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# Ecological niche of allis shad during reproduction : consequences at the population level in a global warming context

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L'UNIVERSITÉ DE BORDEAUX**

ÉCOLE DOCTORALE Science et environnements (304)

Spécialité Ecologie évolutive, fonctionnelle et des communautés

Par Alexis PAUMIER

Sous la direction de : Patrick LAMBERT

(Co-directeur : Hilaire DROUINEAU)

**Niche écologique de l'alose pendant la reproduction :  
conséquences au niveau de la population dans un  
contexte de dérèglement climatique**

Soutenue le 16 décembre 2019

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Dissertation submitted in fulfilment of the requirement for the degree of

**DOCTOR OF PHILOSOPHY  
BORDEAUX UNIVERSITY**

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Specialty evolving, functional and community ecology

By Alexis PAUMIER

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(Co-supervision: Hilaire DROUINEAU)

**Ecological niche of shad during reproduction:  
consequences at the population level in a global  
warming context**

Dissertation date: 16<sup>th</sup> December 2019

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**À pépé**



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---

*"Il y a des instants qui ont de la mémoire. L'éphémère vit d'éclairs et je ne demande pas au bonheur une rente."*

Romain Gary

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# Résumé étendu

## Chapitre I : Introduction générale

Cette thèse se place dans un contexte de dérèglement climatique (IPCC 2018) et de déclin généralisé des espèces de poissons. Dans les écosystèmes d'eau douce, le pourcentage de mammifères et de poissons menacés était de 23 % en 2014 (Collen et al. 2014). Cette disparition est préoccupante. En effet, si les rivières ne représentent seulement que 0.8% de la surface du globe, elles représentent des « hotspots » de biodiversité abritant plus 6% des espèces connues (Dudgeon et al. 2006). Les effets du dérèglement climatique sont difficiles à prévoir pour ces écosystèmes, mais il est attendu un réchauffement de la température de l'eau et une dégradation du cycle hydrologique naturel. Cette dernière s'ajouterait aux dégradations anthropiques déjà existantes, causées par les barrages et les utilisations de l'eau (Postel et Richter 2003). Le débit annuel diminuera jusqu'à -40 % avec le pire scénario du dérèglement climatique (RCP 8.5) contre -10 % avec le scénario RCP 2 en Garonne (Dayon 2015).

Les poissons sont plus touchés par les changements climatiques que les animaux terrestres avec un taux d'extinction deux fois plus élevé que celui des espèces terrestres (Pinsky et al. 2019). Les poissons sont plus susceptibles d'être touchés par les dérèglements climatiques, car ce sont des animaux ectothermes, c'est-à-dire que leur température corporelle suit de près celle de leur habitat (Angilletta 2009). Les poissons anadromes, qui partagent leurs cycles de vie entre l'océan pour la phase de croissance et les rivières pour la reproduction (McDowall 1988) seront plus impactés par le dérèglement climatique que les espèces marines

ou catadromes car, les impacts du dérèglement climatique seront plus importants sur les continents que dans les océans.

Les principales réponses des êtres vivants face au changement climatique sont notamment l'adaptation, le changement de distribution et les réponses phénologiques. Cette thèse s'intéresse aux réponses phénologiques. Celles-ci sont des modifications d'événements périodiques du cycle de vie liées à des perturbations dans la variation naturelle et saisonnière du climat. Avec le dérèglement climatique, on observe d'ores et déjà dans les régions tempérées un printemps plus précoce et un automne plus tardif, ce qui a des conséquences sur le cycle de vie des espèces. Chez les poissons migrateurs, les réponses phénologiques les plus étudiées sont la migration et la période de reproduction (Crozier et Hutchings, 2014). À titre d'exemple, la migration des juvéniles de saumons a progressé d'environ quatre jours par décennie (Kennedy et Crozier, 2010 ; Russell et al., 2012). Sous l'effet des dérèglements climatiques, les facteurs environnementaux qui régulent la phénologie des poissons peuvent changer, comme la température et le débit des rivières. Ces changements auront des conséquences inconnues en termes de succès de reproduction.

Dans ce contexte, ce travail de doctorat s'intéresse au contrôle environnemental de la reproduction chez la grande alose, *Alosa alosa* (Linneaus, 1758). Pour ce faire, nous avons développé à la fois des modèles corrélatifs et des modèles mécanistes afin de définir la niche écologique durant la reproduction. Après avoir défini la niche écologique de la grande alose, nous avons utilisé des scénarios du dérèglement climatique afin de déterminer si la reproduction a été affectée dans le passé par une dégradation de l'habitat dans les frayères, et s'il sera affecté par le climat futur.

## **Chapitre II : Cas d'étude**

A l'échelle mondiale, les poissons diadromes font face à de multiples pressions anthropiques qui entraînent un déclin mondial de ces espèces migratrices (Limburg and Waldman, 2009). La Garonne et la Dordogne abritaient les plus fortes abondances de grande alose en Europe avant le 20ème siècle (Castelnaud et al. 2001). Les captures par unité d'effort (c.-à-d. le nombre de poissons/jour de filet) ont indiqué que la population était stable de 1983 à 1999 et qu'elle a même augmenté après 1993 (Castelnaud et al., 2001). Cette légère augmentation serait liée à la création de passes à poissons sur certains barrages (Travade et al. 1998). Un changement a été observé après le XXe siècle et un déclin spectaculaire a d'abord été observé chez les juvéniles en 2000 et ensuite chez les géniteurs en 2005. Ce déclin a conduit à un moratoire sur la pêche en 2008 (Rougier et al. 2012 Cette espèce vient récemment d'être classée en danger critique d'extinction en France

Le contrôle environnemental sur la reproduction a été exploré avec huit facteurs environnementaux: la température de l'eau, la température de l'air, le débit d'eau, la durée du jour et les variations quotidiennes de chacun de ces quatre facteurs. Ces huit facteurs environnementaux ont été présélectionnés sur la base d'un contrôle documenté du cycle de vie des aloses et de leur disponibilité à une échelle quotidienne. Contrairement aux salmonidés dont la reproduction est principalement déclenchée par la photopériode (Scott 1990), la température et le débit de la rivière semblent être les principaux déclencheurs de la maîtrise de la reproduction et de la migration des aloses (Mohr 1941 ; Dottrens 1952 ; Hoestlandt 1958 ; Cassou-Leins 1981 ; Philippart, et Vranken, 1982 ; Menneson-Boisneau et Boisneau 1990 ; Cassou-Leins et Carette 1995 ; Aprahamian et al. 2003 ; Bagliniere et al. 2003). La migration semble également être contrôlée par la température et, dans une



moindre mesure, par le débit de la rivière (Roule 1925 ; Boisneau et al. 1985 ; Aprahamian et al. 2003). La température contrôle notamment les capacités de nage de l'alose, car leur vitesse de nage est inhibée lorsque la température de l'eau descend en dessous de 12°C (Steinbach et al. 1986).

En Garonne et en Dordogne, la température de l'eau est corrélée négativement avec le débit de la rivière et la variation de la longueur du jour. Elle est également corrélée positivement avec la longueur du jour. Les autres corrélations restent faibles. La fonction d'autocorrélation (ACF ; Fig. II7) souligne que la température de l'eau à la fois est fortement autocorrélée par rapport aux 15 jours précédents. La fonction d'autocorrélation partielle souligne que les autocorrélations observées jusqu'à 15 jours étaient un effet résiduel de l'autocorrélation pour les décalages de 1 et 2 jours (PACF ; Fig. II6). Il en va de même pour le débit fluvial avec un décalage de plus de 20 jours dans l'ACF dû à la corrélation des résidus pour les décalages 1 jour, 2 jours et 3 jours (ACF et PACF ; Fig. II7). En conséquence, nous avons utilisé des méthodes statistiques qui garantissent la prise en compte de ces données corrélées et non indépendantes, avec notamment le choix des Boosted Regression Trees (BRT) dans deux articles de cette thèse.

### **Chapitre III : Approches explicatives**

Dans ce chapitre "Approches explicatives", nous avons cherché à définir le contrôle environnemental sur la reproduction des aloses et à améliorer notre compréhension du lien complexe entre migration et reproduction. La définition du contrôle environnemental sur la reproduction de l'alose a été réalisée en utilisant deux modèles corrélatifs. L'étude du lien entre migration et reproduction a été réalisée à l'aide de deux modèles mécanistes développés durant la thèse.

Dans les approches corrélatives, nous définissons le contrôle environnemental sur plusieurs étapes. Tout d'abord, nous nous sommes concentrés sur la température. Ensuite, nous nous avons complété cette description du contrôle environnemental de la reproduction de l'aloise, en y intégrant la durée du jour et le débit.

Pour le premier modèle corrélatif (publié dans *Environmental Biology of Fishes*) nous avons utilisé un indice d'électivité (indice de Manly) afin de définir le comportement thermique de l'aloise pendant la reproduction en Garonne et en Dordogne. Un des objectifs était de tester l'hypothèse de Quinn et Adams (1996) qui formule une optimisation des règles comportementales de reproduction afin de maximiser la survie de leur progéniture chez certains migrateurs. La première évaluation a porté sur la température en raison de la sensibilité documentée des jeunes stades à ce facteur (Jatteau et al. 2017). Une préférence thermique (définie comme la plage de température la plus étroite dans laquelle 80 % de l'activité reproductrice annuelle totale a lieu) entre 14,5 °C et 23 °C a été observée chez les géniteurs pendant la reproduction pour les 14 années d'études. Malgré les fluctuations annuelles, on a observé une similitude générale des gammes de températures entre les deux rivières. La préférence thermique est très proche de la tolérance thermique des jeunes stades (16,2°C à 24,8°C) établie par Jatteau et ses collaborateurs (2017). Ce recouvrement confirme que les géniteurs d'aloise adoptent des règles comportementales de reproduction afin de maximiser la survie de leur progéniture (Quinn and Adams 1996; Lambert et al. 2018).

Le second modèle corrélatif (publié dans *Freshwater Biology*) se proposait de fournir un premier diagnostic sur la sensibilité de la grande alose face au dérèglement climatique. Une technique d'apprentissage automatique (Boosted Regression Trees ; BRT) a été calibrée à l'aide d'une série temporelle de 14 ans composée de mesures quotidiennes des facteurs

environnementaux et de la présence de poissons en reproduction sur les frayères. Le BRT a fourni un aperçu de la relation entre la probabilité de frai, c'est-à-dire la probabilité de reproduction d'un poisson, et les facteurs environnementaux qui pourraient évoluer avec le changement climatique. La probabilité de frai était positivement liée à la longueur du jour (44,6 %) et à la température de l'eau (34,7 %), et négativement liée au débit des rivières (20,7 %). Les conditions optimales de reproduction pour la population étudiée correspondaient à une différence de longueur de jour entre 0 et 0,04 heure, une température de l'eau entre 15 °C et 26 °C et un débit fluvial entre  $55 \text{ m}^3 \text{ s}^{-1}$  et  $665 \text{ m}^3 \text{ s}^{-1}$ . Cette étude laisse à penser que ce changement climatique pourrait entraîner un changement dans la phénologie de la reproduction, car la température de l'eau et le débit de la rivière changeront dans le futur. Il s'agit donc d'un premier diagnostic qui sera complété par des prédictions dans le chapitre IV.

Dans l'approche mécaniste, deux modèles ont été développés. Le modèle le plus développé (HoOS pour Hasty or Omniscient Shad) a exploré les conséquences de la migration et de deux comportements stéréotypés de reproduction (décision de se reproduire) en termes de survie de la descendance. Le second modèle (flirtyShadBrain), plus complexe, cherchait à dépasser les comportements stéréotypés de reproduction développés dans HoOS et de calibrer en parallèle la migration et le comportement de frai (décision de pondre en fonction des facteurs environnementaux). Malheureusement, la calibration de ce modèle est toujours en cours et n'a pas atteint le niveau de publication au moment de la rédaction de ce doctorat. L'activité de reproduction des poissons migrateurs est le résultat de choix comportementaux multiples. Elle peut être dissociée en deux comportements liés : la migration et la décision de pondre. Cependant, le lien entre les deux processus reste flou. Par exemple, Acolas et ses collaborateurs (2006) ont observé que le pic d'abondance pendant la migration en amont n'est pas synchronisé avec le pic de reproduction.

L'hypothèse de Quinn et Adams (1996) affirme que les poissons optimisent la reproduction pour améliorer la survie au début de la vie. Cependant, les processus dans lesquels cette optimisation a eu lieu ne sont pas très clairs dans cette théorie. Le premier modèle mécaniste HoOs visait à comprendre l'importance de la migration et de la décision de pondre sur la survie des jeunes stades. L'approche expérimentale étant très coûteuse et complexe, nous avons choisi de simuler la chaîne de décision dans un cadre conceptuel qui incluait : le temps de migration de l'estuaire jusqu'à la frayère et la décision de se reproduire. La décision de pondre a été décrite à l'aide de deux comportements stéréotypés : une alose "hâtive" qui fraie dès son arrivée dans les frayères et une alose "omnisciente" qui attend les conditions environnementales les mieux adaptées pour la survie des jeunes stades. Le modèle a démontré que la survie des jeunes stades présentait une période optimale en fonction du temps de migration. Par ailleurs, le comportement de fraie régule l'influence de la migration, les géniteurs "omniscients" retardant leur reproduction par rapport aux géniteurs "hâtifs". En conclusion, ce modèle HoOs a mis en évidence le compromis entre la migration et le comportement de fraie sur la survie de la progéniture. Cet article sera soumis prochainement dans *Ecological Modelling*.

Dans la lignée du modèle HoOs, nous avons développé un nouveau modèle mécaniste *flirtyShadBrain* qui cherchait à simuler l'arrivée sur les frayères et la "vraie" décision de fraie à partir des facteurs environnementaux (c'est-à-dire au-delà des deux comportements stéréotypés de fraie précédents). L'objectif était de reproduire la série chronologique des activités de ponte observée. Malheureusement la calibration de ce modèle *flirtyShadBrain* n'a pas pu aboutir par manque de temps. Cependant, malgré cet échec, ce modèle mécaniste permet de comprendre la complexité des interactions entre migration, décision de

reproduction et contraintes physiologiques. Cela a permis de garder une réflexion critique pour le développement du modèle BRT.

## **Chapitre IV : Approche prédictive**

Après la définition du contrôle environnemental de la reproduction chez la grande alose lors du chapitre précédent, nous avons souhaité fournir un diagnostic fiable sur l'impact du dérèglement climatique. Dans cette optique, nous avons collaboré avec des scientifiques du CERFACS/CNRS (Julien Boé et Gildas Dayon) pour obtenir des données simulées, passées et futures, de température de l'air et débit des rivières (de 1950 à 2010 dans les deux rivières). Dans cette approche prédictive, nous avons utilisé le modèle le plus abouti de cette thèse, le BRT calibré dans le second article. Nous avons forcé le modèle BRT avec deux scénarios contrastés : un scénario compatible avec l'accord climatique de Paris 2015 (RCP 2.6) et un scénario du pire (RCP 8.5). Les résultats indiquent qu'il n'y a eu aucun changement majeur dans la favorabilité de des frayères (en termes combinés de température, de débit et de durée du jour) et qu'aucun changement majeur n'est détecté dans le cadre de ces scénarios.

Cette approche explicative conclut les travaux sur la reproduction de la grande alose. Cependant, les dernières corrections de Julien Boé et Gildas Dayon doivent encore être prises en compte (notamment sur la correction du canon et de quelques terminologies pour les modèles climatiques) avant de soumettre cet article dans *Global Change Biology*.

## **Chapitre V : Discussion**

L'objectif de cette thèse était de définir le contrôle environnemental sur la reproduction de la grande alose. A l'aide de 4 études principales avec plusieurs outils de modélisation (l'indice de Manly, le modèle BRT, le modèle HoOS et le modèle flirtyShadBrain), nous avons étudié ce contrôle environnemental et évalué l'impact futur du dérèglement

climatique. La première étape pour évaluer l'impact des changements d'habitat a été de tester l'influence des facteurs environnementaux sur la reproduction de l'alose (papier #1, papier #2 et flirtyShadBrain). Nous avons d'abord exploré l'influence de la température, puis nous avons testé plusieurs facteurs environnementaux sur la reproduction de l'alose. Concrètement, nous évaluons que l'alose est une espèce photopériodique. La durée du jour est peut-être la donnée saisonnière qui déclenche la migration, et la température et le débit sont utilisés pour les décisions à court terme (choix final de se reproduire avec les repères sociaux). Selon nos projections multifactorielles, il semblerait que les géniteurs de grande alose ne seront pas touchés par le futur réchauffement de la planète pour le scénario RCP 2.6, et que même dans le pire des scénarios (RCP 8.5), la favorabilité de l'habitat devrait même augmenter avec toutefois une période favorable plus précoce. Ainsi, le changement climatique n'apparaît pas comme une menace majeure pour cette espèce, du moins si elle est capable de suivre le léger déplacement du centroïde des conditions les plus favorables.

La science de la prévision des impacts du changement climatique sur la biodiversité est pleine d'incertitudes (Zimmer 2007). Ainsi, l'utilisation d'une gamme de scénarios fournit un panel de "futurs" possibles pour l'alose et peut servir de guide pour la planification des mesures de gestion. Dans cette thèse, nous avons vu que nous nous attendions à peu d'impact du changement climatique, et que la gestion des mesures pourrait donc se concentrer sur d'autres pressions ou d'autres phases du cycle de vie, et notamment sur les premiers stades de la vie.



# Preface

This PhD is structured in five chapters. A general introduction presents the general positioning of this thesis on fish responses to climate change, with a focus on allis shad and finally on the methodological concepts developed in this PhD. The second chapter “Case study” introduces deeply the data used to calibrate the different models developed in this PhD. The third and four chapters, “Explanatory approaches” and “Predictive approach”, are based on manuscripts that have either been published on international reviewed journals or that will be submitted soon:

- Chapter III: In this chapter three manuscripts were written, two were published (*Freshwater Biology* and *Environmental Biology of Fishes*) and the third one is based on the internship realised by Camille Poulet, a student (master level) that I supervised, this paper will be submitted to *Ecological Modelling*.

Paper #1: **Paumier, A.**, Drouineau, H., Carry, L., Nachón, D.J., and Lambert, P. 2019a. A field-based definition of the thermal preference during spawning for allis shad populations (*Alosa alosa*). *Environ. Biol. Fishes*. doi:10.1007/s10641-019-00874-7.

Paper #2: **Paumier, A.**, Drouineau, H., Boutry, S., Neftalí, S., and Lambert, P. 2019b. Assessing the relative importance of temperature, discharge and day length on the reproduction of an anadromous fish (*Alosa alosa*). *Freshw. Biol.* doi:10.1111/fwb.13418.

Paper # 4: Poulet, C., **Paumier, A.**, Lassalle, G., Pierre, M., Tentelier, C., Daverat, F., Lambert, P. *in prep.* Allis shad offspring survival: Disentangling migration patterns from reproduction behaviors.



- Chapter VI: In this chapter, one manuscript was written and will be submitted in *Global Change Biology*.

Paper # 3: **Paumier, A.**, Boé J., Drouineau, H., Gildas, D., Boé, J., Lambert, P. *in prep*. Back to the future: riverine spawning habitat suitability for a migratory fish species between 1950 and 2099 under RCP scenarios.

Furthermore, I participate in an article during the first month of this PhD. This article is presented in annexe as I only participated in the review of this article (annexe I).

Paper # 5: Lambert, P., Jatteau, P., **Paumier, A.**, Carry, L., and Drouineau, H. 2018. Allis shad adopts an efficient spawning tactic to optimise offspring survival. *Environ. Biol. Fishes* 101(2): 315–326. doi:10.1007/s10641-017-0700-4.

Most of the content of the third chapter has been presented as oral presentation in international and national conferences.

- Paumier, A., Drouineau, H., and Lambert, P. Association Française d’Halieutique. « Adaptation au changement climatique au travers de la plasticité comportementale. Cas de la tactique de ponte de la grande alose pour la population menacée du bassin de la Garonne Dordogne » Pêches et Changements Globaux. Ifremer Nantes. 28-30 June 2017
- Paumier, A., Drouineau, H., and Lambert, P. “Reproduction and adaptation: a definition of the thermal niche of spawning for a French metapopulation of Allis shad in a global warming context”. American Fisheries Society. 28th August 2018.

- Paumier, A., Drouineau, H., and Lambert, P. "Assessment of environmental control on fish reproduction: case of the allis shad populations" Société Française d'Écologie et d'Évolution. 22th October 2018.
- Paumier, A., Drouineau, H., and Lambert, P. Analyse de sensibilité et exploration de sorties de modèles. « flirtyShadBrain: un modèle de reproduction simulée pour les populations d'aloses (*Alosa alosa*) » 12 November 2018.
- Paumier, A., Drouineau, H., and Lambert, P. Association Française d'Halieutique. 'Back to the future: A look back and forward at an anadromous fish reproduction between 1950 and 2099' Acidification, réchauffement et désoxygénation. Université de Caen Normandie. 26-28 June 2019.

This PhD was supported by the Regional Council of Nouvelle Aquitaine (FAUNA project) and the Water Agency of Adour-Garonne (SHAD'EAU project).



# **Chapter I**

## **Introduction**



## I. CLIMATE CHANGE

### A. *A component of global change*

Ongoing human induced modifications on worldwide ecosystems are unprecedented (Steffen 2004), a situation referred as *global change*. Global change involves natural and anthropogenic changes on the Earth system. Earth system is defined as the interaction between physical, chemical and biological process that promotes life (Steffen 2004). Drivers of global change include changes in land and sea use, direct exploitation of natural resources, climate change, pollution, and invasion of alien species (Díaz et al. 2019). Most of these components emerge from the human population growth (around 7.7 billion people in August 2019).

Climate change (which would be more appropriately named climate deregulation), one of the components of global change, is induced by human activities (IPCC 2018). Climate change is defined by the Intergovernmental Panel on Climate Change (IPCC) as “a change of climate which is attributed directly or indirectly to human activity that alters the composition of the global atmosphere and which is in addition to natural climate variability observed over comparable time periods”. The climate change is notably measured by the warming of surface temperature (Fig 11). This index shows a dramatic change in natural climate (described below).

### B. *Climate change in the 20<sup>th</sup> century*

In 2017, the global warming ranged between 0.8°C and 1.2°C above the pre-industrial level (Fig. 11). Over the past 30 years, air temperature increased by from 0.1°C to 0.3°C per decade (IPCC 2018). The average warming over continental lands was higher than over the oceans,

and therefore has more impacted freshwater than marine ecosystems (IPCC 2018). Moreover, multiple modifications of global environment were documented in association with the warming temperature, such as shrinking ice sheets, glacial retreat, decreased snow cover, sea level rise, declining arctic sea ice, ocean acidification and changes in the frequency and intensity of climate extreme events (Stocker et al. 2010; Field et al. 2011; IPCC 2012; Wuebbles et al. 2017).

### *C. Climate change projected for the 21th century*

In order to explore the impact of future climate change, four scenarios of future radiative forcing pathways (RCP) were developed (Moss et al. 2010). RCPs refer to “the change in the balance between incoming and outgoing radiation to the atmosphere caused by changes in atmospheric constituents, such as carbon dioxide” (Moss et al. 2010). These scenarios encompass plausible trajectories of greenhouse-gas emission, from the scenario in accordance with the 2015 Paris climate agreement (RCP 2.6) to the “worst-case” scenario (RCP 8.5). A global average surface air temperature warming between 1.8°C to 4°C is expected depending on considered RPCs (Fig. I1). Warming is expected to be greatest at most high northern latitudes (IPCC 2018). The two extreme scenarios (RCP 2.6 and 8.5) diverge mostly after 2050 because of the inertia of past emissions (Fig. I1). Warming from anthropogenic emissions will persist for millennia and will continue to cause long-term changes in climate (IPCC 2018).

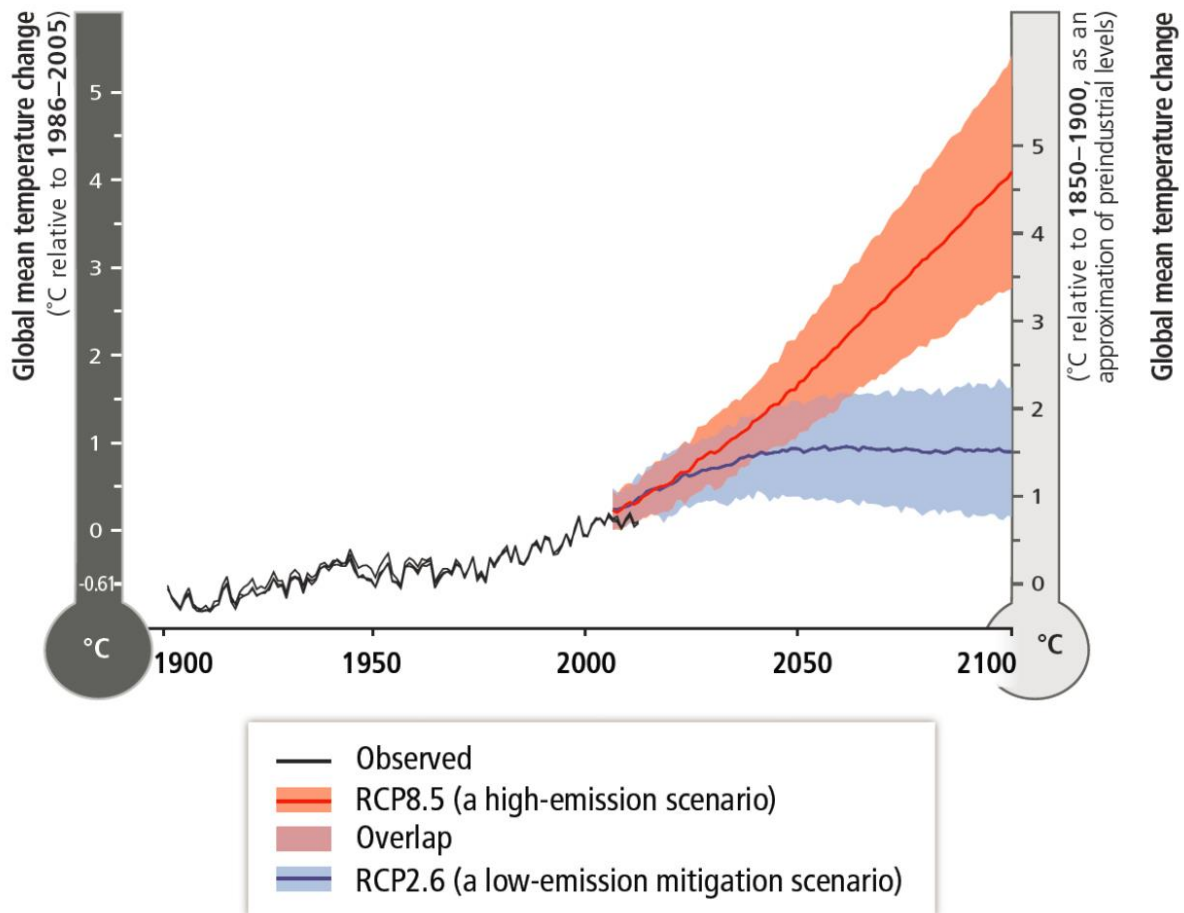


Figure 11: Projected rise in surface air temperature through 2100, compared to the rise observed since 1900. Two emission scenarios are represented: high emission of greenhouse gas emissions (RCP 8.5 in red; 4 °C above recent temperatures), and low-emission (RCP 2.6 in blue, 1 to 2 °C above recent temperatures). This diagram is from the Fifth Assessment Report (AR5) of Working Group II (WGII) of the United Nations' (UN) Intergovernmental Panel on Climate Change (IPCC 2014).



#### ***D. Climate change in rivers***

Freshwater ecosystems cover only around 0.8% of the overall world's surface and 0.01% of overall water stock. However, they represent a hotspot of biodiversity with 6% of the species (Dudgeon et al. 2006). Climate change is expected to drastically increase river temperature but also change hydrological cycle such as river flows (Allan et al. 2005b). Moreover the hydrological cycle is also deeply altered by other human activities such as water withdrawals or dams (Postel and Richter 2003).

Trends in river water temperature are difficult to project under climate change scenarios (Lennox et al. 2019), as the stream temperature depends on the balance of numerous physical processes such as “heat transfer between air and water, direct conduction from the stream bed, friction created by water flow over the bed, and adjectives heat gains from precipitation and groundwater inputs” (Isaak et al. 2012). Most streams are characterised by nonlinear relationships between air and water temperatures (Morrill et al. 2005) but for sure global warming will result in the warming of river water. On average, a 1 °C increase of air temperature generates about 0.6 to 0.8 °C (Morrill et al. 2005). These thermal changes will also lead to changes in water physico-chemistry in rivers as reductions in dissolved oxygen (Morrill et al. 2005).

The degradation of natural hydrological cycle by dams and water uses (Postel and Richter 2003) could be compounded by climate change: evapotranspiration in spring and winter are expected to increase in the future while summer precipitations will decrease (Fig I2; Dayon 2015). In France, upstream parts of rivers in the Pyrenees will likely suffer strong decrease of flow (40% ±15%), because of an earlier snowmelt and a decrease in summer precipitations (Dayon 2015).

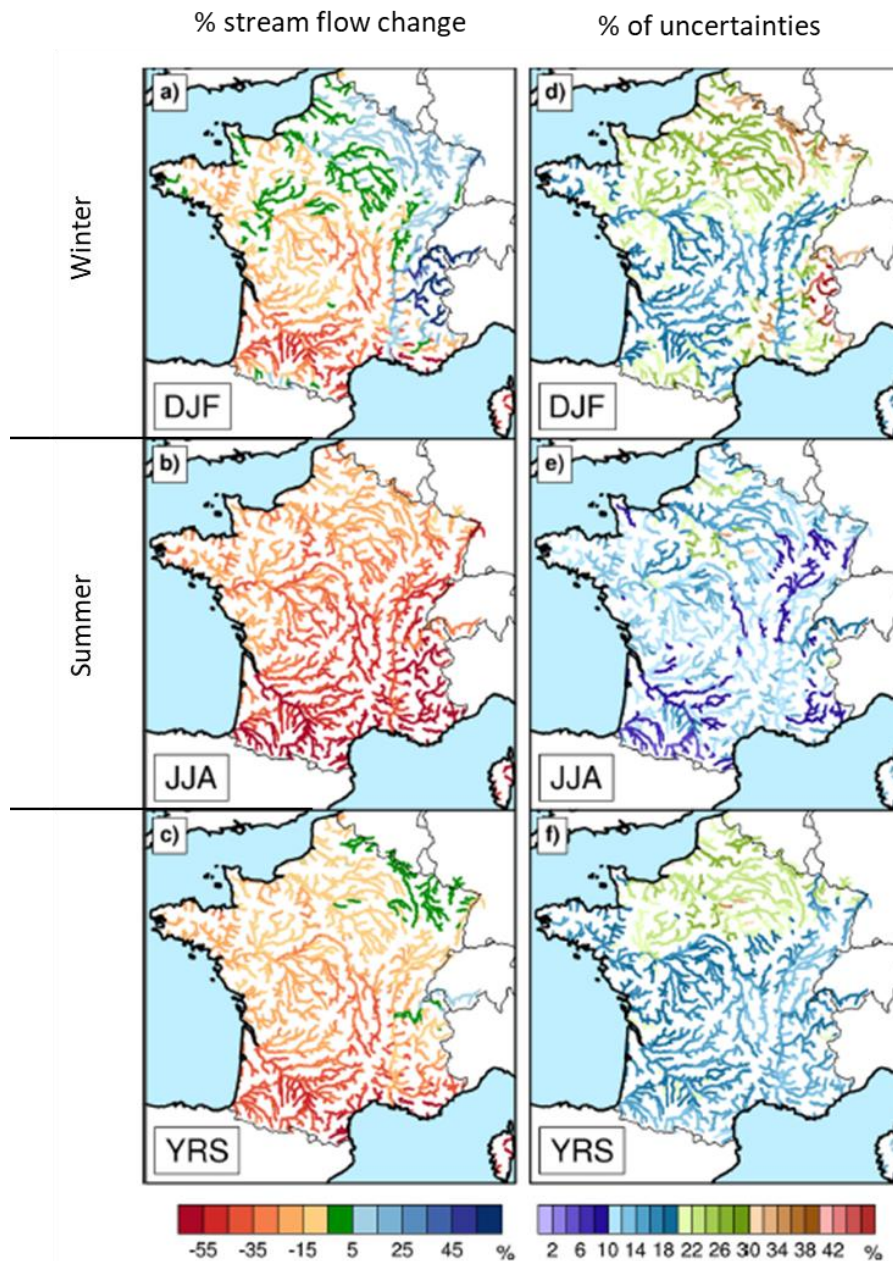


Figure 12: Hydrological change projected in France according to Dayon (2015). Panel (a–c) represent the ensemble means of relative streamflow changes (%) between the 1960–1990 and 2070–2100 periods under the RCP8.5 scenario in winter (DJF), in summer (JJA) and for the entire year (YRS). Panel (d–f) represent the estimation of the uncertainty range at [5–95%] due to GCMs, estimated by a 1.64 standard deviation between simulations.

Additionally, changes in the snowpack is projected (Dayon 2015). Earlier snowmelt implies runoff of cold water over spring (Dayon 2015). The annual streamflow will decrease up to -40% with the RCP 8.5 compared to -10% with the RCP 2.6 in the Garonne River (Dayon 2015). Although the pattern of climate change is straightforward at a global and regional scales, local changes are more complex and dependant of natural activities close to rivers. Spatial variations will depend on the anthropogenic fingerprints in the vicinity of the river such as the presence or absence of riparian forests, dams, water discharges from power. To conclude, river habitats are likely to experience elevated temperatures in association with decreased flow rates and increasing incidence of hypoxic conditions.

## **II. BIOLOGICAL RESPONSE TO CLIMATE CHANGE**

### ***A. The great acceleration of the Anthropocene***

#### a) Global scale

Global biodiversity is defined as the abundance of species that occurs naturally in biomes (Sala 2000). Earth system has already undergone planetary-scale critical transitions in biodiversity with the 'Big Five mass extinctions' that changed the course of life's evolution: the Ordovician–Silurian (ended ~443 Myr ago) , the late Devonian (ended ~359 Myr ago) , Permian–Triassic (ended ~251 Myr ago), Triassic–Jurassic (ended ~200 Myr ago) extinction event and Cretaceous–Paleogene (ended ~65 Myr ago) extinction events (Barnosky et al. 2011). These critical transitions were relatively fast, about 5% of the time over the period (Barnosky et al. 2011). The time of these transitions ranged from several 10 000 years to 2,000,000 years. Nowadays, Earth system is in the midst of its sixth great critical transitions (Steffen 2004). Compared to the previous "Big Five", this sixth extinction differs by a very short transition time and by the fact that it results from the activity of a single biological

species, *Homo sapiens*. The human induced extinction rate is thought to be tens to hundreds times higher than over the past 10 million years (Díaz et al. 2019).

Climate change is expected to cause more species extinction by exacerbating the impact of ongoing anthropogenic pressures (Díaz et al. 2019), but strong uncertainties remain about the magnitude of these pressures. Climate change in association with the many components of global change has led to a widespread impact on biodiversity (Díaz et al. 2019). As an example, a dramatic species turnover of over 60% of the present biodiversity was predicted for 2050 using a sample of 1066 exploited marine fish and invertebrates, with notably poleward shifts, extinctions and species invasion (Cheung et al. 2009). Future climate-related risks will depend on the rate, peak and duration of climatic events: “Limiting global warming to 1.5°C compared to 2°C is projected to lower the impacts on terrestrial, freshwater and coastal ecosystems and to retain more of their services to humans” (IPCC 2018).

b) In rivers

For freshwater ecosystems, the greatest negative impact (relative to other pressures) is land use, followed by fish harvesting (Díaz et al. 2019). In freshwater ecosystems, the percentage of threatened mammals and fishes was 23% in 2014 (Collen et al. 2014). Fishes are more prone to be impacted by climate change than land animals, with a rate of extinction twice as important as the rate of land-based species (Pinsky et al. 2019). First, fishes are ectothermic animals, *i.e.*, their body temperature closely follows the temperature of their habitat (Angilletta 2009). Therefore, fishes will be directly impacted by warmer temperatures of streams. Furthermore, fish living in freshwater ecosystems are more prone to extinction than species living in marine or continental ecosystems (Abell 2002; Xenopoulos et al. 2005; Dudgeon et al. 2006; Kostoski et al. 2010). Indeed, inland fish lived in fragmented habitat that

could hamper the accessibility to thermal refuges (*i.e.*, cooler areas; see Frechette et al. 2018 for salmon behaviour in summer), simply because these thermal refuges are too far away in the catchment or because they are located upstream dams or not connected to other habitat.

### ***B. Fish response to climate change***

Fishes, as other animals, may respond to climate change in four main ways: effect on physiology, effect on phenology, effect on distribution and adaptations (Hughes 2000). These responses may lead to changes in community structure and ecosystem function (Buisson et al. 2013; Díaz et al. 2019). Since these changes will be species-dependant, the temporal and spatial interactions between species could be disrupted (Hughes 2000). Time scales of these four responses are different (a gradient from several years for adaptation to day for behaviour). A behavioural adjustment is the first organism's response (Wong and Candolin 2015). This behavioural adjustment included tracking the suitable environment in time (phenology) or in space (distribution). Ultimately, the species could evolve to the new environment (adaptation *in situ*).

#### a) Adaptation

Evidence of evolutionary change has been observed for natural populations (Hendry et al. 2008), indicating that adaptation could be a way to cope with climate change (Hoffmann and Sgrò 2011). Evolutionary response could be the only one for species unable to disperse from unsuitable environment in fragmented habitat. The adaptation will depend on the generation time and growth rate of species. As such, the *Drosophila* characterised by short generation time and fast growth rate has undergone *in situ* microevolutionary change in response to climate change (Rodríguez-Trelles and Rodríguez 1998). The population has lost 18.3% of chromosomal diversity in 16 years, indicating a fast response to climate change. For fish, an

extensive review reveals that only two studies have undoubtedly related phenotypic changes (*e.g.*, changes in timing of migration and reproduction, age at maturity, growth, etc.) to evolutionary mechanisms as a response to climate change (Crozier and Hutchings 2014). Indeed, detection of evolutionary change is complex for fish (Crozier and Hutchings 2014). “Direct monitoring of evolutionary change in the wild are rare, making it difficult to assess the relative contributions of changes in trait means versus changes in plasticity to climate change responses” (Kelly 2019). A solution may be a long-term study of temporal shifts in reaction norms, defined as the “graphical representations of phenotypic change along an environmental gradient” (Crozier and Hutchings 2014). Moreover there is a risk that adaptations may fail to keep pace with the ongoing climate change given the rapid rate of changes and the long time scale required for adaptive divergence (thousands of generations).

b) Distribution

The ongoing climate change has led to shift in distribution of species with contraction and expansion (Hughes 2000; Walther et al. 2002; Pearson and Dawson 2003). For highly mobile species such as marine fishes, a shift towards either higher latitudes or depth is observed/projected (Cheung et al. 2009). As such, two thirds of 90 exploited and unexploited North Sea fishes have responded markedly to climate change with shifts in latitude and in depth over a 25-year period (Perry 2005). In rivers, freshwater fish distributions will be affected by climate change with reduction and shift to higher altitude or latitude for most cold-water species and expansion for cool- and warm-water species (Buisson et al. 2013). The fish response may depend on dispersal capabilities and availability of suitable habitat. However, it appears that life history characteristics such as generation time and body size

influence shifting behaviour, as fishes with faster life cycles and smaller body sizes have changed their distribution to a greater extent (Perry 2005).

c) Phenology

Phenology is the study of seasonal phenomena, especially in relation to climate and plant or animal events. In mid to high latitudes, many organisms live in seasonal environment where key environmental factors such as temperature, day length or food supplied vary over the year. Organisms in this seasonal environment may follow annual routines (McNamara and Houston 2008), *i.e.*, the life cycle is synchronised with the seasonal changes and therefore is scheduled in a regular way over the year. With climate change, the seasonal activities are showing shifts in times. For salmon species, the phenology of migration and spawning are well documented (Crozier and Hutchings 2014) and some authors have observed that migration timing of juveniles has advanced by around 4 days per decade (Kennedy and Crozier 2010; Russell et al. 2012).

### ***C. Reproduction and climate change***

The success of survival of the earlier life stages (eggs, larvae and juveniles) is a key feature of population dynamics for fish (Hjort 1914; Toresen and Østvedt 2000; Brunel and Boucher 2006). Early life stages are usually more sensitive than adults to environmental fluctuations (Hjort 1914) and many species have adopted reproductive strategy that ensures suitable biophysical conditions for offspring (Quinn and Adams 1996; Lyons et al. 2015). Beside parental care (Balon 1975), an aspect of the reproductive strategy is when to reproduce (Munro et al. 1990; Stearns 1992). As such, climate change is a major threat to fish populations and change in spawning time is one of the most document effects of climate change on fish (Crozier and Hutchings 2014). Indeed, fishes live in habitats where

environmental conditions favourable to their offspring are available only for a specific time of year, *i.e.*, ultimate factors such as water quality and availability of appropriate food (Balon 1975; Munro et al. 1990). When there is a close match between the spawning season and optimal conditions for offspring survival, reproduction is supposed to be the response, from an evolutionary perspective, of a long-term reproductive adaptation to the environment that maximises recruitment success. The proximate factors used by the fish to time the reproduction needs to be correlated with the environmental fluctuations.

Under climate change, several environmental cues driving fish reproduction may change such as temperature and rivers discharge. These changes will lead to unknown consequences in terms of reproductive success. Climate change may influence the timing of reproduction, depending on how well the *proximate* cues will predict future conditions. In fact, reproduction could become desynchronise to the optimal conditions for offspring if the cues used to time the reproduction are no longer reliable under climate change. Such mismatch was observed for the spawning period and the peak of plankton production (Chevillot et al. 2017). A deeper assessment is needed about the environmental control on fish reproduction in order to predict the effect of climate change of the population dynamics.

### **III. Allis shad in river systems**

Animal migration is one of the most visible and a widespread nature's phenomena. One of the most complex and remarkable type of migration for fish is diadromy (Talbot 1958; McDowall 1988; Bloom and Lovejoy 2014). Diadromy is a life history behaviour that leads fish to move between ocean and freshwater habitat to complete their life cycle (McDowall 1988). Three types of diadromy are described (McDowall 1988): anadromy for fishes that reproduce in rivers and growth in sea, catadromy for fishes that reproduce in sea and growth in river,



amphidromy for fishes that reproduce in rivers and growth between river and sea. Diadromous species can be seen as inland fishes that that life part of their live in freshwater environments (Allan et al. 2005a; Myers et al. 2017). Several hypotheses were formulated to determine the origin of diadromy such as the productivity hypothesis (the differences between marine and freshwater productivity determine whether anadromy or catadromy: oceans have higher productivity than freshwater in temperate regions promoting anadromy derived from freshwater ancestors that began migrating to oceans to exploit the higher productivity, and conversely in tropical regions with catadromy), predation, competition and geological history but it still remains unclear and origins may vary between species and latitudes (Bloom and Lovejoy 2014).

Anadromous fishes include iconic, food or sports fishes as salmon (Bloom and Lovejoy 2014; Liebich et al. 2018). Anadromous fishes fascinate biologists due to the tuning of key events between habitats that required physiological and behavioural adaptation. Furthermore, biologists as well as societies have recognized anadromous fish to provide major ecosystem services (Limburg and Waldman 2009) such as food supplies with harvested (Castelnaud 2001) or farmed fish (Castelnaud 2011; Kobayashi et al. 2015), recreation value (Verspoor et al. 2008) and importation of marine-derived nutrients in river systems with the carcasses of spawners (Quinn et al. 2018).

### ***A. The allis shad (*Alosa alosa*)***

In this PhD, I studied the potential response of allis shad, *Alosa alosa* (Linnaeus 1758), to climate change (Fig. 13). Allis shad have been intensively studied in the last decades (Lambert et al. 2001, 2018; Rochard 2001; Aprahamian et al. 2003; Bagliniere et al. 2003; Acolas et al. 2004, 2006; Alexandrino et al. 2006; Lassalle et al. 2008, 2009; Lassalle and Rochard 2009;

Lochet et al. 2009; Rougier et al. 2012, 2015; Martin et al. 2015; Jatteau et al. 2017; Randon et al. 2017). Here, I propose a short review about this species' life cycle and the population trend (see Aprahamian et al. 2003 and Bagliniere et al. 2003 for complete reviews). Allis shad is a member of the order of Clupeomorpha and belongs to the Clupeidae family (as herrings and sardines). Two closed species of shad can be found in France, the studied species and the twaite shad, *Alosa fallax* (Lacépède, 1803). The timing and the geographical location of spawning grounds are different between the two species. Allis shads spawn more upstream and later than twaite shads (Bagliniere et al. 2003). However, hybridisation of the two species has been observed (Alexandrino et al. 2006) due to shared spawning grounds with the construction of dams that block access of upper spawning grounds.

### ***B. Allis shad's life cycle***

Allis shad is an anadromous species (McDowall 1988) (Fig. I4). In France, the majority of adults die after the spawning season (*i.e.*, semelparous life history). Adults are batch spawners *i.e.*, they reproduce several times during a spawning season (Acolas et al. 2006). The adults mature between 3 and 8 years, with a majority of spawners observed at 5 years old (Lambert et al. 2001). The timing of reproduction migration is latitude dependent, with southern populations migrating earlier in the year than those further North (Aprahamian et al. 2003; Bagliniere et al. 2003). In France, adults move toward coasts in February, and start to migrate to the rivers when the temperature exceeds 10 to 12°C (Roule 1925). The migrating spawners stop to feed, causing a gradual loss of condition.

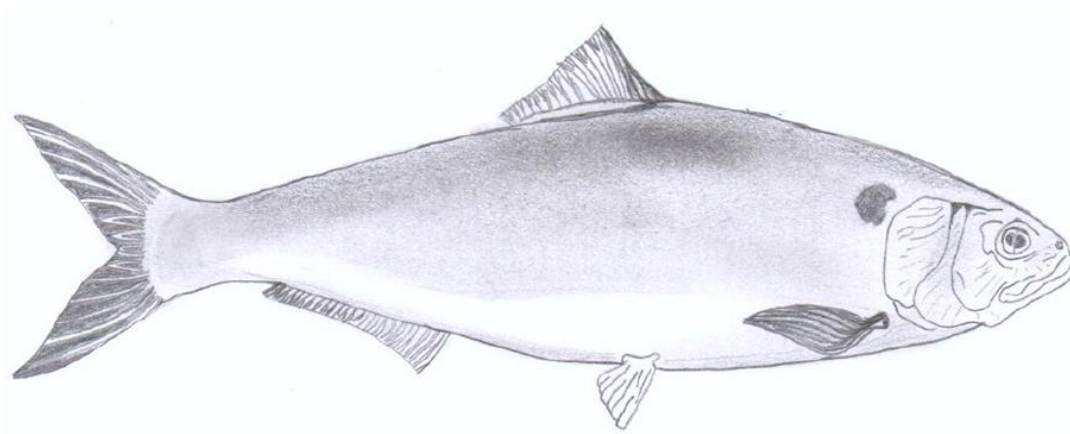


Figure I3: illustration of *Alosa alosa* (©Alexis Paumier)

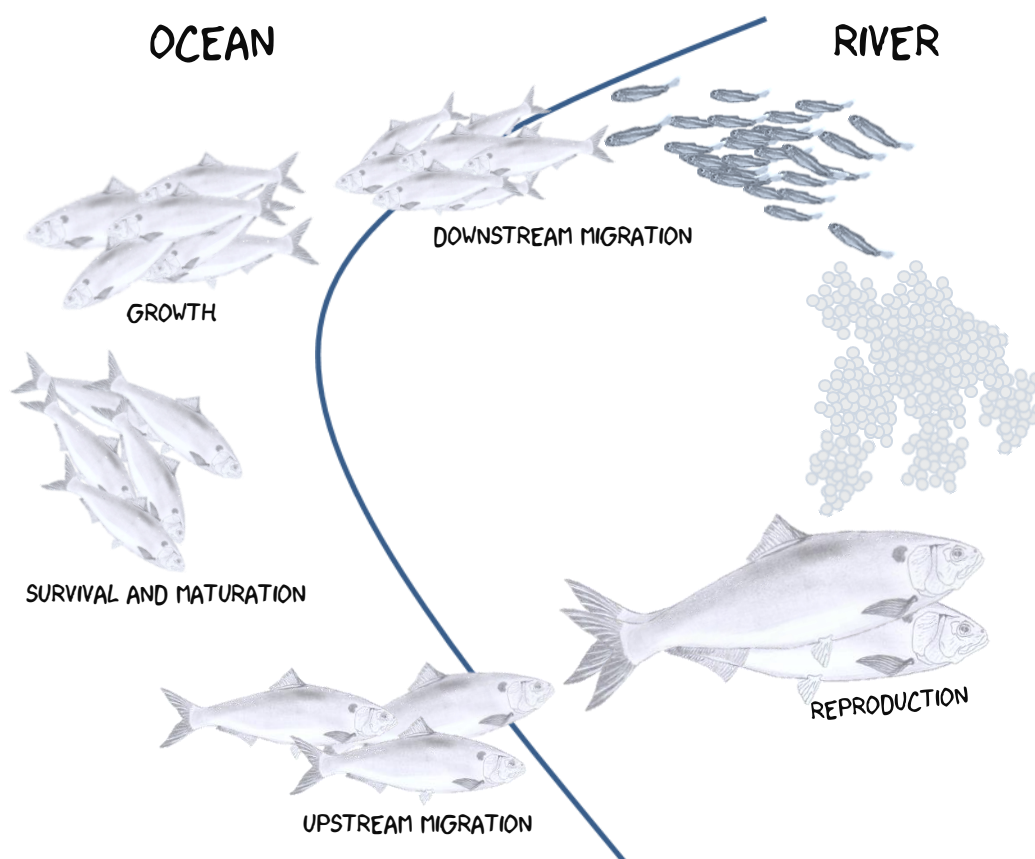


Figure I4: Schematic allis shad's life cycle(©Alexis Paumier)

The spawning migration is rather unimodal in high river discharge or bimodal in low discharge (Rochard 2001; Acolas et al. 2006). The timing of spawning is also latitude dependent (Aprahamian et al. 2003). Indeed, it has been documented that Moroccan shad spawned much earlier (early April) than French and Portuguese stocks (early May). Reproduction is even later for shad in the British Isles (late May). Spawning takes place between May and July in the Gironde System (Cassou-Leins et al. 2000). The links between peaks of migration and reproduction are not clear (Acolas et al. 2006), suggesting a complex behaviour in the spawning grounds. The typical spawning ground is a shallow area near a pool with a fairly strong current and a clean gravel bottom (Bagliniere and Elie 2000). During the day, fish shelter in rest areas away from the spawning ground (Acolas et al. 2004). The reproduction starts at night and is maximal around 3am (Cassou-Leins 1981; Menneson-Boisneau and Boisneau 1990). Allis shad are highly fecund species with an absolute fecundity up to 600,000 eggs (Aprahamian et al. 2003).

During the reproduction, a couple of fish swim side by side, thrashing caudal fin on water surface. The fish swim circularly while expulsing gametes. Expulsed oocytes are fertilised by sperm in the mid-water and then sink in the gravel bottom. The reproduction behaviour produces a sound of between 35 and 50 decibels (Cassou-Leins et al. 2000). At the end of summer, most of the juveniles have migrated in the estuary. At sea, allis shads are a schooling fish that eat predominantly zooplankton by filtering the water column (crustaceans, cladocerae, copepods and ostracods). Historically, fishes were thought to return to their natal spawning grounds, but recent studies suggested a metapopulation dynamics with rivers acting as source or sink, and therefore a homing at the watershed scale (Tomas et al. 2005; Martin et al. 2015; Randon et al. 2017).

### *C. Population trend in the distribution range*

Studying the population trend is key to assessing a species' status and take conservation measures accordingly (Freyhof and Brooks 2011). The populations of allis shad were historically present all along the East Atlantic coast, ranging from Norway in the North, to Morocco in the South and to the Baltic Sea in the East (Bagliniere et al. 2003). Nowadays, the allis shad populations are mostly distributed in France and Portugal.

The Garonne and Dordogne rivers sheltered the most abundant population of spawners in Europe until the 20<sup>th</sup> century (Castelnaud et al. 2001). Catch per unit effort (i.e., number of fish/net day), indicated that the population was stable from 1983 to 1999 and even increased after 1993 (Castelnaud et al. 2001). The slight increase was thought to be related to the creation of fish facilities in the rivers (Travade et al. 1998). A dramatic decline was observed firstly for juveniles in 2000 and afterwards for spawners in 2005 (Fig I5). This decline led to a fishing moratorium in 2008 (Rougier et al. 2012).

The stock–recruitment relationship for this population indicated that a minimum of 0.17 million spawners to reopen the fishery (Rougier et al. 2012). In Europe, the species is on the red list of threatened species (IUCN 2019) and has been included in Appendix III of the Bern Convention and into annexes II and V of the EC Habitats Directive. Giving the population trend in France, the species' status of the ICUN in France should be re-evaluated from “Least concern” to “vulnerable” that is defined as a species facing a high risk of extinction in the wild in the immediate future (IUCN 2019).

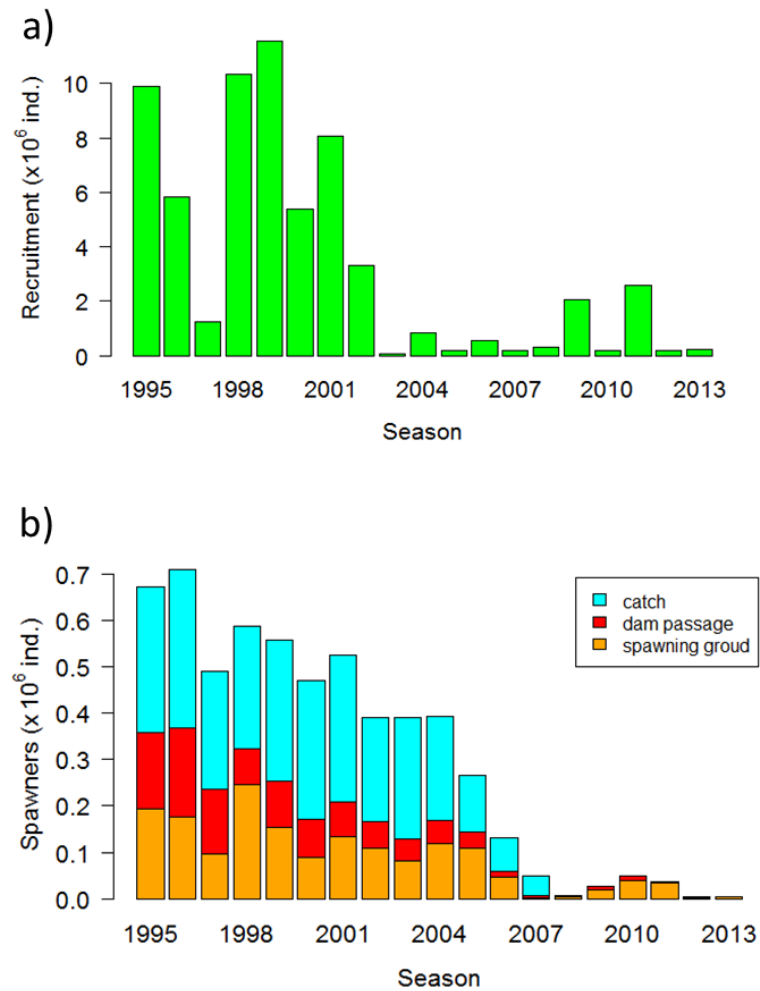


Figure 15: a) Trend in recruitment ( $\times 10^6$  individuals) in the Gironde Watershed; b) Trend in number of spawners from different survey measures (catches, count in dam passage, and counting on spawning grounds) in the Gironde Watershed.

#### **IV. Review of potential threats**

Allis shad suffer multiple anthropogenic pressures that have dramatically impacted shad species worldwide, leading ultimately to collapse of population (Limburg and Waldman 2009). The causes of decline may differ between populations and rivers and are suspected to be cumulative (de Groot 2002; Aprahamian et al. 2003; Limburg and Waldman 2009). However, the main cause is rarely demonstrated (Lassalle et al. 2008). The potential threats to shad can be included to the components of the global change (IPCC 2001): dam construction, fishing mortality, pollution and habitat degradation, alien species and climate change.

##### ***A. Dams construction***

Dams' construction has been identified for decades as the major threat for migratory species, as it hampers the free access to suitable habitats (Poff 1997). The first dam upriver of an estuary is now usually the end point for the migration, though fishway have been installed in the Garonne and Dordogne Rivers since 1987 (Travade et al. 1998). The loss of habitat was suspected to result in extinction of several populations, e.g. Rhine population (De Groot 1990). Even when fishway improve upstream passability, hydropower plants can impact juvenile survival during downstream migration through turbine induced mortality. Finally, the outflow is managed for hydropower purpose and thus affects the natural river discharge regime (Lassalle et al. 2009). In the Gironde system the first dams are located far upstream (270 km in the Garonne River and 200 km in the Dordogne River). Furthermore, the dams construction occurred decades before the first sign of decline (CIGB/ICOLD 2003).

Therefore, it is unlikely that dams are the unique cause of the dramatic decline of the shad population in the Gironde systems.

## ***B. Fishing mortality***

The fishing season of allis shad is synchronised with the spawning migration during which individuals gather in the estuary and become easier to capture (Martin-Vandembulcke 1999; Aprahamian et al. 2003). In the Gironde system, the exploitation rates ranged between 47.5% and 87.5% over the 1987-1998 period (Martin-Vandembulcke 1999), 61% over the 1987-2001 period (Chanseau et al. 2005) and 58% over the 1991-2003 period (Rougier et al. 2012). The overfishing in the estuary was proposed to be the main cause of the allis shad population collapse in the Gironde system (Rougier et al. 2012). However, no sign of recovery have been observed since the fishing moratorium in 2008.

The stock–recruitment relationship was originally thought to be a Ricker curve (Martin-Vandembulcke 1999). However, later a Beverton–Holt model better described the population dynamics (Rougier et al. 2012). A regime shift was suspected in the 1990s although no environmental fluctuations were detected (Rougier et al. 2012). The Beverton–Holt stock–recruitment relationship for *A. alosa* incorporated an Allee effect (Rougier et al. 2012). This depensation effect introduces a relationship between the population size and the individual fitness (Allee 1931). The mechanism of Allee effect could be explained by a mate limitation (Gascoigne et al. 2009), *i.e.*, it is more difficult for spawners to find a mate. The loss of reproductive facilitation could also explain the depensation effect, *i.e.*, individuals are less likely to reproduce if they do not perceive other reproductions. Indeed, shads are referred as hearing specialists as they respond to sound up to 180 khz (Mann et al. 2001). Therefore, we could expect that shad detect the sound of other mate reproducing, involving social facilitation (Koizumi and Shimatani 2016). Finally, the loss of large school of juveniles could



increase the risk of predation (Rougier et al. 2012). The depensation effect may have strongly hamper the recovery of the Garonne-Dordogne population (Rougier et al. 2012).

### ***C. Pollution and habitat degradation***

Massive water quality degradation has occurred with the urbanization and industrialization of watershed during the late 19<sup>th</sup> and in the 20<sup>th</sup> century (Freyhof and Brooks 2011). The urban wastewaters coupled with the industrial effluents may strongly impact the water quality and thus implied high mortality during the freshwater phases. High industrial pollution has notably led to a documented collapse of *Alosa fallax* in the Thames River (Bagliniere and Elie 2000). The abstraction for agriculture could degrade the spawning sites of shad by changing the natural cycle of discharge. Granulate extraction has led to degradation and loss of both spawning grounds and nursery area for juveniles (Bagliniere and Elie 2000). For the Gironde, significant metal pollution has been detected, with high cadmium concentrations in particular (Pierron et al. 2007; Courrat et al. 2009). Fishing ban on shad have been imposed due to the high concentration of PCB. This watershed presents a risk on pesticides with the presence of viticulture.

### ***D. Introduced species***

The shad populations can notably be impacted by newly introduced predators. The European catfish (*Silurus glanis*) has been introduced quite recently in France and may represent a huge shad predator to spawners closed to dams and fish passes (Guillerault et al. 2017).

### *E. Climate change*

In the last decades, climate change has been identified as an emerging threat for shad populations (Lassalle et al. 2008; Lassalle and Rochard 2009; Limburg and Waldman 2009). However, it remains unclear whether the climate change has impacted or will impact these populations. In the one hand, studies suggested that climate change will not be a main threat considering the thermal tolerance of juveniles (Jatteau et al. 2017), and lack of evidence of recruitment failure due to environmental changes (Rougier et al. 2012). Furthermore, studies dealing with species distribution models demonstrated that allis shad may exhibit a robust and optimistic response to climate change with suitable stable basins and gain of northern basins (Rougier et al. 2015). On the other hand, studies predict a reduction of suitable habitat (Lassalle and Rochard 2009) and a higher sensibility of the population due to the low abundance of spawners (Thuiller 2004; Lassalle et al. 2009).

## **V. Ecological concepts and modelling approaches developed in this PhD**

### *A. Ecological concepts*

The understanding of environmental constraints that shaped where and when organisms occur has long stood as the root of ecological studies. From casual observers to ecologists, anyone may deduct simple and global correlation between climate and distribution of species. As a silly example no one would expect a piranha to be naturally distributed in French rivers (luckily for allis shad). Despite the apparently simple link it is difficult to deeply understand what constrains a species distribution. Here, we define the components of environmental control on fish, from the habitat to the individual perception of environment that led to decision rules, with a special focus on the reproduction of allis shad ultimately.

a) Habitat versus ecological niche

A habitat is an area where a community of species lives, and could be considered as the “real” place of an ecosystem. One could define the habitat by its location with latitude and longitude. Even if habitats and ecological niches are sometimes considered as synonymous, we have chosen to differentiate these two concepts. The major difference is that niche should ideally be based on a more mechanistic understanding of the organism's response to environment, and could include biotic mechanisms as competition. As such, latitude is a good factor for the habitat but not when defining the ecological niche as the fish does not know the latitude. In other words, habitat is composed of several niches as it shelters numerous species, whereas, niche is an ecological component of habitat that needs to be defined with a specific set of environmental factors (as proximal as possible) for a single species.

Several definitions of ecological niche were proposed through the time (Sillero 2011). Ecological niche was originally proposed in 1904 as a subdivision of the habitat that enables organisms of a species to survive and reproduce (Grinnell 1904). This definition was based on environmental factors without consideration of biotic effects such as species density (Hirzel and Le Lay 2008; Wiens et al. 2009). Elton (1927) proposed an alternative definition that takes into account biotic effects and especially trophic interactions. In his “Concluding remarks”, Hutchinson proposed the cornerstone of niche conceptualisation with the first distinction between the realised and the fundamental niche (Hutchinson 1957). A species' fundamental niche refers to a fraction of an n-dimensional volume in the environmental space where a species can maintain a viable population (Hutchinson 1957). The realised niche refers to the occupied fundamental niche (Fig. 16), the unoccupied part of the fundamental niche being due to solely competition (Hutchinson 1957). The realised niche is therefore generally

narrower than the fundamental niche. However, some populations could occur in unsuitable environments, *i.e.*, habitats not contained in the fundamental niche, due to a sink-source relationship with healthier populations nearby (Pulliam 2000). Two ramifications of the Hutchinsonian niche were then proposed: the potential niche (Jackson and Overpeck 2000) and the occupied niche (Pearson 2010). The potential niche is the fundamental niche available at a specific moment in time. The realised niche is thus a proportion of this potential niche. The occupied niche is a fraction of the realised one that is constrained by geographical, historical and all types of biotic interactions. Thus, the occupied niche refers to the geographical distribution of the species (Fig. I6).

b) From ecological niche towards decision rules during the reproduction

At some point in their lives, allis shad must decide when (and probably with whom) to reproduce. The final observation of reproduction emerges from a collection of several individual reproductive choices, from the beginning of the upstream migration to the final choice to reproduce. In this PhD, we aimed to define the ecological niche during the reproduction and refine this definition to the final decision rules to reproduce. What is the difference between these two definitions?

The answer lies in the shad life cycle (Fig I4). Indeed, the reproduction in rivers depends on the final decision rule but also on the migration. Thus when we define the ecological niche during the reproduction, we implicitly integrate migration into it. The decision rule is different from the niche because the influence of migration must be explicitly explained, and therefore we focus essentially on the choice of when reproduce (*i.e.*, decision rules).

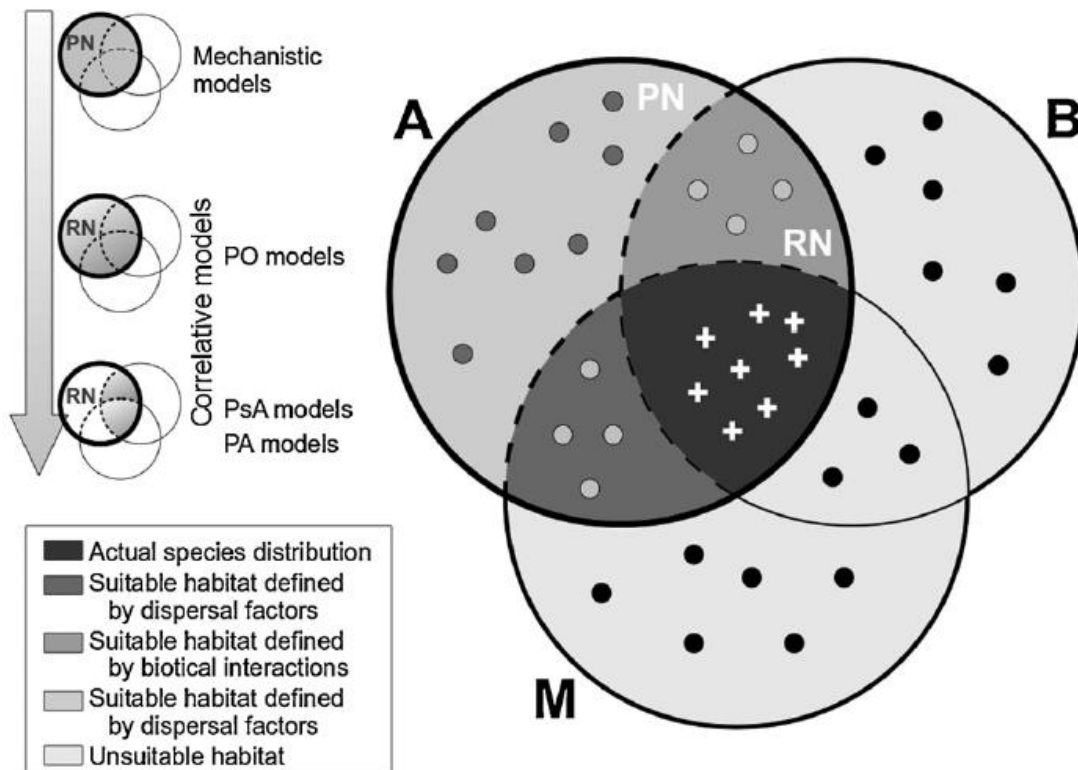


Figure 16: The BAM diagram from Sillero (2011). The three main factors limiting the distribution of a species are represented: abiotic (A), biotic (B) and dispersal (M). The habitat is unsuitable for the species outside the area common to the three factors where the species actually occurs (presence in cross and absence in dots). The circle (A) represents the fundamental niche (FN), the area common to (A) and (B) represents the realised niche (RN). The fundamental niche (FN) can be identified by mechanistic models. The realised niche (RN) can be identified by correlative models (presence-only (PO) models, pseudo-absence (PsA) models and presence/absence (PA) models).

This is not the first time that a niche was refined to a biological process. In the past, the case of diadromous fish has been questioned when applying niche modelling, and in particular on the impact of their dispersal capacity when predicting their distribution (Leathwick et al. 2008). Leathwick *et al.* (2008) analysed the distribution of 15 diadromous and 15 non-diadromous fish species from 13,369 sites and interpret that the difference in their biogeography's reflected the interaction between their marked differences in dispersal ability. This extent of integrating life history parameters represents a promising approach to gain in ecological realism when defining ecological niche. Moving further from the traditional use of ENMs on simple occurrence, different parts of the life cycle can be targeted when performing ENMS: reproduction, growth and survival (Pulliam 2000; Sax et al. 2013; Brambilla and Saporetti 2014; Feng and Papes 2017). This simple idea is more than an option for anadromous fish because these highly mobile species use different habitats and have different physiological tolerances during these three stages. The definition of ecological niche will be analysed with correlative models, whereas decision rules will be defined with mechanistic models (Fig. 17).

### ***B. Methodological approach***

We must follow a procedure in order to gain in model realism when defining either the ecological niche or the decision rule (Fig. 17). The model realism depends on three key processes: the choice of relevant modelling method, the selection of relevant factors and the extent of extrapolation when forecasting future conditions (Elith and Leathwick 2009).

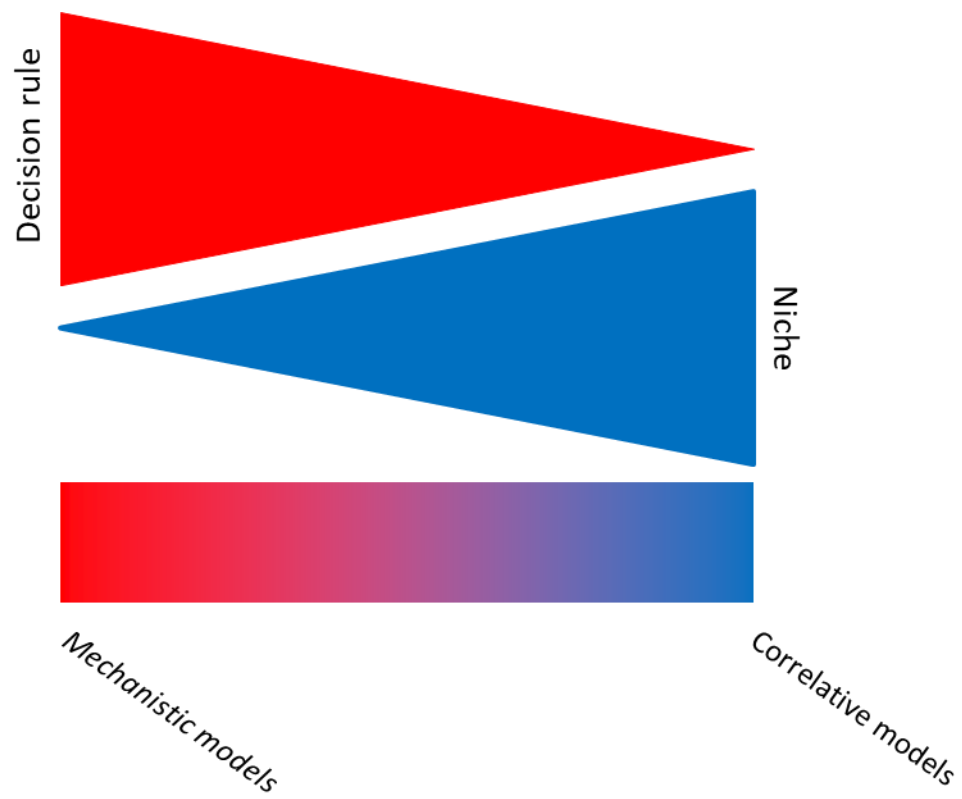


Figure 17: Thematic gradient between the mechanistic model that seeks to define decision rules and correlative models that define the ecological niche

## a) Correlative and mechanistic approaches

In order to describe the environmental constraints on fish distribution across time and space, modellers used correlative procedures to relate field observations of fish with environmental predictor variables. This discipline that aims at defining the ecological niche could be named in many ways, and fails to reach a consensus (Sillero 2011). It could be named Ecological Niche Models (ENMs), Species Distribution Models (SDMs), habitat suitability maps (HSMs), habitat distribution model, species-habitat model or climatic envelope models (Sillero 2011). Even if Species Distribution Models (SDMs) is the most used terminology, my work will refer to Ecological niche models (ENMs), rather than Species Distribution models (SDMs). SDMs predict the distribution of suitable habitats whereas ENMs refer to prediction of the species' distribution *per se* (Sillero 2011) and is more attached to the niche concept (developed below). To my mind ENMs was more adapted to this PhD, as no spatial output of suitable habitats was developed. Most ENMs used correlative approaches that provide occurrence probability in the context of Hutchinsonian niche and excluded mechanistic models (Elith and Leathwick 2009 but Kearney and Porter 2009; Sillero 2011 include mechanistic models in SDMs).

A large array of techniques is available to model ecological niches. Here, I propose a decision tree (Fig. 18) adapted from the niche classification of Sillero (2011). The choice of the ecological niche to model is highly dependent on the biological data available. As such, the choice to model a potential or a realised niche is highly dependent on either physiology or occurrence data are available (Fig. 18). Mechanistic models are complementary approaches to ENMs that provide a process-based conceptualisation of the ecological niche (Fig. 17).



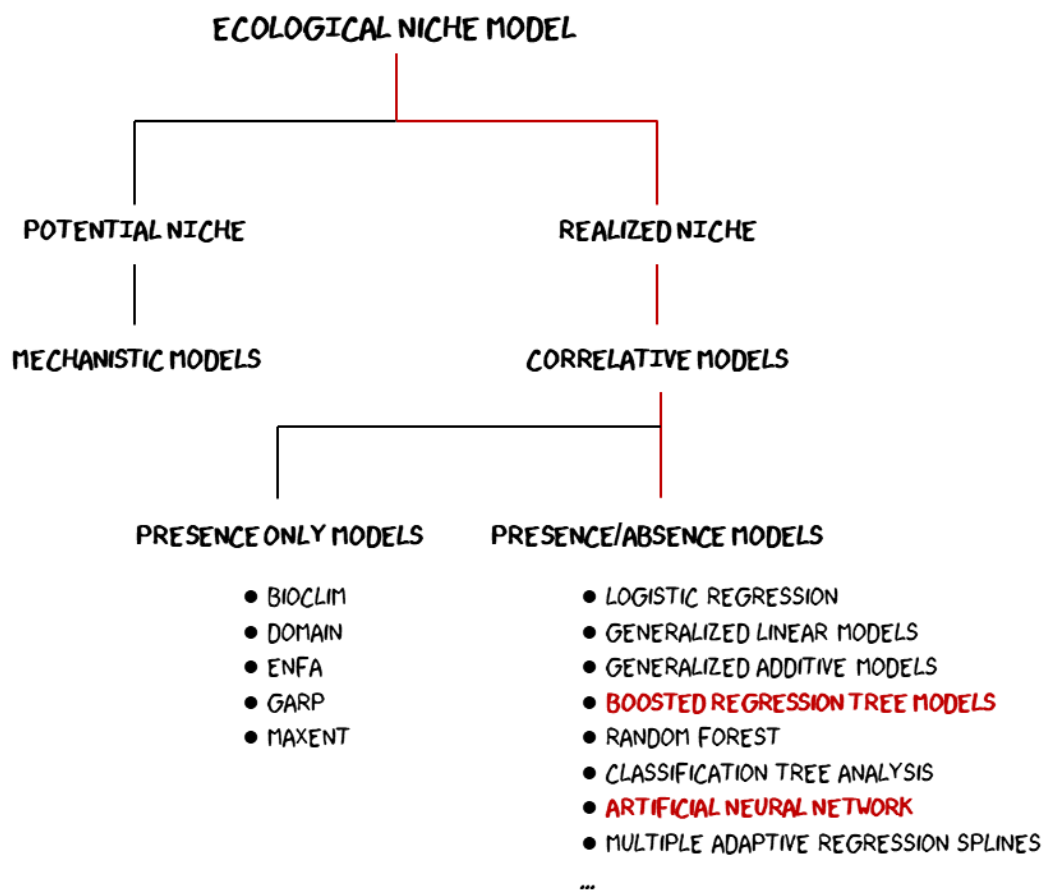


Figure 18: Decision tree of available model use according to the type of niche and data available (modified from a personal communication from Sillero).

Mechanistic models provide an explicit formulation of the underlying processes whereas correlative models can implicitly incorporate any factors associated with independent variables. In this PhD, the mechanistic models explore deeply the reproduction by disentangling the migration and the decision rules. The advantages of mechanistic models are highly transferable across environments but with potentially low precision whereas correlative models perform local analysis with a better precision (Kearney and Porter 2009).

b) The selection of relevant data

The first step is gathering reliable biological data (occurrence or abundance) with relevant environmental factors (Fig. 18). The quality and quantity of available data is the cornerstone of this PhD.

The data used in this PhD could be classified in four categories: abundance, presence data, absence data and background data. Abundance is a count of individuals reproducing; a presence refers to the occurrence (in space of time) of the species reproduced, while conversely, absence corresponds to the non-occurrence of reproduction. Background data is the set of environmental factors selected to model the species' niche from the study area. Here, we tried to select the most proximal environmental factors available, consistently with a mechanistic understanding of the organism's response to environment. As such, though some ENMs latitude is reliable proxy of environmental conditions to model the distribution of diadromous fishes (Lassalle et al. 2009; Rougier et al. 2015), latitude is more related to habitats than niches, and here, we chose to use directly temperature.

A recent debate about the need of proximal factors was conducted by McGarvey *et al.* (2018). McGarvey *et al.* (2018) studied the reliability to use air temperature as a surrogate of instream conditions (water temperature) when modelling the distribution of freshwater fish.

Surprisingly, it appears that predictions were quite similar when using either air or water temperature for modelling 15 freshwater fishes' distributions at the scale of the Columbia Basin (McGarvey et al. 2018). Thus, air temperature seems to be a reliable proxy of instream conditions. However, it is, of course, preferable to use water temperature because fish will perceive directly this environmental factor.

c) Predictive and explanatory approaches

Beyond the difference between mechanistic and correlative approaches, this PhD aimed at fulfilling two distinct objectives: explanation and prediction.

The first goal aims at exploring the control of environmental factors on reproduction of allis shad with both mechanistic and correlative models. This definition of the fish's spawning niche as a function of temporally variable environmental factors was then used to quantify the sensibility of the species to climate change. Ultimately, we aimed to predict the effect of climate change with the model developed for the explanatory approaches.

The prediction approach is increasingly being asked by decision makers in order to implement strategic conservation plans (Wiens et al. 2009; Elith and Leathwick 2009). In fact, given the magnitude of anthropogenic pressures and especially climate change, understanding the consequences of such threats on biodiversity become critical. ENMs then represent useful tools to incorporate these future unprecedented conditions into biodiversity management policies. ENMs can be used to predict future spatial or seasonal distribution of fishes, which are two of the main responses of organisms to climate change: changes in distribution and changes in phenology (Hughes 2000). As such, Thuiller *et al.* (2005) predicted the distributions of 1,350 European plants species under seven climate change scenarios, and forecasted that half of these species could be vulnerable or threatened by 2080. For fish,

Perry *et al.* (2005) demonstrated a major shift in fishes 'distribution likely due to climate change and profound impacts on commercial fisheries as well. In conclusion, prediction in ENMs may have several implications in conservation and management of species.

In these prediction applications, a particular attention should be paid to the extent of extrapolation in order to produce reliable predictions. Extrapolation refers to the use of a rule described by a model outside the domain where it was calibrated. As such, it refers in ENMs to new combinations of environmental predictors absent in the training data. Therefore, the extrapolation is inherently risky. Several methods are available to evaluate the risk of extrapolation (model robustness). First of all, the environmental factors combinations used for calibration can be represented and compared with the set used for projections. This will enable to identify combinations of factors for which the model has not been calibrated. Second, cross-validation is a model validation technique that tests the model's ability to predict with data not used for the training. Cross-validation involves partitioning multiple times a sample of data into two subsets: the training data in which the model is calibrated and the testing data in which the model outputs are compared with observed data.

## **VI. General aim of the PhD**

During this PhD, I explored the control of environmental factors on reproduction of allis shad (Fig I9). For this, I developed both correlative models and mechanistic models. After defining the environmental control on allis shad, I used this understanding to respond whether reproductive behaviour of shad spawners has been impacted by possible habitat degradation on spawning grounds in the past, and will be impacted by future climate change.

This PhD is divided in four sections: description of the study (chapter II), explanatory approaches (Chapter III), predictive approach (chapter IV) and discussion (chapter V).

The case study (chapter II) will briefly present the data set proceeded in this PhD and the allis shad population in the Garonne and Dordogne rivers. In the explanatory approaches (chapter III), we developed four methods: Manly index, a boosted regression trees model, the FlirtyShadBrain model and the HOOS model. The two correlative models (paper #1 and paper #2) will enable to define the thermal niche first and then to define a more comprehensive niche that is composed of temperature, discharge and day length. Then, two mechanistic approaches will be presented to disentangle the migration from the decision rules. The ecological understanding developed in the chapter III is critical for the final application of ENMs (chapter IV). In chapter IV, I will propose insight of the possible impact of climate change on the reproduction of the allis shad population in the Garonne and Dordogne rivers.

A general discussion will conclude this manuscript. It will explain first the knowledge improvement on allis shad reproduction and finish on a personal perspective about modelling in ecology.

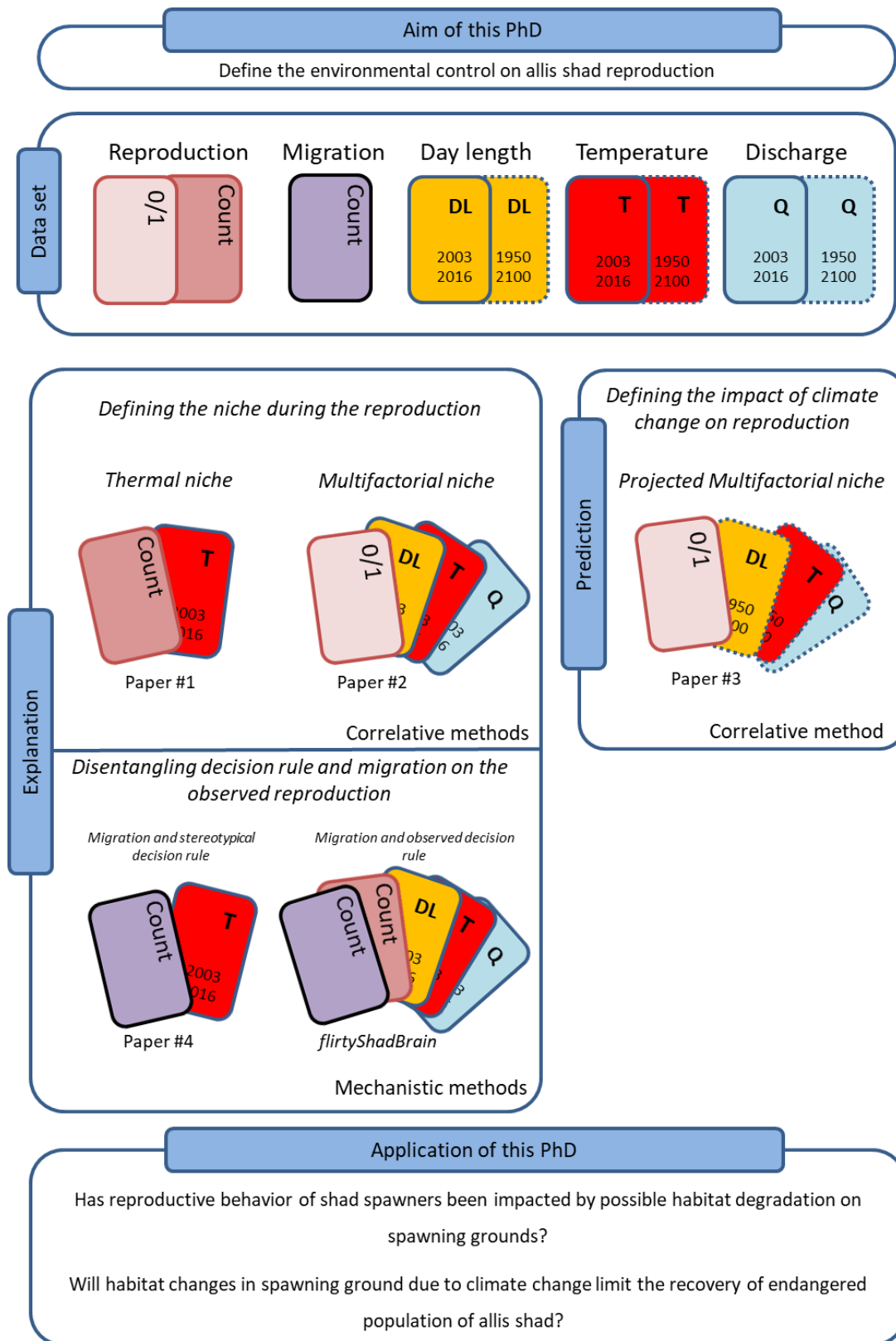


Figure I9: Conceptual diagram representing the articulation of the different parts of this PhD.







# **Chapter II**

## **Case study**



In this chapter II, I will present briefly the data set used in this PhD, which are composed of both biological (observations of reproduction, and migration) and environmental factors that can explain the studied biological processes (Fig II1). In the next chapter, these different data were coupled in order to calibrate different statistical and mechanistic models that aimed at explaining and predicting the response of shad to environment.

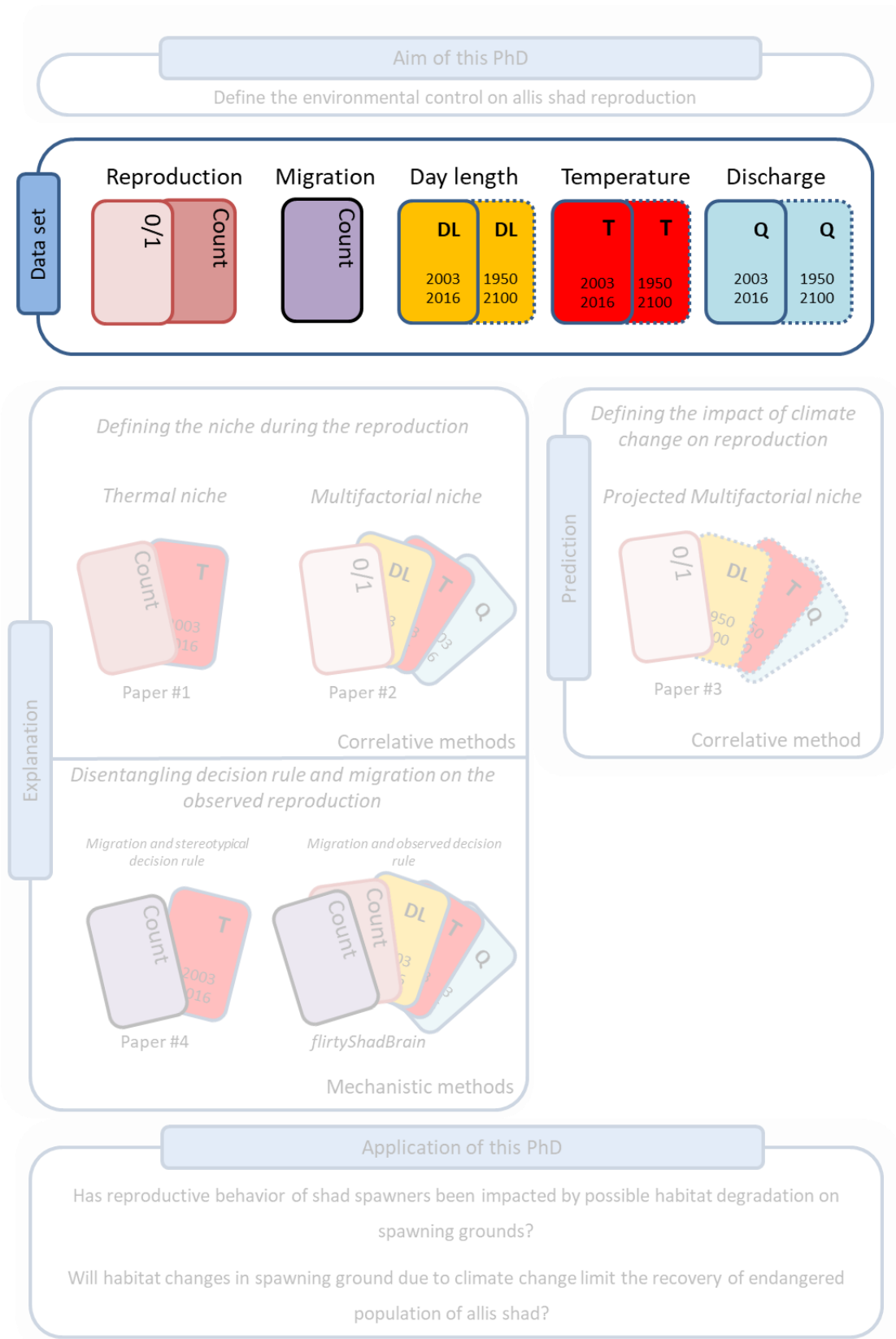


Figure II1: Conceptual diagram representing the articulation of the different parts of the PhD.

The highlight part represents the chapter developed (here the data set)

## **I. Biological data**

### ***A. Spawning grounds***

The data used in our studies were collected in the Garonne and Dordogne rivers (Fig. II.2). These two rivers are located in South-Western of France. The first barrier is at 270 km from the sea on the Garonne River (Golfech dam) and at 200 km on the Dordogne River (Tuilières dam). The allis shad reproduction is monitored by Migado (non-profit association, <http://www.migado.fr/>).

Seven main spawning grounds are known in the Garonne River. Four spawning grounds were selected, as there were regular visits by spawners during the 13 years. These 4 spawning grounds (namely Sauveterre, St Nicolas, St Sixte and Lamagistère) are concentrated in 20 km downstream the Golfech dam (Fig II.2). The flow and temperature regime of the Garonne River are influenced by the melting of snow in early summer.

Fourteen main spawning grounds are known in the Dordogne River. Among them four sites were analysed based on regular visits by spawners from 2003 to 2016. These spawning grounds are from downstream to upstream: Gardonne, Prignonrieux, Castang and Nébouts (Fig II.2). In the Dordogne River, shad spawned upstream than the selected spawning grounds in 2003, 2008, 2012 and 2016, therefore these years were excluded in our analysis. The flow regime is more artificial in the Dordogne Rivers, particularly through dams.

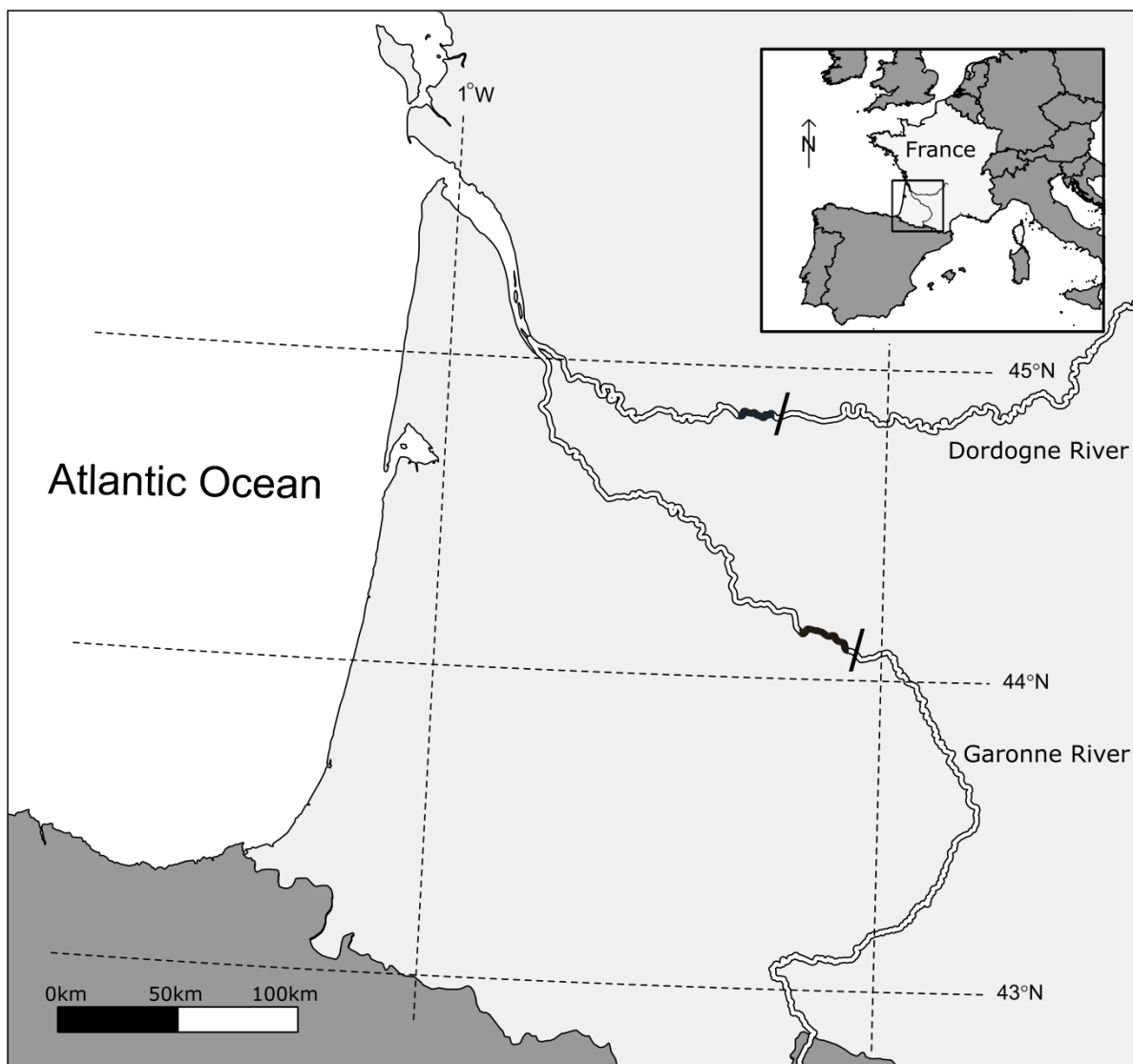
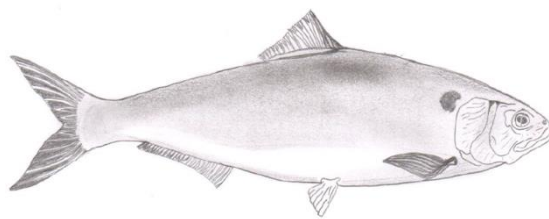


Figure II2: Location of spawning sites monitored by the Migado association (coloured sections). Temperatures and discharges were recorded close to the two dams (symbol: /).

The reproduction was monitored in two ways: either directly by hearing (direct counting) or by audio recording (indirect acoustic counting). For direct counting, the observer was equipped with a manual counter and stood on the shoreline in front of the most active area (Gaillagot and Carry 2016; Gracia and Caut 2016). Indirect counts were carried out using audio digital recorders that record the noisy behaviour (Gaillagot and Carry 2016; Gracia and Caut 2016). The daily observations per spawning grounds were pooled for each river to obtain a sufficient number of observations and was justified by the low environmental variation between them (Gaillagot and Carry 2016; Gracia and Caut 2016). Data were available from 2003 to 2016, which constituted 1143 presence-absence data.

### ***B. Preliminary analysis on biological data***

The monitoring period, *i.e.*, first and last date of monitoring within a spawning season fluctuated during the 14-year period in the two rivers (Fig. II3). The onsets of the reproduction closely follow the start of the monitoring window. This is consistent with the monitoring approach of Migado that waits the first passage at the control dam (upstream the spawning grounds) to begin the monitoring (personal communication Laurent Carry). Therefore, few sooner reproductions were potentially not monitored. This is likely in the Garonne River when reproduction was observed from the first day of monitoring (Fig. II3).

The number of reproduction fluctuated during the studied period with a spectacular fall beginning in 2006 in the two rivers (Fig. II4). Reproduction has remained very low since 2007, with a moderate peak in reproduction in 2011, caught up by a synchronised decline in reproduction in both rivers.

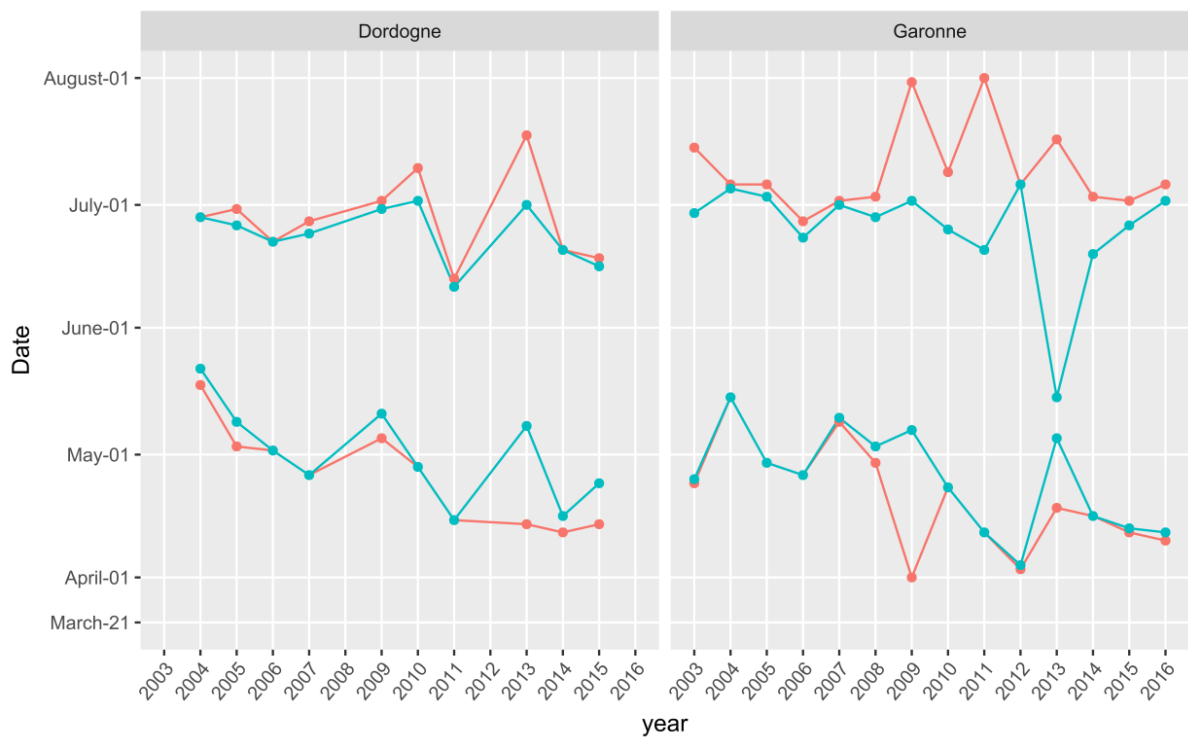


Figure II3: Trends in the onset and cessation (blue lines) of the spawning period in the Garonne and Dordogne rivers for the 14-year period. Trends in the observation period, *i.e.*, start and end of the monitoring carried out by MIGADO (red lines).



The trend in number of reproduction revealed that the possible extirpation of shad populations in the Gironde system can no longer be excluded (Fig. II4) as observed by Rougier *et al.* (2012). This synchrony in the decline may be due to a synchronised degradation of environmental factors in the spawning grounds or by the metapopulation dynamic for this species in France (Randon *et al.* 2017).

## **II. Environmental factors**

### *A. Selection of factors*

Eight environmental factors were used in this PhD: water temperature, air temperature, water discharge, day length and the daily variations of each of these four factors. These eight environmental factors were pre-selected based on documented control over the life cycle of allis shad and their daily availability. Contrary to salmonids for which the reproduction is mainly triggered by photoperiod (Scott 1990), temperature and river discharge also appear as main triggers of shad reproduction and migration (Mohr 1941; Dottrens 1952; Hoestlandt 1958; Cassou-Leins 1981; Philippart, and Vranken, 1982; Menneson-Boisneau and Boisneau 1990; Cassou-Leins and Carette 1995; Aprahamian *et al.* 2003; Bagliniere *et al.* 2003; Acolas *et al.* 2006). The migration also seems to be controlled by both temperature and to a lesser extent by river discharge (Roule 1925; Boisneau *et al.* 1985; Aprahamian *et al.* 2003). The temperature controls notably the swimming capabilities of shad, as their swimming speed is inhibited when water temperatures fall below 12°C (Steinbach *et al.* 1986).

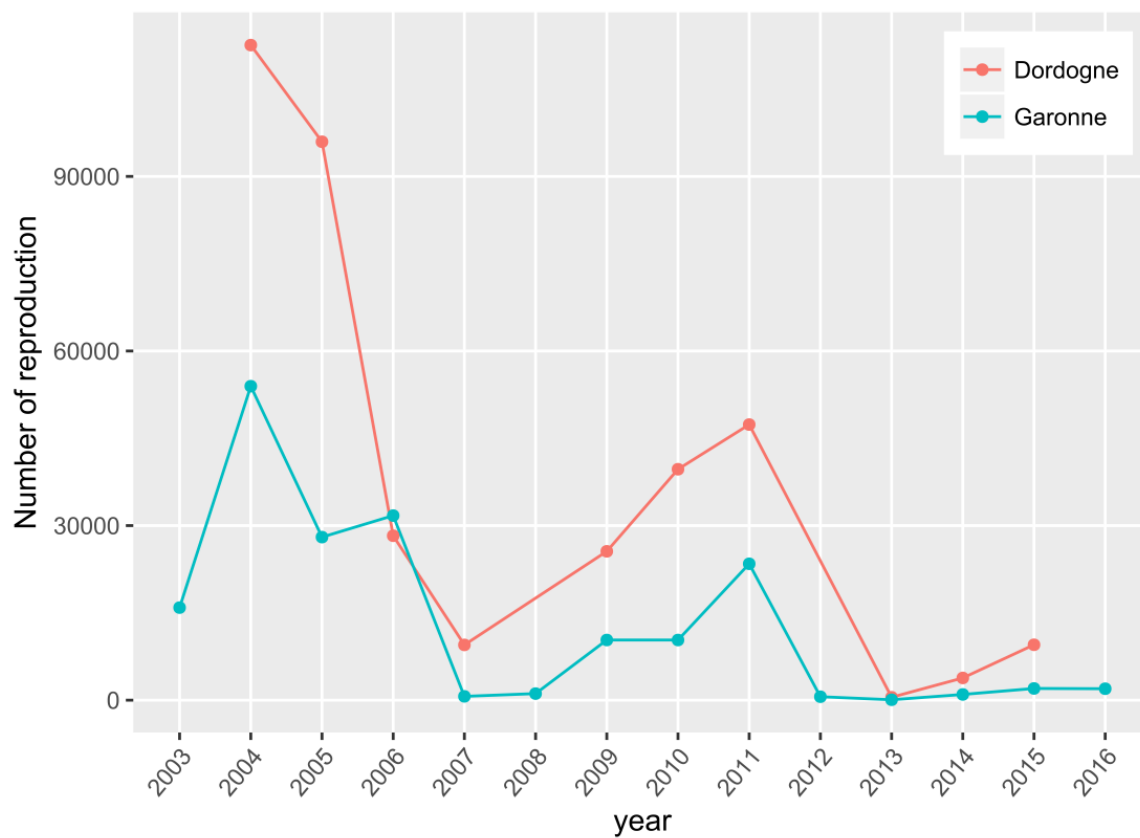


Figure II4: Trend in number of reproduction monitored by MIGADO in the Dordogne and Garonne rivers.

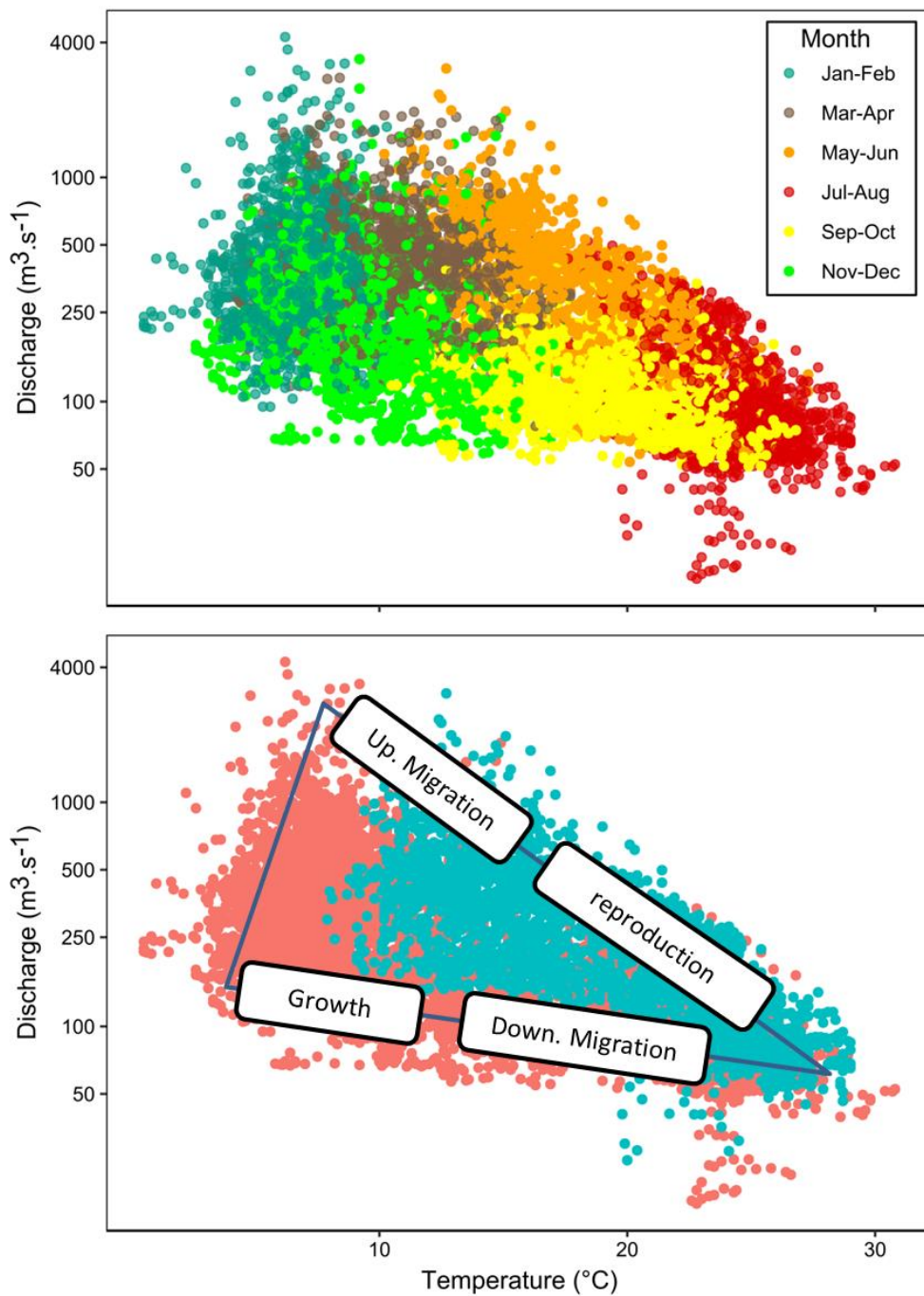


Figure II5: Ichthyograph of allis shad based on Flitcroft *et al.* (2016). 14 years of river daily discharge and water temperature (the y axis is log-scaled): (top panel) the colours represent each of the six two-month periods representing the annual cycle of hydrologic conditions; (bottom panel) the colours represent the reproduction period (in blue) and the background data (in red).

Finally, experiments on embryonic and larvae survival demonstrated that daily survival is strongly dependent on temperature and could impact the success of recruitment of allis shad in France (Jatteau et al. 2017). The action of river flow on migration is less clear-cut and of varying importance depending on the time of migration. It could act as a secondary modulator when the temperature is favourable (Rochard 2001). The river discharge is thought to moderate the spawning migration only during strong peaks ceasing the spawning migration (Bellariva 1998).

The influence of the environment on the allis shad life cycle could be represented with an *ichthyograph*. An *ichthyograph* is a graphical tool that visualise relationships between hydroclimate and fish phenology (Flitcroft et al. 2016). We used the 14-year data sets of temperature and discharge to examine relationships between hydroclimate and the expression of life-history phenology by allis shad. This graphical representation gave a first look about the environmental control on reproduction. We can see that the reproduction takes place during a wide range of temperatures whereas the range of river discharge is moderate through low values (Fig. II5).

Water temperature ( $^{\circ}\text{C}$ ) and river discharge ( $\text{m}^3.\text{s}^{-1}$ ) were measured near the spawning grounds throughout the year. Water temperature was recorded every hour by data loggers at the Golfech Dam (Garonne River; Fig. II.2) and at the Tuilières Dam (Dordogne River; Fig. II.2). We average the temperature per day. Daily air temperature at the grid cell closest to the spawning grounds (8 km by 8 km grid) in the two rivers is extracted from the SAFRAN dataset (Vidal et al. 2010). SAFRAN is based on observation stations over France collected by Météo-France and an optimal interpolation algorithm. SAFRAN is available on a 8 km by 8 km grid from 1950 to 2018. The average daily river discharge was obtained from the French “Banque

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Hydro” (<http://www.hydro.eaufrance.fr>). Water and air temperatures (Temp) were calculated as the average daily temperature ( $^{\circ}\text{C}$ ) and the variation of average temperature from one day to the next ( $\Delta T$  in  $^{\circ}\text{C}$ ). The daily river discharge (Q) was log-scaled in order to normalise the distribution in the two rivers and the variation of logged daily river discharge from one day to the next ( $\Delta Q$  in  $\text{m}^3 \cdot \text{s}^{-1}$ ). Day length (DL) was defined as the interval between sunrise and sunset based on the latitude and longitude of the spawning grounds (Corripio 2003), and the variation of day length from one day to the next ( $\Delta \text{DL}$  in hours).

### ***B. Dealing with correlated predictor variables***

The water temperature was negatively correlated with the river discharge and the variation of the day length (Fig. II6). The water temperature was positively correlated with the day length (Fig. II6). Other correlations were weak. The auto-correlation function (ACF; Fig. II7) highlighted that the water temperature at a given day was strongly auto-correlated with temperatures from the previous 15 days. The partial auto-correlation function highlights that the autocorrelations observed were a residual effect of the partial autocorrelation for the 1-day and 2-day offsets (PACF; Fig. II6). The same applies for the river discharge with a lag of more than 20 days in the ACF due to residual correlation for the 1-day, 2-day and 3-day offsets (ACF and PACF; Fig. II7).

As there is a strong autocorrelation for the three environmental factors (the dataset has indeed a temporal structure), we choose to use methods that could deal with such non-independent and correlated data such as the Boosted Regression Tree (BRT) that has been proven to deal great with any type of data such as non-independent data (Fabricius and De’Ath 2008; Buston and Elith 2011).

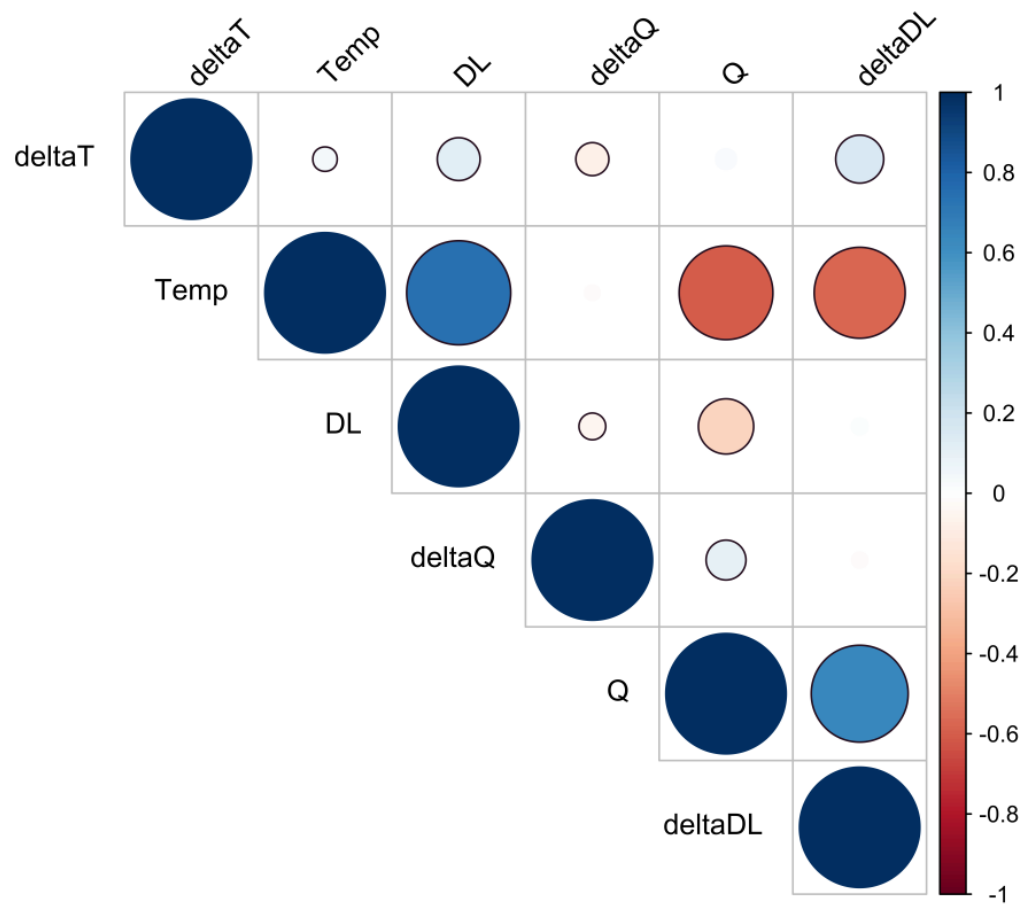


Figure II6: Correlation matrix between the 6 environmental factors. The colour and the size of the circles indicate the intensity and direction of the correlations (positive correlation in blue circles and negative correlation in red circle)

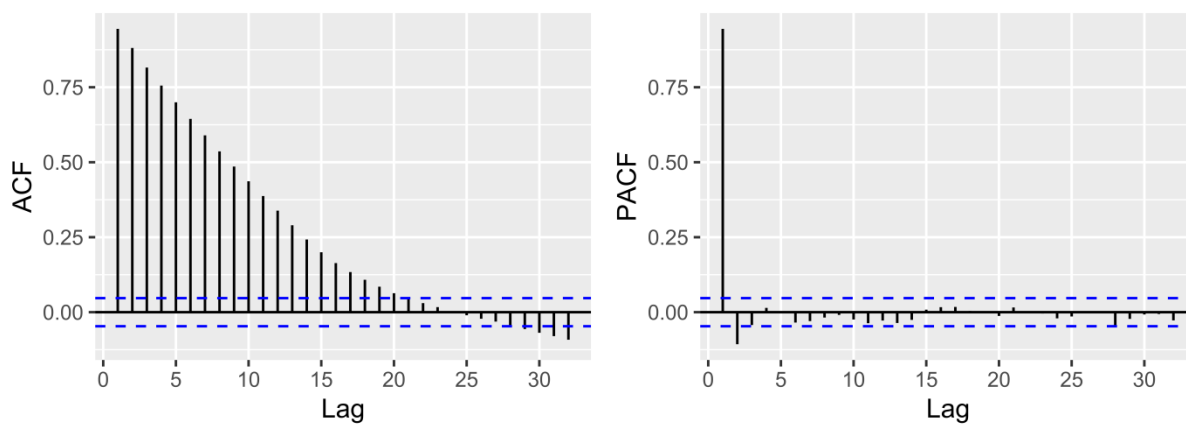


Figure II7: The auto-correlation function (ACF, left panel) and the partial auto-correlation function for the water temperature (PACF, right panel). The analysis was coupled for the two rivers.

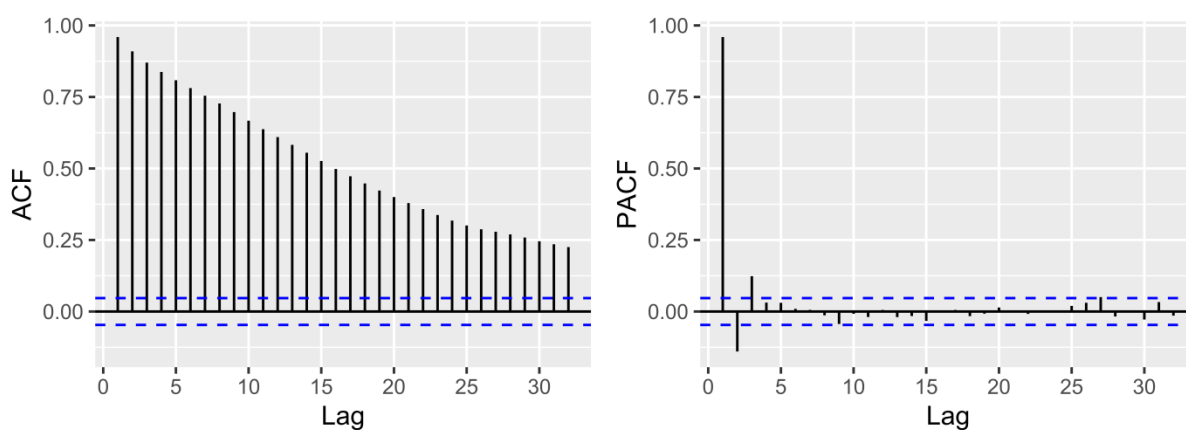


Figure II8: The auto-correlation function (ACF, left panel) and the partial auto-correlation function for the discharge (PACF, right panel). The analysis was coupled for the two rivers.





# **Chapter III**

## **Explanatory approaches**



In this chapter “Explanatory approaches”, we aimed at defining the environmental control on allis shad reproduction and at improving our understanding about the complex link between migration and reproduction (Fig. III1). The definition of the environmental control on allis shad reproduction was achieved by using two correlative models, whereas the disentangling of migration and reproduction was performed by two mechanistic models.

In the correlative approaches, we defined the environmental control on several steps as the reproduction is a complex event. First, we focused on temperature as the early life stages are documented to be sensitive to this environmental factor. Then, we extended to a more integrated description of the environmental control on shad’s reproduction based on temperature, discharge and day length.

In the mechanistic approach, we presented two mechanistic models, which aimed to disentangle the migration from the reproduction. The most developed model (HoOS) successfully explored the consequence of the migration and two stereotypical spawning behaviours (reproduction *per se*) in terms of early life survival. The second one (flirtyShadBrain) was the most complex model. The idea was to move beyond the stereotypical behaviour and simulated in parallel the migration and the spawning behaviour (decision to spawn according to environmental factors).

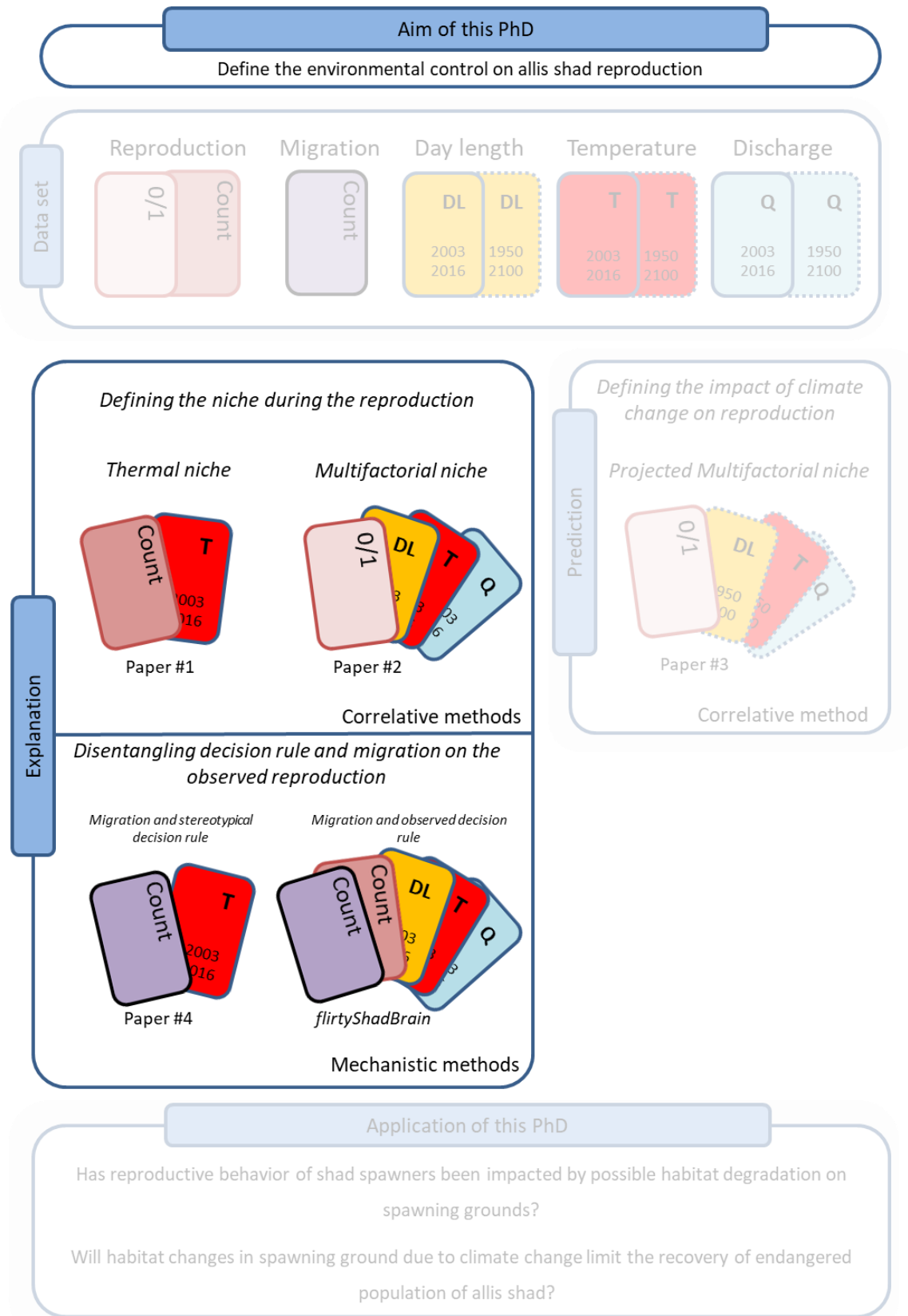


Figure III1: Conceptual diagram representing the articulation of the different parts of the PhD.

## I. CORRELATIVE APPROACHES

### A. Paper #1: “A field-based definition of the thermal preference during spawning for allis shad populations (*Alosa alosa*)”

In this paper we aimed at testing whether temperature plays a role in allis shad’s reproduction (Fig. III2). The idea was to demonstrate that shad select specific temperature range. For this purpose, we used an innovative metric (Electivity index of Manly) to study thermal preference during reproduction for allis shad. Our results demonstrate a true selection of certain temperature ranges during the reproduction. Ultimately, we illustrated the overlapping of temperature range selected by spawners with the thermal tolerance of early life stages, which tends to confirm the Quinn and Adams’ hypothesis (1996), that states that fish optimise the reproduction to enhance the early life survival.

This paper was submitted in September 2018 and published in *Environmental Biology of Fishes* in March 2019. The reference of this article is: Paumier, A., Drouineau, H., Carry, L., Nachón, D.J., and Lambert, P. 2019a. A field-based definition of the thermal preference during spawning for allis shad populations (*Alosa alosa*). *Environ. Biol. Fishes.* doi:10.1007/s10641-019-00874-7.

NB Erratum, a word is misspelled in the second sentence of this article (“exothermic” should be replaced by ectothermic).

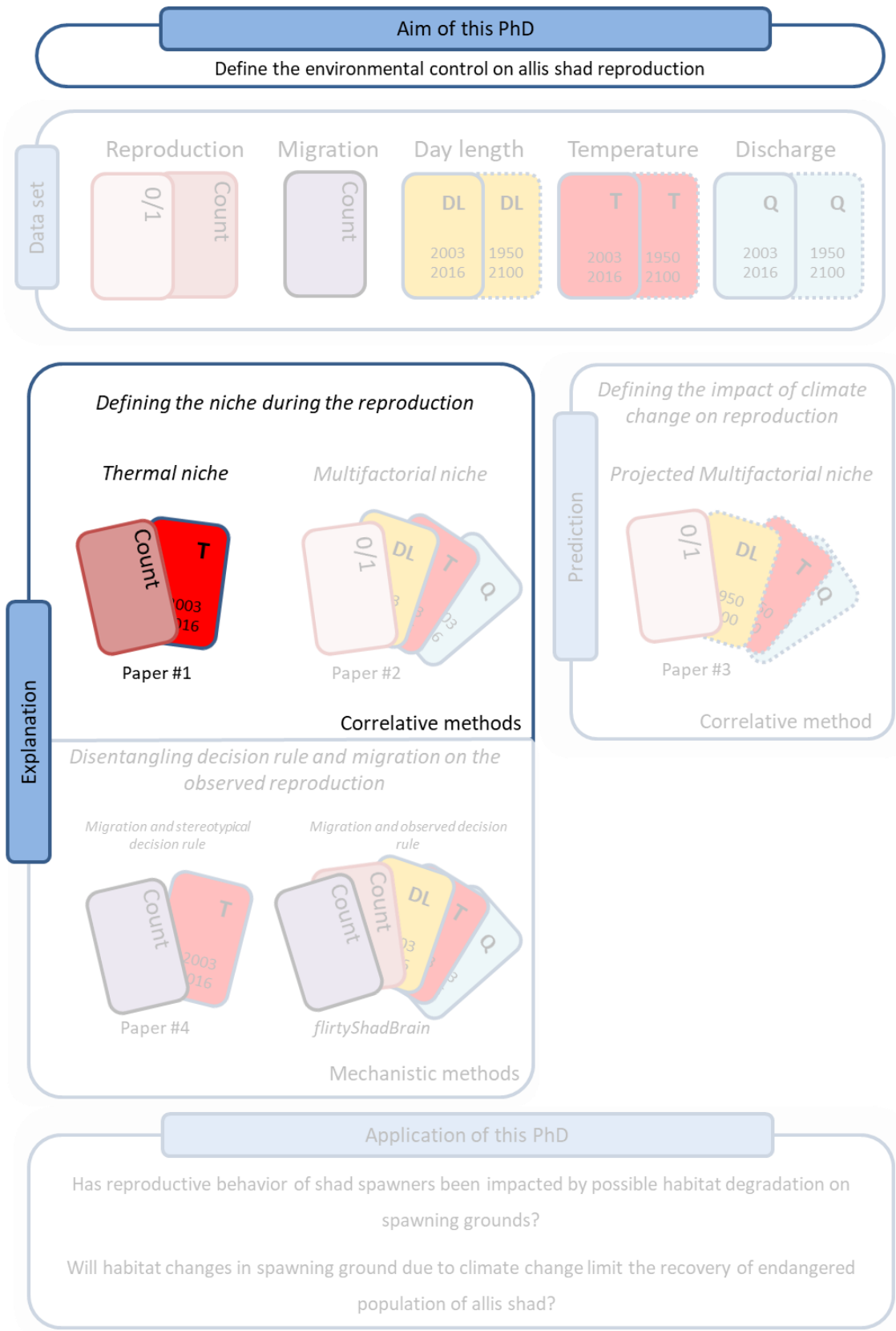


Figure III2: Conceptual diagram representing the articulation of the different parts of the PhD.



## A field-based definition of the thermal preference during spawning for allis shad populations (*Alosa alosa*)

Alexis Paumier · Hilaire Drouineau · Laurent Carry · David José Nachón · Patrick Lambert

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**Abstract** All around the world, diadromous fish are facing multiple anthropogenic pressures resulting in a global decline in these migratory species. In Gironde, the allis shad populations which were the most abundant in Europe are no exception and have dramatically declined since 2000. Failure in reproduction success is one of the proposed explanations for this collapse. In light of this, we studied the reproductive strategy of the allis shad populations in the Gironde watershed. We used an original methodology to define the thermal behavior of allis shad during reproduction using an electivity index for 14 years of field monitoring in two rivers, composed of daily reproduction activity and temperature. For the first time, this study deeply explores and defines the thermal preference of a shad species during the reproduction. A temperature preference between 14.5 °C and 23 °C by spawners during the reproduction was observed. Despite annual fluctuations, an overall similarity of temperature ranges between the two rivers was observed. The thermal preference matched with the thermal tolerance of early stages (16.2 °C to 24.8 °C) and confirms that allis shad spawners adopt behavioral rules

of reproduction in order to maximize the survival of their offspring. The similarity of shad thermal behavior may indicate the phylogenetic basis of thermal preference for fish species.

**Keywords** Diadromous fish · Reproduction · Temperature · Thermal preference · Fitness · Allis shad

### Introduction

Biologists have demonstrated the undisputed link between temperature and all major life cycle processes from the cell to the organism level (Hochachka and Somero 2002; Rome 2007; Angilletta 2009). The high thermal conductivity together with the strong heat capacity of water causes the body temperature of exothermic aquatic organisms, like fish, to closely follow the temperature of their habitat (Angilletta 2009). Therefore, temperature is a major component of freshwater habitat and can be seen as a component of the ecological niche (Hutchinson 1957). Accordingly all aspects of behavior and physiology of fish are sensitive to temperature (Huey and Kingsolver 1989; Quinn and Adams 1996; Golovanov 2006). Fish have evolved to perform well in very specific ranges of temperature (Brett 1956, 1971; Fry 1964, 1971). In the context of global warming (IPCC 2014), a major challenge for ecologists is to predict how this phenomenon will affect the biology, abundance and distribution of organisms (Hughes 2000). Like other species, diadromous fish, which migrates between sea and river during their life cycle (McDowall 1988), have proved to be sensitive species

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to these climatic modifications (Lassalle and Rochard 2009). Indeed, these species have multiple thermal requirements to complete their life cycle (Quinn and Adams 1996; Quinn et al. 1997; Hodgson and Quinn 2002; Jatteau et al. 2017). Early life stages are the most sensitive to environmental fluctuations and are characterized by high mortality rates, as observed for bay anchovy and striped bass (Houde 1989) and for the cod and herring stocks (Hjort 1914). The success of survival of the earlier stage is a key feature of population dynamics for fish (Hjort 1914, 1926; Toresen and Østvedt 2000; Brunel and Boucher 2006). Thus, the spawning strategy, defined as the reproduction timing, is a major life history trait, as it influences the biophysical conditions that offspring experience (Quinn and Adams 1996; Lyons et al. 2015).

The allis shad, *Alosa alosa* (Linnaeus, 1758), is an anadromous species belonging to the Clupeidae family. The adults spend most of their life in the ocean, returning to their natal river to reproduce between 3 and 6 years old (McDowall 1988; Lambert et al. 2001; Martin et al. 2015; Randon et al. 2017). Reproduction takes place in the intermediate and higher reaches of the rivers (Bagliniere et al. 2003). Allis shad populations are spring spawners (Hasnain et al. 2013); the period of reproduction is spread out in less than 2 months, from late April to late June (Bagliniere et al. 2003). During the reproduction, a fast and noisily circular movement is observed near the river surface. The spawning act lasts between 3 and 10 s and produces a characteristic sound between 35 and 50 dB at 1 m (Cassou-Leins et al. 2000). This noise is used to monitor the spawning activity (Menneson-Boisneau 1990). Allis shad spawn in very specific habitats characterized by a deep area followed by a shallow coarse substrate beach. Shad spawn in the upstream deepest areas and the fertilized eggs drift downstream to the shallowest area (Bagliniere et al. 2003). After the reproduction, the spawners die and the eggs hatch in less than 10 days (Cassou-Leins 1981; Jatteau et al. 2017). The short incubation time allows to study the reproduction under the Quinn and Adams (1996) hypothesis: fish species may develop reproductive strategies to enhance the survival of their offspring, as the environmental conditions experienced by spawners and earlier stages are very similar (Leggett and Carscadden 1978; Quinn and Adams 1996; Lambert et al. 2018).

Allis shad populations were largely distributed along the European Atlantic coasts from Norway to Morocco and were even present in the western part of the

Mediterranean, but their distribution has decreased since the middle of the twentieth century because of anthropogenic pressures (Bagliniere et al. 2003). Until the end of the twentieth century, the population in the Gironde Basin (Southwestern France; Fig. 1) was the most abundant in Europe, but it suddenly collapsed in the early 2000s (Bagliniere et al. 2003; Rougier et al. 2012). Recruitment failure in continental waters was suspected (Rougier et al. 2012). Dam constructions, riverine habitat degradation, overfishing, and water pollution also contributed to this collapse (De Groot 2002; Bagliniere et al. 2003; Lassalle et al. 2008; Limburg and Waldman 2009; Rougier et al. 2012; Drouineau et al. 2018). Despite a fishing ban in 2008, the populations of shad have failed to recover to the historical abundance.

Temperature has already proved to influence many ecological processes of allis shad, such as spawning activity, spawning migration or young stage survival (Cassou-Leins et al. 2000; Acolas et al. 2004, 2006). The best survivals from embryos to 14 day after hatching larvae were found between 16.6 °C and 24.8 °C (Jatteau et al. 2017). Lambert et al. (2018) demonstrated that spawners are able to adopt an efficient spawning tactic to anticipate favorable thermal conditions for survival of their offspring but they do not demonstrate whether this result from a thermal preference during the reproduction.

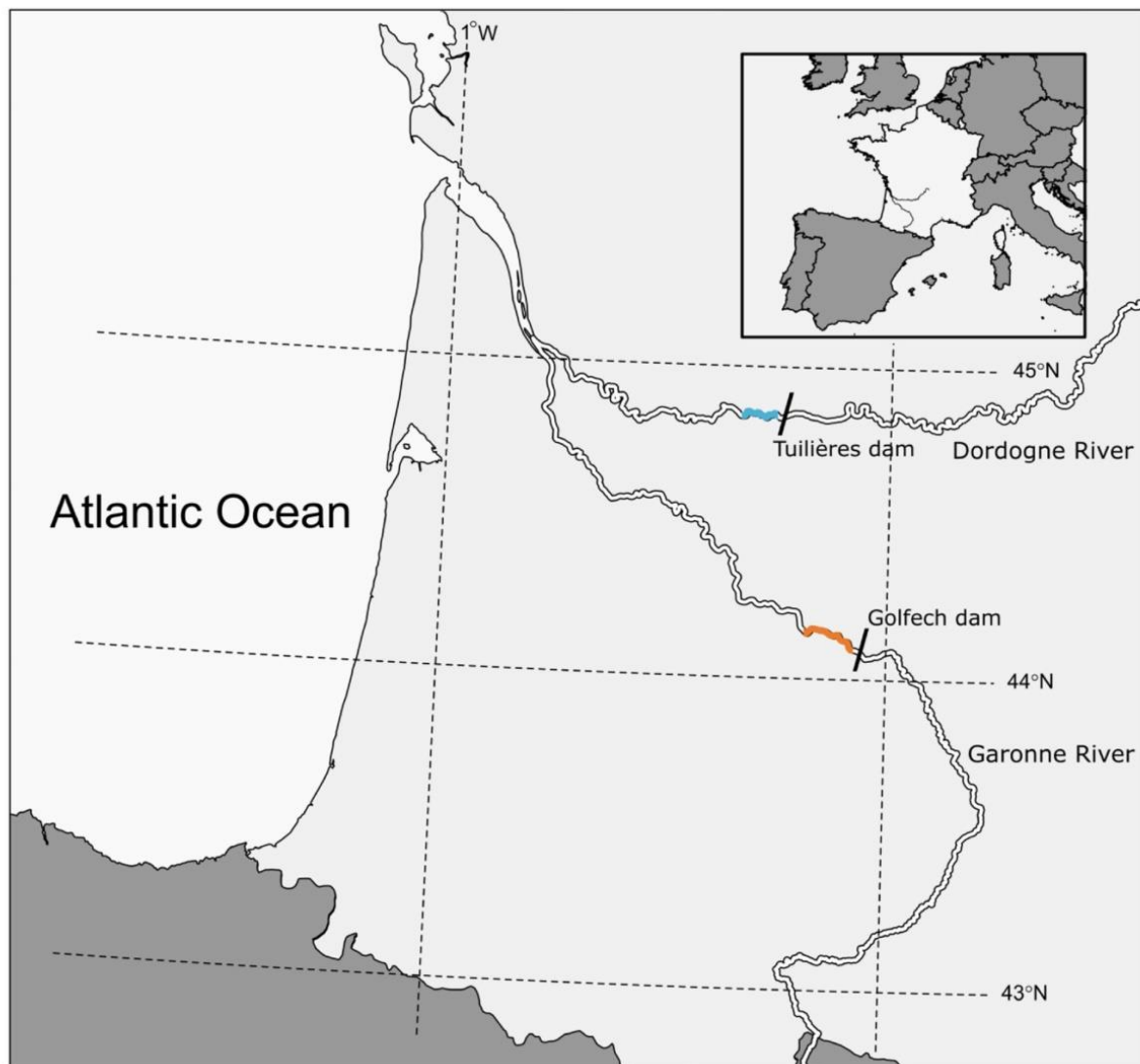
In this context, this study aims at exploring whether adult allis shads display a specific reproduction behavior to ensure that they spawn in specific temperature conditions that can latter enhance their offspring survival. To do this, we combined time series of water temperatures and spawning monitoring and we used electivity scores (Manly 1974) to answer the following questions: (i) Do spawners exhibit a thermal preference during the reproduction? (ii) Are thermal preference for reproduction consistent with thermal tolerance of early stages, as proposed by Quinn and Adams (1996) hypothesis?

## Material and methods

### Study area

Temperature preference during reproduction was investigated in the Garonne River and in the Dordogne River, the two main rivers of the Gironde watershed (Southwestern France; Fig. 1). In each river, we used spawning activity monitoring from seven spawning grounds located





**Fig. 1** Location of Garonne and Dordogne rivers in the Gironde watershed. The reproduction acts were recorded in the Garonne and Dordogne spawning grounds (colored sections). Temperatures

were monitored at the two dams in the Garonne and Dordogne Rivers

downstream of the first barrier to upstream migration, the Tuilières hydroelectric dam in the Dordogne River and Golfech hydroelectric dam in the Garonne River (Fig. 1). These spawning grounds are concentrated in 20 km and are the most frequented in both rivers (Carry and Jo 2012; Gaillagot and Carry 2014).

The reproductive monitoring and environmental data

From 2003 to 2016, spawning acts were recorded by both direct and indirect acoustic counting (Gaillagot

and Carry 2014). The collected spawning data consisted of the daily number of spawning acts for each river throughout the spawning season. Numbers of reproductive acts were summed over the spawning grounds of each river.

This pooling allowed the analysis of the relationship between temperature and reproduction with a sufficient number of observations. It was justified by both the low distance between spawning grounds and the low variability of environmental conditions between them (Fig. 1; Carry and Jo 2012; Gaillagot and Carry 2014). In the

Dordogne River, shad spawned upstream than the selected spawning grounds in 2003, 2008, 2012 and 2016. Therefore, these years were excluded for further analysis due to the few observations of spawning acts. Temperatures in each river were recorded at the dams every hour by data loggers during the same period and were averaged per day.

#### The spawning temperature range

For each spawning season and river, the spawning temperature range (STR) was defined as the narrowest range of temperature in which 80% of the total annual reproductive activity took place.

#### The thermal preference during reproduction

The thermal habitat, defined as the occurrence of days in each of the 18 temperature classes ( $T, T + 1$  °C) during monitoring periods, was used to identify years and sites with similar temperature regimes.

An electivity score ( $\alpha$ ) was used to measure the overall thermal preference of shad spawners during the reproduction, taking into account the available temperatures (Manly 1974). The electivity score was computed by gathering the data for all the surveys in the two rivers (Eq. 1).

$$\alpha_i = \left( \frac{n_i}{g_i} \right) / \left( \sum_{j=1}^{18} \frac{n_j}{g_j} \right) \quad (1)$$

where  $n_i$  is the relative reproduction acts of a particular 1 °C class of temperature  $i$  for the 14-year surveys in the two rivers and  $g_i$  is the proportional availability of this particular temperature class. The electivity score ( $\alpha$ ) varies from 0 to 1: 0 standing for an absolute avoidance of a given temperature while 1 indicates an absolute preference for this temperature during reproduction (Pledger et al. 2007). The thermal preference was detected by checking whether the electivity score ( $\alpha$ ) for a given temperature class was superior to 1/18 corresponding to a use of 18 temperature classes in proportion of their availability (Manly 1974; Pledger et al. 2007; Cagnazzi et al. 2013).

The statistical significance of the thermal preference was tested using a randomization test associated with null model. The test was constructed by considering the expected usage  $E(n_i)$  under the assumption of a random selection of temperature in proportion to

the thermal availability ( $H_0$ ), and the results were obtained by randomly assigning the reproduction 10,000 times to each 1 °C temperature class with a probability  $g_i$  following a multinomial distribution of availability (Pledger et al. 2007). The Bray-Curtis index of dissimilarity was used to compare the similarity between the observed and the expected value (Eq. 2) (Bray and Curtis 1957; Pledger et al. 2007). The test was run using R software version 3.3.1 (R Core Team 2018).

$$BCD = \frac{\sum_{i=1}^{18} |n_i - E(n_i)|}{\sum_{i=1}^{18} |n_i + E(n_i)|} \quad (2)$$

## Results

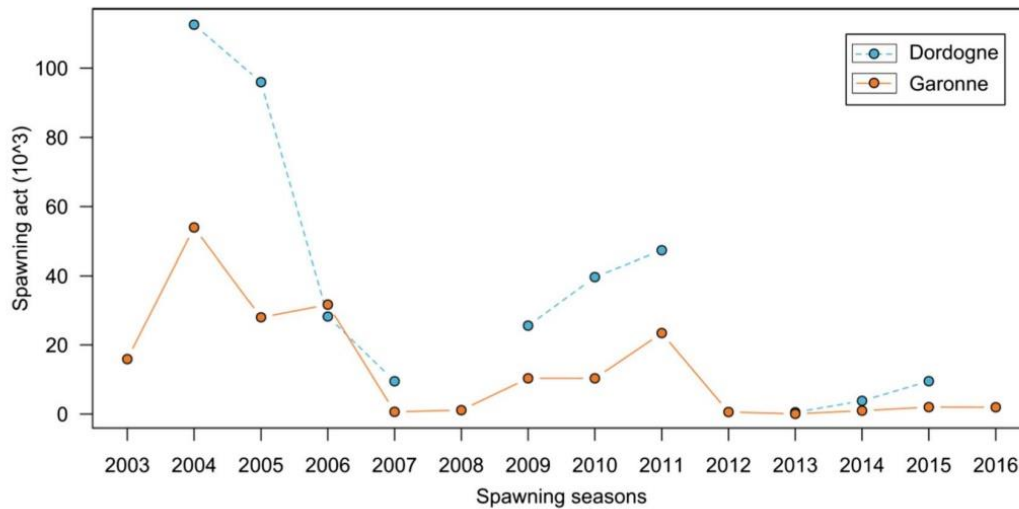
### Description of spawning seasons

From 2003 to 2016, 181,116 spawning acts were recorded in the Garonne River and 385,735 were recorded in the Dordogne River. A common decline in spawning activity until 2007 was observed in both rivers (Fig. 2). Then, the reproduction weakly increased but remained at a low level. In fact, a very low number of reproduction acts was observed during the last 5 years (Fig. 2).

The thermal conditions differed between the two rivers and years (Fig. 3). The coldest temperature class was [10 °C, 11 °C] for 6 years (2010 and 2013 in the Dordogne River; 2009, 2010, 2012 and 2013 in the Garonne River) and the highest temperature class was [27 °C, 28 °C] for 3 years (2005 in the Dordogne River; 2003 and 2009 in the Garonne River). Several years were characterized by strong frequent cold temperatures during the spawning period (below 15 °C), especially at the end of the monitoring period. The remaining years were characterized by high availability of moderate temperatures (between 17 °C and 24 °C) or characterized by contrasted regimes with alternating warm and cold periods (Fig. 3).

### The annual spawning temperature ranges

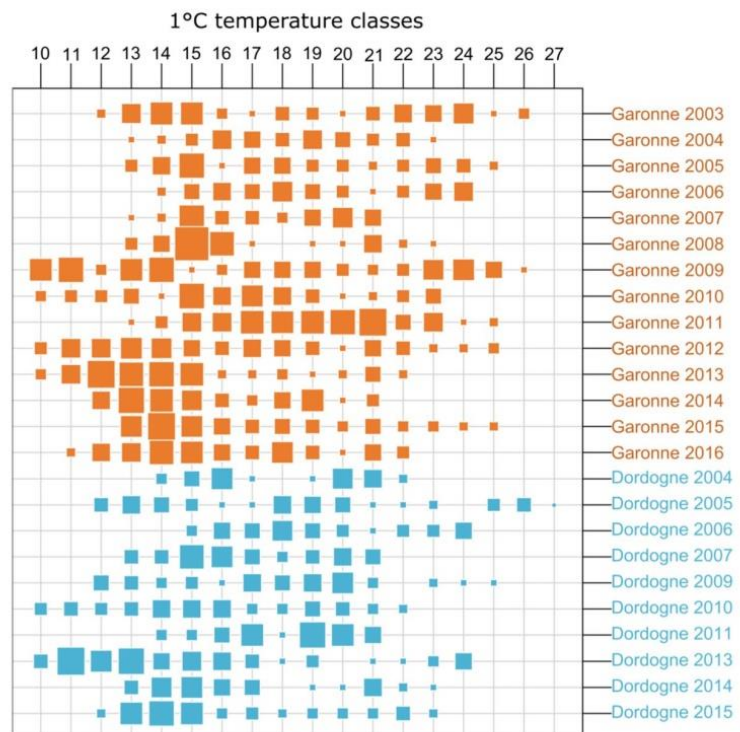
For the 10 seasons in common between the two rivers, the STR ranged between 10.7 °C and 23.4 °C in the Dordogne River (Fig. 4a) and between 13.3 °C and 25.7 °C in the Garonne River (Fig. 4b). The width of the 24 STR varied from 0.7 °C to 8.7 °C-wide,



**Fig. 2** Evolution of the annual spawning acts in the Garonne River and in the Dordogne River

respectively in the Garonne River in 2013 and 2012 (Fig. 4). Most STRs overlap the thermal tolerance of the early stages, though slightly shifted toward colder temperatures (Fig. 4). For seven combinations of site-year, at least half of their STRs were below the lower limit of the thermal tolerance for the early stages (Fig. 4; e.g. Garonne in 2013).

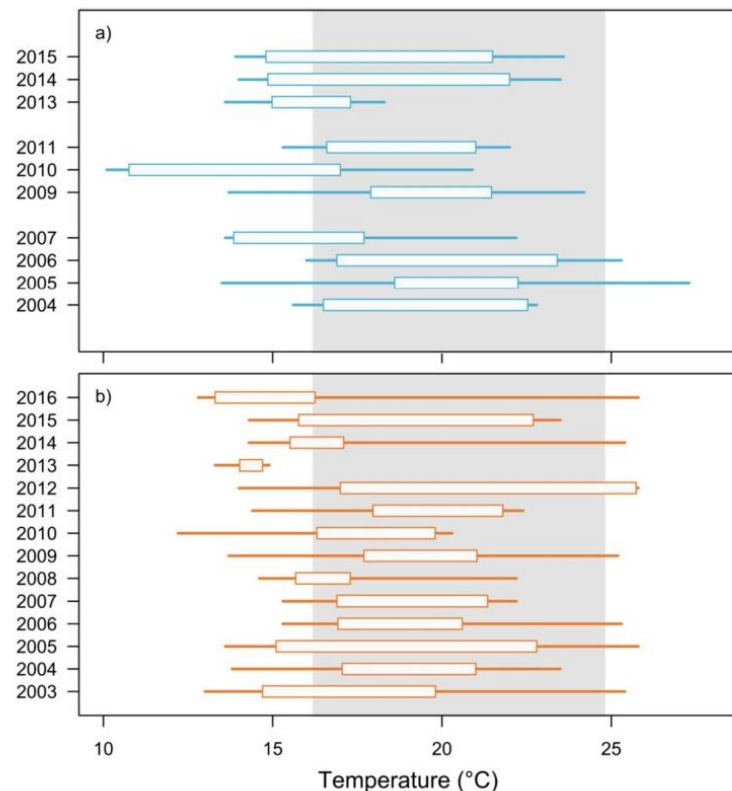
**Fig. 3** Thermal habitats for each river and year. The square size is proportional to the number of days in each of the 18 1 °C-temperature classes (T, T + 1 °C) during the monitoring periods



The thermal preference and the reproductive success

The Bray-Curtis index of dissimilarity (BCD) demonstrated a thermal preference for reproduction, with a difference between the use and the temperature availability ( $BCD_{obs} = 0.199$ ,  $BCD_{H0} = 0.003$ ). Based on electivity scores higher than 1/18, the shad spawners

**Fig. 4** The annual spawning temperature ranges (STR) in **a** the Dordogne River and in **b** the Garonne River. Black lines represent minimum and maximum temperatures at which the reproduction took place; white filled rectangle, the annual spawning temperature range; grey rectangle, the thermal tolerance for early stages (Jatteau et al. 2017)



reproduce preferentially between 14.5 °C and 23 °C (Fig. 5). Temperatures colder than the lower limit were strongly avoided while temperatures beyond the upper limit seem to be used more commonly.

## Discussion

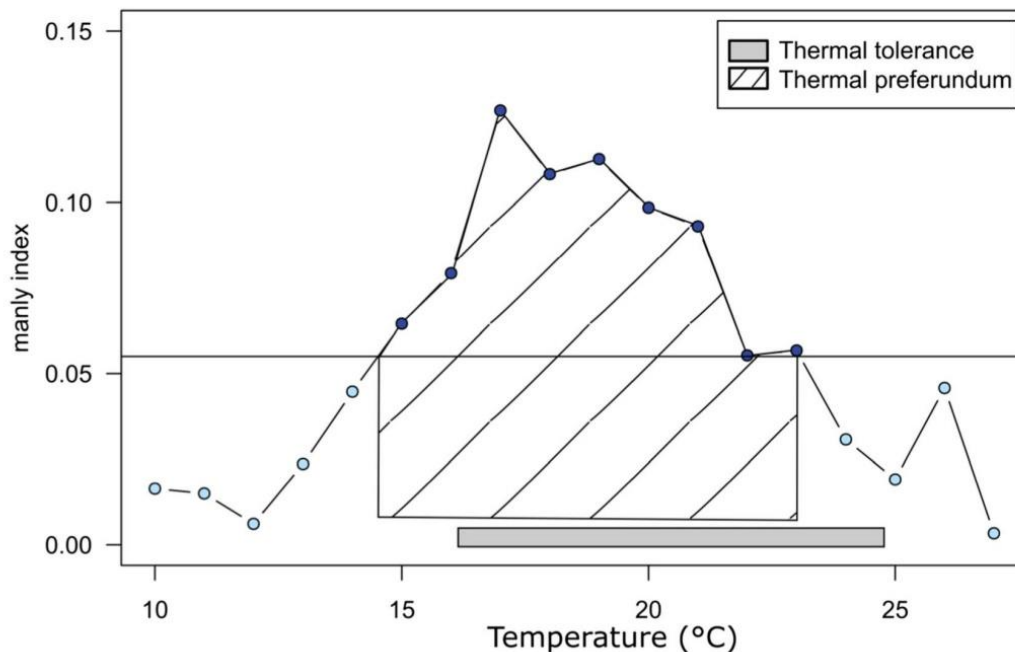
The present study combined long-term monitoring of reproduction with regime of temperature profiles in two rivers. Our electivity results provided for the first time a robust description of the thermal behavior of allis shad during reproduction at the population scale. The overlap with the thermal requirement of juveniles supports the hypothesis that spawners exhibit reproductive tactics to enhance the survival of their offspring (Quinn and Adams 1996).

### Suitability of the field-based model

Estimating thermal preference using field data is not straightforward. Indeed, the temperature is a fluctuating factor, displaying strong spatial and temporal variations

at local and global scale. As such, temperature could be seen as a resource (Magnuson et al. 1979) and fish spawning in the natural environment results from both the availability of this resource (occurrence of days with an appropriate thermal conditions) and of fish intrinsic thermal preference. Consequently, disentangling the relative effect of resource availability and thermal preference in observed spawning pattern is still challenging. However, the Manly index is a well-known efficient resource selection index that compares the use of a resource in relation to availability of this resource (Manly 1974; Pledger et al. 2007; Cagnazzi et al. 2013).

This thermal preference can be considered as a proxy of the thermal niche of reproduction. The niche definition is ambiguous and different definitions have been proposed (Kearney 2006). The modern conceptualization of the niche is based on the Hutchinsonian niche (Kearney 2006), defined as ‘n-dimensional hypervolume in where each dimension limits an organism’s survival and reproduction (Hutchinson 1957). However, further experiments in controlled environments are required to avoid confusion with other potentially correlated environmental factors.



**Fig. 5** Thermal preference analysis using the Manly's electivity index. The points represent the evolution of the electivity score for each of 18 1 °C-temperature classes. The hatched polygon represents the temperature range in which the electivity scores were

superior to 1/18 (i.e. temperature between 14.5 °C and 23 °C). The grey rectangle represents the thermal tolerance for early stages (Jatteau et al. 2017)

Moreover, here we focused on observed spawning at the population scale. New observations at the individual scale through tagging experiments (Acolas et al. 2004, 2006) or experimental studies (Jatteau et al. 2017) would allow to validate that the thermal preference observed at the population scale is the result of individual spawning behaviors. For example, modern telemetry tags that combine fish positioning and temperature monitoring have proved to be useful to determine the thermal selection of fish (Acolas et al. 2004; Harrison et al. 2016). Experiments in controlled environment are major tools used by thermal biologists to assess thermal behavior (Angilletta 2009; Peck et al. 2012; Golovanov 2013; Jatteau et al. 2017). However, a common pitfall of experimental design is the use of unnatural thermal regimes during a short period (Wehrly et al. 2007), potentially disconnected with thermal availability. This field-based study was a good trade-off to determine the thermal behavior using a long-scale field-based monitoring. The wide range of temperatures experienced by spawners, ranging from 10 °C to 28 °C, provided a realistic picture of the behavioral temperature selection during the reproduction.

#### The annual spawning temperature range

This study is the first to highlight the interannual variation of temperature ranges during the reproduction of allis shad using a long-term monitoring field data. The similarity of the STRs for the same year between the two rivers, despite the different thermal availability, suggests that the shads adopt a common thermal behavior. This common behavior can be due to the likely strong gene flow between these two sub-populations (Randon et al. 2017) and the genetic basis of the thermal preference (Beitinger and Fitzpatrick 1979; Johnson and Kelsch 1998; Hasnain et al. 2013).

Despite an overall similarity between the two rivers, we observed annual fluctuations of the STRs. We state that these fluctuations mostly result from the interannual variability of thermal availability associated with the thermal preference of allis shad (Johnson and Kelsch 1998; Cassou-Leins et al. 2000). For example, years when reproduction occurred mainly at cold temperatures in the Garonne (2013, 2014 and 2016) were characterized by extremely cold temperatures during the spawning season. However, the thermal availability failed to entirely explain the STR fluctuations. For example, the year 2003 in the

Garonne River was characterized by a STR between 14.7 °C and 19.8 °C, whereas this thermal range was not the most available during the spawning season. Indeed, the fish behavior is not only influenced by temperature but by a complex combination of biotic and abiotic factors (Righton et al. 2010). First, the length of the day (photoperiod) is a well-known abiotic factor controlling the reproduction of anadromous fish (Bagliniere et al. 2003). But the constant pattern of photoperiod between years cannot explain the annual variability of spawning activity (Forsythe et al. 1995). The stream velocity is also a main factor controlling the reproduction by blocking it above a certain threshold (Bagliniere et al. 2003). Increase water velocity due to peak of river discharge is likely to affect reproductive behavior (Acolas et al. 2006). However, the spawning period is characterized by rather rare episodes of extreme flow.

Biotic factors can also have an influence on the observed thermal range of reproduction. As reproduction needs at least two organisms at the same place and time, the arrival of organisms on spawning ground could also explain STR fluctuations. Indeed, spawners have a limited time of residence on the spawning grounds or nearby (i.e. close to 1 month; Chittenden 1976; Acolas et al. 2006; Olney et al. 2006; Aunins and Olney 2009), therefore their arrival on spawning grounds will determine the temperatures set available for the reproduction. In light of this, atypical reproductions could result from earlier arrivals associated with cold temperatures, in which spawners were not able to wait for suitable conditions. Another biotic effect is social facilitation that usually leads to biological processes more aggregated in time than expected from seasonality alone (Koizumi and Shimatani 2016). In light of this, few reproductions at a certain range of temperature could lead to a snowball effect of numerous reproductions if other spawners are in the vicinity (Berdahl et al. 2017). These individual's interactions lead to socially induced reproductive synchrony, and thus to a restricted temperature range of spawning.

#### The thermal preference during the reproduction

The relative similarities between the STRs when compared to the fluctuating temperature availability may be explained by the behavioral preference of spawners for a specific range of temperature (Johnson and Kelsch 1998). Indeed, the present analysis showed that spawners reproduce preferentially between 14.5 °C and 23 °C. To

our knowledge, this work is the first truly determination of the thermal preference of shad during the reproduction. Indeed, previous study focused on the minimum and maximum temperature in which the reproduction occurred, without a demonstration of an actual preference (Cassou-Leins 1981; Menneson-Boisneau 1990; Acolas et al. 2006). Furthermore, these previous studies used a short observation period and a few years to conclude (Cassou-Leins 1981; Menneson-Boisneau and Boisneau 1990; Acolas et al. 2006). Here, we used a 14 years of field data in two main rivers, and demonstrated the thermal preference with an original methodology. However, it is still interesting to compare our thermal preference range with former thresholds determined for allis shads and other anadromous fishes. The range of allis shad in the Gironde system is consistent with thresholds observed in other rivers (Table 1). This result suggests a strong genetic basis of the thermal preference for allis shad populations (Beitinger and Fitzpatrick 1979; Johnson and Kelsch 1998). The slight differences may arise from local adaptations (Ohlberger et al. 2008; Eliason et al. 2011; Hasnain et al. 2013).

The thermal preferences (14.5 °C to 23 °C) found here is also quite similar to other shad species. The similarity may result from the shared evolutionary history, and of the shared thermal conditions experienced during their life cycle (Freckleton and Jetz 2009). The thermal preference was either similar to the sea lamprey or different with colder temperature preferred for the Atlantic sturgeon or the brook lamprey (Table 1).

#### Spawning behavior and survival requirements of early stages

The overlap of the thermal preference with the thermal tolerance of early stages (16.2 °C to 24.8 °C; Jatteau et al. 2017) confirms that allis shad spawners adopt behavioral rules of reproduction in order to maximize the survival of their offspring. The present study brought additional evidence of the relationship between thermal preference and earlier life survival (Beitinger and Fitzpatrick 1979; Hasnain et al. 2013) that supports the Quinn and Adams hypothesis (Quinn and Adams 1996; Lambert et al. 2018).

Nevertheless, a 2 °C shift of the thermal preference to colder temperatures was observed relative to the thermal tolerance range. This kind of difference in thermal preference between early life and adult stages is already observed in other species (Magnuson et al. 1979; Sinclair et al. 2016). For example, a difference of more than 9 °C

**Table 1** Documented spawning temperature ranges of anadromous fish

| Species                                      | Spawning temperature ranges (°C) | References                            |
|--|----------------------------------|---------------------------------------|
| Allis shad                                   | 14-23                            | Acolas et al. (2006)                  |
| <i>Alosa alosa</i>                           | 12-25                            | Menneson-Boisneau and Boisneau (1990) |
|  | 18-24                            | Cassou-leins & Cassou-leins (1981)    |
| Twaite shad                                  | 18-22                            | Breder and Rosen (1972)               |
| <i>Alosa fallax</i>                          | 14-20                            | Nachón et al. (2016)                  |
| (Lacépède, 1803)                             |                                  |                                       |
| American shad                                | 12-21                            | Walburg and Nichols (1967)            |
| <i>Alosa sapidissima</i>                     |                                  | Leggett and Carscadden (1978)         |
| (Wilson, 1810)                               |                                  |                                       |
| Alewives                                     | 15-19                            | DiMaggio et al. (2015)                |
| <i>Alosa pseudoharengus</i>                  |                                  |                                       |
| Sea Lamprey                                  | 15-23                            | Tavemy and Elie (2008)                |
| <i>Petromyzon marinus</i>                    |                                  |                                       |
| (Linnaeus, 1758)                             |                                  |                                       |
| Brook lamprey                                | 8.5-17                           | Tavemy and Elie (2008)                |
| <i>Lampetra fluviatilis</i> (Linnaeus, 1758) |                                  |                                       |
| Atlantic sturgeon                            | 7.7-22                           | Rochard et al. (1990)                 |
| <i>Acipenser sturio</i>                      |                                  |                                       |
| (Linnaeus, 1758)                             |                                  |                                       |

was experimentally found for the alewife between adults and young-of-the-year (Otto et al. 1976). However, the shift might not be disadvantageous given the likely rise of temperature during the spawning period in spring.

#### Implication for conservation

This study revealed that the possible extirpation of shad populations in the Gironde system can no longer be excluded given the general trend of declining spawning acts. However, the effective spawning strategy may facilitate adaptation by preventing population reduction, and thus save time needed to accumulate genetic changes, the so-called Baldwin effect (Wong and Candolin 2015). The definition of the thermal requirement during the reproduction could be used by wildlife managers to detect favorable river habitat for reproduction that need to be preserved.

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**Author contributions** Paumier A. analysed the data and wrote the paper, Drouineau H. analysed the data and wrote the paper, Carry L. performed the field work, Nachón D.J wrote the paper and Patrick L. analysed the data and wrote the paper.

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***B. Paper #2: “Assessing the relative importance of temperature, discharge and day length on anadromous fish reproduction”***

The ambition of this second paper was to move from a thermal behaviour to a multifactorial rule (Fig. III3). Indeed, we aimed at defining a more complete niche as the Hutchinson’s niche is composed of several factors. In this context, we selected perceivable factors (day length, river discharge and water temperature), that we defined as the most proximal factors as possible. Furthermore, we used a machine learning algorithms (Boosted regression tree) to deeply explore the relative importance of each factor on the reproduction. Our results demonstrate that the reproduction was positively related to day length (44.6%) and water temperature (34.7%) and negatively related to river discharge (20.7%). Optimal reproductive conditions corresponded to a difference in day length between 0 and 0.04 hours, a water temperature between 15 °C and 26 °C and a river discharge between 55 m<sup>3</sup>.s<sup>-1</sup> and 665 m<sup>3</sup>.s<sup>-1</sup>; conditions that are currently being utilised by allis Shad populations in the Garonne and Dordogne rivers, around the end of spring. Experiments in controlled environments would be necessary to validate our results.

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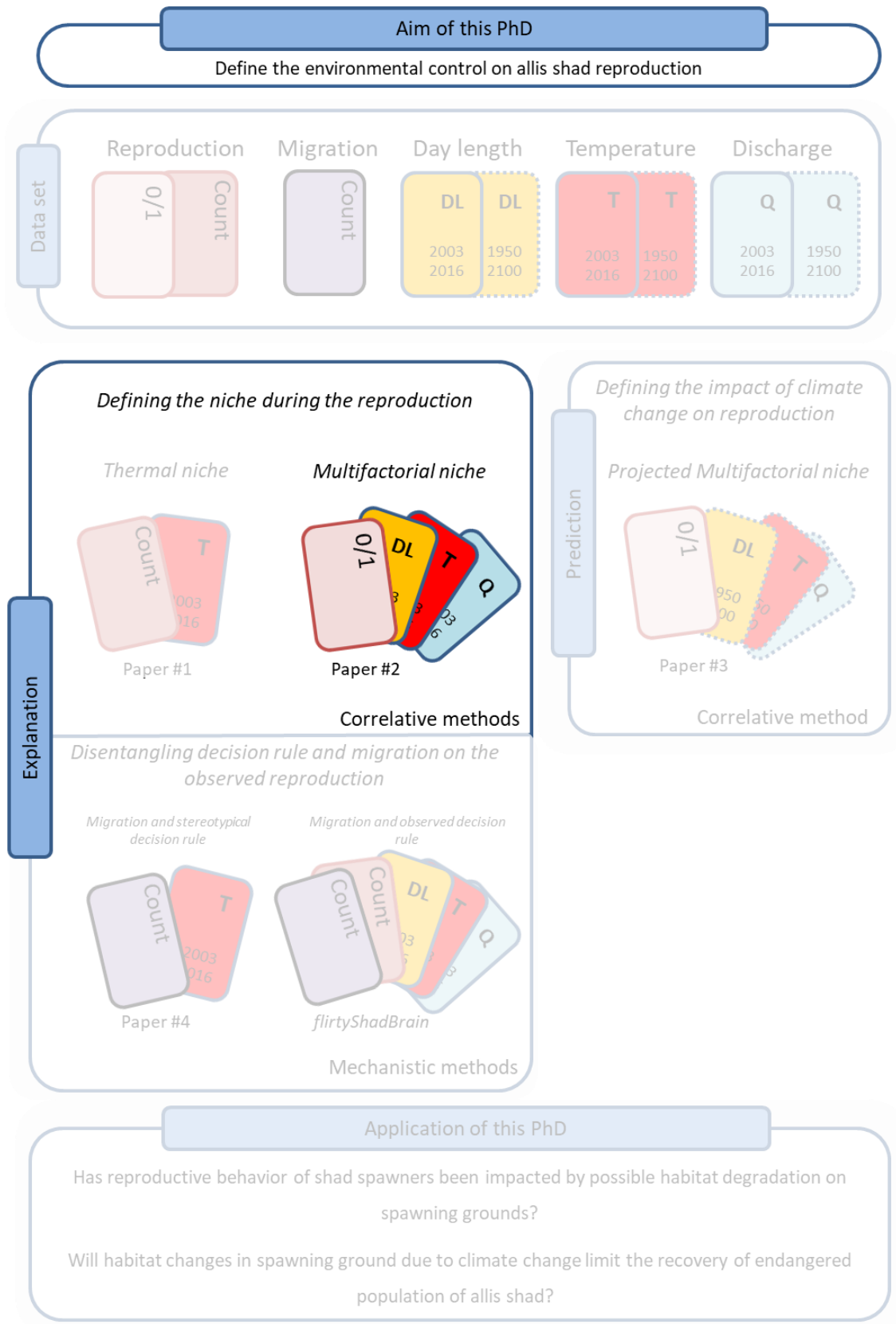



Figure III3: Conceptual diagram representing the articulation of the different parts of the PhD.

# Assessing the relative importance of temperature, discharge, and day length on the reproduction of an anadromous fish (*Alosa alosa*)

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#### Abstract

1. Climate change threatens anadromous fishes such as the allis shad (*Alosa alosa*) populations of which have declined since the 20th century in Europe. Sensitivity to climate change could be quantified by determining the fish's spawning behaviour, defined as the timing of reproduction (i.e. spawning events) as a function of temporally variable environmental factors. The cues that fish use to time reproduction could determine their response to climate change.
2. A machine learning technique (boosted regression tree) was calibrated using a 14-year dataset composed of daily measures of environmental factors and fish occurrences during reproduction. The boosted regression tree provides complete insight into the complex relationship between the spawning probability, i.e. the probability for a fish to reproduce, and environmental factors that might evolve with climate change.
3. The spawning probability was positively related to day length (44.6%) and water temperature (34.7%) and negatively related to river discharge (20.7%). Optimal reproductive conditions corresponded to a difference in day length between 0 and 0.04 hr, a water temperature between 15 and 26°C and a river discharge between 55 and 665 m<sup>3</sup>/s; these conditions are currently being utilised by allis shad populations in the Garonne and Dordogne rivers, France.
4. This study highlights the relative influence of environmental factors on the observed spawning period as well as the evolution of habitat suitability during the 14-year period. The novelty of this study stems from assessing population process data, i.e. the occurrence of fish reproduction, rather than mere occurrence data in an ecological niche model study. Climate change may lead to a shift in spawning phenology, as the water temperature and river discharge will also change. Therefore, conservation plans need to integrate these effects on spawning grounds.

#### KEYWORDS

boosted regression tree, climate change, ecological niche, ecospat, migratory fish

## 1 | INTRODUCTION

Anadromous fishes that migrate between oceans and rivers to complete their life cycles (McDowall, 1988) have undergone dramatic declines due to marine and continental overfishing, habitat degradation and fragmentation, and water pollution (Drouineau et al., 2017, 2018; Limburg & Waldman, 2009). Over the past few decades, global warming has been identified as an additional threat (Drouineau et al., 2018; Lassalle, Béguer, Beaulaton, & Rochard, 2008) as a growing number of fishes in both the marine and freshwater environments have been impacted by climate change (Buisson, Thuiller, Lek, Lim, & Grenouillet, 2008; Cheung, Watson, & Pauly, 2013; Portner & Peck, 2010; Rijnsdorp, Peck, Engelhard, Mollmann, & Pinnegar, 2009).

Assessing the vulnerability of anadromous species is a prerequisite for determining whether global warming will exacerbate the decline of anadromous fishes (Foden et al., 2019). Vulnerability is defined by a complex combination of species sensitivity, adaptive capacity, and the magnitude of human actions (Foden et al., 2019; IPCC, 2007). Species sensitivity is defined as the degree to which the species is affected by climate variability (Foden et al., 2019; IPCC, 2007) and this sensitivity could be explored by the species' preference to environmental factors during a key life event, such as reproduction.

Many fishes, such as shad, lay eggs under conditions that optimise growth and offspring survival (e.g. a specific temperature range; Lambert, Jatteau, Paumier, Carry, & Drouineau, 2018). Concerns have been raised about a potential mismatch, driven by global warming, between reproductive events and optimal freshwater conditions. Species' spawning behaviour, defined as the ability to decide when to reproduce depending on environmental conditions, should be taken into account in assessing the effects of climate change on population viability. For example, if anadromous fishes, such as salmon, base their spawning behaviour on factors that are unaffected by global warming, such as photoperiod (Scott, ; Quinn & Adams, 1996), the conditions triggering spawning may become desynchronised from the conditions that determine the optimal time for reproduction, and spawners may reproduce in suboptimal conditions. The spawning period may not match the peak of prey for juveniles (Chevillot et al., 2017) and could ultimately affect offspring survival, as observed in migratory birds (Visser, Noordwijk, Tinbergen, & Lessells, 1998).

Understanding the relationship between habitat and population processes is crucial to monitoring species recovery (Martin, Camaclang, Possingham, Maguire, & Chadès, 2017). Ecological niche models (ENMs), also known as species distribution models (Sillero, 2011), explore the relationship between environmental factors and species occurrences. Ecological niche models are based on the ecological niche concept, defined as "the environmental requirements needed for a species to subsist without immigration" (Grinnell, 1917; Hirzel & Le Lay, 2008; Hutchinson, 1957; Sillero, 2011). Ecological niche models are challenging for anadromous fishes because of the multiplicity of ecological niches required at different life stages, such as feeding areas in the open sea and spawning grounds in rivers.

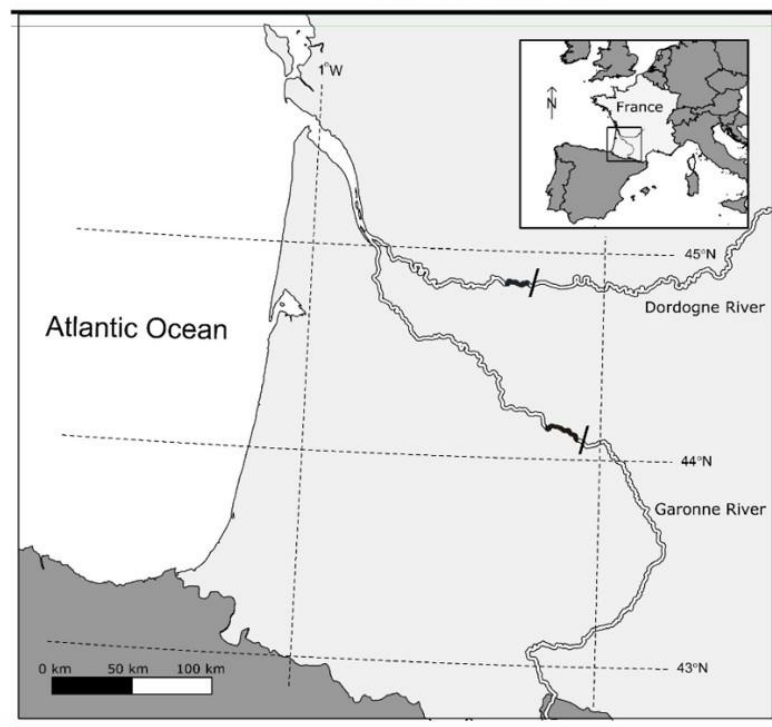
Furthermore, the physiological limits differ with life stages (Feng & Papes, 2017; Sax, Early, & Bellemare, 2013), especially for shad (Coutant, 1977; Souchon & Tissot, 2012).

The common outputs of correlative ENMs are the probabilities of a species occurrence in a particular habitat (Brambilla & Ficetola, 2012; Brambilla & Saporetti, 2014; Feng & Papes, 2017; Unglaub, Steinfartz, Drechsler, & Schmidt, 2015). However, occurrence does not necessarily imply that the habitat is suitable (Brambilla & Ficetola, 2012). The novelty of this study stems from assessing population process data, i.e. occurrence of fish reproduction, rather than mere occurrence data in an ENM study. In this study, the output of the ENM model is spawning probability, defined as the probability for a fish to reproduce in a particular habitat. The influence of environmental factors on spawning probability was explored to assess the sensitivity to climate change.

It is essential to select ecologically relevant factors when implementing an ENM (Elith & Leathwick, 2009). The environmental factors used in this study are known to influence fish behaviour directly or indirectly: day length, temperature, and discharge. Day length is known to affect the circannual clock of teleost fishes, triggering migration and reproductive maturation (Scott, ; Yeates-Burghart, O'Brien, Cresko, Holzapfel, & Bradshaw, 2009). Second, temperature affects all aspects of the behaviour and physiology of fishes, as they are ectothermic (Angilletta, 2009; Golovanov, 2006; Huey & Kingsolver, 1989). Third, most fish perceive flow because of their lateral line (Ryder, 1889). Although these factors have already been identified as affecting the distribution and abundance of fish in streams (Jackson, Peres-Neto, & Olden, 2001; Lobón-Cerviá, 2003), the relative influence of these factors on reproduction is poorly studied.

Allis shad, *Alosa alosa* (Linnaeus, 1758), is an anadromous fish of the Clupeidae family (e.g. herrings and sardines). Allis shad populations were historically abundant along the European coast. The most abundant population has suffered a dramatic reduction since the middle of the 20th century (Rougier et al., 2012). This population reproduces in the Garonne and Dordogne rivers in south-western France (Figure 1), where a fishing moratorium has been implemented since 2008 (Rougier et al., 2012). In the French shad population, the adults spend 5 years in the ocean and return to rivers to reproduce before dying (Lambert, Martin Vandembulcke, Rochard, Bellariva, & Castelnaud, 2001; McDowall, 1988). In France, reproduction generally takes place over <2 months in the spring, from late April to late June (Bagliniere, Rochard, & Aprahamian, 2003; Paumier, Drouineau, Carry, Nachón, & Lambert, 2019). Spawners reproduce at night, with a peak in reproduction at 03.00 (Cassou-Leins, 1981; Menneson-Boisneau & Boisneau, 1990). Typical spawning behaviour involves a couple of fish swimming side by side in a circle while ejecting eggs and sperm. During this swim, the spawners thrash their caudal fins on the water surface, producing a loud sound that is between 35 and 50 dB (Cassou-Leins, Cassou-Leins, Boisneau, & Bagliniere, 2000), which are recorded for surveys measuring spawning events on sites in rivers (Gaillagot & Carry, 2016). A metapopulation dynamic was revealed in these two adjoining rivers (Randon et al., 2017).

**FIGURE 1** Location of spawning sites monitored by the Migado association (coloured sections). Temperatures and discharges were monitored closed to the two dams (symbol:/)



A machine learning technique, relatively new in ecology, was applied to fully explore the relationships between environmental factors and reproduction: boosted regression trees (BRT). This method has innovative features compared to traditional approaches, such as the ability to process any type of data without assumptions about the distribution function and interactions (Buston & Elith, 2011; Elith, Leathwick, & Hastie, 2008).

The objectives of this study were to highlight: (1) the relative influence of environmental factors on the reproduction of allis shad in a global warming context; (2) understand how these factors determine the observed spawning period; and (3) visualise how the favourability of the habitat has evolved during the study period. To achieve these objectives, a BRT model was calibrated using a 14-year dataset of daily environmental and fish surveys.

## 2 | METHODS

### 2.1 | Field collection

In south-western France (Figure 1), allis shad reproduction is monitored every year on the Garonne and Dordogne rivers by the non-profit association Migado (<http://www.migado.fr/>). Seven main spawning grounds are monitored per river and concentrated in a single 20-km reach in each river (Figure 1). Reproduction was monitored in two ways: either by observing spawning events on site (direct counting) or via audio recordings (indirect acoustic counting). The sound of spawning events from direct and indirect

observations corresponded to the count data. For direct counting, the observer was equipped with a manual counter and stood on the shoreline in front of the most active area (Gaillagot & Carry, 2016; Gracia & Caut, 2016). Indirect counts were carried out using audio digital recorders (Gaillagot & Carry, 2016; Gracia & Caut, 2016). All daily observations were pooled into a single daily value for each river to obtain a sufficient number of observations, as there is low environmental variation between areas (Gaillagot & Carry, 2016; Gracia & Caut, 2016). In this study, the occurrence of fish reproduction (presence-absence data) was used to calibrate the statistical models. Data were available from 2003 to 2016, which constituted 1143 presence-absence values. Water temperature ( $^{\circ}\text{C}$ ) and river discharge ( $\text{m}^3/\text{s}$ ) were measured near the spawning grounds throughout the year. Water temperature was recorded every hour by data loggers at the control station at the Golfech Dam (Garonne River; Figure 1) and at the control station at the Tuilières Dam (Dordogne River; Figure 1). Average daily river discharge was obtained from the French *Banque Hydro* (<http://www.hydro.eaufrance.fr>).

Six environmental factors were used to model spawning probability: water temperature, water discharge, day length, and the daily difference in each of these factors. Water temperature was calculated as the average daily temperature ( $^{\circ}\text{C}$ ) and the difference in average temperature from one day to the next (in  $^{\circ}\text{C}$ ). The daily river discharge was log-scaled in order to normalise the distribution in the two rivers and the difference in daily river discharge from one day to the next (in  $\text{m}^3/\text{s}$ ). Day length was defined as the interval between

sunrise and sunset (Corripio, 2003) and the difference in day length from one day to the next (in hr).

## 2.2 | Statistical method

### 2.2.1 | Data aggregation test from the two rivers

A preliminary analysis of niche overlap determined whether it was appropriate or not to aggregate data from the two adjacent rivers. Aggregation was considered because the rivers have similar hydrological regimes and their shad populations are linked in metapopulation dynamics (Randon et al., 2017). The aggregated dataset provided a sufficient number of observations to properly calibrate the BRT model. The Ecospat package in R quantified the niche overlap between the two river spawning grounds (see Broennimann et al., 2012; Di Cola et al., 2017 for a complete description of the method). Ecospat first estimated reproduction occurrences in the environmental space (principle component analysis), created with the environmental conditions pooled for the two rivers during the 14 years as background data; then, Ecospat measured the niche overlap along the principle component analysis axes and quantified the niche equivalency and similarity between rivers (Di Cola et al., 2017). Niche overlap was computed using the D metric (Warren, Glor, & Turelli, 2008), which varied from 0 (no overlap) to 1 (complete overlap).

The niche equivalency test determines whether the niches of two entities in two geographical ranges are equivalent. For this, the occurrences of both entities are merged, and the resulting merged database is split into two datasets 100 times with the same sample size as the original datasets. The D metric is calculated for each pair of datasets. The null hypothesis of niche equivalency can be rejected when the observed D value falls above 95% of simulated values.

The niche similarity test examines whether the overlap between two observed niches is different from the overlap between the observed niche of one entity and random niches from the other entity. Ecospat randomly shifts the entire set of occurrences 100 times in one entity and calculates overlap between the simulated niche and the observed niche of the other entity. When the observed overlap is higher than 95% of the simulated values, the occupied environments in both ranges are more similar to each other than expected by chance.

### 2.2.2 | Influence of environmental factors on reproduction

The influence of environmental factors on reproduction was assessed using BRTs (Buston & Elith, 2011; De'Ath, 2007; Elith et al., 2008; Friedman, Hastie, & Tibshirani, 2000; Leathwick, Elith, Chadderton, Rowe, & Hastie, 2008; Leathwick, Elith, Francis, Hastie, & Taylor, 2006; Schapire, Denison, Hansen, Holmes, & Mallick, 2001). The BRT is a machine learning algorithm that is considered to be an advanced form of regression (Friedman et al., 2000; Schapire et al., 2001). This machine learning technique has been increasingly

used in ecology due to its innovative characteristics compared to traditional statistical approaches (Buston & Elith, 2011; Elith et al., 2008). First, the combination of regression trees and boosting algorithms enables the modelling any type of data, such as non-independent data and correlated independent data. Second, complex relationships can be modelled without any assumptions (Buston & Elith, 2011; Elith et al., 2008; Schapire et al., 2001). Third, BRTs combine multiple simple models and thereby improve model predictions (Elith & Graham, 2009; Elith et al., 2006, 2008). Finally, BRTs provide clear graphical and numerical outputs, making them suitable for studying complex ecological issues (Cappo et al., 2005; Fabricius & De'Ath, 2008).

The BRT model was used to predict spawning probabilities based on environmental factors. According to the procedure of Elith et al. (2008), the BRT model was tuned with a tree complexity of 5, a learning rate of 0.001 and a bag fraction of 0.5 with a binomial error distribution (see more detail of these parameters in Elith et al., 2008). Ten-fold cross-validation was applied to address the non-independent structure of the data (Buston & Elith, 2011; Fabricius & De'Ath, 2008). This established method was equivalent to adding a random effect to a mixed model to account for non-independent structure of the data (Buston & Elith, 2011).

The relative importance of the six environmental factors was assessed by Friedman's procedure, which quantified the percentage of variance attributed to each factor (Elith et al., 2008; Friedman, 2001; Friedman & Meulman, 2003). The relative value is scaled from 0 to 100%: a high value indicates a greater influence on the spawning probability. Selection of variables was performed in order to drop redundant factors that increased the model variance (see Appendix S2 in Elith et al., 2008). The six factors were ranked by decreasing importance and dropped in descending order until a significant increase in residual deviance was assessed between the prior and the simplified model (Elith et al., 2008). Model performance was assessed with the area under the curve (AUC) of the receiver operating characteristics (Hanley & McNeil, 1982; good performance was established at AUC > 0.8). Joint partial dependence plots were used to visualise the effects of the selected factor on the spawning probability after accounting for the average effects of the remaining factors and strongest interactions (Elith et al., 2008).

### 2.2.3 | Trend in spawning probability

The calibrated BRT model was used to predict spawning probabilities in the observed environmental conditions from 2003 to 2016. First, the spawning probabilities during the whole year were computed for the 14 years in the two rivers and visualised with the average spawning probabilities per Julian day in the 5–95% quantile range. This analysis identified the spawning period when the most favourable environmental conditions were met, i.e. the highest spawning probability.

Finally, the BRT model predicted the spawning probabilities for a common constant spawning period based on the method mentioned above, e.g. 1 April–1 July. The predicted spawning probabilities were



used to compute two annual indices that reflected the changes in the physical habitat: the habitat suitability index (HSI) computed as the annual means of the predicted spawning probabilities, and the mid-season day (MSD), which was computed as the spawning probability-weighted timing. The MSD reflects the temporal centroid of the most suitable conditions regarding the physical cues.

$$\text{MSD} = \sum (t_i p_i) / \sum p_i$$

where  $t_i$  is the Julian day and  $p_i$  is the corresponding spawning probability for that day.

All analyses were performed in R (R Core Team, 2017), including the packages Ecospat (version 3.0) for the data gathering test and dismo (version 1.1-4) and gbm (version 2.1.4) for the boosted regression trees.

### 3 | RESULTS

#### 3.1 | Aggregation of data from the two rivers

The two niches were distributed mainly along the axes of temperature, discharge, and difference in day length (Figure 2d). Reproductive niches highly overlapped between the two rivers (D metric = 0.75; Figure 2-5a,b,c), with a significant niche equivalency

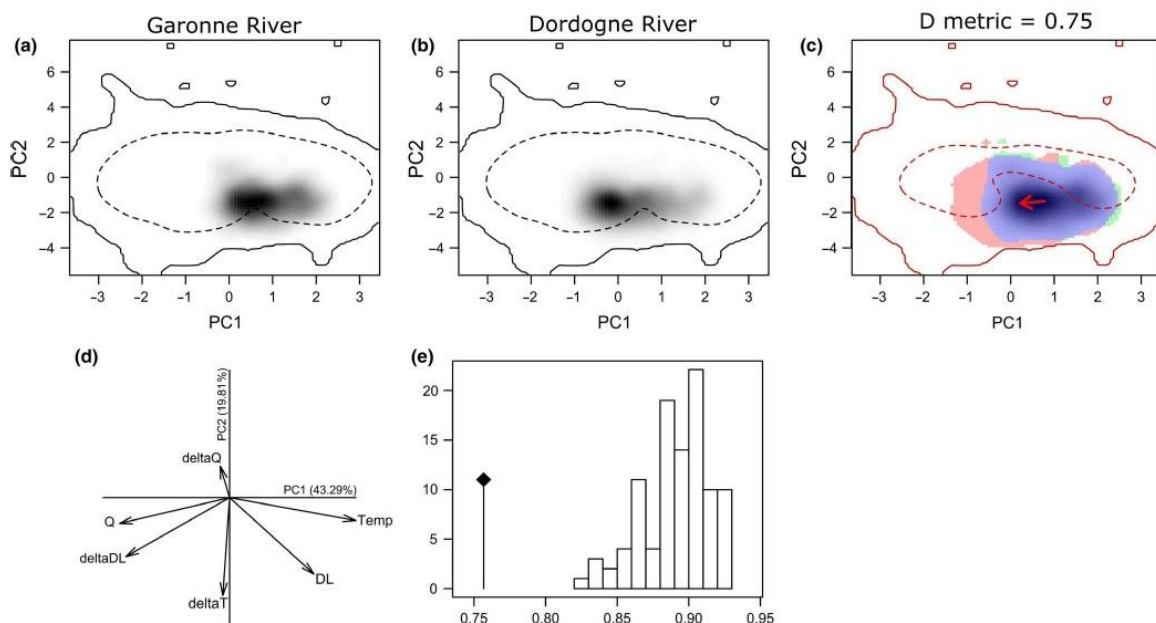
test ( $p > 0.999$ ) and similarity tests ( $p$  value = 0.01 from Garonne to Dordogne and  $p$  value = 0.03 from Dordogne to Garonne; Figure 2e). The overlap enabled us to aggregate the datasets from the two adjacent rivers for the BRT analysis.

#### 3.2 | Influence of environmental factors on reproduction

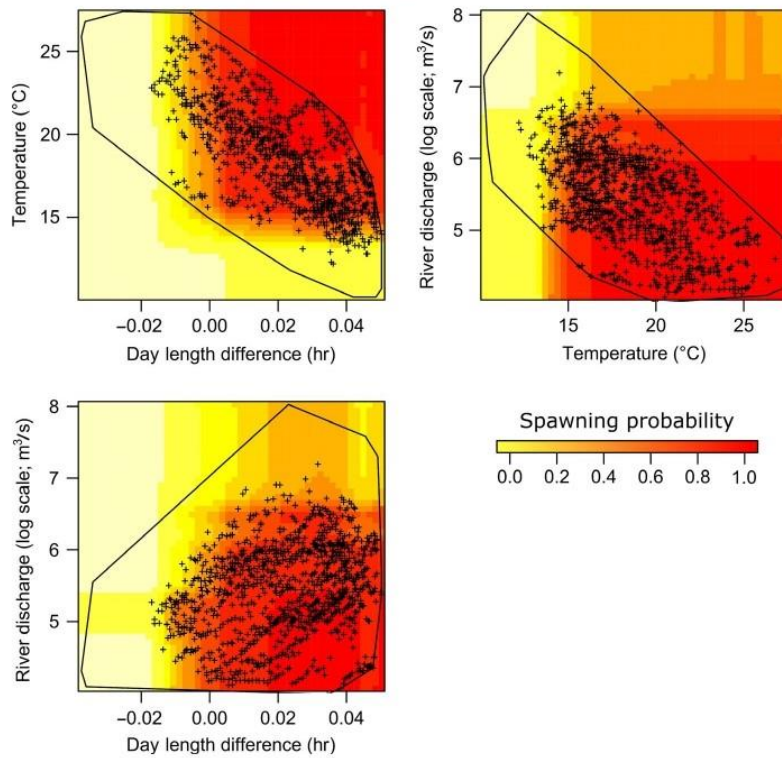
The AUC value (0.93) indicated the high performance of the BRT model. Three factors were selected: difference in the day length (44.6%), water temperature (34.7%), and river discharge (20.7%). The magnitudes of the second-order interaction effects were high between temperature and difference in day length (553.19), as well as between river discharge and difference in day length (237.42). The interaction was moderate between temperature and river discharge (88.89). The optimal combination for reproduction according to the BRT is a difference in day length between 0 and 0.04 hr, a water temperature between 15 and 26°C and river discharge between 55 and 665 m<sup>3</sup>/s (Figure 3).

#### 3.3 | Trends in spawning probability

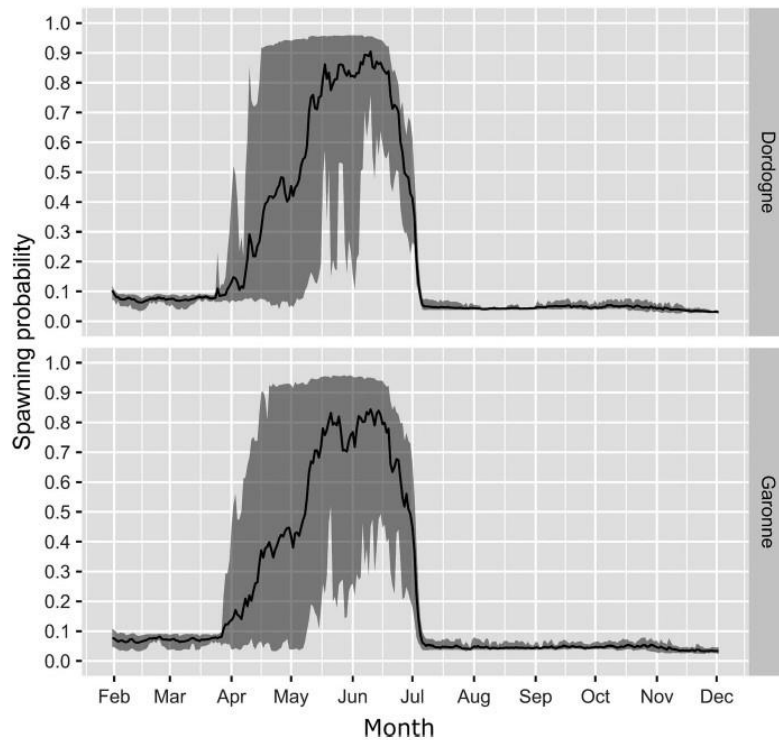
The average spawning probability for the 14 years was high between mid-May and the end of June for the two rivers (Figure 4). Variability



**FIGURE 2** (a, b) The density plots of the spawners of *Alosa alosa* in the environmental space projected on the first two principal components, respectively in the Garonne River and the Dordogne River. Density of the occurrences of spawners is grey shaded. The solid and dashed contour lines illustrate, respectively, 100 and 50% of the available environmental space. (c) Niche overlap between the two populations of the Garonne and Dordogne rivers. The arrow represents how the centroid differs between the Garonne and Dordogne. Dordogne population is represented in red, the niche overlap in blue, and the Garonne population in green. (d) The contribution of the environmental factors on the two axes of the principle component (PC) analysis and the percentage of inertia explained by the two axes (PC1: 43.29%; PC2: 19.81%). (e) Histogram of observed and randomly simulated overlaps, with  $p$ -values of equivalency



**FIGURE 3** Predicted spawning probability in three-dimensional partial dependence plots for the most influential environmental factors in the model. The omitted variable is set by the mean. Each black cross represents a single observation of fish reproduction in the two rivers during the 14 years. The polygon represents the convex hull of the combination of the two environmental factors during the spawning period



**FIGURE 4** Mean of spawning probability per day for the 2003-2016 period in the Garonne and Dordogne rivers (solid lines and points) and the 5-95% range of the confidence interval (shading)

was relatively high at the beginning of the spawning season between mid-April and mid-June. This variability implies that there was a year-to-year fluctuation at the beginning of the spawning season in the two rivers.

The MSD varied around the end of May (Figure 5). There was no shift in the centroid of the most favourable conditions (Figure 5). The annual HSI patterns were similar between rivers and fluctuated around 0.51 in the Dordogne River and around 0.48 in the Garonne River (Figure 5). In the Garonne River, unsuitable conditions (HSI < 0.5) were observed in 2004, 2008, and 2009, with dramatic unsuitable conditions in 2013 (HSI < 0.2). In the Dordogne River, unsuitable conditions were observed in 2004, 2013, and 2016.

#### 4 | DISCUSSION

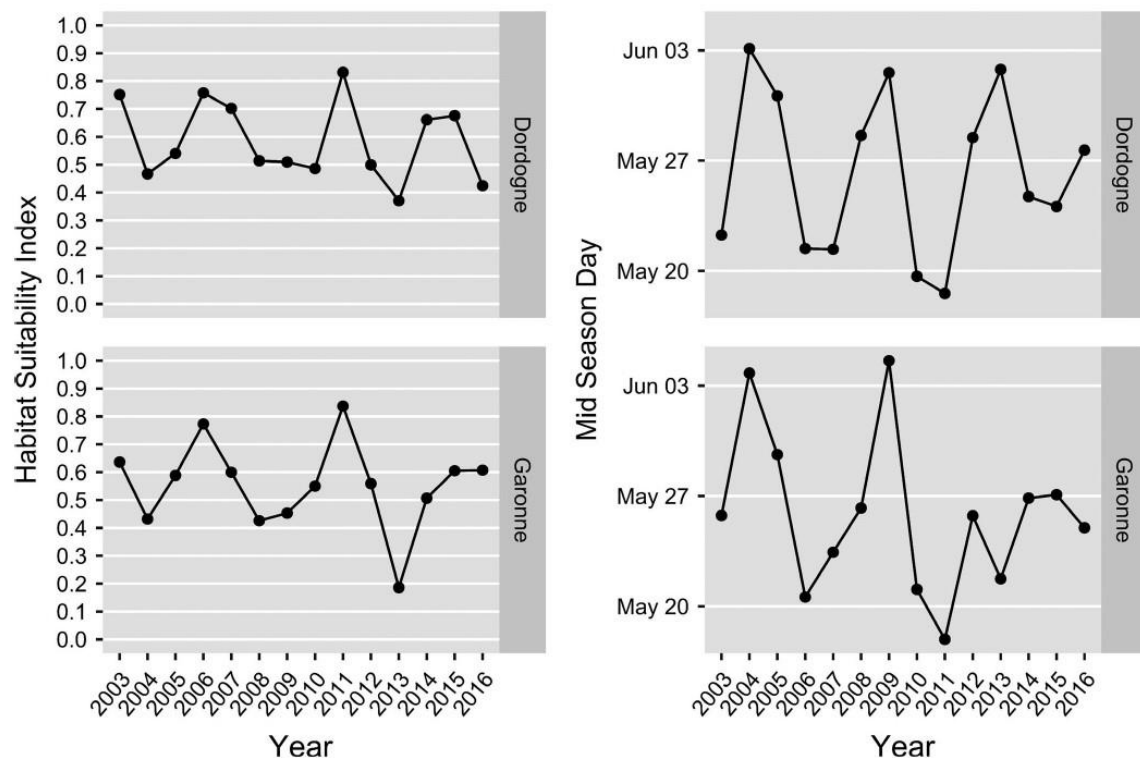
##### 4.1 | Environmental influence on reproduction

The selected environmental factors were identified as important for controlling both the migration and reproduction of shad (Acolas et al., 2006; Aprahamian, Aprahamian, Baglinière, & Alexandrino, 2003; Leggett & Whitney, 1972; Munro, Munro, Scott, & Lam, 1990; Quinn & Adams, 1996; Walburg & Nichols, 1967). The two statistical analyses (Ecospat and BRT model) highlighted similar influences of the environment on the reproduction of allis shad: reproduction

was mostly controlled by difference in the day length and the water temperature and to a lesser extent, river discharge.

The 15–26°C temperature range is consistent with previous analyses of shad reproduction (Acolas et al., 2004, 2006; Cassou-Leins, 1981; Menneson-Boisneau & Boisneau, 1990; Paumier et al., 2019) and matches the thermal tolerance of embryos and larvae (Jatteau et al., 2017). The influence of discharge was lower than differences in day length and temperature. Only river discharges exceeding 665 m<sup>3</sup>/s significantly reduced reproduction. The sensitivity of shad to discharge was consistent with that in previous studies, demonstrating that extreme water speeds (>0.80 m/s) halted reproduction (Acolas et al., 2006; Aprahamian et al., 2003; Menneson-Boisneau & Boisneau, 1990). Experiments in controlled environments would be necessary to validate the ranges of factors that promote reproduction.

Some combinations of environmental factors in the BRT model predicted a high probability of reproduction when no reproduction was observed. An example of these unexploited climatic niches is a combination of temperatures above 25°C and day length differences above 0.04 hr. The absence of fish observations can be explained by the absence of such environmental combinations in both rivers. This finding corresponded to the concept of the potential niche: the part of the fundamental niche that exists in the current environmental conditions (Jackson & Overpeck, 2000). Therefore, part of the



**FIGURE 5** Time series of annual habitat suitability index (left panel) and mid-season day (right panel) from 2003 to 2016 in the Garonne and Dordogne rivers (solid lines and points) and the 5–95% range of the confidence interval (shading)

fundamental niche is not expressed because the specific environmental conditions are not available.

#### 4.2 | Spawning over time

The synchronisation of the reproductive period with suitable conditions for the survival of young stages is a requirement for successful reproduction. According to the BRT model, reproduction may be promoted during the end of spring, around the end of May. This finding is consistent with the seasonality of spawning described for allis shad (Acolas et al., 2006; Aprahamian et al., 2003; Bellariva, 1998). The seasonality of environmental conditions in rivers may explain the propensity of shad reproduction to occur around the end of May when conditions are favourable (McNamara & Houston, 2008). However, the rule is not fixed in time but in environmental fluctuations, and, consequently, year-to-year fluctuations of spawning probability were observed during the 14-year period.

The selective pressures on spawners to optimise offspring survival and the observation of a reproduction routine suggest that natural selection has led spawners to follow external cues to coordinate the spawning period, such as difference in the day length, water temperature, and river discharge (see optimal routines in McNamara & Houston, 2008). Many species with limited incubation times have developed reproduction strategies to spawn in environmental conditions that promote offspring survival (Lambert et al., 2018; Quinn & Adams, 1996). The thermal range during reproduction coincided with the physiological tolerance of the offspring, which depends strongly on temperature (Jatteau et al., 2017). Therefore, it appears that reproduction tends to favour suitable conditions for the offspring. The differences in the day length and temperature were highly influential factors. These two factors may be used by the fish to predict the best time to breed, as they could be reliable proxies of food abundance (McNamara & Houston, 2008). Indeed, the larvae's diet is mostly composed of zooplankton (Aprahamian et al., 2003) that emerge as a function of the temperature and day length. The sensitivity of discharge during reproduction could be explained by the egg-laying strategy. Shad spawn in a deep area; then, the fertilised eggs are carried by the current drift upwards to a shallow area after ultimately sinking to a gravel bottom (Aprahamian et al., 2003). Therefore, the egg habitat is dependent upon the flow, and strong spates will drag the eggs out of the area chosen by the spawners.

#### 4.3 | Management implications

Planning habitat management is a complex task because many species exhibit complex ecological requirements. Habitat management is crucial for enhancing the chance of recovery of endangered species, as habitat degradation is one of the major threats to biodiversity (Travis, 2003). The interaction between habitat degradation and ongoing climate change could put fish populations at high risk of extinction. It was necessary to identify and rank the environmental factors that control the population process to put appropriate management measures in place.

First, our results suggest that a temperature below 15°C as associated with discharge exceeding 665 m<sup>3</sup>/s would reduce reproductive activity and therefore impact population dynamics. These stressful conditions may occur during the spawning season due to global warming by causing early snow melt and early cold water flooding during the spawning season in snow-fed rivers (Blösch et al., 2017). The impact of global warming on reproduction will depend on the magnitudes of these environmental changes in the freshwater habitat and on the ability of shads to adapt to them (Foden et al., 2019). As the cumulative influence of environmental factors disrupted by global warming is greater than those that are undisturbed, spawners could follow optimal freshwater conditions with spatial and temporal shifts (McQueen & Marshall, 2017; Nack, Swaney, & Limburg, 2019; Quinn & Adams, 1996; Wedekin & Küng, 2010). However, low abundance will enhance the sensitivity of these populations to environmental stress (Froeschke & Froeschke, 2016; Hidalgo et al., 2011). The current BRT model could be used to predict the effect of climate change on the species distribution in different scenarios.

Second, the current BRT model could identify the most favourable spawning grounds that need to be preserved among the potential spawning grounds in France and in the historical distribution ranges. The most favourable spawning ground would share the same physical habitat conditions as the potential spawning grounds, such as grain size or water depth, but would have more favourable thermal and hydrological conditions. This concept has been developed for salmon in the context of climate change with the notion of thermal refuge (Frechette, Dugdale, Dodson, & Bergeron, 2018). A thermal refuge is a spawning ground with cooler temperatures during summer heat (Newell & Quinn, 2005). The identification of these potential spawning grounds will require databases of environmental factors and hydroclimatic models in French rivers at high resolutions. Finally, the documented decrease in population abundance in the spawning rivers (Paumier et al., 2019; Rougier et al., 2012) can only be partially explained by the fluctuations of environmental conditions. However, the cause of the decline needs to be explored for other habitat components and life stages, such as low levels of dissolved oxygen for juvenile in estuaries (Chevillot et al., 2017; Ficklin, Stewart, & Maurel, 2013; Portner & Knust, 2007).

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#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon request from the corresponding author: <http://www.migado.fr/> and <http://www.hydro.eaufrance.fr/>.

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### *C. Concluding remarks on correlative models*

The two correlative models were successfully accepted in two journals and provide a deep understanding of shad's reproduction. First, we demonstrated an active selection of temperature during the reproduction (paper #1), then we defined more completely this behavioural rule by completing the set of environmental factors (paper #2). However, the spawning behaviour *per se* is still unexplored, along with the influence of migration in the final observation of spawning. At this point of this manuscript, the remaining questions could be formulated as follows: (i) "Can we explicitly define the spawning behaviour?"; (ii) "Can we integrate the migration explicitly in the reproduction activity?". These two questions were partially addressed with two mechanistic models.



## II. MECHANISTIC APPROACHES

Reproduction activity is the result of complex behaviours that involve multiple behavioural choices. The reproduction of migratory fish can be dissociated in two linked behaviours: the spawning migration and the spawning behaviour. However, the link between the two processes is rather unclear and poorly studied. For example, Acolas et al. (2006) observed that the peak of abundance during the upstream migration did not synchronise with the peak of reproduction. Here, we present two mechanistic models: *HoOs* and *FlirtyShadBrain*, which both aimed at disentangling these two behaviours and to understand the environmental control on the decision to spawn (Fig. III4). One of these two models consists of a theoretical exploration of 2 stereotypical egg laying behaviours (HoOS model) and the other represents an attempt to calibrate the egg laying behaviour on real data (*flirtyShadBrain*).

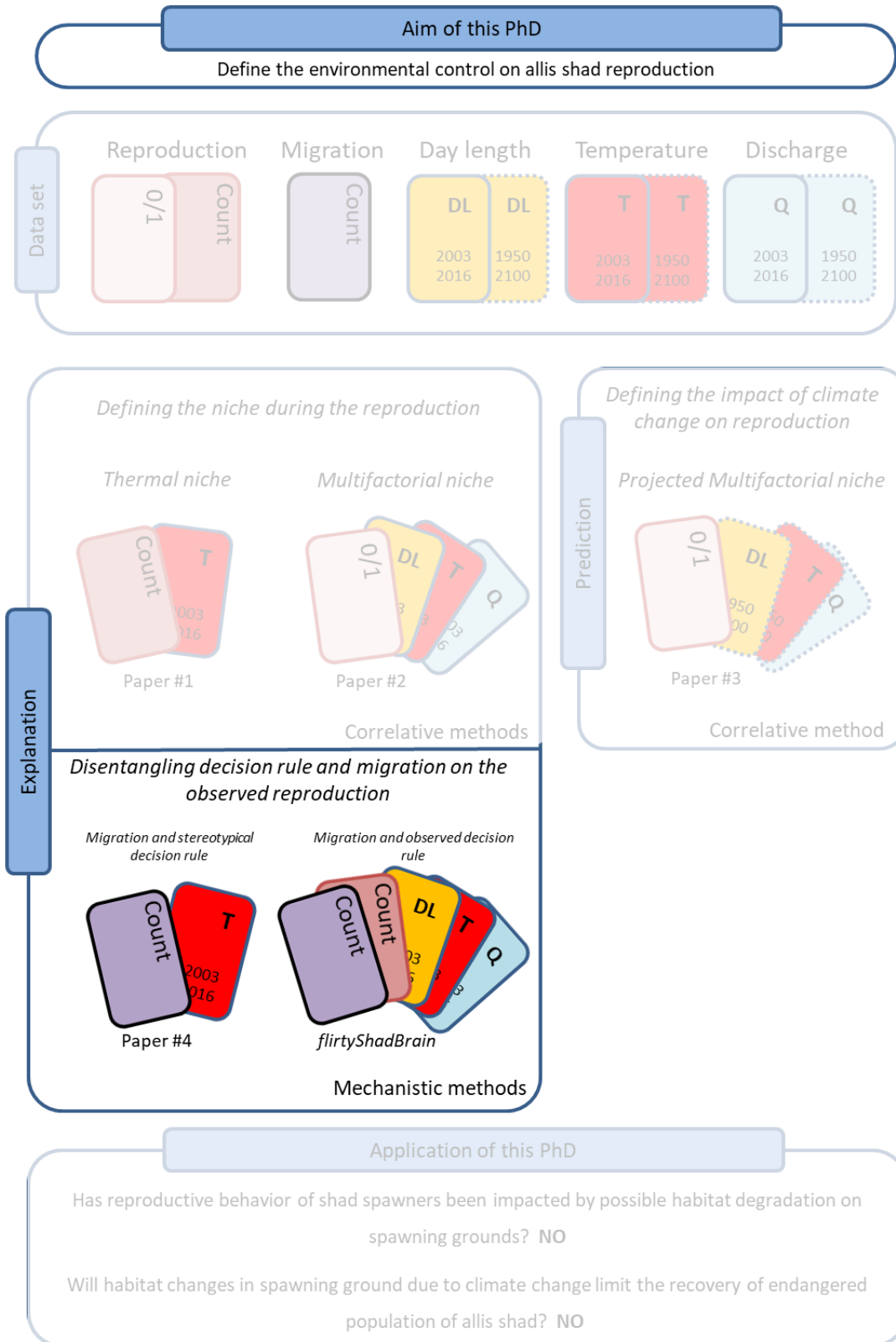


Figure III4: Conceptual diagram representing the articulation of the different parts of the PhD.

### *A. The HoOS model*

The Quinn and Adams 'hypothesis (1996) states that fish optimise the reproduction to enhance the early life survival. However, in which process, migration or reproduction, this optimisation takes place is rather unclear in this theory. Here, we developed the HoOs model (**H**asty or **O**mniscient **S**had) that aimed to understand the importance of migration and spawning decision on the early life survival (Fig. III5). The spawning behaviour was described with two stereotypical behaviours a "hasty" shad that spawn as soon as he arrives in the spawning grounds and an "omniscient" shad that is able to wait for the most suitable environmental conditions.

This study is the first exploration of the survival differences between the two reproductive behaviours for migratory fishes. The HoOS model demonstrated that early arrivals (that are less favourable) can be compensated by an 'omniscient' behaviour, whereas in intermediate time transit the 'hasty' behaviour is sufficient. By exploring the interactions between migration and reproduction, the HoOS model provided evidence that the migration and the spawning behaviour can balance each other in such way to ensure maximum fitness outcome.

This article is the result of the internship work of Camille Poulet (master 2) that I supervised and a 3-month contract that led to this article. This paper is currently a draft and will be submitted by Camille Poulet *et al.*, in *Ecological Modelling*.

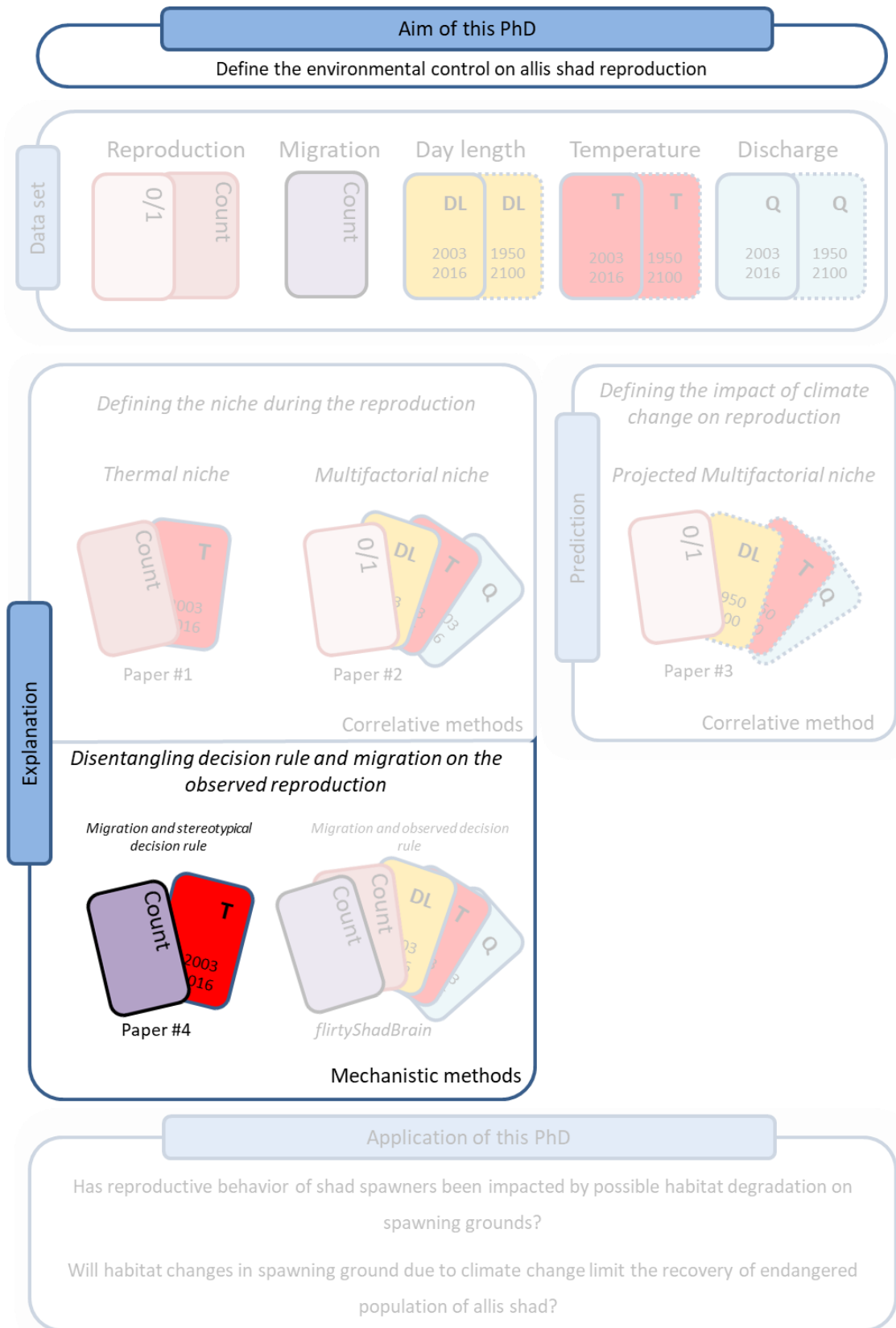


Figure III5: Conceptual diagram representing the articulation of the different parts of the PhD.

***Paper #4: “The first holistic exploration of the interactions between migration and spawning behaviour. Implication on the reproductive success of an anadromous fish”.***

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### **Abstract**

The migration and reproduction have been studied for decades and fascinated biologists in particular for anadromous fishes that migrate from oceans to rivers to reproduce. For such migratory fishes, ecologists studied independently the migration and the reproduction. However, it would be more consistent to study reproduction as a process that occurs from the beginning of migration towards the final choice of when to spawn. As an experimental approach being very expensive and complex, we chose to simulate the decision chain within a conceptual framework that included: (i) the time transit of migration (ii) the decision to reproduce. Ultimately, this holistic approach evaluated how spawning behaviour and migration influenced the offspring survival in terms of thermal sensitivity. The offspring survival was dome-shaped relative to the migration time, which implied an optimal period for reproduction. The spawning behaviour regulates this influence of migration, by delaying the reproduction for the “omniscient” spawners compared to “hasty” spawners. In conclusion, this HoOs model (Hasty or Omniscient Shad) highlights the trade-off between migration and spawning behaviour on the offspring survival.

**Keywords:** Fitness, strategy, reproduction, migration, anadromous fish

## 1 Introduction

In seasonal environments, fishes adapt their behaviour to environmental factors in many respects, and notably by the timing of life-cycle events such as reproduction. In fact, the favorability of the spawning habitat is restricted to a limited period of time (as we saw in the paper #2 of this PhD). Anadromous fishes migrate from ocean to river to complete their life cycle (McDowall 1988). Populations of anadromous fishes migrate and reproduce following seasonal routines, *i.e.*, reproduction is scheduled in a regular way and inter-annual variations are correlated with inter-annual fluctuations of environmental conditions (McNamara and Houston 2008). For example, at temperate latitudes, shads migrate at early spring and reproduce during spring (Arahamian et al. 2003), salmon species reproduce during the spring and reproduce in fall winter (Scott 1990) and sturgeon species between January and October, with a reproduction starting in May (Castelnaud 2011).

The reproductive activity is the combination of arrivals on the spawning grounds of mature spawners and the expression of a spawning behaviour (Bagliniere and Elie 2000). The behavioural sequence from the choice to migrate to the choice to spawn is still poorly known, mainly due methodological limitations in field surveys and experiments (Acolas, 2004, 2006). First, the reproductive journey begins with the triggering of the migration from ocean to rivers. The time of arrival is conditioned by several factors such as the initial onset of migration and the swimming speed. Migrating at favourable times can reduce '*en route*' mortality and can save energy latter needed to compete for mates and ensure quality breeding locations that enhance reproductive success (Crossin et al. 2004; Cooke et al. 2014). Therefore, an early arrival probably will not have the same fitness-related outcomes than a later arrival. As such, as a decreasing reproductive success during the breeding season is

commonly observed for migratory species. Second, the reproductive journey ends with the choice of when to spawn controlled by the spawning behaviour. The choice to spawn may modulate the effect of migration timing on fitness, by determining in which environment early stages may experience. Therefore, this final step may compensate a bad timing of migration. Here, we explored the potential influence of spawning behaviour by simulating two contrasted behaviours, *i.e.*, a virtual shad that only spawn in optimal conditions in terms of temperature and a virtual shad that tolerates no delay for reproduction. These two behaviours enable to confine all the possible spawning behaviours performed by shad in the natural world. The HoOs model (Hasty or Omniscient Shad) highlights the trade-off between migration and spawning behaviour on the offspring survival.

## 2 Material and method

### 2.1 Case study

The analysis is based on ecological data of allis shad in the Garonne River. Given the issue at play for the population in the Garonne and Dordogne rivers, a better understanding of the mechanisms regulation the reproductive success is crucial to propose solutions for population recovery. The data set is composed of 3 years of fishing data and spawning activity associated with temperature in the Garonne river, *i.e.*, 2005, 2006 and 2007 (before the fishing ban in 2008). The migration departure of allis shad was estimated using the catch per unit effort (CPUE) from the drift net commercial fisheries, located around 100 km downstream to the spawning areas. The temperature and reproduction data are similar to those published in the first and second paper.

### 2.2 Modelling procedure

In order to test the influence of the reproduction and migration timing on the early stage survival, we first simulated the arrivals time series on spawning grounds (2.2.1) and then considered two contrasted spawning behaviours (2.2.2) to examine their influence on the early stages survival (2.2.4). However, an intermediate step was necessary to integrate the physiological constraints of shad during the reproduction (2.2.3.)

#### 2.2.1. Simulated arrivals time series

Upstream migration of allis shad were simulated by using CPUE times-series and a Gaussian mixture model (GMM) (Reynolds 2015). Allis shad upstream migration is characterised by intermittent pulses or waves over the season and, as such, follows a multimodal distribution (Rochard 2001a). Hence, using Gaussian functions to approximate migration events appeared fairly relevant if we assume that the timing of migration is a quantitative trait (Miller 2002; Jonzen et al. 2006). We defined each Gaussian wave by a mean, corresponding to the day of the migration peak, a standard deviation defining the wave duration and a relative proportion of fish belonging to each wave within a reproductive season. The Gaussian mixture model was implemented with the R: “mixdist” package (Macdonald 2018) using the maximum likelihood method and the iterative expectation maximisation algorithm (Dellaert 2002; McLachlan and Krishnan 2008). The standard deviations were constrained to be equal for all waves in a given year in order to avoid flat waves. The starting values of the means in the algorithm were defined with a fixed interval between each migration peak. Numbers of waves per year, from 1 to 6, were selected according to the lowest corrected Akaike’s information criterion adjusted for small sample size (AICc) (Burnham et al. 2011). Time series of arrivals were simulated by adding to this migratory pattern a time transit until the spawning grounds. We considered a range of transit



times from 0 to 60 days to explore the impact of different swimming capabilities of fish. The range of tested transit times was defined to encompass the migration speeds found in the literature, *i.e.*, shads can spend between 2 and 10 days to travel the 100 km from the downstream part of the river to the spawning grounds (Rochard 1992, 2001b; Bellariva 1998; Tétard et al. 2016).

### 2.2.2. Simulated spawning behaviour

Two contrasted spawning behaviours were considered in this analysis. First, the 'omniscient' behaviour corresponds to a virtual fish that reproduce according to the time series of temperature in order to maximise the offspring thermal survival (Jatteau et al. 2017). This hypothesis corresponds to a predictive behaviour in response to environmental cues *sensu* Lucas and Baras (2001). Second, the 'hasty' behaviour corresponds to a fish that spawned just after the arrival and thus is constrained by the arrival time and the physiological constraints (described below).

### 2.2.3. Physiological constrained

The migration and spawning timings cannot be examined without reference to physiological constraints. As such, many anadromous commercial species are semelparous and batch spawners, *e.g.*, Atlantic salmon, shad, eels and sea lampreys. Semelparous fishes participate once in their lifetime to reproduction and die. Batch spawners developed and release several batches of eggs within single spawning seasons (McBride et al. 2015). The number of batches, the intervals between two lays of eggs and the maximum residence time on spawning ground could be seen as physiological constraints. The number of batches and the minimum intervals between two lays of eggs are adaptations of non-synchronous oocyte development for fecund fishes. Indeed, physical limitation of the body cavity occurs during

the hydration phase of oocytes because of the increasing egg volumes (Murua and Saborido-Rey 2003). The maximum residence time results from a physiological stress of starvation and osmoregulation in freshwater (Dodson et al. 1972; Glebe and Leggett 1981).

These three physiological constraints were considered in the HoOS model: maximum number of spawning nights (whether 2, 4 or 6 nights of spawning) and minimum day intervals between spawning nights (whether 0, 2 or 4 days) and maximum residence time (that should be higher than  $6 * (4 + 1) = 30$  days, whether 30, 35 or 40 days). These physiological constraints were based on the literature on shad ecology (Olney et al. 2006; Aunins and Olney 2009; Maltais et al. 2010; Lowerre-Barbieri et al. 2011; McBride et al. 2015; Rosset et al. 2017; Tentelier et al. 2018). At the end, with the 3 levels for each of the 3 physiological constraints, 27 combinations of physiological constraints were simulated, corresponding to a range of constraints for many semelparous fish species. The offspring survival was then simulated with an existing survival model (Jatteau et al. 2017), which predict the survival off early life stages (from hatch to up to 14 days post hatching) according to the daily water temperature time series. For each set of physiological constraints and transit time, we computed the advantage to adopt a 'hasty' rather than 'omniscient' behaviour by averaging the differences of offspring survival between these two behaviours.

### 3 Results

#### 3.1. Migration pattern calibration

The allis shad spawning runs upstream the tidal limit occurred from the end of March to the beginning of June and lasted from 42 to 68 days depending on the year. The AICc criterion allowed selecting the number of migration waves: a 2-wave pattern in 2006 and 2007 and a 5-wave pattern in 2005.

### 3.2 Trade-off between reproduction and migration

Not surprisingly, the survival rates corresponding to the ‘omniscient’ behaviour were always higher than those associated with the ‘hasty’ behaviour regardless of transit time and combination of physiological constraints (Fig III6; always positive difference). Higher differences between the two spawning behaviours were observed for early arrival times on the spawning grounds (<20 days of time transit). For intermediate time lags, the difference between the two behaviours became weak (around 40 days of time transit), but rose again for late arrival.

## 4 Discussion

### 4.1 Strengths and limitations

This study combined explicitly migration dynamics and spawning behaviour for the first time. The HoOS model overpassed the information scarcity about the physiology of shad by exploring the space of possible physiological characteristics (27 sets of potential physiological constraints). This model could be refined by a deeper understanding of shad’s physiological constraints. As such, new exploration of the relative influence of migration and physiology on reproductive success began with the use of telemetry (Minke-Martin et al. 2018).

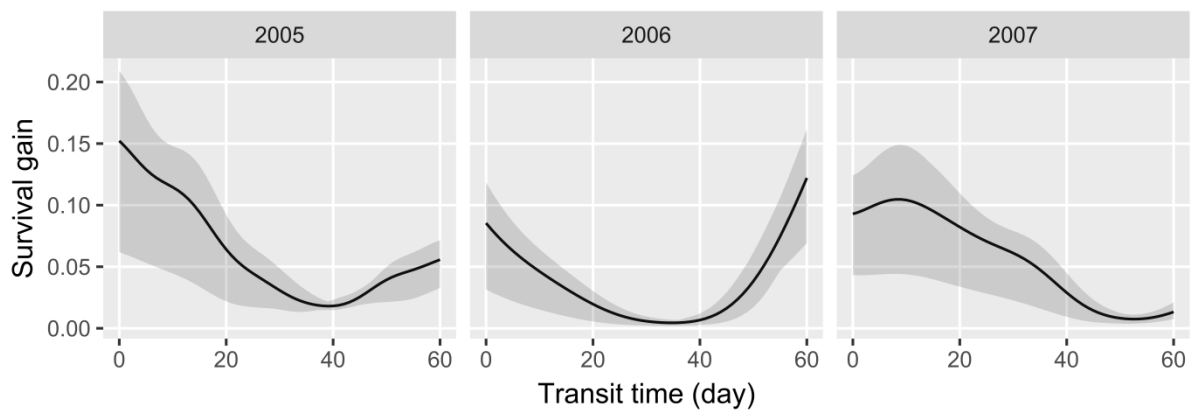


Figure III6: Survival gain (based on thermal tolerance of Jatteau *et al.*2017) between the “omniscient” against the “hasty” behaviour. The envelop represent the difference for the 27 combination of physiological constraints, and the solid line represents the means of the difference of these 60 physiological constraints. The three panels represent the analysis for each of the three years in the Garonne River.

The HoOS model did not consider all the factors which are likely to influence the reproductive success. For instance, the simulation of migration did not take into account the influence on environmental factors during the journey (Boisneau et al. 1985; Tétard et al. 2016) which probably reshape the timing of spawning ground arrivals from the downstream passage signal. Indeed, the possible laying time on the spawning ground must probably depend on the level of energy remaining in the shad, which depends precisely on migration conditions. Therefore this approach underestimated the possibility (or the impossibility depending of the year) for fish to arrive on the spawning grounds at the best time. In that sense, simulation of migration with a more complex approach (*i.e.*, with a transit time for each migration wave depending on environmental factors) may greatly improve the model.

#### 4.2 Migration and reproduction trade-off

Although it is commonly assumed that the timing of migration is an important factor for the reproductive success, evidences are relatively scarce and generally target birds (Brinkhof et al. 1993; Gienapp and Bregnballe 2012; Bejarano and Jahn 2018). To date, the HoOS model is the first model to explore the survival differences between the two reproductive behaviours for migratory fishes.

The HoOS model demonstrated that early arrivals (that are less favourable) can be compensated by an 'omniscient' behaviour, whereas in intermediate time transit the 'hasty' behaviour is sufficient. In that case, using environmental cues to appropriately spawn become not crucial because arrivals time on spawning grounds coincide with suitable ecological conditions for reproduction and subsequent offspring survival. For fish displaying a 'hasty' behaviour, the breeding timing only depends on physiological constraints induced by batch spawning; therefore, they have limited ability to wait for more suitable conditions on

spawning grounds. Conversely, 'omniscient' fishes can delay their breeding timing regarding to the arrival date that requires to foresee future thermal conditions by using proximate environmental cues such as water temperature (Paumier et al. 2019), photoperiod (Roberts et al. 1978) or water discharge (Acolas et al. 2006). Such prospect seems conceivable because temporal autocorrelations conveys information about future environmental conditions (Sabo and Post 2008).

These findings bring evidence of the close relationship between migration timing, spawning behaviour and reproductive success and raise the question of what is the most advantageous strategy. Early migration followed by waiting has been highlighted several times in many populations of salmon (Hodgson and Quinn 2002; Morbey 2003; McBride et al. 2015). For spring spawners, such as shads, spawning occurs under conditions of decreasing water flow and rising in water temperature. As such, early migrants could be exposed to faster currents that can interrupt their migration (Rochard 2001). However, once at spawning grounds, 'omniscient' fish can display plasticity in spawning timing that could be advantageous when environmental conditions are unsuitable.

#### 4.3 Conclusion and perspectives

By exploring the interactions between migration and reproduction, the HoOS model provided evidence of the need to consider the reproduction as a complex combination of migration and spawning behaviour. The two processes can balance each other in such way to ensure maximum fitness outcome. This study should motivate further exploration of the complex reproduction of anadromous species. A perspective to this virtual experiment is to explore how fish used environmental cues to properly time reproduction and migration.

### ***B. The flirtyShadBrain model***

Moving further from the HoOS model, we aimed at modelling the arrival on spawning grounds and the “true” spawning decision, *i.e.*, beyond the two stereotypical spawning behaviours used in the HoOS model (Fig. III7). The goal of the flirtyShadBrain model was to mimic the observed reproduction with rules based on the environmental factors used in the second paper. Contrary to the statistic approaches, we tried to simulate the abundance of spawners reproducing. This model was firstly coded by Patrick Lambert in Java, and recoded by myself in R, with the precious help of Hilaire Drouineau and Sebastien Boutry to validate the code. I think that we are not far from a successful calibration of this model, but I ran out of time during this PhD to finish the work.

This is without a doubt the most frustrating part of this PhD. However, despite the actual unsuccessful calibration, this mechanistic model enables to understand the complexity of the interactions between migration, decision to reproduce and physiological constraints and it constitutes an important step in the reflection that was critical to develop the BRT model.

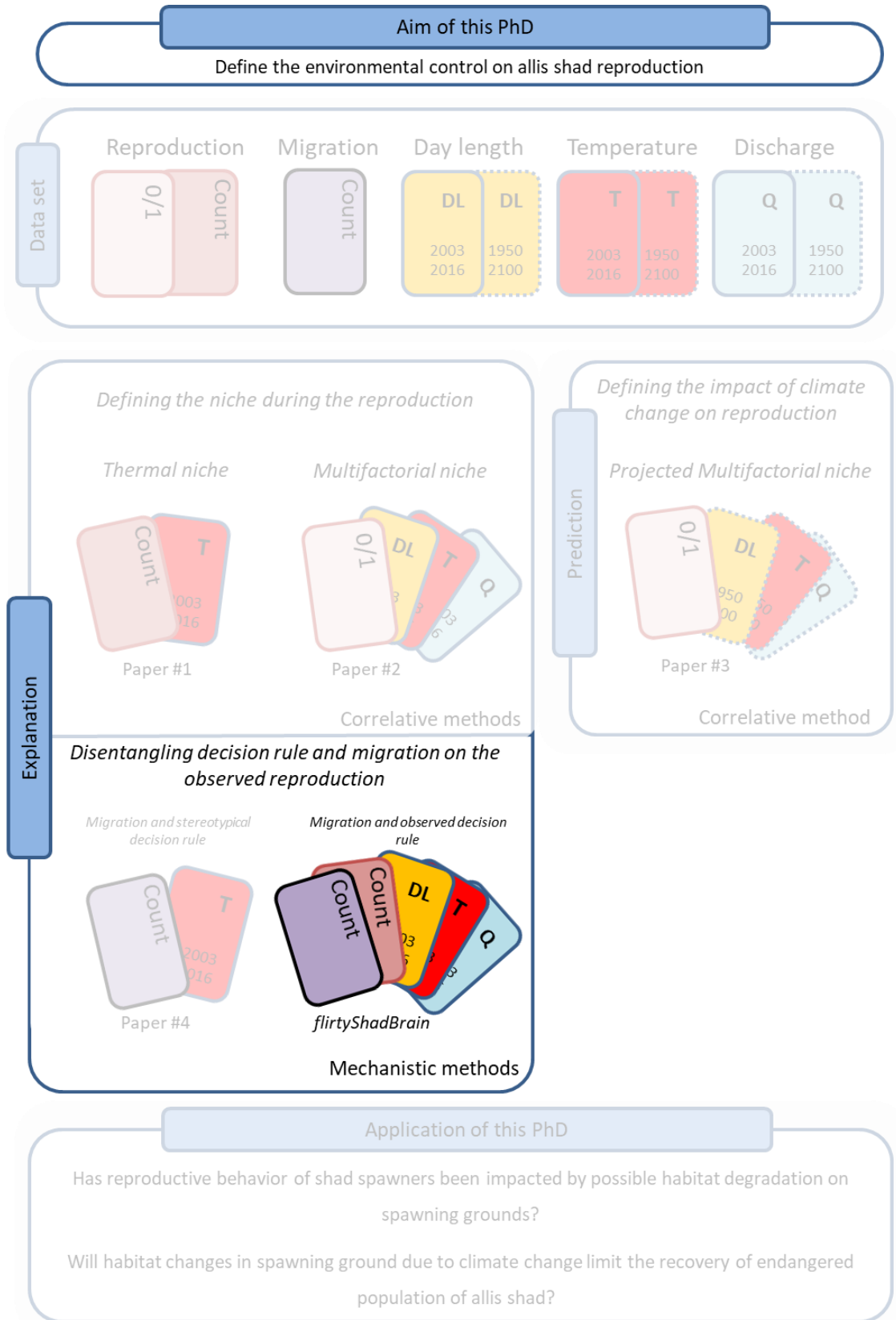


Figure III7: Conceptual diagram representing the articulation of the different parts of the PhD.



## 1 Introduction

In this study, we tried to simulate the arrival on spawning ground and the spawning behaviour of allis shad in the Garonne and Dordogne rivers. The disentangling of these two behaviours enables to explicitly define the decision rule of shad during the final choice of spawning. This decision rule was simulated with a machine learning tools (Artificial neural networks; ANN), which is documented to handle non-linear relationships and to provide accurate results in simulations (Lek et al. 1996; Olden et al. 2008; Franceschini et al. 2018). Artificial neural networks (ANNs) are used in ecology to predict the impact of climate change but also to evaluate the most important factors controlling biological processes (Maravelias et al. 2003; Franceschini et al. 2018). The relative influences of environmental factors on freshwater fish distribution were notably assessed by ANNs (Lek et al. 1996; Maravelias et al. 2003; Ibarra et al. 2003; Konan et al. 2015; Olaya-Marin et al. 2015; Muñoz-Mas et al. 2015; Giam and Olden 2015). Here, we present the *flirtyShadBrain* model that aimed to simulate the migration process explicitly with the arrival on spawning grounds and the decision rule based on 6 environmental factors using ANNs.

## 2 Materials and methods

### 2.1 The *flirtyShadBrain* model

The *flirtyShadBrain* model encapsulated two processes: the arrival on spawning grounds (end of the spawning migration) and the spawning behaviour (decision to reproduce) (Fig. III8). The reproduction process was simulated in four steps.

Step 1) for sake of simplicity (and contrary to HoOS model), the arrival on spawning grounds was simply simulated by a unimodal migratory pattern based on Gaussian distribution with the mean date of arrival, the standard deviation that shapes the duration of the arrival wave, and the number of individuals. It gave the number of fish per day arriving on the spawning ground (Fig. III8).

Step 2) for each date of arrival, the probability to spawn during the next days was computed with an artificial neural network (ANN) according to environmental factors “perceivable” by a fish (Fig. III8). The spawning behaviour was simulated with a 3-layer artificial neural network with bias. The network configuration was composed of an input layer with 6 neurons (scaled environmental factors), one hidden layer with 3 neurons, and one output layer with a single neuron (spawning probability) (Fig. III9). This configuration is one of the simpler that could be used with 6 inputs and 1 output.

Step 3) the proportion of reproduction acts for each day after one arrival was computed with the previous time series in respect with the three biological constraints already considered in HoOS model (one of the parameters sets: a maximum of 3 nights with egg expelling spaced by a minimum of 3 days (*i.e.*, 2 nights without reproductive acts between them within 30 days of presence on the spawning grounds, Fig. III8).

Step 4) the time series of proportions of reproduction acts of the date of arrival were summed up per day to give the daily reproduction activity within a spawning season that can be compared with the field observations. Thus fish reproduce several times depending on their arrival date, conditions and physiological constraints. The sum of these “individual stories” gives the series of global breeding activity over the season (Fig. III8).

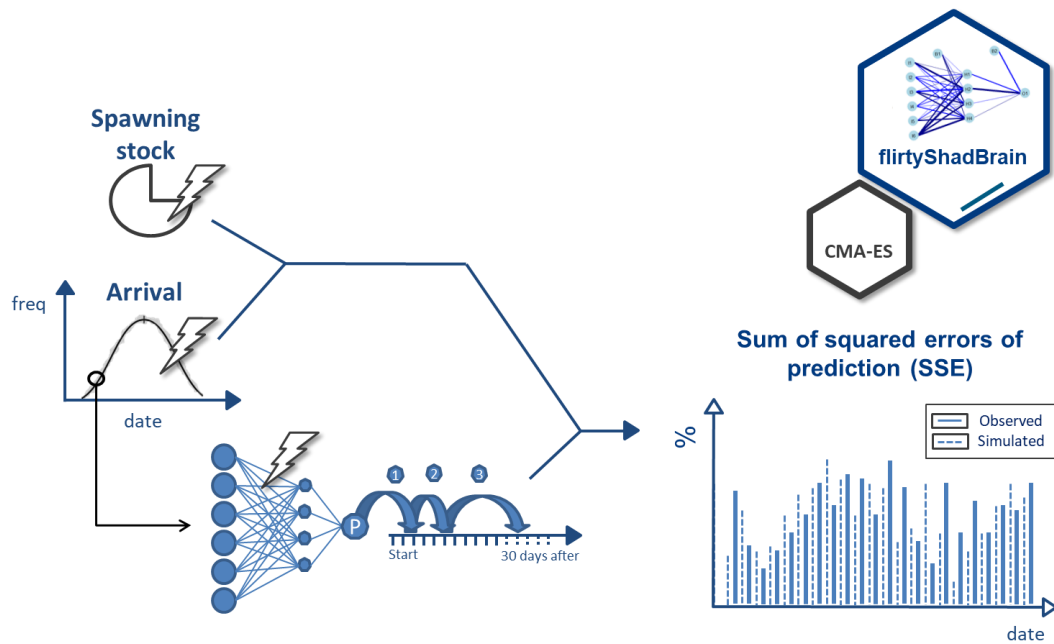


Figure III8: Structure and calibration of the *flirtyShadBrain* model. Lightning flashes represent the parameters to be optimised by CMAES.

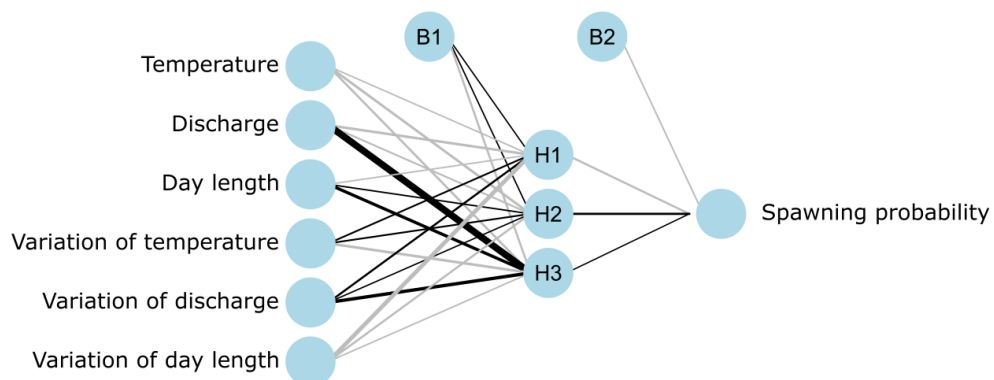


Figure III9: Structure of the neural network used in the *flirtyShadBrain* model. The leftmost layer is the input layer with input neurons (6 nodes; temperature, discharges, day length, variation of day length, variation of discharge, and variation of temperature and one bias); the rightmost is the output layer with a single output neuron (1 node; spawning probability). The middle layer is the hidden layer (neither inputs nor outputs) with hidden neurons (3 nodes; H1:H3 plus one bias).

## 2.2 Data collection

The environmental data used to calibrate the *flirtyShadBrain* model were daily abundance of fish reproducing and the 6 environmental factors used in the BRT models (paper #2): water temperature  $T$  ( $^{\circ}\text{C}$ ) and variation of water temperature  $\text{delta}T$  ( $^{\circ}\text{C}$ ), water discharge  $Q$  ( $\text{m}^3 \cdot \text{s}^{-1}$ ) and variation of water discharge  $\text{delta}Q$  ( $\text{m}^3 \cdot \text{s}^{-1}$ ), day length (hours) and variation of day length (hours). The 6 input variables were normalised in a  $[0, 1]$  intervals by a min-max scaling in order to be proceeded by artificial neural networks (ANNs). For temperature and day length, the minimum and maximum were computed from the 1<sup>st</sup> of January 2003 to 31 December 2016 in the two rivers. Discharge was log-scaled on the same period but grouped by the river, the river cross sections being different.

## 2.3 Model calibration based on an evolution strategy

Since there are calculation (migration patterns and biological constraints) between the ANN output (probability to spawn a given day) and the *flirtyShadBrain* output (the daily reproductive activity) the ANN calibration referred to a reinforcement learning (Salimans et al. 2017). All the model parameters were calibrated to minimise an objective function (Eq. 1). The model parameters were the weights of neural networks, migration parameters and number of spawners (Fig. III8).

Equation 1: objective function minimised by CMA-ES

$$\sum_{site*season} \sum_t (simulated(t) - observed(t))^2 +$$

$$\sum_{site*season} 1000 * (\sum_t (simulated(t)) - 1)^2 +$$

$$\sum_{site*season} 1000 * [sd(probability(t) < 0.1) * (sd(probability) - 0.1)^2]$$

The objective function is a sum of squared errors of prediction (SSE;  $\sum_{site*season} \sum_t (simulated(t) - observed(t))^2$ ), defined as the sum of the squares of residuals (deviations predicted from actual empirical values of daily reproductive activities). Two constraints were added to the SSE. The first constraint avoiding error compensation between site-season ( $\sum_{site*season} 1000 * (\sum_t (simulated(t)) - 1)^2$ ), which implies that we prevented a site-year combination with a very poor SSE from being compensated by another site-year combination with a very good SSE. The second constraint limiting a very flat Gaussian distribution of spawning probability ( $\sum_{site*season} 1000 * [sd(probability(t) < 0.1) * (sd(probability) - 0.1)^2]$ ), that implies that we prevented that the flirtyShadBrain model was only calibrated on the migration process. The calibration was done using the covariance matrix adaptation evolution strategy CMA-ES (Hansen and Ostermeier 2001). Since this optimisation algorithm is stochastic, 50 calibrations with simply different initial seeds for the pseudo-random number generator were performed to ensure the convergence of the calibration.

## 2.5 ANN sensitivity analysis

After the calibration of flirtyShadBrain, a sensitivity analysis of the ANN was performed to assess the relative importance of the 6 inputs (*i.e.*, environmental factors), and therefore to

specify the spawning behaviour *per se* (more specific than in the second paper because without integrating the migration). Three methods of sensitivity analysis were used: the Olden method, the lek-profile and the variance decomposition based on the Sobol method (Olden et al., 2004). The Olden method computes the relative variable importance and the sign of the contribution, as the product of the raw connection weights between each input-output neuron and sums the product across all hidden neurons (Olden et al., 2004; Saltelli et al. 2010). The variance decomposition based on the Sobol method quantifies (i) the importance of the variance of one input while the others are averaged (first order indices,  $S_i$ ) (ii) quantify the contribution of all input variance and their interaction (Saltelli et al. 2010). This analysis was performed using the “*soboljansen*” function from the “*sensitivity*” packages which implements the Monte Carlo estimation for both Sobol indices (Jansen 1999; Saltelli et al. 2010). The lek-profile method was applied to obtain information about the form of the relationship between variables rather than a categorical description provide by the Olden method (Lek et al. 1996; Gevrey et al. 2003). The final product is similar to the marginal plot of the BRT-model (paper #2 and paper #3): a set response curves across the range of values for one explanatory variable, while holding all other explanatory variables constant to specific quantiles.

### 3 Results

#### 3.1 Calibration robustness

The 50 calibrations of the *flirtyShadBrain* model provided reliable predictions of reproduction. The adjusted R-squared between the simulated reproduction activity and the observed reproduction activity were high (up to 70%; Fig. III10).

Despite reliable predictions, the exploration of the 50 calibrations showed that the calibration did not converge toward a unique solution. Different sets of neural network weights emerged from the 50 calibrations. They led to different distributions of spawning probabilities even if they resulted in the same simulated reproduction (Fig. III11).

The sensitivity analysis of the ANN showed highly variable relative importance and sign for the 6 environmental factors between the 50 calibration replicates. According to the Olden method, the day length and the river discharge appeared to globally have a negative impact on the spawning behaviour whereas day-length difference and temperature had positive impacts (Fig. III12). Variations of both temperature and discharge fluctuated between positive and negative effects (Fig. III12). This method highlighted that the relative importance of the 6 factors differed between the 50 calibrations, as the boxplot of each factor highly overlapped (Fig. III12).

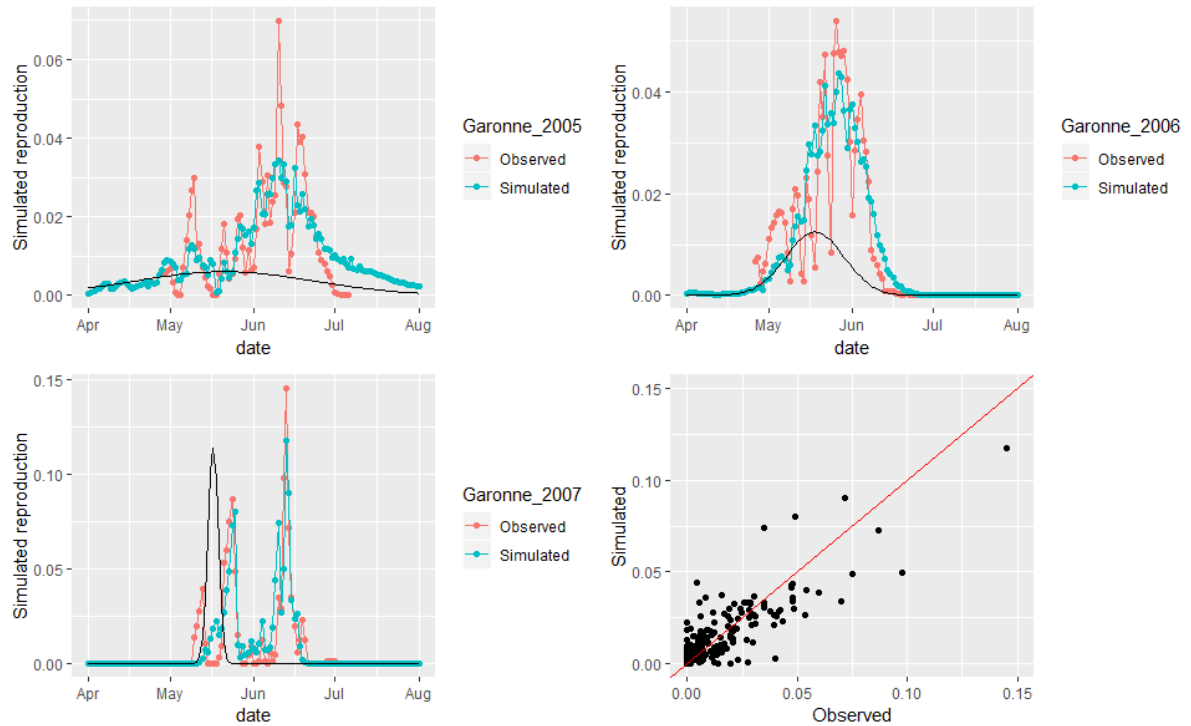


Figure III10: Output of one calibration of the flirtyShadBrain model in the Garonne River in 2005, 2006 and 2007. The black line represents the simulated migration pattern, the blue line is the simulated reproduction activity, and the red line is the observed reproduction activity. The bottom right panel represents the simulated reproduction versus the observed reproduction for the three years.



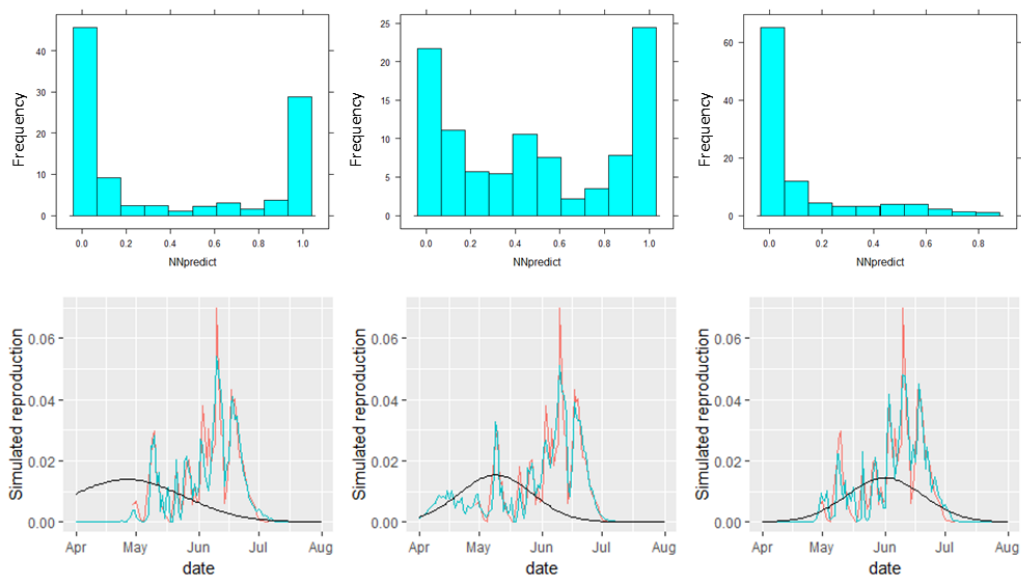


Figure III11: Top panel represents the distribution (frequency) of spawning probabilities computed one spawning season for 3 calibration replicates of the *flirtyShadBrain* model. Bottom panel represents the output of these three calibration replicates. The black line represents the simulated migration pattern, the blue line is the simulated reproduction activity, and the red line is the observed reproduction activity.

The Sobol first order indices ( $S_i$ ) and the Sobol total indices ( $ST_i$ ) for day length variation, day length and temperature did not overlap, which indicated strong interactions between these 3 environmental factors (Fig. III12).  $S_i$  and  $ST_i$  for the river discharge and the difference of temperature and discharge overlapped, which indicated weak interactions between these 3 environmental factors. The two Sobol indices indicated that day length variation, day length and temperature were the most influential factors and that remaining factors had weak influence. However, these three most influential factors cannot be ranked as the relative influence highly overlapped. The marginal plots of the Lek-profiles were highly variable between the 50 calibration replicates of the *flirtyShadBrain* model and no global relationship arose from these 50 Lek-profiles. Here, we chose to represent only one of the 50 replicates (Fig. III13). In this Lek-profile, the temperature positively impacts the reproduction whereas the 5 remained factors negatively impact the reproduction, with notable a strong relationship for the river discharge.

#### 4 Discussions

The *flirtyShadBrain* model was able to mimic the observed time series of reproductive acts by simulating a migration wave and spawning rules. However, the behaviour rules could not be understood with the present model since the relative influence of environmental factors highly fluctuated between each of the 50 calibration replicates. Therefore, a unique decision rule did not emerge from the present *flirtyShadBrain* model calibration. Nevertheless this failure gave some insights to understand the reproduction process. The different calibrations revealed that many decision rules could end in a similar pattern of reproduction.

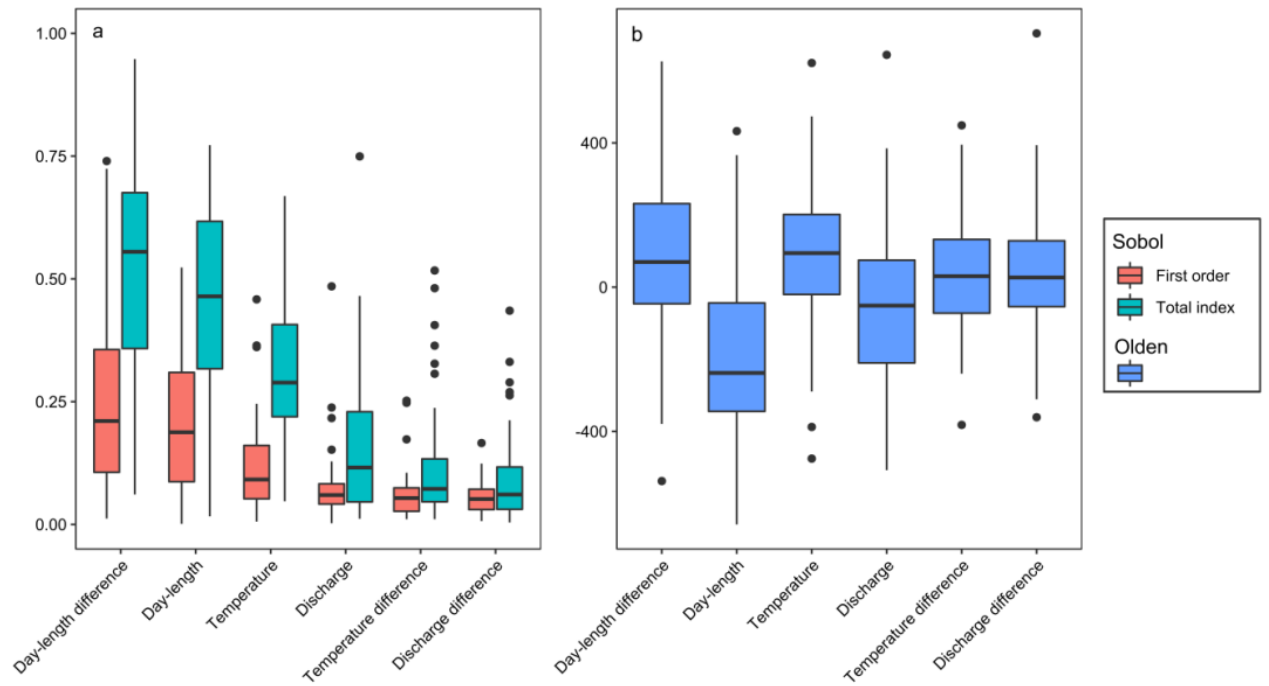


Figure III12: Boxplot of the Sobol and Olden indices for the 6 environmental factors for the 50 calibration replicates of the *flirtyShadBrain* model.

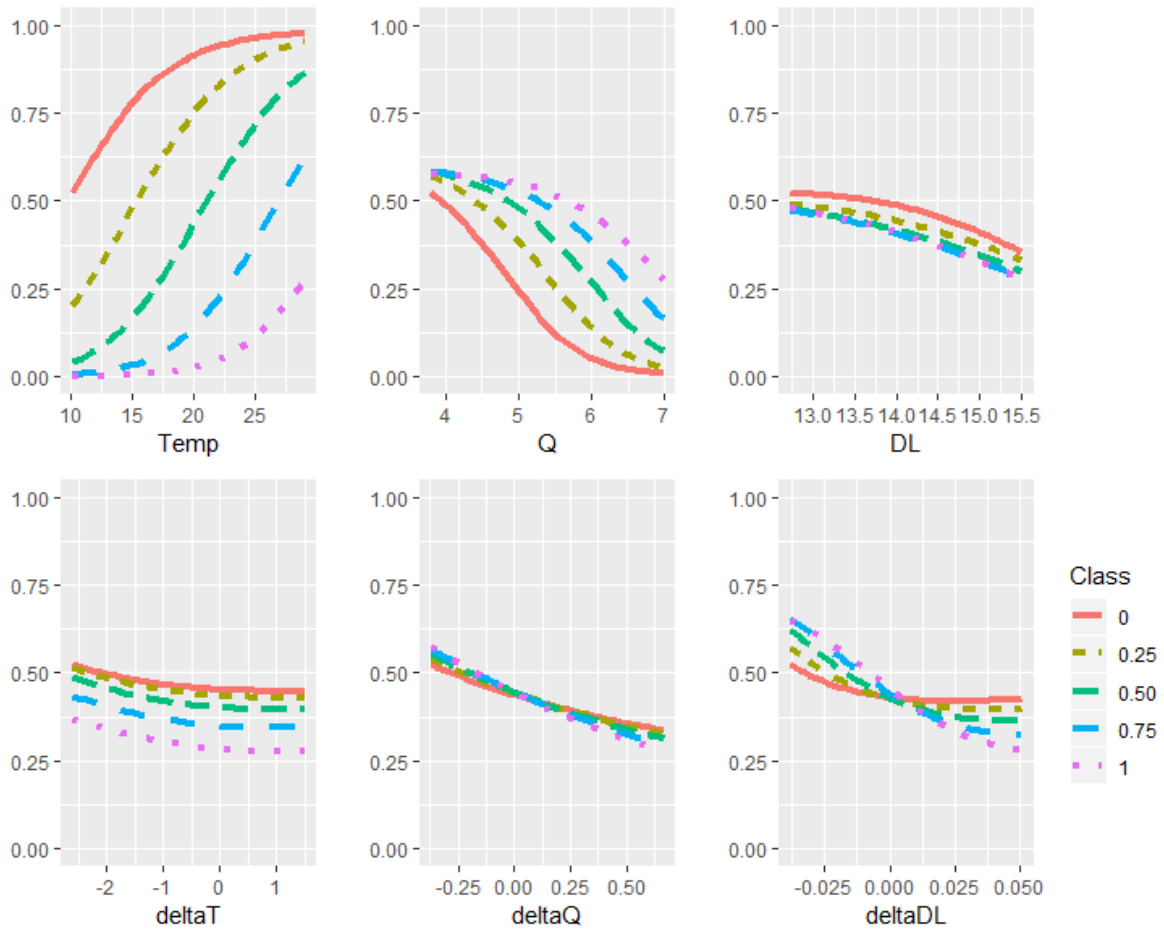


Figure III13: Lek profiles for the 6 environmental factors for one calibration run of the *flirtyShadBrain* model.

It can be easily explained by the correlation between environmental factors, leading to a redundancy of information in nature. Therefore we may speculate on a phenotypic variability for shads with spawners responding to different stimuli but resulting in a similar final reproductive activity. In that case, the interactions between the spawning behaviours and the physiological constraints should be deeply analysed to highlight how these constraints limit the consequences of the spawning behaviour on the reproductive pattern. Coming back to the failure of the *flirtyShadBrain* model calibration (before endorsing this biological speculation), I propose plausible explanations and research perspectives.

First, the optimisation algorithm could not be adapted to or not well tuned to well perform the calibration. One way could be to apply an elastic net regression which linearly combines lasso and ridge penalties (Zou and Hastie 2005). The first one, based on the sum of absolute value of the parameters, tends to discard the least important weights in the neural network. The second one based on a quadratic form of parameters lead to shrink the parameter ranges (avoid large weights). Some preliminary tests did not show a great improvement in the calibration. But such technic is still empirical and needs some very fine tuning. Another way could be to test other optimisation algorithm as the more classical gradient descent (Barzilai and Borwein 1988).

Second, the *flirtyShadBrain* model should be considered over-parametrised. The well-known flexibility of the neural network at a price of a high number of parameters (25 weights in our model) can be incriminated. With only 1700 observations, the calibration leads the model to simulate the reproduction activity as a white noise. Two “obvious” (but not so simple) solutions can be proposed. On the one hand, the number of observations of reproductive acts should be increased. But only about a hundred observations are recorded

on a river each year. So the best way is probably to gather information from other basins, not so different from the Garonne-Dordogne basin to increase the learning data set. On the other hand, the idea is to reduce the numbers of parameters. The number of neurons in the hidden layer can be decreased. But it is difficult to use less 3 neurons in that layer. However, since the response curves seems to be sigmoidal, other tools than the neural networks can be tested as a combination of simple logistic functions.

A more radical but still speculative proposal (because of lack of time in this PhD to test it) would be to dissociate the calibration of the spawning rules and the migration pattern. The main idea is that the spawning decision module could be calibrated by assuming it is shaped directly by the offspring survival (Quinn and Adams 1996; Lambert et al. 2018). Indeed it is not easy to observe in the field the decision to spawn independently of the migration pattern. In accordance with the optimised spawning hypothesis, a binary time series indicating whether it is better to spawn today or later could be created according to the computation of the offspring survival: 0 if the juvenile survival born the next day is better than today, 1 if survival born today is better than tomorrow. The offspring survival will be computed according to Lambert et al (2018) methodology based on thermal tolerance. An ANN (with an error back propagation learning) or more simply a BRT model could be calibrated according to the 6 environmental factors to predict this computed indicator. Finally, the time series of observed reproductive acts will be used to fit the annual patterns of arrivals on the spawning ground using the previous calibrated spawning decision module and the physiological constraints. This modified *flirtyShadBrain* model could give more insight about the migration behaviour in the estuary and river journey, and notably explain the link between peak of abundance of fishes migrating and peak of reproduction (Acolas et al. 2006).







# **Chapter IV**

## **Predictive approach**



In the chapter III “explanatory approaches”, we defined the environmental control on allis shad’s reproduction. Despite this definition it was difficult at this point to provide a robust diagnostic about the impact of climate change on reproduction. To this extent, we collaborated with scientists from the CERFACS/CNRS (Julien Boé and Gildas Dayon) to obtain simulated data of past and future environmental cues (air temperature and river discharge from 1950 to 2010 in the two rivers). These data enables to develop a predictive approach (Fig IV1).

We used the most developed model in this PhD (BRT calibrated in the paper #2) but replacing water temperature by air temperature. Two indicators previously developed in the paper #2 were used: the habitat suitability index and the mid-season day. We choose to force the calibrated BRT model under two contrasted Representative Concentration Pathways (RCP): a scenario roughly compatible with the 2015 Paris climate agreement (RCP 2.6) and a worst-case scenario (RCP 8.5). Finally, we projected the multifactorial niche to respond to two concerns: 1) has reproductive behaviour of shad spawners been impacted by possible habitat degradation on spawning grounds? 2) Will habitat changes in spawning ground due to climate change limit the recovery of endangered population of allis shad? According to our multifactorial projection, it appears that shad spawners may not be impacted by the future global warming under the RCP 2.6, and that even in the worst scenario, RCP 8.5, habitat suitability is expected to increase though shifting in time towards earlier dates.

This third article is not in its final form for the moment, the last corrections by Julien Boé and Gilas Dayon still need to be taken into account (especially on the cannon’ correction and some model terminology). We would like to make these corrections before the PhD defence and submit the article to the journal *Global Change Biology*.

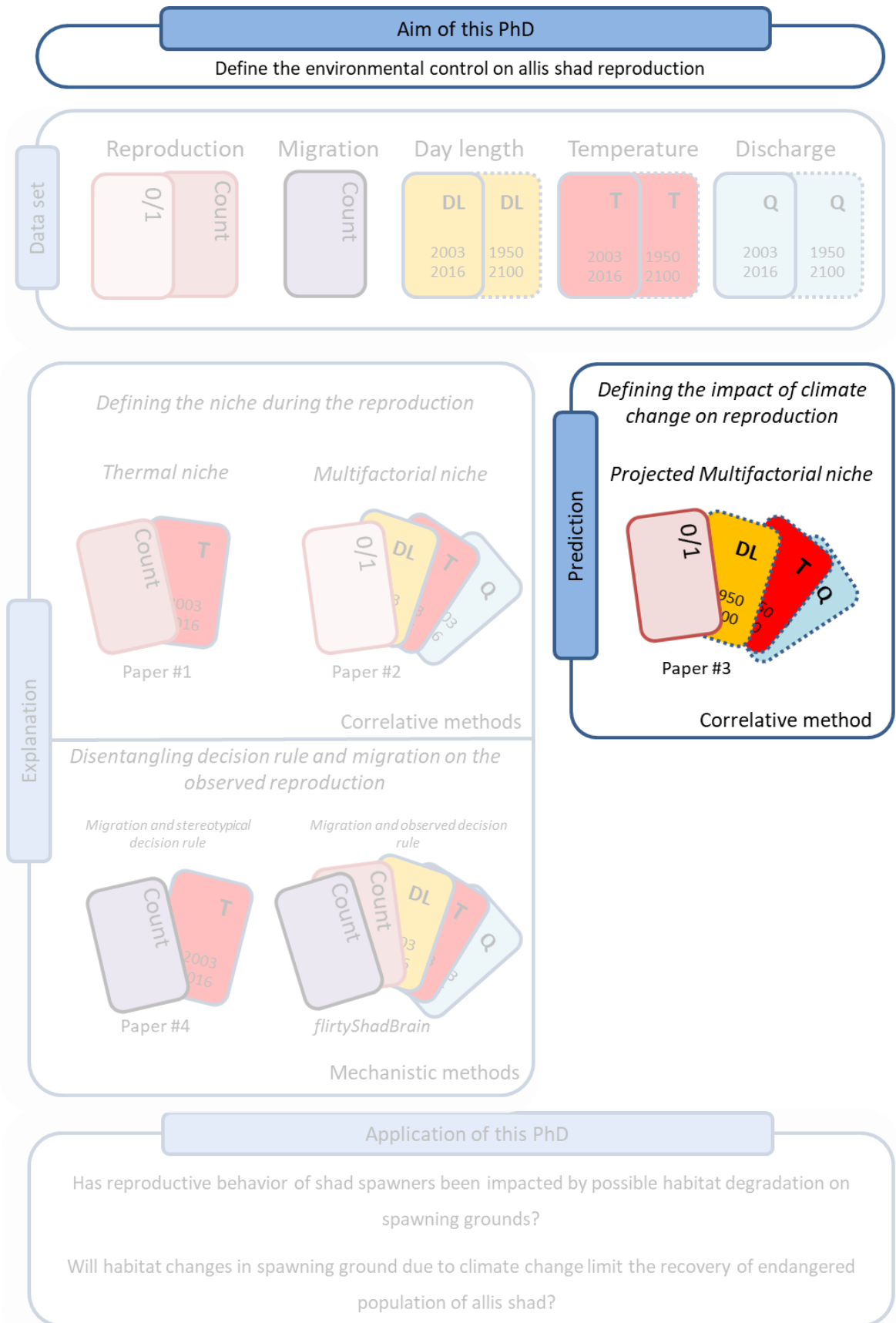


Figure IV1: Conceptual diagram representing the articulation of the different parts of the PhD.

## **Back to the future: riverine spawning habitat suitability for a migratory fish species between 1950 and 2099 under RCP scenarios**

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## Abstract

Environmental cues driving fish reproduction are changing with climate change leading to unknown consequences in terms of reproductive success. A deeper assessment of the causal links between fish reproduction and climate change might be of crucial importance especially for endangered species such as allis shad (*Alosa alosa*). As such, a boosted regression tree model (BRT) was applied to predict allis shad reproduction as a function of key climate-related and environmental factors. Environmental suitability was characterised by two indicators: the habitat suitability index and the mid-season day. The three explanatory variables selected in the analysis were the variation of day length, air temperature and river discharge. The calibration was based on data collected in the observed spawning grounds from 2003 to 2016 in the Gironde-Garonne-Dordogne system. Then, the calibrated BRT model was used to calculate the historical suitability of environmental conditions in the spawning grounds from 1950 to 2018 using simulated time series of environmental factors. Finally, the BRT model was applied to simulate the evolution of environmental suitability from 1950 to 2099 according to 'projected' times series of environmental variables under RCPs 2.6 and 8.5. Results suggested that no major changes in environmental suitability at the spawning grounds had occurred and are expected in a near future. This study pointed towards the importance of studying climate change impacts on additional life-history phases such as early stages.

**Keyword:** Climate change, phenology, reproduction, ecological niche model, diadromous fishes.

## 1 Introduction

Inland fish that live all or part of their lives in freshwater habitat (Allan et al. 2005; Myers et al. 2017), are under threat due to combined human-induced pressures, such as habitat fragmentation, water withdrawal, introduction of alien species, pollution and overfishing (Limburg and Waldman 2009; Vörösmarty et al. 2010; Buisson et al. 2013). Additionally to these pressures, climate change may represent an additional major stressor for all types of inland fishes (Sala 2000; Buisson et al. 2008, 2013; Heino et al. 2009; Lassalle and Rochard 2009; Lyons et al. 2010; Strayer and Dudgeon 2010; Booth et al. 2011; Almodóvar et al. 2012; Nack et al. 2019). Therefore, climate change is of primary concern for ecologists (Parmesan and Yohe 2003; Lassalle et al. 2010; Myers et al. 2017). River flows and their seasonality will be modified by the climate change in France (Dayon 2015) and may compound the significant degradation of the natural water cycle with the dam and water use (Xenopoulos et al. 2005). Over France, expected environmental changes are warmer stream temperatures, earlier spring peaks of discharge in snow-fed rivers and long-lasting low-flow periods notably during summers and autumn (van Vliet et al. 2013; Jiménez Cisneros et al. 2014; Dayon 2015).

The timing of seasonal activities (*i.e.*, phenology) such as migration and reproduction of fishes are demonstrated to be indirectly controlled by the quality of riverine habitats (Poff 1997; Huijbers et al. 2012; Tillotson and Quinn 2018). Fish synchronise their activities with physical cues (Wenger et al. 2011; Paumier et al. 2019), directly and indirectly relying with temporally and spatially limited resources (Cushing 1990; McNamara and Houston 2008; Chevillot et al. 2017). Changes in the spawning period are particularly critical as this will determine the environmental window in which offspring will have to survive and grow (Quinn

and Adams 1996). As a result, the spawning period is tightly linked with offspring survival (Lambert et al. 2018).

Among inland fishes, anadromous fishes are reliable indicators of river degradation as they rely on highly specific habitats to perform their complex life cycle (McDowall 1988). These fishes migrate between the ocean, where they feed and grow, to rivers where they spawn (McDowall 1988). Addressing the sensitivity of these fishes to climate change requires a thorough understanding of key life-cycle events, such as reproduction. Every year, thousands of allis shad (*Alosa alosa*) spawners breed in rivers flowing into the North-Eastern Atlantic Ocean, heralding the beginning of the warmer season. The life history characteristics make this species an appropriate biological model for studying the effects of climate change on fish in rivers. Shad spawn in spring and will therefore be affected by early warming of water temperatures and disruption of flow due to climate change. Here, we used a dataset of high spatial and temporal resolution in the two rivers sheltering historically the most abundant populations of allis shad in Europe. These datasets is composed of 150 years of daily measures and projections of environmental cues (air temperature and discharges).

Moving further from Paumier *et al.* (*in press*) that sought insight into the causal driver of shad reproduction, we developed an Ecological Niche Model (ENM) in order to respond to two major concerns: as reproductive behaviour of shad spawners had been impacted by possible habitat degradation on spawning grounds? Will habitat changes in spawning ground due to climate change limit the recovery of endangered population of allis shad? Based on simulated spawning probabilities, *i.e.*, probability for a fish to reproduce, we investigate how two annual indices of habitat suitability had evolved from 1950 to 2099. The models used to predict the future response to climate change were forced under two contrasted



Representative Concentration Pathway (RCP): a scenario roughly compatible with the 2015 Paris climate agreement (RCP 2.6) and a worst-case scenario (RCP 8.5). Finally, as downscaled hydro-climate projections do not integrate the array of anthropogenic disturbance (Dayon et al. 2018), we applied a newly developed bias correction (Cannon 2018) in order to partially take into account the effects of global change.

## **2 Material and methods**

### *2.1 Case study*

Allis shad is an anadromous clupeid that has dramatically declined through its historical range (Aprahamian et al. 2003). Despite restoration efforts including a fishery ban starting in 2008 in the Gironde-Garonne-Dordogne basin, the most abundant populations in Europe have undergone an unstoppable and still unexplained decline (Rougier et al. 2012; Paumier et al. 2019). Fish spend around 5 years at sea before achieving their maturation (Lambert et al. 2001). Then, fish schools migrate from the ocean to the rivers without feeding and ultimately reproduce (Aprahamian et al. 2010). During the spawning period, fish spawn multiple nights with noisy behavioural sequences that allow observers to monitor the events (Acolas et al. 2004, 2006).

### *2.2 Observed biological and environmental datasets*

Daily monitoring of shad reproduction and the physical environment were available in the Dordogne and Garonne rivers from 2003 to 2016. Daily observations of reproduction in these rivers were performed by Migado (non-profit association, <http://www.migado.fr/>). Seven main spawning grounds are identified and monitored in the Garonne and Dordogne rivers. These spawning grounds are concentrated over 20 km in each river. The reproduction was

monitored following two protocols: either directly on sight and hearing, or by audio recording (Gaillagot and Carry 2016; Gracia and Caut 2016). The observations at each spawning ground were pooled by the river given the low environmental variations between sites in order to obtain a statistically sufficient number of observations (Gaillagot and Carry 2016; Gracia and Caut 2016). In this study, the occurrence of fish reproduction (i.e., binary data with 0 and 1) was used to calibrate the statistical models. This occurrence variable had 1143 observations.

Six environmental factors were used to model spawning probability (Table IV1): air temperature, water discharge, day length and the daily difference in each of these factors one day to the next. Daily air temperature at the grid cell closest to the spawning grounds in the two rivers is extracted from the SAFRAN dataset (Vidal et al. 2010). SAFRAN is based on observation stations over France collected by Météo-France and an optimal interpolation algorithm. SAFRAN is available on an 8 km by 8 km grid from 1950 to 2018. The daily river discharge was obtained from the French “Banque Hydro” from 1960 to 2018 (<http://www.hydro.eaufrance.fr>). The daily river discharge (Q) was log-scaled in order to normalise the distribution in the two rivers and the difference in daily river discharge from one day to the next ( $\Delta Q$  in  $m^3.s^{-1}$ ). Day length (DL) was defined as the interval between sunrise and sunset (Corripio 2003).

### **2.3 Hydro-climate scenarios**

A large multi-scenario and multi-model ensemble of statistically downscaled hydro-climate projections for the two rivers were used (Table IV2). Ten global climate models (GCMs) of the Coupled Model Intercomparison Project phase 5 (CMIP5; Taylor et al 2012) were statistically downscaled on a 8 km by 8 km grid following the method described in Dayon *et al.* (2015).

Table IV1: Biological and environmental datasets used in the present study.

| Dataset  | Time period | Data owner           |
|--|-------------|----------------------|
| Day length   | 1950-2099   | None                 |
| Observed reproduction                                      | 2003-2016   | Migado               |
| Observed river discharge                                   | 1960-2018   | Banque Hydro         |
| Observed air temperature                                   | 1950-2018   | SAFRAN, Météo France |
| Simulated air temperature<br>(reconstructed and projected) | 1950-2099   | (Dayon et al. 2018)  |
| Simulated river discharge<br>(reconstructed and projected) | 1950-2099   | (Dayon et al. 2018)  |

Table IV2: Summary of the 46 environmental datasets used in the present study. GCMs and number of time series per scenarios (Historical, RCP2.6 and RCP8.5) were given. The 46 datasets were available for the two rivers (i.e., 46 time series x 2 rivers = 92 datasets).

| GCMs          | Reconstructed | RCP2.6 | RCP8.5 |
|---------------|---------------|--------|--------|
| ACCESS1-3     | 1             | 0      | 1      |
| bcc-csm1-1-m  | 1             | 1      | 1      |
| BNU-ESM       | 1             | 0      | 1      |
| CanESM2       | 5             | 5      | 5      |
| CNRM-CM5      | 1             | 1      | 0      |
| CSIRO-Mk3-6-0 | 1             | 0      | 1      |
| GFDL-CM3      | 2             | 0      | 0      |
| IPSL-CM5A-MR  | 3             | 1      | 1      |
| MIROC5        | 5             | 0      | 3      |
| NorESM1-M     | 3             | 1      | 1      |

We used historical simulations on the 1950-2005 period and simulations with two Radiative Concentration Pathways - RCPs (Moss et al. 2010) from 2006 to 2099. In historical simulations, natural and anthropogenic forcing are those observed during the past period (Meinshausen et al. 2011). Natural forcings mainly include variations of the solar activity and volcanic aerosols. Anthropogenic forcings mainly include anthropogenic aerosols and greenhouse gas (GHG). The RCP 2.6 scenario leads to a global warming close to 1 (K) at the end of the 21<sup>st</sup> century compared to 1986-2005 period while the RCP8.5 scenario leads to a global warming of roughly 4 K (Collins et al. 2013). Downscaled climate variables were used to force the ISBA-MODCOU hydrological system (Habets et al. 2008). ISBA is a land surface scheme that computes the surface energy and water budgets and MODCOU routes the runoff simulated by ISBA in the hydrological network. The hydrological projections are described in Dayon *et al.* (2018). Downscaled temperature at the grid point the closest to the study sites and simulated river discharges at the observation stations were studied.

As climate projections may be biased in comparison to observations (Cannon 2018), a multivariate bias correction algorithm (MBCn) was applied on air temperature and river discharge. Biases may arise because of models and downscaling errors. Additionally, biases in river flows may be due non-anthropogenic climatic influences such as water withdrawal and dams that are not taken into account in the hydrological model. This algorithm transferred all aspects of the observed continuous multivariate distribution (here past observation of air temperature and river discharge from 1950 to 2018; Table IV1) to the corresponding multivariate distribution of the air temperature and river discharge from the ten GCMs (Table IV1 & Table IV2). Changes in quantiles of each variable between the past observation and the projection period are preserved taking into account of dependence between them (Cannon 2018).

## 2.4 Boosted regression trees (BRT) model

A presence-absence algorithm, boosted regression trees (BRT), was used to predict daily spawning probabilities in function of the 6 environmental factors. The BRT was calibrated using the 13 years of field monitoring of reproduction and environmental cues in the Garonne and Dordogne rivers (Table IV1). Following the procedure recommended in Elith *et al.* (2008), the BRT model was tuned with a tree complexity of 5, a learning rate of 0.001 and a bag fraction of 0.5 with a binomial error distribution. Tenfold cross-validation (CV) was applied to address the non-independent structure of the data (Fabricius and De'Ath 2008; Buston and Elith 2011). The relative importance of the 6 environmental factors was assessed by the Friedman's procedure (Friedman 2001; Friedman and Meulman 2003; Elith *et al.* 2008). A variable selection was performed in order to drop redundant predictors that could have increased the model variance. The 6 factors were dropped until a significant increase in residual deviance was assessed between the prior and simplified model ("gbm.simplify" of the "dismo" package).

The model performance was assessed with the area under the curve (AUC) of the receiver operating characteristics (ROC) plots (Hanley and McNeil 1982). One partial dependence plot per environmental factor was plotted to visualise its effect after accounting for the average effect of the two remaining factors (Elith *et al.*, 2008). This analysis was completed in R (version 3.5.1 R Development Core Team) using the "dismo" and the "gbm" packages (respectively version 1.1-4 and version 2.1.4).

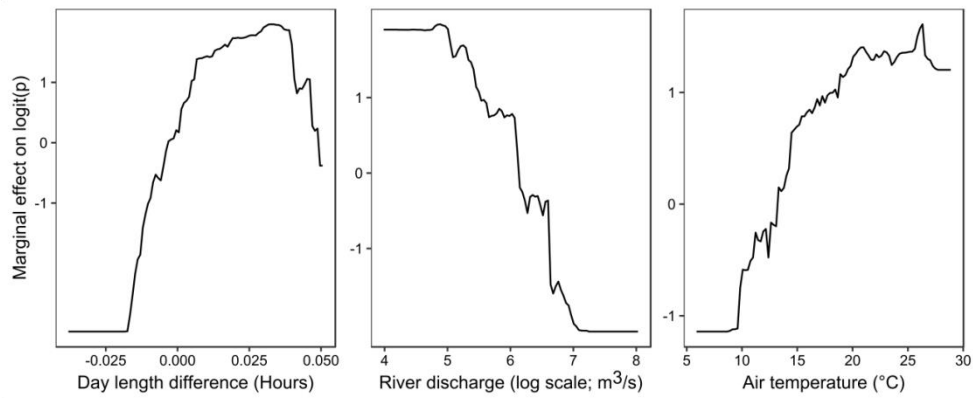


Figure IV2: Two-dimensional partial dependence plots for the three most influential predictors in the BRT model. For each plot, the two remaining variables are heading at their mean. the Y-axes are on the logit scale.

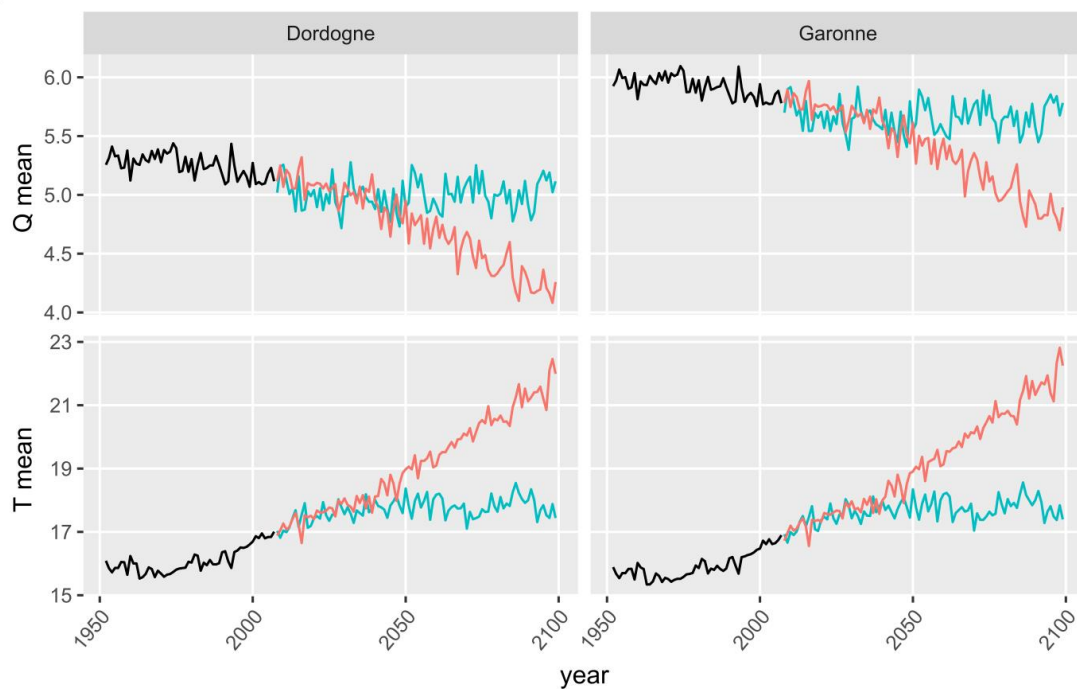


Figure IV3: Time series of annual mean river discharge (Q mean, log-scaled, m<sup>3</sup>.s<sup>-1</sup>) and annual mean air temperature (T mean, °C). Projections are shown for the two RCPs for the multi-model mean: black for Historical, red for RCP 8.5 and blue for RCP 2.6

## 2.5 *Habitat index definition*

The calibrated BRT model was used to predict spawning probabilities in the observed environment (1950-2018); (ii) the simulated environment (1950-2018) and (iii) the projected environment (2019-2099). For each of the datasets (Table. IV2), the BRT model predicted the spawning probabilities on a constant spawning period that we defined as the wider spawning period: 21<sup>st</sup> of March until 1<sup>st</sup> of August (Aprahamian et al. 2003).

The predicted spawning probabilities were used to compute two annual indices that reflected the changes in the physical habitat. We assumed that the spawning probabilities are proportional to the habitat quality. Firstly, the habitat suitability index (HSI) was computed as the means of the predicted spawning probabilities during the spawning period. Secondly, the mid-season day (MSD) was computed as the spawning probability-weighted timing that reflects the temporal centroid of the most suitable conditions regarding the physical cues.

$$MSD = \sum (t_i p_i) / \sum p_i$$

Where  $t_i$  is the Julian day and  $p_i$  is the corresponding spawning probability for that day.

## 2.6 *Statistical analysis*

The non-parametric Mann-Kendall test was employed to detect any significant monotonic trends in HIS and MSD series (Table IV2). We qualified the trend according to the statistical significance and how the index evolved during the time series (positively, negatively, no change).

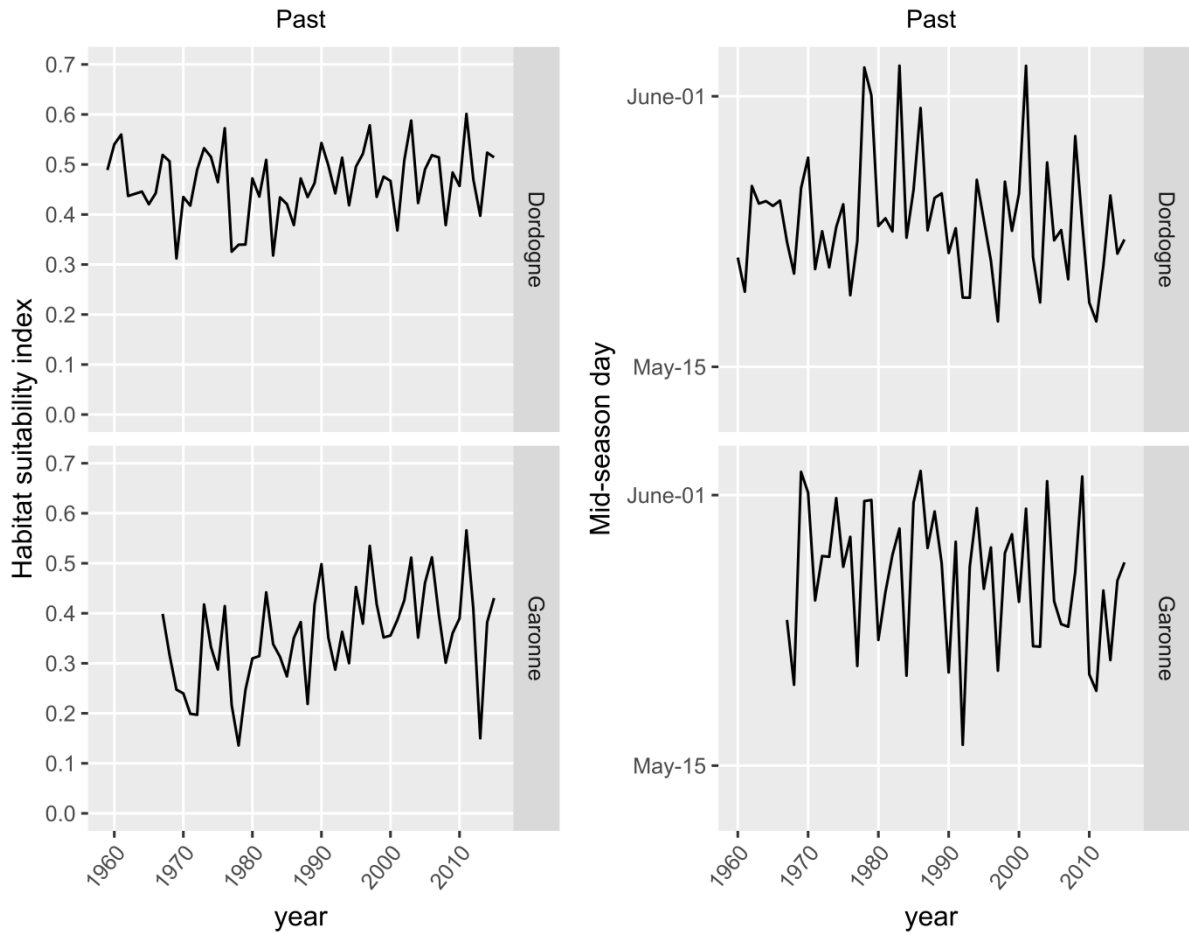


Figure IV4: Time series of annual Habitat Suitability Index (HSI; left panel) and annual Mid-season day (MID; right panel) from 1960 to 2018 in the Garonne and Dordogne rivers



### 3 Results

#### 3.1 Model calibration and response curves

The AUC value (0.92) indicated a high performance of the BRT model calibrated on the 13 years of observed historical data. Three explanatory factors were retained after the variable selection procedure. The most influential factors were: the variation of day length (47 % of the total variance), river discharge (35.2 %) and air temperature (17.8 %). According to the BRT model, allis shads start to reproduce at 20°C. Reproduction is associated to strong and positive variations in the duration of the day. On the contrary, high discharges (*i.e.*, beyond 403 m<sup>3</sup>.s<sup>-1</sup>) are predicted to stop the reproduction (Fig. IV2). An increasing sigmoid relationship was calculated between reproduction and air temperature. A decreasing sigmoid curve was obtained between reproduction and river discharge (Fig. IV2). Finally, a dome-shaped relationship was found with the variation of day length.

#### 3.2 Trends in temperature and discharge from 1950 to 2099

Simulated, *e.g.*, reconstructed and projected, air temperature and river discharge changes were very similar between the two rivers (Fig. IV3). During the spawning period (from the 21<sup>st</sup> of March to the 1<sup>st</sup> of August), a positive trend in air temperature was shown over the historical period, from 1950 to 2005. On the opposite, a negative trend in river discharge was shown on the same period of time. Based on GCMs' projections, these trends intensified during the 21<sup>st</sup> century under RCP8.5, but the stabilisation of both temperature and discharge were projected after the first two decades of the 21<sup>st</sup> century under RCP2.6.

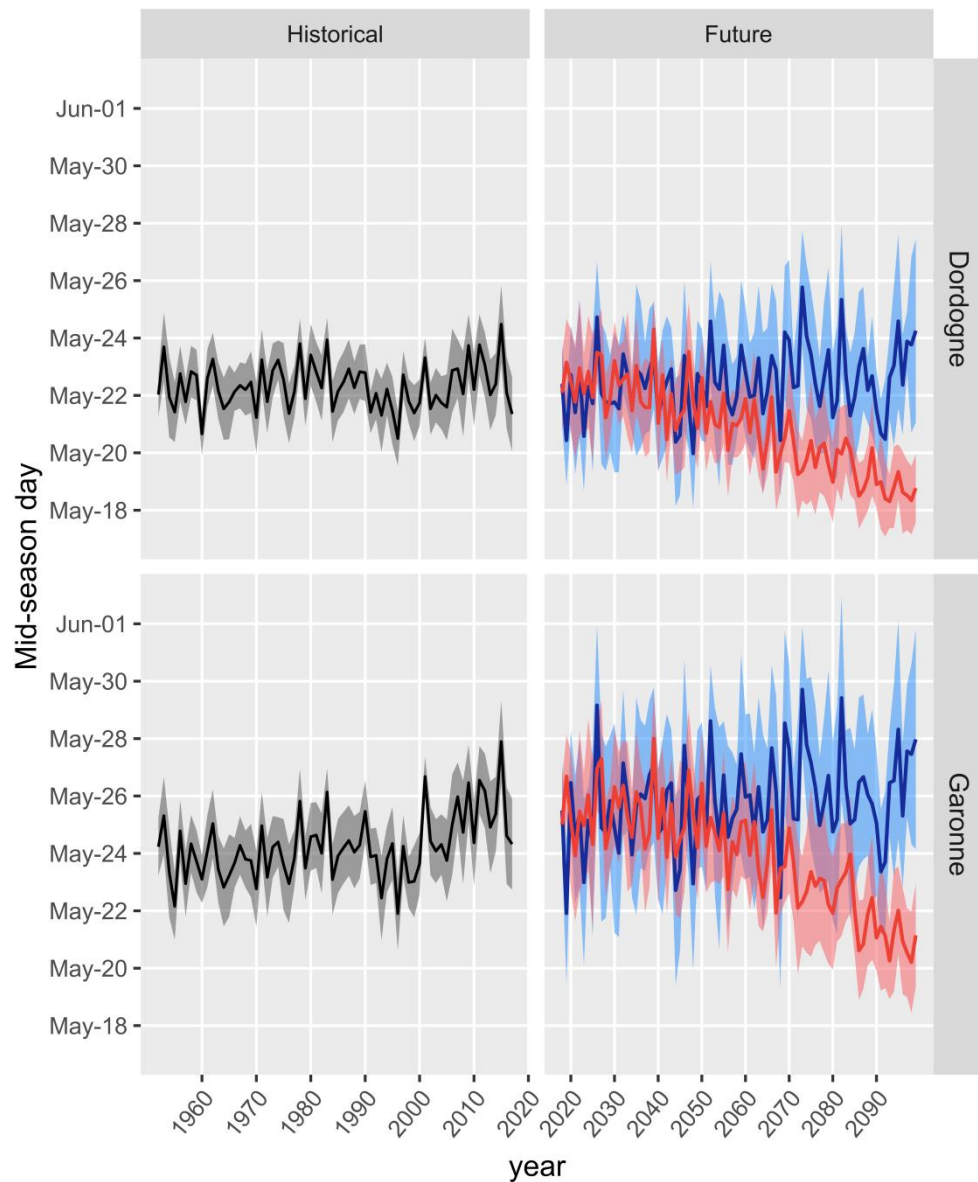


Figure IV5: Time series of annual Mid-Season Day (MSD; left panel) from 1950 to 2018 (left panel) and from 2019 to 2099 (right panel) in the Garonne and Dordogne rivers. Projections are shown for the two RCPs for the multi-model mean: black for Historical, red for RCP 8.5 and blue for RCP 2.6 (solid lines) and the 5 to 95% range of the confident interval across the distribution of individual models (shading).

### ***3.3 Trends in the two habitat indices following changes in hydro-climatic variables***

#### **3.3.1 With past observed environmental conditions**

In the Garonne River, a significant positive trend was estimated for the HSI calculated with observed air temperature and river discharges in the past (Table IV3; Fig. IV4). A large interannual variability in habitat suitability was also noted during this 40-year period (Fig. IV4). In the Dordogne River, no significant trend was detected for the HSI, with again a strong interannual variability. Generally, we observed higher HSI values for the Dordogne River (Fig. IV4). The MSD index highly fluctuated near the end of May for the two rivers (Fig. IV4). No significant trend for this index was estimated in the past for any of the two rivers (Table IV3; Fig. IV4).

#### **3.3.2 With simulated past environmental conditions**

The MSD values calculated with the environmental data series were consistent with results obtained from past observed environmental conditions, *i.e.*, no significant trend in the ensemble mean was estimated for any of the two rivers (Table IV3; Fig. IV5). Consistently with the exercise with observed environmental data, a significant positive trend in the ensemble mean was estimated for the HSI in the Garonne River for the period 1950-2018 (Table IV3; Fig. IV6). A significant positive trend of the HSI was also estimated in the Dordogne River with environmental datasets while the trend was not significant with past observed environmental conditions (Table IV3; Fig. IV4&6).

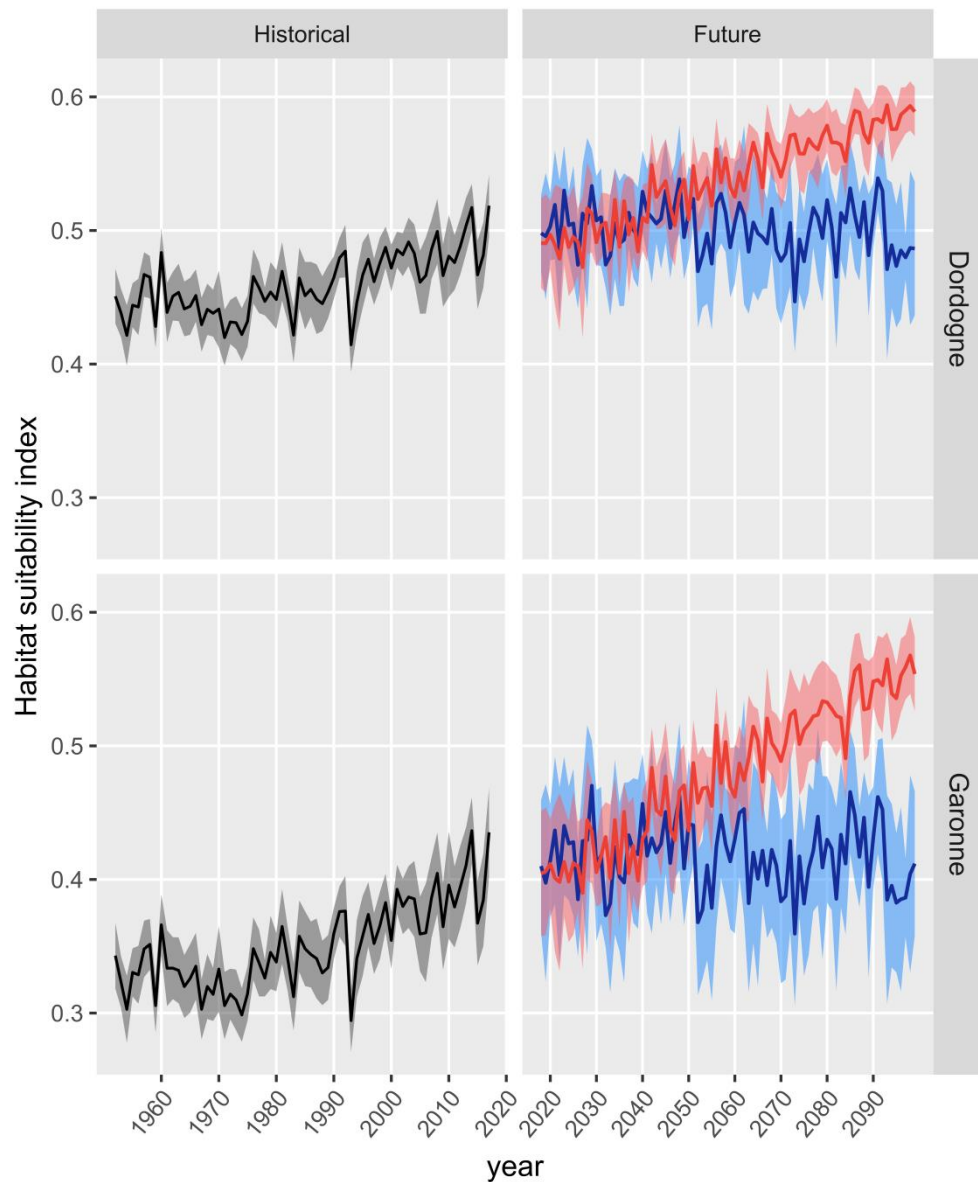


Figure IV6: Time series of annual Habitat Suitability Index (HSI; left panel) from 1950 to 2018 (left panel) and from 2019 to 2099 (right panel) in the Garonne and Dordogne rivers. Projections are shown for the two RCPs for the multi-model mean: black for Historical, red for RCP 8.5 and blue for RCP 2.6 (solid lines) and the 5 to 95% range of the confident interval across the distribution of individual models (shading).

### 3.3.3 With projected environment

For the two indices and under RCP2.6, no significant trends in the ensemble mean were projected for the two rivers (Table IV3; Fig. IV5&6). A significant negative trend was calculated for the MSD under RCP 8.5 in the two rivers (Table IV3; Fig. IV5). A significant positive trend was estimated for the HSI under RCP 8.5 in the two rivers (Table IV3; Fig. IV6).

## 4 Discussion

In this study, we explored the response of the reference population of allis shad in Europe to past environmental changes and future climate change. A look back allowed us to find out whether the ongoing decline of this population was related to deterioration in the physical habitats (temperature and discharge). Then, a look forward allowed us to project/assess whether climate change might be acting as an additional threat for this endangered species.

### 4.1 *Future impact of climate change on allis shad reproduction*

If the objective to limit climate change by 2 degrees as set by the international community is met, which is roughly consistent with the RCP2.6 scenario, the spawning habitats were calculated to be favourable for allis shad spawners. A different conclusion arose with the worst-case climate scenario. Under RCP 8.5, habitat suitability was predicted to increase and shift in time. The spawners will have to track this temporal shift (Dahl et al. 2004; Wedekind and Küng 2010; Pankhurst and Munday 2011; McQueen and Marshall 2017). Nonetheless, it remains unknown whether possible environmental-driven shifts in spawning timing will result in a phenological synchrony with optimal conditions for offspring.

Table IV3: Results of the Mann-Kendall trend test for the two rivers and the habitat suitability index (HSI) and for the mid-season day (MSD) obtained with the two periods: 1950-2006 (observed and reconstructed environment) and 2006-2099 (RCP 2.6 and 8.5). The simulated environmental conditions are shaded. An arrow was drawn if a significant trend was detected by the Mann-Kendall trend test (negative trends: ↘; positive trends: ↗)

| River    | Index | 1950-2006     |       | 2006-2099 |       |
|----------|-------|---------------|-------|-----------|-------|
|          |       | Dataset       | Trend | Dataset   | Trend |
| Dordogne | MSD   | Observed      |       | RCP2.6    |       |
|          |       | Reconstructed |       | RCP8.5    | ↘     |
|          | HSI   | Observed      |       | RCP2.6    |       |
|          |       | Reconstructed | ↗     | RCP8.5    | ↗     |
| Garonne  | MSD   | Observed      |       | RCP2.6    |       |
|          |       | Reconstructed |       | RCP8.5    | ↘     |
|          | HSI   | Observed      | ↗     | RCP2.6    |       |
|          |       | Reconstructed | ↗     | RCP8.5    | ↗     |

A step forward is to investigate the trends in juvenile survival for different RCP scenarios, as for diadromous fishes, reproduction might have even more dramatic consequences for earlier stages (Limburg and Waldman 2009). Indeed, life-stage transitions are precisely tuned because favourable conditions are very limited in time and space (McNamara and Houston 2008). Climate change could notably lead to phenological mismatches between the spawning period and the peak of plankton production (Chevillot et al. 2017). This desynchronisation over time with the peak of plankton production could cause allis shad to potentially spawn during unsuitable periods for larvae survival, that depend on this food resource.

#### ***4.2 From climate change to global change***

The trend in the two indices for the past and observed environment indicate first that the riverine habitat has been degraded and that favourable conditions do not shift in time. Accordingly, the potential degradation of the habitat, based on the 3 selected environmental factors, is rejected here, and could not explain the decline of these populations and the lack of recovery. Although these three physical cues in the spawning grounds did not appear to be too 'degraded' for spawners based on the present analysis, other physical cues could be more severely altered by climate change as dissolved oxygen (Portner and Knust 2007; Ficklin et al. 2013). Simulating potential effects of climate change on fish populations is a complex topic that requires to consider uncertainties and biases operating at different levels (Payne et al. 2016). Key advances in the understanding of climate change effects on inland fishes are notably to compare observations and (Myers et al. 2017). As such, we compared the trend in MSD and HSI from past and past observed environmental factors in order to address these biases. For most of the indices and rivers, the trends were similar between past and observed environment.

However, a difference of trend was observed for the HSI in the Dordogne River. This difference of trend implies that non-anthropogenic climatic pressure has been greatly impact the riverine habitat in the Dordogne River. These non-climatic pressures have been implicitly measured in past observed hydrological data and not included in the reconstructed past by the hydrological model. As such, an attempt was made to include these non-climatic pressures in the projection under RCP 2.6 and 8.5 with the multivariate quantile-quantile correction (Cannon 2018). This correction of climate projections is a first step towards assessing the impacts of global change on fish.

### *Acknowledgments*

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# **Chapter V**

# **Discussion**

*“We demand an answer to the question “How do you know,” when the simple answer is that we do not know but try from our background knowledge to formulate hypotheses and devise how these can be tested in order to (temporarily) select the one which best corresponds with facts”*

Ulltang, Øyvind (1998) in “Explanations and predictions in fisheries science - problems and challenges in a historical and epistemological perspective.”

## I. MAJOR CONTRIBUTIONS OF THIS PHD

The purpose of this PhD was to define the environmental control on allis shad reproduction. Ultimately, this definition enables to respond either (i) past habitat degradation has had an impact on allis shad spawners and (ii) will climate change limit the recovery of these threatened populations. The strength of this PhD was to combine rich datasets and several kinds of models to define this environmental control: Manly index, boosted regression tress and the HoOS model and flirtyShadBrain (Fig V1). In addition, the use of climate models coupled with a hydrological model and a "biological" model is innovative for river studies.

### A. *Spawning behaviour: from temperature to a multifactorial rule*

The first step to evaluate the impact of habitat changes was to test the influence of environmental factors on shad's reproduction (paper #1, paper #2 and flirtyShadBrain). First, we explored the influence of temperature, and then we tested multiple environmental factors on shad's reproduction. The first assessment focused on temperature because of the documented sensitivity of young stages (Jatteau et al. 2017). Jatteau *et al.* (2017) evaluated the potential effects of climate change on the survival of allis shad early life and demonstrated a thermal tolerance of early stages between 16.2 °C and 24.8 °C (Jatteau et al. 2017). In view of this, we checked whether observed spawning temperature ranges (STRs; defined as the narrowest range of temperature in which 80% of the total annual reproductive activity took place) matched this thermal tolerance of early stages.

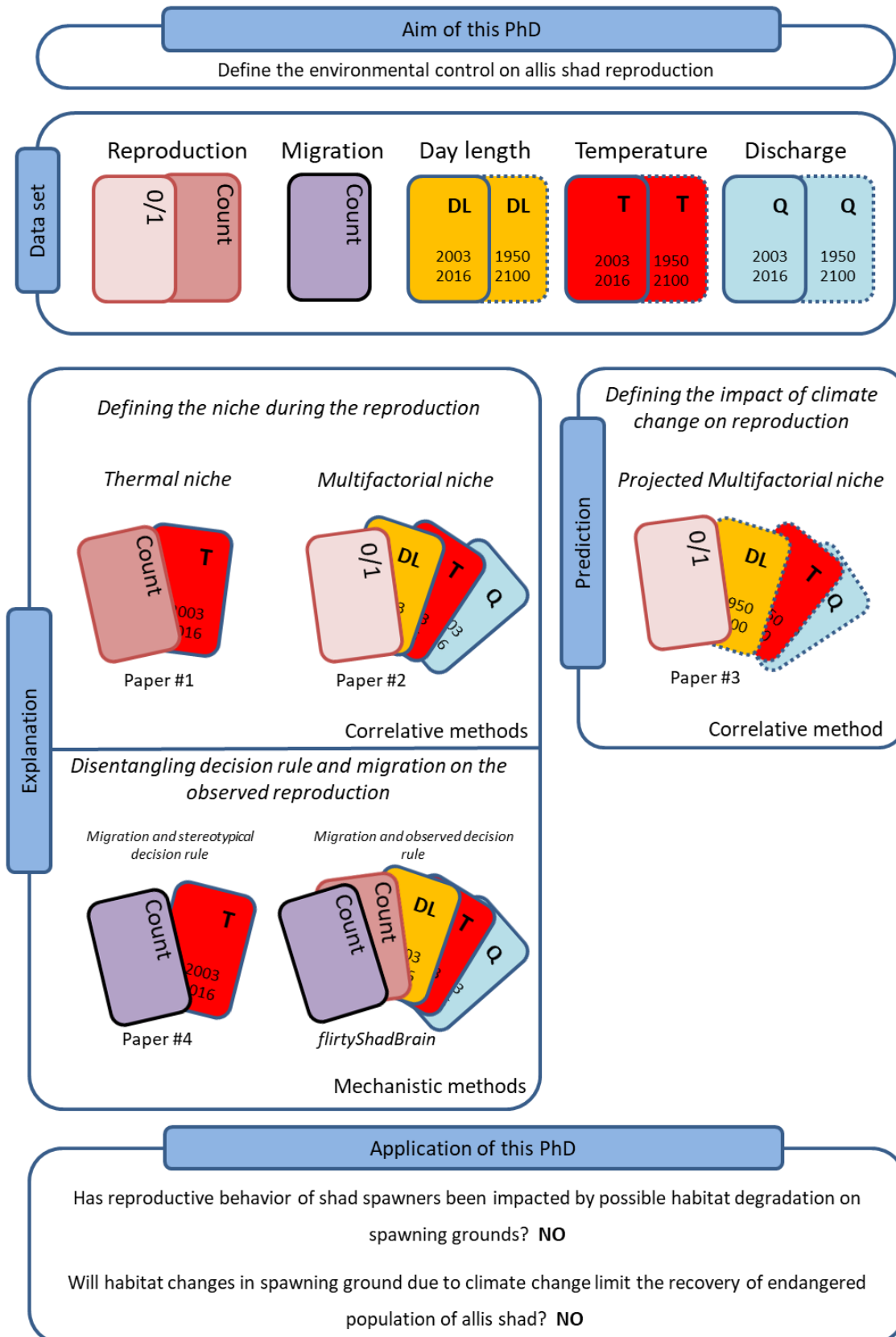


Figure V1: conceptual diagram representing the articulation of the different parts of this PhD.

I present here the final application of this PhD.

Indeed, we observed a strong overlap between the STRs and the range of early-stage survival, consistently with the Quinn and Adams' hypothesis that postulates that spawners adopt behaviour rules of reproduction to maximise their offspring survival (1996). Beyond the overlap, we used an electivity index to check that spawners display a true thermal preference. We demonstrated that spawners reproduce preferentially between 14.5 °C and 23 °C. This paper provided a robust description of the thermal behaviour of shad during the reproduction.

Moving further from this first paper, we aimed to have a more integrated picture of the spawning behaviour of shad. Indeed, shad behaviour is not only influenced by temperature but by a complex combination of biotic and abiotic factors. Therefore, in the second paper we explored the role of 6 environmental factors on the shad's behaviour: temperature, discharge, day length and the daily difference of these three environmental factors. A machine learning technique (boosted regression tree; BRT) provided insights on the complex relationship between the spawning probabilities and these 6 environmental factors. The range of temperature in which the spawning probability was high (>0.8 for a 15°C -26°C range) and consistent with the first paper (14.5 °C and 23 °C), the 3°C difference toward warmer temperature is probably due to the interaction with the other environmental factors. According to the rule defined by our model, the model identified the most favourable environmental conditions between mid-April and mid-June, that is consistent with the seasonality of spawning described for allis shad (Bellariva 1998; Aprahamian et al. 2003; Acolas et al. 2006).

Moreover, we demonstrated that allis shad is a photoperiodic species, which is defined as *"the ability of an organism to assess and use the day-length as an anticipatory cue to time"*

*seasonal events in their life histories*" (Bradshaw and Holzapfel 2007). Indeed, we estimated a relative importance of 44.6% for the variation of day length, 34.7% for the water temperature and 20.7% for the river discharge. The importance (rank) of environmental cues may determine the future response of shad to climate change because reproductive behaviour seems to be based on cues that do not vary from year to year (variation of day length) and cues which do vary (temperature/discharge). The BRT model assessed that photoperiod may provide the "go/no-go" signal for the seasonal reproduction of allis shad, along with temperature and discharge. Perhaps day length is the seasonal cue that triggers migration, and temperature and discharge are used for short-term decision (final choice to reproduce along with social cues). However, the BRT model could not give this temporal importance of factors during the reproduction, it only gives the relative importance of factors in a statistical procedure, but a shad is not a statistician. Moreover, there are correlations between environmental factors and therefore there may be confusion even if the statistical tool is designed to process these correlations.

### ***B. Impact of climate change on allis shad***

This PhD improves the knowledge on shad, with the first assessment of influence of a set of environmental factors on reproduction (paper #1 and #2). We used these insights to explore the potential impact of climate change. For the congeneric species American shad *Alosa sapidissima* and the striped bass *Morone saxatilis* in the Hudson River estuary, Nack et al. 2019 estimated that a 15 days earlier onset of the spawning seasons for 2100. However, their analysis was restricted to the effect of temperature and therefore may be biased especially, because other factors seem to control its European congeneric species (*Alosa alosa*). According to our multifactorial projection, it appears that shad spawners may not be



impacted by the future global warming under the RCP 2.6, and that even in the worst scenario, RCP 8.5, habitat suitability is expected to increase though shifting in time towards earlier dates. Thus, climate change does not appear as a major threat for this species, at least if shads are able to track the slight centroid shift of the most suitable conditions.

The major methodological strength of this projection was (i) to produce probability output rather than binary output (presence-absence; this novelty is also shared in the second article) and (ii) to use a range of RCPs to simulate the potential response of fish. First, we need to strengthen out that the BRT model does not predict the change in reproduction of shad but more precisely the changes in the most suitable habitat for the reproduction. The transition between favourable habitat to shad's reproduction involves integrating other components that are not environmental factors (dispersal capacity, competition, adaptation; Thuiller et al. 2008). As such, I believed that it is needed to keep the probability of presence and not to transform them in binary presence-absence response (by introducing a threshold) considering the several limitations of ENMs. Second, the science of predicting the climate change impacts on biodiversity is rife with uncertainties (Zimmer 2007). As such, the use of a range of scenarios provides a panel of possible "futures" for shad, and may offer guidance for planning managing measure. In this PhD, we saw that we expect few impacts of climate change, and thus management measures can probably focus on other pressures or other phases of life cycle, and notably the early life stages (mismatch with optimal conditions for growth and survival).

### ***C. Implication for allis shad's conservation plan***

This PhD tested whether a past habitat degradation has had an impact on allis shad spawners in the Garonne and Dordogne rivers. This hypothesis was formulated by Rougier *et*

*al.* (2012) which aimed to detect whether there had been a regime shift between 1991 and 2009. Although, Rougier *et al.* (2012) failed to detect such regime shift, we tried to explore this hypothesis with a more complete dataset from 1950 to 2018. It appears that the habitat suitability did not decrease, when focusing on day length, air temperature and river discharge (paper #3). Like Rougier *et al.* (2012), we have not seen any environmental degradation likely to explain the collapse. The cause is therefore probably to be found elsewhere.

However, this does not exclude other types of spawning ground degradation such as oxygen concentration and chemical pollutants. Furthermore, we could test other components of the habitat, such as the mortality in spawning grounds by predation. Indeed, an hypothesis to explain the complex life history of the anadromous fish is the 'loophole-seeking' strategy, which states that spawners performed "perilous migrations in order to deposit progeny in extremely sterile but predation-free freshwater environments" (Bakun and Broad 2003). The invasive European catfish (Guillerault *et al.* 2017) may put this 'loophole-seeking' strategy at risk, as they predate shad notably in "forced" spawning grounds and fish passes (Guillerault *et al.* 2015, 2017, 2019; Cucherousset *et al.* 2018; Boulêtreau *et al.* 2018). As such, a study about the mortality induced by such invasive species may give another insight about the causes of the allis shad's decline. Keeping up with predation, the nocturnal behaviour of spawning is seen as a way to avoid egg predation for animals that don't provide parental care (Šmejkal *et al.* 2018). However, public lighting is increasingly present on river banks (Manfrin *et al.* 2017), particularly on spawning grounds, which could also increase predation.

The Allee effect suspected by Rougier *et al.*, (2012) indicated that the viability of the stock is threatened when the effective number of spawners is inferior to 0.17 million (in a no-harvest situation, *i.e.*, actual situation since 2008). At the current level of abundance (see

population trend figure in Chapter II), the extirpation of the allis shad population in the two rivers is likely. Furthermore, the other French watersheds that may shelter the shad spawners are composed of small rivers with low carrying capacity and with low population abundance (in Brittany: Vilaine, Blavet and Aulne rivers or in the Basque country: Nivelle River). Given this dramatic decline in France, the IUCN status in France was recently revised from “Vulnerable” (in 2010) to “Critically endangered” (in July 2019) but is still in “least concern” in global scale. We strongly advocate for an update of this Global evaluation (as well as Rougier *et al.*, in 2012), as it was evaluated in 2008 when the crash was partially observed in the Gironde systems (IUCN 2019). Full monitoring of potentially inhabited rivers is necessary to assess the trend in population abundance at the global level. For example, in Spain, historically monitored rivers show a dramatic decline in population whereas unmonitored rivers are suspected to shelter spawners (Nachón, *personal communication*).

#### ***D. From habitat to behaviour***

In the literature, analysis of the environmental control on allis shad reproduction and migration have mainly focused on temperature and discharge (Acolas *et al.* 2004, 2006; Rougier *et al.* 2015; Jatteau *et al.* 2017; Lambert *et al.* 2018). Although I confirmed these roles in the paper #1 (active selection of temperature during the reproduction) and in the papers #2 (complementary influence of discharge), I demonstrated that photoperiod has also an important role that is 10 % higher than the water temperature (paper #2), 29 % higher than the air temperature (paper #3) and around 20% higher than the discharge (see relative importance in paper #2 and paper #3). This is an interesting illustration of the risk of confusion between correlation and causality and therefore on the need to postulate biological mechanisms. In a concrete way, if we had not integrated the photoperiod, the BRT

would have concluded a relative importance of temperature and flow and the conclusions would have been different. This raises the issue of the validity of the transition between habitat and behaviour. As we discussed earlier, we produced probability output rather than presence-absence because of the complex transition between habitat and behaviour (Growth and West 2008). Hereafter, we developed the idea of using the more 'perceivable' environmental cues and about how it was difficult to apply in this PhD.

In this PhD, we tried to select the more 'perceivable' environmental factors before defining the ecological niche, but we were limited by the data availability. Indeed, if we used distal cues the relationship between environment and distal cues could change, notably with climate change, and the projection of ecological niche could be biased. The major difficulty was to find appropriate data. As such, water velocity is a more proximal cue than discharge for fish. This is an issue because the same discharge can correspond to very different velocities given the variability of the wet section between spawning grounds of the same river and between the two rivers. A model is currently developed to predict the velocity at any point in French rivers (Morel et al. submitted), and could be used in future ENMS models in French rivers. Beyond the data availability, the definition could be tricky. As such, a question still remains: is the variation of day length perceivable at a 24-hour scale for allis shad?

Second, the difficulty is to classify cues between distal and proximal. The first difficulty is that these variables are all correlated with each other as we saw in chapter II (Fig. II4). Despite these correlations, it was more difficult than I used to think to approximate the fish's perception. In statistics, the parsimony principle leads to reduce a dataset to limited set of uncorrelated variables, therefore, in this situation a statistician tends to reduce the environment to one or two uncorrelated cues. However, shad behaviour does not necessarily

follow the parsimony principle and we cannot exclude neither that shads potentially use a complex set of correlated environmental cues as behavioural trigger, nor that shad use only one variable and that we are not able to disentangle the cues because of their intrinsic correlations. In an evolutionary perspective, tracking several environmental factors imply costs to maintain energetic, regulator and sensorial mechanisms, and to develop the appropriate response. This line of thought emerged when different neural networks of several flirtyShadBrain calibrations (rules based on different factors) resulted in the same reproduction observation. This implies that several behaviours, several ANNs, can lead to similar simulated reproductions. From an epistemological perspective, we could quote Protagoras transcribed by Platon in Théétète: "Man is the measure of all things" (Platon and Narcy 2016). Despite the common interpretation that the universe is made for Man, we could see this discourse as a very humble statement from a scientific point of view. This quotation can be understood as the impossibility for Man to understand the ecosystems without referring to his own human measure. In other words, this quote could illustrate the awareness of the lack of access to the true measure of things for us, but just the access to things only to the extent of our humanity. So the only criterion for moving away from my "human" scale could be statistics, but it's not the true approximation of fish's perception.

To conclude these two points, I believed that one simple way to test our results would be to experiment on allis shad to test these different "triggers" of reproduction. However, in view of the small populations it is not obvious that we can "sacrifice" valuable shad reproduction.

### *E. From reproduction to fitness*

From the first to the third paper, climate change does not appear to be an issue for shad's reproduction, but what about the impact of climate change on early life stages? Although this PhD focused on the reproduction and that two PhDs are currently assessing the sensitivity of early life stages to temperature, hypoxia and pollutants (PhD of Baumann Loic and Blaya Marion), I believed that there is a need to transform the reproductive behaviour into survival of young stages. First, the reliability of this photoperiodism raises questions in a global change context because the correlation between temperature and day length or between discharge and day length will be degraded in the near future, *e.g.*, much warmer temperature or lower discharge with the same day length. Therefore, the simulated reproduction in the RCPs could lead to poor survival. The daily spawning probabilities can be transformed on survival of the young stages according to the laying temperature (Jatteau et al. 2017; Lambert et al. 2018). This perspective is currently impossible because we need spawning probabilities according to water temperature to compute the daily survival, and projections of water temperature are currently unavailable.

The HoOS model is the only study in this PhD for which we tend to study the fitness implication of reproduction. Of course, we only measure the thermal survival and not the fitness that depends on various biotic and abiotic factors. Still, the HoOS model enables to better understand how the migration and the reproduction interfere in the reproduction output that we measure as the early life survival (Jatteau et al. 2017).

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## ***F. Assumptions and perspectives of this PhD***

This section focuses on the main assumptions made in this PhD and therefore on the limits of our results and also on the new perspectives for shad research in the future. We classify those assumptions in two categories: research on migration and research beyond the species.

### ***Assumptions***

First, in the correlative approaches, we focused on the daily prediction of spawning acts. We indirectly assumed that spawners on the spawning grounds were not limited in number during the entire reproduction season. However, it is well-known that the reproduction of shads depends on the migratory behaviour, which is also influenced by various environmental cues such as temperature, river discharge and photoperiod, and many others acting in the estuarine part of river systems. The strength of this PhD was therefore to develop mechanistic models that integrated the migration. As such, migration was integrated in the *HOOS* model which highlights the central role of migration in the reproductive output. Second, we considered the allis shad population as being ‘Gleasonian’ (Gleason 1926), *i.e.*, organisms respond individually (*i.e.*, independently from other fish’s choice) to environmental factors. However, it appeared that adding biotic interactions did not significantly enhance the ENM model performances (Bucklin et al. 2015). Moreover, the level of intraspecific interaction, either competition or facilitation, has likely varied because of the decline of the population abundance in the recent years (Arahamian et al. 2010). Competition could occur for the female, and facilitation could be a trigger to spawning when other fish are reproducing around a potential couple. Still, this ‘Gleasonian’ approach means that we rather modelled the favorability of habitat rather than the true presence of shad during the reproduction. Third, we supposed a niche conservatism (Wiens and Graham 2005) that implies a fixed

niche envelope in space and time. In other words, we neglected potential adaptive capacities as a response to environment modifications when we predict the impact of climate change. A question still remains: does shad have the adaptive capacity to respond to climate change? Allis shad have a rather short generation time (around 5 years) that may provide 16 generation for a gene pool  $((2100-2019)/5 \sim 16$  generations). Does these generation are sufficient for adaptation? As such, the *Drosophila* characterised by shorter generation time (around 2 weeks at 22°C) have undergone in situ microevolutionary change in response to climate change in 16 years (Rodríguez-Trelles and Rodríguez 1998). The *Drosophila* has around 417 generations to adapt for one gene pool  $(52.1429 \text{ week} * 16 \text{ years} / 2 \text{ weeks})$ . Coming back for fish, we could take the example of the population divergence between an anadromous form and a landlocked form (freshwater resident) of Alewife, *Alosa pseudoharengus*. As an example of the time necessary to adaptation, the divergence time was estimated between 300 years and 5000 years ago depending on the microsatellite mutation rate assumed (Palkovacs et al. 2007).

### **Perspectives**

Beyond the degradation of spawning grounds explored in this PhD, the downstream conditions can be explored. Indeed, the upstream migration can be stopped by both low water discharges as migratory fishes needs a minimum river discharge to migrate (Drouineau et al. 2017), or high discharge (Rochard 2001). As the natural regime of discharge has been modified and will be by climate change, research on shad migration is mandatory. Research is needed on the fragmentation of rivers that hamper the access to spawning grounds (Soule 1991; National Research Council (U.S.) et al. 2000; Fahrig 2001; Brooks et al. 2002; Seabloom et al. 2002), and particularly of migratory species that rely on specific habitat (Limburg and



Waldman 2009; Drouineau et al. 2018). Indeed, it is unknown whether “forced” spawning grounds are of worse quality than “historical” ones. Finally, analyses developed in this PhD for allis shad could be applied to other shad populations and species. These works could be firstly used in order to compare with allis shad’s response, secondly to predict their response in their distribution area. We think notably to the other French rivers, such as in Brittany where population seemed to fall after colonization (IUCN 2019). A comparison with the twaite shad (*Alosa fallax*) may give some clues about the sensitivity of shad to environmental changes in the Garonne and Dordogne rivers. A potential collaboration with Karin Limburg (SUNY-ESF, Maine) could allow applying the methodology developed in the PhD to predict the potential response of the American shad in the East-coast.

### **Concluding remarks...**

In conclusion, this PhD has provided new insights into habitat use by allis shad during reproduction, with evidence that allis shad bases its behaviour on day length, as salmon does (Scott 1990), which is supplemented by other factors such as temperature and flow. These decision rules should be validated by experiments in controlled environment, but remains the most complete description to date of shad behaviour during reproduction. Despite this knowledge, the non-recovery of the population after a fishing ban of more than ten years has not been explained yet, and the suspected habitat degradation during reproduction is currently refuted. In the same line, future conditions regarding spawning behaviour should not compromise the recovery of the population. The future of this species is therefore uncertain, but reproduction does not seem to be the priority lever for action according to our results.

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## II. ON THE CONTRIBUTION OF MODELLING TO THE ASSESSMENT OF THE IMPACT OF CLIMATE CHANGE

### A. *Is Ecology becoming a predictive science?*

Ecological systems have always fascinated mankind by their extraordinary complexity (Loreau 2010). It is not astonishing that ecology's purpose was originally to understand this complex phenomenon and develop theory about it (Currie 2019). "The central goal of ecology is to understand the causes of the patterns that we observed in the natural world," said Tilman in 1988 when introducing the resource-ratio hypothesis in community ecology (Tilman 1988). At a time of great perturbations of natural systems (*i.e.*, global change), ecology might change its inherent goal from understanding pattern to predict them (Mouquet et al. 2015). During this PhD, I developed models both to understand the shad's reproduction and to predict the response to climate change. Therefore, we pursued these two apparent distinct modelling goals in ecology (Evans et al. 2013). Is ecology becoming a predictive science? This broad question is challenging, because ecology encompasses many disciplines with different practices. Moreover, few authors have yet studied this subject and there is no consensus on the trend towards an increase in prediction and its validity (Evans et al. 2013; Petchey et al. 2015; Schindler and Hilborn 2015; Mouquet et al. 2015; Houlahan et al. 2017; Dietze 2017; Currie 2019). Mouquet *et al.* (2015) advocated for a rise in ecological prediction whereas Houlouhan *et al.* (2017) said that prediction plays a peripheral role in ecology. In order to have a clear idea, I realised a very simple bibliometric analysis: I made a request on Scopus about the number of articles in "ecology" from 1950 to 2018 (Fig. V2), and then I made a request about the number of articles with "prediction" in the title, abstract and keywords among these articles in ecology (Fig. V2). Finally, I computed the relative proportion of article dealing with prediction among articles in ecology (Fig. V2).

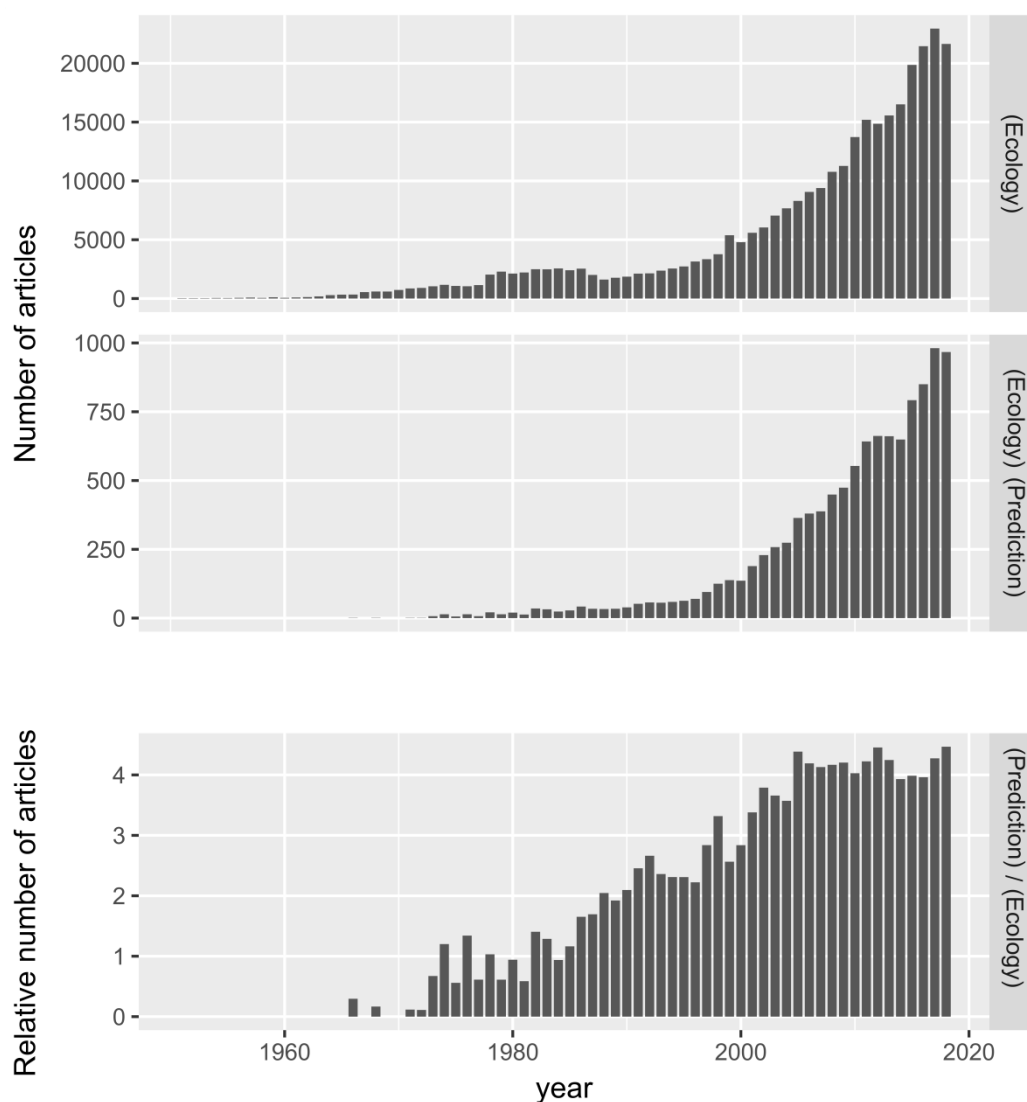


Figure V2: The two upper barplot illustrates the number of articles per year that have (i) 'ecology' or (ii) 'prediction' and 'ecology' in their title, abstract and keywords. The bottom panel represents the percentage of article dealing with prediction relative to the total number of articles published in ecology. Scopus was used with the following search criteria: (TITLE-ABS-KEY (ecology); TIMESPAN = [1950; 2018]) for the first panel and ((TITLE-ABS-KEY (ecology) AND TITLE-ABS-KEY (prediction)); TIMESPAN = [1950; 2018]) for the second panel.

This analysis demonstrated that the increase in citations of article dealing with prediction illustrated in Mouquet (2015) is only the result of the explosion of studies in ecology and not the growth of interest for prediction in this discipline (Fig. V2). The relative number of articles dealing with prediction increased until 2000s, but the trend flattens in 2005 and is stable around 4% of the total published articles, confirming Houlouhan *et al.* (2017) observation of the peripheral role of prediction in ecology. Despite this peripheral role in ecology (4% of article; Fig. V2), the use of prediction is common in some disciplines of ecology closely connected to decision-making. Fishery science is a waxing example. The need to sustainably harvest fish stocks has led fishery scientists to develop models that predict the future abundance of populations. The present global ecological crisis urges ecology to take into account management and societal questions (Mouquet et al. 2015), but without sacrificing conceptual considerations. The political and social awareness will push ecology to becoming a more predictive science, concerning global change, conservation and ecosystem management. A prompt example is the *Nereus* program (<http://nereusprogram.org/>) that is an international research network created to evaluate future scenarios for managing fisheries.

Now even if I have just argued for more prediction in ecology, is this approach feasible? I think that that there is an opportunity for ecology to becoming a 'Big science' (Hampton et al. 2013). It seems to me that the need to predict therefore makes the use of modelling and data inevitable. The combination of growing available ecological data and the development of computation force with complex statistical tools gives an opportunity to develop *anticipatory* prediction (Mouquet et al. 2015). However, if ecology can become a "big science", it is not a question of letting data speaks for itself in a data-driven process, but on the contrary, it is a question of confronting ecological theories with these now abundant data, an approach that

is process driven. In fishery science, complex models such as 'end-to-end' models are increasing. These models such as OSMOSE (Shin and Cury 2004; Moullec et al. 2019) or APESCOM (Maury and Poggiale 2013), explore and predict major trends, particularly with regard to climate change. In ENMs, successful prediction of global warming is also available (see for example: Guisan and Thuiller 2005; Harrison et al. 2006; Buisson et al. 2008, 2013).

Despite the opportunity for ecology to become more predictive, the ecological predictability is challenging (Evans et al. 2013). Indeed, ecological systems are inherently complex with numerous biological, chemical and physical processes, with infinite interactions responsible for nonlinear dynamics; which leads to threshold effects, spatial and temporal heterogeneity (Coreau et al. 2009). Furthermore, feedback mechanisms can lead a system apparently stable towards abrupt shifts. Therefore, the ability to predict accurately is limited to a rather short period of time, *i.e.*, forecast proficiency (Petchey et al. 2015). Therefore, the complexity of systems has led to think that reliable predictions of ecosystems trajectories unreachable (Schindler and Hilborn 2015). A way to overcome the apparent unpredictable of ecosystem could be to study the global trend of system dynamics despite the short-term uncertainties (Petchey et al. 2015). A great example is the projection of alternative futures of our ecosystems simulated by the United Nations' (UN) Intergovernmental Panel on Climate Change (IPCC 2018) that we used in the third paper. The development of such scenario is a great opportunity to strengthen collaboration between scientists of different discipline, including social sciences and policymakers (Mouquet et al. 2015), ultimately making ecology a more operational science as in the third paper of this PhD.

## ***B. Managing perspective from the manager sight***

Regarding the uncertainty about the future states of ecosystems, a new environmental policy is needed. Herein I listed the components of that effective environmental policy.

First, management have to emphasis the central role of monitoring. A routine monitoring is required to evaluate the ecological response to pressure and management policy. The financing of sampling campaigns is crucial. In fact, the delay of response of stakeholders for the allis shad stock, leading to a fishing ban in 2008, is notably due to uncertainties about the indicators, *i.e.*, abundance of spawners versus abundance of juvenile (Lambert, *personal communication*). Therefore, reliable indicators are needed in order to promote greater reactivity of decision makers (*e.g.*, PLAGECOMI, COGEPOMI, CMEA, and CNPMEM). A better flexibility and responsiveness based on reliable indicators would have potentially prevented the crash of the population. In other words, reacting quickly enough when something worries is important, and this reactivity must be based on the most reliable indicators (from adequate monitoring). Finally, ecosystems can abruptly change in response to past perturbations. Ideally, robust management should react rapidly to pressures before the system is too degraded to be restored. As such, in a retrospective way, the fishing pressure could have been significantly reduced for shad population before 2008 in order to prevent crash and to maintain a proper fishing sector. However, the indicators were not considered reliable enough to detect the ongoing decline (Lambert, *personal communication*).

Second, the cause of the decline (multifactorial with probably overfishing as a main driver) must be separated from the leverage actions for species recovery. Although fishing seems to be the main cause (Rougier et al. 2012), it is important to limit the effects of all other anthropogenic pressures that affect the survival of the population and therefore represent

drivers for restoration. For the allis shad, the restoration plan consists in identifying the environmental issues to which the allis shad is sensitive in order to determine the conditions for the success of the species' recovery program (SHAD'EAU project). The aim of the SHAD'EAU project is to fill the "black boxes" in the allis shad life cycle. The main hypotheses to explain the decline of shad at the scale of the study area were: (i) the impact of climate change in rivers (this PhD), (ii) the impact of climate change at sea, (iii) a potential lower survival of early life stages in rivers and estuaries (increased contaminant pressure on young life stages, warmer temperature, and low oxygen saturation). Once one of the pressures has been identified as a possible cause for the decline and lack of recovery (not necessarily the same factors for the decline and lack of recovery), some actions will have to be considered. The effectiveness of these measures will depend on the willingness of stakeholders to limit their activities in order to encourage the return of the population and therefore a fishing activity. It is therefore a balance between different ecosystem services. As such, if the pressure of contaminants on young life stages is considered as the main cause of the decline, will industrialists or farmers agree to reduce their activities for shad restoration? Nothing is less certain.

In conclusion, it appears that the restoration of highly impacted fish stocks is complex and takes a long time because their life cycle makes them sensitive to the 5 components of global change (Drouineau et al. 2018). Therefore, everything must be done to move beyond safe biological limits. The most famous example is the decline of Northern cod that show a the slight increase of after almost two decades of fishing ban (Rose and Rowe 2015). Restoring allis shad is difficult because no factor limiting its restoration has been identified. This does not mean that management actors should do nothing in the meantime. However, the levers

are not yet identified well and there is therefore a lack of effectiveness in restoring this species, from my point of view.

### ***C. Managing perspective from the scientist sight***

I think that sharing data should be a central goal in ecology, as the accessibility of ecological data remains relatively limited (Hampton et al. 2013). Open access data would enable new use with new ecological questions. A great example is how we used data set that was not produced to respond to our studies: the count of reproduction acts by Migado was never developed to define the niche of reproduction but for monitoring the population (number of individuals based on the number of spawning events); the river discharge provide by the “Banque hydro” does not aim at studying the impact on fish but for managing the river water quantity (*e.g.*, prediction of floods).

The second point (closed to the first) is the need to strengthen interdisciplinary collaborations. We tried in this PhD to collaborate with other fields, with notably the third paper (Chapter IV – Prediction), which was based on time series of environmental factors from 1950 to 2100 from Dayon's thesis (Dayon 2015). These data emerge from a collaboration of several researchers and data exchange. These time series were available because the World Climate Research Programme's Working Group on Coupled Modelling produced data (CMIP) makes available their model outputs. Météo France was also involved by providing the SAFRAN data and contribution to the development of the SAFRAN–ISBA–MODCOU system.



### III. A PERSONAL PERSPECTIVE: REVIEW OF THE PHD EXPERIENCE

#### A. *What is a good model?*

If I distance myself from the species in terms of ecology and management and focus on what the thesis has brought me as knowledge and methodology, I learned a lot about the modelling process. I explore a myriad of methods (not all were presented in the manuscript) to gain of deep knowledge on allis shad's reproduction, with both correlative and mechanistic models: quantile regression, generalized linear model, generalized additive models, Manly index, mechanistic model, EDM, Ecospat and Boosted regression trees. During the PhD, I seek for the most adapted statistical tools to describe the reproduction of shad. This diversity of model tends to gain in ecological robustness of the published results, as such, some package for niche modelling combine multiple models for accurate prediction, "ensemble forecasting" (Thuiller et al. 2009). At the end, it became clearer that beside the model performance, the quantity and quality of the data proceed was the cornerstone of reliable studies. It appeared that (i) a modeller should not be trapped by his favourite modelling tool, and that (ii) a simple model could provide a deep understanding. These two points were counter-intuitive from me at the beginning of my PhD, as I seek for the most complex model in order to respond a rather simple question. I spent one year trying to make quantile regressions with smoothers, without success (which delayed all my publications), although a simpler model (Manly index in the first paper) was sufficient for the ecological question. Globally, I learned that the model is just a tool and that we need to know precisely "what is the ecological question?" before developing a model. If it may seem obvious, the young modeller I was (and still I am) first tried to be very technical in code, without enough implication on the ecological question. For such

understanding, I strongly acknowledge my two supervisors that guided me on the path of this consideration.

### ***B. Precision requirement when predicting***

“Much of the weakness of attempts so far to relate individual life history characteristics (growth, migration, reproduction) to environmental conditions is that the latter could not be measured directly on individual fish” (Brander 2010). The scale in ecology is a central question (Levin 1992), and is currently used to delimit subfield of ecology, *e.g.*, macroecology or population vs community ecology. All scales are relevant and the choice may depend on the ecological issue, however, I was surprised to discover during the PhD that publication in high-impact journals (impact factors > 3) is sometimes more limited by the scale used rather than the method or ecological question. This was a comment for one of the high-impact journals that rejected the second paper ““While I enjoyed reading your work, [the study is] too limited in scope to attract the broad audience readership [...]’. As we focused on only one species in two rivers, we had to insist on the transferability of the approach to publishing in journals. Since academic position is based primarily on publications in high impact journals, I am convinced global scale is a strategic choice for a young researcher. However, I do not see global scale as the preferred scale in ecology. I think finer scale is necessary to explain deeply the mechanism observed at global scale. As such, the daily observation enables to gain in knowledge about the behaviour of shads in rivers. During the submission of the first paper, we tried to give a perspective in adaptive ecology, and the reviewer rejected the paper as we did not have individual measures. Thus, fine scale (one species in one location) could be interesting, but need high quality data that are very expensive. I think that global scale is relevant not only because of its attractiveness to journal publishers, but also because it is a

more appropriate scale for prediction, particularly in the context of climate change. Indeed, when we simulate the effect of climate change, we do not seek for a prediction at a particular day but we aimed to detect average trends with several scenarios. Given the societal and scientific attractiveness of climate change, I think I will select studies in a global scale in my future work. Furthermore, beside the study scale it appears clear that the studied species is critical to the “publishing power” (this is probably related to the societal attractiveness of species). As such, many people manage to publish in prestigious journals as *Nature* although they studied a single species in a single area. A speaking example for migratory species is the salmon.

### ***C. Mechanistic models: an appealing work from scratch***

To close this manuscript, I would like to discuss my experience about the use of correlative versus mechanistic models. As I said before, these two types of ENMs can be used for both explanation of distribution and prediction of impacts of climate change. Correlative models are much more used than mechanistic models. The appeal of the correlative models comes from the simplicity of both the using with freeware packages, and the data requirement. However, we saw that several assumptions and limitations make correlative models limited tools that need to be used carefully. Accordingly, mechanistic models are seen as an alternative approach that is more reliable.

In this section, I aim to discuss about the “publishing power” of these two methods rather than their ecological relevance. Being a young researcher, one of practical choice in order to have a research position is the number of publications, in addition to the networks and specialisation. The experience of the PhD is that mechanistic model, even if they failed; enable to gain in understanding simply because the hypothesis must be clearly stated.

However, these models are often made from scratch, which means that developing a mechanistic model takes much more time than a correlative model. However, once the model is calibrated, several uses can result from it, I think of GR3D for Camille Poulet's PhD in IRSTEA (Rougier et al. 2015), or OSMOSE model (Shin 2001) with several uses (more than 40 articles; <http://www.osmose-model.org/publications?page=1>) and therefore a strong publication potential. I think that a beginning of a scientific career, with few articles (around five), the choice of a mechanistic model is rather risky and I plan to continue my career with correlative models with a rather short production time between analysis and submission. First, beyond the time to code the model, the data formatting was time consuming in this PhD, the selection of relevant environmental factors, the standardisation and the choice of spawning grounds took around the first 6 months of the PhD. Then, quantile regression with splines took the next 6 months to code (unpublished), the Manly index took around 1 month to code (paper #1), the BRT model took around 2 weeks to code (paper #2), the perspective of this second paper in a climate change context took 1 month (*submitted*), the FlirtyShadBrain took 4 months to code (*unpublished*) and finally the HOOS model took 2 months to code (*in prep* by Camille Poulet). Of course the time to code was shortening at the end because we knew exactly what we wanted to simulate, so this time can be misleading. It appears that correlative models are simpler to use and therefore take less time to develop when the goal is crystal clear. However, the development of the mechanistic model has made it possible to formulate hypotheses and to be more cautious about the outcome of correlative models and in particular about the extent of migration of reproductive production.

Again, I have positioned myself as a "young" researcher, but if you look at it from a permanent researcher's point of view, this question is even more complex, which is as follows: Should we encourage a research system that makes it extremely complicated to work

on mechanistic approaches? In other words, it is mainly young researchers who can develop mechanistic models (researchers can only support and train them, due to lack of time to seek funding). So if young researchers do not develop the models, who will develop them? There is thus a deadlock in my reasoning, because mechanistic models can provide a better understanding of systems. In short, I do not have the solution, but I am convinced that ecology cannot be a "data-driven" science only, *i.e.*, without understanding systems, but also a "process-driven" science that explicitly tests mechanistic hypotheses with mechanistic models or implicitly with correlative models.



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# Annex I

Lambert, P., Jatteau, P., **Paumier, A.**, Carry, L., and Drouineau, H. 2018. Allis shad adopts an efficient spawning tactic to optimise offspring survival. *Environ. Biol. Fishes* 101(2): 315–326. doi:10.1007/s10641-017-0700-4.



## Allis shad adopts an efficient spawning tactic to optimise offspring survival

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**Abstract** The potential effects of global warming on the allis shad population were tested by combining a time series of spawning acts with expected thermal survival rates for embryos and larvae until 14 days post hatching. The yearly mean survival of spawn for each reproductive season was calculated and an index of reproductive efficiency based on this survival rate was proposed. The randomness of the spawning tactics was evaluated by shuffling the spawn acts time series. This approach was applied to the Gironde-Garonne-Dordogne (south-west France) population, which recently collapsed. The yearly mean thermal survival of spawn is slightly variable at approximately 55% over 2003–2012 despite fluctuating temperatures. An especially low survival (35%) was recorded for the last season (2013). For eight of the 11 reproductive seasons, the index of reproductive efficiency was high (> 80%) and largely above indices obtained by a random spawning tactic. Therefore shad are able to adopt an efficient spawning tactic to anticipate favourable thermal conditions for survival of their offspring. However, thermal behavioural rules still need to be expanded to understand the failures in their reproduction efficiency.

**Keywords** *Alosa alosa* · Spawning tactic · Behavioural plasticity · Temperature · Adaptation to environmental change

### Introduction

Species are expected to display different responses to climate changes, including (i) physiological modifications, (ii) shifts in species distribution, (iii) changes in phenology and (iv) adaptation by genome evolution (Hughes 2000). The last point clearly results in genetic changes, whereas the other three responses are mainly based on mechanisms of phenotypic plasticity (Crozier et al. 2008). The phenotypic plasticity is the ability of an organism with a given genotype to change its phenotype in response to environmental changes (West-Eberhard 1989; Pigliucci 1996). Among plastic traits, behaviour plasticity plays a special role in evolution and adaptation. Behaviour is often the first adaptive response (West-Eberhard 1989): in such a mechanism, the individuals adapt to environmental variability by switching behaviours according to the environmental conditions (Stearns 1989).

Temperature is a main driver of metabolism and ontogenetic development for ectotherms and thereby indirectly influences the phenology and the life history traits (Angilletta et al. 2002; Brown et al. 2004). More specifically, the water temperature influences growth, development, feeding, reproduction, behaviour and distribution of fish (Golovanov 2013). Early life stages are particularly sensitive to temperature fluctuations and to

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the temporal variability of primary and secondary production because of their limited energetic storage and lower trophic levels (Houde 1989). Discharge may directly or indirectly impair the recruitment success. For example, May and June discharges explained 80–87% of recruitment variability in year-class strength of American shad in the Connecticut River between 1966 and 1980 (Crecco and Savoy 1987) and a stock-recruitment model including a discharge-dependent mortality rate has been proposed for this species (Lorda and Crecco 1987). Mechanistically, high flow may increase abrasion of eggs on hard substrate (Ulanowicz 1975; Stoll et al. 2010), transport embryos and larvae to unsuitable habitats of low food density and high predator abundance (Reichard and Jurajda 2004; Nack et al. 2015; Walton et al. 2017), increase turbidity which may interfere with the feeding ability (Mion et al. 1998), reduce water temperatures thereby delaying the development of eggs and larvae (Lorda and Crecco 1987). In this context, many species have developed spawning tactics to optimise their offspring survival in variable environmental conditions (Lambert 1990; Murua et al. 2003; Durham and Wilde 2006). Reproductive behaviour in freshwater is triggered by environmental cues such as water temperature and discharge (Quinn and Adams 1996). When spawners and offspring experience very similar environmental conditions because of a limited incubation period and limited eggs and larvae drift, Quinn and Adams (1996) postulated that adults should behaviourally adjust the spawning timing (or the migration timing in their study cases) to optimise the environmental conditions for offspring survival.

The allis shad (*Alosa alosa*), which is an anadromous species, was originally distributed from Norway to Morocco (Baglinière et al. 2000). Many shad populations have declined in the last several decades, which have resulted in a contraction of the species distribution (Lassalle et al. 2008). River fragmentation, pollution, habitat degradation and overfishing are more frequently cited causes of these declines (Taverny et al. 2000). Consequently, the species was listed as vulnerable in the Red List of Threatened Species of the International Union for Conservation of Nature and in many European conservation initiatives (Habitat Directive, Annexes II and V; OSPAR Convention, Annex V; Berne Convention, Annex III).

The Gironde Basin (south-west France) was previously the reference for the European allis shad population, i.e., large effectives and well documented (Martin

Vandembulcke 1999; Chanseau et al. 2004). However, the population recently collapsed (Rougier et al. 2012) and recruitment failure in continental waters is suspected. Juvenile abundance has markedly declined since 2000, and the adult abundance has only declined since 2005 (Rougier et al. 2012). A moratorium on fishing was enforced in 2008 without any clear signs of recovery since then (ICES 2014).

Allis shad is a semelparous species where sexual maturity is triggered by a size threshold around 55 cm (Rougier et al. 2015). Consequently, female age at maturity ranges between 4 and 6 years with a majority of the 5-year spawners (Cassou-Leins et al. 2000). The incubation duration for allis shad is less than 10 days long (Cassou-Leins and Cassou-Leins 1981; Jatteau et al. 2017). Therefore, this species is a good candidate to test the Quinn and Adams (1996) hypothesis. Shad spawners need specific environmental conditions to spawn. The temperature at the onset of spawning has been reported to be in the range of 15 to 20 °C (Roule 1922; Cassou-Leins and Cassou-Leins 1981; Boisneau et al. 1990). In Brittany, upstream spawning migration is stopped when temperature are below 10–11 °C (Mennesson-Boisneau et al. 2000; Acolas et al. 2006) and the reproduction activity itself is inhibited below 14 °C (Acolas et al. 2006). In the Gironde Estuary, only a few migrants were caught by commercial fishermen when the water temperature was lower than 11 °C (Rochard 2001) and no spawning occurred in this basin at temperatures below 12 °C (unpublished data). These thresholds vary with latitude (Cassou-Leins et al. 2000). The high discharges can also explain the limited success of the reproduction activity (Boisneau et al. 1990).

In addition to its role in spawning, temperature affects shad embryos and larvae survival (Crecco et al. 1983; Crecco and Savoy 1985; Savoy and Crecco 1988; Aprahamian and Aprahamian 2001). Recently, Jatteau et al. (2017) estimated a thermal survival curve for allis shad early life stages based on laboratory experiments. The optimal range, corresponding to a survival higher than 80% of the maximum survival, was between 16.6 °C and 24.8 °C, which was consistent with the results of Hundt et al. (2015b). The tolerance range, which corresponded to survival higher than 5% of the maximum survival, was between 10.3 °C and 29.9 °C.

The date of the egg laying is a phenotypically plastic trait. The proximate environmental cues that trigger laying are not necessarily the same environmental factors that influence subsequent offspring survival and

growth. Temperature, photoperiod and other environmental variables can serve as proximate cues if they predict the future via a correlation with environmental factors that determine the selection of the optimal laying tactic (Visser 2008). The laying date is affected by temperatures earlier than those influencing the juvenile mortality. Therefore, timing of the reproduction date is probably strongly selected by the close match between the offsprings' thermal sensitivity and the temperature conditions during embryogenesis and after hatching.

This study first describes the annual reproductive efforts exhibited by female allis shad and the expected survival of early stages based on Jatteau et al. (2017) curves and temperatures between 2003 and 2013. It then explores whether the reproductive activity influences early stage survival. The efficiency of allis shad reproduction for the 11 spawning seasons is compared to a random tactic (i.e. shuffled spawn acts time series). Finally, adaptation capacity of the species to address environmental fluctuations and the subsequent risk of population extirpation due to climate warming are discussed.

## Method

### Field data

The reproductive activities of allis shad in the Garonne River were obtained from the Lamagistère spawning ground, which was one of the most important spawning grounds (Fig. 1) (around 30% of the total activity; Gaillagot and Carry 2014). The reproductive activity was estimated as the daily number of spawning acts corresponding to fast, circular nocturnal movements of at least two side-by-side spawners at the water's surface (Roule 1923; Acolas et al. 2006). A detailed description of the protocol to count spawner acts was provided by Gaillagot and Carry (2014). Briefly, the evaluation of spawning acts was based on auditory survey which was performed one night out of two at the beginning and the end of the reproduction season and three nights out of four during the period of high activity. The counting of spawning acts took place between 2 am and 3 am, period corresponding to the peak of activity (Cassou-Leins et al. 2000). These figures were extrapolated to the all night with a nocturnal pattern regularly updated during the season. The missing nights were estimated by linear interpolation. The observation period is

defined as the period ranging from the first night to the last night of effective auditory survey. It includes nights with no reproduction activity. The spawning season was estimated as the period between the first and the last days when spawning acts were recorded.

Mean daily water temperature data were recorded at the control station at the Golfech Dam fish pass located two kilometres upstream of the study site. Temperature was recorded every hour (automatic probe NKE S2 T) and averaged by day. Daily temperatures were grouped into five classes based on tolerance and optimal ranges proposed by Jatteau et al. (2017): below the minimum tolerance range ( $\leq 10.8$  °C), between the minima of the tolerance and the optimal ranges ( $> 10.8$  °C and  $\leq 16.6$  °C), within the optimal range ( $> 16.6$  °C and  $\leq 24.8$  °C), between the maxima of the tolerance and optimal ranges ( $> 24.8$  °C and  $\leq 29.8$  °C), and above the maximum tolerance range ( $> 29.8$  °C). In 14 days, temperatures do not vary a lot so that for each spawning act, temperatures during the 14 days post hatch (dph) belong to two classes at most. In view of this, each spawning act was assigned to the worst class associated with the temperature between egg laying and 14 dph.

### Thermal survival of recruitment (TSR)

The TSR evaluates the expected yearly mean spawn survival from fertilisation up to 14 dph and thus provides information on the reproductive success for different spawning seasons. The limit of 14 days corresponds to the duration of Jatteau et al. (2017) experiments of early stage survival.

The TSR index is based on the combination of experimental thermal survival curves and field measures of water temperature. The computation required four steps:

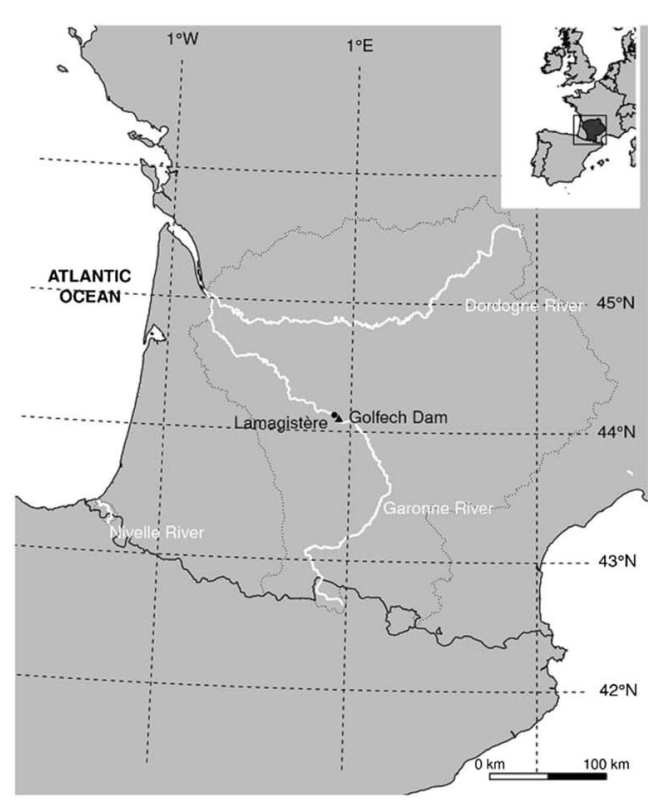
1. The computation of incubation duration  $d(j)$  in days for the embryos spawned on day  $j$ .

Jatteau et al. (2017) found an exponential relationship between the incubation duration and the temperature, which is as follows:

$$d = 1124 T^{-1.83} \text{ or } dT^{1.83} = 1124$$

However, field temperatures are not constant and therefore it was necessary to modify the formula to account for daily temperature variability as observed in nature. The previous formula was modified to link the

**Fig. 1** Location of the study site. Reproduction acts were recorded from the Lamagistère spawning ground (black point) on the Garonne River. Temperatures were monitored at the Golfech dam (black triangle). Thermal performance curve were estimated on shad from the Nivelle River by Jatteau et al. (2017)



incubation duration of the embryos spawn on the day  $j$  and the temperatures of the following days:

$$\sum_{i=0}^{d(j)-1} T(j+i)^{1.83} = 1124$$

where  $T(i+j)$  denotes the temperature  $i$  days after spawning on day  $j$ .

The incubation duration (rounded down to the next whole number) was then calculated by solving the following inequality:

$$d(j) = \max(k) \mid \sum_{i=0}^{k-1} T(j+i)^{1.83} < 1124$$

where  $k$  is the number of days since fertilisation.

2. The computation of expected cumulative embryo survival  $S_{CUMembryo}(j)$  for embryos spawn on day  $j$ .

Jatteau et al. (2017) used a logistic regression with a cubic polynomial of temperature to assess the embryo survival from :spawning to hatching

$$S_{CUMembryo} = \frac{1}{(1 + e^{-1.24+1.12T-7.83 \times 10^{-2}T^2-6.11 \times 10^{-4}T^3})}$$

which produced a daily survival by assuming a constant survival rate over the incubation period:

$$S_{embryo} = \frac{1}{(1 + e^{-1.24+1.12T-7.83 \times 10^{-2}T^2-6.11 \times 10^{-4}T^3})^{1/1124T^{1.83}}}$$

Considering the variable temperatures during the incubation phase, the expected embryo survival from spawning to hatching for embryos spawn on day  $j$  became:

$$S_{CUMembryo}(j) = \sum_{i=0}^{d(j)-1} \frac{1}{(1 + e^{-1.24+1.12T(j+i)-7.83 \times 10^{-2}T(j+i)^2-6.11 \times 10^{-4}T(j+i)^3})^{1/1124T(j+i)^{1.83}}}$$

3. The computation of the expected larvae cumulative survival  $S_{CUMlarvae}(j)$  over 14 days after the hatch for larvae issued from the spawn of day  $j$ .

This computation was performed with the Jatteau et al. (2017) formula applied with temperatures of the 14 days following the hatch.

$$SCUMlarvae(j) = \sum_{i=d(j)}^{d(j)+13} e^{(1.85-5.13 \times 10^{-1} T(j+i)+1.02 \times 10^{-2} T(j+i)^2+7.01 \times 10^{-2} T(j+i)^3)}$$

4. Computation of the  $TSR(k)$  as the weighted mean of expected embryo survival and expected 14 dph larvae cumulative survival using the daily number of spawns  $Nspawn_k(j)$  over spawning season  $k$ ,

$$TSR(k) = \frac{\sum_{j=1}^{n_k} Nspawn_k(j) SCUMembryo(j) SCUMlarvae(j)}{\sum_{j=1}^{n_k} Nspawn_k(j)}$$

where  $n_k$  is the number of days in the reproduction season  $k$ .

$TSR(k)$  can be simply interpreted as the average expected survival of all eggs laid during the season  $k$ .

Randomness of the reproduction behaviour and an index of reproduction efficiency ( $I_{TSR}$ )

$TSR_{min}(k)$  and  $TSR_{max}(k)$  correspond to the minimum and maximum values that  $TSR(k)$  can take during season  $k$ . These values are calculated with a time series of the spawning acts number and embryo-larval survival sorted into the opposite (one increasing and one decreasing) and the same (both increasing) orders. The former corresponds to the highest number of spawns associated with the dates of the worst survival and the latter to the highest numbers of spawn associated with the dates of best survival.

To test the randomness of the reproduction behaviour, the distribution of the  $TSR(k)$  is calculated by shuffling the spawn act time series for a spawning season  $k$  10,000 times. This illustrates the value of  $TSR$  irrespective of the date of spawning but with the same distribution of the reproduction activity. The quantiles 0.025 and 0.975 define the range of  $TSR(k)$  corresponding to a random reproduction activity.

Based on these previous indicators, the efficiency of the reproduction activity relative to the expected thermal survival of the young stages for season  $k$  was evaluated

with an index ranging from 0 and 1 and was calculated as follows:

$$I_{TSR}(k) = \frac{(TSR(k) - TSR_{min}(k))}{(TSR_{max}(k) - TSR_{min}(k))}$$

The distribution of  $TSR(k)$  based on shuffling the spawning acts series was used to calculate the distribution of  $I_{TSR}$  and to similarly test the randomness of the reproduction behaviour.

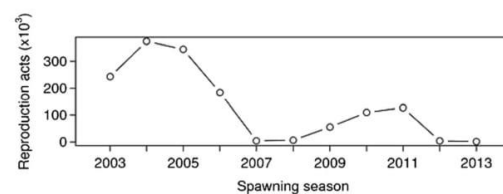
To sum up,  $TSR$  assesses whether survival was good (high  $TSR$ ) in a specific year while  $I_{TSR}$  assesses whether fishes could have done better (low  $I_{TSR}$ ) with a more appropriate spawning tactic.

## Results

The four strongest reproduction activities occurred during the first several seasons, which were then followed by two years (2007 and 2008) of low activity. Then, the number of reproduction acts increased until 2011. The last two seasons (2012 and 2013) were again very low (Fig. 2).

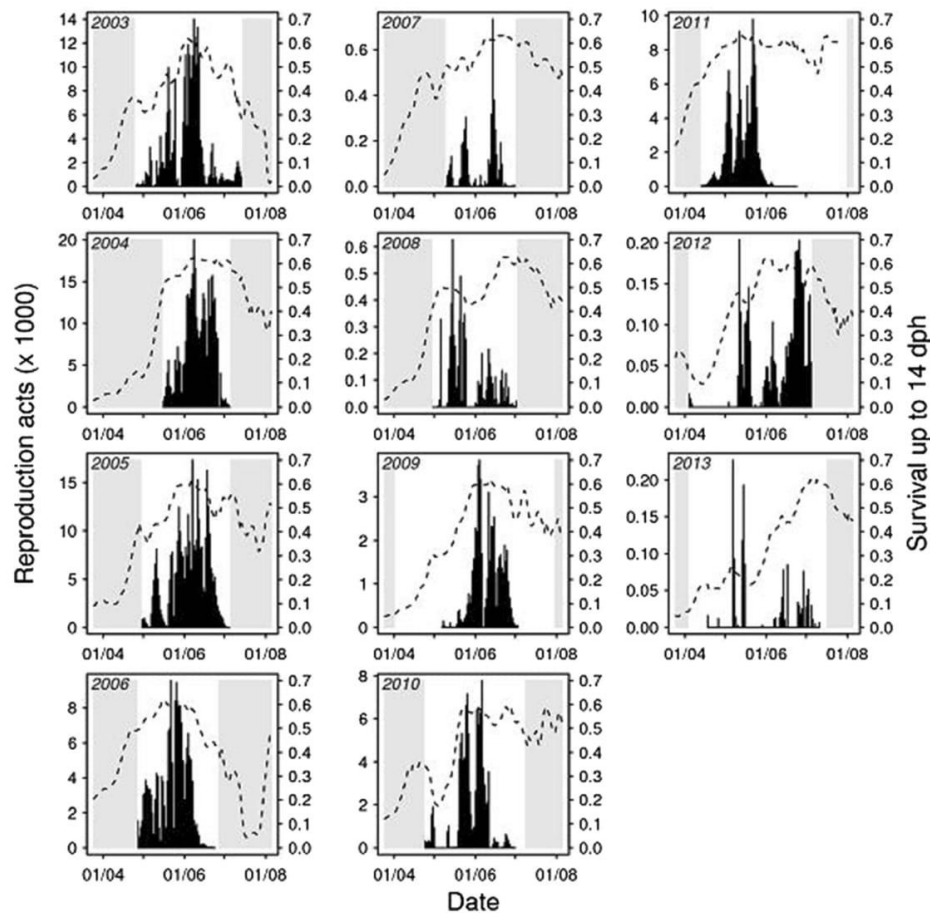
Figure 3 details the correspondence between spawning acts and the expected cumulative survival up to 14 dph. The survival time series resembles dome-shaped curves with high values located mainly between mid-May and mid-June. Most spawning acts were recorded during day associated with high values of juvenile survival (conversely, few spawning acts occurred during days associated with low survival; Fig. 3). The start of the reproduction season usually fluctuates between the end of April and the first days of May, but an early beginning was observed in the last three years. The spawning seasons were finished between mid-June and mid-July with no obvious trend.

The proportion of spawning acts assigned to the worst class associated with the temperature



**Fig. 2** Evolution of the total number of reproduction acts according to the 11 studied reproduction seasons





**Fig. 3** Evolution of the spawning acts number (bar) and the survival from embryos up to 14 dph (dotted line) for the 2003–2013 seasons. The x axis labels correspond to the day and the

month (dd/mm) in the reproduction season. The white rectangles correspond to the observation window of the spawning activity (effective auditory survey)

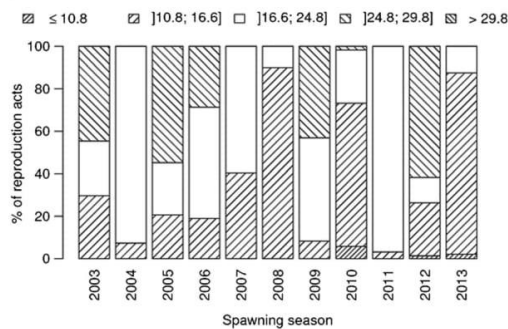
between egg laying and 14 dph was plotted for each season in Fig. 4. Exposure to low temperatures (below the minimum of the optimal range) affected a higher proportion of spawning acts, particularly in 2008, 2010 and 2013, than exposures to high temperatures (above the maximum of the optimal range).

$TSR$  remained stable at approximately 55% of the survival except for the 2013 season when an especially low survival (35%) was recorded (Fig. 5a). For eight of the 11 studied seasons, the efficiency of reproduction is higher than the one obtained by random reproduction activity (Fig. 5b). In these cases, the efficiency is higher than 80%.

## Discussion

Interest of cumulative mortality from 14-dph larvae,  $TSR$  and  $I_{TSR}$

This work corresponds to the first application of thermal performance curves of embryos and larvae (Jatteau et al. 2017) to field temperatures according to the seasonal time series of reproduction acts. It was possible to estimate the global efficiency of allis shad reproduction in terms of offspring survival for 11 spawning seasons in the Garonne River. This study also offers the possibility to test whether the laying tactic exhibited by this species optimises the survival of its early development stages as



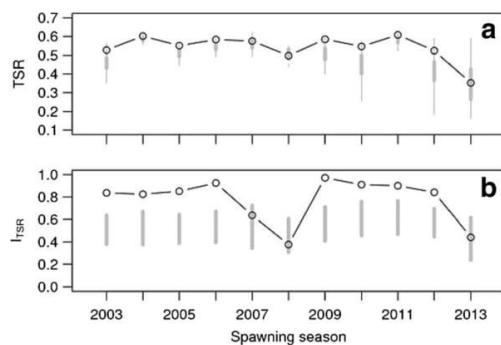
**Fig. 4** Evolution according to spawning season of the proportion of spawning acts assigned to the worst class associated with the temperature between egg laying and 14 dph. The class limits are based on tolerance and optimal thermal ranges of Jatteau et al. (2017)

postulated by Quinn and Adams (1996) for species with a close temporal and spatial connection between the environments experienced by spawners and their progeny. More generally, it provides insights on the adaptive abilities of allis shad in response to climate warming.

#### TSR assumptions

The computation of the TSR relies on several assumptions.

- 1) Jatteau et al. (2017) estimated survival curves on shad from the Nivelle River (Fig. 1), whereas the field data used in this application were collected from the Garonne River, which is approximately



**Fig. 5** Evolution of (a) the thermal survival of recruitment ( $TSR$ ) and (b) the reproductive efficiency ( $I_{TSR}$ ) according to the spawning seasons (thin vertical segments indicate the difference between the minimum and maximum of  $TSR$ , thick segments indicate the range corresponding to a 95% distribution of  $TSR$  or  $I_{TSR}$  for random reproduction behaviour)

250 km away. The possible local differences in thermal tolerances are implicitly neglected. First, Hundt et al. (2015b) found similar optimal thermal ranges for fish from the Garonne River. This putative local adaptation to temperature is impaired by straying between the catchments in the Bay of Biscay though individuals from the Nivelle Catchment displayed a higher level of genetic differentiation (Martin et al. 2015). Moreover, the Nivelle River displays less suitable thermal conditions for early stage survival than the Garonne River (Jatteau et al. 2017).

- 2) Survival models of embryos or larvae that were calibrated at a constant temperature are applied to the fluctuating temperatures in the natural conditions. This assumption does not take into account the possible acclimation (Moss 1970; Reynolds 1978), which will lead to an overestimation of the survival.
- 3) Mean daily temperatures mask fluctuations throughout the day (Wehrly et al. 2009) and variations at the microhabitat scale. More extreme conditions may be experienced by the fish, and, thus, the survival calculation may also be inflated.
- 4) The egg number per spawning act is assumed to be constant throughout the reproductive season. Shad are fractional spawners with batch fecundity that is highly variable between individuals (Olney and McBride 2003; Hyle et al. 2014). However, even if the variability of the batch fecundity during a batch sequence for an individual or the evolution of the batch fecundity along the reproduction season are suspected (Chambers and Leggett 1996), no information is available for the allis shad.

Accepting these assumptions, the TSR can be used to explore direct consequences of temperature on the off-spring survival in the Garonne River.

#### Effect of cold temperatures

The TSR indicated that the most affected years in regard to spawning were not those with high temperatures. Indeed, the highest mortality obtained for 2013 coincided with a high proportion of spawning acts affected by extremely low temperatures (Figs. 4 and 5a). The slightly high mortality obtained for 2003, 2008 and 2012 also coincided with low temperatures, although to a lesser extent. Similar temperature optimal ranges for American

and allis shad early stages allow comparison between the two species (Jatteau et al. 2017). Higher mortality with lower temperatures was also reported for the American shad (Nack et al. 2015). This result is in agreement with the more numerous reports in the literature of death due to low temperatures than those attributed to heat (see Beitinger et al. 2000 for a review).

#### Effect of warm temperatures

Increased larval survival of *A. sapidissima* was associated with higher water temperature (Crecco and Savoy 1985). Likewise, Ross et al. (1993) did not observe a reduction in American shad larval density during field sampling between 26 and 27 °C. Individuals in the embryonic stage rarely (or never) encounter a temperature higher than 25 °C because the spawning period is early in the season (Cassou-Leins et al. 2000) and because the potential future spawners can be blocked or die before spawning, which was suspected during the 2003 heat wave (Travade and Carry 2008). Nevertheless, older larvae could potentially be affected by higher temperatures and low levels of oxygen. Preliminary laboratory experiments for three-month-old juveniles have shown high sensitivity to hypoxia at 25 °C (Jatteau and Fraty 2012). These conditions were occasionally recorded during the summer migration of allis shad in the Gironde Estuary (Lanoux et al. 2013). Even with their higher tolerance, the negative impact of warm temperature risks to be exacerbated by climate change in the future.

#### Stability in survival

A clear survival sensibility to temperature was experimentally shown for allis shad until 14 dph (Jatteau et al. 2017). Surprisingly, the present estimations of  $TSR$  suggest that the mean survival only fluctuated between 50% and 61% between 2003 and 2012 and dropped to 35% only in 2013 (Fig. 5a). This relative stability cannot be explained by a lack of temperature changes (Fig. 4). Seasons 2004 and 2011 can be considered suitable with more than 90% of the reproduction within the optimal temperatures when seasons 2003, 2005 and 2010 are unfavourable with only 25% of the reproduction acts within the optimal range. The objective of this work was not to discuss all the possible causes of the collapse (see Rougier et al. 2012 for a review) but the present result confirms that the unfavourable thermal conditions, at least for fish up to 14 dph, were probably

not responsible for the recruitment failures. Nevertheless, an explanation of the population decline may be explored in the survival of older juveniles, possibly affected by the extreme thermal and oxic conditions in mud plug during estuarine migration. Alternatively, this result may suggest that allis shad adapted its spawning tactic to be able to mitigate the negative effects of extreme temperatures.

#### $I_{TSR}$ assumptions

For the sake of simplicity, computation of the randomness in  $I_{TSR}$  does not integrate any constraints in the seasonal distribution of the reproductive act number that may be induced by environmental conditions, internal fish states or interactions between individuals. A more comprehensive but more complex approach based on migrating and spawning behavioural rules (Jonsson and Jonsson 2009) should exceed this limitation. Data on timing of the arrival at the spawning grounds, evolution of the spawner density on the spawning grounds and variability of the spawning interval will be required but not easily available. Interannual variation in migratory timing is correlated with river temperature, i.e., colder temperatures delay migration while warmer temperatures advance it (Leggett and Whitney 1972; Quinn and Adams 1996). River discharge also influences the river temperature (Acolas et al. 2004). These relationships will have indirect consequences on the young stages of survival. On average, a female shad copulates from two to 10 times in a season (Olney and McBride 2003; Acolas et al. 2004, 2006; Hyle et al. 2014) with a 2–3 day spawning interval (Olney and McBride 2003; Hyle et al. 2014). This variability induces differences in the residency times on the spawning grounds and thus differences related to environmental conditions that the spawners experience.

#### Spawning tactics

The  $I_{TSR}$  evolution clearly showed that allis shad exhibits a spawning tactic that is more efficient than a simple random tactic in eight seasons among the 11 that were studied (Fig. 5b). This is in accordance with Quinn and Adams (1996) who predicted that shad would employ plasticity to respond to river conditions because of the short-time interval between adult migration timing and larval emergence. For example, the females can anticipate the conditions that their offspring will

experience a few days later by starting spawning when the temperature is still under the optimal range but increasing.

The 3 seasons with a suboptimal spawning tactic (2007, 2008 and 2013) are similar to cases of low spawning activity. This could be explained by a lack of breeding synchrony due to less social facilitation (Clayton 1978; Ochi 1986). Nevertheless, this mechanism is not the only one because in 2012, the abundance was also very low but  $I_{TSR}$  was high (Figs. 2 and 5b). Furthermore, cold temperatures can explain spawning tactic failures in 2008 and 2013 (Fig. 4). However the cold 2010 season was not associated with a low spawning efficiency. Discharge is also suspected of playing a role in spawning tactic failures (Acolas et al. 2006). The 2008 and 2013 seasons showed low  $I_{TSR}$  (Fig. 5b) and recorded floods during the spawning period ([www.hydro.eaufrance.fr](http://www.hydro.eaufrance.fr)). However, the high discharge peaks observed in 2010 and 2012 were not reflected in the poor efficiencies of the spawning tactic. Consequently, underlying thermal behavioural rules still need to be expanded to clearly understand the failures in the reproduction efficiency.

#### Adaptation and shift distribution

Modelling studies of allis shad distribution suggests a preference of warm water for this species (Béguer et al. 2007) and predicted a northward shift in future climate change scenarios (Lassalle and Rochard 2009; Lassalle et al. 2009). Field observations reported the first signs of a natural recolonisation of the Seine River watershed (Belliard et al. 2009), which may herald this northern movement. Movement to the northern basins will likely be facilitated if the temperatures continue to increase during the spawning season (Rougier et al. 2015). The present results indicate that allis shad in the early stages of development are not strongly constrained by high temperatures because of suitable thermal tolerance of the early stages and the efficient egg laying tactic of the spawners.

However, even though it is unlikely in the near future, increasing temperatures could impair the efficiency of the spawning tactic (dramatic declines of  $TSR$  and  $I_{TSR}$ ) and lead to a possible maladaptive response to climate change (Kennedy and Crozier 2010; Crozier and Hutchings 2014). In this case, behavioural plasticity alone will not be sufficient to allow a shift in shad distribution, and hence, genetic evolution in the

reaction norm will be needed to face ongoing global warming (Visser 2008).

#### Management perspectives

From a management perspective,  $TSR$  can be used to predict recruitment survival and anticipate when anthropogenic mortalities (fishing, pumping, etc.) should be reduced to strengthening the weak cohorts. The  $TSR$  could be easily used in a report card similar to that for the shad population in Gironde (Collin and Rochard 2012). It can also help to explain the efficiency variability of a stocking programme similar to the one implemented in the Rhine (Hundt et al. 2015a) and to optimise the release procedure. In the medium term, a higher frequency of low  $I_{TSR}$  will provide information concerning the risk of maladaptation of the spawning tactic to new environmental conditions and then the need to reinforce population protection.

#### Conclusion

A combined analysis of reproduction activity and fluctuations of expected embryo-larval mortality due to temperature confirms Quinn and Adams' (1996) hypothesis that shad selection favours an efficient spawning tactic to anticipate favourable thermal conditions for the survival of their offspring. Underlying behavioural rules still need to be explicitly formulated. New environmental conditions induced by ongoing climate change will challenge this behavioural plasticity. In the case of maladaptation coupled with no genetic evolution, the shift of shad distribution would be undermined.

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# NICHE ECOLOGIQUE DE L'ALOSE PENDANT LA REPRODUCTION : CONSEQUENCES AU NIVEAU DE LA POPULATION DANS UN CONTEXTE DE RECHAUFFEMENT CLIMATIQUE

## RESUME

Cette thèse se place dans un contexte de dérèglement climatique (IPCC 2018) et de déclin généralisé des espèces de poissons. L'objectif de cette thèse était de définir le contrôle environnemental sur la reproduction de la grande alose. A l'aide de 4 études combinant plusieurs outils de modélisation (l'indice de Manly, le modèle BRT, le modèle HoOS et le modèle *flirtyShadBrain*), nous avons étudié ce contrôle environnemental et évalué l'impact futur du dérèglement climatique.

La première étape a consisté à définir l'influence des facteurs environnementaux sur la reproduction de l'alose (papier #1, papier #2 et le modèle *flirtyShadBrain*). Nous avons d'abord exploré l'influence de la température, puis nous avons testé plusieurs facteurs environnementaux sur la reproduction de l'alose (température, débit et durée du jour). Cette étape a permis de démontrer que l'alose est une espèce photopériodique. La durée du jour est peut-être la donnée saisonnière qui déclenche la migration, et la température et le débit sont utilisés pour les décisions à court terme. Nous avons utilisé ces connaissances pour explorer l'impact potentiel du dérèglement climatique (papier #3). Selon nos projections multifactorielles, il semblerait que les géniteurs de grande alose ne seront pas touchés par le futur réchauffement climatique pour le scénario RCP 2.6, et que même dans le pire des scénarios (RCP 8.5), la favorabilité de l'habitat devrait même augmenter avec toutefois une période favorable plus précoce. Ainsi, le changement climatique n'apparaît pas comme une menace majeure pour cette espèce.

## MOTS CLES :

Niche écologique ; Dérèglement climatique ; Réponse adaptative ; Modélisation ; Poissons diadromes

## ECOLOGICAL NICHE OF SHAD DURING REPRODUCTION: CONSEQUENCES AT THE POPULATION LEVEL IN A GLOBAL WARMING CONTEXT

### ABSTRACT

Climate change threatens anadromous fishes such as the allis shad (*Alosa alosa*) populations of which have declined since the 20th century in Europe. The objective of this PhD was to define environmental control over the reproduction of the allis shad. Using 4 main studies with several modelling tools (Manly index, BRT model, HoOS model and *flirtyShadBrain* model), we studied this environmental control and assessed the future impact of climate change.

The first step in assessing the impact of climate changes was to test the influence of environmental factors on shad reproduction (paper #1, paper #2 and the *flirtyShadBrain* model). We first explored the influence of temperature, then tested several environmental factors on shad reproduction. Our results demonstrate that the shad is a photoperiodic species. Day length may be the seasonal data that triggers migration, and temperature and flow are used for short-term decisions (final choice to reproduce). We used this knowledge to explore the potential impact of climate change (paper #3). According to our multifactorial projections, it would appear that allis shad spawners will not be affected by future global warming for the RCP 2.6 scenario, and that even in the worst case scenario (RCP 8.5), habitat favorability should even increase, although with an earlier favourable period. Thus, climate change does not appear to be a major threat to this species.

### KEY WORDS:

Ecological niche; Climate change; Adaptive response; Modelling; Diadromous fish