Atlantic salmon mortality at sea: Developing an evidence-based "Likely Suspects" Framework

Walter Crozier, Ken Whelan, Mathieu Buoro, Gerald Chaput, Jason Daniels, Sue Grant, Kim Hyatt, James Irvine, Niall Ó'Maoiléidigh, Etienne Prévost, Etienne Rivot, Ian Russell, Michael Schmidt and Brian Wells

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www.atlanticsalmontrust.org
11 Rutland Square,
Edinburgh, EH1 2AS
Tel: 0131 221 6550
Email: info@atlanticsalmontrust.org

Contents

Foreword

The Atlantic salmon (Salmon salar) has suffered from significant declines in survival at sea since the late 1990s, manifest in persistently poor return rates of various sea ages for a wide range of wild stocks across the north Atlantic range. While observed survival trends differ among individual stocks, there are also common trends across groups of stocks; from which it can be inferred that local and wider scale factors may be implicated.

In this regard, the EU-funded SALSEA research collaboration led to a step change in the state of knowledge of European Atlantic salmon at sea. SALSEA established the concept of an annual "conveyer belt" of northward migrating smolts. Along this route, the number of smolts declines due to cumulative effects of natural mortality as well as any fishing mortality. In particular, SALSEA identified the existence of "choke points" in the ocean, where there is coalescence of migrating smolts in relatively restricted geographical areas and where there is believed to be potential for variations in oceanic conditions to alter the destinations of migrating smolts. Additional mortality factors likely operate during the overwinter feeding phase and on the return migration to home waters and entry to rivers.

While SALSEA identified potential sources of mortality during the initial smolt migration to the feeding grounds, it did not aim to quantify or fully understand these. It is evident however, that since these factors can vary in time and space, such variation may be expected to account for some, if not most of, the variability in return rates observed among salmon stocks and between years. However, although much of the research on Atlantic salmon marine survival in the past 15 years has focused on factors at sea, it is acknowledged that conditions experienced by juvenile salmon before and during the critical phase of migration from freshwater to the sea may also impact survival during the subsequent marine phase.

The scale and complexity of survival problems facing Atlantic salmon pose unique challenges for conducting scientific research both in freshwater and the marine environment, and we must consider how it can best be coordinated and targeted. This is particularly the case with "at sea" research programmes since these are very expensive and typically require international collaboration across several countries.

Over the course of 2017, the Atlantic Salmon Trust has been developing a concept that seeks to provide coherent guidance on how future research on salmon survival can be targeted and prioritised. This has become known as the "AST Likely Suspects Framework". In June 2017 AST presented an overview of this concept to technical meetings at the North Atlantic Salmon Conservation Organisation (NASCO) and received the endorsement of the NASCO International Atlantic Salmon Research Board (IASRB). Funding was made available from the Board to support a workshop in autumn 2017 to further refine and develop the Framework. International Year of the Salmon representatives, who attended the NASCO meetings, suggested that the scope of the workshop be expanded to include modellers from west coast North America, as many of themes in the AST presentation to NASCO were common to salmon from both the Atlantic and the Pacific. As a result, the North Pacific Anadromous Fish Commission (NPAFC) partnered the workshop, via the

International Year of the Salmon (IYS) initiative. http://www.npafc.org/new/science_IYS.html

Additional funding for the workshop was also made available by the UK Department of Environment, Food and Rural Affairs (Defra) and Fisheries and Oceans Canada DFO, while AST also received valuable support and advice from our colleagues in the Atlantic Salmon Federation.

Following discussions within the IYS International Steering Committee it was agreed that the Likely Suspects Framework Workshop would be the first joint science project of the International Year of the Salmon.

The scientific workshop was held at NASCO headquarters, from 7-9th November 2017 and involved scientists from both the Atlantic and Pacific areas. The overall purpose of the workshop was to:

"Assess the scope for further development and refinement of the AST Likely Suspects Framework concept, taking account of previous and on-going related research in the North Atlantic and the wider salmosphere, including the Pacific Basin".

The AST believes that this workshop marked a milestone in our understanding of how to target research to further refine the estimates of the scale of, and variation in, mortality during the freshwater and marine phases of the salmon's lifecycle. This is likely to improve understanding of local mortality factors relative to those that operate on a wider scale. This would be of particular interest to local managers who wish to understand where their management actions can have greatest impact.

We believe the joint participation of salmon scientists from the Pacific and Atlantic areas has provided valuable comparative insights into factors influencing survival in the ocean, at both basin and hemispherical scales and has established a momentum to drive collaboration between Atlantic and Pacific research groups on common issues affecting salmon. We are grateful to all of our contributors, who provided a wide range of fascinating and important scientific findings and insights to the workshop.

Sarah Bayley Slater *CEO, Atlantic Salmon Trust*

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The Atlantic Salmon Trust wishes to gratefully acknowledge the generous support of the Likely Suspects Workshop sponsors.

Setting the scene: The AST Likely Suspects Framework

This summary report starts with a description of the AST Likely Suspects Framework concept and then discusses the topics covered by the workshop sessions, drawing on the papers presented at it:

- The utility of the Likely Suspects Framework to tease out and partition the mortality factors operating at different geographical scales and to assess their cumulative effects.
- Populating the Framework with evidence - data requirements.
- The scope for modelling approaches to populate the Framework with mortality estimates accounting for evolutionary change.
- The potential to move from a high level conceptual framework to incorporate a number of modelling approaches to help further assess the various mortality factors.
- The potential for application of the likely suspects concept to the wider salmosphere, including Pacific Basin salmon species.
- Development of a web-based tool for demonstration and outreach purposes.

A final over-arching section provides a summary of workshop outcomes and actions.

The likely suspects concept

The concept of likely suspects arose from scientific work carried out to explain why the stock assessment of cod in the Irish Sea estimated apparently much higher total mortality than could be accounted for by reported landings by the fishing fleet combined with natural mortality (ICES, 2016). This unaccounted for mortality was difficult to reconcile with a large reduction in fishing effort by whitefish trawlers in recent years and raised the question of what factor or factors in combination could account for the “missing” cod? ICES recommended that research should focus on identifying the sources of unaccounted for mortality or causal factors. Candidate “likely suspects” included discards, emigration from the stock, survey bias, underreporting of catches and the assessment model itself. Part of the work arising from the initial examination of the likely suspects led to an EU funded cod tagging project aimed at addressing the migration question. The ICES WKIRISH benchmark meeting held in January 2017 (ICES, 2017) reviewed evidence on more accurate catch reporting, lack of evidence on high grading of cod and increased observer coverage for discard observation and also noted that there was not sufficient evidence to suggest movement of a significant proportion of the stock into/out of the stock assessment area. Application of a different assessment model and changes in the input data resulted in a change in the perception of the stock and ICES now considers information on landings and discards as unbiased estimates of removals.

While the outcome of the cod re-assessment is not directly relevant to Atlantic salmon, the approach adopted is relevant, in that various candidate mortality factors (or in some cases bias factors) were looked at in the context of whether they could singly or in combination feasibly account for the apparently high level of unexplained mortality.

The "AST Likely Suspects Framework": general principles

The likely suspects approach as applied to Atlantic salmon seeks to explain the main sources of additional mortality at sea, to try and account for the observed reductions in sea survival in recent years compared to earlier periods of higher survival. To this end it places candidate mortality factors within an overall spatio/temporal framework covering the freshwater migration/sea entry phases and the marine phase of the life cycle. The objective is to identify the various mortality factors involved and quantify the potential for each factor to influence survival (i.e. the "likely suspects"). In an approach more akin to financial accounting than mathematical modelling, the cumulative effect of these factors is made to account for the observed overall marine survival variations between particular periods. This can be used to identify the likely impact both individually and cumulatively of the "likely suspects".

The initial approach is to quantify the number of salmon in recent years that are dying on their initial migration and at sea, in comparison to earlier periods of high marine survival (corrected for differences in numbers of spawning fish), and to allocate these "lost" fish to the various known or hypothesised sources of mortality.

This concentrates research on identifying where and how mortality factors may have changed since earlier periods of higher marine survival. Can we narrow this down to the really important suspects? Perhaps the missing numbers and the big numbers are where research should be concentrated?

A key part of this approach is to prompt specific testable hypotheses about the operation of the factors involved and hence aid targeting of research to further refine the estimates of the potential scale of, and variation in, mortality at each part of the marine phase.

Implementation of the Likely Suspects Framework

There is empirical evidence for the existence of some of the candidate mortality factors and the locations and scales at which they may operate and this forms the starting point for constructing the Framework.

Start by identifying zones or "ecosystem domains" in the life cycle where significant mortality is believed to be taking place. Domains can be placed at geographical locations (e.g. Mork et al., 2012) and/or allocated to particular phases where significant marine mortality factors operate (such as: estuarine/coastal; near-shore; migration to feeding grounds, coastal return/river entry). However, what happens during other phases lying outside the marine environment (such as smolt migration through freshwater) may influence subsequent survival at sea and these must also be represented in the Framework. Some hypothetical domains for an example Northern Irish salmon stock are shown in Figure 1.

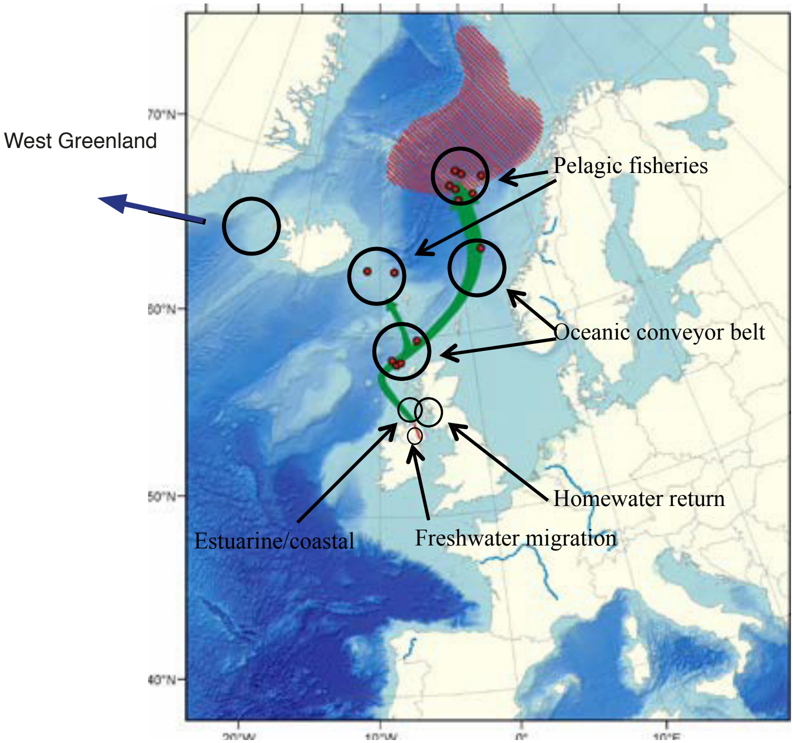


Figure 1: Example domains for a Northern Irish salmon stock as envisaged in a hypothetical Likely Suspects Framework

A simple diagrammatic view of how a life cycle based Likely Suspects Framework might look is shown in Figure 2.

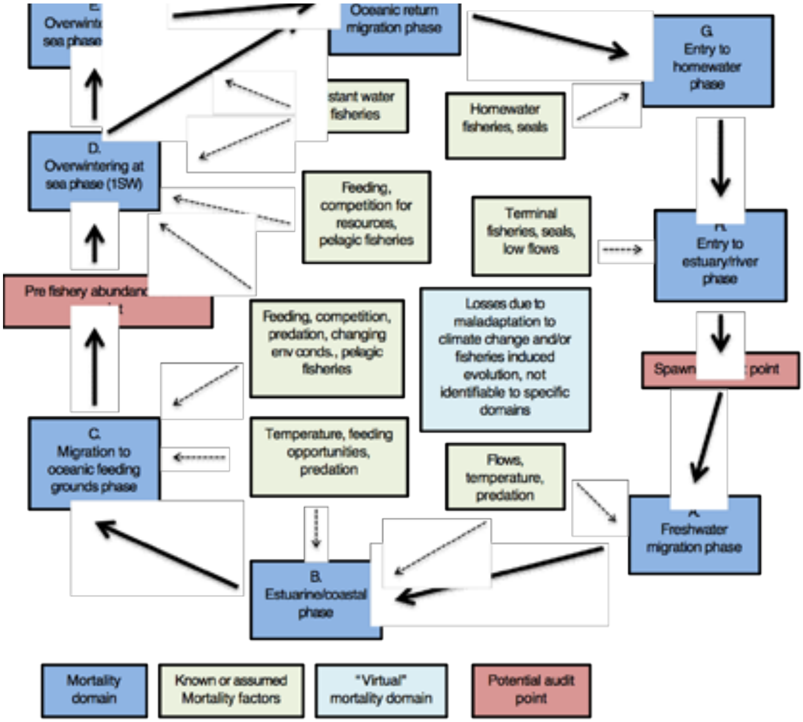


Figure 2: A diagrammatic view of how a life cycle based Likely Suspects Framework might be constructed

This example framework is based around a preliminary list of candidate mortality factors (including capture fisheries) and their associated domains representing particular geographical locations/areas or periods in the life cycle where identified or hypothesised mortality factors are thought to operate. An important feature is the use of life cycle audit points, as these are necessary to allow comparison of salmon abundance between different periods being examined. One such audit point would be pre-fishery abundance (PFA), which is the abundance of salmon at sea on 1st January of the second year at sea, as estimated by the International Council for the Exploration of the Sea (ICES) as part of its annual stock assessment procedures (ICES, 2017a).

The effects on mortality of factors such as loss of genetic "fitness" due to maladaptation to rapid environmental change and effects of fisheries-induced evolution (e.g. Piou et al., 2015) cannot be ignored. Since the geographical locations and/or periods during the life cycle where these effects take effect is not yet understood, it is necessary to introduce a different type of domain…a "virtual domain".

Initially, we can begin to populate the Framework with known or even hypothesised ranges for each mortality factor, but these would subsequently be refined as each targeted piece of research (including modelling where applicable) produced updated or new estimates.

An initial approach might attempt to populate the Framework at stock-complex level, where time series data exist about changes in overall abundance of salmon among various stock groupings, such as changes in PFA as estimated by ICES. This would involve comparing current and earlier periods between which survival at sea is known to have changed (declined). For example:

- Start at broad scale such as ICES stock complex level (e.g. southern North East Atlantic Commission (sNEAC), northern North East Atlantic Commission (nNEAC), and North American Commission (NA)).
- Quantify overall additional losses in recent years compared to earlier decades of higher survival (e.g. compare ICES PFAs 1971-75 vs. 2012-16). These represent the "missing" fish that have to be accounted for.
- Make preliminary numerical allocations to all the mortality domains…ie start to partition the overall unaccounted for mortality based on what is known or thought to be the case.

A key question is: What additional mortality in terms of numbers of salmon is needed to account for the difference and where should this be allocated?

A comparative study among stock complexes may highlight differences in amount and patterns of change and might point to some of the differing factors involved and in particular the scales over which they operate. This leads us towards starting to tease out scales of mortality. Comparisons between European and North American stock complexes would be important in this regard to identify mortality factors that cannot be common to both stock complexes and factors that are likely to be common. For example:

- Pelagic fishery by-catch in NEA and predation by harp seals in Labrador Sea are non-common factors.
- Factors impacting salmon at West Greenland (such as a >20% reduction in capelin biomass since 1970s (ICES, 2017a)) may be common to MSW stock components from NA and NEAC stock complexes.

Since several mortality factors of interest may operate only in localised areas or on small groups of stocks, it is recognised that populating the proposed mortality domains at stock complex level may not establish a full picture of the mortality factors at work on any given stock. However, a key attribute of the Likely Suspects Framework approach is that it can be adapted to various scales.

It is therefore proposed that the Framework would subsequently evolve to adopt a cohort approach, whereby variation of marine mortality would be considered on an individual stock basis on selected stocks from each stock complex. The ICES "index" rivers are an example of this approach, where much more detailed data are available, including annual stock-specific indices of marine mortality (ICES, 2017a). A single stock approach would allow comparison between individual cohorts, which may give insight into year on year changes in mortality at sea.

As well as census and biological data from ICES "index" stocks, migration data from the increasing number of stocks with tracking/location studies will also help populate this approach. These studies often give insight unto losses during very specific periods along the estuarine/near shore migration routes and in some cases quantitative estimates of predation (e.g. see *NASCO IASRB progress Report on SALSEA-track ICR(17)3, and NASCO IASRB Inventory of Research Relating to Salmon Mortality in the Sea SAG(17)2)*.

Provisional values to populate "virtual domains" incorporating, for example, estimates of mortality due to loss of genetic adaptation under rapidly changing environmental conditions might be obtained from individual based salmon eco-genetic modelling at individual stock level.

It is emphasised that the Likely Suspects Framework is not a model and it may be necessary to evolve it from a high level conceptual framework to incorporate a number of modelling approaches to help further assess the various mortality factors?

Further developments of the approach must keep in mind the management requirements. Though not designed to have predictive capability, the Likely Suspects Framework may be capable of indicating where variations in marine mortality factors have the greatest impact and where some further partitioning of the marine phase of salmon stock forecast models used for catch advice may be contemplated.

What does adopting this framework imply for future research on salmon at sea?

The value of the proposed framework is to link together patterns of mortality at appropriate geographical and temporal scales and, if suitably populated with data, can enable the development of testable hypotheses about salmon mortality at sea. It therefore offers an adaptive framework from which appropriate new research can be identified and prioritised. The Likely Suspects Framework can subsequently be populated with emerging data from various ongoing and future research projects. As outlined later in this report, there is also much scope for closer collaboration between oceanographers, ecosystem modellers and salmon scientists. The AST Likely Suspects Framework could provide a clear strategic focus for supporting such developments.

The establishment of a conceptual framework would also support consortium groups in targeting bids for research on salmon at sea, as it will help avoid overlap/duplication and will help funders target resources at the most important domains in the marine phase of the life cycle. Through updates it will also indicate the state of progress in research on mortality at sea.

As an example, the proposed framework would provide a valuable new perspective on the research activities listed in the IASRB *Inventory of Research Relating to Salmon Mortality in the Sea"*, as it would allow "mapping" showing the degree of alignment of these activities to the various mortality domains identified in the framework. Such a framework is also relevant to developing the research priorities of individual organisations. For example, it provides clear linkage between many of the components within the "Ocean" and "Inshore and Coastal" key pillars of the draft *AST 10 Year Science Strategy*:

Pillar 1: In the Ocean

- Salmon migration in the ocean / SALSEA Track
- Real-time monitoring and assessment of salmon cohorts in the ocean
- Pelagic by-catch

Pillar 2: Inshore and Coastal

- Post-smolt migration routes and survival
- Impacts of aquaculture
- Predation

Pillar 3: In Fresh Water

- In-river juvenile and smolt survival

A further application of the framework would be for outreach activities. A simple web based interactive tool could be developed, that would present users with a map based version of the marine phase of the life cycle and allow users to vary the impact of changing the various mortality factors within ranges to be established during development of the framework. This would demonstrate how variation in these factors impacts cohort survival and, through this, how trends in stock abundance become established.

Examining the utility of the Likely Suspects Framework to partition the mortality factors operating at different geographical scales (local, regional, oceanic)

Key Questions

- *How can we identify the main mortality "domains" and candidate mortality factors operating at the various spatial scales?*
- *Can marine survival be considered as starting with the physiological process of smoltification and during subsequent passage to the sea?*
- *Which are likely to be the important domains from a management perspective?*

Identifying domains in the framework

The workshop considered that one way to try to identify the key mortality domains at sea could be to collate marine environmental covariates thought to be associated with salmon survival during marine life. These covariates could be laid out spatially and correlated to survival patterns of individual stocks representative of the stock complexes of interest. This will reveal hotspots in the ocean for spatial and temporal correlation. This would extend previous work by Friedland et al. (2000, 2014) and numerous unpublished studies and would link well with hypothesised choke points identified by SALSEA (SALSEA-MERGE, 2012) that appear to be of importance for smolts migrating in the NEA from home waters to their feeding grounds.

There is empirical evidence for the existence of several such domains or chokepoints in estuarine and coastal waters and during post-smolt migration to feeding/over wintering oceanic areas; can others be hypothesised?

There will be domains where mortality factors impact many stocks, while others where only a few stocks or even a single stock are impacted. In visualising this, it may be useful to think of salmon from a given stock on their migratory journey passing through successive mortality domains, where they are joined by salmon from other stocks, and so on. The overall survival at sea of each cohort of a stock will vary according to the balance between, and cumulative effects of, the various mortality factors. This presents a particular challenge in identifying the various domains of interest, since any given stock is likely to pass through domains local to that stock (e.g. estuary and nearshore areas), migrate along a pathway where several to many stocks coalesce (e.g. marine conveyer belt) and spend time feeding and overwintering in oceanic areas where many stocks combine for several months (e.g. Labrador Sea, W Greenland, N Norwegian Sea).

We must not get lost in the weeds though, as not all domains are of equal significance in influencing mortality at sea, so a strategy would be to concentrate initially on those where many stocks overlap (for example at West Greenland) and are all doing the same thing for a period of time. It is important to concentrate on the big numbers and on places/periods where any mortality impacts are likely to affect a large number of stocks (this knowledge is important from a management perspective). Major areas of interest are not necessarily at oceanic scale. Another aspect to be considered when looking at domains is that space/time axes in freshwater and estuaries can be very discrete hotspots where fish get slowed down and get preyed upon.

This should be done for North American as well as European stock complexes and also for one sea winter (1SW) and multi sea winter (MSW) components, as this will help to identify factors that cannot be common and also those that might be common. Some early refinement of the relative importance of various domains may be possible. For example, pelagic fisheries in the Norwegian Sea can hardly be impacting North American post-smolts in the Labrador Sea, while a reduction in capelin biomass and energetic content at west Greenland since 1970s (ICES, 2017a) may be commonly impacting MSW stock components from NA and NEAC stock complexes.

The geographical locations and/or periods during the life cycle where the effects on mortality of factors such as loss of genetic "fitness" due to maladaptation to rapid environmental change and effects of fisheries-induced evolution (e.g. Piou et al., 2015) are not yet understood. The corresponding virtual domains are considered separately in a later chapter of this report.

The work would also start to partition (segment) the marine phase into important staging areas that are domains of particular interest. Identifying the location and spatial/temporal extent of such domains is of central importance in drawing up hypotheses about the potential factors driving mortality and when contemplating further research focusing on the functional mechanisms at work.

An important question was raised as to whether it is mean or annual variation in mortality at sea that is of interest? The workshop agreed that both were important, and that while much of the annual variability in marine survival is likely to be stochastic, it is the overall cumulative impact of the main factors negatively influencing mortality over broad scales that drives productivity on a downward trajectory (i.e. rate of adults returning per migrating smolt is lower in recent years on average (ICES, 2017a)). But evidence from Pacific salmon studies also show that we must be aware of the impact of particular single year events where exceptional survival change occurs. This mix of directional and exceptional single year events implies that the timescales chosen for examining survival patterns is of some importance. Choice of appropriate temporal bookkeeping or audit points in the Framework is important for capturing changes in survival between key parts of the life cycle.

Where does marine survival start?

It is important to consider the question of where the marine survival process actually starts, as there is evidence that what happens during the freshwater phase of the life cycle may influence subsequent survival at sea and must therefore be accounted for in the Framework. The cumulative effects of size, timing and condition of fish entering the marine environment may be significant. For example, climate change impacts in freshwater may change smolt migration timing, which some studies have shown may affect subsequent survival at sea (Kennedy and Crozier, 2010). While the process of smoltification may be considered the physiological start of preparation for marine life, factors impacting marine survival may begin well before smoltification, and may include epigenetic effects (Mirbahai and Chipman, 2014) originating from the adults that gave rise to the smolt cohort.

At a recent Conference organized by the Atlantic Salmon Trust and the Tweed Foundation (Barry et al., 2017) evidence was presented which clearly demonstrated the range of potential impacts encountered by smolts during the estuarine and freshwater phases of their migration to sea. In addition to manmade influences such as chemical pollution and barriers, predation and climate change are also impacting severely on some Atlantic salmon populations. However, what is considered most important is that the smolts enter the marine environment during a narrow "window of opportunity" when conditions in the sea are at their optimum in terms of water temperature and prey suitability, which allows survival to be maximised (McCormick et al., 1998).

One of the consistent findings from the smolt Conference was that climate change is impacting directly on the migration patterns of salmonid smolts. This has two potential consequences: smolts will be younger, smaller and less fit; smolts may reach the sea when conditions are less than optimal for their survival, with colder sea temperatures and reduced feeding opportunities. Both these effects are likely to reduce marine survival, as there is increasing evidence that smaller smolts display lower rates of marine survival. There is growing evidence from some of the key index monitoring sites in the North East Atlantic that smolt age is dropping, with increasing numbers of smaller, 1+ smolts running to sea. Smolt run timing across the geographic range has also been earlier, at an average rate of almost 3 days per decade (Barry et al., 2017).

Which are the important domains for managers?

One key consideration in identifying mortality domains is to recognise the practical relevance of various scales of domains to management of the resource. Hence, managers at national/international level may be more interested in the impacts of large scale factors at the domains where, say many stocks from several stock complexes coalesce. Here variation is likely to impact stocks at the level of management units used for international management, reflecting the scale that the stock assessment and catch advice models have been established. At that scale, the broad picture of what is happening at stock complex level is of interest. In contrast, local river managers will be more focused on where the local mortality factors that affect their stocks are operating, not least because they may be able to influence these (e.g. predation, water quality, barriers to migration, contaminants). For local managers the oceanic factors are almost seen as overheads and a mortality penalty that stocks must endure and over which they have no control. In the local context therefore, a sensible management strategy would be to maximise output of smolts and their chances of success at the critical freshwater/marine interface and during the early marine period by controlling estuarine/coastal impacts on single stocks.

Populating the Framework with evidence - data requirements and unknowns

Key Questions

- The key question is "what mortality factor or factors have changed in recent years?"
- Can we estimate mortality at different parts of the marine phase?
- What data will be required to populate the Framework at different scales? Where are the data gaps?
- Can the Framework, if suitably populated with data, enable the development of testable hypotheses about salmon mortality at sea?

Has marine mortality changed and over what scales?

Given that the basis for establishing a Likely Suspects Framework is to attempt to partition the effects of mortality factors on salmon stocks, a key question arising is what mortality factor or factors have changed in recent years? A core issue is to determine how marine survival in Atlantic salmon has changed and at what scale to address the question; i.e. do we need understanding at individual population level or at aggregate scale?

In the Atlantic area, a series of monitored rivers in each stock assessment unit provides annual data on smolt output and subsequent returns and spawners by sea age. These are assumed to be representative (i.e. an index) of that unit. The workshop considered that direct examination of index river data might facilitate some progress in resolving spatial and temporal components of changes in patterns of marine survival. We are using the term index river in this context, because we are inferring that survival trends of salmon from a monitored river show some degree of representativeness with surrounding rivers in that region/management unit.

At present a total of 56 river/stock datasets are available to ICES for smolt to adult return rates from 1969-2015 smolt migration years. These comprise 27 wild stocks and 29 hatchery stocks. The wild stocks split into 16 rivers in the NE Atlantic and 11 in the North West Atlantic areas. Not all have data for the full time series, probably limiting time series analysis to around 20 wild stocks. Given that these index rivers typically hold annual data on sex ratios, scale samples (growth and age structure, DNA) and other biological parameters, the workshop also considered what types of relevant analyses could be supported by these data?

An initial analysis of patterns in marine survival across the ICES index river series was reported by Chaput (2012) and this was extended and updated for the workshop.

In performing such analyses it is noted that return rates to index rivers are proxies for marine survival. This is because, for each cohort of migrating smolts, survivors return during two or more subsequent years. For example, return rates of two-sea winter (2SW) salmon do not equal survival, since a proportion of that smolt cohort has already returned as maturing 1SW fish. Results indicated:

- In general, return rates for 1SW stocks are higher than for Multi Sea Winter (MSW) stocks.
- Return rates for salmon stocks in Iceland and Europe are greater compared to Eastern N. America.
- Return rates in index rivers show declines over the past four decades in southern regions of N. America and in most regions in the NE Atlantic.
- Pre-fishery abundance (an audit point in the LS Framework) has declined strongly in the three major stock complexes of the N. Atlantic (nNEAC down 53%; sNEAC down 63%, N. America down 45%)…peak estimated abundance of 10 million fish at sea in the 1970s has fallen to an average of less than 3.5 million fish in the past 10 years.

There is some evidence of large spatial scale effects. Relative productivity (PFA abundance/eggs) is annually highly variable, but shows a sharp decline around 1989-1991 for North American and sNEAC stock complexes (Figure 3). This appears to coincide with an ecosystem regime shift as characterised by a change in phytoplankton community structure around the same period (Figure 3).

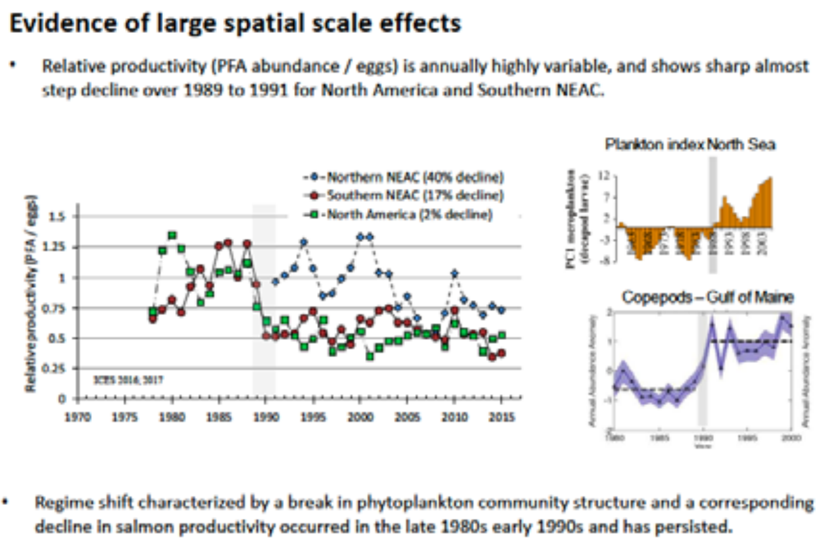


Figure 3: Trends in an index of productivity for the three major stock complexes of Atlantic salmon over several decades. Also shown are two indicators of phytoplankton community structure.

Further analysis of trends in returns for management regions within the N. American stock complex (Figure 4) illustrates contrasting trends at a regional level:

- Increasing returns of small and large salmon in northern regions (Labrador/ Newfoundland).
- Decreasing trends of returns of large salmon in the other regions of eastern Canada, with severe declines in the two most southern regions, despite reductions in mixed stock fisheries harvests.
- Small salmon returns decreased in the Maritime Provinces (Gulf and Bay of Fundy/Atlantic Nova Scotia), despite reductions in mixed stock fisheries harvests. No noted decline in Quebec.

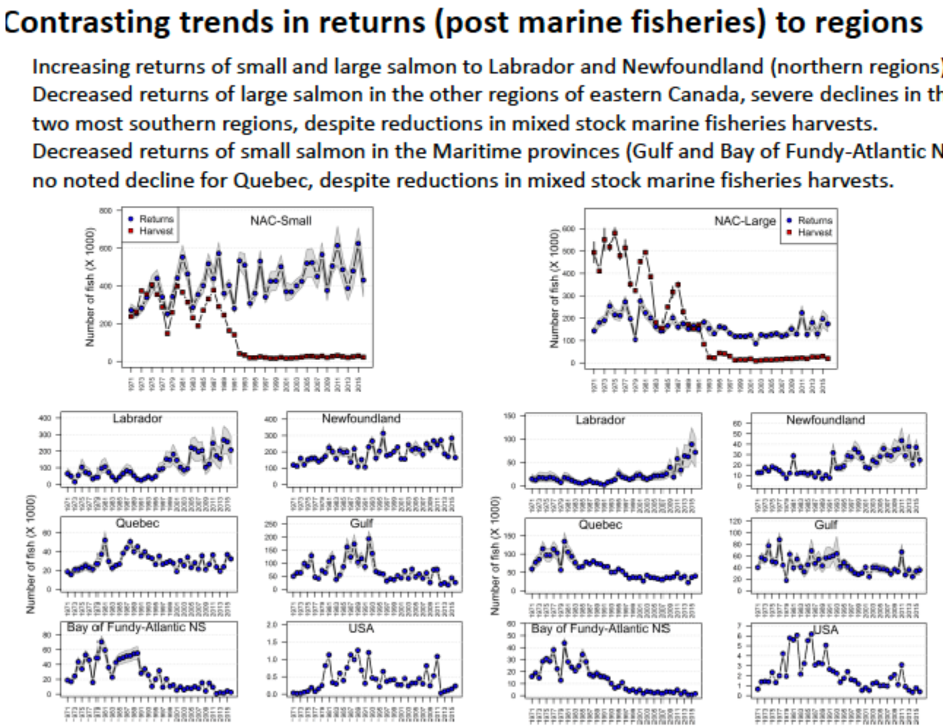


Figure 4: Trends in returns of small and large salmon to management regions in eastern North America.

Moving to individual river level, patterns in returns to individual rivers in these N. American management areas are shown in Figure 5 below as anomalies with respect to the standardised time series from 1984.

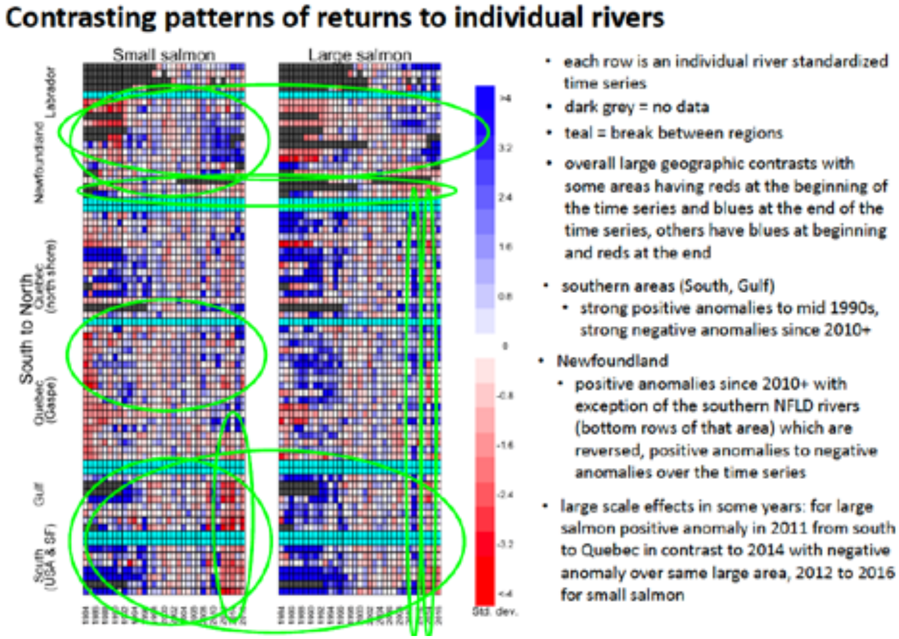


Figure 5: Patterns of Atlantic salmon returns to individual rivers in eastern North America using standardised time series.

This analysis showed there are overall large geographical contrasts, such as returns improving over the time series for Newfoundland/Labrador, while declining for southern N. American stocks. In addition, there are large-scale effects where every area follows the same trend, with a strong positive anomaly for large salmon from USA to Quebec, while for 2014 there was a negative anomaly for small salmon over the same large area. This analysis shows that differences between impacts at local and broader scales are very important. This serves to illustrate the complexity of resolving scales of variation in marine survival (and by extension, the factors influencing marine survival).

Regarding linkage of this information with the populating the LS Framework, the workshop recommended further analysis to examine/scan Atlantic salmon populations by ecoregion (rather than management unit), to look for differences and similarities; i.e. domains with multiple populations present with common survival patterns, versus separate domains with different un-coherent properties. Inferences can perhaps be drawn from the network of time series indicators from stocks that enter different marine domains or leave different freshwater regions. It was suggested in the workshop that covariance (and similar) analysis may resolve spatial scales at which coherence in survival operates, as indicated for example by similar analysis of Pacific salmon in the Salish Sea (Ruff *et al.*, 2017, Zimmerman et al., 2015)

Can we estimate mortality at different parts of the marine phase?

The workshop then considered in detail the potential for estimating ranges of natural mortality operating at or between particular domains or life cycle stages, such as during the first and second years at sea…in effect can we partition out marine mortality? Ricker (1976) summarised a number of approaches, termed maturity schedule methods, to derive estimates of mortality at age. A modification of the maturity schedule method allows estimation of total mortality rates (Z) during the first and second year at sea based on information on abundance and sex ratios of out-migrating smolts and return rates for male and female 1SW and 2SW salmon (Figure 6). Assumptions are that survival at sea age is similar for males and females, while maturation schedules differ for males and females, but not after the first sea year since the maturation decision has already been taken.

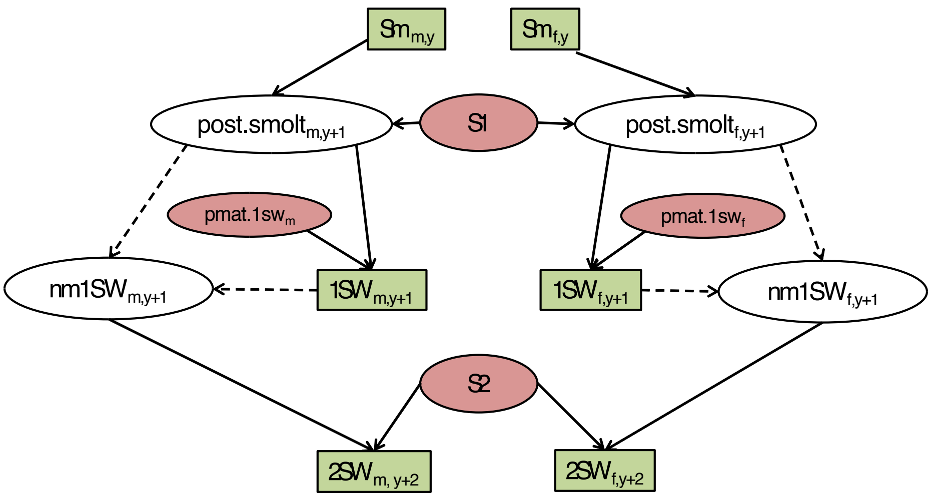


Figure 6: Using the maturity schedule method to estimate salmon marine survival by year at sea.

Application of this approach to a selection of index rivers in Canada that have characteristically different population dynamics in terms of sea age structure and sex ratio by sea age showed some contrasts and similarities:

- In the de la Trinite River, where 1SW were mostly male and 2SW mostly female, survival during the first year was <10% but dropping further to 2-3% since the 1990s. In contrast, second year survival was high, up to around 80%, but subsequently dropping down to around 20%. The salmon in the second year are mostly females, since the probability of male maturating as 1SW's is very high (around 80%+).
- In contrast, in the Saint Jean River, where the smolts are mainly females, the 2SW male component is 30-40% male due to much lower (and highly variable) proportion of males maturing during the first sea winter. For this stock, survival during the first year at sea is low, but even lower during the second year at sea, particularly for males.
- In addition, for both stocks survival at sea was seen to differ over time in both the first and second years a sea.

This illustrates that the sex ratio and proportion maturing by sea age in a stock are fundamental to differing levels of survival at sea between 1SW and 2SW components. Since these characteristics differ between stocks it is important to interpret marine survival data in the light of these influences, since variations in sex ratio and maturation tempo between stocks and over time, may account for some of the observed variability in marine survival regardless of other factors.

Conclusions from this analysis were that:

- Index rivers where smolt production and adult return rates are monitored provide an opportunity to estimate total mortality in the first and second years at sea:

o This needs data on abundances and sex ratios for smolts and returning adults by sea age.

o If smolt production estimates are not available, information on smolt sex ratio with full information on returns and sex ratios by sea age can still provide estimates of mortality in the second year and the probability of maturing after one year at sea for males and females.

o Knowing total mortality in the first and second years may provide a means of developing the weight of evidence for marine harvests as a likely suspect in the observed declines of salmon.

In particular the workshop noted that, while index rivers are likely to have the type of data required for spatial and temporal analysis of survival at sea using the above methods, those rivers where smolt abundance is not known could still provide useful information.

If smolt production estimates are not available, information on smolt sex ratios with full information on returns and sex ratios at sea ages provide estimates for total mortality in the second year at sea and the probability of maturing after one year at sea for males and females. New DNA based sex determination methods could be used to provide a more reliable basis for obtaining sex ratios for smolts and adults (via scales for example), hence extending estimates of survival during the second year at sea to many more river stocks than at present.

The workshop recommended that, given the availability of data from index rivers, emphasis should be given to further analysis of second year natural mortality (M) across as wide a range of Atlantic salmon stocks as possible. One of the assumptions used in the run-reconstruction model used by ICES to estimate pre fishery abundance in Atlantic salmon is that, accounting for fishery losses, M between the PFA stage and return to home river, is constant. An instantaneous monthly rate of 3% is currently used (ICES, 2014), therefore, updated/improved estimates of spatial and temporal variation in "M" would be of great interest. The analysis described here provides evidence against the constant mortality rate assumption made by ICES. The workshop therefore recommended that, given the availability of data from index rivers, emphasis should be given to further analysis of second year natural mortality (M) across as wide a range of Atlantic salmon stocks as possible.

This might involve analysis of covariance in M across various geographical ranges of salmon and changes over time for individual stocks, as well as concordance among stocks. The scale over which there is coherence in second year M is important because this may point to more appropriate stock groupings used in the ICES stock assessments. Similarly, if the assumed constant value for M used by ICES does not capture changes in M over time periods, these changes should be reflected in the run reconstruction models embedded within the ICES stock assessments. Perhaps M is greater in recent years compared to the 1960s, 70s and 80s?

Relating this back to populating the Likely Suspects Framework, it was concluded that it should be possible to begin to partition out mortality during the marine life cycle. For example, data from acoustic tracking work can provide estimates of mortality for the initial period (<2 months) at sea. Combining these data with estimates of mortality during the second year at sea would, for example, allow an understanding of the relative scale of mortality in the first two months at sea versus during the second year at sea, for fish returning from West Greenland.

Data requirements

The spatial extent of mortality domains can differ greatly. Domains in freshwater may be very discreet, for example locations where predation is high or migration is delayed, whereas oceanic domains may be on a very much wider scale (e.g. an extensive area of ocean bounded by two isotherms). In a practical sense, this implies very different types and extent of data needed to populate domains and to start to examine the mechanisms linking to mortality in salmon. Again, this emphasises that individual research projects at single stock/local level can provide very valuable data to identify and populate domains of local relevance, whereas at the oceanic scale a different magnitude of data requirements will demand a different scientific approach. The process of populating the Likely Suspects Framework will clearly guide researchers towards identifying and prioritising the necessary work.

The Workshop emphasised that the time series from the ICES index rivers was of critical importance and furthermore that other monitored rivers with perhaps less complete data can still contribute data; for example, sex ratio based analyses of second year mortality. Similarly, rivers having tracking studies can contribute information on mortality rates in the freshwater to marine transition, including early marine life.

Since the data from the index rivers are used annually by ICES for stock assessment purposes, it is the data relating to that which are usually emphasised. It is clear that an initiative is needed to focus on what data sets are required (existing and new) to populate the Likely Suspects Framework, as this has a different purpose.

The workshop reviewed experiences from Pacific salmon species, which illustrated the importance of developing data systems that will hold data on a range of relevant metrics, with defined uncertainties associated with the data points and time series from difference countries and continents. Opportunities to assemble and fully document these data (including metadata) are needed.

In the Likely Suspects Framework context, there is a particular need to compile good documentation on the survival time series of wild Atlantic salmon. That approach was adopted by the EU SALMODEL project (Crozier, *et al.*, 2003) which looked at stock and recruitment data throughout the Atlantic range of salmon in order to drive research into setting and transporting conservation limits. There is a need therefore for a workshop format (perhaps under the auspices of ICES?) to evaluate/document this. Data will then need to be standardised and made accessible to import into analyses at domain scale. It was agreed that it is not just data from river and coastal locations/study sites that are needed, but also from those domains representing stages at sea where salmon are in a common area.

The current workshop made a start, by developing an illustrative spreadsheet of the required data attributes at various scales (broadly aligned with LSF domains). The required dataset would include other relevant information such as: growth (from scales); genetic diversity (DNA); migration history (otolith trace elements) and other sources of data on biological characteristics of Atlantic salmon populations (ICES, 2010). Such a dataset could be further developed in conjunction with the SALSEA_PGNAPES databases of biological information on salmon marine samples.

http://www.nasco.int/sas/pdf/salsea_documents/salsea_merge_finalreports/D%202.4%20Electronic%20data%20bases%20of%20biological%20information%20on%20marine%20samples.pdf

Data on hatchery releases would be valuable, as they may help to "tune out" variations in freshwater mortality observed in wild stocks, though at risk of introducing confounding influences of hatchery practices.

A benefit realised from having joint Atlantic and Pacific representation at the workshop was that agreement was reached that specific follow up tasks would include developing a common language/currency, establishing an operating framework for working together (e.g. meetings/discussion forum), and sharing information to align approaches so that data are comparable. Alignment of terminology and data across the salmosphere is seen as a necessary step to facilitate collaborative working, especially at hemispherical scale.

Prioritising research: Identifying hypotheses to test

The workshop concluded that prioritising future research can be achieved primarily through two complementary approaches; defining the questions that need answered and constructing a series of hypotheses that can be tested.

A typical simple set of high level questions might include the following:

- What do we know about survival rates at sea over time?
- There are lots of environmental and ecosystem proxies at sea; things we can measure (e.g. sea surface temperature (SST), primary productivity). How do we relate these to temporal and spatial patterns of salmon survival at sea?
- Where are the common patterns, over what scales do they exist and how does this vary?
- How important is the second year at sea; if most losses are during the first year is mortality in the second year only marginal?
- Can we partition mortality between the first and second years at sea and has relative mortality been switching between these phases?

In order to make significant advances towards answering the sort of marine survival questions as shown above, the workshop agreed that we need to start with a clear set of hypotheses.

In framing hypotheses we should aim to approach this systematically, such that we find out more about the evolution of marine survival and the dynamics of how the process (or processes) actually work. Lessons from the Pacific are that marine survival is a very dynamic process and factors that cause significant losses to some stocks in some years, may be less significant or absent in other years. For example, in some years there are widespread drops in marine survival, but in others these reductions are localised and for different reasons. For example, in years when there is significant upwelling on the California coastal current there is a superabundance of seabirds and these prey heavily on Chinook salmon *(Oncorhynchus tshawytscha)*, yet in other years this effect is less evident. Similarly, climate change impacts at oceanic scale may also have an impact on salmon while still in freshwater. Hence the overall impact is accumulated over both parts of the life cycle. The message is that we need to factor these types of dynamics into hypotheses being developed for Atlantic salmon.

The workshop agreed that a systematic attempt should be made to draw up hypotheses for Atlantic salmon marine mortality addressing the primary questions to be answered. This would be based on the initial set of LSF domains and a list of likely candidate variables/drivers influencing marine survival and would be drawn up using expert opinion and with reference to previous research where hypotheses have been identified (e.g. SALSEA-Merge, 2012). The list of hypotheses should be prioritised, and should be cross-matched to the data consolidation exercise to reveal what data are available and where data gaps exist. Such a list would act as a reference list against which progress of future research could be evaluated; therefore assessment status should be formally and regularly updated.

An example from the Pacific regions illustrates the use of hypotheses to help develop a comprehensive, multi-disciplinary and highly coordinated research programme at an ecologically relevant scale, to investigate survival of juvenile Pacific salmon and steelhead (Oncorhynchus mykiss) in the Salish Sea: https://marinesurvivalproject.com/the-project/key-hypotheses/

Testing the scope for individual based salmon modelling approaches to populate the Likely Suspects Framework with mortality estimates accounting for evolutionary change

Key Questions

- *Is it likely that candidate mortality factors include loss of genetic adaptation due to rapidly changing environmental conditions?*
- *Could a general and widespread loss of genetic "fitness" be the most likely suspect of all?*
- *Should fisheries-induced evolution also be considered in this context, as it has the potential to influence life history characteristics, such as maturation tempo, which in turn may impact cumulative mortality at sea?*
- *Since the geographical scales or locations where evolutionary change impacts take effect are not yet understood, how do we take account of them in the Likely Suspects Framework?*

The cumulative and synergistic effects of factors such as environmental change and fisheries induced evolution on life history traits and fitness components and hence survival at sea cannot be ignored among the likely suspects. For example, delayed maturation inevitably increases cumulative mortality at sea. Since the locations and times where these "stressors" take effect are not known or poorly understood, this may involve introducing a different type of domain; a "virtual domain" that would incorporate estimates of increased mortality in that stock due to lack of phenotypic plasticity and/or loss of genetic adaptation under rapidly changing environmental conditions.

Sensitivity to environmental change

In considering how to deal with the effects of environmental/ecosystem change on mortality of Atlantic salmon at sea, in the context of the Likely Suspects Framework it is necessary to attempt to understand the mechanistic basis of how salmon may respond to these pressures. Importantly, in salmon there is a complex interplay between life history traits, in short the relationships between growth, survival and maturation, with potentially opposing selection between freshwater and marine phases of the life cycle; a recipe for maladaptation under conditions of rapid change.

The response of populations to climate change and fisheries induced evolution depends on:

- The rate of environmental change (associated with the strength and direction of induced selection)
- Phenotypic Plasticity
- Genetic diversity and heritability
- Constraints (e.g. physiology, genetic, etc)

Because selection acts on phenotype, a core concept is that adaptation and persistence of a population depends on the diversity of phenotype expressed and exposed to selection. If environmental change is too fast, salmon may be unable to keep up at population level.

Phenotypic plasticity (i.e. the ability for an organism to change its phenotype in response to environmental signals) favours the persistence of populations to environmental fluctuations (Chevin et al., 2010). Under scenarios of unprecedented environmental change, both in terms of speed and magnitude, phenotypic plasticity may not suffice to ensure populations persist. Indeed, under low plasticity and high rates of environmental change a population may go extinct. But phenotypic plasticity mechanisms are themselves genetically determined. If genetic diversity is reduced, a population might not be able to express optimal phenotype under new environmental conditions. In worst case scenarios, plasticity could even be detrimental to population persistence. Plasticity mechanisms genetically selected to be adapted to a certain regime of environmental fluctuations may become maladapted if the regime changes. Phenotypic plasticity may also dampen the effects of natural selection, an undesirable property when the environment is changing directionally and fast.

Studies on long-term changes in key attributes such as length, mass, and migration phenology in Atlantic salmon from rivers in three areas of France (Bal et al., 2017), suggested a response to common environmental drivers jointly affecting the marine phase of the life cycle of different populations spawning in distant rivers. This may suggest the evolution of a maturation reaction norm in response to environmental covariation in growth and mortality. It appears likely that an evolutionary trade-off is at work, where maturing earlier increases cohort survival up to reproduction, while maturing late increases fecundity (Marty *et al*., 2011).

One of the emerging hypotheses was that changes in large-scale climate conditions in the Northwest Atlantic have apparently caused a *"phase shift"* in ecosystem productivity, altering trophic pathways that influence growth, survival and abundance of many species. For example, along the coast of West Greenland, lower quality boreo-Atlantic squid were nearly absent from historical data, but have become of moderate importance in contemporary samples, while higher quality capelin (the regional keystone forage species) have decreased in importance (Renkawitz *et al.*, 2015). It is observed that energy density (i.e. kJ/g/wet weight) has declined over this period (Figure 7); with for example mean energy density estimates of capelin having decreased by approximately 34%. It may therefore be helpful to consider the impact on growth, maturity, and mortality of a reduction in the abundance and also the quality of key forage species in energetic terms.

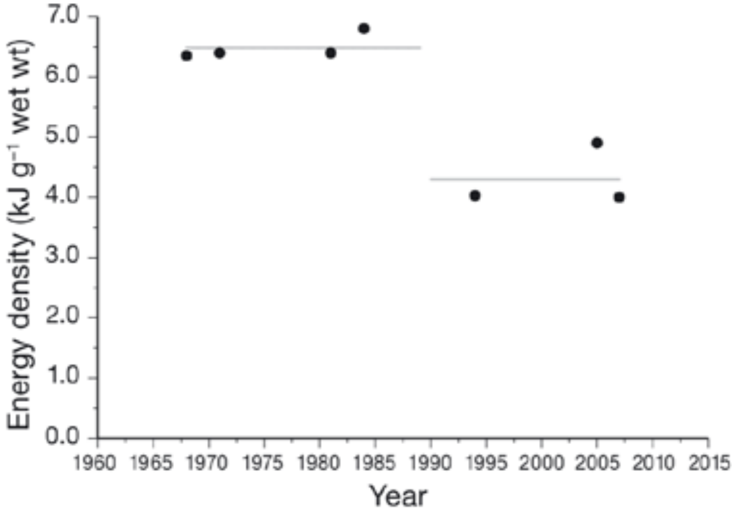


Figure 7: Energy density of capelin sampled at West Greenland (illustration from Renkawitz et al., 2015).

Based on Dynamic Energetic Budget theory, the K-rule (Martin *et al.*, 2017) shows that energy assimilated from feeding is partitioned, being allocated between maintenance, growth and storage/reproduction (Figure 8).

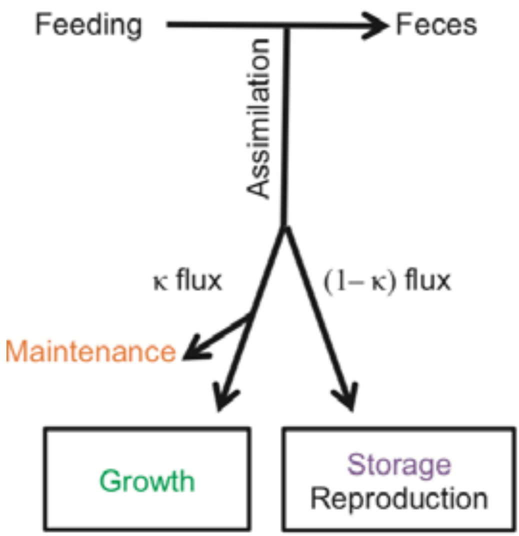


Figure 8: Simplified diagram showing allocation pathways of energy assimilated from feeding (illustration from Martin et al., 2017)).

Allocation is not random, as "k" fraction of assimilated energy is allocated to pay maintenance costs first and then any surplus is allocated to growth. The remainder ("1-k") is allocated to accumulating storage lipids (in juveniles) and later to reproduction (adults). Maturation is triggered when an energetic threshold is surpassed and then individuals decrease investment in growth and invest energy in reproduction (Martin et al., 2017). However, because there is individual variation for the threshold of maturation, some have to accumulate more energy (and stay longer at sea) before eventually initiating maturation.

The pattern of energy allocation is not constant and varies with age; notably in salmon species it undergoes a major shift associated with transition from freshwater to marine life. For example Martin *et al*. (2017) have shown that in Chinook salmon growth is prioritised over lipid storage after the initial transition to the marine environment. They hypothesise this is an adaptation to reduce predation risk in the ocean. However, when the feeding rate at sea declines, there is a decreased investment in growth and assimilation and relatively increased investment in storage. Hence environmental variability drives trade-offs between growth and age at maturity.

There is therefore a potential dependency between total resource acquisition and resource allocation (Descamps *et al*., 2016), implying that when feeding conditions (resources) decline there is a change in energy allocation strategy with consequent impacts on growth, maturation and mortality. In general, when growth is fast salmon mature early, while if growth is poor they mature later and remain at sea longer.

In accordance with this hypothesis, Sydeman *et al.* (2015), in a review of climate change and marine vertebrates, suggested that the interplay of metabolism and ecosystem productivity appears key to predicting future effects on marine vertebrates. In particular, they illustrate that intrinsic properties of individuals, populations, species and communities, together with the extrinsic properties of the environments they inhabit, shape their exposure and sensitivity to climate change.

Could loss of genetic adaptation due to rapidly changing environmental conditions be a candidate mortality factor?

Information on investigating the demogenetic responses of Atlantic salmon populations to climate change was presented to the workshop. It is impossible to conduct experiments *in natura* on responses to climate change scenarios at the population or larger scale; *in silico* investigations using virtual populations is the only alternative for prospective studies. IBASAM, an Individual Based Atlantic Salmon Model (http://ibasam.github.io/IBASAM/), was developed to simulate the eco-genetic dynamics of S. salar populations in southern Europe (Piou and Prévost, 2012) and explore the consequences of climate change scenarios (Figure 9).

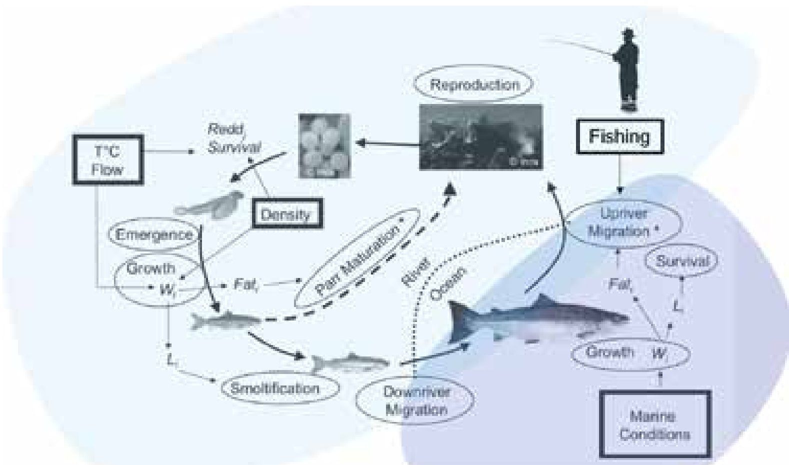


Figure 9: Schematic of an Individual Based Atlantic Salmon model (IBASAM), that allows simulation of the response of salmon to climate change scenarios.

The model allows investigation of population response (demography) to climate change scenarios, taking account of inter-individual variability (raw material for selection), individual phenotypic response to environmental change (phenotypic plasticity) and mechanisms of transmission of individual traits (allowing genetic adaptation). The model takes a mechanistic approach; growth is influenced by variation in environmental conditions in freshwater and at sea, while survival at sea is size dependent and age at maturation depends on energy allocation (fat), an individual threshold for maturation. Both growth and maturation thresholds are genetically determined. The model was parameterised using data from the River Scorff in Brittany (an ICES index river) and validated using field observations that showed close concordance with field observations on size of parr, smolts, adults, age at maturity and numbers of fish in the population at various life stages.

Illustrative results from simulations were shown based on population parameters from the R. Scorff and run for 50 years with a temperature rise of 3oC, river flow amplitude increasing by 25% and oceanic growth conditions decreasing by 25%. The outcome was that the changed flow regime and oceanic growth conditions had a greater influence than river temperature on population persistence. An increase in river flow amplitude of 25% and decrease in oceanic growth conditions by 25% produced a probability of extinction over 50 years of P=0.19 i.e. 19% (Piou and Prévost 2012). Note these simulations were obtained with the first version of IBASAM that did not include genetic heritability of growth.

The authors acknowledge that the IBASAM model as described is evolving and more detailed mechanisms could be developed. For example, there is only one parameter for describing effects of climate change at sea (i.e. ocean growth conditions) and the genetic architecture for age at maturation seems too simplistic (Barson *et al*., 2015). It is seen as a tool for research, allowing testing of environmental conditions never observed but which might be experienced in the future. IBASAM also has a role as a decision support tool, identifying the relative importance of the different potential stressors, including selective fisheries (see next section), to inform management strategies to reduce the probability of extinction (Piou *et al.*, 2015).

A further point is illustrated by Figure 10 (taken from Piou and Prévost, 2013) and is that climate change impacts on salmon populations are likely to be spread over several parts of the life cycle, with responses to changes in river growth, growth at sea and hence overall cohort survival having cumulative and confounding effects on population persistence.

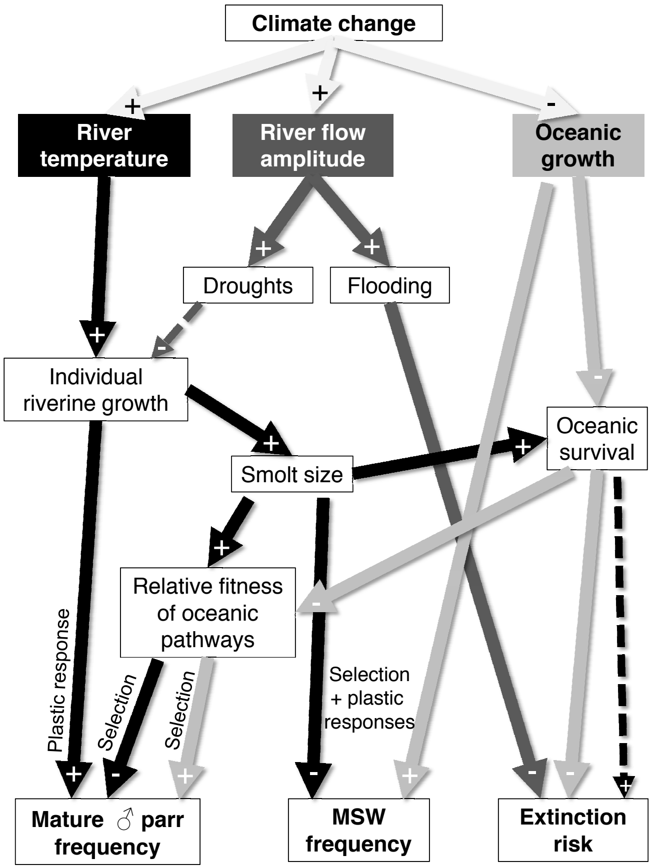


Figure 10: How climate change may cause pressures spread over several parts of the Atlantic salmon life cycle, resulting in complex and cumulative responses.

Considering fisheries-induced evolution

Having considered climate change impacts, we also need to ask should fisheries-induced evolution also be considered in this context of the Likely Suspects Framework, as it has the potential to influence life history characteristics, such as maturation tempo, which in turn may impact cumulative mortality at sea?

Barston *et al.* (2015) have shown that sex dependent dominance at a single gene locus maintains variation in age at maturity in salmon, with two different alleles one for early maturation (E) and one for later maturation (L). These alleles are closely linked to lipid storage, thus genotype influences allocation of energy. Genotype at this locus explains almost 40% of the variation in age at maturity. The ability of a population to maintain variation in age at maturity (an evolutionary advantage) therefore depends on selective processes maintaining genetic polymorphism (multiple alleles) in the gene pool of that population (Barston *et al*., 2015).

However, simulations over 300 year timescales conducted by Kuparinen and Hutchings (2017) show that the genetic architecture of age at maturity can generate divergent and disruptive harvest-induced evolution. This means that the evolutionary outcome of a specific harvesting strategy can be highly uncertain. Other simulations carried out by Piou *et al.* (2015) on the interactive effects of selective fishing and environmental change on Atlantic salmon demo-genetics (using IBASAM), showed that increased fishing pressure on MSW fish resulted in an evolutionary effect, in the form of a lower maturation threshold for females, resulting in an increase in the proportion of 1SW fish. The authors concluded that fishing strategies targeting MSW fish were likely to worsen the effects of oceanic environmental change that would lower growth at sea.

How can we take account of mortality due to environmental/ecosystem change?

The workshop considered how to account for adaptation/change in response to changing environmental/ecosystem conditions in the Likely Suspects Framework.

The workshop evaluated whether the IBASAM could be used to identify key domains in the Likely Suspects Framework. An approach to achieve this would be to consider how we can identify key domains based on how salmon allocate energy and how this varies as the environment changes. In a period when salmon have to adapt to rapid environmental change, this approach might point to where key domains exist where the ability of salmon to adapt (plasticity) becomes critical. For example the beginning of the marine phase appears to be significant in terms of marking a major change in energy investment (as noted above) and therefore this could be a very important domain in the Likely Suspects Framework.

IBASAM as described to the workshop is not predictive, but may be used for scenario testing (prospective). Scenario modelling of changing marine conditions (including feeding and energetics) at or near the freshwater-marine transition phase could be used to test hypotheses in terms of the consequences on subsequent growth, maturation and survival. In testing the effects of the underlying mechanisms, it would be possible to use long term datasets from index rivers on size, returns sex ratio etc. to confront and verify model outputs. Additional information would be required on productivity at sea, food history reconstruction (e.g. otoliths) and analysis of fish growth at sea (scales). Indeed, it would be valuable to investigate (sample) energy density variation in space and time in the marine phase of the life cycle.

One of the major limitations of sampling programmes for salmon is that we tend to see only the fish that survive, therefore survivor bias is nearly always present and we can only infer what may have happened to the fish that died. In the near absence of fisheries at sea, we need renewed salmon sampling at key periods at sea; as we need to see a mixture of potential survivors at the same time as potential mortalities.

Hence, a research theme was proposed to investigate the energetic changes (energy density variation) needed to explain the changes in growth and maturation profiles that we are seeing. In broad terms, can we correlate energy density variation in salmon to potential environmental drivers? This is a different type of approach to accounting for salmon losses at sea:

- What are the drivers determining energy in salmon prey items (temperature, primary productivity etc) and can we measure those drivers?
- Can we take account of what degree of shortage of energy in the ecosystem is sufficient to impact Atlantic salmon?
- In taking an *"energetics of the ocean"* approach, can we model the differences in energetic balance/allocation of those salmon that die at sea compared to these that survive?

A specific example might be researching the partitioning of the energy budget in salmon at sea during critical phases where many stocks coalesce (e.g. W. Greenland). This would imply a targeted at-sea sampling programme involving salmon as well as key prey species and environmental parameters.

Two complementary approaches can be considered:

a. Explore the potential influence of ocean productivity shifts (energy density changes) on resource allocation strategies and life history traits by exploring how patterns of covariation match with some theoretical mechanistic hypotheses.

b. Explore the evolutionary and demographic consequences of such patterns using IBASAM. The latter approach might require gathering data on spatio-temporal trends in resources (prey energy density) and energy density content of salmon; 1SW vs. 2SW.

The workshop noted that the above approach requires much greater links with pelagic surveys, in order to maximise information of relevance to salmon research, perhaps to the extent of designing modifications (or additions) to methods and or coverage of existing international marine surveys or even contemplating some new targeted at-sea surveys.

Evaluating the potential to move from a high level conceptual framework to incorporate a number of modelling approaches to help further assess the various mortality factors

Key Questions

- *How can a high level conceptual framework, such as the Likely Suspects Framework be used?*
- *How can a conceptual framework be further developed into a conceptual model or models?*
- *How can this be applied to Atlantic salmon?*

How can a high level conceptual framework, such as the Likely Suspects Framework be used?

The Likely Suspects Framework shares some of the characteristics of conceptual frameworks developed in the Pacific area. The workshop suggested the Framework could be further developed along those lines to help identify and prioritise research. Changes in growth at sea and age at maturation of salmon are most probably responses to underlying changes in oceanic and ecosystem conditions. Therefore any such conceptual framework should include the main ecosystem components, typically; physical environment, primary production, forage and predator species and competitors. It would be of benefit to include the management drivers applicable at various scales, from river to ocean, not least to show how management drivers operate at different scales within the overall marine ecosystem. Notably, climate change is a key management driver because of its overarching scale of cause and effect.

A North American example was presented to the workshop (Figure 11), where a conceptual framework was developed to help define salmon research on the Pacific west coast. The framework is arranged in layers, specifically:

- How is the ecosystem structured,
- What is the effect on salmon, and
- What are the different levels of management drivers?

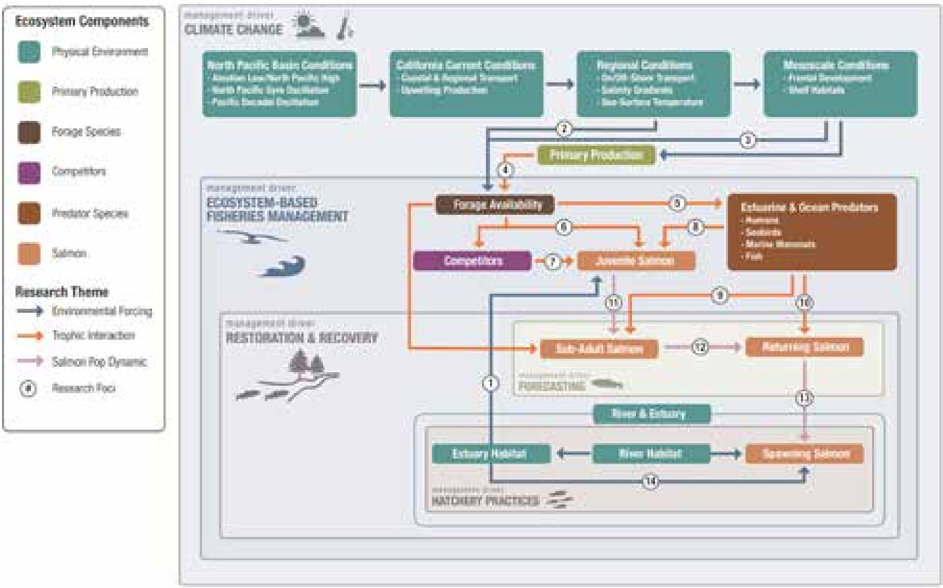


Figure 11: Example of a conceptual framework used to define a salmon research programme on the Pacific coast of N. America.

The arrowed lines in the above example include broad scale environmental forcing, trophic interactions between ecosystem components at local, coastal and oceanic scales, and population dynamics through the various life stages of salmon (juveniles in the river/ estuary, sub-adults at sea and returning adult salmon). These directional linkages represent research themes, while numbered circles are research foci, which prompt a series of specific research questions. Four of the numbered themes are shown below as examples:

2. *How does transport affect regional forage species on the shelf? How do freshwater plumes and upwelling fronts aggregate or diffuse forage species? Is there a strong, direct effect of SST on salmon growth and survival?*
5. *For salmon predators what are the main alternative prey species? When unavailable, how does that affect predation of salmon? Do predators change foraging behaviour under different forage assemblages?*
8. *Which species are salmon predators and what is their abundance and distribution? How do salmon migration timing, abundance and size alter predation rates?*
12. *What demographic rates relate to maturation? How do the environment, forage base and early growth history interact to affect maturation?*

The workshop agreed that it should be possible with some further analysis to refine the draft Atlantic salmon Likely Suspects Conceptual Framework using information already available, as well as expert opinion, to identify the main domains, pressures and response variables. This would take the Framework to a stage similar to the example above. Suggested steps were as follows:

- Using mainly data from ICES Index rivers, conduct covariance analysis on marine survival and abundance across the range of Atlantic salmon, looking for trends in similarities and differences at various scales, in order to refine the Likely Suspects Framework and **to identify the key domains/areas of interest**, particularly those where mortality is thought to be high and those where many stocks coalesce.
- **First attempts can be made at identifying the appropriate mechanistic relationships/ linkages, as this will point to gaps and suggest exploratory projects.** Bear in mind the different scales of effects when doing this.
- At the same time, **review and develop hypotheses that will be tested in the further phases**, prioritising those relating to functional links between pressures and response variables.

How can a conceptual framework be further developed into a conceptual model or models?

Given a revised conceptual framework, with ecosystem domains chosen, candidate mortality factors provisionally mapped to these and a series of hypotheses in place, the next development phase would focus on particular domains. It would attempt to quantify mortality where possible and also begin to examine the underlying mechanistic relationships between the pressures and response variables and how responses influence salmon mortality.

Isolating both the primary and contributing mortality factors (the causes) and the mechanisms by which they operate is important. However, synergistic and cumulative effects are bound to be occurring and it will be impossible to answer all the questions about what is driving survival. In approaching this, it is perhaps just as important to pose a different question *"what can you do about it"?* Therefore, **concentrate effort on those that are associated with large-scale pressures affecting many stocks, but also those where research outcomes can underpin management actions.**

It was agreed that for progress in this direction a multi-disciplinary approach is vitally important, as will be necessary to try to develop a deeper understanding of key overall ecosystem components and how these link with salmon survival and mortality rates.

An example of how this might evolve is given below (Figure 12), where a conceptual ecosystem model of Chinook salmon recruitment is being developed (Wells et al., 2016). The example relates to the California coastal current and impacts of upwelling on ecosystem components where migrating Chinook salmon enter from neighbouring coastal rivers.

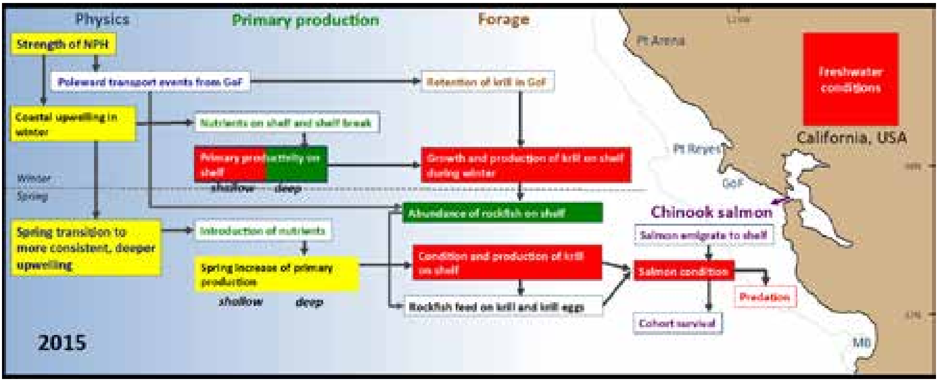


Figure 12: A conceptual model of Chinook salmon recruitment relating to the California current.

This model framework incorporates the main boxes or domains representing locations and times where significant interactions between salmon and ecosystem components take place. For example, coastal upwelling influences nutrient availability and hence primary production. In turn this links to secondary production and availability of forage species, which in turn impacts on Chinook salmon growth and condition on the coastal shelf. The boxes are colour coded to reflect an annual assessment (2015 in this example) of whether conditions have changed (green =positive, red=negative, yellow= average). Where possible the boxes and the current status are based on ecosystem indictors for forage items. For example salmon time series of abundance, biological characteristics (such as growth and condition) and insight into the functional relationships linking them.

Clearly, this conceptual ecosystem model cannot be fully paramaterised from the start, and will take some years to finalise, but it reflects part evidence base and part guesstimated structure sitting in the middle of an end to end ecosystem model. The approach is to start anyway and build as information on functional relationships becomes available (this is where the targeting and prioritising of research becomes important). In taking this approach it is necessary to recognise the gaps and the weaknesses and work to fill in the unknowns, at least initially including use of simulations to fill in the gaps in empirical data.

It is important to decide on the purpose of developing such a conceptual model; is it for researchers to help understand ecosystem processes, or is it output driven to support management? The probable answer is both, but a balance must be struck. It is not of itself a management framework, but rather a decision support tool, providing guidance but not advice. It does not tell you what to do, but says *"here are the green lights and the red lights; do what you feel needs to be done"*. The key output is in seeing enough of the picture from the conceptual model of what is happening to the salmon and why, thus allowing managers to consider their options. This approach is a very powerful tool to present to regional management organisations and to commissions or enquires set up in response to concerns about salmon stocks.

Managers need to be convinced that the ocean matters! Freshwater practices affect the contribution of the juvenile salmon to the ocean and managers need to understand ocean systems to make sense of the impact of freshwater decisions. One of the main benefits therefore in the management context of developing conceptual frameworks is that they emphasise the importance of functional linkages through the ecosystem. For example under conditions of poor ocean productivity, local mortality factors (such as local shifts in predator abundance or behaviour) may suddenly become of crucial importance, and managers need to know that.

A synthesis of hypothesis-driven research on predation on Chinook salmon in the California Current system presented at the Workshop illustrated the value of the approach being suggested for Atlantic salmon. A conceptual framework was first established defining key ecosystem domains, with research questions and hypotheses driving specific research to populate the key pathways with data and simulations. Predators were a major focus of this series of studies (seabirds, fish and mammals). The conclusions reached serve to illustrate the complexity of interactions in the marine ecosystem, but also show it is possible via carefully targeted research to meaningfully account for variation in salmon success at sea. In this particular case the key conclusions were:

- Bottom-up dynamics lead to top down impacts on Chinook salmon from fishes, seabirds and mammals.
- The mechanism is related to differential foraging behavior between good and bad productivity years.
- Specifically, incidental or directed predation on salmon may increase during poor productivity years and this impact will relate to the availably of alternative prey.
- The impact on returns of salmon can be significant.

Building a conceptual model providing insight into key factors and ecosystem relationships driving salmon abundance variation can be envisaged at different scales. The Pacific example cited above refers to the scale of the California Coastal Current and adjacent coastal Chinook salmon stocks, however applying this approach to a much wider supra-regional scale (say southern European Atlantic salmon stock complex) would present significant additional challenges. There will be ecosystem domains where mortality factors impact many stocks, while others where only a few stocks or even a single stock are impacted.

We cannot represent all of this in a single ecosystem conceptual model framework right at the start, so must develop our approach based on what is known (or thought to be the case) about the ecosystem. When taking a broad scale approach, a simple structure encompassing the main hypothesised drivers of salmon mortality may be possible.

Development should initially concentrate on those domains and processes that are thought likely to be most important influencers of salmon survival; analogous to a triage approach. What are the *"most likely"* of the likely suspects? This is where the hypotheses are a critical first step. This triage process should be discussed with managers, as it would be important to agree the main areas of interest. Probably these core areas fall into a relatively few categories of cause and effect, such as below:

- Indirect impacts:
  - o Changing ocean- primary production?
  - o Prey distribution, abundance and energetic content?
- Direct mortality impacts:
  - o Predator abundance and distribution (seabirds/mammals)
  - o Commercial directed salmon fisheries (much reduced now).
  - o By-catch in pelagic fisheries
- Main hypothesis for underlying mechanism:
  - o Food availability impacts salmon growth and energetic storage, leads to change in maturation tempo and hence survival at sea.

In an example of what can be resolved through broad scale analyses, Wells et al., (2008) analysed over 20 years of biological and physical data from the North East Pacific and were able to resolve the spatial scales of oceanic conditions affecting growth across much of the species range of Chinook salmon. Scale growth increment data from returning fish was used in path analysis and partial least squares regression to quantify the relationships between growth and regional and large scale oceanic conditions (sea level height, sea surface temperature, upwelling etc.).

Similarly, DFO Canada reported comparative studies of changes in salmon population attributes (e.g. total returns, survival rates) or traits (e. g. size, age at return) along environmental gradients within Canada's Pacific region. This Salmon Indicators Research Approach was developed under the Salmon in Regional Ecosystems Program (SIRE-P). Comparing and contrasting a network of time series indicators for <20 out of >260 populations spanning >10 degrees of latitude showed covariance at coarse scale, with northern and southern populations showing different tends in return pattern (Hyatt et al., 2017). This initially simple approach supported further development and application of biophysical forcing models to account for environmentally induced changes in salmon distribution, abundance and survival. This allowed testing of speculative hypotheses such as operation of coast-wide vs. sub-regional factors. The main steps in this were:

- Step 1: Scan populations for similar vs. contrasting patterns by eco-region.
  - In this case Alaska down welling domain and the California Current upwelling domain.
- Step 2: Identify environmental factors associated with variations in salmon numbers (or even between stage-specific survivals) to partition freshwater vs. marine effects.
  - These include NOAA forecast SST anomalies and winter effects of El Niño events on temperature and precipitation. For example, in the California Current domain, sub-average and above-average survival variations exhibited by Okanagan Sockeye are anticipated by El Niño and La Niña events at the time of sea entry.
- Step 3: Build and test models (statistical, food web processes, life history processes) and use time series to test hypotheses for consistent prediction outcomes.

For example, Figure 13 shows the schema of a two-state, production model (cold ocean vs. warm ocean), reflecting Pacific Decadal Oscillation (PDO)- El Niño/Southern Oscillation (ENSO) induced reorganisation of biophysical properties of the Northern California Current System into which Okanagan and Barkley Sound Sockeye salmon enter (Hyatt *et al*., 1989).

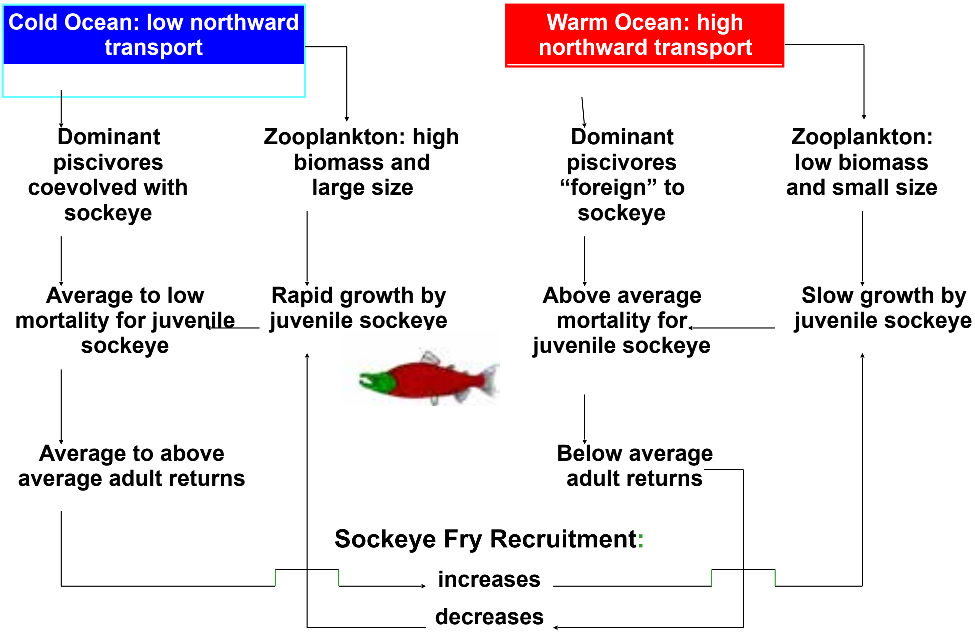


Figure 13: Schematic of a two-state, production-model (cold ocean vs. warm ocean), reflecting biophysical properties of the Northern California Current System.

This type of process supports creation and verification of statistically sound biophysically meaningful models, providing better insight into the causes and geographic origins of production variations; therefore narrowing down the suspects into a list of the most likely suspects.

The benefits of conceptual models have been usefully summarised by Harvey and Garfield (2017) as follows:

- They put indicators into context; each box or line corresponds to one or more indicators.
- They facilitate discussion around which issues are thought to be most important in the ecosystem.
- They can be readily simplified or made more in-depth and complex as desired.
- Relating the focal component (e.g. salmon or ground fish) to its linked components and processes may help us anticipate how changes in the ecosystem will affect managed species.
- Conceptual models with up-to-date information on status and trends of relevant indicators could provide information for “ecosystem considerations” sections of stock assessments. [Note: this is directly relevant to the annual ICES Atlantic salmon stock assessments]
- They serve as consistent reminders to account for human dimensions and potential management tradeoffs in different human sectors.

How can this be applied to Atlantic salmon?

In terms of building such a conceptual ecosystem model for Atlantic salmon, the message from the Pacific experience is to start with one or two domains, even with only one or two environmental driver correlations and functional relationships boxes and subsequently expand the model.

The key message is to restrict this to a few domains we suspect are important and about which something is known or can be hypothesised. The workshop suggested that a productive start might be to concentrate on domains representing the early phase of marine life (say first 2 months after sea entry) and on study of the functional relationships between energetics of the forage species and the partitioning of the energy budget in salmon at sea at overwintering feeing areas at west Greenland. The outcomes of this work would slot into the overarching conceptual framework and would encourage further research to fill in the gaps at other domains.

The underlying challenge is how to go from nothing to something; from data free conceptual framework to data informed model? To start with, simple structured equation models can be contemplated, for example taking a bottom up approach. What does the system look like; fill in for oceanography first? A sequential approach can be adopted to fill in the functional relationships as information becomes available.

It was felt that data on marine environmental drivers are initially more likely to be readily available than data on for example predators on salmon in the Atlantic; this implies that a bottom-up approach to modelling is likely to produce earlier gains than a top-down approach. In some cases, marine environmental indicator time series may provide proxies for variability in lower trophic levels where for example comprehensive data on salmon prey trends are not available.

It was noted that simulations could be used to fill in the gaps inherent in the spatial and temporal restrictions of empirical data. Their use together gives great emergent capability to build hypotheses and test scenarios.

There will be scalability issues…. some areas are particularly challenging; especially where stocks pass through many spatially defined marine ecosystems. Local vs broad forcing is hard to put in a simple model. However, co-variation analysis layered with hypotheses is a great tool in these situations. We must retain an oceanic scale aspect in the Likely Suspects Framework and must still try to account for the unaccounted for mortality while the work on the chosen domains continues to evolve.

It was not immediately clear if ICES or other databases are organised in such a way as to support access both to metadata and time series data that can be used in researching functional links between diverse ecosystem components such as fish, birds and mammals. This may pose a challenge as well as bringing an opportunity for ICES to consider the extent to which their various databases can support this work and where the gaps in data and/or capability lie. The workshop noted that:

- The conceptual ecosystem modelling approach being suggested for Atlantic salmon is very closely aligned with understanding the underlying drivers for th changes in status of Atlantic salmon assessed by ICES.
- Development would depend largely on data on salmon and other ecosystem components, some of which may be available within ICES databases.
- The purpose of such a framework would be to develop a decision support tool that would be of benefit to NASCO as well as national and local managers.
- ICES has a strong focus on ecosystem approaches to their fish stock assessments, and an Atlantic salmon ecosystem modelling framework could provide information for the “ecosystem considerations” sections of stock assessments.

Such a programme, applied to Atlantic salmon, would be intended in the medium term to evolve the Likely Suspects Framework from a conceptual basis towards building an ecosystem modelling framework and decision support tool. This will enhance understanding of ecosystem processes and impacts of climate change on Atlantic salmon and in turn feed into refinement of predictive models used to develop management advice.

It is noted that typically such an ecosystem modeling framework is not a single model itself, but rather consists of sub-models, each addressing particular areas of interest, but fully coupled together. The example on Chinook salmon cited above consists of an ocean circulation sub-model (ROMS, Shchepetkin and McWilliams, 2005), a biogeochemical sub model and an individual based sub model for salmon. This allows simulation and testing of hypothesis on the mechanistic relationships between ecosystem parameters. Fiechter *et al.* (2015) describe how this model framework was used to determine if model simulations could be used to identify favourable or unfavourable growth conditions for juvenile salmon and relate them to potential environmental drivers affecting salmon feeding success.

The workshop also discussed the Atlantis ecosystem model; for description see: https://www.nwfsc.noaa.gov/research/divisions/cb/documents/atlantis_ecosystem_model.pdf Atlantis is a flexible modular modelling framework capable of running simulations of whole ecosystem dynamics and serves as a decision support tool for ecosystem based management. Sub-models represent ecosystem dynamics, covering biophysical (food web, biogeochemistry, habitat), oceanography and human activities. The user can chose the level of complexity for the simulations, ranging from simple trophic interactions to extensive runs with complicated stock structure, detailed economics and multiple management actions. A consequence of the flexibility and complexity is that Atlantis is parameter-intensive and fine scale spatial resolution is not possible. Characteristically achieving whole ecosystem capability involves tradeoffs; in Atlantis the ocean part is handed coarsely and the freshwater portion greatly simplified. The workshop felt that the tradeoffs involved in trying to use that Atlantis type approach for Atlantic salmon was unlikely to yield significant (or early) gains over the more salmon-focused approach outlined earlier in this chapter.

An integrated ecosystem assessment (IEA) approach (where it is the state of the regional ecosystem that is being assessed annually rather than focus directed on salmon) is a much longer-term goal (>5 years), but depends on much wider availability of data on ecosystem components and evidence of functional relationships between those components. For examples, see Chandler et al. (2017) for an assessment of the state of the physical, biological and selected fishery resources of Pacific Canadian marine ecosystems, while the California Current Integrated Ecosystem Assessment (CCIEA) status report 2017 is available at:

https://www.integratedecosystemassessment.noaa.gov/Assets/iea/california/Report/pdf/2017-iea-main-report.pdf

Opportunities for interfacing the Likely Suspects Framework with the life cycle catch advice model being developed for ICES

Key Questions

- *What is the life cycle catch advice model being developed for ICES?*
- *Are their opportunities for interfacing the Likely Suspects Framework with the life cycle model?*

What is the life cycle catch advice model being developed for ICES?

A life cycle modelling approach is being applied to improve on the methods currently used by ICES (ICES, 2017a) to estimate abundance of post smolts at sea before fisheries take place (Pre-Fishery abundance; PFA) and to forecast the impact of various catch options at sea on the returns of salmon to Europe and N. America (Rago et al., 1993; Potter *et al.*, 2004). The life cycle approach also provides a framework to examine the drivers and mechanisms of change on Atlantic salmon population dynamics and productivity in the N. Atlantic. This approach is intended to address limitations of the present ICES catch advice process, where three different models are run for the three stock assessment complexes (nNEAC, sNEAC, NA) and where some core demographics are not explicitly stated and not harmonised across these groups. The existing approach does not support collective analysis of the population dynamics across stock units and precludes identification of the drivers and mechanisms of response of Atlantic salmon to ecosystem changes.

Researchers have been developing a model framework (Figure 14) that embeds stock assessment and forecasting in a single age and stage-based life cycle model within a probabilistic Bayesian rationale (Massiot-Granier *et al.*, 2014; Olmos *et al*., 2017).

The principles of the modelling strategy are that salmon are impacted by multiple factors that operate at various life stages and in a hierarchy of scales. The premise is that aggregation of data at the scale of large groups of populations will diminish sample noise, but still allow separation out of the effects of natural mortality vs fishing mortality at sea. The scales involved maximise the environmental gradient; while the geography of covariation allows analyses of correlation in a hierarchy of spatial scales and helps identify key factors impacting populations locally vs. factors susceptible to simultaneously impact large groups of populations.

The model is an age and stage based life cycle model developed within a data-driven state-space framework designed to reconstruct past variations in abundance at sea and marine productivity. It is built on data aggregated at the scale of groups of populations (stock units). The model is fitted to data collated by ICES WGNAS for (presently 13) stock units in European and North American continental groupings, using time series from 1971 to present and provides forecasts for three years ahead.

The model considers the variability of life histories, including river age distributions of outgoing smolts, sea age of returns and egg production per sea age group. It models covariation in the dynamics of the populations that share migration routes and feeding areas at sea and are harvested at mixed stock fisheries, particularly at West Greenland. This approach allows disentanglement of the effects of fisheries from those of environmental and ecological factors at a hierarchy of spatial scales. Inputs comprise adult returns to homewaters, homewater catches, sex ratio and egg yield per female by sea age, egg to smolt survival, proportion of smolt ages and catches in mixed stock fisheries (which get allocated among the stock units).

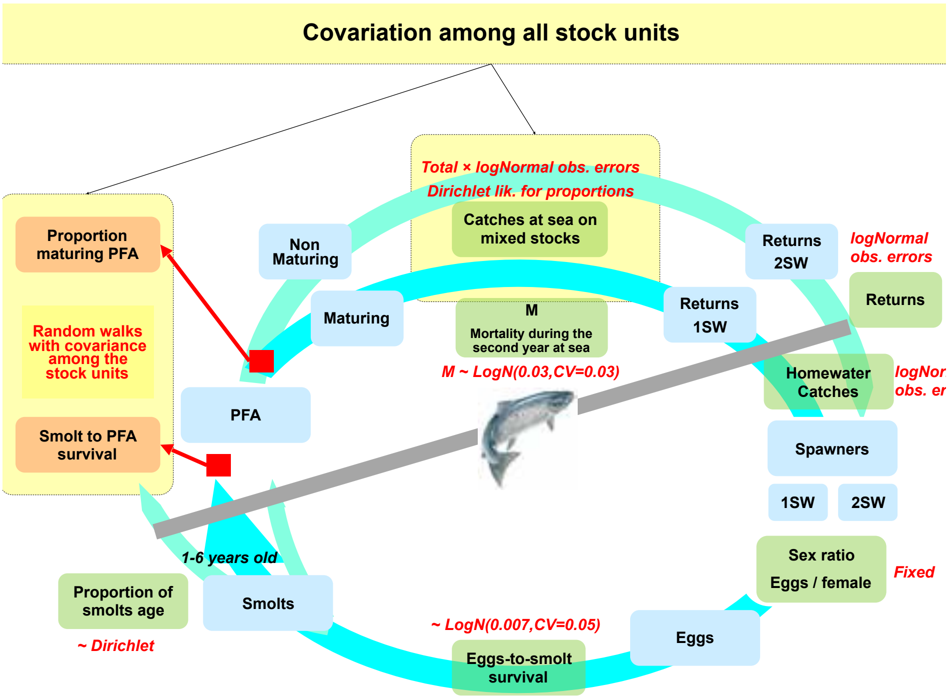


Figure 14: Model framework being developed to provide catch advice for Atlantic salmon which embeds stock assessment and forecasting in a life cycle model within a probabilistic Bayesian rationale

The model estimates the trends for each stock unit in marine productivity (post-smolt survival rate to January 1st of the first winter at sea = PFA stage) and the proportion maturing as 1SW. These parameters form the basis for forecasting homewater returns, conditional on catch options for the mixed stock sea fisheries.

The outputs also allow collective analysis of trends in the population dynamics among the stock units, uncovering common temporal trends in both the post-smolt survivals and proportion of the fish that mature after one year at sea (Olmos *et al.*, 2017). These include a decline in marine survival, and a decline in the proportion of late maturing fish (sight increases recently). However, there are differences among continental stock groupings and among stock units (Friedland *et al.*, 2014) and correlations are higher between stock units within similar migration routes.

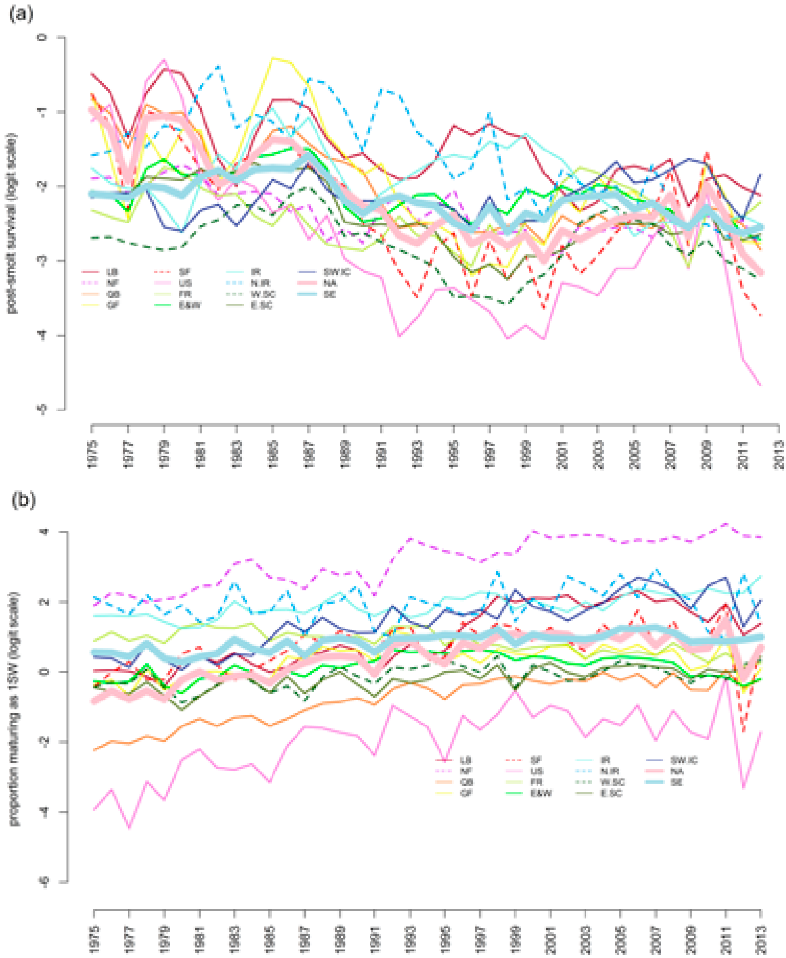


Figure 15: Outputs from the Bayesian life cycle model being developed for Atlantic salmon, showing (a) temporal trends in post-smolt to PFA survival and (b) proportion of the fish that mature after one year at sea.

Examination of model outputs lends support to the hypothesis of a synchronous response to large-scale ecosystem changes in the N. Atlantic during the last three decades with simultaneous impacts on distant origin populations during their marine migrations and/or at their common marine feeding grounds (ICES, 2017a). Results suggest a response of populations to changes in the N. Atlantic ecosystem involving a bottom up mechanism with a decline in trophic conditions. (Beaugrand and Reid, 2012, Mills *et al*., 2013).

The model framework as presently formulated has some limitations. The data sources are heterogeneous. The model uses estimates of the number of salmon returning to homewater in each stock unit that are derived from data compiled at the scale of each stock unit (i.e. typically the total catches raised by estimates of harvest rates). Other data (i.e. sex ratio, fecundity) are derived from river index and extrapolated at the scale of stock units. Also the data are only available for particular model nodes. Demographics are coarsely represented and some parameters are presently fixed; such as natural mortality (M) in the second year of sea life, also smolt output is estimated by assuming a fixed egg to smolt survival rate of 0.7%.

Available data on monitored rivers could be used to provide better information on egg to smolt survival rate dynamics, including parameterisation of density dependent survival rates and variability among stock units. ICES is also encouraging improvement of a number of input data streams, including new stock origin data on the composition of mixed stock fisheries. The nNEAC stock units are presently not included due to that data time series being 12 years shorter than the others, however, extension to include nNEAC is currently under development.

The purpose of the workshop reviewing this model framework is to determine whether there is potential for interfacing the Bayesian life cycle model, with the Likely Suspects Framework. This is considered further below.

Are their opportunities for interfacing the Likely Suspects Framework with the life cycle model being developed for ICES?

The advantages noted for the Bayesian hierarchical framework approach are that it is an open and expandable framework. Additional data can be assimilated in order to refine demographics, such as density dependence in the freshwater phase. It can also be used to test hypotheses on mechanisms of drivers of change. It is therefore worth exploring whether the life cycle model can be used to support the evolution of the Likely Suspects Framework from a conceptual framework to an ecological model framework, as envisaged in a previous chapter.

The workshop suggested the Bayesian life cycle model could be applied to test hypotheses generated by the Likely Suspects Framework about where the fish are in space and time to further investigate what the likely mortality suspects are? There is a clear link between both approaches, in that inferences on time trends in smolts to PFA survival and the proportion of the PFA maturing as 1SW fish from the Bayesian model are conditioned by explicit hypotheses that can and should be challenged. In other words, the Bayesian model could be used for "what-if" scenario testing, quantifying the effects of various mortality factors individually or synergistically.

The life cycle model structure allows analysis of correlation in a hierarchy of spatial scales and helps identify key factors impacting populations locally vs. factors susceptible to simultaneously impact large groups of populations. The outputs will also allow collective analysis of trends in the population dynamics among the stock units, uncovering common temporal trends in both the post-smolt survivals and proportion of the fish that mature after one year at sea. These analyses would greatly support the further development of the Likely Suspects Framework towards an ecological model framework. Another possibility is to embed the life cycle model in the Likely Suspects Framework. Since some of the life cycle model nodes align well with some of the potential domains considered under the Likely Suspects Framework, the estimates of survival from smolt to PFA stage and proportion maturing that are outputs from the life cycle model could become inputs to populate key parts of the developing Likely Suspects Ecosystem Model Framework. This would be especially valuable as the life cycle model develops further along the lines described below.

One of the biggest challenges in understanding salmon marine survival lies in partitioning in time and space the mortality experienced during the marine phase, therefore the workshop explored how further partitioning of survival in the life cycle model could be investigated. Two main areas were considered:

- Partitioning the relative influence of freshwater vs. marine dynamics.
- Further partitioning of the marine mortality along the migration routes at sea.

Partitioning the relative influence of freshwater vs. marine dynamics

There are no data available on wild smolt production at the scale of the stock units used in the model, therefore egg to smolt survival is implicitly considered constant in time and homogeneous among the stock units. All variations (in time and among stock units) are therefore attributed to variations in marine survival.

It is considered that data from index rivers could be used to partition freshwater and marine phase mortality; typically using tag return data to estimate smolt to adult return rates and hence marine survival independent of the freshwater phase, while spawner to smolt data series could estimate egg to smolt survival (de Eyto *et al.*, 2014). For such rivers this would allow parameterisation of density dependent egg to smolt survival and therefore evaluation of the impact of this on estimated trends in marine survival. It was suggested that the model should also use marine survival data from hatchery reared fish at index rivers to test/control for wild fish marine survival variation, since these would not have been influenced by density-dependent variation in fresh water (at risk of introducing confounding effects of hatchery practices).

Massiot-Granier *et al.* (2014) considered the effects of density dependence on smolt production, noting that it will change estimates of trends in marine survival and will also change ecological inferences and forecasting. These changes will be different among stock units depending on parameterisation. In simulations on salmon rivers in Eastern Scotland they showed that density dependence in freshwater, being compensatory, will dampen temporal variations in egg abundance over the time series, this is turn dampening the decline in smolt to PFA survival (which ,however, still declines).

The workshop was told of plans to collate the index river data on stock and recruitment available from circa 20 rivers in the N. Atlantic to provide input parameters to upscale from individual river level to stock unit level. It is anticipated that a compensatory stock and recruit model will be fitted to the data series and density-dependent survival parameters will be scaled to a common scale such as wetted area. These parameters will be transported to other rivers lacking such data using covariates; probably latitude, since these parameters vary with latitude (Prévost et al., 2003). It has not yet been decided how to scale up the productivity from one index river in a stock unit to all the rivers, since this can be done either by adding together the surface areas to get a total and applying average S/R parameters, or instead use the sum of many rivers with different estimated parameters. The latter is more realistic but is more complex.

Further partitioning of marine mortality along the migration routes at sea

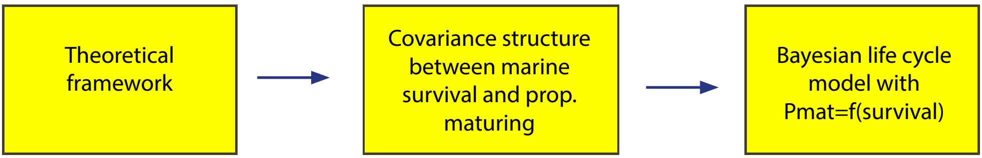
In the Bayesian modelling framework being developed for use at ICES, the marine survival rate after the PFA stage is treated as constant and homogeneous among all stock units. This means that all changes in the relative proportion of 1SW/2SW in returns are interpreted as changes in the proportion of fish maturing at the PFA stage, but could conceivably result from changes in marine survival after the PFA stage as well. This suggests that a priority in development of this Bayesian model approach should be further partitioning of the marine mortality during the marine phase.

One possibility currently being explored would involve combining a time series model approach with knowledge on marine migration routes to partition mortality at sea. Information from the literature could be used to identify windows in time/space where fish are (for example the April to September "early" marine period) and then assume after that they are elsewhere. This splits the first year at sea into a together period vs. a segregated period. It may be possible to construct a hierarchical model to partition global (synchronous) and specific (asynchronous) time trends in marine survival. A problem arises in identifying factors that impact locally vs factors that synchronise over broader scales, which requires identification of covariables in these space/time windows. In reality salmon do not "eat" SST (sea surface temperature), therefore more directly linked covariables such as primary production measurements would be targeted. While this would be valuable in understanding some aspects of early vs later first year survival at sea, it does not address the question of partitioning mortality during the first and second year at sea.

The maturity schedule methods (as outlined in an earlier chapter) offer a means of further examining mortality variation during the period after January 1st of the first sea winter, allowing estimation of total mortality rates during the first and second year at sea, based on information on abundance and sex ratios of out-migrating smolts and return rates for male and female 1SW and 1SW salmon. Some of the ICES index rivers would have biological data necessary for such analysis.

Another path to development could involve growth-mediated mechanisms to relate marine survival and proportion maturing. There is evidence from empirical and theoretical life histories that survival and maturation negatively co-vary; implying a growth mediated maturity and survival relationship. There are tradeoffs between the two and both are related to growth conditions during the first few months of post-smolt life at sea.

It is suggested therefore to interface a theoretical model framework with the Bayesian life cycle model in the manner shown below:



The theoretical framework would be used outside the life cycle model (i.e. relying on the individual based modelling approaches) to extract the covariance structure between marine survival and proportion maturing and correlate this pattern to proxies of trophic conditions at sea. The above-mentioned IBASAM or Dynamic Energy Budget modelling might be, among others, options for such preliminary pattern identification. The covariance structure could then link to and inform the Bayesian life cycle model. If marine survival before the PFA stage and proportion maturing are a *priori* strongly correlated, marine survival after the PFA stage could be better estimated.

A hemispherical perspective: Learning from each other

Key Questions

- *What are the parallels and contrasts between Atlantic and Pacific salmon?*
- *How can we improve dialogue at hemispherical scale?*
- *What is the potential for joint research activities involving Pacific and Atlantic salmon?*

What are the parallels and contrasts between Atlantic and Pacific salmon?

Significant benefits were realised from having joint Atlantic and Pacific representation at the workshop, in terms of sharing knowledge and techniques and in scoping the potential for future collaborative research. A particularly valuable experience was hearing about the status of salmon in both basins and comparing and contrasting our assessments of the underlying drivers for change in the salmosphere.

The workshop noted that there exist some similarities between the magnitude and timing of productivity dynamics of Atlantic salmon and some species in the Pacific that may not be coincidental. Declining survivals for Atlantic Salmon are similar to those of many populations of Coho *(Oncorhynchus kisutch)*, Sockeye *(Oncorhynchus nerka)*, Chinook *(Oncorhynchus tshawytscha)*, and even-year returning pink salmon *(Oncorhynchus gorbuscha)* and steelhead *(Oncorhynchus mykiss)* in the southern portion of their range of the eastern North Pacific, as well as Masu salmon *(Oncorhynchus masou)* in the western North Pacific. In contrast, most populations of chum and odd-year pink salmon are doing well.

At the same time, there are huge differences between Atlantic and Pacific in overall salmon abundance and temporal patterns. Numbers of maturing Atlantic Salmon declined from ~10 -> 3.5 x 106 million from the early 1970s to recent years while in the North Pacific, numbers increased from ~500 -> 750 x 106 during the same period (Ruggerone and Irvine, 2018).

It was clear from the workshop presentations and discussions that researching key mortality factors and the scales at which they operate in Pacific and Atlantic salmon populations will involve common approaches:

- We need to isolate the primary and contributing factors responsible for declines (and increases) in order to understand mechanistic linkages driving these changes.
- It is important to understand that survival drivers and outcomes can be similar among species/areas while mechanisms may differ.
- To understand linkages, research needs to be interdisciplinary. Ecologists, oceanographers and climate scientists must conceive of and investigate research avenues together.

- Testable hypotheses need to be clearly stated (as they have in some areas of the Pacific).
- There is a need to investigate interactions between bottom-up (e.g. prey changes, inability of salmon to adapt) and top-down (e.g. predation) drivers while recognising that multiple factors (cumulative effects of habitat loss, disease, contaminants etc.) are involved.

Although identifying causes of salmon declines was not the theme of the workshop, the examples reviewed led to some general observations about similarities in drivers of change in the Pacific that likely have parallels in the Atlantic basin:

- Freshwater factors influence subsequent survival at sea; these can be population-specific or broader in impact.
- In the marine, there are local, regional and basin scale drivers at work. These operate cumulatively as salmon pass through various ecosystem domains (in time and space) and in some cases operate synergistically.
- Climate change is a likely driver of major significance, with effects being felt at very broad scales and in different ways; for example there are trends for general ocean warming, but also there is potential for short term or single year anomalous "big" events having high impact.
- Climate change has impacts in freshwater as well as at sea, therefore mechanisms of change are complex and multi factorial. Climate change may have a hemispherical impact on salmon species.
- Some mortality factors become critical in years of bad oceanic conditions, but matter less in good years.
- Size selective mortality of salmon is high during years of low ocean production. In bad years the small salmon get eaten.

The Pacific provided some good examples of how these scales of impact operate:

- The example of Chinook salmon in Californian Rivers cited earlier in this report illustrates how the ecosystem impacts of a single current system (the California Current) can strongly influence the fortunes of salmon as they enter the ocean. While freshwater and wide oceanic factors have influence on marine survival, the dominant effect on Chinook marine survival is the contrast between good years and poor years of upwelling at the shelf edge (almost on/off switching). The strength of upwelling drives variation in primary productivity and skews predator/prey relationships; in turn impacting Chinook salmon.

- In contrast, marine survival success of chum salmon in the Bering Sea off Alaska is thought to be strongly influenced by basin-wide factors. Total salmon production in the N. Pacific is higher than it has been in the past 60 years and it is hypothesised that the N. Pacific may have reached carrying capacity for salmon (Ruggerone and Irvine, 2018). This is thought to cause reduced growth, leading to changes in age at return and survival. For example, odd-year pink salmon are more abundant and growth at sea is reduced relative to even-year cohorts; suggesting competition between the odd-year pink salmon. The presence of vast numbers of hatchery salmon in the N. Pacific (Chum dominate biomass and 60% of Chum are from hatcheries) is thought to play a key role in density dependence. Climate variation is thought to influence competition effects, with Chum salmon growth reduced in years of higher North Pacific Gyre Oscillation (NPGO) and this effect is exacerbated by biomass (Debertin *et al.*, 2017). Covariation in growth is observed among Chum salmon in different areas of ocean, suggesting broad scale climate change and density-dependent effects at work.

Both examples above point to the importance of considering the diversity of oceanic impacts as an integral part of understanding what drives changes in salmon status and suggests that Atlantic salmon researchers should look closely for differing scales and mechanisms of effect across the Atlantic range. The message as it relates to the Likely Suspects Framework domains, is that sometimes the domain is constrained and all the signals are contained there, while in other cases the signal is widely spread across a number of domains. This should be taken into consideration when developing hypotheses from the Likely Suspects Framework.

How can we improve dialogue at hemispherical scale?

The workshop concluded that there would benefits to improving dialogue among scientists between the Atlantic and the Pacific. Agreed specific follow up tasks should include:

- Developing a common language/currency to be shared by Pacific and Atlantic salmon researchers.
- Establishing an online operating framework for working together (e.g. meetings /discussion forum) in order to foster and enable collaboration and to coordinate and share information pertinent to research bids and on funding opportunities.
- Sharing information to align approaches so that data are comparable. Data harmonisation would be essential to support joint research (as outlined below) on hemispherical scale climate change linked effects on salmon.

What is the potential for joint research activities involving Pacific and Atlantic salmon?

The workshop agreed that more research could be done to investigate the reasons why salmon in both basins are dying at sea and how the patterns of productivity are influenced at various scales. Some of that research would be best done together, especially where broad scale drivers such as climate change are involved. Evidence on climate change driven impacts on salmon species at hemispherical scale is a major research gap.

Pacific researchers should investigate options for applying a "Likely Suspects" approach, while recognising that multiple species and populations complicate the Pacific situation. This raises the additional question of how and whether we can link an Atlantic Likely Suspects Framework to comparable Pacific frameworks at hemispherical scale? What would this look like? This may be a way to conceptually show the potential global impact of wider scale climate drivers such as E Niño on salmon species (telekinetic effects).

Attributes of the Likely Suspects Framework were that, as an overarching framework, it could adapt as data become available and it can accommodate inputs from modelling scenarios and simulations to "fill in" the various ecosystem domains. The cumulative impacts of mortality and the accountancy approach to try and account for mortalities as "missing fish" were seen as conceptually important features.

Pacific attendees at the workshop also found the Atlantic salmon Bayesian life cycle model framework and the IABASM model development very useful (particularly the evolutionary genetics theme) and would be interested in applying similar approaches to the Pacific salmon species.

The workshop identified some research priorities at hemispherical scale:

- One research proposal is to assess similarities and differences in marine survival/ abundance trends across salmon species at hemispherical scale.
- Similarly, a new research priority will be jointly investigating climate change drivers and impacts on salmon at hemispherical scale.

These research topics would help identify broader scale factors potentially contributing to changes in salmon productivity and they align well with International Year of the Salmon (IYS) priorities. The workshop also felt that pursuing joint research on the hemispheric scale impacts of climate change on salmon species would capture the public imagination; portraying salmon in the Pacific and Atlantic as highly visible indicators of ecosystem change (aquatic canaries!).

Development of a web-based tool for demonstration and outreach purposes

The workshop noted that a further benefit envisaged for the likely suspects concept, is that the framework being developed would be a valuable tool to help managers and stakeholders visualise and understand the impact of the various mortality factors impacting salmon stocks at sea.

A web based tool could be developed that would present users with a map based version of the marine phase of the life cycle and allow users to vary the impact of changing the various mortality factors within ranges to be established during development of the framework. Users could visualise the challenges faced in assessing salmon mortality at sea and understand why research was being targeted in certain areas.

One novel benefit would be in demonstrating how the amounts of salmon thought to be “saved” by management measures, such as restrictions on netting at sea and catch-and-release in rod fisheries, compare to numbers potentially “lost” due to the impacts of other mortality factors. Again, this is where an accountancy approach is helpful, as it presents the issue as being one of losses and gains and the overall balance between these.

As an example of what is envisaged, the workshop was given a demonstration of the web-based Salmon Population Modeller developed by the AST and the Institute of Fisheries Management (IFM): http://www.atlanticsalmontrust.org/modeller/

This tool is designed to provide everyone interested in salmon with a clearer understanding of how salmon stocks work (stock dynamics) and what the constraints are on increasing salmon numbers. It is intended to illustrate typical levels of loss at the different stages of the salmon life cycle, and the impact that changing these can have on the viability of the stock. It is based on a notional pristine river stock, because all stocks in Britain and Ireland are impacted to varying extents by human activities, and it would be very difficult to come up with a typical impacted stock. Using a theoretical pristine (i.e. un-impacted) stock as the base line for the Modeller makes it possible to illustrate the effects of impacts at different stages. It is then possible to show the effect of reducing the losses caused by these impacts by reversing the process. The Modeller allows impacts to be imposed at different stages in the life cycle, simulating, for example, the effects of a dry spring resulting in reduced survival of emigrating smolts or a dry autumn preventing some adults from reaching the spawning areas. It also allows the amount of available spawning and parr habitat to be increased or decreased.

Under completely stable conditions the population would be expected to reach an equilibrium state where the numbers at each life stage will, on average, be the same from one generation to the next. A change to a new set of conditions would cause the population to move to a new equilibrium state after several generations. In real life, numbers of even a stable stock will fluctuate, sometimes dramatically, from year to year, but the Modeller removes this year-to year variation to show how a typical stock is affected on average by changes in survival at different stages.

The workshop agreed that a similar tool based on the Likely Suspects Framework would be very useful in explaining to a wide audience the challenges and issues with marine survival and how the mortality factors impact at various phases of marine life and at various scales. The new web tool would therefore expand the marine part of the existing Salmon Modeller, which has a single marine survival box where the user can change overall survival to 1SW and 2SW. The new tool could be integrated with the Salmon Modeller as an expanded marine area, or be a freestanding tool.

The workshop thought the two stage colour coded system used in the Salmon Modeller to illustrate sustainable vs. unsustainable population status was a very good feature and colour could be adopted by the new Likely Suspects Framework tool (perhaps Red/Amber/Green coding) to show degree of impact of mortality changes at various domains?

The way forward: Summary of Workshop Outcomes and Actions

Refining and developing the Likely Suspects Framework

It is important to decide on the purpose of developing a conceptual framework. The workshop agreed that the AST Likely Suspects Framework will provide a basis for conceptualising marine survival issues in Atlantic salmon and will act as a focus for discussion and development of research priorities.

A programme would subsequently be developed to evolve the Likely Suspects Framework from a high level conceptual framework towards building an ecosystem modelling framework and decision support tool:

- This will enhance understanding of ecosystem processes and impacts of climate change on Atlantic salmon and in turn feed into refinement of predictive models used to develop management advice.
- The key output is seeing enough of the picture from the ecosystem modelling framework of what is happening to the salmon, and why, thus allowing managers to consider their options.
- This approach is a very powerful tool to have to present to regional management organisations and to local managers also.

The Likely Suspects Framework shares some of the characteristics of conceptual frameworks developed in the Pacific area and the workshop suggested the Framework could be further developed along those lines, for example, including the management drivers applicable at various scales, from river to ocean. The initial phase of development would seek to identify appropriate domains that are the key phases or points in the life cycle where mortality factors are having particular impacts. In terms of further refining possible domains, evidence was presented that influences on marine survival start even before smoltification, with the precondition of smolts being one such factor. Domains must, therefore, include relevant periods during freshwater life. We also recognise spatial marine units along migration path of various sizes; with cause and effect driving change. It is particularly important to identify staging/transition areas, which may be domains of particular interest. The process of identification of domains also leads towards consideration of the potential mechanisms driving variation in mortality.

It was suggested to initially examine/scan Atlantic salmon populations by Ecoregion, to look for differences and similarities; i.e. domains with multiple populations present with common survival patterns, vs separate domains with different un-coherent properties. Inferences can be drawn from the network of time series indicators from stocks that enter different marine domains or leave different freshwater regions.

Of course, not all domains will be of equal significance. Therefore, concentrate on important ones where many stocks overlap (e.g. W. Greenland); matching of time and space domains where they are all doing the same thing. For example, a viable strategy may be to assemble a range of environmental covariates, lay these out spatially and correlate them to survival of a stock or stocks. This will reveal "hotspots" in the ocean for spatial and temporal correlation and may point to spatial domains where many stocks are responding to similar pressures.

At the same time, develop and review hypotheses that will be tested in the further phases, prioritising those relating to functional links between pressures and response variables.

The workshop agreed that identifying both the primary and contributing mortality factors (the causes) and the mechanisms by which they operate is important. However, synergistic and cumulative effects are bound to be occurring and it will be impossible to answer all the questions about what is driving survival. In approaching this, it is perhaps just as important to pose a different question *"what can you do about it"*; thus concentrating research on areas where information can underpin management actions in support of Atlantic salmon recovery.

With a revised conceptual framework in place and an initial portfolio of hypotheses, the next phase would focus on particular domains and where possible quantifying mortality. This phase could also begin to examine the underlying mechanistic relationships between the pressures and response variables and how response influences salmon mortality. To understand linkages, research needs to be interdisciplinary. Ecologists, oceanographers and climate scientists must conceive of and investigate research avenues together.

This progression is in line with the original stated objective of the concept, which was ***"to prompt specific testable hypotheses about the operation of the factors involved and hence aid targeting of research to further refine the estimates of the potential scale of, and variation in, mortality at each part of the marine phase".***

The workshop also agreed the potential of the Likely Suspects Framework to be developed as a simple web based tool for outreach to manager/stakeholders. A simple interface showing the key domains in the Framework would enable users to change various candidate mortality pressures to show the cumulative impacts on marine survival and hence stock status trends.

What steps are needed to implement this process?

The workshop suggested a series of steps, as follows:

Step 1.

- Better assess marine survival (and abundance) trends for similarities and differences…. analysis of spatial and temporal patterns of covariance.
- In parallel, continue to improve the Atlantic salmon life-cycle model, including better partitioning of mortality (freshwater v marine, ocean age 1 v 2) and better consideration of the effects of timing of maturity on this partitioning.
- Consider including Pacific salmon for a hemispheric look at the same time as looking at the Atlantic.

Step 2.

- Refine the Likely Suspects Framework and establish the appropriate linkages for embedding the improved Bayesian life cycle model.
- Ensure response variables are apparent and distinct from pressures/drivers of mortality.
- An attempt could be made to do this with all the information gathered from the workshop, then brought back for review. Decide at what scale the ecosystem modelling framework should be constructed. To an extent this will depend on the data available vs. data gaps, however it was thought that a broad scale framework should be attempted (mainly to capture the processes going on at oceanic domain scale), while one or more regional/local examples could be developed to focus on a specific relationship that is thought to have strong local impact (similar to the predation example from the California Current).
- The scale chosen for the ecosystem modelling framework(s) will also have implications for funding, since oceanic scale proposals are likely to be of interest at intergovernmental level.

Step 3.

- Simultaneously review and compile hypotheses (and briefly summarise affiliated findings to date) from previous efforts as basis for this work. Use this to create initial working list.
- This can be done up front, and reviewed after identifying domain(s) of focus.
- Testable hypotheses need to be clearly stated (as they have in some areas of the Pacific).

Step 4.

- Use the trends analysis (Step 1) combined with the revised ecosystem framework to help isolate what domain(s)/region(s)-life stage(s) should be considered area(s) of likely high mortality and consistent among populations. These may or may not be a shared location.

Step 5.

- Within the domain of focus, quantify mortality where possible (or clearly explain the mechanistic relationships between the pressure/driver and salmon mortality) and where not, develop research to help do so.
- Consider starting with exploratory projects.

Actions specific to the Atlantic Basin

In order to progress the steps listed above, the workshop identified several specific actions for the Atlantic, as outlined below:

- **Getting the scientists together**

There is a clear need to routinely integrate non-salmon scientists into our world. Progress on salmon mortality at sea will depend on a multidisciplinary approach and therefore, oceanographers, predator and competitor experts will have to become involved. The workshop suggested that an initial step towards integration would be that ICES WGNAS should request that ICES arrange for an oceanographer to attend their meetings to provide an annual update on oceanic conditions/events.

- **Getting the data together**

There is a need to compile good documentation on the survival time series of wild Atlantic salmon. Such an approach was adopted by the EU SALMODEL project that looked at stock and recruitment data throughout the Atlantic range of salmon, in order to drive research into setting and transporting conservation limits. There is a need therefore to get together in a workshop format (perhaps under the auspices of ICES) to evaluate/document this. Data will then need to be standardised and made accessible to import into analysis at domain scale. The AST workshop made a start, by developing an illustrative spreadsheet of the required data attributes at various scales. This should be extended to include other relevant data such as growth (scales), genetic diversity (DNA) and migration history (from otolith trace elements) and should be further developed in joint consideration with other databases.

It was not immediately clear if ICES databases are organised in such a way as to support access both to metadata on ecosystem components and time series data series that can be used in researching functional links between diverse ecosystem components such as fish, birds and mammals.

- **Salmon as a pelagic indicator species**

Steps should be taken through ICES, NASCO and the EU to promote the Atlantic salmon as a pelagic species and a key indicator of marine ecosystem health. This form of leverage will be necessary to ensure that appropriate ecosystem surveys are carried out in the N. Atlantic in areas of relevance to salmon and that support is generated for any new targeted "salmon at sea" surveys judged necessary.

- **Natural mortality during the second year at sea**

It was agreed that there is scope for a broad comparative analysis of natural mortality "M" during the period following the 1st January of the first winter at sea for a range of stocks across the Atlantic range of salmon. This would examine the variations in natural survival during the second year at sea (i.e. after the decision to mature has been taken). ICES needs to know whether M varies temporally and spatially, especially at the assessment unit level.

- **An "energetics of the ocean" approach to researching salmon mortality**

A research theme was proposed to investigate the energetic changes (energy density variation) needed to explain the changes in maturation profiles that we are seeing. A specific example might be researching the partitioning of the energy budget in salmon at sea during critical phases where many stocks coalesce (e.g. W. Greenland). Two complementary approaches could be considered:

  - o Explore the potential influence of ocean productivity shifts (energy density changes) on resource allocation strategies and life history traits; use a theoretical mechanistic approach to explore patterns of covariation.
  - o Explore the evolutionary and demographic consequences of such patterns using IBASAM. The latter approach might require gathering data on spatio-temporal trends in resources (energy density) and energy density content of salmon; 1SW vs 2SW.

- **Survivor bias**

Survivor bias is a problem. We only see the salmon that survive and have also lost sources of data as at sea fisheries for Atlantic salmon decline. This perhaps justifies a renewed "at-sea" sampling programme.

- **Atlantic salmon Bayesian life cycle model development**

The workshop endorsed further development of the Bayesian life cycle model for Atlantic salmon being developed for stock assessment and catch advice at ICES, with an emphasis on partitioning marine mortality along the migration routes at sea.

- **Linking the Likely Suspects Framework with Atlantic salmon models**

A further project would seek to integrate the IBASAM model, or any other theoretical framework approach developed under the *"energetics of the ocean"* approach above with the Bayesian life cycle model. For example, IBASAM modelling could be used to set up scenarios that would be tested as prior assumptions in an enhanced Bayesian life cycle model.

Atlantic and Pacific working together

Significant benefits were realised from having joint Atlantic and Pacific representation at the workshop. The workshop concluded that there would benefits to improving dialogue among scientists between the Atlantic and the Pacific. Agreed specific follow up tasks should include:

- Developing a common language/currency to be shared by Pacific and Atlantic salmon researchers.
- Establishing an operating framework for working together (e.g. meetings/ discussion forum) in order to foster and enable collaboration and to coordinate and share information pertinent to research bids and on funding opportunities.
- Sharing information to align approaches so that data are comparable. Data harmonisation would be essential to support joint research (as outlined below) on hemispherical scale climate change linked effects on salmon.

The workshop agreed that more work could be done to investigate the reasons why salmon in both basins are dying at sea and how the patterns of productivity are influenced at various scales. Some of that work would be best done together, especially where broad scale drivers such as climate change are involved.

Evidence on climate change driven impacts on salmon species at hemispherical scale was identified as a major research gap. Is there a potential hemispherical impact of wider scale climate drivers such as El Niño on salmon species (telekinetic effects)? The workshop identified two particular research priorities at hemispherical scale:

- One proposal is to assess marine survival/abundance trends across species and oceans for co-variance. This would be a powerful connector and might help to further isolate some of the broader factors at play and functionally how they are leading to changes in salmon productivity.
- A particular research priority would be jointly investigating climate change drivers and impacts on salmon at hemispherical scale.

These research topics would help identify broader scale factors potentially contributing to changes in salmon productivity and they align well with International Year of the Salmon (IYS) priorities.

Appendix 1. List of participants-Likely Suspects Workshop 2017.

Chair: Walter Crozier, Atlantic Salmon Trust

Rapporteur: Ken Whelan, Atlantic Salmon Trust

Sarah Bayley Slater, AST, UK

Emma Hatfield, NASCO/IASRB

Jason Daniels ASF, Canada

Gerald Chaput DFO, Atlantic Canada.

Niall O'Maoiléidigh, Marine Institute, Ireland.

Ian Russell, Cefas, United Kingdom.

Etienne Prévost, INRA, France

Mathieu Buoro, INRA, France

Etienne Rivot, Agrocampus Ouest, France.

Kim Hyatt, DFO Pacific Region, Canada.

Michael Schmidt – Long Live the Kings - University of Washington, Seattle

Brian Wells, NOAA Fisheries, Santa Cruz, California

James Irvine, DFO Pacific Region, Canada

Sue Grant, DFO Pacific Region, Canada

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Summary of the Work of the Atlantic Salmon Trust

Since 1967 the Atlantic Salmon Trust (AST) has supported research into key aspects of the lives of migratory salmonids. AST is the UK's only charity whose work is devoted exclusively to the conservation of wild Atlantic salmon and sea trout. The Trust facilitates research, partners research projects, organises scientific meetings, workshops and conferences. It communicates its findings to anglers, fishery managers, fishery owners and the public.

The role of the Trust is to demonstrate how both species can be conserved and managed to enable their value to society to be realised sustainably. The Trust's work concentrates on improving our knowledge of these fish, their habitats and their complex and fascinating life histories, and the threats to their survival. Until relatively recently this knowledge was confined mainly to the freshwater aspects of their life cycle, but the AST is now focusing on the migration and marine phase of their life cycle.

The abundance of Atlantic salmon, prior to any fisheries exploitation, has declined over the last forty years; from 8 – 10 million fish in early 1980s to 3 – 4 million fish at present (ICES, 2017a). At present AST's major concern is the dramatic decline in marine survival in the Atlantic, which has fallen from over 15% in the 1980s to, at times, less than 5% in the last five years.

AST is now focusing a large part of its research activities on the coastal zone and wider ocean. Once considered the 'black box' in terms of knowledge, new scientific and technological advances are making research into this vast area possible.

Atlantic Salmon Trust,
11 Rutland Square,
Edinburgh EH1 2AS
Scotland