Risks, benefits and management implications of harvesting small and large size salmon in wild Atlantic salmon populations, with an emphasis on Quebec

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SUMMARY

- Many fisheries management activities result in non-random harvesting of individual fish based on their size, age, sex, and timing of reproduction.
- Where harvesting rates are moderate to high, such selectivity can induce evolutionary changes in wild fish populations with negative consequences for population persistence, productivity and recovery.
- This review first broadly investigates the biological (ecological, genetic, evolutionary) benefits and risks of conserving small (1SW) and large size (MSW) salmon in wild Atlantic salmon populations.
- The review then focuses on assessing risks associated with the current practice of harvesting only (or mainly) 1SW salmon in populations found in Quebec.
- Where known, current harvesting rates of small size salmon in most Quebec populations are not sufficiently high to generate *rapid* evolutionary changes within populations.
- However*, incremental* evolutionary changes may be expected in some Quebec populations if their current harvest rates (~0.35-0.40) are continued for several more generations.
- The simplest way to avoid (or dramatically reduce) harvest-induced evolutionary change (and any risks associated with it) is to simply reduce overall fishing mortality to low or moderate levels (~0.10-0.30).
- The relative benefits of conserving small and large size salmon vary widely depending on their relative proportions within a population.
- In the face of increasing environmental change and pressures on wild Atlantic salmon populations, a long-term adaptive management strategy could consider (i) improved monitoring of a series of population metrics on select populations spanning a wide range of life history variation, and (ii) experimental manipulation of harvest regimes across groups of rivers in order to better forecast their full risks and benefits from conservation and harvesting perspectives.

INTRODUCTION AND REVIEW OBJECTIVES

Sustainable exploitation of wild fish populations remains a long-term societal challenge, both from a socio-economic, environmental and policy perspective. Unsustainable exploitation is detrimental to Canadian industry and the environment, as evidenced by well-known collapses of northwest Atlantic cod and several high value recreational fisheries (Hutchings & Myers 1994; Post et al. 2002). Development of sustainable fisheries harvesting practices depends heavily on sound scientific principles and evidence-based knowledge from a diversity of biological sub-disciplines (e.g. ecology, evolution, genetics, behaviour) and levels of biological organization (e.g. population, species, community, ecosystem) (Palkovacs 2011; Fraser 2013; Dunlop et al. 2015; Kuparinen & Festa-Bianchet 2017).

Within this context, fisheries science is increasingly recognizing that, intentionally or inadvertently, many fisheries management activities elicit what is referred to as selectivity. I define selectivity here as any non-random harvesting of individuals within exploited populations based on their size, age, sex, timing of reproduction, behaviour, or life history type (e.g. Kuparinen & Merila 2007; Hutchings & Fraser 2008; Heino et al. 2015; Tilletson & Quinn 2017). In fishes, most of these characteristics show genetic variability among individuals (e.g. Carlson & Seamons 2008; Wood et al. 2015). Therefore, whenever fishing is persistently selective, by non-randomly targeting such genetically-based characteristics over successive generations, evolutionary change can occur in the exploited populations (Kuparinen & Merila 2007; Hutchings & Fraser 2008).

When the rate of selective harvesting is moderate over time, such fisheries-induced evolution (hereafter abbreviated FIE) is expected to be *incremental* over several generations; when selective harvesting rates are very high, FIE is expected to be very *rapid*, within one to a few generations (Conover & Munch 2002; Dunlop et al. 2015; Uusi-Heikkila et al. 2017). Although it is extremely difficult to conclusively demonstrate FIE in natural populations, it is likely common in many fisheries, including for salmonid fishes (Ricker 1981; Hard 2004; Edeline et al. 2007; Kendall & Quinn 2012; Heino et al. 2015). Very importantly, FIE can subsequently elicit ecological change on short time scales that affect harvest biomass and population persistence, in some cases potentially equal to or exceeding the changes brought on by classical ecological effects (Palkovacs 2011; Fraser 2013). Specifically how fisheries selectivity and evolutionary change may negatively or positively affect population persistence and productivity (directly or indirectly) is only recently being addressed theoretically and empirically (Fraser 2013; Heino et al. 2013; Dunlop et al. 2015; Eikeset et al. 2016; Kuparinen & Hutchings 2017).

In the case of wild Atlantic salmon (*Salmo salar*), adults returning to spawn in rivers have either spent one winter at sea (1SW, otherwise known as 'small size' or 'grilse') or multiple winters at sea (MSW, comprising 2SW, 3SW and occasionally 4SW or older fish, otherwise known as 'large size') before they are exposed to exploitation by anglers. Due to this major age difference in growth opportunity, MSW fish are much larger in body size than 1SW fish (e.g. Hutchings & Jones 1998, Cauchon & April 2018).

Populations also vary dramatically in their proportions of 1SW vs. MSW fish (e.g. Klemetsen et al. 2003; MFFP 2017). In many regions, Atlantic salmon management permits the harvesting of 1SW salmon, whereas most MSW salmon are mandatorily or voluntarily released (e.g. DFO 2015; MFFP 2017). Quebec has the highest proportion of MSW salmon of any Canadian province, and remains the only place in North America where recreational anglers can harvest MSW fish. The number of rivers on which such practice is allowed has been reduced over the past decade. For instance, since the implementation of the Plan de gestion du saumon 2016-2026 (MFFP 2016), harvesting of MSW salmon is allowed only from mid-season (the middle of the spawning run) onwards, and only if mid-season counts indicate that the optimal conservation number of spawning adults will be reached for that specific river (MFFP 2017). As a result, it is common that only 1SW salmon are harvested annually in many of the province's rivers (MFFP 2017).

The potential benefits of conserving large-sized, older fish (e.g. MSW salmon) have been heavily discussed in the primarily literature in recent years (e.g. Birkeland & Dayton 2005; Gwinn et al. 2013; see below). Nevertheless, annual harvesting of only 1SW salmon may also generate selectivity. Moreover, in many populations, 1SW salmon are disproportionately male (Hutchings & Jones 1998). Hence, continued harvesting of only 1SW salmon may ultimately generate evolutionary changes to wild Atlantic salmon life history characteristics, especially in males. The degree to which such evolutionary changes may be manifest has not been considered, nor have the potentially undesirable consequences to Atlantic salmon population persistence or harvesting productivity.

This review firstly synthesizes the benefits and risks of harvesting small and large size salmon based on existing and emerging literature on FIE and the biology of Atlantic salmon. I then use this synthesis to assess risks associated with current harvesting regimes in Quebec, with implications for Atlantic salmon management considerations in the province. The review's five main objectives specifically investigate:

- Genetic and ecological benefits of conserving large size (MSW) and small size salmon (1SW)
- Ecological, genetic and evolutionary risks to wild salmon populations from harvesting only 1SW salmon (including in relation to population diversity, life history evolution, mating system and sex ratios)
- Conditions under which harvesting only 1SW salmon would be considered a negligible risk to wild populations
- Risk assessment of harvesting only 1SW salmon in Quebec's wild Atlantic salmon populations
- Management recommendations in relation to wild salmon harvesting and wild salmon sizes in Quebec

GENETIC AND ECOLOGICAL BENEFITS OF CONSERVING BOTH LARGE SIZE AND SMALL SIZE SALMON

The fisheries literature has a long history of reporting the potential negative consequences of size-selective harvesting (Law & Grey 1989; Law 2007; Jorgensen et al. 2007; Kuparinen & Merila 2007; Heino et al. 1998, 2008, 2015; Hutchings & Fraser 2008; Laugen et al. 2013; Dunlop et al. 2015; Kuparinen & Festa-Bianchet 2017). Fishing commonly targets large-sized individuals with faster growth rates. Increased mortality on such individuals from fishing is therefore expected to favour faster life histories directly or indirectly, in the form of earlier age-at-maturation, increased reproductive investment, or reduced post maturation growth (Heino et al. 2015; Kuparinen & Festa-Bianchet 2017). Because genetic variability underlying growth and maturation traits can also co-vary with genetic variability underlying other traits, size-selective harvesting results directly or indirectly in selection on an array of traits, including behavior (Uusi-Heikkila et al. 2015), timing of reproduction (Tilletson & Quinn 2017) and physiology (Philipp et al. 2015). Over successive generations, evolutionary changes to the properties of fish populations can be manifest, in turn potentially influencing their dynamics and productivity.

Benefits of conserving large size salmon – As a result of the risks associated with large fish removal, a wide body of literature has focused on the potential benefits of reducing or avoiding harvest of larger sized adults within natural fish populations. Larger, older fish have exponentially greater fecundity, can produce more and faster-growing or higher-quality offspring, be more experienced and successful with spawning, may be more effective at cropping down competitor prey species and, in some cases, benefit younger individuals that learn migration routes from older individuals (Grey & Law 1987; Berkeley et al. 2004a,b; Birkeland & Dayton 2005; Venturelli et al. 2010; Gwinn et al. 2013). Hence conserving larger fish maintains individuals with higher reproductive potential, which may contribute towards a faster recovery in populations that have experienced declines due to environmental or human-induced causes (Birkeland & Dayton 2005). Conserving older fish also means that the average generation time of a population is greater. This can have positive effects on the stability of trophic cascades in aquatic ecosystems (Birkeland & Dayton 2005). It can also result in a greater likelihood that genetic diversity is retained at smaller population size, through dampened genetic drift and inbreeding over time periods of concern to management (Fraser 2013).

Benefits of conserving small size salmon – There are also several benefits to ensuring that small-sized adult fish are conserved within populations. In many fishes, spawning occurs at different times and locations for individuals of different size/age (Wright & Trippel 2009), including within salmonid fishes (Hutchings & Myers 1994; Quinn et al. 2016). This can provide a clear buffer against environmental stochasticity (Hsieh et al. 2010). Timing of reproductive events in fishes is also thought to reflect local evolutionary optima based on selective pressures on adults and their offspring (Tilletson & Quinn 2017), and both body size and reproductive timing commonly have moderate to high heritability (Carlson & Seamons 2008). Thus, conserving smaller, younger individuals is likely to increase overall reproductive output of a population whilst extending the spawning season and increasing the likelihood that spawning times are matched with local environmental optima and prey availability. Note that the same

benefit applies to conserving large, older fish, which tend to spawn either earlier or later than smaller-sized fish over a reproductive season depending on the species.

Smaller-sized adults are most often also younger in age; their conservation means that a mixture of age classes is present in any one spawning season, which increases the retention of genetic diversity in different age cohorts within a population, should there be recruitment failure in a given year (Hutchings & Jones 1998; Perrier et al. 2014). Sexual-size dimorphism is common in many fishes (Parker 1992; Ritchie et al. 2007; Zastavniouk et al. 2017), including some Atlantic salmon populations (Klemetsen et al. 2003). Therefore, conservation of smaller-sized fish can also reduce the likelihood that size-selective fishing of smaller-sized individuals will predominantly target only one sex, which poses a number of risks (see below).

ECOLOGICAL, GENETIC AND EVOLUTIONARY RISKS TO WILD SALMON POPULATIONS FROM HARVESTING ONLY SMALL SIZE SALMON

Harvesting of only small size salmon is expected to increasingly pose a number of potential ecological, genetic and evolutionary risks to wild Atlantic salmon populations as the harvest rate within a population increases from moderate to very high.

Ecological risks – Harvesting of only small salmon (and predominantly males) may alter mating systems and perhaps sex ratios of spawning salmon (Gross 1991; Fraser 2013). Nevertheless, there is substantial empirical evidence that Atlantic salmon populations are regulated primarily by density-dependent mortality at early life stages and by density-independent factors at reproductive stages (Jonsson et al. 1998; Einum & Nislow 2005; Imre et al. 2005; Einum et al. 2006). Therefore, harvesting of only small size salmon – especially if these are less likely to be females (or females with lower fecundity) – is not expected to have major density-dependent consequences for population recruitment unless the harvest rate is persistently moderate or higher (~0.30-0.40 or greater: see below and Dunlop et al. 2015; Kuparinen & Hutchings 2017). Additionally, within most Atlantic salmon populations, including in Quebec, males are composed of anadromous and nonanadromous, precocial parr (Hutchings & Jones 1998; Perrier et al. 2014). Precocial male parr are capable of spawning with, and fertilizing the eggs of, females even when anadromous males are absent (Hutchings & Jones 1998). From the perspective of fertilizing eggs and egg deposition within salmon populations, the presence of mature male parr helps to dampen any negative effects of reducing the number of returning small salmon.

Genetic and evolutionary risks – Harvesting only small size salmon is a form of selectivity. If such selective harvesting is moderate or higher and persists over time, FIE may arise, especially given that age-at-maturity and related traits (e.g. propensity to migrate or migrate to sea in males) have a significant genetic component (Carlson & Seamons 2008; Barson et al. 2015). Life history changes generated from FIE may subsequently affect abundance and harvestable productivity of an Atlantic salmon population in undesirable ways for management.

Shifts in life history expression – As harvesting of small-size salmon in Quebec specifically targets males disproportionately, a resulting consequence might be reduced fishery yields (biomass and catchable numbers of individuals) through alterations to alternative life history tactics. Expression of anadromous and nonanadromous life histories in salmonids is associated with a threshold body size and influenced by both genetic and plastic effects (Theriault et al. 2008; Piche et al. 2008; Yates et al. 2015). The much larger migratory anadromous individuals are of primary interest for fisheries harvesting whereas the nonanadromous individuals are often too small to harvest at all. Intense fishing of males will directly select against anadromous individuals, potentially favouring a shift towards an increased probability of expressing the nonanadromous life history; the reduced population size of anadromous individuals also decreases mating competition among nonanadromous individuals where the two forms exhibit alterative mating tactics (Gross 1991; Fraser 2013).

Population-specific sensitivities to life history changes induced by harvesting – Atlantic salmon populations probably vary in the likelihood that harvesting will induce an increase in the frequency of precocial male maturation. From a fishery-perspective, the most sensitive populations might be those with (i) no males maturing as MSW fish (only as 1SW fish), (ii) a higher proportion of anadromous vs. precocial maturation and/or (iii) a greater mean fitness difference between the precocial and anadromous life history at any point in time. These are all cases where selection from harvesting 1SW males only might be expected to be strongest against an anadromous life history, and where the cost of reducing the anadromous component of male life histories is most impactful for fishery yields. Unfortunately, good data for (ii) and (iii) are unavailable for most wild populations (e.g. see Hutchings & Jones 1998). Reductions in fishery yield resulting from an increased frequency of precocial male maturation would, again, be expected more under high harvesting rates over multiple generations.

Altered phenology from harvesting – Given the aforementioned links between body size and either reproductive timing within populations or spawning area use (and the often high heritability of body size/phenology traits), size-selective harvesting of smaller size individuals may also contract the reproductive season in Atlantic salmon. This is because it would reduce the abundance of smaller adults with either particularly early or later (in the case of many salmonids) spawn timing (Hixon et al. 2014; Tilletson & Quinn 2017). Thus, harvesting of only smaller, younger individuals – if sufficiently intense – might be expected to decrease overall reproductive output of a population, contract the spawning season, and decrease the likelihood that all suitable spawning times and areas were used by returning adults.

Loss of genetic diversity – Potential genetically-based shifts in male size-at-maturation and overall reproductive timing induced by FIE discussed above are associated with quantitative traits in Atlantic salmon. Loss of genetic diversity *per se* (e.g. neutral genetic diversity not under current selection) as a risk from harvesting only small size salmon seems less likely to occur. Namely, precocial males in freshwater will contribute to the annual generation of new cohorts within the population (e.g. see Perrier et al. 2014). The only exception may be in very small populations (e.g. <100-200 adults)

because the loss of genetic diversity from stochastic events is more likely in such populations (Palstra & Ruzzante 2008), though presumably such populations are already largely protected from high harvesting rates.

CONDITIONS UNDER WHICH HARVESTING ONLY SMALL SIZE SALMON WOULD BE CONSIDERED A NEGLIGIBLE RISK TO WILD POPULATIONS; OTHER SUSTAINABLE HARVESTING CONSIDERATIONS

Negligible risk is defined here as *an impact on the productivity of a population which can be mitigated by a wild population within one generation once the impact ceases.* Undoubtedly, harvesting of small salmon at high rates over successive generations within largely 1SW-based populations would render wild population recovery difficult within a generation. Persistent, intense harvesting of small salmon over multiple generations would also be expected to result in FIE and possible changes to the productivity of wild populations; again, such FIE would be more severe at higher harvesting rates and/or when the selectivity in harvesting is more pronounced (e.g. by disproportionately harvesting only specific traits or components of the populations) (Kuparinen & Merila 2007; Hutchings & Fraser 2008; Audzijonyte et al. 2013; Kuparinen & Festa-Bianchet 2017). Currently, however, there is little specific empirical information to guide management efforts regarding the exact conditions wherein harvesting only 1SW salmon poses a negligible risk to a wild Atlantic salmon population (aside from populations with a very small proportion of 1SW spawners where risk is inherently low). Given this, below I draw inferences from modelling studies, focus on ways in which risks can be avoided or reduced in relation to harvesting itself, and then discuss some additional uncertainties not accounted for in existing modelling.

Avoiding fisheries-induced evolution by reducing harvesting rate – The simplest way to ensure that harvesting of small size salmon is a negligible risk for wild populations is to simply avoid (or dramatically reduce) FIE by reducing overall fishing mortality to low or moderate levels (Law 2007; Hutchings & Fraser 2008; Hutchings 2009; Kuparinen & Festa-Bianchet 2017). For example, at low harvest levels (~0.10-0.30), existing modelling simulations suggest that any incrementally generated FIE over a 100 year period had a minimal effect on population growth rate for different fish species (cod, perch, whitefish; Dunlop et al. 2015). Moderate to high levels of harvesting induced more significant and rapid impacts on population growth rate (Dunlop et al. 2015). These simulations may not adequately typify exactly what would be expected in Atlantic salmon given their different life history characteristics and genetic basis of traits (see below). Nor do they account for other potentially undesirable aspects for harvesters (e.g. changes in average size of harvested fish). Yet even more recent modeling efforts that accounted for Atlantic salmon genetic intricacies did not detect major FIE at fishing mortalities of ~0.35-0.45 until after 40-50 years of simulated harvesting (approximately 12-15 generations for the species) (see Figures 2 and 4 in Kuparinen & Hutchings 2017). In sum, results of existing modelling simulations suggest that, provided low to moderate levels of harvesting are practiced, harvesting of only small salmon likely poses a negligible risk to wild Atlantic salmon population productivity, unless continued for a considerable number of harvesting generations.

Balanced harvesting: a more sustainable way to harvest? – Inherently, the risks and uncertainties posed from harvesting either large or small size salmon raise a fundamental question: what is the optimal way to harvest wild Atlantic salmon populations? It is not possible to harvest salmon randomly according to their size, age, timing of migration, behaviour, etc. in a way that would entirely remove any selectivity. 'Balanced' harvesting is one alternative harvesting strategy to common, size-based management practices.

Advantages of balanced harvesting – <u>Balanced harvesting is intended to distribute fishing mortality across the widest range of sizes in a given ecosystem or population, in proportion to their natural productivity; by doing so, it has the potential advantage of more effectively mitigating the ecological and evolutionary effects of fishing while supporting sustainable fisheries</u> (Garcia et al. 2012, 2016), potentially even more productive ones (Law et al. 2014). Indeed, maintenance of fish size spectra under intense and diverse harvesting regimes which cause high mortality but low selectivity is cited as support for balanced harvesting (Garcia et al. 2012).

Uncertainties/disadvantages of balanced harvesting – <u>Unfortunately, the relative efficacy of balanced harvesting in retaining population-productivity relationships compared to size-selective harvesting has not been evaluated under controlled experimental conditions using natural populations of any fish species</u>. Balanced harvesting is also not without potential disadvantages, which should be factored in if adopted as an exploratory approach for sustainable harvesting. First, balancing selection does not completely rule out selectivity. Heino et al (2015) point out that a uniform rise to fishing mortality across all body sizes still will cause selective pressures on many traits in many situations. This is because the advantages of becoming older become less important in life history trade-offs, leading to faster life history evolution (e.g. mature earlier, enhance current reproduction). Second, critics of balanced harvesting point to a number of potentially impractical limitations of the approach for implementation. These include the requirement of harvesting all sizes of fish, difficulties in obtaining a truly balanced harvesting distribution even if a population's size distribution is well-known (and temporally unchanging), and effectively regulating a balanced harvest distribution (Froese et al. 2016).

Other uncertainties – Modelling exercises that have investigated conditions wherein FIE is manifested and expected to influence population growth rate may not adequately portray population responses in the wild. Therefore, several additional uncertainties should be considered for any harvest regime that imposes selectivity. The first is that the extent of FIE also depends on the genetic architecture underlying traits. Most traits under selection will be polygenic in nature, which should shift life histories in a directional fashion (e.g. smaller size and earlier age at maturity when size selective harvesting targets large-sized fish). However, age at maturity in Atlantic salmon was recently determined to be largely under genetic control at a single locus (Barson et al. 2015). This trait characteristic recently modeled to result in largely divergent and disruptive selective pressures in Atlantic salmon (Kuparinen & Hutchings 2017),

implying that the evolutionary outcome of a specific harvesting strategy is likely to be very uncertain.

The first uncertainty is compounded by a second one: the difficulty of understanding indirect effects of selectivity on correlated traits that influence each sex. For instance, it has been suggested that male-specific selectivity (which typifies small size Atlantic salmon harvesting in many rivers) indirectly affects adaptive female traits and potentially affect population dynamics (Kuparinen & Festa-Bianchet 2017). Nevertheless, evidence for this is, at present, slim for any organism (Pigeon et al. 2017).

A third chief uncertainty in the interpretation of phenotypic trends in harvested populations is that the plastic changes to phenotypes and vital rates expected from harvest-based reductions in population density can be similar to changes induced by harvest-selection (Kuparinen & Festa-Bianchet 2017); mere detection of life history trends within Atlantic salmon populations may not be adequate for assessing the full existence of FIE (Kuparinen & Hutchings 2017). Similarly, in many modelling simulation exercises, trait heritabilities are assumed to be constant within populations over harvesting intervals, yet these vary over time within fish populations and are often highly variable within trait classes (Carlson & Seamons 2008; Heino et al. 2015).

In summary, we are still a long way off from a complete understanding of what the direction of fisheries-induced selection imposed by a specific type of harvesting/gear will be for a given trait, how strong the selection will be, and how quickly FIE might ensue (Audzijonyte et al. 2013; Kuparinen & Festa-Bianchet 2017). Evolutionary and ecological variables (density, age structure, recruitment, population growth) can interact in complex ways within populations and across life stages, vary temporally and affect different fitness components (Dunlop et al. 2015; Eikeset et al. 2013, 2016; Kuparinen & Festa-Bianchet 2017; Pigeon et al. 2017). While the rate of FIE has been observed to be low in some modelling exercises (e.g. 0.1-0.6%/year Anderson & Brander 2009), such low rates are significant if they persist for decades (Heino et al. 2015). Hence, many authors recommend applying the precautionary principle and minimizing FIE (Eikeset et al. 2013; Laugen et al. 2013; Dunlop et al. 2015).

RISK ASSESSMENT OF HARVESTING ONLY SMALL SIZE SALMON SPECIFICALLY IN QUEBEC'S WILD ATLANTIC SALMON POPULATIONS

The province of Quebec contains more than 100 wild Atlantic salmon populations, the vast majority of which are harvested annually when adults return to rivers to spawn (MFFP 2017; Figure 1). Since approximately 2002, the mandatory release of most or all MSW salmon has been implemented on many rivers (MFFP 2017). Harvesting of MSW salmon is only permitted mid-season onwards if the optimal conservation limit in a specific river is achieved (MFFP 2016). Most harvested salmon in the province are therefore 1SW salmon (MFFP 2017), and most of these salmon are males (O'Connell et al. 2016, Cauchon & April 2018). This time period constitutes approximately 3-4 generations for the species in which the small size-selective harvesting practice has been implemented.

Variability in life history and harvest rates among Quebec salmon populations –
The life history of Atlantic salmon populations in Quebec is highly variable (Hutchings &
Jones 1998; MFFP 2017), as is the harvesting rate between populations (MFFP 2017).
This variability is tremendously important to factor in when determining potential risks
associated with harvesting only small size salmon in Quebec's rivers, or alternative
harvesting regimes. Five specific populations exemplify this variability (locations in
Figure 1). For example, virtually all or most adult spawners in some populations are
large size salmon (e.g. Moisie, Saint-Jean (Gaspesie)). Others have more intermediate
proportions of both large and small size salmon (Matane, Trinite), while small size
salmon dominate spawning runs in Du Vieux-Fort (Table 1). Similarly, mean harvesting
rates of small size salmon vary substantially among these populations, from as low
~0.05 in the Moisie and Du Vieux-Fort since 2002, to ~0.20 in the Trinite, and to ~0.38-
0.40 in the Saint-Jean and Matane (Table 1; extracted from MFFP 2017). I have
included an additional five populations in Table 1 (Grande Riviere, Sainte Anne, Cap
Chat, Sainte Marguerite, Jupiter; geographic locations in Figure 1). <u>These additional five</u>
<u>populations span a similar proportion of 1SW:MSW life history components as the</u>
<u>Matane and Saint-Jean; along with the Matane and Saint-Jean, these are the most</u>
<u>heavily exploited salmon populations in Quebec of the 37 populations with long-term</u>
<u>monitoring data available (assessed from MFFP 2017). Hence, they provide the best</u>
<u>insight into whether current harvesting regimes pose a significant, negative risk to the</u>
<u>life history, persistence and/or productivity of Quebec's wild Atlantic salmon populations.</u>

Are current harvest rates in Quebec salmon populations generating FIE of
conservation concern? When considering data since 2002, harvesting rates in the
Moisie and Du Vieux-Fort, and probably the Saint-Jean and Trinite, have been
sufficiently low for any FIE generated from harvesting only small-size salmon to be a
conservation concern. Furthermore, in the Moisie and Saint-Jean, the proportion of
males that comprise 1SW vs. MSW fish is very small or small (~0.05-0.20). At such a
low proportion, any selection that disfavors 1SW males with even a ~0.40 harvesting
rate may not generate large-scale changes in the life history and yield of small size
salmon, unless continued on for many generations, and most likely only the male
component of the small size salmon would be affected.

In the Matane and remaining five rivers (Grande Riviere, Sainte-Anne, Cap-Chat and
Saint-Marguerite; Jupiter), small size salmon comprise a considerable proportion of the
annual spawning run (~0.40-0.55) and are also exploited at a mean annual rate of ~0.40
(in some years ~0.60-0.70). Yet interestingly, there is only an indication in 2 of 6 rivers
(Sainte-Anne, Cap-Chat) that the ratio of small vs. large salmon is declining since 2002
(15 years or 3-4 generations), which might be expected if disproportionate harvesting of
small size salmon favors a shift towards an older, large size salmon life history; in the
Sainte-Anne, salmon abundance has actually increased since 2002 and it is stable in
the Cap-Chat (assessed from MFFP 2017). Longer timespans (>20-33 years) in the
other 4 of 6 rivers reveal general stability in adult abundance (Grande Riviere, Matane)
or continuous declines (Saint-Marguerite, Jupiter). Other explanations than harvesting
of small size salmon per se could explain population declines; if existing rates of small

size salmon harvesting have affected population abundance or productivity in the past 15 years, they may have only done so in 2 of 6 of the most candidate populations.

Overall, these numbers are encouraging from a management perspective as they suggest a minimal overall impact of harvesting only small size salmon in most Quebec rivers with the highest current harvesting rates (mean ~0.35-0.40). Nevertheless, I reiterate two previous points drawn from recent modelling simulations (Dunlop et al. 2015; Kuparinen & Hutchings 2017): (i) the highest current harvest rates in some Quebec populations may elicit incremental FIE if continued for several more generations, and (ii) a lack of life history changes within Atlantic salmon populations may not detect the full existence of FIE. As discussed above, for example, a major uncertainty is how potential shifts in precocial male maturation in freshwater affect future Atlantic salmon harvest yield, and by how much.

Simulating harvesting rates versus egg deposition and harvest yield – Another way to approach risk to Quebec salmon populations is to assume no FIE occurs and simulate the potential consequences to egg deposition and harvest yield of harvesting different proportions of 1SW and MSW salmon in populations with varying life histories (i.e. different proportions of 1SW and MSW fish). This is cursorily summarized for four of five main focal populations in Table 2 (excluding Moisie, see below), assuming that salmon and large salmon weigh 2kg and 5kg, and produce 2025 eggs vs. 1745 eggs per kg, respectively, along with exploitation rates of 0%, 25%, 50%, and 75%.

Broadly speaking, with simulated, increased harvest rates of only 1SW salmon, egg deposition unsurprisingly decreases as the proportion of 1SW fish in the population increases, but this drop is only significant in populations that have very high proportions of 1SW fish (≥0.90) (Table 2). Adopting a 3:1 ratio of 1SW:MSW fish increases the harvest biomass relative to harvesting 1SW fish only, but only in populations with higher proportions of MSW fish (≥0.60) (Table 2). Adopting a harvesting approach where 1SW and MSW fish are harvested in the same proportion as they are represented in the adult return within a given population also increases the harvest biomass relative to harvesting 1SW fish only. However, these benefits are only obtained when the proportion of MSW fish is higher, and they come with the most cost in relation to reduced egg deposition (Table 2). The two salient points for management are as follows. First, optimal harvesting proportions of 1SW vs. MSW fish in relation to overall harvest biomass and egg deposition are highly population dependent; these metrics are not necessarily highest when only small salmon are harvested. Second, in many instances, egg deposition can be maintained without that much cost (reduction) to egg deposition if only 1SW fish or mainly 1SW fish are harvested. These general trends can be broken down further per population to relate costs and benefits of harvest relative to egg deposition.

In the Moisie, it is not possible to adopt a harvesting strategy of 1SW fish only if the harvest rate is ≤ 0.05 because there are so few small salmon in the population (Table 1).

In the Saint-Jean, harvesting only 1SW fish generates a harvest biomass that is 45% of the harvest based on harvesting the same proportion of 1SW and MSW fish as in the adult returns, without having virtually any impact on egg deposition (Table 2). Harvesting small amounts of MSW fish in this population can also improve yield without reducing egg deposition that much (Table 2). Overall, there are benefits to harvesting only (or mainly) 1SW fish in the Saint-John population.

In the Matane and Trinite, the benefits of harvesting only 1SW fish become even clearer, with yields of 53-73% relative to scenarios including harvesting of MSW fish, with little effect on overall egg deposition. Very low harvest rates of MSW fish in these populations could be permitted if increasing harvest biomass is really important for management (Table 2).

In Du Vieux Fort, there is little impact from harvesting 1SW fish only, in terms of both maintaining harvest biomass and egg deposition. Conversely, harvesting of any MSW fish does not appreciably increase harvest biomass and only substantially reduces egg deposition, especially at increased harvest rates (Table 2).

How many males are required to fertilize total egg deposition and maintain genetic diversity in harvested Atlantic salmon populations? Another aspect of risk for management to consider is – again, in the absence of FIE – how many anadromous males would be required in a given population to (i) fertilize the total number of eggs deposited in that population and (ii) maintain the genetic diversity within the population?

The answer to the first question is hypothetically zero: in some Atlantic salmon populations, a high percentage of males mature as precocial parr, and such parr are capable of spawning with and fertilizing a large percentage of female eggs within a population (e.g. Myers et al. 1984; Hutchings & Jones 1998; Taggart et al. 2001). However, our knowledge of male parr biology (including in Quebec) is far from complete to formulate prescriptive numbers and robust recommendations at the present time for a given salmon population. For example, while parr can have high levels of reproductive success relative to anadromous males, their study has been limited to single, small river systems whose spatial dynamics of spawning probably do not apply to larger rivers (e.g. Taggart et al. 2001; Weir et al. 2010). Little is known on the extent of movement of individual mature parr, their spawning lifetimes, or how quickly they can replenish sperm, although their large numbers and spatial distribution tend to suggest that a propensity to find and fertilize females in different stream areas (e.g. Taggart et al. 2001; Weir et al. 2010).

The question of how many anadromous males are required in a given population to retain that population's genetic diversity is also difficult to answer and is hypothetically zero, for the same reasons as above. Namely, precocial parr help to maintain effective population size through their fertilization of female eggs; their large numbers in many streams contain much of the standing, neutral genetic diversity within a population (Taggart et al. 2001), even when anadromous males are largely absent (Johnstone et al. 2013). Nevertheless, the presence of *at least some* anadromous males is probably

important for maintaining competitive and adaptive rigor within the vast majority of Atlantic salmon populations and has other biological benefits (e.g. gene flow between anadromous populations).

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS IN RELATION TO WILD SALMON HARVESTING AND WILD SALMON SIZES IN QUEBEC

- Existing primary literature suggests that, where existing harvesting proportions of wild Atlantic salmon are known, these are not sufficiently high to generate *rapid* FIE within *most* of Quebec's rivers (since 2002).

- Provided that low to moderate levels of harvesting are practiced (~0.10-0.30), harvesting of only small salmon likely poses a negligible risk to wild Atlantic salmon population life history characteristics or productivity.

- Nevertheless, where currently known, harvest rates of small size salmon may be sufficiently high in *some* Quebec populations (~0.35-0.40) to incrementally elicit FIE if continued for several more generations, according to recent modelling simulations (Dunlop et al. 2015; Kuparinen & Hutchings 2017).

- The simplest way to avoid (or dramatically reduce) FIE and any risks associated with FIE is to simply reduce overall fishing mortality to low or moderate levels (Law 2007; Hutchings & Fraser 2008; Hutchings 2009; Kuparinen & Festa-Bianchet 2017). Management strategies aimed at reducing overexploitation will also reduce FIE.

- There are benefits to conserving both small and large size salmon, among them being to buffer wild Atlantic salmon populations from environmental stochasticity.

- In general, however, large and small salmon are not equal in a fitness/evolutionary sense for each size of fish. Size-selective harvesting of large size salmon has more negative consequences for population recruitment and productivity than selective harvesting of small size salmon, because the advantages of becoming older (and larger) become less important in life history trade-offs. Even when the harvesting rate of each size of salmon is equal, it still becomes less valuable for a salmon to postpone reproduction because any gain from doing so (enhanced growth, survival, future reproduction) is lost when an MSW fish is harvested (see Heino et al. 2015). This is important for management to consider even in populations with high MSW:1SW ratios, given the global declines in MSW Atlantic salmon (ICES 2015).

- Strongly male-biased harvesting of 1SW fish is a form of fisheries-selectivity within harvested Atlantic salmon populations. Populations likely vary in their sensitivity to shifts towards greater precocial male maturation induced by harvesting. At present, the consequences of such shifts for the productivity of

salmon populations are uncertain but are expected to manifest only if moderate or higher harvest rates persist over time (~0.30-0.40 or greater).

- The relative benefits of conserving each size of salmon vary widely depending on their relative proportion within a population. This makes it difficult to recommend simple, prescriptive harvesting strategies across populations.

- A general approach to monitoring wild Atlantic salmon populations in Quebec given their extensive life history variability would be to treat harvesting strategies for 'groups' of populations in relation to similar 1SW:MSW components, population annual harvesting rates, population sizes, population sizes of precocial male parr, etc. to better represent population nuances (while accounting for genetic population structure). Redundancy analyses would provide one statistical means to best partition populations into groups based on variation in their characteristics.

- Harvesting rates within Quebec populations are known with reasonable confidence for 37 of more than 100 rivers in the province. Molecular DNA and eDNA approaches provide promising avenues for inferring and monitoring adult salmon abundance where this is not feasible to carry out using traditional approaches (Lacousiere-Roussel et al. 2016; Yates et al. 2017). Any such monitoring endeavor, however, must carefully consider the strengths and limitations of such approaches in relation to Atlantic salmon biology (Ferchaud et al. 2016; Yates et al. 2017).

- Because a lack of life history changes within Atlantic salmon populations may not detect the full existence of FIE (due to intricacies in the genetic basis of traits underlying functional traits in salmon), annual collection of a number of basic data on harvested fish and spawning runs is recommended where feasible.

- These monitoring data would include information on harvested/non-harvested fish size, sex, capture date, run-timing, as well as sex ratio and MSW:1SW ratio.

- The demographic contribution of precocial male parr to salmon recruitment remains a major research gap in Atlantic salmon. Focused studies on male parr (e.g. their numbers, patterns of reproductive success) where numbers and harvesting rates of anadromous males are known could help to inform the question of how many anadromous males are required to fertilize female eggs whilst maintaining genetic diversity within a given population.

- A select group of populations representing a wide range of life history characteristics could be prioritized for monitoring data collection to (i) detect potential incremental changes over time that may be warning signals of undesirable FIE (in fish size, phenology, and by sex etc.), and to (ii) facilitate future, province-wide decision-making on harvesting policies. Some of these data are already being collected on a few select rivers.

- Continued harvesting coupled with increasing climate change may result in new and rapidly changing harvest rates such that these become much higher than current rates. If certain Atlantic salmon populations experience continued declines, the likelihood of generating FIE will likely increase, with associated impacts on population productivity and persistence.

- For improved, future preparedness on how to balance conservation needs vs. harvesting interests, one adaptive management approach would be to experiment with different harvesting regimes on multiple rivers as 'treatments' in the next decade or two, with rigorous, ongoing monitoring of the metrics listed above. A 'treatment' could involve 4 to 5 rivers with the same harvesting regime (small salmon only, mix of small and large salmon, balanced harvesting etc.).

- By manipulating harvesting regimes in a controlled, replicated way across selected populations, the full benefits/risks of different harvesting regimes for all Quebec rivers could be determined before such information was needed in a given case.

Q1
1. Rivière Kedgwick
2. Rivière Patapédia
3. Rivière Causapscal
4. Rivière Matapédia
5. Rivière Nouvelle
6. Rivière Cascapédia
7. Petite rivière Cascapédia
8. Rivière Bonaventure

Q2
9. Petite rivière Port-Daniel
10. Rivière Port-Daniel du Milieu
11. Rivière Port-Daniel Nord
12. Rivière Anse à la Barbe
13. Rivière du Grand Pabos Ouest
14. Rivière du Grand Pabos
15. Rivière du Petit Pabos
16. Grande Rivière
17. Rivière Malbaie
18. Rivière Saint-Jean
19. Rivière York
20. Rivière Dartmouth

Q3
21. Rivière Madeleine
22. Rivière De Mont-Louis
23. Rivière Sainte-Anne
24. Rivière Cap-Chat
25. Rivière Matane
26. Rivière Mitis
27. Rivière Rimouski
28. Rivière Sud-Ouest
29. Rivière Ouelle

Q5
30. Rivière Jacques-Cartier
31. Rivière du Gouffre
32. Rivière Malbaie

Q6
33. Rivière Petit Saguenay
34. Rivière Saint-Jean
35. Rivière à Mars
36. Rivière Sainte-Marguerite principale
37. Rivière Sainte-Marguerite Nord-Est

Q7
38. Rivière des Escoumins
39. Rivière Laval
40. Rivière Betsiamites
41. Rivière aux Anglais
42. Rivière Mistassini
43. Rivière Franquelin
44. Rivière Godbout
45. Rivière de la Trinité
46. Petite rivière de la Trinité
47. Rivière du Calumet
48. Rivière Pentecôte
49. Rivière aux Rochers

Q8
50. Rivière Moisie
51. Rivière Matamec
52. Rivière Pigou
53. Rivière au Bouleau
54. Rivière Sheldrake
55. Rivière au Tonnerre
56. Rivière Jupitagon
57. Rivière Magpie
58. Rivière Saint-Jean
59. Rivière Mingan
60. Rivière Romaine
61. Rivière de la Corneille
62. Rivière Piashti
63. Rivière Watshishou
64. Petite rivière Watshishou
65. Rivière Nabisipi
66. Rivière Aguanus
67. Rivière Nathasquan

Q9
68. Rivière Kégaska
69. Rivière Musquaro
70. Rivière Musquanousse
71. Rivière Washicoutai
72. Rivière Olomane
73. Rivière Coacoachou
74. Rivière Etamamiou
75. Rivière Nétagamiou
76. Rivière du Petit Mécatina
77. Rivière Véco
78. Rivière du Gros Mécatina
79. Rivière Kécarpoui
80. Rivière Saint-Augustin Nord-Ouest
81. Rivière Saint-Augustin
82. Rivière Coxipi
83. Rivière Chécatica
84. Rivière du Vieux Fort
85. Rivière Napetipi
86. Rivière Saint-Paul
87. Ruisseau au Saumon
88. Ruisseau des Belles Amours
89. Rivière Brador-Est

90. Rivière à l'Hulle
91. Rivière MacDonald
92. Rivière à la Patate
93. Rivière Vauréal

Q10
94. Rivière aux Saumons
95. Rivière du Renard
96. Petite rivière de la Loutre
97. Rivière Bell
98. Ruisseau Box
99. Rivière Dauphiné
100. Rivière de la Chaloupe
101. Petite rivière de la Chaloupe
102. Rivière Maccan
103. Rivière Ferré
104. Ruisseau Martin
105. Rivière du Pavillon
106. Rivière aux Plats
107. Rivière Chicotte
108. Rivière Galiote
109. Rivière du Brick
110. Rivière Jupiter
111. Rivière à la Loutre
112. Rivière aux Cailloux
113. Rivière Sainte-Marie
114. Rivière Bec-Scie

Q11
115. Rivière aux Feuilles
116. Rivière Koksoak
117. Rivière à la Baleine
118. Rivière George

Q: Zones salmonicoles

ÎLES DE LA MADELEINE

QUÉBEC

HULL

MONTRÉAL

Q1. Baie des Chaleurs
Q2. Péninsule de la Gaspésie
Q3. Bas-Saint-Laurent et
    Rive Nord de la Gaspésie
Q4. Région des Appalaches
Q5. Région de Québec
Q6. Région du Saguenay
Q7. Haute Côte-Nord
Q8. Moyenne Côte-Nord
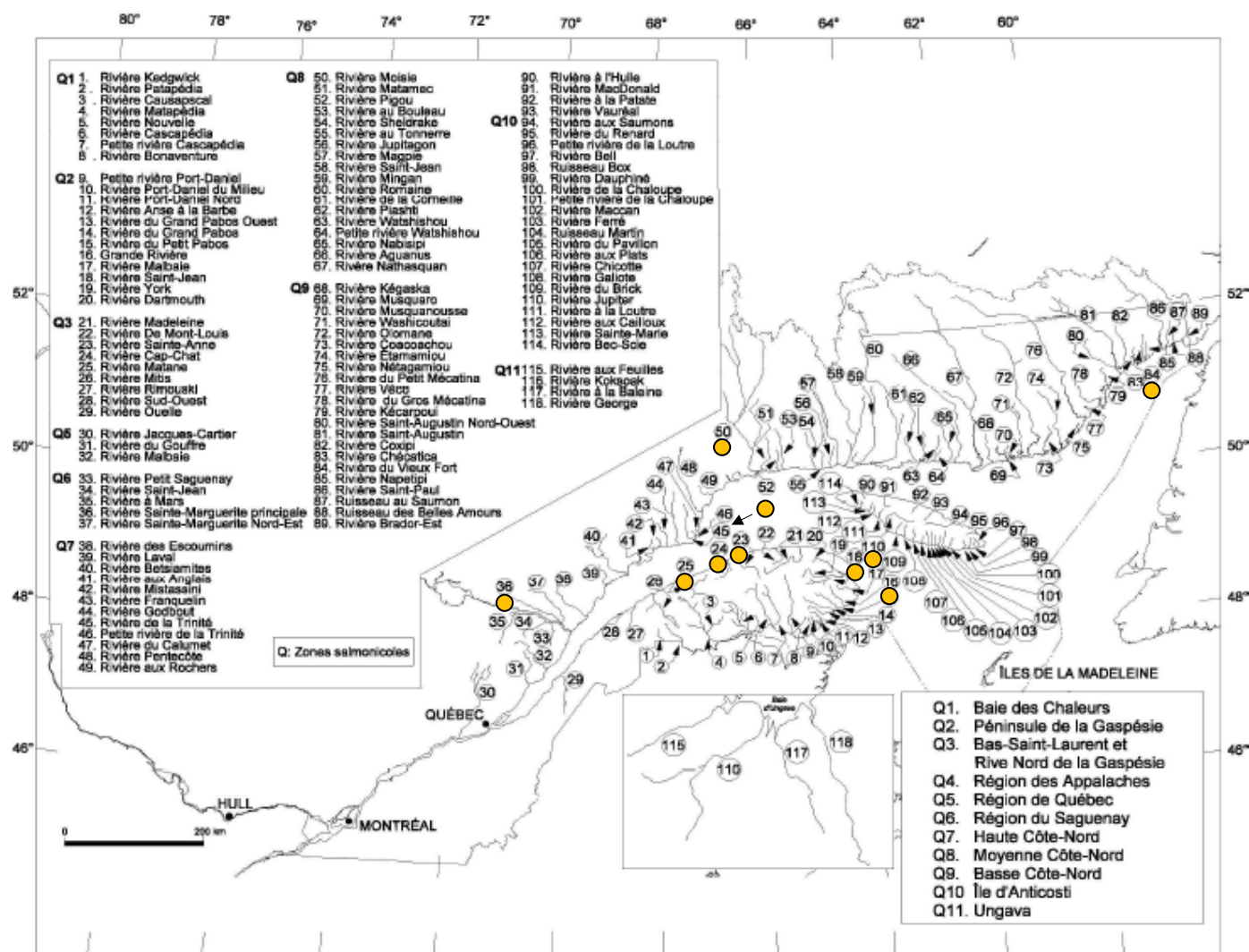Q9. Basse Côte-Nord
Q10 Île d'Anticosti
Q11. Ungava

Figure 1. Map of Atlantic salmon rivers in Quebec from MFFP 2017; orange circles below specific rivers denote the focal rivers included in the section "Risk assessment of harvesting only small size salmon specifically in Quebec's wild Atlantic salmon populations".

Table 1. The varying proportions of small and large size wild Atlantic salmon in selected Quebec Rivers. Data were extracted or summarized from MFFP 2017, or were provided by J. April, MFFP. Notes on harvesting refer to rates for 1SW salmon only, or 1SW and MSW salmon combined ('all').

River	Notes on average harvesting rate of small salmon and of the total spawning run (ranges since 2002)	Prop. MSW	Prop. of MSW as males	Prop. of MSW as females	Prop. of 1SW as males	Prop. of 1SW fish as females	Ratio of 1SW:MSW males
Moisie	1SW: Likely very low All: Likely <0.10 contemporarily; 0.09-0.33 historically	0.95	0.45	0.55	0.99	0.01	0.0495
Saint-Jean (Gaspésie)	1SW: 0.38 (0.20-0.60) All: 0.143 (0.06-0.27), vast majority harvested fish were 1SW - Usually 2-3X MSW than 1SW in spawning run, fluctuates widely.	0.80	0.35	0.65	0.99	0.01	0.198
Matane	1SW: 0.393 (0.27-0.61) All: 0.321(0.21-0.39) mix of 1SW and MSW, more 1SW harvested	0.60	0.30	0.70	0.85	0.15	0.34
De la Trinité	1SW: 0.187 (0.10-0.24) All: 0.125 (0.05-0.17), all 1SW (but 1SW + MSW present)	0.40	0.10	0.90	0.80	0.20	0.48
Du Vieux-Fort	1SW: 0.046 (0.2-0.12) All: 0.04 (0.02-0.1), mainly 1SW harvested vast majority of spawners are 1SW	0.10	0.10	0.90	0.5	0.50	0.45
Grande Riviere	1SW: 0.438 (0.21-0.68); All: 0.185 (0.08-0.38); ~0.45-0.65 of spawners are MSW						
Sainte-Anne	1SW: 0.405 (0.25-0.59); All: 0.173 (0.13-0.26); ~0.50-0.70 of spawners are MSW						
Cap-Chat	1SW: 0.440 (0.25-0.77); All: 0.172 (0.10-0.30); ~0.50-0.75 of spawners are MSW						
Sainte Marguerite	1SW: 0.364 (0.26-0.46); All: 0.099 (0.05-0.16); ~0.55-0.80 of spawners are MSW						
Jupiter	1SW: 0.387 (0.29-0.50); All: 0.229 (0.13-0.29); ~0.30-0.45 of spawners are MSW						

Table 2. Simulated harvest biomass and egg deposition under different harvesting types and harvesting rates, across select Quebec Atlantic salmon populations varying in the proportion of 1SW and MSW fish. For each population, harvesting types listed are for (i) 1SW fish only, (ii) the same proportion of 1SW versus MSW fish as their proportion in the adult returns for that population, and (iii) a 3:1 ratio of 1SW versus MSW fish. Harvest biomass is reported as total harvest (kg) and as the proportion of the total biomass of the population. Also included is the proportion of harvest biomass for 1SW only versus the other two harvest types. The proportion of egg deposition for each harvest type and rate listed is relative to the total egg deposition of the population under no harvest. For the simulations, small and large salmon were assumed to weigh 2kg and 5kg, respectively, and produce 2025 eggs vs. 1745 eggs per kg, respectively. Mean census population size of anadromous adults (33 year average except for Du Vieux Fort (7 years)) used to calculate harvest biomass: 1227 (Saint-Jean), 2700 (Matane), 1056 (Trinite), 1437 (Du Vieux Fort). The Moisie population is not included because the low numbers of 1SW fish in this population mean it does not reach any harvest quotas for the harvesting rates simulated (see text for further details).

Population	Harvest type (1SW:MSW)	Harvest rate	Harvest biomass (kg)	Prop. Of total biomass (kg) in population	Prop. Biomass for 1SW only vs. specified harvest type	Prop. Egg deposition relative to no harvest
Saint-Jean	1SW only	10%	245	0.05		0.999
Saint-Jean	1SW only	25%	614	0.11		0.998
Saint-Jean	1SW only	35%	859	0.16		0.997
Saint-Jean	1SW only	50%	1227	0.23		0.996
Saint-Jean	0.20:0.80	10%	540	0.10	0.45	0.900
Saint-Jean	0.20:0.80	25%	1350	0.25	0.45	0.750
Saint-Jean	0.20:0.80	35%	2699	0.35	0.45	0.650
Saint-Jean	0.20:0.80	50%	4049	0.50	0.45	0.500
Saint-Jean	0.75:0.25	10%	337	0.06	0.73	0.968
Saint-Jean	0.75:0.25	25%	844	0.16	0.73	0.920
Saint-Jean	0.75:0.25	35%	1181	0.22	0.73	0.888
Saint-Jean	0.75:0.25	50%	1687	0.31	0.73	0.841
Matane	1SW only	10%	540	0.15		0.980
Matane	1SW only	25%	1350	0.13		0.960
Matane	1SW only	35%	1890	0.18		0.950
Matane	1SW only	50%	2700	0.26		0.920
Matane	0.40:0.60	10%	1026	0.10	0.53	0.900
Matane	0.40:0.60	25%	2565	0.25	0.53	0.750
Matane	0.40:0.60	35%	3591	0.35	0.53	0.650
Matane	0.40:0.60	50%	5130	0.50	0.53	0.500

Table 2 continued.

Population	Harvest type (1SW:MSW)	Harvest rate	Harvest biomass (kg)	Prop. Of total biomass (kg) in population	Prop. Biomass for 1SW only vs. specified harvest type	Prop. Egg deposition relative to no harvest
Matane	0.75:0.25	10%	743	0.07	0.73	0.950
Matane	0.75:0.25	25%	1856	0.18	0.73	0.870
Matane	0.75:0.25	35%	2799	0.25	0.73	0.820
Matane	0.75:0.25	50%	3713	0.36	0.73	0.750
Trinite	1SW only	10%	211	0.06		0.980
Trinite	1SW only	25%	528	0.16		0.940
Trinite	1SW only	35%	739	0.22		0.920
Trinite	1SW only	50%	1056	0.31		0.890
Trinite	0.60:0.40	10%	338	0.10	0.63	0.900
Trinite	0.60:0.40	25%	845	0.25	0.63	0.750
Trinite	0.60:0.40	35%	1188	0.35	0.63	0.650
Trinite	0.60:0.40	50%	1690	0.50	0.63	0.500
Trinite	0.75:0.25	10%	290	0.09	0.73	0.930
Trinite	0.75:0.25	25%	726	0.21	0.73	0.820
Trinite	0.75:0.25	35%	1016	0.30	0.73	0.750
Trinite	0.75:0.25	50%	1452	0.43	0.73	0.650
Du Vieux Fort	1SW only	10%	287	0.09		0.920
Du Vieux Fort	1SW only	25%	719	0.22		0.810
Du Vieux Fort	1SW only	35%	1006	0.30		0.730
Du Vieux Fort	1SW only	50%	1437	0.43		0.610
Du Vieux Fort	0.90:0.10	10%	331		0.87	0.900
Du Vieux Fort	0.90:0.10	25%	826		0.87	0.750
Du Vieux Fort	0.90:0.10	35%	1157		0.87	0.650
Du Vieux Fort	0.90:0.10	50%	1653		0.87	0.500
Du Vieux Fort	0.75:0.25	10%	395	0.12	0.73	0.870
Du Vieux Fort	0.75:0.25	25%	988	0.30	0.73	0.670
Du Vieux Fort	0.75:0.25	35%	1383	0.42	0.73	0.530
Du Vieux Fort	0.75:0.25	50%	1976	0.60	0.73	0.330

References cited

Andersen K.H., Brander K. 2009. Expected rate of fisheries-induced evolution is slow. Proc. Natl. Acad. Sci. U.S.A. 106: 11657-11660.

Audzijonyte, A., Kuparinen, A., and Fulton, E.A. 2013. How fast is fisheries-induced evolution? Quantitative analysis of modelling and empirical studies. Evol. Appl. 6(4): 585–595. doi:10.1111/eva.12044.

Barson, N.J., Aykanat T., Hindar K., Baranski M., Bolstad G.H., Fiske P. et al. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature 528: 405-408.

Baskett M.L., Levin S.A., Gaines S.D., Dushoff J. 2005. Marine reserve design and the evolution of size at maturation in harvested fish. Ecol. Appl. 15: 882-901.

Berkeley S.A., Hixon M.A., Larson R.J., Love M.S. 2004a. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. Fisheries 29: 23-32.

Berkeley S.A., Chapman C., Sogard S.M. 2004b. Maternal age as a determinant of larval growth and survival in a marine fish. Ecology 85: 1258-1264.

Birkeland C., Dayton P.K. 2005. The importance in fishery management of leaving the big ones. Trends Ecol. Evol. 20: 356-358.

Carlson, S.M., and Seamons, T.R. 2008. A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. Evol. Appl. 1: 222–238.

Cauchon, V., April, J. 2018. Suivi des populations témoins de saumon atlantique au Québec : rapport scientifique 2017, Québec, ministère des Forêts, de la Faune et des Parcs, Direction générale de la gestion de la faune et des habitats, Direction de l'expertise sur la faune aquatique, 54 p.

Conover, D.O., and Munch, S.B. 2002. Sustaining fisheries yields over evolutionary time scales. Science 297: 94–96.

DFO. 2015. Update of stock status of Atlantic Salmon (*Salmo* salar) in DFO Gulf Region (New Brunswick Salmon Fishing Areas 15 and 16) for 2014. DFO Can. Sci. Advis. Sec. Sci. Resp. 2015/008.

Dunlop, E.S., Eikeset A.M., Stenseth, N.C. 2015. From genes to populations: how fisheries-induced evolution alters stock productivity. Ecol. Appl. 25: 1860-1868.

Edeline, E., Carlson, S.M., Stige, L.C., Winfield, I.J., Fletcher, J.M., James, J.B.,

Haugen, T.O., et al. 2007. Trait changes in a harvested population are driven by a dynamic tug-of-war between natural and harvest selection. Proc. Natl. Acad. Sci. U.S.A. 104: 15799–15804.

Eikeset A.M., Richter A.P., Dunlop E.S., Dieckmann U., Stenseth N.C. 2013. Economic repercussions of fisheries-induced evolution. Proc. Natl. Acad. Sci. U.S.A. 110: 12259-12264.

Eikeset A.M., Dunlop, E.S., Heino, M., Storvik, G., Stenseth, N.C., Dieckmann, U. 2016. Roles of density-dependent growth and life history evolution in accounting for fisheries-induced trait changes. Proc. Natl. Acad. Sci. U.S.A. 113: 15030-15035.

Einum, S., and Nislow, K.H. 2005. Local-scale density-dependent survival of mobile organisms in continuous habitats: an experimental test using Atlantic salmon. Oecologia 143: 203-210.

Einum, S., Sundt-Hansen, L., and Nislow, K.H. 2006. The partitioning of density-dependent dispersal, growth and survival throughout ontogeny in a highly fecund organism. Oikos 113: 489-496.

Ferchaud A-L, Perrier C, April J, et al (2016) Making sense of the relationships between Ne, Nb and Nc towards defining conservation thresholds in Atlantic salmon (*Salmo salar*). Heredity (Edinb) 117:1–11.

Fraser DJ (2013) The emerging synthesis of evolution with ecology in fisheries science. Can. J. Fish. Aquat. Sci. 70:1417-1428.

Froese R., Walters C., Pauly D., Winker H., Weyl O.L.F. et al. 2016. A critique of the balanced harvesting approach to fishing. ICES J. Mar. Sci. 73(6): 1640-1650.

Garcia, S.M., Kolding J., Rice J., Rochet M.J., Zhou S. et al. 2012. Reconsidering the consequences of selective fisheries. Science 335: 1045-1047.

Garcia, S.M., Rice J., Charles A. 2016. Balanced harvesting in fisheries: a preliminary analysis of management implications. ICES J. Mar. Sci. 73(6): 1668-1678.

Grey D.R., Law R. 1987. Reproductive values and maximum yield. Funct. Ecol. 1: 327-330.

Gross, M.R. 1991. Salmon breeding behavior and life history evolution in changing environments. Ecology 72: 1180–1086. doi:10.2307/1941091.

Gwimm, D.C., Allen, M.S., Johnston, F.D., Brown, P., Todd, C.R., Arlinghaus, R. 2013. Rethinking length-based fisheries regulations: the value of protecting old and large fish with harvest slots. Fish Fish. DOI: 10.1111/faf.12053.

Heino, M. 1998. Management of evolving fish stocks. Can. J. Fish. Aquat. Sci. 55: 1971-1982.

Heino, M., Baulier L., Boukal D.S., Dunlop E.S. et al. 2008. Evolution of growth in Gulf of St. Lawrence cod? Proc. R. Lond. Biol. Sci. 275: 1111-12.

Heino, M., Baulier, L., Boukal, C.S., Ernande, B., Johnston, F.B., et al. 2013. Can fisheries-induced evolution shift reference points for fisheries management? ICES J. Mar. Sci. 70(4): 707-721.

Heino, M., Diaz-Pauli B., Dieckmann U. 2015. Fisheries-induced evolution. Ann. Rev. Ecol. Evol. Syst. 46: 461-480.

Hixon M.A., Johnson D. W., Sogard, S.M. 2014. BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES J. Mar. Sci. 71: 2171-2185.

Hsieh C., Yamauchi A., Nakazawa T., Wang W.F. 2010. Fishing effects on age and spatial structures undermine population stability in fishes. Aquatic Sci. 72: 165-178.

Hutchings, J.A. 2009. Avoidance of fisheries-induced evolution: management implications for catch selectivity and limit reference points. Evol. Appl. 2: 324–334. doi:10.1111/j.1752-4571.2009.00085.x.

Hutchings, J.A., Jones M.E.B. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, Salmo salar. Can. J. Fish. Aquat. Sci. 55 (S1): 22-47.

Hutchings, J.A., and Fraser, D.J. 2008. The nature of fisheries- and farming induced evolution. Mol. Ecol. 17: 294–313.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. 51(9): 2126–2146.

ICES 2015. Report of the working group on North Atlantic salmon. ICES WGNAS Report, 2015. 332 pages.

Imre, I., Grant, J. W. A. and Cunjak, R. A. (2005), Density-dependent growth of young-of-the-year Atlantic salmon *Salmo salar* in Catamaran Brook, New Brunswick. J. Anim. Ecol., 74: 508–516.

Johnstone, D., O'Connell M., Palstra F.P., Ruzzante D.E. 2013. Mature male parr contribution to the effective population size of an anadromous Atlantic salmon population over 30 years. Mol. Ecol. 22: 2394-2407.

Jonsson, N., Jonsson, B. and Hansen, L. P. (1998), The relative role of density-dependent and density-independent survival in the life cycle of Atlantic salmon *Salmo salar*. J. Anim. Ecol. 67: 751–762.

Jorgensen C., Enberg K, Dunlop E.S., Arlinghaus R., Boukal D.S., et al. 2007. Managing evolving fish stocks. Science 318: 1247-1248.

Kendall, N.W., and Quinn, T.P. 2012. Quantifying and comparing size selectivity among Alaskan sockeye salmon fisheries. Ecol. Appl. 22: 804–816.

Klemetsen, A., Amundsen P.A., Dempson J.B., Jonnson B., Jonsson N., O'Connell, M.F., Mortensen E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Fish Fish. 12: 1-19.

Kuparinen, A. and Merila J. 2007. Detecting and managing fisheries-induced evolution. Trends Ecol. Evol. 22: 652-659.

Kuparinen, A., and Hutchings, J.A. 2012. Consequences of fisheries-induced evolution for population productivity and recovery potential. Proc. R. Soc. B Biol. Sci. 279: 2571–2579.

Kuparinen, A., Festa-Bianchet, M. 2017. Harvest-induced evolution: insights from aquatic and terrestrial systems. Phil. Trans. R. Soc 372: 20160036.

Kuparinen, A., Hutchings J.A. 2017. Genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. Phil. Trans. R. Soc. 372: 20160035.

Lacoursière-Roussel, A., Côté, G., Leclerc, V. and Bernatchez, L. (2016), Quantifying relative fish abundance with eDNA: a promising tool for fisheries management. J. Appl. Ecol. 53: 1148–1157.

Law, R. 2007. Fisheries-induced evolution: present status and future directions. Mar. Ecol. Prog. Ser. 335: 271-277.

Law, R., and Grey, D.R. 1989. Evolution of yields from populations with agespecific cropping. Evol. Ecol. **3**: 343–359.

Law, R., Plank M.J., Kolding J. 2014. Balanced exploitation and coexistence of interacting, size-structured, fish species. Fish Fish., doi:10.1111/faf.12098.

Laugen, A.T., Engelhard, G.H., Whitlock, R., Arlinghaus, R., Dankel, D.J., Dunlop, E.S., et al. 2013. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. Fish Fish. doi:10.1111/faf.12007.

MINISTÈRE DES FORÊTS, DE LA FAUNE ET DES PARCS. 2016. *Plan de gestion du saumon atlantique 2016-2026*, ministère des Forêts, de la Faune et des Parcs, Direction générale de l'expertise sur la faune et ses habitats, Direction de la faune aquatique, Québec, 40 p.

MINISTÈRE DES FORÊTS, DE LA FAUNE ET DES PARCS. 2017. *Bilan de l'exploitation du saumon au Québec en 2016*, ministère des Forêts, de la Faune et des Parcs, Secteur de la faune, 299 p.

Myers, R. A. 1984. Demographic consequences of precocious maturation of Atlantic salmon (*Salmo salar*). Can. Fish. Aquat. Sci. 41: 1349-1353.

O'Connell, M. F., Dempson, J. B., & Chaput, G. 2006. Aspects of the life history, biology, and population dynamics of Atlantic salmon (*Salmo salar* L.) in eastern Canada. Fisheries and Oceans Canada, Science.

Palkovacs, E.P. 2011. The overfishing debate: an eco-evolutionary perspective. Trends Ecol. Evol. doi:10.1016/j.tree.2011.08.004.

Palkovacs, E.P., Kinnison, M.T., Correa, C., Dalton, C.M., and Hendry, A.P. 2012. Fates beyond traits: ecological consequences of human-induced trait change. Evol. Appl. 5: 183–191.

Palstra, F. P., Ruzzante, D.E. 2008. Genetic estimates of contemporary effective population size: what can they tell us about the importance of genetic stochasticity for wild population persistence? Mol. Ecol. 17: 3428–3447.

Parker G.A. 1992. The evolution of sexual size dimorphism in fish. J. Fish Biol. 41: 1-20.

Perrier C, Normandeau E, Richard A, Dionne M, Bernatchez L. 2014. Alternative reproductive tactics increase effective population size and decrease inbreeding in wild Atlantic salmon. Evol. Appl. 7:1094-1106.

Philipp, D.P., Claussen J, Koppelman J, Cooke S.J., Suski C., Sutter D.A.H., Arlinghaus R. 2015. Fisheries-Induced Evolution in Largemouth Bass: Linking Vulnerability to Angling, Parental Care, and Fitness. Trans. Am. Fish. Soc. 82: 223-234.

Piche, J., Hutchings, J.A., and Blanchard, W. 2008. Genetic variation in threshold reaction norms for alternative reproductive tactics in male Atlantic salmon, Salmo salar. Proc. R. Soc. B Biol. Sci. 275: 1571–1575.

Pigeon G., Ezard T.H.G., Festa-Bianchet M., Coltman D.W., Pelletier F. 2017. Fluctuating effects of genetic and plastic changes in body mass on population dynamics in a large herbivore. Ecology, in press.

Post, J.R. M. Sullivan, S. Cox, N.P. Lester, C.J. Walters. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries 27: 6-17.

Quinn, T.P., Peterson J.P., Reed, T. E. 2016. The paradox of 'premature migration' by adult anadromous fishes: patterns and hypotheses. Can. J. Fish. Aquat. Sci. 73: 1-16.

Ricker, W.E. 1981. Changes in the average size and average age of Pacific salmon. Can. J. Fish. Aquat. Sci. 38:1636-56.

Ritchie, M.G., Hamill R.M., Magurran A.E., Webb S.A., Macias-Garcia C. 2007. Sex and differentiation: population genetic divergence and sexual dimorphism in Mexican goodeid fish. J. Evol. Biol. 20: 2048-2055.

Taggart, J.B., MacLaren I.S., Hay D.W., Webb J.H., Youngson A.F. 2001. Spawning success of Atlantic salmon (*Salmo salar*): a long-term DNA profiling-based study conducted in a natural stream. Mol. Ecol. 10: 1047-1060.

Theriault, V., Dunlop, E.S., Dieckmann, U., Bernatchez, L., and Dodson, J.J. 2008. The impact of fishing induced mortality on the evolution of alternative life history tactics in brook charr. Evol. Appl. 1: 409–423.

Tillotson, M.D., Quinn T.P. 2017. Selection on the timing of migration and breeding: a neglected aspect of fishing-induced evolution and trait change. Fish Fish. doi:10.1111/faf.12248

Uusi-Heikkila S., Whiteley A.R., Kuparinen A., Matsumura S., Venturelli P.A., Wolter C., Slate J., Primmer C.R., Meinelt T., Killen S.S., Bierbach D., Ploverino G., Ludwig A., Arlinghaus R. 2015. The evolutionary legacy of size-selective harvesting extends from genes to ecosystems. Evol. Appl. 8: 597-620.

Uusi-Heikkilä S, Sävilammi T, Leder E, Arlinghaus R, Primmer CR. Rapid, broad-scale gene expression evolution in experimentally harvested fish populations. Mol. Ecol. 26: 3954–3967.

Venturelli P.A., Murphy C.A., Shuter B.J., et al. 2010. Maternal influences on population dynamics: evidence from an exploited freshwater fish. Ecology 91: 2003-2012.

Weir, L.K., Breau C., Hutchings J.A., Cunjak R.A. 2010. Multiple paternity and variance in male fertilization success within Atlantic salmon *Salmo salar* redds in a naturally spawning population. J. Fish Biol. 77: 479-493.

Wood, J. L. A., Tezel, D., Joyal, D. and Fraser, D. J. 2015. Population size is weakly related to quantitative genetic variation and trait differentiation in a stream fish. Evolution, 69: 2303–2318.

Wright, P.J., Trippel E.A. 2009. Fishery-induced demographic changes in the timing of spawning: consequence for reproductive success. Fish and Fisheries 10: 283-304.

Yates, M.C., Debes P.V., Fraser, D.J., Hutchings J.A. 2015. The influence of hybridization with domesticated conspecifics on alternative reproduction phenotypes in male Atlantic salmon in multiple temperature regimes. Can. J. Fish. Aquat. Sci. 72: 1138-1145.

Yates, M.C., Bernos T.A., Fraser, D.J. A critical assessment of estimating census population size from genetic population size (or vice versa) in three fishes. Evol Appl. 10: 935-945.

Zastavniouk C., L.K. Weir, Fraser D.J. 2017. The evolutionary consequences of habitat fragmentation: body morphology and colouration differentiation among brook trout populations of varying size. Ecol. Evol. 7: 6850-6862.