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Evolutionary Ecology of Kerguelen Islands Colonization by Introduced Salmonids: SALMEVOL 1041-2 project

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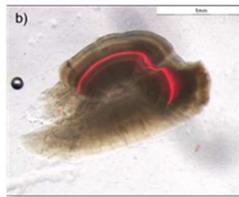
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Evolutionary Ecology of Kerguelen Islands Colonization by Introduced Salmonids.

SALMEVOL-1041-2 IPEV Project

Scientific Report

(2015-2020)



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Abstract:

The present report is a synthesis of all studies conducted around the long-term ecological research (LTER) monitoring of introduced salmonid species in the sub Antarctic Kerguelen islands over the 2015-2020 period, within the SALMEVOL-2 project. The monitoring encompasses the history of eight species, five of which are still present in Kerguelen, the data and collections spanning five decades and tenths of rivers. Based on this monitoring, but also thanks to various field experiments, we have undertaken to study the evolutionary ecology of these species, using the invasive Brown trout as flagship model, under the premise that the Kerguelen situation, where rivers were previously void of any fish species, could be an anticipation lab of the situation developing at the poles due to climate change. Our findings pertain to life history traits such as individual growth, migration between freshwater and marine ecosystems, microbiomes, but also proximal and ultimate mechanisms of adaptation in relation to the local environment. We also begin to investigate how the expanding metapopulation structure, resulting from multiple invasion events, may affect life history traits evolution.

Preamble

The present SALMEVOL report aims at describing the status of colonization of Kerguelen Is. by introduced salmonid species, at describing the status of our data and sample collections, and at presenting the various results mostly in the field of Evolutionary Ecology, obtained since the previous SALMEVOL-1 project led between 2009-2013. This second iteration of the SALMEVOL long term project (hereafter referred as to SALMEVOL-2) started in 2015 and ended in 2021. 3 summer field campaigns were initially planned, but the 2016-2017 campaign could not be led as expected due to reduced access to field, in relationship with the scientific ship “La Curieuse” problems. An additional summer campaign was thus conducted in 2018/2019 thanks to the Polar Institute, in order to fully reach our initial objectives.

Acknowledgements:

This scientific report is a testimony to long term investment into ecological research in the polar regions. This sustained investment is in large part due to the French Polar Institute policy. Such policy, when replicated over a number of scientific projects, is the backbone of the French LTER Zone Atelier Antarctique et Terres Australes (ZATA), that has also helped steering our work over the years. Such long-term investment is a rare thing at the international level, and therefore, we are particularly thankful to the Polar Institute, for it allows us now to explore patterns and hypotheses that would otherwise have remained inaccessible. Additionally, we are also grateful to the logistic teams of the Polar Institute, that have deployed continued efforts and creativity to help us in our protocols and experiments. They have also cared for our security, in coordination with the staff from the Terres Australes et Antarctiques Françaises (TAAF). We also thank the Ocean Tracking Network (OTN, Frederick Whoriskey) for assisting us in the acoustic tracking of Brown trout, and lending us costly equipment to deploy on the field. Finally, we are also enthusiastic at the growing interest from our Institute (INRAE) and our University (UPPA). Funding came mainly from the French Polar Institute, INRAE, UPPA, ZATA, OTN.

2. THE SALMEVOL Long Term Monitoring

2.1. General situation

As a brief reminder, 8 salmonid species were introduced in the subantarctic Kerguelen islands, with the first efforts carried out in 1954, and the first natural reproduction in Kerguelen rivers observed in 1962. The last introductions occurred in 1993. The number of transports, origins, and introductions depend on the species (annexes 1 & 2, Lecomte et al 2013). 3 species never reproduced naturally in Kerguelen and disappeared. 5 species remain nowadays. Preceding the SALMEVOL research project focusing on evolutionary ecology and initiated in 2009, several other projects allowed to collect data and samples since 1967. The ECOBIOP lab maintains a long term ecological monitoring of all these events, including also natural colonizations of new rivers, density census, and tissue sampling. Historical as well as many methodological aspects of this monitoring were described in the previous SALMEVOL report (Labonne et al. 2013a).

1.2 Status of our databases and collections.

Our effort in the long term monitoring is two-fold. First, we endeavour to maintain the present monitoring with a reasonable frequency given our personal and financial investment. This frequency must allow to keep track of new colonizations, potential extinctions, and to increase our capture database and our collections of sample in consequence. This explains also why we generally build a new iteration of the SALMEVOL project every 6 years approximately. Second, we also devote substantial effort to integrate all past data and samples in our monitoring: before 2009, no general standard for data and sample collections was established. We thus constantly work to add data and samples collected between 1962 and 2003 in a standardized framework. This effort initiated since 2009 is now close to an end: most past captures and samples data have been integrated, and we predict another 2 to 3 years of work to integrate all census data (sampling protocols allowing to estimate local density).

Sample type	Estimated count (1962-2019)	Now recorded in our database	Salmevol 1 contribution (2009 - 2015)	Salmevol 2 contribution (2016 -2019)
Scale	About 70 000 envelopes	57060	4655	2130
Adiposis fin	> 7354	7354	830	410
Other fins	> 1314	1314	680	537
Pectoral fin radius	> 586	586	586	0
Stomach content	> 5757	5757	532	188
Otolith	> 2398	2398	946	129
Whole fish	> 1259	1259	358	397

Table 1: Number of samples of various type available in our collections.

Table 1 indicates the current state of our collections of samples regarding the Kerguelen (and Crozet) islands monitoring. SALMEVOL 1 & 2 projects also contributed to the collections significantly. Two

factors however have begun to change the way we collect samples. First, the duration of field campaigns, which is a trade-off between ship rotation and our staff availability. Second, some types of samples require fish sacrifice, an act that deserves some consideration, notably due to European regulation on Animal ethics. Development of less invasive approaches are in order, so to avoid or minimize animal sacrifices in the field. Additionally, some samples of different nature are not yet included in this accounting: river drift sampling and additional whole fish, all tracing back to the 1970's. These samples were often stored in formalin, and are currently sorted and characterized, so to make them available later for the scientific community.

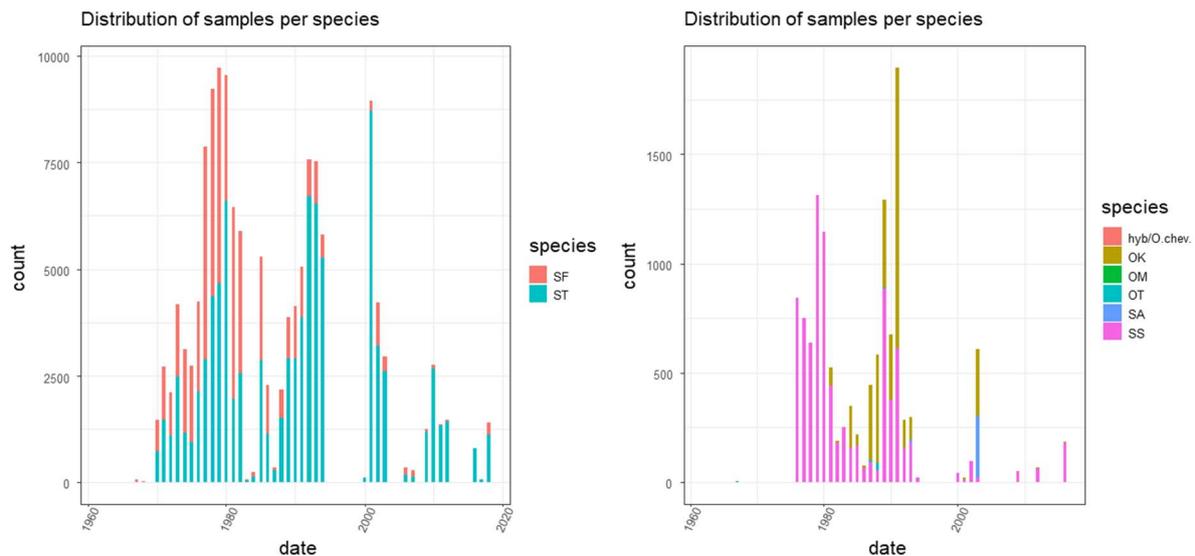


Figure 1: distribution of samples per species as a function of sampling year. The two dominant species, Brown trout (ST) and Brook trout (SF) are displayed on the left panel, Coho salmon (OK), Rainbow trout (OM), Chinook salmon (OT), Atlantic salmon (SS) and Arctic char (SA).

Figure 1 reflects our sampling effort across the decades (up to 2017). Two species represent 91.5% of our samples overall: the Brown trout (*Salmo trutta*) and the Brook trout (*Salvelinus fontinalis*). These two species have benefited from a large introduction effort, and were also able to maintain their population in introduced sites, or even colonize many new rivers, in the case of Brown trout. Most of the scientific interest from 1970 to 2000 was concentrated on Brown trout demography and acclimation, explaining also the prevalence of the species in our data. The Brook trout however is less present in our recent sampling, notably due to sympatric competition with the Brown trout in most systems, as described in our previous report (Labonne et al. 2013a). The remaining 8.5% of the samples in our database regroup several species: Atlantic salmon (*Salmo salar*), Arctic char (*Salvelinus alpinus*), Coho salmon (*Oncorhynchus kisutch*), Rainbow trout (*Oncorhynchus mykiss*), Chinook salmon (*Oncorhynchus tshawytscha*) as well as some *Salvelinus* spp. Hybrids. The Atlantic salmon was abundantly captured before 2000, but due to the extinction of the Korrigans population, their number dramatically declined even in our samplings.

The number of captures per campaign is also declining: this is due to several factors. First, previous teams during the 1970's and 1980's spent complete campaigns (i.e., wintering) in Kerguelen. Second, our focus has changed from pure detailed demographic studies on some focus populations to large scale monitoring, in order to track the progress of colonization, or because we favour experimental

investigations of patterns, often requiring lighter samplings. This is illustrated in Figure 2, where we can observe the growing numbers of rivers sampled as a function of time.

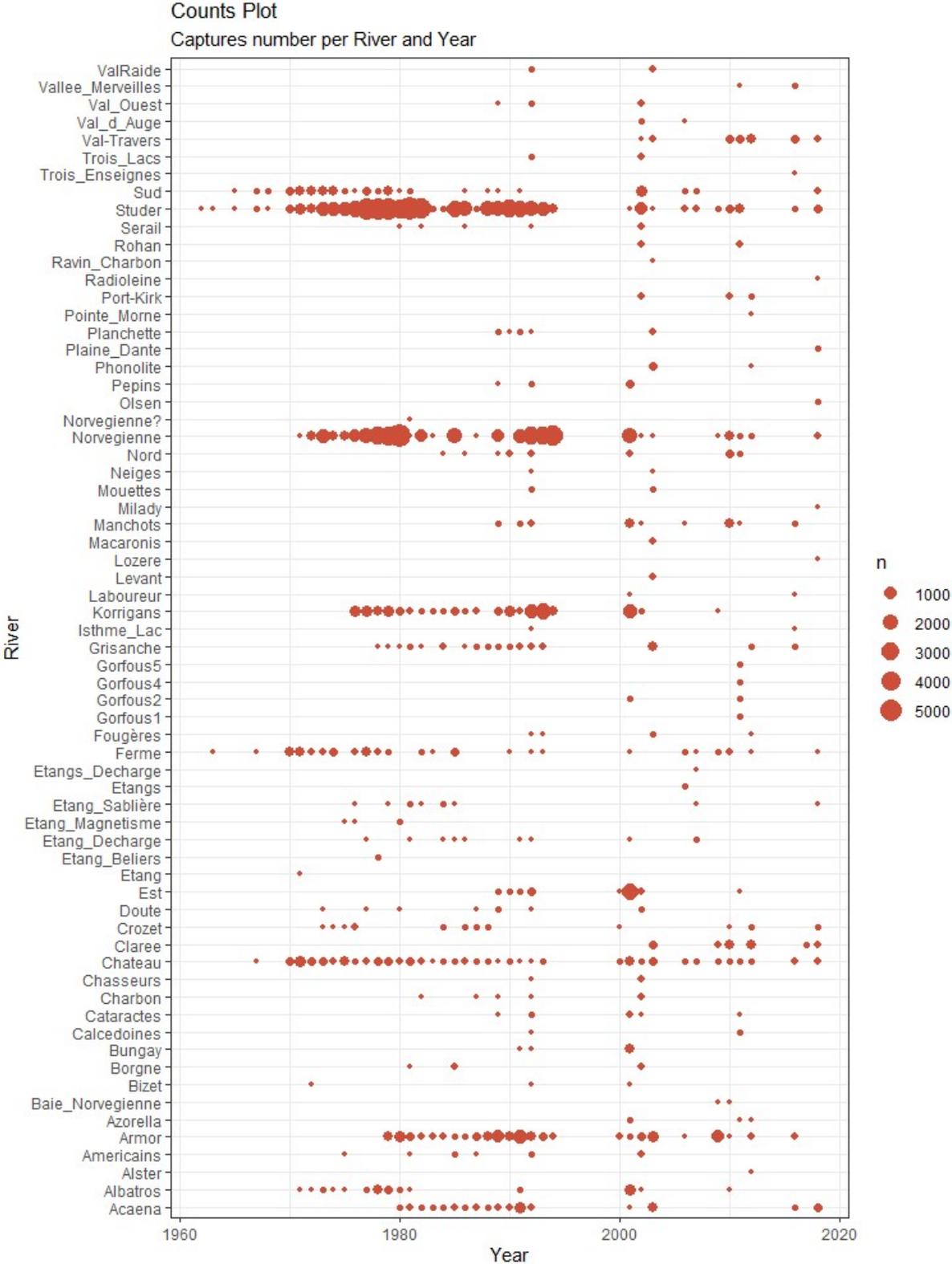


Figure 2: Number of captures (all species considered), per river or lake system, as a function of sampling year.

1.3 Access to data and sample collection

Paralleling our efforts to build capture and samples databases, as well as our collections, we also started to provide access to some of our data and collections.

Our scale collection is integrated to the Colisa CRB (part of the RARE Research Infrastructure), a joint effort of INRAE and OFB (Office Français de la Biodiversité) accessible here:

<https://colisa.fr/>

Several datasets regarding punctual experiments or analyses are also accessible on the INRAE data portal, notably the colonization dynamics data for the 8 introduced salmonid species:

<https://data.inrae.fr/dataverse/ecobiop>

Additionally, part of our data (colonization matrices for the 8 species, individual capture data) are currently being integrated in the ZATA LTER Observatory, an initiative from the ZATA LTER aiming at creating a biodiversity Observatory for the Antarctica and sub Antarctic islands.

Finally, most of the publications cited in the present report provide open access to their various datasets.

3. The current status of colonization

Of the 8 species that were introduced, reproductions were only observed for 5 species (Table 2). Species whose introduction failed will not be reported here (but see details in Lecomte et al., 2013 and Appendices 2a and 2b). The special status of hybrids will be discussed below when describing the status of the species concerned.

During the SALMEVOL 1 and 2 projects, a detailed assessment of the current state of colonization was carried out for the period 2009-2019. The assessments (Table 2) suggest an evolution in the number of colonised rivers which is linked (1) to the colonization of new rivers, but also (2) to a more systematic survey of rivers which had not been visited for a long time or never visited. Annex 1 provides a precise overview of the species present in 2019 and the dates of the last survey. Two maps of the current distribution of species have been produced, one for *Salmo* and *Oncorhynchus* (Figure 3) and the other one for *Salvelinus* (Figure 4). These tools will be updated thanks to the survey of future missions, and they allow to prioritise some sites over others, depending on the age of previous samplings.

The Brown trout (or common trout), *Salmo trutta*, is the species that has colonised the largest number of rivers in Kerguelen (Figure 3). From the 10 introduction sites, it is now established in 55 rivers total, among which 41 are in allopatry (Annexe 1). A colonization model has been built based on the data in our possession in 2012 (Labonne et al., 2013b). It is possible that some rivers that had not been visited before 2012 were already populated when this work was carried out. This is notably the case for the tributaries of the Bay of Audierne where a high-density Brown trout population was discovered at the end of 2018 in the Plaine de Dante river. "Smolts of undetermined species" (probably trout) were also observed in the same period in the rivers coming out of the Plaine Ampère and a sea trout was caught "by hand" in La Mouche valley. These sites should be carefully explored during future missions.

Species	Number of rivers colonized (closed ponds excluded)					
	Stocked over 1955-92	Survived introduction	Reproduced after introduction	Settled in 2012	Settled in 2019	Strayers in 2016-19
<i>Salmo trutta</i>	11	10	10	42	55	3 (+ 2 unknown spp)
<i>Salmo salar</i>	3	2	2	1	1	
<i>Oncorhynchus mykiss</i>	5	1	0	0	0	
<i>Oncorhynchus kisutch</i>	2	2	2	2	3	1
<i>Oncorhynchus tshawytscha</i>	1	1	0	0	0	
<i>Salvelinus fontinalis</i>	6	6	6	11	10	
<i>Salvelinus namaycush</i>	2	0	0	0	0	
<i>Salvelinus alpinus</i>	2	1	1	2	2	
Hyb. <i>S. trutta</i> x <i>S. salar</i>	2 ?	?	?	1	1	
Hyb. <i>S. fontinalis</i> x <i>S. alpinus</i>	1	1	1	1	2	
Rivers with ≥ 1 species	18	17	15	45	58	4

Table 2: Summary of the colonization of the archipelago's rivers, from the first introductions to 2019.

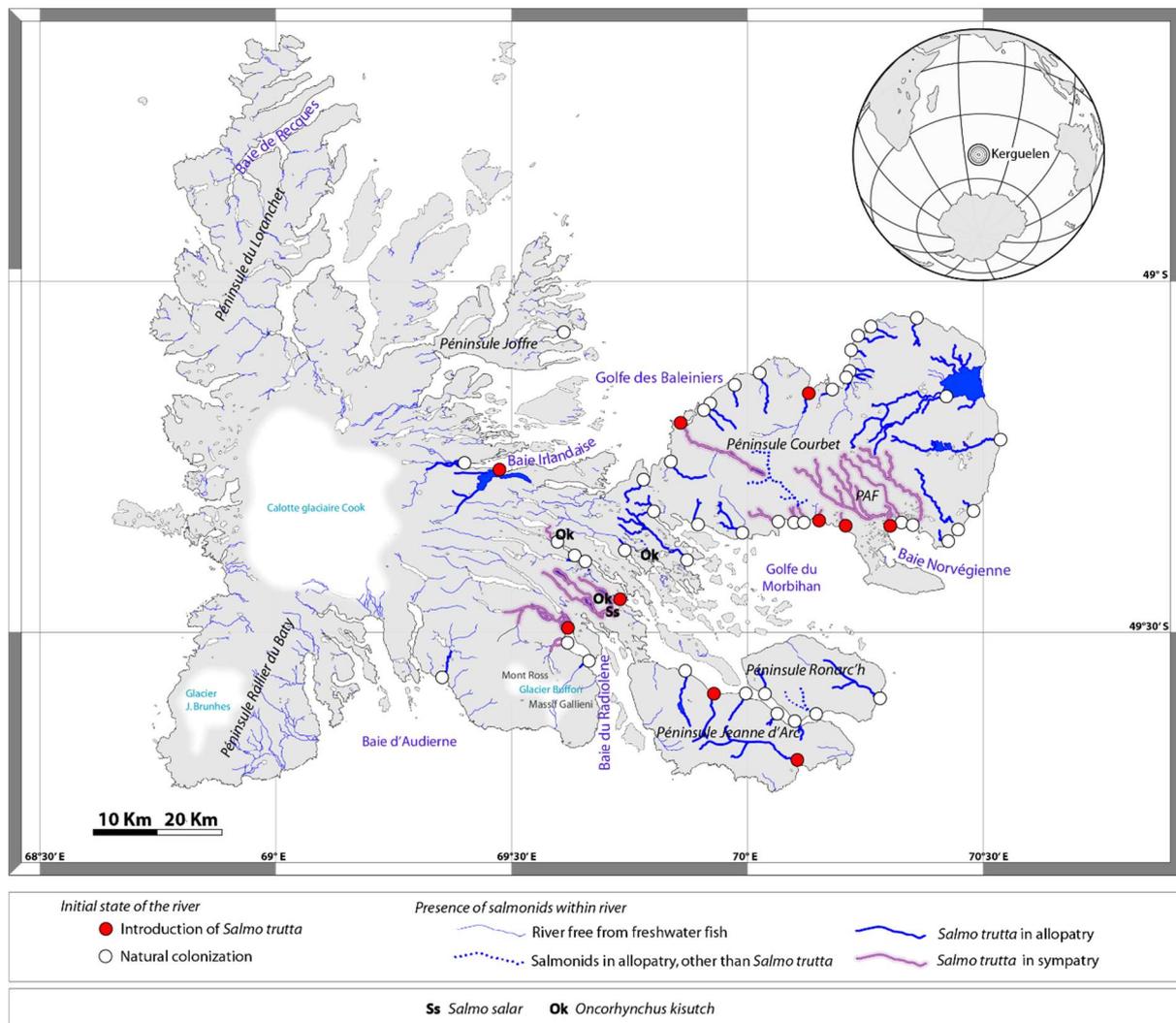


Figure 3: Current status of the colonization of Kerguelen islands by Brown trout (*Salmo trutta*), Atlantic salmon (*Salmo salar*) and Coho salmon (*Oncorhynchus kisutch*).

Other colonizations in agreement with the predictions of the model could be dated quite precisely on this same southern coast. Two new populations were discovered in the Baie du Radiolène, probably founded by individuals coming from the population introduced in La Clarée. On the north coast of the island, in the Golfe des Baleiniers, fry and juveniles were observed in 2017 in the river Val-Froide, a tributary of the Baie Irlandaise, whereas the river was apparently virgin in 2012. In 2017-2019 alevins and juveniles were sampled in the Cascade du Lozère which had never been explored before. These two sites are quite close to sites where trout had been introduced (rivers Studer and Val Travers). Finally, we must mention the Bay of Recques, In the North of the Loranchet peninsula, where we have suspicions of sea trout presence. It is likely that these sites will warrant further exploration and sampling to identify the origins of these populations and refine our predictions. The metapopulation model indeed did not predict long range colonizations.

For Atlantic salmon, *Salmo salar*, the situation is much simpler. It was only introduced at two sites (the Armor and Korrigans basins in the Gulf of Morbihan), but it quickly disappeared from the Korrigans

site. It only survives on the Armor site but no return of marine migrants has been observed. The individuals surviving on this site constitute a small non-anadromous population which hybridises in situ with Brown trout.

Coho salmon, *Oncorhynchus kisutch*, was introduced to the Armor site and to the Grisanche river, which neighbours the Armor basin. It was mass-reared in the Armor fish farm in 1977-1991. It is likely that this breeding is also the cause of accidental introductions. This species migrates to the sea during its first year in fresh water and the adults are semelparous. The capture of adults during their freshwater life only for reproduction can only take place during the southern winter. It is very uncertain due to the weather conditions in Kerguelen. So the only possibility to validate its presence on a site is to capture fry during the austral spring before their migration at sea. A few juveniles of this species were reported in 2012 in the rivers Grisanche and Valdotaine (a small tributary very close to the Grisanche), but no sampling has been carried out since then on this site. But, in 2016, juveniles were caught for the first time and in very large numbers in a small stream in the Bras Jules Laboureur (left bank downstream, Figure 3 and annexe 1). It is likely that this small stream, not colonised by trout, is now the main breeding area for this species. Smolts 1+ were also observed in 2016 in the estuary of another small stream flowing into the Anse de St Malo, not far from this breeding site. These small streams with low flows and little access to common trout will require more attention in the coming years to monitor the possible expansion of Coho salmon.

The Brook trout, *Salvelinus fontinalis*, is the species which, after Brown trout, has been introduced to the greatest number of sites. It had colonised only 5 rivers, but is no longer present in the Acaena where it was reported in 1984. There are now only 4 colonizations. It is only present in allopatry in 2 sites where Brown trout have never been introduced. It only became established in sympatry with the Brown trout when both species were introduced simultaneously. The known colonizations have all taken place in very close rivers from their origin. In Kerguelen, this species therefore has a limited colonization potential, probably in connection with the existing colonization by Brown trout.

Arctic char, *Salvelinus alpinus*, was successfully introduced into the Lac des Fougères, on the right bank of the Fjord Bossière, from where it colonised the Grisanche river, that is an upstream tributary of the Fjord Bossière.

Hybrids of these two species (*S. fontinalis* and *S. alpinus*) have been produced in fish farms and introduced into the Rivière des Galets, which shares its estuarine braided zone with the river La Clarée where Brown trout was introduced simultaneously. They have colonised the Olsen river, which is very close to this shared estuarine zone.

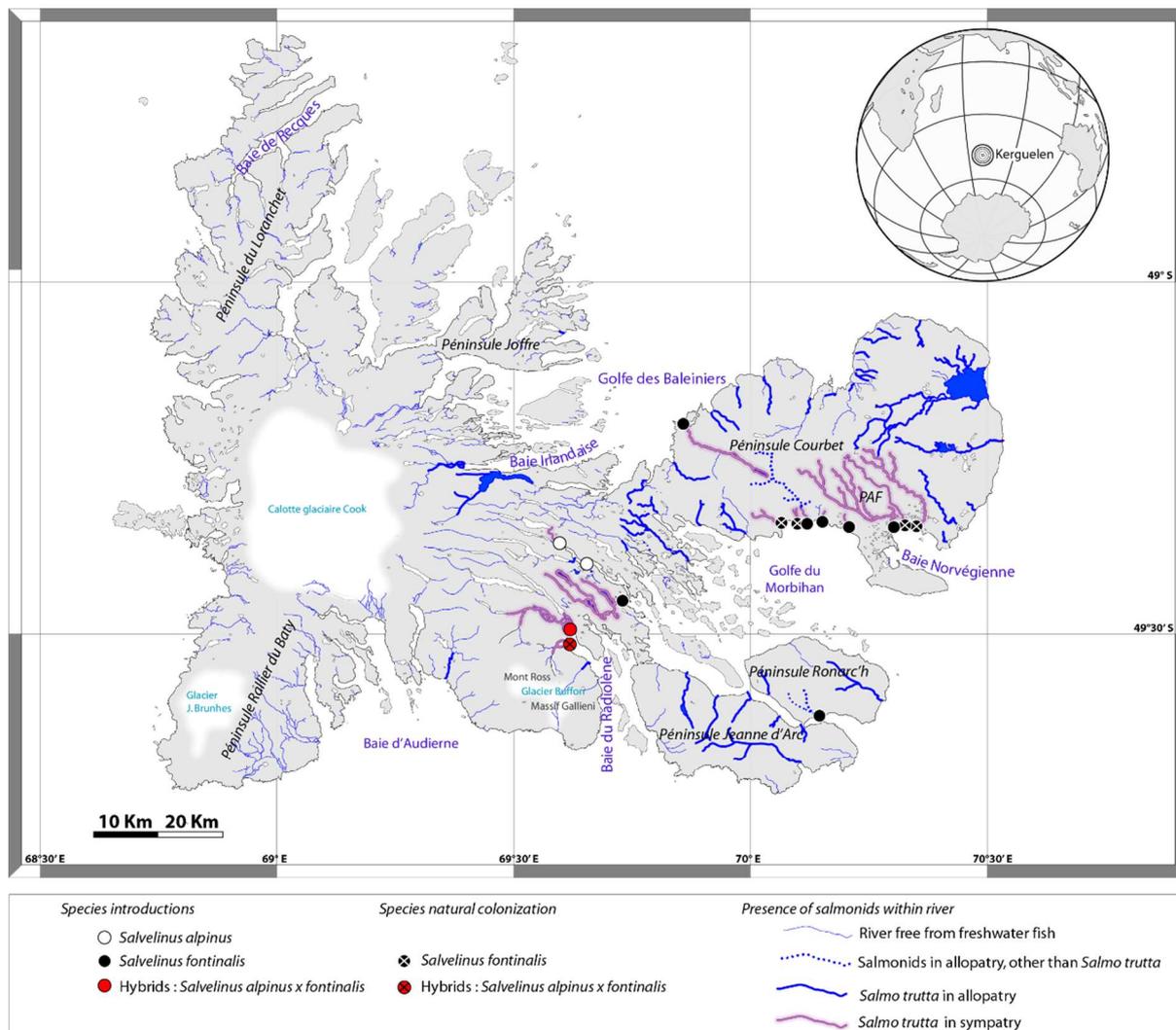


Figure 4: Current status of the colonization of Kerguelen islands by Brook trout (*Salvelinus fontinalis*), Arctic char (*Salvelinus alpinus*) and their hybrid (*Salvelinus alpinus x fontinalis*).

Some conclusions:

The survey effort may have exaggerated the effect of colonization by the Brown trout, but it is clear that this species has acclimatised very well to Kerguelen and still has a strong potential for colonization, far superior to other species, even if it has benefited from a greater introduction effort (Figure 5).

Some colonizations discovered far from the source rivers during SALMEVOL-2 are puzzling and could have been introductions by humans without our knowledge, particularly for Brown trout. Considering this uncertainty, it is important to carry out a new genetic analysis of all trout populations in Kerguelen Is.

Coho salmon are struggling to establish themselves in the presence of Brown trout. Their fry emerge slightly earlier than Brown trout fry, in the late southern spring. They could therefore suffer from

strong predation by sedentary Brown trout at the end of the cold period. In order to monitor the possible expansion of this species, it is important to keep a close eye on small streams not colonised by Brown trout.

Number of rivers colonized by five introduced salmonid species at Kerguelen

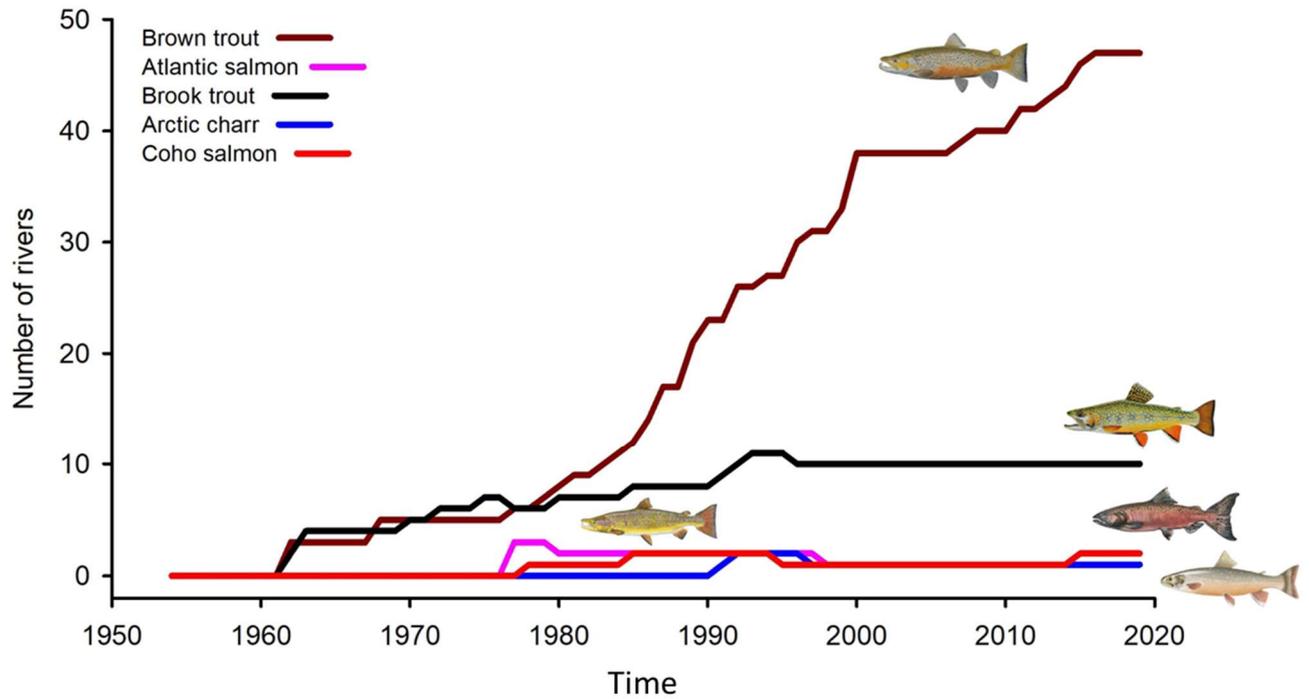


Figure 5: number of rivers colonized by the 5 remaining salmonid species in the Kerguelen islands as a function of time (graph produced by C. Barbraud). A river is deemed colonized when evidence of local reproduction has been confirmed.

4. Scientific results

We here present a collection of new results obtained these last years. Some are directly the consequences of the SALMEVOL-2 field campaigns, other results stem from long term data analyses. For each study, we synthesize the question, protocols and findings, and discuss the potential perspectives. The objective here is to provide the reader with the essential of our findings. In each case however, we point at the source material (reports, thesis manuscript, journal articles) that contains additional details and references.

- Part 3.1 details various aspect of growth patterns in Brown trout, the most common salmonid species in Kerguelen Is., and also the only massively invasive one. We study individual growth at different life stages, in different ecosystems, at various scales, from within population variation to metapopulation approaches.

- Part 3.2 describes the ecology of the Arctic char in the Lac des Fougères, a study proposed and led by our Norwegian collaborators from NTNU.

- Part 3.3 is an original collaboration with physiologists from the NUMEA lab (INRAE), that illustrates why studying populations expansions in novel or post-glacial environments brings new knowledge.

- Part 3.4 focus on the study of sea migration, a facultative life history decision in Brown trout. We look both at the behaviour of sea trout during their marine migration, and the evolution of the reaction norm that leads to sea migration.

- Part 3.5 regroups several studies revolving around local adaptation in newly founded populations, using Brown trout as a model species.

- Part 3.6 describes a novel approach developed in a collaboration with the MUSSELKER IPEV project, allowing to investigate the skin and blood microbial signatures in Brown trout.

4.1. Patterns and evolution of individual growth in Brown trout

Individual growth is a proxy of fitness in most fish species. Large body size is generally associated to lower mortality, increased dispersal ability, and may also provide benefits for reproduction (higher fecundity, higher competitive ability to access partners, higher attractiveness in some cases, Dieterman et al., 2012; Werner and Gilliam, 1984; Vincenzi et al., 2014). Rapid growth could therefore be a mean to escape predation. It might be achieved however at some costs: first, fast growing strategies can be risky with regard to predation, second, growth can be potentially traded-off against fecundity, although such pattern is not commonly observed among salmonid species. Salmonids however add a layer of complexity, since they have the ability to migrate between ecosystems with contrasted growth opportunities (river, lakes, estuaries, sea). Rivers generally offer lower growth opportunities, but are a mandatory stage of development since spawning occurs in freshwater. At the other end of the spectrum, growth opportunities at sea are generally the highest, but predation risks might also be increased.

The Kerguelen environment presents a large variation of ecological contrast in riverine environment, thanks to heterogeneous geology, west-east climatic gradient, past and present exposure to ice. The introduced salmonids populations show generally non stable demography, as opposed to most other situations studied throughout the world, adding a layer of ecological contrast. In the present part of our report, we seek to investigate the different patterns of growth in terrestrial and marine ecosystems, focusing our analyses sometimes on some known and thoroughly documented

populations, other time benefiting from our large data cover over many systems and sample collections. Using the latter, we aim at unravelling general trend that could occur along the colonization front, under the direct effect of ecological factors but also in relationship with eco-evolutionary processes.

4.1.1. Factors driving growth prior to migration

In partial migratory population, the study of growth before potential migration may help to unravel the key processes that control individual decision, or tactic: resident or migratory. According to the future migratory status (resident or migratory), differences in growth have already been observed in fish (Gillanders et al., 2015), and the energetic status determines the migration destination (Boel et al., 2014). As the local density increases, the available resources per individual are expected to decrease, under the assumption that the ecosystem resources do not vary. Under the fasting endurance hypothesis and in these circumstances, one can expect that growth will decrease with time.

In this section, we used our longitudinal monitoring, focusing on some well documented Brown trout populations (where scales samples were available and already analysed) to investigate patterns of growth during their first years of life. Scales readings provide proxies of age at capture, as well as proxies of the relationship between body size and age all along the development of the fish. 4750 fish sampled in 7 rivers (Acaena, Château, Manchots, Nord, Norvégienne, Port-Kirk and Rohan) from 1962 until 2019 were included in the study. We analysed up to the 6 first years of individual life in fresh water (when available). Using these data, we were able to fit individual-based formulations of Von Bertalanffy growth function (vBGF) model in a Bayesian framework. In such model, the size at capture L can be related to growth exponent (k), size at asymptote (L_∞), and theoretical time at size 0 (t_0).

$$L_{i,j} \sim N(m_{i,j}, \tau)$$

$$m_{i,j} = L_\infty (1 - e^{-(k_{r,p} + \varepsilon_t)(j - t_0)})$$

Our primary goal was to investigate whether the future migratory status of the fish (resident or migrant), the local habitat (differences between populations), and the cohort (temporal effect) were influencing the patterns of individual growth. Various models were tested, accounting for each of these three factors effects on each of the three parameters of the model.

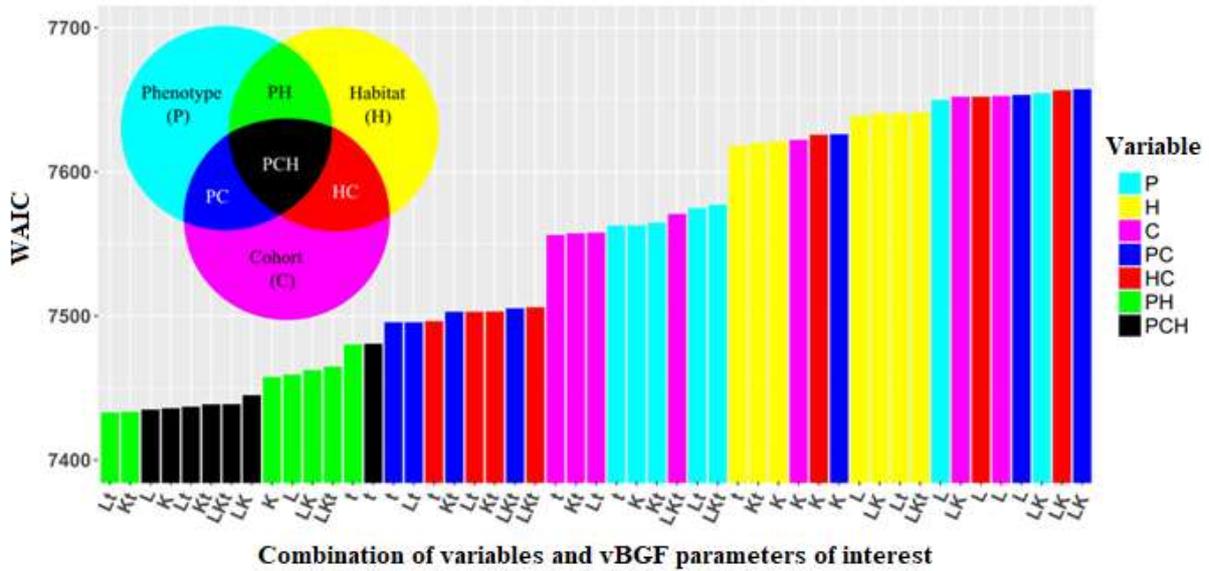


Figure 6: Weighted Akaike Information Criterion for 49 alternative vBGF models, ordered by increasing score. Lowest values indicate best fit conditional on model parsimony.

Model selection (Figure 6) indicated that the future phenotype, in conjunction with habitat and cohort factors had all significant effects on the model parameters. This was further confirmed and analysed using recursive partitioning of the data (Figure 7). Two periods were distinguished: during the early period of colonization in these populations, habitat effects were the more important. However, during the later period, the future phenotype also had an effect on growth.

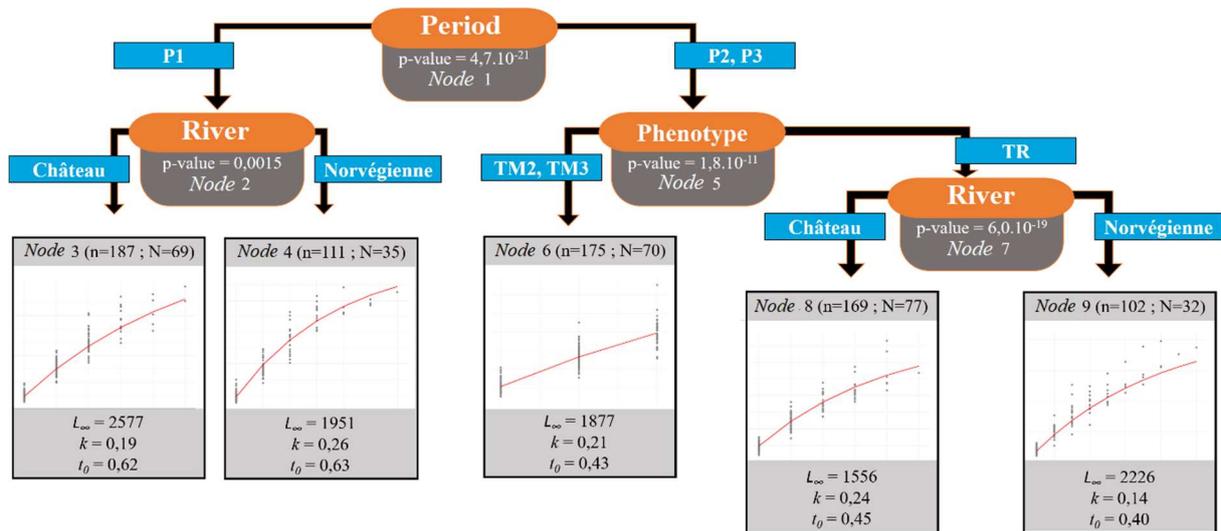


Figure 7: Decision trees obtained from recursive partitioning, considering river, period and phenotype, and their modalities (n =number of data, N =number of individuals). TM stands for migrant trout and TR for resident trout.

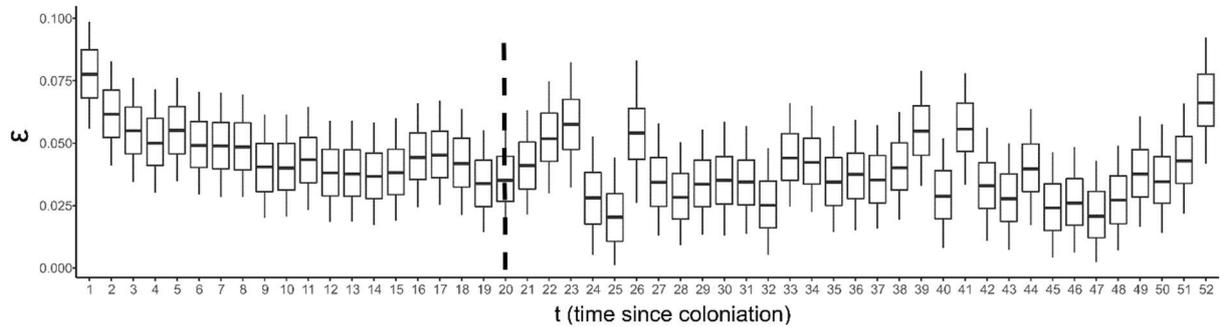


Figure 8: Cohort random effects estimates (ϵ_t). The median value (bold dark line) is given with the confidence interval at 50% ($CI_{50\%}$, plain boxplot segments) and the confidence interval at 95% ($CI_{95\%}$), thin segments).

The cohort or temporal effect on these populations generally shows a decline in individual growth over time since colonization during the two first decades. The negative density-dependence of growth (increase in competition for resources, e.g., food or mates) has already been proven in numerous studies (in fish: (Imre et al., 2005; Vincenzi et al., 2014), in mammals: (Loe et al., 2009; Mysterud et al., 2011), in amphibians: (Grayson and Wilbur, 2009). After that, temporal variation occurs without trend, although it seems that growth was increased during the last years, but these patterns are only noted in the oldest populations (Chateau and Norvegienne for instance, Figure 8). We also found that future migrants generally had a higher growth rate k than future resident (Figure 9), an interesting finding confirming existing literature. It is often demonstrated that individuals with the highest energy demand are those who grow fastest and are the fastest to migrate (Bohlin et al., 1996). Equally, once migration is chosen by some individuals, they might start to allocate more to growth to reach larger size necessary to survive the early marine period. The higher average growth rate for migrant trout seems to suggest that migrant are faster growers, but growth differences may either drive migration decisions or follow from migration decision. That result was however nuanced in some populations (Norvegienne notably), indicating that the mechanisms triggering migration might be of various natures, under environmental and / or genetic control.

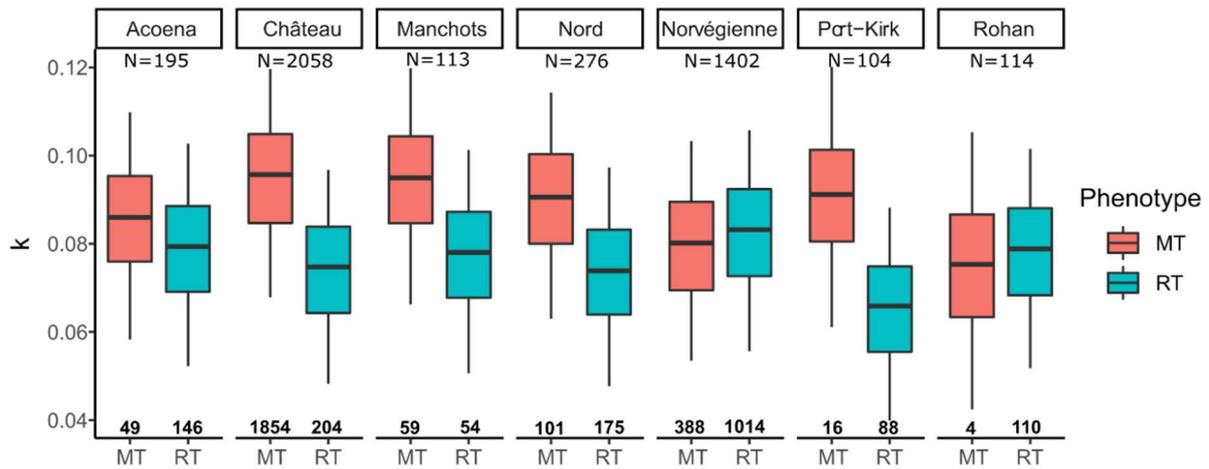


Figure 9: Estimates of growth exponent k according to river and phenotype. MT stands for future migrant trout and RT for resident trout. N summarize the number of total available samples by river. The number of samples by phenotype-category is given in bold below each boxplot. The median value (bold dark line) is given with the confidence interval at 50% ($[[CI]]$ (50%), plain boxplot segments) and the confidence interval at 95% ($[[CI]]$ (95%), thin segments).

What have we learned ?

- Individual growth may change as a function of future migratory status, but it is also influenced by environmental and temporal effects.
- Future migrants seem to have higher growth rate than future resident, in most populations.
- Temporal variation in growth rates over the decades has certainly occurred in this subset of populations.

These results are extracts from Lucie Aulus-Giacosa's PhD manuscript (Aulus-Giacosa 2021), and from several Master theses from G. Magne, V. Santanbien, H. Rogissart, and undergraduate internships (L. Baron, P. Gouzou, J. Levy, see § 6). These students actively contributed to scale readings and analyses, producing data that have been used for other studies in the present report and another publication (Aulus-Giacosa et al. 2019).

4.1.2. Large scale analysis of juvenile body size evolution

Early growth in freshwater remains a challenge in the eutrophic waters of Kerguelen Islands. The low primary production, the lack of prey that appears to trigger alternative diet (see § 3.3), as well as the low winter temperatures, all these mechanisms indicate that this early stage of life could be very selective. The previous study (§ 3.1.1) indicates various sources of variation in individual growth. The environmental and temporal effects though can include several mechanisms.

Granted, each new population is founded in a new environment, that may differ ecologically from the previous ones, thereby affecting individual growth through resource availability. Second, at the scale of the whole archipelago, temporal variation in ecological conditions can happen, for instance in relationship with climate change or due to the impact of other invasive species. Such effect should therefore affect all populations. But not all populations have been founded at the same date, and may therefore present contrasted densities: it may indeed take several generations before the carrying capacity of the population is reached. Additionally, as new populations are founded on the margins of the expanding metapopulations, environments with null to low density can constantly be found. These populations are founded by dispersers, and these dispersers may represent a non-random part of the origin population in terms of phenotypic and genetic variation (for instance, regarding growth, as evidenced in the previous paragraph). Thus, we might expect that the patterns in growth observed in old populations, with regard to local density, might not be the same in recently founded populations, because of this spatial sorting of phenotypic variation due to dispersers.

We here however face a challenge: to disentangle the effects of these various factors would require a large data set encompassing an important number of populations at representing various stages of colonization, and also integrating general temporal variation. Such undertaking now becomes possible thanks to our long term monitoring of populations. In the present analysis, we browsed our complete database regarding individual captures over 42 populations and 57 years of data (for Brown trout). In order to be able to lead a comparative analysis, we focused on body size at capture during the second year of life (between 1+ and 2+ ages). This age ensures that all fish lived their whole life in freshwater yet. To capture this part of the age pyramid however would require also to have ascertained the age of all these individuals. We first targeted individuals with body size ranging between 50 and 240 mm: we found 46241 occurrences in our data. Between these boundaries, we expected to have 1+ to even 4+ fish. Looking more closely, 6191 of these fish had already been aged using scale readings. We then trained a learning algorithm on these 6191 fish, in order to predict the age of any other fish based only on its body length and day of capture in the year (Julian day). Using the knn package for neural networks in R, we found 97% efficiency in age prediction. We therefore used the algorithm to infer the age of all the 40050 remaining fish, and select only the 1+ (Figure 10). We narrowed down again the sample to only encompass data sampled during the growth season (between the 150th and 280th day of the year, starting from the 1st July), thus discarding again 5% of our samples. We then obtained 21639 1+ fish.

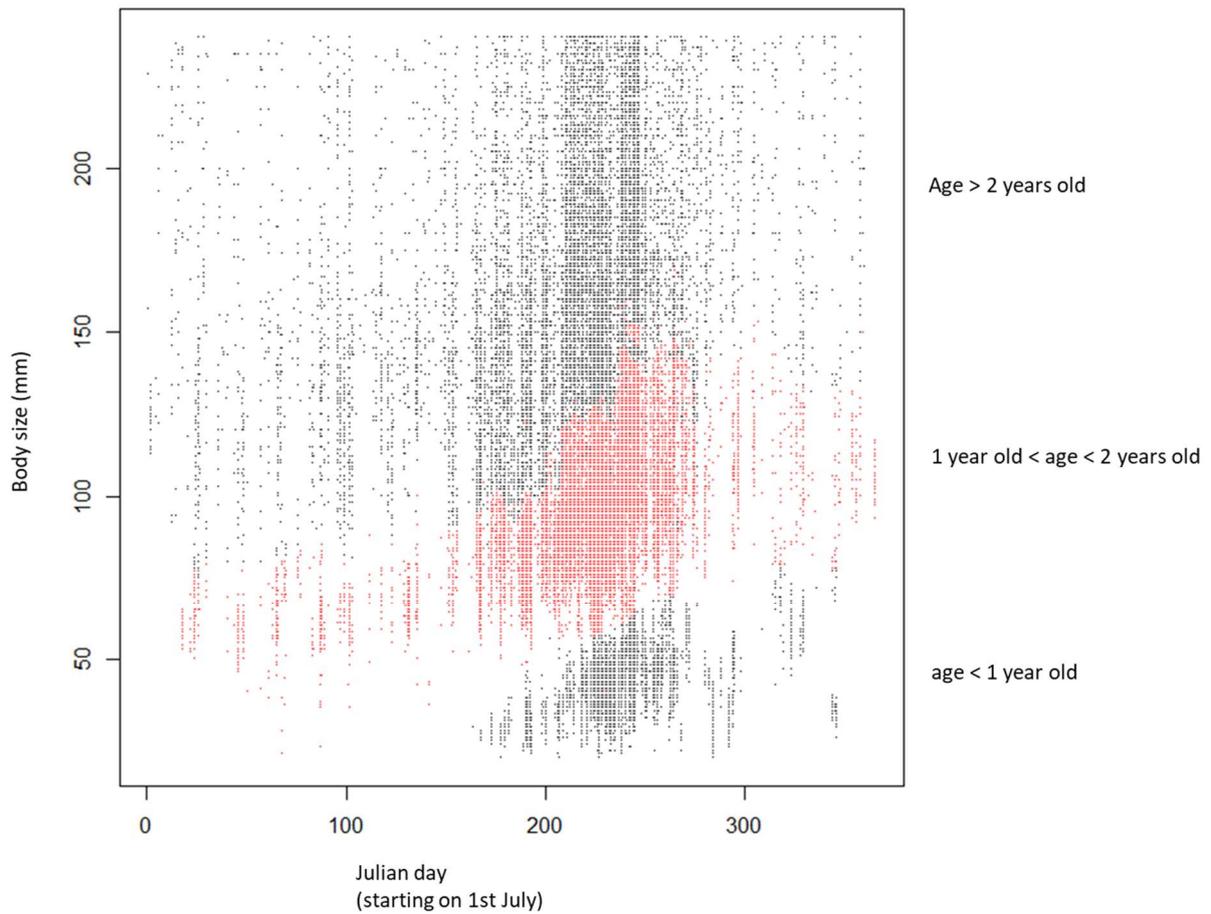


Figure 10: Relationship between body size (in mm) and Julian date of capture in the year in our whole dataset (all shown points) and for one-year-old fish (as detected by the neural network learning, in red).

As explained earlier, these fish represented 42 populations over 57 years (1962-2019). But these populations also present substantial variation in their founding dates, and have often been sampled multiple times (Figure 11).

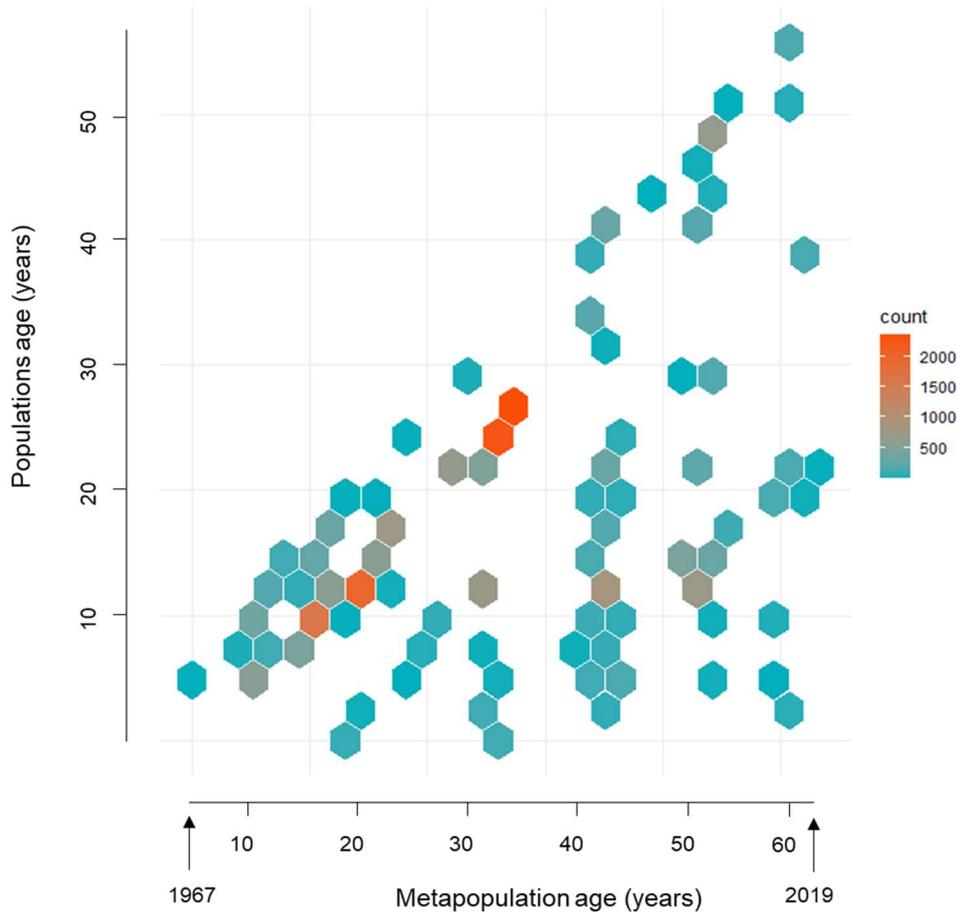


Figure 11: Density of sampling as a function of metapopulation age and populations age.

We name “metapopulation age” the time spent between the founding of the metapopulation and the date of a sample collection. Likewise, we name “population age” the time spent between the founding of the local population and the date of a sample collection. We then analysed these data using a mixed-effect linear model, in order to test the effect of metapopulation age, population age, and their interaction on the slope of the relationship between body size and Julian date of capture, that is, growth. We also included a categorical variable to contrast populations naturally colonized with introduced populations. The local environment effect related to each population was modelled as random effects on the intercept and slope of the relationships. Our findings are summarized in Figure 12, that predicts body size as a function of metapopulation age and population age in naturally colonized or introduced populations (at the 226th day of the year as a standard).

In naturally colonized populations, we found that body size evolved slowly and positively on the colonization front: body size in young populations founded recently was higher than in young populations founded at the beginning of the metapopulation expansion, an expected outcome of the spatial sorting hypothesis. It is also relatively consistent with the previous analyses on the drivers of migratory tactic (§ 3.1.1). In each population however, while local density likely increased as a function of time since founding, body size decreased very quickly, as expected under the competition for resource hypothesis.

In introduced populations however, body size appeared to evolve differently. First, initial body size was always lower than in naturally colonized populations. Second, it evolved slowly and positively in

newly founded populations as the metapopulation got older, but this potential evolution cannot be the result of spatial sorting here, since the population were not founded by dispersers. Second, and somewhat surprisingly, as populations got older, body size did not decrease. In fact, it even appeared to increase in the last two decades.

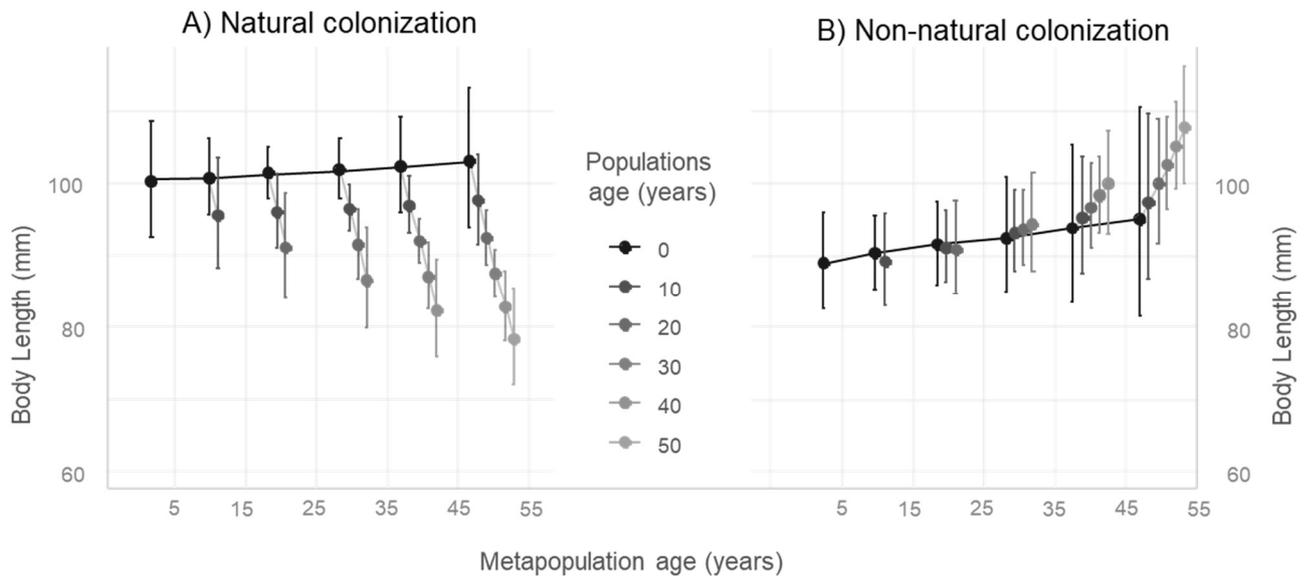


Figure 12: Average body size (mm) predicted (using fixed effects of the model) at the mean capture date (226th day of the second year) by the best model, as a function of metapopulation age and population age for A) naturally colonized rivers and B) non-naturally colonized rivers. The black lines indicate the evolution of body size in newly founded populations, the grey lines indicate the evolution of body size when populations get older.

The differences in body size evolution between naturally colonized and introduced population might be explained by several facts. First, it is likely that the rivers where fish were introduced are not a random subset of the ecological spectrum available: these systems are usually large, with an easy access to sea, and generally not far from human presence. They also bear the ecological footprints of human presence: they can therefore undergo selection on body size through fishing, community assemblages are modified through various species introductions, affecting ecosystem dynamics and productivity (Lebouvier et al. 2011). Finally, the various genetic origins, numbers and life stages of propagules used to stock these rivers (reported in Lecomte et al 2013) may also have profound evolutionary consequences, in shaping the genetic and phenotypic foundation of these man introduced populations, notably the relationship between density and growth rate of individuals (Brunsdon et al 2017), whereas dispersal conditions the founder effects in naturally colonized systems.

These results on the one hand confirm the role of expected drivers (spatial sorting and local density) of the evolution of body size in an expanding metapopulation, apparently leaving durable footprints on phenotypic diversity. The contrast between naturally colonized and introduced populations however was not anticipated. Human induced evolution has been recently investigated in details (Hendry et al 2017), and human impact in subantarctic ecosystems is also well described now (Lebouvier et al. 2011). Our study however goes one step beyond, by showing how human footprints in the subantarctic environments alters evolutionary trajectories in an expanding invasive species. There is

little reason to think that other species, including native ones, may not be equally influenced, and this fact should be especially considered in restoration plans.

What have we learned ?

- *The expanding metapopulation of Brown trout drives the evolution toward bigger body size on the colonization front.*
 - *density-dependent regulation of body-size proceeds as expected under a competition for resource mechanism*
 - *But human influence dramatically alters these evolutionary trajectories.*
-

These results are extracted from a article published in Biology Letters (Aulus-Giacosa et al. 2021), based on L. Aulus PhD manuscript (Aulus-Giacosa 2021).

3.1.3 Growth at sea during the early steps of the colonization

As a partial migratory species, every Brown trout faces a choice: to stay in the river where they were born until they reach sexual maturity, or to migrate downstream, possibly reaching the marine environment. The subantarctic islands present rather small watersheds, and therefore, most of the time, access to sea is easy. The evolution of partial migratory tactics remains a central question for salmonids and beyond, and it always involves the cost and benefits that each tactic entails. Migrating at sea thus potentially offers better growth prospects, although it can be traded against increased predation risks (especially in Kerguelen where predation in rivers might be reduced, notwithstanding cannibalism). An increased growth can later provide a benefit in terms of mating success. But it can also be a tactic to counteract parasites, since all external parasites will not tolerate the osmotic contrast that salmonids undergo through the smolting process. We are aware of parasites in marine environments in Kerguelen. It is less clear for freshwater environments: for instance, we do not know yet if the nematodes found in stomach contents are active parasites. Finally, migration can allow individuals to disperse to other rivers, and possibly colonize new rivers. In such cases, a successful founder of a new population may sire hundreds of offspring that will themselves reach sexual maturity and reproduce: the fitness of such individuals is thus very high.

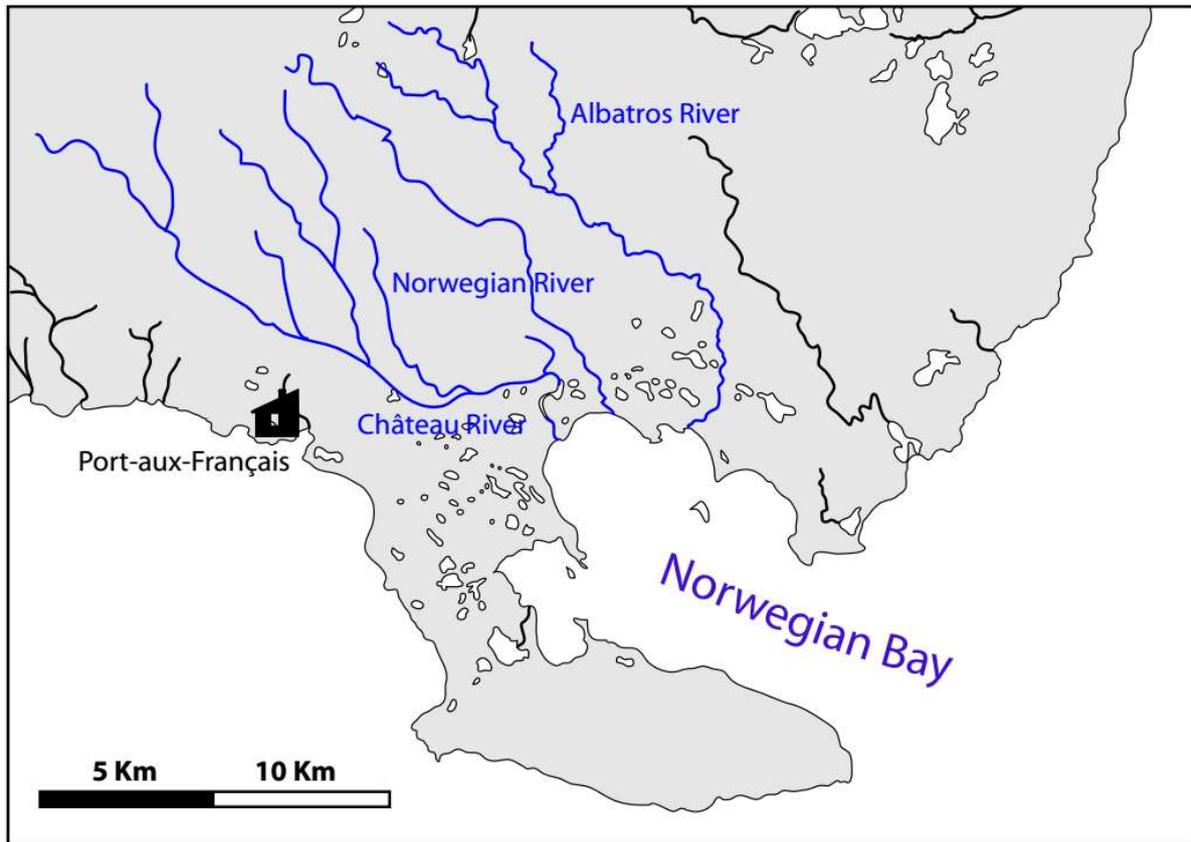


Figure 13: Map of the Norvégienne Bay with the three rivers where sea trout were sampled.

We here report result on growth at sea during the early steps of the colonization of Kerguelen Is. In the Norvégienne bay (Figure 13). In this bay, the Chateau, Norvégienne and Albatros rivers are mouthing together. For the record, natural reproduction occurred in 1962 for the first time in the Chateau river, in 1968 in Norvégienne river and in Albatross river. During the 1971-1984 period, regular samplings occurred in these rivers and their estuaries, as well as along the bay shoreline (using either electrofishing, rod fishing or nets) at nearly any time of the year. A total of 1089 sea trout were caught, measured for weight and length, and phenotypic sex was established by examining gonads for 486 of these individuals. Scales samples were taken for ageing. Individuals smolting at age 2 and 3 were kept for further analysis (N = 1016). Observed sex-ratio among these sea trout was favouring females (between 54% and 57% of the samples). Looking at the body size and weight distribution within and between years of development, it was possible to ascertain several facts. First, males and females achieved different growth during their first two years at sea, but these differences were compensated later on. Second, the observed growth in the coastal marine environment of the Norvégienne Bay was excellent, with individuals reaching 2 to 3 Kg and 60 cm during their fifth year on average (Figure 14), these numbers ranking among the best known growth worldwide for this species. Third, loss of weight during winter could be used to approximate reproductive investment. This investment represented about 18 to 19% of the total weight for females and 15 to 21% for males, a range of values that are quite high. It therefore seems that rapid growth at sea is not traded against fecundity, and possibly not against survival. Age distribution indicates that individuals older than 7 years are rather frequent – something that is not often observed in the initial distribution area. It also might be possible that sea migrant can survive better than resident fish, although we have not yet specifically investigated this matter. Finally, during this 1971-1984 in the Norvégienne bay, we did not find any obvious trend in

growth at sea, implying that ecological conditions in the marine coastal ecosystem remained stable at that time.

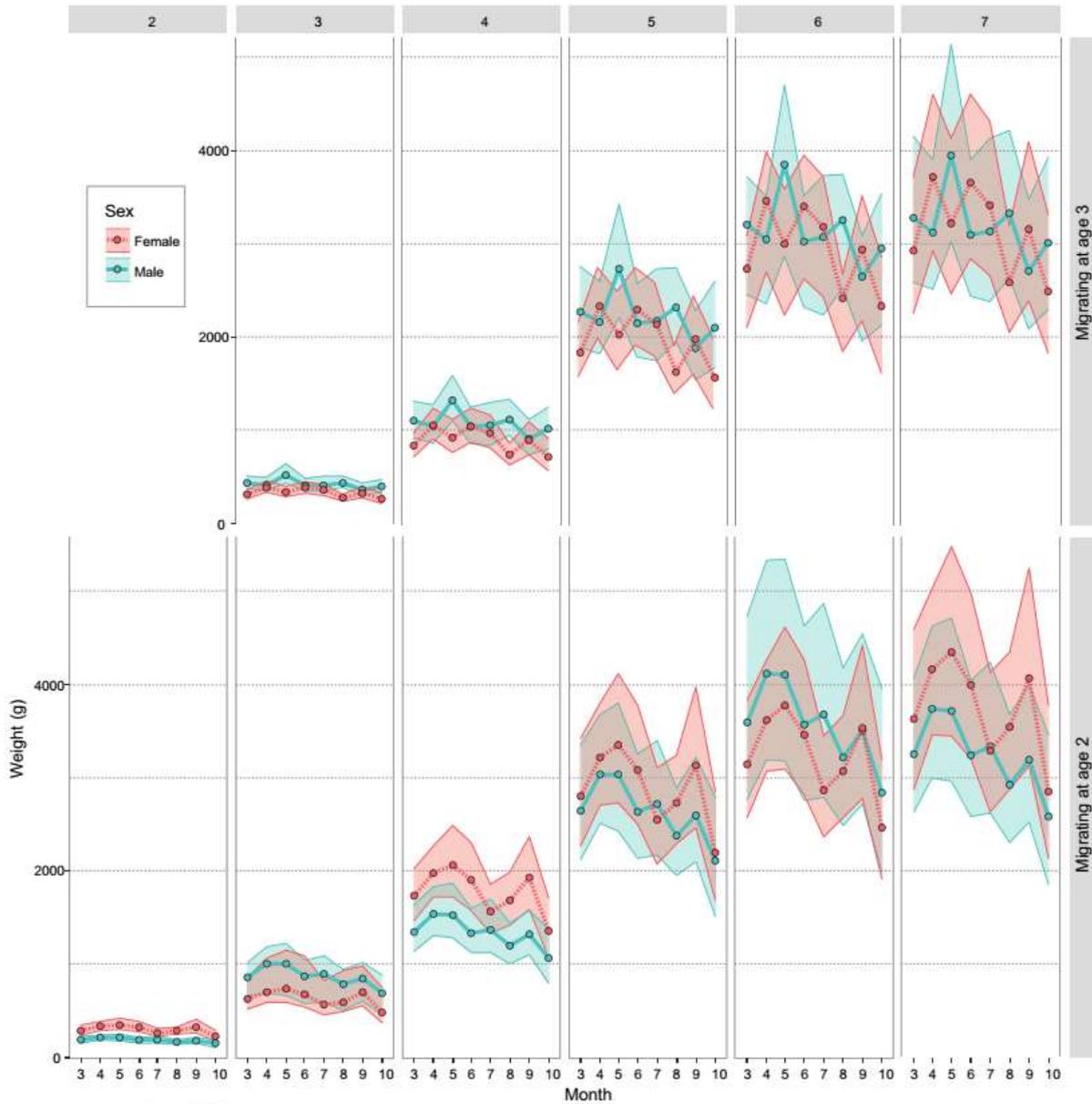


Figure 14: Median growth in weight (g) for male and female individuals migrating at 2- and 3-year-old (as predicted from the mixed-effect model fitted on our observations). Envelopes indicate 95% credibility interval. Reproductive investment is estimated by comparing month 5 and month 8 (May and August)

What have we learned ?

- Growth at sea during the early steps of population increase in the Norvégienne bay was excellent, for both males and females
 - Reproductive investment and lifespan were also high, possibly indicating a lack of trade-off between the migratory strategy and these traits, at that time of the colonization in this area.
 - Growth conditions at sea appear to have remained stable during the 1971-1984 period.
-

These results are extracted from a manuscript published in *Polar Biology* (Jarry et al. 2018).

4.2. Ecology and growth in lakes for *S. alpinus*.

Arctic char (*Salvelinus alpinus*) was introduced in Kerguelen islands in 1991 in Lake Fougères and in 1992 in Lake Armor. But our long-term monitoring found no occurrence of the species in Lake Armor afterward, it was only found in the outlet of the Fougères lake, mouching in the Fjord Bossières (Figure 15). This species, as its name indicates, is however no stranger to seemingly harsh polar environment. It is also known to show repeatable divergence in morphology and behaviour related to eutrophic conditions: dwarf morphs occupy the less productive bottoms of lakes, whereas faster growing morphs are observed in the pelagic and coastal areas. Often too, a third carnivorous morph is observed, generally feeding on conspecifics.

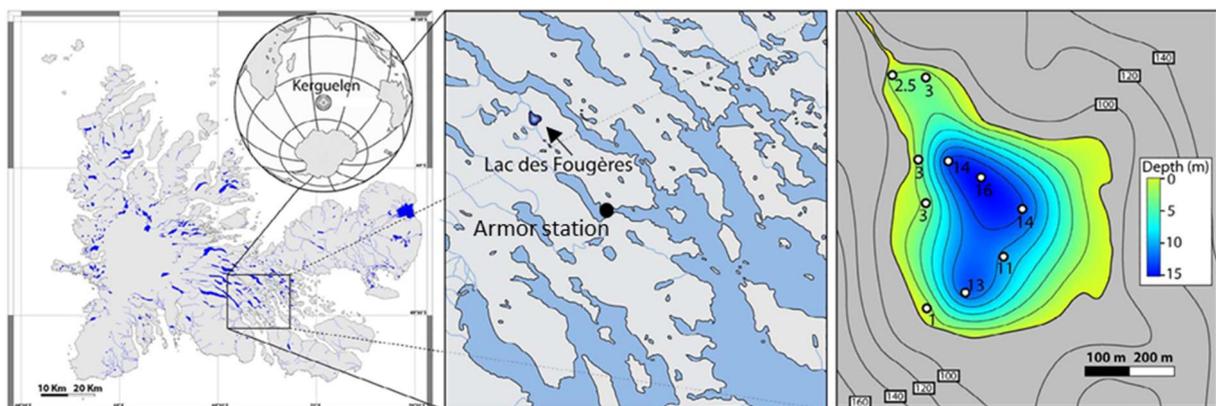


Figure 15: Map of Kerguelen Island and position relative to southern hemisphere land masses (left panel), sampling location for Kerguelen Island Arctic char (middle panel) and bathymetry of Lac des Fougères (right panel)

During SALMEVOL-2, we conducted a sampling of the outlet and of the Lake Fougères itself, using electrofishing and gillnet sampling. Weight, body size, sex, maturity stage and stomach fullness were recorded. Age was determined using otoliths, and dorsal muscle tissue were sampled and frozen for isotopic analyses. We also sampled for benthic invertebrates and zooplankton using standardized benthic invertebrate sampling methods and a 90 μ m zooplankton net towed either manually by wading

and troughing, or behind a small inflated boat. Using these samples, we were able to investigate variation in trophic ecology of the arctic char. In particular, using $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, we estimated an index termed Percentage Littoral Reliance (PLR), that describes how much an individual relies on littoral productivity versus pelagic productivity in its feeding behaviour.

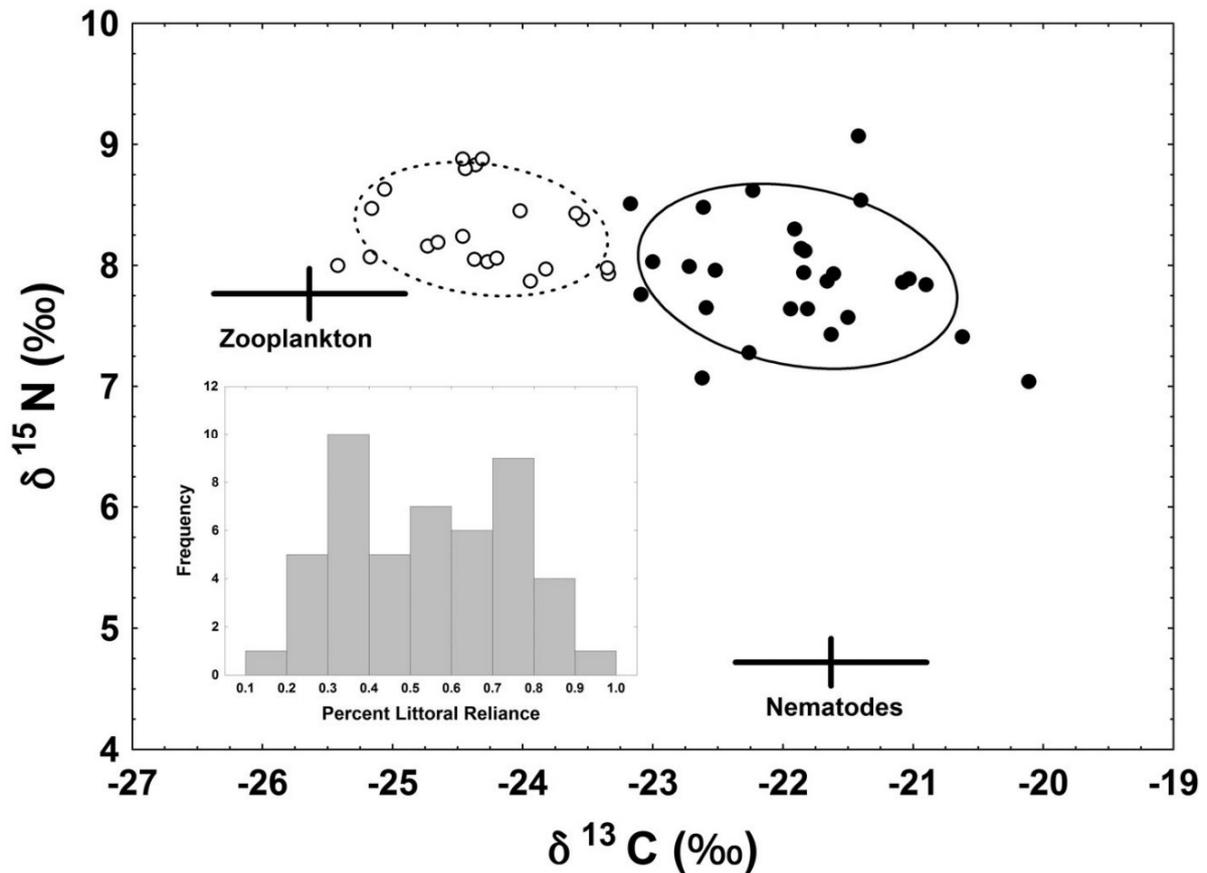


Figure 16: Bivariate stable isotope plot of Lac des Fougères for *S. alpinus*. Black circles indicate the predominantly littoral feeding individuals, while open circles indicate predominantly pelagic feeding individuals. Ellipses correspond to approximately 1 S.D. Crosses denote the mean \pm 1 S.D. of pelagic zooplankton and littoral captured nematodes used to define the two-compartment mixing model end members required to determine percent littoral reliance. The inset histogram plots percentage littoral reliance of all Lac des Fougères *S. alpinus* computed using the mixing model.

The results of our sampling first indicate that 29 years after the introduction, Arctic char have grown and reproduced in the lake. Life history traits values found here generally equated those known for sub-Arctic populations, but not Arctic ones: mortality rates appeared indeed higher and maximum ages (about 7 years old) lower than in Arctic populations. The population seemed to split evenly between littoral feeders (48.8%) and pelagic feeders (51.2%, Figure 16). Smaller fish generally relied more heavily on pelagic feeding (Figure 17). Although the development of resource polymorphism is known in Arctic char, it generally results in morphological adaptation, something that was not apparent in the Lake Fougères population: this might be indicative of the temporal time scale needed to witness the effect of trophic divergence on phenotypic evolution. One other surprising fact was the lack of detection of cannibalism in our samples. This might be related to maximum fish size, that did not exceed 40 cm here, a size threshold above which cannibalism is generally observed. It is possible that the reduced seasonality in primary production and temperature in Kerguelen compared to the initial

distribution area of the species might preclude the appearance of cannibalism: individuals may achieve slower but more stable growth at reduced maintenance cost.

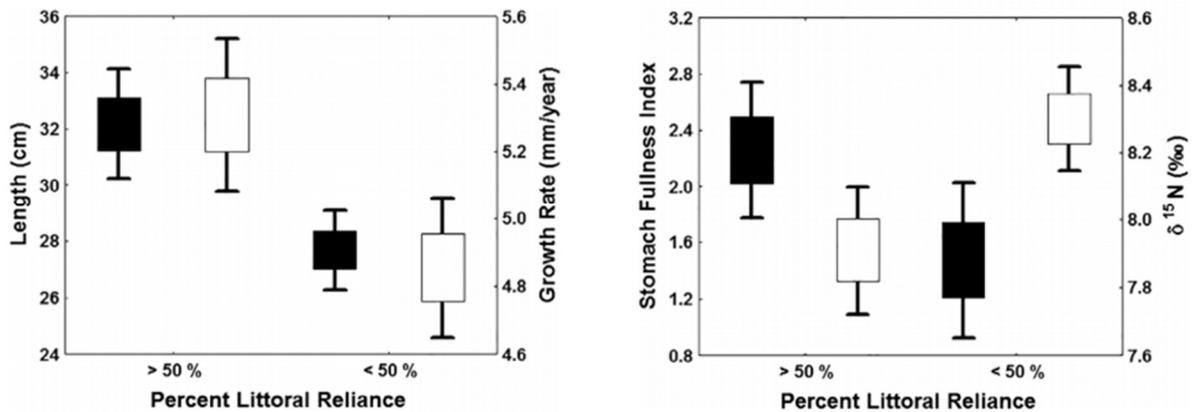


Figure 17: Means \pm S.E. (filled bars) and means \pm 95% confidence intervals (whiskers) of length and average growth rate (top panel), stomach fullness index and trophic level index, $\delta^{15}\text{N}$, (bottom panel) for Lac des Fougères *S. alpinus* having high (>50%) and low (<50%) littoral reliance as computed using a standard two-compartment mixing model. In the top panel length is plotted with black bars and whiskers, and growth rate with white bars and whiskers. In the bottom panel stomach fullness index is similarly plotted with black bars and whiskers, and $\delta^{15}\text{N}$ with white bars and whiskers

These results show that incipient divergence process observed on long established populations of Arctic char in their initial distribution area is reproduced on a very short time scale here in Kerguelen: size-dependent strategies are clearly at work. However, the effect on morphotypes are not yet detectable. Because the trophic ecology of lakes is strongly related to climate variation, it is very likely however that such situation will evolve quickly, since the subantarctic region is undergoing a strong and rapid temperature and rainfall change. Our personal field observations vividly confirm these predictions: all ponds around the lake were dried up, and the lake outlet was also dried up – a fact we had not witnessed during any previous field campaigns.

What have we learned ?

- Arctic char persists in Lake Fougères in the Kerguelen islands.
 - Incipient divergence process was observed as in other sub-arctic ecosystems where the species occurs.
-

These results are extracted from a manuscript published in *Journal of Fish Biology* (Eldøy et al. 2020), and are the results of a collaboration with the NTNU (Norway).

4.3. Unforeseen plasticity in diet

As advocated before, terrestrial ecosystems in Kerguelen island have low productivity, a fact that can impose strong constraint on early life history in salmonids. Salmonids indeed belong to a high trophic level, and are generally considered as strictly carnivorous species, metabolically adapted for high catabolism of proteins, and low utilization of dietary carbohydrates. A puzzling fact however is that they appear to have conserved a “mammalian-type” nutritional regulation of glucids: their glucokinase encoding gene and its enzymatic activity can be regulated by carbohydrates (as observed in captivity, Panserat et al. 2001). Yet, no study ever reported any evidence for natural substantial ingestion of carbohydrates in wild populations. But the Kerguelen environment is more akin to a post-glacial ecosystem that the initial area of distribution of many salmonids, with reduced diversity in food, and eutrophic ecosystems. Additionally, colleagues from the IMMUNOTOXKER project found a puzzling observation in Kerguelen Brown trout: many individuals presented advanced symptoms of hepatic disorders (Jaffal et al 2015), but they were unable to relate such disorders to any of the investigated factors at the time (they were aiming at potential effects of contaminants). We therefore assumed that some salmonids could be more plastic than previously envisioned regarding their feeding behaviour, and could partly rely on the ingestion of carbohydrates to sustain their development.

To investigate this assumption, we sampled 45 Brown trout with body size ranging between 12 and 24 cm on the upper part of River Chateau. This sampling therefore targeted fish born locally, that had never migrated yet to marine environment. We analysed their stomach content in order to check for feeding behaviour. We sampled their blood and centrifuged it to separate the plasma fraction that was stored at -20°C, in order to measure various metabolites concentrations. Fresh livers were placed in -80°C nitrogen tanks, to later analyse the expression of *g6pc* (glucose-6-phosphatase) and *gck* (glucokinase) encoding genes (using RT-PCR protocols) and their respective enzymatic activity. These samples were compared to available literature on salmonids, but also to another batch of samples originating from fish farm, wherein captive individuals (*Oncorhynchus mykiss* sp.) were either kept fasting, fed with classical diet without carbohydrates, or fed with 30% carbohydrates diet.

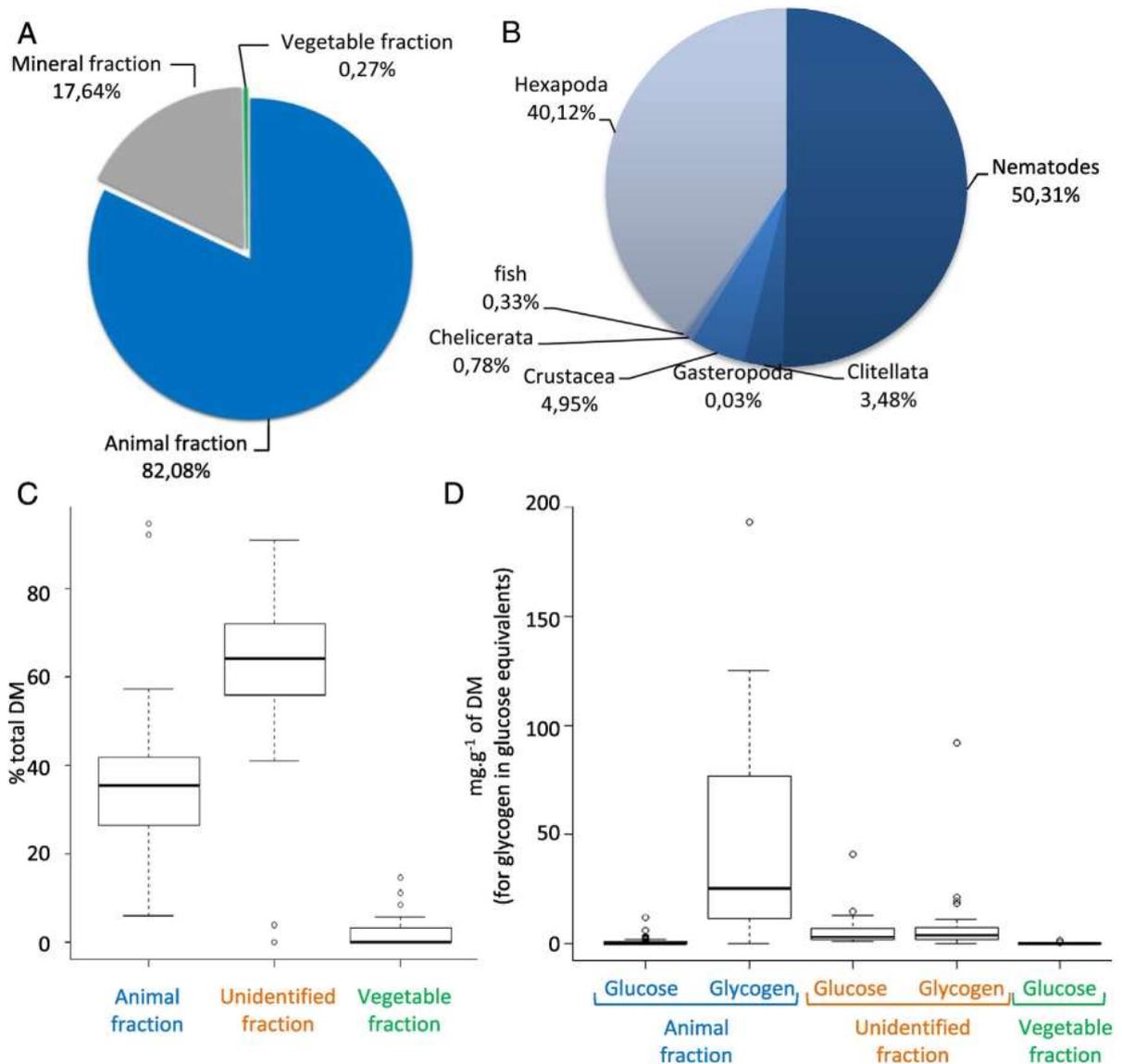


Figure 18: Stomach contents of Kerguelen trout. (A) Portion of animals, vegetables and minerals in the stomach, (B) description of species found in the animal fraction, (C) portion of animal, vegetable and unidentified fractions in percent of dry matter (DM), (D) glucose and glycogen content in animal, vegetable and unidentified fractions in percent of dry matter.

We found that the diet of the 45 sampled Brown trout was mostly composed of animal preys (Figure 18). Vegetal fraction was very reduced in this sample. We also notably found a substantial mineral fraction. The species targeted by Brown trout were in accordance with previous studies in Kerguelen performed at the same season (Lesel et al 1971, Wojtenka and Van Steenberghe 1982). Yet our personal observations of stomach contents in other populations at different times in the year indicate that it is also possible to find a substantial vegetal fraction. But despite the lack of this vegetal fraction in the contents in the present samples, we found a surprisingly high amount of glycogen in the ingested preys. This glycogen content is likely due to hexapoda (mainly caterpillars) that store reserves in this form.

Having confirmed that Brown trout ingested carbohydrates, we analysed the plasma to assess the glucose concentration in blood. Under fasting or usual diet, this concentration is known to remain below 0.8 g.L⁻¹. Under high carbohydrates diet in captivity, the concentration sky rockets above 1 g.L⁻¹. In Kerguelen trout, high values were found, characteristic of hyperglycaemia (Figure 19A). It therefore appeared that ingested glycogen was indeed digested.

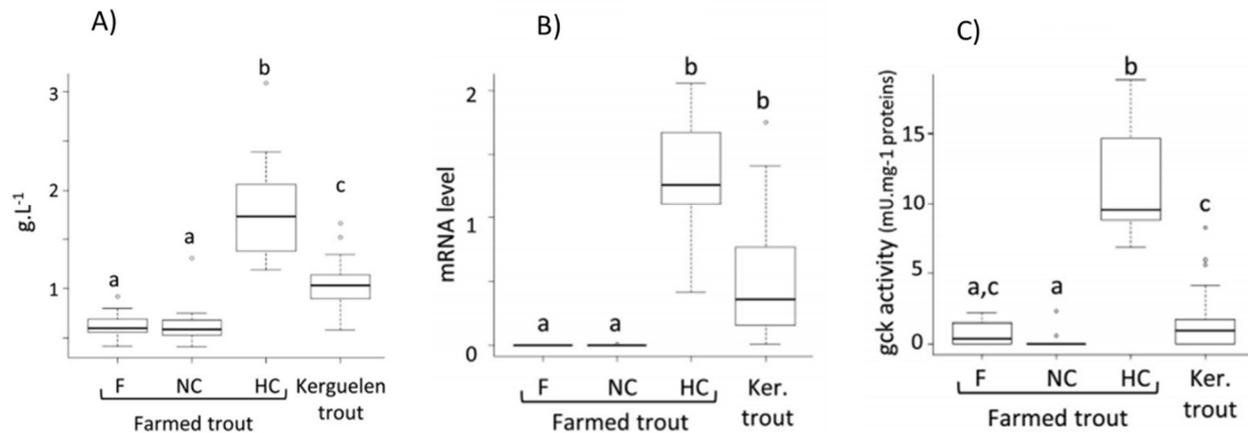


Figure 19: A) Concentration of glucose (g.L⁻¹) in blood B) Relative expression of *gckb*, C) *gck* activity. These measures are provided for various lots of salmonids, F: fasting, NC: normally fed, HC: high carbohydrate feeding (30%), all three lots being farmed rainbow trout, Kerguelen trout: Brown trout sampled in Chateau river.

We then investigated whether the glucokinase genes (only one showed here, the *gckb*, Figure 19B) were expressed in our samples. These genes encode for the glucokinase enzyme which catalyses the phosphorylation of glucose into gluco-6-phosphate, and acts as an ON/OFF system regarding the glycolysis cycle. While the *gckb* was not expressed in captive fasting or normally fed fish, it was clearly expressed in captive fish fed with high carbohydrates diet, and it was also expressed in wild Brown trout of Kerguelen. Additionally, we also found that the enzymatic activity of the *gck* in Kerguelen Brown trout was intermediate between captive normally fed fish and captive fish fed with high carbohydrate diet (Figure 19C). So, our fish in Kerguelen not only ingest and digest carbohydrates, but they also metabolize these carbohydrates to produce energy. Finally, we also found that the use of carbohydrates was more pronounced in smaller fish (12-16cm) but was unrelated to condition index, possibly indicating a critical stage in the development.

These findings have several implications. First, the Brown trout species here again show how much plastic it can be when environment is changing from the initial distribution area. Second, that the conservation of a regulation system of carbohydrates has a possible evolutionary explanation: salmonids are typical pioneer species able to quickly colonize post-glacial landscapes, as they have done multiply during the Eocene. Being able to switch to carbohydrate-based production of energy is certainly a perk in very eutrophic environment generally found after ice retreat. Third, we may not have sampled in the best conditions to measure the strongest effect of carbohydrate diet. As hinted before, we have witnessed stomach content of fish in November or December on other populations with significant amount of vegetal matter, such as algae. Additionally, we did not find in the present sample evidence of hepatic steatosis status as reported by Jaffal et al. (2015), although it is likely that such status is visible later in the life cycle. In any case, early growth appears to present a challenge to

salmonids in Kerguelen, and might have a strong selective effect, since body growth is usually a proxy of fitness, and is related to other traits such as dispersal, or fecundity.

What have we learned ?

- *Brown trout displayed an unforeseen ability to metabolize carbohydrates in Kerguelen islands*
 - *This phenotype is especially frequent among young fish (2+), indicating a potential selective filter that could affect population structure.*
 - *The conservation of this function in the salmonids genomes may be related with the pioneer status of these species, making them efficient colonizers of very eutrophic environments.*
-

These results are extracted from a manuscript published in Science of the Total Environment (Marandel et al. 2018), as a result of a collaboration with the NUMEA INRAE/UPPA lab in Saint-Pée sur Nivelle.

4.4. Partial migration

Migration is a major process that determines the distribution of organisms in space and time, with consequences at different scales of biological organisation, i.e. from individuals to ecosystems (Chapman et al. 2012). But migration is often a facultative life history tactic for individuals within populations. Only a fraction of a population may migrate while the other remains resident in its native habitat. This is known as partial migration and is common in many taxa, including insects, fish, birds and mammals. (Chapman et al., 2012). Salmonids are emblematic species of partial migration behavior as fish from a population may complete their entire life cycle in freshwater streams (residency) whereas another part may migrate to sea (anadromy) or to larger rivers or lakes before returning to freshwater streams to spawn (Dodson et al. 2013).

Migrants experience costs and benefits associated with transfer and settlement in both habitats. Indeed, migration can be costly in terms of energy expenditure, physiological development or risk of predation at the expense of survival, but can offer substantial benefits in terms of growth opportunities (e.g. better feeding habitat) and fecundity (e.g. increasing with size), promoting higher reproductive success. Migration, when leading to dispersal (the movement of individuals away from their natal population for reproduction), may also have an adaptive advantage at the population and species levels if it allows the colonization/recolonization of new habitats, ensuring the stability and resilience of metapopulations. The maintenance and evolution of these alternative migration tactics relies on short term balance between absolute fitness of these tactics and long-term eco-evolutionary advantages (bet-hedging, frequency-dependent selection and balancing selection).

However, evidence of eco-evolutionary causes and consequences of partial migration are extremely limited and identifying the proximate and ultimate mechanisms underlying partial migration in salmonids is still challenging. At the individual level, it is assumed that the migratory behaviour and physiological changes associated are triggered by a developmental pathway comparing a proximal trait with a genetically based development threshold. These alternative migration tactics are then seen as an adaptive phenotypic plasticity, allowing a plastic (via proximate cue) and/or an evolutionary

response (via threshold) to environmental changes. The threshold is expected to evolve in response to changes of absolute fitness of each tactic, as a function of the proximate cue (Tomkins & Hazel 2007). The proximate cue is a labile trait such as energetic state, metabolic rate, lipid storage or hormone levels (Ferguson et al., 2019), the expression of which is the result of multiple interacting factors. It can be determined by abiotic factors (e.g. temperature) as well as by biotic factors (e.g. inter/intra-specific competition). In salmonid species, this cue is commonly associated with a morphological trait, such as body size or mass, which serves as a proxy. Indeed, it is generally assumed in anadromous salmonids that body size positively influences the probability of migration because of size-dependent survival at sea. But this effect may vary with the age of the individual and other life history decisions (e.g. maturation). However, it is important to distinguish between factors involved in the migration decision from those that act as stimuli for the timing of the actual migration.

Indeed, conflicting hypotheses have emerged regarding the role played by body size and growth in the expression of migratory tactics (see Dodson et al. 2013 and Ferguson et al. 2019). Briefly, one hypothesis states that fast-growing individuals migrate to more productive feeding areas, while the other hypothesis states that rapid early life growth (and low density) is associated with freshwater residence. Using an experimental design to explore the proximate drivers of facultative migration in Brown trout, Archer et al. (2019) show that the frequency of migration tactic increased with food restriction. Thus, it is increasingly recognised that growing conditions may trigger the migration decision while size may influence the timing of migration (migrate this year or later), suggesting the existence of multiple thresholds for migration.

Migration propensities are likely to vary temporally and among populations because of environmental and biotic changes (e.g., population density) (Ferguson et al. 2019) which affect growth, survival and/or reproductive success. Populations exposed to similar environmental conditions can also express different migratory traits due to genetic variability in the threshold and in the genetic component of the cue. Indeed, variation among populations is also expected due to different genetic characteristics induced by selection (natural, sexual or anthropogenic). Phillis et al. (2016) estimated a higher migration threshold in an anadromous steelhead (*O. mykiss*) population above an impassable barrier than the population below. Archer et al. (2019) also found a higher migration propensity (smolting rate) in the naturally anadromous Brown trout population than the non-anadromous population in similar growth conditions. Interestingly, they also found that even individuals from the non-anadromous population can express the migrant phenotype, implying the capacity for migration was lying “dormant”.

Disentangling the role of proximate and ultimate effects on migration tactics decisions remains challenging, especially in natural populations because both processes act concurrently and the relative contribution of genetic versus environmental variation is rarely known (Ferguson et al. 2019). But the long-term monitoring of populations and the phenotypic changes observed allow us to shed some light on ongoing processes.

4.4.1. Migratory behaviour on the colonization front

The vector of colonization in salmonids is their anadromous form, which is achieved through a behavioural and physiological process termed as “smoltification”. Understanding the ecology of this part of the life cycle in brackish and marine waters is mandatory, since it can shed light on the benefits of anadromy, especially in Brown trout for which it is a facultative process. It can also help forecasting the process of colonization, notably accounting for the physical and chemical structure of the marine ecosystem used by sea trout. Such parameters may help us improve our colonization models through a better mapping of favourable marine areas between river systems.

To investigate these questions, we worked in the north-western part of the Brown trout distribution area in Kerguelen, focusing our efforts on the Val Travers population. This system is already studied in its freshwater area (see §3.5.1 and §3.5.3). For the present study, 31 sea-run Brown trout were first sampled in Lac Bontemps (freshwater), and at its outlet (marine water side), as well as in Rivière du Nord and Cascade du Lozère (Figure 20). Part of the fish were killed for various sampling and analyses, including ageing, body length and weight, muscle tissue for isotopic analysis, blood samples for metabolites analyses, stomach content for diet. Another 50 sea trout were captured downstream the Lac Bontemps outlet, anaesthetised, and tagged with acoustic transmitters. In the meantime, 50 acoustic receivers were deployed in several areas around the outlet, barring the Baie Irlandaise, and other accessible rivers systems either virgin of fish or already colonized (Figure 20). During one year, these tagged fish were monitored using the acoustic receivers, allowing to trace part of their movements, controls for entries in new rivers, or assess the physical and chemical parameters selected in marine water (temperature, salinity). While more than 50% of the Brown trout were regularly detected up to 10 months after release, a number of individuals (n=11) were lost to the study through mortality, tag expulsion or predation followed by the predator excreting the tag.

Somewhat contrarily to our expectations, nearly none of the tagged fish were detected outside the Baie Irlandaise area (Figure 20). They therefore were not particularly seeking new rivers to colonize. 9 individuals however were detected in Vallée des Merveilles, a recently colonized system, hinting at very substantial exchanges between Val Travers and Vallée des Merveilles.

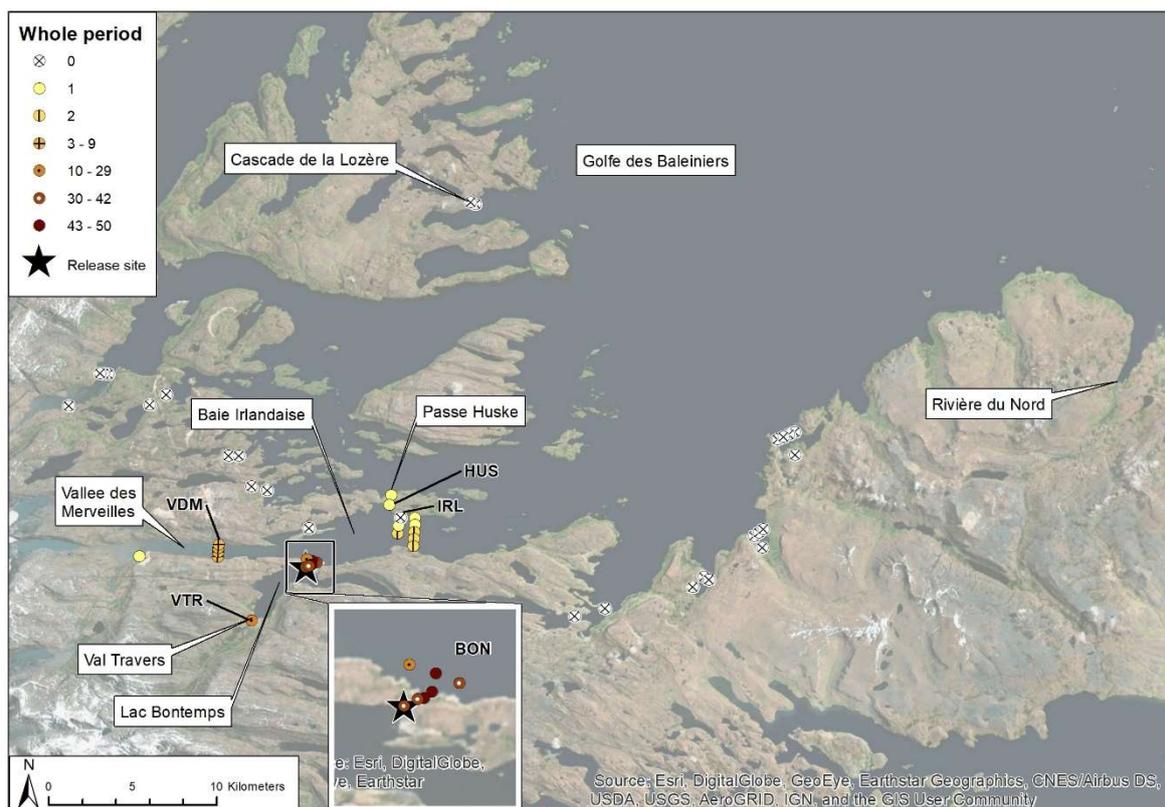


Figure 20: Map of the acoustic receiver array deployed (n = 50 receivers). Symbols give the location of individual receivers and number of individual sea trout registered at each receiver. The tagging site (large star) was located next to the outlet of Lake Lac Bontemps.

Ample variation in movement and feeding behaviour was observed. First, fish were distributed between either freshwater, brackish water or marine water throughout the year, but with different

proportions depending on the period of the year (Figure 21B). Temperature profiles corresponding to these three groups of fish showed that amplitude was greater in freshwater, and smaller in marine water (Figure 21A). Fish were more present in freshwater during austral winter (in relation to reproduction), but some of them stayed in marine water. During other periods of the year, a large portion of the fish preferred brackish water, which provides better feeding prospects than freshwater but higher temperatures than marine water. This result tends to confirm coastal dispersal modality as inferred from metapopulation dynamics approach (Labonne et al. 2013b). Fish preyed mainly on amphipods and fish (respectively 68% and 23% of the stomach contents). Isotopic signatures for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ were contrasted between sampling sites: higher values were observed for instance for the trout sampled in Rivière du Nord than for the ones sampled in Baie Irlandaise (Figure 22). Very few marine parasites were observed on fish. Metabolic and feeding status of Baie Irlandaise trout appeared to be very good, which might explain why they did not seem to migrate very far.

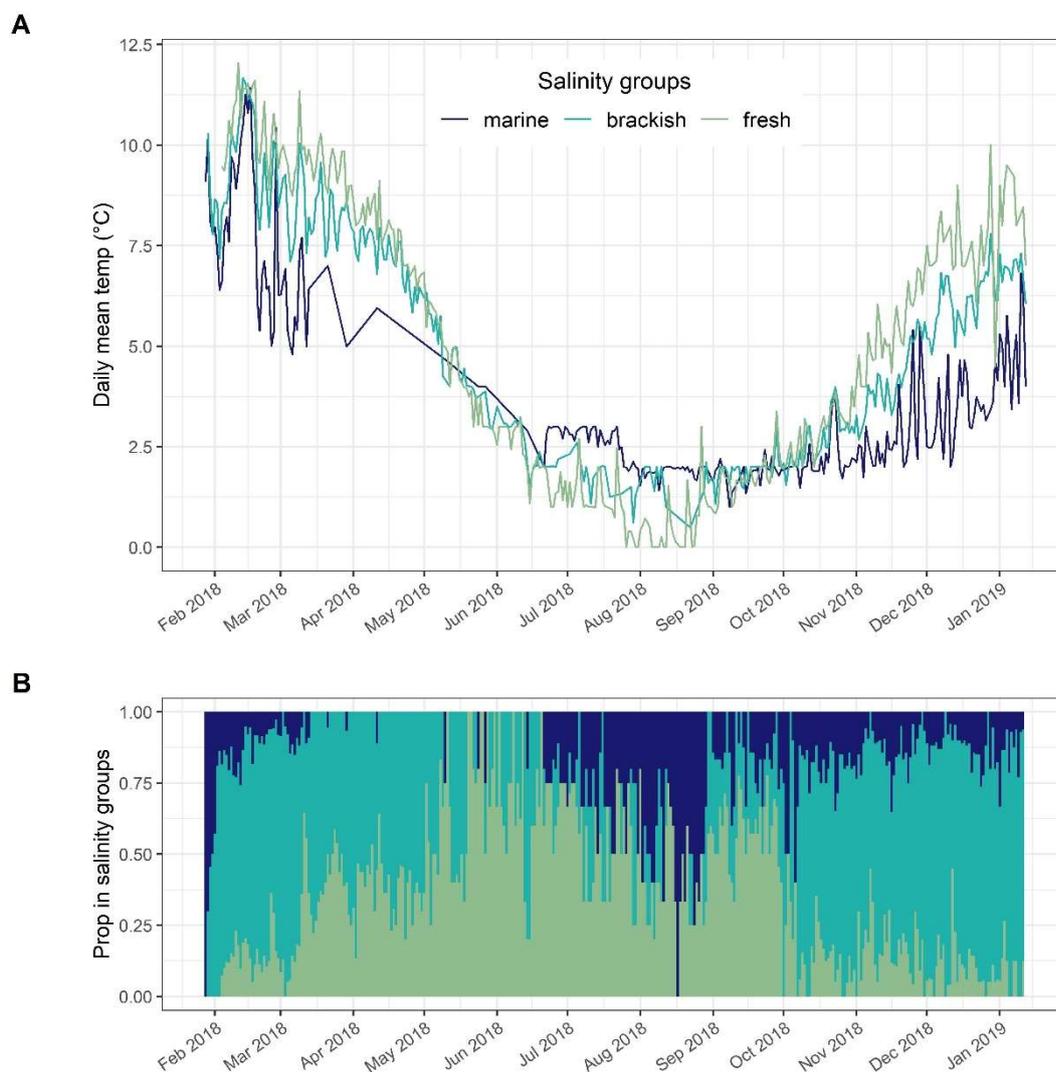


Figure 21. Salinity and temperature levels experienced by Brown trout tracked in the Lake Bontemps estuary and nearby areas. A) daily mean temperature experienced by the fish divided in the three salinity categories (fresh (<5‰), brackish (5-30‰) and marine waters (>30‰); B) daily proportion of

fish divided in to three salinity categories (fresh, brackish and marine waters). The proportions are based on the relative sample size for the actual day.

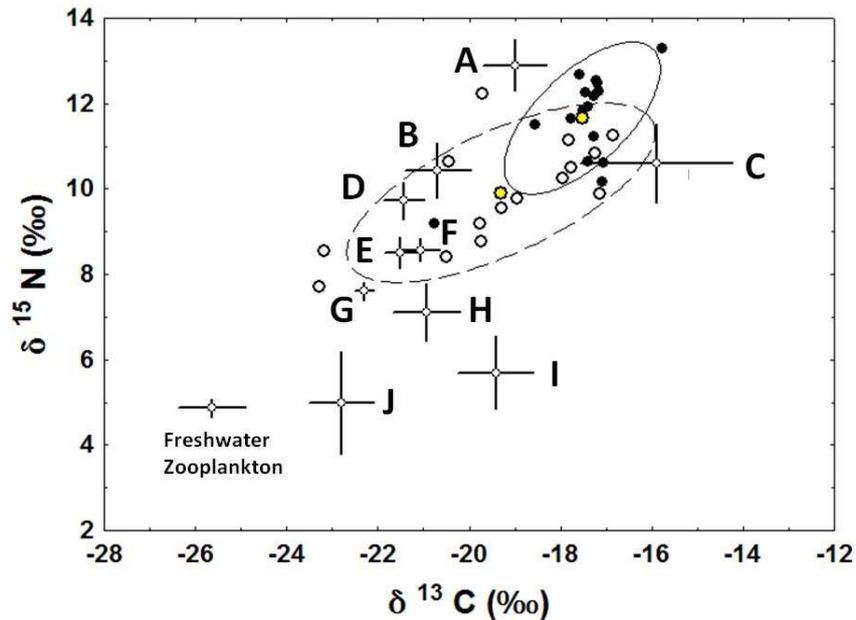


Figure 22: Stable isotope crossplot of Brown trout (circles) and Kerguelen invertebrate and fishes (black squares and crosses) grouped by Genus. Solid and dotted lines, respectively, plot the standard ellipse area (SEAC) for Rivi re du Nord (black circles) and Golfe des Baleiniers (open circles) sampled Brown trout. Ellipse means are denoted by the yellow circles. Freshwater zooplankton are labelled and provided as a freshwater reference value. Species plotted (and data sources) include: A - *Dissostichus eleginoides* (Cherel et al. 2008); B - *Cephalopod* sp. (Cherel et al. 2008; Guerreiro et al. 2015); C - *Ecinoderms* (Saucede et al. 2019); D - *Gymnoscopelus* sp. (Cherel et al. 2010); E - *Protomyctophum* sp. (Cherel et al. 2010); F - *Electrona* sp. (Cherel et al. 2008; Cherel et al. 2010); G - *Krefflichthys andersonii* (Cherel et al. 2008); H - prey fish species samples obtained from Brown trout guts (this study); I - nearshore sampled amphiod sp. (this study); J - *Thermisto* sp. (Cherel et al. 2008).

What have we learned ?

- Sea trout remained close from their tagging site in Baie Irlandaise, and no potential dispersers were detected in our sample.
 - Fish mostly selected brackish water with intermediate temperatures most of the year, except during reproduction period, when fish returned to freshwater.
 - Fish in the Baie Irlandaise presented different marine diet than fish from Rivi re du nord, stressing the probable contrast in marine environment.
-

These results are extracted from a manuscript published in Scientific Reports (Davidsen et al., 2021). This is a collaboration with the NTNU (Norway), the University of Dalhousie (Canada) and the Ocean Tracking Network (OTN, they provided all the acoustic receivers), and its success is in large part related to the presence of the scientific ship “La Curieuse” on Kerguelen, its dedicated crew, and the constant support from the Polar Institute Logistics. We have a specific thought for Captain Michel Beilloeil.

4.4.2. Evolution of migration age

Although most salmonids are anadromous species, they show different life history patterns with regard to marine migration. Some are said to follow mandatory migration, like the Atlantic salmon (although landlocked populations exist, like in Kerguelen). Other, like Brown trout, are termed as partial migratory species: they can either favour a full life cycle in freshwater, or alternate with marine (or brackish) water. These interspecific differences however must not shadow the wondrous intraspecific variation that can also be observed. For instance, in Atlantic salmon again, age of departure from freshwater vary within populations and between populations. In Brown trout, this is also very much the case, with the added difference that one should also account for the fact that a proportion of the population will remain resident. Under the conditional strategy framework, such strategy is expected to be maintained by frequency dependent cost/benefits balance between the two tactics: resident or migratory (Roff 1996, Gross 1996). One convenient way to summarize condition is to focus on some integrative traits related to fitness (the liability trait), such as body size, for instance, and to assume that above a given threshold value of this trait, the individual will change its tactic (Tomkins and Hazel 2007). Variation of this threshold is investigated using the probabilistic reaction norm approach, wherein ones model a probabilistic choice as a function of a continuous variable. Here, several approaches are found in the literature, but salmonids offer a yet unexploited opportunity: as scale reading allows to read in the past decisions of each fish, it is not only possible to estimate the age and size at which an individual decides to migrate to sea, but it is also possible to estimate the age and body size at which the same individual decides to stay in freshwater. In fact, each individual may take this decision each year of its growth, and such information can be extracted and statistically analyzed in the reaction norm framework.

Benefiting from this framework, we used our data collections on several populations of known history (Chateau, Norvégienne, Nord mainly – but other data were analysed too from Acaena, Rohan, or Manchots). For each population, we were able to gather samples at different times since colonization, in order to investigate whether the threshold for partial migration might have evolved, notably in response to increase in local density: we indeed assumed that increased density should tip the scale in favour of earlier migration to sea, since access to resources would decrease fitness benefits for residents. Part of our results are synthesized in Figure 23. We found that the probability to migrate (here for 3 years old fish) was highly controlled by body size. For the three populations envisioned, the probability to migrate to sea increased when fish reached about 200 mm. However, the exact threshold changes between populations, but also as a function of time since colonization. The most striking result is that in Chateau and Norvégienne rivers, the threshold for migration decreased: fish now migrate at a smaller body size than what they did 40 years ago. It is not however the case in Nord, where the threshold is much more difficult to estimate, and does seem to evolve in the opposite direction (but the population is more recent, so the effect of time since colonization might be more difficult to infer).

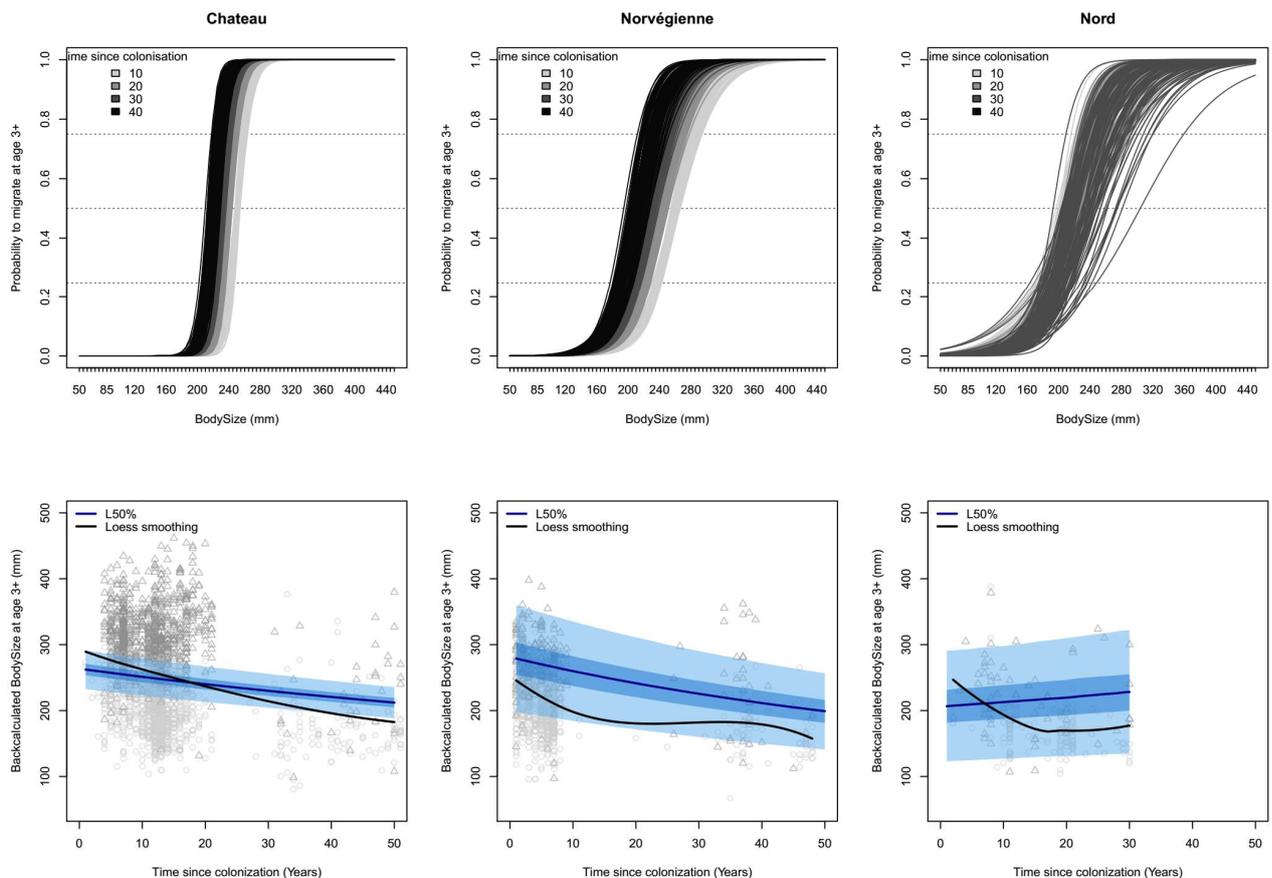


Figure 23: (upper panel) Probability to migrate as a function of body size and time since colonization for 3+ fish in Chateau, Norvégienne and Nord rivers. Each line corresponds to a projected reaction norm based on a posteriori parameter values. (lower panel) Size-specific probabilities of migration as a function of time since colonization reaction norm for 3+ fish in Chateau, Norvégienne and Nord rivers. The size at reaction norm midpoint (i.e. projected size for a probability to migrate of 50% or L50%, solid blue line) and envelope (L25%–L75%, dark blue; and L2.5% - L97.5%, light blue) are reported. Back calculated size for residents (grey circles) and migrants (grey triangles) are also given. The black line shows the trend in size over time since colonization (loess smoothing).

These results indicate that it is likely that the reaction norm to migration is currently evolving in the Kerguelen islands. This is clear enough in the Norvégienne Bay systems – that are also among the earliest colonized systems. The direction of this evolution seems to match what we could expect from the dynamics of balance between cost and benefits between the two tactics of the strategy, assuming that the coastal marine environment has not varied substantially, whereas the freshwater environment benefits are diminishing in correlation with the local increase in density. But this result is not replicated in Nord river for the moment, possibly because the balance between freshwater and marine benefits and costs is not the same. Other studied populations produced also variable results, but data availability for these populations also prevents to draw any solid conclusions from the observed patterns. We also have to remind here that body size itself is also evolving meanwhile (see § 3.1.2), and it does so in different directions depending on the river status (naturally colonized or introduced). Therefore, the final patterns of migration for each river will depend on the evolution of

body size on the one hand, and the evolution of the migration reaction norm on the other hand. A potential outcome for some rivers, like Norvégienne for instance, is that the *age* of migration itself will not change much. Again, some scientific expectations can be verified on our dataset, but we also uncover less anticipated directions in evolution. We therefore conclude that while general mechanisms are at work, the fabric of intraspecific phenotypic diversity might follow various pathways, and we yet have to unravel what dictates these differences.

What have we learned ?

- *It is possible to track changes in the threshold for sea migration in Brown trout*
 - *It seems that this threshold is decreasing: fish leave rivers at a smaller size now than at the foundation of the populations, possibly as a function of increased density in freshwater.*
 - *But this pattern is likely not homogenous among rivers.*
-

These results are extracted from a manuscript in preparation (Aulus-Giacosa et al., in prep).

4.5. Local Adaptation

Over the course of metapopulation expansion, and as discussed before, a variety of environments are encountered. While some general evolutionary patterns can be investigated in relationship to density gradients and dispersal on the colonization fronts, environmental heterogeneity between colonizable rivers are expected to drive local evolution through local adaptation. However, such adaptation is also expected to be supported by phenotypic – and therefore genetic – variation, a quantity that might be in short supply on the colonization front. If only a pair of dispersers found a new population, and if dispersal is relatively low, then these two dispersers will have a tremendous founder effects in genetic terms on the local population. And along this founder effect unavoidably comes a strong inbreeding, since the first offspring will probably later mate with each other.

4.5.1. Inbreeding and selection against homozygosity

These particular conditions we were able to study in Kerguelen Is., by focusing on two populations (Val Travers and Clarée, Figure 24) introduced in 1993 with offspring sired by parents of known number (2 and 3 respectively) and origins. These two populations thrived, and we were able to monitor them in 2003, 2009-2012, 2016 and 2018.

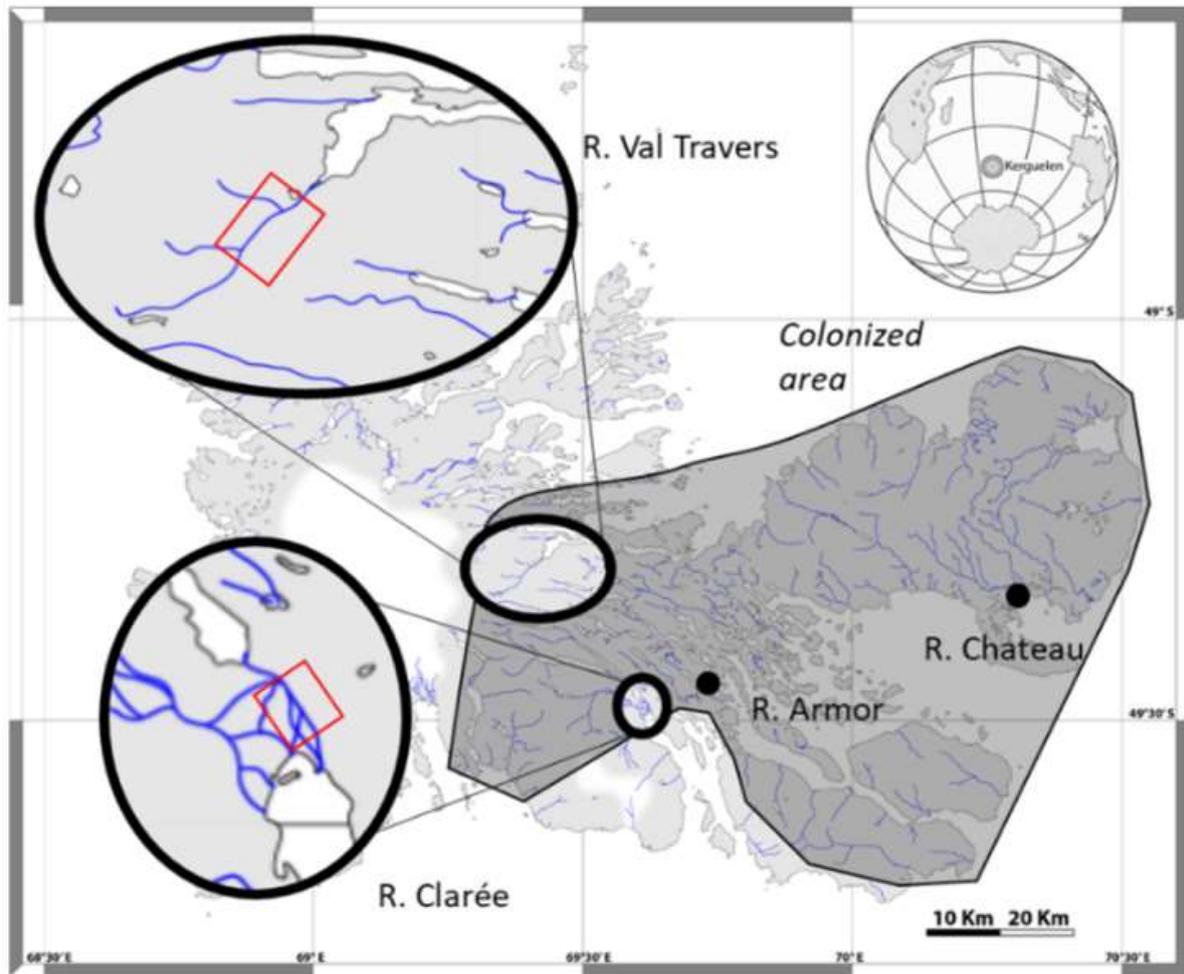


Figure 24: Locations of the two studied populations close to the western colonization front.

First, we investigated whether inbreeding was possibly an obstacle to local adaptation. Inbreeding is indeed expected to multiply the occurrence of homozygosity in the genome, possibly uncovering deleterious mutations in face of natural selection. When looking at the distribution of homozygosity level (HL) among individuals at 2 dates, 2003 and 2010, we found that HL was indeed very high in 2003 in Val Travers, and significantly decreased in 2010. However, such result was not repeated in Clarée where HL was initially lower but remained constant (Figure 25).

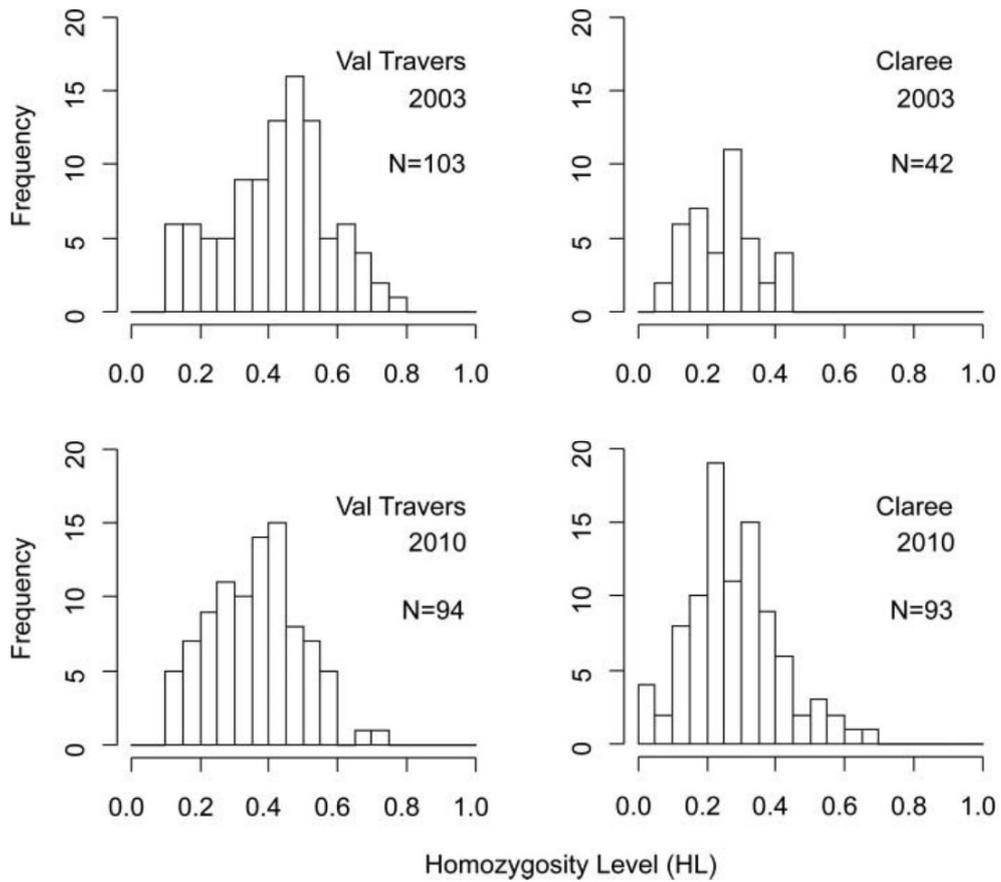


Figure 25: Distribution of homozygosity level (HL) in Val Travers and Clarée for the two sampling years (2003 and 2010).

We also found that age of capture of individuals was negatively correlated with individual homozygosity: individual captured at high ages had lower HL (Figure 26). The pattern however was clear in Val Travers, but it was more variable and sex dependent in Clarée. To sum up: inbreeding was very high as expected, but it was selected against mainly in Val Travers population, whereas it did not appear to be so in Clarée population.

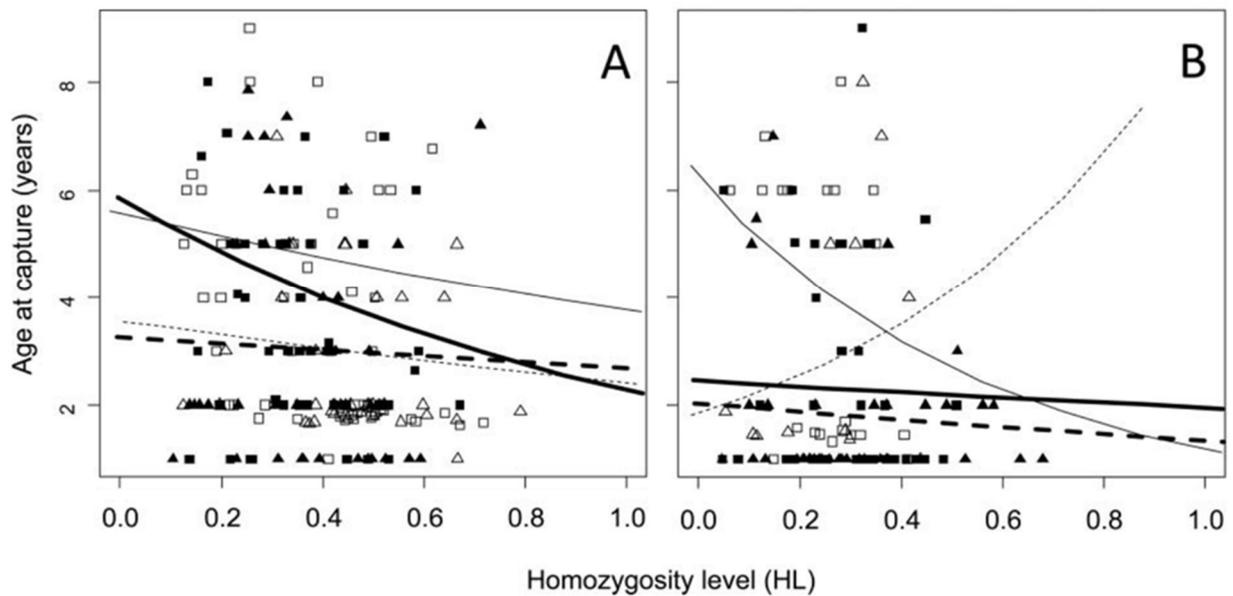


Figure 26: Effect of homozygosity level (HL) on age at capture for the Val Travers (A) and Clarée (B) populations. Open symbols indicate data sampled in 2003 and solid symbols indicate data sampled in 2010 (triangles for females, squares for males). Curves show predictions from the quasi-Poisson generalized linear model (full lines for males, dashed lines for females; thin lines indicate 2003 predictions and bold lines indicate 2010 predictions).

So, selection is occurring, in populations with very little genetic variation available, in a somewhat predictable way against homozygotes, although not systematically, depending on the population considered. But is that selection related to local adaptation? Are individuals of recent generations better adapted to their local environment than their sire?

What have we learned ?

- Inbreeding is a reality in populations founded by only a few parents.
 - Selection against homozygotes in relation to inbreeding can happen. But it is not mandatory.
-

These results are extracted from a manuscript published in *Evolutionary Ecology Research* (Labonne et al. 2016), in collaboration with the Redpath Museum of McGill University in Montreal, Canada.

4.5.2. Founder effects and morphological variation

In the previous report (Labonne et al. 2013a), we analysed the morphological variation of body shape in these two populations (Val Travers and Clarée), and concluded that clear divergence occurred, but such divergence could be mainly plastic. These results however pointed at different trophic and hydrological conditions between Val Travers (bottom feeding, low current speed) and Clarée (dwelling feeding, fast current speed). Again, the question of genetic variation, effect of selection on phenotypic diversity is of major interest, since such diversity will possibly shape the structure of populations along the metapopulation expansion gradient. But beyond the relationship between a morphotype and the local environment, founder effects should in fact controls the amount of morphological variation in populations.

We investigated this latter question by blending our data on these two populations with three other populations' data from Kerguelen (Manchots, Chateau and Norvégienne rivers), and 3 other Brown trout colonization fronts throughout the world (New Zealand, Newfound Land, Chile) and France as a control (i.e., stabilized populations), amounting to a total of 32 populations and 1991 individual morphological data (Figure 27).

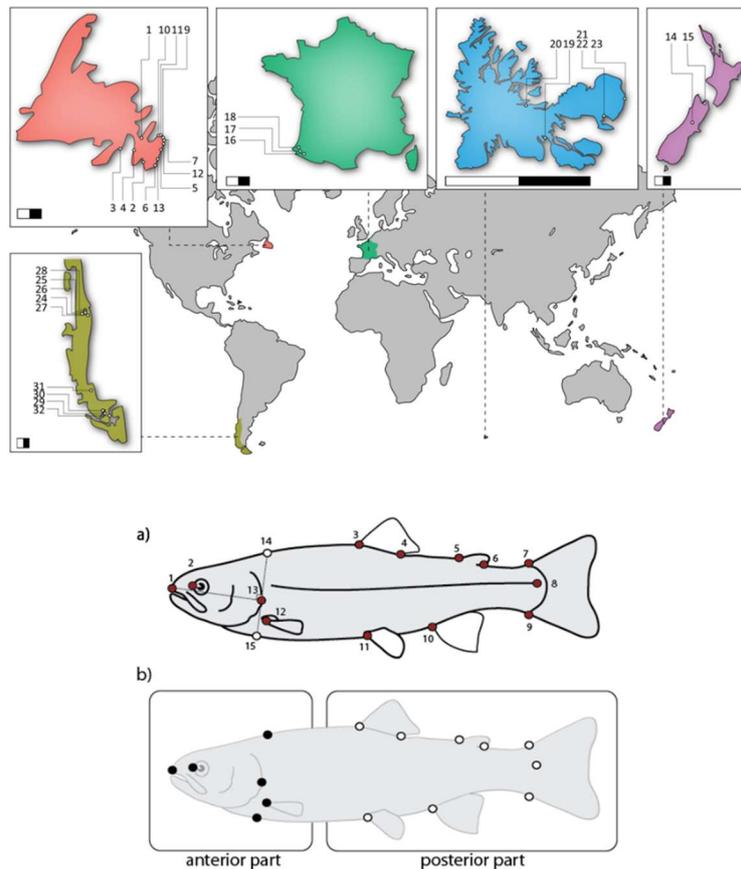


Figure 27 Top Panel: sampling locations. Numbers refer to population numbers in Table 1. The grey bar in each submap equals to a 100 km distance. Bottom panel: a) Position of the 13 landmarks (red dots) and 2 semi-landmarks (white dots) on the body shape, b) partition of landmarks in two functional modules (respectively black and white landmarks).

Based on these morphological data, we calculated three indices. The first one, shape variance (SV), describes how much variation is observed among possible forms within each population, or region. We found that SV was generally high on several colonization fronts around the world, since it was higher than the France populations (Figure 28). Then, we looked at overall body morphological integration (OBI), an indicator that investigates whether morphological variance is channeled in some specific variation axes, or if each morphological landmark evolves independently. In this analysis, Kerguelen appeared to present some of the less integrated morphological variation (Figure 28). When narrowing morphological integration to known functional sub-units (anterior part of the body versus the posterior part of the body, FI indicator), we found that, again, the Kerguelen populations ranked among the lowest values, indicated no strong morphological channelization in morphology development.

It thus appears that phenotypic variation, here at the morphological level, is in no short supply on most colonization fronts. In particular, Kerguelen populations appear to show no strong selection for channelized morphology, meaning that individuals within population appear to evolve along different pathways, at least for the time being.

There are also differences between colonization fronts, and within each colonization fronts, difference between populations. We sought to explain these differences by investigating the relationship to the age of these colonization fronts (introduction date), and the possible founder effect (propagule numbers). Introduction date would control for the time available for populations to adapt, and propagule number would correlate to initial available genetic variation. We however found no consistent relationship between these two variables and our three indicators of morphological variance (SV, OBI, FI, Figure 29). It is very possible that our explanatory variables poorly captured more complex process affecting genetic variation and past selection, such as local environment effects.

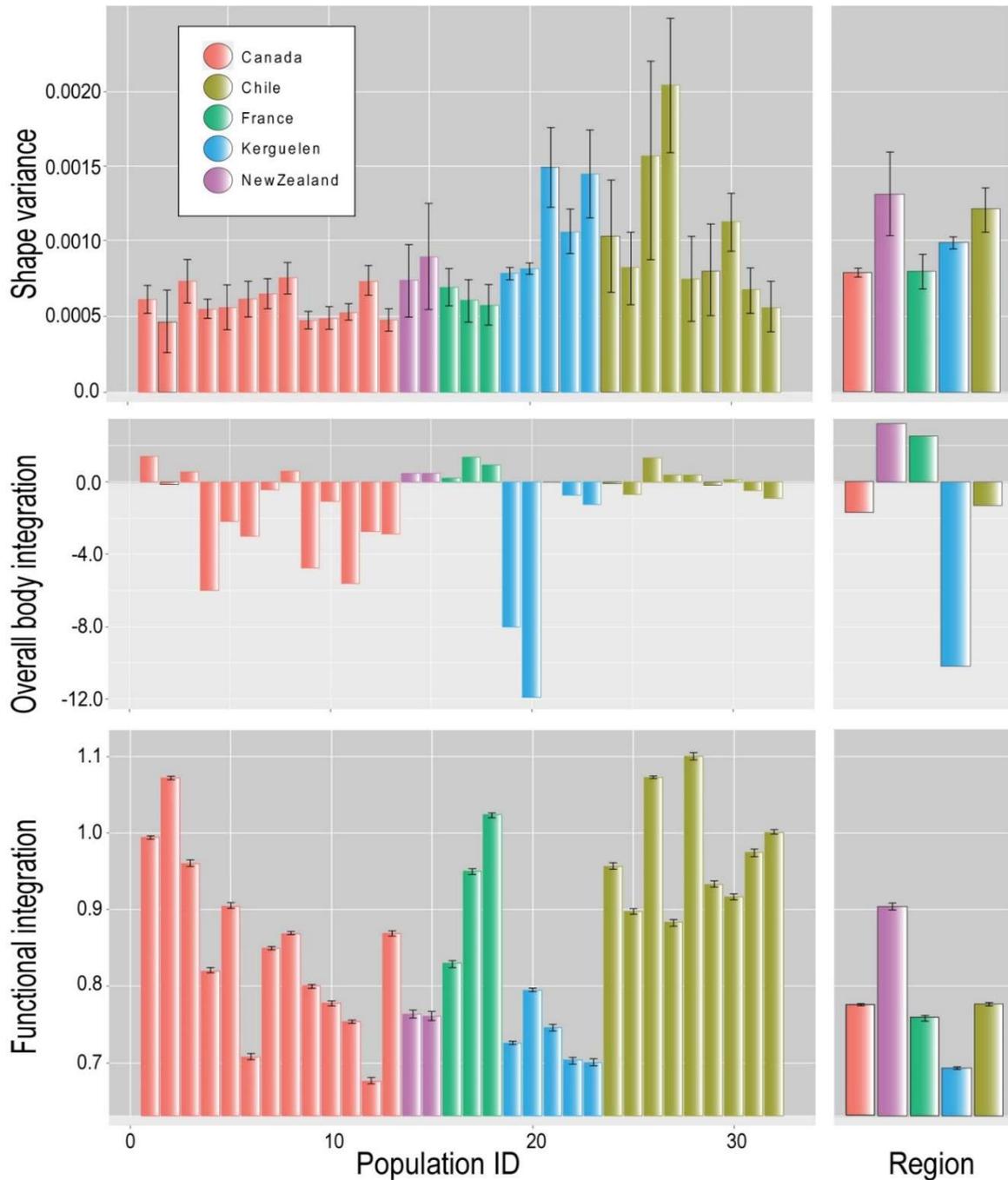


Figure 28: Indicators of morphological variance per region and per population within regions. A) Shape variance (Foote's index) and its 95% confidence interval for all rivers (white bars) over the 2500 bootstrap iterations. B) Overall Body Integration measures how much the morphological variation is concentrated in just few dimensions or spread across many directions of shape space within a sample, conditional on sample size. It is here calculated as the distance to the mean expected value, using a bootstrap approach. C) Functional Integration, and its 95% confidence interval, measured as the degree of covariation between anterior and posterior modules, relatively to covariation to other modules.

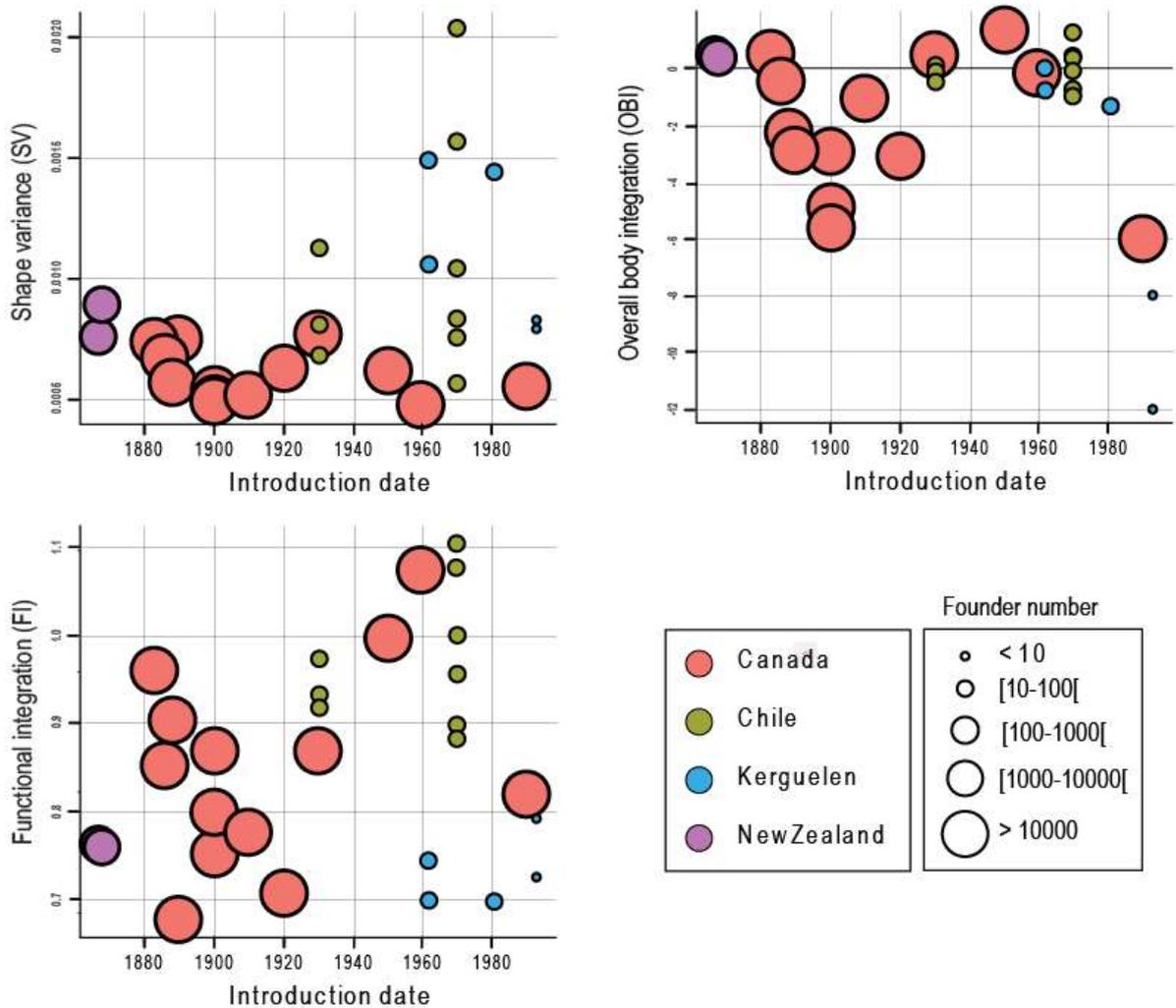


Figure 29: Variation of shape variance (SV), overall body integration (OBI) and functional integration (FI) as a function of introduction date, founder number and region.

What have we learned ?

- There is no evidence that morphological variation is reduced in young populations located in colonization front throughout the world.
 - The Kerguelen populations appear to present particularly variable morphological variation, wherein within population variation is maximized, notably when genetic variation was potentially reduced.
-

These results are extracted from a manuscript in review (Vignon et al., submitted), in collaboration with the Redpath Museum of McGill University in Montreal, Canada, Universidad Austral del Chile (Chile), University of Alaska at Fairbanks, the University of Canterbury in New-Zealand, and EDB Lab in Toulouse, France.

4.5.3. In situ experimental approach of local adaptation and genetic rescue

To go further in the investigation of local adaptation, we proceeded to a wide scale experiment. We argued that, if local adaptation (LA) was an efficient process in the shaping of intraspecific diversity on colonization fronts, we should be able to show that local individuals should have a higher selective values than foreign immigrant individuals. If LA does not occur, then foreign individuals should have the same fitness than local individuals. Additionally, if genetic variation is too reduced for local adaptation to take place quickly, then we should observe a higher fitness in individuals being genetically more diverse than local ones. If genetically poor local and foreign individuals were to mate together, their offspring should logically present more diversified genome. Such diversity should then boost their fitness, and in turn improve the fitness of the whole population by means of selection after the next generations.

In 2010, we proceeded to a reciprocal transplant between Val Travers and Clarée populations. In each population, 261 individuals were caught, individually tagged, photographed, aged using scale readings, and genetically analysed. 151 of these individuals were transported and released in the other populations, while the 110 remaining were released in their population of origin, as a control. All these individuals are hereafter termed as the C0 group. Our expectations were multiple.

Under local adaptation:

- Transplanted (foreign) individuals would not survive as well as local individuals.
- Foreign individuals would have lower reproductive success than local individuals – through either reduced early survival of their offspring, or by being less attractive than locally adapted mates.

Alternatively, if reduced local genetic variation was preventing LA to occur quickly:

- Hybrid individuals originating from possible matings between local and foreign parents would have a higher fitness than both parental lineages. Such fitness being the product of their survival and their reproductive success, it could be tracked by monitoring the outcome of our experiment over at least 2 generations following the transplantation stage, and calculating the reproductive success of foreign, local and hybrid individuals.

We thus sampled offspring (6 months old) in 2012 and 2018. The 2012 samples (hereafter C1 group) encompass the first possible offspring produced by the fish tagged in 2010. This C1 group is thus informative of the respective fitness of foreign and local individuals: we analyzed whether these offspring were sired by local or foreign parents, or both (i.e., F1 hybrids). Assessing the proportion of foreign and local parents in each population, it was therefore possible to calculate their respective contribution to offspring production in the population.

Then in 2018, we sampled offspring again (C2 group), so to assess also the fitness of individuals born in 2012. This meant we could expect to detect foreign, local, F1 hybrids, but also F2 hybrids and backcrosses between F1 and either local or foreign lineages, see Figure 30).

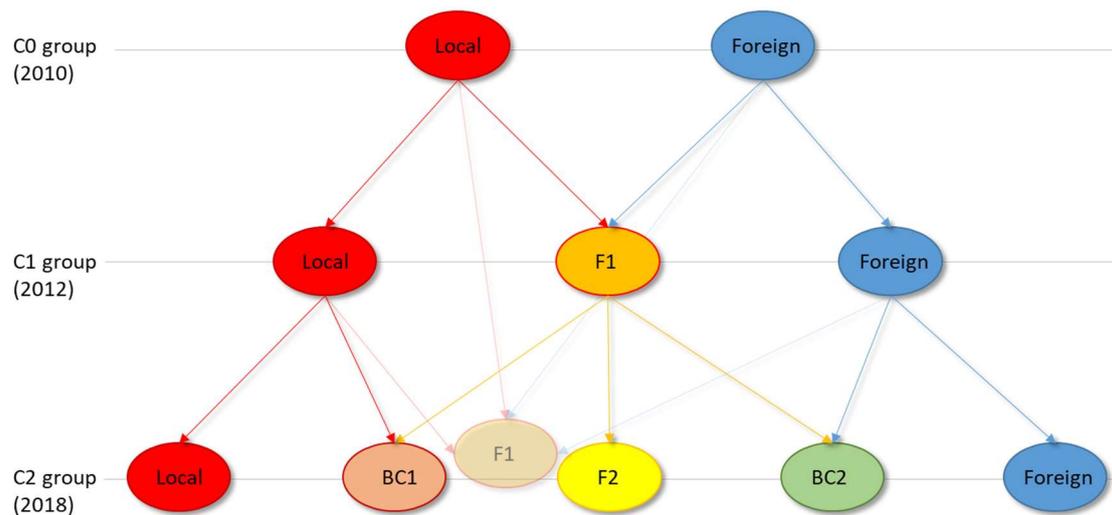


Figure 30: Possible pedigree obtained from our transplantation experiment: the C0 group is composed of local and foreign (transplanted) parents analyzed in 2010. The C1 group represents the first possible generation where hybrid offspring could be found (F1). C2 group corresponds to the first generation where offspring of hybrids (F2), or backcrosses between hybrids and either local or foreign individuals could be found (BC1 and BC2 respectively).

The figure 31 represents the number of offspring assigned to each possible genotypic category in C1 (2012 samples) and C2 groups (2018 samples). In the Clarée population, we found very few hybrid offspring or offspring originating from purely foreign parents. The gene flow occurred, but was therefore very reduced. Calculating the fitness of the different parental origin (foreign, local, and F1) we found no clear differences: footprints of local adaptation could not be found. In the Val Travers population, an important gene flow occurred: many F1 hybrids were detected in 2012, and many F1, F2 and backcrosses were detected again in 2018. Investigating further if there were unequal fitness values between genotypic categories, we found that foreign individuals always had a clearly higher fitness than local or F1 individuals. Additionally, F1 and local individuals had equal fitness.

So, we found no trace of LA. We found no clear footprints of genetic rescue: hybrids did have a higher genetic diversity (i.e., higher heterozygosity, results not shown) but not a higher fitness. And in one population only, we found that foreign individuals had a higher fitness, and this was mainly due to a higher mating success. This means that they were either more attractive to local mates, or more competitive in securing mating opportunities. In either case, it was unrelated to natural selection, but it underlined the role of sexual selection in shaping fitness and therefore genetic variation on colonization fronts.

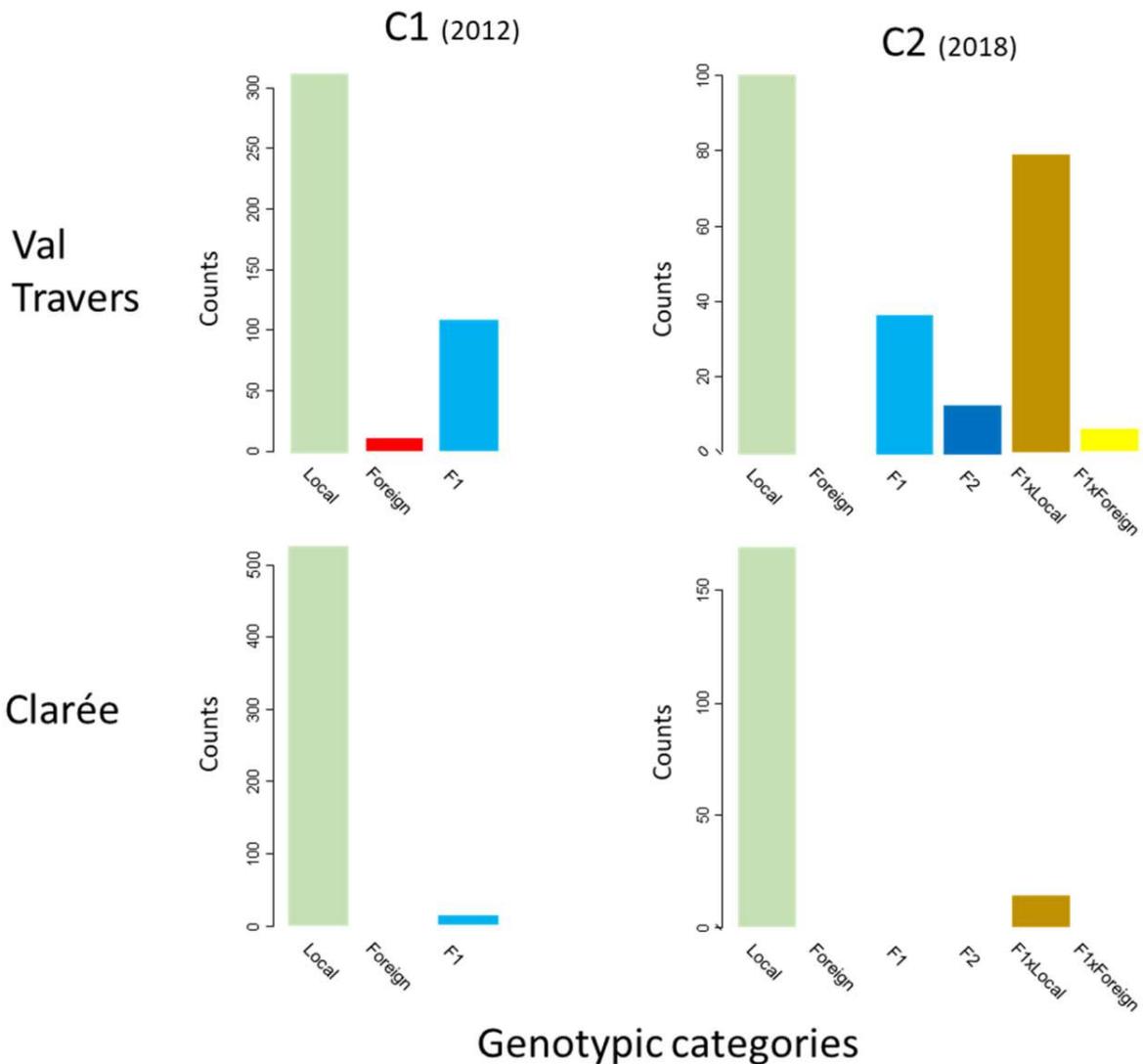


Figure 31: Counts of the different genotypic categories detected for C1 (left) and C2 (right) gene pools, in Val Travers (top) and Clarée (bottom) populations.

Small populations founded on the colonization front might not really suffer from reduced genetic variation. First, we detected no evidence of population extinction (for Brown trout) throughout all our monitoring (Labonne et al. 2013b). We found evidence of selection against homozygosity though (even in the recent years, Labonne et al. 2020), and no indication of local adaptation for the time being, but not obvious genetic rescue effect too. And phenotypic variation was as much available than in many other population of different status in other context. These results of course deserve now to be extended to a larger sample of populations in Kerguelen, but what we could achieve here in details will certainly help us interpret patterns on large scale in the future. Partly puzzling is the notion that sexual selection appeared to influence fitness evolution and genetic structure more so than natural selection. It is however compatible with the recent renewed interest for the role of sexual selection in shaping biodiversity at micro evolutionary scale.

What have we learned ?

- *Neither local adaptation nor genetic rescue appear to strongly influence diversity in these inbred populations.*
 - *Surprisingly, gene flow seems mainly related to apparently non adaptive contrast in sexual selection.*
-

These results are extracted from a manuscript published in Genes (Labonne et al. 2020), in collaboration with the Redpath Museum of McGill University in Montreal, Canada. The reciprocal transplantation protocol was only successful due to the full support and dedication of the Polar Institute logistic staff.

3.6. Investigating skin and blood microbial signatures in Brown trout

The microbiome, or the pool of microbial DNA in a host species, is known to be affected by genetic and environmental factors. Characterization of the microbial communities of specific tissue compartments can thus be used to evaluate the health status of a given species and to determine its adaptation to specific environments. Our understanding on how these microbiome signatures are modulated in wild fish populations remains, however, poorly known and has, until now, mostly been inferred from studies in commercial and/or farmed fish populations. In the particular case of introduced salmonids in the Kerguelen islands, such approach could serve at least two purposes:

- to detect pathogens affecting the fitness of introduced fish, and possibly assess whether said pathogens originate from the local environment, or have been brought to the Kerguelen islands through human mediation,
- to use the fish as a sampling tool to evaluate microbial diversity in several areas of the Kerguelen Archipelago.

The MUSSELKER project (PI: Yves Saint-Pierre, funded by the French Polar Institute) developed a logistically-simple and minimally-invasive sampling platform adapted for remote regions, so to assess microbial diversity from DNA extracted in various compartments of the ecosystem. SALMEVOL and MUSSELKER agreed to collaborate so to apply these new developments to introduced salmonids, and in particular, to Brown trout. Blood as well as mucus samples were collected on individuals originating from 6 different populations around Kerguelen (Figure 32), using FTA cards. Both resident and migratory phenotypes were sampled, in order to reflect possible environmental control on microbial signatures. Mucosal and blood circulating DNAs were extracted and the 16S rRNA amplified, then compared to available databanks.

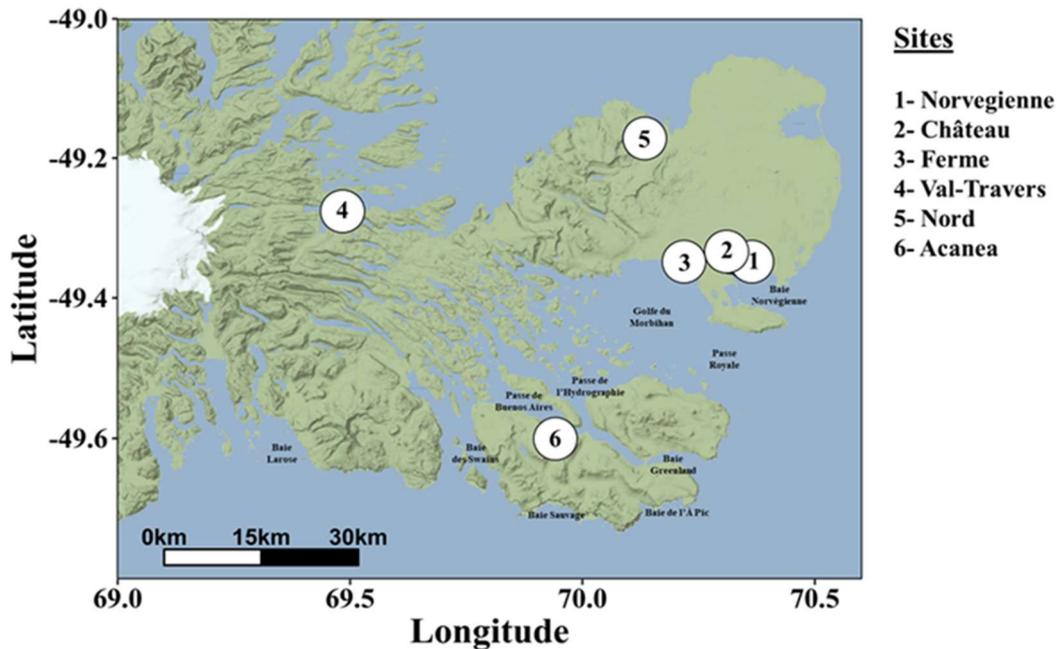


Figure 32: Map of the French sub Antarctic Kerguelen Islands showing the location of the sites. Sedentary trout were collected from freshwater (FW) and migratory trout were collected from the mouth of the river (seawater (SW)).

Our results first showed that Brown trout in Kerguelen has a microbiome signature that is clearly distinct from those of salmonids of the Northern hemisphere: the dominant genera were not the same for instance between Kerguelen results and results obtained from Atlantic salmon in Norway (Lokesh and Kiron 2016), even the difference between resident and migratory forms of salmonids differed between regions. Focusing now on Kerguelen Brown trout; we found clear differences between resident and migratory phenotypes, as well as between blood and skin samples, as shown in Figure 33, at both phylum and genus levels. The most striking difference is observed in migratory phenotypes, for skin samples, indicating that the coastal marine ecosystem was likely to produce a very different bacterial diversity. In particular, out of 28 phyla found, 5 phyla were specific to the marine environment only, and none were specific to freshwater environment. More impressively, these 5 marine specific phyla were composed of 321 marine specific genera, representing 46% of all the genera detected in all samples (migratory, resident, blood, skin, N=688). Contrastingly, only 85 genera were freshwater specific.

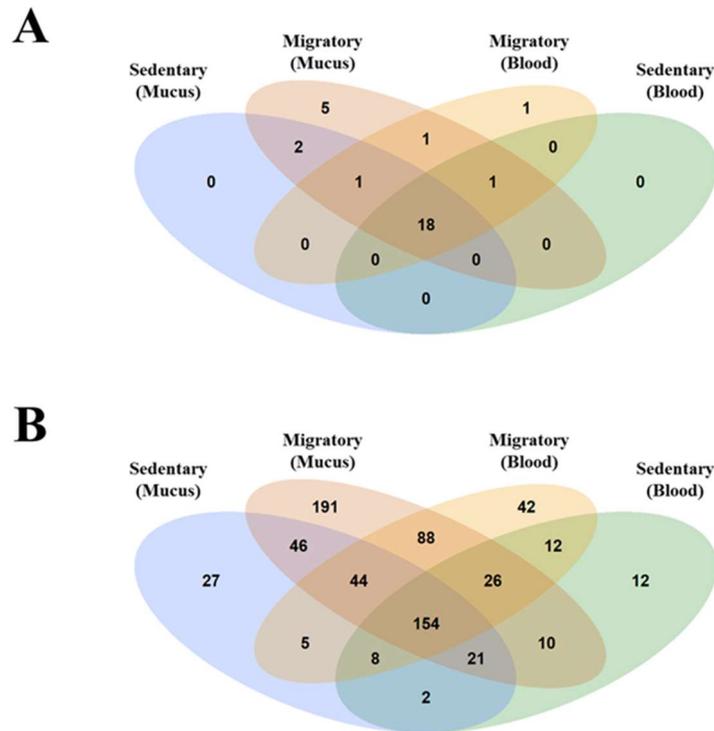


Figure 33: Venn diagrams showing the number of unique and shared (A) bacterial phyla and (B) genera in mucosal and circulating compartments in both resident and migratory Brown trout (*S. trutta*).

Analysis at the phylum and genus levels in both compartments showed that the microbiome signatures undergo significant site-specific variations which correlates, in some cases, to the peculiarity of specific ecosystems (Figure 34). For instance, at the phylum level, blood circulating microbiome showed striking contrasts between sites. For instance, the Val-Travers sites exhibited a clear dominance of proteobacteria for migratory phenotype only, something that was not found for any other sites. Contrastingly, such domination of proteobacteria was found for the resident fish of the Nord river. More specifically, two potential pathogenic genera were found, *Aliivibria* and *Renibacterium*. The first one is extremely harmful for the Atlantic salmon (*Salmo salar*), a species that was introduced in two sites of Kerguelen (Korrigans, Armor). It is remarkable that one of these two populations is already extinct, and the other one in extremely poor status right now, and that in both populations, no migratory Atlantic salmon was never found (whereas the migratory tactic is close to mandatory for this species). It was then assumed that no migratory routes existed for the species, and therefore, salmon got lost. The present results however indicate that they might instead have contracted *Aliivibria* bacteria in the marine coastal areas of Kerguelen and died of it. The Brown trout however appears not as sensitive to the pathogen, but it might impact the fitness of the migratory form indeed: individuals carrying *Aliivibria* spp were found in various sites. The second genus, *Renibacterium*, includes the *salmoninarum* species, which is the causative agent of the Bacteria Kidney Disease (BKD): this pathogen was, contrarily to *Aliivibria* spp, introduced with the importation from the United-States of Chinook salmon (*Oncorhynchus tshawytscha*) in the Armor basin, for the “Aquasaumon” sea ranching project in 1987. This pathogen is actually one of the reasons for the failure of this project. We found its presence in Acaena Brown trout population, not so far from the Armor system. Again, Brown trout seems to be way more resistant to BKD than their Chinook cousins.

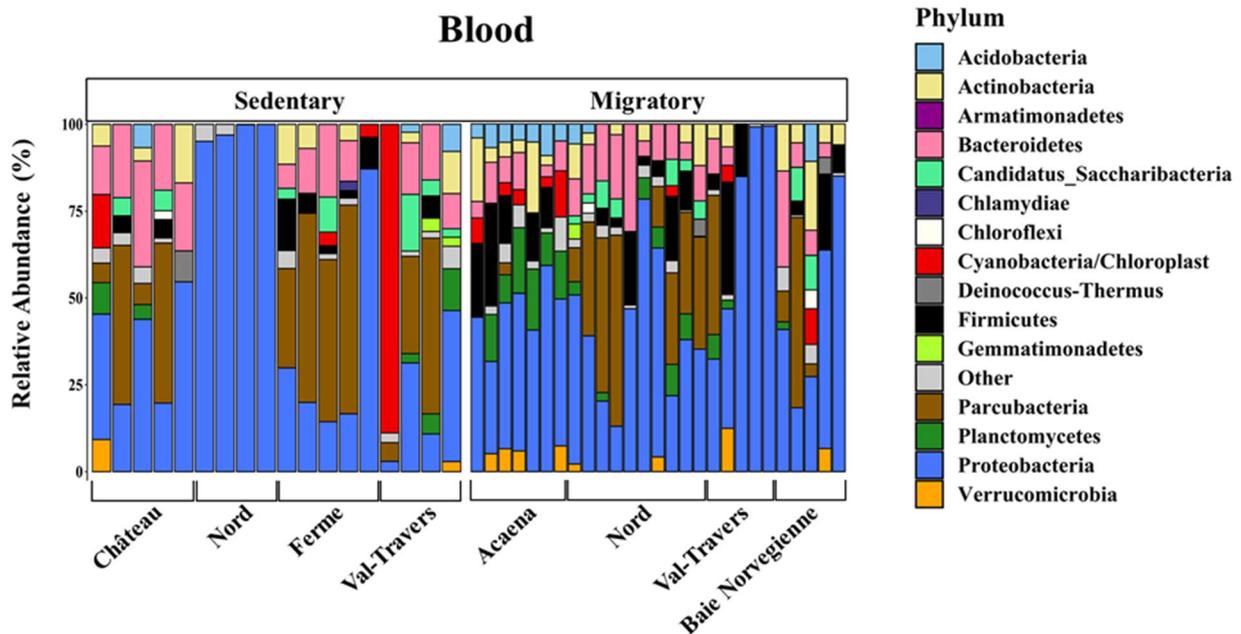


Figure 34: Inter-individual variability of circulating microbiomes at phylum level. Bar plots display the major phyla between sedentary (left) and migratory (right) Brown trout (*S. trutta*) collected at different sites. Phylum with a relative abundance of $\leq 1.5\%$ are represented as "Other".

Finally, we also discovered that the Brown trout could be used as a sampling actor of the surrounding ecosystem. For instance, in the Acaena river, an abundance of hydrocarbon degraders was found in the microbiome of migratory trout. We hypothesize that their presence at the mouth of the Acaena river is possibly due to the nearby presence of multiple lignite deposits, also called “brown coal”, at the Ravin du Charbon and the Ravin Jaune near the Acaena river (Frey et al. 2000).

What have we learned ?

- Capturing mucosal and blood circulating DNAs on FTA cards opens new avenues to explore microbiomes diversity. In particular, the mucus sampling is especially simple and informative, with little impact on the organism itself.
 - These microbiomes differ wildly between sites and between resident and migratory phenotypes.
 - the methodology was able to find footprints of past human intervention (presence of BKD agent’s DNA) or to reveal local environment characteristics.
-

These results are extracted from a manuscript in revision (Ferchiou et al. in review), in collaboration with the MUSSELKER project. The SALMEVOL team mainly gathered initial samples, and assisted in the writing of the manuscript, while the MUSSELKER team developed the ideas, the sampling and analytic methodologies, produced the results and wrote most of the manuscript.

5. Perspectives for future research

As part of the ZATA LTER, it is mandatory that we keep on maintaining our collections and our monitoring of salmonids species spread and populations structure in the Kerguelen islands.

Demography, traits, and genetics.

Our databases and collections are now in a much better shape, and allow us to address large scale questions.

- In 2013, we published a first model to describe the dynamics of colonization (Labonne et al. 2013b). Our recent findings show that the colonization progresses further on. Additionally, this approach was using a classical metapopulation approach, with a binary approach of patch occupation. We now have the option of updating the colonization model, but we can also refine it, using intra-patch dynamics based on density estimates.

- Second, we have now investigated the general trends regarding individual growth patterns, at several scales, and in both freshwater and marine ecosystems. We have also investigated the evolution of body size as well as the reaction norm for partial migration. We therefore benefit from a much deeper insight on the evolution of life history traits, and this knowledge can be now paired with an improved approach of population dynamics, as mentioned above.

- Finally, our collections, as well as the progress of genomics and molecular biology techniques, should now allow us to plan a large-scale population genetics investigation of the whole colonization process. Using whole genome-wide association frameworks, we could investigate migration-related candidate loci that influence partial migration in Brown trout or other salmonid species (e.g. Lemopoulos et al. 2018) and better understand the evolution of migratory behavior by studying the associated changes in allele frequencies over time (and across populations).

Taken together, these three questions can actually be merged in a single framework, wherein evolution of traits in the metapopulation expansion framework can be directly linked to an actual modelling of population dynamics based on density census, while investigating the neutral and non-neutral genetic forces at work in shaping evolution.

A second general avenue for further developments is to improve some of our sampling approaches. The sampling of scales on fish that is the backbone of our monitoring, it is a very efficient and cheap approach to build samples databank. It allows to analyze life histories, genetics, and chemical composition. We however feel that more comprehensive sampling methods should be explored, such as what was done in collaboration with the MUSSEKER research project (previously IMMUNOTOXKER, Y. Saint-Pierre, S. Bétouille): we have indeed collaborated during the first SALMEVOL project (2019-2013), and during the SALMEVOL-2 project, we have conducted some technical trials. Based on simple FTA cards, that can be conserved for at least a decade, the MUSSELKER project showed that diverse information could be obtained from simple mucus sampling, such as the mucosal microbiome. We endeavor at further developing this kind of sampling, and associated studies (host DNA, microbiome DNA, and other environmental DNA).

Finally, a third path lies in extending our project to the recently created International Lab MACLIFE, for Management of extreme CLimate Impacts on Freshwater Ecosystems. This international Lab regroups our own lab, UMR ECOBIOP 1224 UPPA/INRAE, with the Stream Ecology Group in Bilbao, Spain (UPV),

and the Berkeley Freshwater Group, USA (UC). Its ambition is to connect organizational levels from genes to ecosystem in order to pursue integrative research to forecast effect of extreme climate events. The sub Antarctic islands are particularly exposed to such events, and we believe the SALMEVOL project could host new experimental approaches at community and ecosystems levels (Where Bilbao and Berkeley teams are especially skilled) to complete our own approaches on salmonids intraspecific dynamics.

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7. Training

Niveau	Année	Durée du stage	Nom du stagiaire	Thématique
L3	2017	3 mois	Lucille Baron	Caractérisation des traits de vie chez la truite commune. Mise en place de méthodologie par scalimétrie et modélisation de la croissance.
M1	2018	5 mois	Gautier Magné	Comparaison de trajectoires de croissance entre deux populations de truites de Kerguelen.
L3	2018	3 mois	Paul Gouzou	Etude de la croissance compensatoire chez la truite commune.
L2	2018	1 mois	Jon Levy	Caractérisation de traits de vie chez la truite commune.
M2	2019	6 mois	Valentin Santanbien	Comparaison de trajectoires de croissance entre deux populations de truites de Kerguelen.
M1	2019	6 mois	Hervé Rogissart	Caractérisation de traits de vie chez la truite commune.

8. Annexes

7.1 Annexe 1:

Status of knowledge in 2019 on presence of *Salmo trutta*, including other introduced salmonids in streams and waterbodies grouped by geographic zone of the Kerguelen Islands. Names follow the 1/100 000 IGN (French Geographic Institute) map nomenclature of the Kerguelen. Most of names are from the repertoire of the Commission Territoriale de Toponomie (1973). For some unnamed streams, we gave temporary names or numbers according to geographic or topographic features. Holding ponds are shown by *. NV: not visited; NS: not sampled. Code in the first column refer to previous works of Labonne et al., 2013. (Updated from Appendix 4 in Lecomte et al, 2013). For the rivers not considered in previous works, we choose numbers from 80 to 200 or we added a letter index to the number.

Code	Site	GPS position of estuary	Estimated 1 st repro Only for <i>Salmo trutta</i>	Date last sampling	Species present at last sampling	Strayers (date seen)	Colonization possible	Comments (for successful introductions, year of the first reproduction)
NORTHERN IS. & PENINSULAS								
190	Peninsula Loranchet, Anse Excursion (river?)	48°52'58" S 68°57'51" E	?	2018		<i>Salmo trutta</i> (2018)	Yes (several rivers)	Rod fishing, 11 sea trouts
191	Peninsula Loranchet, Anse du Jardin (river?)	48°51'13" S 69°00'49" E		2018			Yes (several rivers)	Rod fishing
192	Peninsula Loranchet, Port Léontine (V. Rapides)	48°59'08" S 68°59'46" E		2018			Yes	Rod fishing
193	Peninsula Loranchet, Anse du Ring (V. du Ring)	49°05'25" S 68°58'36" E		2018			Yes (several rivers)	Rod fishing
194	Baie Française, Anse du Cartographe (river?)	49°07'47" S 69°12'44" E		2018			Yes	Rod fishing
195	Cascade de la Lozère (outlet Lac d'Astée)	49°05'00" S 69°36'30" E	?	2017			Yes	
196	La Basille R.	49°02'18" S 69°33'35" E		NV			Unknown	
199	Sinat R.	49°09'16" S 69°19'52" E		NV			Unknown	
200	Mont Ventoux R.	49°09'58" S 69°18'39" E		NV			Unknown	
1	Val des Entréacs	49°10'50" S 69°18'22" E		2019			Yes	
2	Inlet Bassin Victoria	49°12'17" S 69°19'02" E		2019			Yes	
3	Outlet of Croix du Sud Lake	49°13'13" S 69°24'51" E		2019			Yes	
4	Outlet of Lake Euphrasine	49°14'14" S 69°25'50" E		2019			Yes	
5	Bellon R.	49°14'41" S 69°26'27" E		2011			Yes	
6	Sannom R.	49°14'52" S 69°26'26" E		2011			Yes	
7	Brook Ile aux Skuas	49°14'55" S 69°25'32" E		NS			No	Low discharge
7a	Brook Ile aux Skuas	49°14'46" S 69°55'01" E		2011			Yes	
8	Brook 1 S Ile du Port	49°12'36" S 69°37'17" E		2011			Yes	
9	Brook 2 Ile du Port	49°12'10" S 69°37'59" E		2011			Yes	
10	Brook 3 Ile du Port	49°11'10" S 69°38'37" E		2011			Yes	
11	Brook 4 Ile du Port	49°10'36" S 69°38'10" E		NS			No	Low discharge
11a	Brook 5 N Ile du Port	49°09'28" S 69°38'17" E	1998-2015	NV			Unknown	
12	Vallée R.	49°16'11" S 69°24'03" E		2017		<i>Salmo trutta</i> (2011)	Yes	
CENTRAL PLATEAU NORTH								
13	Val Travers R. & Bontemps estuary	49°16'48" S 69°28'38" E	1993	2019			Yes	Successful human introduction (<i>Salmo trutta</i> , 1992)
14	Brook N of Port-Couvreux	49°16'49" S 69°41'26" E		2012			Yes	
15	Brook S of Port-Couvreux cabin	49°17'05" S 69°41'41" E		2012			No	
16	Brook W end of Havre du Beau Temps	49°18'10" S 69°34'05" E		2011			Yes	
17	Bassin de la Gazelle Brook	49°18'48" S 69°40'16" E		2011			No	
17a	Anse Sablonneuse Brook	49°18'50" S 69°42'05" E		2011			Yes	
COURBET NORTH								
18	Port Kirk R.	49°17'28" S 69°47'19" E	1997	2019			Yes	
19	Val de l'Ouest R.	49°16'02" S 69°50'50" E	1987	2002			Yes	
20	Studer Basin	49°12'48" S 69°52'12" E	1962	2018			Yes	Successful human introduction (<i>Salmo trutta</i> , 1959 ; <i>S fontinalis</i> , 1962)
20a	Port-Elizabeth Brook	49°12'39" S 69°53'31" E		1973		<i>Salmo trutta</i> (1973)	Yes	
21	Doute R.	49°11'44" S 69°55'34" E	1985	2002			Yes	
22	Vallée du Charbon R.	49°11'39" S 69°55'53" E	1986-1992	2002			Yes	
23	Sérial R.	49°11'39" S 69°55'53" E	1988-1992	2002			Yes	
24	Chasseurs R.	49°08'31" S 70°02'35" E	1986	2002			Yes	
25	Nord R.	49°10'27" S 70°08'13" E	1985	2019			Yes	
26	Pépins R.	49°09'57" S 70°11'31" E	1989	2001			Yes	
27	Cataractes R.	49°09'01" S 70°13'36" E	1985-1989	2011			Yes	Successful human introduction (<i>Salmo trutta</i> , 1981)
28	Hautes Mares South Brook (Gorfous 1)	49°08'10" S 70°14'06" E	2000	2011			Yes	
29a	Hautes Mares North Brook (Gorfous 2)	49°07'57" S 70°13'52" E	1991-2000	2011			Yes	
29b	Gorfous 3	49°07'15" S 70°13'52" E		2011			Uncertain	
30	Pointe des Cabanes Brook (Gorfous 4)	49°06'11" S 70°14'05" E	1998-2000	2011			Uncertain	
31	Cap Rouge Brook S (Gorfous 5)	49°04'47" S 70°16'09" E	1997-2000	2011			Uncertain	
32	Cap Rouge Brook N (Gorfous 6)	49°04'18" S 70°16'45" E		2011			Uncertain	
32a	Gorfous 7	49°03'50" S 70°17'09" E		2011			No	
COURBET EAST								
33	Cap de Rohan R.	49°03'28" S 70°22'24" E	1995-1999	2019			Yes	
33a	Cap Digby Brook	49°06'23" S 70°31'25" E		2019			Yes	
34a	Lac Manville north tributary 1 (West)	49°08'43" S 70°25'39" E	1982-1989	1992			NS	
34b	Lac Manville north tributary 2	49°08'40" S 70°25'42" E	1982-1989	1992			Yes	
34c	Lac Manville north tributary 3	49°07'41" S 70°26'58" E	1982-1989	2001			Yes	
34d	Lac Manville north tributary 4	49°07'24" S 70°28'05" E		2001			Unknown	
34e	Lac Manville north tributary 5 (East)	49°07'23" S 70°28'11" E		2011			Unknown	
34f	Est R.	49°09'04" S 70°30'41" E	1982-1989	2011			Yes	
34g	Volcan R.	49°10'12" S 70°30'24" E	1982-1989	2001			Yes	
34h	Lac Manville south tributary	49°10'10" S 70°25'58" E	1982-1989	2001			Yes	
35	Menchois R.	49°10'30" S 70°30'02" E	1982-1989	2001			Yes	
36	Pointe des Calédoines R.	49°13'43" S 70°33'12" E	1982-1989	2010			Yes	
37	Bungey R.	49°10'45" S 70°20'45" E	2003-2006	2011			Yes	
38	Abatros R.	49°21'27" S 70°28'11" E	1984-1988	2001			Yes	
39	Norvegiemne R.	49°21'03" S 70°22'31" E	1968	2010			Yes	
40	Château R.	49°21'10" S 70°19'35" E	1962	2018			Yes	Successful human introduction (<i>Salmo trutta</i> , 1962 ; <i>Salvelinus fontinalis</i> , 1962)

Code	Site	GPS position of estuary	Estimated 1 st repro Only for <i>Salmo trutta</i>	Date last sampling	Species present at last sampling	Strayers (date seen)	Colonization possible	Comments (for successful introductions, year of the 1st reproduction)
MORBIFAN NORTH								
41	PAF Ferme R.	49°21'03" S 70°13'21" E	1962	2018	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		Yes	Successful human introduction (<i>Salmo trutta</i> , 1962 ; <i>Salvelinus fontinalis</i> , 1962)
41a	*PAF Sablière Pond	49°20'25" S 70°12'03" E	?	2005	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		?	Successful human introduction, year unknown (<i>Salmo trutta</i> & <i>Salvelinus fontinalis</i>)
41b	*PAF Magnétisme Pond	49°20'58" S 70°12'23" E	?	2001	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		?	Successful human introduction (<i>Salmo trutta</i> , 1970 ; <i>Salvelinus fontinalis</i> , unkn)
41c	*PAF Décharge Pond	49°20'46" S 70°12'39" E	1970	2009	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		1/2 isolated site	Successful human introduction (<i>Salmo trutta</i> , 1970 ; <i>Salvelinus fontinalis</i> , unkn)
41d	*PAF Collets Pond	49°20'41" S 70°12'51" E	1970	2005	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		1/2 isolated site	Successful human introduction (<i>Salmo trutta</i> , 1970 ; <i>Salvelinus fontinalis</i> , unkn)
41e	*Fono Pond	49°20'57" S 70°15'14" E	1960	2010	Information not available		No	Information not available
41f	*Bâliers Pond	49°20'46" S 70°13'57" E			Information not available		No	Information not available
42	Borgne R.	49°20'44" S 70°10'13" E	1973	2016	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		Yes	Successful human introduction (<i>Salmo trutta</i> , 1973 ; <i>S. fontinalis</i> , 1972)
42a	Otarie R.	49°20'45" S 70°09'55" E					No	Falls
43	Sud R.	49°20'47" S 70°07'54" E	1979	2016	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		Yes	Successful human introduction (<i>Salvelinus fontinalis</i> , 1962)
44	Pointe de l'Épave Brook	49°20'36" S 70°06'56" E	1991	2018	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		Yes	
45	Américains R.	49°22'07" S 70°04'48" E	1978-80	2016	<i>Salmo trutta</i> / <i>Salvelinus fontinalis</i>		Yes	
46	3 Lacs R.	49°22'01" S 70°00'40" E	1988	2016	<i>Salmo trutta</i>		Yes	Falls
46a	Lac Christiane outlet	49°20'25" S 69°51'18" E	1994-98	2016	<i>Salmo trutta</i>		No	Falls
47	Val d'Auge R.	49°20'23" S 69°49'17" E					No	Falls
48a	Lac des Trois Enseignes outlet	49°20'11" S 69°48'48" E	2003-2014	2016	<i>Salmo trutta</i>	<i>Oncorhynchus kisutch</i> (smolts 2016)	Yes	
48b	Anse de St. Malo R. = Port Raymond R.						Yes	
MORBIFAN WEST								
49	Basin downstream of Korrigans Lake	49°23'32" S 69°51'32" E	1975-1979	2016	<i>Salmo trutta</i>	<i>Oncorhynchus kisutch</i> (2009)	Yes	Successful human introduction (<i>Salmo trutta</i> , 1975 to 1979 ; <i>Salmo salar</i> , 1975)
50	Baie de l'Observatoire R.	49°23'55" S 69°52'38" E	2003-2014	2016	<i>Salmo trutta</i>	<i>Salmo trutta</i> (2002)	Yes	
51	East Brook on Bras Jules Labourer	49°23'58" S 69°48'57" E			<i>Oncorhynchus kisutch</i>	<i>O. kisutch</i> , <i>S. trutta</i> (2010)	Yes	
51a	Lac Saturne outlet	49°24'23" S 69°47'38" E					Yes	Low discharge
51b	SW Brook on Bras Jules Labourer	49°24'42" S 69°48'37" E					Yes	Low discharge
51c	E Brook on Bras Jules Labourer	49°25'20" S 69°48'12" E			possible introduction (species unknown)	<i>Oncorhynchus kisutch</i> (2001)	Yes	Low discharge
51d	East Brook on Bras Baudouin	49°23'53" S 69°45'41" E					Yes	Low discharge
51e	Gave de l'Azouella	49°23'35" S 69°45'02" E					No	Falls
52	Valdaine R.	49°23'03" S 69°36'26" E	2003-2007	2011	<i>Salmo trutta</i> / <i>Oncorhynchus kisutch</i>		Yes	Falls 200m from sea
52a	Alster R.	49°23'13" S 69°36'27" E	2003-2007	2012	<i>S. trutta</i> / <i>O. kisutch</i> / <i>S. alpinus</i>		Yes	Successful human introduction (<i>Oncorhynchus kisutch</i> , 1978)
53	Lac des Fougères + outlet	49°24'17" S 69°38'18" E			NS		No	
54	Lac d'Armor Basin	49°24'43" S 69°39'39" E			<i>Salvelinus alpinus</i>	<i>Salmo trutta</i> (2012)	Yes	Successful human introduction (<i>Salvelinus alpinus</i> , 1991)
55	Anse J. Bourcart Brook	49°27'59" S 69°43'44" E	1994	2012	<i>Salmo trutta</i> / <i>S. salar</i> / <i>Salvelinus fontinalis</i>	<i>Oncorhynchus kisutch</i> (2012)	Yes	hum. Intro. (<i>S. salar</i> , 1977 ; <i>O. kisutch</i> , 1978 ; <i>S. trutta</i> , 1991 ; <i>S. fontinalis</i>)
55a	Anse J. Bourcart Brook	49°29'17" S 69°46'02" E				<i>Oncorhynchus kisutch</i> (1989)	Yes	
MORBIFAN SOUTH								
55a	*Port Bisset Pond (Ile Longue)	49°31'30" S 69°54'18" E	1969	2010	<i>Salvelinus fontinalis</i>		No	Successful human introduction (<i>Salvelinus fontinalis</i> , 1975)
55b	*NW Ponds (Ile Longue)	49°31'12" S 69°53'25" E	1975	2009	<i>Salvelinus fontinalis</i>		No	
55c	*Ile du Clématis Pond	49°29'38" S 70°04'33" E	2001	2009	<i>Salmo trutta</i>		No	
56	Bassin du Charbon R.	49°33'01" S 69°49'08" E				<i>Salmo trutta</i> - <i>Salmo salar</i> (2003)	Yes	
57	Vallée des Neiges Basin	49°33'51" S 69°52'55" E	?-2003	2003	<i>Salmo trutta</i>		Yes	
58	Acana R.	49°35'49" S 69°56'38" E	1979	2019	<i>Salmo trutta</i>	<i>Salvelinus fontinalis</i> (1984)	Yes	Successful human introduction (<i>Salmo trutta</i> , 1979)
59	Vallée de la Planchette R.	49°35'49" S 70°01'11" E	1984	2003	<i>Salmo trutta</i>		Yes	
60	Val Baïde Brook	49°38'09" S 70°07'50" E	1987	2003	<i>Salmo trutta</i>		Yes	
61	Nouettes R.	49°35'36" S 70°03'17" E	1987	2003	<i>Salmo trutta</i>		Yes	
SOUTH COAST (Jeanne d'Arc & Ronarc'h peninsulas)								
62	Macaronis R.	49°35'54" S 70°18'13" E	1995-99	2016	<i>Salmo trutta</i>		No	Successful human introduction (<i>Salvelinus fontinalis</i> , 1993)
63	Vallée phonolite Basin	49°37'16" S 70°10'17" E			<i>Salvelinus fontinalis</i>		No	Falls
64	Mhicric R.	49°40'57" S 70°14'29" E			NS		No	Successful human introduction (<i>Salmo trutta</i> , 1992)
64a	Val du Levant R.	49°41'24" S 70°07'28" E	1993	2003	<i>Salmo trutta</i>		No	Falls
65	Cap du Challenger R.	49°43'49" S 70°04'55" E			NV		probably no	
66	Crête des Laves R.	49°39'27" S 69°49'47" E			NV		Yes	Falls low discharge
67	Crête des Laves R.	49°38'17" S 69°47'40" E			NS		Yes	
67a	Relais des Swains R.	49°35'02" S 69°46'33" E			NS		Yes	
68	Relais des Swains R. aux Escuells Brook	49°34'45" S 69°46'26" E			NS		Yes	
SOUTH COAST (Gallieni Mountains & Audierne Bay)								
69	La Clérée Basin; Hermance Lake & Gallets R.	49°30'01" S 69°37'37" E	1993	2018	<i>S. trutta</i> / <i>S. fontinalis</i> X <i>alpinus</i>		Yes	Successful human intro. (<i>Salmo trutta</i> , 1993 ; <i>Salvelinus fontinalis</i> X <i>alpinus</i> , 1993)
70	Olsen R.	49°31'29" S 69°40'18" E	2014-2016	2018	<i>S. trutta</i> / <i>S. fontinalis</i> X <i>alpinus</i>		Yes	
71	Vallée du Radiolaire R.	49°33'00" S 69°40'16" E	?-2016	2018	<i>Salmo trutta</i>		Yes	
72	Val des Sikaus	49°36'29" S 69°35'20" E			NS		No	Glacier near beach high slope + pinguins
73	River between Le Peligné & Doigt-Sainte Anne	49°35'07" S 69°22'31" E			NV		Possible	
74	Plaine de Dante R.	49°34'17" S 69°21'26" E	? - 2015	2018	NV		Yes	
75	Torrent des cristaux (outlet Marfoz lake)	49°27'49" S 69°17'31" E			<i>Salmo trutta</i>		Unknown	
80	Plaine Ampère Basin	49°29'10" S 69°12'46" E			NS		Yes	
83	Porres Noires R.	49°29'06" S 69°05'30" E			NS	Smolts unknown sp (2018)	Unknown	
90	Des Contacts Valley	49°32'24" S 69°05'01" E			NV		Unknown	
98	Vallée de La Houche Bassin	49°35'01" S 69°03'36" E			NS	<i>Salmo trutta</i> (2018)	Yes	1 sea trout hand caught in a small pool
100	Larmor R.	49°39'49" S 69°05'13" E			NV		Unknown	
103	Plage Jaune R.	49°43'18" S 68°55'10" E			NV		Unknown	
105	Des Sables R.	49°42'28" S 69°00'50" E			NV		Unknown	

7.2 Annexe 2a

Available data on salmonids (genera *Oncorhynchus* and *Salvelinus*) introduced to the Kerguelen Islands (originally published in Lecomte et al 2013).

A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	
Species Common name	Import #	Year import	Intro or transfer #	Trial #	Origin	Acquiculture or Wild	Comments on spawners, quality of eggs or released fish	# imported or produced on site	Import or production stage	Survivors	Date of release	Total released	Stage at release	River or bush	Site of release & comments	Isolated site	Survival	Natural reproduction	
<i>Oncorhynchus kisutch</i> (Walbaum, 1792)	12	1977	Intro 1	1	Coville R. (USA)	Wild, sea ranching	From rivers in Washington State (Trout Lodge hatchery, Tacoma)	15 600	Egg	14 600	06/03/1978	6 020	Fry	Griscaille	Downstream from Lake Tristan	No	Yes	Yes	
<i>Coregonus alpinus</i>	15	1983	Intro 2	2	Puyallup R. (USA)	Wild		200 000	Egg	199 000	22-25/12/1984	22 560	Smolt	Amnor	Outlet of Amnor Lake, last pool	No	Yes	Yes	
											11/03/1985	215	Smolt		Outlet of Amnor Lake, last pool	No	Yes	Yes	
											08/03/1985	3 900	Parr		Amnor Lake	No	Yes	Yes	
											22/12/1985	893	Smolt		Outlet of Amnor Lake, last pool	No	Yes	Yes	
											01/01/1986	11 090	Parr		Amnor Lake	No	Yes	Yes	
											14/01/1986	18 660	Smolt		In brackish water below falls	No	Yes	Yes	
											09/02/1986	18 200	Smolt		In brackish water below falls	No	Yes	Yes	
											10/02/1986	100	Smolt		Amnor Lake	No	Yes	Yes	
											19/02/1986	18 770	Smolt		In brackish water below falls	No	Yes	Yes	
											24/12/1986	4 500	Parr		Amnor Lake	No	Yes	Yes	
											31/12/1986	2 408	Parr		Amnor Lake	No	Yes	Yes	
											08/01/1987	100	Smolt		In Bate Hurley	No	Yes	Yes	
											10/01/1987	12 000	Smolt		Outlet of Amnor Lake, last pool	No	Yes	Yes	
											17/02/1987	12 150	Smolt		Outlet of Amnor Lake, last pool	No	Yes	Yes	
											19/02/1988	18 180	Smolt		Amnor	No	Yes	Yes	
											18-22/07/1989	32 197	Smolt		Downstream fence	Semi	Yes	Yes	
											07/01/1989	33 792	Smolt		Downstream fence	Semi	Yes	Yes	
											198 600	18-22/07/1990	40 413	Smolt		Downstream fence	Semi	Yes	Uncertain
											193 660	10/01/1990	63 120	Smolt		Amnor Lake	Semi	Yes	Uncertain
											6-11/2/1990	21 086	Smolt		Downstream fence	Semi	Yes	Uncertain	
											05-08/02/1991	43 517	Smolt		Downstream fence	Semi	Yes	Uncertain	
											19/01/1991	15 397	Parr		Amnor Lake	Semi	Yes	Uncertain	
											15/01/1992	2 459	Smolt/Parr		Upstream fence	Semi	Yes	Uncertain	
											27/12/1992	7 465	Smolt/Parr		Amnor Lake	Semi	Yes	Uncertain	
											0	0	Egg						
											02-03/02/1956	100	Egg		R. de la Ferme, downstream dam	No	No	No	
											06/04/1948	7 500	Egg		Downstream Hall Fusse	No	No	No	
											05/04/1948	6 250	Egg		Downstream falls	No	No	No	
											7/03/1959	721 (mixed to S. trutta)	Parr		Outlet Lac Supérieur and left bank lac des Trinités	Semi	Yes	No	
											29/12/1961	~ 2600	Egg			Semi	Yes	No	
											7/01/1962	?	Sac fry		R. des Américains	No	No	No	
											0	0	Egg						
											07/07/1987	80 000	Parr		Amnor Lake	Semi	Yes	No	
											29/12/1961	~ 3400	Egg		Outlet Lac Supérieur	Semi	Uncertain	No	
											02/01/1962	~ 500	Sac Fry		Lac Blen	Semi	Uncertain	No	
											29/12/1961	6 500	Egg		Outlet Lac Supérieur	Semi	Yes	Yes	
											02/01/1962	2 000	Spec Fry		Outlet Lac Supérieur	Semi	Yes	Yes	
											01/02/1962	500	Fry		Upstream near Grande-Munille	No	Yes	Yes	
											02/01/1962	2 000	Spec Fry		Upstream falls	Semi	Yes	Yes	
											11/01/1963	48	Parr		R. du Sud	No	Yes	Yes	
											Jan-May 1963	50	Parr		Small risk of confusion with R. Norvégienne ?	No	Yes	Yes	
											22/03/1972	60	Fry		R. de la Ferme, downstream dam	No	Yes	Yes	
											07/04/1974	60	Adult + parr		Mid-stream, Doubt on release	Semi	Yes	Probable	
											18/12/1975	~ 12	Adult		R. du Sud	Semi	Yes	Yes	
											19/03/1991	284	Parr		Downstream falls	Semi	Yes	No	
											26/12/1992	14	Adult		Amnor Lake	Semi	Yes	Yes	
											27/12/1992	470	Fry		Amnor Lake	Semi	Yes	Yes	
											09/01/1993	2 282	Egg		Mid-stream, near shelter	No	Yes	Yes	
											7/8/1991	2 000	Parr		4 release sites in the lake	No	Yes	Yes	
											27/12/1992	808	Parr		Amnor Lake, infected by BKD	Semi	Uncertain	No	
											09/01/1993	350	Fry		Last tributary downstream on left bank of Lac d'Hernance	No	Yes	Yes	

7.3 Annexe 2b

Available data on salmonids (genus *Salmo*) introduced to the Kerguelen Islands (originally published in Lecomte et al 2013).

