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Food for Thought

The likely suspects framework: the need for a life cycle approach for managing Atlantic salmon (*Salmo salar*) stocks across multiple scales

C. D. Bull [1,2,*], S. D. Gregory [3,4,5], E. Rivot [6], T. F. Sheehan [7], D. Ensing [8], G. Woodward [9] and W. Crozier [1]

[1]Atlantic Salmon Trust, Battleby House, Redgorton, Perth PH1 3EW, UK
[2]Biological and Environmental Sciences, University of Stirling, Stirling FK9 4LA, UK
[3]Salmon and Trout Research Centre, Game and Wildlife Conservation Trust, Wareham, Dorset BH20 6BB, UK
[4]The Centre for Environment, Fisheries and Aquaculture Science, Barrack Road, Weymouth, Dorset DT4 8UB, UK
[5]Department of Life and Environmental Sciences, Faculty of Science and Technology, Bournemouth University, Poole BH12 5BB, UK
[6]DECOD (Ecosystem Dynamics and Sustainability), Institut Agro, INRAE, IFREMER, 35042 Rennes, France
[7]NOAA Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole MA 02543, USA
[8]Fisheries and Aquatic Ecosystems Branch, Agri-Food and Biosciences Institute Northern Ireland, Belfast BT9 5PX, UK
[9]Georgina Mace Centre for the Living Planet, Department of Life Sciences, Imperial College London, Silwood Park, Ascot, Berkshire SL5 7PY, UK

[*]Corresponding author: tel: +44(0) 7736644192; e-mail: colin@atlanticsalmontrust.org

The ongoing declines in Atlantic salmon populations across its range underscore the need for co-ordinated scientific-based knowledge to support management and decisions for their conservation. Current salmon management actions remain largely focused on addressing bottlenecks to production in the freshwater phase of the life-cycle, whereas the continued declines observed in the recent decades are thought to be driven primarily by constraints on the marine phase. The challenges brought by global warming and other emerging stressors require immediate actions, requiring us to re-think the methods behind stock assessment and forge stronger linkages between data, models and policies to promote more effective management actions. We outline a scientific framework that takes a wider ecosystem view, designed to evaluate holistically a suite of indicators and potential drivers of salmon mortality at key phases of the life cycle. The aims of the proposed "Likely Suspects Framework" are to enhance cross-fertilisation of ideas between assessment processes at the stock-complex scale and stock-specific focused management activities, and to develop new decision support tools to improve management efficiencies and scenario testing. Adopting such an approach provides a new way to catalyse the acquisition and deployment of both existing and new data and models that are urgently needed for assisting the conservation and future stewardship of salmon stocks on both sides of the Atlantic.

Keywords: ecosystem-based-management, life-cycle approach, Salmo salar, stock assessment.

The status of Atlantic salmon stocks and their assessment

Atlantic salmon (*Salmo salar*) is one of the most economically, socially, and ecologically important fish species in both North America and Europe, reproducing in more than 2500 rivers and spending up to 7 years as juveniles in the freshwater phase and 1–4 years at sea (Thorstad *et al.*, 2011). In recent decades its stocks have been in decline, driven largely by reduced marine survival rates (Chaput, 2012; ICES, 2021) across most of its North Atlantic range. Atlantic salmon population dynamics are shaped by multiple biotic and abiotic drivers from local (stock-specific, e.g. Rosseland and Kroglund, 2011) to basin-wide (multi-stock, e.g. Olmos *et al.*, 2020) scales. These have their counterparts in current stock management measures whereby different systems operate at different geographical scales, from local rivers to regional, national, and ultimately entire ocean basin scales. This tiered system of management creates unique opportunities, as it links local expertise and data from across scales, but also considerable challenges. These include an incomplete knowledge of the mechanisms driving population changes (Thorstad *et al.*, 2021), combined with limited acquisition and mobilisation of existing knowledge from across the life cycle (ICES, 2020). This creates the potential to allow misalignment between the scales of the management actions employed and the relevant pressures influencing stock status. Here, we present the "Likely Suspects Framework" as a vision for improving management of Atlantic salmon by co-ordinating knowledge transfer more effectively across scales and expanding our view beyond the single-species focus that has prevailed to date to more explicitly consider interactions between salmon and their ecosystems.

The growing crisis in Atlantic salmon stocks across most of their native range has been ongoing since at least the 1990s, despite widespread moratoriums on their harvest in high-seas and home-water fisheries (Beugrand and Reid, 2012; Mills *et al.*, 2013; Chaput, 2012; ICES, 2021). The mechanisms underpinning the declines in marine survival (or more generally, the smolt-to-adult return rate) are currently unknown (see Thorstad *et al.*, 2021 for review), but suggestions include

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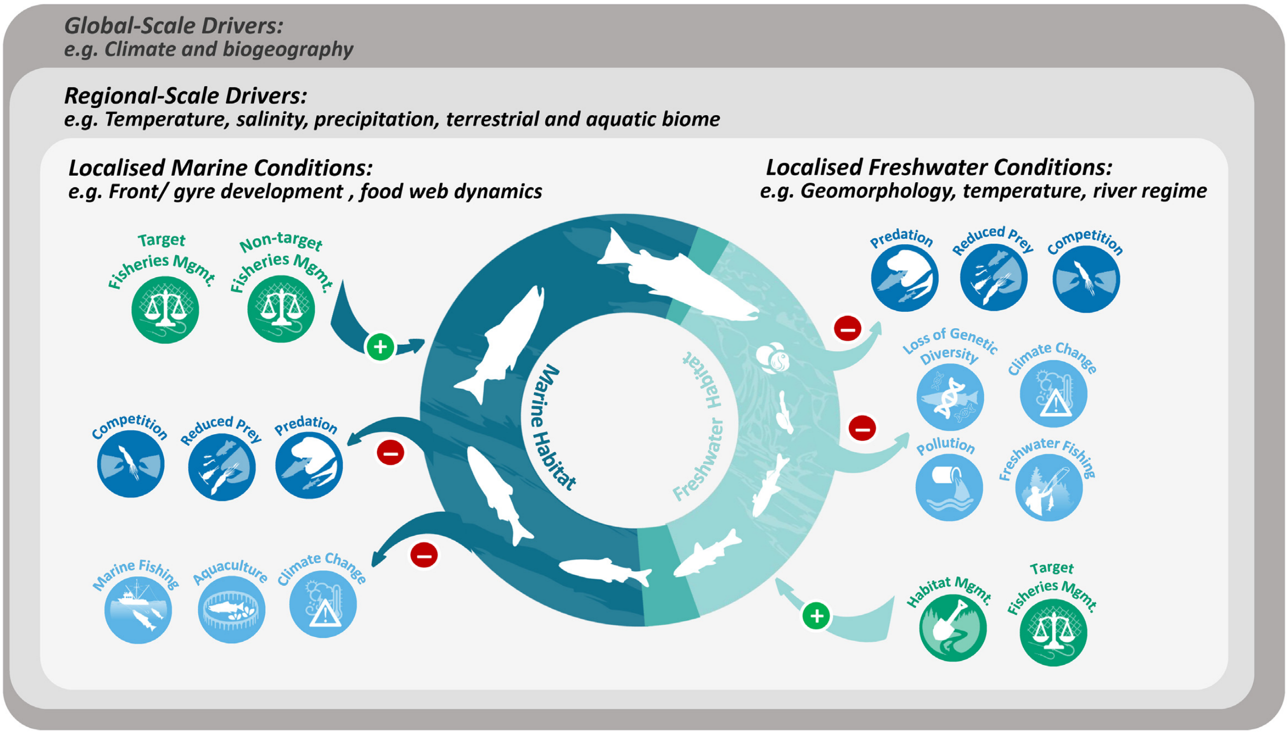

Figure 1. Conceptual overview of the life cycle of the Atlantic salmon showing hierarchical scaling of primary environmental drivers influencing stock dynamics across the marine and freshwater life stages. Processes leading to salmon mortality (red negative symbols) arise from multiple natural (dark blue circles) and anthropogenic (light blue circles) sources. Focused management strategies (green circles) intending to counter these losses (green positive symbols) and enhance stock status require benefit from knowledge of the processes acting across the life-cycle to optimise their effectiveness.

mechanisms related to changes during both the freshwater and marine phases of their life cycle. The connections between these phases could be particularly critical bottlenecks, as changes in freshwater conditions have been linked to shifts in the timing and size of seaward migrating juveniles (Russell *et al.*, 2012; Thorstad *et al.*, 2012; Otero *et al.*, 2014; Armstrong *et al.*, 2018; Gregory *et al.*, 2018, 2019; Simmons *et al.*, 2021, in press). Whilst we are not looking at the imminent global extinction of the Atlantic salmon, the recent declines in abundance have rendered it a species of conservation concern and effectively non-viable commercially in some areas where it was previously numerous. There is a need to deepen our understanding of what is driving changes in salmon abundance and to prioritise the threats and management actions to mitigate them.

Altered abiotic ocean conditions have been linked to declines in the abundance, growth and survival of salmon at sea (Beaugrand and Reid, 2003; 2012; Mills *et al.*, 2013; Friedland *et al.*, 2014; Olmos *et al.*, 2020; Todd *et al.*, 2021; Trehin *et al.*, 2021; Harvey *et al.*, 2022; Vollset *et al.*, 2022). Changes in biotic drivers, including the abundance and feeding of marine predators (Strom *et al.*, 2019), prey distribution, abundance and quality (Renkawitz *et al.*, 2015; Jansen *et al.*, 2021; Utne *et al.*, 2021a, b) and the broader activities of marine fisheries (ICES, 2021), have also been implicated in stock declines (Figure 1). These (and other) drivers have the potential to affect the time spent in various habitats by different life stages (Thorpe *et al.*, 1998) and thus cumulative mortality risks (Mangel and Satterthwaite, 2008). Drivers influencing state, duration and functional traits of the different life stages can operate across multiple scales, often in interaction (Brook *et al.*, 2008), and several may be operating either in synchrony or asynchronously—as stressors rarely occur singly in space or time (Jackson *et al.*, 2021). Atlantic salmon stock assessment and management operates at multiple organisational scales, ranging from local through to national and international levels. Local (e.g. single river stock) management activity is largely focused on actions maximising freshwater production or adult spawners and egg deposition, using locally available and specifically compiled data. At the other end of the organisational scale, cooperative management and conservation efforts in the mixed stock fisheries at West Greenland and Faroes are coordinated internationally by the North Atlantic Salmon Conservation Organisation (NASCO), supported by stock advice from the International Council for the Exploration of the Sea (ICES). These assessments are generated by the ICES Working Group on North Atlantic Salmon (WGNAS) using outputs from three separate but linked models (run-reconstruction, stock forecast and catch-advice) underpinned by data on returning stock estimates and commercial and recreational catches (ICES, 2021). The objectives of these models are to reconstruct time series of abundance at sea (starting in the early 1970s) before any targeted marine fisheries (Pre-Fishery Abundance) take place and to forecast the annual returns of adult salmon to their homewaters. The model captures environmental stochasticity on the marine survival and the proportion of fish maturing as in the first year at sea. It assumes that ocean climate effects are random as there are no climate or environmental variables used to explain the temporal variability. On the hindcasting phase of the analysis, time series (random walk) models are fitted to the observed year-to-year variations of survival and maturation to capture the past variation. The same time series models are then used to forecast the returns 3 years ahead while propagating uncertainty based on the amount of variance estimated from the hindcasting phase. Model outputs are incorporated into a risk analysis framework to assess the consequences of mixed-stock marine salmon fisheries on the returns, and to assess compliance of forecasted spawning escapement against conservation limits (biological reference points below which the stocks should not fall).

Conventionally, in Europe, conservation limits are defined as the number of spawners required to achieve egg deposition that maximises average harvest of adult fish, commonly known as the Maximum Sustainable Yield (MSY) (Prévost and Chaput, 2001). An alternative biological reference point now applied in Canada, but not yet in US or Europe, is the egg deposition needed to maximise recruitment to the marine stage (i.e. maximum smolt production) (Chaput *et al.*, 2015). Conservation limits are produced across the national/regional stock units in each of three continental stock complexes (North America and the southern and northern North East Atlantic) and compared to Pre-Fishery Abundance forecasts for the next three years. The probability of achieving aggregate conservation requirements for each national/regional stock unit and for the three continental stock complexes are calculated and considered against current management objectives, to produce fishery catch options.

ICES' efforts are focused largely on forecasting salmon stock status to underpin advice on allowable catch in mixed-stock marine fisheries and to guide homewater fisheries advice, relying on the coordination of salmon population monitoring across a network of "index" rivers and catch statistics from commercial and recreational fisheries (ICES, 2021). In response to declining stock status in recent decades the work of WGNAS has been evolving to more fully consider how the results from new research and wider ecosystem influences may impact the productivity of Atlantic salmon stocks across the North Atlantic and how future assessment model development may better consider these factors. The current WGNAS assessment model is likely to be superseded within the next three years by a new single Bayesian Life Cycle Model to harmonise future stock assessments (hereafter Life Cycle Model; Massiot-Granier *et al.*, 2014; Olmos *et al.*, 2019; ICES, 2021).

Linking stock assessment to management of Atlantic salmon populations

Stock assessment simply seeks to quantify and compare fish numbers against a desired state and (in theory) does not require any understanding of fish ecology or behaviour: it is phenomenological rather than truly mechanistic or predictive, and so it has limited forecasting ability, especially under changing conditions, such as warming or altered food supplies. Stock management, on the other hand, requires a more mechanistic understanding of why certain stock units, or wider complexes of stock units, change and how management actions affect them in a predictable manner.

The international Atlantic salmon stock assessment process is undertaken to provide catch advice for the mixed stock fisheries at West Greenland and the Faroes, as requested by NASCO, and is not designed to provide quantitative management advice at the scale of regional or individual river salmon stocks. As single-species stock advice, its provision does not currently take full advantage of the huge volumes of available data and knowledge relating to potential ecosystem controls and drivers. For instance, the assessments do not incorporate key environmental variables or possible interactions with other marine species in the Atlantic food web. The capacity to forecast how multiple biotic and abiotic drivers shape current and future salmon stocks currently remains limited.

International Atlantic salmon management is bound by the legislative catch controls derived by NASCO, and the trends and modelled projections of stock abundance. Management planning may be further informed to varying degrees by national and regional guidance generated from individual countries. Despite these multiple levels of acquisition and input and transfer of knowledge across the management scales, some gaps remain that may be limiting success. For example, the implementation of many salmon management activities remain largely constrained by our poor understanding of the mechanisms driving temporal patterns in abundance, and how these relate to stock-specific actions. Addressing these constraints will require new cooperative research efforts. We believe these should include (but not be limited to) investigations on how altered energy flow within the North Atlantic ecosystem and changing energy densities of important Atlantic salmon prey items may be altering salmon growth and survival, how conditions experienced during the freshwater phase may effect life history during the marine phase, and on the evolutionary responses to various anthropogenic and naturogenic influences. Coupled with advances in these key research areas, an improved understanding of the marine migrations undertaken by salmon is still required to support future spatiotemporal-explicit hypothesis testing.

Developing stock-specific management strategies to address impacts of Atlantic basin-wide drivers such as climate change would benefit from a wider life-cycle context to assist with making resource allocation decisions. New knowledge on the growth and survival responses of salmon at particular life stages needs to be combined with an understanding of cumulative responses across the life-cycle, and what these mean for predicting adult population dynamics. These bottlenecks are now being recognised within the stock assessment process, with moves to address them more explicitly within life-cycle modelling approaches (e.g. Olmos *et al.*, 2020), but these approaches will remain constrained by the sparse and incomplete data and forecasts available from the large suite of candidate environmental variables suspected to drive salmon population dynamics. An accessible framework that links information on the ecological processes governing salmon survival across the life-cycle, and across scales (e.g. global, regional and local environmental drivers: Figure 1), would be highly beneficial for delivering new knowledge to assist salmon management efforts.

We recommend targeting the gaps between the existing stock-complex focused assessment process and the requirements of single-stock focused management by utilising all available information to expedite the development of more effective Atlantic salmon management strategies. New approaches can be harnessed alongside the mobilisation of existing data to better integrate knowledge on key ecosystem processes and salmon population dynamics for building more informed management and decision-making frameworks. Pacific salmon management has already begun this transition by developing tools that span the assessment and management realms to improve knowledge flow and provide management tools (e.g. the Risk Assessment Methodology for Salmon or RAMS approach; Hyatt *et al.*, 2017), including the integration of life history and life cycle modelling (Hare *et al.*, 2016; Crozier *et al.*, 2019; 2021; Scheuerell *et al.*, 2006; 2021; Walsh *et al.*, 2020). Indeed, work is also underway to include spatial data on migration and catches at sea for Atlantic salmon stocks in the Baltic Sea (Whitlock *et al.*, 2021). Building this more holistic understanding of the Atlantic salmon's ecosystems for improving stock assessment and management is a considerable challenge, but it potentially offers high rewards. These include more effective management based on new insights into how the multiple pressures can lead to the nonlinear, time-lagged, and often unexpected outcomes we see in the real world, but which cannot be captured by current approaches. To improve the current situation, we need to shift our focus from single-species observations to more sophisticated systems-based approaches that offer better approximations of reality.

Embedding Atlantic salmon within an Ecosystem-based management framework

The ecosystem-based management approach to resource use has evolved in recent years due to the growing realisation that focal species are just one component of a much larger and more complex ecosystem (Morishita, 2008; Levin *et al.*, 2009; Curtin and Prellezo, 2010; Link, 2010; Link and Browman, 2014; 2017 and references therein). This broader management view considers how biotic and abiotic components are interlinked, emphasising the need for understanding ecosystem properties and the services they deliver (Curtin and Prellezo, 2010). In the context of fisheries management, ecosystem-based approaches can provide better quality management advice for specified components of an ecosystem (e.g. a target fish species) by linking it with other dynamic components (e.g. via predator-prey relationships, environmental forcing, habitat overlaps) (Pikitch *et al.*, 2004; Link, 2010) and they also have predictive power for defining expected baselines and deviations from them at these higher organisational levels (e.g. Nicholson and Jennings, 2004). These benefits have led to ecosystem approaches becoming broadly accepted as crucial for effective marine resource management, including multi-species stock assessments and rebuilding damaged ecosystems (Levin *et al.*, 2009).

Implementing an ecosystem-based approach requires data on the likely abiotic and biotic drivers operating within the system (reviewed by the NASCO-ICES Salmon Mortality at Sea workshop in 2019; ICES, 2020a) and key indicators (e.g. abundance of prey and predators) that can provide useful proxies for stock status and ecosystem productivity (Jennings, 2005; Link, 2010; Large *et al.*, 2013, 2015; Otto *et al.*, 2018). For example, large basin-scale climatic and oceanographic indicators (e.g. the North Atlantic Oscillation) have been used to represent abiotic conditions that influence salmon survival in the ocean (e.g. Friedland *et al.*, 2014; Todd *et al.*, 2021). Regional trends in salmon population dynamics have also been linked to sea surface temperature or primary productivity (Olmos *et al.*, 2020). Typically, these large-scale indicators only weakly represent variability shown in individual salmon populations, likely because they are influenced by multiple layers of drivers operating at different scales, with some (e.g. predation and resource competition in local food webs) coming into play increasingly as spatial scale is reduced (e.g. Winship *et al.*, 2015), and also because different populations with different genetic pools can respond differently to the same driver. Ecosystem complexity and the intricate interactions with individual populations may limit the success of some environmentally-based forecast processes (e.g. Wainwright, 2021), and the design of new management systems that rely on their outputs will need to be robust enough to accommodate uncertainties. These early insights into high-level ecosystem indicators nonetheless merit deeper investigation and eventual integration into existing modelling frameworks for Atlantic salmon, and as coverage improves, they will help to direct future ways of disentangling proximate and ultimate drivers of change. We suggest that considering these largely ignored relationships will generate important new opportunities for evaluating and refining the biological reference points used in stock status evaluation both now and in the future.

To combat issues of scale, suites of indicators representing different scales could be used to represent different drivers of stock dynamics (Pardo *et al.*, 2021), especially as salmon move through the food web over both space and time as they grow. For example, developing marine prey species indicators could exploit datasets used by ICES for annual fish stock assessments, integrating spatial parameters from recent salmon migration studies (e.g. Gilbey *et al.*, 2021; Rikardsen *et al.*, 2021) and dietary changes. Salmon feed mostly on various fish larvae and large zooplankton during their early marine migration (Rikardsen *et al.*, 2004; Haugland *et al.*, 2006; Hvidsten *et al.*, 2009; Renkawitz and Sheehan, 2011) and larger fish prey, such as capelin (*Mallotus villosus*), blue whiting (*Micromesistius poutassou*) and sandlance (*Ammodytidae* spp), as they grow and mature (Jacobsen and Hansen, 2001; Rikardsen and Dempson, 2011; Renkawitz *et al.*, 2015; ICES, 2017). Species interactions (Huse *et al.*, 2012) will influence the feeding and growth of salmon both directly (e.g. metabolic constraints on individual salmon) and indirectly (e.g. metabolic constraints on their prey, competitors and predators) (Utne *et al.*, 2012; 2021a, b). Developing suitable indicators for salmon that reflect these interactions will require the consideration of population data not only from other fish species (Lacroix, 2013; Strom *et al.*, 2019), but also for other taxa, such as seabirds (e.g. Montevecchi, 2007) and marine mammals (e.g. Middlemas *et al.*, 2003).

Identifying data sources, developing suitable indicators, setting thresholds and translation into decision-making criteria are challenging, but they move us considerably closer to capturing ecosystem complexity and the multivariate reality of management issues on the ground (Link, 2005). Following from the start made in identifying potential marine data sources by NASCO-ICES (ICES, 2020), we now need to identify how best to marshal our existing data and models to better prioritise future actions to meet these goals. This will require new levels of international cooperation and integration to join the dots from across the existing knowledge base and to identify the key gaps to fill in the next phases of the process (Woodward *et al.*, 2021). A key next step will be to garner the existing data for identifying which are the best indicators across relevant temporal and spatial scales, to help prioritise the next phase of modelling, validation and subsequent targeted data collection to plug the remaining critical gaps iteratively.

Promoting a new approach for future management of Atlantic salmon stocks

The Likely Suspects Framework for Atlantic salmon was conceived by a consortium of scientists and stakeholders to unify past and future efforts to understand the mechanisms affecting salmon survival across all life stages (Crozier *et al.*, 2017). It is an organisational approach to provide the resources necessary to test robust hypotheses about the relative strength, direction and shape of putative drivers (i.e. the *"likely suspects"*) associated with mortality at each part of the life-cycle. The overall objective is firmly focused on developing and providing the scientific basis for a more ecosystem-based management framework for salmon and the provision of a wider range of decision support tools. This will be advanced via four routes:

1. Better describe conditions facing salmon during the marine phase of their life-cycle,
2. Mobilise existing evidence and synthesise new data to test the resulting hypotheses relating to reduced ocean survival,
3. Test and rank these against competing hypotheses,
4. Assist the movement away from single-species stock status and catch advice towards a wider ecosystem management and assessment-based system.

Although these form a natural progression, in terms of the logical order of an ascending hierarchy of complexity and data-needs and availability (Woodward *et al.*, 2021), each of the four areas of work can be at least partially addressed in parallel, so it is not a single linear timeline and rapid progress can be made in each of these areas even in the near term. To advance the Likely Suspects Framework process, a consortium of UK-based salmon conservation organisations—the Missing Salmon Alliance (https://missingsalmonalliance.org/)—launched a programme to work in 2019 collaboratively with salmon stock assessment and management groups worldwide. The programme is providing resources, focusing future research initiatives, assisting with the improvement of salmon stock assessment and the generation of management guidance. It is designed explicitly to align with other such programmes (Levin *et al.*, 2009; NMFS, 2016; Hare *et al.*, 2019; Wells *et al.*, 2020) to maximise its transferability and begins with identifying objectives and priorities to underpin development. It is recursive by design, so lessons that are learned can help refine objective(s) that enter the cycle again. The first steps in the Likely Suspects Framework process are focused on the marine environment, given its impact on population productivity and the state of the current assessment methods and processes, and it will then fan out to include drivers of salmon survival across all life stages.

The research objectives and candidate mortality hypotheses for the Likely Suspects approach have been formulated by expert-led assessment. Examples of this type of approach towards identifying mortality hypotheses are provided by O'Neil *et al.* (2000), Cairns (2001), Peterman *et al.* (2010), Beauchamp *et al.* (2012), Ó Maoiléidigh *et al.* (2018) and Olmos *et al.* (2020). Candidate mortality hypotheses cover the entire life cycle and represent the current focus and future vision for collaborative research.

Collating the necessary datasets and building the analytical framework to test mortality hypotheses is challenging. There is still a paucity of data at certain spatial and temporal scales that can be matched to salmon-specific datasets, and inadequate data mobilisation frameworks and incomplete understanding are common obstacles to advancing this approach (ICES, 2020). Facilitating improved organisation and mobilisation of relevant information began within the Likely Suspects Framework with the development of a central data resource—a database that adheres to FAIR data standards (Wilkinson *et al.*, 2016). Since it is initially focused on collating data resources identified by NASCO-ICES (ICES, 2020) it includes the concept of "space-time domains" occupied by in the Atlantic salmon during the different phases of their life cycle (Olmos *et al.*, 2020). This approach is used as an organisational structure to incorporate spatially- extensive knowledge resources and assist with making them useable in testing mortality hypotheses. This organisation is further informed by recent studies on the ocean migration of Atlantic salmon (e.g. Ounsley *et al.*, 2020; Gilbey *et al.*, 2021; Rikardsen *et al.*, 2021) that provide opportunities for spatial and temporal refinement on the key space-time domains occupied.

Once organised into the database, resources can be mobilised and used to evaluate the current state of knowledge on relevant mortality hypotheses, associated mechanisms and drivers, and for identifying knowledge gaps that still need to be filled. Testing hypothesised influences on salmon survival could then follow a multidisciplinary Integrated Ecosystem Assessment approach (Levin *et al.*, 2009; Möllmann *et al.*, 2014) as a means of providing a coherent strategy to map onto ecosystem-based objectives and for informing decisions across sectors, scales and species. Ultimately, as the database matures over time the capacity to consider additional new types of information, such indigenous knowledge systems (e.g. Sethi *et al.*, 2011; Reid *et al.*, 2021), will grow as its range of coverage expands, although this is currently out of scope for the first round of iterations. Similarly, its increasing depth and breadth of temporal and spatial coverage will help to disentangle historical drivers from newly emerging threats, such as climate change and the ongoing invasion of pink salmon *Oncorhynchus gorbuscha* (Sandlund *et al.*, 2019). It is imperative that we seek to capture these baselines and emerging trends now, whilst we still can, and before previous phenomenological approaches lose more of what limited predictive power they still have.

We have conceptualised where the phases in developing the Likely Suspects Framework could link to the evolution of existing international stock assessment methods and emerging space-time domains of interest to provide important new information to guide management interventions focused at the river stock-specific scale (Figure 2). The Likely Suspects Framework will facilitate the mobilisation of new knowledge as it evolves, drawing from a growing range of sources (Table 1), with the potential to catalyse the development of the stock assessment and ecosystem-based management approaches. It provides a common platform for re-synthesis, cooperative analysis and sharing of new knowledge to support hypothesis-testing and the development of future management support tools.

Improved data mobilisation provided by the central data resource will be integral to the requirement for developing suites of abiotic and biotic indicators of relevance to salmon population dynamics, and to inform on stock prospects. These could include environmental forcing and predator and prey dynamics, all of which could be used within life cycle modelling efforts to provide more realistic stock assessments and forecasts based on a more complete understanding of the roles of various drivers of Atlantic salmon productivity. Developing a weighting scheme for suitable indicators will be critical for the successful implementation of an ecosystem-based framework, and to integrate with population models, and there are

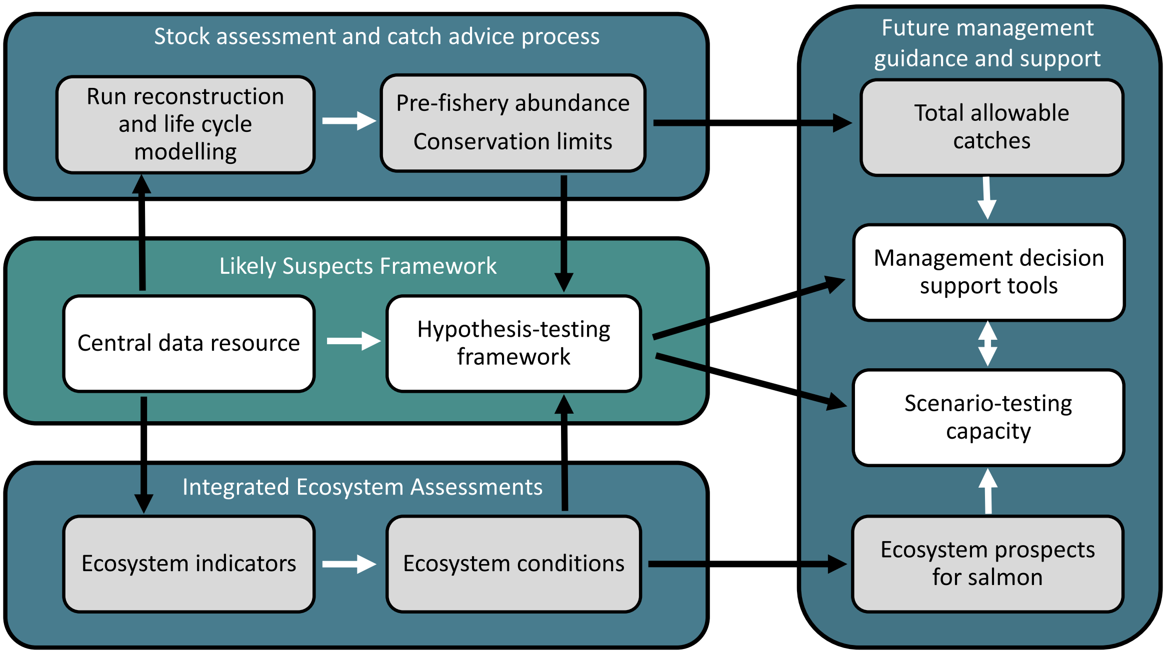

Figure 2. Conceptual outline of how the components of the Likely Suspects Framework process could facilitate the development of new river stock-specific management guidance and support, linking the processes of stock assessment and catch advice for Atlantic salmon (at the stock-complex scales) and wider Integrated Ecosystem Assessments.

Table 1. Exemplar datasets and compiled model estimates drawn from the Likely Suspects Framework database along with their relevance to hypothesis testing and construction of a panel of ecosystem indicators to integrate with the development of ecosystem-based management for Atlantic salmon.

Resource title	Description	url	Relevance for developing a more life-cycle approach to salmon management
Freshwater habitat quality assessment	River ecological quality assessment indices (Scotland)	https://www.sepa.org.uk/data-visualisation/water-classification-hub/	Extraction of variables that describe ranges and temporal change on drivers of growth and survival in freshwater stages of development
Smolt migration phenology	Daily Fish Counts at Burrishoole index river, Newport (Ireland)	https://erddap.marine.ie/erddap/tabledap/newport_daily_fish_counts.html	Emigration timing reflects variation in previous growth opportunity during freshwater stage. Timing of migration may inform the development of suitable marine ecosystem indicators
Annual marine survival rates	Monitoring abundance of migratory salmon in the River Scorff salmon index river (France)	https://doi.org/10.15468/yvcw8n	Underlying temporal change in the stage survival reflecting outcome of multiple influences including environmental drivers in marine domains
Plankton abundance and composition	Continuous Plankton Recorder distribution, seasonal cycles and changes in abundance of plankton over the Northern Hemisphere.	https://www.gbif.org/dataset/67c54f85-7910-4cbf-8de4-6f0b136a0e34	Temporal and spatial variation at key points along migration routes and main feeding grounds in response to basin-scale water temperature change. Important factor when considering developing future marine phase ecosystem indicators due to influence on salmon growth, maturation, stage duration and cumulative mortality
Oceanographic conditions	The Scottish Shelf Waters Reanalysis Service is a 26 year hind cast of one year climatology	https://sites.google.com/view/ssw-rs/home	Access to multiple-scales of environmental control data reflecting drivers of growth and survival (both direct and indirect) during entire marine phase
Annual stock abundance estimates of pelagic fish species	ICES Working Group on Widely Distributed Stocks compiles annual data on large stocks of pelagic species, as well as other widely distributed and highly migratory species.	https://www.ices.dk/community/groups/pages/wgwide.aspx	Patterns of abundance and distribution of competitors, prey and alternative forage for predators that may inform development of indicators of salmon growth and survival
Coastal seabird abundance	Seabird 2000 Census Data 1998–2002. Joint Nature Conservation Committee (UK)	https://webarchive.nationalarchives.gov.uk/20190301135521/http://jncc.defra.gov.uk/page-4460-theme = default	Temporal variation in the abundance and distribution of potential predators of salmon during critical early marine migration stage

several examples of marine fish species for which this has been done. For example, Bedford *et al.* (2018) illustrate the value of surveying the planktonic community to indicate changing oceanic conditions for informing statutory reporting under the Marine Strategy Framework Directive. Indicators have also been applied in ecosystem-based modelling (e.g. Lindegren *et al.*, 2011) to improve Baltic cod (*Gadus morhua*) stock assessment (Gardmark *et al.*, 2013). Bils *et al.* (2017) also combined metrics of larval Atlantic herring (*Clupea harengus*) with that of mesoplankton, highlighting the potential for surveying small planktonic organisms as a means of understanding the factors affecting larval fish feeding, growth and survival. Bentley *et al.* (2017) provide tantalising insights into the potential for linking species models within wider frameworks for identifying proximate drivers and indicators that could also be useful for salmon management in marine ecosystems.

Discussion about what indicators may be of use, how they will be weighted, and what determines "Ecosystem conditions" (Figure 2) for critical space-time domains during the marine phase could be informed by analyses of ecosystem conditions before versus after the sudden Atlantic regime shift in the 1990s (Chaput *et al.*, 2005). For instance, the temperature dependence of growth and survival (Litzow *et al.*, 2019; Tillotson *et al.*, 2021) could ultimately be accounted for by developing a suitably weighted panel of environmental and biological indicators (e.g. Harvey *et al.*, 2020). These could help to identify potential ecological thresholds (Large *et al.*, 2013; Satterthwaite *et al.*, 2020) and early warning signals (Litzow and Hunsicker, 2016) of future reduced survival at sea.

Directing efforts to identify and interpret signal shifts within the food web around these major transitions could help to unearth new ecological indicators that could also be used for hindcasting to explain past growth challenges (Todd *et al.*, 2020; Tillotson *et al.*, 2021; Trehin *et al.*, 2021; Harvey *et al.*, 2022; Vollset *et al.*, 2022), as well as for forecasting responses to future environmental change.

In the freshwater environment, examination of the primary indicators influencing growth and survival have helped guide management strategies towards maximising the number and resilience of pre-smolts (Thorstad *et al.*, 2021) and while this is logical, the newly emerging science is highlighting new tools (e.g. Bell-Tilcock *et al.*, 2021) that can address the often neglected linkages between pre-smolt performance in fresh waters and their growth and survival as post-smolts at sea (McLennan *et al.*, 2018; Gregory *et al.*, 2018, 2019; Austad *et al.*, 2021; Tian *et al.*, 2021; Simmons *et al.*, in press). By integrating new and emerging science outputs into the development of the more holistic Likely Suspects Framework approach there is increasing potential to uncover new mitigating actions for freshwater-based salmon management that ultimately fan out across the full life cycle.

As the Likely Suspects Framework approach becomes established it can consider suitable initial suites of indicators for salmon conditions in freshwater domains, and during these critical marine-freshwater transitions, extracted from the decades of work by government agencies in creating indices of Good Ecological Status for legislative frameworks (e.g. EU Water Framework Directive: Kallis and Butler, 2001). In addition, there is an extensive complementary knowledge base of the processes leading to variability in marine recruitment (i.e. smolt production from the freshwater phase, Crozier *et al.*, 2003) with adult stock characteristics, egg deposition abundance, cohort survival influenced by predation, prey abundance, intra and interspecific competition and freshwater habitat quality all being important (Jonsson and Jonsson, 2004).

Once an initial suite of suitable indicators has been agreed across salmon domains, an analytical framework needs to be constructed to test competing mortality hypotheses. A range of possible population modelling approaches could be embedded within this more integrative, interdisciplinary future framework and this could mirror what has been used to improve Baltic cod stock assessment (Gardmark *et al.*, 2013) and ecosystem modelling tools such as Atlantis (Audzijonyte *et al.*, 2019) or EcoPath-Ecosim and Ecospace (Pauly *et al.*, 2000) that interweave ecological sub-models and approaches. We envisage new opportunities arising in the development of agent-based modelling of the dynamics of salmon and other ecosystem components, and how stocks could respond to climate change and varying management scenarios. Spatially explicit agent-based models have already been developed for several species that might be linked to salmon survival, including mackerel (*Scomber scomber*) (Boyd *et al.*, 2018, 2020), herring (Hufnagl and Peck, 2011) and North Sea cod (Romagnoni *et al.*, 2020).

Ecopath with Ecosim EwE models have been used to simulate and evaluate changes to climate scenarios in the Norwegian and Barents seas ecosystem, suggesting warming will lead to increased biomass of pelagic species like blue whiting and herring (potential competitors with salmon) and decreases in boreal species of redfish (*Sebastes* spp), prawns (*Pandalus borealis)* and capelin (potential prey for salmon) (Haughland *et al.*, 2006; ICES, 2017). The current hierarchical Bayesian life cycle model for Atlantic salmon (Olmos *et al.*, 2019; ICES, 2021) could potentially be extended to include more ecological realism (e.g. multi-species and food web approaches) and combined within an Integrated Ecosystem Assessment framework to gauge ecosystem status and trends. Individual components can be designed to address specific mortality hypotheses targeting Atlantic salmon, or to investigate the influence of the wider ecosystem or communities within particular salmon domains (Olmos *et al.*, 2019). Lessons could be learned from the development of individual based models (Piou and Prévost, 2012) to test hypothesis on individual process affecting salmon growth, survival, and life history, and from recent Pacific salmon (*Onchoryhnchus spp.*) decision-making processes that have partially fused modelling outputs (biogeochemical, individually based) and expert opinion to provide lay guidance for managers. For instance, the Climate Vulnerability Assessment methodology (NOAA, 2020) uses a variety of data on species sensitivities and distribution to assess vulnerability to communicate risks to salmon managers. Similarly, the Risk Assessment Method for Salmon (Hyatt *et al.*, 2017)—adapted from Ecological Risk Assessment methodology (Hobday *et al.*, 2011)—can be modified to help identify limiting factors to salmon production across the various phases of life cycle. A Priority Threat Management framework (Gregory *et al.*, 2012) has also been adapted to aid decision-making in assigning limited resources for maximising Pacific salmon population recovery potential (Walsh *et al.*, 2020). In this vein, recent collaborative research to understand mortality drivers for salmon in the California Current (Wells *et al.*, 2017) has identified proximate drivers of survival as variation in prey abundance and associated predator responses (Friedman *et al.*, 2019) and has prioritised management options (Wells *et al.*, 2020). The Likely Suspects

Framework programme will evaluate these past efforts and work to develop a management framework that builds from these early successes, but also is tailored to the unique challenges of managing Atlantic salmon across the Atlantic basin.

Meeting the goals of the Likely Suspects Framework to improve the linkages amongst processes underpinning salmon management will require careful consideration to ensure the most appropriate integration of knowledge, the correct use of inputs (Dickey-Collas *et al*., 2014) and minimising the potential misuse of outputs in management actions. For the process to capitalise on the full spectrum of opportunities scientists, managers, and stakeholders will need to worktogether (DePiper *et al*., 2021). Whilst plenty of scientific tools have been developed for implementing the general approach (Smith *et al*., 2007), many have been considered "too complex" for adoption by non-technical audiences (Patrick and Link, 2015) and can fail on translation into management practices. Co-design from the outset, which is central to the Likely Suspects Framework premise, should help to make the transition of outputs into management actions as smooth and rapid as possible.

Addressing challenges of the future

Modifying current salmon management systems and providing new ecosystem indicators should neither immediately detract from already identified pressures nor should they supersede existing "good guidance" (e.g. Hansen *et al*., 2012; Thorstad *et al*., 2021). Rather, they offer a broader view of prospects across the life cycle for prioritising actions and potential trade-offs in areas over which managers may be able to exert some control. The value of advancing this approach is not simply in providing management prescriptions for any particular course of action to address a mortality pressure (although it can), but in presenting new guidance in terms of risk and expectation.

By developing resources that can bring greater biological realism to stock modelling and improved forecasting of salmon survival to inform management, the central questions posed within the Likely Suspects Framework can be revised, including: what data resources exist already, what are the appropriate scales at which to assess salmon survival, and what higher-level metrics are best able to predict performance of salmon across the lifecycle under different management and environmental conditions? Thus, the development of the data resources and mobilisation programme together with future workshops focused on salmon mortality at sea can be steered by feeding back iteratively as these gaps and challenges are addressed over time.

In addition, we also need to review how this information can be communicated and deployed: too often the highly technical outputs from salmon research, and from stock assessment outputs, are not translated into positive actions because they are not readily accessible to salmon managers, and the *ad hoc* and patchy uptake of the current scientific state of the art can embed biases in salmon management strategies, leading to ineffective resource allocation. For the Likely Suspects Framework approach to succeed, communication tools must be appropriate and accessible for integration into future salmon management. Viable decision or assessment support tools (Hyatt *et al*., 2017 Crozier *et al*., 2019; 2021; Scheuerell *et al*., 2006; 2021; Walsh *et al*., 2020) must also deliver scientific outputs that address "what-if" questions and future scenarios that are realistic for specific stock or river management operations. Key considerations in designing suitable applications for salmon management will be user-friendliness, engaging recognised formats to describe risk levels and survival expectation, and the use of simple messaging and tools to offer guidance in terms of balancing risks and expectations.

Progress from single-species fisheries management towards a more ecosystem-based methodology has generally been slower than might be hoped for or expected, reflecting historical inertia among both the individuals and institutions involved and project management path dependencies (Fulton, 2021). Progress towards accommodating ecosystem assessments in the context of the Atlantic salmon management will be shaped by the rate at which these hurdles can be overcome, and how effectively it can improve our still limited understanding of ecosystem resilience under future scenarios.

In summary, we have outlined a new process that starts to build the long-term approach and data infrastructure we need urgently for improving knowledge, understanding and prediction of future Atlantic salmon stocks across their range. The Likely Suspects Framework will facilitate and focus future cooperative research, and integrate the results into the development of improved management guidance. Allowing managers access to more comprehensive support tools when weighing the effectiveness of their actions within the context of the salmons' life-cycle will help them to meet the myriad of challenges posed by climate change and other pressures that salmon face, both now and in the future. The challenge now is to harness the huge potential of the salmon science and the management communities and channel our collective resources towards building an ecosystem based approach fit for the 21st century and beyond.

Authors' contributions

WC led on the conceptualization of the Likely Suspects Framework, and CB led on writing the paper. All authors contributed to drafting and revising the manuscript.

Data availability

No new data were generated or analysed in support of this research.

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