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New strategies for sustainable fisheries management: A case study of Atlantic salmon

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Headlines

- Fish stocks have declined globally in recent years, including wild Atlantic salmon populations throughout their geographic range, this is a cause for concern as Atlantic salmon are ecologically and socio-economically important.
- There have been significant efforts to manage and restore Atlantic salmon but declines and local extinctions continue across many populations.
- Incorporating a more holistic approach to Atlantic salmon management –
 considering the entire life cycle, feeding interactions, and integrating the wider
 food web and ecosystem effects can offer additional insights to help improve
 current conservation efforts.
- Sustainable management can best be achieved through continued coordinated efforts amongst researchers and stakeholders as well as through more targeted efforts.
- The holistic approaches described in this paper can be applied to managing other important fish species and the ecosystems they inhabit.

Introduction

The United Nations began to highlight the threats to global fish stocks to ensure their sustainable production soon after its formation in 1945¹. Despite this, many stocks have continued to decline, particularly since the 1970s, with the rate and spread of collapses accelerating globally².³. Fisheries are critically important for food security, livelihoods, and economies, but can be depleted rapidly if they are not managed sustainably, with negative consequences for natural ecosystems and economic development. Given the recent dramatic declines of iconic aquatic species in UK waters, such as the Atlantic cod (*Gadus morhua*) and Atlantic salmon (*Salmo salar*), it has never been more important to monitor, model and manage fish stocks within biologically sustainable limits.

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Domestic legislation surrounding fisheries changed in 2020 as the United Kingdom left the European Union (EU) Common Fisheries Policy (CFP), which had been in place since 19834. This has been superseded by a Fisheries Act that sets rules for fisheries within the UK's Exclusive Economic Zone⁵ (see Glossary for definitions). There is ongoing debate around the best way to manage fisheries sustainably, but policy should evolve through an iterative process based on the scientific evidence base and being refined and adapted when and if that evidence changes. The overall aim for such policies is to be able to manage stocks sustainably, such that fish stocks remain viable resources for future generations. However, delivering this approach is challenging, especially as fishes do not respect international borders, with some species not only traversing vast areas and multiple jurisdictions, but also spanning freshwater and marine realms. Further to this, consideration of how stocks may be affected by a changing climate and other emerging stressors such as habitat loss or pollution will also become increasingly important as current baselines of what 'healthy fisheries' look like will change over time (e.g., poleward migration of fish to track their thermal optima will result in range shifts).

To date, fisheries science and policy have largely operated in narrow disciplines focused on a few target species and/or specific regions, although there has been movement towards more integrated ecosystem-based approaches in recent years. Despite these advances, the field remains fragmented even for many key species and if we are to track, predict and manage populations sustainably, new approaches will be needed to refine data gathering and to organise these resources more effectively. This briefing paper will consider these issues through the lens of a focal species – the Atlantic salmon.

Atlantic salmon are an ecologically important species, as well as having high cultural and economic value. They support subsistence, commercial and recreational fisheries throughout their range, with their importance highlighted by the Atlantic salmon being the only fish species to have its own International Treaty: The Convention for the Conservation of Salmon in the North Atlantic Ocean⁶. Atlantic salmon were once common and widespread across both North American and European Atlantic coasts and their inland waters, but have undergone dramatic population declines in recent years across much of their original range, with many populations facing local extinction⁷. These declines are of concern because although

Glossary

Anadromous fish Fish species that migrate to rivers from the sea to spawn, as for Atlantic salmon.

Before-After-Control-Impact

(BACI)

A methodology that statistically compares control sites against impacted sites, represented by data before and after the impact. This makes is possible to account for pre-existing differences between the sites, leading to a more accurate estimate of the impact variable

(e.g. a management action) over space and time.

Catch-and-release A conservation practice within recreational fishing whereby rod-caught fish are returned live

back to the rivers, aimed to prevent overharvesting of fish stocks.

Environmental DNA (eDNA) "Free" DNA that is released from an organism into the environment, including through

excretion or shed scales, which can enable screening of water or sediment samples to detect cryptic, rare, or endangered species that are difficult to track using traditional surveying

methods.

Exclusive Economic ZoneAn area of water and seabed extending 200 miles from the shore of a coastal country for

which that country assumes jurisdiction over the exploration and exploitation of marine

resources.

Food web An interconnection of food chains describing feeding relationships among species in an

ecological community.

MSW (multi sea-winter)

Atlantic salmon

An adult Atlantic salmon that has spent two or more winters at sea, and which may be

a repeat spawner.

Productivity (In ecology) refers to the rate of generation of biomass in a system, typically expressed in

units of mass per volume (or area) of habitat per unit of time.

Smolt A life stage of Atlantic salmon when it migrates from freshwaters to the sea.

1SW (one sea-winter) Maiden adult

Atlantic salmon

Maiden adult Atlantic salmon that have spent one year at sea as an adult.

Atlantic salmon still numbers in the many millions globally and is not under imminent threat of global biological extinction, it faces effective commercial and functional extinction in many systems where it was previously abundant. Due to experiencing multiple pressures that span their anadromous life cycle through time and over large spatial scales in both freshwater and marine systems, Atlantic salmon are useful indicators of the overall state of the ecosystems they inhabit, as well as being exemplars of the wider sustainability challenges facing fisheries management and conservation in general, as such, they are key bellwethers of such human impacts.

Threats to the Atlantic salmon

Wild Atlantic salmon are found in the North Atlantic Ocean and in over 2,000 of the rivers that flow into it⁸ (Figure 1). As an anadromous species, they spawn and spend their juvenile stages in fresh waters (e.g., rivers and lakes) before migrating to the marine environment and finally returning to fresh waters to complete their life cycle. Eggs are usually laid in autumn or winter and hatch in the spring. The juveniles can then remain in freshwater for one to seven years, depending on the location, temperature, and the productivity of the system⁹, before migrating to sea, where they exploit the often far more productive marine food web to rapidly increase in body mass. Adult Atlantic salmon then return to spawn in their natal rivers after typically spending between one to five years at sea. Such migrations connect habitats and species, thus providing a crucial

ecological energy flow between ecosystems over a wide range of scales, from small headwater streams to the Atlantic Ocean¹⁰.

Globally, Atlantic salmon populations have declined dramatically in recent decades, as well as disappearing altogether from many rivers, with these losses intensifying in many areas 11,12,13. The annual report from the International Council for the Exploration of the Seas (ICES) Working Group on North Atlantic Salmon (WGNAS) stated that 2019 catches of Atlantic salmon from almost every country were the lowest in the 40 years studied, with 2020 catches below the previous fiveand ten-year averages7. To account for factors that influence catches (e.g., exploitation rates and non-reported landings within catch statistics), ICES WGNAS developed a pre-fishery abundance (PFA) model to estimate and forecast the abundance of Atlantic salmon prior to any fishing mortality. As with the actual catch data, these models also show considerable overall declines in adult Atlantic salmon, with numbers dropping by more than half over the last 30 years7. More specifically, in the Northeast Atlantic region between the 1980s and 2020, the estimated abundance dropped from around 3.8 million to 1 million for 1SW fish (Figure 2). These declines have been attributed to several factors that affect the species' life cycle, including anthropogenic and environmental drivers. Some of these pressures affect populations across the whole life cycle and at large scales (e.g., climate change), with others being more localised and restricted to the marine (e.g., trawler bycatch) or freshwater (e.g., dams, weirs, and other barriers to migration) phases (Figure 3).

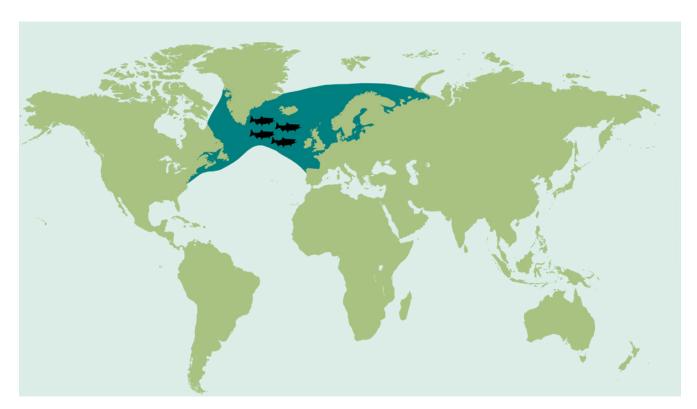


Figure 1: The global distribution of wild Atlantic salmon (shaded dark blue)

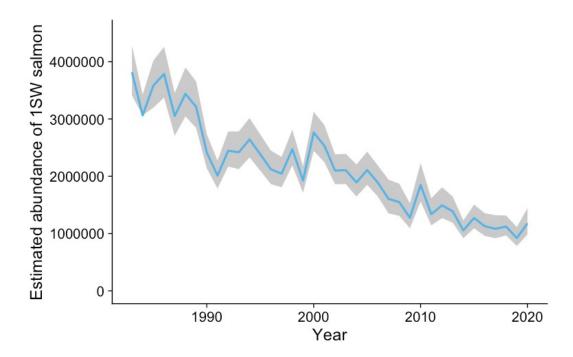


Figure 2: The estimated abundance of maturing 1SW Atlantic salmon (potential 1SW returns) in the Northeast Atlantic from ICES WGNAS using a run–reconstruction model to predict the pre-fishery abundance (as opposed to simply the catch), data is from ICES WGNAS annual reports⁷.

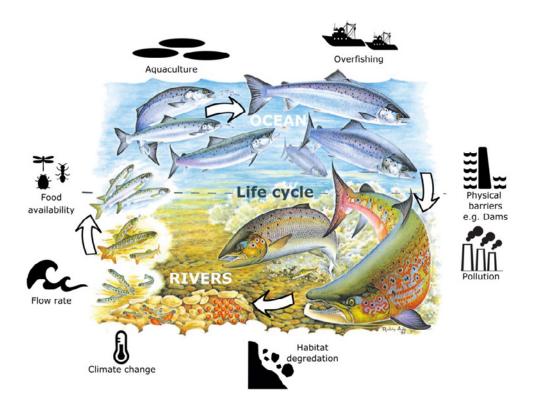


Figure 3: A depiction of the life cycle of Atlantic salmon and the environmental and human drivers that can affect it in both marine and freshwater realms: identifying the key bottlenecks and potential synergies among these drivers and other stressors is key to predicting impacts on individual stocks (life cycle artwork provided by The Atlantic Salmon Trust¹⁴).

Current Atlantic salmon management

In the face of these declines, numerous regional and national management strategies have been implemented with preserving and enhancing Atlantic salmon stocks as their focus. These have previously concentrated on exploitation management – such as reducing fishing and introducing catchand-release quotas – and have benefited some Atlantic salmon populations³. It is of concern, however, that management of exploitation is not enough to prevent further declines, and attention must be focused on other additional conservation efforts and on addressing the underlying causes of falling population abundance.

Efforts to restore Atlantic salmon populations have, so far, commonly included managing or regulating the rivers and lakes where the fishes spend the freshwater phase of their life cycle, as this is more feasible than managing their marine environment¹⁵. Techniques have included restoring and enhancing their habitat; supplementing wild populations (e.g., stocking with hatchery-raised 'wild' Atlantic salmon or the translocation of spawners); and protecting or enhancing spawning and nursery areas (e.g., building 'salmon ladders' to open previously inaccessible spawning and juvenile feeding grounds) (Figure 4).

Some of these techniques have successfully mitigated localised declines in certain cases^{16,17,18}, but the effects of others are unknown and may even be inadvertently detrimental^{16,19}. A systemic lack of rigorous Before-After-Control-Impact data gathering makes it difficult to discern generalities in the efficacy of conservation or restoration measures and overall, such efforts have clearly not been sufficient to halt ongoing global declines. The general scientific consensus is that stocking typically has negligible benefits (largely due to densitydependent mortality setting the carrying capacity of a given river); habitat restoration can have some positive benefits, but these are often transient; and pollution remediation can have benefits at the river catchment scale, but climate change and multiple stressors – including those that affect marine mortality - complicate the picture at larger scales. This indicates that traditional approaches will need to be augmented with additional data and new tools to help halt this iconic species' decline across its range.

Additional insights for Atlantic salmon conservation

To address global declines in Atlantic salmon, research is needed to uncover the underlying mechanisms driving population dynamics. To achieve this, it is important to look beyond targeting particularly vulnerable life stages or habitats (e.g., the focus on restoring breeding grounds for egg-laying in the headwaters) and start to consider Atlantic salmon as an integral part of the wider food web and the ecosystems it



Figure 4: A salmon ladder built in the rock to allow access above a previously impassable waterfall.

inhabits throughout its entire life cycle. More than a century of ecological research has shown that species interactions are critically important, yet most Atlantic salmon monitoring still disregards most of the food web, including the many prey species that sustain them, as well as the other competitors and predators of Atlantic salmon.

Continued monitoring and many current conservation efforts remain critically important, but these should be also supplemented wherever possible with monitoring, modelling and interventions that consider population drivers more rigorously so we can then prioritise them effectively based on hard evidence (e.g., see Box 1). Unfortunately, conducting research into Atlantic salmon in the marine phase, which is suspected as being where especially critical pinch points may lie, is far more challenging than working in the freshwaters where most of the data are located. This is because of the vast geographic range involved, the presence of numerous and mixed populations that span many jurisdictional areas, as well as the higher costs involved of operating research at these scales. As a result, there is still a lack of understanding among scientists about how Atlantic salmon operate in the marine realm and how their success in freshwaters (e.g., larger size, better condition) translates into success in the sea, and vice versa. The many decades of data collated on focal Atlantic salmon populations will be invaluable in building towards

these more holistic approaches at larger scales in both time and space. There are few species on Earth with such a wealth of population time-series data, and yet information on the drivers of those populations remains much more elusive. Nonetheless, progress is being made and ultimately understanding population drivers and life cycle responses in their entirety will help management efforts focus accordingly, looking beyond single species population demographics towards more predictive approaches (outlined in Figure 5). To move to a more holistic and predictive ecosystems-based approach, new initiatives such, as the Likely Suspects Framework (Box 2), are engaged in gathering and standardising data on the potential drivers of salmon population dynamics across their entire life cycle.

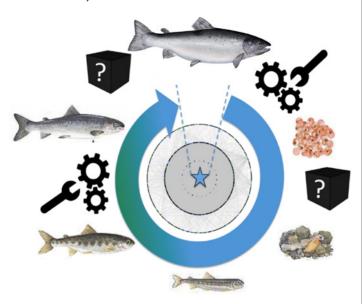


Figure 5: Understanding key points in the Atlantic salmon life cycle and in the food web (central circles – Atlantic salmon identified in the centre of this by the blue star) to address the gaps in our knowledge (black boxes) such as survival during the marine phase and egg development phase which may offer further insight into causes of declines in Atlantic salmon populations. Management interventions (cogs and wheels) throughout the life cycle can be implemented.

Freshwater and marine ecosystem linkages

The link between the Atlantic salmon in its freshwater juvenile phase and its future survival in the marine environment is described as a 'carryover effect'. The vast marine migrations that Atlantic salmon undertake and the difficulty in tracking them at sea, mean that attempts to uncover carryover effects have typically been pursued via mathematical modelling in the absence of strong data^{22,23}. For example, one recent model suggests that larger Atlantic salmon smolts migrating to the sea, result in higher return rates of 1SW fish back to rivers (Figure 6)²³. This indicates that factors during the freshwater phase potentially have a great influence on later life stages and return rates, which ultimately could lead to greater potential for

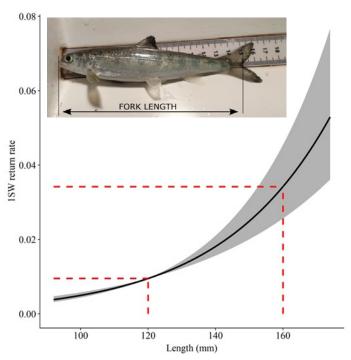


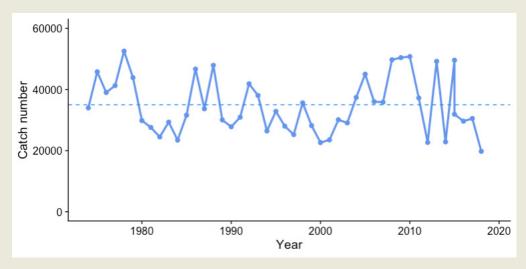
Figure 6: Bigger fish have greater survival: estimated 1SW return rate as a function of salmon fork length (the measurement from the tip of the snout to the end of the middle caudal fin ray: see inset picture) of individual Atlantic salmon smolt from a river in the UK (River Frome). The black solid line is the estimated effect with the grey bands the estimated error in this relationship (graph from Gregory et al. 2019²³).

spawning. These factors are particularly important to consider due to reduced survival rates observed in recent years during the Atlantic salmon's marine phase⁷.

The importance of the relationship between the freshwater phase and the carryover effects into the marine phase, as well as the underlying mechanisms, is slowly becoming clearer, but even so, the available data and models do not yet cover all the relevant intricacies of population dynamics and evolutionary adaptive behaviours involved²⁴. Whilst many studies continue to increase scientists' understanding, a key development is required for the models to bring these together at the population (instead of individual) scale. Such mechanisms, like the timing of migration and how this relates to predation or synchrony with food availability, could have significant impacts on Atlantic salmon success at sea. To address these knowledge gaps, high-resolution tracking data, through a range of emerging tagging and tracking methods, are needed to validate model predictions and reveal patterns. A number of ambitious marine tagging programmes are now underway^{25,26}, but these require considerable resources. Continued coordinated efforts across large spatial and temporal scales will therefore be key to their success, especially in terms of linking up to the much larger data resources already available on the freshwater side to understand and ultimately to forecast population dynamics across the whole life cycle.

Box 1: Iceland as a model system for Atlantic salmon: The final refuge?

Iceland's relatively pristine rivers provide conditions favourable for Atlantic salmon and it is often the dominant freshwater fish in these systems. Thus, any declines in the abundance of wild Atlantic salmon populations here (e.g., due to increasing human and environmental pressures) would be a particular cause for concern across the wider species range. To monitor this, the governmental Marine and Freshwater Research Institute (MFRI) in cooperation with many of the river owners' fishery associations, has conducted long-term fisheries research throughout Iceland, with detailed records on catches spanning many decades across the country's one hundred Atlantic salmon rivers. The MFRI have used these data to regularly assess the health of their stocks and to provide advice on sustainable management to maintain them in a good condition. Within Icelandic rivers, abundances of wild Atlantic salmon have remained (on average) relatively consistent since the early 1970s when large-scale standardised monitoring began (Box 1 Figure). In that period, the effort (the number of fishing rods), as well as the length of the annual and daily fishing period has remained stable. However, large fluctuations occurred between 2012 and 2015, with year-on-year declines in catches leading to some of the lowest ever recorded levels from 2015 onwards. To understand and prevent these river systems from facing similar declines to those seen elsewhere, conservation projects such as the Six Rivers Project²⁰ are now investigating population dynamics within the wider ecosystem context. In these relatively simple systems, researchers are better able to pull the signal from the noise in terms of what is driving population change, and hence are better placed to gauge what may be required to sustain stocks for future generations. Long-term individual- and population-level data are critical to understanding population dynamics and to bring about effective management. These data will be essential for informing the next generation of predictive models to forecast future scenarios that can then inform more adaptive and targeted management interventions.



Rod catch numbers for wild Atlantic salmon corrected for catch and release recordings (recorded Atlantic salmon caught and released back into the river) within Icelandic rivers from 1974 to 2020. The dashed blue line is the average catch for the time series (data source: MFRI reports²¹).

Any Atlantic salmon management programmes should ideally be as fully integrated as possible in a systems-based approach since any intervention at one stage can have implications on the rest of the life cycle. Management that ignores potential carryover effects could be futile, or at worst, detrimental²⁴ and we urgently need to understand these fundamental population drivers so that policy and management can target interventions and restoration more effectively and efficiently.

Where do Atlantic salmon go at sea? Understanding migration patterns

The Atlantic salmon as a species is not only distributed across a vast geographical range, but individual fish also move over large distances during their life cycle. There is still limited knowledge of the exact migration routes and stopover points, but Figure 7 illustrates the current best estimate of major routes that are taken by populations from different freshwater source locations. Recent studies into migratory patterns have revealed that different populations use different seas, and that this can even apply to different individuals from the same regional population²⁷. Migrations also vary with the age of individual fish, as different sea winter age Atlantic salmon may also exploit different regions²⁴.

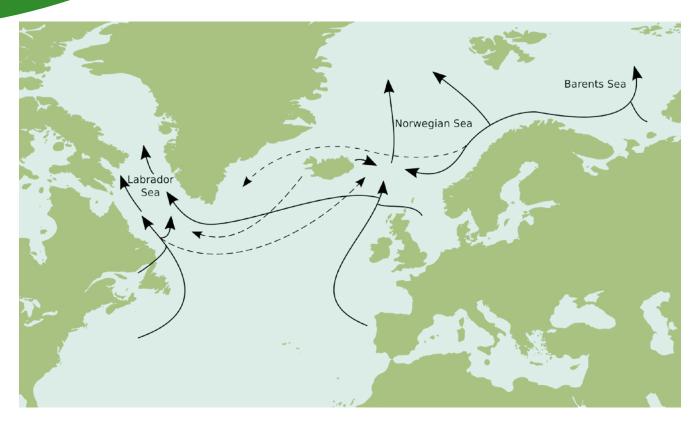


Figure 7: Estimated Atlantic salmon marine migratory routes, adapted from NASCO²⁸. The dashed migration lines on the map highlight the smaller proportion of Atlantic salmon that travel even greater migratory distances across the North Atlantic.

It is still unclear what exactly determines many aspects of migration, such as where, when, or how far Atlantic salmon travel, as well how many winters are spent at sea before returning to freshwaters. However, the answers to these questions are now beginning to emerge, with recent connections made to food availability, temperature changes and growth rates. For example, sea winter age has been linked to the body size of migrating Atlantic salmon smolts entering the ocean, with examples of smaller fish spending longer at sea²⁹. A recent genomic study has also indicated that sex ratios for Atlantic salmon differ between 1SW and MSW fish³⁰, this is important for management as female fecundity is strongly positively correlated with body size. However, what ultimately determines these drivers and what the implications are for the survival of the species remains unclear. More rigorous validation is needed to understand the freshwater carryover effects and how these translate into beneficial migratory patterns. New data and models are starting help fill these gaps, particularly via the increased international collaboration and ecoinformatics integration activities that are now underway (e.g., ICES WGNAS Life Cycle Modelling Workshop^{7,31}).

The importance of sustainable management in a changing climate

The drivers of Atlantic salmon population dynamics are especially important in the context of climate change. Freshwater and marine environments will continue to be

affected by both progressive warming as well as more unstable and severe conditions, such as fluctuations in hydrology and temperature, especially pronounced in the freshwater phase. Temperature is a key environmental variable that ultimately drives changes in biological processes from the individual- to ecosystem-level³². For cold-blooded animals (ectotherms), such as Atlantic salmon, the surrounding environmental temperature is important for respiration, digestion, growth rates, and the timing of life cycle events, including migration and spawning (Figure 8a). These rates will also vary as an individual grows and develops through its life stages, with temperature influencing body size differently due to changes in metabolic rate (Figure 8b). Temperature therefore sets the pace of life, from individual fish through to the entire food web and ecosystem within which it operates. This also demonstrates the need for these traits to be considered in both the life cycle and the food web of Atlantic salmon, as body size and temperature are key factors that underpin many ecological theories that can help explain how these species operate; not just now, but under future climate change in both freshwater and marine environments33,34.

The impact of temperature on growth and survival will also shape the species' distribution across the globe over time; as the southernmost populations face increasing temperatures, these regions will be the first to lose their Atlantic salmon populations, and a northward movement is expected as the species tracks its shifting thermal niche³⁵. Further to this, climate change is not occurring in isolation, and how this interacts with the increasing threats from other anthropogenic

stressors such as pollution and habitat alteration, is poorly understood³⁶. Disentangling such effects will be vital for predicting this species' response to different environmental drivers and having a solid understanding of the fundamental role of temperature will give important new insights into deviations from baseline conditions caused by other stressors in the system. One pertinent example of the need to gather these baseline data with urgency is the exponential spread of Pacific pink salmon (Oncorhynchus gorbuscha) across much of the Atlantic salmon's range^{37,38,39}. This alien species, which was introduced for aquaculture, represents a potential stressor as it shares the same prey and habitats so could alter the fundamental ecology of the native species, putting further pressure on populations that may already be under threat in many areas. Pacific pink salmon numbers are now in the millions across the Atlantic and spreading at an accelerating rate, with breeding already recorded in UK rivers⁴⁰. Unlike the threat of 'gene swamping' by escapees of farmed Atlantic salmon, which is one of the major concerns about the loss of genetic diversity in wild stocks, Pacific salmon are more likely to cause rewiring of the food web and could also compete for prey and/or space at key junctures of the lifecycle.

Towards a more holistic ecosystem approach

As the species range of Atlantic salmon spans the North Atlantic (Figure 1), it is also important to understand how populations and their drivers vary across different locations. Most studies have focused on individual systems or regions, but comparisons of populations across their range are now needed to offer

insight into the whole species' resilience, especially under scenarios of future change.

Figure 9 shows marked differences, but also some striking commonalities, in feeding interactions amongst Atlantic salmon from different rivers and latitudes. The UK River Frome (red) has many more species and feeding interactions (or links) compared with the Icelandic Vesturdalsá river (blue). These networks of feeding links show how closely Atlantic salmon are connected to all other species in each river. In both cases, even though these food webs are comprised of different species, Atlantic salmon are no more than two feeding links from any other species. Both rivers also flow into the even more complex Northeast Atlantic marine food web, where there are almost no species shared with the riverine food webs. However, even within this complex marine food web, Atlantic salmon are still no more than three links away from any other species.

Consideration of these feeding interactions is therefore important for effective and sustainable ecosystem-based management, as any major changes in their predators, prey, and competitors (including Pacific pink salmon) are likely to alter the population dynamics and ultimately the stock size of Atlantic salmon. Understanding the wider food web will provide much needed insights into the food resources that support it and if these can be more easily predicted or forecasted this could improve our ability to understand migration patterns and marine survivorship, where directly observed data are much harder to obtain⁴². This can also be achieved through trait-based approaches, in which species are linked by their functional traits (e.g., body size as a trait captures many other attributes, including the metabolic demands of an individual) and can therefore be used to determine the most likely interactions

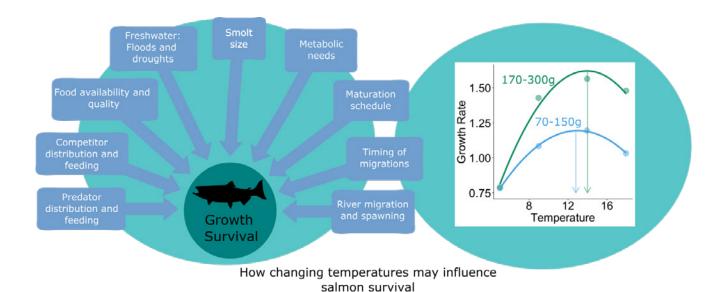


Figure 8: Temperature sets the pace of life: (a) The factors affected by variation in temperature which impact Atlantic salmon growth and survival and (b) thermal performance curve examples showing changes in specific growth rate (percentage per day) over a thermal gradient for two different size classes of hatchery Atlantic salmon smolts in saltwater with unlimited food resources. The two size classes (70-150g and 170-300g) show different optimum temperatures for growth (12.8°C and 14°C, respectively), adapted from Handeland et al. 2008⁴¹.

that can help to identify drivers of Atlantic salmon population change. In particular, the new generation of size-based approaches, as opposed to the more traditional speciesaveraged approaches (whereby each species is given a single value in the food web, irrespective of variation in individual body size) can offer far more powerful models than those

currently in common usage. This is especially useful in analysing entire aquatic ecosystems, where body size is far more important than species identity for predicting how an individual will move through the food web as they grow, shifting from being prey to ultimately becoming predators of other species.

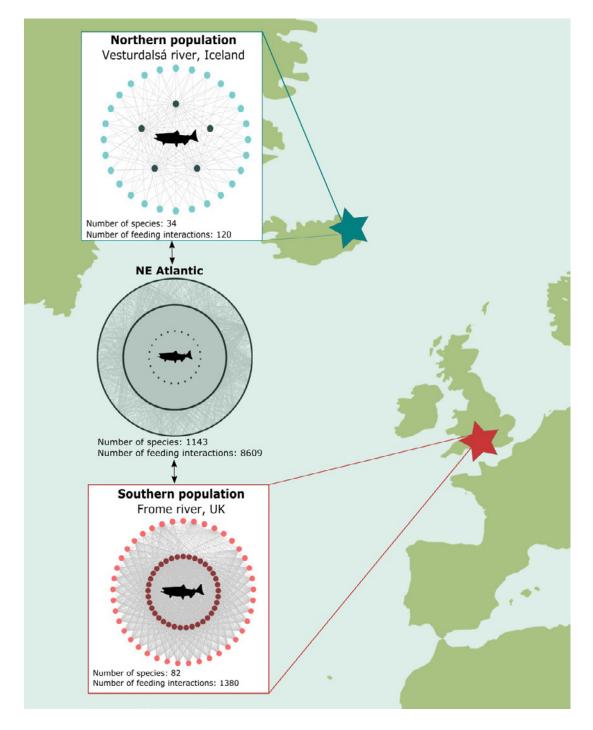


Figure 9: Feeding interactions between two focal ICES rivers. The Vesturdalsá is a relatively unproductive and nutrient-poor Icelandic river, compared to the River Frome in the UK, although both flow into the Atlantic. The food webs from these freshwater systems and the Northeast Atlantic Ocean vary in the number and type of species, and their complexity (number of feeding interactions), with this increasing from the Icelandic to the UK river as well as increasing within the oceanic food web. This indicates feeding interactions across and within populations will require more consideration in Atlantic salmon management (unpublished data from Woodward et al.).

The close connectivity of Atlantic salmon with other species demonstrates how they are an integral part of the wider ecosystem. Considering them in isolation can therefore only ever provide a partial view of their ecology and highlights the need for an ecosystem approach to fishery management that goes beyond the traditional focus on single species (and single sites). Ecosystem-Based Fisheries Management (EBFM) has risen in prominence in recent years, and its implementation can help deliver more knowledge-based decisions when assessing trade-offs among and between fisheries, aquaculture, protected species, biodiversity, and their habitats⁴³. Biological interactions with members of both their own and other species will shape the growth and survival of Atlantic salmon (Figure 10), so their consideration will be vital in the next generation of both models and monitoring programmes.

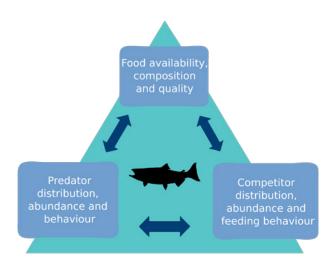


Figure 10: Biological interactions determine Atlantic salmon growth and survival, which directly influence their stock size, and should thus be considered for effective sustainable management.

Box 2: The Likely Suspects Framework (LSF): a coordinated approach to uncover causes of mortality during the Atlantic salmon life cycle

The LSF approach for Atlantic salmon is spearheaded by the Missing Salmon Alliance⁵⁹, a group of conservation focused organisations to develop interdisciplinary research collaborations and the cooperative support needed for a single guiding international management strategy.

This evidence-based approach uses science to collate and evaluate potential suspects driving the decline in Atlantic salmon population abundance. The LSF draws on existing data resources to carefully link and describe changes in the ecosystems of Atlantic salmon at key points in the life cycle where mortality pressure fluctuates. The framework sets out how to assess the evidence and understand how prey, competitors and predators of Atlantic salmon interact, and

Implications for policy and management

The need for a more holistic approach to Atlantic salmon management is being increasingly recognised, and collaborative research efforts are underway to address the reasons for recent population declines7. Means of accessing long-term monitoring data to address gaps in knowledge are improving, as well as technological advances that have made the rapid generation of the new ecosystem-level data that is needed feasible. For example, molecular tools and the use of environmental DNA (eDNA) can potentially reveal the presence of all species in the food web, including Atlantic salmon and their relatives, from a simple water sample⁴⁴. Further to this, species diets can be easily characterised using next-generation molecular tools45 and genomic and genetic analyses can reveal population structure and stock composition of functional traits⁴⁶, as well as informing the mechanisms that determine behaviours and drive migration and maturation^{47,48}. Acoustic tracking⁴⁹, tagging individuals⁵⁰, isotopic analyses of body tissues^{51,52,53} and mixed stock analysis⁵⁴ can also reveal large-scale Atlantic salmon movements in rivers and seas, as well as potential introgression (genetic mixing) of farmed Atlantic salmon into wild populations55. This breadth of knowledge and advancing technological opportunity can provide vital additional information to Atlantic salmon conservation efforts and better inform management strategies.

International collaboration on new data-harvesting and syntheses is becoming more commonplace, and coordination of research approaches that address the management challenge is also underway (e.g., Box 2). The suggested coordinated approach can be seen as part of an Integrated Ecosystem Assessment focusing on Atlantic salmon, that will provide methods and protocols that integrate quantitative and qualitative sources of data and information to optimise the evaluation of trade-offs.

are influenced by changes in their environment. By using this structure to interrogate datasets and build a comprehensive international programme of assessment and research, it will be far easier to discern the drivers of Atlantic salmon survival. The LSF will make this information readily accessible for managers, allowing them to prioritise strategies and actions for conservation of wild Atlantic salmon stocks in the present.

Where this approach differs from previous Atlantic salmon management efforts is in being removed from the process of providing a numerical assessment of stock abundance to inform catch advice. Instead, it prioritises understanding of the wider ecosystem and providing the information that managers require to do their job more effectively. This provides a significant step-change in how to manage not only the Atlantic salmon as a resource itself, but the knowledge resources needed to make decisions, how to prioritise new research initiatives and how to share method development amongst a wider community.

This will be a necessary step to facilitate the dialogue between science, policy, and society, ensuring the required provision and co-creation of integrated knowledge, advice, and solutions to move toward sustainability and conservation of Atlantic salmon. Such efforts need continued recognition and support to succeed but new technologies and organisational structures are emerging that will help disseminate key information more effectively, both nationally and internationally, to help shape more integrated future research priorities, policy, and management interventions.

For Atlantic salmon in particular, policy and interventions should be designed that consider both the freshwater and marine realms, as well as the transitional waters connecting them, especially as areas such as river mouths and estuaries are increasingly suggested as a bottleneck in Atlantic salmon survival⁵⁶. In many cases much of the core data that are needed already exist, and rapid progress can be made now by targeted action to plug the remaining gaps by focusing on a few key 'model systems' across the species range to view the bigger picture (e.g., Box 1). Coordinating the use of standardised methods to resolve data gaps in the life cycle and the food web can be done through tagging of individuals, eDNA, and metabarcoding of entire communities. Given the rapid emergence of a host of these novel technologies in recent years, focused taskforces in these areas could be set up to augment existing research bodies and to forge the new standard operating procedures and open-source data repositories that are needed to both test and inform policy.

Atlantic salmon management efforts have not yet fully embraced these more 'systems-based' approaches and the current piecemeal approach has made it difficult to discern the bigger picture or to link cause to effect – and hence to devise appropriate and effective policy and management actions. Simply coordinating ongoing activities more efficiently could produce major advances across this field within just the next few years. This could include using replicated Before-After-Control-Impact designs⁵⁷ to test the efficacy of planned management activities, such as the removal of weirs and dams or bankside reafforestation¹⁶) and using standardised currencies (e.g., DNA, body mass, metabolic rate).

Coordinating and sharing data to inform models and to test policy in a more iterative and proactive manner will be critical in the development of this more holistic and mechanistic approach58. This will require a prioritisation of effort by researchers, their funders, and practitioners on the ground to maximise returns most rapidly: attaining the deeper understanding and predictive capacity required is currently most feasible within the freshwater realm, as this is where most of the core data currently reside, where policy and management interventions can be manipulated and tested most easily, and where the key knowledge gaps can be filled with least effort. Understanding the marine phase of the Atlantic salmon life cycle more completely will need continued effort, as those data are

still not sufficiently comprehensive. However, as they emerge in the coming years, and can be linked to the freshwater phase, the last pieces of the puzzle can be put together to provide the more holistic understanding required to manage Atlantic salmon stocks sustainably across its geographic range into the future.

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