THE SECOND ICES/NASCO WORKSHOP ON SALMON MORTALITY AT SEA (WKSALMON2; OUTPUTS FROM 2022 MEETING)

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i Executive summary

ICES, in consultation with the North Atlantic Salmon Conservation Organisation (NASCO), convened a series of workshops to explore how to use biological and environmental data in models to advance the conservation of wild Atlantic salmon (*Salmo salar* L.) at sea. This workshop set out to consider multiple candidate hypotheses contributing to changes in the temporal patterns of abundance, and agree the priority research questions.

No agreement on the development of a set of priority marine mortality hypotheses was reached. This resulted from the recognition of the hierarchical nature of ecosystem controls, and important complexities introduced by evolutionary diversity. An integrated ecological-evolutionary framework was proposed for the evaluation of hypotheses, and to identify key points in space and time. There was an agreed need for the continuation of cooperative initiatives to examine drivers of marine growth change using standardized approaches, and in the evolutionary delineation of stock units. These were seen as productive pathways to significantly enhance understanding of the marine factors affecting species abundance.

The workshop recognized that options for developing and testing hypotheses remain constrained by the availability and quality of data, and identified ways to mobilize existing knowledge resources on key aspects of salmon ocean ecology. These focused on the synthesis of physical ocean data and model outputs, involving ocean basin-wide evaluations of available energy from surveys of lower trophic levels, and updating of population-specific biological information. The workshop agreed on the need for a specific call for data from pelagic commercial fisheries, given the broad scale of this activity and potential overlap with salmon migrations. There was also the recognition that Atlantic salmon should be included in the ICES Working Group on Bycatch of Protected Species (WGBYC) Protected, Endangered and Threatened Species list.

Much of the work required to mobilize useful data sources was recognized as being outside the scope of existing ICES data calls, or the constituted core work of ICES Working Group on North Atlantic Salmon (WGNAS). Recommendations for the third workshop are for 1. More detailed consideration of how to access the work needed for data mobilization, and 2. The identification of well-defined, achievable outcomes.

ii Expert group information

Expert group name	Second ICES/NASCO Workshop on Salmon Mortality at Sea (WKSalmon2)
Expert group cycle	Annual
Year cycle started	2022
Reporting year in cycle	1/1
Chairs	Colin Bull, UK
	Glenn Nolan, Ireland
Meeting venues and dates	15 June 2022, online, 59
	30 August – 01 September 2022, Copenhagen, Denmark, 59

1 Introduction and Terms of Reference

The overall goal of the WKSalmon workshop series is to improve the assessment of Atlantic salmon river stocks by identifying and testing key hypotheses regarding at-sea mortality, and partitioning these declines or losses among possible or likely "suspects". This can be used to help identify in which domain (i.e. key points in time and space where a substantial amount of the mortality occurs) actions may need to be focused upon to ensure the future abundance of this iconic species.

The original terms of reference for WKSalmon were as follows:

WKSalmon 1: The first workshop in 2019 (ICES, 2020) provided a comprehensive review of salmon marine ecology and identified potential marine data resources that may be of use in considering the plausibility of multiple candidate hypotheses as mechanisms contributing towards the temporal patterns of abundance.

WKSalmon 2: The second workshop will build on workshop 1 by agreeing on a subset of priority research questions, seeking consensus on how to define the space and time "domains" used by salmon during their marine growth phase, and focusing action on the mobilization of the knowledge resources that are required to test specific mortality hypotheses.

WKSalmon3. The third workshop will further develop modelling options and identify pathways that can lead to specifically testing mortality hypotheses.

This report summarizes the progress during the second workshop 2 (WKSalmon2).

1.1 Terms of Reference for the Second Workshop in a series on Salmon Mortality at Sea (WKSalmon2)

The terms of reference for the WKSalmon2 workshop were as follows:

1. A one day scoping meeting in June 2022 will provide the framing for an efficient and productive outcome of the WKSalmon2 process.

a) In advance of this scoping meeting, participants will be apprised of the current state of the science in a working document prepared by the chairs, work that builds on the output of WKSalmon1, developing hypotheses about at sea mortality and the salmon "domains" concept. This scoping meeting will then discuss these hypotheses;

b) Agree to a focused set of high priority hypotheses. The hypotheses should focus on examining sources of at sea mortality that are thought to be limiting the conservation potential of North Atlantic salmon. These hypotheses will be tested in the final workshop in this series, WKSalmon3; and,

c) Propose an approach to represent and integrate the salmon "domains" concept within the likely suspects framework (LSF) hypotheses-testing framework.

2. A three day workshop in late August/early September 2022 will:

a) Agree to a final set of high priority hypotheses, based on the discussions in the one day scoping meeting;

b) Identify opportunities and mechanisms to leverage existing data sources within the ICES region and beyond to investigate the set of high priority hypotheses and salmon "domains" concept (ToR 1b); and,

c) Draft an ICES Data Call in preparation for WKSalmon3. The data requested in the Data Call should support testing of the hypotheses identified in ToR2a. Testing these hypotheses is an attempt to improve the our scientific understanding, the stock assessment, and the ICES advice for North Atlantic salmon.

2 Update on progress on identified actions from WKSalmon1

2.1 Preparatory candidate mortality hypothesis development

In preparation for WKSalmon2, identification of an initial subset of marine mortality hypotheses for further consideration was conducted by the Missing Salmon Alliance Likely Suspects Framework team (https://missingsalmonalliance.org/likely-suspects-framework-home). Following review of relevant methodologies (O'Neil *et al.*, 2000; Cairns, 2001; Peterman *et al.*, 2010; Greene *et al.*, 2012; Ó Maoiléidigh *et al.*, 2018) the aim of the process was to capture expert opinion on the plausibility and realism of the proposed mechanisms being suggested in the candidate hypotheses statements in a qualitative way, and allow narrowing down to a smaller group of candidate hypotheses for more rigorous appraisal. Eleven candidate general mortality hypotheses were proposed (Table 2.1) and presented in a preparatory working paper alongside an initial sweep of possible factors and mechanisms and an initial review of evidence that provides support for, or against, the mortality hypotheses.

With reference to the process of developing and testing of marine mortality hypotheses, it was noted that:

1. There is a strong likelihood that multiple causal mechanisms may act simultaneously, with additive, synergistic or offsetting effects contributing to the patterns in salmon abundance through time.
2. Potential drivers for the patterns we see in marine growth and survival of salmon will invariably not only differ spatially and temporally among salmon stocks (Olmos *et al.*, 2020: Tillotson *et al.*, 2021; Vollset *et al.*, 2022), but likely be associated with relatively high or low frequency ecosystem changes (Mills *et al.*, 2013), be sensitive to period of study (Harvey *et al.*, 2020: Tillotson *et al.*, 2021), and be of relevance as potential explanatory factors over mortality variation during the early (Olmos *et al.*, 2020; Todd *et al.*, 2021; Trehin *et al.*, 2021; Utne *et al.*, 2022) or late stages of marine life (Barajas *et al.*, 2021).
3. Our knowledge of spatial distribution of salmon in the sea, while advancing rapidly, needs to account for remaining uncertainties with regard to late-ocean phase feeding locations (e.g. Feeny *et al.*, 2021) and long distance transatlantic migrations (Bradbury *et al.*, 2021).

With these issues in mind, the group cautioned that any proposition regarding the strength of factors and mechanisms put forward in support of any hypotheses could be considered as guidance only, providing assistance with the identification of further evidence sources to evaluate hypotheses that are more specific.

Table 2.1. Candidate marine mortality hypotheses proposed for consideration during the workshop alongside an indication of the life stage and space-time domain that controls are likely occurring.

Candidate general hypotheses thought to represent significant mortality factors contributing to the patterns of marine survival in Atlantic salmon	Salmon domain and life stage				
	Freshwater		Estuary	Specific-Ocean	Common-ocean
	juv.	smolt	smolt	post-smolt	post-smolt/ subadult
Seasonal variation in the physical habitat in freshwater lead to reduced feeding and growth	🟩				
Latent (carry-over) effects originating in freshwater lead to reduced growth or survival in later stages	🟩	🟩			
Changes in the rate of survival during smolt migration through freshwaters		🟩			
Changes in the rate of survival during smolt migration through estuaries			🟩		
Interactions with coastal aquaculture in the coastal / nearshore zone				🟩	
Synergistic effects of feed restriction and predator–prey interactions in the coastal / nearshore zone				🟩	
Variation in the timing of post-smolt entry to the marine phase and a mis-match with suitable prey			🟩	🟩	
Lower survival expectations of smaller-body size smolts during their marine migration			🟩	🟩	🟩
Seasonal variation in the physical habitat in shelf seas/ open ocean zones leading to reduced feeding and growth				🟩	🟩
Synergistic effects of feed restriction and predator–prey interactions in shelf seas/ open ocean zones				🟩	🟩
Bycatch of salmon by commercial fisheries in shelf seas/ open ocean zones				🟩	🟩

2.2 A shared data repository for salmon and salmon ecosystem data sources

In response to a perceived need to improve the accessibility of knowledge resources available to test marine mortality hypotheses the Salmon Ecosystem Data Hub (SalHub) has been developed

(Diack *et al.*, 2022). This web application begins a comprehensive catalogue of salmon research data, with around one third of the described resources including a link (URL) to the data itself. Following the initial effort made in WKSalmon1 to compile and populate a metadata spreadsheet (ICES, 2020), around 360 data sources are now described in SalHub. This will provide the salmon research community with new opportunities for sharing data, developing new synthesis pathways, data products and support the future work of the WKSalmon series.

SalHub is further described in Section 4.10 and can be accessed upon registration using the following link: https://shiny.missingsalmonalliance.org/SalHub/

2.3 Using ocean model results as synoptic proxies for marine conditions

WKSalmon1 identified a need to evaluate the potential for integrating ocean model simulations into developing a more comprehensive picture of the salmon marine ecosystem drivers. They noted that understanding of marine survival would be enhanced by the use of recently available high-resolution regional models but that these vary in range, quality and coverage. In addressing this issue, The Missing Salmon Alliance Likely Suspects Framework team commissioned a study on the utility of two European ocean models (AMM7 and SSM-RS models) to provide outputs of a spatial and temporal resolution to be considered in the evaluation of possible ecosystem indicators of change. Results from this study (Tyldesley, 2021) are discussed in more detail in Section 4.3, but it concluded that these ocean models do provide environmental information relevant to salmon during their early marine phase and provide synoptic proxies for observed data for the purposes of statistical and mechanistic modelling of environmental conditions.

3 Developing marine mortality hypotheses: a hierarchical integrated evolutionary-ecological approach

Advancing the robust formulation and testing of hypotheses to explain temporal patterns in the marine survival in Atlantic salmon is a stated aim of the Likely Suspects Framework process (Bull *et al.*, 2022). The group considered the intersessional proposal of eleven candidate marine survival hypotheses (Table 2.1) to further develop an agreed process to formulate, prioritize and evaluate hypotheses on marine growth, maturation and survival in Atlantic salmon as questions to focus and drive future research. The initial preparatory online session of WKSalmon2 in June 2022 was used to evaluate and critique these candidate hypotheses using focused discussions in small-groups. This process was exploited to highlight where general interest lay in advancing certain hypotheses where possible needs were in alignment, and where data might exist to facilitate hypothesis testing.

This process was successful in focusing attention on how to frame important (and often difficult) questions regarding the quest for an improved (and mechanistic) understanding of marine survival patterns of Atlantic salmon river stocks. However, it proved largely inconclusive. This resulted largely from obstacles encountered with the individuals' interpretations of the hypotheses statements with regard to issues of spatial and temporal scale, and confounding effects of growth and maturation on marine return rates. Within the group, a general perception existed of a need to try to account for notable variations in river-stock specific responses across spatial and temporal scales in the development of hypotheses for evaluation. As biological processes are often best understood in the context of evolutionary theory (Mace and Purvis, 2008; Millstein, 2010; 2013), it is essential to develop hypotheses on the impact of environmental factors on growth, mortality and maturation, within an integrated ecological and evolutionary framework.

3.1 Integrating evolutionary considerations into ecological research, assessment and monitoring

An integrated consideration of evolutionary and ecological processes is essential to effective conservation programmes (e.g. Lande, 1988; Conover *et al.*, 2006), including when modelling species' responses to environmental change (Bay *et al.*, 2017). Ecological processes and outcomes (e.g. growth, survival, maturation, and distribution) are conditioned by environmental and evolutionary factors e.g. gene flow, selection and migration, adaptive population divergence (Clutton-Brock and Sheldon 2010; Dimmick *et al.*, 1999; Hughes *et al.* 2008; Palkovacs and Hendry 2010; Graham *et al.* 2014). However, its integrated consideration in ecological studies (Mace and Purvis 2008), or modelling (Pierson *et al.*, 2014) is rare. It does occur in respect of applied freshwater studies of Atlantic salmon (Garcia de Leaniz *et al.*, 2007; Taylor 1991; Fraser *et al.*, 2011)but is notably absent in studies of the species marine ecology (e.g. Dadswell *et al.*, 2010; Thorstad *et al.*, 2011; Crozier *et al.*, 2018).

The basic nature and extent of evolutionary population structuring in the Atlantic salmon is well understood, with what is known coming largely from studies of the distribution of molecular genetic variation. The species shows a basic division into eastern and western phylogeographic groups (King., 2007; Bourett *et al.*, 2013). Recent work confirms widespread hierarchical structuring with each group (e.g. Europe: Gilbey *et al.*, 2017; North America: Jeffery *et al.*, 2018), down to the smallest spatial scale, the existence of evolutionarily (i.e. genealogically) distinct populations within larger river systems (e.g. Verspoor and Cole, 1989; Dillane *et al.*, 2008). A more nuanced and profound insight into evolutionary structuring may be realized by the completion of a synthesis integrating across existing studies (Figure 3.1: Verspoor *et al.*, *in prep*). However, most studies are based on small sets of arbitrarily chosen polymorphic loci, providing limited genomic coverage and an uncertain power for resolving evolutionary population units (Capella-Gutierrez *et al*., 2014).

This is also true of the nature and extent of adaptive differentiation of such diversity. Adaptive and phylogenetic population diversity for freshwater traits, while incompletely understood appears widespread (e.g. Garcia de Leaniz *et al.,* 2007; King *et al.*, 2007; Bourett *et al.*, 201; Oserov *et al.* 2017; Scanlan *et al.*, 2018) as well as other salmonids (Fraser *et al.*, 2011; Hutchings 2011; Snorrason and Skúlason 2004; Eizaguirre and Baltazar-Soares 2014) while little is known about adaptive diversity in respect of marine traits. What is known is that population divergence can evolve even when there is some gene flow among populations and, it is difficult to detect as the loci involved appear to be located in small "genomic islands" (Feder *et al.* 2012, 2014; Hemmer-Hansen *et al.,* 2013; Egan *et al.* 2015), including in genomes of salmonid fishes (Larson *et al.* 2017, 2019). Thus, a detailed account of population diversity and its evolutionary structuring is still lacking and current studies almost certainly underestimate its full extent, particularly in respect of evolved marine diversity.

Historical tag return and scale data provide clear evidence of distributional differences between Eastern and western Atlantic groups (e.g. Dadswell *et al.,* 2010) as well as for Baltic Sea and Inner Bay of Fundy groups within these, with known cases of local estuary migrating populations (Webb *et al.,* 2007). This migratory diversity is likely to be evolved as is the post-glacial evolution non-anadromous population types from anadromous colonists (Webb *et al*., 2007). Evidence that is more recent supports such diversity being widespread, as argued by Hansen and Quinn (1998). Gilbey *et al.,* (2021) found that post-smolts captured in research trawls in the NE Atlantic could be assigned to the phylogeographic groups identified by Gilbey *et al.* (2017) using molecular genetic markers. Most notably, individuals from the groups geographically closest to the main identified feeding aggregation (around the Vøring Plateau, in the Norwegian Sea), where more southerly groups dominated, were absent (those from Iceland) or in low abundance (those from central and northern Norway). Scanlan *et al.,* (2018) and Minkoff *et al.,* (2020) provide compelling evidence of migrational diversity among populations in magnetic field responses. This appears to relate to the sequential use of magnetic data (Mouritsen, 2018) and aligns with salmonids possessing and inherited sensory ability to discriminate both the inclination and intensity of magnetic fields (Putnam *et al.,* 2014a,b; Lohmann and Lohmann, 2019).

Collectively these studies make it clear for the potential for evolved adaptive population diversification for marine traits. For example, it a strong case can be made for it to occur in respect of the initial migrations of post-smolts from different spawning rivers to shared, or different, marine feeding areas. Storage of a magnetic "foot print" is suggested to be the basis of the homing of mature salmon back to their natal rivers (Lohmann and Lohmann, 2019), possibly exploiting epigenetic or other developmental mechanisms. Cryptic adaptive population diversity may also potentially exist for other aspects of migratory behaviour (Kjærner-Semb *et al.,* 2021) or traits such as prey preferences and success in energetically exploiting different prey types.

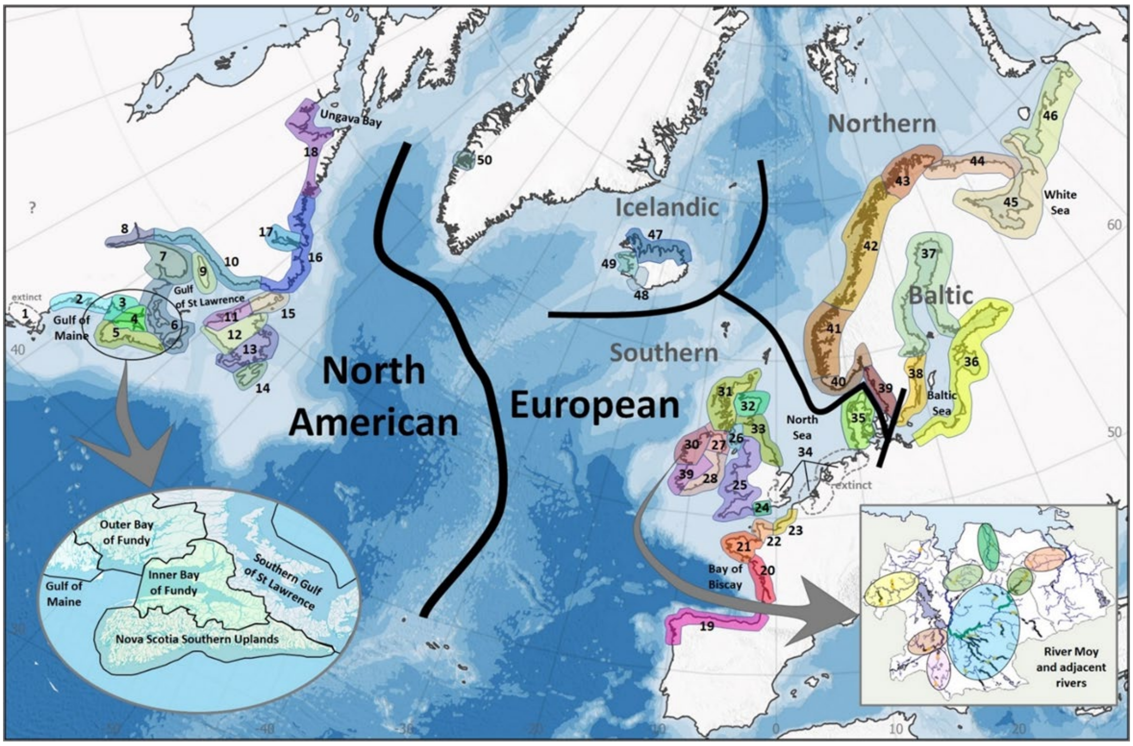


Figure 3.1. **A synthesis of trans-range phylogeographic structuring observed across studies in Atlantic salmon resolved by screening of phylogenetically informative nuclear microsatellite and SNP variation. Colours and numbers represent the main phylogeographic groupings. Figure is from Verspoor *et al*. (in prep)**

Both theoretical and observational evidence support the view that studies of the marine ecology and the marine conservation of the Atlantic salmon will be most insightful when carried out within an evolutionary framework. This must encompass both ecological and evolutionary processes, including their interactions, and focus on evolved units of population diversity (e.g. Conover *et al*., 2006). The framework for so doing is the focus of the new field of eco-evolutionary dynamics (Schoener, 2011, Hendry, 2016) and such studies have started to emerge for Atlantic salmon (Czorlich *et al*. 2018, 2022, Jensen *et al*. 2022). Although we recognize that a thorough discussion of eco-evolutionary dynamics is beyond the scope of this report, we stress the importance of considering phylogeographic structuring in developing approaches to understand marine mortality.

Despite the strong academic support for taking an integrated ecological-evolutionary approach, few conservation management programmes explicitly do so in their applied research, assessment and monitoring work (Casey *et al*., 2016). Brodersen and Seehausen (2014) ascribe this to: 1) biodiversity managers not having taken on board the importance of evolutionary diversity and processes, and 2) a lack of evolutionary biologists in applied conservation management. This is not helped by two further factors: 3) the loose, inconsistent, use of “stock”, “population” and associated terms in fisheries management literature (Waldman, 2005; Waples and Gaggiotti, 2006; Casey *et al*., 2016; https://www.lawinsider.com/dictionary/fish-stock), and 4) the historical difficulty of identifying evolved diversity (King and Burke, 1999; Waples and Naish, 2009).

3.2 Considerations of interactions among growth, maturation and survival at sea in marine mortality hypothesis development

Salmon marine return rate has declined dramatically across the Atlantic, indicating a degradation of environmental conditions during the marine life of salmon. Return rate is generally estimated at the population level, as the ratio of returning adults to out-migrating smolts, per smolt cohort. Return rate depends on the 'instantaneous' survival rate, and the duration of the marine phase which is driven by the timing of the maturation decision. It is assumed that the longer the salmon spends at sea, the lower are their chances of survival.

Marine growth has been positively correlated to return rate in several studies (e.g. Tillotson *et al.*, 2021; Todd *et al.*, 2021; Tréhin *et al.*, 2021; Vollset *et al.*, 2021). Good growth conditions in the early months at sea would allow salmon to build up lipid stores and better survive the harsh winter period. Good marine growth is thus assumed to improve 'instantaneous' survival rate. There is also empirical evidence that marine growth is negatively correlated with the 'age at maturation' decision. Good growth conditions would therefore allow salmon to reach a hypothetical threshold of physiological conditions suited for initiating maturation and return after only one winter at sea (Mobley *et al.*, 2021; Tréhin *et al.*, 2021). Thus, good marine growth is expected to lead to reduced duration of the marine phase and an early return. Thus, the negative effect of a decrease in marine growth on return rate can be biologically explained by either one or the combination of those two processes, namely I) a decrease in 'instantaneous' survival rate and/ or ii) an increase in the duration of the marine phase.

In addition, the influence of marine growth during the early months at sea on the maturation decision is likely to be very different between males and females, as females need to reach a higher threshold of physiological conditions than males to mature (Mobley *et al.*, 2021; Tréhin *et al.*, 2021). Hence, the interactions between growth, survival and maturation also depends upon the sex of the fish, which further complicates the demographic consequences of changes in growth at sea.

The intricate links between growth, survival and maturation and the underlying eco-evolutionary dynamics (section 3.1) create difficulties when attempting to draw conclusions regarding underlying mechanisms driving declines in salmon return rate. An integrated life cycle approach, explicitly providing for key demographic transitions (e.g. the Life Cycle Model approach being developed by the ICES-WGNAS group) could be recommended as a way to develop further research in this area.

3.3 Taking marine growth variation as an example of issues relevant to the development of marine survival hypotheses

Many studies have analysed growth patterns of Atlantic salmon in individual rivers or multiple rivers in close proximity to each other (e.g. Hogan and Friedland, 2010; Peyronnet *et al.*, 2007; Barajas *et al.*, 2021). However, larger-scale studies (e.g. Vollset *et al.*, 2022) provide unique opportunities to discern common or distinct trends in growth patterns that may be related to changes in ecosystem conditions and population dynamics at regional to basin scales. Whether reduced marine growth leads to reduced marine survival, a change in the sea age at returns, and therefore declines in abundance is an obvious hypothesis to be tested.

Studying marine growth at the basin scale can be informative for several reasons (Friedland *et al*., 2000, 2006, 2009; Peyronnet *et al*., 2007; McCarthy *et al*., 2008; Hogan and Friedland, 2010; Tillotson *et al*., 2021; Barajas *et al*., 2021; Todd *et al*., 2021; Vollset *et al*., 2022). First, temporal and spatial synchrony can inform the extent to which different salmon populations are affected by the same environmental factors. Second, common trends or shifts in growth among populations can reveal large-scale alterations in the marine environment. Third, differences in marine growth are likely related to variation in survival, abundance and sea age composition of returns. Lastly, variations in marine growth can be linked to variations in environmental variables (e.g. sea surface temperature), providing insight into how changes in marine condition affect salmon biology. Hence, a pan-Atlantic study of marine growth and its relation to the ocean environment and its effect on survival and age at maturation would be highly informative to better understand the biology of the Atlantic salmon at sea. In turn, such knowledge may allow us to better understand historical changes in abundance and build predictive models and scenarios for the future. However, there are several biological, methodological, and statistical considerations to be made for such a study.

3.3.1 Biological considerations

1. Survivor bias: Marine growth is typically only retrieved from fish that survived their ocean migration. Hence, one can question the representativeness of these returned fish for the marine growth experienced by all fish at sea. If good growth is positive for survival, the fish that grew poorly will not have survived and the average growth of the returned fish will be an overestimate of the average growth of all fish. This survival filter may reduce heterogeneity between individual growth trajectories, thus resulting in low statistical power to detect underlying ecological mechanisms. Aligning marine growth datasets from individual cohorts sampled at different times, and ideally before their return (i.e. fish harvested at Greenland or Faroes and subsequent adult returns from major contributing stocks) may however provide insights into the dynamics of this survivor bias.
2. Survivalvs.maturation: Growth may affect both survival probability and the probability of maturing (Tréhin *et al*., 2021). Both affect salmon abundance, as the fish delaying maturation have lower survival probability because they stay longer at sea. On the other hand, delaying maturation may not be negative for population growth, as fecundity increases with sea age (through body size).
3. Spatio-temporal distribution: Our ability to identify where and when salmon are in the ocean, and to align this information with patterns of individual growth rings and microchemistry of scales, is currently limited. Hence, it is hard to know whether an observed synchrony in growth is due to fish sharing feeding grounds or synchrony in food availability across feeding grounds. In addition, we also lack specificity on the timing of formation of certain scale features (e.g. annuli, winter minimum) although recent progress has been made in estimating the timing of marine annulus deposition (Carlson *et al*., 2021). Having a clearer spatio-temporal understanding of salmon marine distribution and the temporal dynamics of feature deposition would strengthen our ability to explain the ecological drivers of change in marine growth

3.3.2 Methodological considerations

1. Scale sampling: The location of where the scale sample is taken on the fish should be standardized to reduce heterogeneity in scale shape and increase the probability of obtaining a complete scale (i.e. not a replacement). Standard sampling for this species has previously been defined as scales coming from the left side of the fish, 3 – 6 rows above the lateral line and posterior to the dorsal fin (Shearer, 1992).
2. Intra-individual and intra-scale heterogeneity: Typically, only a single scale per fish and a single scale radius per scale are measured for growth increment analysis due to the time required to extract information. However, heterogeneity exists in radius measures and number of circuli both among and within scales. It is not clear yet the degree to which this heterogeneity is statistically important when making comparisons in growth among individuals or stocks.
3. Growth measurements: There are several different methods to measure the growth from the circuli spacing in the scales. Some experts have measured growth along the longest radius of the scale while others measured it along a line at an angle to the longest radius. Growth is often divided into first summer and winter growth for the different years, and what is considered the end of these zones may vary. Some labs do not differentiate between summer and winter and only measure the total yearly growth in the scale. Some of the current data are based on so-called back-calculated growth that uses both the fish length and the growth measure in the scale to calculate how much the fish has grown in body length according to a formula. There exist different formulae for performing back-calculation (Francis, 1990) – though the Dahl-Lea method is most often applied to Atlantic salmon – and different metrics to quantify fish length (e.g. fork lengthvs.total length). However, very few empirical data exists to parameterize these formulae. A more recent technique for measuring growth is to measure the distance between each circuli in the scales. This gives a more complete and accurate picture of scale growth throughout the life of each fish that is independent of the back-calculation method used. However, methods on how to compare scales with different number of circuli are still in their infancy (e.g. Todd *et al* ., 2021; faster growth generates both longer distances and more circuli) and the rate of circuli deposition on scales seems to be variable (as opposed to deposition rate in otoliths), which makes their interpretation challenging (Thomas *et al* ., 2019). Emerging techniques in image analysis and machine learning may be applicable to images of salmon scale to automatically measure inter-circuli distances along any number and position of scale radii. This method would be less resource-intensive in that it requires scale preparation and imaging, but not detailed increment detection by scale readers. This could be applied to more scales and more measurements within scales. However, the challenges remain in comparing scales/radii with different number of circuli and the interpretation of inter-circuli spacing, as outlined above.
4. Spatial scale of the observations: Growth is measured on individual fish from individual rivers, while abundance is often estimated at relatively large geographic scales (e.g. stock complexes encompassing many rivers). If the growth of the fish measured from scale sampling programmes in-river that do not fully represent the average marine growth of groups at the larger geographic scale, the effect of growth will be most likely be downwardly biased due to attenuation (see e.g. Hansen and Bartoszek 2012).
5. Sample size: As growth measurement is time consuming, the number of individuals included in a study may be a sub-selection of the available samples. Reduced sample size may underestimate heterogeneity in growth trajectories (see 4, above). Use of automated scale reading tools has the potential of bolstering sample sizes.
6. Scale erosion: When adult salmon stay in freshwater, their scales are increasingly eroded, resulting in a “spawning mark” (Shearer, 1992). In this process, some of the most recently

deposited circuli will be missing – sometimes whole winter bands may be eroded if the fish stays in freshwater for several months (ICES, 2011). Removing eroded scales from a study may bias the sample against late returning fish, which may potentially have a different growth trajectory. Erosion of scales also challenges our ability to track growth trajectories in multiple spawners.

3.3.3 Statistical considerations

1. Correlationvs.causation: Time-series analyses attempting to link marine growth with survival, abundance, or environmental variables suffer from the well-known statistical problem that whereast correlation may imply causation, it cannot be used to prove it. For example, if both growth and abundance have declined over time, we will find a positive correlation, but we do not know whether abundance has declined because of reduced growth or because of other factors temporally correlated with growth. There are, however, statistical methods that attempt to mitigate this problem such as de-trending, or using part of the data as a training dataset and the rest as a test dataset (i.e. to test predictiveness), and the application of the Granger causality test.
2. Non-stationarity in ecological mechanisms: As the environment changes, the responses of individuals to the environment may change too. It is likely that the relationship between growth and survival or any key environmental driver is not linear and may change in direction over time. Strong evidence of a non-stationary influence of growth on survival has already been demonstrated for Atlantic salmon sampled at West Greenland from 1968-2018 (Tillotson *et al.*, 2021). Non-stationarity, as well as the duration of the time-series analysed, may affect our ability to identify and predict individual responses (Claireaux *et al.*, 2022).
3. Separating the effect of growth on survival and maturation probability: This is not an easy task. First, ratios of the number (N) of returners (N1SW/(N1SW + NMSW) reflect probability of maturing given survival, and therefore a strongly upwardly biased estimate of probability of maturing across all individuals at sea. The bias may vary among years due to variation in the ratio of pre- and post-maturation survival. Second, sampling effort varies between capture years for a given river, and needs to be controlled when calculating the N1SW/(N1SW + NMSW) ratios for smolt cohorts.
4. Time-series of growth: Typically, scale growth patterns are delineated into discrete periods (e.g. all marine growth, first summer growth, second summer growth) which may not be statistically independent. Consideration of variations in the continuous series of scale growth measurements from individual fish through, for example, hierarchical time-series clustering may elucidate important patterns in growth among salmon not detectable by traditional feature analyses.

3.3.4 Conclusions

A pan-Atlantic study of marine growth and how it relates to salmon population dynamics is promising, ambitious, but not at all impossible. A first step towards such a study is to generate an inventory of available data including the methods and criteria used to extract the growth data. Second, one should examine the degree to which different measures of growth taken in the fish scales are comparable across datasets, and then whether potential differences are of importance to the biological question (e.g. whether differences affecting growth trends would be discerned among datasets). If differences in methodology are suspected, a standard set of scales could be processed by the participating laboratories and the resulting data could be analysed to look for biases. From such an exercise, one would learn whether it is possible to combine existing datasets or account for differences in methodology statistically among the analyses. If this is not possible, one may consider measuring growth in scales from the different regions using a standardized method. In this regard, machine-learning algorithms may provide an interesting opportunity to develop a unified approach to retrospective growth analysis at the basin scale. However, we know that the interpretation of growth periods on scales is highly reliant on the opinion of experts who developed a detailed knowledge of scale patterns in their study rivers, and an automatic approach may have its own caveats. Based on these inter-calibration exercises, recommendations could be proposed to orientate future data acquisition. The feasibility of the work needed to address all these key challenges will greatly depend on the resources available.

3.4 Developing the concept of space-time domains for marine mortality hypothesis testing

In their evaluation of spatial synchrony in the responses of salmon population abundance to climate change Olmos *et al.*, (2020) applied two marine space-time domains applicable at the Stock Unit level. The authors provide an important spatial and temporal framework to represent the general conditions for the first part of the marine phase and the most comprehensive review of the literature available (Olmos *et al.*, 2020 Supplementary Information is included in a working paper) to build a theoretical outline of marine domains used during the seven month post-smolt period until 1st January (Figures 2 and Figure 3). Domains are presented either as early phase transitional (three months) specific to stock units, or geographically proximate groups, or common/ shared (four month) areas that multiple groups of post-smolts use during the later phase of the first year at sea.

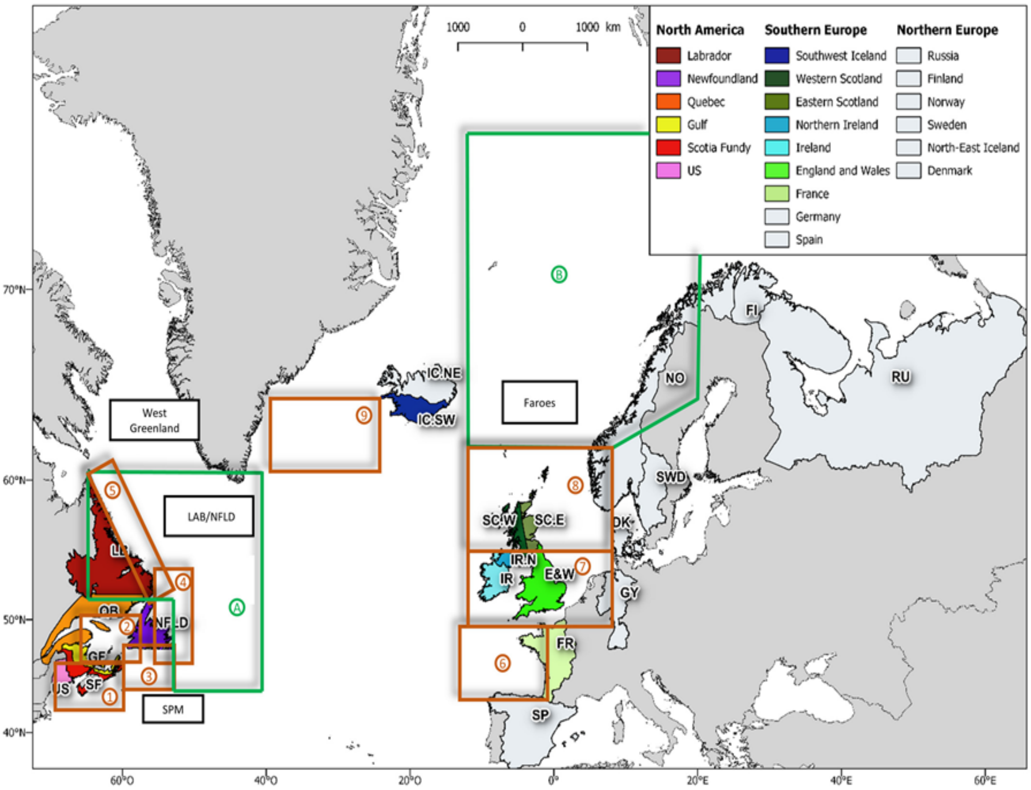


Figure 3.2. Location of the 13 SU and specific and common space–time domains considered in North Atlantic. SU of North America: GF, Gulf; LB, Labrador; NFLD, Newfoundland; QB, Quebec; SF, Scotia-Fundy; US, USA. SU in Southern Europe: E&W = UK (England and Wales); E.SC, UK (Eastern Scotland); FR, France; IR, Ireland; N.IR, UK (Northern Ireland); SWIC, Southwest Iceland); W.SC, UK (Western Scotland). Specific and common CSG space–time domains are in orange and green respectively (Source: Olmos *et al.*, 2020).

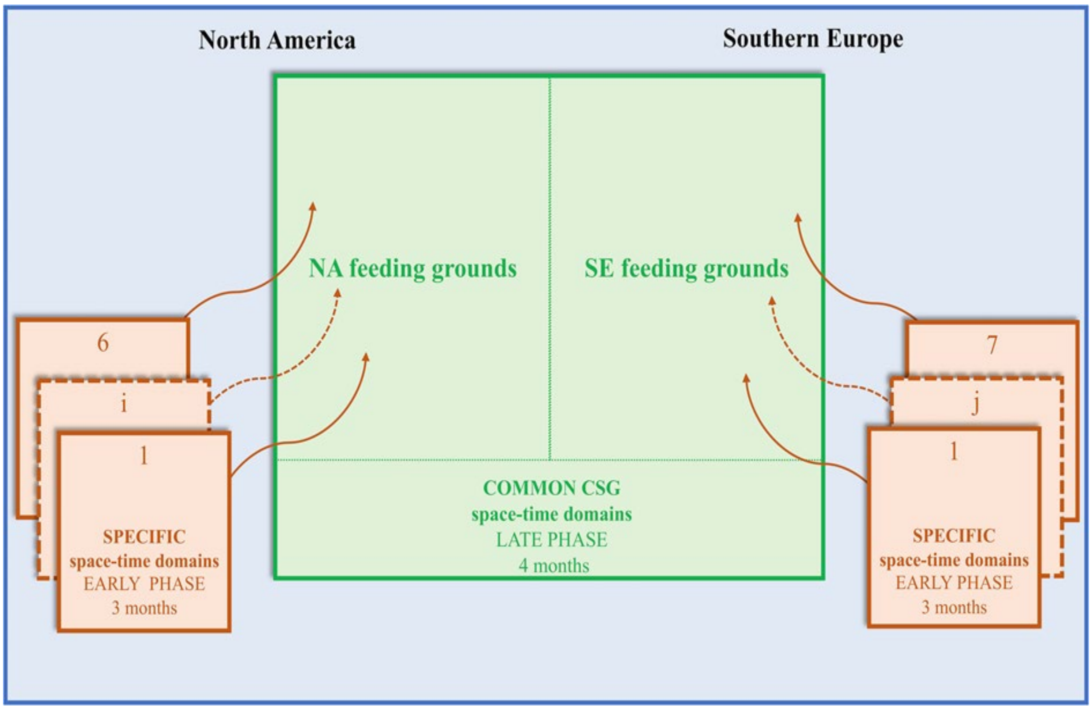


Figure 3.3. Theoretical representation of the hierarchy of space–time domains. Orange: space–time domains defined as transit habitat occupied by post-smolts during their first two months at sea (specific domains). Green: space–time domains corresponding to the habitat occupied by salmon in the later phase of the first year at sea, associated with feeding areas, common to all SU within the same CSG (Labrador Sea and the Norwegian Sea for NA and SE CSG respectively; common domain). SU, stock units (source: Olmos *et al*., 2020).

Agreeing on an approach for considering how to effectively partition the marine phase into stock-grouping relevant “marine domains” (e.g. Olmos *et al*., 2020) may provide a level of organizational structure within which wider resources can be mobilized and shared at the temporal and spatial scales required to advance cooperative hypothesis testing efforts. Including options to propose space-time domains as “theatres” within which certain processes and mechanisms are driving salmon mortality would appear to be an important step.

Specifically, including an appraisal of marine domains may facilitate more effective and efficient targeting of:

1. Future data scoping and matching;
2. Future data acquisition;
3. Data averaging/integration; and
4. Synthesis of new data.

Considering how to effectively partition the marine phase of the salmon life cycle may also be of use when attempting to source and refine ecosystem datasets that could generate appropriate condition indicators, and assist forecasting efforts. To build on the start made in WKSalmon1 (ICES, 2020) in considering options for developing the domains concept, questions were posed in a working paper and discussed by the group.

The group agreed to adopt the initial framework of space-time domains proposed by Olmos *et al.*, (2020) but also discussed options for possible refinement and extension. Clearly, there are many locations that Atlantic salmon occupy during their marine phase, with migration corridors specific to continental stock groups and shared feeding grounds where these groups converge (Olmos *et al.*, 2020). With such diverse and multiple migration routes, and mixing of stocks in common shared feeding areas, there must be recognition that asynchronous or synchronous signals and responses will likely be encountered. Additionally, data/knowledge deficiencies are likely to be widespread among the marine salmon domains, which will likely inhibit progress. Where there appears to be little prospect of identifying signals that can be linked to one or more of the marine domains this represents a current knowledge gap but does not in itself prevent progressing with the hypothesis evaluation. Otherwise, the only signals that could be used to generate hypotheses, testable across the default "marine phase," would be those spanning the time between the commonly used audit points of smolt migration and adult return.

The Norwegian Sea is an important migratory pathway and feeding area for European salmon. Post-smolts from a range of European countries, from Spain in the south to Norway in the north, are found in the Norwegian Sea in the period June-September (Gilbey *et al.*, 2021). The Norwegian Sea may also be an important feeding area for salmon during winter (Jacobsen and Hansen 2001) and early spring (Hansen and Jacobsen, 2000). There are regional differences in oceanographic conditions and species composition and abundance of plankton and small fish within the Norwegian Sea. Hence, the post-smolt diet varies geographically according to prey availability (Utne *et al.*, 2022). In addition, post-smolts from different European regions have been shown to have varying temporal and geographic distributions within the Norwegian Sea (Gilbey *et al.*, 2021). For feeding Atlantic salmon it was suggested that the Norwegian Sea can be further divided, from the single common domain proposed in Olmos *et al.*, (2020), into three main regions (Figure 3.4: Utne *et al.*, 2022).

Following these directions, it was possible to propose modifications to the 'Marine Domains Concept' (Olmos *et al.*, 2020) to reflect varying responses for growth occurring during particular times of the marine life phase (Table 3.1). There may be merit in developing collective thoughts on the drivers of marine mortality changes to include domains where we believe pressures on salmon growth and survival may be acting in very local areas or specific time periods (e.g. during the initial day or two of marine entry or before river re-entry as an adult). Transition for post-smolts and returning adults through estuary and coastal areas has long been considered as an important and highly variable factor in influencing the eventual marine survival (e.g. Butler *et al.*, 2011; Russell *et al.*, 2012; Thorstad *et al.*, 2012). These periods are therefore proposed as 'Hyper-specific domains' (e.g. within 50km of a river mouth). The 'Freshwater domain' is included for completeness, representing a growing body of evidence highlighting the influence of changes to freshwater growth on eventual marine survival (e.g. Gregory *et al.*, 2019).

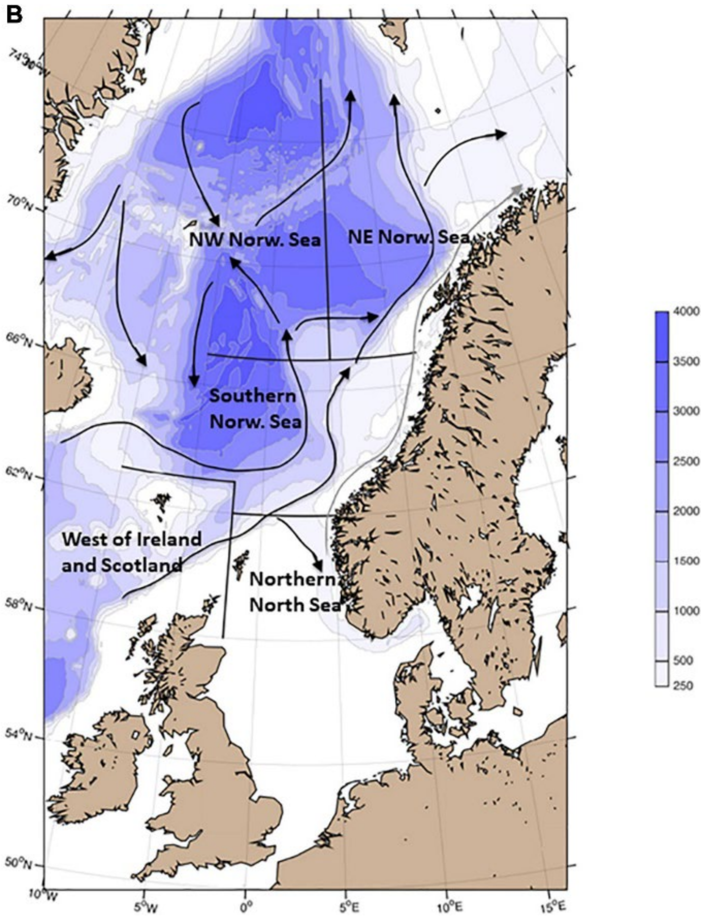


Figure 3.4. **Three proposed Atlantic salmon feeding areas within the Norwegian Sea. The arrows represent the general currents in the NE Atlantic Southern Norwegian Sea (62-67 ˚N). The migratory pathway for post-smolts in this region is along the slope on the eastern side of the Norwegian Sea in warm Atlantic water flowing northwards. A general pattern is that post-smolts when reaching the Vøring plateau at 67˚N either migrate northwestward or follow the slope further northeastward. The migration pattern seems to vary greatly in the region of the Northeastern Norwegian Sea (north of 67˚N and east of 5˚E). Source: Utne *et al*. (2022).**

Table 3.1. Proposed list of Atlantic salmon space-time life phase 'domains' for consideration and incorporation in further development and testing of specific hypotheses about growth, maturation and survival

Proposed space-time domain	Description	Note
1	Hyper-specific rearing juvenile freshwater	https://nasco.int/rivers-database/
2	Hyper-specific transit post-smolt (estuary and coast): 50km from river mouth	
3	Specific transit early post-smolt (shelf seas)	Encompassed within early phase specific transit domain proposed by Olmos *et al.,* (2020)
4a	Common feeding Labrador Sea	
4b	Common feeding Southern Norwegian Sea	
4c	Common feeding Northwest Norwegian Sea	
4d	Common feeding Northeast Norwegian Sea	
4e	Common feeding West Greenland Sea	
4f	Common feeding Faroes	
5	Specific transit adult return (shelf seas)	
6	Hyper-specific transit adult return (coast and estuary)	
7	Hyper-specific adult migration freshwater https://nasco.int/rivers-database/	

3.5 Developing a marine mortality hypothesis evaluation framework for Atlantic salmon

Widely agreed general factors considered of importance in determining marine survival were extracted from the list of candidate hypotheses and proposed as: growth, predation, disease, salmon aquaculture, marine fisheries and freshwater carry-over effects (Table 3). These were viewed as critical topics for collective attention to determine their linkage to environmental drivers, and the development of auditable and repeatable testing of marine mortality hypotheses.

The factors represented the most likely drivers to explain the regional patterns of decreasing marine return rates observed in Atlantic salmon, and were discussed by the group with reference to:

- Strength of evidence for possible mechanisms behind changes in these factors;
- Possible causal agents associated with the mechanisms, and
- Provision of links to resources required to further assess their relative importance for evolutionarily defined river-specific and regional salmon conservation units.

Although responses from specific factors are often not easily separated, their relevance was initially discussed from the perspective of their direct or indirect effects on growth and physiological condition.

Table 3. Possible factors of importance in directing the temporal patterns of marine return rates in Atlantic salmon

Possible factors of importance in directing the temporal patterns of marine return rates in Atlantic salmon	**Description**
Growth	Changes in the observed patterns of marine growth (from analysis of scale and/or otoliths) indicating poor feeding conditions and suboptimal energy acquisition leading to higher mortality
Predation	Changes in the incidence rate of predation due to marine predator community abundance or behavioural changes
Disease	Changes in the prevalence, and/or severity of known salmon diseases or new sources
Salmon aquaculture	Recognized negative effects on growth and survival as a consequence of effects associated with a growing salmon aquaculture industry
Marine fisheries	Possible changes in the capture incidence rate and overall severity of the activities of both targeted and non-target marine fisheries
Freshwater carry-over effects	Changes to conditions during freshwater growth stage that contribute to reduced survival during the marine phase

Although there was overall agreement on the likely importance of the factors proposed and general organization of data requirements in support of testing, a considerable range of opinions on the current state of knowledge of, and evidence in support of, many of these factors were evident. For example, some concerns were expressed about how to represent and decipher any signals of change. This was discussed in relation to evidence suggesting the existence of differential responses from individual stocks and region-specific stock complexes to similar marine changes (e.g. Vollset *et al.,* 2022), non-stationarity in these responses through time (e.g. Tillotson *et al.,* 2021 and regionally varying responses in salmon growth across time periods (Todd *et al.,*2021; Vollset *et al.,*2022).

The group recognized a need to be able to document the support for acceptance of any given hypothesis for any particular evolutionarily defined conservation unit at a given spatial and temporal scale of examination. There was agreement that further development and testing of any specific mortality hypotheses would require a system to allow careful evaluation in light of supporting evidence, data gaps and high levels of response variation at the level of the individual, populations and higher order evolutionary population complexes. Organization of wide ranging data resources relating to the six general factors was also proposed for discussion using the existing data groupings in an existing online data catalogue database (Table 3.2). Using a small number of initial factors, standardized data descriptors and organization using a hierarchy of data categories, this demonstrated how data resources from multiple sources might be organized and mobilized for cooperative analysis and hypotheses testing.

Table 3.2. Possible factors of importance in directing the temporal patterns of marine return rates in Atlantic salmon and outline data groupings currently used in the SalHub online data catalogue that could be useful for future hypothesis testing.

Possible factor	Possible mechanism	Climate change drivers-ocean and atmosphere	Salmon marine distribution	Salmon marine growth and condition	Salmon freshwater growth and condition	Smolt migration phenology	Predator popn dynamics and feeding behaviours	Prey availability and quality	Competitor popn dynamics	Commercial fishing pressure	Salmon farming data	Fish diseases
1 Predation	Increased predation pressure	■	■				■			■		
	Post-smolts in poorer physiological state are more susceptible to predation	■	■	■	■		■	■	■			■
	Smaller post-smolts are more susceptible to predation	■	■	■	■	■	■	■	■			
2 Growth	Variation in the quality and quantity of suitable prey	■	■	■				■	■	■		
	Increased competition for available prey	■	■	■				■	■	■		
	Mis-match between initial marine migration phenology and availability of prey resources	■	■	■		■		■	■			
	Energetic costs in marine phase increasing	■	■	■	■			■	■			

	Smaller post-smolts have less energy storage and lower resilience during period/s of reduced feeding opportunity	🟨	🟦	🟦	🟦			🟩	🟧			🟨
3 Disease	Cumulative stressors increasing disease severity	🟨	🟦	🟦				🟩	🟧		🟥	🟨
4 Salmon aquaculture	Increased mortality risk resulting from aquaculture mediated ectoparasite encounters	🟨	🟦	🟦	🟦	▨		🟩	🟧			
5 Fisheries	Variation in the incidence and severity of commercial bycatch	🟨	🟦							🟩		
6. Carry-over	Changes to conditions during freshwater growth stage that contribute to reduced survival during the marine phase	🟨	🟦							🟩		

Previous attempts to evaluate and focus efforts on testing priority marine survival hypotheses for salmon have advanced untangling the complex relationship among marine growth, maturation and survival but have not comprehensively described the wealth of supporting evidence, or attempted to mobilize data sources. This restricts the opportunity for re-analysis and extension to improve our understanding. To advance this topic we assess how we can provide sufficient robust evidence to support our acceptance of any mortality hypotheses that identify mechanisms acting during particular time periods, stages and areas during the salmon's marine phase. Any mechanisms that are proposed as a result of hypothesis testing must adequately explain the historical changes in survival rates. Knowledge of the detrimental mechanisms may then allowfurther consideration of how to correct them or, more likely, to allow prediction of whether they will persist or change in the future.

The workshop proposed the development of a more comprehensive hypothesis evaluation framework and a process that could allow:

- The collective input and assessment of the current state of knowledge in support of the acceptance of particular hypotheses regarding the causes of reduced marine survival;
- The identification and mobilization of resources in support of future cooperative research to further test hypotheses and identify knowledge gaps; and
- The identification of resources required to develop hypotheses further and allow a more mechanistic approach to evaluate the importance of potential "suspects".

One way in which this process could be developed is proposed in Figure 3.5. This represents a hierarchical decision process for considering general factors and hypothesis development alongside gathering and organising supporting information. It provides an opportunity to progressively advance from the identification of general ecosystem signals, to possible mechanisms and associated causal agents. Identifying the unit and period of study are important qualifiers for initially framing any hypotheses, and advancing through the steps requires credible (and accessible) evidence to be presented allowing further refinement of options. At each step, the information presented can be linked to a database for subsequent targeted retrieval and further cooperative evaluation.

An important first step in the process is to ensure the units of study are properly defined within an evolutionary framework, wherever possible, rather than by arbitrary geographical or national delineations. These units may be considered at the level of individual salmon population, metapopulation or phylogeographic group.

One way of advancing and developing the management of information gathered using such an approach could be via hosting it as an accessible online tool. This could be made available to WKSalmon participants (and a wider agreed-upon group of expert users) to access and input their information, appropriate to where their expertise lies. Contributions would be securely managed and organized to allow focused retrieval of information linked to the development of ideas to promote future group evaluation.

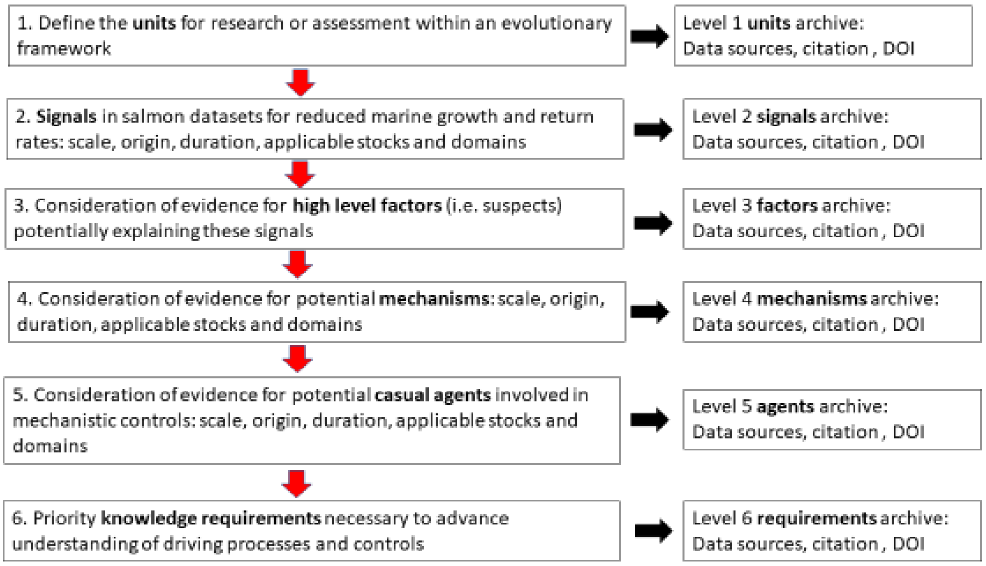


Figure 3.5: A schematic of proposed steps in a Hypothesis Evaluation Framework

Step 1. Evolutionary units to be characterized: Given that evolved population diversity defines the fundamental units that must be focused on to understand the demographic and ecological dynamics of Atlantic salmon in the marine environment, the focus of data collection, analysis and modelling must be on the performance and state of these units.

Step 2. Assess signals from salmon data: To provide support for the existence of the wide scale changes in the marine survival rates we are seeking to explain. This is further defined by providing a specified time period for subsequent consideration of evidence in support of any hypotheses. The discovery and source of signals recorded at each level in the decision process provide an audit trail for the subsequent evaluation of supporting evidence and the existence of knowledge gaps.

Step 3. High-level factors: Candidate factors (*or suspects*) can be selected for development of more specifically targeted hypotheses. Supporting evidence from research and associated ecosystem datasets collated.

Step 4. Mechanisms. Developing ideas on the potential mechanisms behind proposed factors and indications for the scope, extent and the space-time periods (domains) where the mechanisms may be exerting effects over the patterns of marine returns that we see.

Step 5. Causal agents. Evaluation of available evidence in support of identification of potential causal agents involved in the controlling mechanisms. Further expansion identification of possible mechanisms, with opportunity to list supporting evidence (and identify knowledge gaps).

Step 6. Priority knowledge requirements. Identify current limitations and resources necessary to advance understanding. Group assessment of the evidence trail highlighting weaknesses and knowledge gaps, along with possible actions to address them.

4 Mobilizing key data sources in support of marine mortality hypothesis testing

4.1 Data issues and complexity of mobilization

Salmon are a heavily researched and managed group of species. They are data rich, with many monitoring campaigns producing time-serieslong time-series, but there remains a lack of knowledge flow from these activities towards actions that address the issue of population declines. A key issue that must be acknowledged and addressed in advancing the mobilization of salmon and salmon ecosystem data will be its' assignment to the appropriate level of evolutionary conservation units (e.g. population, meta-population, phylogenetic group).

There is a critical requirement to understand the existing data landscape so that salmon researchers can judge the analytical power of the evidence available, and have a realistic way to initiate collaborations with the data owners. Improved data sharing is proposed as part of the solution to this problem by improving research power and confidence, leading to more confident knowledge mobilization.

A catalogue to capture the breadth of existing data that can describe salmon biology, related biological processes and their physical environment has been proposed before (e.g. Hutchings and Jones, 1998; ICES, 2010; ICES 2020). Addressing data accessibility issues is currently a priority area in the current science plan for the Atlantic Salmon Research Joint Venture programme in North America (https://www.dfo-mpo.gc.ca/science/publications/asrjv/plan/index-eng.html). This desire was reiterated during the WKSalmon2 2 meeting and the group identified data mobilization as an issue requiring attention within the salmon science community:

ICES (2020): *"Despite being publicly available, it is not easy or straightforward to navigate and extract the data of interest"*, and *"In the longer term, a fuller compilation of such metadata with search variables would facilitate the exchange and the development of larger collaborations."*.

The NASCO/IASRB "Metadatabase" went a way towards this goal. As described in the NASCO Board's Scientific Advisory Group (SAG) in 2013 the purpose of the Metadatabase was to:

'... [be a] means to advertise the availability of the valuable and unique datasets related to the marine phase of Atlantic salmon. It would contain details of where databases and sample collections are held, together with details of the data or samples and conditions governing their accessibility.'

Uptake of this tool as a community resource has not been as hoped, and the metadatabase is soon to have a final update and will then become a static resource.

Despite a clear desire, for more openness, the current state of the salmon 'Research Data Landscape' is still opaque. There is an acknowledgement that many data exist (Birnie-Gauvin *et al.*, 2019; Woodward *et al.*, 2021), but they are not clearly signposted online, are widely dispersed, and are minimally accessible outside relatively narrow research silos (ICES, 2020). Greater openness and clarity could increase opportunities for data collaboration, inform the community which hypotheses can be tested, allow unique insights, and drive knowledge creation.

Many factors sustain this status, e.g. interoperability issues, concerns regarding uninformed usage/misuse, and technical barriers. They are not peculiar to the salmon research community, and are explored in depth in many papers regarding ecological informatics and data mobilization (e.g. Perrier *et al.*, 2020). What is peculiar to salmon research in this respect is the widespread scale of data gathering and research activities. To break down some common data mobilization hurdles that all ecological research struggles with, it is important to have a support mechanism in place that can guide a specific community to the best tools and practices that already exist. Now, Data Mobilization for Atlantic salmon is confounded by a plethora of standards and available mobilization tools.

It is important for a solution to be developed for researchers to more quickly and easily make their data findable in a contextualised space to directly deal with the opacity problem. WKSalmon1 created the beginnings of a comprehensive and context rich list of salmon relevant data resources. This provided a starting point to develop standardized descriptions of data sources and present them via a keyword or topic-led search- interface.

Before exploring how data sources may be made more readily accessible for hypotheses testing, there were a number of areas that the group discussed in relation to building up a comprehensive data resources list.

4.2 Mobilizing relevant salmon biological data from other sources

A large variety of data sources will be needed to support future marine mortality support hypothesis testing for Atlantic salmon. These data sources may include measures of Atlantic salmon abundance and productivity at varying geographic and conservation-unit scales (e.g. river population-specific, regional, basin-wide), a wide variety of oceanographic data types (e.g. physical, chemical, and biological), or the abundance and effect of salmon predators and the activities of fisheries.

An additional data type describing the biological characteristics of individual salmon conservation units at varying scales over time will also be useful towards evaluating if changes in phenology are associated with changes in salmon productivity and/or environmental change.

4.2.1 Study Group on Biological Characteristics as Predictors of Salmon Abundance

In 2009, ICES hosted a study group meeting entitled Study Group on Biological Characteristics as Predictors of Salmon Abundance (SGBICEPS). The meeting was intended to further the work of the WGNAS to *'continue the work already initiated to investigate associations between changes in biological characteristics of all life stages of Atlantic salmon, environmental changes and variations in marine survival with a view to identifying predictors of abundance'*. The terms of reference (ToRs) for SGBICEPS were as follows:

a) Identify data sources and compile time-series of data on marine mortality of salmon, salmon abundance, biological characteristics of salmon and related environmental information;
b) Consider hypotheses relating marine mortality and/or abundance trends for Atlantic salmon stocks with changes in biological characteristics of all life stages and environmental changes; and
c) Conduct preliminary analyses to explore the available datasets and test the hypotheses.

In total, two SGBICEPS meetings were held (ICES, 2009; 2010). A standardized database template was developed and forwarded to various salmon experts from across the North Atlantic. The database template was meant to facilitate the collation of river-specific biological characteristics data related to smolt emigration timing, freshwater and marine age of adult returns, adult return size and sex and maiden spawners proportions. Data were submitted from over 30 rivers within Canada, USA, Iceland, Russia, Finland, Norway, Sweden, UK (England and Wales, Northern Ireland and Scotland) and France. A few time-series of data were initiated in 1910, but the majority of the dataseries started in 1971 with 2009 being the last year of available data. A number of exploratory analyses were conducted by SGBICEPS looking at the spatial and temporal trends of biological characteristics as well as an exploration of potential two-way relationships within the database. SGBICEPS also reviewed a large number of published and unpublished case studies that investigated time-series of biological characteristics and changes in salmon productivity relative to environmental variables. SGBICEPS concluded that the study group had gone as far as it could in addressing their ToRs and that further progress might best be made by other groups.

The work of the SGBICEPS was continued after the study groups met and resulted in a peer reviewed manuscript that investigated the influence of freshwater factors and biological characteristics of smolts on trends in Atlantic salmon marine mortality (Russell *et al.*, 2012). This investigation used only a small proportion of the biological characteristics data collated by SGBICEPS, but highlighted the utility of having such a database for conducting large-scale investigations into the drivers of Atlantic salmon productivity across the range of the species.

The archived SGBICEPS database is constrained both spatially and temporally as only a small fraction of the available monitored rivers data is contained within and the last update of the data occurred in 2009. An updated and more comprehensive database would be beneficial to future investigations into the marine mortality and productivity of Atlantic salmon. However, there are a number of considerations before embarking on such an effort.

4.2.2 Updating SGBICEPS

a) By what mechanism should the update be conducted?

- Should the update be conducted by a new ICES Working or Study Group, the WGNAS, NASCO, individual researchers?
- Should the update be conducted by some official mechanisms (ICES data call, NASCO request to Parties) or informally peer to peer?
- Should the update be conducted sporadically as needs arise or annually?

b) SGBICEPS noted a number of caveats of the collated data and provided a number of suggestions for future efforts.

- These suggestions should be revisited and formally addressed prior to any subsequent updating/expansion effort.

c) Should the database be updated in its current form or should it modified to be more comprehensive?

- Should data from additional monitored rivers be included? If so, should this be on a volunteer basis or a more targeted and systematic approach?
- Should additional data types be considered for inclusion?

d) How should the resulting dataset be maintained and archived?

- Should the ICES Data Centre be utilized or the new Salmon Ecosystem Data Hub (SalHub; Diack *et al.*, 2022)?

e) When the collated data are used and published, how will the data suppliers be acknowledged?

- Would data providers be included as authors on published manuscripts or simply acknowledged for data provision?

The value of the large number of Atlantic salmon monitoring programmes across the North Atlantic cannot be understated. The collection of abundance, age, growth and other biological data from these systems are extremely useful and provide a measure of performance over time that can be used to investigate the drivers of Atlantic salmon productivity. The ability to combine biological characteristics data from numerous populations across the species range greatly increases the value of these data when compared to analysing a single river's data. There is a need to better utilize and collate these available datasets to maximize the benefit that can be provided by them towards our efforts to understanding of the marine (and freshwater) drivers of Atlantic salmon productivity.

4.3 Mobilizing physical oceanographic data

4.3.1 Making use of existing oceanographic products to describe past changes in salmon domains

Physical oceanography data provide context for key physical water column processes that affect ocean chemistry and pelagic and benthic living resources. Some of the processes of importance include major current pathways, frontal systems, gyres and retention zones, water column stratification and ocean salinity. There is a wide array of data collection platforms for such data including conventional conductivity, temperature, depth (CTD) profiles from ships, moored buoys with oceanographic sensors, ocean gliders, tide gauges, autonomous profiling floats (e.g. Argo) and satellite remote sensing of the photic zone. Many data originators have systematic long-term data collection programmes for physical oceanographic data to underpin real-time decision-making in support of ocean health and climate applications and reporting obligations.

A trend in recent decades is towards the aggregation of physical oceanographic datasets in large data aggregation initiatives such as the ICES data centre, EMODNet, Copernicus and SeaDataNet in Europe and the World Ocean Atlas and the CLIVAR and Carbon Hydrographic Data Office (CCHDO) at the global level. In many cases, ocean climatologies based on oceanographic observations from a range of available platforms are produced and updated periodically (see Berx and Hughes, 2009; Troupin *et al.*, 2010; Locarnini *et al.*, 2018).

4.3.2 Potential of ocean model simulations

The salmon research community can also benefit from the synoptic data provided by ocean model simulations. The WKSalmon1 review of available data noted that:

"Data from hind-cast model simulations are available but availability varies with domain and model selection. There is a range of different oceanographic models that potentially can provide simulated data. The quality of model simulations varies spatially and temporally, and different models have different strengths and weaknesses. These were not documented at WKSalmon." (ICES, 2020; Section 3.3.1.3)

Ocean simulations could help to fill data gaps and allow marine growth, maturation and survival hypothesis testing if they provide relevant variables in the domains used by salmon at sea and reproduce real-world patterns and trends. Global ocean model hindcasts have been used to investigate the effectaffect of environmental variability on salmon survival (e.g. Olmos *et al.*, 2019).

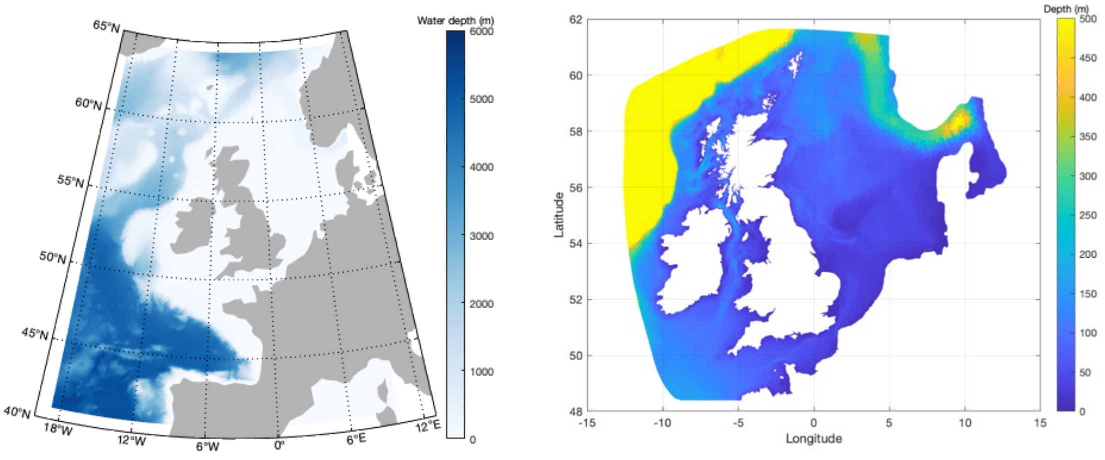
Understanding of marine survival will be enhanced by the use of recently available high-resolution regional models.

4.3.3 Example – AMM7 and SSW-RS

An example assessment is summarized here of two recently available regional hindcasts for the NE Atlantic: the Atlantic Margin Model reanalysis (AMM7v5) and the Scottish Shelf Waters Reanalysis Service (SSW-RS) (Figure 4.1). The study focused on the models' ability to represent changing ocean conditions along a key post-smolt migration route (the NE Atlantic shelf edge to the Norwegian Sea) during April to August. Relevant variables were compared with published studies and satellite data.

AMM7v5 is a coupled physical-biogeochemical three-dimensional ocean model hindcast (1993-2021) for the northwest European Shelf at 7 km lateral resolution and terrain following depth layers that are interpolated onto fixed depth bands down to 5000 m (Tonani and Ascione, 2021). Model outputs are daily and monthly means of physical (e.g. horizontal currents, temperature and salinity) and biogeochemical (e.g. concentrations of dissolved oxygen, nutrients and phytoplankton) components.

SSW-RS is a physical three-dimensional ocean model hindcast (1993-2019) of the Scottish shelf seas (Campbell and O'Hara Murray, 2021). It has an unstructured grid that allows bathymetrically complex areas to have high resolution: horizontal resolution varies from 1 km near the coast to 20 km in the open ocean. Terrain-following depth layers resolve the water column. Outputs are hourly instantaneous horizontal currents and sea surface height and daily mean temperature, salinity and horizontal currents.



(a) (b)

Figure 4.1. **Model domains for (a) AMM7 and (b) SSW-RS.**

It was concluded that data from these models could be used as a proxy for observed data for modelling environmental conditions during early marine migration. For example, the models reproduce expected variability of SST and seasonal phytoplankton dynamics along the migration route. The high spatial resolution of the SSW-RS model could be of particular use for modelling nearshore migration in detail. There were noted spatial limitations, e.g. the Vøring Plateau shared feeding area is beyond the northern edge of the model domains, and temporal limitations, e.g. the hindcasts only extend back as far as the start of the satellite oceanography era (1993 for SST and 1998 for ocean colour). This illustrates the need to combine these with other data sources.

The following outputs illustrate the sort of salmon-specific information, on a variety of space-time scales that can be derived from such models:

- Regional-scale perspective of the changing marine ecosystem, e.g. trend in SST over 1993-2020 in the AMM7v5 domain (Figure 4.2).
- Mean conditions over specific space/time domains, e.g. areas of migration track shared by different stocks.
- A salmon's-eye view of the marine environment, e.g. phytoplankton bloom timing derived from phenology metrics applied to AMM7v5 modelled phytoplankton concentrations "sliced" along the shared Atlantic shelf migration route used by many southern European stocks (Figure 4.3).
- Combine monitored river information with ocean model outputs to get stock-specific information, e.g. coastal SST from the high-resolution SSW-RS model on the date of post-smolt migration for different rivers (Figure 4.4).

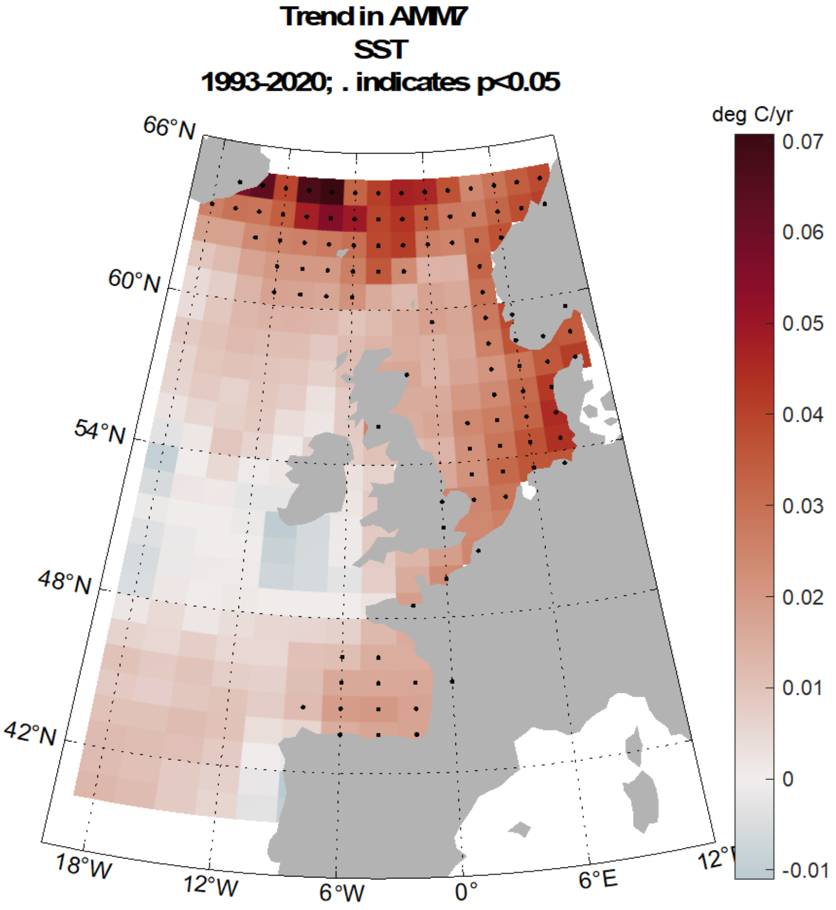


Figure 4.2. Regional overview of environmental change – trend in SST in AMM7 model domain over 1993-2020

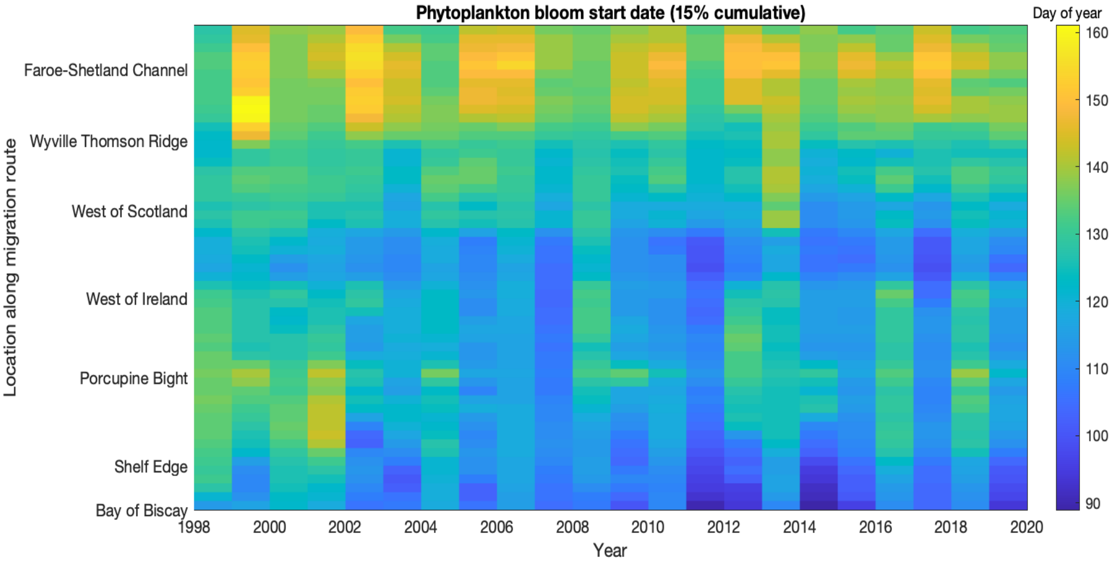


Figure 4.3. **Salmon's-eye-view – interannual variability of phytoplankton bloom initiation along shared migration route "slice".**

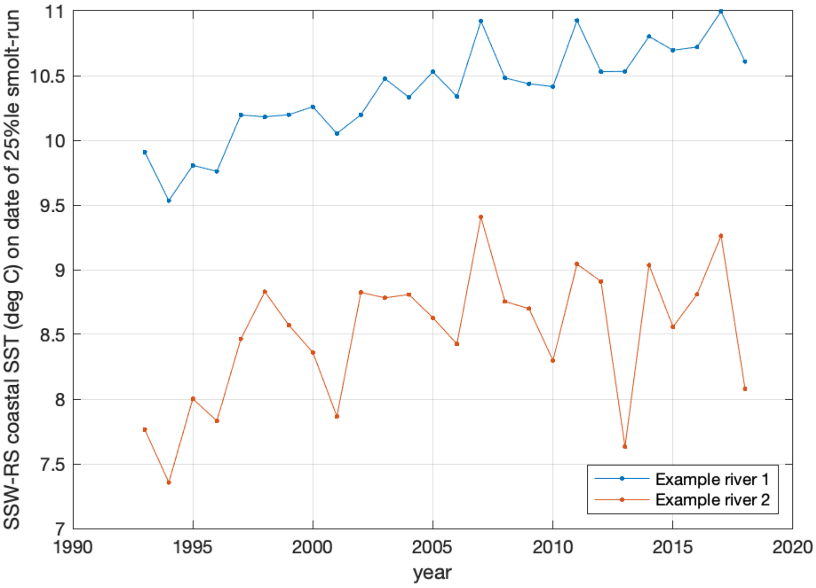


Figure 4.4. **Stock-specific marine indicators – coastal SST at time of post-smolt migration for two example populations making use of the shared migration route (the NE Atlantic shelf edge to the Norwegian Sea).**

4.3.4 Ongoing work

The assessment above illustrates that ocean simulations can assist in building marine ecosystem indicators for salmon survival. Ongoing work will focus on:

- Making model outputs visible and accessible to salmon researchers. This can be achieved through a shared data repository (see section 4.10) which can document model simulations by salmon domains as well as host salmon-focused outputs generated from such models.
- Creation of an inventory of ocean models covering the marine domains used by salmon throughout the Atlantic from ocean-basin to regional scale (e.g. Capet *et al.*, 2020) Again, this will permit researchers to see where a model exists that may fill gaps for a specific research question. For example, the Scottish Shelf Model, which underlies the SSW-RS, has a supplementary suite of higher-resolution models covering coastal regions around the UK.
- Using ocean simulation outputs as inputs to other modelling studies, either as explanatory variables in statistical studies or in a mechanistic approach, to test priority hypotheses. Current examples include using outputs as driving fields for modelling higher tropic levels in the salmon foodweb; statistical modelling of the influence of environmental variability on survival at a range of scales from ocean-basin to stock-specific; and particle tracking modelling of migration movement and variability.
- The challenge of making predictions, both short term for management purposes, and on a decadal time-scale to understand the potential effect of ongoing environmental change on salmon survival. With ongoing work to link physical and lower trophic levels to the rest of the salmon ecosystem, there is the potential to model changes under future climate change projections.

4.4 Mobilizing biological data from lower trophic levels

Ocean conditions have long been hypothesized to have bottom-up effects on salmon survival via the energetics of the food chain (Beaugrand and Reid, 2003; 2012; Mills *et al.*, 2013). Tracing these effects is far from straightforward because of the length of the trophic chain supporting salmon post-smolts, the diversity of prey species at each of those trophic levels, the role of life history and behavioural strategies from the zooplankton upwards, and above all, the sparsity of data. For example, diet studies suggest that the key taxa in the diet of Southern European post-smolts in the first summer at sea are the larvae of sandeel, blue whiting, herring and possibly other clupeids, as well as the largest crustacean zooplankton, euphausiids and amphipods (Haugland *et al.*, 2006; Utne *et al.*, 2022). Sandeel, herring and blue whiting, taken together, are dependent upon a wide spectrum of zooplankton from euphausiids and amphipods down to small copepods like Oithona and Acartia. These prey items represent a 10,000x range of energy per individual (Olin *et al.*, 2021, Dolmaire, 2022). These zooplankton are in turn directly dependent on phytoplankton production, but some of the zooplankton taxa are long-lived, long-distance integrators (Heath *et al.*, 1999; Hatun *et al.*, 2009; Edwards *et al.*, 2021) while others are likely to respond to phytoplankton conditions more directly in the coastal waters where they are found (Martin *et al.*, 2021).

In general, using the biological variables available from large-scale, biogeochemical ocean models (or from satellite remote sensing) as proxies for post-smolt feeding conditions (e.g. Olmos *et al.*, 2020) necessarily requires skipping over all the trophic complexity above. At the intermediate trophic levels (large zooplankton and forage fish), the dataset that best matches the spatial scale of Atlantic salmon migrations, the multidecadal scale of our historical questions, and the breadth of the trophic pyramid supporting post-smolts remains that derived from Continuous Plankton Recorder (CPR) sampling, 1958–present (cprsurvey.org). CPR data have long been applied to salmon marine survival questions (Beaugrand and Reid 2003; Mills *et al.*, 2013), and recent studies have used it to describe very long-term (Edwards *et al.*, 2021) and multispecies, whole-diet-based (Olin *et al.*, 2022) patterns in elements of the trophic pyramid described above. The CPR does sample fish larvae, but mostly this category has not been disaggregated by species, and so CPR data are likely to be useful primarily as a descriptor of the prey of the post-smolts' prey, rather than the post-smolts' own total prey field.

Major limitations remain in the regional and temporal coverage of CPR sampling, from a salmon-centred perspective. For example, the Nordic Sea has, in general, been poorly sampled. Sampling in the Norwegian Sea 2008–present (Strand *et al.*, 2020) does provide a seasonal view of Calanus copepod distribution and density in the seas between Norway and Iceland, intersecting important summer feeding grounds for many European salmon stocks, but the record is very short compared with the records of historical declines in those stocks. Net-sampling-based time-series for zooplankton and forage fish in the post-smolt trophic pyramid do exist for the Norwegian Sea and other regions poorly sampled by CPR (Vollset *et al.*, 2022; Skagseth *et al.*, 2022). However, the question of how best to integrate net-sampling and CPR-based time-series into a unified, multistock picture of change in the food available to post-smolts and their prey is an open research problem, because of mismatches in abundance/biomass units and species coverage, as well as in space and time. There are a number of specific research tasks that could advance such an integration:

- Integrating views of changes in zooplankton energy (abundance multiplied by the typical energy per individual) summed over many taxa (European shelf and Norwegian Sea). Recent papers have described zooplankton declines on the Northwest European shelf and in the Subpolar Gyre interior as long-term, gradual declines (Schmidt *et al.*, 2020, Edwards *et al.*, 2021), matching the pattern in salmon returns from western UK/Irish rivers (Tyldesley *et al.*, in prep). In contrast, Vollset *et al.*, (2022) describes declines in the marine growth of southern and central Norwegian salmon, and a variety of associated marine conditions, as a step change in the early 2000s. Is this a matter of scale, or an actual regional difference? It is likely that this picture could be clarified by integrating data held in the IMR Norwegian Plankton Database with published time-series and ongoing European shelf CPR analysis following Olin *et al.*, (2022). It is not clear whether this (and the other regional data integrations described below) would best be done at species/genus level, or at a higher level of aggregation (e.g. plankton lifeforms, Ostle *et al.*, 2021).
- Integrating views of changes in zooplankton energy, (abundance multiplied by the typical energy per individual) summed over many taxa (European shelf and NW Atlantic). A series of studies over >2 decades has explored the effect of basin-scale climate-ocean processes on the key zooplankton taxa in the salmon food chain: influences that begin in the Subpolar Gyre and affect the shelf seas through physics, biogeochemistry, or an actual shelfward transport of organisms. More recently, Schmidt *et al.* (2020) and Olin *et al.* (2022) have explained bottom-up changes in available zooplankton energy on the European shelf (and sandeel diet and condition over the same area) through local summer primary production dynamics, as opposed to remote, basin-scale influences. It would advance the harmonizing of these perspectives to determine whether the same lower-trophic changes that have occurred on the European shelf have also occurred on NW Atlantic shelf and its adjacent basins. One starting point could be to generalize the CPR methodology developed for the European shelf by Olin *et al.*, (2022) to the Gulf of Maine, Scotian Shelf, and Newfoundland Shelf, potentially using time-series from net sampling (AZMP/AZOMP) for pattern validation. A locally appropriate taxon list could be assembled either by working downward from the diet of capelin and other planktivorous fish

found in post-smolt diet data (WGNAS, 2017), or through zooplankton functional groups (Ostle *et al.*, 2021).

- Linking zooplankton time-series to physical water mass time-series. Zooplankton changes in European waters have previously been interpreted in terms of water mass associations (for example, subpolarvs.subtropical, oceanicvs.shelf), but this topic is worth revisiting in light of recent changes in both the ocean itself and the development of physical and biological indicators (Gonzalez-Pola *et al.*, 2020; Skagseth *et al.*, 2022). It would be useful to intercompare the longest (pre-1980) deep salinity time-series, ocean-climate indices (including SPG, Norwegian Sea Relative Freshwater Content), and CPR zooplankton time-series developed for other ongoing studies. This intercomparison would provide important guidance on the question of how to move from historical description to future prediction: do we believe that climate model projections of, for example, salinity changes could be translated into implications for salmon growth, and if so where and how?

On a longer time horizon, it would also be valuable to advance the development and application of zooplankton and forage-fish numerical models that attempt to simulate the dynamics that the time-series above directly measure. Most large-scale biogeochemical ocean models only climb the foodweb as far as a highly aggregated and simplified view of zooplankton production, but a few spatial, life-history and diversity-resolving models of crustacean zooplankton and forage fish do exist or are under development (Banas *et al.*, 2016; Huse, 2016; Brennan *et al.*, 2019; Dolmaire, 2022). These could be applied to salmon oceanography more widely, and contribute to the task of translating historical, mechanistic understanding into projected futures.

4.5 Mobilizing data on marine predators of salmon

4.5.1 Fish predators

Little is known about salmon predators while at sea, but they are thought to include a range of commercial fish depending on their life-history stage (e.g. the European sea bass, Atlantic cod, whiting, hake, etc.) (Friedland *et al.*, 2012; Gillson *et al.*, 2022; Wheeler *et al.*, 1974). From existing studies, predation on post-smolts during their first few months at sea is thought to contribute to significant mortality (49%) due to their small size (reviewed by Gillson *et al.*, 2022). Predation on post-smolts after their first summer at sea and adults is less well studied (reviewed by Gillson *et al.*, 2022).

Ideally, the study of predator prey dynamics is undertaken through stomach content and or stable isotope analysis (reviewed in ICES, 2020). Inferences can also be made from predated tagged salmon (see Lacroix, 2014; Strøm *et al.*, 2019; ICES, 2020; Renkawitz *et al.*, 2021), but these studies do not provide enough data to relate predator abundance to Salmon declines. The study of salmon predators could provide insight into causes for their decline and even their potential migration routes. For example, Friedland *et al.* (2012) hypothesized that changes in predation distribution may be having an affect salmon abundance within the Gulf of Maine. Predators and prey can also be used to predict the distribution of a more vulnerable species of interest (e.g. Pendleton *et al.*, 2020). Since there is evidence that some commercial fish species are salmon predators (e.g. hake, Atlantic cod, whiting, European sea bass;; reviewed by Gillson *et al.*, 2022), studying abundance and distribution trends of these species, for which large long-term spatialized datasets are freely accessible, could be an area of future research.

If long-term existing data were to be used to understand salmon-commercial fish predator prey dynamics, long-term (1965 to present, depending on the survey) annual scientific bottom-trawl surveys (SBTSs) exist at a precise resolution, within numerous ICES biogeographic regions (e.g. the Celtic Sea, Greater North Sea, Baltic Sea and the Bay of Biscay and Iberian Coast). These are collated and accessible within ICES DATRAS portal (https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx). SBTSs are, however, undertaken annually (some biannual surveys are undertaken) and since the precise timing and migratory routes of salmon are not known, there may be a temporal or spatial mis-match between the period when salmon are thought to migrate through a specific area and surveys with potentially relevant data on salmon predators. For example, from predicted NE Atlantic post-smolt migration by Gilbey *et al.*, (2021), there appears to be slight spatial overlaps with the North Sea International Bottom Trawl surveys (IBTS; collected since 1965) undertaken in quarter 1 (January-February) and quarter 3 (August-September), and Irish Groundfish Surveys (IE-IGFS; collected since 2003) undertaken in quarter 4 (November to December). These surveys do not overlap with the quarter 2 early marine migration period of post-smolts, spatially detailed by Gilbey *et al.*, (2021).

Although references exist on the predation of salmon by demersal fish, Salmon is a pelagic species with a potentially low vertical overlap with demersal species (Guðjónsson *et al.*, 2015; Kristensen *et al.*, 2018). Relatively long-term acoustic and pelagic trawl surveys with potential pelagic predator records are also available from ICES data portals but have a more limited spatial and temporal coverage than SBTS (https://www.ices.dk/data/data-portals/Pages/acoustic.aspx). For example, PELGAS (collected between April and June) is undertaken in the Bay of Biscay (2000 to date); WESPAS (collected in July, 2014 to date) is undertaken within the Celtic Sea; and HERAS (2009 to date) at set locations within the Celtic Sea (UK waters, July) and North Sea (Norway, Germany, Netherlands and Danish waters, July). Pelagic surveys which spatially and potentially temporally overlap with the known post-smolt migration pathways (Gilbey *et al.*, 2021), include those of HERAS (Norway) and WESPAS (Ireland).

Landings (logbook) data (also used for stock assessments) can also be georeferenced through Vessel Monitoring System (VMS) with precise spatial resolution (Hintzen *et al.*, 2012). Fisheries data could therefore be an alternative source of data to investigate the temporal trends and spatial distribution of salmon predators. Gear specific fisheries-dependent data are collected throughout the year and could be matched more precisely to salmon migration at sea in space (X, Y and Z) and time than fisheries- independent data. There is also a higher likelihood of accessing salmon records from fisheries- dependent data than fisheries-independent data to help validate models. Working with fisheries dependent data does require more complex modelling techniques due to the targeted nature of the fishing vessels and issues with accurately recording Catch Per Unit Effort (CPUE) from the varying, often non-comparable, gear types (Bourdaud *et al.*, 2017; Alglave *et al.*, 2022; Elliott *et al.*, 2022). Furthermore, fisheries-dependent data needs to be requested through individual country government bodies which can be reluctant to share this information at a fine enough resolution due to the commercial sensitivity of fishing data.

4.5.2 Cetaceans

Thirty-nine cetacean species have been recorded in European seas (Evans, 2020), but of those, only bottlenose dolphins and killer whales are known to take salmonids more than just casually. However, little is known about salmonid predation by cetaceans in offshore waters.

Seasonal density distribution maps are available for a number of cetacean species including bottlenose dolphins and killer whales in NE Atlantic waters (Waggitt *et al.*, 2020; Evans *et al.*, 2021). Density and distribution data/maps are also available for a number of cetacean species in Irish and NE Atlantic waters from the SCANS and ObSERVE programmes (Rogan *et al.*, 2018; Lacey *et al.*, 2022).

Fine scale distribution data and maps are also available for a number of species over smaller spatial scales. Of most relevance are likely those of coastal populations of bottlenose dolphin, for example, the distribution of the population on the east coast of Scotland (Civil *et al*., 2019). The 2022 ICES Working Group on Marine Mammal Ecology (WGMME) report outlines many of the most recent regional surveys conducted for cetaceans in the NE Atlantic (ICES, 2022). Wide-ranging aerial observations of cetacean abundance/distribution are also available for eastern Canada (Lawson and Gosselin, 2009).

Population trend information is available for a number of populations e.g. Northern European coastal bottlenose dolphins, from the east coast of Scotland, Cardigan Bay, and the Shannon Estuary SAC (Lohrengel *et al*., 2017; Rogan *et al*., 2018; Civil *et al*., 2019).

There are several marine mammal diet data collections and campaigns in the NE Atlantic, summarized and referenced in the WGMME report (ICES, 2021). Information on the diet of a number of cetacean species that may overlap with, and/or compete with, salmon were provided as a working paper, and a general review can be found in Pierce *et al*., (2022). A selection of the most relevant references is provided here in relation to the diet of bottlenose dolphins (Santos Vazquez, 1998; 2001; 2007; Walker *et al*., 1999; Hernandez-Milian and Rogan 2009; Hernandez-Milian *et al*., 2015). Killer whales are well known to feed regularly upon salmon in coastal waters of the eastern North Pacific (Ford and Ellis, 2006), but have also been recorded taking salmon in Norwegian waters (Vester and Hammerschmidt, 2013).

It was referenced during the workshop that similar data are likely to be available for cetacean species in NW Atlantic and the Gulf of St Lawrence.

4.5.3 Seals

Grey seals and harbour seals are well-known to predate salmonids (Jounela *et al*., 2006; Sharples *et al*., 2009; Königson *et al*., 2013) but there is no evidence that ringed seals predate salmonids (Suuronen and Lehtonen, 2012).

Distribution maps based on telemetry data and on onshore counts are available for seal species (grey and harbour seals) around Britain and Ireland (Cronin *et al*., 2014; SCOS, 2021; Carter *et al*., 2022). Similarly, this has also been completed for grey and harbour seals tracked from the Dutch coasts (e.g. Aarts *et al*., 2016). Additionally, tracking studies have been carried out in other areas from which distribution could be modelled. The 2022 ICES WGMME report outlines many of the most recent regional surveys conducted for seals in the NE Atlantic (ICES, 2022).

The 2022 ICES WGMME report outlines many of the most recent regional surveys conducted for seals, and available trends for both grey and harbour seal species in the NE Atlantic (ICES, 2022).

There are a number of seal data collections and campaigns in the NE Atlantic, summarized and referenced in the WGMME report (ICES, 2021). At the Scottish Mammal Research Unit (SMRU), the results of an analysis of hard parts in faecal samples (scats) for grey and common seals have been published (Wilson and Hammond, 2016), as have those in the Baltic Sea along with calculations of prey consumption (Lundström *et al*., 2010; Mantyniemi *et al*., 2012; Tverin *et al*., 2019).

Trends in abundance of grey seals on the Scotian Shelf and in the Gulf of St Lawrence, and of harp seals in the Labrador/Newfoundland areas, are also available (Hammill *et al*., 2021 ; DFO, 2022).

4.6 Mobilizing data from commercial fisheries

4.6.1 Data access issues to assess existence of spatial and temporal changes in bycatch pressure on salmon at sea from pelagic fleet

Due to the declines in salmon abundance, targeted at sea fishing no longer occurs throughout much of its range (ICES, 2020; 2021a; b; Dadswell *et al.*, 2022; Gillson *et al.*, 2022). Because of declines s, targeted Faroe fishing stopped in 1991 (ICES, 2021b) and within Greenland, no exportation of salmon is permitted (NASCO, 2014). Much of the remaining known catch occurs within coastal waters (ICES, 2020; 2021b).

As part of the EU data collection framework, bycatch monitoring is mandatory. Most fish species have low bycatch survival rates, and for some gears they are not easily observed, and therefore not recorded. Various methods exist to log bycatch, including fisheries observer records, logbook data (also referred to as landings data) to fish market data collection methods. Salmon are mainly taken as bycatch in pelagic trawls and static net fisheries such as gillnets (ICES, 2005; Gilbey *et al.*, 2021; Elliott *et al.*, 2022 ;). They are, however, also caught by bottom trawls, bottom longline and purse-seine fisheries (ICES, 2005; 2020; Elliott *et al.*, 2022).

Although bycatch of salmon is difficult to access (particularly at a fine spatio-temporal resolution), it can provide key information on mortality and the spatial distribution of salmonids (Elliott *et al.*, 2022). With enough and sufficiently detailed data, estimations of bycatch can be undertaken (ICES, 2004; 2005; 2020). Little effort has to date been undertaken to collate and monitor salmon bycatch since it is thought to be minimal (ICES, 2005; Borges *et al.*, 2008; Ulleweit *et al.*, 2010). Nonetheless, even a small amount of bycatch could affect populations given the current low salmon abundance. For example, bycatch rate from Icelandic trawlers has been estimated at 5.4 fish/1000 tonnes of mackerel (Olafsson *et al.*, 2016). Whereas in 2012 within Polish waters it was estimated that some 16,480 salmon were misidentified as other species (ICES, 2013). According to ICES (2021b), in 2020, an estimated 276 tonnes of salmon were unreported in catches within the NASCO area. It is not however, possible to partition this unreported catch to specific coastal, estuarine and river areas. Since bycatch data are difficult to fully understand, eDNA analysis could also be used to monitor the location of any bycatch and improve understanding of salmon migratory pathways (Atkinson *et al.*, 2018; Bracken *et al.*, 2018).

ICES Working Group on Bycatch of Protected Species (WGBYC) has embarked upon a detailed plan to monitor bycatch of Protected Endangered and Threatened Species (PETS) (ICES, 2022a). Since Atlantic salmon has been assessed as being ‘Vulnerable’ within the IUCN European Red List of freshwater fish (Brooks and Freyhoff, 2011), and is protected through the various national and international conventions and Directives that exist (e.g. OSPAR, HELCOM, EU CFP prohibited list, Bern Convention, EU Habitats Directive, the Marine Strategy Framework Directive, etc.) (ICES, 2021a), salmon should be a listed WGBYC species. Nonetheless, because of their commercial nature they are not listed on the ICES WGBYC roadmap to date (October 2022). Accessing Salmon bycatch data (i.e. unreported, observer and landings data) from respective nations at a fine enough resolution (ideally precise latitude and longitude) and with sufficient detail (vessel size class, gear, métier, target species), could help give a better understanding of commercial fisheries bycatch in space and time and by gear type, even with likely misreporting occurring (ICES, 2021a).

4.6.2 Landings data and gillnet fisheries

Landings data can provide information on bycatch but is rarely recorded and difficult to access. Landings data can be spatialized through Vessel Monitoring System (VMS) data with a precise spatial resolution (Hintzen *et al.*, 2012). Only vessels >12m are, however, equipped with VMS. Unreported catches are also required by each country, but the method to report 'unreported catches' varies from country to country (e.g. some countries only report illegal catches while others estimate unreported catches by illegal gear (ICES, 2021b)). Illegal, unreported and unregulated fishing is known to occur (e.g. Waugh, 2004; ICES, 2005; 2013), and has been suggested to be a significant mortality factor (Dadswell *et al.*, 2022).

Taken as bycatch salmon from gillnets (targeting mullet, sea bass and sea trout) (Sumner, 2015; Elliott *et al* , 2022) are relatively easy to record due to the nature of the fishery (fish removed from the nets). Smaller vessels (<12 m) fishing closer to the coast, that are not equipped with VMS, are more difficult to board by fisheries observers and their salmon bycatch may therefore not be recorded. Adult salmon are more likely to be caught than post-smolts by static gear due to their size, and because return timings can span a larger proportion of the year (Gillson *et al.*, 2022).

4.6.3 Pelagic fisheries

The commercial fishery for pelagic fish in the NE Atlantic includes different fleets. Most of the landings are taken by pelagic trawling, but purse-seines are also applied (especially by the Norwegian fleet). The spatial distribution of the commercial catches can together with knowledge of known migration routes for salmon (Gilbey *et al.*, 2021) be used to pinpoint areas with potential high bycatch of salmon (ICES, 2005). Such data for all countries participating in the different fisheries are however not available as open access, and an ICES data call to make such data available for salmon research is therefore necessary.

Most pelagic fisheries which are at risk of bycatching salmon (e.g. mackerel, sardine, herring, blue whiting, capelin and sprat; ICES, 2005; 2014; 2022b; Sumner 2015; Elliott *et al.*, 2022) are large-scale fisheries which are easier for observers to board. Discarding from pelagic fisheries is more sporadic than from demersal fisheries since target species are schooling fish that often have a low diversity in species and sizes (Borges *et al.*, 2008; Ulleweit *et al.*, 2010; ICES, 2022b). In addition, fish caught by these fisheries are taken straight below deck and frozen in large holding tanks due to the quantity of catch (Borges *et al.*, 2008). Only a small and variable proportion of hauls are therefore sampled for bycatch (ICES, 2004; 2005).

Access to weekly disaggregated catches from large pelagic fisheries in key locations for Northeast Atlantic stocks have previously been analysed by ICES study groups on salmon bycatch risk. The Study Groups on Bycatches of Salmon in Pelagic Fisheries (SGBYSAL) in 2004 and 2005 (ICES 2004; 2005) examined the disaggregation of commercial catch data of mackerel and herring from areas of the Norwegian Sea, North Sea and West of Ireland and Scotland by ICES Division and standard week. Data were presented in (among other ways) a series of figures mapping fishing activity. Although these suggested that there were certain areas and times of concern for salmon post-smolt migration where there was potential overlap with commercial fishing activity, the catches were rather small at the time when the salmon were thought to move through these areas. Unfortunately, the SGBYSAL commercial pelagic activity dataset in this form is not currently readily available post-2005, leaving doubt over the potential influence of shifts in the distribution and intensity of more recent fishing fleet activity. The group agreed that revisiting this methodology in some way and accessing frequent up to date data on pelagic fishing activity at this level of spatial and temporal disaggregation would be of use in any analysis of temporal change in salmon marine survival.

In addition to bycatch recordings from observers on pelagic vessels, slippage (when part of the catch is released back out to sea prior to sorting) sometimes occurs. This sort of bycatch can be qualitatively recorded as it is released back to sea and species length and composition is determined by samples from the hold or from the following or previous haul (Borges *et al.*, 2008). It is thought that slippage might be an important component of discards in pelagic trawlers but it is frequently not recorded due to estimation difficulties (e.g. ~3000 t of fish a year, mainly from the North Sea; Borges *et al.*, 2008). In a report by Couperus *et al.*, (2004), discards from Dutch pelagic freezer trawls constituted 18% of the catch. 12% of this came from slippage, 17% was pumped directly overboard, 14% from gear damage and the rest was sorted on the conveyer belt.

Methods of recording and calculating discards can also vary between fisheries (e.g. Couperus *et al.*, 2004; Ulleweit *et al.*, 2010). These biases may therefore lead to underreporting (Olafsson *et al.*, 2016; ICES, 2013, 2022b). Bycatch of post-smolts is particularly difficult to observe (because of their small size and the loss of scales), and variable according to the timing and location of the haul (ICES, 2005). In 2015, the EU introduced landings obligations for small pelagic fish. This obligation has been generally effective since 2019 (ICES, 2022b) and so bycatch within pelagic fisheries may now be easier to monitor. A former ICES working group addressed the bycatch of salmon and stated that the mackerel and herring (North Sea and Norwegian Spring-Spawning) fishery have the highest potential for bycatch, but that it may also occur in blue whiting, horse mackerel and capelin fisheries (ICES, 2004). The North Sea herring fishery and the mackerel fishery in the Norwegian Sea spatially overlap with known post-smolt migration routes while the other fisheries can primarily overlap with sea-winter salmon in the feeding grounds or on their return migrations to rivers.

North Sea herring fishery – There is a fishery with pelagic trawl or purse-seine targeting North Sea herring in late April, May and June. The fishery takes place in northern parts of the North Sea and can potentially have bycatch of both post-smolt and returning adult salmon from, among others, British, Swedish, Danish, German and Norwegian rivers.

Mackerel fishery – There is a substantial mackerel trawl fishery around the Britain and Ireland during winter (December-March). The fishing effort during spring, when the post-smolts leave the rivers, is however limited. The first period of the post-smolt migration does therefore not overlap in space and time with a large mackerel fishery. Mackerel migrate into the Norwegian Sea from June onwards, supporting a large trawl fishery in this region. Furthermore, mackerel has expanded north- and westwards in recent years (Nøttestad *et al.*, 2016), and the total landings of mackerel from this fishery have increased. Bycatch of salmon in the summer fishery for mackerel has previously been investigated (ICES 2004, 2005) and estimated as up to 1M individuals, although this estimate has a huge uncertainty. A quality assured estimate is currently not possible due to lack of observations and samples from the fishery.

Data on commercial landings of mackerel in the Norwegian Sea with fine spatial and temporal resolution is submitted to ICES through the Working Group on Widely Distributed Stocks(WGWIDE) and is used as input for the mackerel stock assessment. Such data would be valuable for further studies on bycatch of salmon in the mackerel fishery. A data call asking for these data will be addressed to ICES on behalf of WKSalmon.

Catch data from the Norwegian Sea can be combined with scientific survey data from the mackerel survey (IESSNS) in the region in July for the years 2010-2021. The probability to catch salmon, or the catch rates from the scientific survey, can be used to estimate the total potential bycatch for the mackerel fishery in the Norwegian Sea considering the temporal and spatial dynamics of both salmon migrations and the commercial mackerel fishery. IESSNS trawl data are stored in the PGNAPES database at the Faroe Islands and are not available as open-access. The countries participating in this survey have nevertheless indicated that salmon catch data from trawl hauls can be made available for a study on salmon bycatch from pelagic trawling in the area.

Use of commercial pelagic trawlers to perform targeted sampling of bycatch from mackerel caught with pelagic trawls in the Norwegian Sea or other areas (e.g. from the Spring blue whiting fishery along the European continental shelf post-smolt migration route) may be a possibility to improve understanding of salmon bycatch and marine distribution. Hiring commercial trawlers with quotas for such sampling would have to compensate the vessels for a potential lower price of the catch, as well as lower catch rates compared to their ordinary fishery. However, these costs would be less than for operating scientific survey vessels. Support would also be required to cover the cost of any scientific personnel involved in the fishery or sampling of the catch, for instance during a complete screening at a fish processing plant. Such sampling would be valuable to reduce the uncertainty around bycatch of salmon in the mackerel (or other pelagic species) fisheries.

4.7 Formulating an ICES data call in support of WKSalmon

Discussions reported in Section 4.6 were instructive in providing the focus for developing an ICES WKSalmon-specific data call. Guidance was obtained from the chair of WGWIDE and from ICES data specialists on the specific purpose, format and limitations of the data call process and its applicability. Considering these points, a targeted approach was agreed to develop a data call building on constructive dialogue with WGWIDE to formulate a data call request for spatially explicit and temporally distinct time-series records of pelagic fishing fleet catches (mackerel, herring and blue whiting targeted species) from ICES member states.

The group agreed that an ICES WKSalmon-specific data call be generated to provide species-specific and total pelagic fleet recorded catch broken down by species month of the year and spatially by ICES statistical rectangle. This request would be for data spanning the period 2000 - present (or however long records are available) and would be used for the purpose of evaluating potential risk for migrating Atlantic salmon from bycatch.

The subject matter for the WKSalmon2 data call were also concordant with a recent request from NASCO to ICES for information pertaining to "*advise on the risks of salmon bycatch occurring in pelagic and coastal fisheries, and report on effectiveness and adequacy of current bycatch monitoring programs*". It was therefore considered as an efficient mechanism to support the future work of WKSalmon and ICES.

4.8 Mobilizing data on salmon aquaculture

Salmon aquaculture may affect wild salmonids in various ways. This includes direct and indirect effects that may ultimately reduce marine survival and population viability of wild Atlantic salmon populations. Such effectshave now been thoroughly investigated in a number of scientific studies, and efforts to assess and develop measures to mitigate these effects are partly in place in some countries.

Experimental studies in Ireland and Norway have demonstrated that escaped farmed salmon entering salmon rivers and interbreeding with the wild salmon populations may disrupt local adaptation and reduce fitness of the population, and reduce marine survival (Fleming *et al.*, 2000; McGinnity *et al.*, 2003; Skaala *et al.*, 2019). See also Glover *et al.*, (2017) for a review of the knowledge status regarding genetic interactions. Recently, the effects of introgression on life-history traits of wild salmon populations have been demonstrated by Bolstad *et al.*, (2017; 2021). There is therefore a need to closely monitor the situation with respect to the distribution of escaped farmed salmon to allow development of more effective management measures to reduce or eliminate this problem

Parasite spillover of salmon lice (*Lepeophtheirus salmonis*) from farmed to wild salmon is, together with genetic introgression, assessed to be the most critical man-made risk factor for wild Atlantic salmon in Norway (Forseth *et al.*, 2017). The effect of salmon lice on wild fish has been documented through studies that correlate parasite loads to infestation pressure from fish farms (Vollset *et al.*, 2018, Johnsen *et al.*, 2021, Bøhn *et al.*, 2022). Laboratory studies on the physiological effects of salmon lice (e.g. Finstad *et al.*, 2000; Fjelldal *et al.*, 2022) and randomized control trials releasing parallel groups of treated and untreated hatchery salmon (Vollset *et al.*, 2016) clearly show that infestation levels on wild fish are heavily affected by the presence of farmed fish, and that infestations can lead to reductions in marine survival.

An example of how mobilizing data from several monitoring programs is utilized to develop a risk assessment process is provided by Norway (Grefsrud *et al.*, 2022). Among assessed factors relevant to marine survival of Atlantic salmon are infections from sea lice, transmission of infectious diseases, and genetic introgression of farmed salmon into wild populations. Further details, relating to the Norwegian monitoring programme, are provided below:

- Every year, the proportion of escaped salmon is estimated in approximately 200 to 250 salmon rivers. The estimates are based on analysis of scale samples collected from rod fisheries in the sports fishing season, research fisheries in autumn closer to the spawning season and drift diving counts in rivers (Skoglund *et al.*, 2021). The level of genetic introgression from escaped farmed salmon into wild populations are also assessed in a monitoring program. Samples from recreational rod fisheries and broodstock collections are analysed for a set of SNP-markers and compared to a farm-wild baseline, as described by Karlsson *et al.*, (2016).
- To assess the temporal and spatial effect of fish farms on infestation levels in different regions and assess the effect of parasite spillover a surveillance program on wild salmonids has been established. The results from the field observations are combined with the models for sea lice dispersion (Asplin *et al.*, 2020), and a virtual post-smolt migration model (Kristoffersen *et al.*, 2018; Johnsen *et al.*, 2021) and an estimate for the sea lice induced post-smolt mortality is developed for 401 salmon rivers.
- In 2017, a new management regime for salmonid aquaculture was implemented. Under this management regime, the level of Norwegian aquaculture production in 13 defined production areas along the coast is regulated and adjusted according to environmental indicators and whether the indicators suggest that environmental impact of the farm in production region is acceptable or not. As of 2022, the only operational environmental indicator is the estimated added mortality in the production areas from salmon louse infections due to the presence of fish farms.
- An expert group evaluates the effect of sea lice from fish farms on wild salmon every year. The expert group consists of 10 experts overlooked by a steering group of scientists from the three major environmental research institutes in Norway IMR, NINA and VI. The mandate of the expert group is to use and assess all available data and models. In reality, most surveillance data are provided by the surveillance program from IMR. Other data sources are models from VI and SINTEF as well as river-specific data migration time of salmon smolt from rivers collected by other research institutions. The expert groups work has recently been evaluated by an international evaluation committee (https://www.forskningsradet.no/en/about-the-research-council/the-traffic-light-system-for-aquaculture/).

Similar approaches to the Norwegian method for assessing the risks posed by salmon aquaculture, and in framing mitigation measures, are currently being developed and adopted by other countries where the industry is present. In developing and further testing of hypotheses relating specifically to establishing the effect of salmon aquaculture on patterns of salmon marine mortality (focused on the appropriate unit of study) it is clear that continued and enhanced data mobilization from the industry, wild fisheries and environmental sources will be required.

4.9 Mobilizing data on current salmon diseases

Over the past two decades, there have been numerous reports of Atlantic salmon prespawners suffering from skin diseases, following river entry. These have occurred in freshwater systems draining into the Atlantic Ocean and adjacent sea areas, such as the Baltic Sea. One of these skin diseases, Ulcerative Dermal Necrosis (UDN) is well known and defined clinically and histologically. The more recently described Red Skin Disease (RSD) is clinically and histologically different from UDN. However, both diseases have unknown causes. Furthermore, prespawners may also suffer from other skin anomalies, which occur following entry into freshwater, or in the period prior to spawning. These skin anomalies, often found on the flanks or associated with the fins of the fish, include small (petechial) or large haemorrhages, ulcers, areas of discolouration, scale loosening or scale loss, areas covered with a thick mucus layer, and small to large areas affected by different species of "fungi" (oomycetes). In the case of UDN and RSD, as mentioned above, the aetiology of these skin diseases is unknown. In addition, they all lack a formal case definition, and a disease name.

Parallel with the apparent increase in wild Atlantic salmon skin diseases during the last two decades, there has been a documented increase in skin diseases in farmed salmonids, especially freshwater-farmed rainbow trout but also in farmed marine fish (Schmidt *et al.,* 2018). Many of these diseases have a name and defined disease characteristics (Oidtmann *et al.,* 2013; Maddocks *et al.,* 2015). However, as for UDN, RSD and other skin anomalies in wild Atlantic salmon, the aetiology of the farm fish skin diseases are unknown. For some of the skin diseases in farmed fish, treatment with the antibiotic oxytetracycline has proven helpful. This could indicate that bacteria are involved in the development of the disease (Schmidt *et al.,* 2018; 2021).

Recently, Red Mark Syndrome (RMS) in farmed rainbow trout in Europe which is the same disease as Strawberry Disease in farmed rainbow trout in North-America (Metselaar *et al.,* 2022), has been associated with a bacterium which is in many ways similar to the recently described *Midichloria mitochondrii*, within the family Midichloriaceae, in the order Rickettsiales (Cafiso *et al.,* 2016; Orioles *et al.,* 2022). This a group of small, intracellular bacteria that are very difficult to cultivate and diagnosis of their presence is based on genetic analysis. As the bacterium involved in RMS is very similar to *M. mithochondrii,* it is referred to as a *Midichloria*-like organism (MLO). A pattern similar to that of an MLO infection has been found in the skin of diseased wild Atlantic salmon. However, the identification of a clearly defined organism and clarification of its significance in the overall health of the host requires a great deal of diagnostic work and research.

A review workshop on the current state of knowledge of salmon diseases was organized by the Atlantic Salmon Trust in 2022, in cooperation with the Norwegian Institute for Nature Research. Workshop presentations are available at (526) Atlantic Salmon Trust - YouTube. and a written report is being prepared (Whelan and Mo, *eds*, *in press).*

The mobilization of data that may provide useful insights into the scale and severity of skin diseases in wild salmon at sea is currently poor, and often only available by request for sporadic individual cases and diagnostics. To understand the causes and the significance of the increasing incidence of these skin diseases, and their potential role in contributing to the patterns of marine mortality, it is clear that increased cooperative efforts are required. Increased resourcing of targeted collective sampling and research programmes would improve not only our understanding of mechanisms underlying the disease outbreaks, but in providing the data to allow their severity to be comprehensively evaluated alongside other mortality factors.

4.10 Mobilizing salmon and salmon ecosystem data for co-operative research

The Salmon and ecosystem data hub (SalHub: Diack *et al.*, 2022: https://shiny.missingsalmonalliance.org/SalHub/) is an online resource that has been developed to promote an incremental approach towards the Findable, Accessible, Interoperable and Reusable (FAIR) principles of data use applied to salmon and salmon ecosystem datasets. A critical element of success is that SalHub is developed by an engaged community of users who want to ensure that it becomes and remains a useful resource. A goal is to catalogue available datasets so that when researchers have a salmon question to answer, there is a central location that shows if data exists to answer that question.

The resource is currently hosted by the Missing |Salmon Alliance (https://missingsalmonalliance.org/) (whose future existence is not guaranteed) and the front end is available on Github. SalHub's long-term security needs to be addressed if it is to provide a useful tool for future co-operative research. It is a resource is in its infancy, and iterative development is required.

Some elements of the SalHub resource as it currently stands are:

- Through the search interface, resources are presented both in tabular form and in a geographic context (a map). Filters are available that utilize the annotations directly to present the data landscape in the context of salmon domains and variable classes, alongside free text search which filters on metadata content.
- It is accessible via a free to register login interface. Users must agree to abide by the Terms of Use as outlined on the site prior to registering. These terms reflect the ethical framework that exists within academia and are not a legal agreement.
- The key feature of the metadata submission process is the short time frame within which a user can complete the form and click submit by way of reduced metadata fields that are required for submission. More details are required to describe a data resource. Salmon research community specific annotations (e.g. Domains and Variable Classes) can be easily attached to the described resources. These annotations add relationships between data sources that put them in context of each other and of the salmon life cycle.

5 Summary of key points

The WKSalmon2 group discussions reiterated how complex marine research targeting the assessment of the importance of supposed "suspects" or driving forces behind the temporal patterns of salmon marine mortality actually are. For these efforts to have real effect they cannot, and should not, be considered in isolation from the evaluation of the interconnected effects over growth and the maturation schedule. In addition, the innate genetic diversity, varying evolutionary pressures and flexibility of responses to perturbation that can occur in Atlantic salmon directed from the individual and population levels (Section 3.2) require considerable attention and thought. Evidence of non-stationarity in growth and maturation responses to changes in marine conditions through time and space further deepen the requirement for a considered approach to the period being examined in any hypothesis testing exercise. Simplifications in the development and testing of general hypotheses risk incurring errors in any attribution of causal agents. This introduces the possibility of misdirecting attention away from other possible factors of importance.

The issues outlined in Sections 3.1 to 3.3, required caution when addressing WKSalmon2 Terms of reference 1b and 2a (to advance development of mortality hypotheses). The group agreed that advancing this area would require a concerted group effort that was not achievable within the time allocated for the workshop.

There was general support for more cooperative studies on growth as an integrator of ecosystem change and with clear influence over the marine survival prospects. There was agreement that a new basin-wide cooperative research programme could provide considerable new and important knowledge towards understanding the drivers of trends in Atlantic salmon marine survival. It was suggested that this be supported with a concerted effort on the analysis of patterns of marine growth from existing scale samples (Section 3.3).

Consideration of possible refinement and integration of the concept of space-time domains into the development of testable hypotheses (Section 3.4) led to agreement to build on the specific marine transit and common shared feeding domains proposed by Olmos *et al.*, (2020). Discussions led to the proposal of an extended space-time marine domains structure that recognizes additional regional-specific coastal domains, and refinement of common feeding domains (Table 3.1).

The development of a rigorous hierarchical hypothesis evaluation system (Section 3.5) to build up evidence and options for future hypothesis testing was proposed. With further participation, this would provide a shared resource that reviews the current knowledge, assists with sifting through possible priority research areas, and identifies possible ecosystem indicators for salmon marine survival. This approach was also considered as a useful tool to forge and focus future research cooperatives. To this end it should be noted that the group were conscious that, if this were to be prioritized, considerable further effort would be required in developing, completing and evaluating the content in such a system (Figure 4.1), and that resources would be required.

Several preliminary areas for collective attention were subsequently suggested when establishing a hierarchical hypothesis evaluation (Table 5.1) to ensure the integration of a consideration of evolutionary diversity and processes (Section 3.1).

The WKSalmon group identified multiple potential actions that would provide considerable future benefits to any future hypotheses testing initiatives by the updating, mobilizing and FAIR treatment of specific data resources. These were spread across a wide variety of disciplines and sources, reflected in Section 4. These include the evaluation of existing ocean models for informing salmon research, updating dataseries from one off study groups and supporting new collaborations to permit new analysis of up-to-date datasets. Significant progress has been made by the WKSalmon workshops in a number of key areas to address the terms of reference for the workshop series, including providing opportunities to identify and mobilize new resources for furthering understanding.

An updated and more comprehensive database of Atlantic salmon biological information would be beneficial to future investigations into the marine mortality and productivity of Atlantic salmon. Challenges remain to organize and update valuable biological information from the ICES SGBICEPS study group (Section 4.2) but there was general agreement to pursue this as a group. Several outstanding issues remain to be resolved in agreeing on the future scope and actual mechanism for the delivery and sharing of the salmon biological information from major salmon rivers around their native range. Important salmon biological data (e.g. age, body length, and sex ratios of smolt stage and adult returners) could be collated, made available for future investigations and shared (e.g. via SalHub).

It was clear from discussions that the expanding range and options associated with ocean surveillance systems and modelling is providing growing opportunities for building up a picture of the salmon's ecosystem changes during its marine phase (Section 4.3). Increasing use of these tools is warranted, as are increased interdisciplinary efforts to define key marine domains for salmon, to refine and synthesizesynthesize appropriate portions of these synoptic proxies. Such cooperative ventures to mobilize and interpret outputs will be important in advancing our understanding of salmon marine survival.

Table 5.1. Actions suggested ensuring integration of evolutionary structuring within an emerging hierarchical hypothesis evaluation system

Suggested action	**Further details and justification**
Promote raising of awareness: Promote wider recognition of the nature and importance of evolutionary factors in ecological studies among applied ecologists and conservation managers.	Greater awareness is required: 1) of the potential for evolved, adaptive intraspecific population diversity in migrational behaviour (i.e. spatial distributions) and in the exploitation of marine resources (e.g. in respect of feeding ecology or ability to find optimal temperature habitats); 2) that overall biological responses and outcomes of a species represent the additive effects of its individual populations (i.e. *"portfolio effect"* (Schindler *et al*., 2015)); 3) responses and outcomes being determined by complex, multi-factorial genotype-environment interactions (e.g. Garcia de Leaniz *et al.,* 2007) encompass gene-gene interactions (Murren *et al.,* 2015); 4) of the potential for heritable population variation in the degree of phenotypic plasticity in trait expression (Crozier and Hutchings, 2013); and 5) the scope for adaptive epigenetic as well as Mendelian change (Vercelli, 2004; Hu and Barrett, 2017).
Clarification of terminology: Apply a consistent set of different term to evolutionary and non-evolutionary units used in ecological studies to make clear when arbitrary study units are being used.	Agreeing a clear differentiated use of "stock" and "population" as the use of the two terms currently overlaps and is thus confusing. This can lead to a failure to recognize that arbitrary units are being used and result in a an inaccurate and potentially misleading account ecological and demographic dynamics (Kerr *et al*., 2016) and an erroneous take on a species' local, regional and trans-range conservation status and management needs e.g. see "portfolio effects" (Schindler *et al*., 2015). How such clarity might be achieved in the marine context for Atlantic salmon should be identified and promoted.
Resolution of evolutionary structuring: Resolving cryptic evolutionary population diversity in Atlantic salmon.	Many regional studies of evolutionary population structuring have been carried out over the last 17 years using a range of different phylogenetically informative molecular marker types (e.g. Bradbury *et al.,* 2015; Gilbey *et al.,* 2017; Cauwelier *et al.,* 2018; Jeffery *et al.,* 2018; Wennevik *et al.,* 2019; Ozerov *et al*., 2017). While each has advanced understanding, a more nuanced and profound insight into evolutionary structuring can be realized by an integrated synthesis across studies. An initiative to generate such a synthesis is now underway as part of the SeaSalar project (Verspoor *et al.,* in prep.). Most existing molecular genetic baselines for assigning individuals to evolutionary units are based on relatively small marker sets. These are able to successfully resolve and assign individual salmon to the most deeply divergent phylogeographic population groups (Gilbey *et al.,* 2017; 2021; Jeffery *et al.,* 2018). Expanding the

	numbers of markers used could, to some degree, to increase assignment success to already resolved evolutionary groups and possibly provide a more nuanced picture of structuring.
Establishment of distributional diversity among evolutionary units: Acquisition of accurate spatial-temporal accounts of populations to support their conservation management	This can be advanced in part by the accurate assignment of fish captured at sea to their respective higher order evolutionary units and individual populations. However, achieving this objective will in reality be problematic due to data scarcity given the number of such units that are likely to exist, and the logistic challenges of gaining robust spatial-temporal samples across the salmon's potential marine distribution. This is a challenge faced in respect of all widely distributed, rare marine species (DFO, 2021), and is currently being explored by Verspoor *et al.,* (in prep) to advance understanding of early marine Atlantic salmon post-smolt distributions.
Determine the extent and nature of ecological performance variation among evolutionary units: Adoption of evolutionarily defined units as opposed to arbitrarily defined ones	This will ensure that an accurate account of the dynamics of ecological processes and outcomes in relation to spatial-temporal environmental change is gained, at a local, regional and trans-range level. This approach can already be progressed using data from fish that have already been assigned to evolutionary population groups (e.g. Gilbey *et al.,* 2021).
Determine the nature of adaptive divergence among evolutionary units for marine traits: Advancement in the understanding of evolved adaptive diversification of populations and phylogeographic population groups	This can be achieved through studying additive genetic variation and ecological dynamics in relation to environmental variation, and in particular, in respect of showing the same or difference phenotypic outcomes under shared environmental conditions i.e. genotype-environment interactions. Toward this end, the emerging field of "wild quantitative genomics" Johnston *et al*., (2022) is promising.
Assessment of the effects of introgression of farm genes on marine fitness: Integration of a suite of negative effects of salmon farming on the character, fitness and survival of river stocks	Research is needed into whether introgression has disrupted the genomic adaption of populations in respect of marine traits such as migration and feeding behaviour and success, depressing adaptation and increasing marine mortality rates. Such work can be carried out by exploiting approaches such as used by Bourret *et al.,* (2014), including targeted analysis of changes in functionally associated loci (e.g. Bolstad *et al.,* 2021) and comparing the marine performance, survival and return rates of introgressed, and non-introgressed, conspecifics within and across evolutionary units.

The value of accessing and viewing spatial and temporal "layering" of datasets that shed some light on the changing marine conditions and potential pressures was discussed as well as advances made in highlighting opportunities and synthesising existing data. Considerable group effort was directed in the meeting towards advancing the steps towards accessing data in many areas including physical ocean modelling (Section 4.3), potential links between available energy (abundance times typical energy per individual, summed over many taxa) of lower trophic levels to salmon growth and survival (Section 4.4) and various datasets accessible to describing changes in marine predator abundance, distribution and behaviour (Section 4.5). The important issue of how data collected from other ICES working groups might be used to provide information of relevance to testing salmon mortality hypotheses, and promote a more ecosystems-based approach to future management was explored in several of these Sections. It was clear that increased data access and cooperation between existing ICES working groups would facilitate this approach in future. This is currently being developed via dialogue with WGWIDE on changing patterns in the distribution and effort in the commercial pelagic fishing fleet in key areas of shared salmon migration and feeding (Section 4.6).

Re-analysis of data that can be used to represent patterns of spatial and temporal changes in populations of lower trophic levels (e.g. in the available energy as prey for the salmon post-smolt prey) was an area of interest and potential (Section 4.4). Although early stage investigations are revealing useful associations between indices of zooplankton and salmon marine return rate, work is needed to determine how to integrate this into a unified, multistock picture of change in the food available to post-smolts. Several potential development options were presented for consideration, including integration of views of zooplankton energy between European, Norwegian and North American marine zones and advancing the application of zooplankton and forage-fish numerical models. There was agreement that developing this energetics approach and applying it to salmon oceanography more widely, could contribute to the task of translating a historical, mechanistic understanding into future projections.

Several opportunities for mobilizing and integrating knowledge that could assist with future hypothesis testing and possible attribution of causal agents were provided during discussions on salmon predators (fish, cetaceans and seals discussed here), and their current and historic data sources (Section 4.5). It was clear that while there remain restrictions on the spatial and temporal extents of many predator data resources, the range of data options available are increasing. Sources now include time-series of population census data, focused telemetry and diet studies (to evaluate actual predation risk). Much of these resources are either freely available to download from reports and publications or potentially accessible for use on request to WGMME..

Several areas were outlined in WKSalmon2, which could lead to developing the knowledge landscape for how salmon survival fluctuations are linked to the evolution of commercial marine fishing activity (e.g. bycatch issues). The group agreed that revisiting the approaches taken in the SGBYSAL one-off study groups (ICES, 2004; 2005) and accessing frequent up-to-date data on pelagic fishing activity at this level of spatial and temporal disaggregation would be of use in any analysis of temporal change in salmon marine survival.

There was a general agreement that this approach should be considered, updated and revisited, especially in light of recent advances in our understanding of salmon migration routes and stock specific use of marine areas (e.g. Gilbey *et al*., 2021; O'Sullivan *et al*., 2022). Section 4.6 also included recognition of the need for:

- A meta-analysis on the spatial temporal variation in pelagic fisheries activities and salmon migration as both smolts and adults;
- Development of an ICES data request for observer, landings, and unreported salmon catches to get a better understanding of bycatch risks;
- Collation of coastal static net fisheries being undertaken within proximities of salmon rivers;
- *S. salar* to be added toWGBYC roadmap;
- A request that WGWIDE establish a protocol for screening discards and bycatches in pelagic fisheries (mackerel and herring; ICES, 2005); and
- Support being considered for hiring commercial vessels to trawl for mackerel in the Norwegian Sea in June/July, (and other species at key domains for salmon) and have the total catch screened for salmon.

In light of previous issues surrounding the proposal and testing of multiple hypotheses to explain salmon mortality, the development of a wide-ranging ICES data call that was envisaged as being required in support of the workshop was not advanced. Instead, the outline for a more focused and specific data call was formulated (Section 4.7) to access valuable information relating to pelagic commercial fishing activity. This will advance objectives and our understanding on the potential for fisheries bycatch and its contribution to marine mortality.

The importance of considering the negative effects of salmon aquaculture on the status of wild Atlantic salmon populations was provided from a Norwegian perspective in Section 4.8 making full use of the risk assessment process outlined in other areas, and integrating effects into a more comprehensive evaluation of mortality factors at the appropriate unit scale, will present challenges. However this approach is advanced and made applicable to areas within the salmons' range with similar intensity of coastal aquaculture, it will undoubtedly benefit from improving mobilization of resources. This will allow the appropriate and careful consideration of the effects of local physical ocean systems (Section 4.2) and developing knowledge of salmon marine migration routes (Section 3.4), among others.

The risks posed by disease to wild salmon stocks require more attention (Section 4.9), but the growing body of evidence does suggest an increasing pressure on marine survival. It is clear that in the context of increasing stress factors associated with climate change and other man-made impacts, salmon skin is particularly sensitive to major changes in its environment (e.g. Red Skin Disease (RSD)). However, to fully understand the causes and the significance of the increasing incidence of these skin diseases, additional collective efforts will be required, directed by governmental fish health diagnostic laboratories.

In the SalHub tool (Diack *et al.,* 2022) researchers interested in pursuing exploration of Atlantic salmon marine mortality variation have access to a new a tool for assisting with sourcing knowledge and mobilizing data on salmon and ecosystem components (Section 4.10). The future shared development of this resource will require concerted effort and support, but could prove important to group initiatives such as future NASCO-ICES WKSalmon workshops, and focused study groups.

In light of the workshop discussions it is clear that advancing collective efforts to allow for testing of multiple marine mortality hypotheses is both complex to attempt and was not universally agreed upon as priority work. A more focused and considered approach was favoured to develop very clearly defined lines of agreed enquiry and to test very specific hypotheses, and this will require considerable time and resources. In addition to actions identified to advance data-mobilization, resourcing for future activities will require consideration by parties engaged in the WKSalmon process. The goals for the third workshop will require careful consideration to provide clearly defined and achievable outcomes that integrate with the current priorities of the WGNAS.

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Annex 2: Resolutions

WKSalmon2 - Second Workshop in a series on Salmon Mortality at Sea

Approved on the Resolutions Forum in April 2022

2021/2/FRSG35 **The Second NASCO/ICES Workshop on Salmon** (WKSalmon2), co-chaired by Colin Bull (UK) and Glenn Nolan (Ireland) will be established and conducted in two sessions: WKSalmon2 will meet online on 15 June 2022 for a one day scoping workshop and on 30 August to 01 September 2022 for a 3-day workshop at the ICES Secretariat in Copenhagen with hybrid meeting access for all participants. The objective of WKSalmon2 is to identify key hypotheses on the mechanisms behind the declines in wild Atlantic salmon stocks and to identify the data resources available and needed to test these hypotheses.

The overall goal of the WKSalmon workshop series is to improve the assessment of Alantic salmon stocks by identifying and testing key hypotheses regarding at sea mortality, and partitioning these declines or losses among possible or likely “suspects”. This Likely Suspects Framework (LSF) can be used to help identify in which domain (i.e. key points in time and space where a substantial amount of the mortality occurs) actions may need to be focused to ensure the future abundance of this iconic species.

1. A one day scoping meeting in June 2022 will provide the framing for an efficient and productive outcome of the WKSalmon2 process.

a) In advance of this scoping meeting, participants will be apprised of the current state of the science in a working document prepared by the chairs, work that builds on the output of WKSalmon1, developing hypotheses about at sea mortality and the salmon “domains” concept. This scoping meeting will then discuss these hypotheses;
b) Agree to a focused set of high priority hypotheses. The hypotheses should focus on examining sources of at sea mortality that are thought to be limiting the conservation potential of North Atlantic salmon. These hypotheses will be tested in the final workshop in this series, WKSalmon3; and,
c) Propose an approach to represent and integrate the salmon “domains” concept within the likely suspects framework (LSF) hypotheses-testing framework.

2. A three day workshop in late August/early September 2022 will:

a) Agree to a final set of high priority hypotheses, based on the discussions in the one day scoping meeting;
b) Identify opportunities and mechanisms to leverage existing data sources within the ICES region and beyond to investigate the set of high priority hypotheses and salmon “domains” concept (ToR 1b); and,
c) Draft an ICES Data Call in preparation for WKSalmon3. The data requested in the Data Call should support testing of the hypotheses identified in ToR2a. Testing these hypotheses is an attempt to improve the our scientific understanding, the stock assessment, and the ICES advice for North Atlantic salmon.

WKSalmon2 will report by 14 October 2022 for the attention of the Advisory Committee.

Supporting information

Priority	Providing the best available scientific advice for the conservation of North Atlantic salmon is a high priority for NASCO and ICES. This workshop will provide the scientific foundation to advance the assessment of the state of North Atlantic salmon.
Scientific justification	To improve the scientific assessment and advice for the conservation of wild Atlantic salmon, ICES in consultation with the North Atlantic Salmon Conservation Organisation (NASCO), convened a series of three workshops to explore how best to integrate available data on salmon, specifically data on marine survival, for use in models to advance the conservation of wild salmon at sea as part of WKSalmon3. In agreeing to a set of priority Likely Suspects Framework (LSF) hypotheses (ToR 1), the workshop should: • Characterize and agree to a list of questions and priority hypotheses to test within the LSF programme. • Evaluate and agree to the appropriate process of testing priority hypotheses. • Agree how the concept of salmon "domains" should be represented and integrated within the LSF hypotheses-testing framework. For ToR 2, the workshop should: • Explore mechanisms to mobilize and share data for assessing salmon mortality at sea • Identify how to prioritize the access to the datasets that have greatest utility to match and advance the hypothesis-testing process, and ensure agreed, focused requests. • Refine our understanding of the nature of existing data gaps, and assess the options for addressing them. • Agree common architecture and data sharing for metadata and data organization within the context of the limits set by ToR 2.
Resource requirements	There are no additional resource requirements. This workshop series comprises a scoping workshop (WKSalmon1 held in 2019), a data meeting (WKSalmon2), and finally a modelling meeting (WKSalmon3). WKSalmon1 convened in 2019 with the first workshop held at ICES headquarters from June 24-28 2019. The workshop report is available at (https://nasco.int/wp-content/uploads/2020/08/ICES-wksalmon_2019.pdf).
Participants	Participants anticipated from the oceanographic, marine survey and data collection, and salmonid ecology and stock assessment communities.
Secretariat facilities	Web conferencing and SharePoint facilities, as requried

Financial	No financial implications.
Linkages to advisory committees	FRSG, ACOM
Linkages to other committees or groups	WGNAS, WGDIAD, WGWIDE, SCICOM
Linkages to other organizations	NASCO, NPAFC