Regular paper

The brook trout *Salvelinus fontinalis* (Mitchill, 1814) in the Saint-Pierre and Miquelon archipelago: a review

by

Julie VIANA (1, 2), Eve BRIAND (1), Loic PERRIN (3), Edgard GUSTAVE (1), Céline AUDET (2) & Fabrice TELETCHEA* (1)

Abstract. – The French archipelago of Saint-Pierre and Miquelon (SPM) is located in eastern North America. Brook trout *Salvelinus fontinalis* (Mitchill, 1814) is the key angling species in SPM's freshwater. Here we provide a synthesis of local studies and rearing trials performed on this fish. Dozens of documents were found dating back from the beginning of the 1980s that aimed to elucidate its biology and ecology. At that time, the first farming trials were conducted in Miquelon and then in Saint-Pierre, generally by volunteers, and mainly for restocking purposes or to develop sport fishing. As a result, thanks to the work of many enthusiasts occasionally supervised by outside researchers, knowledge was acquired on the biology, ecology and farming of brook trout on the archipelago. Finally, some suggestions for further works (*e.g.* genetic diversity, connectivity and gene expression) are presented.

Submitted: 17 May 2022
Accepted: 11 Oct. 2022
Editor: F. Teletchea, D. Pauly

Key words
Brook trout
Aquaculture
Angling
Ecotourism

Résumé. – L'omble de fontaine à Saint-Pierre et Miquelon.

L'archipel français de Saint-Pierre et Miquelon (SPM) est situé à l'est de l'Amérique du Nord. L'omble de fontaine *Salvelinus fontinalis* (Mitchill, 1814) est la principale espèce pêchée à la ligne dans les eaux douces de SPM. Nous présentons ici une synthèse des études locales et des essais d'élevage réalisés sur ce poisson. Nous avons retrouvé des dizaines de documents datant du début des années 1980 qui visaient à élucider sa biologie et son écologie. À cette époque, les premiers essais d'élevage ont été réalisés à Miquelon puis à Saint-Pierre, généralement par des bénévoles, et principalement à des fins de repeuplement ou pour développer la pêche sportive. Ainsi, grâce au travail de nombreux passionnés encadrés occasionnellement par des chercheurs extérieurs, des connaissances ont été acquises sur la biologie, l'écologie et l'élevage de l'omble de fontaine sur l'archipel. Enfin, quelques suggestions pour des travaux ultérieurs (par exemple, la diversité génétique, la connectivité et l'expression génétique) sont présentées.

INTRODUCTION

Aquaculture is a growing economic activity worldwide, with an annual growth rate around 10% since the early 1980s (FAO, 2020). The increase in fish production is largely based on a few species, which have been introduced globally (Teletchea, 2016, 2019). However, introduction of non-native fish species is one of the major causes of biodiversity disruption (Teletchea and Beisel, 2018). For this reason, these practices are increasingly restricted or even prohibited in several European countries (Teletchea and Le Doré, 2011) and some regions of North America (Escobar *et al*., 2018). A diversification of production by enhancing native species could allow the development of a more sustainable, resilient and better adapted aquaculture, targeting both conservation issues and economic development of territories (Fontaine and Teletchea, 2019). However, the concerns associated with such a practice must be taken into account because domestication can lead to introgression of wild populations and induce a loss of their adaptive diversity (Krueger and May, 1991; Carvalho, 1993; Barrett and Schluter, 2008; George *et al*., 2009; Fraser *et al*., 2011; Lutz *et al*., 2021). To succeed when dealing with this issue, it is essential to build on the scientific knowledge acquired over the years (Teletchea, 2015, 2016).

In Saint-Pierre and Miquelon (SPM), a small French archipelago of 242 km² located 25 km southwest of the Canadian province of Newfoundland (Fig. 1A), a project called OMBLESPM was launched in 2018 (https://www.facebook.com/Omblespm). This project aims to support the transition towards the development of an aquaculture and ecotourism activity around an emblematic species of the archipelago: the brook trout *Salvelinus fontinalis* (Mitchill, 1814). This salmonid, native to eastern North America (MacCrimmon and Campbell, 1969; Dutil and Power, 1980), is a symbol of the freshwater fishery of these islands and represents the central part of SPM's angling heritage. Thus, as part of this new project, a synthesis of the work and rearing trials conducted over the last few decades in the archipelago, was realized (Briand *et al*., 2021).

(1) Université de Lorraine, INRAE, URAFPA, 54000 Nancy, France. viana.julie40@gmail.com, eve.briand@hotmail.fr, edgard-7@live.fr, fabrice.teletchea@univ-lorraine.fr
(2) Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, Rimouski, QC, Canada. Celine_Audet@uqar.ca
(3) Fédération Territoriale de Pêche de Saint-Pierre et Miquelon, Saint-Pierre, France. loic.perrin@ftpspm.com
* Corresponding author

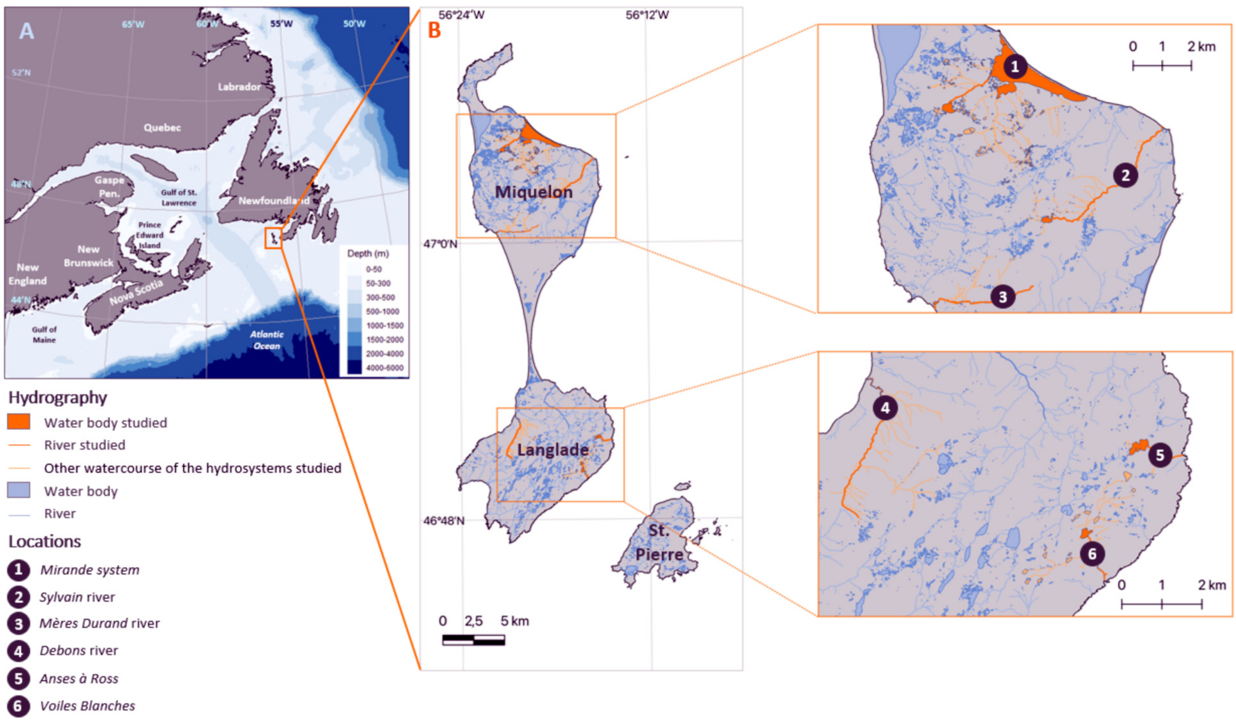

Figure 1. – Geography of Saint-Pierre and Miquelon (SPM). **A**: Location of the SPM archipelago (France) relative to the coast of eastern Canada (box in the upper left). **B**: Main islands of SPM. Some water bodies mentioned in this review are shown (see the numbers in the legend).

The aims of this review are *(i)* to synthesize information on brook trout populations in SPM, (*ii*) to recall the history of aquaculture on the archipelago and to highlight the issues and challenges of the implementation of such a practice and *(iii)* to suggest some work that needs to be carried out to deepen the knowledge of these populations, which differ in several ways from other North American populations.

RECREATIONAL FISHING: A TRADITIONAL ACTIVITY IN THE ARCHIPELAGO

Historically, both angling and hunting are popular activities in the archipelago. Once a vital source of additional proteins, they remain today core recreational activities for the inhabitants of SPM. Even though brook trout is still a very popular species, a depletion of the stocks, likely due to excessive fishing pressure (Champigneulle *et al.*, 2000; Gerdeaux, 2000; Cloutier *et al.*, 2003) and/or parasitism (Preynat, 2013), has occurred in the past decades. To counter this depletion, stock enhancement from local hatcheries was attempted (see below). Also, the importation of eggs from genetically distinct populations, such as those from Canada, was performed until the end of 1980s. The eggs, originating from the Alléghanys fish farm (Philemon, Quebec), were raised in hatcheries and then released in several water bodies. However, this practice was discontinued when it was realized that it would lead to introgression of the native strains by an external strain (Müller, 2006). From 1979 on, eggs from spawners taken from the archipelago waters by electric fishing were used (Briand *et al.*, 2021), with the seeding done by fishing groups from 1982 on. In 1988, for example, 3,000 char were purchased by the Miquelon fishing association and 1,000 for the Saint-Pierre/Langlade association. In 1990, a fish farm was set up by the *Joyeux Pêcheurs de Miquelon* to replace the one initiated by the *Association de Recherche pour le Développement de l'Aquaculture* (ARDA). From 1992 to 1997, the broodstock originated from Terre-Grasse (Mirande, Miquelon). The fry produced were then released in different rivers of the archipelago. On Saint-Pierre, another fish farm was created in 2000. It operated in a similar way and the broodstock came from the Savoyard and the Goéland rivers (Müller, 2006). Despite this attempt, and although fishing pressure appeared to have decreased (Fig. 2), the stocks of brook trout still appear to be in poor condition due to multiple pressures (*e.g.* degradation of the environment through roads and impoundments, parasitism, climate change), including fishing, which may still be too high to allow recovery.

During summer, angling is practiced by holders of a fishing licence, which also allows ice fishing during winter (Briand *et al.*, 2021). Since the 1990s, each year, it is up to

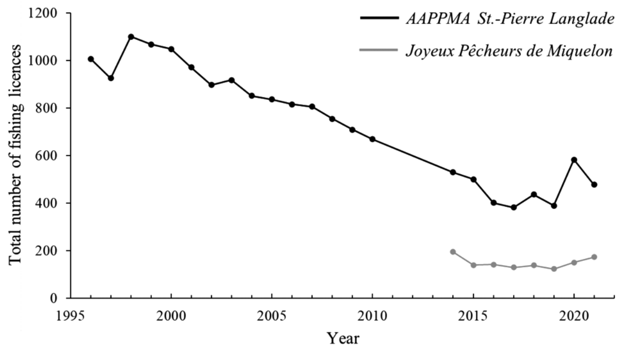

Figure 2. – Annual evolution of the number of fishing licenses issued from 1996 to 2021 by the two fishing associations of the Saint-Pierre and Miquelon archipelago: the *AAPMA de Saint-Pierre-Langlade* (in black) and the *Association des Joyeux Pêcheurs de Miquelon* (in grey). No data are available from 2011 to 2013.

Figure 3. – Ecotypic diversity of brook trout populations in the Saint-Pierre and Miquelon; two individuals fished in the *Mère* Durand River (see location in Fig. 1B). **Above**: anadromous ecotype; **Below**: resident ecotype (©: Edgard Gustave).

the fishing associations to set up fishing regulations (Grant *et al.*, 2017), according to the recommendations made in the management plans elaborated by the *Fédération Territoriale des Pêches de Saint-Pierre et Miquelon* (FTPSPM). The FTPSPM then communicates these proposed regulations to each fisher holding a fishing licence. The opening and closing dates of the fishing season are indicated, as well as the sites where fishing is authorized, along with some associated restrictions, the species that can be fished with their bag and size limits, and the gears that may be used. These regulations may vary according to the island and water body where the activity is practiced and can vary within a season. If it is impossible to set up permanent fishing reserves, renewable prefectural decrees may however identify certain fishing sectors as reserves for a maximum period of five years (Claireaux, 2005).

CHARACTERIZATION OF THE NATURAL BROOK TROUT POPULATIONS OF SAINT-PIERRE AND MIQUELON: AN OVERVIEW SINCE THE LATE 1980S

Biology and ecology

In the early 1980s, a sampling campaign was conducted in two major environments: the main courses of four small streams connected to the ocean and the tributaries of the Grand Étang de Mirande in Miquelon, where spawning occurs (Champigneulle *et al.*, 2000) (Fig. 1B). Two main age groups of brook trout were found (late 0^+ to early 1^+ and early 2^+ to > 2^+). The average densities and biomasses appeared to be higher for the tributaries of the Grand Étang de Mirande than the coastal streams sampled; also, a high variability in the sizes of brook trout of the same age was noted between these habitats. This work also demonstrated a habitat preference of 1^+ individuals for deep areas with substantial vegetation cover and slow flow (< 10 cm.s^{-1}) during the winter period. In summer, on the other hand, no significant preference was detectable among these individuals. Finally, large brook trout (41.5 cm) aged 5^+ were sampled at the mouth of the Grand Étang de Mirande and its tributaries indicated that the largest ponds of the archipelago may be good growth areas for the species.

Ecotypic variability and migratory dynamics

The study of the different ecotypes (Champigneulle *et al.*, 2000; Preynat, 2013), highlighted the presence of resident populations in fresh waters (ponds and tributaries) and anadromous populations in several streams (Fig. 3). For the latter ecotype, two forms of migration were observed: between coastal streams and the ocean (Fig. 4A) and within the Mirande system (Figs 2B, 4B). For the coastal streams, the anadromous individuals stayed a few months at sea, from May to September, and the return to fresh water, essential for spawning, does not necessarily involve the natal stream; however, the fraction of spawners that fail to return to their natal stream still remains to be estimated. Similar trends were observed in brook trout populations outside the archipelago, although the timing and periods of marine residency vary (Dutil and Power, 1980; Naiman *et al.*, 1987; Montgomery *et al.*, 1990; Lenormand *et al.*, 2004; Curry *et al.*, 2006). For example, in Prince Edward Island, in the Gulf of St. Lawrence (Fig. 1A), another island in Eastern Canada, seaward movements of anadromous brook trout were observed throughout the year with a peak during the months of October to December, while the return to freshwater of these individuals occurred from April to early July (Smith and Saunders, 1958). This marine migration is thought to be an advantage for access to richer food resource areas and

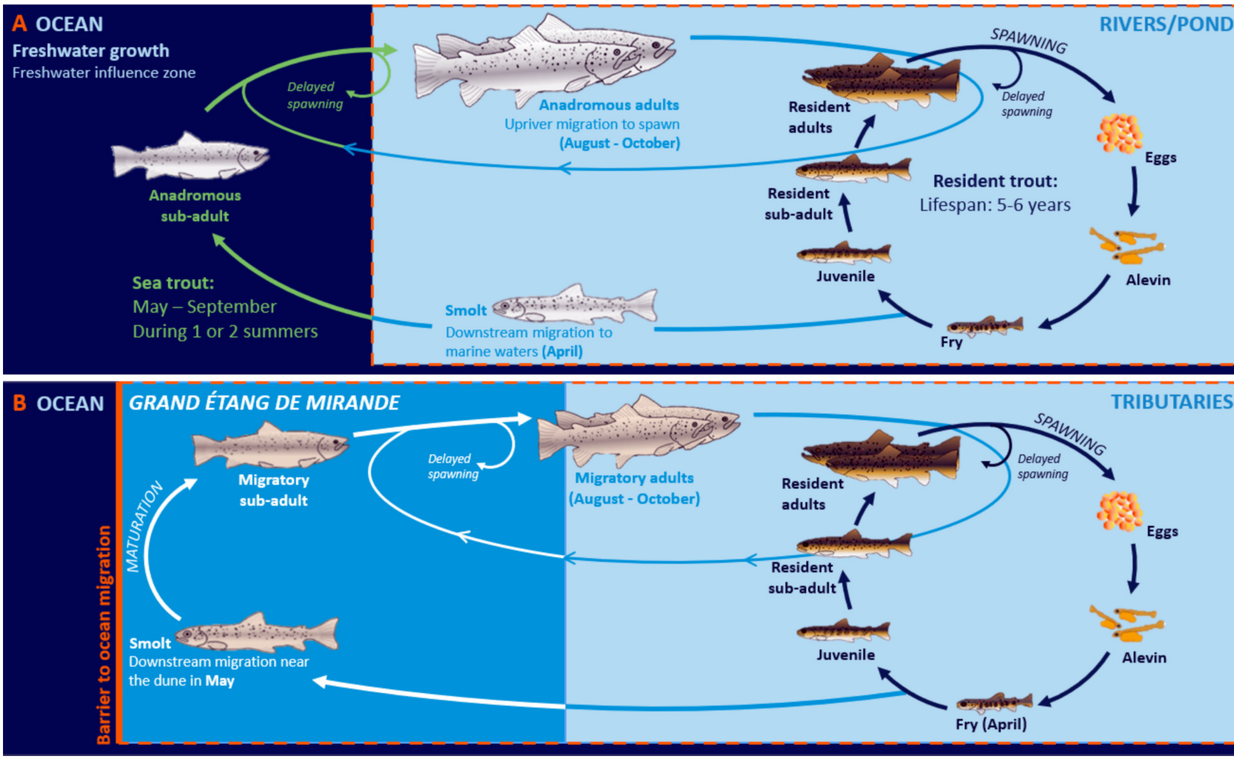

Figure 4. – Ecotypic diversity of brook trout populations in the Saint-Pierre and Miquelon archipelago. **A**: Life cycle of anadromous and resident freshwater brook trout in the coastal ponds and streams of the archipelago. **B**: Life cycle of migratory and resident freshwater brook trout in the Mirande system. Green (**A**) and white (**B**) arrows show movements in the marine environment (**A**) or the Grand Étang de Mirande (**B**). The blue arrows (light and dark) correspond to movements in the rivers/ponds (**A**) or tributaries of the Mirande (**B**).

thus growth, which is also positively correlated with the reproductive success of individuals (Blanchfield and Ridgway, 1999).

The second type of migration concerns the Grand Étang de Mirande system. In 1950, the construction of a road led to the closure of the main pond, which was previously connected to the ocean. The anadromous individuals were then no longer able to migrate to the sea. The surveys conducted in 2000 and in 2013 within the Mirande system (Fig. 4B) showed a concentration of brook trout along the barrier beach during the spring (end of April), including some individuals with a 'pre-smolt' appearance. These individuals were recaptured in May near the same area, and they had a silvered coat, a feature of the smoltification process that normally precedes the passage into salt water. At the end of August and until the end of October, the return migration to the tributaries of the majority of brook trout occurred. The females, less numerous than the males, were captured at the beginning of the migration phase, indicative of a spawning migration into the Mirande system. This spawning period, which reached its peak from the end of September to the beginning of October, was followed by the return of the spawners to the pond, with an earlier return of females than males.

Overall, it seems that many rivers have insufficient or no reliable spawning areas. When conditions are optimal for reproduction, females establish nests in the gravel of well-oxygenated stream sections, while the males compete to fertilize the eggs. In the rivers of the archipelago, favourable conditions are not always met, and some brook trout seem to have adapted, by depositing their gametes on gravel beds in lacustrine environments (Chapuis, 2011). There could also be a genetic component to this observed phenotypic variation. However, no experimental test of this hypothesis has been performed so far. Other ecosystems in SPM are characterized by brook trout populations with particularities: the Anse à Ross has brook trout that are morphologically roughly similar to capelin (*Mallotus villosus*), while the Voiles Blanches are characterized by brook trout populations with a strongly orange coloration (Fig. 1B). These phenotypes are likely the consequence of different habitat characteristics and food resources (Saito and Regier, 1971; Meyers, 1994; Rainville *et al.*, 2021).

Issues associated with parasitism

The annual survey of brook trout populations in the archipelago, initiated in 2010 with the creation of the *Comité de Pêche et Protection des Milieux Aquatiques* (CCPMA), aims at assessing parasite load and their impacts, in particular, the Blackspot parasite (*Posthodiplostomum cuticola*) (Preynat, 2013). This parasite, which has fish-eating birds as its final hosts, uses brook trout as its last intermediate host (Ondračková *et al.*, 2004). The presence of cormorants (*Phalacrocorax carbo*) in the Mirande pond is a concern for the transmission of the Blackspot to other bodies of water in the archipelago (Kanarek and Zaleśny, 2014; Briand *et al.*, 2021). Nevertheless, even though its presence has often been reported, little seems to be known about its transmission and its effects on local brook trout populations. A second parasite present in SPM, *Salmincola edwardsii* (Olsson 1869), is known to affect fish of the genus *Salvelinus* and particularly brook trout (Hoffman, 1967; Margolis and Arthur, 1979; Conley and Curtis, 1994). It is commonly found on fins, and the gills of its fish host (Kabata, 1969).

DIVERSITY OF AQUATIC ENVIRONMENTS IN THE ARCHIPELAGO

Saint-Pierre and Miquelon, despite its small size, possesses a variety of aquatic ecosystems (Durand, 2021). At the end of the 20th century, these ecosystems are generally in good health (Gerdeaux, 2000). The few exceptions concern highly impacted rivers that would require restoration work for their connectivity and diversification of flow facies to be restored (Durand, 2021). Although not exhaustive, studies conducted on the archipelago tend to show that brook trout populations in ponds subject to anthropogenic pressures are much less abundant than in areas where such disturbances are restricted or absent (Cloutier *et al.*, 2003).

In Saint-Pierre, which is the most populated island, habitat degradation is considered the most worrying (Gerdeaux, 2000; Durand, 2021). All water bodies and watercourses are to an extent disturbed by human activities (*e.g.* urbanization, destabilization of the banks, pollution linked to economic activities, dams preventing the upstream migration of anadromous brook trout during spawning periods; Drogue *et al.*, 2021; Durand, 2021; Gustave, 2021). The presence of parasites is also a problem for the brook trout populations on this island.

In Miquelon, fishing pressure and the presence of logjams seem to be the main reasons for the overall decline observed in the brook trout populations (Briand *et al.*, 2021). Indeed, although woody debris can help the productivity of salmonid populations by offering suitable fish habitat (Warren and Kraft, 2003; Abbe and Brooks, 2011), they can also represent an obstacle to the return of migratory individuals (Ligon *et al.*, 1995; Pess *et al.*, 2008). The Sylvain River (Fig. 1B), in particular, had to be closed to fishing in 2000 because of the excessive decline in brook trout catches, even though this stream seems to offer very favourable habitats for the species (Gerdeaux, 2000).

Finally, Langlade is the least impacted, even though some water bodies, such as the Debons River (Fig. 1B), have been strongly modified by anthropogenic activities that results, in some places, in blocking the migratory pathways of brook trout.

AQUACULTURE TRIALS

At the end of the 1980s, an aquaculture project, initiated by ARDA with the technical assistance of the *Institut Scientifique et Technique des Pêches Maritimes* (ISTPM, since became Ifremer, see Forest, 2022), resulted in the establishment of an experimental farm in Miquelon. The structures using freshwater included a hatchery, located on the Renard River, and grow-out and overwintering located in the vicinity of the Carcasse de l'Ouest River (Fig. 5). The Renard River was selected because of its year-round accessibility and its slope, which was sufficient for a gravity-fed water supply. For the saltwater stage, the Grand Étang de Miquelon (Fig. 5) appeared to be the most suitable for floating cages. This lagoon, which connects to the sea via a narrow opening, had the necessary characteristics for the rearing of salmonids: it is subject to the influence of the tides and has a salinity varying from 24 to 32.5‰, depending on the area and the seasons, which allows for good growth of brook trout (Champigneulle *et al.*, 1983).

Various studies were carried out to develop farming, notably on the suitability of different stocking densities and on growth (by scalimetry), and migrations related to the possibility of 'sea ranching.' Besides brook trout, two other salmonids, Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) were tested, the latter being non-native to the archipelago. The aim of these studies was to allow the establishment of a local production of salmonids, both for human consumption (for the three species) and restocking brook trout in potentially deficient environments (Champigneulle *et al.*, 1983).

However, numerous difficulties were encountered (*e.g.* the archipelago's distance from markets in Canada and metropolitan France, difficult climatic conditions, limited technical and human resources, significant mortality of the stocks) which put an end to this initiative, and all activities ceased in 1989. For brook trout, trials were abandoned early because this species, while well adapted to local conditions, was considered to have low potential for the production of large fish (Puyo, 1982). Other initiatives were launched in Saint-Pierre (see Briand *et al.*, 2021 for more details) for restocking, but each of them was eventually abandoned due to difficulties encountered similar to those of the first project carried out by ARDA.

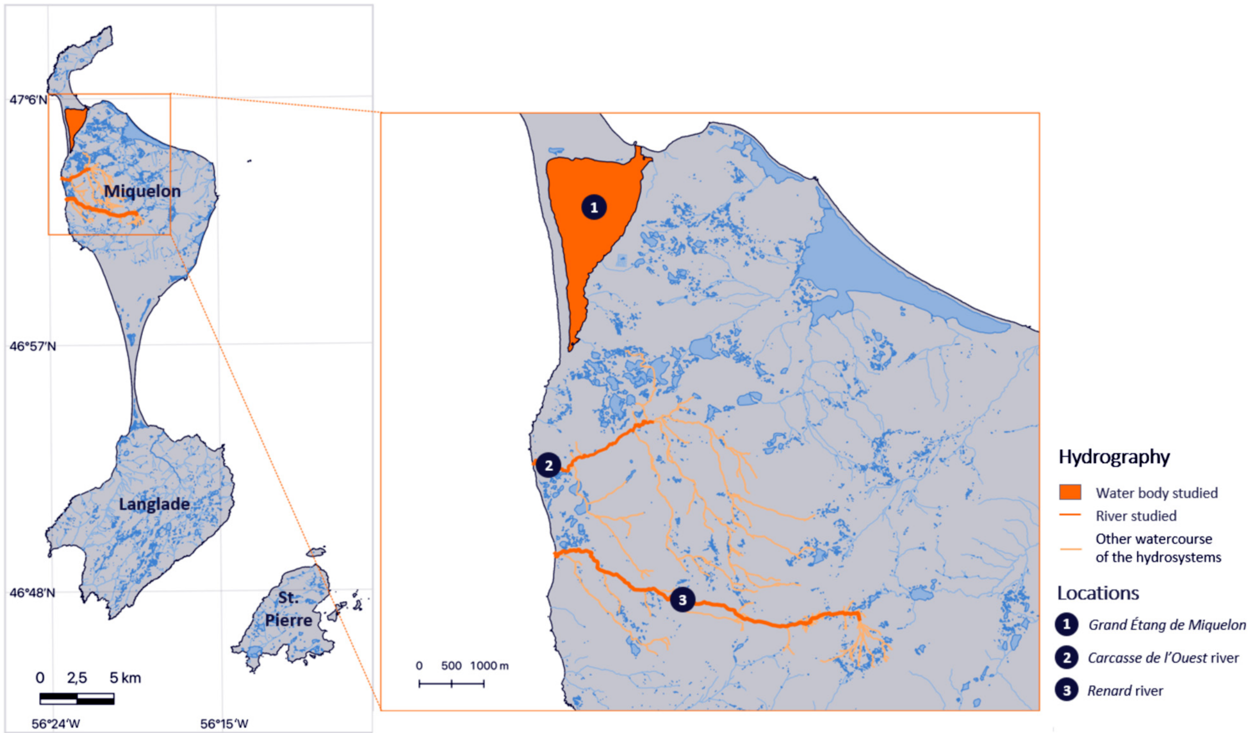

Figure 5. – Locations of the three hydrographic systems used for the aquaculture project initiated by the *Association de Recherche pour le Développement de l'Aquaculture* (ARDA) and the *Institut Scientifique et Technique des Pêches Maritimes* (ISTPM) at the end of the 1980s in Saint-Pierre and Miquelon.

Domestication: contribution and issues of the practice for stocking purposes

Stocking captive-reared individuals has been a common management practice since the late 19th century (U.S. Commission of Fish and Fisheries, 1888; Olla *et al*., 1998; Östergren *et al*., 2021). This practice is one of the most widespread fisheries management strategies in North America (Halverson, 2008) to offset the impacts of anthropogenic disturbances (*e.g*. dams, overexploitation, habitat degradation) and global change on natural populations, Jackson *et al*., 2004; Létourneau *et al*., 2017). Stoking can meet different objectives ranging from improving recreational fisheries to supporting natural populations (Näslund, 2021). The implementation of a restocking using captive-bred (and even domesticated) fish may have negative consequences because these specimens are used to an environment without predators, diseases or parasites, and a high food supply (Näslund, 2021).

However, given current and future anthropogenic pressures, it is very likely that restocking, despite its drawbacks, will continue (Young *et al*., 2016; Näslund, 2021). It is therefore important to consider the difficulties of acclimatization of the reintroduced specimens to ensure the success of the restocking program.

Domestication corresponds to a long-term process allowing the progressive adaptation of captive animals to humans and to the captive conditions (Teletchea, 2015). These conditions, however, differ from those in the natural environment, and individuals under domestication selection may thus develop different behavioural, physiological, morphological, and genetic traits compared to individuals growing in the wild (Einum and Fleming, 2001; Johnsson *et al*., 2014; Jonsson and Jonsson, 2014; Christie *et al*., 2016; Wringe *et al*., 2016; Gering *et al*., 2019). Captive (domesticated) strains develop traits that are favourable for a controlled aquaculture environment, which are not necessarily adapted to a natural environment (Araki *et al*., 2008; Islam *et al*., 2020; Solberg *et al*., 2020). The release of captive/domesticated animals into the wild could therefore produce deleterious effects on wild populations regardless of the intended purpose of the stocking (Mittelbach *et al*., 2014). For example, exposure of domesticated individuals to fishing practice disturbances, coupled with the absence of the food source typically used in aquaculture, could make them less likely to take bait, negating the value of seeding to enhance recreational fishing (Koeck *et al*., 2019).

Added to this is the problem of strains selected during domestication process. They too often originate from source populations that are genetically divergent from the wild populations they are meant to support (Humston *et al*., 2012; Bruce *et al*., 2018; Kazyak *et al*., 2018; White *et al*., 2018). These hatchery strains are unlikely to share the same local adaptations as the wild populations affected by stocking (Fraser *et al.*, 2011). Yet, natural freshwater fish populations often have low genetic diversity and high local adaptation in response to long reproductive isolation (Lamphere and Blum, 2012). The use of a non-adapted domesticated strain could therefore disrupt local adaptations in wild populations through introgression and lead to homogenization of the regional gene pool. This would compromise the ability of populations to persist under varying environmental conditions (Barrett and Schluter, 2008; George *et al.*, 2009; Glover *et al.*, 2017; Lutz *et al.*, 2021), reducing the resilience of metapopulations (Krueger and May, 1991; Carvalho, 1993).

The implementation of a restocking program for brook trout in Saint-Pierre and Miquelon therefore requires a real dialogue on the aims of the project, as numerous studies conducted on this species have revealed important genetic and ecological differences (*e.g.* survival, growth, diet) between wild and introduced populations (Wesner *et al.*, 2011; Annett *et al.*, 2012; Humston *et al.*, 2012). This highlights the importance of correctly identifying the donor population that will be farmed and subsequent restocking process and considering the rearing conditions of the brood stock that will be used (Näslund, 2021). Attention to diversity in trait expression among domesticated individuals could also increase post-release success (Watters and Meehan, 2007; Cordero-Rivera, 2017). Prior exposure of domesticated individuals to conditions similar to the environment in which they will be introduced (Tetzlaff *et al.*, 2019) could increase the likelihood of adaptation and survival of these individuals. Time spent in captivity will also need to be minimized to limit the effects of domestication (Teletchea, 2017). The goal should be to breed individuals with morphological, physiological, genetic, and behavioural phenotypes are as close as possible to those expressed by the wild population to be supported (Lorenzen *et al.*, 2012; Daly *et al.*, 2020). Finally, it is crucial not to view domestication as the only answer to declines in wild populations. This solution can only be viable if coupled with projects to restore the physical, chemical, and hydrological habitat used by these populations (Wohl *et al.*, 2015) and the implementation of regulations on fishing practice.

NEW PERSPECTIVES TO BETTER UNDERSTAND THE NATURAL BROOK TROUT POPULATIONS OF SAINT-PIERRE AND MIQUELON

The only “administrative European” indigenous brook trout are found in Saint-Pierre and Miquelon (Langlois, 2021), and their management and long-term conservation present different challenges. In particular, global warming could lead to a 50 to 100% decline in brook trout abundance by 2100 throughout their native range (EPA, 2015). It is important to deepen current knowledge on these populations and this is one of the objectives of the OMBLESPM project. Significant adaptive diversity is usually found in small populations, despite their vulnerability to genetic and demographic stochasticity (Gilpin and Soulé, 1986). Witnesses of past climatic changes in North America (Magnan *et al.*, 2002), they may have been through numerous evolutionary processes which resulted in the morphological, ecological and genetic plasticity expressed by the species. The management of these small populations is therefore an essential measure for the safeguard of the species (Segelbacher *et al.*, 2022). The Mirande system, in particular, may be ideal to document morphs differentiation (Salisbury and Ruzzante, 2022) and the effects of anthropogenic pressures on migration patterns.

Future issues for research will therefore focus on the characterization of brook trout populations in the three main islands to evaluate their degree of connectivity and their adaptive potential. To achieve this, further studies at three geographic levels: islands, rivers, and location within these rivers are proposed. The first step will be to define the genetic diversity and structures between the three main islands. Curry *et al.* (2006) have shown that salinity may restrict coastal movements of brook trout, which could therefore limit migratory movements between the three main islands. Finally, the influence of habitat characteristics and local environmental conditions will be studied on the gene flow and isolation of brook trout populations within the archipelago to determine the dominant environmental forces influencing the structure of the populations and how this is reflected in terms of phenotypic plasticity. Such information will highlight environmental variables to prioritize in habitat restoration efforts (Castric *et al.*, 2007; Bradbury *et al.*, 2014; Hargrove *et al.*, 2022).

Acknowledgements. – Thank you to all persons that kindly exchanged with Eve Briand about the work performed on this species in the archipelago. These data are invaluable. This work was supported by the *Fondation de France* and European BEST project (BEST2.0+-2020-PO-86). Julie Viana has a PhD grant from *Institut France-Québec Maritime* (IFQM). The authors thank two anonymous reviewers for their useful comments.

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