

NASCO WORKSHOP FOR NORTH ATLANTIC SALMON AT-SEA MORTALITY (WKSALMON)

VOLUME 2 | ISSUE 69

ICES SCIENTIFIC REPORTS

RAPPORTS
SCIENTIFIQUES DU CIEM



International Council for the Exploration of the Sea Conseil International pour l'Exploration de la Mer

H.C. Andersens Boulevard 44–46
DK-1553 Copenhagen V
Denmark
Telephone (+45) 33 38 67 00
Telefax (+45) 33 93 42 15
www.ices.dk
info@ices.dk

The material in this report may be reused for non-commercial purposes using the recommended citation. ICES may only grant usage rights of information, data, images, graphs, etc. of which it has ownership. For other third-party material cited in this report, you must contact the original copyright holder for permission. For citation of datasets or use of data to be included in other databases, please refer to the latest ICES data policy on ICES website. All extracts must be acknowledged. For other reproduction requests please contact the General Secretary.

This document is the product of an expert group under the auspices of the International Council for the Exploration of the Sea and does not necessarily represent the view of the Council.

ISSN number: 2618-1371 | © 2020 International Council for the Exploration of the Sea

ICES Scientific Reports

Volume 2 | Issue 69

NASCO WORKSHOP FOR NORTH ATLANTIC SALMON AT-SEA MORTALITY (WKSALMON)

Recommended format for purpose of citation:

ICES. 2020. NASCO Workshop for North Atlantic Salmon At-Sea Mortality (WKSALMON, outputs from 2019 meeting). ICES Scientific Reports. 2:69. 175 pp. <http://doi.org/10.17895/ices.pub.5979>

Editors

Gérald Chaput • Niall Ó Maoiléidigh

Authors

Hlynur Bárðarson • Gérald Chaput • Jonathan Gillson • Stephen Gregory • Erica Head • Jan Arge Jacobsen
• Priscilla Licandro • Niall Ó Maoiléidigh • Ana Ribeiro Santos • Kjell Rong Utne



ICES
CIEM

International Council for
the Exploration of the Sea
Conseil International pour
l'Exploration de la Mer

Contents

i	Executive summary	vi
ii	Expert group information	vii
1	Introduction.....	1
	1.1 Overview of Atlantic salmon in the North Atlantic.....	1
	1.2 Overview of trends in at sea dynamics	4
	1.3 'Likely Suspects' framework.....	5
	1.4 Definitions.....	7
	1.4.1 Atlantic salmon life stages	7
	1.4.2 Types of observations	7
2	Atlantic salmon marine knowledge.....	9
	2.1 Salmon distribution and occurrence.....	9
	2.1.1 Catches in marine fisheries.....	9
	Value of catch data for describing salmon distribution and occurrence at sea	10
	Limitations of catch data for describing salmon distribution and occurrence at sea	10
	Availability of data.....	11
	2.1.2 Tag recaptures in marine fisheries.....	11
	2.1.2.1 Tagging in home rivers and recaptures in marine fisheries.....	12
	Value of these data.....	12
	Limitations of the data	12
	2.1.2.2 Tag recaptures from oceanic tag and release programmes	13
	Value of these data.....	13
	Limitations of the data	13
	Availability of data.....	13
	2.1.3 Marine research surveys.....	14
	2.1.3.1 Northwest Atlantic.....	14
	2.1.3.2 Northeast Atlantic.....	15
	Value of these data.....	17
	Limitations of these data.....	18
	Availability of data.....	18
	2.1.4 Bycatch in marine fisheries.....	18
	2.1.4.1 Northwest Atlantic.....	18
	2.1.4.2 Northeast Atlantic.....	18
	Value.....	19
	Limitations.....	19
	2.1.5 Diet studies of predators – direct observation	19
	2.1.6 Inferences from stable isotopes and isoscape patterns – sequential observation.....	19
	Value.....	20
	Limitations.....	20
	Availability of data.....	20
	2.1.7 Telemetry - repeat observation type.....	21
	2.1.7.1 Acoustic tags	21
	2.1.7.2 Archival tags - non-transmitting	23
	2.1.7.3 Archival tags - transmitting.....	24
	Value.....	25
	Limitations.....	25
	Availability of data.....	25
	2.1.8 Migration modelling	26
	2.2 Salmon ecology at sea – physical habitat features.....	26
	2.2.1 Single observation - direct or modelled.....	26
	Value.....	27

Limitations	27
Availability of data	27
2.2.2 Repeat observation – direct or modelled	28
2.2.2.1 Archival tags - non-transmitting	28
2.2.2.2 Archival tags - transmitting	29
Value	30
Limitations	30
Availability of data	30
2.3 Salmon ecology at sea – diet	30
2.3.1 Diet studies - single observation	31
Value	33
Limitations	33
Data availability	33
2.3.2 Stable isotopes – sequential observation	33
Value	34
Limitations	34
Availability of data	35
2.4 Salmon ecology at sea – predation	35
2.4.1 Diet studies of predators - single observation	35
2.4.2 Modelled observations	35
2.4.2.1 Acoustic tags	35
2.4.2.2 Archival transmitting tags	36
Value	37
Limitations	37
Availability of data	38
2.5 Salmon abundance	38
2.5.1 Fisheries catches as indicators of abundance	38
Value of data	38
Limitations	38
Availability of data	38
2.5.2 Continental scale abundance	38
Value	41
Limitations	41
Availability of data	41
2.5.3 Individual river scale abundance	41
2.5.3.1 North America (NAC)	42
2.5.3.2 Northeast Atlantic	43
Value	44
Limitations	45
Availability of data	45
2.6 Population dynamics – survival rates	45
2.6.1 Continental and regional scale (life-cycle modelling)	45
Value	48
Limitations	48
Availability of data	48
2.6.2 Population specific survival rates	49
2.6.2.1 Smolt to maiden salmon	49
Value	50
Limitations	50
Availability of data	50
2.6.2.2 Repeat spawner survival rates	53
Value	55
Limitations	55

	Availability of data	55
	2.6.3 Individual estimates - telemetry	55
	Value	58
	Limitations	58
	Availability of data	58
	2.7 Population dynamics – maturation rates	59
	Value	61
	Limitations	61
	Availability of data	61
	2.7.1 Continental and regional scale (life-cycle modelling)	61
	Value	61
	Limitations	61
	Availability of data	62
	2.8 Biological characteristics	62
	Value	63
	Limitations	64
	Availability of data	64
	2.8.1 Proxies for growth based on scale patterns	64
	Value	65
	Limitations	65
	Availability of data	65
3	North Atlantic ecosystem – physical features	66
	3.1 Contemporary conditions	67
	3.2 Circulation data	67
	3.3 Oceanographic data: physical features	70
	3.3.1 Sea surface temperature	70
	3.3.1.1 <i>In situ</i> data	70
	3.3.1.2 Satellite data	71
	3.3.1.3 Hind-cast model simulations	73
	3.3.2 Ice cover	73
	3.3.2.1 Ice cover in the Gulf of St Lawrence and on the Newfoundland Shelf	74
	3.4 Atmospheric forcing indices	75
	3.4.1 North Atlantic Oscillation (NAO)	75
	3.4.2 Atlantic Multidecadal Oscillation (AMO)	76
	3.4.3 East Atlantic Pattern (EAP)	77
	3.4.4 Atlantic Meridional Overturning Circulation (AMOC)	78
4	North Atlantic ecosystem – biological features	79
	4.1 Primary and secondary production in the North Atlantic	79
	4.1.1 The Northwest Atlantic ecosystem	79
	4.1.2 The Northeast Atlantic ecosystem	80
	4.1.3 Satellite-derived estimates of phytoplankton biomass and production	80
	4.1.4 <i>In situ</i> observations of phytoplankton and zooplankton concentration	82
	4.2 Mesopelagic community	84
	4.3 Pelagic fish community	84
	4.3.1 Northwest Atlantic	85
	4.3.2 Northeast Atlantic	88
	4.3.2.1 Norwegian spring spawning herring (NSSH)	90
	4.3.2.2 Blue whiting	90
	4.3.2.3 Mackerel	91
	4.3.2.4 Redfish (<i>Sebastes</i> sp.)	91
	4.3.2.5 Sprat	91
	4.3.2.6 Sandeels	95
	Data sources	99

	4.3.3	Characteristics of pelagic fish community	99
	4.4	Predator community.....	102
		Limitations.....	103
	4.4.1	Seabirds.....	103
	4.4.1.1	Northern gannet	104
	4.4.2	Marine mammals.....	106
	4.4.2.1	Seals (Phocidae).....	107
	4.4.2.2	Cetaceans.....	110
	4.4.3	Fish.....	115
	4.5	Commercial pelagic fisheries and bycatch of salmon	115
	4.5.1	Spatial and temporal distribution of fisheries catches and effort (ICES) (InterCatch; DATRAS; STECF; RDB).....	117
	4.5.1.1	ICES InterCatch database.....	117
	4.5.1.2	STECF Fisheries Dependent Information database (STECF FDI).....	117
	4.5.1.3	Regional Database (RDB)	118
	4.6	Spatial and temporal overlap of salmon and monitored marine ecosystem components.....	120
		Availability of data.....	121
5		Contribution to the ‘Likely Suspects’ framework	123
	5.1	Progress to date on identification of domains and regulatory factors.....	123
	5.1.1	Spatial synchrony in the response of a long-range migratory species (<i>Salmo salar</i>) to climate change in the North Atlantic Ocean; Olmos <i>et al.</i> (2020).....	124
	5.1.2	Climate-driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations; Almodóvar <i>et al.</i> (2019)	125
	5.1.3	Differential response of continental stock complexes of Atlantic salmon (<i>Salmo salar</i>) to the Atlantic Multidecadal Oscillation; Friedland <i>et al.</i> (2014).....	125
	5.1.4	Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations; Mills <i>et al.</i> (2013)	126
	5.1.5	Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon; Friedland and Todd (2012).....	127
	5.1.6	Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic; Beaugrand and Reid (2012)	128
	5.1.7	Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers; Otero <i>et al.</i> (2012).....	129
	5.1.8	The recruitment of Atlantic salmon in Europe; Friedland <i>et al.</i> (2009)	129
	5.1.9	Multidecadal North Atlantic climate variability and its effect on North American salmon abundance; Condrón <i>et al.</i> (2005).....	130
	5.1.10	Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (<i>Salmo salar</i> L.) in the North Sea area; Friedland <i>et al.</i> (2000)	130
	5.1.11	Marine survival of North American and European Atlantic salmon: effects of growth and environment; Friedland <i>et al.</i> (1993)	131
	5.2	Identification of audit points	135
	5.3	Data gaps	136
	5.4	Next steps	136
6		SALSEA_PGNAPES database	140
	6.1	Use of the databases	140
7		New projects initiated addressing salmon ecology at sea	145
	7.1	SeaSalar: Atlantic salmon at sea—factors affecting their growth and survival.....	145
	7.1.1	SAlmonids Management ARound the CHannel (SAMARCH)	145
8		Metadata compilation of salmon datasets discussed during WKSAlmon	147
9		References cited.....	148

Annex 1:	WKSAlmon list of participants.....	172
Annex 2:	List of presentations at WKSAlmon.....	173
Annex 3:	ICES resolution	175

i Executive summary

Reductions in marine survival have been implicated as the primary reason for the North Atlantic pattern of declines in Atlantic salmon abundance over the past five decades. With the goal to improve the scientific assessments and advice for the conservation of wild Atlantic salmon (*Salmo salar* L.) in the North Atlantic, ICES in consultation with the North Atlantic Salmon Conservation Organisation (NASCO) convened a series of workshops to explore how best to integrate available data on salmon for use in models to advance the conservation of wild salmon at sea. The first workshop (WKSalm) was held 24–28 June 2019 for the purpose of identifying data sources that could inform estimates of at-sea salmon mortality as well as ecosystem data including oceanographic time-series, plankton surveys, pelagic or demersal fish surveys that describe the marine ecosystem occupied by Atlantic salmon.

Atlantic salmon populations are broadly distributed in the western and eastern continental areas of the North Atlantic (42 to 68°N). There are extensive population-specific data on life-history traits including growth rates, maturation, marine survival and fisheries exploitation across the distributional range of the species. Reconstructions of abundance extending five decades are available for regional groups of populations. Atlantic salmon is a pelagic marine species, and groups of populations from the North Atlantic utilize common feeding areas at key points of the marine phase. The absence of synoptic and systematic marine surveys for Atlantic salmon preclude a full understanding of its distribution and population dynamics at sea.

Knowledge of marine ecosystem components relevant to Atlantic salmon including physical and biological oceanography, prey, competing species, and potential predators is extensive although the temporal (seasonal, annual) and spatial scales of coverage of these data is highly variable and does not overlap with the entire anadromous phase of salmon. The physical oceanographic features monitored by remote sensing including sea surface temperature and indices of primary production have the highest spatial resolution, and the broadest domain coverage that encompasses the entire North Atlantic and months when salmon are at sea. The indices of secondary production have a broad spatial and temporal coverage, but a lower resolution compared to remote sensing indices. The pelagic fish community is sparsely sampled, with the best coverage in the Northeast Atlantic for May, and July–August and no current coverage in the Northwest Atlantic.

The options for testable hypotheses are constrained by the availability and representativeness of monitoring data for the components of the marine ecosystem occupied by Atlantic salmon. Few of the datasets described, in particular for Atlantic salmon, are readily available as open data or from websites. The most readily available data are for climate indices and physical oceanographic features. The large amount of ecosystem information is compiled and maintained within a diverse community of scientific experts with to date limited cross-fertilization and networked analyses. The time scales and spatial scales of observations are variable, of differing complexity requiring a range of analytical skill sets, but seemingly extractable with some concerted effort.

ii Expert group information

Expert group name	NASCO Workshop for North Atlantic Salmon at Sea Mortality (WKSALMON)
Expert group cycle	Annual
Year cycle started	2019
Reporting year in cycle	1/1
Chairs	Gérald Chaput, Canada Niall Ó Maoiléidigh, Ireland
Meeting venue and dates	24–28 June 2019, Copenhagen, Denmark (24 participants)

1 Introduction

With the goal to improve the scientific assessments 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. Parallel initiatives are being planned elsewhere to refine and integrate freshwater and inshore marine data, particularly on the survival of migrating smolts and post-smolts, to provide a comprehensive understanding of the key mortality factors affecting the entire life cycle of Atlantic salmon. These data would support the further development of the Likely Suspect Framework (see http://www.nasco.int/sas/pdf/archive/papers/2018/SAG_18_04_AST%20Likely%20Suspects%20Framework%20Update.pdf), an initiative that will link patterns in at-sea mortality of Atlantic salmon to appropriate geographic and temporal scales. Ultimately, the work achieved would improve the ICES advice for Atlantic salmon through enabling the provision, collation and standardisation of salmon data that are currently unavailable to ICES outside the expert group responding to specific questions of advice from NASCO.

WKSALMON, convened June 24–28, 2019, is the first of these workshops with the purpose of addressing the first of the five following objectives:

- a) Identify data sources that could inform estimates of at-sea salmon mortality and the associated available data, including data for Atlantic salmon as well as ecosystem data (such as oceanographic time-series, plankton surveys, International Ecosystem Summer Survey in the Nordic Seas (IESSNS), pelagic or demersal fish surveys);
- b) Develop a data call that will integrate these sources with existing ICES databases;
- c) Evaluate the appropriateness of data and methods used to estimate at-sea salmon mortality;
- d) Identify data gaps and develop recommendations for future data acquisition;
- e) Evaluate modelling approaches to integrate marine data fully to cover the whole life cycle of Atlantic salmon in the context of the 'Likely Suspects' Framework.

This report is focused on data related to the marine phase of anadromous populations of Atlantic salmon in the North Atlantic. The report is organized as follows:

- Section 2 addresses specifically Atlantic salmon related datasets that can be informative of salmon ecology at sea.
- Section 3 considers the physical components of the marine environment.
- Section 4 considers the biological components of the marine ecosystem occupied by salmon.
- Section 5 provides an overview of recent work of relevance to the development of the 'Likely Suspects' framework and identifies data gaps.

1.1 Overview of Atlantic salmon in the North Atlantic

Atlantic salmon (*Salmo salar* Linnaeus, 1758) is a species within the Family Salmonidae with a wide distribution in the northern hemisphere. The Atlantic salmonine species diverged from the Pacific salmon complex approximately 20 million years before present, and isolation of these groups has been essentially complete (King *et al.*, 2007). *Salmo salar* and *Salmo trutta* (Brown trout) diverged from a common ancestor less than 5 million years before present (King *et al.*, 2007).

Subsequent evolutionary processes driven by geological and climate events resulted in the formation of two phylogenetic groups, represented by North America and Europe, approximately 600 to 700 thousand years before present (King *et al.*, 2007; Lehnert *et al.*, 2019) (Figure 1.1). The isolation of the western and eastern Atlantic groups of *Salmo salar* has not been complete, termed secondary contact, with colonization of some regions of North America following the most recent glacial period considered to have involved salmon from both western and eastern Atlantic refugia (King *et al.*, 2007). Lehnert *et al.* (2019) provided evidence of this, particularly in the northern (Labrador) and eastern (Newfoundland) populations of eastern North America. Further, approximately 18 thousand years before present, the Baltic subgroup of European salmon diverged and it has remained isolated from the North Atlantic group and important biogenetic differences have been set, the most striking being the resistance of the Baltic Salmon group to the freshwater ectoparasite *Gyrodactylus salaris*, which is otherwise pathogenic to the North Atlantic populations of Atlantic salmon (Figure 1.1).

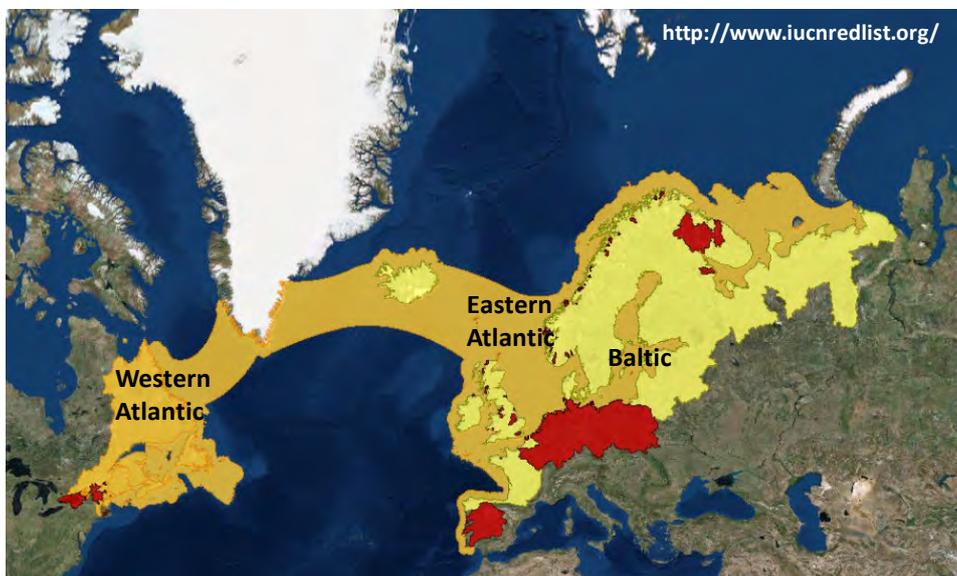


Figure 1.1. Continental and marine occurrence of anadromous populations of Atlantic salmon in the North Atlantic. Red shaded polygons represent areas where contemporary Atlantic salmon populations have been lost.

Over the recent 700 thousand years of Atlantic salmon evolution, the range of Atlantic salmon has repeatedly contracted and expanded (particularly for northern populations) associated with advances and retreats of glaciers, changes in sea levels, and loss or creation of freshwater habitat and marine habitat. These glaciation events have shaped intraspecific diversity.

Atlantic salmon is an obligate freshwater spawner with anadromy as an optional and widespread life-history strategy. It is the anadromous form of Atlantic salmon that has attracted the most human interest because of the large body size, achieved by individuals going to sea to feed and grow before returning to their natal river to spawn. Atlantic salmon have evolved plastic life histories across populations characterized by wide variations in age at smoltification, growth rates, sea age at maturity, size-at-age, etc. Although these variations have to some extent a genetic foundation which is maintained by high natal river fidelity of spawners, they also largely reflect the flexibility of population level responses to climatic and environmental variations.

River age at smoltification is one example of a plastic response which is strongly related to growth conditions and potential. Metcalfe and Thorpe (1990) reported on the negative relationship between the mean age (log scale) of smolts within a salmon population and an index of growth potential for combined samples of populations from North America and Europe. The similarity in mean age and growth potential index between the two continental complexes, illustrates the strength of the environmental association, and hence the smaller direct genetic effect,

of residence time in freshwater of anadromous Atlantic salmon. Seaward migration timing is another example, whereby seaward migrating juvenile Atlantic salmon, known as smolts, from populations around the North Atlantic were found to be migrating approximately 2.5 days earlier per decade in response to freshwater and ocean temperatures changes (Otero *et al.*, 2014).

There is also large variation among populations with spatial correlations in the mean sea age at maturity of anadromous Atlantic salmon. In contrast to the freshwater age at anadromy, sea age at maturity has a relatively strong heritable component (Barson *et al.*, 2015). The proportion of sea-age at maturity is a stock-specific characteristic, and populations can be characterized as one-sea-winter maturing and multi-sea-winter stocks (1SW, 2SW and other ages at maturity). Across the North Atlantic, there are important large regional differences in the proportions at sea age of return with populations in Newfoundland (eastern North America) and Ireland (Europe) dominated by 1SW maturing adult returns, in contrast to higher proportions of multi-sea-winter ages in most other regions of the North Atlantic (Figure 1.2).

In multi-sea-winter stocks, there is frequently a sex bias in the age at maturity. Males in these stocks are proportionally more abundant as 1SW salmon and females as 2SW and older ages at maturity. Multi-sea winter salmon are larger bodied than 1SW salmon. Consequently, multi-sea-winter salmon females have a much higher fecundity than 1SW females. Atlantic salmon spawn a relatively small number (2000 to 18 000 per female) but large (4.5 to 7 mm diameter) eggs, which are deposited in constructed gravel and small cobble pockets, called redds, that provide oxygenated and flowing water to remove metabolic byproducts. The overwinter incubation of eggs over a period of several months is followed by hatch and fry emergence in suitable habitat. These are the most sensitive periods of the salmon life cycle.

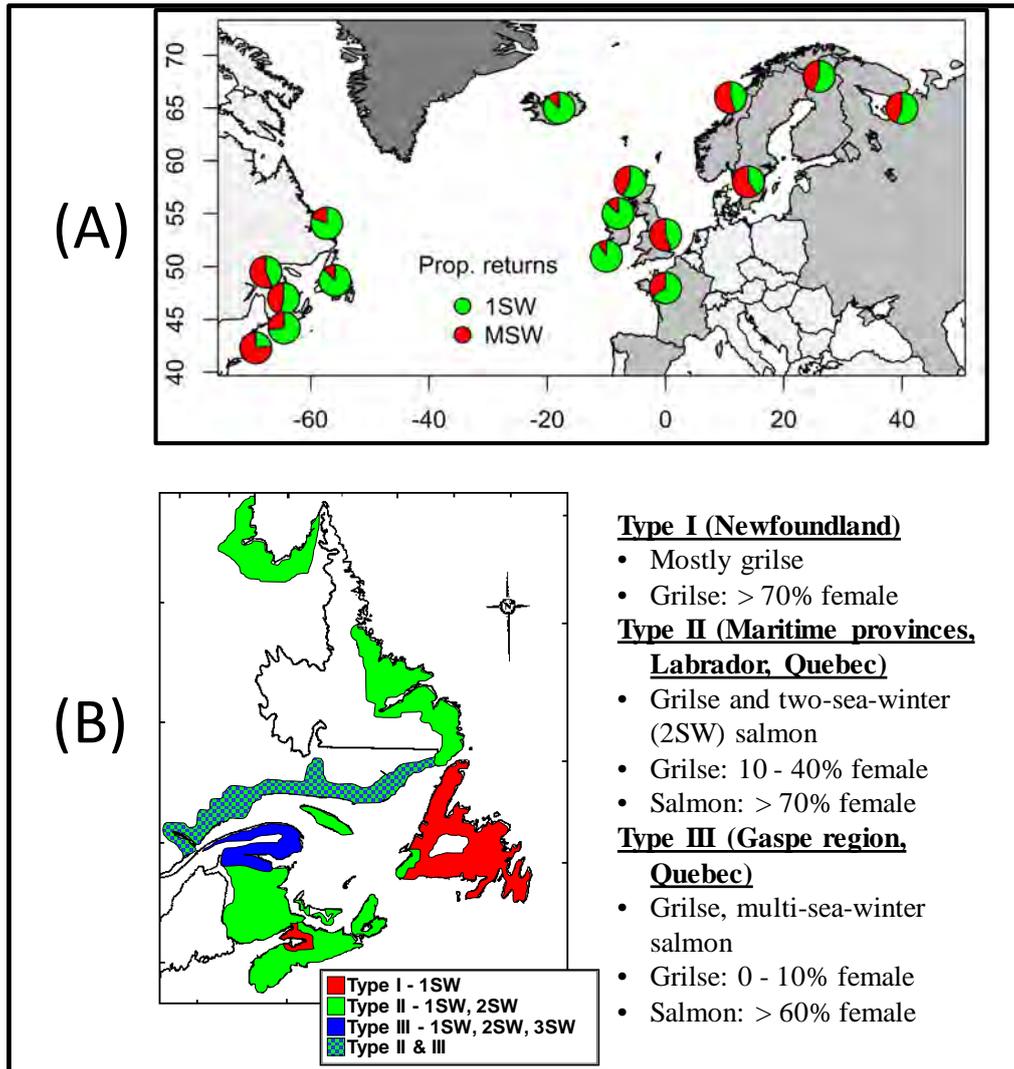


Figure 1.2. Regional variations in the general proportions of sea age at maturity of Atlantic salmon in the North Atlantic. The upper panel (A) summarized the proportions of one-sea-winter (1SW) and multi-sea-winter (MSW) returning adult salmon by country/jurisdiction based on abundances reported in ICES (2019a). The bottom panel (B) illustrates the broad geographical groups of the adult characteristics (sea age at maturity, proportion female) of anadromous Atlantic salmon in eastern Canada (from Porter *et al.*, 1986; O'Connell *et al.*, 2006).

1.2 Overview of trends in at sea dynamics

Time-series of return rates (ratio of total adult returns over all sea ages to smolts going to sea from a smolt migration year) from monitored rivers in the North Atlantic illustrate geographical differences in their variability within and between the continental complexes. There are highly variable return rates among monitored stocks (spatial variability) with those from the Northeast Atlantic being generally higher than in the Northwest Atlantic area (Figure 1.3).

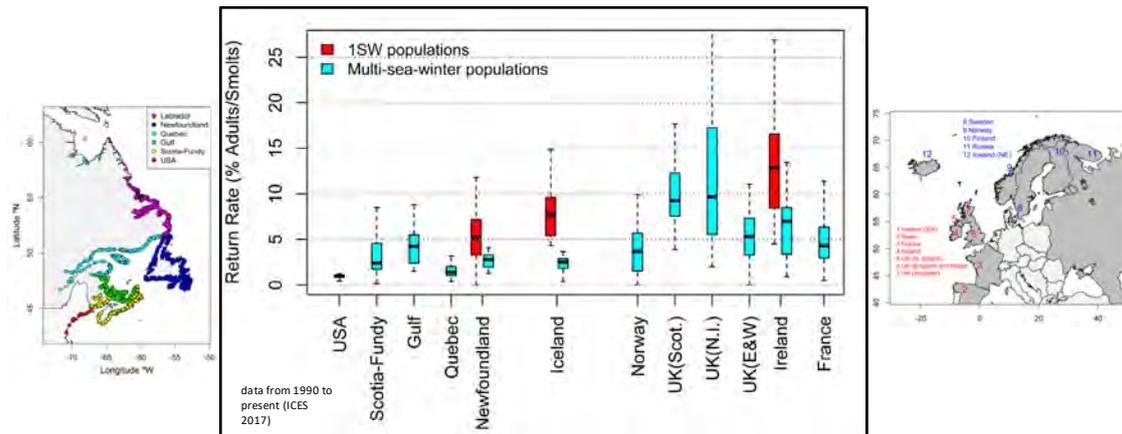


Figure 1.3. Summary of country and continental differences in measured marine return rates of Atlantic salmon in the North Atlantic. The figure is summarized using data from ICES (2017).

When viewed across individual populations over time, a number of patterns arise:

- Important declines over the period 1970s/1980s to 2000s;
- More important declines in southern stocks;
- Since mid-1990s, annual changes in northern stocks are less severe than those prior to the mid-1990s; and
- For southern stocks, especially in Europe, annual changes are more severe since mid-1990s.

Survival at sea is not a random process and is likely related to the freshwater life stages (Russell *et al.*, 2012). Evidence for this comes from the lower return rates of hatchery origin juveniles compared to wild salmon juveniles from the same river. If survival at sea was purely a random process, then return rates between release groups of different origin would be expected to be similar. Returns rates are rather driven by individual fitness. Individual based monitoring methods are shedding some light on some potential mechanisms. Gregory *et al.* (2019), using Passive Integrated Transponder (PIT) tags which are sufficiently small to monitor individual Atlantic salmon juveniles and to assess return rates, showed that marine return rates after one winter at sea (1SW) were positively associated to fork length of individual Atlantic salmon smolts emigrating from the River Frome (Dorset, UK). Such smolt size to survival relationships suggest that mortality may not be expressed equally at all stages of life at sea and that there are likely more vulnerable life stages, for example, during the initial smolt and post-smolt stage when fish are small.

Thorstad *et al.* (2012) provide a comprehensive summary of the smolt and post-smolt life stage:

- Migration is not passive drifting, but rather there is an active component;
- Migration is rapid in freshwater, generally nocturnal, but changes as the season progresses;
- Slowing down in the initial brackish water phase, with day and night movements;
- Evidence of tidal driven behaviours (back and forth movements in estuaries / bays);
- Near surface migrations with some shallow diving behaviours;
- Subject to intense estuarine and nearshore predation in some areas;
- Larger smolts generally have higher estimated survivals than smaller smolts; and
- The location and timing of the components mortality of salmon at sea remains elusive.

1.3 'Likely Suspects' framework

A conceptual framework ('Likely Suspects') has been developed to provide coherent guidance on how future research on marine survival can be identified and prioritised. The framework,

developed by the Atlantic Salmon Trust, places candidate mortality factors within an overall spatial-temporal matrix covering the freshwater migration and marine phases of the life cycle (Figure 1.4). Key geographical areas and periods where mortality factors are known or thought to operate are characterised as ecosystem domains. The domains can be identified at various locations, ranging from freshwater to overwintering feeding areas, and would be associated with different mortality factors. Mortality factors associated with some local domains at or near individual rivers will be encountered by only a few stocks, whereas at larger domains in the ocean, for example in overwintering/feeding areas, the mortality factors will be encountered by many stocks as they coalesce in that area.

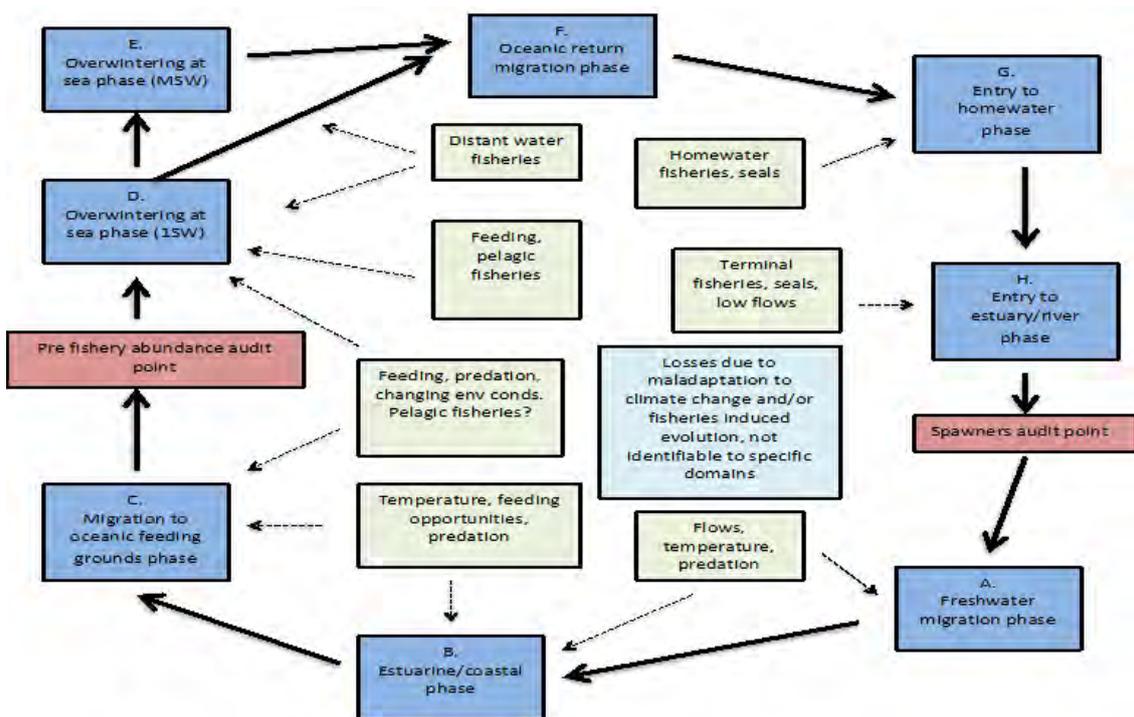


Figure 1.4. A schematic figure representing the major components of the Likely Suspects Framework. The figure is taken from www.atlanticsalmontrust.org.

The identification of the various domains and matching candidate mortality factors will assist in the specification of testable hypotheses and hence aid targeting of research to improve knowledge of the marine phase of the life cycle of Atlantic salmon. A useful strategy may be to concentrate research priorities on domains where suspected losses are greatest and/or at domains where managers can do something about the pressures (e.g. predation, bycatch, water quality, barriers, contaminants, etc.). A first workshop held in November 2017 (workshop report, <http://www.atlanticsalmontrust.org>) initiated the thinking of how such a framework could be set up. Drawing jointly upon experience in both the Pacific and Atlantic oceans with marine survival trends and mortality drivers, the workshop reached several conclusions:

- The framework shares many of the characteristics of conceptual frameworks developed in the Pacific area and the framework will provide a basis for conceptualising marine survival issues for Atlantic salmon and act as a focus for discussion and development of research priorities.
- The framework should include the management drivers applicable at various scales, from river to ocean.
- A programme could subsequently be developed to evolve the framework from a high-level conceptual framework towards building an ecosystem modelling framework(s) and decision support tool.

The next phase of development would focus on particular domains and quantify mortality where possible, and also begin to examine the underlying mechanistic relationships between the pressures and response variables and how these influence salmon mortality. It is a complex problem and the first step is to consider what is known (or thought to be the case) about the ecosystem, hence the purpose of WKSALMON to compile existing data sources which can serve to inform on the possible domains, information that already exists to support hypotheses testing, and gaps. It was noted that ICES has an important role in such questions and encourages the use of their ecosystem databases and products to assist with developing such frameworks and research into the underlying mechanistic relationships between variability of ecosystem drivers at particular domains and trends in salmon mortality.

1.4 Definitions

1.4.1 Atlantic salmon life stages

- fry: juvenile salmon in freshwater in its first year (young-of-the-year; age-0 parr);
- parr: juvenile salmon in freshwater in second and older years;
- smolt: juvenile salmon leaving freshwater to continue its life at sea;
- post-smolt: immature salmon in the first year at sea;
- small salmon: adult (mature) salmon < 63 cm fork length (usually), convenient, also called grilse, 1SW, ...;
- large salmon: adult (mature) salmon \geq 63 cm fork length (usually), convenient, also called salmon, MSW, ...;
- maiden salmon: adult (mature/maturing) salmon returning to spawn for the first time;
- bright salmon: adult (mature) salmon returning to spawn from the sea;
- kelt or black salmon: post-spawned (spent) salmon still in the river or returning to sea post-spawning (usually in the spring);
- one-sea-winter (1SW): adult maiden salmon that spent one full year at sea before returning to rivers to spawn the summer / fall following the smolt migration year;
- two-sea-winter (2SW): adult maiden salmon that spent two full years at sea before returning to rivers to spawn;
- three-sea-winter (3SW): adult maiden salmon that spent three full years at sea before returning to rivers to spawn;
- multi-sea-winter (MSW): a fish that spends more than one full year at sea, includes 2SW, 3SW, ... and repeat spawners;
- repeat spawner: adult (mature) salmon returning for a second or additional spawning (more later);
- consecutive repeat spawner (C): salmon returning to spawn again in successive years after a short period of reconditioning;
- alternate repeat spawner (A): salmon returning to spawn again after having spent a full year at sea reconditioning.

1.4.2 Types of observations

Observations are categorized in terms of the type of observation and the scale to which the observation applies:

- Single observation: a specific datapoint in time and space. Examples include the fork length of a fish, a stomach sample, a detection of an acoustic tag at a receiver, a measurement of sea surface temperature.

- Sequential observation: a sequence (generally temporal) of observations from a single instrument. The instrument can be a fish (for example, the growth metrics along an axis of a scale from a fish, stable isotope metrics from scales or otoliths), an instrument attached to a fish (archival tag data), a continuous plankton recorder, environmental data from a fixed station, etc.
- Direct observation: the observation is an actual datapoint. Examples include measured length of a fish, catch in a gear, prey identified from a stomach sample, sex by internal examination.
- Indirect observation: the observation is inferred from a model of varying complexity. Examples include total catch of salmon in a fishery (based on samples and raising factors), age of a salmon (interpreted from scales or otoliths), location at sea of salmon based on data from archival tags, daily sea surface temperature at specific locations (from satellite data), reconstructed climate indices (Atlantic Multidecadal Oscillation), chlorophyll concentration from satellite imagery, predation events based on archival tag data, pelagic community indices from acoustics.
- Individual observation: the observation applies to an individual fish sampled within a group (sampled fish in a catch). Examples include fork length from a single fish, marking and subsequent recapture of individual fish (single recapture with external batch mark), sequences of recaptures with individual marks (from PIT or archival tags).
- Population level observation: the observation applies to a group of related individuals. Examples include return rates of smolts to a specific river (known for the population but not for individual fish), proportion maturing at sea age, sex ratio, egg depositions in a river, zooplankton community from a sample, total catch of salmon from a river.
- Multiple population observation: the observation applies to a large region comprising multiple individual populations. For example, catches in mixed-stock fisheries, catches of post-smolts in research trawls, genetic origin of salmon to continent or region, run reconstructed estimates of abundance.

2 Atlantic salmon marine knowledge

2.1 Salmon distribution and occurrence

Information on the distribution and occurrence of Atlantic salmon at sea is available from several sources. The most readily available information is from direct observations of fish collected at specific points in time and space, referred to as single observation data. The longest time-series of observations are from directed fisheries for Atlantic salmon and more recently from directed research surveys for Atlantic salmon or from monitoring of bycatch in other fisheries. With the advent of telemetry technologies in the form of data storage tags and acoustic/radio transmitting tags, individual observation data from the same fish have been obtained. These two observational types are discussed separately.

2.1.1 Catches in marine fisheries

Harvests in marine fisheries provide the longest time-series of information on Atlantic salmon distribution in time and space. In most jurisdictions, harvests are compiled at jurisdictional specific scales and time periods. At the ICES Working Group on North Atlantic Salmon (WGNAS), participants from jurisdictions report on total harvests, and in some jurisdictions, catches are reported by regions within the jurisdictions. The combined spatial and temporal categories of catches are generally not available.

In eastern North America, the commercial marine salmon fisheries occurred near the coast as there was no industrial offshore fishing. The fisheries occurred during the ice-free season (April to October) and corresponded to the return migration of salmon to home water areas. Return migrations to rivers are earlier in the southern areas of the distribution. In northern areas the fishing seasons and locations were determined by the retreat and onset of sea ice from the coastal areas. Fish migration to rivers were later in some years due to the late retreat of sea ice; this provided insights into the locations of salmon at sea.

The high seas Atlantic salmon mixed-stock fisheries catches at Greenland are compiled by sub-areas designated by the Northwest Atlantic Fisheries Organization (NAFO) in the WGNAS reports. The harvest summaries show variations in the percentages of the annual catches reported by NAFO subarea along the coast of West Greenland (Figure 2.1). Catches by combined area and date are generally not available, particularly since 1995 following on the closure of the commercial export fisheries.

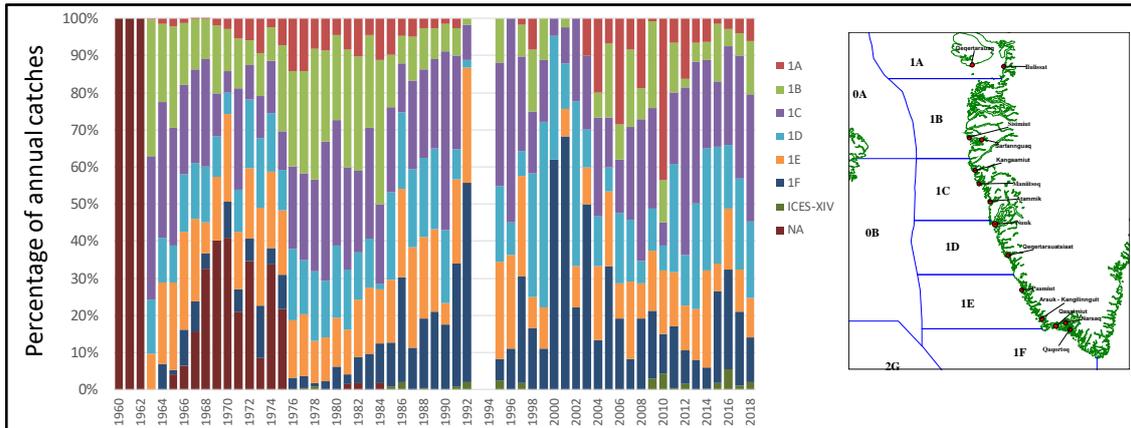


Figure 2.1. Summary of the percentage of reported annual catches (in weight) at Greenland by NAFO subarea and for eastern Greenland (ICES-XIV). Data from ICES (2019a). NA means no location reported for the catches.

Some similar information is available for the marine fisheries in the Faroes Exclusive Economic Zone (EEZ) that occurred from December to June from 1983 to 1995 (Figure 2.2). Catches by month are compiled in ICES WGNAS reports and maps of annual catch per unit of effort by statistical rectangles within the Faroes EEZ are shown in the annual reports of ICES WGNAS (see ICES, 1995 for example, Figure 4.1.3.1), but again the combination of location and time is not reported.

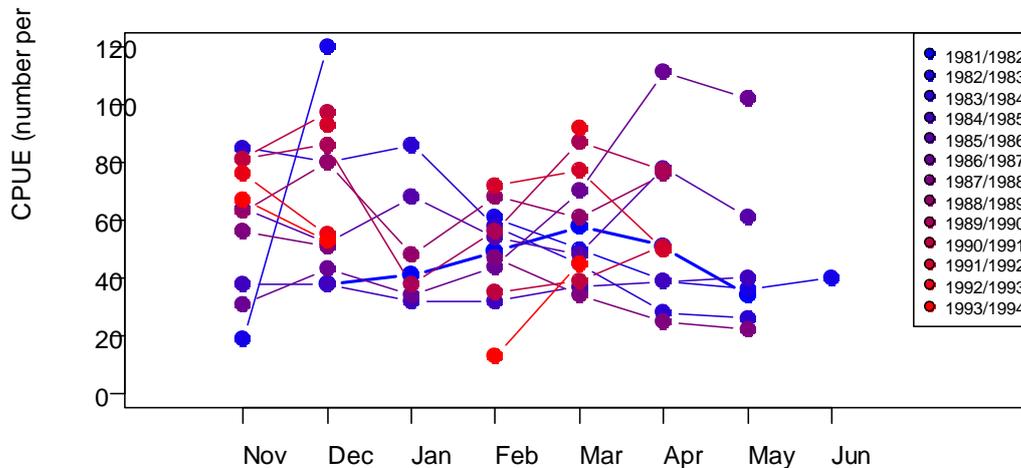


Figure 2.2. Reported catches by month of Atlantic salmon in number per unit effort (1000 hooks) in the Faroes longline fishery south of 65°30'N in the seasons 1981/1982 to 1993/1994. Data from ICES (1995, Table 4.1.3.1).

Value of catch data for describing salmon distribution and occurrence at sea

- Provides the longest-term perspective, although limited in spatial coverage of where salmon occurred.

Limitations of catch data for describing salmon distribution and occurrence at sea

- Very limited perspective of salmon distribution at sea: fisheries occur in limited locations and time periods within the year, i.e. data are biased by the location of fisheries.
- Many of the fisheries were size selective and in many areas it was illegal to land / keep salmon under set weights, so fisheries do not necessarily sample all life stages at sea, e.g. 1SW and MSW salmon.
- With exceptions of the Faroes fishery, the historical Greenland fishery and Norwegian Sea fisheries, the majority of fisheries occurred in coastal areas, near home waters, and

particularly so since the late 1990s, as concerns over mixed-stock fisheries were highlighted.

- Most if not all marine fisheries, even those that occur near the coast, catch salmon from a number of individual river populations. Hence, catches in fisheries can be informative of where and when salmon are located, however in the absence of additional monitoring and analyses, they are not informative of their fine scale distribution.
- The majority of the catch data at finer geographic scale are in paper reports and would be challenging to capture in electronic format. Some jurisdictions compiled catch data from individual purchase slips but these would not be accessible prior to the mid-1980s (in Canada for example).
- With successive closure of marine fisheries for salmon, the observational opportunities of presence of salmon at sea have been lost.
- Harvests are not representative of abundance due to the incompleteness of reports, changes in management, variable exploitation rates, different origin of the salmon, etc.

Availability of data

- The ICES Working Group on North Atlantic Salmon (WGNAS) reports archive the harvest by weight of the combined (freshwater and marine) Atlantic salmon fisheries by country/jurisdiction beginning in 1961 (Tables 2.1.1.1, 2.1.1.2; ICES, 2019a). The catch data are provided by country/jurisdiction, and for some years and jurisdictions by sea age (1SW, MSW) or size group (small ~ 1SW; large ~ MSW) and are available in a csv file format with the following fields: continent complex, region, report-type, origin, size, year, weight (in tonnes).

2.1.2 Tag recaptures in marine fisheries

Atlantic salmon have been marked and released for the purpose of understanding their marine migrations and distribution for more than a century; the first marking efforts occurred at the beginning of the 20th century by anglers in Scotland (reported by Calderwood, 1912, as cited in Hubbard, 1990). Since that time, most countries with Atlantic salmon stocks in the North Atlantic have conducted tagging programmes on salmon of various life stages (see ICES, 2019b). Tagging activities consisted of two types: tagging and release in home waters of juvenile stages with recaptures in marine and home water fisheries, and tagging and release of salmon captured at sea with recoveries in marine and home water fisheries.

ICES conducted a series of four workshops to compile, review, and summarize the extensive tagging programs on Atlantic salmon of the North Atlantic. Ó Maoiléidigh *et al.* (2018) summarized the findings of these workshops. The tag-recovery database (North Atlantic Salmon Tag Recovery (NASTR)) comprises four Excel workbooks relating to Greenland salmon tag recoveries, Faroes salmon tag recoveries, Faroes tagged adult tag recoveries, and Norwegian tagged adult tag recoveries which provide details of the recaptures of individual tagged salmon around the coast of Greenland and within the Faroes EEZ, and adult salmon captured, tagged, and released around the Faroe Islands, respectively. Included in the data files are details of tag recoveries in home waters from the adult tagging experiments in Greenland and the Faroes. Each entry includes three groups of information related to: (i) the tag, (ii) the tagging and release (Tagging) event, and (iii) the recovery (Reporting) event.

The databases were largely compiled during two ICES workshops (WKDUHSTI; ICES, 2007 and WKSHINI; ICES, 2008) by representatives from various countries. Further tag records were incorporated during subsequent workshops (WKLUSTRE; ICES, 2009a and WKSTAR; ICES, 2013b), with some extra validation during the intervening periods. The NASTR database is held at ICES Data Centre and documented throughout this report. The intention was for the data to

be accessible on ICES website (<http://ices.dk/marine-data/>) subsequent to the report being published.

Ó Maoiléidigh *et al.* (2018) also summarize the key results from the relevant papers presented at the ICES/NASCO salmon symposium in LaRoche (France) in 2011. Several relevant papers from this workshop were published in the ICES Volume 69(9) in 2012, namely Jacobsen *et al.* (2012) for recaptures in the Faroes fisheries, Reddin *et al.* (2012) for recaptures in the Greenland fisheries.

2.1.2.1 Tagging in home rivers and recaptures in marine fisheries

Ó Maoiléidigh *et al.* (2018) provide a compilation of information from salmon tagged in home waters and subsequently recaptured in the oceanic salmon fisheries around the Faroe Islands, Greenland, and in the Norwegian Sea. The tag-recovery databases developed from this work are in two Excel workbooks, one relating to Greenland salmon tag recoveries and the other to the Faroes salmon tag recoveries.

ICES (2007; WKDUSTI Annex 4) provides a summary of recaptures of salmon in various home water and high seas fisheries originating from various release locations.

Miller *et al.* (2012) summarize the recaptures of salmon marked and released as smolts from USA rivers and recaptured in the marine fisheries of eastern North America and at Greenland. Bowlby *et al.* (2014) summarize the recapture information by month and life stage in marine fisheries of eastern Canada and Greenland for salmon marked and released from rivers of the eastern portion of Nova Scotia (Canada). There were substantial recaptures of salmon in the offshore mixed-stock driftnet fisheries in Ireland originating from various rivers and jurisdictions in the north-east Atlantic; an example is summarized in Table 3.1 of Ó Maoiléidigh *et al.* (2018).

Value of these data

- Provides population specific information on location and time of occurrence of salmon at sea in areas where fisheries were prosecuted.
- In many instances, biological characteristics of recaptured salmon are available.
- In many cases, annual tagging programmes were undertaken thus providing information on annual variations in spatial and temporal salmon occurrence.

Limitations of the data

- There is no single database or clearing house of recaptures of salmon in marine fisheries (offshore, and in home waters) and there is no formal structure for reporting tagging and recapture programmes.
- With few exceptions (e.g. Miller *et al.*, 2012; Bowlby *et al.*, 2014; ICES, 2008 Figures 4 to 11), there are no synthesis summaries of recaptures in home water fisheries that are comparable to those provided for recaptures in the Greenland and Faroes fisheries (Jacobsen *et al.*, 2012; Reddin *et al.*, 2012; Ó Maoiléidigh *et al.*, 2018).
- Information (date, location, biological characteristics) is frequently incomplete.
- Spatial information on recovery location is frequently of low resolution.
- Recapture data are from fisheries and thus limited to where fisheries occur both in time and space and the scale of the fishing effort; there are more recapture data in areas where fisheries are most intense therefore it is not known if the number of tags returned from an area is representative of the relative distribution of fish rather than the relative distribution of fishing effort. As marine fisheries have progressively declined in intensity, recapture opportunities have also declined.
- Salmon are marked and released from a limited number of rivers within countries / jurisdictions and not all countries / jurisdictions have tagging programmes.
- Many tagging programmes use hatchery fish.

- Many tagging programmes use coded-wire tags which would not be noticed in the catches by fishermen unless there were systematic and directed sampling programmes scanning for these tags.
- Tagging programmes in individual countries / jurisdictions have declined in line with reductions in mixed-stock fisheries and the interest in quantifying origin of catches in these mixed-stock fisheries.

2.1.2.2 Tag recaptures from oceanic tag and release programmes

Ó Maoiléidigh *et al.* (2018) also summarized information from adults tagged in oceanic areas in the North Atlantic. The data are arranged according to an agreed framework recommended at the 2007 workshop (WKDUHSTI; ICES, 2007) and stored for easy access and retrieval as two datasets: adult tagging in Norwegian waters, and adult tagging in Faroese waters. The datasets are referred to as the North Atlantic Salmon Tag Recovery database (NASTR). Not included in NASTR are the data from marine tagging programs conducted in the Northwest Atlantic which are otherwise summarized by Reddin and Lear (1990).

Marine tagging programmes provide a different perspective of salmon distribution at sea than tag and release programs of juveniles. These programmes indicate the origin, location and timing of salmon at sea prior to their return to home waters and individual rivers.

Value of these data

- Provides population specific information on location and time of occurrence of salmon at sea in areas where tagging programmes are conducted.
- In many instances, biological characteristics of salmon at time of tagging at sea and recaptured in home waters or rivers are available.
- Not dependent on specific tagging and release programmes in individual rivers and countries.

Limitations of the data

- Limited in spatial location and time (season, years).
- Many tagging studies are of small sample sizes (Reddin and Lear, 1990).
- Recaptures in home waters and rivers are few in number and generally dependent on recoveries and reporting from fisheries catches. As recapture data are generally limited to where fisheries occur both in time and space and the scale of the fishing effort, recapture data may be biased to areas where fisheries are most intense, therefore it is not known if the number of tags returned from an area is representative of the relative distribution of fish in the tagging location rather than the relative distribution of fishing effort.
- Spatial information on recovery location, unless taken in rivers, is frequently of low resolution.
- Tagging programmes are directed at large-bodied salmon, after the post-smolt stage.

Availability of data

- For eastern Canada, data describing the application, distribution and recovery of individually unique identifiable tags applied externally to Atlantic salmon initiating mostly, but not exclusively, from Canadian government funded research to 1985 are registered with the Atlantic Salmon Tag Clearing House of the Department of Fisheries and Oceans, Science Branch, Maritimes Region. These data are held and maintained in an Oracle database at the Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada. This database contains data from the Maritimes Provinces of eastern Canada from 1964 to

1985, but does not include tagging information from Newfoundland or Quebec. The ORACLE database of tagging and recoveries of Atlantic salmon from Fisheries and Marine Service has been summarized by Ritter (1989) and portions of the database content are described Price (1975) and Newbould (1989).

- Cefas (Centre for Environment, Fisheries and Aquaculture Science) Lowestoft (UK) is the tag clearing house for tag recoveries at Greenland.
- Marine Institute (Ireland) is the tag clearing house for recoveries at Faroes (ICES CRR report annex 5). There is no single tag recapture database for home water fisheries in Northeast Atlantic.
- Ó Maoiléidigh *et al.* (2018) indicated that the datasets, referred to as the North Atlantic Salmon Tag Recovery database (NASTR), are available two Excel workbooks, one relating to Greenland salmon tag recoveries and the other to the Faroes salmon tag recoveries.
- Not included in NASTR are the data from marine tagging programs conducted in the Northwest Atlantic, which are otherwise summarized by Reddin and Lear (1990).

2.1.3 Marine research surveys

2.1.3.1 Northwest Atlantic

There have not been any systematic and repeated marine survey efforts for Atlantic salmon in the Northwest Atlantic. The first marine campaigns focused on Atlantic salmon began in 1965 in the Labrador Sea and at Greenland, and the last directed survey was conducted in 2009 (Figure 2.3). Most of the surveys used surface gillnets to capture salmon. Pelagic trawls were first used in 2000 in the southern range of the Bay of Fundy and Gulf of Maine, and then used in the Labrador Sea surveys of 2008 and 2009 (Figure 2.3).

Sampling season varied but the majority of surveys in the Labrador Sea were conducted in the spring (March to June) or fall (August to October) during the 1960s and in the 1980s to 2000s. The survey on the Grand Banks was conducted in late winter (February to May) whereas the inshore surveys in Bay of Fundy and Penobscott Bay were conducted in May to early June shortly after the migration of smolts to the sea.

Survey catch data that includes individual fish characteristics, locations, and time of capture and other details have been analysed and reported previously (Reddin, 1985, 1988, 2006; Reddin and Shearer, 1987; Reddin and Short, 1991; Reddin and Friedland, 1993). Most of these data should be available in electronic files. More recently, samples from some contemporary surveys have been analysed for region of origin showing the mix of European and North American salmon in the Labrador Sea (I. Bradbury, DFO Canada, unpubl.data).

There are no directed pelagic research surveys in the Northwest Atlantic of the type conducted in the Northeast Atlantic.

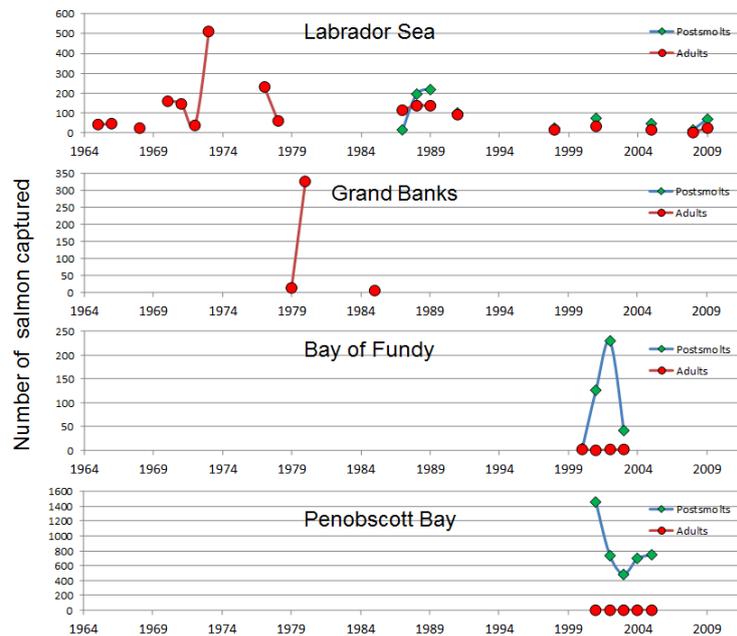


Figure 2.3. History of directed marine surveys for Atlantic salmon conducted in the Northwest Atlantic since 1965. Pelagic trawls were used in the surveys of the Bay of Fundy and in Penobscot Bay. Salmon were sampled with surface gillnets in the Labrador Sea and the Grand Banks over the entire period and a pelagic surface trawl was additionally used in 2008 and 2009 (Sheehan *et al.*, 2012).

2.1.3.2 Northeast Atlantic

Directed marine surveys targeting salmon in the Northeast Atlantic were conducted during the 1990s and 2000s. These surveys provided the first scientific sampling programme for post-smolts in the Norwegian Sea and demonstrated the capacity to capture post-smolts away from the coast.

The surveys took place between May and September and the spatial coverage varied from west of the United Kingdom and Ireland to the Barents Sea. Results from surveys conducted in the years 1990 to 1998 are presented in Holm *et al.* (2000) (Figure 2.4). Surveys in May were normally carried out west of the United Kingdom and Ireland, or along the Norwegian coast to target post-smolt shortly after leaving the rivers. There were a few surveys in June and these normally covered the northern North Sea or the southern Norwegian Sea. Most of the surveys were in July and these often covered the Norwegian Sea. Surveys later than July covered the northern Norwegian Sea or the Barents Sea. All surveys, with a few exceptions in the early 1990s, applied pelagic trawling to catch salmon. Longline was applied on the remaining surveys. Most of fish were post-smolt but there have also been catches of larger salmon.

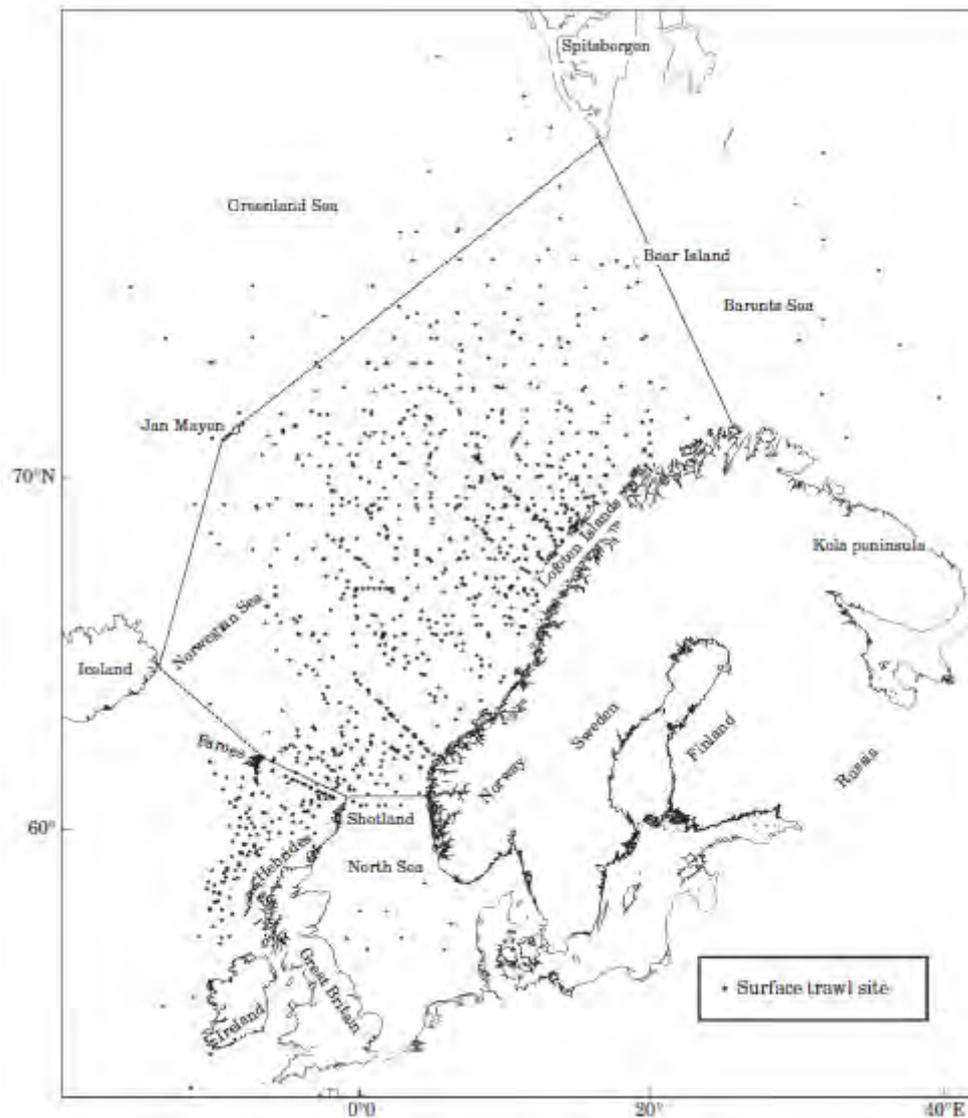


Figure 2.4. Positions of surface trawling for salmon in the years 1990–1998. Each dot represents one trawl site. Figure from Holm *et al.* (2000).

The last directed surveys for salmon were conducted during the months of May to July in 2008 and 2009 as part of the SALSEA-Merge project (SALSEA-MERGE, 2012). A total 1727 post-smolts were captured and sampled during SALSEA-Merge. The detailed data from the SALSEA-Merge surveys were entered into the Planning Group on Northeast Atlantic Pelagic Ecosystem Surveys (PGNAPES) database (see Appendix 6.1).

There are a range of surveys targeting other species that encounter salmon as bycatch. These surveys mainly use pelagic trawling during surveys targeting mackerel or herring and most of the catches are from the Norwegian Sea. However, there have also been occasional bycatch of salmon in the Barents Sea and the North Sea.

The surveys were carried out by institutions from Norway, Scotland, Russia, Faroe Islands, Ireland and Iceland. A detailed description of the surveys will not be given here as the data is still being processed and prepared for publication. Once all data have been published, the data should be available through collaboration, but it does require permission from the institutions performing the respective surveys.

Salmon, both post-smolts and older age groups, have been captured and sampled during the International Ecosystem Survey in Nordic Seas (IESNS) surveys of the Norwegian Sea which have been conducted annually since 2010 during the months of July and August (Figure 2.5). These systematic surveys, conducted with large pelagic surface trawls sample the most important pelagic fish communities in the Norwegian Sea (herring, mackerel). The data are entered and available in PGNAPES (see Appendix 6.1). Processing, including genetic analyses for region of origin, stomach contents and other analyses of the salmon samples from these surveys is ongoing.

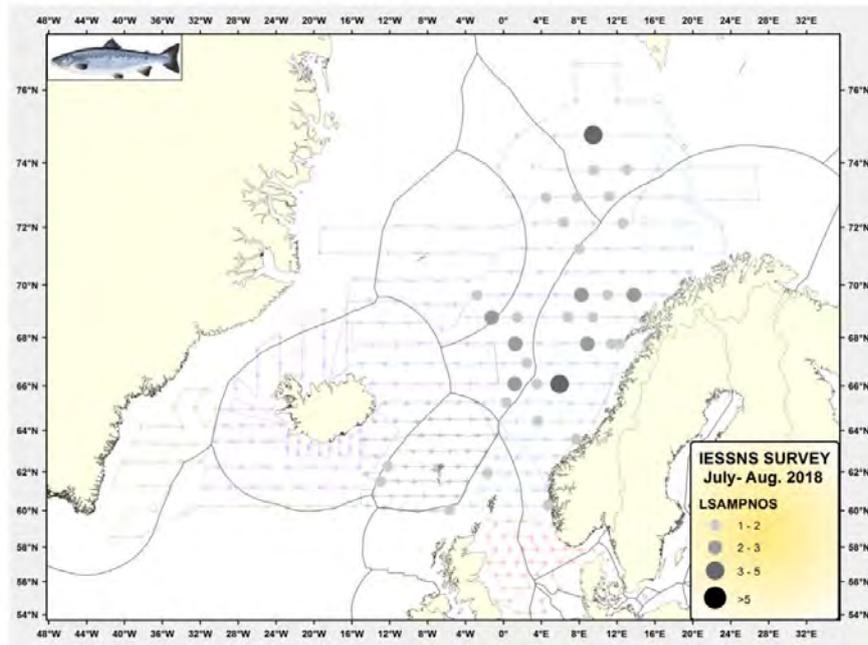


Figure 2.5. Stations occupied and stations with Atlantic salmon catches during the July and August 2018 IESSNS pelagic fish surveys in the Norwegian Sea (ICES, 2019a).

The total dataset of salmon catches in the Northeast Atlantic from directed surveys for salmon and the IESSNS pelagic fish surveys are presently being analysed and prepared for publication (Gilbey *et al.*, in prep). The dataset includes catches from 37 surveys directly targeting salmon, but also holds data from more than 200 other surveys catching salmon as bycatch. The total number of salmon caught at surveys in the Northeast Atlantic for the years 1995–2018 exceeds 7000 individuals. Of these, nearly 4000 individuals have been genetically assigned to their region of origin. As the dataset is being prepared for publication, the details are not yet available.

Value of these data

- Surveys are conducted following a sampling design that allows the characterization of relative occurrence of salmon within a defined sampling frame.
- Sampling is standardized in terms of gear and effort therefore catch rates can be assumed to be representative of relative abundance.
- Surveys have been conducted annually at relatively similar times and cover a large portion of the Norwegian Sea (for the Northeast Atlantic surveys)
- Salmon catches can be processed for detailed characteristics including tissues for the genetic identification of river or region of origin.
- Data are entered in PGNAPES: a database constructed for ecosystem marine surveys.

Limitations of these data

- There has not been any systematic, repeated, and sustained marine survey efforts for Atlantic salmon in the Northwest Atlantic.
- The surveys conducted as part of SALSEA-Merge in 2008 and 2009 were not systematic, as they were designed to capture post-smolts along a pre-defined and hypothesized migration corridor. Due to the location of sampling, the majority of the fish captured were from the southern stocks of the Northeast Atlantic. Smaller pelagic trawls were used and these were less efficient at capturing larger Atlantic salmon.
- The pelagic ecosystem surveys occur over a narrow window of salmon life at sea and do not cover the potential range of distribution of all salmon life stages in the North Atlantic.

Availability of data

- Survey catch data directed in North America that includes individual fish characteristics, locations, and time of capture and other details have been analysed and reported previously (Reddin, 1985, 1988, 2006; Reddin and Shearer, 1987; Reddin and Short, 1991; Reddin and Friedland, 1993; Sheehan *et al.*, 2012). Most of these data should be available in electronic files.
- More recent samples from some contemporary surveys have been analysed for region of origin and data would be available from Ian Bradbury, Fisheries and Oceans Canada.
- The detailed data from the SALSEA-Merge surveys were entered into PGNAPES.
- The systematic surveys of the Norwegian Sea, conducted with large pelagic surface trawls to sample the pelagic fish communities, are entered and available in PGNAPES.

2.1.4 Bycatch in marine fisheries

2.1.4.1 Northwest Atlantic

ICES (2004a) reviewed the potential for bycatch of salmon in fisheries of the Northwest Atlantic. ICES concluded that there was insufficient information to quantify bycatch although, based on information reviewed, there was no obvious concern about bycatch of salmon in these fisheries. Historical data provided some evidence of bycatch as salmon had been reported in commercial landings but the location of this bycatch was not well defined. Based on the Canadian data, the bycatch occurred most frequently in gillnet fisheries. No catches of salmon from purse-seines or trawls were reported.

2.1.4.2 Northeast Atlantic

Most commercial fisheries targeting large demersal or pelagic fish stocks in the Northeast Atlantic have occasional incidental bycatches of salmon. However, the frequency of such bycatch varies considerably between fisheries, areas and seasons. Bycatch of salmon has been reported from bottom trawl, bottom longline and purse-seine fisheries (ICES, 2004b; ICES, 2017a; Rosseland, 1971). Some of the fish caught in coastal areas may however be escaped farmed salmon. The number of salmon caught in bottom trawling, Danish seines and bottom gillnets are most likely low due to the depths at which these gears operate. Considering the extent of the industrial pelagic fisheries in the Northeast Atlantic, the number of salmon caught in the pelagic fishery, either with purse-seine or pelagic trawling, could potentially be high (ICES, 2004b).

Olafsson *et al.* (2016) reported on the origin and biological characteristics of 186 samples of marine-caught salmon collected over the period 2007–2010. The salmon samples were obtained primarily by the Directorate of Fisheries in Iceland during monitoring of pelagic mackerel fisheries in Icelandic waters in 2010, and from bycatch of vessels in the Icelandic fishing fleet in 2007 to 2009, or for a few specimens in research cruises by the Marine Research Institute. The results indicated that the seas south and east of Iceland are important as feeding areas for Atlantic

salmon that had spent at least one winter in the sea, particularly for salmon originating in the UK, Ireland, and southern Europe. Furthermore, the lack of adult Icelandic fish so close to Iceland is remarkable and suggests that Atlantic salmon from Icelandic stocks are using different feeding grounds.

More recently, a new tagging and wide-scale tag screening programme for mackerel and Norwegian Spring-spawning herring was initiated in the Northeast Atlantic (ICES, 2015a). The programme involves automated screening of commercial landings at 23 European (UK, Iceland, Norway, Denmark, Faroe Islands) factories processing pelagic fish for human consumption. The catch is passed through a line that allows for the automatic detection of PIT tags therefore any PIT tagged salmon in the catches scanned at the factories would be expected to be detected during automatic screening of pelagic fish landings. ICES (2019b) noted that in 2018 more than 120 000 salmon were released with such tags.

Lists of unknown tags detected at factories have in previous years been distributed to countries with PIT-tagging programs, and salmon post-smolts in catches have been identified. This list includes 339 unknown tags as of September 2018. An updated list is distributed to the National Tagging coordinators and to the members of the WGNAS.

Value

- Automatic detections of PIT tags are an efficient way of scanning for tagged fish in large catches to obtain temporal information.

Limitations

- Few areas where fish are PIT tagged, hence salmon from large regions will never be detected among the screened commercial catches of pelagic fish.
- Location of captures at sea is not always precisely known for salmon detected by automatic screening in fish processing plants as several vessels may deliver their catch simultaneously.

2.1.5 Diet studies of predators – direct observation

Diet studies of potential salmon predators have provided information on distribution and timing of salmon at sea.

Recoveries of external tags from a gannet (*Sula bassanus*) colony near Newfoundland (Canada) being monitored by the seabird researchers have provided information on stock-specific occurrence across time. The exact location of salmon recovery is limited by the uncertainties in the feeding range of gannets which can be quite extensive (up to 180 km from the colony), although the time of recovery was well known based on the digested condition of the regurgitated prey (Montevecchi *et al.*, 1988). Additionally, diet studies of gannets based on regurgitation samples have provided observations of persistent occurrence and periods of higher levels of predation on post-smolts by gannets (Montevecchi *et al.*, 2002). Fish in good condition were also measured with accompanying information on sizes of other prey consumed by gannets. There were no other studies or publications found on salmon in gannet diet or other seabird diet that would be informative of salmon occurrence and distribution at sea.

2.1.6 Inferences from stable isotopes and isoscape patterns – sequential observation

Stable isotope analysis is a powerful tool that has transformed understanding of the diet, feeding and movement of Atlantic salmon at sea.

Naturally occurring stable forms of elements with unique atomic masses due to the presence of equal numbers of protons but differing numbers of neutrons are known as stable isotopes (Ehleringer and Rundel, 1989). More than 90 natural elements have over 250 stable isotopes that do not undergo radioactive decay and behave differently in biogeochemical processes. Among these, the stable isotopes involved in important biogeochemical processes are hydrogen, carbon, nitrogen, oxygen and sulphur (Kaplan, 1975). These stable isotopes are absorbed from the environment and assimilated into an organisms' tissues providing 'isotopic signatures' that can be used to reconstruct the diet, feeding and movement histories of animals (West *et al.*, 2006). The value of stable isotopes for studying the foraging and spatial ecology of animals is related to the strong relationship between the isotopic composition of the environment, assimilated food sources and an animals' tissues (DeNiro and Epstein, 1978, 1981). Generally, the isotopic composition of samples of animal tissues (e.g. blood, muscle, scales or otoliths) and possible prey items are measured to estimate the relative contributions of different food sources to an animal's diet.

Isotope ratio mass spectrometry is used to measure the ratio of heavy to light stable isotopes (e.g. $^{13}\text{C}/^{12}\text{C}$) in a given sample and the values are reported relative to international standards prepared by the International Atomic Energy Agency (IAEA), expressed in delta (δ) notation as parts per thousand (‰) using the following equation (Fry, 2006):

$$\delta^H X = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$$

where δ is the notation specified for a particular element ($X = \text{hydrogen, carbon, nitrogen, oxygen or sulphur}$), H gives the atomic mass of the heavy isotope for that element ($2\text{H, }^{13}\text{C, }^{15}\text{N, }^{18}\text{O or }^{34}\text{S}$), and R is the ratio of the heavy to light isotope for the element ($2\text{H}/^{1}\text{H, }^{13}\text{C}/^{12}\text{C, }^{15}\text{N}/^{14}\text{N, }^{18}\text{O}/^{16}\text{O or }^{34}\text{S}/^{32}\text{S}$). Accepted international standards for stable isotope ratios include Vienna Standard Mean Ocean Water (V-SMOW) for hydrogen and oxygen, PeeDee Belemnite (V-PDB) for carbon, atmospheric air for nitrogen and Canyon Diablo Troilite (CDT) for sulphur.

Value

- Stable isotope ratios vary in a predictable manner because differences in the reactivity kinetics of isotopes to biogeochemical processes are well understood (Rubenstein and Hobson, 2004).
- Geographic gradients in stable isotope ratios can be used to produce maps of the isotopic composition of the environment, commonly referred to as isoscapes (West *et al.*, 2010).
- Isoscapes are useful for tracking animal movements by relating the isotopic composition of an animal's tissues to known spatial variations in isotope distribution in the environment (Hobson, 1999). For example, maps produced by matching time-series of $\delta^{13}\text{C}$ ratios from archived salmon scales of UK origin to sea surface temperature records have revealed geographic segregation in marine feeding areas between salmon populations and age classes in the North Atlantic (Figure 2.6; Mackenzie *et al.*, 2011).
- The accuracy and precision of isoscapes depends on the amount of variation in isotopic signatures due to changes in climate, ocean circulation and plankton community composition (Trueman *et al.*, 2012b).

Limitations

- A large number of biotic and abiotic factors can generate variation in isotopic signatures, making comparison across studies problematic (Boecklen *et al.*, 2011).
- Studies of isotopic signatures have been limited by unrealistic assumptions with little experimental support and an over-reliance on obtaining key parameter values from the literature (Gannes *et al.*, 1997).

Availability of data

- Data are described in publications.

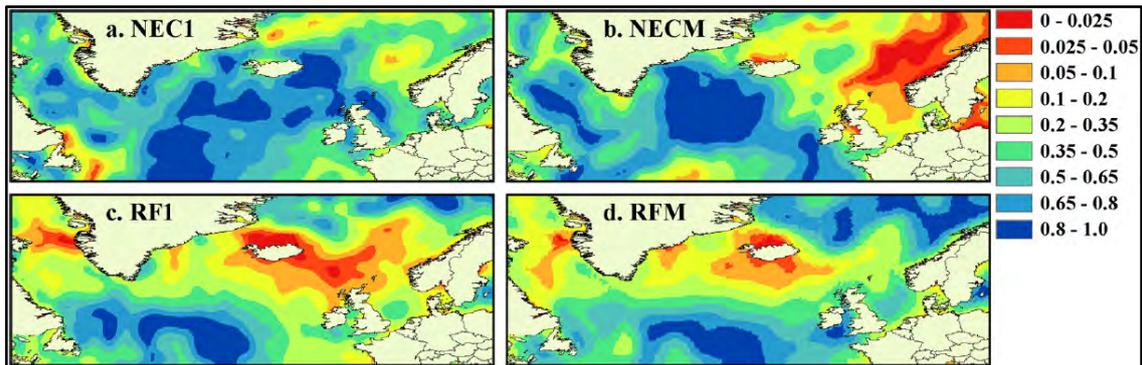


Figure 2.6. Proposed marine feeding areas for two salmon populations of UK origin indicated by the strength of correlation between sea surface temperature records and scale $\delta^{13}\text{C}$ ratios. Colours indicate the significance of the correlation (p-value) after adjustment of effective degrees of freedom to account for autocorrelation in both time-series. Each map represents feeding areas for a specific population and cohort: (a) Northeast Coast 1SW, (b) Northeast Coast MSW, (c) River Frome 1SW, and (d) River Frome MSW. Modified from Mackenzie *et al.* (2011).

2.1.7 Telemetry - repeat observation type

Telemetry is a valuable tool for learning about the timing and location of mortality events as you can get repeat observations of marked individuals, over time and in different locations, without having to catch them (Strom *et al.*, 2019). There are two main types of telemetry electronic tags for monitoring the distribution and migration of salmon at sea: archival tags and transmitting tags.

Archival tags, also called data storage tag (DST), are inserted or attached to the fish and they monitor, record, and archive data from sensors that measure elements of the environment of the fish. Environmental parameters most often recorded are temperature, pressure and light intensity. Simpler archival tags must be physically retrieved in order to extract the data. Popup satellite archival tags (PSAT) are tags attached externally to the fish and if the tag is released from the fish, based on pre-timed or behavioural triggers of the fish, they float to the surface and attempt to contact and transmit the stored data to satellites.

Transmitting tags, either as acoustic tags that function in fresh and salt water environments or radio tags that function in freshwater, differ from archival tags in that they generally do not log data but rather repeatedly transmit an acoustic signal representing a unique identifier. Receivers deployed at various points along the migration route listen for the transmissions and if the tag is in the proximity of a receiver, the tag id will be registered. Transmitting tags require the deployment of receiving stations and provide information on fish location when within range of a receiver.

2.1.7.1 Acoustic tags

The miniaturization of transmitting tags that are subsequently detected by deployed acoustic receivers has provided new opportunities to learn about salmon ecology at sea, particularly for the smaller-bodied post-smolts in the initial migration period. Deployment of receiver arrays in estuarine and coastal areas in the North Atlantic are providing opportunities to characterize the timing and location of the early post-smolt stages. The majority of ongoing research is summarized in the inventory of marine research (<http://www.nasco.int/sas/research.htm>) compiled by NASCO's International Atlantic Salmon Research Board (IASRB) and in NASCO's SALSEA-Track Progress Report of 2017 (<http://www.nasco.int/sas/>).

The Ocean Tracking Network (<http://oceantrackingnetwork.org/>) has an inventory of acoustic detection platforms that have been deployed through the world's oceans.

A summary of an unpublished review of literature, just over 75 published studies dating from 1975 to 2018, that used either acoustic or radio telemetry technologies to research various aspects of Atlantic salmon smolt and post-smolt migratory phase indicated (Figure 2.7):

- The research objectives included describing the movement dynamics (timing, pathways, speed, depth) and estimating stage-specific inferred survival estimates (modelled detections) in freshwater and in the early marine phase.
- Temporal coverage begins in the mid-1970s with most studies reported since the 2000s (Figure 2.7).
- Temporal replication and spatial coverage is low; most studies are of one or two year duration, there is a handful of telemetry projects that have been replicated at the same location for more than five years, and the longest study at the same location was 14 years.
- Overall locations and years, 60% of individual studies had tagged and monitored less than 50 salmon smolts, with only 14% of studies using more than 100 salmon smolts. Small sample sizes constrain the ability to follow sufficient animals in time and space resulting in greater uncertainty in sequential estimates of survival. The technology remains expensive.
- Smolts have been captured, tagged and released at various distances from the head of tide (<1 km to 187 km) and smolts and post-smolts have most often been tracked at sea over relatively short distances (< 100 km); maximum distance monitored from head of tide to the last marine monitoring point is ~800 km for smolts from the Gulf of St Lawrence (exit to the Labrador Sea) (Chaput *et al.*, 2018).
- The size distributions of smolts used in individual marine monitoring studies are variable and stock specific; hatchery smolts are bigger than wild smolts and in many studies, wild smolts are quite small with mean lengths of 130 to 150 mm (Figure 2.7).
- With current telemetry technologies, the challenge is to move away from the coast and later into the marine phase.

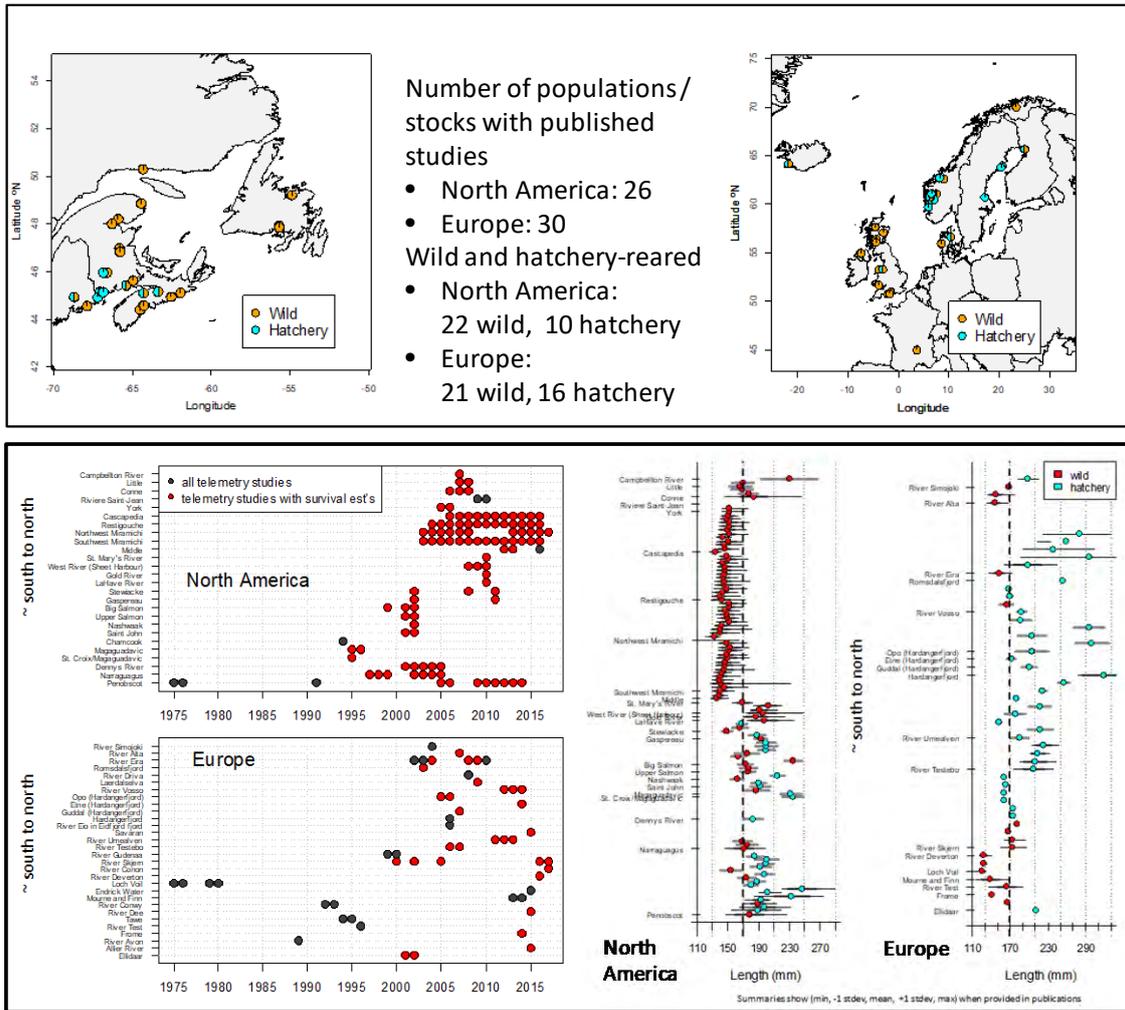


Figure 2.7. Summary of the locations, timing, and size distribution of Atlantic salmon smolts (wild, hatchery origin) in reviewed studies using telemetry technology to research the migration dynamics and survival of the smolt and post-smolt stages.

2.1.7.2 Archival tags - non-transmitting

Archival tags, also called data storage tags (DST), are inserted or attached to the fish and they monitor, record, and archive data from sensors that measure elements of the environment of the fish. Environmental parameters most often recorded are temperature, pressure and light intensity. Non-transmitting archival tags must be physically retrieved in order to extract the data. There are a few studies reporting on distribution of salmon at sea using archival tag implanted in salmon smolts and salmon kelts (Table 2.1).

Salmon smolts

Gudjonsson *et al.* (2015) published the only study to date covering an entire period of sea migration from smolt to returning adult. The authors were able to retrieve data collected by an archival tag on temperatures, depths, and diurnal activity from seven individual salmon tagged and released as smolts and returning as 1SW salmon to a river in Iceland. These data were used to estimate daily locations during an entire period at sea. The authors concluded that the salmon in the study stayed southwest of Iceland in the Irminger Sea during the first summer months, but moved towards the Faroe Islands in the fall and then back to the Irminger Sea where they stayed, until returning to the river (Gudjonsson *et al.*, 2015).

Salmon kelts

In an analysis of kelt data, Chittenden *et al.* (2013a) matched temperatures recorded on the tags to sea surface temperature profiles and a probabilistic model inferring location based on these data to infer that the probable locations of these fish overlapped with the polar front area during the months of November to April. Strøm *et al.* (2018, 2020) summarize results of extensive tagging programmes on salmon kelts with archival tags. The purpose of these studies was to investigate and map the spatial distribution and investigate the vertical behaviour of adult Atlantic salmon from a North Norwegian river during the entire ocean migration. This was done by tagging post-spawned Atlantic salmon, before they left the river in the spring, with high resolution light-based geolocation archival tags that recorded temperature, depth, and light intensity at 30-s intervals. Geolocation estimates obtained from the light data, in combination with depth and temperature measurements, were incorporated into a hidden Markov model (HMM) to geolocate the fish during the entire period of ocean residency.

Table 2.1. Summary of studies using archival tags implanted on salmon smolts and salmon kelts that describe salmon distribution and occurrence at sea.

Life stage (period)	Location	Parameters measured	Number of tags retrieved (number released)	Reference
Smolt (2005, 2006)	River Kidafellsa (Iceland)	Temperature pressure	7 (598)	Gudjonsson <i>et al.</i> (2015)
Kelt (2006–2008)	Alta River (Norway)	Temperature	14 (316)	Chittenden <i>et al.</i> (2013a)
Kelt (2013–2015)	Alta River (Norway)	Internal and external temperatures, pressure, and light	6 (197)	Strøm <i>et al.</i> (2018)
Kelt (2006–2015)	Alta River (Norway)	Various (internal and external temperatures, pressure and light)	49 (1044)	Strøm <i>et al.</i> (2020)

2.1.7.3 Archival tags - transmitting

Archival tags that have transmitting capacity to satellite systems have been used to obtain information on salmon at sea. These tags, called pop-up satellite archival tags (PSAT), are attached externally to the animals. The tags may be pre-programmed to detach from the anchoring harness on the fish at a predetermined date or can be programmed to detach in response to a perceived mortality of the fish carrying the tag, such as due to constant depth profiles over a determined period of time. When detached from the fish, either because of the pre-determined release date, mortality, mechanical failure of the harness or predation, the positively buoyant tags float to the surface and begin to transmit their archived data to the Argos satellite system. Retrieved archived data from these tags can be used to reconstruct the movement and behaviours of individual fish using various models, such as hidden Markov models, which predict the probability of individuals occupying different geographic positions by time. The tags are currently still quite large and published studies are of post-spawned kelt salmon.

Recent projects to tag salmon during their second summer and fall at sea to learn about this life stage and phase are described in the inventory of marine research compiled by NASCO's International Atlantic Salmon Research Board (IASRB) (<http://www.nasco.int/sas/research.htm>) and in NASCO's SALSEA-Track Progress Report of 2017 (<http://www.nasco.int/sas/>).

To date results of post-spawned salmon migrations show a wide range of migration patterns and distributions for salmon from eastern North America (Lacroix, 2013; Strøm *et al.*, 2017) and from Europe (Chittenden *et al.*, 2013b; Strøm *et al.*, 2019) (Table 2.2). Lacroix (2013) reported on individual fish tracks that extended from five to 169 days at sea, and distances of 20 to almost 5000 km. Strøm *et al.* (2017) summarize movement data of kelts up to 150 days post release, and migration distances exceeding 2000 km. In both studies, daily georeferenced positions for fish are modelled from such data.

Table 2.2. Summary of life stages studies, locations, parameters measured and references for studies of Atlantic salmon migration and distribution at sea using transmitting archival tags (PSAT).

Life stage	Location	Parameters measured	Number of tags retrieved (number released)	Reference
Kelt (2008–2011)	Bay of Fundy rivers (Canada)	Ambient light, temperature, pressure	39 (55)	Lacroix (2013)
Kelt (2012–2015)	Miramichi River (Canada)	Ambient light, temperature, pressure	16 (43)	Strøm <i>et al.</i> (2017)
Kelt (2008)	Alta River, Norway	Ambient light, temperature, pressure	2	Chittenden <i>et al.</i> (2013b)
Kelt (various)	Canada, Norway, Denmark, Ireland, Spain	Ambient light, temperature, pressure	156	Strøm <i>et al.</i> (2019)

Value

- Individual sequential modelled observations of fish location over time and space.
- Results from studies to date confirm the consistent observations of behaviour (pelagic mostly in surface waters, deep diving, temperature ranges).
- Provide data on position used to describe migration paths.

Limitations

- Time-series of observations (number of years) are relatively recent.
- In some studies (kelts), there are few individuals monitored.
- Spatial resolution for PSAT tags is not accurate enough to precisely determine the exact location of fish.
- More precise positioning can be obtained with acoustic tags and deployed receivers, however receiver deployments are localized, near shore, and sparsely distributed.
- Number of populations monitored is small.
- Life stage constraints for using the larger transmitting archival tags which currently can only be used on large-bodied fish, such as kelts or salmon in their second year at sea.
- Acoustic tags have some limits related to size of smolts which can be tagged, and tracking to date has been restricted to coastal and nearshore environments.

Availability of data

- Data are described in publications.

2.1.8 Migration modelling

Individual based modelling (IBMs), numerical models focusing on individual fish movements and their behaviour, can be a useful approach to understand the mechanisms driving fish migrations and to understand populations dynamics. There are several publications where this has been applied for salmon (Booker *et al.*, 2008; Byron *et al.*, 2014; Burke *et al.*, 2014; Bracis and Anderson, 2012; Chittended *et al.*, 2013a; Mork *et al.*, 2012; Ohashi and Sheng, 2018). The results indicate that there are several variables affecting salmon migrations, for example temperature, geomagnetic fields, ocean currents and salinity. However, correlations between the variables makes it difficult to understand the driving mechanism (Byron and Burke, 2014). Model validation require recordings or observations from the marine environment, for instance trawl catches or DST-tag data. Lack of such data can limit model development and understanding.

The model for the Northeast Atlantic applied by Mork *et al.* (2012) is operational but requires assistance of modellers who normally do not work on Atlantic salmon questions. The possibility to apply other published models are not known.

A new IBM is presently being developed under the SeaSalar project (Appendix 6.2.1). One of the objectives of the model is to explore the spatial and temporal link between post-smolt and prey, a link that has not been properly explored by previous salmon IBMs (Byron and Burke, 2014). The model domain will cover the Norwegian Sea and surrounding areas, but not the areas south and west of Greenland. Model simulations are expected to be initiated in 2020.

2.2 Salmon ecology at sea – physical habitat features

2.2.1 Single observation - direct or modelled

Conditions, including water temperature, depth of water column, salinity may be available to describe the characteristics of the habitat occupied by salmon which are captured in fisheries or research programmes. In most cases, information on water characteristics (e.g. temperature, salinity) are not available from fisheries catches or even for recaptures of tagged salmon at sea.

Water temperatures corresponding to the time and location of recaptured fish were interpolated for some of the recapture data from the Faroes fishery analysed by Ó Maoiléidigh *et al.* (2018; Figures 7.10–7.14). For the most part, salmon were not recaptured in water < 4°C and sea surface temperature when fish were recaptured ranged from 4 to 10°C in fall and winter.

Directed marine surveys for salmon provide more detailed information on sea surface temperatures and other characteristics of the physical habitat in which salmon are captured. Reddin (2006) summarizes the temperature preferences of adult and post-smolt salmon based on research vessel catch rates and temperature profiles at locations of capture. Post-smolts were most frequently captured in temperatures from 5 to 8°C whereas adult salmon catch rates were highest in sea surface temperatures of 4 to 10°C (Figure 2.8). Water temperatures in areas and at times corresponding to captures of salmon post-smolts at sea from sampling in August and September in the Northwest Atlantic (Sheehan *et al.*, 2012) and from sampling in May and June in the Northeast Atlantic (SALSEA-Merge, 2012) reported highest catch rates at temperature of 10°C and above (Figure 2.8).

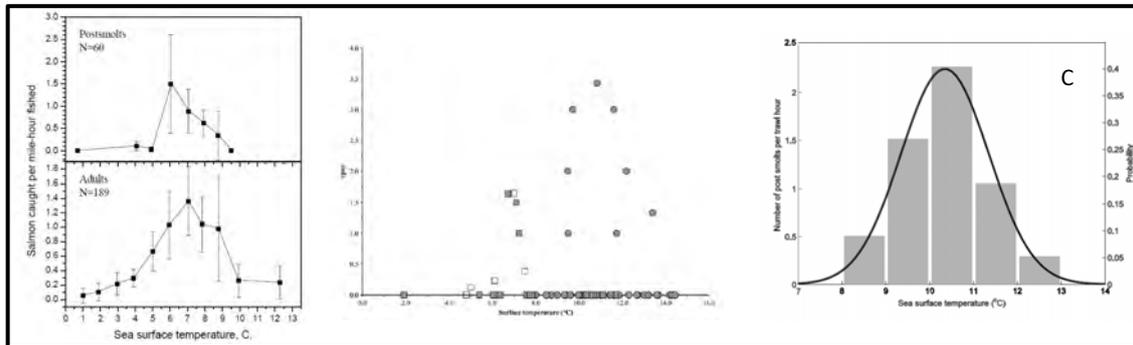


Figure 2.8. Summary of catch rates of Atlantic salmon in directed marine surveys in the North Atlantic. Panel A from Reddin (2006) and panel B from Sheehan *et al.* (2012) are from sampling in the Northwest Atlantic. Panel C from SALSEA-Merge (2012) is from sampling for post-smolts in the Northeast Atlantic.

There were directed surveys targeting salmon in the Northeast Atlantic in the 1990s and early 2000s (see Section 2.1.3), but oceanographic data from these surveys are not always available. It would require a larger effort to get an overview of the available data and its location. For the surveys after 2010, there are oceanographic data sampled with an instrument that records conductivity, temperature and depth (also known as a CTD) at regular stations covering the survey areas. These surveys were mainly targeting mackerel or other pelagic species, and salmon was taken as bycatch. The available oceanographic data include both temperature and salinity with 1 m vertical resolution and are available through collaboration.

There are also available historic satellite data of sea surface temperature provided by the National Oceanic and Atmospheric Administration (NOAA) (see description in Section 3.3.1). These data could be a useful replacement or addition to the oceanographic data sampled *in situ* during the surveys.

Value

- Provides information on temperatures in which salmon are found and relative abundances over temperature ranges in which salmon are captured.

Limitations

- Not appropriate to call these observations temperature preferences, as not all temperatures ranges over seasons and in the North Atlantic were sampled.
- Temperature at the time of capture by the gear is not known. An average temperature over the time the fishing gear was sampled, which can cover a few kilometres, is calculated and applied to all fish in the sample. Based on geography, temperature would not be expected to be so variable over the duration of the sampling set (30 minute set using surface trawl). Gillnet sets, which were the source of the majority of salmon captured in the surveys described by Reddin (2006), often extended over several hours and the nets were drifting.

Availability of data

- Individual temperature data at time of capture should be available by contacting researchers directly.

2.2.2 Repeat observation – direct or modelled

The greatest advance in knowledge on physical characteristics of the habitat which is occupied by salmon comes from telemetry monitoring of migrations of individual fish. Multiple and temporally sequential data on some features of the physical habitat encountered by salmon at sea can be logged using telemetry technologies.

Acoustic and radio telemetry provides an opportunity to collect some physical features of the habitat occupied by salmon, although no such data were presented at WKSalmor. Acoustic tags with depth and temperature sensors are available from manufacturers, however, these tags tend to be quite large and would not be suitable for smolt and post-smolt monitoring. Temperature and pressure data would be recorded when a tagged fish is in range of a receiver; the data transmitted corresponding to the conditions at the time of data transmission. There are no data storage capacity and transmittal features for these tags.

2.2.2.1 Archival tags - non-transmitting

Archival tags have provided detailed data on temperature and depth occupied by individual fish during their migration at sea (Table 2.3). Reddin *et al.* (2006) reported on temperatures registered by archival tags during short durations of time at sea of smolts; most of the tag recoveries occurred within three to 28 days post-release, with two tags recovered on post-smolts returning to freshwater 59 and 71 days post-release. Gudjonsson *et al.* (2015) compiled data on temperatures and depths encountered during an entire period of migration of 1SW salmon from Iceland. The archival tag data consisted of time-stamped temperature and depth data from seven salmon returning as 1SW salmon. From these data, it was concluded that salmon stayed close to the surface most of the time and showed diurnal diving behaviour, with slightly deeper waters occupied during day. The salmon occupied habitat ranging in water temperatures from 6 to 15°C, with warmer temperatures in the summer.

There is substantially more data from archival tags placed on salmon kelts prior to their return to sea post-spawning. Reddin *et al.* (2011) report on temperatures and depths of 13 kelts during the reconditioning migration phases that lasted an average of 62 days at sea prior to returning to the river to spawn. Water temperatures recorded on the archival tags over the period at sea showed a wide range for all fish (from <0 to nearly 20°C), with modes of cooler temperatures 6–7°C corresponding to daytime profiles and slight warmer temperatures of 11–12°C at night. Variations in depth were also recorded; salmon dove more frequently and spent less time near the sea surface during the day. Similarly, Chittenden *et al.* (2013b) and Strøm *et al.* (2018, 2020) reported on temperature data retrieved from archival tags placed and retrieved in kelts from a northern Norway River. Temperatures encountered by the fish were relatively cool, averaging 2.7°C in the spring in some years with maximum temperatures of just above 8°C recorded during the summer period. Strøm *et al.* (2020) summarize sea temperature ranges for salmon from available studies in the North Atlantic, based on archival tags and from sea sampling programmes.

Table 2.3. Summary of life stages studied, locations, parameters measured, number of tags applied and retrieved and references for studies that characterize physical characteristics of habitat utilized by Atlantic salmon from non-transmitting archival tags.

Life stage	Location	Parameters measured	Number of tags retrieved (number released)	Reference
Smolt (2002)	Campbellton River (Canada)	Temperature	15 (311)	Reddin <i>et al.</i> (2006)
Smolt (2005, 2006)	River Kidafellsa (Iceland)	Temperature, pressure	7 (598)	Gudjonsson <i>et al.</i> (2015)
Kelt (1998)	Various rivers in Newfoundland (Canada)	Temperature	11 (139)	Reddin <i>et al.</i> (1999, 2004)
Kelt (2007)	Campbellton River (Canada)	Internal and external temperatures, pressure and light	13 (26)	Reddin <i>et al.</i> (2011)
Kelt (2006, 2007, 2008)	Alta River (Norway)	Temperature	14 (316)	Chittenden <i>et al.</i> (2013b)
Kelt (2008–2012)	Orkla River, Alta River, Neiden River (Norway)	Temperature, depth	38 (634)	Hedger <i>et al.</i> (2017a,b)
Kelt (2013–2015)	Alta River (Norway)	Internal and external temperatures, pressure and light	6 (197)	Strøm <i>et al.</i> (2018)
Kelt (2006–2015)	Alta River (Norway)	Various (internal and external temperatures, pressure and light)	49 (1044)	Strøm <i>et al.</i> (2020)

2.2.2.2 Archival tags - transmitting

A common tag type used for larger bodied animals is the pop-up satellite archival tag (PSAT) which is attached externally to the animal and records a number of physical characteristics of the habitat occupied by fish, including primarily temperature, pressure and luminance (for assisting in geo-referencing). Several studies report on data obtained with this technology including Lacroix (2013, 2014) for salmon kelts from populations of the Inner Bay of Fundy Canada, Strøm *et al.* (2017) for salmon kelts from the Gulf of St Lawrence Canada, and Hedger *et al.* (2017a, 2017b) for salmon kelts from Norway (Table 2.4).

These studies have provided empirical data on sequential temperatures encountered by salmon at sea and depths utilized by salmon during the marine phase. As has been shown for maiden salmon based on archival tags, previously spawned salmon are predominantly a pelagic, upper column fish spending the majority of the time in the upper 10 m of the water column but in offshore areas will undertake dives to depths exceeding 500 m (Lacroix, 2013; Hedger *et al.*, 2017a; Strøm *et al.*, 2017).

Table 2.4. Summary of life stages studied, locations, parameters measured, number of tags applied and retrieved and references for studies that characterize physical characteristics of habitat utilized by Atlantic salmon from archival transmitting tags.

Life stage	Location	Parameters measured	Number of tags with useable data (number released)	Reference
Kelt (2008–2011)	Bay of Fundy rivers (Canada)	Ambient light, temperature, pressure	39 (55)	Lacroix (2013)
Kelt (2012–2015)	Miramichi River (Canada)	Ambient light, temperature, pressure	16 (43)	Strøm <i>et al.</i> (2017)
Kelt (2008–2012)	Orkla River, Alta River, Neiden River (Norway)	Temperature, depth	38 (634)	Hedger <i>et al.</i> (2017a, 2017b)

Value

- Multiple, temporally sequential data on temperature and depth that describes diurnal, seasonal and annual variations in behaviour of salmon at sea.
- PSAT technologies can provide data on salmon which survived back to home waters but also for salmon which did not return.

Limitations

- Current technology limits the life stage of salmon that can be studied to large-bodied fish (kelts, and possibly 1SW non-maturing salmon in the second summer at sea), but note the exception of study by Gudjonsson *et al.* (2015) which involved archival tags in relatively large smolts.
- There may be an effect of larger PSAT tags on salmon behaviour, growth and survival (Hedger *et al.*, 2017b).

Availability of data

- Time stamped depth and temperature archival tag data from 50 kelts of the River Alta (Norway) over the period 2006 to 2015 with migration routes inferred for six fish (personal communication J.F. Strøm).
- PSAT ocean migration modelled data from 57 kelts in Norway (2008–2010), 29 from Denmark (2011–2014), eleven from Ireland (2010–2011), five from Spain (2013–2014) and two from Iceland (2011) (personal communication J.F. Strøm).
- Initiatives in SEASALAR include archival tag data from the Alta River for 2018 and 2019 (archival tags recording temperature, depth, light) from River Lakselva for 2018 and 2019, river Etne for 2019, and the River Nidelva for 2019 (PSAT; temperature, depth, light) (personal communication J.F. Strøm).

2.3 Salmon ecology at sea – diet

There have been many studies of Atlantic salmon diets (reviewed by Rikardsen and Dempson, 2011), although they are usually restricted to specific locations at specific times, and often suffer from small sample sizes. There is evidence for an ontogenetic shift in diet (Rikardsen and Dempson, 2011). For example, Rikardsen *et al.* (2004) analysed the stomach contents of post-smolts from eight Norwegian fjords and found that fish larvae, including sandeels and herring, constituted a large proportion of diet biomass in several fjords, although insects and crustaceans were major dietary components in other fjords. Although diets of non-maturing and maturing adult

salmon included these same fish species, they also included several different fishes, including blue whiting, lantern fish and capelin, together with amphipods and euphausiids (Rikardsen and Dempson, 2011 and references within). Again, there is some suggestion that the differences in diets could be due to spatio-temporal variation in feeding opportunities, and perhaps individual specialism.

Diet content, including amount and relative composition, is purported to have implications for Atlantic salmon stocks, presumably through its effect on individuals. For example, Kallio-Nyberg *et al.* (2006) found that the abundance of age 0+ herring stocks in the Baltic Sea was associated with the recapture rate of wild River Simojoki post-smolts, although July sea surface temperature had a stronger and dominant association. The same study found that herring and sprat populations were not associated with the survival of older Atlantic salmon, suggesting that the impacts of diet on survival might be strongest during the first few months at sea (Kallio-Nyberg *et al.*, 2006). Similarly, Mantyniemi *et al.* (2012) found that the survival rate of hatchery and wild post-smolts was best described by a measure of herring recruits available to each post-smolt, and that sprat were less important. They also found that grey seal abundance was associated with post-smolt survival rate and suggested that it might explain the observed declining trend in Baltic Sea post-smolt survival, whereas prey abundance might better explain the interannual variability (Mantyniemi *et al.*, 2012). Despite the wealth of studies on post-smolt survival in the Baltic Sea, the overall picture is still not clear. While some studies have considered sea surface temperature and smolt length among their explanatory variables, others have omitted them in favour of prey and predator abundance.

2.3.1 Diet studies - single observation

In 2017, NASCO asked ICES to provide a summary of the available diet data for the marine life stages of Atlantic salmon and to identify key prey species at different life stages. In addition, ICES was requested to comment on any significant changes in population dynamics (i.e. abundance, distribution, size structure, and energy density) of key prey species which may be associated with changes in salmon abundance, distribution, and marine ecology, while also providing information related to fisheries which catch significant numbers of the identified key prey species (i.e. direct harvest or bycatch).

The key findings reported in ICES (2017a) include:

- Feeding intensity and diet composition varies with life stage, fish size, season and location, and correlates to water depth.
- Some of the key prey species identified are important during multiple life stages in multiple locations.
- There are large temporal and spatial differences in the diet for salmon in the Northeast Atlantic and differences in the diet relative to body size of the salmon.
- In the Northeast Atlantic, post-smolt feed on fish larvae in coastal regions and on large zooplankton in oceanic regions.
- As for post-smolt, there are temporal and spatial differences in the diet for larger salmon. Their diet consists of small pelagic fish, large zooplankton and mesopelagic fish. The general picture is that larger salmon feed on larger prey and are opportunistic predators capable of switching diet according to availability.
- The key prey species of Atlantic salmon fall into two general categories: fish harvested in fisheries (capelin, Atlantic herring, sandeel, and other pelagic species) and unharvested prey, including fish (barracudina and sandlance), crustaceans (amphipods and euphausiids), and cephalopods (armhook squid). More information was available for commercially important fish species, but for all the other unharvested species, fish and invertebrates, very little is known besides basic life history and distribution.

Diet studies of Atlantic salmon have been summarized in a few key papers, notably Lear (1972), Jacobsen and Hansen (2001), and Rikardsen and Dempson (2011).

In the Northeast Atlantic, salmon stomachs have been sampled from 1995 to 2019. However, it is not a consecutive time-series as there are several years without samples. Further, the sampling period has varied from May to August. Most of the historic sampling has been done in the Norwegian Sea but there are also samples from west of the British Isles, the Barents Sea and from along the Norwegian coast (Figure 2.9). Sampling has been undertaken in Norwegian, Irish and Faroese surveys. The sampling method has been visual identification, splitting the prey into species group and measure the weight of each prey group. The dataset holds stomach samples from more than 3200 individual fish (Table 2.5). The genetic origin is known for some of the fish where the stomach content has been analysed, but the exact number is not clear. Diet information from stomachs sampled in the 1990s and early 2000s have been published by Haugland *et al.* (2006) and the remaining samples are now being prepared for publication. Preliminary analyses of the new data support earlier findings, but there are indications of a reduced proportion of fish larvae in the post-smolt diet.

Table 2.5. Month and year of Atlantic salmon stomach sampling and number of samples (N) aggregated to large scale areas in the Northeast Atlantic.

Area	Months	Years	Number of post-smolt samples	Number of 1SW and older salmon samples
West of British Isles	May/June	1995, 1996, 1997, 2004, 2008	454	7
Norwegian coast	May/June	1998, 1999, 2000, 2001	1102	8
Barents Sea	July	2000	177	0
Norwegian Sea	June/July/August	1995, 1996, 1997, 1998, 1999, 2001, 2002, 2003, 2008, 2009, 2018	1513	26

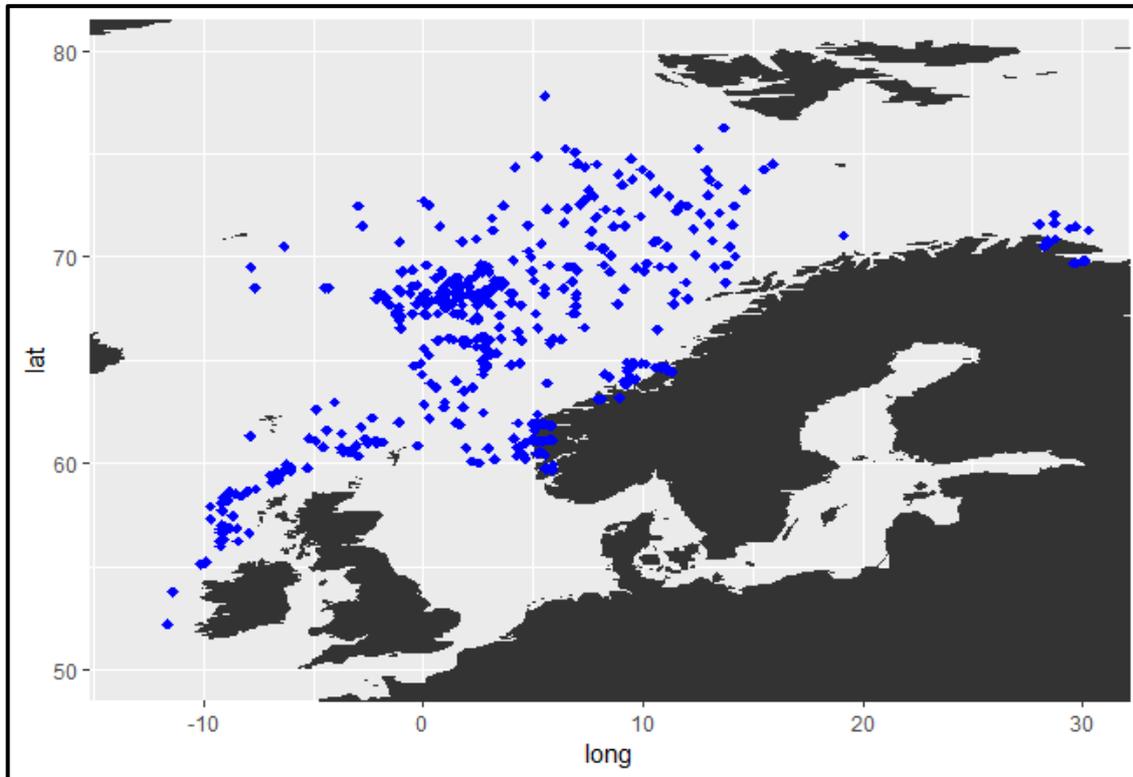


Figure 2.9. Geographic presentation of locations of Atlantic salmon stomach samples collected from the Northeast Atlantic.

Value

- Provides information on prey items consumed by individual salmon.
- Can be used to monitor temporal differences in the prey community being consumed by salmon, as well as prey quality.

Limitations

- Point in time samples only.
- Because of digestion, not all prey items can be identified and prey with hard bony parts can be identified more readily than soft-bodied prey.
- Prey items identified indicate interactions over a recent short period of time.
- Cannot infer prey selection because generally indices of prey availability are not known.
- Temporal coverage of sampling is low, most samples come from summer and fall.
- Spatial coverage is also limited, generally collected from fisheries or directed surveys with minimal replication.

Data availability

- The stomach data are available through contact with the relevant research institutes.

2.3.2 Stable isotopes – sequential observation

Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) stable isotope ratios can be used to estimate the dietary sources and trophic position of an animal (DeNiro and Epstein, 1978, 1981). $\delta^{13}\text{C}$ ratios do not change with increasing trophic level and provide information on the primary producer responsible for energy flow at the base of the foodweb (Peterson and Fry, 1987). Productive benthic and nearshore regions supported by algae and sea grass have higher $\delta^{13}\text{C}$ ratios than less productive pelagic and oceanic regions supported by phytoplankton (Graham *et al.*, 2010). $\delta^{15}\text{N}$ ratios are

indicative of an animal's trophic position, because $\delta^{15}\text{N}$ ratios consistently rise with increasing trophic level as the lighter nitrogen isotope is preferentially excreted (Cabana and Rasmussen, 1994). Sulphur ($\delta^{34}\text{S}$) stable isotope ratios vary widely and reflect sources of nutrients in food-webs (Fry, 2006). Oxygen ($\delta^{18}\text{O}$) and hydrogen ($\delta^3\text{H}$) stable isotopes have fewer ecological applications due to their relatively homogeneous spatial distribution in the marine environment.

Stable isotope analysis is a powerful tool that has transformed understanding of the diet, feeding and movement of wild Atlantic salmon at sea. Early investigations using stable isotope analysis demonstrated that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in salmon are temporally and spatially variable, suggesting that salmon occupy a wide range of different marine feeding areas in the North Atlantic (Trueman and Moore, 2007; Sinnatamby *et al.*, 2009; Dempson *et al.*, 2010). An analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in archived salmon scales of UK origin from the Faroes and West Greenland fisheries indicated that salmon are size-structured pelagic predators, adults feed in different marine areas before returning to natal UK rivers to spawn, and salmon from the UK do not forage in the same regions of the Northwest Atlantic used by 1SW salmon from Newfoundland, Canada (Mackenzie *et al.*, 2012). A more recent investigation into $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in scale samples of salmon captured returning to the Miramichi and Nashwaak Rivers in New Brunswick, Canada found that the diet and marine feeding areas of salmon varied depending on spawning strategy (Kelly *et al.*, 2019). Repeat alternate spawners that return to rivers to spawn after spending more than one year at sea mainly consumed hyperiid amphipods and capelin (*Mallotus villosus*), while repeat consecutive spawners that return to the Miramichi and Nashwaak Rivers following a brief period of a few months reconditioning at sea largely preyed on sandlance (*Ammodytes* sp.) and amphipods, respectively.

Investigations using stable isotope analysis have provided insight into the mechanisms driving the increased marine mortality of wild Atlantic salmon populations over the last three decades. Differences in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios of archived scales collected from two UK salmon populations between 1979 and 2002 have revealed that climate-driven fluctuations in phytoplankton community composition are related to the increased marine mortality of salmon feeding in the Norwegian Sea but not the Iceland Basin (Trueman *et al.*, 2012a). The marine mortality of salmon in the Iceland Basin is likely to be more strongly influenced by top-down (e.g. predation risk) than bottom-up (e.g. prey availability) processes. More recently, an investigation into $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ratios in archived scales collected from salmon returning to the St John River in New Brunswick, Canada between 1980 and 2011 indicated that warmer ocean temperatures are unlikely to be the main cause of increased mortality, because 1SW and MSW populations occupy different marine feeding areas and experience different ocean temperature regimes (Soto *et al.*, 2018).

Value

- To some extent, allows a reconstruction and inference of trophic feeding state of salmon, and the extent of pelagic vs benthic sources.
- Data can be extracted from archived tissue samples thus able to reconstruct time-series of trophic state indices.
- Based on scales, there are extensive spatial and temporal collections, no need to sacrifice fish or to store samples in any particular medium.

Limitations

- When collected from returning salmon, results are for survivors only and that the study is limited to those individuals that were able to compete and feed successfully, and it ignores those unsuccessful individuals that may have been influenced more heavily by changes in the marine ecosystem.
- Marine portion of the scale represents the integration over a large time spent at sea rather than finer points in time.

- Resolution of trophic levels only, does not identify specific prey consumed.

Availability of data

- As far as known, there is no repository of stable isotope data developed for Atlantic salmon. Data reside in individual research laboratories or institutions and contacts would be available from the publication author and contact details.

2.4 Salmon ecology at sea – predation

2.4.1 Diet studies of predators - single observation

Cairns (2006), in a summary of prey–predator interactions of Atlantic salmon, concluded that Grey, Harp, and Harbour seals, along with common murre and northern gannets were the most commonly reported predators of Atlantic salmon in marine waters. The identification of salmon in gastro-intestinal samples was very rare; in part because salmon are a minute fraction of total prey biomass in the North Atlantic and of individual predator diet.

Diet studies are usually based on the collection of gastro-intestinal tracts from predators and the identification of prey is often based on bony body parts, primarily otoliths and atlas vertebrae, when prey items are too digested. The stomach samples of potential predators are also dependent upon the ease of sampling of the predators; usually available from animals in coastal or estuarine areas, or for seabirds, collections during the breeding season. Sample sizes from individual locations and periods may be quite small and coverage of predators when they are away from coastal areas and haul out areas or in less dense aggregations is generally not possible.

2.4.2 Modelled observations

Predation of Atlantic salmon has been inferred directly and indirectly using telemetry technologies (Table 2.6). One example of a direct predation observation using telemetry is a study reported by Dieperink *et al.* (2002) of predation of Atlantic salmon and sea trout smolts by seabirds (herring gull *Larus argentatus*, cormorant *Phalacrocorax carbo sinensis*); predation was inferred from the recovery in seabird colonies of radio tags which had been placed in migrating salmon and trout smolts. In many cases using telemetry, the specific predator is not known.

2.4.2.1 Acoustic tags

Predation of a tagged fish can be detected using new “predator tags” that signal a consumption event of the tag, and presumably the fish carrying the tag, based on a change in identification code in response to a sensor which is sensitive to a lowering of pH when the tag is ingested and becomes separated from the fish in the predator’s gastrointestinal tract (Halfyard *et al.*, 2017). Daniels *et al.* (2019) reported on an experiment involving such predator tags inserted in 50 Atlantic salmon smolts released to the Northwest Miramichi River; 24 of 41 subsequently detected tags in the estuary had signalled a predation event. The specific predator was not known but because most tags were detected over multiple days, it was concluded that it was the result of fish predation rather than bird or mammal predation. Predator tags thus provide an opportunity to gain insights into the locations, timing, and rates of predation on tagged animals; however it is not possible to identify the predator species based exclusively on the change in signal of the tag.

Behavioural modelling of telemetry tag detections have provided an alternate means of inferring predation on tagged salmon smolts. Thorstad *et al.* (2011) used detections of acoustic tags equipped with depth sensors to make inferences on potential predation events on tagged smolts.

Previous studies had described the generally surface dominated behaviour of smolts migrating through estuaries and fjords, and hence abrupt changes in transmitted depth metrics from the assumed “normal” depths utilized by smolts and subsequent transmissions of greater depths was used to infer that predation had occurred, mostly likely by Atlantic cod (*Gadus morhua*) and saithe (*Pollachius virens*). The authors concluded that nine of 12 smolts lost in the fjord were consumed by fish predators (Thorstad *et al.*, 2011). Gibson *et al.* (2015) first reported on inferred predation of acoustically tagged Atlantic salmon smolts by striped bass (*Morone saxatilis*) based on unusual tag detection patterns that were more representative of the movements of predators rather than smolts. This modelling of tag detection patterns resulted in inferred predation rates ranging from 2.4% to 13.6% of tagged smolts, i.e. tags originally placed in smolts that exhibited migration patterns most similar to the predator (Gibson *et al.*, 2015). A similar modelling approach was reported by Daniels *et al.* (2018), again inferring predation by striped bass on salmon smolts using detection metrics for contrasted tagged striped bass and tagged salmon smolts. These authors concluded that over the three years of analysis of tagged smolts emigrating from two rivers and meeting in a common estuary, that between 1.9% and 17.5% of tags placed in smolts exhibited detection histories in the estuary that were most similar to detection histories of a tagged potential predator species.

2.4.2.2 Archival transmitting tags

Archival transmitting tags that record three key parameters (temperature, pressure, light intensity) have provided data with which to infer predation events and in many cases, the predator itself (endotherm, ectotherm). The consumption and retention of the archival transmitting tag and the associated changes in light intensity (associated with ingestion), temperature (core body temperature of the predator) and pressure (attributed to behaviours of potential predators from parallel telemetry studies of predators of salmon) have been used to describe predation events.

Lacroix (2014) first reported on predation of large-bodied salmon by sharks, and bluefin tuna. Depth and temperature profile data recovered from PSAT tags that had been ingested and subsequently ejected by a predator were indicative of the species of predator and approximate locations of predation events were inferred from the first transmitted location of the tags. Time of predation was inferred from the time-stamped changes in light, temperature and depth data of the tags.

Strøm *et al.* (2019) provides a compilation of the more recent data and summarized the predation events and likely predators inferred from such data. Tagging studies on a large number of potential predators of salmon have provided the behavioural information to infer the species which would have ingested an archival tag attached to salmon. Strøm *et al.* (2019) reported that predation events were inferred from data as having occurred eight to 159 days after release, and accounted for 14% of the reporting tags. Based on temperature profiles from 22 tags during the period of time the tag was retained in the predator digestive tract, five profiles were consistent with consumption by marine mammals, four by ectothermic fish (e.g. swordfish, blue shark), and 13 were consumed by endothermic fish (e.g. Bluefin tuna, porbeagle shark). Positions and dates of predation events are inferred from these data.

Table 2.6. Summary of studies using telemetry technologies to infer predation, predation rates, and likely predators of Atlantic salmon.

Life stage	Country	Technology	Number of tags reporting (released)	Number of predation events (%)	Number of unknown mortalities	Reference
Smolt	Norway	acoustic	(20)	9 of 12	na	Thorstad <i>et al.</i> (2011)
Smolt	Canada	acoustic	(113 smolts ; 44 predators)	(2.4% to 13.6%)	na	Gibson <i>et al.</i> (2015)
Smolt	Canada	acoustic	(105 to 160 smolts per year; 66 to 82 predators per year)	(1.9% to 17.5%)	na	Daniels <i>et al.</i> (2018)
Smolt	Canada	acoustic	(50)	25 of 41	na	Daniels <i>et al.</i> (2019)
Kelt	Canada (Bay of Fundy)	PSAT	27	11	16	Lacroix (2014)
Kelt	Norway	PSAT	65		10	Strom <i>et al.</i> (2019)
Kelt	Denmark	PSAT	32	2	11	Strom <i>et al.</i> (2019)
Kelt	Ireland	PSAT	19	5	10	Strom <i>et al.</i> (2019)
Kelt	Spain	PSAT	12	5	2	Strom <i>et al.</i> (2019)
Kelt	Canada (Gulf of St Lawrence)	PSAT	28	10	5	Strom <i>et al.</i> (2019)

Value

- When matched to behavioural data of potential predators, these data can be informative of the location and timing of predation events.
- Provides data on fish not subject to predation events thus allowing an inference of locations and times of lower predation risk.
- Predator species can be inferred.
- New generation of predator acoustic tags provides finer spatial and temporal resolution for predation events, and confirmation of predation as a contributor to mortality.

Limitations

- Current technology limits the life stage of salmon that can be studied with PSAT to large-bodied fish (kelts, and possibly 1SW non-maturing salmon in the second summer at sea).
- There may be an effect of telemetry tags on salmon behaviour, growth and vulnerability to predation.
- Predator species cannot be specifically identified.
- The high cost of tags tends to prohibit large sample sizes.

Availability of data

- Data reside in individual research laboratories or institutions and contacts would be available from publication author and contact details.

2.5 Salmon abundance

2.5.1 Fisheries catches as indicators of abundance

Variations in fisheries reported catches have been promoted as indicators of salmon abundance and some researchers have used reported Atlantic salmon landings as a proxy for abundance. Fisheries catches can vary, and be unrelated to abundance, for a number of reasons including variations in exploitation rates (proportions of the stock that is removed), and these are usually associated with fisheries management measures, changes in gear technology (generally improvements). ICES (2019a) provides summaries of the estimated exploitation rates on 1SW salmon (or small salmon for NAC) and MSW salmon (or large salmon for NEAC) over the period 1971 to 2018; exploitation rates in the North Atlantic have declined substantially from the high values of the 1970s that exceeded 50% to levels of 10% or less for NAC and 20% or less for NEAC areas. The decline in exploitation rate thus exaggerates the change in the abundance that would be inferred from catches, compared to the changes corresponding to abundance.

Harvest weight of Atlantic salmon in the North Atlantic has declined from peak catch values of 12 000 tonnes per year to the lowest value of the time-series in 2018 of less than 1000 tonnes (ICES, 2019a). Catches in 2018 in NAC, southern NEAC and northern NEAC were the lowest or near lowest values on record (ICES, 2019a).

Value of data

- If fisheries management measures and fishing technologies are homogeneous, then catches may be a reasonable proxy of abundance when accounting for fishing effort.

Limitations

- Changes in fisheries management, frequently associated with closures of fisheries, result in a biased representation of variations in abundance.
- Exploitation rates in both NAC and NEAC stocks have been shown to decline.

Availability of data

- Catch data available from ICES Working Group on North Atlantic Salmon (WGNAS) report tables.
- Fisheries catches (harvested fish; weight) of Atlantic salmon for the North Atlantic, by country, are available in ICES (2019a) for the period 1961 to 2018.
- Catches in weight and number by size / age group are available from several countries for a shorter period are also available in ICES (2019a).
- Finer scale specific catch data available by contacting jurisdictions.

2.5.2 Continental scale abundance

Estimates of abundance, by sea age class or size group as proxy for sea age, at large geographic scales are provided by ICES (2019a) based on a reconstruction of returns to home water jurisdictions, raised to earlier periods at sea by accounting for marine fisheries removals in mixed-stock fisheries and correcting for natural mortality. Returns and spawners are derived by jurisdictions and countries using the jurisdiction specific approaches and data. The run reconstruction approach for estimating pre-fishery abundance (PFA) was developed by Rago *et al.* (1993) and

adapted for the Northeast Atlantic by Potter *et al.* (2004). Reconstructions of abundance of spawners (mature salmon that survive all fisheries), returns (mature salmon in home waters prior to home water fisheries) at the continental scale complex (North America, NAC; Northeast Atlantic, NEAC) and sub-complexes (Southern NEAC, Northern NEAC) as well as regions within each complex are available for the period extending from 1971 to 2018, and from 1983 to 2018 for Norway (ICES, 2019a) (Table 2.7).

Table 2.7. Summary of spatial scale and years for which Atlantic salmon returns, spawners, and pre-fishery abundance are available by continental complexes, and for individual countries/jurisdictions as reported in ICES (2019a).

Spatial scale	Returns	Spawners	Pre-fishery abundance (year)
North America (NAC)	1971 to 2018	1971 to 2018	1971 to 2017
Labrador	1970 to 2018	1970 to 2018	1978 to 2016
Newfoundland	1970 to 2018	1970 to 2018	1978 to 2016
Quebec	1970 to 2018	1970 to 2018	1978 to 2016
Gulf	1970 to 2018	1970 to 2018	1978 to 2016
Scotia-Fundy	1970 to 2018	1970 to 2018	1978 to 2016
USA	1971 to 2018	1971 to 2018	1978 to 2016
Southern Northeast Atlantic (S-NEAC)	1971 to 2018	1971 to 2018	1971 to 2017
France	1971 to 2018	1971 to 2018	1971 to 2017
Ireland	1971 to 2018	1971 to 2018	1971 to 2017
UK (Northern Ireland)	1971 to 2018	1971 to 2018	1971 to 2017
UK (England and Wales)	1971 to 2018	1971 to 2018	1971 to 2017
UK (Scotland)	1971 to 2018	1971 to 2018	1971 to 2017
Iceland (southwest)	1971 to 2018	1971 to 2018	1971 to 2017
Northern Northeast Atlantic (N-NEAC)	1983 to 2018	1983 to 2018	1983 to 2017
Iceland (northeast)	1971 to 2018	1971 to 2018	1971 to 2017
Sweden	1971 to 2018	1971 to 2018	1971 to 2017
Norway	1983 to 2018	1983 to 2018	1983 to 2017
Finland	1971 to 2018	1971 to 2018	1971 to 2017
Russia	1971 to 2018	1971 to 2018	1971 to 2017

Pre-fishery abundance is estimated to 1 January of the first winter at sea for NEAC stocks whereas it is estimated to 1 August of the second summer at sea for NAC stocks. The year of PFA is expressed according to 1 January or 1 August and does not correspond to a year class as it includes a mixture of fish of varying smolt (freshwater) ages. To estimate the total abundance for a PFA year requires the returns of 2SW (for NAC) or MSW (for NEAC) for the year following the PFA year. For NAC, PFA by region is not estimated in the run reconstruction; catches in marine

fisheries are added to the sum of returns to regions to estimate PFA for NAC and this is available to the 2017 PFA year (ICES, 2019a). The non-maturing 1SW PFA by region in NAC is estimated within the PFA inference / forecast / catch advice model used by ICES; it does not include PFA by region for the 1SW maturing component. The most recent 1SW non-maturing PFA abundances for regions in NAC are from ICES (2018), including estimates to the 2016 PFA year. For NEAC, the proportions of the catches of NEAC salmon at Faroes and West Greenland are assumed known and constant over time, hence PFA by region is calculated as part of the run reconstruction and are available for both 1SW maturing and 1SW non-maturing salmon to the 2017 PFA year (Table 2.7; Figure 2.10; ICES, 2019a).

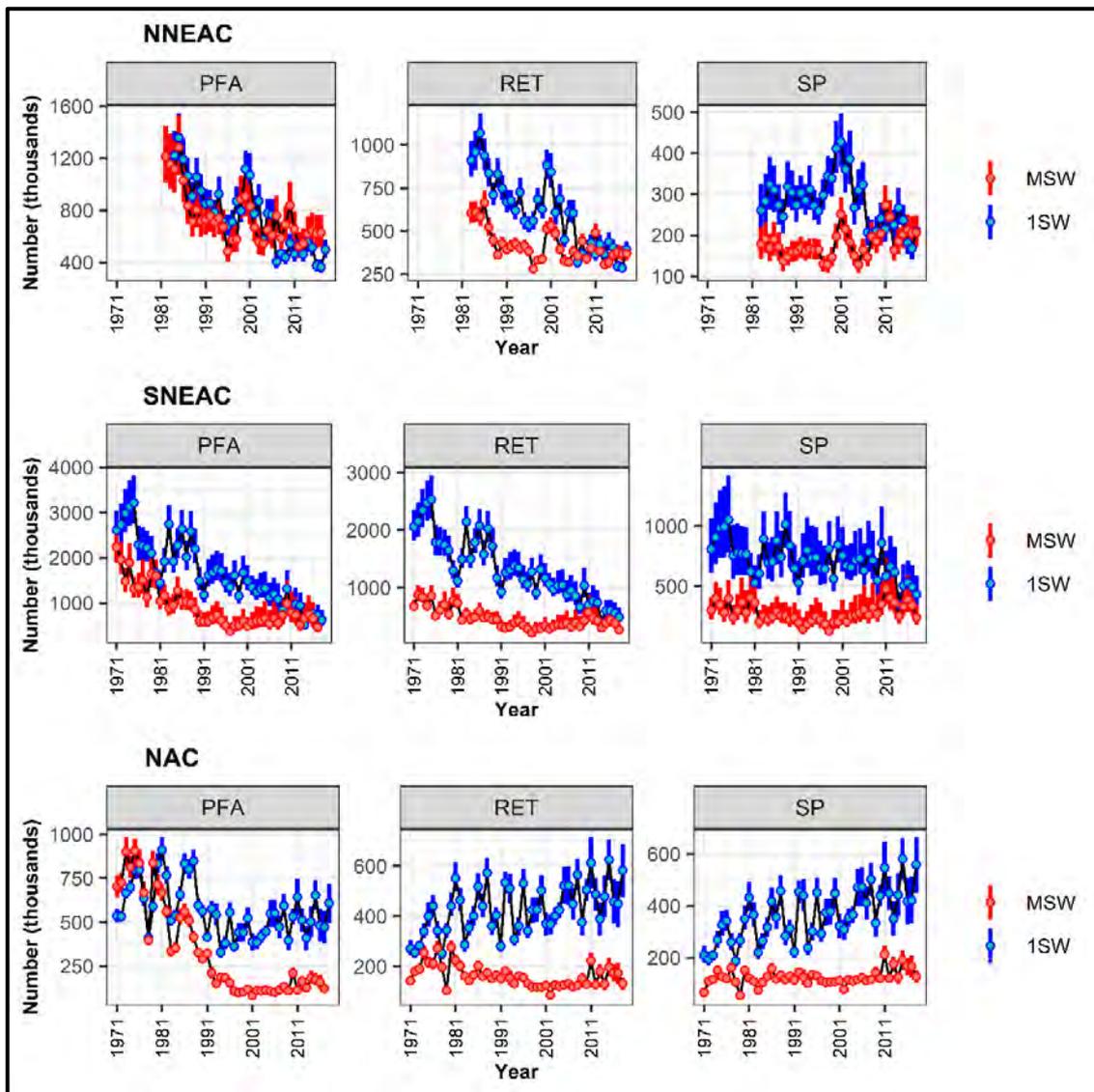


Figure 2.10. Run reconstructions of PFA, returns, and spawners for 1SW and MSW sea age (size group for NAC) for Northern NEAC (NNEAC), Southern NEAC (SNEAC), and North America (NAC), from 1971 to 2018 (2017 for PFA) (source: ICES, 2019a).

Run reconstructed estimates of returns and spawners by sea-age class at sub-country scales are available from ICES; eleven subregions for Northern NEAC and seven subregions for Southern NEAC (see Section 2.6.1).

Value

- Best estimates of relatively long time-series of abundance of Atlantic salmon as returns to home waters and prior to marine fisheries.
- Reconstructions by jurisdiction take account to some extent the phenotypic diversity (sea ages at maturity) of salmon populations across its range in the North Atlantic.

Limitations

- Represent estimates for large spatial scale by summing returns and spawners across a large number of individual populations.
- Groupings are based on jurisdictions rather than biological / populations.
- Reconstructions of PFA are based on a strong assumption of natural mortality (M) in the second year at sea being constant over time and fixed at 0.03 per month.
- In many jurisdictions, the estimates are largely driven by catches and assumed / derived exploitation rates or limited monitoring sites within each larger geographic unit.

Availability of data

- Annual run reconstructions of spawners, returns, and pre-fishery abundance at the continental scale complex (North America, Northeast Atlantic), for sub-complexes (Southern NEAC, Northern NEAC), and by regions within sub-complexes are available for the period 1971 to 2018 (1983 to 2018 for Norway) from the WGNAS reports.

2.5.3 Individual river scale abundance

Atlantic salmon spend one or more years feeding and growing at sea before reaching sexual maturity and returning as adults to spawn in their river of origin (Klemetsen *et al.*, 2003). Returns of adult salmon typically commence in spring, but peak in summer and early autumn, with salmon entering coastal waters and rivers several months prior to spawning (Thorstad *et al.*, 2008). Declines in the numbers of returning adult salmon have been observed in many rivers since the 1980s (Chaput, 2012).

Returns of wild and hatchery-reared Atlantic salmon are estimated using counts of the numbers of returning adults obtained from fish counters and traps, mark-recapture studies and spawner surveys, or derived from catches raised by exploitation rates. A limited number of monitored rivers flowing into the North Atlantic Ocean report verified counts of the numbers of returning adult salmon using fish counters and/or traps. In other monitored rivers, estimates of abundance of returning salmon are provided by mark-recapture studies and surveys of the abundance of spawning females and redds. For most rivers, however, the usual procedure involves deriving estimates of the numbers of returning adults from catches raised by exploitation rates.

Annual estimates of the numbers of adult salmon returning to spawn in rivers are an invaluable metric for assessing the status of salmon stocks. The provision of annual estimates of returning adult salmon is essential for the derivation of important stock status estimates, including the marine return rates of emigrating smolts, the size of the spawning stock and egg deposition in rivers. Conservation limits for salmon-producing rivers are often calculated using stock–recruitment relationships along with estimates of the numbers of returning adults to calculate the spawning stock required to achieve maximum sustainable yield. Such is their importance that annual estimates of returning adults are included as input data in the pre-fishery abundance model used in the annual assessment of the status of salmon stocks across the North Atlantic (ICES, 2019a). Furthermore, estimates of returning salmon are included as an indicator in the NASCO Framework of Indicators, which provides an interim assessment of the status of salmon stocks and determines whether the previously provided multi-annual management advice for

the Faroese salmon fishery is still appropriate (NASCO, 2019). Careful monitoring and assessment of the numbers of returning adults is therefore crucial to inform management decisions to protect and restore salmon populations.

Assessments of returns to individual rivers are frequently provided by a number of countries and jurisdictions based on full counts at counting fences, fishways, acoustics, resistivity counters, and other techniques or estimates from mark and recapture experiments. These individual river assessments are often used to derive exploitation rate estimates which are applied at alternate spatial scales to catches and used in the run reconstruction at regional and continental complex scales (see Section 2.5.2).

2.5.3.1 North America (NAC)

Individual river counts were tabled until 1998 (ICES, 1999a) but this was discontinued. For NAC, individual rivers return data for 1999 are not provided in a table but a summary figure (Figure 4.2.1.1 in ICES, 2000) presents the returns to 54 monitored rivers in eastern Canada relative to those of 1998 for small salmon separately from large salmon. As of 2000, ICES WGNAS has not included the individual river return data in its report but these individual returns are compiled by countries / jurisdictions.

The returns or indices of returns by size group (small salmon, large salmon) to 129 rivers in eastern North America have been compiled from published river assessments (G. Chaput; DFO Canada unpublished data). The time-series begins in 1970 and has been updated to 2018 (Figure 2.11). For 73 of the 129 rivers, the time-series of return values extends at least 20 years and includes rivers from the southern range of eastern North America (US) to northern Labrador, at the exclusion of data from the most northern range in Ungava Bay.

For illustration of the qualitative spatial and temporal patterns of returns abundance, the river-specific returns were standardized (mean, std. dev.) using the period 1998 to 2007 and the river-specific anomalies (in units of standard deviations) were plotted as a heat map by years and individual river dimensions (Figure 2.11).

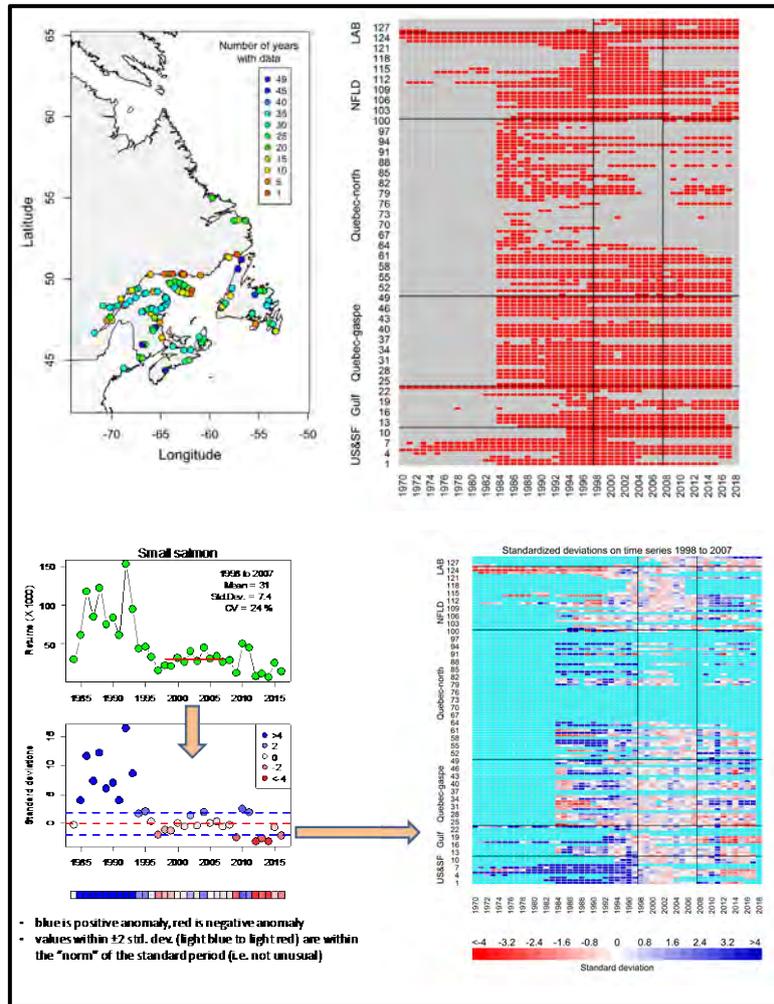


Figure 2.11. Summary of locations, time-series and spatial/temporal patterns of river-specific return anomalies (based on the standard period 1998 to 2007) to eastern North America, for the period 1970 to 2018. The returns are for size/age groups combined.

2.5.3.2 Northeast Atlantic

ICES (2000) has tables (see Table 3.4.3.1 of ICES report) of wild adult salmon counts (sea-age groups combined) for 36 rivers in the NEAC area (Iceland, Sweden, Russia, UK, France, Norway, and Ireland); some series begin in 1952, with most beginning in the mid-1980s. These tabulations were discontinued thereafter and run reconstructed estimates of returns and spawners by jurisdiction became the primary indicator of status.

Many countries / jurisdictions report individual river count data within their annual stock status reports provided at ICES WGNAS. An example of the time-series of estimated numbers of salmon (sea age / size groups combined) from counters in UK (England & Wales) is shown in Figure 2.12, as extracted from the national report for 2018.

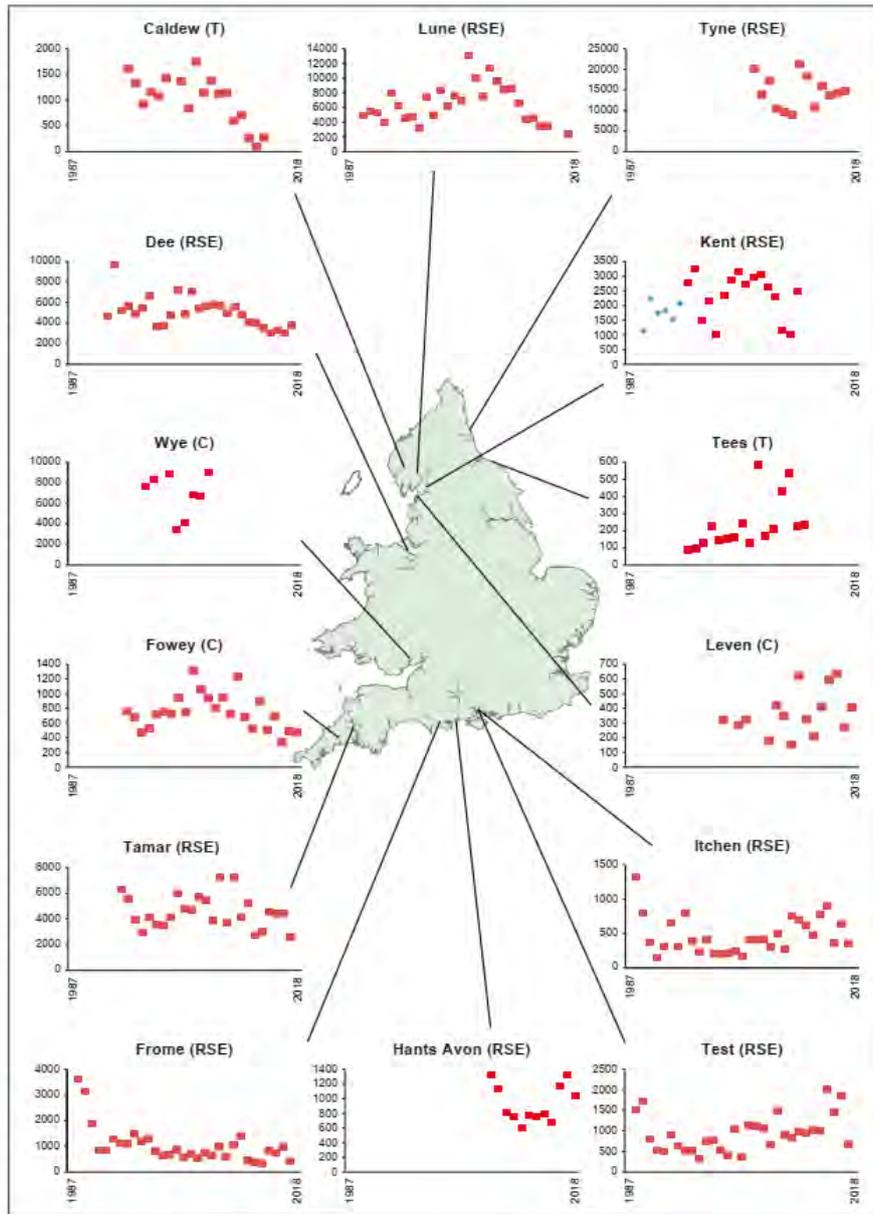


Figure 2.12. Counts of Atlantic salmon from electronic counters (C) and monitoring traps (T), and returning stock estimates (RSE) (based on trapping and tagging, or validated counts plus catch below counter) for selected salmon stocks in UK (England and Wales), 1988–2018 (Salmon Stocks and Fisheries in England and Wales, 2018. Cefas Salmon and Freshwater Fisheries and Environment Agency and Natural Resources Wales).

Value

- These individual river data can provide important spatial and temporal contrasts in abundance of salmon. Similar data have been analysed in a number of Pacific salmon species to examine spatial covariance components of population dynamics.
- These data are essential elements of the Framework of Indicators developed by ICES for monitoring status and assessing for significant changes in status during the intervening years of the multi-year catch advice cycle for NASCO.
- These data are often the basis for the run reconstruction inputs for country / jurisdictions.

Limitations

- The returns to rivers are after all sea fisheries and the trends in abundance may also reflect changes in fisheries management measures rather than variations in abundance. For example, in Canada the returns are after mixed-stock sea fisheries (in Newfoundland and Labrador, Greenland, and Saint Pierre and Miquelon) and the rivers in Newfoundland in particular show a response in increased returns to rivers following the closure post-1992 of the salmon marine commercial fisheries. Similar increased returns to rivers following on closures of marine fisheries were reported in Ireland.
- There are limitations involved with using estimates of the numbers of adults returning to spawn in rivers to assess the status of salmon stocks.
- Fish counters positioned upstream of the tidal limit have the potential to underestimate the numbers of returning adult salmon and confound estimates of marine mortality. Adult salmon spawning downstream of the counter will not be included in adult return estimates.
- Counts of returning adult salmon are only reported for a limited number of monitored rivers.
- For most rivers, estimates of returning adults are derived from catches raised by exploitation rates. However, uncertainty in derived estimates of returning adults has increased due to the very low numbers of retained salmon in catches resulting from the implementation of fisheries management measures.
- Caution should be exercised when interpreting variation in the numbers of returning adult salmon. Factors affecting salmon during both the freshwater and marine phases of the life cycle influence the survival of emigrating smolts and the resultant numbers of returning adults (Russell *et al.*, 2012; Gregory *et al.*, 2019).

Availability of data

- The data for eastern North America are available as csv files that include the geo-reference information for the rivers, by request and acknowledgement of the jurisdictional contributions.
- Currently, the individual rivers return data for NEAC has not compiled into a database. Individual jurisdiction / country data would need to be requested.

2.6 Population dynamics – survival rates

Friedland *et al.* (2009) found that survival of post-smolts in the Northeast Atlantic was positively associated with plankton and possible post-smolt food abundance, including marine copepod *Calanus finmarchicus* and krill that make up the majority of biomass in that region, and these prey abundances have declined notably since the 1970s. Friedland *et al.* (2009) also found that longer bodied smolts survived better compared to shorter smolts, but only for the River Figgjo in Norway. Together, these results suggest that marine conditions affect post-smolt survival, but that freshwater conditions can also affect post-smolt survival through their effects on individual smolt development (Russell *et al.*, 2012). For example, Gregory *et al.* (2019) showed that a 12 cm smolt leaving the River Frome in the UK was 3–4 times less likely to survive their first sea winter compared to a 16 cm smolt.

2.6.1 Continental and regional scale (life-cycle modelling)

ICES (2015, 2016a, 2017a, 2018b, 2019a) has for a number of years been working on developing and improving large scale population dynamics models for the provision of catch advice for high

seas marine mixed-stock fisheries. The current modelling efforts are focussed on the development of an Atlantic salmon Bayesian life-cycle model to estimate abundance of post-smolts at sea before any fisheries (Pre-Fishery Abundance; PFA), and to forecast the influence of catch options at sea on the returns in the different jurisdictions in Europe and North America. The life-cycle model also provides a framework to improve understanding of the drivers and mechanisms of changes in Atlantic salmon population dynamics and productivity in the North Atlantic. Progressive versions of the model have been published in Massiot-Granier *et al.* (2014) and Olmos *et al.* (2019, 2020).

In 2019, the life-cycle model was further developed for the joint estimation of life history and abundances for all stock units in NAC, Southern NEAC and Northern NEAC in a single hierarchical model (Figure 2.13). The model provides the opportunity for modelling covariation in the dynamics of the different populations that share migration routes and feeding areas at sea, and which are harvested in mixed-stock fisheries, particularly at West Greenland for NAC and Southern NEAC and at Faroes for Southern and Northern NEAC.

The model provides estimates of trends in marine productivity (expressed as post-smolt survival rate to January 1 of the first winter at sea) for all stock units in Northern and Southern NEAC, and NAC (Figure 2.14).

Additionally, a single model is now used to forecast the population dynamics of all stock units simultaneously, which is of particular interest when assessing catch options for mixed-stock fisheries operating on a mixture of stocks from both NAC, Northern and Southern NEAC (West Greenland) or both Northern and Southern NEAC (Faroes). The model also provides a major improvement to the assessment and forecast models of Atlantic salmon currently used by ICES, by enabling the provision of catch options for the West Greenland and Faroes salmon fishery simultaneously (Figure 2.13).

In a more recent publication, Olmos *et al.* (2020) have examined the environmental drivers and the demographic mechanisms of the widespread decline of marine survival rate in Atlantic salmon in the North Atlantic Ocean for the 13 stocks units from the NAC and Southern NEAC complexes. The model was used to investigate whether the temporal variations in the post-smolt survival were best explained by environmental variations encountered by salmon during the early phase of the post-smolts marine phase when salmon use transitional habitat, or during the later phase of the first year at sea when salmon of different origin concentrate in common foraging areas. To test this hypothesis, an extensive review of the literature on post-smolt migration routes was conducted to define different space-time domains associated with the early phase or with the late phase of the first year at sea. Such a framework allows for assessing the relationships between the temporal variations of marine survival and environmental covariates (Sea Surface Temperature (SST) and Primary Production (PP)) defined in different space-time domains, and as well with proxies of large scale environmental conditions, the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO).

Results show a strong coherence in the temporal variation in post-smolt survival among the 13 stocks units of NAC and Southern NEAC. The common trend of the temporal variation of the post-smolt survival for the 13 stocks units explains 37% of the temporal variability and declines by a factor 1.8 over the 1971–2014 time-series. Synchrony in survival is stronger between stocks within each complex. The common trends at the scale of the NAC and the Southern NEAC complexes capture 60% and 42% of the total variance of temporal variations, respectively. The remaining part of the variability was explained by local variations. Temporal variations of the post-smolt marine survival are best explained by the temporal variations of SST (negative correlation) and PP (positive correlation) encountered by salmon in space-time domains corresponding to late summer/early autumn feeding areas, specifically, in the Labrador Sea/Grand Banks for the NAC complex and the Norwegian Sea for the Southern NEAC complex. Variation of SST and PP

explain 27% and 26% of the variance of the common trends for the NAC complex, respectively and 21% and 14% of the variance of the common trends in the Southern NEAC complex, respectively. Temporal variations of SST and PP measured in specific space-time domains were much weaker predictors of the post-smolt marine survival.

Those findings support the hypothesis of a response of salmon populations to large-scale bottom-up environmentally driven changes in the North Atlantic susceptible to simultaneously impact several populations originating in distant continental habitats, but also that ecological drivers and/or mechanisms could be different between NAC and Southern NEAC populations in relation to partially different migration routes at sea.

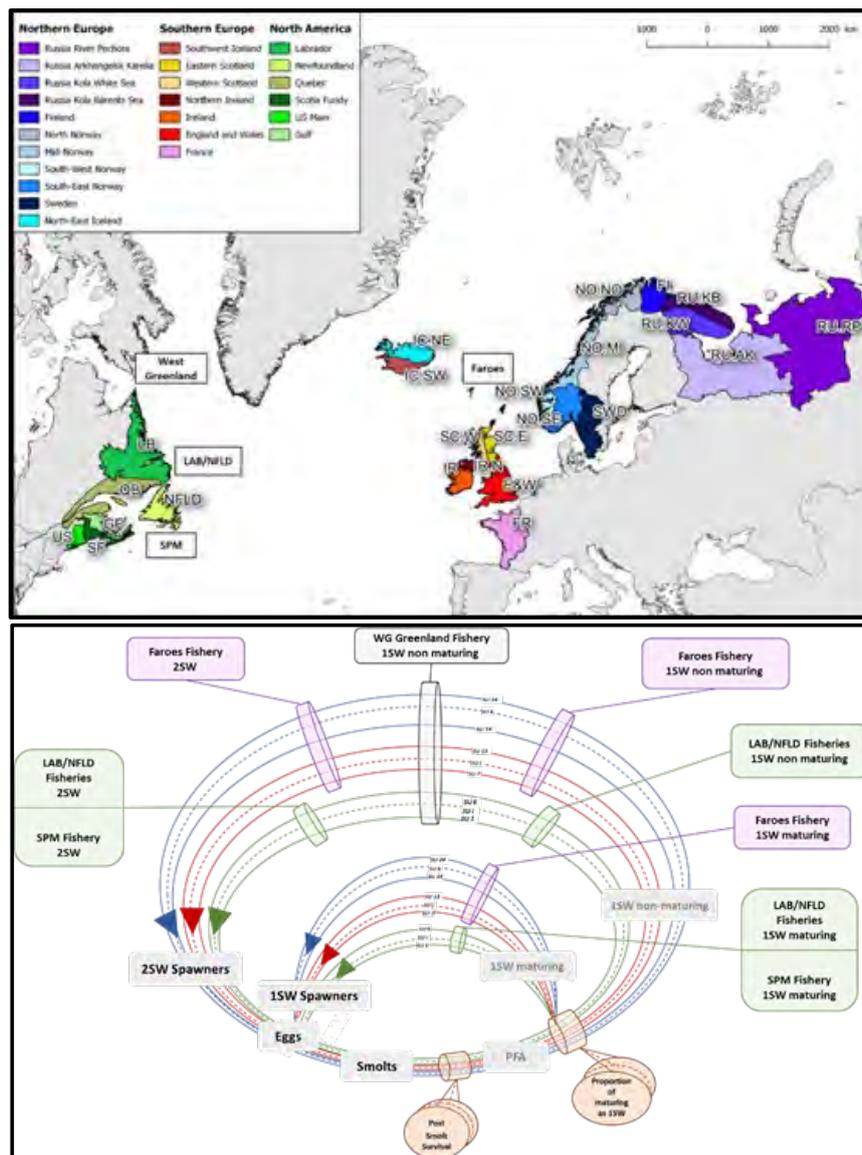


Figure 2.13. Schematic of the life-cycle model applied to the 24 stock units of Northern and Southern NEAC and North America. Variables in light blue are the main stages considered in the stage-structured model. The smolt-to PFA survival (post-smolt survival) and the proportion of maturing PFA are estimated for the time-series (1971 to 2014) and modelled as a random walk with covariation among stock units. Stock units of the Northern and Southern NEAC complex are potentially harvested by the mixed-stock fishery operating around the Faroes islands as 15W maturing and non-maturing fish, and as 25W fish. Stock units of the NAC complex are potentially harvested by the mixed-stock fishery operating around the Labrador and Newfoundland and Saint Pierre and Miquelon as 15W maturing and non-maturing fish, and as

2SW fish. Stock units of the Northern and Southern NEAC complex are potentially harvested by the mixed-stock fishery operating at West Greenland as 1SW non maturing fish.

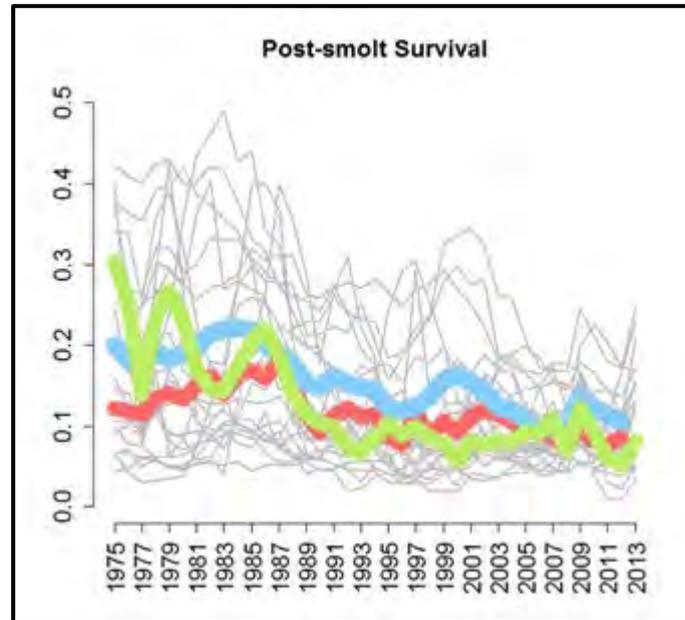


Figure 2.14. Time-series of smolt-PFA survival (plotted in the natural scale) for the 24 stock units (thin grey lines) and averaged over the three continental stock groups (thick colour lines). NAC=green, NNEAC= blue, SNEAC=red. (ICES, 2019a).

Value

- Modelling approach that considers the covariation in life history dynamics (post-smolt survival rate; proportion of PFA maturing as 1SW salmon) of salmon by regional groups that share common environments at sea.

Limitations

- Abundances and population dynamics are inferred from modelling rather than empirical observations.
- Simplification of life history in second year at sea by assuming natural mortality is known and constant across stocks and years.
- Abundances in the second year are an amalgam of sea ages older than 1SW in NEAC and for NAC, excludes all sea ages other than 1SW and 2SW. In some areas of eastern Canada, repeat spawners contribute important proportions of the eggs spawned.
- Building on input data from run reconstructions, the regions and subregions used in the life-cycle model are defined by jurisdictional boundaries rather than on biological considerations.

Availability of data

- From publication authors (E. Rivot) but ultimately from ICES WGNAS as part of core assessment output.

2.6.2 Population specific survival rates

2.6.2.1 Smolt to maiden salmon

Declines in the marine survival of Atlantic salmon have been reported in many rivers flowing into the North Atlantic Ocean since the 1980s (Chaput, 2012). Marine survival rates have declined to a record low with less than 10% of the emigrating wild smolts surviving the seaward migration and returning to rivers as adults (ICES, 2019a). Low marine survival rates are therefore a major factor hindering the recovery of salmon populations (Jonsson and Jonsson, 2004).

Although fisheries exploitation likely contributed to declines in the numbers of returning adult salmon during the early 1980s (Parrish *et al.*, 1998), recent broad-scale environmental changes in the North Atlantic Ocean are thought to have reduced the growth and survival of smolts by decreasing the availability of food resources and the growth potential of the fish (Friedland *et al.*, 2009; Beaugrand and Reid, 2012; Mills *et al.*, 2013). Reductions in smolt growth and survival are linked to the unusually small numbers of adult salmon returning to rivers (Todd *et al.*, 2008; Jonsson *et al.*, 2017; Armstrong *et al.*, 2018). Fluctuations in sea surface temperature and primary production in the Labrador Sea/Grand Banks regions for North American populations and the Norwegian Sea for southern European populations, best explain variation in the marine survival of salmon (Olmos *et al.*, 2020).

Mortality can be more readily measured in Atlantic salmon than virtually any other pelagic fish species (Cairns, 2003a). Counts of the numbers of smolts and returning adults obtained from fish counters and traps, mark-recapture studies and acoustic telemetry enable estimates of marine survival rates to be derived (Davidsen *et al.*, 2009; Chaput, 2012). Marine return rates measure the proportion of smolts that return to home waters or their river of origin as adults. Annual estimates of marine return rates are available for 23 wild and 18 hatchery populations from monitored rivers flowing into the North Atlantic Ocean (ICES, 2019a). Empirical data from monitored rivers indicate that salmon suffer considerably higher mortality (~65–95%) than other pelagic fish species (~20%) due to their rapid growth rate at sea (Cairns, 2003a, 2003b). Reported survival rates during the first year at sea are highly variable, ranging from 1.3% to 17.5% (Hutchings and Jones, 1998). The proportion of smolts surviving the seaward migration is higher in the Northeast than the Northwest Atlantic, with return rates to the coast of River Bush to 1SW salmon as high as 35% (Crozier and Kennedy, 1994) and return rates to other rivers often in excess of 10% (Ó Maoiléidigh *et al.*, 2003). In the Northwest Atlantic, marine survival is generally lower, in the order of 2–7% in Newfoundland in eastern Canada (O’Connell *et al.*, 2006) and up to 13% in the Canadian Maritime Provinces (Hutchings and Jones, 1998).

Although return rates are often used to infer the marine survival of salmon, extrapolation is complicated by differences in sea-age at maturity between stocks (Chaput, 2012). For stocks comprised almost entirely of adults with one sea-age at maturity, return rates can be used as indices of marine survival. However, determining absolute measures of marine survival from return rates is not possible for stocks that have two or more sea-ages at maturity due to differences or confounding in the maturation and survival of the MSW components at sea. Despite these complications, the return rates of smolts to monitored rivers, although variable, have generally declined since 1980 (ICES, 2019a; Figures 2.15 and 2.16). Declines in the return rates of emigrating smolts have been more severe for 1SW than MSW salmon and return rates to rivers have decreased more sharply in the Northwest than the Northeast Atlantic. For many stocks, the return rates of smolts have declined to the lowest levels of the time-series, indicating that the marine survival of salmon has decreased to a record low. At present, less than 10% of emigrating smolts are returning to monitored rivers.

Survival at sea is not a random process. If survival of smolts was purely random, there would not be any systematic differences in survival rates of hatchery origin smolts compared to wild

smolts for co-migrating cohorts (Figure 2.17), nor would size-dependent survival patterns be evident. Larger smolts have a higher probability of returning to rivers than smaller smolts due to their better condition and faster growth which seems to favour survival by providing greater resilience to predation and inhospitable environmental conditions (Gregory *et al.*, 2018, 2019).

Value

- Direct observation/estimation of return rate for individual stocks.
- Additional information on run timing, size, and age of smolts and returning adults generally available from monitored rivers.

Limitations

- There are limitations involved with using marine survival rates estimated from the proportion of smolts returning as adults.
- Proportions are return rates rather than survival rates, reflecting both mortality and maturation dynamics (Crozier *et al.*, 2003).
- Absolute measures of marine survival cannot be determined for salmon populations with two or more sea-ages at maturity given the confusion between mortality and maturation (Chaput, 2012). In the few instances when salmon populations are comprised almost entirely of adults maturing after one sea winter, the return rates of smolts can be inferred to represent marine survival rates.
- Survival rates estimated from counts of salmon passing fish counters and traps positioned upstream of the tidal limit in monitored rivers may confound the mortality occurring in the freshwater and marine environments.
- Marine survival rates obtained from fish counters and traps installed close to river mouths are insufficient to separate the mortality occurring in different habitats during the seaward migration.
- Reported return rates in ICES (2019a) are generally uncorrected for marine fishery removals, i.e. they represent Z (total mortality) rather than M (natural mortality).
- Very few of the 1000s of salmon populations are monitored.
- The number of monitored populations has decreased over time (ICES, 2019a).
- Hatchery origin salmon return rates are generally lower than wild salmon return rates therefore their use as a proxy for wild salmon return rate trends needs to be confirmed.

Availability of data

- ICES (2019a) reports on estimated return rates for a number of monitored rivers in the North Atlantic. The tables in ICES (2019a) do not provide the foundational data (number of outmigrating smolts, number of returning adults at age) that are the basis of the published return rates. These more detailed data would be available by contacting individual jurisdictions and researchers.

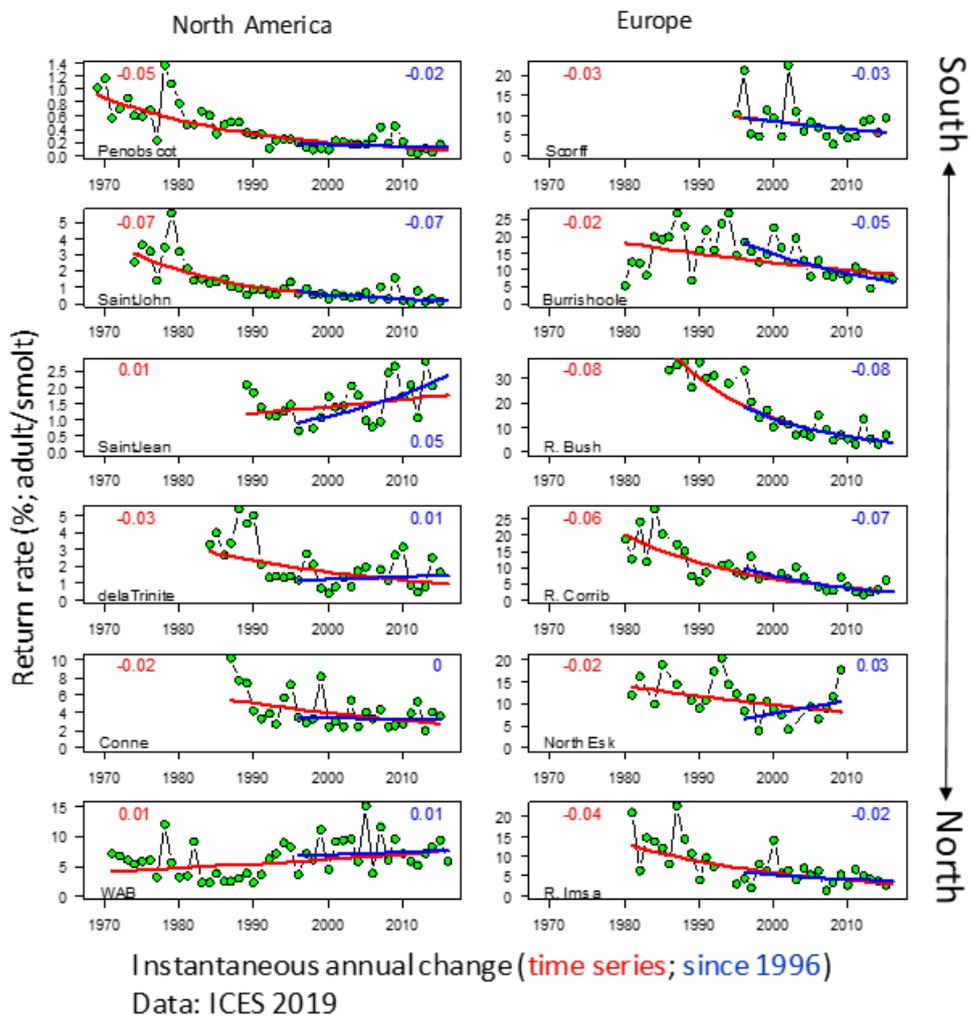


Figure 2.15. Examples of trends in returns rates of wild Atlantic salmon smolts to monitored rivers of North America (left column) and Europe (right column) as reported in ICES (2019a).

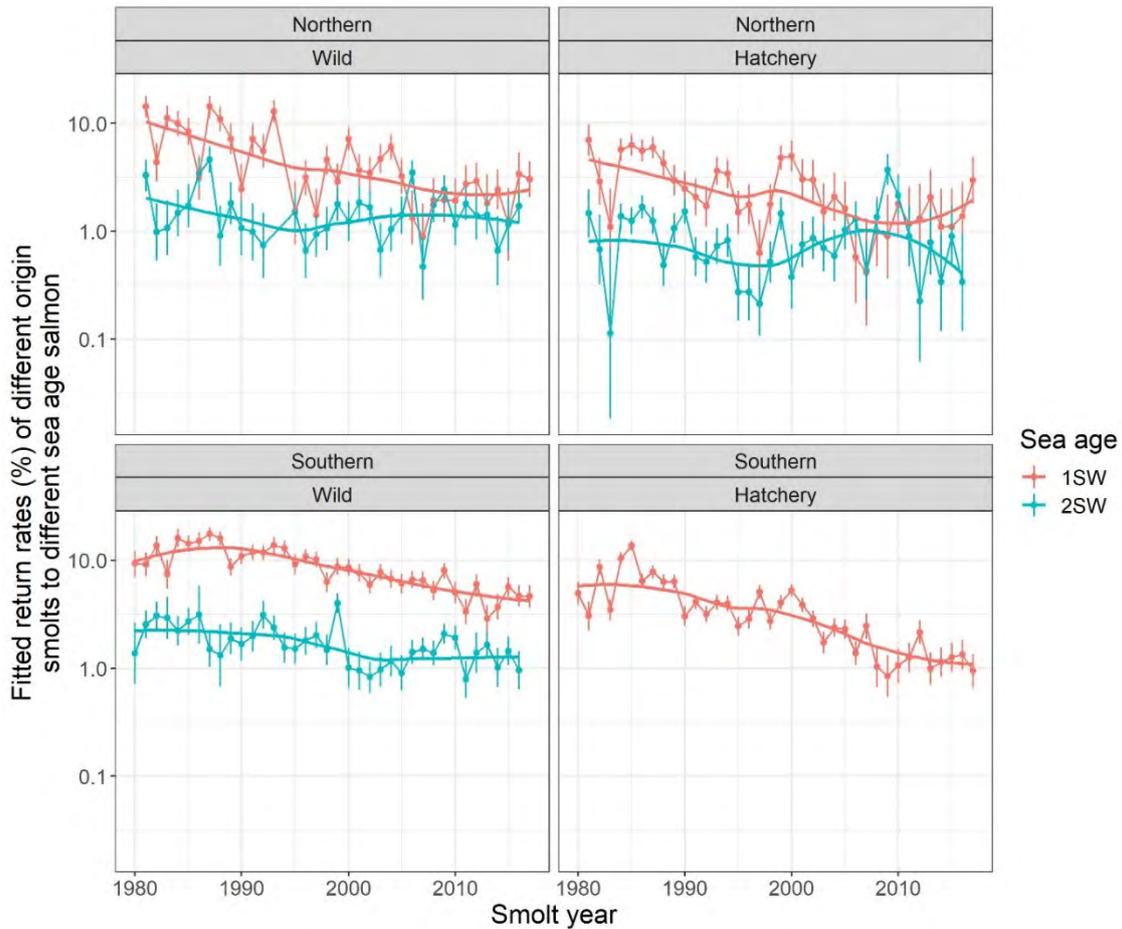


Figure 2.16. Extracted from ICES (2019a). Least squared (marginal mean) average annual survival indices (%) of wild (left hand panels) and hatchery origin smolts (right hand panels) of 1SW (red) and 2SW (blue) salmon to Northern (top panels) and Southern NEAC areas (bottom panels). For most rivers in Southern NEAC, the values are returns to the coast prior to the home water coastal fisheries. Trend lines are from locally weighted polynomial regression (LOESS) and are meant to be a visual interpretation aid.

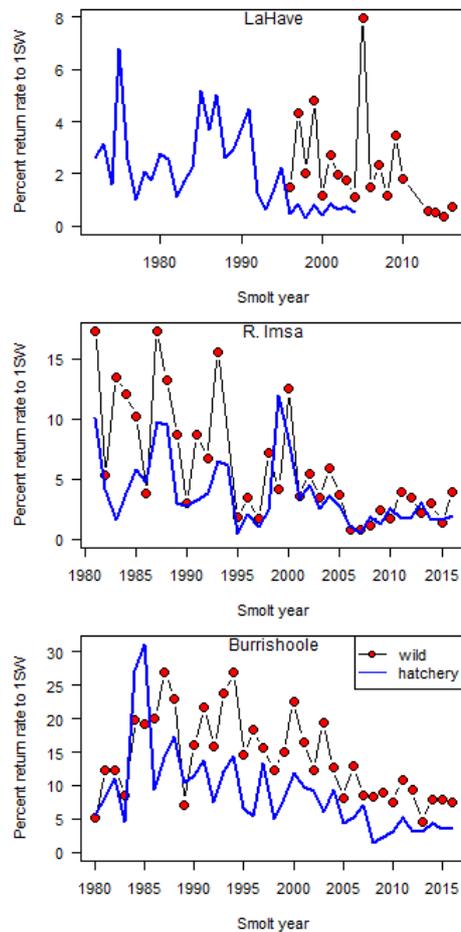


Figure 2.17. Examples of trends in returns rates of wild Atlantic salmon smolts and hatchery origin smolts to monitored rivers of North America (upper panel) and Europe (middle and lower panel) as reported in ICES (2019a).

2.6.2.2 Repeat spawner survival rates

Atlantic salmon are iteroparous with the potential to spawn repeatedly throughout their adult life (Klemetsen *et al.*, 2003). Adult salmon are capable of spawning up to seven times (Chaput and Jones, 2006). However, post-spawning mortality is generally high with most individuals spawning once or twice before dying (Ducharme, 1969; Jonsson *et al.*, 1991). Spawning populations of salmon are comprised of varying proportions maiden (first time) and repeat spawners (Bordeleau *et al.*, 2019). Maiden spawners consist of smaller grilse that return after one winter at sea and larger multi-sea-winter fish that return after two or more winters at sea. Although most (60–80%) maiden salmon survive spawning and return to the sea (Jonsson *et al.*, 1991), only 10% of these fish return to spawn a second time (Hansen and Jonsson, 1994). Salmon that survive the seaward migration can return to rivers as consecutive or alternate repeat spawners (Niemelä *et al.*, 2006; Halttunen *et al.*, 2009). Consecutive repeat spawners return to spawn in successive years following a brief period of a few months reconditioning at sea in the vicinity of their natal river (Niemelä *et al.*, 2006; Chaput and Benoît, 2012; Strøm *et al.*, 2017). Alternate repeat spawners return to spawn after spending more than one year at sea to feed and recondition post spawning (Reid and Chaput, 2012; Lacroix, 2013).

Repeat spawners form a substantial portion of the spawning population in many salmon rivers (Niemelä *et al.*, 2006; Chaput and Benoît, 2012; Bordeleau *et al.*, 2019). Salmon that spawn repeatedly are major contributors to the spawner abundances that can safeguard against successive years of reproductive failure (Halttunen *et al.*, 2009; Bordeleau *et al.*, 2019). A recent study has

shown that the extent of iteropartiy may have a genetic basis and be linked and co-inherited to sea age at maturity (Aykanat *et al.*, 2019).

Maiden salmon surviving the first spawning event move downstream and to the ocean to feeding areas to recondition before returning to the river to spawn again (Klemetsen *et al.*, 2003). Post-spawning mortality for maiden salmon is highly variable both within and among populations (Dempson *et al.*, 2004). The percentage of maiden salmon surviving first spawning ranges from close to 0% to more than 90% (Dempson *et al.*, 2004; Niemelä *et al.*, 2006; Halttunen *et al.*, 2009). Females are more likely to survive than males due to their higher energy reserves and lower likelihood of sustaining injuries during spawning (Jonsson *et al.*, 1997). Reported survival rates for repeat spawners vary substantially. Less than 20% of repeat spawners survive the seaward migration and return to rivers in Newfoundland, Canada (Dempson *et al.*, 2004). Lower numbers of repeat spawners return to the coast of the Saint John River (5%) in New Brunswick and the La Have River (10%) in Nova Scotia (Chaput and Jones, 2006; Hubley *et al.*, 2008). In contrast, the percentage of repeat spawners (20–60%) returning to the Miramichi River in New Brunswick is higher (Chaput and Jones, 2006). In Europe, repeat spawners comprise a small portion of the salmon returning to the River Teno (5%) in the northernmost parts of Finland and Norway (Niemelä *et al.*, 2006), the Shannon River (7%) in Ireland (Went, 1964) and multiple rivers (5%) in Scotland (Shelton, 1986). The percentage of repeat spawners in samples from the fishery at West Greenland has increased over the period 1985 to 2018 (Figure 2.18).

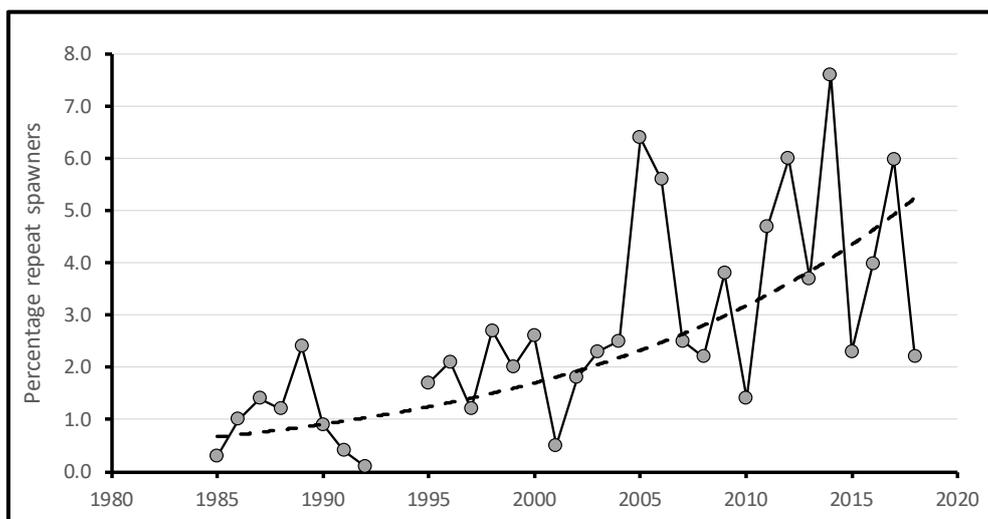


Figure 2.18. Percentage of samples of North American origin salmon sampled from the West Greenland mixed-stock salmon fishery that were repeat spawners, 1985 to 2018. Data are from ICES (2019a).

Adult salmon returning to many rivers in eastern Canada and northern Europe are increasingly comprised of repeat spawners (Niemelä *et al.*, 2006; Chaput and Benoît, 2012; Bordeleau *et al.*, 2019). For example, the numbers of consecutive repeat spawners returning to the Miramichi River in New Brunswick, eastern Canada, has increased from less than 5% before 1984 to more than 25% after the late 1990s (Chaput and Benoît, 2012). Increases in the return rates of consecutive repeat spawners to the Miramichi River were attributed to increased prey availability in the Gulf of St Lawrence (Chaput and Benoît, 2012; Strøm *et al.*, 2017). In contrast, returns of consecutive repeat spawners to the La Have River in New Brunswick and the Nashwaak River in Nova Scotia have decreased since the early 1990s (Hubley *et al.*, 2008; Hubley and Gibson, 2011; Jones *et al.*, 2014; Bordeleau *et al.*, 2019). In northern Europe, the percentage of repeat spawners returning to the River Teno has increased over the last 30 years (Niemelä *et al.*, 2006).

Value

- An important life stage for some salmon populations. The expectation is that the pelagic environment occupied by repeat spawners is similar to that of maiden salmon, hence repeat spawner survival rates could be a proxy for marine conditions of post-smolts and maiden salmon.
- Some monitoring data are long time-series and they show differences in relative abundances of consecutive vs alternate reconditioning strategies.

Limitations

- Repeat spawners are survivors of maiden salmon and may not reflect similar trends or be subjected to similar factors as post-smolts and maiden salmon.
- Return rates of repeat spawners are from population level modelling, and not measured directly from individual fish.
- There are few populations with systematic monitoring data.

Availability of data

- Individual researchers and institutions.

2.6.3 Individual estimates - telemetry

Acoustic telemetry has provided insight into the marine survival rates of Atlantic salmon. Salmon implanted with acoustic transmitters are monitored by receivers deployed in rivers, estuaries and nearshore waters. For example, acoustic telemetry has been used to estimate the survival rates of smolts leaving the River Deveron and entering Banff Bay in Scotland (Lothian *et al.*, 2018). The overall smolt survival rate was 40% and mortality rates were higher in freshwater (0.77% per km) than the marine environment (0.0% per km).

However, most acoustic telemetry studies have been restricted to estuaries within 50 km from the tidal limit or nearshore waters close to the river mouth, and rarely provide sufficient replication to characterise annual variation in survival rates (Chaput *et al.*, 2018). A few notable exceptions exist where acoustic telemetry has been used to evaluate survival rates over successive years, further offshore (Lacroix, 2008; Kocik *et al.*, 2009; Stich *et al.*, 2015). Chaput *et al.* (2018) used acoustic telemetry to estimate the survival rates of smolts migrating from four rivers in the Gulf of St Lawrence, Canada, to the Labrador Sea between 2003 and 2016. Smolt survival in estuarine and nearshore waters was estimated to be 67–90% for two populations migrating through Chaleur Bay and 28–82% for two populations from the neighbouring Miramichi Bay. Lower survival in Miramichi Bay was attributed to high smolt predation by striped bass (*Morone saxatilis*) (Daniels *et al.*, 2018). Once smolts departed the coastal bays, the median survival rates through the Gulf of St Lawrence were 45–78% (Chaput *et al.*, 2018).

Most studies have focused attention on the survival rates of smolts leaving freshwater and entering the early marine phase of the life cycle (Friedland *et al.*, 2000; Jonsson *et al.*, 2003). Mortality rates for smolts are highly variable among salmon populations, ranging from 0% to 85% (Thorstad *et al.*, 2012). Smolts transitioning from freshwater to the sea encounter high predation pressure (Hawkes *et al.*, 2013), physiological stress (Handeland *et al.*, 1996) and novel environmental conditions (McCormick *et al.*, 1998). Much of the mortality occurs during a critical period when smolts pass through estuaries, fjords and nearshore waters close to river mouths (Lacroix, 2008; Kocik *et al.*, 2009; Dempson *et al.*, 2011). Reported mortality rates for smolts range between 0.3–7.0% km⁻¹ (median = 2.3) in freshwater, 0.6–36% km⁻¹ (median = 6.0) in estuaries and 0.3–3.4% km⁻¹ (median = 1.4) in coastal areas (Thorstad *et al.*, 2012). Once smolts enter the ocean, their survival is positively related to body size at ocean entry (Chaput *et al.*, 2018). Larger smolts have

a higher probability of returning to rivers than smaller smolts due to their better condition and faster growth reducing mortality (Peyronnet *et al.*, 2008; Gregory *et al.*, 2019).

In an unpublished review of literature based on acoustic tagging of smolts, a number of studies provide estimates of “survival” rates during different phases of the smolt migration through freshwater and post-smolt migrations through estuaries and nearshore areas. For the freshwater phase, highly variable survival rates post-release are noted (Figure 2.19). In the North American studies (NAC), there is a general negative association between survival and migration distance, but with high variability. Survival declining with distance (or time) since release would be expected, particularly due to the initial tagging and handling effects. In Europe (NEAC), hatchery smolt survival rates through freshwater are generally lower than for wild smolts.

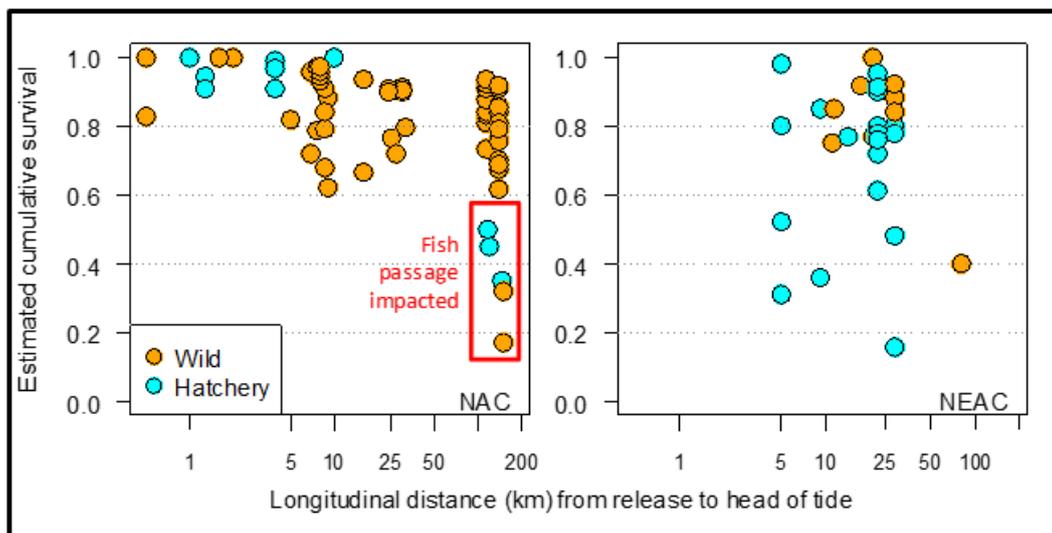


Figure 2.19. Summary of estimated cumulative survival by distance (log scale) from release to detection at the head of tide from studies of telemetry tagged Atlantic salmon smolts in North America (left panel) and in Europe (NEAC; right panel). In the panel for North America, the highlighted low survival rates are from studies assessing the impacts of water regulation and hydro-electric generation on salmon smolt migration dynamics and timing in the Penobscot River (Maine, USA) (Holbrook *et al.*, 2011).

There is a general negative association between cumulative survival in the marine phase and distance to the monitoring point, with the maximum distance monitored ~ 900 km (Figure 2.20). Survival rate estimates are highly variable among locations of similar monitoring distances; these differences may in large part be related to differences in the bio-physical characteristics of the estuary, nearshore, and coastal environments transited by tagged salmon smolts as well as differences in experimental conditions among the studies.

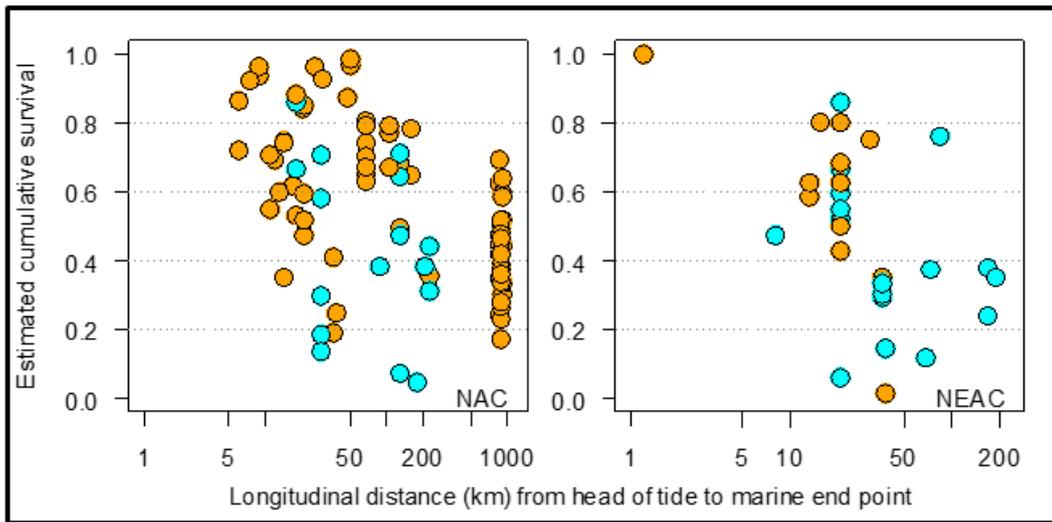


Figure 2.20. Estimated cumulative survival by distance (log scale) from the head of tide to the marine end point for detection of telemetry tagged Atlantic salmon smolts in North America (NAC; left panel) and in Europe (NEAC; right panel).

An example of the annual and spatial variations of survival rates during different phases of the smolt and post-smolt migration through coastal bays and the Gulf of St Lawrence is reported by Chaput *et al.* (2018; Figure 2.21). Over the 2003 to 2016 (smolt migration years) period of study, survival rates per km are lower through the coastal bays than during the offshore migration through the Gulf of St Lawrence. Distance-scaled survivals through Miramichi Bay are lower and declined over time compared to those in the Chaleur Bay; a likely suspect is the high abundance of striped bass in the Miramichi area which are known to prey on salmon smolts and whose single spawning location and spawning period overlap with the smolt migration corridor and timing.

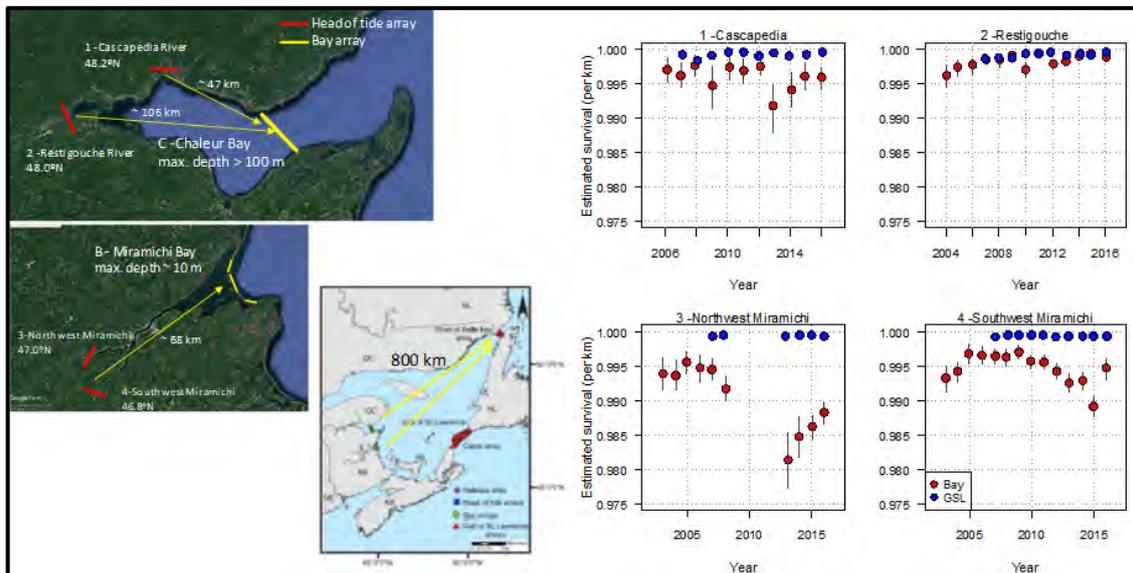


Figure 2.21. Estimated geographic area (bay; Gulf of St Lawrence (GSL)) specific survival rates (per km) of telemetry tagged Atlantic salmon smolts originating from four rivers, migrating through two bays (Chaleur Bay, Miramichi Bay) and collectively through the Gulf of St Lawrence (Canada), 2003 to 2016 (based on data from Chaput *et al.*, 2018).

Value

- Provides opportunity to partition survival at sea in time and space.
- Can study factors that condition survival, including run timing, body size effects, group effects.

Limitations

- In contrast to the historic annually supported marking and recovery programs undertaken by agencies for the purpose of fisheries management, there is substantially less domestic engagement in the establishment and maintenance of standardized annual tracking programmes. This stems in large part from the cost of the electronic technologies as well as the reduced information needs for managing the greatly reduced number of mixed-stock marine salmon fisheries.
- Assumption that survival rates of manipulated and tagged animals are similar to untagged animals is difficult to verify. Biological limits of the experimental animals of interest may well be exceeded by the physical and physiological burden of transporting the current generation of electronic data loggers / transmitters. This is particularly important because the overall objective of these studies is to better understand wild fish dynamics and the assumption that empirical data from tagged animals are representative of un-manipulated animals is not certain.
- With telemetry technologies, the challenge is to move away from the coast and later into the marine phase. As tagged animals die, the estimates of later stage survival rates become more uncertain.
- Tagged fish detection is imperfect and neglecting to account for imperfect detection risks reporting biased survival rates.

Availability of data

- Individual researchers and institutions.

2.7 Population dynamics – maturation rates

Atlantic salmon exhibit substantial variation in the age and size at maturation both within and among populations (Fleming, 1996). Spawning populations of salmon often consist of varying proportions of small (1–3 kg) grilse that attain maturity after one winter at sea (1SW) and large (3–12 kg) multi-sea-winter (MSW) adults attaining maturity after two or more winters at sea (Saunders, 1986). Males tend to mature at young ages and small sizes, either precociously in freshwater or by migrating to the sea to feed and grow before returning as anadromous adults (Fleming, 1996). Females generally mature at older ages and larger sizes than males because they have higher size and growth rate thresholds for maturity (Jonsson *et al.*, 2013). The probability of maturing after the first winter at sea is therefore higher for males (70–90%) than females (4%) (Chaput *et al.*, 2003a). Maturation is energetically costly, particularly for females, and the maturation process cannot be initiated until sufficient energy reserves have been stored to sustain the reproductive process (Jonsson and Jonsson, 2011). The substantial variation in age and size at maturity both within and among salmon populations is regarded as an evolutionary adaptation to varying environmental conditions that maximises reproductive success (Good and Davidsen, 2016).

Maturation in Atlantic salmon is a complex, multifactorial process (Gardner, 1976; Meerburg, 1986). Salmon attain maturity when genetic thresholds for either a critical size-at-age, growth rate or accumulation of energy stores are met in the autumn one year prior to spawning (Thorpe *et al.*, 1998; Duston and Saunders, 1999). If the threshold levels are not met, the maturation process is halted (Mangel and Satterthwaite, 2008). Male parr that mature precociously in freshwater comprise from as little as 12% to as much as 100% of the spawning population (Fleming, 1996). Once smolts leave freshwater, maturation is proportional to the length of time spent at sea. Smolts usually spend one to two and a half years feeding and growing at sea before maturing and returning to rivers as adults (Hutchings and Jones, 1998). Early maturation is generally favoured by increased smolt growth and survival at sea and delayed maturation by decreased smolt growth and survival at sea. However, this is not always the case. High smolt growth rates during the first year at sea increase the age at maturity of salmon returning to Norwegian rivers (Jonsson and Jonsson, 2007). Good feeding opportunities during the first year at sea increase smolt growth rates and the probability of salmon returning as MSW adults. In contrast, poor feeding opportunities during the first year at sea decrease smolt growth rates and age at maturity (Scarnecchia *et al.*, 1991; Nicieza and Braña, 1993; Duston and Saunders, 1999).

The maturation process is influenced by the interactive effects of genetic and environmental factors (Thorpe *et al.*, 1998; Czorlich *et al.*, 2018). Maturation is environmentally dependent, but genetically determined through threshold levels that prevent or permit further reproductive development (Thorpe, 1994). A single gene (VGLL3) has been found to regulate age at maturity (Barson *et al.*, 2015). Furthermore, age at maturity varies in response to environmental factors such as photoperiod, water temperature and salinity (Jonsson and Jonsson, 2011). The numbers of male parr maturing precociously in freshwater are affected by winter rearing temperature, body size and condition factor in spring (Duston and Saunders, 1997). Fluctuations in sea surface temperature in the North Atlantic Ocean affect the proportion of smolts returning to rivers as 1SW relative to MSW salmon (Scarnecchia *et al.*, 1991; Friedland *et al.*, 2000; Otero *et al.*, 2012). Slow-growing smolts generally mature earlier as 1SW salmon and fast-growing smolts later as MSW salmon (Jonsson and Jonsson, 2007). There is an evolutionary trade-off between early and late maturation given the relative costs (e.g. energy requirements and predation risk) and benefits in terms of reproductive success (Piou *et al.*, 2015).

There is also large variation among populations with spatial correlations in the mean sea age at maturity of anadromous Atlantic salmon. The proportion of sea-age at maturity is a stock-specific characteristic and populations can be characterized as one-sea-winter maturing and multi-sea-winter stocks (1SW, 2SW and other ages at maturity). Across the North Atlantic, there are important large regional differences in the proportions at sea age of return with populations in Newfoundland (eastern North America) and Ireland (Europe) dominated by 1SW maturing adult returns, in contrast to higher proportions of multi-sea-winter ages in most other regions of the North Atlantic (see Figure 1.1.2). In multi-sea-winter stocks, there is frequently a sex bias in the age at maturity. Males in these stocks are proportionally more abundant as 1SW salmon and females at 2SW and other ages at maturity. Some of these regional variations are undoubtedly associated with genomic variation; *VGLL3* gene has been shown to explain 39% of the variation in age at maturity of studied salmon populations and promotes earlier maturation in males and later maturation in females (Barson *et al.*, 2015).

Age and size at maturity in Atlantic salmon are sensitive to fisheries exploitation and environmental change. Fisheries exploitation in rivers and at sea has decreased age and size at maturity by selectively removing larger, older salmon from the spawning population (Dempson *et al.*, 2001; Jonsson *et al.*, 2003; Piou *et al.*, 2015). Broad-scale changes in marine environmental conditions have modified the age and size at maturity of many salmon populations over recent decades, generally towards an increasing proportion of smaller, earlier maturing individuals (Chaput, 2012; Otero *et al.*, 2012; Erkinaro *et al.*, 2018). However, there have been reports of salmon delaying maturation in response to changing marine environmental conditions. Warmer temperatures have increased the numbers of MSW salmon returning to rivers in Iceland (Gudjonsson *et al.*, 1995), Norway (Otero *et al.*, 2012), Scotland (Martin and Mitchell, 1985) and England and Wales (Cefas *et al.*, 2019). Otero *et al.* (2012) found that the increase in the age at maturity of salmon returning to Norwegian rivers resulted from changes in the pelagic foodweb affecting post-smolt growth at sea and freshwater conditions influencing pre-smolt growth and subsequent upstream migration. Increased water temperatures are prompting smolts to undertake their seaward migration earlier and adults to delay their return migration from marine feeding grounds (Solomon and Sambrook, 2004; Valiente *et al.*, 2011; Otero *et al.*, 2014).

Determining age at maturity is a key factor in estimating the survival rates and reproductive capacity of Atlantic salmon. Maturity schedules describe the proportion of mature individuals in a salmon population at a given sea-age (Chaput, 2012). Salmon maturity schedules vary by sex and geographically, with some rivers dominated by 1SW grilse and others by MSW adults. Sex ratios differ among sea-ages, with a high proportion of males in grilse-dominated stocks and females in MSW-dominated stocks (O'Connell *et al.*, 2006). The maturity schedules are used in combination with the numbers of returning 1SW and 2SW adults and the sex ratios of smolts to estimate survival rates during the first and second years at sea (Chaput *et al.*, 2003). In addition, maturity schedules are used in combination with the numbers-at-age and sex ratios of returning adults to estimate egg deposition. However, maturity schedules can suffer from several limitations. Firstly, maturity schedules assume that all returning salmon are mature individuals ready to spawn. In reality, however, salmon can leave freshwater and return to the sea without spawning (Jonsson *et al.*, 1990). Secondly, the numbers-at-age of both males and females are usually assumed or modelled for smolts and returning adults because of insufficient sampling (Chaput *et al.*, 2003). Adult sex ratios can be obtained from fishery catch samples, but smolt sex ratios are more difficult to obtain because lethal sampling is undesirable. Less invasive genetic approaches are increasingly being used to estimate sex ratios (Yano *et al.*, 2013; King and Stevens, 2019). Lastly, maturity schedules are static, failing to account for temporal or spatial variation in the proportion of mature adults.

Value

- Can be used to understand dynamics of individual populations and plasticity in their response to climate-driven changes in the freshwater and marine environments.
- Can help explain high variation in measures of population-specific recruitment.

Limitations

- It tends to be confounded with sea survival and can be difficult to relate back to earlier life stages.
- Selective fisheries exploitation can confuse estimation of maturation rates.
- Maturity schedules are fixed and fail to account for variation in the proportion of mature adults.

Availability of data

- Individual researchers and institutions.

2.7.1 Continental and regional scale (life-cycle modelling)

Olmos *et al.* (2019) and ICES (2019a) present results from the life-cycle model showing the proportions of the PFA that comprise 1SW maturing salmon across the stock units of the North Atlantic. Important regional differences in the proportion maturing are shown with general trends of increasing proportions to the mid-2000s followed by a slight decline or levelling off thereafter (Figure 2.22).

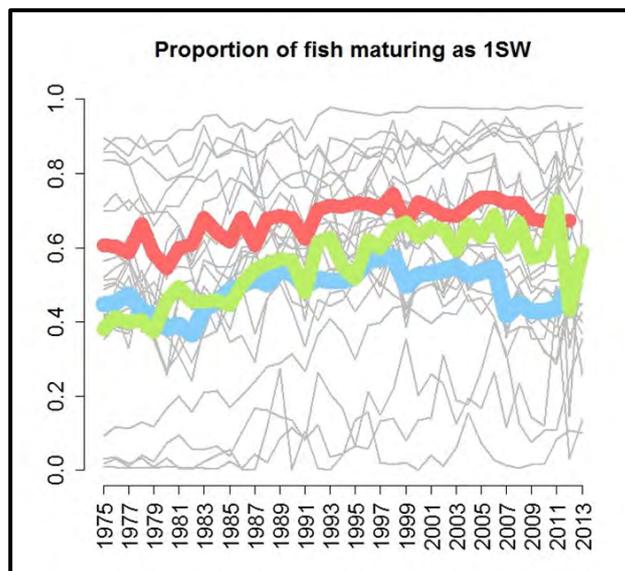


Figure 2.22. Time-series of proportion of fish maturing as 1SW salmon for the 24 Stock Units (thin grey lines) and averaged over the three continental stock groups (thick colour lines). NAC=green, NNEAC= blue, SNEAC=red. Figure from ICES (2019a).

Value

- Age at maturity has been shown to be under relatively strong genotype effect (Barson *et al.*, 2015) but with an important residual environmental component. It is the plastic response of this characteristic which is of most interest in understanding recruitment dynamics of salmon populations.

Limitations

- It is challenging to resolve the confusion between mortality rates and maturation rates.

- For many populations subject to fisheries, the fisheries may be size or sea age selective and can bias the estimates of maturation rates based on abundance post-fisheries.
- The life-history modelling conducted to date has resolved the confusion of the mortality rates and probability of maturing parameters by assuming mortality is known for one of the life stages hence variations in the mortality rates are incorporated as variations in maturation estimates.
- Methods to separate mortality and maturation, such as the Murphy methods, must make simplifying assumptions for some of these life-history rates among subsets of the population, e.g. that survival rates are similar for males and females or for different smolt ages.

Availability of data

- Life-cycle models provide estimates of the proportion of the PFA which matures as 1SW by country / jurisdiction. These would be available from ICES.

2.8 Biological characteristics

ICES convened a study group (SGBICEPS) for the purpose of “identifying and compiling time-series of data on biological characteristics of Atlantic salmon and conducting preliminary analyses on these data as a basis for developing, and where possible testing, hypotheses relating any observed changes in these characteristics to trends in freshwater/marine mortality and/or abundance of Atlantic salmon stocks and/or environmental changes” (ICES, 2009b, 2010a).

ICES (2010a) presents a wide range of analyses of river-specific trends for several biological characteristics including river age, sea age, size-at-age, and run-timing. ICES (2010a) concluded that there was evidence of marked changes in various biological characteristics coincident with a sharp decline in the marine survival for specific stocks, including links between the size of returning 1SW fish and their pre-fishery abundance. Some of the SGBICEPS results were published by Russell *et al.* (2012) and Todd *et al.* (2012).

There are a large number of datasets with river-specific biological characteristics collected systematically over decades (ICES, 2010a). Some of these data have been analysed in primary publications. For example, Bal *et al.* (2017) provide evidence of long-term changes (1987 to 2013) in length, weight and migration phenology of Atlantic salmon populations in different regions of France, with significant declines in weights-at-age of both 1SW and 2SW salmon.

There is an interesting long-term dataset of biological characteristics of Atlantic salmon sampled from the mixed-stock Atlantic salmon fishery at Greenland. A description of the sampling initiatives and the database are available in Sheehan (2019). The database contains information on sizes (fork length, derived whole weight), river ages, sea ages of salmon by continent of origin, some of which are summarized in the annual reports of WGNAS (Figure 2.23).

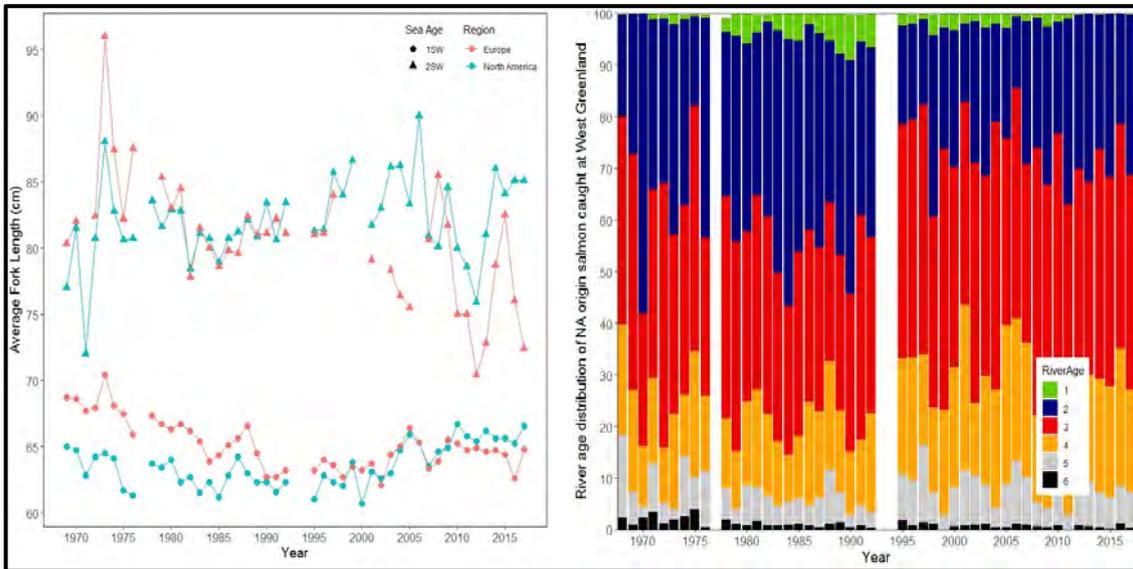


Figure 2.23. Examples of biological characteristics of Atlantic salmon in the samples from the West Greenland fishery. Left panel summarized the mean fork length (cm) of 1SW and 2SW Atlantic salmon by continent of origin over all samples (no correction for date of sampling). The right panel summarizes proportions by river age for North American origin salmon. Data summarized from ICES (2019a).

ICES (2015b) presented an analysis of the trends in predicted whole weights of salmon, by continent of origin at West Greenland, standardized for the date of sampling and fork length (Figure 2.24). The patterns were broadly similar for North American and European origin salmon with short-term variations in condition (predicted weight at length) over the time-series analysed.

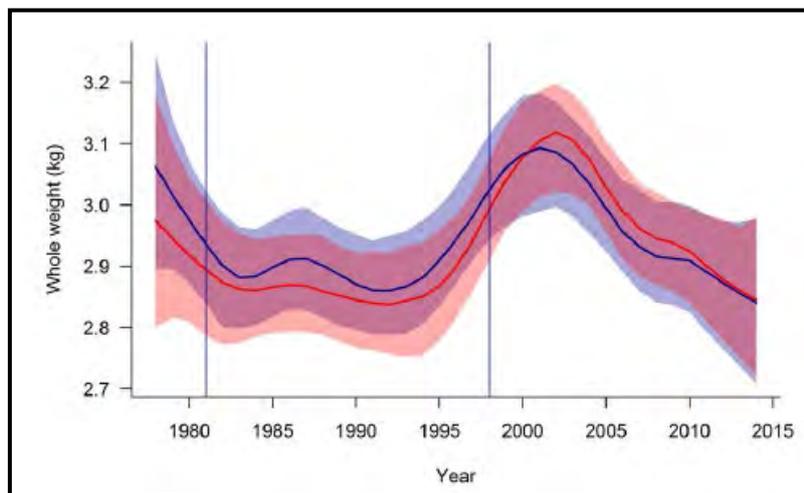


Figure 2.24. Trends in whole weight (kg) for maiden 1 SW fish of North American origin (red) and European origin (blue) over the sampling period (1978–2014). The plot above presents weights for a 65 cm fish on 20 August (ICES, 2015b).

Value

- There are extensive datasets of these characteristics available from a large number of populations in some cases extending over several decades (see Section 2.5.3).
- Non-destructive sampling in most cases but detailed data available from fisheries catches or experimental facilities.
- Often recorded at the level of the individual that allows analyses to account for variation among individuals in different groups.

Limitations

- Fisheries catches tend to be recorded as population averages, rather than at the level of the individual.
- Survivor bias; returning salmon sampled in rivers are survivors and the characteristics are the integration of processes over the entire period of life (freshwater and marine). They may not be informative of characteristics of individuals that did not survive.

Availability of data

- The West Greenland sampling dataset has been reviewed by Sheehan (2019). The workshop report includes consideration for database access and access to historic scale samples from this international sampling programme.
- Individual population data would be available from jurisdictions and individual researchers.
- Data for individual samples would be available from jurisdictions and individual researchers.

2.8.1 Proxies for growth based on scale patterns

Circuli spacing patterns extracted from scales are used to quantify marine growth, with narrow spacings interpreted as representing periods of decreased growth and wider spacings periods of increased growth (Jensen *et al.*, 2012). The analysis of scale patterns allows for the extraction of proxies for growth for different periods of time at sea. Several authors have proposed and reported on the link between growth and growth rates at sea and survival of salmon at sea (Friedland *et al.*, 2000; Peyronnet *et al.*, 2007, 2008; Friedland *et al.*, 2009); in many of these studies, scale growth patterns correlate with survival and or recruitment.

There are a number of published studies of growth patterns from salmon scales and associations with growth conditions, survival, and recruitment. A large number of studies by Friedland and colleagues have analysed scale growth patterns from salmon populations of eastern North America (Penobscot, Machias and Narraguagus rivers USA; Saint John, Margaree and Miramichi rivers Canada; post-smolts captured in the Labrador Sea) and Europe (Burrishoole (Ireland), North Esk and Girnoch Burn (UK Scotland), Drammen and Figgio (Norway), Lagan (Sweden); post-smolts as part of SALSEA-MERGE; and Greenland).

A number of participants at the workshop reported on ongoing work to extract growth features from long time-series of scale collections including:

- Unlocking the archive: using scale and otolith chronologies to resolve climate impacts (Newport Research Cluster Project, GMIT, Marine Research Programme 2014–2020). The project establishes Ireland's first biochronology repository for the purpose of investigating causes of decline in marine survival of salmon using scale growth histories and stable isotope analysis, and to develop novel analytical methods for detecting biochemical markers of stress in archived salmon scales.
- Project within SEASALAR (Norway) to extract circuli-distance data from scales collected from seven rivers, spanning 29 to 71 years per river, with data extraction completed for most rivers for the period 1989–2018, representing approximately 16 000 fish;
- Circuli spacing and growth patterns extracted from 3500 samples comprising approximately 75 salmon of North American origin sampled at West Greenland over the period 1968 to 2018 (M. Tillotson, USA);
- Growth patterns from scales from approximately 30 samples of smolts, 1SW and 2SW adult returns from three rivers in France and two rivers in UK (England and Wales) for

time-series from pre-1989 to 2020, representing 15 000 scale samples (E. Rivot and S. Gregory).

Value

- Can reconstruct proxies of growth histories at various periods of marine life.
- There are extensive collections of scales available from a large number of populations in some cases over several decades.
- Non-destructive sampling, conserving the scale for other analyses.
- Data are available at the level of the individual.

Limitations

- Survivor bias; returning salmon sampled in rivers are survivors and may not provide any information on factors associated with growth that resulted in mortality.
- Assumption is made that circuli number within a stock is a time stamp, but this may vary among populations.
- Growth indices are a proxy for length but not for weight or condition.
- Scale shape and size vary with position on the body of the fish, lack of control of scale collection location adds error to the growth indices within a population and across populations.

Availability of data

There is no existing compilation of extracted circuli spacing or other growth indices from scales across the diverse studies.

3 North Atlantic ecosystem – physical features

The late Quaternary period (the past one million years) during which time the phylogenetic groups of Atlantic salmon evolved, was punctuated by a series of large glacial–interglacial conditions with cycles in the order of approximately 100 thousand years (Petit *et al.*, 1999). Over this period, the geographic range of distribution of Atlantic salmon would have undergone repeated contractions and expansions (particularly northern populations) associated with advances and retreats of glaciers, changes in sea levels, and loss or creation of freshwater habitat and marine habitat.

At the peak of the most recent ice age (20 K years before present), it is estimated that the majority of the area occupied by Atlantic salmon in contemporary times in North America was covered by glaciers with sea ice extending far south of the current distribution (Figure 3.1). In Europe, most of northern Europe and western Russia and most of southern Europe to France was covered by glaciers.

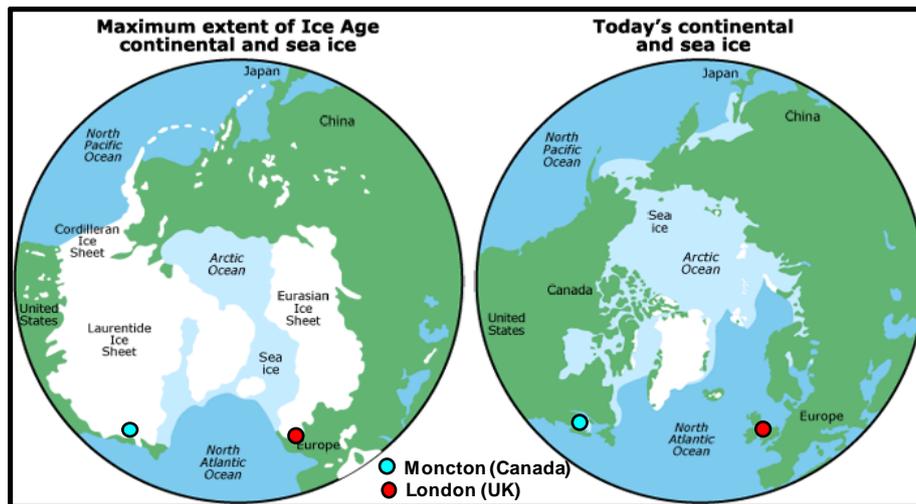


Figure 3.1. Summary figure of the estimated maximum extent of continental and sea ice during the more recent glacial period and approximate sea ice coverage of contemporary times. Image is from <https://www.cdm.org/mammothdiscovery/whenceages.html>.

Sea levels were estimated to have been 120 m lower than present (Figure 3.2) with some offshore banks exposed and potentially acting as refugia for salmon. The most recent warm period (the Holocene) which has persisted for the past 11 000 years, is the longest stable warm period recorded during the past 420 thousand years (Petit *et al.*, 1999). Climate during the last ice age (between about 18 000 and 80 000 years ago) was much more variable (Schmidt and Hertzberg, 2011). The unusually warm and climatically stable period of the Holocene resulted in the continuous and sustained northward expansion of many species, including *Homo sapiens*.

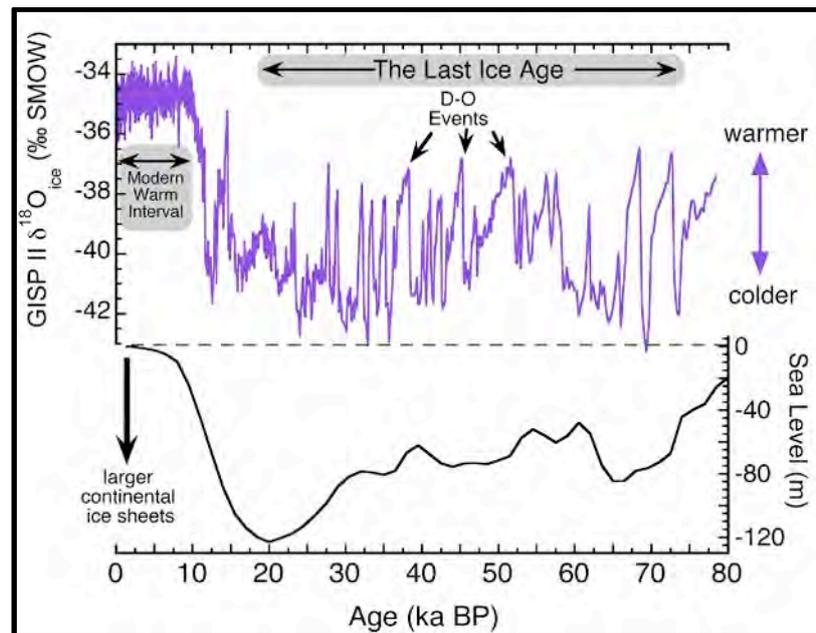


Figure 3.2. Top line shows the oxygen isotope record ($\delta^{18}\text{O}_{\text{ice}}$) from the Greenland Ice Sheet Project II (GISP II) ice core over the last 80 000 years and the bottom panel shows changes in global sea level over the same time period, reflecting the waxing and waning of continental ice sheets during the last ice age. The figure is reproduced directly from Schmidt and Hertzberg (2011).

3.1 Contemporary conditions

Drinkwater (2006) characterizes the warming conditions of the North Atlantic that began in the 1920s and 1930s and persisted into the 1950s and 1960s as the most significant regime shift in the North Atlantic of the 20th century. In a follow-up paper, Drinkwater and Kristiansen (2018) describe the ecosystem responses that resulted following the cold period of the 1970s and 1980s.

Drinkwater *et al.* (2013) is an excellent synthesis of data and analyses of the mean conditions and variability in the climate and physical oceanographic characteristics of the Labrador Sea and surrounding shelves and in the Norwegian and Barents seas of the recent six decades. Key points from the analyses of Drinkwater *et al.* (2013) are:

- Arctic flows are more dominant in the Labrador Sea region, especially on the shelves, while Atlantic flows dominate in the Norwegian and a large part of the Barents Seas.
- General out-of-phase relationship at interannual to decadal scales in the environmental conditions (air and sea temperatures and sea-ice conditions) between the Northwest and Northeast Atlantic, owing to their opposite response to the variability in the North Atlantic Oscillation (NAO).
- From the mid-1990s, air and sea temperatures in both regions generally have been in phase, showing strong warming and reduced ice coverage.

3.2 Circulation data

Good descriptions of circulation patterns and changes in conditions associated with climate change are provided in Reid and Valdés (2011) and Drinkwater *et al.* (2013).

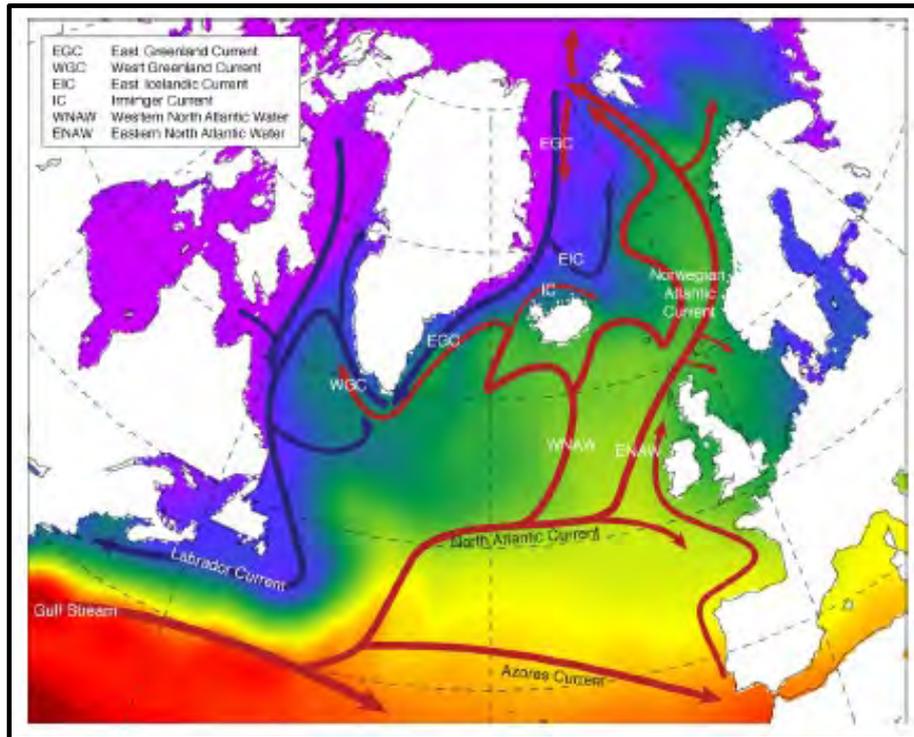


Figure 3.3. Schematic of the pathways of the major near-surface currents of the North Atlantic, superimposed on a map of sea surface temperature for February 2010. Red arrows = the warm, saline waters originating in the Gulf Stream/North Atlantic Current; blue arrows = cold, fresh waters originating in the Arctic Ocean; pink shading = ice-covered regions. This figure is copied directly from Reid and Valdés (2011; Figure 2.1).

One notable feature in the North Atlantic is the subpolar gyre, a large body of cold and low-saline subarctic water, which circulates counter-clockwise south of Greenland and Iceland (Hátún *et al.*, 2005, 2017). From Hátún *et al.* (2005):

“The variability of the Atlantic Inflow salinities is part of a larger picture, which may be illustrated by the changes from a high-index year (1993) to a low-index year (1998) (Figure 3.4). The main features are a southward shift of the frontal zone between the two gyres in the Newfoundland Basin and a substantial salinity increase along the eastern margin of the North Atlantic, including the Iceland Basin... Replacement of the cold and dense water in the Iceland and Irminger Basins with warmer and lighter waters implies an increase in the sea-surface height, whereas colder water replacing warmer water in the Newfoundland Basin likewise implies a decrease in the sea-surface height.... The gyre index is therefore related not only to the strength of the gyre circulation but also to the shape of the gyre. During the high-index period in the early 1990s, the gyre had an east–west shape with strong protrusions into the eastern basins (Figure 3.4A), whereas in the low-index years in the late 1990s, it had a more north–south shape, largely confined to the west of the Mid-Atlantic Ridge (Figure 3.4B).”

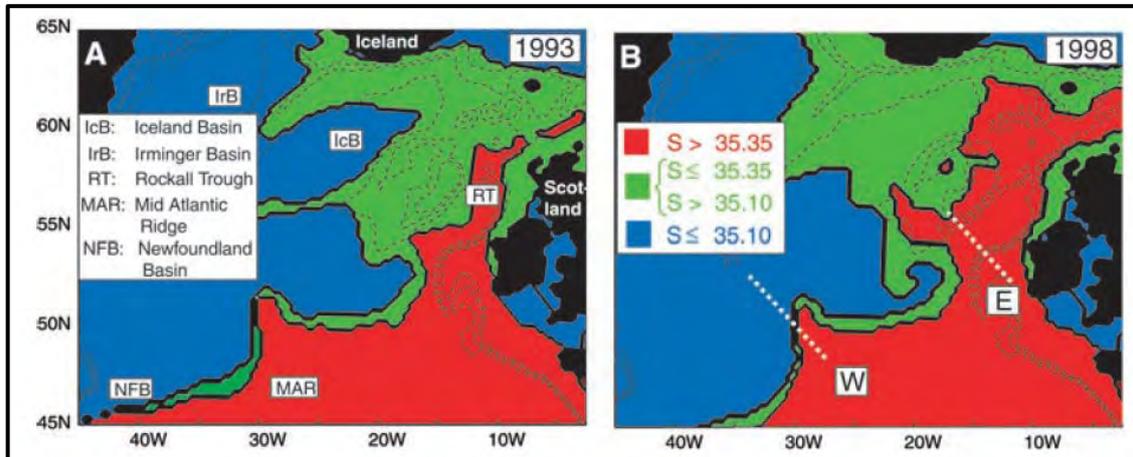


Figure 3.4. This figure is copied directly from Hátún *et al.* (2005). The simulated upper-layer spatial distribution of typical sub-polar gyre water (blue), subtropical gyre water (red), and a mixture, influenced by both gyres (green), averaged for the low-salinity year 1993 (panel A) and the high-salinity year 1998 (panel B).”

During years when the winter mixed layer is anomalously deep in the Labrador-Irminger Sea, the subpolar gyre expands with subsequent increases in abundance of ecologically important zooplankton species, *Calanus finmarchicus*, within the Irminger Sea and on the south Iceland shelf (Hátún *et al.*, 2016, 2017). Associations with a number of trophic level dynamics in the North Atlantic have also been demonstrated (Hátún *et al.*, 2009).

A subpolar gyre index (SGI) has been developed and has previously been used as a metric for the lateral position of the subarctic front and the intensity of vertical winter mixing. The SPG index is dependent on satellite data, as it is calculated from sea surface height (altimetry) and is available since 1993. There are different ways to calculate the index but they are all correlated. The version of the SPI shown in Figure 3.5 is from Berx and Payne (2017) and represents the first principal component of the sea surface height field over the rectangular area defined by 40°N and 60°W to 10°E. The index is available at:

- <https://data.marine.gov.scot/dataset/sub-polar-gyre-index>

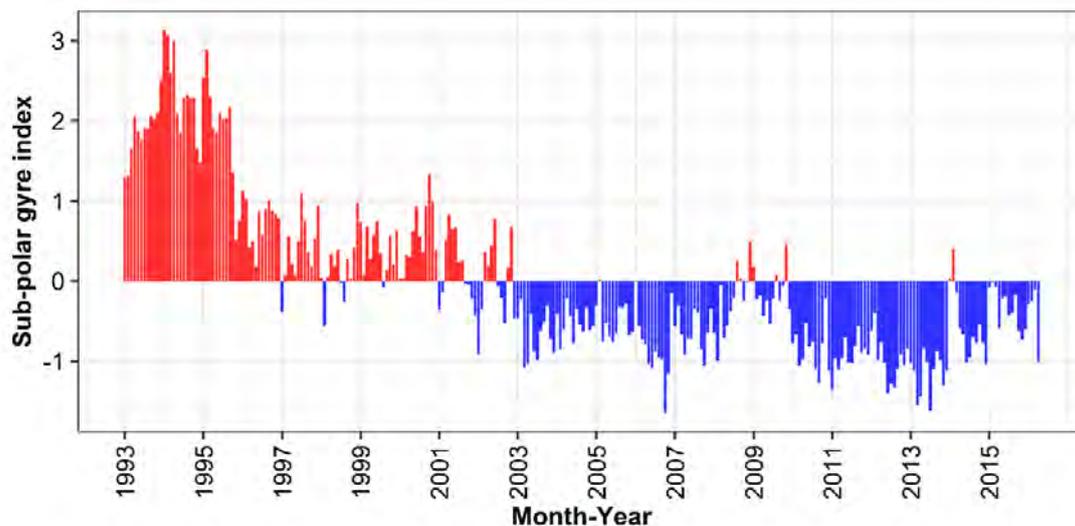


Figure 3.5. Monthly subpolar gyre index values, January 1993 to March 2020. Data for figure derived by Berx and Payne (2017) and available from <https://data.marine.gov.scot/dataset/sub-polar-gyre-index>.

3.3 Oceanographic data: physical features

3.3.1 Sea surface temperature

Sea temperatures in the Northeast Atlantic in the general area of occupancy of Atlantic salmon are warmer than those of the Northwest Atlantic (see Figure 3.3).

Oceanographic data are available from *in situ* measurements (normally a CTD), satellite observations, and hind-casted model simulations.

3.3.1.1 *In situ* data

In situ oceanographic data are available from a range of different surveys in the Northeast Atlantic. They are sampled in all ecosystem surveys and at most other surveys, for instance surveys targeting fish or zooplankton. The most common method is to haul a CTD-sonde from 500 m depth to get a vertical profile of salinity and temperature at the location. This is repeated with even or uneven intervals every 30–100 nautical miles depending on the survey. The weakness of such data is limited temporal resolution. Oceanographic data from surveys are normally available through collaboration with the institutions doing the sampling. It may however require additional work from oceanographers to get data available in a suitable format. The availability of oceanographic data from directed salmon surveys in the 1990s (see Section 2.13) is not known in detail. The majority of the surveys sampled oceanographic data, but there may be exceptions to this routine. The most relevant surveys for WKSalm and their temporal and spatial coverage are described in Section 4.6.

In addition to large-scale surveys, there are also oceanographic sections along the Norwegian coast sampled four times each year. Most of these sections started around 1980. More information and aggregated data from these sections are available (<http://metadata.nmdc.no/UserInterface/#/>). These are data of water temperature or salinity along the Norwegian coast.

Similar large-scale surveys are conducted in the Northwest Atlantic. Such data are collected and reported annually in the Department of Fisheries and Oceans (DFO) Atlantic Zone Monitoring Program (AZMP) and Atlantic Offshore Monitoring Program (AZOMP) (see Section 4.1.1).

Longitudinal and seasonal and depth profiles of temperature and salinity are available for the Labrador Sea based on Argo buoys (DFO, 2019). The temperature ranges at depths below 50 m are quite low, 3 to 8°C, however the extent of cooler water intrusion into near surface layers and reduced density of the water are particularly striking during the 2017 and 2018 winters (Figure 3.6).

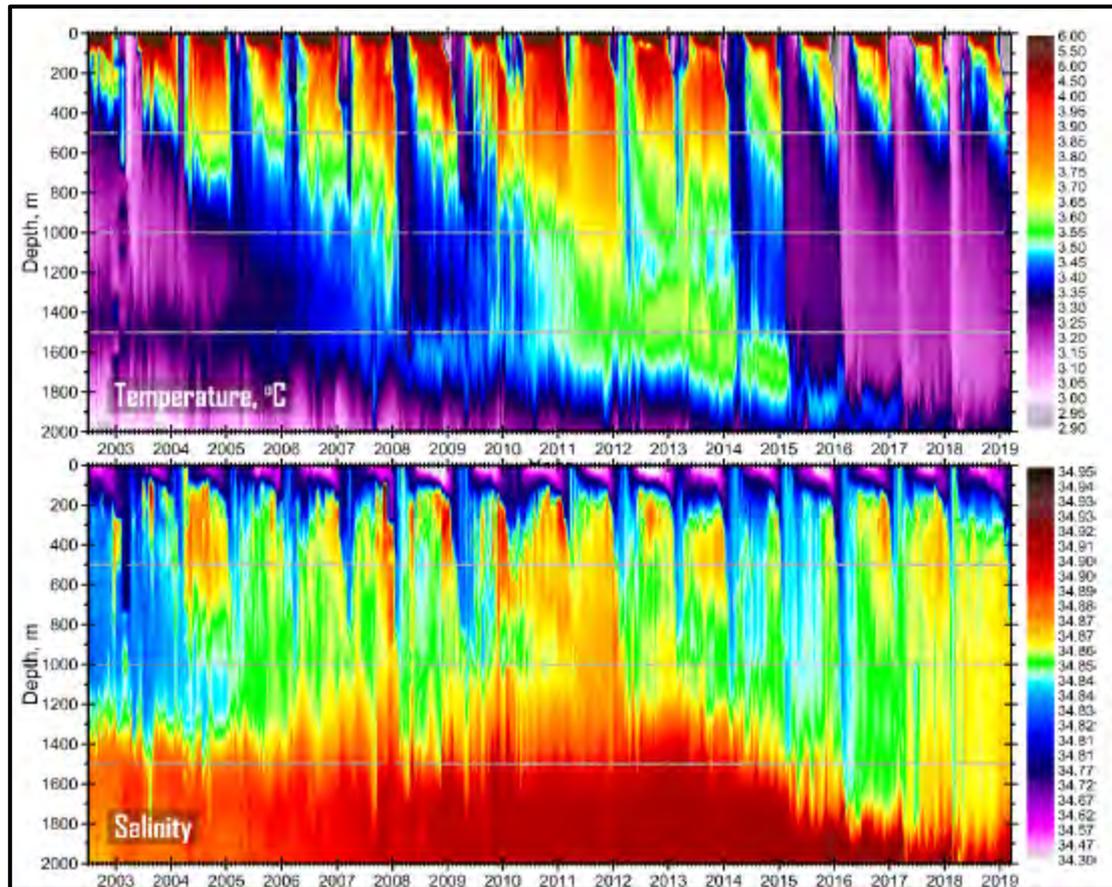


Figure 3.6. Temperature and salinity in the central Labrador Sea based on the measurements collected by the Argo floats and research vessels during 2002–2018 (DFO, 2019).

3.3.1.2 Satellite data

In the Northwest Atlantic, there are important seasonal variations in sea surface temperature along the shelf and coastal areas. The warm Gulf Stream waters form a boundary condition along the southern edge of the Northwest Atlantic with cold waters (Labrador Current) descending along the northern coastal areas of Labrador, Newfoundland and the Gulf of St Lawrence with ice formation in January and persistence into April. Warming of surface waters to temperatures exceeding 15°C occurs in July and persists into September (Figure 3.7).

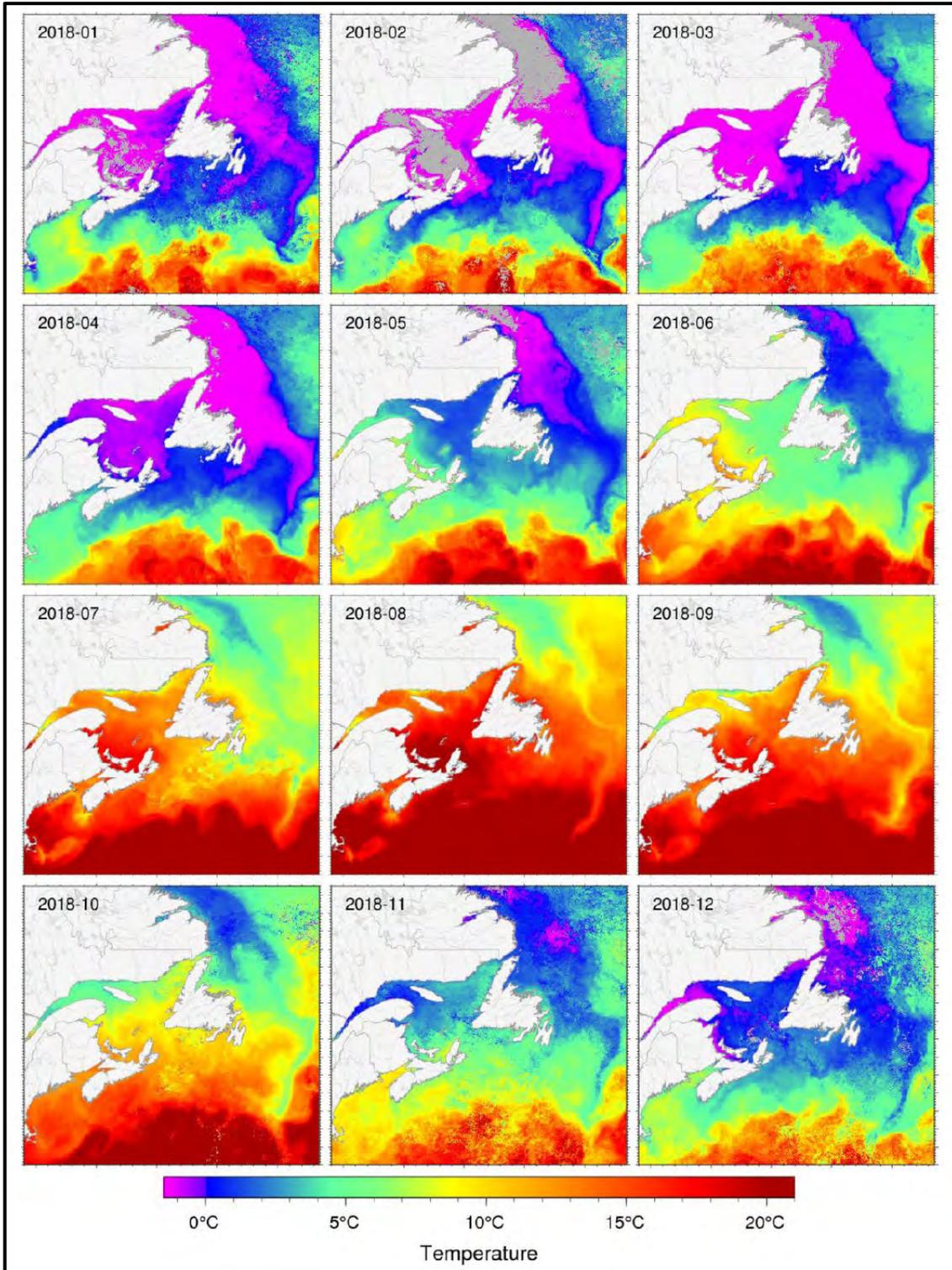


Figure 3.7. Example of seasonal patterns of sea-surface temperatures in the coastal areas of the Atlantic salmon producing areas of eastern Canada. The monthly averages shown are for 2018 (Figure 5 of DFO, 2019).

Satellite data are available as open access provided by NOAA (<https://psl.noaa.gov/data/gridded/data.noaa.oisst.v2.html>).

- The optimum interpolation (OI) sea surface temperature (SST) analysis is produced weekly on a one-degree grid.
- The analysis uses *in situ* and satellite SST's plus SST's simulated by sea-ice cover.

- The weakly mean SST is available for the years 1981–2019 while long-term monthly means derived from data are available for the years 1961–1990 and 1971–2000.
- The geographic domain of the data is the entire world except north of 89.5 N and south of 89.5 S.

Operational Sea Surface Temperature and Sea Ice Analysis (OSTIA) System is produced by the UK Met Office as part of the European Union Global Monitoring for Environment and Security (GMES) MyOcean project (<https://podaac.jpl.nasa.gov/dataset/UKMO-L4HRfnd-GLOB-OSTIA>).

- OSTIA provides sea surface temperature (SST) analysis with global coverage on a daily basis, using satellite SST data provided by international agencies via the Group for High Resolution SST (GHRSST) Regional/Global Task Sharing (R/GTS) framework and *in situ* SST data available over the Global Telecommunications System (GTS).
- It also provides a sea-ice concentration product from the EUMETSAT Ocean and Sea Ice Satellite Applications Facility (OSI-SAF).
- The OSTIA system produces an SST estimate at an output grid resolution of 1/20° (~6 km) and data are adjusted to represent the SST at the same depth as drifting buoy measurements (0.2–1 m).
- Global coverage outputs are provided each day in GHRSST L4 netCDF format. A variety of secondary products are also provided including weekly and monthly mean datasets.
- Reference: UK Met Office. 2005. GHRSST Level 4 OSTIA Global Foundation Sea Surface Temperature Analysis. Ver. 1.0. PO.DAAC, CA, USA. Dataset accessed [YYYY-MM-DD] at <https://doi.org/10.5067/GHOST-4FK01>. Stark, J.D., C. J. Donlon, M. J. Martin and M. E. McCulloch, 2007, OSTIA : An operational, high resolution, real time, global sea-surface temperature analysis system., Oceans 07 IEEE Aberdeen, conference proceedings. Marine challenges: coastline to deep sea. Aberdeen, Scotland.IEEE.

3.3.1.3 Hind-cast model simulations

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.

3.3.2 Ice cover

Salmon distribution at sea has been described as being dependent upon ice cover with the general assumption that salmon avoid ice-covered marine areas. Some studies report on delayed run timing back to home waters and delayed catches in marine fisheries in years with more extensive ice cover in the Labrador Sea (Reddin, 2006). The empirical observations of absence of salmon under ice cover are lacking. There is one study reporting that salmon overwintered successfully in a marine sea cage, which was covered by ice (Dempson *et al.*, 1999). High catches of Atlantic salmon noted in the coastal areas of Svalbard (northern Norway) in the 2000s may be related to the warming of the Atlantic waters west of Spitsbergen at that time, demonstrating to an extent the control ice cover and cold temperatures may have on salmon distribution at sea (Jensen *et al.*, 2014).

The extreme northern areas of the Northeast Atlantic and the western portion of the Northwest Atlantic can have extensive ice cover during the winter. The ice coverage is more extensive in the Northwest Atlantic, extending as far south as 45°N in the Labrador Sea with the Gulf of St Lawrence extensively ice covered during January to March in most years (Figure 3.8).

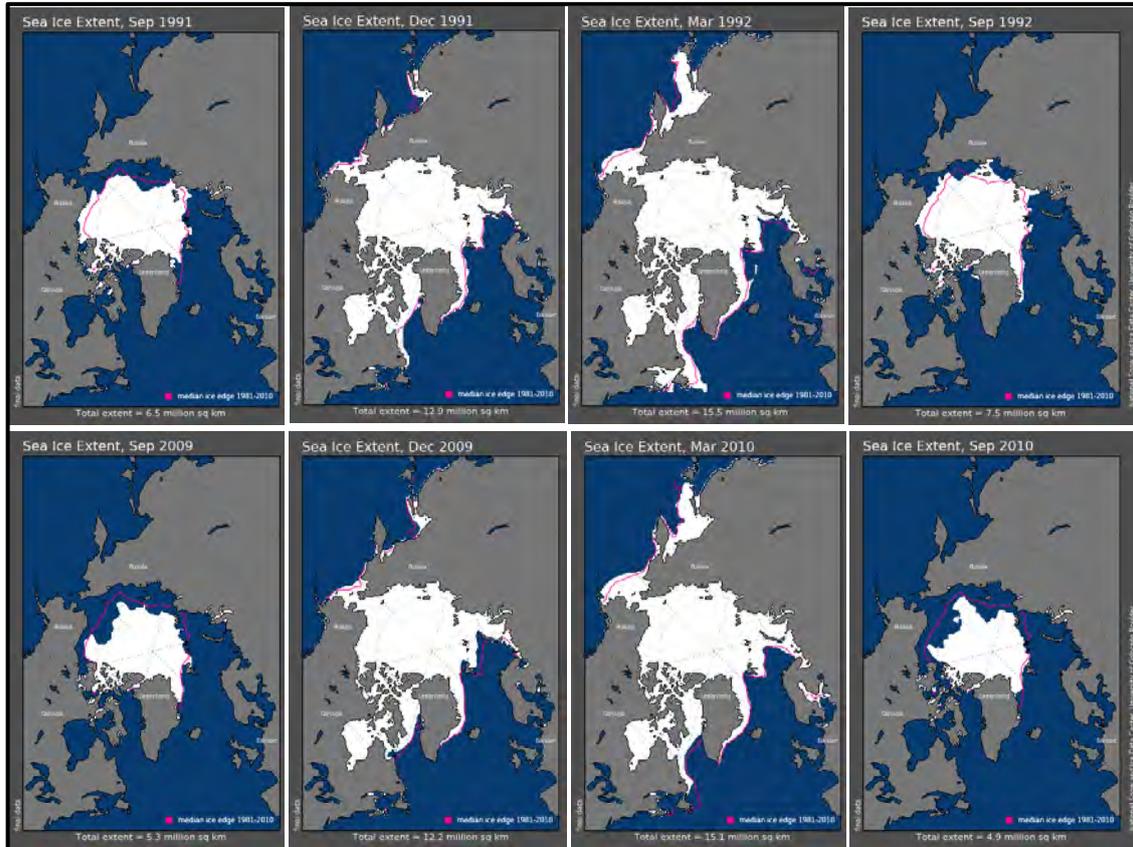


Figure 3.8. Examples of monthly sea ice extent in the North Atlantic for a cold, high ice year period in the Northwest Atlantic (1991–1992; upper row) and contrasted low ice year period (2009–2010; lower row). Source of ice images for Northern hemisphere: https://nsidc.org/data/seaice_index/archives/image_select.

Deser *et al.* (2002) indicated that the winter ice variations in the Labrador Sea are out of phase with those of the Greenland-Barents-Norwegian seas, with advances of the sea ice edge in the Labrador Sea corresponding to retreat of the ice edge in the Northeast Atlantic. These patterns are in large part attributed to the large-scale atmospheric circulation patterns characterized by the North Atlantic Oscillation (NAO). Drinkwater *et al.* (2013) reported the same out of phase patterns for general physical conditions in the Northwest and Northeast Atlantic prior to the mid-1990s but since then responses between the two areas have become generally in phase associated with strong warming and reduced ice cover.

3.3.2.1 Ice cover in the Gulf of St Lawrence and on the Newfoundland Shelf

There is extensive sea ice cover data over large portions of the area of eastern Canada during the winter months (Figure 3.8) associated primarily in support of marine navigation.

Data on ice cover are collected by Environment Canada and reported each year in the Department of Fisheries and Oceans (DFO) Atlantic Zone Monitoring Program (AZMP) reports. The time-series starts in the early 1960s and continues to be updated each year. Annual anomalies for ice cover in the Gulf of St Lawrence and on the Newfoundland Shelf (Figure 3.9) can be found on the DFO website (<http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/climat/ice-glance/coverage-couverture-eng.htm>). Figures showing annual cycles of ice-cover in both regions are also shown on the website and data are also available.

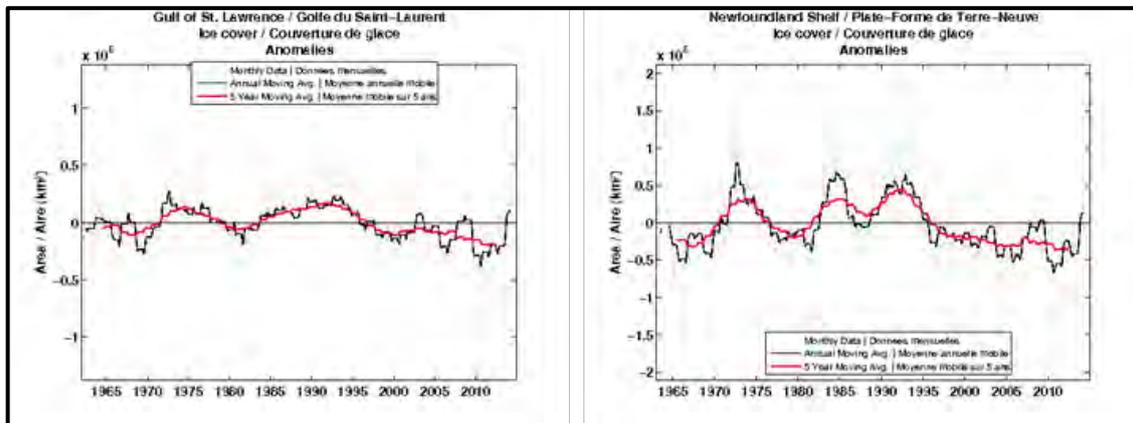


Figure 3.9. Trends in ice cover in the Gulf of St. Lawrence and on the Newfoundland Shelf, Northwest Atlantic.

Additional information on ice cover (e.g. for the Labrador Shelf and Eastern Canadian Arctic) are also collected by Environment and Climate Change Canada. Ice charts are available on a daily basis for navigational purposes, and there is a data archive of images, which is not directly available online, but can (probably) be accessed (<https://www.canada.ca/en/environment-climate-change/services/ice-forecasts-observations.html>).

3.4 Atmospheric forcing indices

The global climate exhibits a number of oscillatory modes of variability on yearly and decadal time scales that are linked over great distances, referred to as atmospheric teleconnection patterns (Reid and Valdés, 2011). An overview of teleconnection indices in the North Atlantic is provided by Reid and Valdés (2011), Alheit *et al.* (2019), and Seip *et al.* (2019).

3.4.1 North Atlantic Oscillation (NAO)

The North Atlantic Oscillation is a pattern of atmospheric variability that has a significant impact on oceanic conditions in the North Atlantic, affecting wind speed, precipitation, evaporation, and the exchange of heat between ocean and atmosphere; its effects are most strongly felt in winter (Hurrell, 1995; Reid and Valdés, 2011). The NAO index is a metric used to describe the state of the NAO, represented as the sea level air pressure difference between the Icelandic low and the Azores high. When the NAO index is positive, there is a strengthening of the Icelandic low-pressure system and the Azores high-pressure system resulting in stronger mid-latitude westerly winds, with colder and drier conditions over the western North Atlantic and warmer and wetter conditions in the eastern North Atlantic (Reid and Valdés, 2011). When the NAO index is negative, there is a reduced pressure gradient, and the effects tend to be reversed.

The NAO index series has been extended back to 1049 using tree-ring based reconstruction. There are variants of the NAO index. The station based index uses the sea-level-pressure (SLP) differences at the two fixed stations (southern station at Lisbon and the northern station at Reykjavik) (Hurrell, 1995). The principal component based indices are a time-series of the leading Empirical Orthogonal Function (EOF) of SLP anomalies over the Atlantic defined by the area 20°–80°N, 90°W–40°E; these PC-based indices track the seasonal movements of the Icelandic low and Azores high. The PC-based indices provide a more optimal representation of the full spatial patterns of the NAO, may be less noisy than station-based indices, but are not available as far back as the station-based indices. Osborn (2011) reported on the record December-January-February NAO index value in 2009/2010 that corresponded to a cold winter and extensive snow cover in the UK Europe but relatively warmer weather in the northwest Atlantic area.

The reconstructed NAO time-series are available from several websites:

- ftp://ftp.ncdc.noaa.gov/pub/data/paleo/historical/north_atlantic/nao_mon.txt.
- <https://crudata.uea.ac.uk/cru/data/nao/>

The annual NAO time-series mean value for December–January–February–March is shown in Figure 3.10.

3.4.2 Atlantic Multidecadal Oscillation (AMO)

The AMO index was defined by Enfield *et al.* (2001) as the detrended, 10-year running mean of North Atlantic (0°–70°N) surface temperature (SST) anomalies. The temporal patterns produced include generally negative or cold periods occurring from the early 1900s through the mid-1920s and from the late 1960s through the mid-1990s with positive or warm periods from the mid to the late 1800s, from the late 1920s through the late 1960s and since the mid-1990s to the present (Alheit *et al.*, 2014; Drinkwater and Kristinsen, 2018) (Figure 3.10). Alheit *et al.* (2014) indicated that the AMO variability is not a true oscillation, and it would be more correct to refer to it as the Atlantic Multidecadal Variability, however, for historical reasons and common usage, the AMO acronym was retained. A number of climatic phenomena have been associated with the AMO, including Atlantic sector hurricane frequency, precipitation in North America, rainfall over the African Sahel zone and northeastern Brazil, as well as global connections to the Tibetan Plateau and the Indian monsoon and an out-of-phase relationship with multidecadal temperature variability in the southern hemisphere (Alheit *et al.*, 2014).

Friedland *et al.* (2014) reported on a strong recruitment coherence between North American and European stock complexes of Atlantic salmon, associated with the Atlantic Multidecadal Oscillation (AMO) but not to the North Atlantic Oscillation (NAO).

Alheit *et al.* (2019) suggested that the contractions and expansions of the subpolar gyre associated with the fluctuations of the AMO could be related to complex ecosystem changes observed in different North Atlantic regions around the mid-1990s.

There is both a smoothed and an unsmoothed AMO-index, both with monthly values available from:

- <http://www.esrl.noaa.gov/psd/data/timeseries/AMO/>

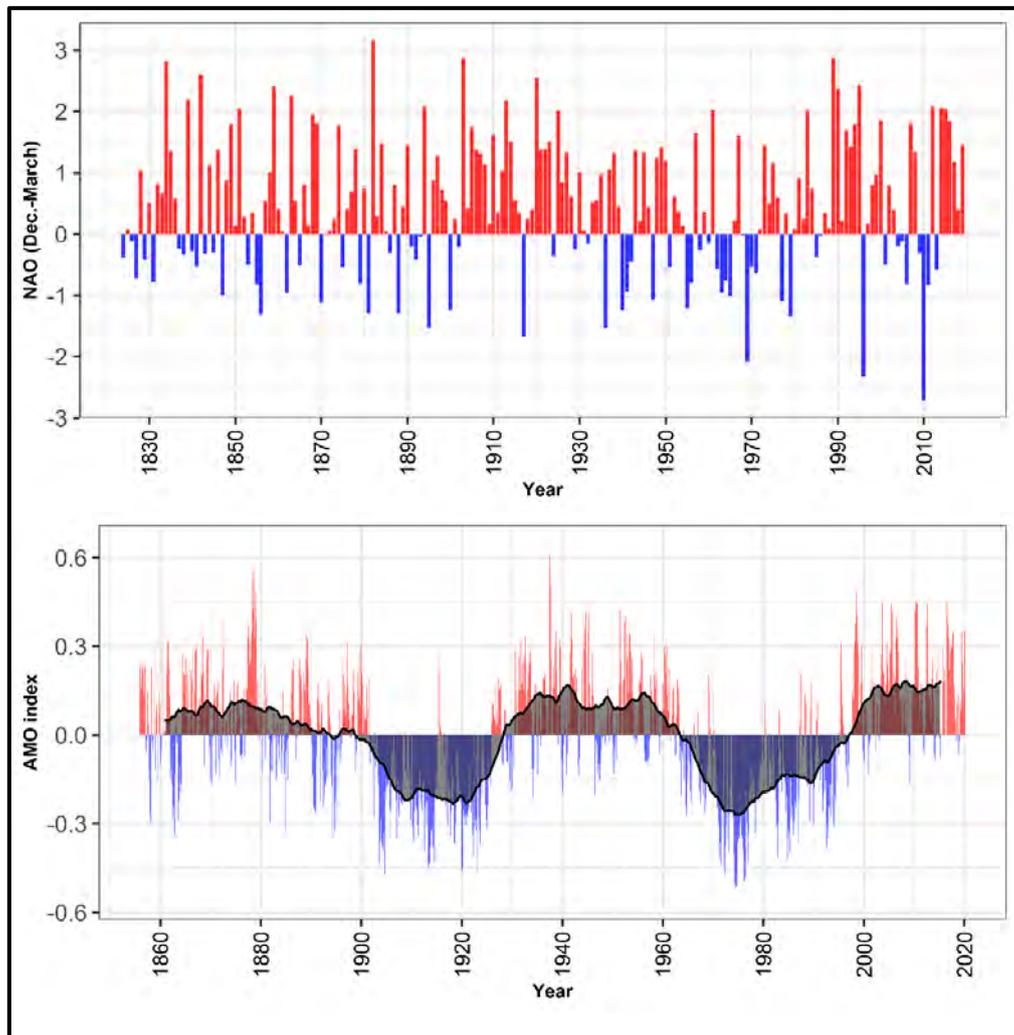


Figure 3.10. Upper panel: North Atlantic Oscillation winter index (December–January–February–March; mean) derived from PC-based data (<https://crudata.uea.ac.uk/cru/data/nao/>). Lower panel: monthly detrended AMO index for the period 1856 to March 2020 and the overlay plot is the smoothed series (120 months running mean) obtained from <http://www.esrl.noaa.gov/psd/data/timeseries/AMO/>.

3.4.3 East Atlantic Pattern (EAP)

The EAP is structurally similar to the NAO, consisting of a low-pressure centre in the Northeast Atlantic and a high-pressure centre over North Africa or the Mediterranean Sea and is important in all months except May to August (Reid and Valdés, 2011). It exhibits strong multidecadal variability, with the negative phase prevailing during much of the period of 1950 to 1976 and the positive phase occurring during much of the time after 1976 (Figure 3.11). The positive phase of the EAP is associated with above-average surface air temperatures in Europe throughout the year and above-average rainfall over northern Europe and Scandinavia, and with below-average rainfall across southern Europe (Reid and Valdés, 2011).

Data are available from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center:

- <http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml>.

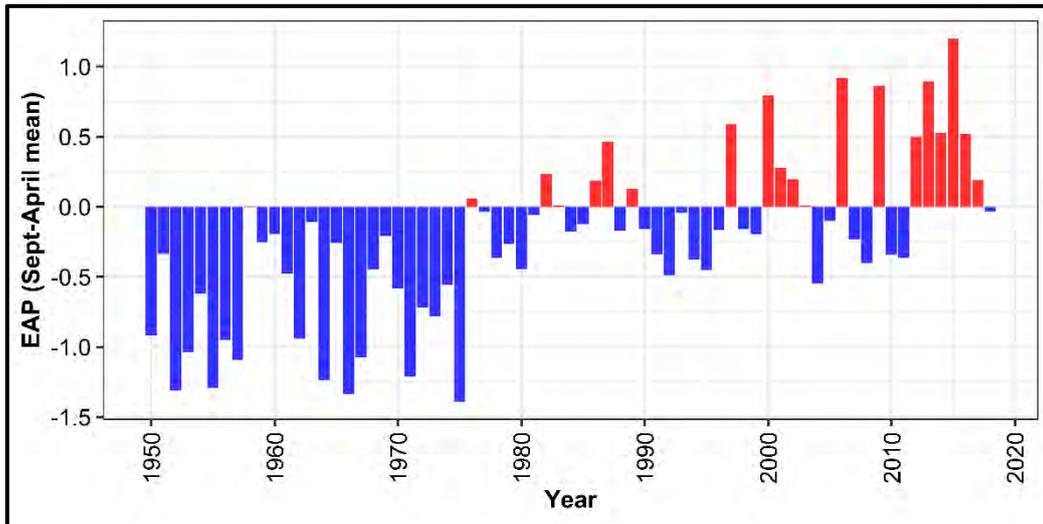


Figure 3.11. The East Atlantic Pattern index (September to April; mean) for the period 1950/1951 (September–April) to 2018/2019. Data are from <http://www.cpc.ncep.noaa.gov/data/teledoc/ea.shtml>. The data are the monthly departures standardized using the 1981–2010 base period statistics.

3.4.4 Atlantic Meridional Overturning Circulation (AMOC)

The Atlantic Meridional Overturning Circulation is a system of currents in the Atlantic Ocean characterised by a northward flow of warm, saltwater in the upper layers of the Atlantic and a southward flow of colder, deep water, which is part of the thermohaline circulation. The surface temperature in the subpolar gyre region, relative to the large-scale temperature trend, has been proposed as an index for the longer term (1871–2018) AMOC variations. The AMOC has a high value when the North Atlantic and the northern hemisphere are warm.

The data analysed by Seip *et al.* (2019) were obtained from Levke Caesar, Potsdam Institute for Climate Impact Research.

4 North Atlantic ecosystem – biological features

4.1 Primary and secondary production in the North Atlantic

The distribution and abundance of phytoplankton and zooplankton are highly variable across time and space, at both small and large scales, and are thought to be related to recruitment and the spatial distributions of fish populations (Friedland *et al.*, 2018; Asch *et al.*, 2019). Plankton encompasses a collection of organisms characterized by a variety of morphologies, functional traits and dynamics, which at times are very different even when considering congeneric species. Changes in plankton abundance and composition can thus significantly impact the energy transferred through the foodweb to top predators, such as salmon. Long-term time-series (i.e. >ten years) allow recognition of changes in plankton stocks and shifts in species composition, and geographical distributions that may be linked to changes in marine ecosystem structure and productivity.

Collectively, much of the world marine primary and secondary production ecological data has been compiled in the “Time-Series Metabase”. This database provides details and graphical results from over 350 marine ecological time-series and includes investigator and project contact information, sampling and methods details, and a collection of standardized summary graphics. More details on the time-series metabase can be obtained at:

- <https://www.st.nmfs.noaa.gov/copepod/metabase/>

4.1.1 The Northwest Atlantic ecosystem

Data required to characterise and quantify changes in ocean physical, chemical, and biological properties on the Canadian Atlantic Continental Shelf and in the Gulf of St Lawrence are collected and reported annually in the Department of Fisheries and Oceans (DFO) Atlantic Zone Monitoring Program (AZMP) and Atlantic Offshore Monitoring Program (AZOMP).

AZOMP sampling is annual, usually in May and includes other metrics to assess the uptake of carbon dioxide and transport to depth via deep convection. The Labrador Sea Monitoring Program, part of the AZOMP, collects and analyses physical, chemical and biological oceanographic observations on a line of stations across the Labrador Sea. The line, referred to as AR7W, is the Atlantic Repeat Hydrography Line 7 West of the 1990–2002 World Ocean Circulation Experiment (WOCE). It has been occupied annually (typically in May) since 1990, with biological measurements since 1994. AR7W extends from Hamilton Bank on the Labrador Shelf to Cape Desolation on the Greenland Shelf. Physical oceanographic properties and the distribution of nutrients, phytoplankton and zooplankton are assessed, as are atmospheric and sea-ice conditions.

AZMP sampling is seasonal and opportunistic along transects (Figure 4.1) and at randomly distributed stations during fish surveys. There is higher frequency temporal sampling at coastal fixed stations. In addition, remote sensing provides broader spatial synoptic coverage of sea surface temperature and chlorophyll concentrations throughout the Northwest Atlantic, while Continuous Plankton Recorder (CPR) sampling provides monthly sampling of plankton along lines between Reykjavik and the Gulf of Maine, often via St John’s and Halifax (Canada).

More detailed descriptions and downloadable data are available on the AZMP and AZOMP websites:

- <http://www.isdm.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html>
- <http://www.bio.gc.ca/science/monitoring-monitorage/azomp-pmzao/azomp-pmzao-en.php>

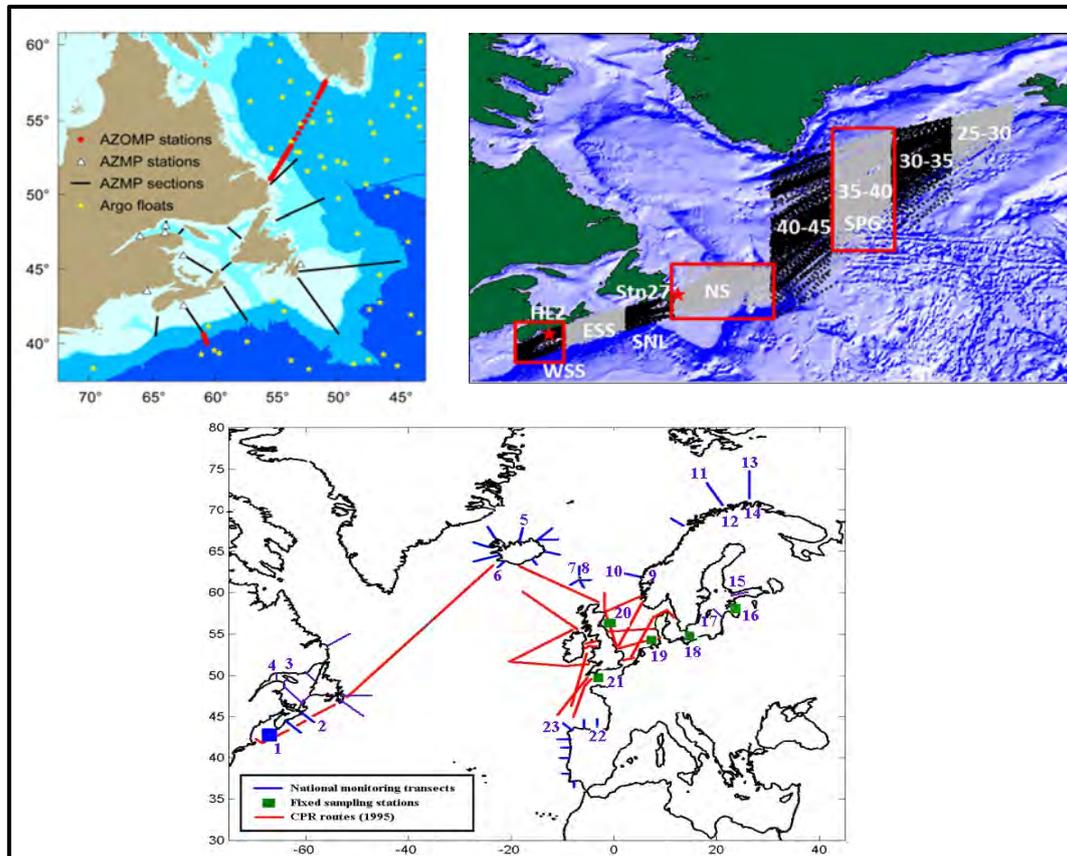


Figure 4.1. AZMP and AZOMP stations and transects (upper left panel) and positions where CPR samples have been collected in the CPR Survey in the NW Atlantic since 1960 (upper right panel). Sampling transects, fixed stations and CPR routes in the NE Atlantic are shown in the lower panel.

4.1.2 The Northeast Atlantic ecosystem

Several nations have programmes to monitor hydrography and plankton in the Icelandic/Norwegian basin, the area most frequented by Atlantic salmon, including Norway, Iceland, The Faroes (Figure 4.1). Other nations, including the UK (Scotland), UK (England and Wales), Estonia, Latvia, Germany, France, Spain, and Portugal sample along transects or at fixed stations in the North Sea, the Baltic, the Bay of Biscay and farther south. Further details of these programmes have been previously published by ICES (2005a), including contact information for those responsible for collecting/collating the data. We are unaware of data repositories that are as readily accessible as those for the AZMP and AZOMP. Most groups submit some of their data to the METABASE database (see below).

4.1.3 Satellite-derived estimates of phytoplankton biomass and production

Remotely sensed images of sea surface chlorophyll concentration (SSC) show areas of the North Atlantic where phytoplankton levels are higher than average to the east and west of Greenland

(Figure 4.2). These areas are indicative of enhanced phytoplankton concentration and/or enhanced primary production and may correspond to areas where zooplankton production is also higher, although unfortunately neither are areas where zooplankton time-series data are available (see below).

Annual primary production rates (photosynthetic rates) can be calculated based on maps of SSC and a database of *in situ* observations including the seasonally varying vertical distributions of chlorophyll concentration, light intensity and experimentally determined relationships between light intensity and photosynthetic rate. For “blue sky” scenarios, annual primary production varies with latitude (i.e. light intensity), but in subpolar regions cloud cover can be significant, and spatial and inter-annual variations may occur.

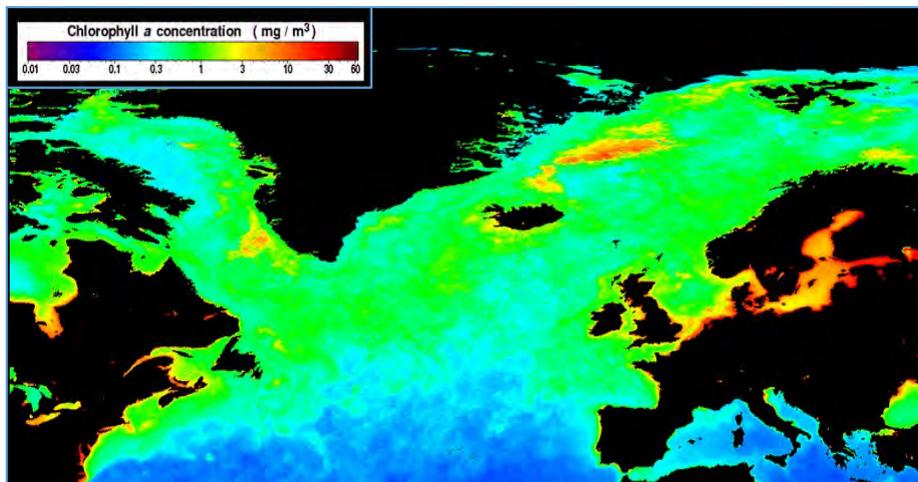


Figure 4.2. Satellite derived sea surface chlorophyll concentrations in the North Atlantic.

Satellite-derived data and metrics are provided on a routine basis for a series of satellite statistical areas (satellite boxes) in the AZMP (Figure 4.3). Metrics include information on the spring bloom dynamics including start date, maximum amplitude, duration and overall magnitude. For example, in the Magdalen Shallows area (outlined in red in Figure 4.3), between 1998 and 2018, the start of the spring bloom varied between the first week of March (2010) and the last week of April (2015), while the maximum amplitude varied between 1.4 mg Chl m⁻³ (1999) and 7.3 mg Chl m⁻³ (2002). Similar calculations could be made for areas in the Northeast Atlantic, but these authors are unaware of any routine reporting or downloadable data sources.

Images and data can be downloaded at:

- <ftp://ftp.dfo-mpo.gc.ca/bometrics/>.

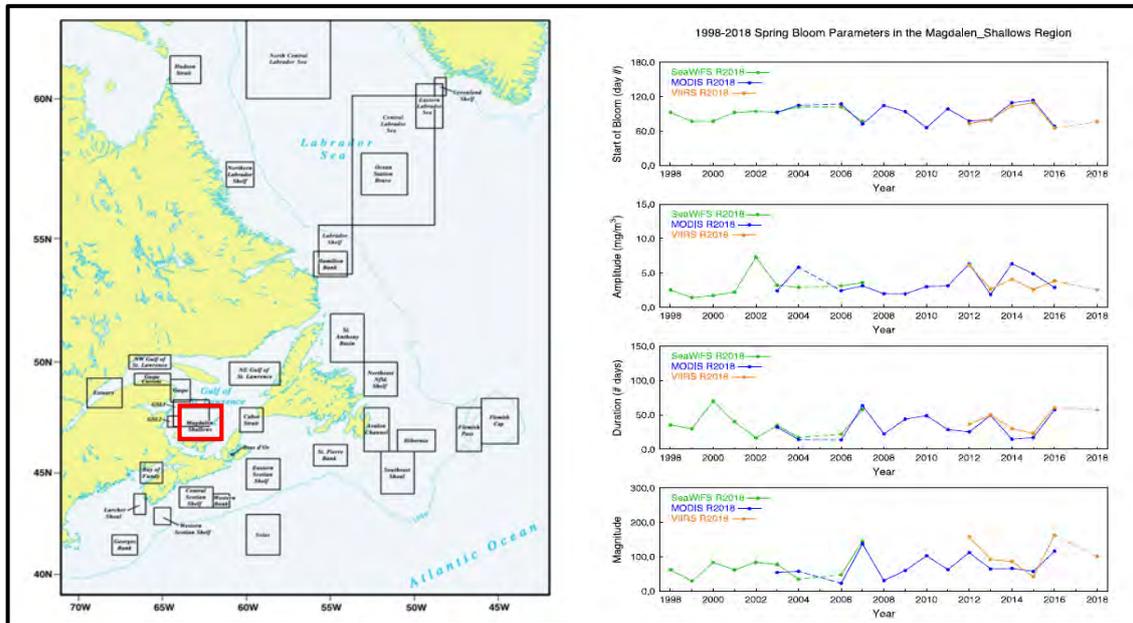


Figure 4.3. Satellite boxes (left panel) for which spring bloom (right panel) metrics are calculated in AZMP.

4.1.4 *In situ* observations of phytoplankton and zooplankton concentration

Time-series of phytoplankton and zooplankton concentrations have been compiled. Many of the time-series stations are coastal fixed stations, which are sampled at monthly, or more frequent, intervals (Figure 4.4). The observations for the open ocean regions are mainly derived from samples collected by Continuous Plankton Recorders (CPR), towed by ships-of-opportunity, such as ferries, cargo ships, etc. For the latter each sample is collected over 10 nautical miles, generally at monthly intervals.

Summary information can be found online at:

- www.st.nmfs.noaa.gov/copepod/time-series/

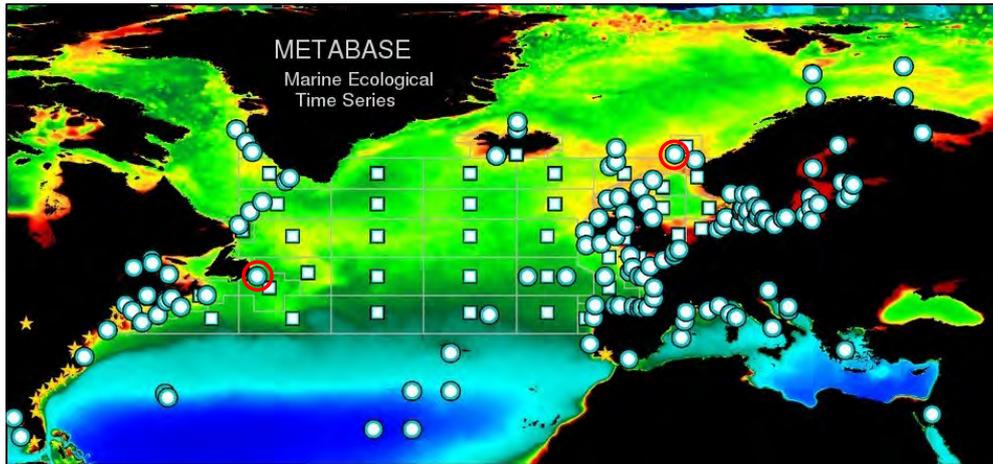


Figure 4.4. Time-series sampling stations in the North Atlantic. The circles indicate stations that are a single position (fixed stations), whereas the small squares are the mid-points of the larger boxes that are sampled by Continuous Plankton Recorders (CPR).

By way of example, time-series observations are shown for two fixed stations; “Stn 27”, off Newfoundland in the Northwest Atlantic and the “Svinoy Transect West” station, off southern Norway in the Northeast Atlantic (Figure 4.5). In general, the coastal time-series observations have been collected over relatively short and recent periods (1980s–present).

Contact details are provided on the website for data requests and additional information regarding methodology and sampling frequency.

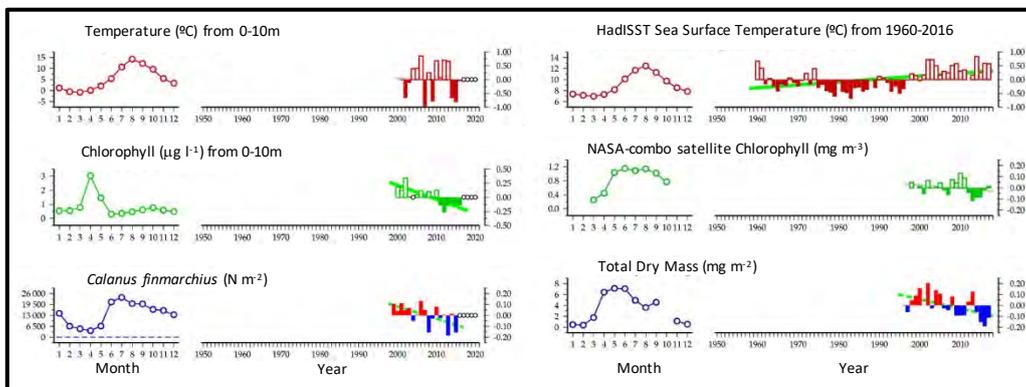


Figure 4.5. Time-series for sea surface temperature and indices of chlorophyll and zooplankton concentration at Stn 27 (left column) and at Svinoy Transect West (right column). The stations are indicated on Figure 4.4 by red circles. Summary figures are from: <https://www.st.nmfs.noaa.gov/copepod/time-series/index-natl-allts.html>.

Longer-term time-series (1960s–present) observations are provided mainly by the CPR Survey. The standard CPR areas and examples of time-series for areas in the Northwest (C8) and the Northeast Atlantic (C4) are shown in Figure 4.6.

For further information and data requests the CPR Survey should be contacted at:

- www.cprsurvey.org.

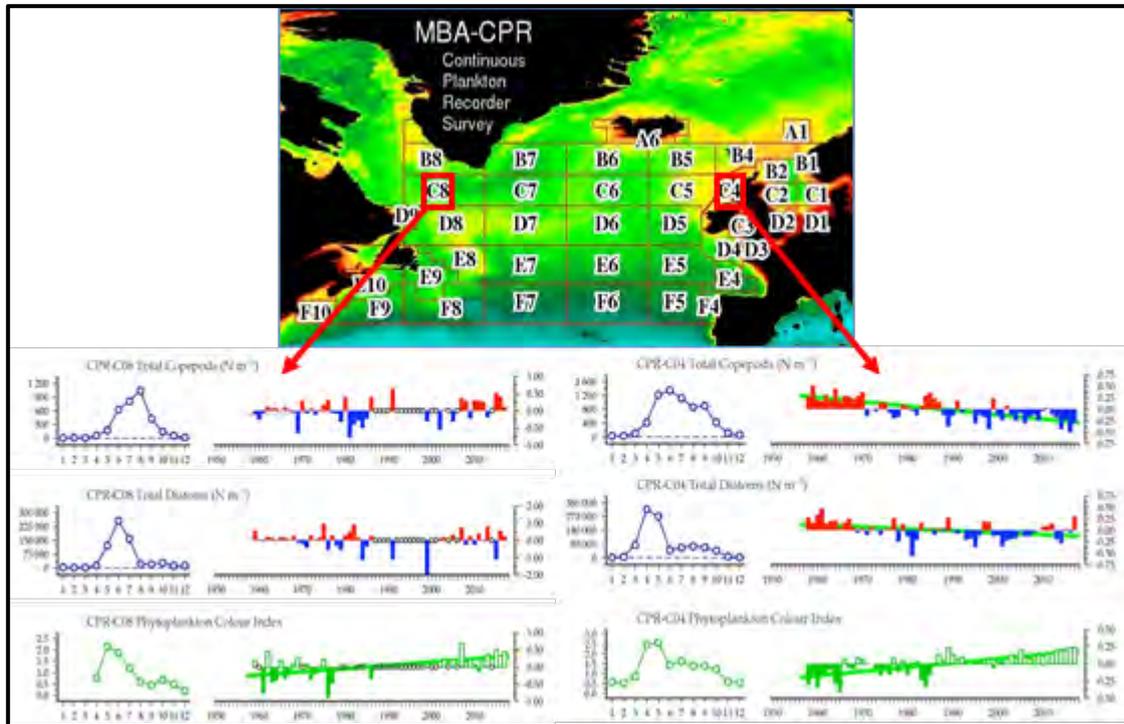


Figure 4.6. Standard Continuous Plankton Recorder (CPR) areas (upper panel) together with average seasonal cycles and annual time-series for zooplankton and phytoplankton indices for areas in the Northwest and Northeast Atlantic areas (lower panels).

4.2 Mesopelagic community

Mesopelagic fish are preyed upon by salmon, especially during the autumn and winter when other prey are scarce. Larvae of mesopelagic fish are also preyed upon by post-smolt (Haugland *et al.*, 2006). The most important species are Mueller's pearlside (*Maurollicus mülleri*), glacier lantern fish (*Benthoosema glaciale*), spotted barracudina (*Arctozenus risso*) and greater argentine (*Argentina silus*). The cephalopod *Gonatus fabricii* is also an important part of the mesopelagic community.

Mesopelagic fish biomass estimates are colossal but this component of the ocean ecosystems is not yet adequately studied and assessed. Six cruises conducted during summer in recent years in the Norwegian Sea around Svalbard, covering in total more than 7800 nautical miles, provide a first description of the distribution of mesopelagic fauna in the region (Siegelman-Charbit and Planque, 2016). There was 3.4 times more acoustic energy recorded at low latitudes than at the highest latitudes.

There are no time-series of mesopelagic fish indices reported at WKSalmon. Ongoing projects on mesopelagic fish, for instance at IMR in Norway, may provide new information about population structure and geographic hotspots.

4.3 Pelagic fish community

Trenkel *et al.* (2014) provide an overview of the abundance and ecology of the pelagic fish communities in the North Atlantic and contrasts these between the Northwest Atlantic and the Northeast Atlantic. The pelagic fish communities of interest to WKSalmon include herring (*Clupea harengus*), mackerel (*Scomber scombrus*), capelin (*Mallotus villosus*), blue whiting (*Micromesistius poutassou*), horse mackerel (*Trachurus trachurus*) and bluefin tuna (*Thunnus thynnus*). Atlantic

menhaden, a pelagic fish with a Northwest Atlantic distribution, is noted but not considered by Trenkel *et al.* (2014). The highlights of the review include:

- Two of the commercial pelagic species considered (blue whiting and horse mackerel) have a distribution essentially restricted to the Northeast Atlantic.
- Commercially important pelagic fish stocks in the North Atlantic undertake extensive seasonal migrations.
- The spatial distribution of pelagic fish in the North Atlantic is very broad, extending into the northern latitudes in the Northeast Atlantic whereas the distribution of most pelagic fish in the Northwest Atlantic has a limited distribution towards the southern edge, the exception being capelin which is a cold-water species inhabiting arctic and subarctic areas.
- Total landings of pelagic fish from the Northeast Atlantic are on average approximately four times those in the Northwest Atlantic.
- Large oceanographic features such as the North Atlantic subpolar gyre play an important role in determining spatial distributions and driving variations in stock size.
- Given the large biomasses and the importance of micro- and macro-plankton to their diets (with exception to Bluefin tuna and mackerel which switch to a larger prey community as they grow), these species can exert significant top-down pressures on the food-web and are important in supporting higher trophic levels.

Several anadromous pelagic fish species in the Northwest Atlantic are not included in the review by Trenkel *et al.* (2014); *Alosa* species including American shad and two species of river herring (and the Northeast Atlantic alosids), and smaller and non-commercially exploited species such as Arctic cod (*Boreogadus saida*) which are found in the Labrador Sea. Notably, Trenkel *et al.* (2014) did not mention Atlantic salmon despite its well-known pelagic and broad distribution in the North Atlantic.

4.3.1 Northwest Atlantic

In contrast to the diverse and broadly distributed pelagic fish community that is fished commercially in the Northeast Atlantic, the commercially exploited pelagic fishes in the Northwest Atlantic (Atlantic herring, Atlantic mackerel) have a distribution that is more generally restricted to the southern extent of the range of Atlantic salmon. The only commercially fished pelagic species found in the northern area of the Northwest Atlantic including the Labrador Sea and at West Greenland is capelin.

Atlantic herring in the Northwest Atlantic are concentrated in the southern areas including the Gulf of St Lawrence, the northeast coast of Newfoundland, the Scotian Shelf, and the Gulf of Maine including the Bay of Fundy (Stephenson *et al.*, 2009; Bourne *et al.*, 2018; Légaré *et al.*, 2014; Surette, 2016; Singh *et al.* 2016). In eastern Canada, the commercial fisheries exploit herring using either fixed gear (gillnets) or purse seines; there is no midwater offshore pelagic trawling for herring in eastern Canada (Singh *et al.*, 2016; Bourne *et al.*, 2018). There are no herring fisheries in the Labrador Sea. The status of exploited herring stocks is variable. Combined fisheries landings in the early 2010s are in the range of 120 000 tonnes annually.

The Atlantic mackerel stock of eastern North America comprises two spawning contingents; a northern component spawning primarily in the southern Gulf of St Lawrence of eastern Canada and a southern contingent spawning in the Mid-Atlantic Bight, Southern New England and the western Gulf of Maine (NEFSC, 2018). The two spawning stocks mix during winter months on the Northeast Shelf of eastern United States. Atlantic mackerel undertakes spring and summer migrations to the Scotian Shelf, Gulf of St Lawrence and the coastal areas of Newfoundland to spawn. Mackerel are fished using primarily driftnets, purse seines, and jiggers (Grégoire and

Savenkoff, 2005), in open water season (spring to fall) along the east coast of Canada. There are no mackerel fisheries in the Labrador Sea and there is no midwater pelagic trawling for mackerel in eastern Canada. Maximum reported landings along the eastern seaboard of North America registered just under 440 000 tonnes in 1973 but averaged 48 000 tonnes during 1978 to 2003 (Grégoire and Savenkoff, 2005).

Capelin are broadly distributed in the Newfoundland and Labrador areas of eastern Canada and the Gulf of St Lawrence but rarely along the eastern Scotian Shelf (Figure 4.3.1.1; Reddin and Carscadden, 1981; Mowbray *et al.*, 2019). Capelin stocks of Newfoundland and Labrador are believed to overwinter on the northern Grand Banks and along the Labrador coast. In addition to the large offshore stocks of capelin there are local stocks distributed in numerous bays of Newfoundland (Reddin and Carscadden, 1981). Capelin are considered a key forage fish, being consumed by seals, whales, groundfish, Atlantic salmon, and seabirds, and provides a vital link in the transfer of energy between zooplankton and upper trophic levels (Mowbray *et al.*, 2019). An offshore foreign fishery developed in the 1970s using midwater trawls that landed in excess of 167 000 tonnes in 1975 but it was closed in 1979. The fishery today has reported landings in the range of 20 000 tonnes, primarily fished by fixed gears (trapnets, cast-nets, dipnets and tucks seines) and purse seiners (Mowbray *et al.*, 2019). The acoustic indices of abundance for offshore capelin in Newfoundland show a dramatic decline post-1990 that has yet to recover (Mowbray *et al.*, 2019; Buren *et al.*, 2019).

The capelin stock in Iceland-East Greenland-Jan Mayen area is assessed by ICES, based on acoustic surveys which have been conducted annually in autumn (September–December) and winter (January–February) since 1978 (ICES, 2016b). This capelin stock spawns in shallow coastal water south and west of Iceland (Vilhjálmsón, 2002) (Figure 4.3.1.2). Year-class abundance is determined by survival during the first winter, and adult growth is positively related to the flow of Atlantic water into the area north of Iceland, when the Irminger Current is strong (Vilhjálmsón, 2002). The fishery utilizes primarily purse seines with a smaller proportion (12% in 2015/2016) of landings taken by pelagic trawl; total landings of capelin in the 2015/2016 season were 517 000 tonnes, primarily during the December to March fishing period (ICES, 2016b). Total landings of capelin in this area exceeded one million tonnes as recently as 2002 (ICES, 2016b).

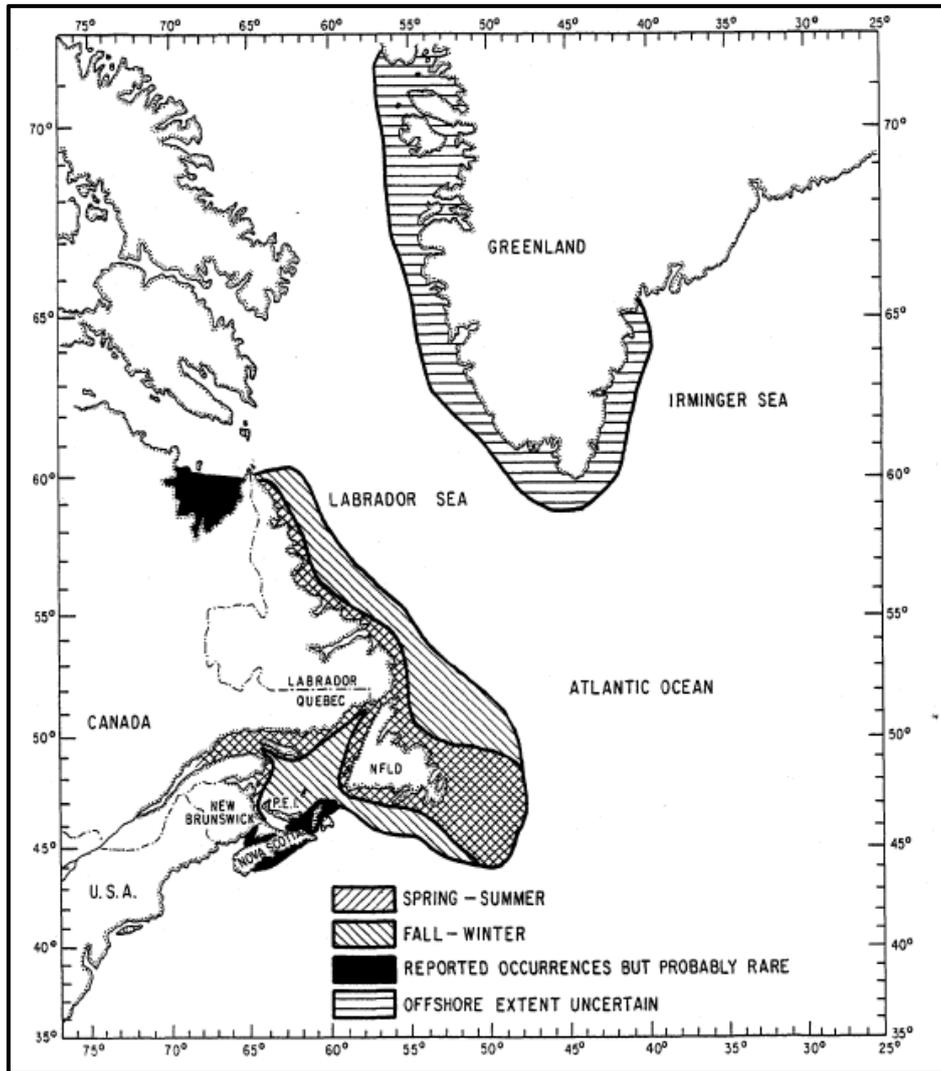


Figure 4.7. Distribution of capelin in the Northwest Atlantic. Figure is copied from Reddin and Carscadden (1981).

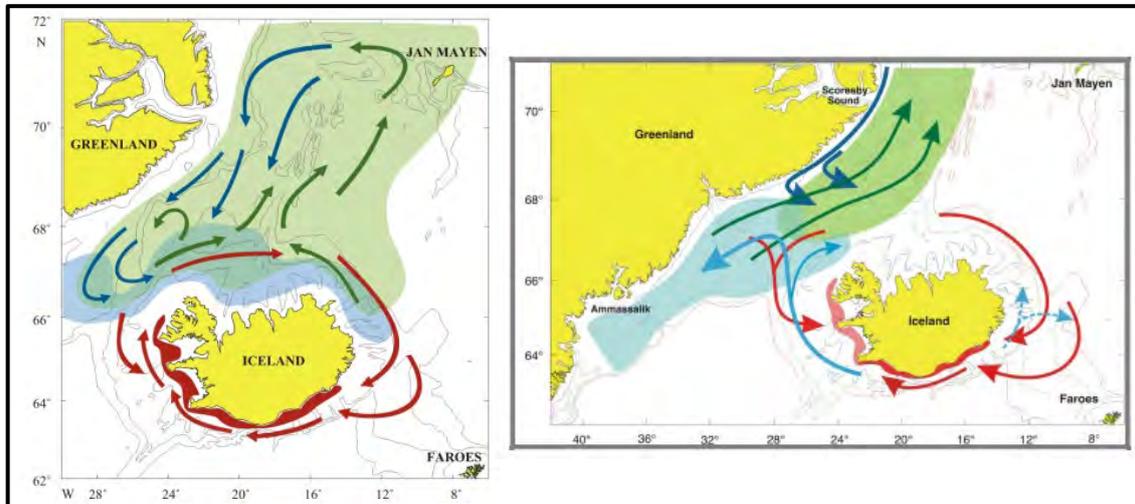


Figure 4.8. Icelandic capelin distribution and migration routes before 2002 (left panel) and after 2002 (right panel) (Figure from ICES, 2012). Areas: Red, spawning grounds; green, adult feeding area; blue, distribution and feeding area of juveniles. Arrows: green, adult feeding migrations; blue, return migrations; red, spawning migrations.

Sand lance (*Ammodytes* sp.) are important forage species that are not fished in Canadian waters (DFO, 1996). Lilly and Simpson (2000) provide distribution maps of catches of sand lance on the Grand Banks of Newfoundland in the autumn and Darbyson and Benoît (2003) show sparse catches of sand lance in the Gulf of St Lawrence. DFO (1996) reported that sand lance were captured at depths ranging between 20 to 150 m with highest concentrations at depths less than 50 m on the Scotian Shelf. Due to their behaviour of burrowing in sand sea bottoms during the day and moving into the water column to feed at night, they are difficult to capture in surveys using bottom trawls hence their distribution and status is difficult to assess (DFO, 1996). Sand lance contribute to the diet of most groundfish species, to large marine mammals such as whales and to most seal species. A recent publication by Staudinger *et al.* (2020) provides an overview of current knowledge of sand lance along the eastern seaboard of the United States.

4.3.2 Northeast Atlantic

The pelagic fish species considered as competitors or prey for salmon in the Northeast Atlantic are capelin, sandeel, sprat, redfish, blue whiting, Norwegian spring spawning herring (NSSH) and mackerel.

Large stocks of blue whiting, Norwegian spring spawning herring (NSSH), and mackerel feed in the Norwegian Sea. These species all spawn elsewhere in the spring and afterwards migrate into the Norwegian Sea and surrounding area for feeding. NSSH (spawning along the Norwegian coast) enter the area in March, while blue whiting and mackerel (spawning west of the British Isles) arrive in May and June. Two species of redfish (*Sebastes mantella* and *Sebastes norvegicus*) also spawn and feed in the Norwegian Sea.

NSSH and redfish larvae are important prey for post-smolt in the eastern Norwegian Sea in spring and early summer (Haugland *et al.*, 2006), while at least blue whiting larvae are important prey for post-smolt west of the British Isles (Haugland *et al.*, 2006).

The pelagic fish are potential competitors with post-smolt as there are both spatial and dietary overlap between the species. However, the degree of interactions between post-smolt and pelagic fish is not known in detail. The geographic distribution of NSSH, mackerel and blue whiting has varied the last decades. The geographic distribution in July based on surface trawl catches is shown in Figure 4.9.

All the pelagic species have fluctuated in abundance in the last decades. The total biomass of NSSH, mackerel and blue whiting increased from the 1980s until 2003, but has been fairly stable thereafter with a total spawning biomass around 14 million tonnes (Figure 4.10). Assessment estimates of recruitment, total stock biomass, spawning–stock biomass and annual landings are available in ICES WG-wide reports (ICES, 2018c). In addition to historic biomass estimates from the assessments, there are annual marine surveys providing snapshots of the spatial distribution and abundance in different regions. For pelagic fish in the Norwegian Sea, the IESSNS survey in May and IESSNS in July are most relevant. The IESSNS also catch salmon as bycatch in pelagic surface trawl hauls. See Section 4.6 for more information about the surveys, the data sampled and access to the data.

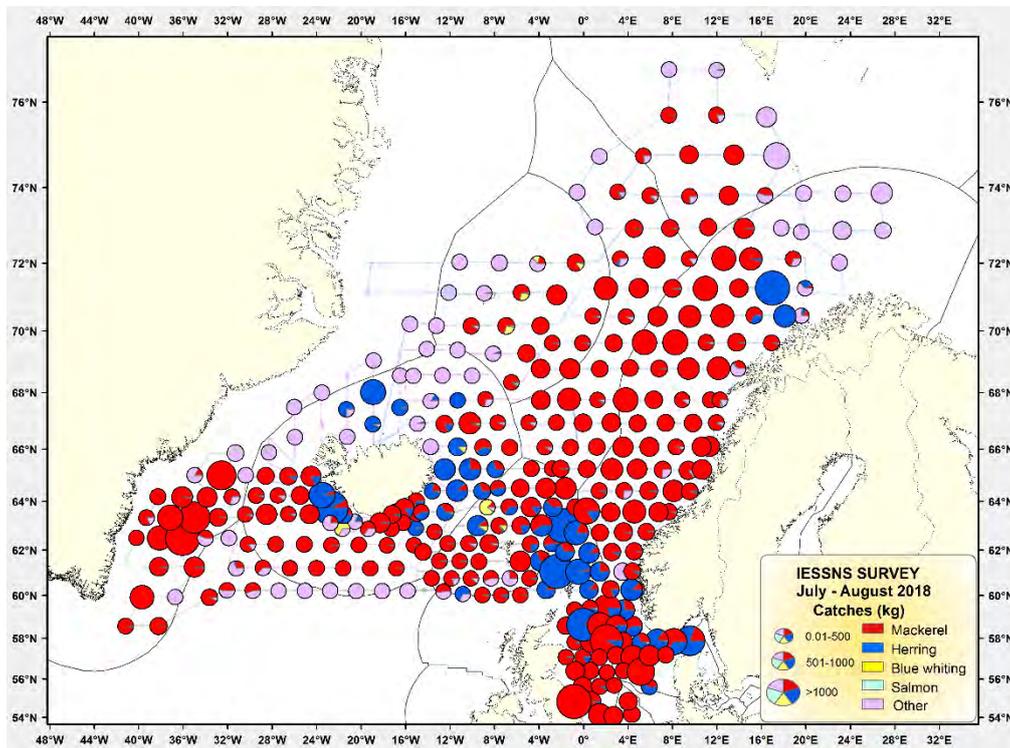


Figure 4.9. Geographic distribution of pelagic fish in the Northeast Atlantic in July 2018. Data from surface trawling during IESSNS. The abundance of blue whiting is underrepresented in the figure as blue whiting are located below the trawl depth. The herring caught during the survey vary geographically and includes North Sea herring, Icelandic herring, NSS-herring and potentially other populations.

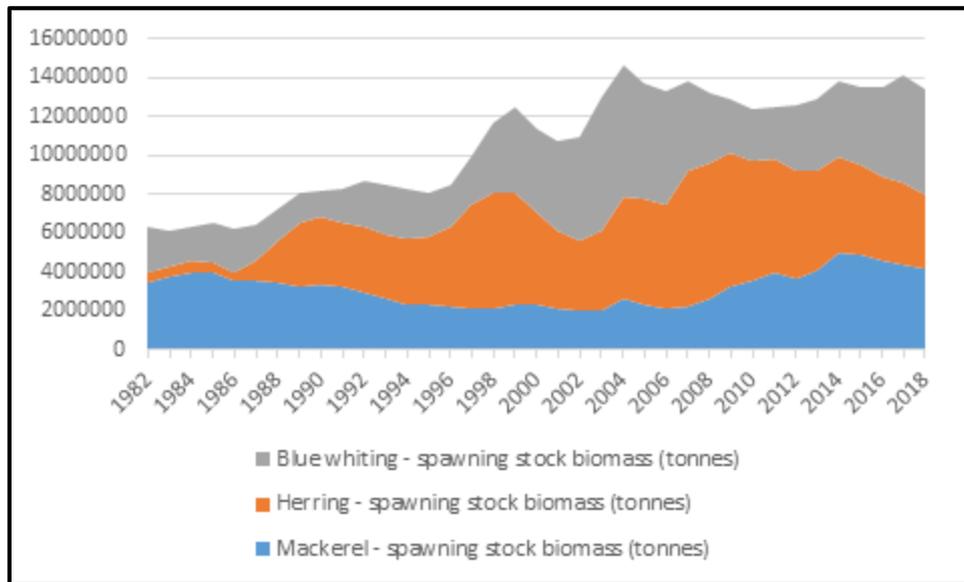


Figure 4.10. Estimated historic spawning-stock biomass (in tonnes) of mackerel, NSS-herring and blue whiting. Data from ICES (2018c) and ICES (2019c).

4.3.2.1 Norwegian spring spawning herring (NSSH)

The NSSH stock collapsed in the late 1960s but recovered again due to a good year class in 1983. Several good year classes in the 1990s brought the stock back to high levels. In the first years after the recovery, herring were feeding east in the Norwegian Sea close to the Norwegian coast during the summer (Røttingen, 1990), but gradually moved the feeding areas further north and later further west (Holst *et al.*, 2004). The peak abundance was reached in 2008–2009 with a spawning-stock biomass around 7 million tonnes. Herring spawn along the Norwegian coast and the larvae drift northwards into the fjords and into the Barents Sea. Herring larvae drifting into the Norwegian Sea are important prey for post-smolt during the summer (Haugland *et al.*, 2006). Juvenile herring are mainly found in the Barents Sea, especially in years with strong year classes.

There are data available with fine spatial resolution of herring larvae along the Norwegian coast in April for the period 1981 to 2016, but with some missing years. These data are available at the Norwegian Institute of Marine Research through collaboration.

4.3.2.2 Blue whiting

Blue whiting spawns further south (mainly west of the British Isles) than NSSH and migrates to the Norwegian Sea to feed in the summer. Juvenile blue whiting inhabits the Norwegian Sea and areas further south throughout the year. Blue whiting has large decadal variation in recruitment success and therefore also stock biomass (ICES, 2018c). It is normally found deeper than 200 m, although juvenile individuals can go all the way up to the surface (Huse *et al.*, 2012). The horizontal overlap with salmon is large since the eastern Norwegian Sea is an important feeding area for blue whiting. The diet overlap with salmon could be large since blue whiting prefers larger zooplankton (amphipods and euphausiids). ICES (2017a) reviewed the potential impacts of bycatch of Atlantic salmon in the blue whiting fishery. None of the information available to ICES suggested that salmon was a frequent bycatch in the blue whiting fishery as the main portion of the fishery occurs in February and March, a time at which there are no post-smolts at sea, and any bycatch of salmon would be of adult size that would be more detectable by the fishing fleets. Furthermore, blue whiting are mainly captured at some depth, while salmon are generally distributed in surface waters. Detection of bycatch in the May–June fishery in the Norwegian Sea would be more challenging and post-smolts may be vulnerable in that time and location (ICES, 2017a).

4.3.2.3 Mackerel

Mackerel spawns further south (mainly west of the British Isles) than NSSH and migrates to the Norwegian Sea to feed in the summer. Mackerel has increased in abundance since the early 2000s and the feeding areas has concurrently expanded north and westward (Nøttestad *et al.*, 2016). The traditional feeding areas are around the United Kingdom and Ireland, the North Sea and the southern and central Norwegian Sea. Adult mackerel are now found north to Svalbard and to the eastern side of Greenland in the west. Juvenile (< 3 years old) mackerel have historically been found in the North Sea and around the United Kingdom and Ireland, but juvenile mackerel has also moved further north along the Norwegian coast in recent years (Nøttestad *et al.*, 2018). Mackerel spatially overlap with post-smolt during the spring and summer, and can potentially be an important competitor.

4.3.2.4 Redfish (*Sebastes* sp.)

Redfish is present in the central and eastern Norwegian Sea. Adult redfish are not expected to impact salmon, but redfish larvae is an important prey for post-smolt. The abundance of beaked redfish has increased since the 1990s and the spawning stock biomass is estimated to be around 800 000 tonnes. The abundance of golden redfish has decreased since the 1990s. The spawning stock is now estimated to be around 20 000 tonnes. Given the large difference in abundance between beaked and golden redfish, it can be assumed that beaked redfish is more relevant for salmon. Both redfish species spawn live larvae in March to May along the Norwegian shelf, but with beaked redfish at deeper waters and presumably over a larger geographic areas than golden redfish. The recruitment of beaked redfish was low around 2000 but has gradually increased (Figure 4.11). Both beaked and golden redfish are handled in the Arctic fisheries working group (<http://ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/acom/2018/AFWG/00-AFWG%202018%20Report.pdf>).

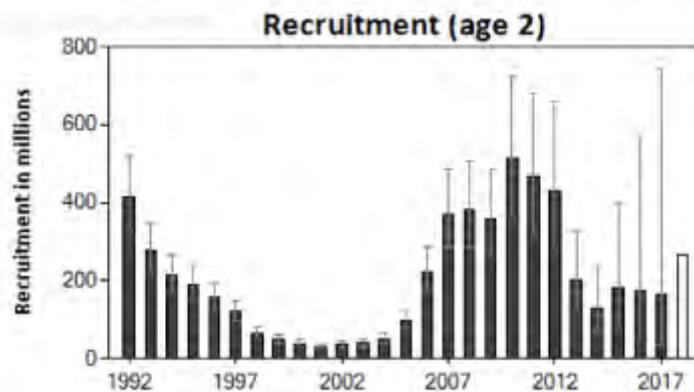


Figure 4.11. Recruitment of beaked redfish. Figure taken from the ICES advice sheet.

4.3.2.5 Sprat

Sprat (*Sprattus sprattus* Linnaeus, 1758) is a small-bodied pelagic and schooling species distributed throughout the Northeast Atlantic from as far north as the Lofoten Area to the west of the British Isles and Baltic Sea and south to Morocco (they are also found in the northern Mediterranean and Black Sea), although their core distribution can be considered the North Sea and adjacent waters (Kaschner *et al.*, 2016; Figure 4.12). They are most abundant in relatively shallow waters, including areas of low salinity, such as the Baltic. There are local populations in several Norwegian fjords. These fjord populations do not interact with the sprat in the central and southern North Sea.

The World Register of Marine Species (WoRMS) Aphia identification number for sprat is 126 425 and information on its taxonomic classification and distribution can be accessed through the

WoRMS database at <http://www.marinespecies.org/aphia.php?p=taxdetails&id=126425>. The FishBase identification number for sprat is 1357 and further information on its taxonomic classification and distribution, together with biometrics and biology, can be accessed through the FishBase website at <https://www.fishbase.se/summary/1357>.

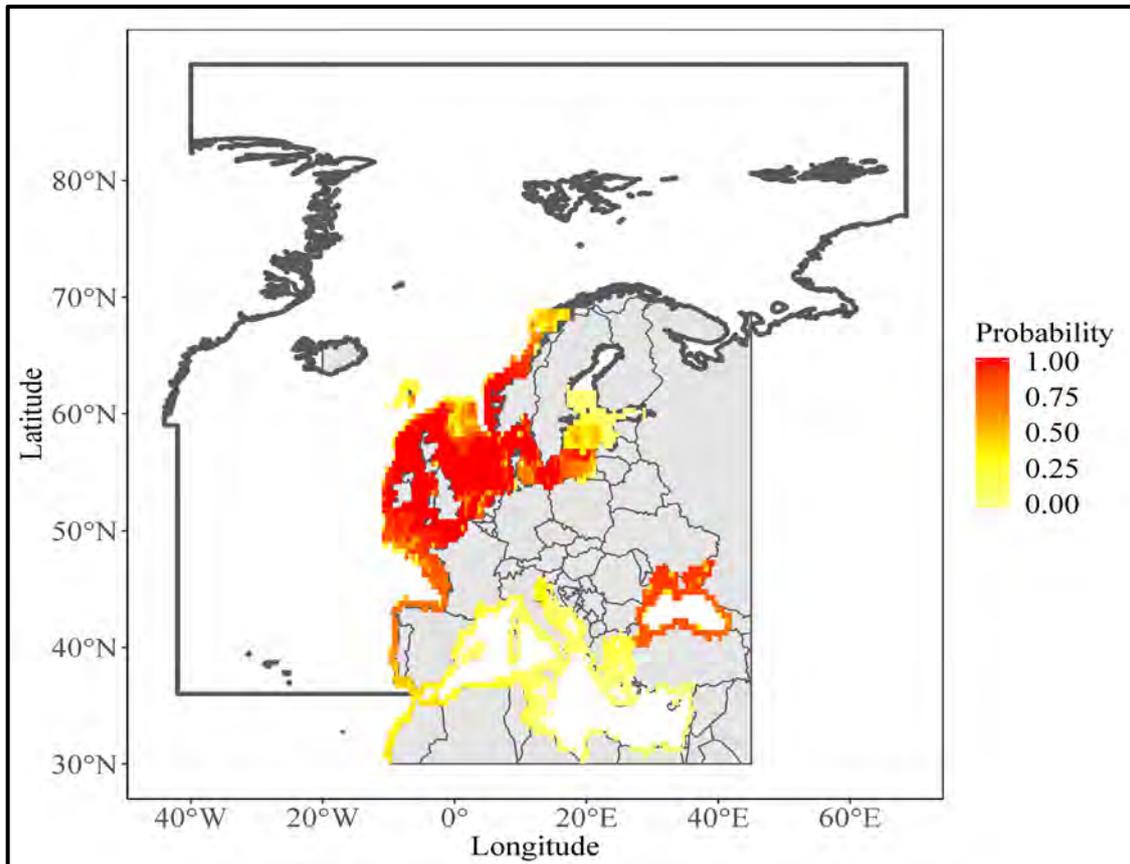


Figure 4.12. A map showing the expected native distribution of sprat (*Sprattus sprattus*) (data from Aquamaps at <https://www.aquamaps.org>). The thick line outlines the boundary of the Food and Agriculture Organisation of the United Nations (FAO) major fishing area 27.

Sprat stocks in the Food and Agriculture Organisation of the United Nations (FAO) major fishing area 27 (<http://www.fao.org/fishery/area/Area27/en>; Figure 4.12) are assessed by ICES. The stock assessment graphs and their underlying stock assessment data (SAG) can be found through the ICES website at <http://standardgraphs.ices.dk/stockList.aspx>. The longest ICES time-series for sprat are the Baltic Sea (spr.27.22–32) and Skagerrak, Kattegat and North Sea (spr.27.3a4) stocks, although the English Channel stock time-series (spr.27.7de) is of similar length, and the West of Scotland and southern Celtic Seas stock (spr.27.67a–cf–k) has been recorded for 35 years (Figure 4.13).

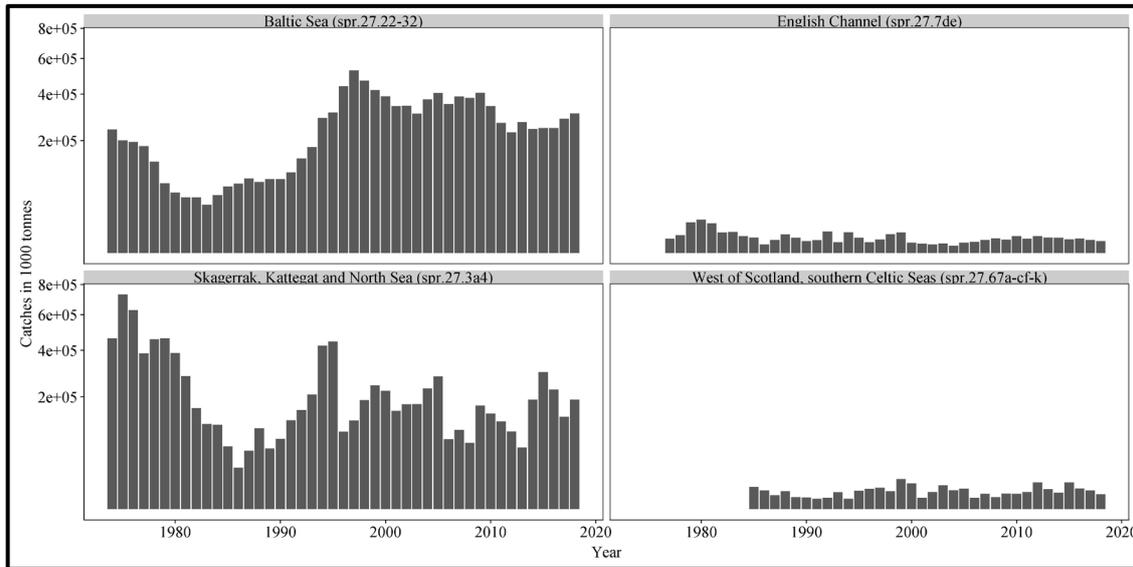


Figure 4.13. Time-series of sprat (*Sprattus sprattus*) catches from four different stocks within their native distribution. Figure generated from ICES Stock Assessment data (<http://standardgraphs.ices.dk/>).

Aside from catch data, the SAG data can provide data on Stock–Recruitment, Fishing pressure (F) and Spawning–Stock Biomass (SSB). For example, see the datasets plotted for sprat in the Baltic Sea (spr.27.22–32) <http://standardgraphs.ices.dk/ViewCharts.aspx?key=12942>.

As part of the ICES stock assessment, sprat are caught and recorded in national and international fishery-independent scientific trawls, such as the North Sea International Bottom Trawl Survey (NS-IBTS). These catches, including those of the NS-IBTS, are submitted to the ICES Database of Trawl Surveys (DATRAS; <https://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>) and can provide finer spatiotemporal resolution data – albeit less complete – than are provided for the ICES stock assessments. To the best extent possible, information entering into the DATRAS database is standardised to promote spatio-temporal consistency, e.g. ICES Working Group on International Pelagic Surveys (WGIPS). For example, Figure 4.14 shows the size and spatial distribution of sprat catches in the NS-IBTS surveys for each year in the DATRAS database.

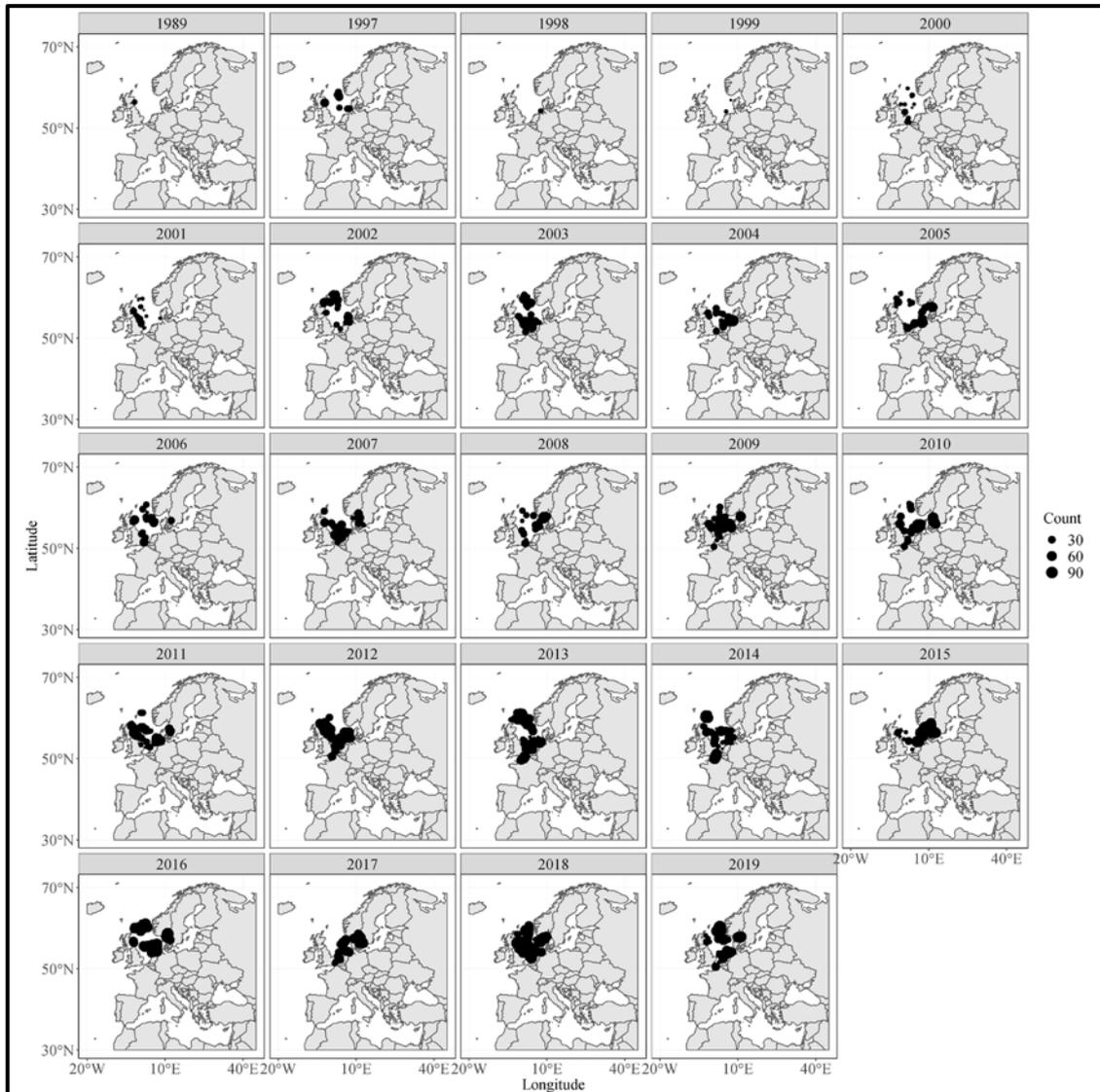


Figure 4.14. Spratt (*Sprattus sprattus*) catches recorded in the North Sea International Bottom Trawl Surveys stored in the ICES Database of Trawl Surveys database plotted in space and time. Data from ICES Datras (<https://datras.ices.dk/>).

The ICES Working Group of International Pelagic Surveys (WGIPS) is tasked with collating and reviewing acoustic survey data and methods used to assess changes in Northeast Atlantic pelagic fish stocks through time (<https://www.ices.dk/community/groups/Pages/WGIPS.aspx>). Their work is summarised in their annual meetings and reported to the ICES Herring Assessment Working Group for the Area South of 62°N (HAWG; <https://www.ices.dk/community/groups/Pages/HAWG.aspx>). All of these data are provided to the Planning Group on North-east Atlantic Pelagic Ecosystem Surveys database (PGNAPES).

Long-term datasets, such as the Baltic Sea spratt SAG data, are well-suited to studies exploring drivers of changes in spratt stock and recruitment. For example, the Baltic Sea spratt SAG data have been used to explore drivers of recruitment in spratt, including environmental variables, competitor and predator stocks, and the spratt spawning stock.

Spratt is thought to be an important food resource for many top predators in the Baltic Sea, including Atlantic salmon (Kallio-Nyberg *et al.*, 2006; Mantyniemi *et al.*, 2012) but less is known about their importance to Atlantic salmon in the North Atlantic. Although spratt are thought to be a source of Atlantic salmon post-smolt food, there is evidence to suggest that their high fatty composition can cause thiamine deficiency in Atlantic salmon and other marine species, such as

birds (Gilbert, 2018). In Atlantic salmon, thiamine deficiency can lead to elevated yolk-sac fry deformities and mortality (Gilbert, 2018), and there is evidence that this can lead to changes in salmon stocks, particularly when stocks of other potential prey, such as cod *Gadus morhua*, are low relative to sprat stocks. Sprat as a prey could also affect Atlantic salmon stocks indirectly, by influencing the population dynamics of their predators. For example, the birth rate of grey seals was significantly related to herring and sprat quality (measured as weight), which were influenced by sprat and cod abundance, as well as zooplankton biomass and plankton size.

By what mechanism sprat might affect Atlantic salmon post-smolt survival is not known. While there have been several studies exploring associations between sprat abundance or quality and Atlantic salmon post-smolt abundance and survival, none of these can evoke causation. Rather, the mechanisms remain speculative and could include sprat as suitable prey (e.g. Rikardsen and Dempson, 2011; Kallio-Nyberg *et al.*, 2006), as unsuitable prey (e.g. Gilbert, 2018) and even as a competitor for plankton and zooplankton (e.g. Haugland *et al.*, 2006) or a predator of Atlantic salmon post-smolts (e.g. Holst, 2018).

4.3.2.6 Sandeels

Sandeels (small sandeel *Ammodytes tobianus* Linneaus, 1758 and lesser sandeel *Ammodytes marinus* Raitt, 1934) are small-bodied demersal and schooling species distributed throughout the Northeast Atlantic from Murmansk to the west of the United Kingdom and Ireland, and Iceland, the Baltic Sea and south to Spain, although their core distribution can be considered the North Sea and adjacent waters (Kaschner *et al.*, 2016; Figure 4.15). They are most abundant in inshore waters, especially sandy bays and beaches where they spend a considerable amount of time buried in the soft substrate. They are also present in the inter-tidal zone and areas of low salinity, such as the Baltic Sea and estuaries.

The World Register of Marine Species (WoRMS) Aphia identification number for lesser sandeel and small sandeel is 126 751 and 126 752, respectively, and information on their taxonomic classification and distribution can be accessed through the WoRMS database. The FishBase identification number for the lesser sandeel is 37 and for the small sandeel is 38 and further information on their taxonomic classification and distribution, together with biometrics and biology, can be accessed through the FishBase website at <https://www.fishbase.se/>.

Although lesser and small sandeels are the main sandeel species in the region, there are several other less significant sandeel species, which have similar behaviours, habitats and ecological roles.

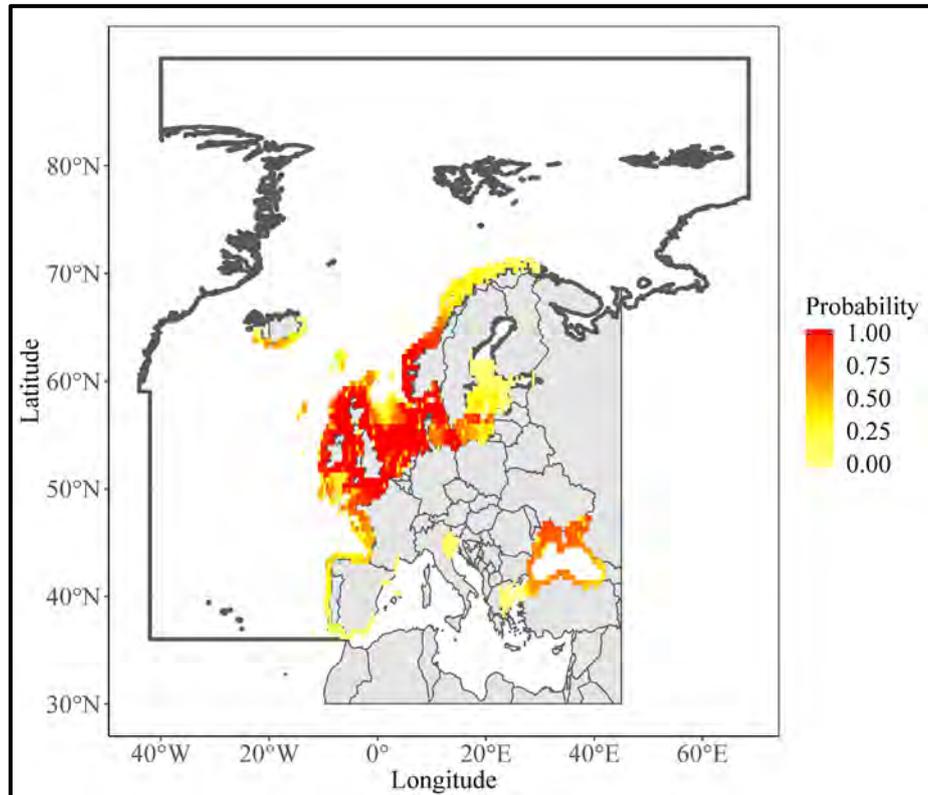


Figure 4.15. A map showing the expected native distribution of sandeels (*Ammodytes tbianus* and *Ammodytes marinus*) (data from Aquamaps at <https://www.aquamaps.org>). The thick line outlines the boundary of the Food and Agriculture Organisation of the United Nations (FAO) major fishing area 27.

Sandeel stocks in the Food and Agriculture Organisation of the United Nations (FAO) major fishing area 27 (<http://www.fao.org/fishery/area/Area27/en>; Figure 4.15) are assessed by ICES. The stock assessment graphs and their underlying stock assessment data (SAG) can be found through the ICES website at <http://standardgraphs.ices.dk/stockList.aspx>. The longest ICES time-series for sandeels is from the Central and southern North Sea and Dogger Bank (san.sa.1r) where their abundance is highest, although the Skagerrak, central and southern North Sea stock (san.sa.2r) time-series is of similar length, and the Skagerrak, northern and central North Sea stock (san.sa.3r) has been recorded for 35 years (Figure 4.16).

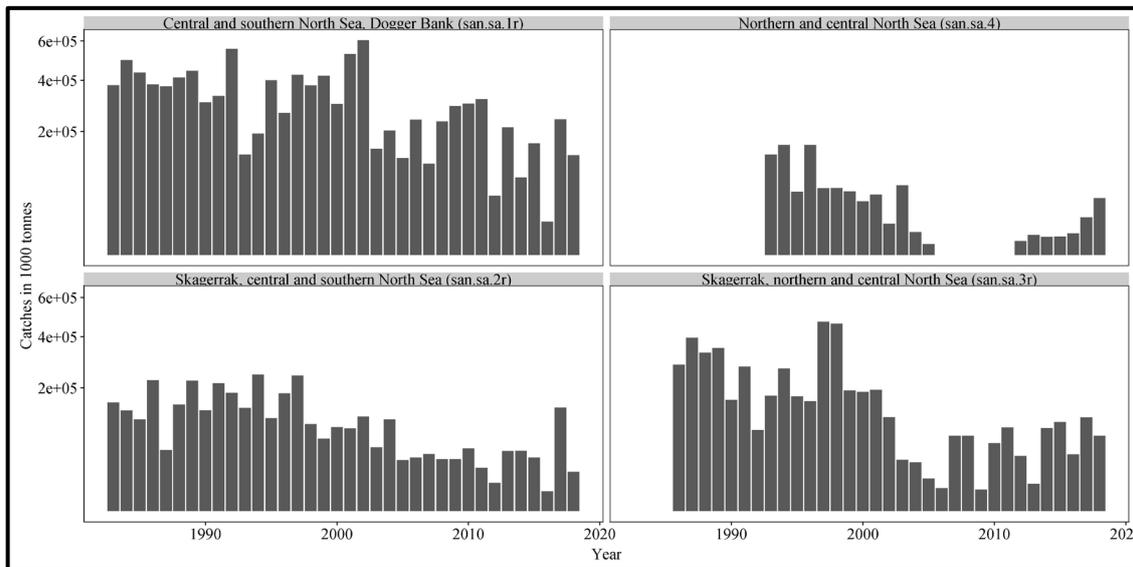


Figure 4.16. Time-series of sandeels (*Ammodytes tobianus* and *Ammodytes marinus*) catches from four different stocks within their native distribution. Figure from ICES Stock Assessment data (<http://standardgraphs.ices.dk/>).

As part of the ICES stock assessment, sandeel are caught and recorded in national and international fishery-independent scientific trawls, such as the North Sea International Bottom Trawl Survey (NS-IBTS). These catches, including those of the NS-IBTS, are submitted to the ICES Database of Trawl Surveys (DATRAS; <https://www.ices.dk/marine-data/data-portals/Pages/DATRAS.aspx>) and can provide finer spatiotemporal resolution data – albeit less complete – than are provided for the ICES stock assessments. To the best extent possible, information entering into the DATRAS database is standardised to promote spatio-temporal consistency, e.g. ICES Working Group on International Pelagic Surveys (WGIPS). For sandeels, however, the data in the DATRAS database are somewhat limited (Figure 4.17).

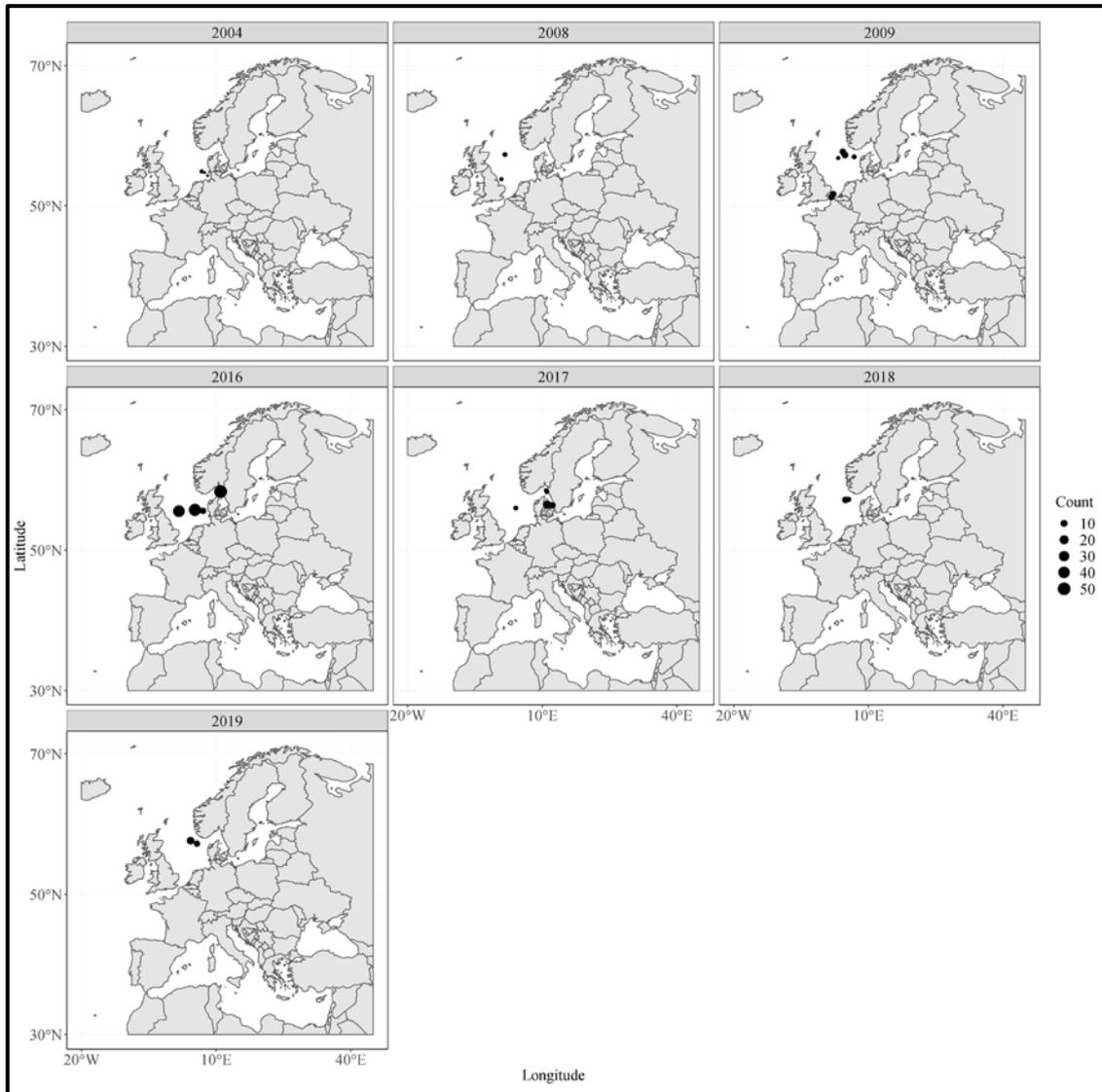


Figure 4.17. Sandeel (*Ammodytes tobianus* and *Ammodytes marinus*) catches recorded in the North Sea International Bottom Trawl Surveys stored in the ICES Database of Trawl Surveys database plotted in space and time. Data from ICES Datras (<https://datras.ices.dk/>).

Where they are present, sandeels make up a significant biomass of the pelagic fish stock. Consequently, they are routinely included in studies designed to better understand the prevailing pressures on the North Sea ecosystem, including climate change (e.g. Heath *et al.*, 2012) and fisheries management (e.g. Dankel *et al.*, 2008). Studies of sandeel stock dynamics have found considerable variation in the stock–recruitment relationship, which is thought to be influenced by top–down and bottom–up processes (Arnott and Ruxton, 2002; Frederiksen, Furness, and Wanless 2007). Sandeels are considered keystone species in the North Sea foodweb; they are the principle food for several predatory fish species, mammals and especially birds, such as the Atlantic puffin (*Fratercula arctica*) and black-legged kittiwake (*Rissa tridactyla*), the latter of which is used as an indicator of sandeel stock size. Commercially, it is landed mainly for industrial processing, including for a source of fishoil and fishmeal, the use of which is increasing sharply with growing offshore aquaculture (Davenport *et al.*, 2009).

Most studies involving sandeels explore the role of these species in the marine foodweb; for example, the reporting of a positive correlation between the recruitment of sandeels, together with six other commercially important North Sea fish stocks, and measures of primary production and copepod abundances. At the opposite end of the trophic cascade, Frederiksen *et al.* (2006)

found a positive relationship between the breeding success of four seabird populations, including the black-legged kittiwake, and the abundance of sandeels. Indeed, the relationship between black-legged kittiwakes and sandeels is thought to be sufficiently robust that kittiwake abundance has been proposed as an indicator of sandeel abundance, particularly age-1 sandeels, although this is still a topic of considerable debate (Eerkes-Medrano *et al.*, 2017).

Arnott and Ruxton (2002), Frederiksen *et al.* (2007) and MacDonald *et al.* (2019) have all explored the role of environmental variables, among other variables, on the recruitment of sandeels. Overall, these have concluded that the recruitment of sandeels is associated with the dynamics of lower trophic levels, including primary producers, and the environmental variables that govern their abundances, such as the North Atlantic Oscillation and sea temperature. For example, MacDonald *et al.* (2019) used data collected from the east coast of Scotland to demonstrate convincingly that there has been a substantial decline in age-1 sandeels in that region, which can be attributed to their poor growth as evidenced in recent declines in age-0 sandeel lengths.

Data sources

- World Register of Marine Species (WoRMS) (<http://www.marinespecies.org/>)
- FishBase (<https://www.fishbase.se/>)
- International Council for the Exploration of the Seas (ICES) (<http://www.ices.dk/>)
- ICES Stock assessment data <http://standardgraphs.ices.dk/>
- DATRAS database <https://datras.ices.dk/>
- FishSource <https://www.fishsource.org/>

4.3.3 Characteristics of pelagic fish community

Changes in size-at-age and condition factor have been addressed for blue whiting (Trenkel *et al.*, 2015), mackerel (Jansen *et al.*, 2015; Olafsdottir *et al.*, 2016) and Norwegian spring spawning herring NSSH (Homrum *et al.*, 2016). Intraspecific competition affects individual growth of all three species. Length-at-age of mackerel shows a decreasing trend since 2005, while blue whiting shows large variation in the last decades as the stock biomass has fluctuated greatly. There is variation but no temporal trend in length-at-age for NSSH. Aggregated data on length-at-age for these three species are available back to 1982 (Figure 4.18) through the ICES Working Group on Integrated Ecosystem Assessments for the Norwegian Sea (WGINOR) (ICES, 2019d). There is geographic variation in the size-at-age and condition factor for mackerel where the length and condition factor increase west and north of the traditional feeding areas in the Norwegian Sea. This is explained by length-dependent swimming speed and spatial variation in prey availability (Nøttestad *et al.*, 1999; Olafsdottir *et al.*, 2019). Juvenile herring are normally located east in the Norwegian Sea, not far from the entrance to the Barents Sea. Older herring are typically found further west in the Norwegian Sea and towards Iceland (Holst *et al.*, 2004). The geographic variation in size and condition factor of blue whiting has not been studied in detail.

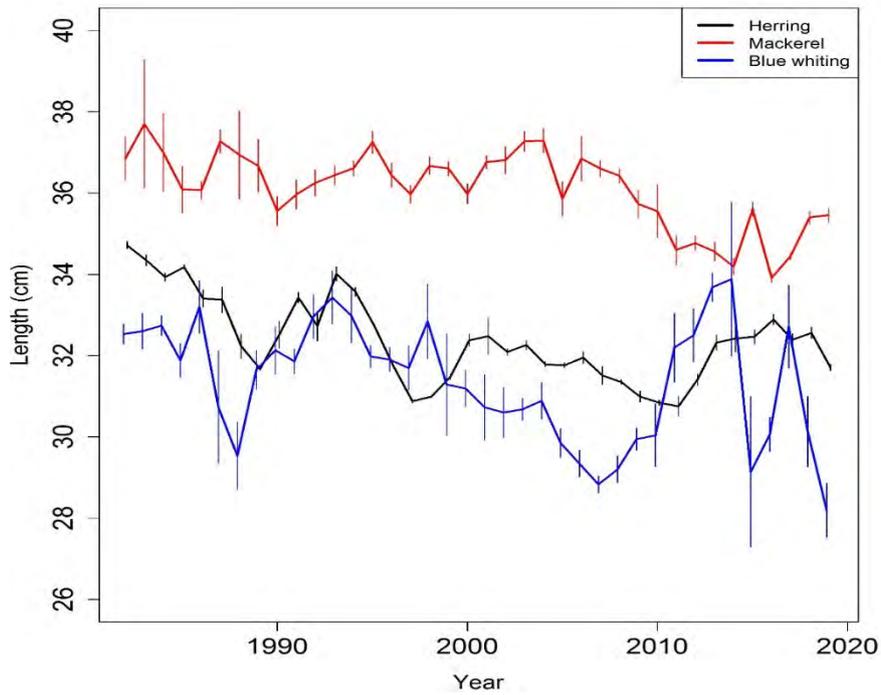


Figure 4.18. Length-at-age for six year old pelagic fish in the Northeast Atlantic. Data from ICES (2019d) (WGINOR).

DATRAS data also include additional data that are not accessible through the SAG data, such as the length, age and gender of individual fish caught in each trawl. Figure 4.19 plots the length-at-age for a sample of female, male and unknown sprat caught in the NS-IBTS and stored in DATRAS. Because this information is stored by trawl, these data can also be considered in space and time. For example, Figure 4.20 shows the length-at-age for the ages 1 to 6 years sprat through time.

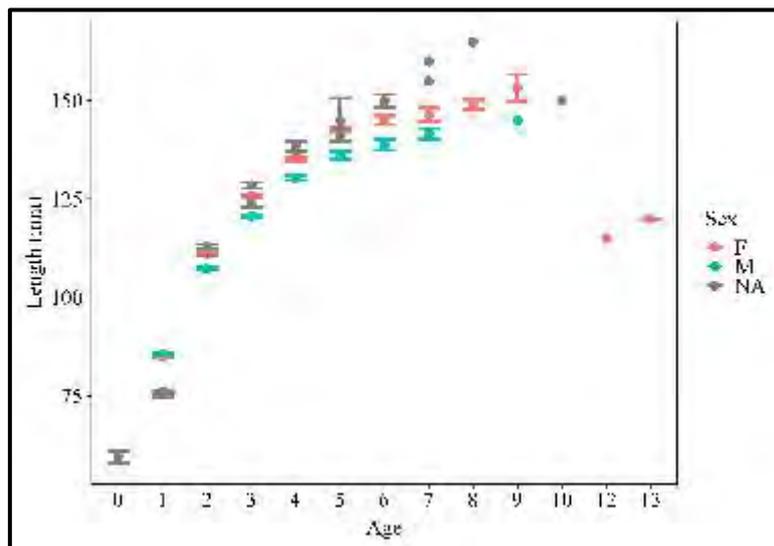


Figure 4.19. Sprat (*Sprattus sprattus*) length-at-age plot split by sex and including individuals of unknown sex (NA). Data from ICES Datras (<https://datras.ices.dk/>).

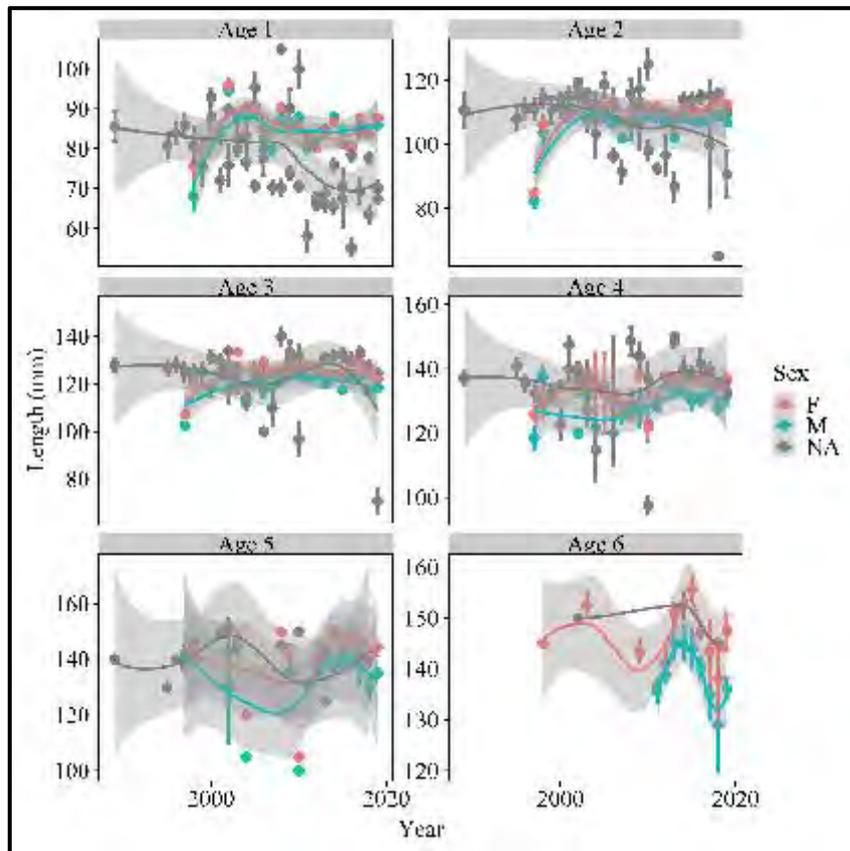


Figure 4.20. Sprat (*Sprattus sprattus*) length-at-age plots by time and split by sex and including individuals of unknown sex (NA). Only ages 1:6 are shown because data are too few for other ages. Regression lines are locally-weighted (loess) regression smooths with standard error bands. Data from ICES Datras (<https://datras.ices.dk/>).

For sandeels, these data are again limited, although Figure 4.21 shows a length-at-age plot for a sample of female, male and unknown sandeel caught in the NS-IBTS and stored in DATRAS. Outside of the ICES data, there are other data collected on sandeels in the commercial sector. Among the most comprehensive datasets appears to come from a longstanding agreement between the Danish Fishermen's Association and the Technical University of Denmark, although another important dataset is collected in Norway. Such commercial data appear to be available, perhaps through collaboration, and have been used in several studies. For example, Rindorf *et al.* (2016) explored characteristics of spatially separated populations and found differences in their weights and age structures. It seems that these data are combined with ICES data and summarised by the ICES Working Group on Sandeels (WKSAN or WKSAND), who hold and publish findings from occasional "Benchmark Workshops", and as part of the ICES Herring Assessment Working Group for the Area South of 62°N (HAWG; <https://www.ices.dk/community/groups/Pages/HAWG.aspx>).

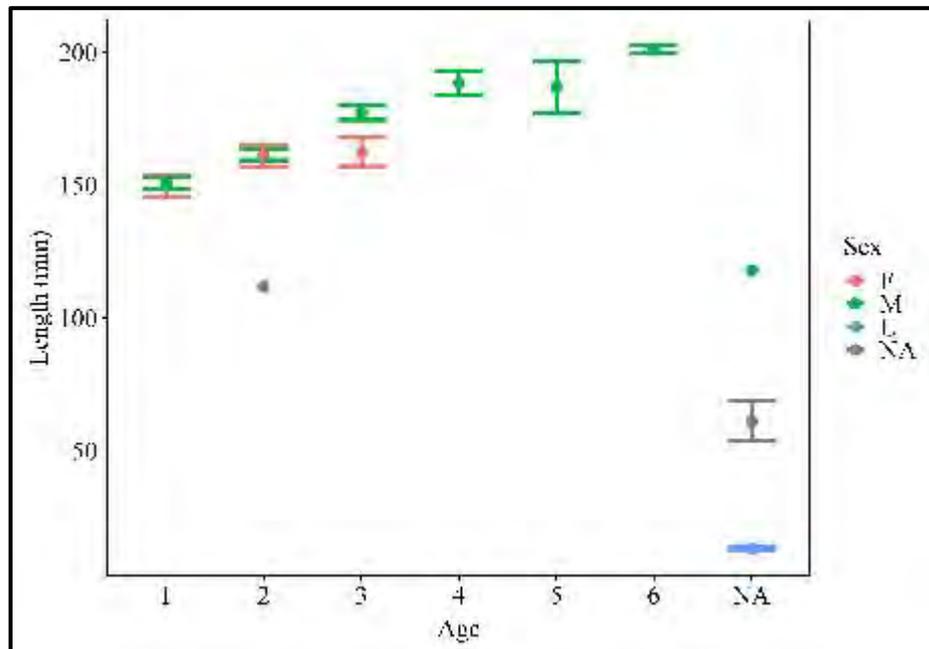


Figure 4.21. Sandeel (*Ammodytes tobianus* and *Ammodytes marinus*) length-at-age plot split by sex and including individuals of unknown sex (NA). Data from ICES Datras (<https://datras.ices.dk/>).

4.4 Predator community

Smolts leaving freshwater and entering the marine phase of the life cycle are particularly vulnerable to predation due to their relatively small body size (Friedland *et al.*, 2012). Predation on smolts during the first months at sea is probably the most important source of mortality impacting the abundance of salmon populations (Hansen *et al.*, 2003).

There is a diverse community of marine predators that reportedly can eat Atlantic salmon in freshwater and at sea (Cairns, 2006). The vulnerability of salmon to predator groups changes as salmon grow and migrate away from coastal areas to the high seas (Cairns and Reddin, 2000). Seabirds are assumed to be able to feed on the smallest range of salmon body sizes and marine mammals on the larger body types (Table 4.4.1; Cairns and Reddin, 2000). Seal species can take marine phase salmon of all sizes but seabirds are restricted to smaller prey. Large fish including sharks and bluefin tuna can consume large-bodied salmon (Lacroix, 2014; Strøm *et al.*, 2019).

Predation rates on salmon are difficult to quantify and alternate approaches are required (Cairns, 2001). In the Northwest Atlantic, Atlantic salmon remains have been identified from stomachs and intestinal tracts of grey seal, harp seal, harbour seal, common murre and northern gannets (Cairns and Reddin, 2000; Montevecchi *et al.*, 2002).

Table 4.1. Range of fish prey sizes consumed by seal and seabird species as summarized by Cairns and Reddin (2000).

Predator species	Fish prey size range (length cm)
Grey seal	5–60
Harbour seal	5–55
Harp seal	2–55
Hooded seal	10–50
Seabirds	
Northern fulmar	2–30
Great black-backed gull	< 40
Murre	< 20
Gannet	? (25 +)

Limitations

- Sampling of predators may not be representative of the period of potential overlap between salmon and the predator. Sampling has often focused on nearshore areas with easy access to animals. Large areas of the high seas are not sampled.
- It is challenging to obtain sufficient sample sizes to detect with some reliability infrequent prey items in individual animals.
- Traditional diet studies from predator stomachs rely on the identification of hard body parts (otoliths) to identify prey, and this technique therefore requires the obtainment of the head of the fish that has been consumed by the predator. Belly biting by marine mammals (seals) has been reported in the literature and therefore larger fish may not necessarily be identifiable from gut contents if the head is not consumed.

4.4.1 Seabirds

There is a large literature on seabirds and no expert in this field was present at WKSAlmon. The following information summarizes a limited number of publications from a preliminary search of the literature using a search logic including the terms “seabirds” and “North Atlantic”.

Seabirds in the North Atlantic represent a diverse range of species and ecological types (pelagic surface-feeding, pelagic diving, coastal benthic-feeding, etc.). Barrett *et al.* (2006) summarized and compared the seasonal composition, abundance, and biomass of seabirds between the Northeast (ICES region) and Northwest (NAFO region) Atlantic fisheries regions. Of particular interest is the finding that seabirds were more abundant by number in the Northwest Atlantic, but the biomass was greater in the Northeast Atlantic. This disparity is due to the seabird fauna in the Northwest Atlantic being dominated by smaller and abundant planktivores, in contrast to the Northeast Atlantic avian communities which are dominated by large alcids (mainly guillemots and Atlantic puffins), which feed primarily on small schooling fish (sandeels, capelin, young herring and gadoids, and sprat). Barrett *et al.* (2006) also summarize relative abundances by season and ICES/NAFO areas, which is important when considering potential predators / competitors of Atlantic salmon.

Eveillard-Buchoux *et al.* (2017), in an analysis specifically of cliff-nesting seabirds in Europe, reported that species richness, population numbers and geographic distribution had remained stable over the approximately 20-year interval of the study. The authors provide maps of species distributions and relative changes for the European countries, including the Faroes, Iceland and eastern Greenland. Estimates of abundance of 30 seabirds in the Northeast Atlantic are provided in Frederiksen (2010). The status, trends and threats for 17 species of seabirds in Norway are reported in Fauchald *et al.* (2015). Barrett *et al.* (2017) report specifically on the northward extension of the distribution of northern gannet in Norway. The Joint Nature Conservation Committee (2020) reports on the abundance and trends of seabirds for the United Kingdom and Ireland, for the period 1968 to 2018; they also show a marked increase in abundance of northern gannet.

Merkel *et al.* (2019) report on estimates of abundance of seabirds in the wintering area of the southwest coast of Greenland and compare estimates from 1999 to those obtained in March 2017.

For the Northwest Atlantic, Gaston *et al.* (2009) review monitoring from the 1970s onwards for six oceanographic regions to assess population trends among Canadian seabirds. The authors report that the trends at Arctic colonies have been decoupled from those at southern colonies around Newfoundland and in the Gulf of St Lawrence, especially since the major cold-water event of the early 1990s which affected the availability of important forage fish species. Changes in food availability for wintering seabirds in Newfoundland waters are also described; murre diets in winter were largely dominated by capelin in the 1950s, Arctic cod, capelin, and euphausiids in the 1980s, capelin and Arctic Cod less abundant and euphausiids replaced by amphipods in the 1990s. Dramatic shifts in diet related to the 1990s cold-water event is illustrated from monitoring of diet of Northern Gannet at the Funk Islands Newfoundland colony (see below). Gjerdrum *et al.* (2012) describe seabird monitoring efforts in the Northwest Atlantic obtained from ships of opportunity for the purpose of providing information on the abundance, distribution and trends of seabirds occurring offshore, to identify important marine habitat sites, and to characterize threats to seabirds in their marine habitat.

Recently, Waggitt *et al.* (2020) used species distribution models and available data from cetacean and seabird surveys to derive distribution maps for 12 seabird species at 10 km and monthly resolution in the Northeast Atlantic. The distribution maps encompassed the areas of the exclusive economic zones of Norway, United Kingdom, Ireland, Sweden, Denmark, Germany, The Netherlands, Belgium, Atlantic coast of France and of northwest Spain. Waggitt *et al.* (2020) show distribution maps for the example months January and June; distribution maps are available via the Dryad Digital Repository (Waggitt *et al.* 2019. Data from: Distribution maps of cetacean and seabird populations in the Northeast Atlantic. Dryad Digital Repository, <https://doi.org/10.5061/dryad.mw6m905sz>).

4.4.1.1 Northern gannet

The northern gannet (*Morus bassanus*) is a large seabird with the greatest potential to feed on post-smolt extending over the period from early migration and into the fall (Cairns and Reddin, 2000). There are a number of gannet colonies in both the Northwest and Northeast Atlantic. In the Northwest Atlantic, the colonies are mainly found within the Gulf of St Lawrence and the northeast coast of Newfoundland (Gjerdrum *et al.*, 2012; Chardine *et al.*, 2013). In the Northeast Atlantic, the colonies extend from Iceland in the west, and the northern part of France to the northern tip of Norway in the eastern portion of the Northeast Atlantic (Barrett *et al.*, 2017).

Gannets have a restricted distribution to continental shelf waters. The species tends to breed at high densities at colonies within foraging distances < 225 km but that varies with the colony (Montevecchi *et al.*, 2002; Garthe *et al.*, 2007). In the Northwest Atlantic, post-breeding gannets forage in the Gulf of St Lawrence, nearshore waters off Labrador, and the east coast of Newfoundland while in winter, the birds are more dispersed along the eastern seaboard of North

America from New England south to Florida, and west along the Gulf of Mexico coast to Texas (Gjerdrum *et al.*, 2012). Gannets in the Northeast Atlantic overwinter in more southern areas, off West Africa, the Mediterranean Sea and Bay of Biscay (Kubetzki *et al.*, 2009).

In the Northwest Atlantic, gannet abundance at the breeding colonies has been continually increasing; passing from 40 thousand pairs in 1984 to 57 000 in 1994, 78 000 in 1999, 102 000 in 2004 to 117 000 in 2009, increases of 3 to 6% per annum (Chardine *et al.*, 2013). Gannets are also increasing in abundance and distribution in the Northeast Atlantic. JNCC (2020) reported a sustained increase in the UK gannet population, passing from 113 000 pairs in 1969/1970, 175 000 in 1984/1985, 218 000 apparently occupied sites (AON) in 2003/2004 to reach 293 161 AON between 2013–2015. Northern gannet along the Norwegian coast has increased drastically. See example from the isle of Runde (Figure 4.22).

Data of seabird counts along the Norwegian coast is coordinated by the Norwegian Institute for Nature Research (NINA) and is available at:

- <http://www2.nina.no/seapop/seapophtml/>.

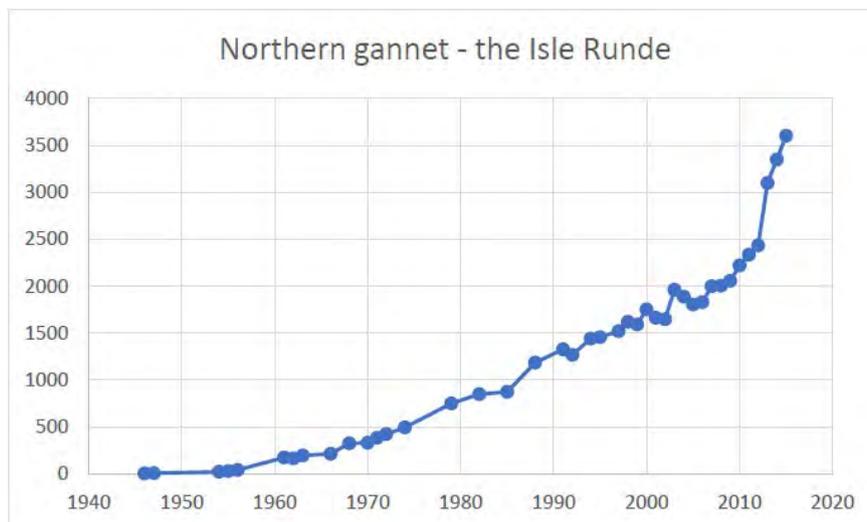


Figure 4.22. Counts of northern gannet at the isle of Runde at the Norwegian coast in the southeastern Norwegian Sea. Data available as open access at NINA's webpages.

Gannet diets monitored in breeding colonies in the Northwest Atlantic are diverse and include capelin, herring, mackerel, sandeels, Atlantic saury, squid, and Atlantic salmon post-smolts (Garthe *et al.*, 2007). Salmon post-smolts were sampled from gannets at Funk Island (Newfoundland, Canada) in August of sizes ranging from 18 to 28 cm; the largest fish prey consumed in that study was mackerel, ranging in size from 34 to 42 cm in length (Montevecchi *et al.*, 2002). There was a large annual variation in the indices of consumption of post-smolt salmon, the variability was in part attributed to a radical shift from warm water (mackerel, saury, squid) to cold water (capelin, herring) pelagic dietary prey driven by physical and biological change on the Newfoundland and Labrador Shelf (Montevecchi *et al.*, 2002; Gaston *et al.*, 2009). Montevecchi *et al.* (2002) concluded that gannet predation on post-smolts could influence the population dynamics of Atlantic salmon in the Northwest Atlantic because of a large potential overlap in the foraging range of gannet colonies for a substantial period between smolt migration from rivers to mid-autumn.

4.4.2 Marine mammals

Atlantic salmon are vulnerable to predation by many species of marine mammals (Middlemas *et al.*, 2003). Marine mammals including pinnipeds (seals and sea lions) and cetaceans (whales and dolphins) have been reported aggregating in river mouths, estuaries and coastal waters to prey on emigrating smolts and returning adult salmon (Halfyard *et al.*, 2012; Thorstad *et al.*, 2012; Lothian *et al.*, 2018). Smolts leaving freshwater and entering the marine phase of the life cycle are particularly vulnerable to predation due to their relatively small body size (Friedland *et al.*, 2012). Adult salmon are most at risk of predation by marine mammals when returning from sea to spawn in rivers (Butler *et al.*, 2008). However, interactions between marine mammals and salmon populations are not well understood because predation offshore is difficult to detect with little known beyond estuaries (Middlemas *et al.*, 2003), and salmon often comprise a small portion of the diet of marine mammals compared to other prey species (Andersen *et al.*, 2004).

Information on the distribution and abundance of marine mammal predators of Atlantic salmon is limited and subject to high uncertainty. Marine mammals are notoriously difficult to study because they have elusive behaviours (e.g. extensive migrations or deep diving) and are widely distributed in remote areas of the world, which poses logistical and economic challenges for assessing the status of their populations (Gerber *et al.*, 2000; Taylor *et al.*, 2007). Abundance estimates are lacking for many marine mammal populations. Accurately estimating abundance trends is difficult in many cases (Taylor *et al.*, 2007), and available abundance time-series often include irregular survey intervals. Furthermore, differences in the methods and coverage of surveys have hindered the assessment of population status (Jewell *et al.*, 2012). However, abundance data have become more widely available through the population monitoring that has accompanied increased conservation efforts over the last fifty years (Magera *et al.*, 2013). Data on the distribution and abundance of marine mammals are collated and assessed by several organisations for management and conservation purposes (e.g. the North Atlantic Marine Mammal Commission (NAMMCO) and International Union for Conservation of Nature (IUCN)).

Historical time-series for many marine mammal species are also available through the ICES Working Group on Marine Mammals (WGMME) reports, such as the 2019 report at:

- https://www.ices.dk/sites/pub/Publication%20Reports/Expert%20Group%20Report/EPDSG/2019/WGMME/wgmme_2019.pdf.

A recent special issue of *Aquatic Conservation* celebrating the 40th anniversary of the Sea Mammal Research Unit at the University of St Andrews, Scotland, includes several potentially useful data sources and is available at:

- <https://onlinelibrary.wiley.com/toc/10990755/2019/29/S1>.

Aside from historical data, a recent study by Waggitt *et al.* (2020) used species distribution models and available data from cetacean and seabird surveys to derive distribution maps for 12 cetacean species at 10 km and monthly resolution in the Northeast Atlantic. The distribution maps encompassed the areas of the exclusive economic zones of Norway, United Kingdom, Ireland, Sweden, Denmark, Germany, the Netherlands, Belgium, Atlantic coast of France and of northwest Spain. Waggitt *et al.* (2020) show distribution maps for the example months January and June; distribution maps are available via the Dryad Digital Repository (Waggitt *et al.*, 2019). Data from: Distribution maps of cetacean and seabird populations in the Northeast Atlantic. Dryad Digital Repository, <https://doi.org/10.5061/dryad.mw6m905sz>.

Further details on individual species, including contemporary population estimates, are summarized below.

4.4.2.1 Seals (Phocidae)

Concerns have been expressed over the impacts of seal predation on the recovery of salmon stocks and the interests of salmon fisheries (Butler *et al.*, 2008, 2011; Lacroix, 2014). Smaller salmon stocks and populations units, such as early-running spring salmon, are particularly vulnerable to seal predation (Butler *et al.*, 2006). Although seals mainly prey on other fish species (Andersen *et al.*, 2004), they have been reported feeding on salmon around river mouths and in estuaries (Middlemas *et al.*, 2003; Sharples *et al.*, 2009), and taking salmon from fishing nets (Jounela *et al.*, 2006). It has been suggested that predation might be limited to a relatively small portion of seals specialising in targeting salmon or foraging around fishing nets (Graham *et al.*, 2011; Harris *et al.*, 2014). However, mortalities of salmon due to seal predation has fuelled conflict between conservationists and fisheries stakeholders (Butler *et al.*, 2011). Seals are perceived to have contributed to declines in salmon abundance, leading to calls from fisheries stakeholders for seal predation to be controlled in the vicinity of salmon fisheries (Butler *et al.*, 2006, 2008, 2011; Graham *et al.*, 2009).

Grey seal (*Halichoerus grypus*)

The grey seal inhabits the temperate waters of the North Atlantic (Figure 4.23; Hall and Russell, 2018). Three grey seal populations are recognised: (1) the Northeast Atlantic; (2) Northwest Atlantic; and (3) Baltic Sea populations (Bonner, 1981). The Northwest Atlantic population is found along the Northeastern United States and southern Canada (Lesage and Hammill, 2001). The Northeast Atlantic population is centred on the British Isles and Ireland, ranging from Iceland, the Faroes, eastward along the coast of France, and north to Norway and the Kola Peninsula (Haug *et al.*, 1994a). The Baltic Sea population is concentrated in the central Baltic area (Karlsson and Helander, 2005).

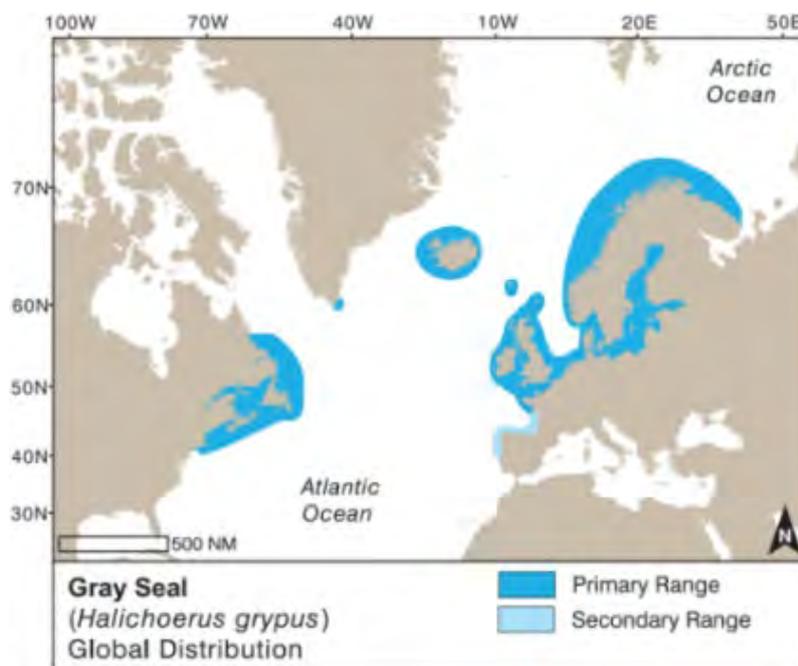


Figure 4.23. Grey seal distribution (from Hall and Russell, 2018).

Grey seals are generalist predators that migrate long distances (≤ 100 km) offshore to forage for a wide variety of fish and invertebrates, mainly in demersal and benthic habitats (Bowen *et al.*, 1993; Jones *et al.*, 2015). Their diet varies seasonally and geographically in response to changes in prey availability (Beck *et al.*, 2007). They typically consume sandeels, gadoids, redfish, and flat-fish species (Hammill *et al.*, 2014; Nilssen, *et al.*, 2019). Although Atlantic salmon can comprise a

substantial portion of their diet when smolts and adults move through estuaries (Boyle *et al.*, 1990; Sharples *et al.*, 2009), predation by grey seals is thought to have less severe impacts on salmon populations than other sources of mortality in the marine environment (Middlemas *et al.*, 2003).

Assessments of the abundance of grey seal populations in the North Atlantic are undertaken by NAMMCO. The abundance of grey seal populations is estimated using counts of adults and pups obtained from visual surveys on land at haul-out sites during the autumn breeding season (Nilssen and Haug, 2007). In total, the abundance of grey seal populations is estimated to be 650 000 animals in the North Atlantic, with the largest numbers present along the east coasts of Canada and the USA (NAMMCO, 2016; DFO, 2017). All three grey seal populations have increased in abundance and expanded their distribution over the last thirty years. The abundance of Norwegian grey seal populations is estimated to have increased to 8740 animals (Øigård *et al.*, 2012). In Britain, abundance has more than doubled, with grey seal populations estimated to number 95 200 animals (SCOS, 2015). Around Iceland, however, population abundance has decreased to about 4200 grey seals (ICES, 2017b). Approximately 1000 to 2000 grey seals are found in the Faroes Islands (Mikkelsen *et al.*, 2002). No recent abundance estimates are available for Russia, but grey seals were estimated to number 3400 in the 1990s (Haug *et al.*, 1994a). In the Northwest Atlantic, grey seal population abundance is estimated to be over 420 000 in Canada (DFO, 2017) and 3300 in the USA (Wood *et al.*, 2007; NAMMCO, 2016). The Baltic Sea population is comprised of about 33 000 greys seals (Harding *et al.*, 2007).

Harbour seals (*Phoca vitulina*)

Harbour seals are the most widely distributed pinniped species, ranging from the temperate to subarctic waters along the eastern and western coasts of the North Atlantic and the North Pacific Oceans (Figure 4.24; Teilmann and Galatius, 2018). In the North Atlantic, they range from France to Svalbard in the east, over to Iceland and Greenland in the central Atlantic. Along the western Atlantic coast, harbour seals are found from New Jersey in the USA and north to Baffin Island in Canada. They are a relatively sedentary pinniped species that undertake limited seasonal migrations (Thompson *et al.*, 1996), rarely moving distances of more than 50 km from the coast (Jones *et al.*, 2015). However, harbour seals are capable of migrating large distances (65–520 km) to find suitable haul-out sites over the course of the year due to seasonal changes in prey availability, movement to breeding areas and avoidance of areas with heavy ice cover (Thompson, 1993; Lesage *et al.*, 2004; Cunningham *et al.*, 2009). Fourteen genetically distinct populations are recognised in the North Atlantic: (1) the USA/Canada; (2) Iceland; (3) Norwegian west coast; (4) Ireland-Scotland; (5) east coast of England; (6) English Channel area; (7) Wadden Sea; (8) Limfjord; (9) Skagerrak; (10) Kattegat; (11) Greenland; (12) Svalbard; (13) West Baltic; and (14) East Baltic/Baltic proper populations (Andersen and Olsen, 2010; Andersen *et al.*, 2011).

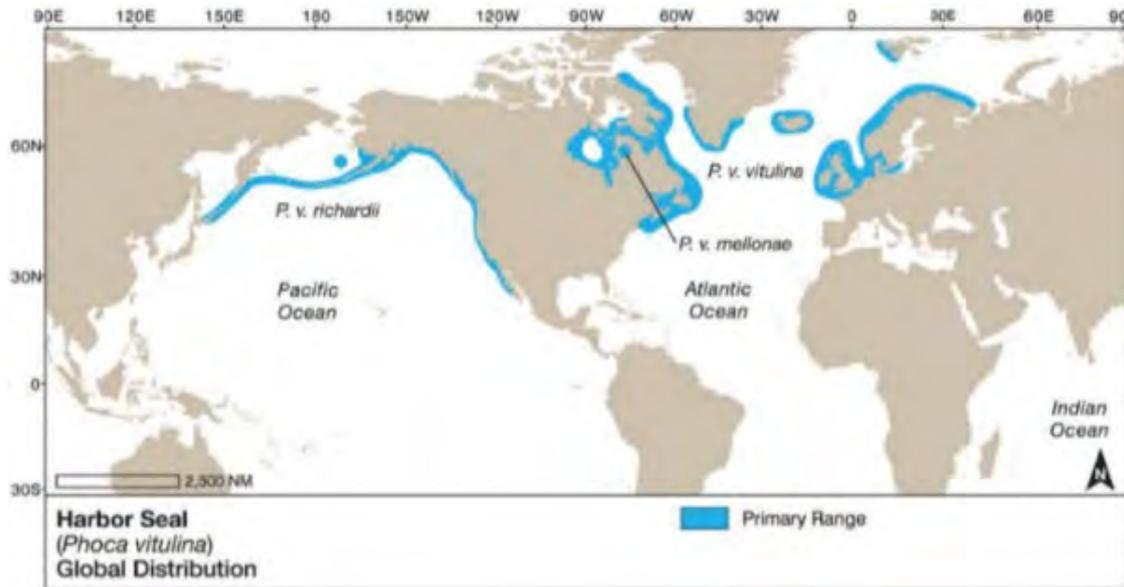


Figure 4.24. Harbour seal distribution (figure reproduced from Teilmann and Galatius, 2018).

As opportunistic predators, harbour seals feed on a wide range of fish, cephalopods and crustaceans (Bowen and Harrison, 1996; Tollit *et al.*, 1998; Anderson *et al.*, 2004). Their diet varies by season and from region to region due to changes in prey abundance (Hall *et al.*, 1998; Ramasco *et al.*, 2017). Harbour seals mainly feed on sandeels, gadoids, herring and flatfish species (Tollit and Thompson, 1996; Hall *et al.*, 1998; Sharples *et al.*, 2009). However, harbour seals are known to exploit seasonal increases in prey abundance by aggregating around river mouths and in estuaries to prey on emigrating smolts and adult salmon returning to spawn in rivers (Middlemas *et al.*, 2006).

The abundance of harbour seals is often estimated using counts of adults and pups obtained from visual surveys on land at haul-out sites during the autumn moulting season (NAMMCO, 2016). Harbour seal populations are estimated to total 200 000 animals in the North Atlantic (NAMMCO, 2016). Fluctuations in the abundance of harbour seal populations have resulted from outbreaks of the phocine distemper virus and anthropogenic factors such as hunting, by-catch, habitat destruction and climate change (Härkönen *et al.*, 2006; Kovacs and Lydersen, 2008). Declines in the abundance of harbour seal populations have been observed in many areas throughout their range, particularly along eastern Canada and northern Britain (Thompson *et al.*, 2001; Bowen *et al.*, 2003; Lonergan *et al.* 2007). Recent estimates of the abundance of harbour seal populations are 8307 off Norway, 12 000 in Iceland, less than 100 around Greenland, 500 along Russia, 19 000 in Sweden and Denmark, 29 100 off the UK, 17 000 in Canada and 75 834 around the USA (NAMMCO, 2016).

Harp seal (*Pagophilus groenlandicus*)

The harp seal is found throughout the North Atlantic and Arctic Oceans from Northern Russia in the east to Newfoundland and the Gulf of St Lawrence in Canada in the West (Figure 4.25; Lavigne, 2018). They are highly migratory, moving large distances (≤ 4000 km) to maintain contact with prey species (Lawson *et al.*, 1995; Bowen and Siniff, 1999). Their annual migration cycle is complex, moving south in the winter, breeding in early spring and moving northward towards feeding grounds in the summer, following the advance and retreat of pack ice (Haug *et al.*, 1994b; Folkow *et al.*, 2004). Three distinct harp seal populations have been identified in the North Atlantic based on differences in morphological, behavioural and genetic characteristics: (1) the Northwest Atlantic; (2) Greenland Sea; and (3) Barents/White Sea populations (Lavigne, 2018).

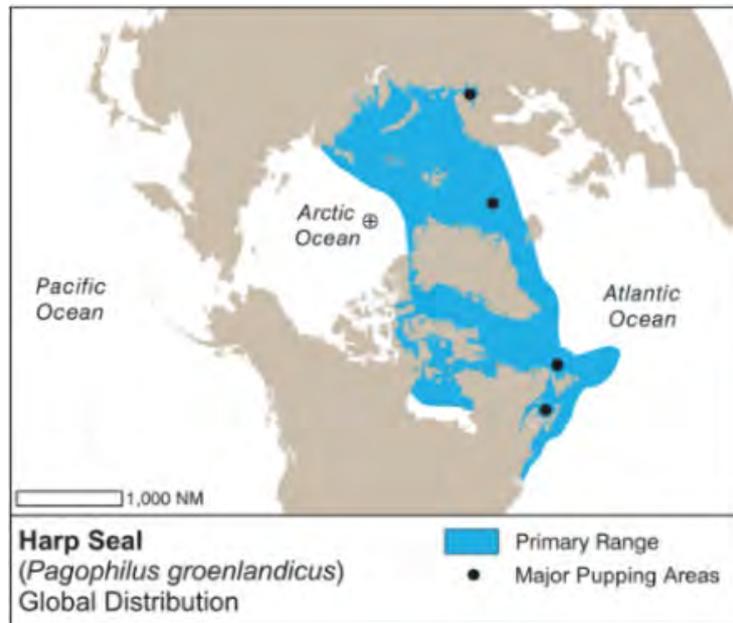


Figure 4.25. Harp seal distribution (figure reproduced from Lavigne, 2018).

Harp seals feed on a wide range of fish and crustaceans, with over 130 prey species reported in their diet (Wallace and Lawson, 1997). Although harp seals exhibit a preference for particular prey species, the composition of their diet is strongly influenced by local prey abundance (Lindstrøm *et al.*, 1998). Much of their diet is comprised of capelin, Arctic cod (*Boreogadus saida*) and Atlantic cod (*Gadus morhua*), Greenland halibut (*Reinhardtius hippoglossoides*), herring and redfish, and various crustaceans including amphipods (Lawson *et al.*, 1995; Hammill *et al.*, 2005). However, Atlantic salmon are reported to be an important component of the diet of harp seals (Tucker *et al.*, 2009), particularly for the Northwest Atlantic population (Hammill and Stenson, 2000).

Precise estimates of the abundance of harp seals are difficult to obtain given their widespread distribution and complex migration cycle. The abundance of harp seals is estimated using counts of pups born on pack ice during winter obtained from a combination of aerial surveys, photographic methods, mark-recapture studies and population models (Hammill *et al.*, 2011, 2015; Øigård *et al.*, 2014). In total, the abundance of harp seal populations is estimated to be over 9 million animals worldwide (Lavigne, 2018). The Northwest Atlantic population is the largest, with an estimated abundance of 7.4 million harp seals (Hammill *et al.*, 2015). In contrast, the Greenland Sea population is the smallest, estimated to comprise around 627 000 harp seals (ICES, 2013a; Øigård *et al.* 2014). The Barents/White Sea population is moderately sized, including an estimated 1.4 million seals (ICES, 2013a). Both the Greenland Sea and Barents/White Sea populations have extended their distribution range southwards into Norwegian coastal waters (Haug *et al.*, 1991), harming commercial fisheries by reducing catches and damaging fishing gear (Nilssen *et al.*, 1992; Haug and Nilssen, 1995).

4.4.2.2 Cetaceans

Cetaceans are apex predators that have important roles in the top-down regulation of marine foodwebs (Katona and Whitehead, 1988). Each year, cetaceans are estimated to consume between 250 and 450 million tonnes of fish, cephalopods and crustaceans worldwide (Tamura and Ohsumi, 2000). There is substantial overlap in the species consumed by cetaceans and those targeted by commercial fisheries (Evans, 2018). As a result, substantial competition exists between cetaceans and fisheries for commercially important species (Tamura, 2003). Reports of cetaceans

feeding on Atlantic salmon in river mouths, estuaries, coastal waters and the open ocean have been documented (Vester and Hammerschmidt, 2013; Samarra *et al.*, 2018; Strøm *et al.*, 2019).

Killer whale (*Orcinus orca*)

The killer whale is the most widely distributed cetacean species in the world (Figure 4.26; Ford, 2018). They are found in all oceans and most seas, but most commonly in coastal temperate waters, particularly in areas of high marine productivity (Forney *et al.*, 2006). In the North Atlantic, their range extends from the east coast of Canada to Norwegian waters. Killer whales are abundant off Norway, common around Iceland and the Faroe Islands, and occasionally observed off Scotland (Forney *et al.*, 2006). Three distinct populations are recognised: 1) population A mainly preys on herring but can switch their diet between fish and marine mammals (Foote *et al.*, 2009; Vongraven and Bisther, 2014; Cosentino, 2015); (2) population B feeds on fish and mammals (Foote *et al.*, 2009; Foote *et al.*, 2011); and (3) population C primarily eats fish, including bluefin tuna (*Thunnus thynnus*) (de Bruyn *et al.*, 2013; Vongraven and Bisther, 2014).

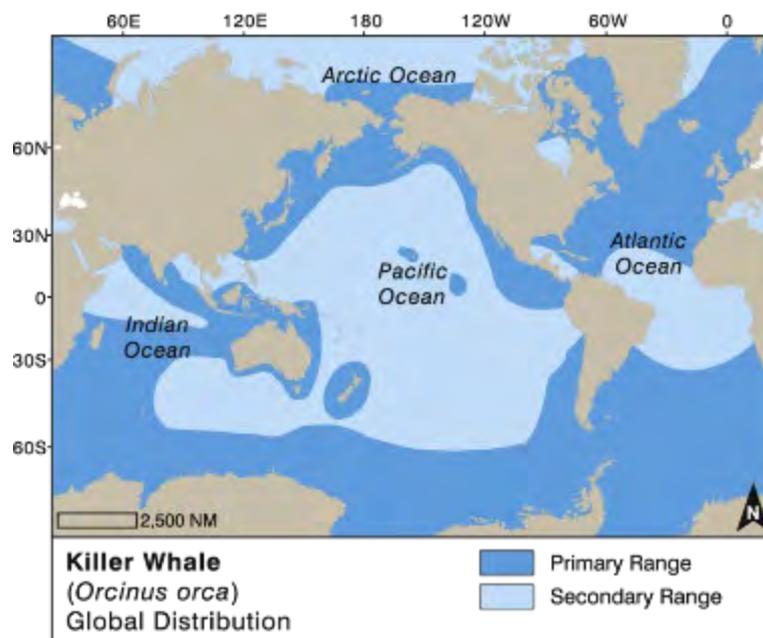


Figure 4.26. Killer whale distribution. (Figure reproduced from Ford, 2018).

Killer whales feed on a diverse array of prey species, including many species of fish, invertebrates, mammals, turtles and birds (Ford *et al.*, 2009). However, different populations of killer whale have specialised foraging behaviours and diets (Ford, 2018). A well-known example is the resident, transient and offshore killer whale populations that coexist in the eastern North Pacific (Ford *et al.*, 2000). Resident killer whales feed exclusively on fish and squid, while transient killer whales are specialists at preying on marine mammals (Ford *et al.*, 1998; Saulitis *et al.*, 2005; Ford and Ellis, 2006). The survival of resident killer whales depends on the abundance of chinook salmon (*Oncorhynchus tshawytscha*) in coastal waters (Ford *et al.*, 2009). The ecology of offshore killer whales is less well understood, but the diet likely comprises fish and marine mammals (Herman *et al.*, 2005).

Limited information on the foraging ecology of killer whales is available in the North Atlantic. Killer whales move long distances to track the seasonal movements of herring and mackerel stocks to Norwegian and Icelandic coastal waters (Luque *et al.*, 2006; Foote *et al.*, 2010). There have been reports of killer whales feeding on Atlantic salmon in the waters around Norway and Iceland (Vester and Hammerschmidt, 2013; Samarra *et al.*, 2018). Diet studies indicate that killer whales mostly feed on marine mammals in Scottish inshore waters (Bolt *et al.*, 2009). In Irish

waters, killer whales mainly consume fish, including ocean sunfish (*Mola mola*), mullet (*Chelon labrosus*) and salmon (Ryan and Wilson, 2003; Ryan and Holmes, 2012). In British waters, herring and salmon are important prey species (Evans, 1988). Less is known about the diet of killer whales in the Northwest Atlantic, but they appear to feed on fish and marine mammals (Lawson and Stevens, 2014).

Providing reliable estimates of the abundance of killer whales is challenging given their widespread distribution throughout the world and scarcity in some regions (Forney and Wade, 2006). Killer whale abundance is estimated using counts of sightings obtained from shipboard or aerial surveys (NAMMCO, 2016). The North Atlantic Sightings Surveys (NASS and TNASS) have collected information on the distribution and abundance of killer whales in the North Atlantic since 1987 (Pike *et al.*, 2009). In total, the abundance of killer whale populations is estimated to be around 15 000 in the North Atlantic (NAMMCO, 2016), with larger numbers found in the Northwest than Northeast region (Lawson and Stevens, 2014). No reliable estimate of the abundance of killer whales is available for the east coast of Canada (NAMMCO, 2016). Killer whales are not abundant in the waters around Greenland (Ugarte *et al.*, 2013). In Icelandic waters, abundance estimates range from 4000 to 6850 animals (Gunnlaugsson and Sigurjónsson, 1990). There are an estimated 7000 killer whales in Norwegian waters (Øien, 1993).

Bottlenose dolphin (*Tursiops truncatus*)

Bottlenose dolphins are widely distributed throughout the world's oceans in temperate and tropical waters (Figure 4.27; Wells and Scot, 2018). Different bottlenose dolphin populations display morphological and behavioural differentiation (Oudejans *et al.*, 2015). Inshore populations tend to be smaller and lighter in colour than offshore forms (Richards *et al.*, 2013; Louis *et al.*, 2014). For the most part, bottlenose dolphin populations have not been clearly defined in the North Atlantic. In the Northwest Atlantic, five distinct populations have been identified: (1) northern migratory; (2) southern migratory; (3) South Carolina/Georgia; (4) northern and central Florida; and (5) western North Atlantic offshore populations (Hayes *et al.*, 2019). All five populations are characterised by differences in abundance, migratory patterns and genetic composition (Toth *et al.*, 2012). In the Northeast Atlantic, population structure is less well understood. Bottlenose dolphins are found off the coasts of Portugal, Spain, France, the UK, and Ireland (Hammond *et al.*, 2013). Around the UK, bottlenose dolphins are patchy distributed with resident populations in Cardigan Bay in Wales and the Moray Firth in north-east Scotland. Three genetically distinct populations are present in Irish waters: (1) a resident population in the Shannon Estuary; (2) a coastal population in the waters off western Ireland; and (3) an offshore population (Oudejans *et al.*, 2015).

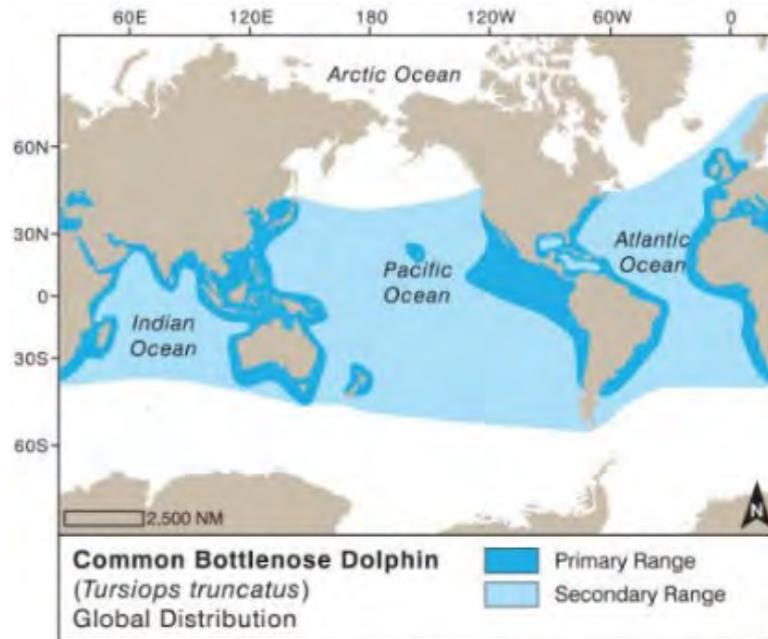


Figure 4.27. Common bottlenose dolphin distribution (figure reproduced from Wells and Scot, 2018).

Bottlenose dolphins feed on a wide variety of prey species, including fish, crustaceans, cephalopods, and small elasmobranchs (Cockcroft and Ross, 1990; Gannon and Waples, 2004). Different bottlenose dolphin populations have specialised foraging behaviours and diets depending on prey availability and habitat conditions (Sargeant *et al.*, 2005). Inshore populations primarily feed on fish, while offshore populations consume more squid (Walker *et al.*, 1999). They move with concentrations of food, entering bays and estuaries in pursuit of prey, and taking advantage of high tides to access shallow coastal areas (Mellink and Orozco-Meyer, 2006). Atlantic salmon can comprise a substantial portion of the diet of bottlenose dolphins at certain times of the year (Hastie *et al.*, 2004; Ryan *et al.*, 2010). Returns of adult salmon are linked to the seasonal movements of bottlenose dolphins into inshore waters (Ingram and Rogan, 2002; Weir and Stockin, 2001; Stockin *et al.*, 2006). For example, resident bottlenose dolphin populations in the Moray Firth (Scotland) and the Shannon Estuary (Ireland) move inshore to feed on salmon when adults return to spawn in rivers during spring and summer (Santos *et al.*, 2001; Ingram and Rogan, 2002; Barker and Berrow, 2016).

Determining the abundance of bottlenose dolphins is challenging because they are a widely distributed marine mammal that often live in large pods (Shane *et al.*, 1986). The abundance of bottlenose dolphin populations is estimated using counts of individuals sighted from shipboard and/or aerial surveys, and mark-recapture studies (Wilson *et al.*, 1999; Speakman *et al.*, 2010). The global abundance of bottlenose dolphins is estimated to be 600 000 animals (Wells and Scot, 2018). Resident bottlenose dolphin populations have provided the most detailed abundance information. Around the UK, the size of resident bottlenose dolphin populations is estimated to be around 250 in Cardigan Bay, Wales and 130 in the Moray Firth, Scotland (Wilson *et al.*, 1999). In Irish waters, the resident population in the Shannon Estuary is estimated to be about 110 animals (Berrow *et al.*, 2012).

Harbour porpoise (*Phocoena phocoena*)

The harbour porpoise is broadly distributed throughout the coastal waters of the North Pacific, North Atlantic and the Black Sea (Figure 4.28; Borge and Tolley, 2018). They are a small cetacean species that mainly inhabits fjords, bays, estuaries and harbours (Reijnders and Lankester, 1990). Although harbour porpoises commonly reside in coastal waters for extended periods of time, they have been known to venture up rivers and migrate long distances ($\geq 10\,000$ km) to deeper

offshore waters in search of prey (Nielsen *et al.*, 2013). Fourteen populations or sub-populations have been proposed in the North Atlantic: (1) the Gulf of Maine/Bay of Fundy; (2) Gulf of St Lawrence; (3) Newfoundland and Labrador; (4) West Greenland; (5) Iceland; (6) Faroe Islands; (7) Norway and Barents Sea; (8) North Sea; (9) Kattegat and adjacent waters; (10) Baltic Sea; (11) Ireland and Western British Isles; (12) Iberia and Bay of Biscay; (13) Northwest Africa; and (14) Black Sea populations (Donovan and Bjørge, 1995; Andersen, 2003).

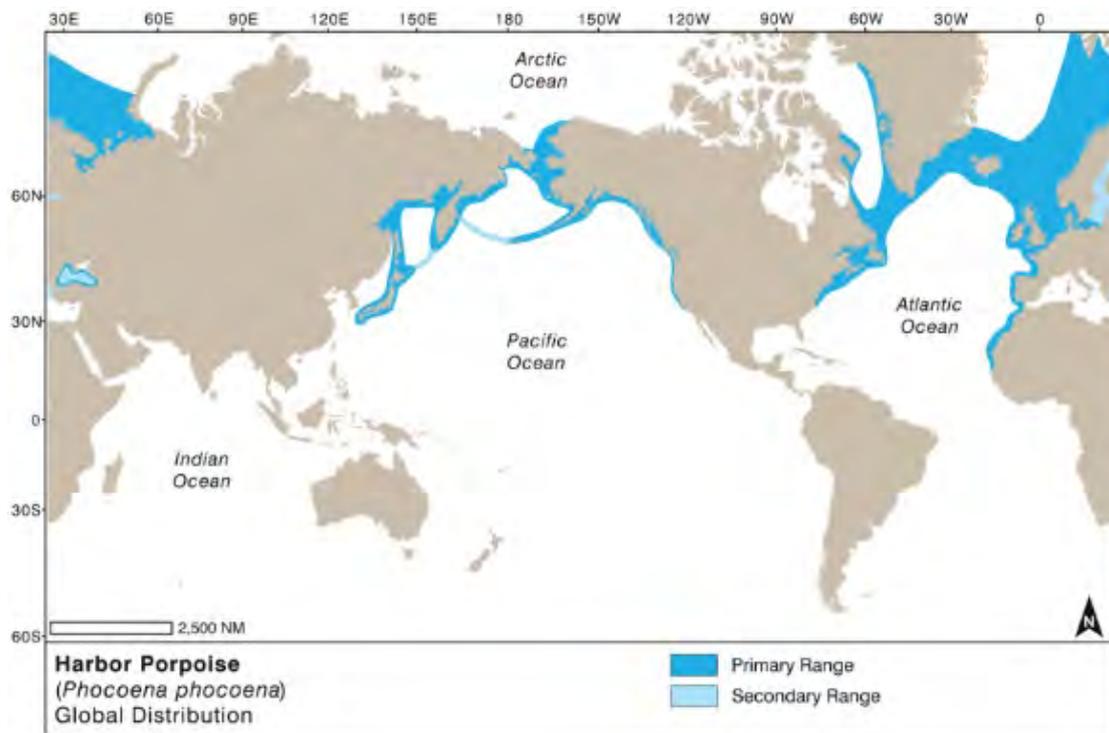


Figure 4.28. Harbour porpoise distribution (figure reproduced from Bjørge and Tolley, 2018).

Harbour porpoise feed on a variety of fish, cephalopods and crustaceans in both benthic and pelagic habitats (Aarefjord *et al.*, 1995; Víkingsson *et al.*, 2003; Spitz *et al.*, 2006). Their diet varies seasonally and geographically depending on prey abundance (Santos and Pierce, 2003). Small pelagic fish such as herring, mackerel, capelin, sprat, whiting and sand eels are their main prey species (Aarefjord *et al.*, 1995; Santos and Peirce, 2003; Mahfouz *et al.*, 2017). There has long been a perception that harbour porpoises prey on Atlantic salmon, particularly around fishing nets (Macintyre 1934; Berry, 1935; Rae, 1965). Predation by harbour porpoises has been suspected of damaging adult salmon returning to spawn in rivers (Thompson and Mackay, 1999). However, no evidence of salmon in the stomach contents of harbour porpoises has been identified in the Northeast Atlantic (Santos and Peirce, 2003).

Obtaining reliable estimates of the abundance of harbour porpoises is particularly challenging because this cetacean species is difficult to count accurately due to their relatively small size, lack of visible surface behaviour, and widespread inshore distribution (NAMMCO, 2016). The abundance of harbour porpoises is estimated using counts of sightings obtained from shipboard and/or aerial surveys (Hammond *et al.*, 2002; Scheidat *et al.*, 2008). The global population abundance of harbour porpoises is estimated to be at least 700 000 (Bjørge and Tolley, 2018). Nearly half (~ 335 000) of the harbour porpoises are found in the North Sea (Hammond *et al.*, 2002). Other large populations are present around the Gulf of Maine and Bay of Fundy (~ 80 000 animals), the mid-southwest coast of Greenland (~ 33 000 animals) and the Gulf of St Lawrence (~27 000 animals) in Canada (Bjørge and Donovan, 1995; Bjørge and Tolley, 2018). The distribution of harbour porpoises has changed over the past decades (Camphuysen, 2004; Thomsen *et*

al., 2006). Harbour porpoises have shifted their distribution southward along the Dutch coast, through the southern North Sea and into the English Channel (Peschko *et al.*, 2016; Hammond *et al.*, 2017). These shifts in porpoise distribution might have resulted from changes in prey availability (Camphuysen, 2004; MacLeod *et al.*, 2007).

4.4.3 Fish

The recent studies of archival transmitting tags placed on salmon kelts has provided insights into the fish community which consume large-bodied Atlantic salmon (Lacroix, 2014; Strom *et al.*, 2019). These include a number of elasmobranchs (porbeagle shark, blue shark) and large pelagic fish (swordfish, Atlantic bluefin tuna).

Information on trends in abundance, distribution both spatially and seasonally of these species was not compiled in this report.

4.5 Commercial pelagic fisheries and bycatch of salmon

Most commercial fisheries targeting large demersal or pelagic fish stocks in the Northeast Atlantic have occasional bycatch of salmon. However, the frequency of such bycatch varies considerably between fisheries, areas and seasons. Bycatch of salmon has been reported from bottom trawl, bottom longline and purse seine fisheries (Rosseland, 1971; ICES, 2004b, 2005b, 2017a). Some of the fish caught in coastal areas may be escaped farmed salmon. The number of salmon caught in bottom trawling, Danish seines and bottom gillnets are most likely low due to the depths at which these gears operate.

In 2002, NASCO asked ICES to “provide an estimate of the bycatch of salmon post-smolts in the pelagic fisheries based on the scientific information currently available”. ICES reviewed the available information on the catch rates of salmon and of mackerel from surveys carried out in the Norwegian Sea during salmon research cruises in 2001–2002 and developed an approach to estimate post-smolt bycatches in the commercial mackerel fisheries (ICES, 2003). Estimates of potential bycatch were very wide, from only a few specimens to as high as just under one million. A specific Study Group on Bycatches of Salmon in Pelagic Fisheries (SGBYSAL) was convened in March 2004, with the task of collating and analysing available information on bycatch of salmon in pelagic fisheries.

The ICES study group (SGBYSAL; ICES, 2004b) examined analytical methods to estimate post-smolt bycatch in commercial fisheries using the Norwegian Sea mackerel fishery as a case study. Based on quarterly catch data, the overlap between post-smolts and the fisheries in the Norwegian Sea appeared high, but the absence of disaggregated data (by week and statistical rectangle), impeded an assessment of the true overlap of post-smolts with the fisheries. The Study Group concluded that the best method presently available would be based on direct observation on board commercial fishing vessels according to agreed sampling protocols. These observations would then need to be combined with disaggregated catch data for week and standard rectangle for the areas in question.

The second study group on bycatch (ICES, 2005b) continued the work and their conclusions, combined with those of ICES (2004b) were:

- Fisheries for mackerel, herring and blue whiting are the principal fisheries of concern, although fisheries for horse mackerel and capelin should also be considered.
- One major drawback for evaluating the potential of salmon being intercepted by pelagic fisheries is that their distribution throughout the year and migration routes in certain areas still are relatively poorly known.

- Using prior knowledge of smolt distribution and the spatial information of the fisheries and depth profiles, the fishery with the highest probability of capture is the surface pelagic trawl fishery.
- Information on salmon movements at sea were used to indicate that the period of potential overlap in the Norwegian Sea mackerel fishery was probably limited to a relatively short period, centred on the latter half of June and early July.
- A review of available information on detection of salmon during screening of catches indicated small but consistently occurring bycatches, mainly in various types of trawl fisheries.
- Some examples of potential overlap in time and space are shown in the distribution of post-smolts and salmon and commercial pelagic fisheries in the Norwegian Sea.
- The detection of salmon bycatch in these fisheries can be challenging. Adult salmon should be relatively easy to distinguish from the pelagic fish even in large catches. Apart from handling the fish individually, it would be very difficult to distinguish the post-smolts from the other species because of their colour and size. If the salmon are substantially smaller than the target species they risk being covered by a larger fish, and if similar in size they will resemble many of the pelagic species due to the change in coloration.
- Reported bycatch rates of salmon were in the range of 0 to 57 fish per 1000 tonnes of pelagic fish catch, dependent on season and fishery (ICES, 2004a, 2004b).
- Considering the extent of the industrial pelagic fisheries in the Northeast Atlantic, the number of salmon caught in the pelagic fishery, either with purse seine or pelagic trawling, could potentially be high (ICES, 2004b).

In Iceland, the data collected from the mackerel fishery with pelagic midwater trawls operating during the summer months within the Icelandic EEZ suggest that the proportion of salmon in the mackerel catches has been relatively stable over the time period of observations, from 4.7 to 6.2 salmon per 1000 tonnes of mackerel (ICES, 2014). Observations from the Faroe Islands in 2011 indicated that the bycatch was most important in May and declined rapidly in season (Table 4.2).

Table 4.2. Estimates of salmon bycatch in the Faroese mackerel fishery in 2011. Screening of mackerel catches at the only land based factory “Kollafjørð Pelagic” during the fishing season. Data provided to WKSALMON in report by Jacobsen and Joensen (2011).

Month	Number of vessels	Number of salmon	Screened catch (t)	Salmon per 1000 t	Total catch (t)	Estimated bycatch of salmon (number)
May	3	57	1520	38	3294	124
June	4	19	2791	7	8715	59
July	13	0	7266	0	43 294	0
August	19	0	9615	0	45 196	0
September	17	0	10 123	0	22 245	0
Total	56	76	31 315	2	122 744	183

ICES (2004a) reviewed the potential for bycatch of salmon in fisheries of the Northwest Atlantic. ICES concluded that there was insufficient information to quantify bycatch although, based on information reviewed, there was no obvious concern about bycatch of salmon in these fisheries. Historical data provided some evidence of bycatch as salmon had been reported in commercial landings, but the location of this bycatch was not well defined. Based on Canadian data, the

bycatch occurred most frequently in gillnet fisheries. No catches of salmon from purse seines or trawls were reported.

Further, ICES (2017a) summarized information on the size, distribution and timing of the blue whiting fishery in the Northeast Atlantic area and observations related to bycatch of salmon. ICES (2017a) concluded that none of the information available suggested that salmon were taken frequently as bycatch in the blue whiting fishery for a number of reasons:

- Much of the blue whiting catch is taken at a time prior to salmon smolts emigrating into the marine environment.
- Blue whiting are mainly captured at some depth, while salmon are generally thought to be distributed in surface waters.

Nonetheless ICES recognised a number of uncertainties:

- There have been essentially no independent observers on board vessels during the blue whiting fishery.
- There are challenges to detecting salmon bycatch in these fisheries including detecting small numbers of salmon in large blue whiting catches that can exceed 2000 tonnes per haul.
- Post-smolts and blue whiting are about the same size and fairly similar in appearance.
- However, the main portion of fishery occurs in February and March, a time period in which there are no post-smolts at sea, and any bycatch of salmon would be of adult size that would be more detectable by the fishing fleets.

4.5.1 Spatial and temporal distribution of fisheries catches and effort (ICES) (InterCatch; DATRAS; STECF; RDB)

In the Northeast Atlantic, there are various databases and data sources of commercial fisheries catches and effort will provide spatial and temporal distributions of fisheries at different scales. This section describes the existent databases and available commercial fisheries data.

4.5.1.1 ICES InterCatch database

InterCatch was developed to ease data handling, standardise procedures and calculations, remove errors and document the national data and process completed at ICES level. The data in InterCatch are used as a basis for advice to the European Commission, NASCO and NEAFC. National institutes upload their commercial catches (landings, discards and effort) and biological data (length and/or age) in InterCatch, as a result of the ICES annual data call. The data are aggregated by ICES area, quarter (year or month for a few stocks) and fleet (normally DCF level 6 métier). The time-series in this database is stock-specific.

Member countries (including Norway and Iceland) should upload their data into InterCatch. However, for the EU Member States this is a mandatory data call.

InterCatch is not publicly available and any data should be requested from the ICES Data Centre. In addition, some catch and effort data might be requested in a different format and these are sent via email to data.call@ices.dk or accessions@ices.dk.

4.5.1.2 STECF Fisheries Dependent Information database (STECF FDI)

The STECF-FDI database holds commercial fisheries catches and effort from the fleets of EU Member States. These data are publicly available and can be found here: <https://stecf.jrc.ec.europa.eu/dd/effort>. The landings and discards are available since 2003 until 2016, by species, year, country, fleet, vessel length, and area:

- <https://stecf.jrc.ec.europa.eu/web/stecf/dd/effort/graphs-annex>.

These data are in different aggregation levels and definitions of fleets from the ones used in the ICES InterCatch, making it difficult to do direct comparisons. This database also holds landings and effort data, by country, rectangle, quarter, fleet and vessel length:

- <https://stecf.jrc.ec.europa.eu/web/stecf/dd/effort/graphs-quarter>.

Despite being publicly available, it is not easy or straight forward to navigate and extract the data of interest and it is necessary to have a knowledge on how the data are organised and defined.

4.5.1.3 Regional Database (RDB)

The Regional DataBase (RDB) is a regionally coordinated database platform for fisheries assessments. The database covers fisheries in the North Atlantic Ocean, the North Sea and the Baltic Sea. It addresses fishery management needs related to the European Union Common Fisheries Policy. Since 2012, RDB is hosted and maintained by ICES for the preparation and analysis of commercial catch and landing data received from the cooperating countries. EU Member States have uploaded fisheries data into RDB since 2009. The database holds:

- Commercial fisheries landings and effort statistics – aggregated by country, month, ICES rectangle, species, commercial category and DCF level 6 métier.
- Raw sampling data from the at-sea and market sampling programmes.

The RDB database access is by login. The data can be requested from ICES, but needs agreement from the EU Member State for the data to be used.

Examples of landings maps by species (Figures 4.29 to 4.31) were presented at the workshop by J.A. Jacobsen (Faroe Marine Research Institute, Faroe Islands).

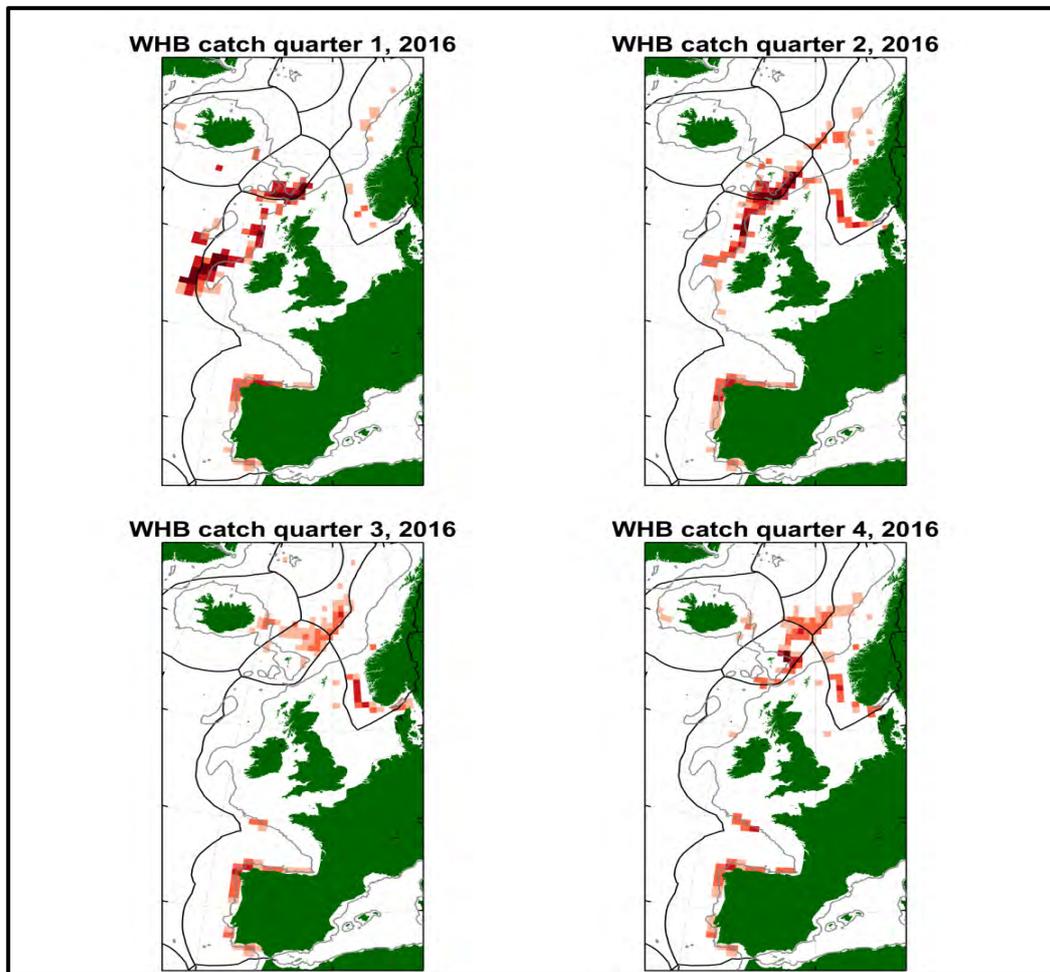


Figure 4.29. Distribution of commercial landings of Blue Whiting, by quarter, in 2016. Figure provided as example to WKSALMON by J.A. Jacobsen, Faroes Institute Marine Research.

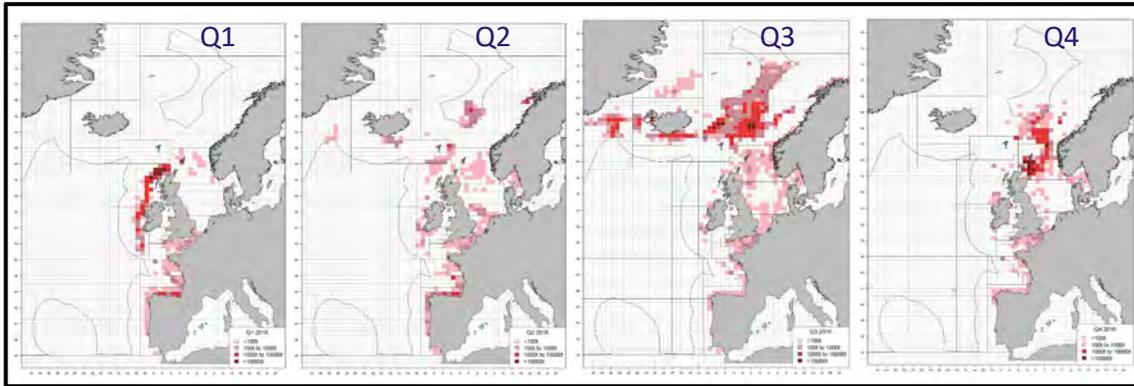


Figure 4.30. Distribution of commercial landings of Atlantic Mackerel, by quarter, in 2016. Figure provided as example to WKSALMON by J.A. Jacobsen, Faroese Institute Marine Research.

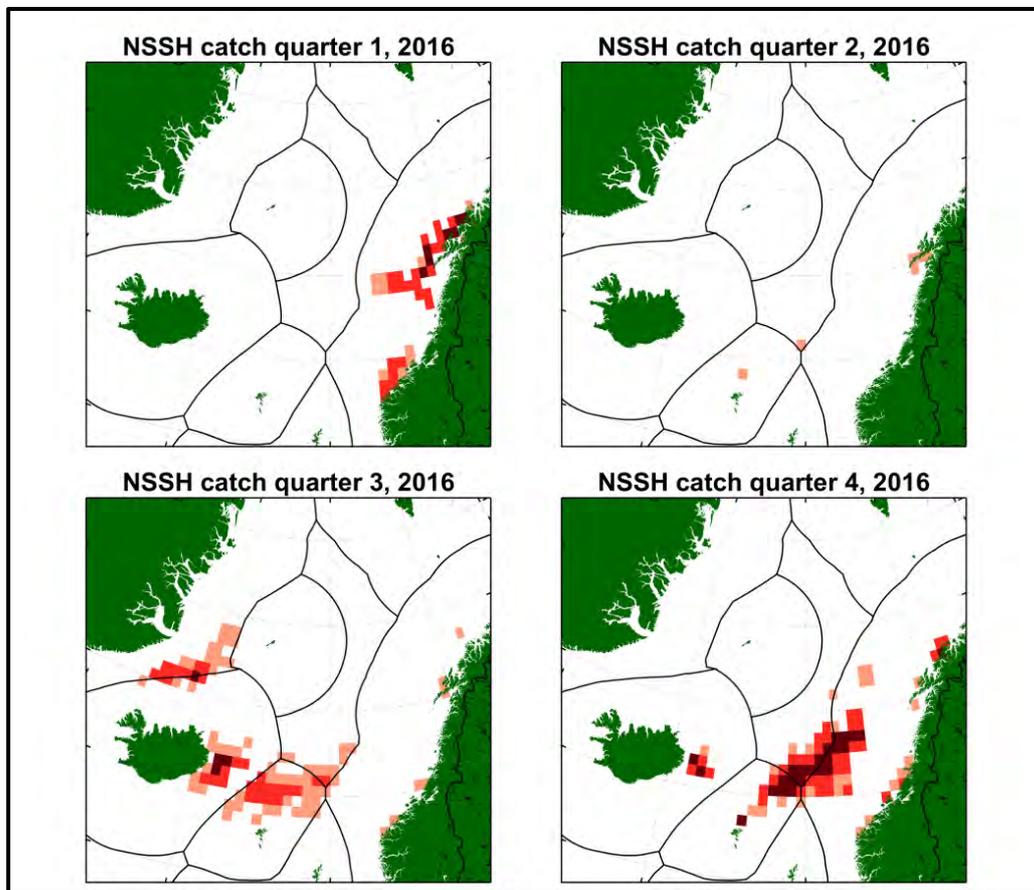


Figure 4.31. Distribution of commercial landings of Atlantic Herring, by quarter, in 2016. Figure provided as example to WKSALMON by J.A. Jacobsen, Faroese Institute Marine Research.

4.6 Spatial and temporal overlap of salmon and monitored marine ecosystem components

There are three large-scale ecosystem surveys with occasional or regular catches of salmon in the Northeast Atlantic: IESNS in the Norwegian Sea in spring, IESSNS in the Norwegian Sea and surrounding areas in summer and an ecosystem survey in the Barents Sea in the autumn (Figure 4.32).

International ecosystem survey in Nordic seas (IESNS) is a collaboration between five research vessels (from Norway, Iceland, Faroe Islands, Russia and Denmark) that cover the Norwegian Sea in May. The first survey was conducted in 1995 and the time-series is still ongoing. The main focus of the survey is to collect abundance estimates of NSSH, but the survey also samples blue whiting and mackerel. Although the primary sampling is of acoustic data, pelagic trawling is used for biological sampling. This includes occasional surface hauls with buoys. There is also sampling of hydrographical data with CTD and zooplankton with WP2 nets and zooplankton trawls. The survey occasionally catch salmon, but the timing of the survey is a somewhat early for post-smolt which enter the Norwegian Sea a couple of weeks after the survey. Further, few and slow surface hauls are not very efficient for sampling salmon returning to their rivers.

International ecosystem summer survey in Nordic seas (IESSNS) started as a Norwegian survey covering the eastern and central regions of the Norwegian Sea in 2007, and has since then expanded to include six vessels from five countries covering the North Sea and the Nordic Seas. The southern and central Norwegian Sea was sampled all years, but the region west of Iceland has only been sampled from 2012 and onwards. The total survey area exceeds 3 million km² and is conducted in July and early August. The survey applies surface trawling for 30 minutes at predetermined locations to get a fishery-independent estimate of mackerel abundance for use in stock assessment. The survey also sample and scrutinize data for herring and blue whiting. It is roughly 60 nautical miles between each trawl haul, but the exact distance varies between regions according to expected density of mackerel. The trawl has a horizontal opening of 70 m, a vertical opening of 30–35 m, and buoys are attached to the wing tips and the center of the trawl to ensure the headline at the surface. The trawl is well suited to catch salmon and tens of salmon are caught annually at the survey. Most of the fish are post-smolts but also include occasional catches of larger salmon. As the survey targets mackerel and other pelagic fish, the survey does not cover potentially important feeding grounds for sea-winter fish where mackerel is absent, such as the Greenland Sea and the Barents Sea. The number of salmon caught as bycatch was low the first years of the survey. In the same period the trawl operation was standardized. Hence, the catchability of salmon probably increased around 2012–2013. The survey also records sea temperature and salinity down to 500 m and sample zooplankton before every predetermined trawl haul (~every 60 nmi). The hydrographical data are sampled with either a Saiv or a Seabird CTD. Zooplankton is sampled with vertical hauls down to 200 m with a WP2-net. The use of WP2 is a cheap and quick way to sample zooplankton. However, large zooplankton are to a large degree able to avoid the gear, and the abundance of for instance euphausiids and amphipods are underrepresented by this method.

The third ecosystem survey is a joint Norwegian and Russian survey taking place in the Barents Sea. The time-series started in 1987 and the survey is undertaken in August–October. The survey targets benthic, demersal and pelagic ecosystems. Pelagic trawling is done at predetermined locations, but the trawl is smaller than the ones applied at IESNS and IESSNS, and most trawl hauls are not at the surface. The samples are used to calculate an annual recruitment index for several important fish stocks, such as herring, capelin, cod and others. This can potentially be useful indices of prey availability for post-smolt migrating out in the Barents Sea. The survey does have occasional catches of salmon but the number is low and bycatch of salmon do not occur annually. The survey also samples oceanographical data, zooplankton and demersal fish. Zooplankton is sampled with both WP2-nets and zooplankton trawls. The latter is time consuming to handle, but it is the only gear with high catchability of large zooplankton.

Availability of data

Trawl catches, zooplankton data and oceanographical data sampled at IESNS and IESSNS are normally available through collaboration. The data are not aggregated and are available with geographic location and date for each sample. As there are several countries involved and the

survey sample oceanography, zooplankton and fish, it may require some work to get the data ready for further salmon studies. It cannot be guaranteed that all institutions organizing the surveys are willing to share all the data.

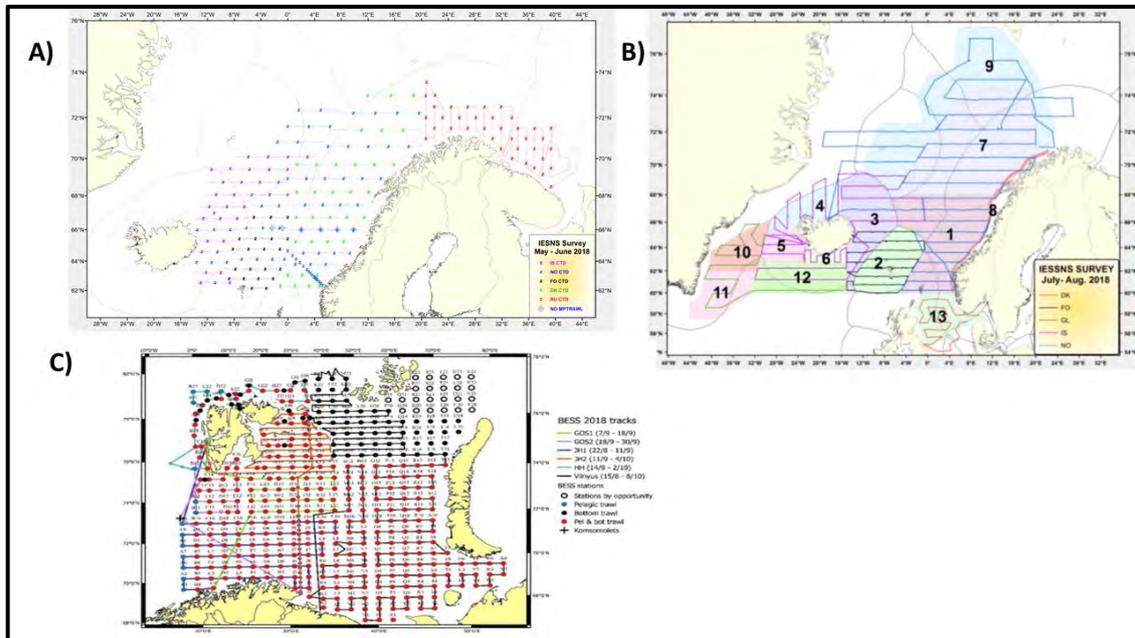


Figure 4.32. Overview of ecosystem surveys coverage in the Northeast Atlantic. A) IESNS in May; B) IESNS in July/August; C) Ecosystem survey Barents Sea in September/October.

5 Contribution to the ‘Likely Suspects’ framework

The ‘Likely Suspects’ conceptual framework proposes to place candidate population dynamics factors within an overall spatial-temporal matrix covering the freshwater migration and marine phases of the life cycle of Atlantic salmon. The identification of key geographical areas and periods, referred to as domains, where mortality or other life-history defining factors are known or suspected to operate, are essential to formulating testable hypotheses (Figure 5.1). These domains can be defined at various locations and times, ranging from freshwater to overwintering feeding areas, and would be associated with factors regulating abundance and life history. The challenge is the matching of these domains to candidate regulatory factors, and the availability of data over sufficient spatial and temporal scales for assessing the contributions of candidate regulatory factors to abundance and life-history variations.

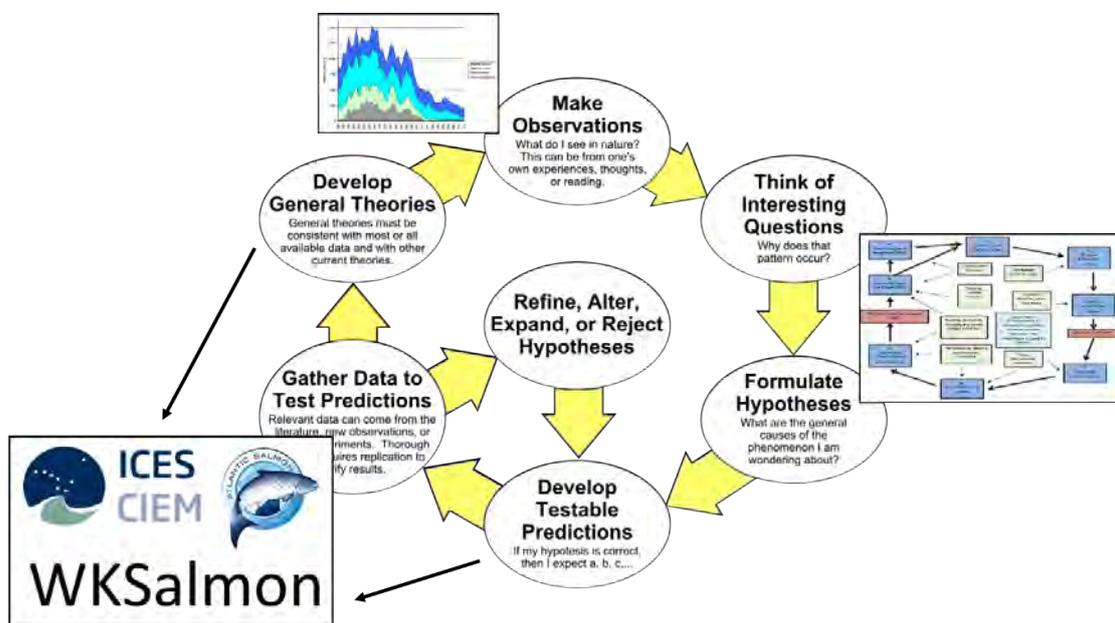


Figure 5.1. A schematic representation of how the Likely Suspects Framework, through the work of WKSALMON, might employ the scientific method to formulate and test hypotheses about the causes of observed declines of Atlantic salmon stocks.

Holt *et al.* (2014) provide a synthesis of the challenges of modelling the marine ecosystems of the North Atlantic. The authors remain optimistic that understanding and modelling the dynamics of the North Atlantic accounting for the complex interactions and feedback of physics, chemistry, biology and phenology of living organisms will be possible.

5.1 Progress to date on identification of domains and regulatory factors

The following examples illustrate the range of hypotheses and the extent to which domains and regulatory factors of salmon dynamics have been examined in published studies of Atlantic salmon. An attempt was made to summarize these studies in the context of the salmon life-history feature examined (e.g. abundance, productivity, survival, maturation), the corresponding regulatory factors, and whether the domains (spatial and temporal) discussed in the study were identified *a priori* or resulted from exploratory correlational analyses.

5.1.1 Spatial synchrony in the response of a long-range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean; Olmos *et al.* (2020)

Olmos, M., Payne, M.R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., Guitton, J., Sheehan, T., Mills, K., and Rivot, E. 2020. Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. *Global Change Biology* 26: 1319–1337.

Using a life-cycle model approach and regionally aggregated estimates of abundance from 13 stock units in Southern Europe and eastern North America over the period 1971 to 2014, Olmos *et al.* (2020) investigated some candidate environmental and biological drivers of post-smolt marine survival rates (smolt emigration to 1 January of the first winter at sea) of Atlantic salmon in the North Atlantic.

- The authors a priori identified domains in which the candidate regulatory factors would act on survival. Based on an extensive review of literature, they characterized space specific (three for North America; five for southern Europe) and time specific (three months) domains associated with the early marine phase and domains for the later phase (one for North America, one for Europe) with stock units in a common area (Olmos *et al.*, 2020; Supplementary Material 2).
- Environmental covariates included primary production indices (PP; April and May) and sea surface temperature indices corresponding to each of the specific and common space-time domains defined for salmon.
- Climate indices examined include the station-based North Atlantic Oscillation index (December to March) and the Atlantic Multidecadal Oscillation (AMO) index (average monthly value May to December) for their associations with larger and common domains for several stock units.
- Olmos *et al.* (2020) found strong coherence in the temporal variation in post-smolt marine survival with a common North Atlantic trend accounting for 37% of the temporal variability of the survivals for the 13 stock units and a survival trend characterized as a decline over the 1971–2014 time-series by a factor of 1.8.
- Synchrony in survival trends was stronger between stock units within each continental stock group. The common trends at the continental scale (North America, southern Europe) accounted for 60% and 42% of the total variance of temporal variation of sea survivals, respectively.
- Sea surface temperature and PP integrated over space domains shared by all stock units within the same continental stock group later in the first year at sea explained a larger proportion of the temporal variation of marine survival than variables integrated in the specific space–time domains.
- The regression coefficients of survivals were positive for PP integrated over common domains for both continental groups whereas they are negative for SST.
- The AMO index was negatively correlated with the trends in post-smolt survivals, with the magnitude of the effect higher for North America than for southern Europe. The AMO index acts as a synchronizing agent of post-smolt survival. In contrast the NAO index is not correlated to post-smolt survival and captured an insignificant part of the variance at any spatial scale.

5.1.2 Climate-driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations; Almodóvar *et al.* (2019)

Almodóvar, A., Ayllón, D., Nicola, G.G., Jonsson, B., and Elvira, B. 2019. Climate-driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations. *Can. J. Fish. Aquat. Sci.* 76: 1581–1595.

Almodóvar *et al.* (2019) examined a suite of factors for their associations with the observed temporal trends in Atlantic salmon catches (as a proxy for abundance of salmon) in Spain. The authors examined a number of North Atlantic scale indices (annual means from CPR samples) of plankton groups and corresponding phytoplankton colour index (indicator of primary production), large scale climate indices including the Atlantic Multidecadal Oscillation (AMO) index (0°N to 70°N domain), North Atlantic Oscillation (NAO) winter (December through March) station-based index, sea surface temperature (SST), and hydrological metrics in Spain. No time space domains, other than year with exploration of lags are used.

- The authors concluded that regime shifts in biophysical conditions in the Atlantic salmon feeding grounds occurred in 1986–1987, driven by the acceleration in anthropogenic warming, as the proximate cause of the collapse of Spanish salmon observed in 1988–1989. Declines in salmon catches continued with increasing ocean and freshwater temperatures, decreasing river flows, and poorer marine trophic conditions.

5.1.3 Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation; Friedland *et al.* (2014).

Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P., and Nye, J.A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *J. Mar. Syst.* 133: 77–87.

Friedland *et al.* (2014) contrast the time-series estimates of total pre-fishery abundance for the North American stock complex with those of the southern European and northern European complexes over the period 1971 to 2010 (pre-fishery abundance years). They conclude that the variations in estimated abundance are negatively associated with the Atlantic Multidecadal Oscillation (AMO) index. They further calculate correlation fields of monthly sea surface temperatures and a catch index from North America, and a tag return index of abundance for stocks from southern Europe. For the North American catch index, there is a significant negative association in springtime corresponding to when smolts migrate to the sea but the correlations dissipate by summer, hence warm springtime conditions, at first entry to seawater, have a detrimental effect on post-smolt survival. For the European tag return index, a coherent pattern of negative correlations is discerned in summer to early fall, that subsequently dissipates later in the year, hence warm conditions in late summer to fall in the post-smolt nursery (Norwegian Sea) have a negative influence on post-smolt survival.

- Run reconstructed estimates of pre-fishery abundance for North America, Southern Europe and Northern Europe stock complexes, by 1SW maturing and 2SW / MSW age groups.
- Catch-based index for North America derived from historical salmon landings in North America and catches at Greenland of North American origin; the time-series was augmented (adjusted?) for contemporary years using a regression model indexed on PFA

estimates. The catch index is not age-disaggregated, analysed using a 2-year lag associated with changes in the 2SW component.

- Tag return index for Europe.
- Thermal habitat (TH) in the Northwest Atlantic based on reconstructed SST dataset, monthly data, 2° grid resolution as the area within the temperature range of 4–8 °C, across the region bounded by 65–41°W and 45–75°N.
- Subpolar gyre index.
- Atlantic Multidecadal Oscillation (AMO) index as the de-trended annual mean of SST variability over the North Atlantic region in the area bounded by 0°–70°N, 75°W–7.5°E.
- North Atlantic Oscillation (NAO) station-based winter index (December through March)
- Arctic Oscillation (AO) index, sea level pressure differences between the Arctic and corresponding locations in middle latitudes.
- The decline in post-smolt survival both for North American and European stock complexes, based on proxy index of pre-fishery abundance, is associated with ocean warming.
- European salmon growth and recruitment appear to be governed by thermal conditions during their first summer at sea.
- North American stocks are affected by thermal variation in coastal waters early in the post-smolt migration during springtime.
- Growth rate during the summer months of the post-smolt year, appears to be key for the survival of Southern European stocks.
- Recruitment control of the North American stock complex is more consistent with variation in predation pressure associated with the variation in springtime ocean thermal conditions although no evidence or analysis of this is in the publication.

5.1.4 Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations; Mills *et al.* (2013)

Mills, K. E., Pershing, A. J., Sheehan, T. F., and Mountain, D. (2013). Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. *Global Change Biology*, 19(10), 3046–3061.

Mills *et al.* (2013) examine the extent to which declines in Atlantic salmon populations, in terms of absolute numbers and in the relative survival from spawners to recruits, in the Northwest Atlantic could be attributed to physical and biological shifts in Northwest Atlantic ecosystems. A major decline in salmon abundance after 1990 was preceded by a series of changes across multiple levels of the ecosystem. A subsequent population change in 1997 identified in the time-series analysis, primarily related to salmon productivity (i.e. corrected for spawner abundance), followed an unusually low NAO event. The authors link the changes in the climate and physical conditions to changes in plankton communities and prey availability, which then condition the abundances of Atlantic salmon. Poor trophic conditions, likely due to climate-driven environmental factors, and warmer ocean temperatures have constrained productivity of North American Atlantic salmon populations. The authors suggest which regulatory factors may be relevant but do not indicate any specific spatial or temporal (monthly) domain which may be most relevant.

- Atlantic salmon region-specific estimates of pre-fishery abundance of 1SW non-maturing salmon (1978–2010) and productivity (PFA/spawners) (1978–2008, year of PFA) for six regions of North America.
- AMO time-series over the region 0° to 70°N, de-trended.

- NAO; principal component based normalized sea level pressure between the subtropical high (Azores) and the subpolar low (Reykjavik, Iceland), December to March index.
- SST; resolved from 2° latitude by 2° longitude grid with spatial interpolation, to calculate an annual SST value, over spatial area corresponding approx. from 44° to 70°N, approximately 63° to 43°W.
- Surface salinity anomalies from observations at Station 27 near St John's, Newfoundland (Canada), computed as deviations from a harmonic regression model of the long-term seasonal salinity cycle.
- Phytoplankton annual anomalies from CPR data collected in the Gulf of Maine (USA) area and a polygon in the North Atlantic (southeast of Greenland and southwest of Iceland).
- Zooplankton annual anomalies from CPR data, based on principal components analyses of five species groups in Gulf of Maine and eight species groups in North Atlantic area (see above) from CPR data collected in the Gulf of Maine (USA) area and a polygon in the North Atlantic (southeast of Greenland and southwest of Iceland),
- Capelin, mean length of spawners index from NAFO Div. 3KL (Northwest Atlantic), 1980–2009.
- Changes in the abundance and productivity of 2SW Atlantic salmon were coherent among six regional groups of eastern North America, over the period 1978 to 2010, with important declines occurring through the late 1980s and early 1990s.
- Direct and indirect associations between climate and Atlantic salmon population declines were noted, with significant correlations between phytoplankton and zooplankton and the salmon population trends and with capelin size the most strongly and consistently associated with Atlantic salmon abundance and productivity.
- No time space domains, other than year were examined.

5.1.5 Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon; Friedland and Todd (2012)

Friedland, K.D., and Todd, C.D. 2012. Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biol.* 35: 593–609.

Friedland and Todd (2012) explored the associations of a suite of ecosystem variables (sea surface temperature, sea ice coverage, chlorophyll concentration, net primary production, and zooplankton abundance) to the variations in the weight of Atlantic salmon of North American origin sampled from the West Greenland fisheries. The purpose of the study was to identify candidate domains (space and time) and the potential drivers of the observed variations in size at age of salmon. The spatial scale of the regulatory factor domains was generally a 5° grid and the temporal scale was generally month.

- Sea surface temperature (SST) and the derived thermal habitat (4–8°C) in the Northwest Atlantic monthly data, 2° grid resolution, in the region bounded by 65–41°W and 45–75°N for the years 1969–2009.
- Monthly sea ice concentrations (%) within a 5° grid box, within the region bounded by 65–40°W and 45–75°N, for the years 1982–2009.
- Chlorophyll concentration, and the timing and dimensions of the spring phytoplankton bloom in the Northwest Atlantic at 8-day temporal resolution and monthly, averaged over 5° grid locations, in the region bounded by 65–40°W and 45–75°N, from 1998–2009.

- Net primary production (NPP), monthly based on chlorophyll concentrations averaged over 5° grid locations in the same region used for the sea ice and chlorophyll data, for the years 1998–2009.
- Abundance of plankton, in four plankton categories, from the Continuous Plankton Recorder (CPR) database, monthly for the period 1991–2006 from six CPR standard areas (three in south Irminger Sea, three in south Labrador Sea and east of Newfoundland). Monthly means were averaged to represent winter (February to April mean) and summer (May to July mean), for the years 1991–2009.
- The authors provide a series of maps with monthly correlation coefficients among various environmental variables and North American salmon weight from samples at West Greenland.
- The authors conclude that for the short time-series of overlap between production at the base of the food web and increasing weight-at-age, the metrics of primary production and plankton biomass are of no consequence to the observed change in size.
- For two regions (bands centered on 55°N, 47°W, and 63°N, 59°W), SST correlated positively with salmon growth, and there was a correlation between weight of 1SW salmon of North American origin and the extent of thermal habitat in February, March and April.

5.1.6 Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic; Beaugrand and Reid (2012)

Beaugrand, G. and Reid, P. C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES J. Mar. Sci.* 69: 1549–1562.

Beaugrand and Reid (2012) revisit a previous paper regarding the long-term changes in three trophic levels (salmon, zooplankton, and phytoplankton) which were shown to be correlated significantly with sea surface temperature (SST) and northern hemisphere temperature (NHT). The updated study confirmed earlier results and reported a new and abrupt shift in 1996/1997. They conclude that hydroclimatic and associated ecosystem changes in the Northeast Atlantic over the past three decades have played a major part in the decline of salmon stocks over the same period and that these changes happened rapidly.

- Considered the nominal catch of Atlantic salmon from southern Europe and northern Europe as a proxy for stock abundance in the Northeast Atlantic, for the period 1960–2009. Country-specific catches by year are post-processed using principal components analysis with retention of relevant components.
- Plankton data from CPR sampling interpolated on a regular grid of 1°longitude × 1°latitude in the spatial domain defined by 40 to 70°N and 30°W to 20°E, for the period 1960–2009. Data are post-processed using principal components analysis.
- Sea surface temperature data, monthly on 2° × 2° spatial grid. Data are post-processed using principal components analysis, for the period 1960–2010.
- Winter NAO principal component analysis index.
- AMO, de-trended and unsmoothed, averaged for the area 25–60°N 7–75°W.
- Northern hemisphere temperature (NHT), 1960–2010.
- No time space domains, other than year were examined.

5.1.7 Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers; Otero *et al.* (2012)

Otero, J., Jensen, A.J., L'Abée-Lund, J.H., Stenseth, N.C., Storvik, G.O., and Vøllestad, L.A. 2012. Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. *Ecol. Evol.* 2: 2192–2203. <https://doi.org/10.1002/ece3.337>

Otero *et al.* (2012) examined the variations in the proportions of sea age groups from the same smolt year class in the recreational catches in 59 Norwegian rivers. They reported that the proportion of 1SW fish in the catches had decreased concomitantly with increasing sea surface temperatures in the autumn of the first year at sea. They propose that the link between maturation rates and sea temperature is via the large-scale changes in the northeastern Atlantic pelagic food-web affecting post-smolt growth. They also reported that the decrease in the proportion of 1SW fish was influenced by freshwater conditions in the year prior to smolt migration although no mechanistic process for this is proposed.

- Nominal rod catch of adult Atlantic salmon for the period 1992–2007 from 59 Norwegian rivers, with sea age composition determined by weight proxies, validated by subsample of scale-interpreted ages.
- Sea surface temperature, monthly, interpolated from data on 1° latitude–1° longitude grid resolution delimited to the range of 55°–80°N and 15°W–30°E (excluding the Baltic Sea), that includes most of the migratory and foraging habitat of Atlantic salmon originated from Norwegian rivers. Monthly SST was derived from the spatial data using Principal Component Analysis and the first principal component was retained to characterize the monthly and annual value of marine SST conditions over the defined area.
- Average discharge in each river during spring–summer (May–August), lagged one-year to correspond to year of smolt migration.
- The proportion of 1SW Atlantic salmon in the catches generally decreased during the smolt year classes 1991 to 2005 across the rivers.
- First principal component of September SST provided the best fit to sea age proportions, with an increasing trend over time.
- Warming was spatially structured with higher correlations centered in the central Norwegian Sea and north of the Faroe Islands.

5.1.8 The recruitment of Atlantic salmon in Europe; Friedland *et al.* (2009)

Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., O' Maoiléidigh, N., and McCarthy, J.L. 2009. The recruitment of Atlantic salmon in Europe. *ICES J. Mar. Sci.* 66: 289–304.

Friedland *et al.* (2009) considered the associations between physical variables (SST, NAO, AMO) and biological factors (plankton indices) to abundance numbers of salmon (PFA by complex in Europe), returns rates to two index rivers, and indices of post-smolt growth from a number of rivers in Europe. The seasonal change in SST was negatively correlated with post-smolt survival during summer in a region that spatially matched the post-smolt nursery area in the Norwegian Sea. Indices of the planktonic foodweb are correlated with indices of salmon survival. Indices of

post-smolt growth during summer are positively correlated with salmon survival and recruitment. Of the climate indices, the Atlantic Multidecadal Oscillation (AMO) was the most strongly correlated to salmon recruitment.

- Sea surface temperature in the Northeast Atlantic (60–80°N and 10°W–20°E), spatial resolution 2° longitude by 2° latitude, calculated as monthly means, 1965–2005.
- Continuous plankton recorder data: seven plankton categories of monthly indices used to derive three-month running mean abundances, four standard areas partially overlapping the region considered to be the post-smolt nursery for salmon in the Northeast Atlantic, 1965–2005.
- Climate indices: North Atlantic Oscillation (NAO) station-based winter index (December through March) and the Atlantic Multidecadal Oscillation (AMO).
- The authors provide a series of maps and plots of monthly correlation coefficients between SST by month / grid, plankton indices by area / month, and growth increments by month to return rates to two index rivers.

5.1.9 Multidecadal North Atlantic climate variability and its effect on North American salmon abundance; Condrón *et al.* (2005).

Condrón, A., DeConto, R., Bradley, R. S., and Juanes, F. 2005. Multidecadal North Atlantic climate variability and its effect on North American salmon abundance. *Geophysical Research Letters*, 32: L23703. 4 p.

Condrón *et al.* (2005) analysed a time-series of salmon abundance indices from the Northwest Atlantic, based on catches, in relation to the Atlantic Multidecadal Oscillation and sea surface temperatures. During the AMO warm / cool phase, salmon abundance was lower / higher, respectively. Based on a multiple correlation analysis, the authors indicate that the changes in sea surface temperature associated with the AMO were most pronounced in the winter season near the Grand Banks of Newfoundland, which is a known overwintering area for salmon and may well be an important time and location for sea survival of salmon.

- Spatial area of interest is the Northwest Atlantic (40°–70°N, 80°–30°W).
- Atlantic salmon abundance proxies based on catch records for the period 1910–1991 and ICES pre-fisheries abundance data (PFA) for the subsequent period.
- Sea surface temperature (SST), monthly means at a 5° latitude by 5° longitude grid, seasonal means for summer (June, July, August) and winter (December, January, February).
- Temporal variations in the multidecadal oscillation were correlated with the winter season SSTs, in an area south of Newfoundland and the Grand Banks.
- SST anomalies in the winter season for the Newfoundland / Grand Banks are negatively correlated with the proxy indices of salmon abundance, suggesting this area and season as an important domain regulating Northwest Atlantic salmon abundance.

5.1.10 Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area; Friedland *et al.* (2000)

Friedland, K.D., Hansen, L.P., Dunkley, D.A., and MacLean, J.C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES J. Mar. Sci.* 57: 419–429.

Friedland *et al.* (2000) examined the time-series of smolt to adult return rates for two rivers in Europe; the North Esk (UK Scotland) and the Figgjo (Norway). The authors demonstrated a strong positive correlation between return rates and the area of thermal habitat in the 6–8°C

range during the month of May and that return rates were also positively associated with indices post-smolt growth (last freshwater circulus and 1SW annulus position). They conclude that the ocean climate variation related to the survival of salmon in the North Sea area occurs in spring when the post-smolts first enter the marine environment and occurs in the area of the North Sea and Norwegian coast. They also conclude that growth is the ultimate factor controlling mortality and hence spring growth rates may establish size-specific mortality dynamics (predation) in the summer that ultimately determines annual recruitment. See also Friedland (1998) and Friedland *et al.* (1998).

- Spatial dimension of the domain examined was defined as the area of thermal habitat in bands of 5–7°C; 6–8°C; 7–9°C; 8–10°C (*a posteriori*) in a spatial area encompassing 22° longitude range centered at 0° (*a priori*).
- Temporal dimension of candidate domain was month, March to July (*a posteriori*).
- Post-smolt growth indices were obtained from scales of return salmon from the North Est (UK, Scotland).
- Return rate indices to two rivers (River Figgio in southern Norway; River North Esk in UK (Scotland)) for the years 1965 to 1993.

5.1.11 Marine survival of North American and European Atlantic salmon: effects of growth and environment; Friedland *et al.* (1993)

Friedland, K.D., Reddin, D.G., and Kocik, J.F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES J. Mar. Sci.* 50: 481–492.

Friedland *et al.* (1993) examined indices of marine survival (return rates of smolts to adults for five populations of eastern North America, growth indices from scales from one river, and indices of abundance based on catches of salmon in North America and Europe) to marine habitat in the North Atlantic defined by sea surface temperature. Four marine areas, two in the Northwest and two in the Northeast Atlantic, and four seasons were defined *a priori* for quantifying the marine domains that could condition survival, growth and abundance. The authors concluded that the factors controlling survival of Atlantic salmon in eastern North America were acting predominantly in the winter months in Labrador Sea and east of Greenland. For the European stocks, lack of data precluded any conclusions on seasonality, however, a limitation was apparent in the spring, the only season examined.

- Sea survival indices from five monitored rivers in eastern North America
- Post-smolt growth indices from scales of salmon from the Penobscott River (USA)
- Catches of North American origin salmon, 1946 to 1988 (smoothed by 4-point moving average).
- Catches of salmon in Europe, 1946 to 1990 (smoothed by 4-point moving average).
- Sea surface temperature anomaly seasonal means (3-month) derived from monthly (5° by 5° spatial grid) data within four predefined polygons in the North Atlantic.
- Monthly thermal habitat areas within four temperature bands for North American stock complex and one temperature band for European stock complex.
- Correlations between survival rate indices suggest that an important cause of mortality acts upon the stocks when they occupy a shared habitat.
- Survival rate of Penobscott River was positively correlated to growth indices from the winter period of the scales, suggesting a season that could be important for survival regulation.

- The patterns of salmon catches of the North American stock were related to winter habitat indices.

Table 5.1. Summary of key research papers, organized by descending chronological order of publication, addressing candidate regulatory factors and the identification of domains in which the regulatory factors may be acting, for Atlantic salmon in the North Atlantic. Details of each publication are provided in Section 5.1.

Reference	Stock group	Salmon metric / regulatory factor	Domains defined			Regulatory factors
			Spatial	Temporal	Assumption	
Olmos <i>et al.</i> (2020)	6 stock units from North America; 7 stock units from Southern Europe	Post-smolt survival	North America (5 stock unit specific areas; 1 common area) Southern Europe (4 stock unit specific areas; 1 common area)	Initial phase (three months); Later phase: North America (August–November) Southern Europe (June–September)	<i>A priori</i>	SST, Primary production, AMO, NAO
Almodóvar <i>et al.</i> (2019)	Spain	Catches	Northeast Atlantic	Annual	<i>A priori</i>	Plankton indices, phytoplankton colour index, AMO, NAO, SST, hydrology
Friedland <i>et al.</i> (2014)	Continental stock complexes; Catch index for North America; Tag return index for Europe	Number of fish (PFA); Catch of salmon; Tag return index	North Atlantic for AMO, SGI, NAO, AO; Northwest Atlantic (65–41°W and 45–75°N) for TH; 2°grid for SST	Annual for AMO, SGI, NAO, AO Monthly for TH, SST	<i>A priori</i> for definition but <i>a posteriori</i> for identification	Thermal habitat (4–8°C); Subpolar Gyre Index, AMO, NAO, Arctic Oscillation (AO), SST
Mills <i>et al.</i> (2013)	North America, six regions, 2SW salmon	Abundance (PFA) Productivity (PFA/spawners)	North Atlantic for AMO, SGI, NAO; SST (~44° to 70°N, ~ 63° to 43°W); Salinity (Station 27, St. John’s, NFLD); CPR (two areas, Gulf of Maine, ~ southeast Greenland); capelin (shelf of southwest Labrador Sea)	Annual indices	<i>A priori</i>	AMO, NAO, SST, salinity, phytoplankton, zooplankton, capelin size
Friedland and Todd (2012)	North America	Weight of 1SW salmon at Greenland	5° grids over defined Northwest Atlantic rectangles; CPR standard areas	Month; Annual mean (CPR)	<i>A posteriori</i>	SST, sea ice, chlorophyll, net primary production, zooplankton

Reference	Stock group	Salmon metric / regulatory factor	Domains defined			Regulatory factors
			Spatial	Temporal	Assumption	
Beaugrand and Reid (2012)	Northeast Atlantic	Catches of salmon	Northeast Atlantic (40 to 70°N by 30°W to 20°E)	Annual	<i>A priori</i>	AMO, NAO, SST, Northern Hemisphere Temperature (NHT), plankton
Otero <i>et al.</i> (2012)	Norway (59 rivers)	Sea age maturity	1° lat. by 1° long. Grid, in domain 55°–80°N, 15°W–30°E; 59 rivers	Monthly SST; summer period discharge	<i>A posteriori</i>	Monthly SST; Discharge
Friedland <i>et al.</i> (2009)	Southern Europe, Northern Europe stock complexes; two rivers Figgio and North Esk; multiple index rivers Europe	Number of fish (PFA); Return rates; Growth rate proxies from scales	Northeast Atlantic SST (60–80°N and 10°W–20°E, 2° grid) CPR four standard areas; North Atlantic (AMO, NAO)	Monthly for SST; Three-month moving average for CPR; Annual for AMO and NAO	<i>A priori</i> for definition but <i>a posteriori</i> for identification	SST, plankton, AMO, NAO
Condron <i>et al.</i> (2005)	North America	Catch as proxy for abundance	North Atlantic (AMO); Northwest Atlantic for SST (40°–70°N, 80°–30°W; 5° grids)	Annual (AMO); Seasonal (SST)	<i>A priori</i> for definition but <i>a posteriori</i> for identification	AMO, SST
Friedland <i>et al.</i> (2000)	Figgio River (Norway) North Esk River (UK Scotland)	Return rates	22° longitudinal band centered on 0°	Month (March to July)	<i>A priori</i> for spatial; <i>A posteriori</i> for temporal	Area of thermal habitat in four bands (5–7; 6–8; 7–9; 8–10)
Freidland <i>et al.</i> (1993)	North America and Europe stock complexes	Return rates; Growth indices; Catches	four polygons: (60–50°W by 40–50°N; 50–40°W by 50–60°N; 20–10°W by 40–50°N; 5°W–5°E by 55–65°N) Thermal habitat (by temperature bands)	Seasonal	<i>A priori</i>	Seasonal SST anomalies in pre-defined polygons; Seasonal thermal habitat in pre-defined temperature bands

5.2 Identification of audit points

The 'Likely Suspects' framework emphasizes the need to develop testable hypotheses based on candidate life-history regulatory processes acting within specific domains (represented by locations/areas or periods in the life cycle). Empirical data are required, termed life-cycle audit points, to confirm or invalidate the hypotheses and processes (Crozier *et al.*, 2018). These audit points could be of various types.

In the summary of example studies in Section 5.1, the most common audit point and value is the abundance of salmon when they return to home waters, based on catches in fisheries, run reconstructions of abundance for regional groups, and return rate metrics derived from the ratio of smolts going to sea and the abundance of adults returning. Examples of life-history processes were also summarized which could also be audit points; weight-at-age of salmon at Greenland, and variations in relative proportions at sea age. Outside these, there are few other audit points available or currently being monitored in the marine portion of the life cycle of salmon in the North Atlantic.

Current and potential audit points, described in Section 2 of this report, are summarized below.

- The return rate time-series from monitored rivers in the North Atlantic (Section 2.6.2) has already been noted. These are critical audit points that quantify the integration of the marine regulatory processes of abundance. Smolt output is an important audit point for understanding the freshwater regulatory processes.
- Monitoring of adult salmon returns to rivers is an important auditing task, from which other life-history metrics including size, condition, lipid content, sea age and sex ratio can provide data for testing hypotheses. With these datasets, survivor bias is an important consideration.
- Audit points for abundance at sea could include catch indices of Atlantic salmon derived from the three large scale ecosystem surveys in the Northeast Atlantic: IESNS in the Norwegian Sea in spring, IESSNS in the Norwegian Sea and surrounding areas in summer and an ecosystem survey in the Barents Sea in the autumn (Section 4.6).
- The fishery at West Greenland, and any historical and contemporary data on relative abundance from catch rate indices, could serve as an audit point for salmon from North America and southern Europe at the high seas feeding grounds in their second summer and autumn at sea.
- Biological characteristics data from salmon captured and sampled at West Greenland could be used as audit points for hypotheses related to for example bottom-up regulatory processes for growth, survival, maturation, as well as migration and distribution at sea of regional groups of salmon (with genetic stock identification tools).
- More recently, acoustic technology tracking programs have been initiated to monitor the migrations and estimate area specific survival rates of salmon post-smolts from four populations migrating through the Gulf of St Lawrence to the Labrador Sea. This program provides a unique auditing opportunity to examine variations and candidate regulatory factors marine survival and migration phenology during the first two months and approx., 1000 km of post-smolt migration. This time-series now extends from 2003 to 2019.
- The accumulation of individual salmon distribution and migration data from archival transmitting tags, if sufficient tagging was conducted over a wide range of populations and years, could provide migration and distribution (and mortality rate) data for hypothesis testing.

5.3 Data gaps

The terms of reference for WKSsalmon were to identify data sources that could inform estimates of at-sea salmon mortality as well as ecosystem data including oceanographic time-series, plankton surveys, pelagic or demersal fish surveys that describe the marine ecosystem occupied by Atlantic salmon. This report summarizes data from a large number of sources but important data gaps remain.

- There are large-scale multi-disciplinary initiatives in ocean modelling that were not described during the meeting of WKSsalmon. Ocean circulation is complex, and descriptions of sea surface temperature and primary production may be relatively accessible for inquiry, however the complex dynamics of the deeper ocean layers is a gap in this report.
- There was no expertise at the WKSsalmon associated with the diverse avian, marine mammal and ectotherm fish community that interacts with salmon. The report summarizes the information on these components based on a review of literature but sources of data regarding variations in abundance, seasonal distribution at sea, and diet data are incomplete.
- The mesopelagic community, those macroplankton (krill) and fish (non-commercial) that serve as prey for salmon, are poorly to not monitored throughout the North Atlantic.
- Outside monitoring of surface conditions by remote sensing, the ecosystem during the winter period (November to April) is poorly to not monitored at all in the North Atlantic. This period has been identified as a key regulatory period of Atlantic salmon at sea.
- Genetics of Atlantic salmon and the capacity for adaptation and evolution of salmon populations is not covered in this report.

Very few of the datasets described in this report are readily available as open data or from websites. The most readily available information is from climate indices and physical oceanographic features. The salmon data, although referred to in a number of studies and reports requires some work to access and would involve contacting individual institutions and governments.

During WKSsalmon, an example of a metadata summary compilation was discussed and a few examples from jurisdictions were provided (see Appendix 6.3). The metadata spreadsheet was populated with examples of salmon related data from Canada, Iceland, and UK (England and Wales). In the longer term, a fuller compilation of such metadata with search variables would facilitate the exchange and the development of larger collaborations.

5.4 Next steps

The options for testable hypotheses within the 'Likely Suspects' framework will be constrained by the availability and representativeness of monitoring data of the components of the marine ecosystem occupied by Atlantic salmon. There is a large amount of information compiled and maintained within a diverse community of scientific experts with to-date limited cross-fertilization and networked analyses. The time scales and spatial scales of observations are variable, of differing complexity requiring a range of analytical skill sets, but seemingly extractable with some concerted effort.

In the mid-2000s, a working group developed a research proposal, SALSEA, to advance the knowledge of salmon ecology at sea. In the development of this proposal, the group constructed a high-level overview (cartoon) of what was known or assumed regarding the spatial and temporal distribution of salmon at sea (Figures 5.2 and 5.3). This conceptualization at the time was adequate for purpose; however, based on the salmon data summarized in this report and contemporary studies, a few corrections are warranted.

- Based on genetic stock identification, Atlantic salmon from southern Europe (primarily the Ireland / United Kingdom group but also Iceland) have been identified from samples collected in the Labrador Sea and to the south coast of Newfoundland.
- North American origin salmon have been identified from samples collected from the Irminger Sea and Iceland Basin with six North American regional groups further confirmed from samples in the Faroes area.

There are actually few audit points for Atlantic salmon at sea (Section 5.2; Figure 5.3) and the spatial by temporal matrix for these is very sparse.

It is the same issue for several ecosystem features of the North Atlantic that define the pelagic environment occupied by salmon. The physical features that are monitored by remote sensing, such as sea surface temperature and indices of primary production, have the highest spatial resolution and the broadest domain coverage that encompasses the entire North Atlantic and months when salmon are at sea (Figure 5.4). The indices of secondary production, for example obtained from Continuous Plankton Recorder monitoring, have a broad spatial and temporal coverage but a lower resolution compared to remote sensing indices. The pelagic fish community is sparsely sampled, with the best coverage in the Northeast Atlantic for May, and July–August (with coverage in the autumn for the Barents Sea) and no coverage in the Northwest Atlantic (Figure 5.4).

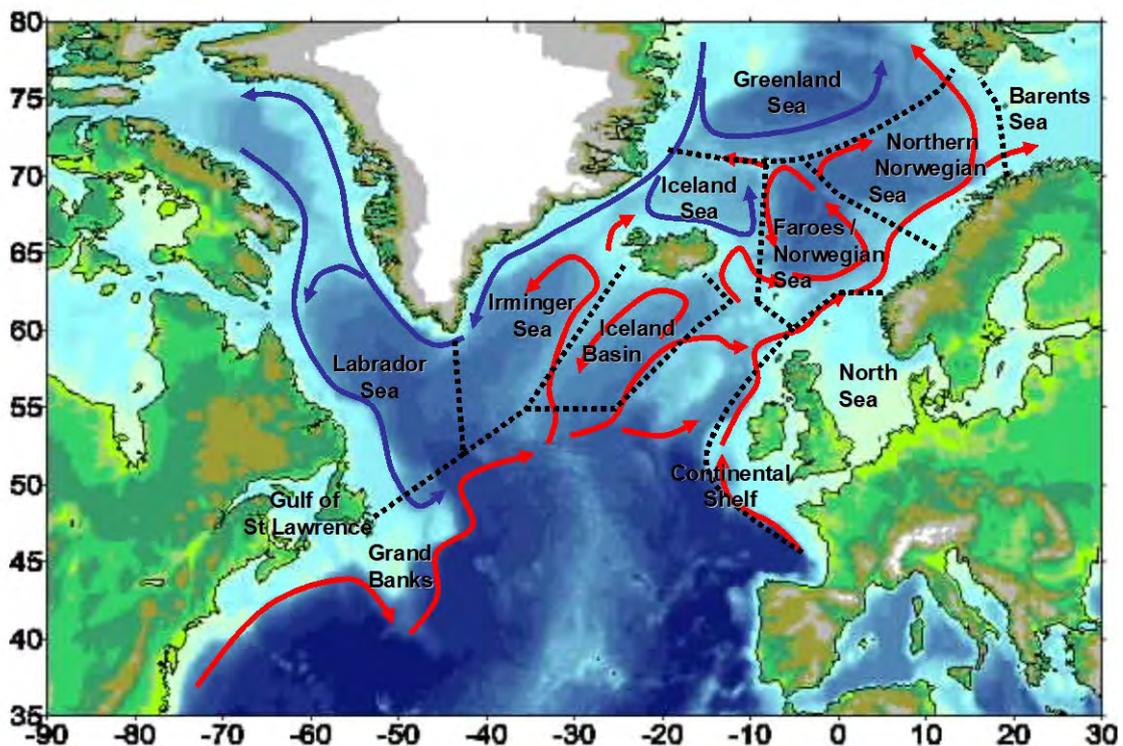


Figure 5.2. General marine areas and currents in the North Atlantic relevant to Atlantic salmon).

Southern NEAC	Smolt		Post-smolt										1SW salmon										2SW salmon				
	April	May	June	July	August	September	October	November	December	January	February	March	April	May	June	July	August	September	October	November	December	January	February	March	April	May	
Estuaries																											
Inshore																											
Faroes / Norwegian Sea			?																								
Northern Norwegian Sea																											
Barents Sea																											
Greenland Sea																											
Iceland Sea																											
Iceland Basin																											
Imringer Sea																											
West Greenland																											
Labrador Sea																											
Northern NEAC	Smolt		Post-smolt										1SW salmon										2SW salmon				
	April	May	June	July	August	September	October	November	December	January	February	March	April	May	June	July	August	September	October	November	December	January	February	March	April	May	
Estuaries																											
Inshore																											
Faroes / Norwegian Sea			?																								
Northern Norwegian Sea																											
Barents Sea																											
Greenland Sea																											
Iceland Sea																											
Iceland Basin																											
Imringer Sea																											
West Greenland																											
Labrador Sea																											
NAC	Smolt		Post-smolt										1SW salmon										2SW salmon				
	April	May	June	July	August	September	October	November	December	January	February	March	April	May	June	July	August	September	October	November	December	January	February	March	April	May	
Estuaries																											
Inshore																											
Atlantic coast NS																											
Gulf of St. Lawrence																											
Grand Bank																											
Labrador Sea																											
West Greenland																											
Imringer Sea																											
Faroes / Norwegian Sea																											
	Audit points																										
	Not found there																										
	Found there																										
	Don't know																										

Figure 5.3. Summary of distribution and occurrence of Atlantic salmon in the North Atlantic for the three stock complexes. Marine areas are shown in Figure 5.4.1. The cells in red represent locations and times that could serve as audit points for obtaining data from Atlantic salmon. Other sea age groups (3SW, 4SW, repeat spawners) are omitted from this figure for simplification.

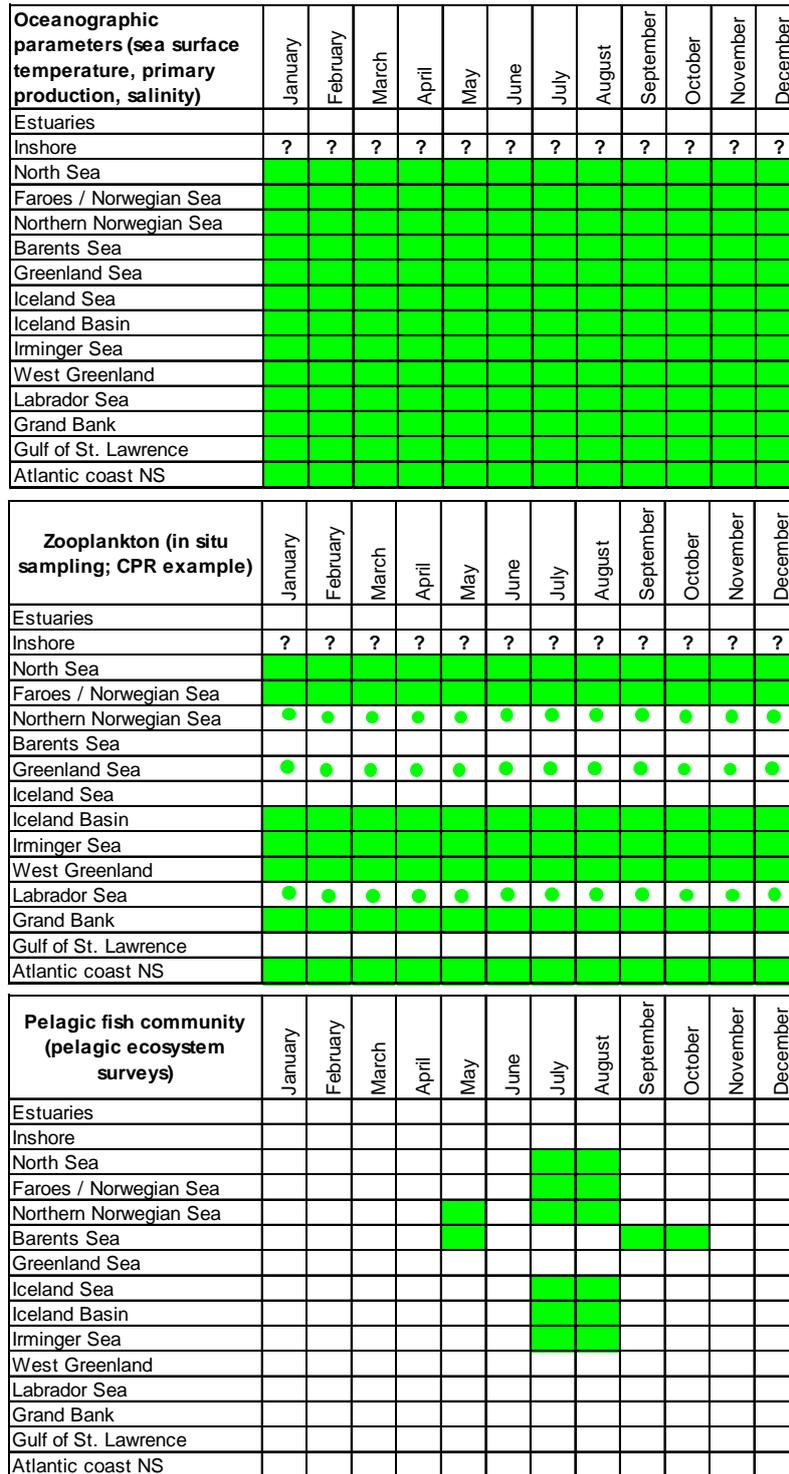


Figure 5.4. Summary of spatial and temporal (by month within year) coverage (green filled cells) of ecosystem variable monitoring in the North Atlantic for physical oceanography (upper panel), secondary production (CPR example middle panel), and the pelagic fish community (ecosystem surveys example, lower panel). Marine areas are shown in Figure 5.2.

6 SALSEA_PGNAPES database

Author: Jan Arge Jacobsen, Faroe Marine Research Institute.

The SALSEA_PGNAPES database was developed on a Microsoft Access platform by the Faroe Marine Research Institute/Faroe Marine Research Institute (formerly the Faroese Fisheries Laboratory, Partner 15), facilitating the collection and organisation of data and ensuring the quality and integrity of the dataset. It was originally developed for the joint international survey for blue whiting and herring in the Northeast Atlantic in the mid-1990s. All data collected during the surveys were entered into the PGNAPES database (logbook, catch or trawl data, biological data, plankton, hydrographic data, and also acoustic data, not shown here). The SALSEA-Merge project chose to build on this development and to store all biological data in the PGNAPES format.

The “SALSEA_PGNAPES_data” is the main database with logbook, biology and sampling data for each fish. All scientific data and analysis on each post-smolt are linked to this main database, even if the data are stored in separated databases.

In the project two work packages were working in parallel, one on the scale growth analysis and one on DNA assignments. These two datasets were stored in separate databases. The “SALSEA_PGNAPES_scales” database holding data on circuli growth analysis (SALMON_Scales and SALMON_Circuli_growth tables), and the “SALSEA_PGNAPES_dna” database holding data on the DNA assignments (SALMON_dna table). These two additional databases are linked up to the main “data” database.

To be able to combine and use the data in all databases, the link must be properly designed. A “unique key” is the key to create useful queries from the database. Basically, the original design was used to create a unique key by combining several parameters in each table, repeat those in each table, and force referential integrity in the “key” between the tables and databases.

Below is a description/picture of the relationships between the tables in the three databases. Further, it is possible to see which tables are linked from the main database into the two additional databases (scales and dna). An arrow (left arrow) pointing to the table name in the “table window” in Access indicate that the table is linked (and thus hold the original data from the main database).

6.1 Use of the databases

In order to safeguard the original data, a copy the bases should be uploaded from the SharePoint. Then a new empty Access database should be created. Into this new database, the tables should be linked from the main “SALSEA_PGNAPES_data”.

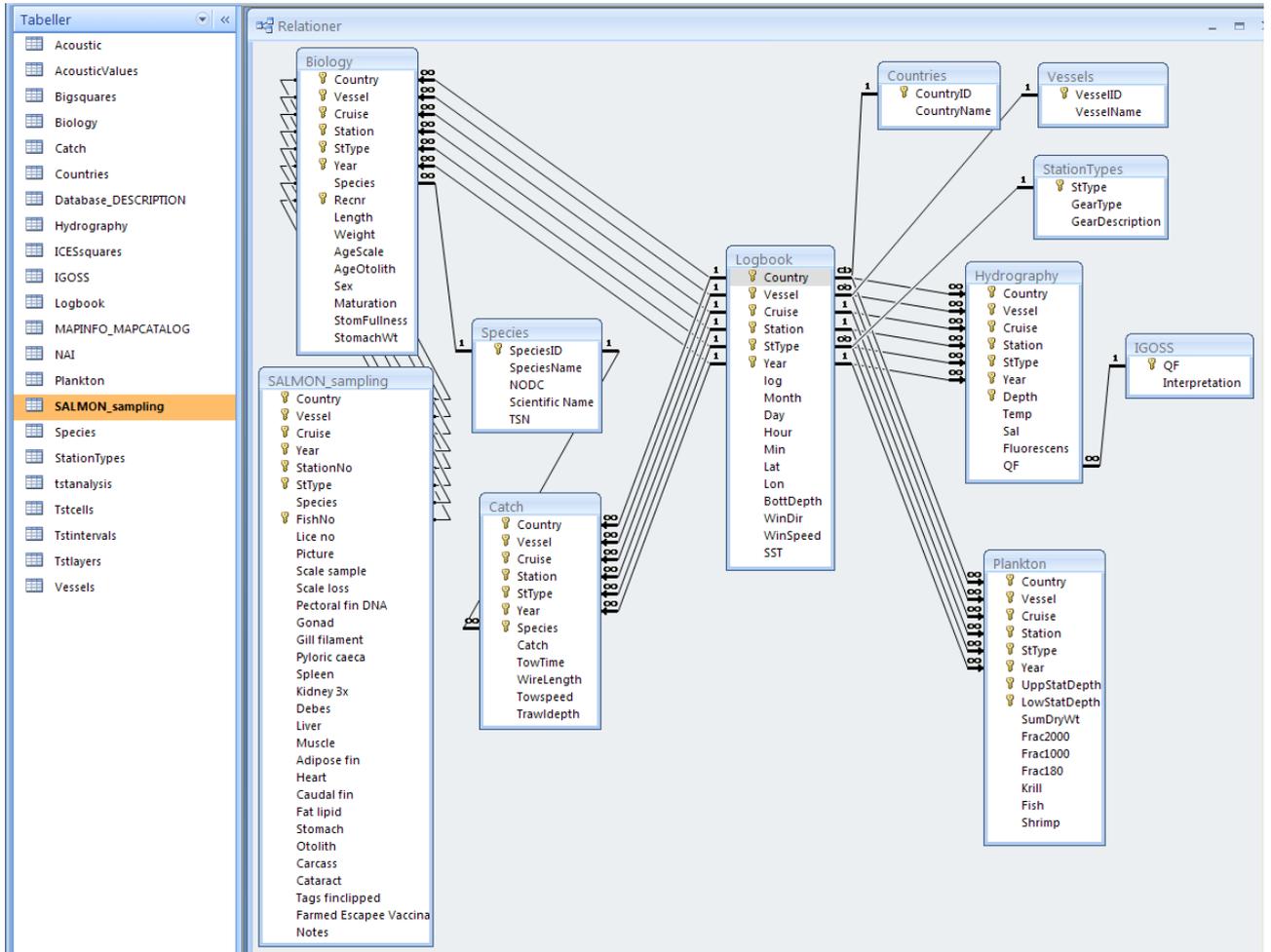


Figure 6.1. SALSEA_PGNAPES_data: Table relationships (Access). This is the main database with Logbook and Biology data for each fish. The two “scales” and “dna” databases link up to the current “data” database.

The screenshot shows a database schema tool with a left-hand pane listing tables: SALMON_Circuli_growth, SALMON_Pictures, SALMON_Scales, Biology, Logbook, SALMON_sampling, and Species. The main area displays two table definitions:

Feltnavn	Datatype	Beskrivelse
Country	Tekst	Post code (or ICES list)
Vessel	Tekst	Call sign (or ICES list)
Cruise	Tekst	Unique cruise identifier
Year	Tal	Four digits
StationNo	Tekst	National station number, link to Station in BIOLOGY
STType	Tekst	CTD, WP2, MIK, TRAWL, PDYP, PBLÅ, PTRAWL, ..., link to STType in StationTypes
Species	Tekst	3 character code, link to SpeciesID in SPECIES
FishNo	Tekst	Fish/record number, link to Recnr in BIOLOGY
GrowthNO	Tekst	Sample number used for growth analyses (key)
Scale image name	Tekst	Name of the file where the image of the scale is stored
Otolith image name	Tekst	Name of the file where the image of the otolith is stored
Location of scale sample	Tal	A number between 1 and 22, indicating the location of the fish where the scale has been taken. 999 = unknown
Scale quality	Tal	A number between 1 and 3, indicating the quality of the scale for detailed growth analyses, focusing on
Type_text	Tekst	Wild, farmed (escapee from the fish farm industry), stocked (for stock enhancement or sea ranching), etc.
Type_No	Tal	Similar to Type_text, but in numbers: wild = 1; farmed = 2; stocked = 3; reared = 4; unknown = 999
SmoltAge_Summary	Tal	Smolt age (integers only) derived from all information available. In cases of discrepancy between scale
SmoltAge_Scale	Tekst	Smolt age derived from scales. If uncertain, describe the uncertainty
SmoltAge_Otolith	Tekst	Smolt age derived from otoliths. If uncertain, describe the uncertainty
Sea age	Tal	Number of winters at sea
Comments	Tekst	Any comments relevant to age and growth analyses
Smolt length	Tal	Backcalculated smolt length from the scale
Scale radius	Tal	Total length of the scale from origo to the scale edge
NoCirculi	Tal	Number of circuli in the marine part of the scale

Feltnavn	Datatype	Beskrivelse
Country	Tekst	Post code, link to Country in BIOLOGY
Vessel	Tekst	Call sign, link to Vessel in BIOLOGY
Cruise	Tekst	Unique cruise identifier, link to Cruise in BIOLOGY
Year	Tal	Four digits, link to Year in BIOLOGY
StationNo	Tekst	National station number, link to Station in BIOLOGY
STType	Tekst	CTD, WP2, MIK, TRAWL, PDYP, PBLÅ, PTRAWL, ..., link to STType in StationTypes
Species	Tekst	3 character code, link to SpeciesID in SPECIES
FishNo	Tekst	Fish/record number, link to Recnr in BIOLOGY
GrowthNO	Tekst	
C_No	Tal	Circuli number, C1 is the first circuli growth in seawater
Growth	Tal	Circuli measurements, mm (growth between to consecutive circuli in scale)

Figure 6.2. SALSEA_PGNAPES_scales: Relationships between the SALMON_Biology table and the added scale-growth tables (SALMON_Scales, SALMON_Circuli_growth).

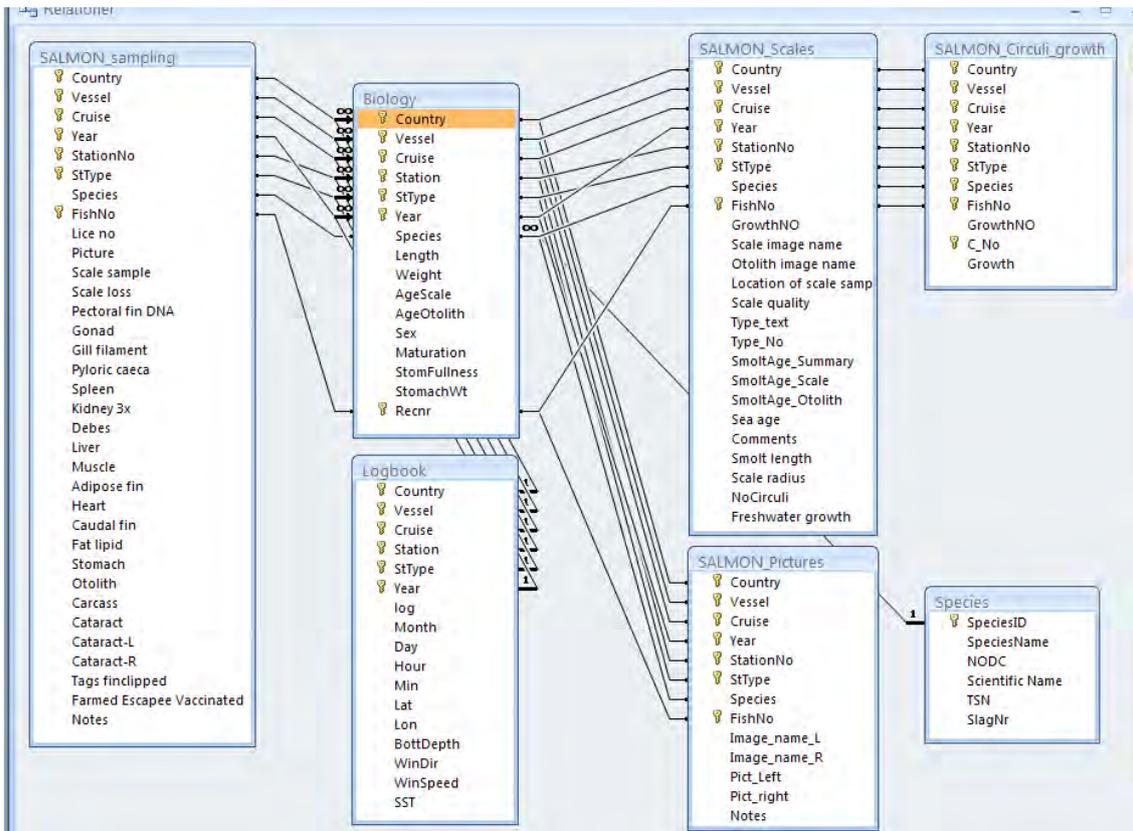


Figure 6.2 (continued).

Feltnavn	Datatype	Beskrivelse
Country	Tekst	Post code
Vessel	Tekst	Call sign
Cruise	Tekst	Unique cruse identifier
Year	Tal	Four digits
StationNo	Tekst	National station number, link to Station in BIOLOGY
StType	Tekst	CTD, WP2, MIK, TRAWL, PDYP, PBLÅ, PTRAWL, ..., link to StType in StationTypes
Species	Tekst	3 character code, libk to SpeciesID in SPECIES
FishNo	Tekst	Fish/record number, link to Recnr in BIOLOGY
SampleID	Tekst	Sample number used in local database (key)
Submitting Laboratory	Tekst	Name of the laboratory submitting the dna sample
Notes	Tekst	
Assigned_Country	Tekst	Assigned country
Level_1	Tekst	regions
Level_2	Tekst	regions, 2- level
Level_3	Tekst	regions, 3- level
Level_4	Tekst	regions, 4- level

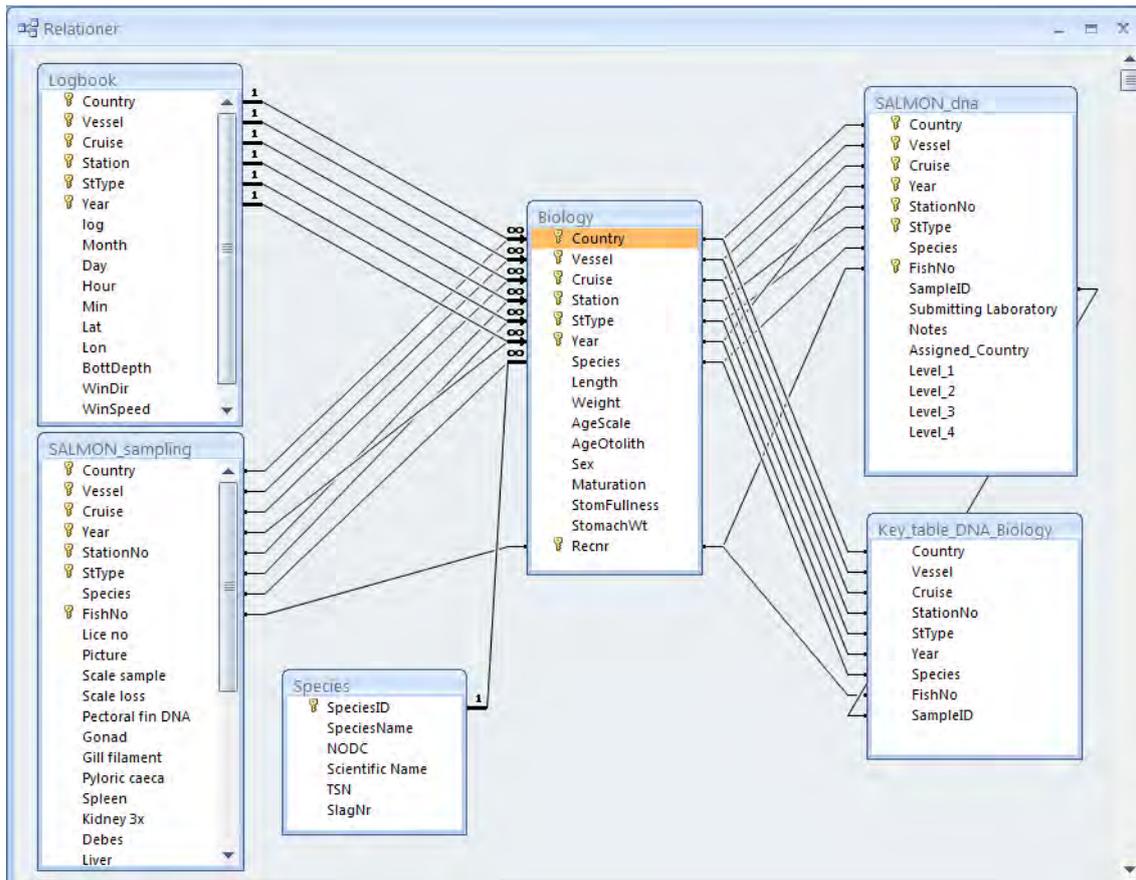


Figure 6.3. SALSEA_PGNAPES_dna: Relationships between the SALMON_Biology table and the added DNA assignments table (SALMON_dna).

Feltnavn	Datatype	Beskrivelse
Country	Tekst	Post code (or ICES list)
Vessel	Tekst	Call sign (or ICES list)
Cruise	Tekst	Unique cruise identifier
Year	Tal	Four digits
StationNo	Tekst	National station number, link to Station in BIOLOGY
StType	Tekst	CTD, WP2, MIK, TRAWL, PDYP, PBLÅ, PTRAWL, ..., link to StType in StationTypes
Species	Tekst	3 character code, link to SpeciesID in SPECIES
FishNo	Tekst	Fish/record number, link to Recnr in BIOLOGY
Lice no	Tal	Number of lice
Picture	Tekst	Photograph taken
Scale sample	Tekst	Scale sample taken
Scale loss	Tal	Scale loss in % of body surface (total loss)
Pectoral fin DNA	Tekst	DNA sample from pectoral fin taken
Gonad	Tekst	Gonad sample taken
Gill filament	Tekst	DNA sample from gill taken
Pyloric caeca	Tekst	Pyloric caeca sample taken
Spleen	Tekst	Spleen sample taken
Kidney 3x	Tekst	Kidney smple (3 places) taken
Debes	Tekst	Special sample for disease (ISA) taken (Debes, Faroes)
Liver	Tekst	Liver sample taken
Muscle	Tekst	DNA muscle sample taken
Adipose fin	Tekst	Adipose fin taken
Heart	Tekst	Heart taken
Caudal fin	Tekst	DNA sample of caudal fin taken
Fat lipid	Tekst	Lipid sample taken (fresh fish only)
Stomach	Tekst	Stomach taken
Otolith	Tekst	Otolith taken, serial number in a station (0 means not found)
Carcass	Tekst	Carcass frozen
Cataract	Tekst	Cataract determined: blank= ok, Left, Right or Left & Right
Cataract-L	Tekst	Cataract on left eye: 0= ok, 1 small white spot in lens, 2 30% lens covered white, 3 60% lens covered, 4 whole lens white
Cataract-R	Tekst	Cataract on right eye: 0= ok, 1 small white spot in lens, 2 30% lens covered white, 3 60% lens covered, 4 whole lens white
Tags finclipped	Tekst	Finnclipped or tagged fish
Farmed Escapee Vaccinated	Tekst	Visual determination whether farmed/vaccinated/escaped fish
Notes	Tekst	Comments

Figure 6.4. SALSEA_PGNAPES database table description. SALMON_sampling (added table linked to the “basic” Biology table in SALSEA).

7 New projects initiated addressing salmon ecology at sea

7.1 SeaSalar: Atlantic salmon at sea—factors affecting their growth and survival

(<https://www.seasalar.no/>)

The Norwegian Institute for Nature Research (NINA) is the lead institution of the project, with the Institute of Marine Research (IMR) and the Arctic University of Norway (UiT) as partners. The project leader is Eva Thorstad (NINA) with Vidar Wennevik as project manager at IMR and Audun Rikardsen as project manager at UiT. Together with experts in the field from several other Norwegian and international research institutions, a consortium was formed with the aim to build a knowledge platform and study how the marine survival of Atlantic salmon is affected by abiotic and biotic variables in the ocean. International collaboration is an important part of this effort, and scientists from England, Canada, Ireland and Scotland participate in the project.

The project consists of the following components: (1) Mapping and modelling the spatial and temporal variation in abiotic and biotic oceanographic data on conditions potentially influencing growth and mortality of salmon. (2) Mapping distribution and migration routes of Atlantic salmon at sea, which is a prerequisite for analysing factors affecting them. (3) Analysing variations in marine growth, survival and population sizes over time and geographical areas. (4) Combining data to identify the environmental and biological factors affecting marine survival. An important part of the project is to utilise existing data and activities to reach these objectives, including salmon collected at sea, genetic material, archival scale samples, survival data, population size data, migration data, and data series on other marine species and oceanic ecosystems. The project will also apply new genetic, stable isotope and electronic tagging technologies and modelling to provide novel results.

The project started 1 August 2018 and will last for four years. Salmon will be tagged with satellite tags in the spring 2019 and 2020, by tagging kelts from rivers in Southern and Western Norway to monitor their sea migration. This has previously not been done in Southern and Western Norway.

7.1.1 SALMONIDS Management ARound the CHannel (SAMARCH)

SAMARCH is a five-year project that started in April 2017 (due to end April 2022) and part funded by the France-England Interreg Channel programme. The project will provide new transferable scientific knowledge to inform the management of salmon and sea trout in the estuaries and coastal waters of both the French and English sides of the Channel. Although the project involves working on a number of rivers in the Channel area, the majority of the data collection and research will focus on five salmon and sea trout monitored rivers in the Channel area. These are the rivers Frome and Tamar in southern England and the rivers Scorff, Oir and Bresle in northern France. The lead organization is GWCT (Exeter University, Bournemouth University, Salmon and Trout Conservation, Environment Agency) with the project manager Dylan Roberts (GWCT) (droberts@gwct.org.uk). Further information about SAMARCH is available online at www.samarch.org.

There are four technical work-packages in the SAMARCH project.

- WP T1 Fish Tracking (Celine Artero (GWCT) cartero@gwct.org.uk).

Uses acoustic tracking technology to follow salmon and sea trout smolts through the estuaries of the rivers Frome, Tamar, Scorff and Bresle in the springs of 2018–2020 to apportion smolt mortality rate between the estuary and the nearshore coast. Sea trout kelts from the Frome, Tamar and Bresle will also be marked with both acoustic and data storage tags to track their movements through the estuary and around the coast.

- WP T2 Genetic Tool Development (Jamie Stevens (Exeter) J.R.Stevens@exeter.ac.uk and Sophie Launey (INRA) sophie.launey@inra.fr)

Collect samples of juvenile brown trout from rivers in northern France and southern England and adult sea trout across the Channel to build a common trout and sea trout genetic dataset to identify the river-of-origin of sea trout caught at sea. Genetic analysis to identify the sex of large numbers of juvenile and adult salmon and sea trout will generate new information for stock assessment models used to manage salmonid stocks in UK (England and Wales) and France.

- WP T3 Salmonid Stock Assessment Models (Marie Nevoux (INRA) marie.nevoux@inra.fr, Etienne Rivot (AO) etienne.rivot@agrocampus-ouest.fr, and Stephen Gregory (GWCT) sgregory@gwct.org)

Involves collecting new data on the marine survival of salmonids and using this and historic data from five monitored rivers to develop new and improve existing models used for salmonid stock assessment in England and France. Historical salmonid scale collections will be analysed to generate data on changes in growth rates and sex ratio over time. The project will also assess the fecundity of salmonids. These new data will feed into the models used to manage salmonid stocks in England and France. See also Section 2.3.7.

- WP T4 Stakeholders and Training

Stakeholder engagement and training activities will be used to ensure the results produced by the project inform, improve and develop new policies for the management of salmonids in estuaries and coastal waters. It will engage with stakeholders in both England and France and further afield to maximise the impact of the results generated by the project.

8 Metadata compilation of salmon datasets discussed during WKSsalmon

Column header	Descriptor	Entry choices	Explanation
ToC index		refers to the table of contents numbering for the report; linked lookup with characteristic column	
Characteristic	refers to the salmon characteristic data and corresponding to the table of contents numbering of the report		
	pull-down	distribution_occurrence physical_habitat diet predation abundance dynamics bio_characteristics parasites_diseases other	
What are the data	user entered; description of the data		
Type	Point or sequential observations (if one fish is sampled, it is point, if a fish is tracked using telemetry, the data are likely sequential)		
	pull-down	single sequential population multi-populations other	one fish is sampled, data collected at single point in time for example multiple positions or multiple temperatures recorded from one pop satellite tag refers to multiple fish (population level) direct or indirect observations e.g. run reconstruction to regions that involves a group of rivers catch all
Data type	Are these direct observations (of individual fish sampled) or modelled (ex. Georeference positions of fish from satellite tags, estimated return rates of smolts, ...)		
	pull-down	direct indirect other	from an actual fish handled estimate (e.g. mean length, return rate) or derived from a model (e.g. position of fish from PSAT, returns to rivers from assessment model, outputs from run reconstruction) catch all
Spatial resolution	Are the position data for the fish at the scale of single point (lat, long), within a degree square, a fisheries unit, or other?		
	pull-down	Lat - Long Degree square ICES units Region Jurisdiction Country Other	specific position where data originated (e.g. salmon sampled from pelagic trawl, mean size of returning 1SW salmon from returns to a river, lat and long refers to river mouth) if appropriate for example (Labrador in North America, south Norway for Norway) for example (UK England & Wales) for example Russia catch all
Main basin	Basin of the North Atlantic corresponding to the data		
	pull-down	Northeast Atlantic Northwest Atlantic North Atlantic	information is from the Northeast Atlantic side information is from the Northwest Atlantic side information encompasses both the Northeast and Northwest Atlantic sides, e.g. Greenland
Spatial location	user entered for the specific detail		
Year coverage begin	user entered (YYYY), first year of data set		
Year coverage end	user entered (YYYY), most recent year of data set		
Temporal resolution	at what temporal scale are the data?		
	pull-down	Point Day Week Month Season Year Other	observation specified with date and time of sampling can have fish sampled daily over an entire season, then data are daily
Temporal period	user entered; specify in the case of month for example May to August, for season Winter (Dec-March), or day (period of coverage June to November)		
Data storage type	How are the data currently stored		
	pull-down	Paper Flatfile Database Mixture Other	in a report or on data forms, not electronic electronic (Excel, csv, txt, R, etc) structured database data in various formats catch all
Data storage name	user entered, name of database (acronym if available)		
Future contact	user entered (name, institution, website, email if possible)		

9 References cited

- Aarefjord, H., Bjørge, A.J., Kinze, C.C., and Lindstedt, I. 1995. Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. Reports of the International Whaling Commission, 16: 211–222.
- Alheit, J., Drinkwater, K.F., and Nye, J.A. 2014. Introduction to Special Issue: Atlantic Multidecadal Oscillation-mechanism and impact on marine ecosystems. J. Mar. Syst. 133: 1-3.
- Alheit, J., Gröger, J., Licandro, P., McQuinn, I.H., Pohlmann, T., and Tsikliras, A.C. 2019. What happened in the mid-1990s? The coupled ocean-atmosphere processes behind climate-induced ecosystem changes in the Northeast Atlantic and the Mediterranean. Deep-Sea Research Part II 159: 130–142.
- Almodóvar, A., Ayllón, D., Nicola, G.G., Jonsson, B., and Elvira, B. 2019. Climate-driven biophysical changes in feeding and breeding environments explain the decline of southernmost European Atlantic salmon populations. Can. J. Fish. Aquat. Sci. 76: 1581–1595.
- Andersen, L.W. 2003. Harbour porpoises (*Phocoena phocoena*) in the North Atlantic: distribution and genetic population structure. NAMMCO Scientific Publications, 5: 11–29.
- Andersen, L.W., and Olsen, M.T. 2010. Distribution and population structure of North Atlantic harbour seals (*Phoca vitulina*). NAMMCO Scientific Publications, 8: 15–35.
- Andersen, S.M., Lydersen, C., Grahl-Nielsen, O., and Kovacs, K.M. 2004. Autumn diet of harbour seals (*Phoca vitulina*) at Prins Karls Forland, Svalbard, assessed via scat and fatty-acid analyses. Can. J. Zool. 82: 1230–1245.
- Andersen, L.W., Lydersen, C., Frie, A.K., Rosing-Asvid, A., Hauksson, E., and Kovacs, K.M. 2011. A population on the edge: genetic diversity and population structure of the world's northernmost harbour seals (*Phoca vitulina*). Biol. J. Linn. Soc. 102: 420–439.
- Armstrong, J.D., McKelvey, S., Smith, G.W., Rycroft, P., and Fryer, R.J. 2018. Effects of individual variation in length, condition and run-time on return rates of wild-reared Atlantic salmon *Salmo salar* smolts. J. Fish Biol. 92: 569–578.
- Arnott, S., and Ruxton, G. 2002. Sandeel recruitment in the North Sea: demographic, climatic and trophic effects. Mar. Ecol. Prog. Ser. 238: 199–210.
- Asch, R.G., Stock, C.A., and Sarmiento, J.L. 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. Glob. Chang. Biol. 25: 2544–2559.
- Aykanat, T., Ozerov, M., Vähä, J.-P., Orell, P., Niemelä, E., Erkinaro, J., and Primmer, C.R. 2019. Co-inheritance of sea age at maturity and iteroparity in the Atlantic salmon *vgl3* genomic region. J. Evol Biol. 2019: 1–13.
- Bal, G., Montorio, L., Rivot, E., Prévost, E., Baglinière, J.-L., and Nevoux, M. 2017. Evidence for long term change in length, weight and migration phenology of anadromous spawners in French Atlantic salmon *Salmo salar*. J. Fish Biol. 90: 2375–2393.
- Barker, J., and Berrow, S. 2016. Temporal and spatial variation in group size of bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. Biology and Environment: Proceedings of the Royal Irish Academy 116(1): 63–70.
- Barrett, R.T., Chapdelaine, G., Anker-Nilssen, T., Mosbech, A., Montevecchi, W.A., Reid, J.B., and Veit, R.R. 2006. Seabird numbers and prey consumption in the North Atlantic. ICES J. Mar. Sci. 63: 1145–1158.
- Barrett, R.B., Strøm, H., and Melnikov, M. 2017. On the polar edge: the status of the northern gannet (*Morus bassanus*) in the Barents Sea in 2015–2016. Polar Research 36:1, 1390384, DOI: 10.1080/17518369.2017.1390384.
- Barson, N.J., Aykanat, T., Hindar, K., Baranski, M., Bolstad, G.H., Fiske, P., Jacq, C., Jensen, A.J., Johnston, S.E., Karlsson, S., and Kent, M. 2015. Sex-dependent dominance at a single locus maintains variation in age at maturity in salmon. Nature, 528(7582): 405.

- Beaugrand, G., and Reid, P.C. 2012. Relationships between North Atlantic salmon, plankton, and hydroclimatic change in the Northeast Atlantic. *ICES J. Mar. Sci.* 69: 1549–1562.
- Beck, C.A., Iverson, S.J., Bowen, W.D., and Blanchard, W. 2007. Sex differences in grey seal diet reflect seasonal variation in foraging behaviour and reproductive expenditure: evidence from quantitative fatty acid signature analysis. *J. Anim. Ecol.* 76: 490–502.
- Berrow, S., O'Brien, J., Groth, L., Foley, A., and Voigt, K. 2012. Abundance estimate of bottlenose dolphins (*Tursiops truncatus*) in the Lower River Shannon candidate special area of conservation, Ireland. *Aquatic Mammals*, 38(2): 136–144.
- Berry, J. 1935. British mammals and birds as enemies of the Atlantic salmon (*Salmo salar*). Reports of the Avon Biological Research, 35: 31–64.
- Berx, B., and Payne, M. 2017. The Sub-Polar Gyre Index - A community data set for application in fisheries and environment research. *Earth System Science Data*.
- Bjorge, A., and Donovan, G.P. 1995. Biology of the phocoenids. Reports of the International Whaling Commission, 16: 1–552.
- Bjorge, A., and Tolley, K.A. 2018. Harbour porpoise (*Phocoena phocoena*). In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 448–451.
- Boecklen, W.J., Yarnes, C.T., Cook, B.A., and James, A.C. 2011. On the use of stable isotopes in trophic ecology. *Annual review of ecology, evolution, and systematics* 42: 411–440.
- Bolt, H.E., Harvey, P.V., Mandelberg, L., and Foote, A., 2009. Occurrence of killer whales in Scottish inshore waters: temporal and spatial patterns relative to the distribution of declining harbour seal populations. *Aquatic Conservation: Marine and Freshwater Ecosystems* 19: 671–675.
- Bonner, W.N. 1981. Grey Seal. In: Ridgway, S.H. and Harrison, R.J. (Eds.). *Handbook of Marine Mammals*. Academic Press, London, pp. 111–144.
- Booker, D.J., Wells, N.C., and Smith, P.I. 2008. Modelling the trajectories of migrating Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 65: 352–361.
- Bordeleau, X., Pardo, S.A., Chaput, G., April, J., Dempson, B., Robertson, M., Levy, A., Jones, R., Hutchings, J.A., Whoriskey, F.G., and Crossin, G.T. 2019. Spatio-temporal trends in the importance of iteroparity across Atlantic salmon populations of the Northwest Atlantic. *ICES J. Mar. Sci.* 77: 326–344.
- Bourne, C., Mowbray, F., Squires, B., and Koen-Alonso, M. 2018. 2017. Assessment of Newfoundland east and south coast Atlantic herring (*Clupea harengus*) stock complexes. DFO Can. Sci. Advis. Sec. Res. Doc. 2018/026. v + 45 p.
- Bowen, W.D., and Harrison, G.D. 1996. Comparison of harbour seal diets in two inshore habitats of Atlantic Canada. *Can. J. Zool.* 74: 125–135.
- Bowen, W.D., and Siniff, D.B. 1999. Distribution, population biology, and feeding ecology of marine mammals. In: Reynolds, J.E.I. and Rommel, S.A. (Eds.). *Biology of marine mammals*. Smithsonian Press, Washington, DC, pp. 423–484.
- Bowen, W.D., Lawson, J.W., and Beck, B. 1993. Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. *Can. J. Fish. Aquat. Sci.* 50: 1768–1778.
- Bowen, W.D., Ellis, S.L., Iverson, S.J., and Boness, D.J. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. *Journal of Zoology London* 261: 15–163.
- Bowlby, H.D., Horsman, T., Mitchell, S.C., and Gibson, A.J.F. 2014. Recovery Potential Assessment for Southern Upland Atlantic Salmon: Habitat Requirements and Availability, Threats to Populations, and Feasibility of Habitat Restoration. DFO Can. Sci. Advis. Sec. Res. Doc. 2013/006. vi + 155 p.
- Boyle, P.R., Pierce, G.J., and Diack, J.S.W. 1990. Sources of evidence for salmon in the diet of seals. *Fisheries Res.* 10: 137–150.

- Bracis, C., and Anderson, J. 2012. An investigation of the geomagnetic imprinting hypothesis for salmon. *Fish. Oceanogr.* 21: 170–181.
- Buren, A.D., Murphy, H.M., Adamack, A.T., Davoren, G.K., Koen-Alonso, M., Montevecchi, W.A., Mowbray, F.K., Pepin, P., Regular, P.M., Robert, D., Rose, G.A., Stenson, G.B., and Varkey, D. 2019. The collapse and continued low productivity of a keystone forage fish species. *Mar. Ecol. Prog. Ser.* 616: 155–170.
- Burke, B., Anderson, B., and Baptista, A. 2014. Evidence for multiple navigational sensory capabilities by Chinook salmon. *Aquat Biol* 20: 77–90.
- Butler, J.R., Middlemas, S.J., Graham, I.M., Thompson, P.M., and Armstrong, J.D. 2006. Modelling the impacts of removing seal predation from Atlantic salmon, *Salmo salar*, rivers in Scotland: a tool for targeting conflict resolution. *Fish. Manag. Ecol.* 13: 285–291.
- Butler, J.R., Middlemas, S.J., McKelvey, S.A., McMyn, I., Leyshon, B., Walker, I., Thompson, P.M., Boyd, I.L., Duck, C., Armstrong, J.D., and Graham, I.M. 2008. The Moray Firth Seal Management Plan: an adaptive framework for balancing the conservation of seals, salmon, fisheries and wildlife tourism in the UK. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 18: 1025–1038.
- Butler, J.R., Middlemas, S.J., Graham, I.M., and Harris, R.N. 2011. Perceptions and costs of seal impacts on Atlantic salmon fisheries in the Moray Firth, Scotland: implications for the adaptive co-management of seal-fishery conflict. *Marine Policy* 35: 317–323.
- Byron, C.J., and Burke, B.J. 2014. Salmon ocean migration models suggest a variety of population-specific strategies. *Rev. Fish Biol. Fish.* 24: 737–756.
- Byron, C.J., Pershing, A., Stockwell, J., Xue, H., and Kocik, J. 2014. Migration model of post-smolt Atlantic salmon in the Gulf of Maine. *Fish. Oceanogr.* 23: 172–189.
- Cabana, G., and Rasmussen, J.B. 1994. Modelling food chain structure and contaminant bioaccumulation using stable nitrogen isotopes. *Nature* 372(6503): 255–257.
- Cairns, D.K. 2001. Approaches and methods for the scientific evaluation of bird and mammal predation on salmon in the Northwest Atlantic. DFO Can. Sci. Advis. Sec. Res. Doc. 2001/011.
- Cairns, D.K. 2003a. Feeding, fasting, and weight-based estimation of natural mortality in marine-phase Atlantic salmon (*Salmo salar* L.). In: Potter, E.C.E., Ó Maoiléidigh, N and Chaput, G. (Eds.). *Marine Mortality of Atlantic Salmon, Salmo salar L: Methods and Measures*. DFO Can. Sci. Advis. Sec. Res. Doc., 2003/101, pp. 162–197.
- Cairns, D.K. 2003b. Temperature-mortality relation in marine-phase Atlantic salmon (*Salmo salar*, L.): The search for underlying mechanisms. In: Potter, E.C.E., Ó Maoiléidigh, N. and Chaput, G. (Eds.). *Marine Mortality of Atlantic Salmon, Salmo salar L: Methods and Measures*. DFO Can. Sci. Advis. Sec. Res. Doc., 2003/101, pp.150–161.
- Cairns, D.K. 2006. A review of predator-prey and competitive inter-specific interactions in Atlantic salmon (*Salmo salar*). DFO Can. Sci. Advis. Sec. Res. Doc. 2006/019.
- Cairns, D.K., and Reddin, D.G. 2000. The potential impact of seal and seabird predation on Northwest Atlantic salmon. DFO Can. Stock Assess. Sec. Res. Doc. 2000/12.
- Camphuysen, C.J. 2004. The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. *Lutra* 47: 113–122.
- Centre for Environment, Fisheries and Aquaculture Science, Environment Agency and Natural Resources Wales. 2019. Salmon Stocks and Fisheries in England and Wales in 2018. Preliminary assessment prepared for ICES, March 2019, 87 pp.
- Chaput, G. 2012. Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality. *ICES J. Mar. Sci.* 69: 1538–1548.
- Chaput, G., and Benoit, H.P. 2012. Evidence for bottom-up trophic effects on return rates to a second spawning for Atlantic salmon (*Salmo salar*) from the Miramichi River, Canada. *ICES J. Mar. Sci.* 69: 1656–1667.

- Chaput, G., and Jones, R.A. 2006. Reproductive rates and rebuilding potential for two multi-sea-winter Atlantic salmon (*Salmo salar* L.) stocks of the Maritime Provinces. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/027, 31 pp.
- Chaput, G., Caron, F., and Marshall, L. 2003. Estimates of survival of Atlantic salmon in the first and second years at sea. In: Potter, E.C.E., Ó Maoiléidigh, N. and Chaput, G. (Eds.). Marine Mortality of Atlantic Salmon, *Salmo salar* L.: Methods and Measures. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/101, pp. 83–109.
- Chaput, G., Carr, J., Daniels, J., Tinker, S., Jonsen, I., and Whoriskey, F. 2018. Atlantic salmon (*Salmo salar*) smolt and early post-smolt migration and survival inferred from multi-year and multi-stock acoustic telemetry studies in the Gulf of St. Lawrence, northwest Atlantic. ICES J. Mar. Sci. 76: 1107–1121.
- Chardine, J.W., Rail, J.-F., and Wilhelm, S. 2013. Population dynamics of Northern Gannets in North America, 1984–2009. J. Field Ornithol. 84: 187–192.
- Chittenden, C.M., Fauchald, P., and Rikardsen, A.H. 2013a. Important open-ocean areas for northern Atlantic salmon (*Salmo salar*) — as estimated using a simple ambient-temperature approach. Can. J. Fish. Aquat. Sci. 70: 101–104.
- Chittenden, C.M., Ådlandsvik, B., Pedersen, O.-P., Righton, D., and Rikardsen, A.H. 2013b. Testing a model to track fish migrations in polar regions using pop-up satellite archival tags. Fish. Oceanogr. 22: 1–13.
- Cockcroft, V.G., and Ross, G.J.B. 1990. Age, growth and reproduction in bottlenose dolphins from the east coast of southern Africa. Fish. Bull. 88: 289–302.
- Condron, A., DeConto, R., Bradley, R.S., and Juanes, F. 2005. Multidecadal North Atlantic climate variability and its effect on North American salmon abundance. Geophysical Research Letters, 32: L23703. 4 pp.
- Cosentino, A.M. 2015. First record of Norwegian killer whales attacking and feeding on a harbour porpoise. Marine Biodiversity Records 8: e108.
- Crozier, W.W., and Kennedy, G.J.A. 1994. Marine exploitation of Atlantic salmon (*Salmo salar* L.) from the River Bush, Northern Ireland. Fish. Res. 19: 141–155.
- Crozier, W.W., Potter, E.C.E., Prevost, E., Schon, P.J., and O'Maoiléidigh, N. 2003. A co-ordinated approach towards development of a scientific basis for management of wild Atlantic salmon in the North-East Atlantic (SALMODEL). An EU Concerted Action - Quality of Life and Management of Living Resources Key Action 5: Sustainable agriculture, fisheries and forestry, and integrated development of rural areas including mountain areas. Contract No. QLK5-CT1999-01546, 431 pp.
- Crozier, W., Whelan, K., Buoro, M., Chaput, G., Daniels, J., Grant, S., Hyatt, K., Irvine, J., Ó'Maoiléidigh, N., Prévost, E., Rivot, E., Russell, I., Schmidt, M., and Wells, B. 2018. Atlantic salmon mortality at sea: Developing an evidence-based “Likely Suspects” Framework. Based on a workshop organised by the Atlantic Salmon Trust, held in Edinburgh Tuesday, 6th November–Thursday, 8th November 2017. Atlantic Salmon Trust, Edinburgh (UK Scotland).
- Cunningham, L., Baxter, J.M., Boyd, I.L., Duck, C.D., Lonergan, M., Moss, S.E., and McConnell, B. 2009. Harbour seal movements and haul-out patterns: implications for monitoring and management. Aquatic Conservation: Marine and Freshwater Ecosystems 19: 398–407.
- Czorlich, Y., Aykanat, T., Erkinaro, J., Orell, P., and Primmer, C.R. 2018. Rapid sex-specific evolution of age at maturity is shaped by genetic architecture in Atlantic salmon. Nature Ecol. Evol. 2: 1800.
- Daniels, J., Chaput, G., and Carr, J. 2018. Estimating consumption rate of Atlantic salmon smolts (*Salmo salar*) by striped bass (*Morone saxatilis*) in the Miramichi River estuary using acoustic telemetry. Can. J. Fish. Aquat. Sci. 75: 1811–1822.
- Daniels, J., Sutton, S., Webber, D., and Carr, J. 2019. Extent of predation bias present in migration survival and timing of Atlantic salmon smolt (*Salmo salar*) as suggested by a novel acoustic tag. Anim Biotelemetry (2019) 7:16, <https://doi.org/10.1186/s40317-019-0178-2>.
- Dankel, D.J., Skagen, D.W., and Ulltang, O. 2008. Fisheries management in practice: review of 13 commercially important fish stocks. Reviews in Fish Biology and Fisheries 18: 201–233.

- Darbyson, E., and Benoît, H.P. 2003. An atlas of the seasonal distribution of marine fish and invertebrates in the southern gulf of St. Lawrence. Can. Data Rep. Fish. Aquat. Sci. no. 1113: iii + 294 p.
- Davenport, J.C, Black, K.D., Burnell, G., et al. 2009. Aquaculture: The Ecological Issues. John Wiley & Sons. 96 pp.
- Davidson, J.G., Rikardsen, A.H., Halttunen, E., Thorstad, E.B., Økland, F., Letcher, B.H., Skarðhamar, J., and Næsje, T.F. 2009. Migratory behaviour and survival rates of wild northern Atlantic salmon *Salmo salar* post-smolts: effects of environmental factors. J. Fish Biol. 75: 1700–1718.
- de Bruyn, P.N., Tosh, C.A., and Terauds, A. 2013. Killer whale ecotypes: is there a global model? Biological Reviews 88: 62–80.
- Dempson, J.B., Pepper, V.A., Furey, G., Bloom, M., Nicholls, T., and Hoskins, G. 1999. Evaluation of an alternative strategy to enhance salmon populations: Cage rearing wild smolts from Conne River, Newfoundland. ICES J. Mar. Sci. 56: 422–432.
- Dempson, J.B., Schwarz, C.J., Reddin, D.G., O'Connell, M.F., Mullins, C.C., and Bourgeois, C.E. 2001. Estimation of marine exploitation rates on Atlantic salmon (*Salmo salar* L.) stocks in Newfoundland, Canada. ICES J. Mar. Sci. 58: 331–341.
- Dempson, J.B., O'Connell, M.F., and Schwarz, C.J. 2004. Spatial and temporal trends in abundance of Atlantic salmon, *Salmo salar*, in Newfoundland with emphasis on impacts of the 1992 closure of the commercial fishery. Fish. Manag. Ecol. 11: 387–402.
- Dempson, J.B., Braithwaite, V.A., Doherty, D., and Power, M. 2010. Stable isotope analysis of marine feeding signatures of Atlantic salmon in the North Atlantic. ICES J. Mar. Sci. 67: 52–61.
- Dempson, J.B., Robertson, M.J., Pennell, C.J., Furey, G., Bloom, M., Shears, M., Ollerhead, L.M.N., Clarke, K.D., Hinks, R., and Robertson, G.J. 2011. Residency time, migration route and survival of Atlantic salmon *Salmo salar* smolts in a Canadian fjord. J. Fish Biol. 78: 1976–1992.
- DeNiro, M.J., and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. Geochimica et cosmochimica acta 42(5): 495–506.
- DeNiro, M.J., and Epstein, S. 1981. Influence of diet on the distribution of nitrogen isotopes in animals. Geochimica et cosmochimica acta 45(3): 341–351.
- Deser, C., Holland, M., Reverdin, G., and Timlin, M. 2002. Decadal variations in Labrador Sea ice cover and North Atlantic sea surface temperatures. J. Geophys. Res. 107, C5, 10.1029/2000JC000683.
- DFO. 1996. Scotian Shelf Sand Lance. DFO Atlantic Fisheries Stock Status Report 96/77E.
- DFO. 2017. Stock assessment of Canadian Northwest Atlantic Grey Seals (*Halichoerus grypus*). DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2017/045.
- DFO. 2019. Oceanographic Conditions in the Atlantic Zone in 2018. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2019/034.
- Dickey-Collas, M., Hintzen, N.T., Nash, R.D.M., Schön, P.-J., Payne, M.R. 2015. Quirky patterns in time-series of estimates of recruitment could be artefacts. ICES J. Mar. Sci. 72: 111–116.
- Dieperink, C., Bak, B.D., Pedersen, L.-F., Pedersen, M.I., and Pedersen, S. 2002. Predation on Atlantic salmon and sea trout during their first days as postsmolts. J. Fish Biol. 61: 848–852.
- Donovan, G.P. and Bjørge, A. 1995. Harbour porpoises in the North Atlantic: edited extract from the report of the IWC Scientific Committee, Dublin 1995. Reports of the International Whaling Commission, 16: 3–25.
- Drinkwater, K.F. 2006. The regime shift of the 1920s and 1930s in the North Atlantic. Prog. Ocean. 68: 134–151.
- Drinkwater, K., Colbourne, E., Loeng, H., Sundby, S., and Kristiansen, T. 2013. Comparison of the atmospheric forcing and oceanographic responses between the Labrador Sea and the Norwegian and Barents seas. Prog. Ocean. 114: 11–25.

- Drinkwater, K.F., and Kristiansen, T. 2018. A synthesis of the ecosystem responses to the late 20th century cold period in the northern North Atlantic. *ICES J. Mar. Sci.* 75: 2325–2341.
- Ducharme, L.J.A. 1969. Atlantic salmon returning for their fifth and sixth consecutive spawning trips. *J. Fish. Res. Board Can.* 26: 1661–1664.
- Duston, J., and Saunders, R.L. 1997. Life histories of Atlantic salmon altered by winter temperature and summer rearing in fresh-or sea-water. *Env. Biol. Fishes* 50: 149–166.
- Duston, J., and Saunders, R.L. 1999. Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (*Salmo salar*) in seawater. *Can. J. Fish. Aquat. Sci.* 56: 201–207.
- Eerkes-Medrano, D, Fryer, R.J., Cook, K.B., et al. 2017. Are simple environmental indicators of food web dynamics reliable: Exploring the kittiwake relationship. *Ecological Indicators* 75: 36–47.
- Ehleringer, J.R, and Rundel, P.W. 1989. Stable isotopes: history, units, and instrumentation. In: Rundel, P.W., Ehleringer, J.R. and Nagy, K.A. (eds). *Stable isotopes in ecological research*. Springer, New York, NY, pp. 1–15.
- Enfield, D.B., Mestas-Nunez, A.M., and Trimble, P.J. 2001. The Atlantic multidecadal oscillation and its relation to rainfall and river flows in the continental U.S. *Geophys. Res. Lett.* 28: 2077–2080.
- Erkinaro, J., Czorlich, Y., Orell, P., Kuusela, J., Falkegård, M., Länsman, M., Pulkkinen, H., Primmer, C.R., and Niemelä, E. 2018. Life history variation across four decades in a diverse population complex of Atlantic salmon in a large subarctic river. *Can. J. Fish. Aquat. Sci.* 76: 42–55.
- Evans, P.G. 1988. Killer whales (*Orcinus orca*) in British and Irish waters. *Rit Fiskideildar*, 11: 42–54.
- Evans, P.G. 2018. Habitat pressures. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 441–446.
- Eveillard-Buchoux, M., Beninger, P.G., Chadenas, C., and Sellier, D. 2017. European Seabirds Show Stable Contemporary Biogeography. *Waterbirds* 40(4): 309–321.
- Fauchald, P., Anker-Nilssen, T., Barrett, R.T., Bustnes, J.O., Bårdsen, B.J., Christensen-Dalsgaard, S., Descamps, S., Engen, S., Erikstad, K.E., Hanssen, S.A., Lorentsen, S.-H., Moe, B., Reiertsen, T.K., Strøm, H., and Systad, G.H. 2015. The status and trends of seabirds breeding in Norway and Svalbard. NINA Report 1151. 84 pp.
- Fleming, I.A. 1996. Reproductive strategies of Atlantic salmon: ecology and evolution. *Rev. Fish Biol. Fish.* 6: 379–416.
- Folkow, L.P., Nordøy, E.S., and Blix, A.S. 2004. Distribution and diving behaviour of harp seals (*Pagophilus groenlandicus*) from the Greenland Sea stock. *Polar Biology* 27: 281–298.
- Foote, A.D., Newton, J., Piertney, S.B., Willerslev, E., and Gilbert, M.T.P. 2009. Ecological, morphological and genetic divergence of sympatric North Atlantic killer whale populations. *Mol. Ecol.* 18: 5207–5217.
- Foote, A.D., Similä, T., Víkingsson, G.A., and Stevick, P.T. 2010. Movement, site fidelity and connectivity in a top marine predator, the killer whale. *Evol. Ecol.* 24: 803–814.
- Foote, A.D., Vilstrup, J.T., De Stephanis, R., Verborgh, P., Abel Nielsen, S.C., Deaville, R., Kleivane, L., Martin, V., Miller, P.J., Øien, N., Pérez-Gil, M., Rasmussen, M., Reid, R. J., Robertson, K. M., Rogan, E., Similä, T., Tejedor, M. L., Vester, H., Víkingsson, G.A., Willerslev, E., Gilbert, M.T., and Piertney, S.B. 2011. Genetic differentiation among North Atlantic killer whale populations. *Mol. Ecol.* 20: 629–641.
- Ford, J.K.B. 2018. Killer whale *Orcinus orca*. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 531–536.
- Ford, J.K., and Ellis, G.M. 2006. Selective foraging by fish-eating killer whales *Orcinus orca* in British Columbia. *Mar. Ecol. Prog. Ser.* 316: 185–199.
- Ford, J.K., Ellis, G.M., Barrett-Lennard, L.G., Morton, A.B., Palm, R.S, and Balcomb III, K.C. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus orca*) in coastal British Columbia and adjacent waters. *Can. J. Zool.* 76: 1456–1471.

- Ford, J.K.B., Ellis, G.M., and Balcomb, K.C. 2000. Killer whales: the natural history and genealogy of *Orcinus orca* in the waters of British Columbia and Washington. UBC Press, Vancouver, BC, and University of Washington Press, Seattle, WA.
- Ford, J.K., Ellis, G.M., Olesiuk, P.F., and Balcomb, K.C. 2009. Linking killer whale survival and prey abundance: food limitation in the oceans' apex predator. *Biology Letters*, 6: 139–142.
- Forney, K.A., Wade, P.R., and Estes, J.A. 2006. Worldwide distribution and abundance of killer whales. In: Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M. and Brownell, R.L. (Eds.). *Whales, Whaling and Ocean Ecosystems*, University of California Press, Berkeley, CA, pp. 145–162.
- Frederiksen, M. 2010. Appendix 1: Seabirds in the North East Atlantic. A review of status, trends and anthropogenic impact. *TemaNord*. 587. 47–122.
- Frederiksen, M., Edwards, M., Richardson, A.J., Halliday, N.C., and Wanless, S. 2006. From plankton to top predators: bottom-up control of a marine food web across four trophic levels. *J. Anim. Ecol.* 75: 1259–1268.
- Frederiksen, M., Furness, R., and Wanless, S. 2007. Regional variation in the role of bottom-up and top-down processes in controlling sandeel abundance in the North Sea. *Mar. Ecol. Prog. Ser.* 337: 279–286.
- Friedland, K.D., and Todd, C.D. 2012. Changes in Northwest Atlantic Arctic and Subarctic conditions and the growth response of Atlantic salmon. *Polar Biol.* 35:593–609.
- Friedland, K.D., Reddin, D.G., and Kocik, J.F. 1993. Marine survival of North American and European Atlantic salmon: effects of growth and environment. *ICES J. Mar. Sci.* 50: 481–492.
- Friedland, K.D., Hansen, L.P., Dunkley, D.A., and MacLean, J.C. 2000. Linkage between ocean climate, post-smolt growth, and survival of Atlantic salmon (*Salmo salar* L.) in the North Sea area. *ICES J. Mar. Sci.* 57: 419–429.
- Friedland, K.D., MacLean, J.C., Hansen, L.P., Peyronnet, A.J., Karlsson, L., Reddin, D.G., Ó Maoiléidigh, N., and McCarthy, J.L. 2009. The recruitment of Atlantic salmon in Europe. *ICES J. Mar. Sci.* 66: 289–304.
- Friedland, K.D., Manning, J.P., Link, J.S., Gilbert, J.R., Gilbert, A.T., and O'Connell Jr, A.F. 2012. Variation in wind and piscivorous predator fields affecting the survival of Atlantic salmon, *Salmo salar*, in the Gulf of Maine. *Fish. Manag. Ecol.* 19: 22–35.
- Friedland, K.D., Shank, B.V., Todd, C.D., McGinnity, P., and Nye, J.A. 2014. Differential response of continental stock complexes of Atlantic salmon (*Salmo salar*) to the Atlantic Multidecadal Oscillation. *J. Mar. Syst.* 133: 77–87.
- Friedland, K.D., Mouw, C.B., Asch, R.G., Ferreira, A.S.A., Henson, S., Hyde, K.J.W., Morse, R.E., Thomas, A.C., and Brady, D.C. 2018. Phenology and time series trends of the dominant seasonal phytoplankton bloom across global scales. *Glob. Ecol. Biogeogr.* 27: 551–569.
- Fry, B. 2006. *Stable isotope ecology*. Springer, New York, NY.
- Gannes, L.Z., O'Brien, D.M., and Del Rio, C.M. 1997. Stable isotopes in animal ecology: assumptions, caveats, and a call for more laboratory experiments. *Ecol.* 78: 1271–1276.
- Gannon, D.P., and Waples, D.M. 2004. Diets of coastal bottlenose dolphins from the US mid-Atlantic coast differ by habitat. *Marine Mammal Science* 20: 527–545.
- Gardner, M.L. 1976. A review of factors which may influence the sea-age and maturation of Atlantic salmon *Salmo salar* L. *J. Fish Biol.* 9: 289–327.
- Garthe, S., Montevecchi, W.A., Chapdelaine, G., Rail, J.-F., and Hedd, A. 2007. Contrasting foraging tactics by northern gannets (*Sula bassana*) breeding in different oceanographic domains with different prey fields. *Mar. Biol.* 151: 687–694.
- Gaston, A.J., Bertram, D.F., Boyne, A.W., Chardine, J.W., Davoren, G., Diamond, A.W., Hedd, A., Montevecchi, W.A., Hipfner, J.M., Lemon, M.J.F., Mallory, M.L., Rail, J.-F., and Robertson, G.J. 2009. Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs. *Environ. Rev.* 17: 267–286.

- Gerber, L.R., DeMaster, D.P., and Roberts, S.P. 2000. Measuring Success in Conservation: Assessing efforts to restore populations of marine mammals is partly a matter of epistemology: How do you know when enough is enough? *American Scientist* 88: 316–324.
- Gibson, A.J., Halfyard, E.A., Bradford, R.G., Stokesbury, M.J., and Redden, A.M. 2015. Effects of predation on telemetry-based survival estimates: insights from a study on endangered Atlantic salmon smolts. *Can J Fish Aquat Sci.* 72: 728–741.
- Gilbert, N. 2018. News Feature: Deadly deficiency at the heart of an environmental mystery. *Proc. Nat. Acad. Sci.* 115.42, pp. 10532–10536.
- Gilbey, J. *et al.* In preparation. Marine distribution and regional origin of Atlantic salmon (*Salmo salar* L.) post-smolts in the North-Eastern Atlantic. Manuscript in preparation.
- Gjerdrum, C., Allard, K., and Bolduc, F. 2012. Pelagic seabird monitoring and research in the northwest Atlantic. Northwest Atlantic Fisheries Organization Serial No. N6055, NAFO SCR Doc. 12/029.
- Good, C., and Davidsen, J. 2016. A review of factors influencing maturation of Atlantic Salmon, *Salmo salar*, with focus on water recirculation aquaculture system environments. *J. World Aqua. Soc.* 47: 605–632.
- Graham, B.S., Koch, P.L., Newsome, S.D., McMahon, K.W., and Aurioles, D. 2010. Using isoscapes to trace the movements and foraging behavior of top predators in oceanic ecosystems. In: West, J.B., Bowen, G.J., Dawson, T.E. and Tu, K.P. (eds). *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer, Dordrecht, pp. 299–318.
- Graham, I.M., Harris, R.N., Denny, B., Fowden, D., and Pullan, D. 2009. Testing the effectiveness of an acoustic deterrent device for excluding seals from Atlantic salmon rivers in Scotland. *ICES J. Mar. Sci.* 66: 860–864.
- Graham, I.M., Harris, R.N., Matejusová, I., and Middlemas, S.J. 2011. Do ‘rogue’ seals exist? Implications for seal conservation in the UK. *Animal Conservation* 14: 587–598.
- Grégoire, F., and Savenkoff, C. 2005. Atlantic mackerel (*Scomber scombrus* L.) fishery, biology, diet composition and predation in NAFO Subareas 3 and 4 in 2004. *DFO Can. Sci. Advis. Secr. Res. Doc.* 2005/056.
- Gregory, S.D., Armstrong, J.D., and Britton, J.R. 2018. Is bigger really better? Towards improved models for testing how Atlantic salmon *Salmo salar* smolt size affects marine survival. *J. Fish Biol.* 9: 579–592.
- Gregory, S.D., Ibbotson, A.T., Riley, W.D., Nevoux, M., Lauridsen, R.B., Russell, I.C., Britton, J.R., Gillingham, P.K., Simmons, O.M., and Rivot, E. 2019. Atlantic salmon return rate increases with smolt length. *ICES J. Mar. Sci.* 76: 1702–1712.
- Gudjonsson, S., Einarsson, S.M., Antonsson, T., and Gudbergsson, G. 1995. Relation of grilse to salmon ratio to environmental changes in several wild stocks of Atlantic salmon (*Salmo salar*) in Iceland. *Can. J. Fish. Aquat. Sci* 52: 1385–1398.
- Guðjónsson, S., Einarsson, S.M., Jónsson, I.R., and Guðbrandsson, J. 2015. Marine feeding areas and vertical movements of Atlantic salmon (*Salmo salar*) as inferred from recoveries of data storage tags. *Can. J. Fish. Aquat. Sci.* 72: 1087–1098.
- Gunnlaugsson, T., and Sigurjónsson, J. 1990. NASS-87: Estimation of whale abundance based on observations made onboard Icelandic and Faroese survey vessels. *Reports of the International Whaling Commission*, 40: 571–580.
- Halfyard, E.A., Gibson, A.J.F., Ruzzante, D.E., Stokesbury, M.J.W., and Whoriskey, F.G. 2012. Estuarine survival and migratory behaviour of Atlantic salmon *Salmo salar* smolts. *J. Fish Biol.* 81: 1626–1645.
- Halfyard, E.A., Webber, D., Del Papa, J., Leadley, T., Kessel, S.T., Colborne, S.F., and Fisk, A.T. 2017. Evaluation of an acoustic telemetry transmitter designed to identify predation events. *Methods Ecol Evol.* 8: 1063–1071.
- Hall, A.J., and Russell, D.J.F. 2018. Gray seal *Halichoerus grypus*. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 420–422.

- Hall, A.J., Watkins, J., and Hammond, P.S. 1998. Seasonal variation in the diet of harbour seals in the southwestern North Sea. *Mar. Ecol. Prog. Ser.* 170: 269–281.
- Halttunen, E., Rikardsen, A.H., Davidsen, J.G., Thorstad, E.B., and Dempson, J.B. 2009. Survival, migration speed and swimming depth of Atlantic salmon kelts during sea entry and fjord migration. In: Nielsen, J.L., Arrizabalaga, H., Fragoso, N., Hobday A., Lutcavage M., and Sibert, J. (Eds.). *Tagging and Tracking of Marine Animals with Electronic Devices. Reviews: Methods and Technologies in Fish Biology and Fisheries 9*, Springer, New York, pp. 35–49.
- Hammill, M.O., and Stenson, G.B. 2000. Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *J. Northwest Atl. Fish. Sci.* 26: 1–24.
- Hammill, M.O., Lesage, V., and Carter, P. 2005. What do harp seals eat? Comparing diet composition from different compartments of the digestive tract with diets estimated from stable-isotope ratios. *Can. J. Zool.* 83: 1365–1372.
- Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T., and Mosnier, A. 2011. Northwest Atlantic Harp Seals Population Trends, 1952–2012. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/099. iv + 28 p.
- Hammill, M.O., den Heyer, C.E., and Bowen, W.D. 2014. Grey seal population trends in Canadian waters, 1960–2014. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/037, pp. 44.
- Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T., and Mosnier, A. 2015. Conservation of Northwest Atlantic harp seals: Past success, future uncertainty? *Biol. Cons.* 192: 181–191.
- Hammond, P.S., Berggren, P., Benke, H., Borchers, D.L., Collet, A., Heide-Jørgensen, M.P., Heimlich, S., Hiby, A.R., Leopold, M.F., and Øien, N. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. *J. Appl. Ecol.* 39: 361–376.
- Hammond, P.S., Macleod, K., Berggren, P., Borchers, D.L., Burt, L., Cañadas, A., Desportes, G., Donovan, G.P., Gilles, A., Gillespie, D., and Gordon, J. 2013. Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. *Biol. Cons.* 164: 107–122.
- Hammond, P., Lacey, C., Gilles, A., Viquerat, S., Börjesson, P., Herr, H., Macleod, K., Ridoux, V., Santos, M.B., Scheidat, M., Teilmann, J., Vingada, J., and Øien, N. 2017. Estimates of Cetacean Abundance in European Atlantic Waters in Summer 2016 from the SCANS-III Aerial and Shipboard Surveys. Sea Mammal Research Unit, University of St Andrews, UK, pp. 40.
- Handeland, S.O., Järvi, T., Fernö, A., and Stefansson, S.O. 1996. Osmotic stress, antipredatory behaviour, and mortality of Atlantic salmon (*Salmo salar*) smolts. *Can. J. Fish. Aquat. Sci.* 53: 2673–2680.
- Hansen, L.P., Holm, M., Holst, J.C., and Jacobsen, J.A. 2003. The ecology of post-smolts of Atlantic salmon. In: Mills, D. (Ed.). *Salmon at the Edge*, Oxford, Blackwell Science, pp. 307.
- Hansen, L.P. and Jonsson, B. 1994. Homing in Atlantic salmon: effects of juvenile learning on transplanted post-spawners. *Animal Behaviour* 47: 220–222.
- Harding, K.C., Härkönen, T., Helander, B., and Karlsson, O. 2007. Status of Baltic grey seals: Population assessment and extinction risk. NAMMCO Scientific Publications, 6: 33–56.
- Härkönen, T., Dietz, R., Reijnders, P., Teilmann, J., Harding, K., Hall, A., Brasseur, S., Siebert, U., Goodman, S.J., Jepson, P.D., and Rasmussen, T.D. 2006. The 1988 and 2002 Phocine distemper virus epidemics in European harbour seals. *Diseases of Aquatic Organisms*, 68: 115–130.
- Harris, R.N., Harris, C.M., Duck, C.D., and Boyd, I.L. 2014. The effectiveness of a seal scarer at a wild salmon net fishery. *ICES J. Mar. Sci.* 71: 1913–1920.
- Hastie, G.D., Wilson, B.E.N., Wilson, L.J., Parsons, K.M., and Thompson, P.M. 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Mar. Biol.* 144: 397–403.
- Hátún, H., Sandø, A. B., Drange, H., Hansen, B., and Valdimarsson, H. 2005. Influence of the Atlantic sub-polar gyre on the thermohaline circulation. *Science* 309, 1841–1844. doi: 10.1126/science.1114777

- Hátún, H., Payne, M.R., Beaugrand, G., Reid, P.C., Sandø, A.B., Drange, H., Hansen, B., Jacobsen, J.A., and Bloch, D. 2009. Large bio-geographical shifts in the north-eastern Atlantic Ocean: from the subpolar gyre, via plankton, to blue whiting and pilot whales. *Prog Oceanogr* 80: 149–162.
- Hátún, H., Lohmann, K., Matei, D., Jungclaus, J., Pacariz, S., Bersch, M., Gislason, A., Ólafsson, J., and Reid, P.C. 2016. An inflated subpolar gyre blows life towards the Northeastern Atlantic. *Prog. Oceanogr.* 147: 49–66.
- Hátún, H., Olsen, B., and Pacariz, S. 2017. The Dynamics of the North Atlantic Subpolar Gyre Introduces Predictability to the Breeding Success of Kittiwakes. *Front. Mar. Sci.* 4:123.
- Haug, T., and Nilssen, K.T. 1995. Ecological implications of harp seal *Phoca groenlandica* invasions in northern Norway. In: Blix, A.S., Walløe, L., Ulltang, O. (Eds.). *Whales, seals, fish and man, Volume 4*, Elsevier, Amsterdam, pp. 545–556.
- Haug, T., Krøyer, A.B., Nilssen, K.T., Ugland, K.I., and Aspholm, P.E. 1991. Harp seal (*Phoca groenlandica*) invasions in Norwegian coastal waters: age composition and feeding habits. *ICES J. Mar. Sci.* 48: 363–371.
- Haug, T., Henriksen, G., Kondakov, A., Mishin, V., Nilssen, K.T., and Røv, N. 1994a. The status of grey seals *Halichoerus grypus* in North Norway and on the Murman coast, Russia. *Biol. Cons.* 70: 59–67.
- Haug, T., Nilssen, K.T., Ien, N., and Potelov, V. 1994b. Seasonal distribution of harp seals (*Phoca groenlandica*) in the Barents Sea. *Polar Res.* 13: 163–172.
- Haugland, M., Holst, J. C., Holm, M., and Hansen, L. P. 2006. Feeding of Atlantic salmon (*Salmo salar* L.) post-smolts in the Northeast Atlantic. *ICES J. Mar. Sci.* 63: 1488–1500.
- Hawkes, J.P., Saunders, R., Vashon, A.D., and Cooperman, M.S. 2013. Assessing efficacy of non-lethal harassment of double-crested cormorants to improve Atlantic salmon smolt survival. *Northeastern Naturalist* 20: 1–19.
- Hayes, S.A., Josephson, E., Maze-Foley, K., and Rosel, P.E. 2019. US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 2018. NOAA Technical Memorandum NMFS-NE-258. NOAA, NMFS, Woods Hole, MA, pp. 291.
- Heath, M.R., Neat, F.C., Pinnegar, J.K., *et al.* 2012. Review of climate change impacts on marine fish and shellfish around the UK and Ireland. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 337–367. DOI: 10.1002/aqc.2244.
- Hedger, R.D., Rikardsen, A.H., Strøm, J.F., Righton, D.A., Thorstad, E.B., and Næsje, T.F. 2017a. Diving behaviour of Atlantic salmon at sea: effects of light regimes and temperature stratification. *Mar. Ecol. Prog. Ser.* 574: 127–140.
- Hedger, R.D., Rikardsen, A.H. and Thorstad, E.B. 2017b. Pop-up satellite archival tag effects on the diving behavior, growth and survival of adult Atlantic salmon *Salmo salar* at sea. *J. Fish Biol.* 90: 294–310.
- Herman, D.P., Burrows, D.G., Wade, P.R., Durban, J.W., Matkin, C.O., LeDuc, R.G., Barrett-Lennard, L.G. and Krahn, M.M. 2005. Feeding ecology of eastern North Pacific killer whales *Orcinus orca* from fatty acid, stable isotope, and organochlorine analyses of blubber biopsies. *Mar. Ecol. Prog. Ser.* 302: 275–291.
- Hobson, K.A. 1999. Tracing origins and migration of wildlife using stable isotopes: a review. *Oecologia* 120: 314–326.
- Holbrook, C.M., Kinnison, M.T., and Zydlewski, J. 2011. Survival of Migrating Atlantic Salmon Smolts through the Penobscot River, Maine: a Prerestoration Assessment. *Trans. Amer. Fish. Soc.* 140: 1255–1268.
- Holm, M., Holst, J.C., and Hansen, L.P. 2000. Spatial and temporal distribution of postsmolts of Atlantic salmon (*Salmo salar* L.) in the Norwegian Sea and adjacent areas. *ICES J. Mar. Sci.* 57: 955–964.
- Holst, J.C. 2018. Let's bring back the salmon, sea birds and G6 mackerel! The hypothesis on overgrazing and predation. Ecosystem Based (Unpublished manuscript).

- Holst, J.C., Røttingen, I., and Melle W. 2004. The herring. In: HR Skjoldal, Editor. The Norwegian Sea Ecosystem. Trondheim: Tapir Academic Press, p 289–300.
- Holt, J.A., Allen, J.I., Anderson, T.R., Brewin, R., Butenschön, M., Harle, J., Huse, G., Lehodey, P., Lindemann, C., Memery, L., Salihoglu, B., Senina, I., and Yool, A. 2014. Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: Physics to fish and coasts to ocean. *Prog. Ocean.* 129: 285–313.
- Homrum E., Óskarsson G.J., and Slotte A. 2016. Spatial, seasonal and interannual variations in growth and condition of Norwegian spring spawning herring during 1994–2015. WD ICES WKPELA 2016.
- Hubbard, J. 1990. Home Sweet Home? A.G. Huntsman and the Homing Behaviour of Canadian Atlantic Salmon. *Acadiensis* Vol. XIX, No. 2 Spring/Printemps. P. 40–71.
- Hublely, P.B., and Gibson, A.J.F. 2011. A model for estimating mortality of Atlantic salmon, *Salmo salar*, between spawning events. *Can. J. Fish. Aquat. Sci.* 68: 1635–1650.
- Hublely, P.B., Amiro, P.G., Gibson, A.J.F., Lacroix, G.L., and Redden, A.M. 2008. Survival and behaviour of migrating Atlantic salmon (*Salmo salar* L.) kelts in river, estuarine, and coastal habitat. *ICES J. Mar. Sci.* 65: 1626–1634.
- Hurrell, J.W. 1995: Decadal trends in the North Atlantic Oscillation and relationships to regional temperature and precipitation. *Science* 269, 676–679.
- Huse, G., Utne, K.R., and Fernø, A. 2012. Vertical distribution of herring and blue whiting in the Norwegian Sea. *Mar. Biol. Res.* 8: 488–501.
- Hutchings, J.A., and Jones, M.E. 1998. Life history variation and growth rate thresholds for maturity in Atlantic salmon, *Salmo salar*. *Can. J. Fish. Aquat. Sci.* 55(S1): 22–47.
- ICES. 1995. Report of the Working Group on North Atlantic Salmon. ICES Headquarters, Copenhagen, 3–12 April 1995. ICES, Doc. CM 1995/Assess: 14, Ref. M, 191 pp.
- ICES. 2000. Report of the Working Group on the North Atlantic Salmon (WGNAS). April 3–13 2000, Copenhagen, Denmark. ICES CM 2000/ACFM: 13. 301 pp.
- ICES. 2003. Report of the Working Group on North Atlantic Salmon (WGNAS). 31 March–10 April 2003, Copenhagen, Denmark. ICES CM 2003/ACFM: 19. 297 pp.
- ICES. 2004a. Report of the Working Group on North Atlantic Salmon. 29 March–8 April 2004 Halifax, Canada. ICES CM 2004/ACFM:20. 286 pp.
- ICES. 2004b. Report of the Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries (SGBYSAL), 9–12 March 2004, Bergen, Norway. ICES CM 2004/I:01. 66 pp.
- ICES. 2005a. Zooplankton monitoring results in the ICES area, Summary Status Report 2003/2004. ICES Cooperative Research Report, No. 276. 34 pp.
- ICES. 2005b. Report of the Study Group on the Bycatch of Salmon in Pelagic Trawl Fisheries (SGBYSAL), 8–11 February 2004, Bergen, Norway. ICES CM 2005/ACFM:13. 41 pp.
- ICES. 2007. Report of the Workshop on the Development and Use of Historical Salmon Tagging Information from oceanic areas (WKDUHSTI), 19–22 February 2007, St. John's, Canada. ICES CM 2007/DFC:02. 64 pp.
- ICES. 2008. Report of the Workshop on Salmon Historical Information – New Investigations from old Tagging Data (WKSHINI), 18–20 September 2008, Halifax, Canada. ICES CM 2008/DFC:02. 55 pp.
- ICES 2009a. Report of the Workshop on Learning from Salmon Tagging Records (WKLUSTRE), 16–18 September 2009, London, UK. ICES CM 2009/DFC:05. 39 pp.
- ICES. 2009b. Report of the Study Group on Biological Characteristics as Predictors of Salmon Abundance (SGBICEPS), 3–5 March 2009, Lowestoft, UK. ICES CM 2009/DFC:02. 119 pp.
- ICES. 2010a. Report of the Study Group on Biological Characteristics as Predictors of Salmon Abundance (SGBICEPS), 24–26 November 2009, ICES Headquarters, Copenhagen, Denmark. ICES CM 2010/SSGEF:03. 158 pp.

- ICES. 2010b. Report of the Benchmark Workshop on Sandeel (WKSAN), 6–10 September 2010, Copenhagen, Denmark. ICES CM 2010/ACOM:57.
- ICES. 2012. Quality Handbook Stock Annex: Capelin in the Iceland-East Greenland-Jan Mayen ecosystem. ICES NWWG REPORT 2012, p. 646–657.
- ICES. 2013a. Report of the working group on harp and hooded seals (WGHARP), 26–30 August 2013, PINRO, Murmansk, Russia. ICES CM 2013/ACOM:20. pp. 65.
- ICES. 2013b. Report of the Workshop on salmon tagging archive (WKSTAR), 19–21 June 2012, ICES Headquarters, Copenhagen, Denmark. ICES CM 2012/SSGEF:16. 19 pp.
- ICES. 2014. Report of the Working Group on North Atlantic Salmon (WGNAS), 19–28 March 2014, Copenhagen, Denmark. ICES CM 2014/ACOM:09. 431 pp.
- ICES. 2015a. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 25 August–31 August 2015, Pasaia, Spain. ICES CM 2015/ACOM:15. 646 pp.
- ICES. 2015b. Report of the Working Group on North Atlantic Salmon (WGNAS), 17–26 March, Moncton, Canada. ICES CM 2015/ACOM:09. 332 pp.
- ICES. 2016a. Report of the Working Group on North Atlantic Salmon (WGNAS), 30 March–8 April 2016, Copenhagen, Denmark. ICES CM 2016/ACOM:10. 363 pp.
- ICES. 2016b. Capelin (*Mallotus villosus*) in subareas 1 and 2 (Northeast Arctic), excluding Division 2.a west of 5 W (Barents Sea capelin). ICES Advice of fishing opportunities, catch, and effort 2016, Book 3.
- ICES. 2017a. Report of the Working Group on North Atlantic Salmon (WGNAS), 29 March–7 April 2017, Copenhagen, Denmark. ICES CM 2017/ACOM:20. 296 pp.
- ICES. 2017b. Icelandic Waters ecoregion - Ecosystem overview. <https://doi.org/10.17895/ices.pub.4669>
- ICES. 2018a. Cooperative Research Report Series No. 343 (Fifty years of marine tag recoveries from Atlantic salmon). 121 pp. <http://doi.org/10.17895/ices.pub.4542>.
- ICES. 2018b. Report of the Working Group on North Atlantic Salmon (WGNAS), 4–13 April 2018, Woods Hole, MA, USA. ICES CM 2018/ACOM:21. 386 pp.
- ICES. 2018c. Report of the Working Group on Widely Distributed Stocks (WGWIDE), 28 August–3 September 2018, Torshavn, Faroe Islands. ICES CM 2018/ACOM: 23. 488 pp.
- ICES. 2019a. Working Group on North Atlantic Salmon (WGNAS). Ed. by M. Robertson. Vol. 1. ICES Scientific Reports 16. International Council for the Exploration of the Sea. DOI: 10.17895/ices.pub.4978.
- ICES. 2019b. WGNAS Addendum. Compilation of Microtags, Finclip and External Tag Releases 2018 by the Working Group on North Atlantic Salmon, 25 March–4 April 2019, Bergen, Norway. ICES CM 2019/FRSG. 25 pp.
- ICES. 2019c. Inter-benchmark Workshop on the assessment of Northeast Atlantic mackerel (IBPNEAMac). ICES Scientific Reports, 1:5. 71 pp. <http://doi.org/10.17895/ices.pub.4985>.
- ICES. 2019d. Report of the Working Group on Integrated Ecosystem Assessments for the Norwegian Sea (WGINOR). ICES WGINOR REPORT 2018 26–30 November 2018. Reykjavik, Iceland. ICES CM 2018/IEASG:10. 123 pp.
- Ingram, S.N., and Rogan, E. 2002. Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. Mar. Ecol. Prog. Ser. 244: 247–255.
- Jacobsen, J.A., and Hansen, L.P. 2001. Feeding habits of wild and escaped farmed Atlantic salmon, *Salmo salar* L., in the Northeast Atlantic. ICES J. Mar. Sci. 58: 916–933.
- Jacobsen, J.A., and Joensen, G. 2011. By-catch estimates of salmon in the Faroese pelagic fisheries in 2011. Unpublished report, Faroe Marine Research Institute, Faroe Islands, October 2011 (provided to WKSALMON).
- Jacobsen, J.A., Hansen, L.P., Bakkestuen, V., Halvorsen, R., Reddin, D.G., White, J., O' Maoléidigh, N., Russell, I.C., Potter, E.C.E., Fowler, M., Smith, G.W., Mork, K.A., Isaksson, A., Oskarsson, S., Karlsson,

- L., and Pedersen, S. 2012. Distribution by origin and sea age of Atlantic salmon (*Salmo salar*) in the sea around the Faroe Islands based on analysis of historical tag recoveries. *ICES J. Mar. Sci.* 69: 1598–1608.
- Jansen, T., Burns, F. 2015. Density dependent growth changes through juvenile and early adult life of North East Atlantic mackerel (*Scomber scombrus*). *Fish. Res.* 169: 37–44.
- Jensen, A.J., O' Maoiléidigh, N., Thomas, K., Einarsson, S.M., Haugland, M., Erkinaro, J., Fiske, P., Friedland, K.D., Gudmundsdottir, A.K., Haantie, J., Holm, M., Holst, J.C., Jacobsen, J.A., Jensås, J.G., Kuusela, J., Melle, W., Mork, K.A., Wennevik, V., and Østborg, G.M. 2012. Age and fine-scale marine growth of Atlantic salmon post-smolts in the Northeast Atlantic. *ICES J. Mar. Sci.* 69: 1668–1677.
- Jensen, A.J., Karlsson, S., Fiske, P., Hansen, L.P., Østborg, G.M., and Hindar, K. 2014. Origin and life history of Atlantic salmon (*Salmo salar*) near their northernmost oceanic limit. *Can. J. Fish. Aquat. Sci.* 71: 1740–1746.
- Jewell, R., Thomas, L., Harris, C.M., Kaschner, K., Wiff, R., Hammond, P.S., and Quick, N.J. 2012. Global analysis of cetacean line-transect surveys: detecting trends in cetacean density. *Mar. Ecol. Prog. Ser.* 453: 227–240.
- JNCC. 2020. Seabird Population Trends and Causes of Change: 1986–2018 Report (<https://jncc.gov.uk/our-work/smp-report-1986-2018>). Joint Nature Conservation Committee, Peterborough. Updated 10 March 2020.
- Jones, R.A., Anderson, L. and Clarke, C.N. 2014. Assessment of the recovery potential for the outer Bay of Fundy population of Atlantic Salmon (*Salmo salar*): status, trends, distribution, life history characteristics and recovery targets. DFO Can. Sci. Advis. Sec. Res. Doc. 2014/008, 94 pp.
- Jones, E.L., McConnell, B.J., Smout, S., Hammond, P.S., Duck, C.D., Morris, C.D., Thompson, D., Russell, D.J., Vincent, C., Cronin, M., and Sharples, R.J. 2015. Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. *Mar. Ecol. Prog. Ser.* 534: 235–249.
- Jonsson, B., and Jonsson, N. 2004. Factors affecting marine production of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 61: 2369–2383.
- Jonsson, N., and Jonsson, B. 2007. Sea growth, smolt age and age at sexual maturation in Atlantic salmon. *J. Fish Biol.* 71: 245–252.
- Jonsson, B., and Jonsson, N. 2011. *Ecology of Atlantic Salmon and Brown Trout: habitat as a template for life history*. Springer, New York.
- Jonsson, B., Jonsson, N., and Hansen, L.P. 1990. Does juvenile experience affect migration and spawning of adult Atlantic salmon? *Behavioral Ecology and Sociobiology* 26: 225–230.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1991. Energetic cost of spawning in male and female Atlantic salmon (*Salmo salar* L.). *J. Fish Biol.* 39: 739–744.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon *Salmo salar*. *J. Anim. Ecol.* 66: 425–436.
- Jonsson, N., Jonsson, B., and Hansen, L.P. 2003. The marine survival and growth of wild and hatchery-reared Atlantic salmon. *J. Appl. Ecol.* 40: 900–911.
- Jonsson, B., Jonsson, N., and Finstad, A.G. 2013. Effects of temperature and food quality on age and size at maturity in ectotherms: an experimental test with Atlantic salmon. *J. Anim. Ecol.* 82: 201–210.
- Jonsson, B., Jonsson, M., and Jonsson, N. 2017. Influences of migration phenology on survival are size dependent in juvenile Atlantic salmon (*Salmo salar*). *Can. J. Zool.* 95: 581–587.
- Jounela, P., Suuronen, P., Millar, R.B., and Koljonen, M.L. 2006. Interactions between grey seal (*Halichoerus grypus*), Atlantic salmon (*Salmo salar*), and harvest controls on the salmon fishery in the Gulf of Bothnia. *ICES J. Mar. Sci.* 63: 936–945.
- Kallio-Nyberg, I., Jutila, E., Jokikokko, E., and Saloniemi, I. 2006. Survival of reared Atlantic salmon and sea trout in relation to marine conditions of smolt year in the Baltic Sea. *Fish. Res.* 80: 295–304.

- Kaplan, I.R. 1975. Stable isotopes as a guide to biogeochemical processes. Proc. Royal Soc. London. Series B. Biol. Sci. 189 (1095): 183–211.
- Karlsson, O., and Helander, B. 2005. Development of the Swedish Baltic grey seal stock 1990–2004. Symposium on the biology and management of seals in the Baltic Area. 15–18 February 2005, Helsinki, Finland, pp. 21.
- Kaschner, K., Kesner-Reyes, K., Garilao, C. *et al.* 2016. AquaMaps: predicted range maps for aquatic species. World wide web electronic publication, www.aquamaps.org, Version 08/2016. <URL: <https://www.aquamaps.org>>.
- Katona, S., and Whitehead, H. 1988. Are cetacea ecologically important. Ocean. Mar. Biol. Ann. Rev. 26: 553–568.
- Kelly, B., Benoît, H.P., Chaput, G., Jones, R.A., and Power, M. 2019. Spawning-strategy-dependent diets in two North American populations of Atlantic salmon *Salmo salar*. J. Fish Biol. 94: 40–52.
- King, R.A., and Stevens, J.R. 2019. An improved genetic sex test for Atlantic salmon (*Salmo salar* L.). Conservation Genetics Resources, 2019: 1–3.
- King, T.L., Verspoor, E., Spidle, A.T., Gross, R., Phillips, R.B., Koljonen, M.-L., Sanchez, J.A., and Morrison, C.L. 2007. Biodiversity and population structure. In: E. Verspoor, L. Stradmeyer, and J.L. Nielsen (eds.). The Atlantic Salmon Genetics, Conservation and Management. Blackwell Publishing, Oxford.
- Klemetsen, A., Amundsen, P.A., Dempson, J.B., Jonsson, B., Jonsson, N., O'connell, M.F., and Mortensen, E. 2003. Atlantic salmon *Salmo salar* L., brown trout *Salmo trutta* L. and Arctic charr *Salvelinus alpinus* (L.): a review of aspects of their life histories. Ecol. Freshw. Fish 12: 1–59.
- Kocik, J.F., Hawkes, J.P., Sheehan, T.F., Music, P.A., and Beland, K.F. 2009. Assessing estuarine and coastal migration and survival of wild Atlantic salmon smolts from the Narraguagus River, Maine using ultrasonic telemetry. American Fisheries Society Symposium 69: 293–310.
- Kovacs, K.M., and Lydersen, C. 2008. Climate change impacts on seals and whales in the North Atlantic Arctic and adjacent shelf seas. Science Progress 91(2): 117–150.
- Kubetzki, U., Garthe, S., Fifield, D., Mendel, B., and Furness, R.W. 2009. Individual migratory schedules and wintering areas of northern gannets. Mar. Ecol. Prog. Ser. 391: 257–265.
- Lacroix, G.L. 2008. Influence of origin on migration and survival of Atlantic salmon (*Salmo salar*) in the Bay of Fundy, Canada. Can. J. Fish. Aquat. Sci. 65: 2063–2079.
- Lacroix, G.L. 2013. Population-specific ranges of oceanic migration for adult Atlantic salmon (*Salmo salar*) documented using pop-up satellite archival tags. Can J Fish Aquat Sci. 70: 1011–1030.
- Lacroix, G.L. 2014. Large pelagic predators could jeopardize the recovery of endangered Atlantic salmon. Can. J. Fish. Aquat. Sci. 71: 343–350.
- Lavigne, D.M. 2018. Harp seal *Pagophilus groenlandicus*. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). Encyclopedia of Marine Mammals. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 455–457.
- Lawson, J.W., Stenson, G.B., and McKinnon, D.G. 1995. Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990–1993. Can. J. Zool. 73: 1805–1818.
- Lawson, J.W., and Stevens, T.S. 2014. Historic and current distribution patterns, and minimum abundance of killer whales (*Orcinus orca*) in the north-west Atlantic. J. Mar. Biol. Assoc. UK 94: 1253–1265.
- Lear, W.H. 1972. Food and feeding of Atlantic salmon in coastal areas and over oceanic depths. ICNAF Res. Bull. 9: 27–39.
- Légaré, B., Beaulieu, J.-L., Girard, L., et Grégoire, F. 2014. Les stocks de hareng (*Clupea harengus harengus* L.) de la côte ouest de Terre-Neuve (Division 4R de l'OPANO) en 2013. Secr. can. de consult. sci. du MPO. Doc. de rech. 2014/091. v + 74 p.

- Lehnert, S.J., Bentzen, P., Kess, T., Lien, S., Horne, J., Clément, M., and Bradbury, I.R. 2019. Chromosome polymorphisms track trans-Atlantic divergence, admixture and adaptive evolution in salmon. *Mol. Ecol.* 28: 2074–2987.
- Lesage, V., and Hammill, M.O. 2001. The status of the grey seal, *Halichoerus grypus*, in the Northwest Atlantic. *Can. Field-Nat.* 115: 653–662.
- Lesage, V., Hammill, M.O., and Kovacs, K.M. 2004. Long-distance movements of harbour seals (*Phoca vitulina*) from a seasonally ice-covered area, the St. Lawrence River estuary, Canada. *Can. J. Zool.* 82: 1070–1081.
- Lilly, G.R., and Simpson, M. 2000. Distribution and biomass of capelin, Arctic cod and sand lance on the Northeast Newfoundland Shelf and Grand Bank as deduced from bottom-trawl surveys. DFO Can. Stock Assess. Secr. Res. Doc. 2000/091.
- Lindstrøm, U., Harbitz, A., Haug, T., and Nilssen, K.T. 1998. Do harp seals *Phoca groenlandica* exhibit particular prey preferences? *ICES J. Mar. Sci.* 55: 941–953.
- Loneragan, M., Duck, C.D., Thompson, D., Mackey, B.L., Cunningham, L., and Boyd, I.L. 2007. Using sparse survey data to investigate the declining abundance of British harbour seals. *J. Zool.* 271: 261–269.
- Lothian, A.J., Newton, M., Barry, J., Walters, M., Miller, R.C., and Adams, C.E. 2018. Migration pathways, speed and mortality of Atlantic salmon (*Salmo salar*) smolts in a Scottish river and the near-shore coastal marine environment. *Ecol. Freshw. Fish* 27: 549–558.
- Louis, M., Viricel, A., Lucas, T., Peltier, H., Alfonsi, E., Berrow, S., Brownlow, A., Covelo, P., Dabin, W., Deaville, R., and De Stephanis, R. 2014. Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. *Mol. Ecol.* 23: 857–874.
- Luque, P.L., Davis, C.G., Reid, D.G., Wang, J., and Pierce, G.J. 2006. Opportunistic sightings of killer whales from Scottish pelagic trawlers fishing for mackerel and herring off North Scotland (UK) between 2000 and 2006. *Aqua. Liv. Res.* 19: 403–410.
- MacDonald, A., Speirs, D.C., Greenstreet, S.P.R., Boulcott, P., and Heath, M.R. 2019. Trends in Sandeel Growth and Abundance off the East Coast of Scotland. *Front. Mar. Sci.* 6:201. doi: 10.3389/fmars.2019.00201.
- Macintyre, D. 1934. Sea enemies of salmon. *Salmon and Trout Magazine* 74: 38–42.
- MacKenzie, K.M., Palmer, M.R., Moore, A., Ibbotson, A.T., Beaumont, W.R., Poulter, D.J., and Trueman, C.N. 2011. Locations of marine animals revealed by carbon isotopes. *Scientific reports*: 1:21.
- MacKenzie, K.M., Trueman, C.N., Palmer, M.R., Moore, A., Ibbotson, A.T., Beaumont, W.R., and Davidson, I.C. 2012. Stable isotopes reveal age-dependent trophic level and spatial segregation during adult marine feeding in populations of salmon. *ICES J. Mar. Sci.* 69: 1637–1645.
- MacLeod, C.D., Santos, M.B., Reid, R.J., Scott, B.E., and Pierce, G.J. 2007. Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: could climate change mean more starving porpoises? *Biology letters* 3(2): 185–188.
- Magera, A.M., Flemming, J.E.M., Kaschner, K., Christensen, L.B., and Lotze, H.K. 2013. Recovery trends in marine mammal populations. *PLoS One*, 8(10): p.e77908.
- Mahfouz, C., Méziane, T., Henry, F., Abi-Ghanem, C., Spitz, J., Jauniaux, T., Bouveroux, T., Khalaf, G., and Amara, R. 2017. Multi-approach analysis to assess diet of harbour porpoises *Phocoena phocoena* in the southern North Sea. *Mar. Ecol. Prog. Ser.* 563: 249–259.
- Mangel, M., and Satterthwaite, W.H. 2008. Combining proximate and ultimate approaches to understand life history variation in salmonids with application to fisheries, conservation, and aquaculture. *Bull. Mar. Sci.* 83: 107–130.
- Mäntyniemi, S., Romakkaniemi, A., Dannewitz, J., Palm, S., Pakarinen, T., Pulkkinen, H., Gårdmark, A., and Karlsson, O. 2012. Both predation and feeding opportunities may explain changes in survival of Baltic salmon post-smolts. *ICES J. Mar. Sci.* 69: 1574–1579.

- Martin, J.H.A., and Mitchell, K.A. 1985. Influence of sea temperature upon the numbers of grilse and multi-sea-winter Atlantic salmon (*Salmo salar*) caught in the vicinity of the River Dee (Aberdeenshire). Can. J. Fish. Aquat. Sci. 42: 1513–1521.
- Massiot-Granier, F., Prévost, E., Chaput, G., Potter, T., Smith, G., White, J., Mäntyniemi, S., and Rivot, E. 2014. Embedding stock assessment within an integrated hierarchical Bayesian life cycle modelling framework: An application to Atlantic salmon in the Northeast Atlantic. ICES J. Mar. Sci. 71: 1653–1670.
- McCormick, S.D., Hansen, L.P., Quinn, T.P., and Saunders, R.L. 1998. Movement, migration, and smolting of Atlantic salmon (*Salmo salar*). Can. J. Fish. Aquat. Sci. 55(S1): 77–92.
- Meerburg, D.J. 1986. Salmonid age at maturity. Canadian Special Publication of Fisheries and Aquatic Sciences 89, 118 pp.
- Mellink, E., and Orozco-Meyer, A. 2006. Abundance, distribution, and residence of bottlenose dolphins (*Tursiops truncatus*) in the Bahía San Jorge area, northern Gulf of California, México. Aquatic Mammals 32: 133.
- Merkel, F.R., Johansen, K.L., Nielsen, R.D., Petersen, I.K., Sterup, J., and Mosbech, A. 2019. Wintering sea-birds in south-west Greenland, 2017. Polar Res. 38, 3462. <http://dx.doi.org/10.33265/polar.v38.3462>.
- Metcalfe, N.B., and Thorpe, J.E. 1990. Determinants of Geographical Variation in the Age of Seaward-Migrating Salmon, *Salmo salar*. J. Anim. Ecol. 59: 135–145.
- Middlemas, S.J., Armstrong, J.D., and Thompson, P.M. 2003. The significance of marine mammal predation on salmon and sea trout. In: Mills D.H. (Ed.). Salmon at the Edge. Blackwell Scientific Publications, Oxford, pp. 42–60.
- Middlemas, S.J., Barton, T.R., Armstrong, J.D., and Thompson, P.M. 2006. Functional and aggregative responses of harbour seals to changes in salmonid abundance. Proc. Royal Soc. London Series B: Biol. Sci. 273: 193–198.
- Mikkelsen B., Haug, T., and Nilssen, K.T. 2002. Summer diet of grey Seals (*Halichoerus grypus*) in Faroese Waters. Sarsia 87: 462–471.
- Miller, A.S., Sheehan, T.F., Renkawitz, M.D., Meister, A.L., and Miller, T.J. 2012. Revisiting the marine migration of US Atlantic salmon using historical Carlin tag data. ICES J. Mar. Sci. 69: 1609–1615.
- Mills, K.E., Pershing, A.J., Sheehan, T.F., and Mountain, D. 2013. Climate and ecosystem linkages explain widespread declines in North American Atlantic salmon populations. Global Change Biology 19: 3046–3061.
- Montevecchi, W.A., Cairns, D.K., and Birt, V.L. 1988. Migration of postsmolt Atlantic salmon, *Salmo salar*, off northeastern Newfoundland, as inferred by tag recoveries in a seabird colony. Can. J. Fish. Aquat. Sci. 45: 568–571.
- Montevecchi, W.A., Cairns, D.K., and Myers, R.A. 2002. Predation on marine-phase Atlantic salmon (*Salmo salar*) by gannets (*Morus bassanus*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 59: 602–612.
- Mork, K.A., Gilbey, J., Hansen, L.P., Jensen, A.J., Jacobsen, J.A., Holm, M., Holst, J.C., O Maoiléidigh, N., Vikebø, F., McGinnity, P., Melle, W., Thomas, K., Verspoor, E., and Wennevik, V. 2012. Modelling the migration of post-smolt Atlantic salmon (*Salmo salar*) in the Northeast Atlantic. ICES J. Mar. Sci. 69: 1616–1624.
- Mowbray, F.K., Bourne, C., Murphy, H., Adamack, A., Lewis, K., Varkey, D., and P. Regular. 2019. Assessment of Capelin (*Mallotus villosus*) in SA2 + Div 3KL in 2017. DFO Can. Sci. Advis. Sec. Res. Doc. 2019/068. iv + 34 p.
- NAMMCO. 2016. Report of the 23rd meeting of the NAMMCO Scientific Committee. NAMMCO SC/23/Report, 4–7 November 2016, Nuuk, Greenland, pp. 271.
- NASCO. 2019. Report on the use of the Framework of Indicators in 2019. WGC(19)03, 11 pp.
- Newbould, K.A. 1989. North American Atlantic Salmon Tagging Programs 1974–1985. Can. Data Rep. Fish. Aquat. Sci. No. 730. v + 66 p.

- Nicieza, A.G., and Braña, F. 1993. Relationships among smolt size, marine growth, and sea age at maturity of Atlantic salmon (*Salmo salar*) in northern Spain. *Can. J. Fish. Aquat. Sci.* 50: 1632–1640.
- Nielsen, N.H., Hansen, R.G., Teilmann, J., and Heide-Jørgensen, M.P. 2013. Extensive offshore movements of harbour porpoises (*Phocoena phocoena*). NAMMCO SC/20/HP/08. Working Group on harbour porpoises, Copenhagen, Denmark, 4–6 November 2013.
- Niemelä, E., Erkinaro, J., Julkunen, M., Hassinen, E., Lämsmä, M., and Brørs, S. 2006. Temporal variation in abundance, return rate and life histories of previously spawned Atlantic salmon in a large subarctic river. *J. Fish Biol.* 68: 1222–1240.
- Nilssen, K.T., Grotnes, P.E., and Haug, T. 1992. The effect of invading harp seals (*Phoca groenlandica*) on local coastal fish stocks of North Norway. *Fish. Res.* 13: 25–37.
- Nilssen, K.T., and Haug T. 2007. Status of grey seals (*Halichoerus grypus*) in Norway. NAMMCO Scientific Publications, 6: 23–31.
- Nilssen, K.T., Lindstrøm, U., Westgaard, J.I., Lindblom, L., Blencke, T.R., and Haug, T. 2019. Diet and prey consumption of grey seals (*Halichoerus grypus*) in Norway. *Mar. Biol. Res.* 15: 137–149.
- Northeast Fisheries Science Center (NEFSC). 2018. 64th Northeast Regional Stock Assessment Workshop (64th SAW) Assessment Summary Report. US Dept Commer, Northeast Fish Sci Cent Ref Doc. 18-03; 27 p. Available from: <http://www.nefsc.noaa.gov/publications/>.
- Nøttestad, L., Giske, J., Holst, J.C., and Huse, G. 1999. A length-based hypothesis for feeding migrations in pelagic fish. *Can. J. Fish. Aquat. Sci.* 56 (Supp 1): 26–34.
- Nøttestad, L., Utne, K.R., Óskarsson, G.J., Jónsson, S.P., Jacobsen, J.A., Tangen, Ø., Anthonypillai, V., Aanes, S., Vølstad, J.H., Bernasconi, M., Debes, H., Smith, L., Sveinbjörnsson, S., Holst, J.C., Jansen, T., and Slotte, A. Quantifying changes in abundance, biomass, and spatial distribution of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic seas from 2007 to 2014. *ICES J. Mar. Sci.* 73: 359–373.
- Nøttestad, L., Utne, K.R., Sandvik, A., Skålevik, Å., Slotte, A., and Huse G. 2018. Historical distribution of juvenile mackerel northwards along the Norwegian coast and offshore following the 2016 mackerel spawning. Working Document to ICES Working Group on Widely Distributed Stocks (WGWIDE), Havstovan, Tórshavn, Faroe Islands, 28. August–3. September 2018, 25 pp.
- O'Connell, M.F., Dempson, J.B., and Chaput, G. 2006. Aspects of the life history, biology, and population dynamics of Atlantic salmon (*Salmo salar* L.) in eastern Canada. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/014, 47 pp.
- Ó Maoiléidigh, N., Potter, E.C.E., McGinnity, P., Crozier, W.W., Hansen, L.P., Gudbergsson, G., Prévost, E., Karlsson, L., and Maclean, J. 2003. Examination of marine survival datasets for Atlantic salmon (*Salmo salar*, L.) in the North-east Atlantic area. In: Potter, E.C.E., Ó Maoiléidigh, N. and Chaput, G. (Eds.). *Marine Mortality of Atlantic Salmon, Salmo salar* L: Methods and Measures. DFO Can. Sci. Advis. Sec. Res. Doc. 2003/101, pp. 10–14.
- Ó Maoiléidigh, N., White, J., Hansen, L.P., Jacobsen, J.A., Potter, T., Russell, I., Reddin, D., and Sheehan, T. 2018. Fifty years of marine tag recoveries from Atlantic salmon. ICES Cooperative Research Report No. 343. 121 pp. <http://doi.org/10.17895/ices.pub.4542>.
- Ohasi, K., and Sheng, J. 2018. Study of Atlantic salmon post-smolt movement in the Gulf of St. Lawrence using an individual-based model. *Regional Studies in Marine Science* 24. 113–132.
- Øien, N. 1993. Abundance of killer whales (*Orcinus orca*) in waters off Norway. Reykjavik, Iceland. Unpublished.
- Øigård, T.A., Frie, A.K., Nilssen, K.T., and Hammill, M.O. 2012. Modelling the abundance of grey seals (*Halichoerus grypus*) along the Norwegian coast. *ICES J. Mar. Sci.* 69: 1436–1447.
- Øigård, T.A., Haug, T., and Nilssen, K.T. 2014. From pup production to quotas: current status of harp seals in the Greenland Sea. *ICES J. Mar. Sci.* 71: 537–545.
- Olafsdóttir, A.H., Slotte, A., Jacobsen, J.A., Óskarsson, G.J., Utne, K.R., and Nøttestad, L. 2016. Changes in weight-at-length and size-at-age of mature Northeast Atlantic mackerel (*Scomber scombrus*) from 1984

- to 2013: effects of mackerel stock size and herring (*Clupea harengus*) stock size. ICES J. Mar. Sci. 73: 1225–1235.
- Olafsdottir, A.H., Utne, K.R., Jacobsen, J.A., Jansen, T., Óskarsson, G.J., Nøttestad, L., Elvarsson, B.P., Broms, C., and Slotte, A. 2019. Geographical expansion of Northeast Atlantic mackerel (*Scomber scombrus*) in the Nordic Seas from 2007 to 2016 was primarily driven by stock size and constrained by low temperatures. Deep Sea Research Part II: Topical Studies in Oceanography 159: 152–168.
- Olafsson, K., Einarsson, S.M., Gilbey, J., Pampoulie, C., Hreggvidsson, G.O., Hjørleifsdottir, S., and Gudjonsson, S. Origin of Atlantic salmon (*Salmo salar*) at sea in Icelandic waters. ICES J. Mar. Sci. 73: 1525–1532.
- Olmos, M., Massiot-Granier, F., Prévost, E., Chaput, G., Bradbury, I.R., Nevoux, M., and Rivot, E. 2019. Evidence for spatial coherence in time trends of marine life history traits of Atlantic salmon in the North Atlantic. Fish and Fish. 20: 322–342.
- Olmos, M., Payne, M.R., Nevoux, M., Prévost, E., Chaput, G., Du Pontavice, H., Guitton, J., Sheehan, T., Mills, K., and Rivot, E. 2020. Spatial synchrony in the response of a long range migratory species (*Salmo salar*) to climate change in the North Atlantic Ocean. Global Change Biology 26: 1319–1337.
- Osborn, T.J. 2011. Winter 2009/2010 temperatures and a record-breaking North Atlantic Oscillation index. Weather Vol. 66, No. 1: 19–21.
- Otero, J., Jensen, A.J., L'Abée-Lund, J.H., Stenseth, N.C., Storvik, G.O., and Vøllestad, L.A. 2012. Contemporary ocean warming and freshwater conditions are related to later sea age at maturity in Atlantic salmon spawning in Norwegian rivers. Ecol. Evol. 2: 2192–2203.
- Otero, J., L'Abée-Lund, J.H., Castro-Santos, T., Leonardsson, K., Storvik, G.O., Jonsson, B., Dempson, B., Russell, I.C., Jensen, A.J., Baglinière, J.L., and Dionne, M. 2014. Basin-scale phenology and effects of climate variability on global timing of initial seaward migration of Atlantic salmon (*Salmo salar*). Global Change Biology 20: 61–75.
- Oudejans, M.G., Visser, F., Englund, A., Rogan, E., and Ingram, S.N. 2015. Evidence for distinct coastal and offshore communities of bottlenose dolphins in the North East Atlantic. PloS one, 10(4): p.e0122668.
- Parrish, D.L., Behnke, R.J., Gephard, S.R., McCormick, S.D., and Reeves, G.H. 1998. Why aren't there more Atlantic salmon (*Salmo salar*)? Can. J. Fish. Aquat. Sci. 55(S1): 281–287.
- Peschko, V., Ronnenberg, K., Siebert, U., and Gilles, A. 2016. Trends of harbour porpoise (*Phocoena phocoena*) density in the southern North Sea. Ecological Indicators, 60: 174–183.
- Peterson, B.J., and Fry, B. 1987. Stable isotopes in ecosystem studies. Ann. Rev. Ecol. Syst. 18: 293–320.
- Petit, J.R., Jouzel, J., Raynaud, D., Barkov, N.I., Barnola, J.-M., Basile, I., Bender, M., Chappellaz, J., Davis, M., Delaygue, G., Delmotte, M., Kotlyakov, V.M., Legrand, M., Lipenkov, V.Y., Lorius, C., Pépin, L., Ritz, C., Saltzman, E., and Stievenard, M. 1999. Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. Nature 399, 429–436 (3 June 1999).
- Peyronnet, A., Friedland, K.D., Ó Maoiléidigh, N., Manning, M., and Poole, W.R. 2007. Links between patterns of marine growth and survival of Atlantic salmon *Salmo salar*, L. J. Fish Biol. 71: 684–700.
- Peyronnet, A., Friedland, K.D., and Ó Maoiléidigh, N. 2008. Different ocean and climate factors control the marine survival of wild and hatchery Atlantic salmon *Salmo salar* in the north-east Atlantic Ocean. J. Fish Biol. 73: 945–962.
- Pike, D.G., Paxton, C.G., Gunnlaugsson, T., and Víkingsson, G.A. 2009. Trends in the distribution and abundance of cetaceans from aerial surveys in Icelandic coastal waters, 1986–2001. NAMMCO Scientific Publications, 7: 117–142.
- Piou, C., Taylor, M.H., Papaix, J., and Prévost, E. 2015. Modelling the interactive effects of selective fishing and environmental change on Atlantic salmon demogenetics. J. Appl. Ecol. 52: 1629–1637.
- Porter, T.R., Healey, M.C., O'Connell, M.F., Baum, E.T., Bielak, A.T., and Côté, Y. 1986. Implications of varying sea age at maturity of Atlantic salmon (*Salmo salar*) on yield to the fisheries. In Salmonid age at maturity, pp. 110–117. D. J. Meerburg [ed.] Can. Spec. Publ. Fish. Aquat. Sci. 89.

- Potter, E.C.E., Crozier, W.W., Schön, P.-J., Nicholson, M.D., Prévost, E., Erkinaro, J., Gudbergsson, G., Karlsson, L., Hansen, L.P., MacLean, J.c., Ó Maoiléidigh, N., and Prusov, S. 2004. Estimating and forecasting pre-fishery abundance of Atlantic salmon (*Salmo salar* L.) in the Northeast Atlantic for the management of mixed-stock fisheries. *ICES J. Mar. Sci.* 61: 1359–1369.
- Price, M.P. 1975. Summary of fish tagging Maritimes Region – 1967–1974. Environment Canada Fisheries and Marine Service Resource Development Branch Data Record Series No. MAR/D-75-3. 87 p.
- Rae, B.B. 1965. The food of the common porpoise (*Phocoena phocoena*). *J. Zool. London* 146: 114–122.
- Rago, P.J., Reddin, D.G., Porter, T.R., Meerburg, D.J., Friedland, K.D., and Potter, E.C.E. 1993. A continental run reconstruction model for the non-maturing component of North American Atlantic salmon: analysis of fisheries in Greenland and Newfoundland Labrador, 1974–1991. *ICES CM* 1993/M:25.
- Ramasco, V., Lindström, U., and Nilssen, K.T. 2017. Selection and foraging response of harbour seals in an area of changing prey resources. *Mar. Ecol. Prog. Ser.* 581: 199–214.
- Reddin, D.G. 1985. Atlantic salmon (*Salmo salar*) on and east of the Grand Bank. *J. Northw. Atl. Fish. Sci.* 6: 157–164.
- Reddin, D.G. 1988. Ocean life of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic. In *Atlantic Salmon: Planning for the Future. Proceedings of the Third International Atlantic Salmon Symposium, Biarritz, France, 21–23 October 1986*, pp. 483–521. Ed. by D. H. Mills, and D. J. Piggins. Croom Helm, London. 587 pp.
- Reddin, D.G. 2006. Perspectives on the marine ecology of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2006/018.
- Reddin, D.G., and Carscadden, J.E. 1981. Salmon-capelin interactions. *Can. Atl. Fish. Sci. Advis. Comm. Res. Doc.* 81/2.
- Reddin, D.G., and Friedland, K.D. 1993. Marine environmental factors influencing the movement and survival of Atlantic salmon. In *Salmon in the Sea and New Enhancement Strategies*, pp. 79–103. Ed. by D. Mills. Fishing News Books, London. 424 pp.
- Reddin, D.G., and Lear, W.H. 1990. Summary of marine tagging studies of Atlantic salmon (*Salmo salar* L.) in the Northwest Atlantic area. *Can. Tech. Rep. Fish. Aquat. Sci.* 1737. 115 pp.
- Reddin, D.G., and Shearer, W.M. 1987. Sea surface temperature and distribution of Atlantic salmon in the Northwest Atlantic Ocean. In *Common Strategies in Anadromous/Catadromous Fishes* 262–275. Ed. by M. J. Dadswell, R. J. Klauda, C. M. Moffitt, R. L. Saunders, R. A. Rulifson, and J. E. Cooper. American Fisheries Society Symposium, 1.
- Reddin, D.G., and Short, P.B. 1991. Postsmolt Atlantic salmon (*Salmo salar*) in the Labrador Sea. *Can. J. Fish. Aquat. Sci.* 48: 2–6.
- Reddin, D.G., Dempson, J.B., Downton, P., Mullins, C.C., and Friedland, K.D. 1999. Migration of Atlantic salmon kelts (*Salmo salar* L.) in relation to sea water temperature in Newfoundland, 1998. *DFO Can. Stock Assess. Sec. Res. Doc.* 99/85.
- Reddin, D.G., Friedland, K.D., Downton, P., Dempson, J.B., and Mullins, C.C. 2004. Thermal habitat experienced by Atlantic salmon kelts (*Salmo salar* L.) in coastal Newfoundland waters. *Fish. Oceanogr.* 13: 24–35.
- Reddin, D.G., Downton, P., and Friedland, K.D. 2006. Diurnal and nocturnal temperatures for Atlantic salmon postsmolts (*Salmo salar* L.) during their early marine life. *Fish. Bull.* 104: 415–428
- Reddin, D.G., Downton, P., Fleming, I.A., Hansen, L.P., and Mahon, A. 2011. Behavioural ecology at sea of Atlantic salmon (*Salmo salar* L.) kelts from a Newfoundland (Canada) river. *Fish. Oceanogr.* 20: 174–191.
- Reddin, D.G., Hansen, L.P., Bakkestuen, V., Russell, I., White, J., Potter, E.C.E., Dempson, J.B., Sheehan, T.F., Ó Maoiléidigh, N., Smith, G.W., Isaksson, A., Jacobsen, J.A., Fowler, M., Mork, K.A., and Amiro, P. 2012. Distribution and biological characteristics of Atlantic salmon (*Salmo salar*) at Greenland based on the analysis of historical tag recoveries. *ICES J. Mar. Sci.* 69: 1589–1597.

- Reid, J.E., and Chaput, G. 2012. Spawning history influence on fecundity, egg size, and egg survival of Atlantic salmon (*Salmo salar*) from the Miramichi River, New Brunswick, Canada. ICES J. Mar. Sci. 69: 1678–1685.
- Reid, P.C., and Valdés, L. 2011. ICES status report on climate change in the North Atlantic. ICES Cooperative Research Report No. 310. 262 pp.
- Reijnders, P.J.H., and Lankester, K. 1990. Status of marine mammals in the North Sea. Netherlands J. Sea Res. 26: 427–435.
- Richards, V.P., Greig, T.W., Fair, P.A., McCulloch, S.D., Politz, C., Natoli, A., Driscoll, C.A., Hoelzel, A.R., David, V., Bossart, G.D., and Lopez, J.V. 2013. Patterns of population structure for inshore bottlenose dolphins along the eastern United States. J. Hered. 104: 765–778.
- Rikardsen, A.H., and Dempson, J.B. 2011. Dietary life-support: The marine feeding of Atlantic salmon. pp. 115–144. In: Aas, Ø., Einum, S., Klemetsen, A. and Skuldal, J. (ed.). Atlantic Salmon Ecology, Wiley-Blackwell, Oxford.
- Rikardsen, A.H., Haugland, M., Bjørn, P.A., Finstad, B., Knudsen, R., Dempson, J.B., Holst, J.c., Hvidsten, N.A., and Holm, M. 2004. Geographical differences in marine feeding of Atlantic salmon post-smolts in Norwegian fjords. J. Fish Biol. 64: 1655–1679.
- Rindorf, A., Wright, P.J., Jensen, H., and Maar, M. 2016. Spatial differences in growth of lesser sandeel in the North Sea. J. Exp. Mar. Biol. Ecol. 479: 9–19.
- Ritter, J.A. 1989. Marine migration and natural mortality of North American Atlantic salmon (*Salmo salar* L.). Can. Manus. Rep. Fish. Aquat. Sci. No. 2041.
- Rosseland, L. 1971. Atlantic salmon fishery in International waters. Jakt og Fiske. 4 (238–242. In Norwegian).
- Røttingen, I. 1990. A review of variability in the distribution and abundance of Norwegian spring spawning herring and Barents Sea capelin. Polar Res. 8: 33–42.
- Rubenstein, D.R., and Hobson, K.A. 2004. From birds to butterflies: animal movement patterns and stable isotopes. Trends Ecol. Evol. 19: 256–263.
- Russell, I.C., Aprahamian, M.W., Barry, J., Davidson, I.C., Fiske, P., Ibbotson, A.T., Kennedy, R.J., Maclean, J.C., Moore, A., Otero, J., Potter, E.C.E., and Todd, C.D. 2012. The influence of the freshwater environment and the biological characteristics of Atlantic salmon smolts on their subsequent marine survival. ICES J. Mar. Sci. 69: 1563–1573.
- Ryan, C., and Holmes, J.M.C. 2012. Killer whale *Orcinus orca* predation on sunfish *Mola mola*. Marine Biodiversity Records, 5: e10.
- Ryan, C., and Wilson, P. 2003. Observations on the behaviour of a pod of killer whales *Orcinus orca* L. that visited Cork Harbour in 2001. The Irish Naturalists' Journal 27: 187–191.
- Ryan, C., Rogan, E., and Cross, T. 2010. The use of Cork Harbour by bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)). The Irish Naturalists' Journal 31: 1–9.
- SALSEA-MERGE. 2012. Advancing understanding of Atlantic Salmon at Sea: Merging Genetics and Ecology to Resolve Stock-specific Migration and Distribution patterns. Project Final Report.
- Samarra, F.I., Bassoi, M., Béseau, J., Elíasdóttir, M.Ó., Gunnarsson, K., Mruszczok, M.T., Rasmussen, M., Rempel, J.N., Thorvaldsson, B., and Víkingsson, G.A. 2018. Prey of killer whales (*Orcinus orca*) in Iceland. PloS one, 13(12): p.e0207287.
- Santos, M.B., and Pierce, G.J. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Ocean. Mar. Biol.: an Ann. Rev. 41: 355–390.
- Santos, M.B., Pierce, G.J., Reid, R.J., Patterson, I.A.P., Ross, H.M., and Mente, E. 2001. Stomach contents of bottlenose dolphins (*Tursiops truncatus*) in Scottish waters. J. Mar. Biol. Assoc. UK 81: 873–878.
- Sargeant, B.L., Mann, J., Berggren, P., and Krützen, M. 2005. Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (*Tursiops* sp.). Can. J. Zool. 83: 1400–1410.

- Saulitis, E.L., Matkin, C.O., and Fay, F.H. 2005. Vocal repertoire and acoustic behavior of the isolated AT1 killer whale subpopulation in southern Alaska. *Can. J. Zool.* 83: 1015–1029.
- Saunders, R.L. 1986. The scientific and management implications of age and size at sexual maturity in Atlantic salmon (*Salmo salar*). pp. 3–6. In: Meerburg D.J (Ed.). *Salmonid age at maturity*. Can. Spec. Publ. Fish. Aquat. Sci. 89.
- Scarnecchia, D.L., Ísaksson, Á., and White, S.E. 1991. Effects of the Faroese long-line fishery, other oceanic fisheries and oceanic variations on age at maturity of Icelandic north-coast stocks of Atlantic salmon (*Salmo salar*). *Fish. Res.* 10: 207–228.
- Scheidat, M., Gilles, A., Kock, K.H., and Siebert, U. 2008. Harbour porpoise *Phocoena phocoena* abundance in the southwestern Baltic Sea. *Endangered Species Research* 5: 215–223.
- Schmidt, M.W., and Hertzberg, J.E. 2011. Abrupt Climate Change during the Last Ice Age. *Nature Education Knowledge* 3(10):11.
- SCOS. 2015. Scientific Advice on Matters Related to the Management of Seal Populations: 2015. SCOS. Sea Mammal Research Unit, pp. 211.
- Shane, S.H., Wells, R.S., and Würsig, B. 1986. Ecology, behavior and social organization of the bottlenose dolphin: a review. *Mar. Mammal Sci.* 2: 34–63.
- Sharples, R.J., Arrizabalaga, B., and Hammond, P.S. 2009. Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Mar. Ecol. Prog. Ser.* 390: 265–276.
- Sheehan, T. 2019. Current status of knowledge, data, and research efforts on Atlantic salmon at Greenland: What do we have, what do we need, and what should we do moving forward? US Dept Commer, Northeast Fish Sci Cent Ref Doc. 19-10; 89 p.
- Sheehan, T.F., Reddin, D.G., Chaput, G., and Renkawitz, M.D. 2012. SALSEA North America: a pelagic ecosystem survey targeting Atlantic salmon in the Northwest Atlantic. *ICES J. Mar. Sci.* 69: 1580–1588.
- Shelton, R.G.J. 1986. Aspects of open sea exploitation of Atlantic salmon and the problems of assessing effects on Scottish home water stocks. In: Jenkins, D. and Shearer, W.M. (Eds.). *The status of the Atlantic salmon in Scotland*. Institute of Terrestrial Ecology, Banchory, Scotland, pp. 28–36.
- Seip, K.L., Grøn, Ø., and Wang, H. 2019. The North Atlantic Oscillations: Cycle Times for the NAO, the AMO and the AMOC. *Climate* 2019, 7, 43; doi:10.3390/cli7030043.
- Siegelman-Charbit, L., and Planque, B. 2016. Abundant mesopelagic fauna at oceanic high latitudes. *Mar. Ecol. Prog. Ser.* 546: 277–282.
- Singh, R., Dalton, A., Knox, D., MacIntyre, A., and Melvin, G.D. 2016. 2015 Evaluation of Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VWX Herring. DFO Can. Sci. Advis. Sec. Res. Doc. 2016/073. vi + 125 p.
- Sinnatamby, R.N., Dempson, J.B., Chaput, G., Caron, F., Niemelä, E., Erkinaro, J., and Power, M. 2009. Spatial and Temporal Variability in the Trophic Ecology of Atlantic Salmon in the North Atlantic Inferred from Analyses of Stable Isotope Signatures. *American Fisheries Society Symposium* 69:447–463.
- Solomon, D.J., and Sambrook, H.T. 2004. Effects of hot dry summers on the loss of Atlantic salmon, *Salmo salar*, from estuaries in South West England. *Fish. Manag. Ecol.* 11: 353–363.
- Soto, D.X., Trueman, C.N., Samways, K.M., Dadswell, M.J., and Cunjak, R.A. 2018. Ocean warming cannot explain synchronous declines in North American Atlantic salmon populations. *Mar. Ecol. Prog. Ser.* 601: 203–213.
- Speakman, T.R., Lane, S.M., Schwacke, L.H., Fair, P.A., and Zolman, E.S. 2010. Mark-recapture estimates of seasonal abundance and survivorship for bottlenose dolphins (*Tursiops truncatus*) near Charleston, South Carolina, USA. *J. Cetacean Res. Manag.* 11: 153–162.
- Spitz, J., Rousseau, Y., and Ridoux, V. 2006. Diet overlap between harbour porpoise and bottlenose dolphin: An argument in favour of interference competition for food? *Est. Coast. Shelf Sci.* 70: 259–270.

- Staudinger, M.D., Goyert, H., Suca, J.J., Coleman, K., Welch, L., Llopiz, J.K., Wiley, D., Altman, I., Applegate, A., Auster, P., Baumann, H., Beaty, J., Boelke, D., Kaufman, L., Loring, P., Moxley, J., Paton, S., Powers, K., Richardson, D., Robbins, J., Runge, J., Smith, B., Spiegel, C., and Steinmetz, H. 2020. The role of sand lances (*Ammodytes* sp.) in the Northwest Atlantic Ecosystem: A synthesis of current knowledge with implications for conservation and management. *Fish Fish.* 21: 522–556.
- Stephenson, R.L., Melvin, G.D., and Power, M.J. 2009. Population integrity and connectivity in Northwest Atlantic herring: a review of assumptions and evidence. *ICES J. Mar. Sci.* 66: 1733–1739.
- Stich, D.S., Zydlewski, G.B., Kocik, J.F., and Zydlewski, J.D. 2015. Linking behavior, physiology, and survival of Atlantic salmon smolts during estuary migration. *Mar. Coastal Fish.* 7: 68–86.
- Stockin, K.A., Weir, C.R., and Pierce, G.J. 2006. Examining the importance of Aberdeenshire (UK) coastal waters for North Sea bottlenose dolphins (*Tursiops truncatus*). *J. Mar. Biol. Assoc. UK* 86: 201–207.
- Strøm, J.F., Thorstad, E.B., Chafe, G., Sørbye, S.H., Righton, D., Rikardsen, A.H., and Carr, J. 2017. Ocean migration of pop-up satellite archival tagged Atlantic salmon from the Miramichi River in Canada. *ICES J. Mar. Sci.* 74: 1356–1370.
- Strøm, J.F., Thorstad, E.B., Hedger, R.D., and Rikardsen, A.H. 2018. Revealing the full ocean migration of individual Atlantic salmon. *Anim Biotelemetry* (2018) 6:2 <https://doi.org/10.1186/s40317-018-0146-2>.
- Strøm, J.F., Rikardsen, A.H., Campana, S.E., Righton, D., Carr, J., Aarestrup, K., Stokesbury, M.J.W., Gargan, P., Javierre, P.C., and Thorstad, E.B. 2019. Ocean predation and mortality of adult Atlantic salmon. *Scientific Reports* | (2019) 9:7890 doi.org/10.1038/s41598-019-44041-5.
- Strøm, J.F., Thorstad, E.B., and Rikardsen, A.H. 2020. Thermal habitat of adult Atlantic salmon *Salmo salar* in a warming ocean. *J. Fish Biol.* 96: 327–336.
- Surette, T.J. 2016. Abundance indices of Atlantic herring (*Clupea harengus*) from the southern Gulf of St. Lawrence based on the September multispecies bottom trawl survey. *DFO Can. Sci. Advis. Sec. Res. Doc.* 2016/064. vii + 33 p.
- Tamura, T. 2003. Regional assessment of prey consumption and competition by marine cetaceans in the world. In: Sinclair, M. and Valdimarsson, G. (Eds.). *Responsible Fisheries in Marine Ecosystems*. Food and Agricultural Organisation of the United Nations and CABI Publishing: Wallingford, UK; pp. 143–170.
- Tamura, T., and Ohsumi, S. 2000. Regional assessments of prey consumption by marine cetaceans in the world. Paper SC/52/E6 presented to the IWC Scientific Committee, June 2000, pp. 42.
- Taylor, B.L., Martinez, M., Gerrodette, T., Barlow, J., and Hrovat, Y.N. 2007. Lessons from monitoring trends in abundance of marine mammals. *Mar. Mammal Sci.* 23: 157–175.
- Teilmann, J., and Galatius, A. 2018. Harbour seal *Phoca vitulina*. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 451–455.
- Thompson, P.M. 1993. Harbour seal movement patterns. *Symposia of the Zoological Society of London* 66: 225–239.
- Thompson, P.M., and Mackay, F. 1999. Pattern and prevalence of predator damage on adult Atlantic salmon, *Salmo salar* L., returning to a river system in north-east Scotland. *Fish. Manag. Ecol.* 6: 335–343.
- Thompson, P.M., McConnell, B.J., Tollit, D.J., Mackay, A., Hunter, C., and Racey, P.A. 1996. Comparative distribution, movements and diet of harbour and grey seals from the Moray Firth, NE. *J. Appl. Ecol.* 33: 1572–1584.
- Thompson, P.M., Van Parijs, S., and Kovacs, K.M. 2001. Local declines in the abundance of harbour seals: implications for the designation and monitoring of protected areas. *J. Appl. Ecol.* 38: 117–125.
- Thomsen, F., Laczny, M., and Piper, W. 2006. A recovery of harbour porpoises (*Phocoena phocoena*) in the southern North Sea? A case study off Eastern Frisia, Germany. *Helgoland Mar. Res.* 60: 189–195.
- Thorpe, J.E. 1994. Reproductive strategies in Atlantic salmon, *Salmo salar* L. *Aqua. Res.* 25: 77–87.

- Thorpe, J.E., Mangel, M., Metcalfe, N.B., and Huntingford, F.A. 1998. Modelling the proximate basis of salmonid life-history variation, with application to Atlantic salmon, *Salmo salar* L. *Evol. Ecol.* 12: 581–599.
- Thorstad, E.B., Økland, F., Aarestrup, K., and Heggberget, T.G. 2008. Factors affecting the within-river spawning migration of Atlantic salmon, with emphasis on human impacts. *Rev. Fish Biol. Fish.* 18: 345–371.
- Thorstad, E.B., Uglem, I., Arechavala-Lopez, P., Økland, F., and Finstad, B. 2011. Low survival of hatchery-released Atlantic Salmon smolts during initial river and fjord migration. *Boreal Environ. Res.* 16: 115–120.
- Thorstad, E.B., Whoriskey, F., Uglem, I., Moore, A., Rikardsen, A.H., and Finstad, B. 2012. A critical life stage of the Atlantic salmon *Salmo salar*: behaviour and survival during the smolt and initial post-smolt migration. *J. Fish Biol.* 81: 500–542.
- Todd, C.D., Hughes, S.L., Marshall, C.T., Maclean, J.C., Lonergan, M.E., and Biuw, E.M. 2008. Detrimental effects of recent ocean surface warming on growth condition of Atlantic salmon. *Global Change Biology* 14: 958–970.
- Todd, C.D., Friedland, K.D., MacLean, J.C., Whyte, B.D., Russell, I.C., Lonergan, M.E., and Morrissey, M.B. 2012. Phenological and phenotypic changes in Atlantic salmon populations in response to a changing climate. *ICES J. Mar. Sci.* 69: 1686–1698.
- Tollit, D.J., and Thompson, P.M. 1996. Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Can. J. Zool.* 74: 1110–1121.
- Tollit, D.J., Black, A.D., Thompson, P.M., Mackay, A., Corpe, H.M., Wilson, B., Van Parijs, S.M., Grellier, K., and Parlane, S. 1998. Variations in harbour seal *Phoca vitulina* diet and dive-depths in relation to foraging habitat. *J. Zool.* 244: 209–222.
- Toth, J.L., Hohn, A.A., Able, K.W., and Gorgone, A.M. 2012. Defining bottlenose dolphin (*Tursiops truncatus*) stocks based on environmental, physical, and behavioral characteristics. *Mar. Mammal Sci.* 28: 461–478.
- Trenkel, V.M., Huse, G., MacKenzie, B.R., Alvarez, P., Arrizabalaga, H., Castonguay, M., Goñi, N., Grégoire, F., Hátún, H., Jansen, T., Jacobsen, J.A., Lehodey, P., Lutcavage, M., Mariani, P., Melvin, G.D., Neilson, J.D., Nøttestad, L., Óskarsson, G.J., Payne, M.R., Richardson, D.E., Senina, I., and Speirs, D.C. 2014. Comparative ecology of widely distributed pelagic fish species in the North Atlantic: Implications for modelling climate and fisheries impacts. *Prog. Ocean.* 129, Part B: 219–243.
- Trenkel, V.M., Lorance, P., Fässler, S.M.M., and Høines, A.S. 2015. Effects of density dependence, zooplankton and temperature on blue whiting (*Micromesistius poutassou*) growth. *J. Fish Biol.* 87: 1019–1030.
- Trueman, C.N., and Moore, A. 2007. Use of the stable isotope composition of fish scales for monitoring aquatic ecosystems. *Terrestrial Ecol.* 1: 145–161.
- Trueman, C.N., MacKenzie, K.M., and Palmer, M.R. 2012a. Stable isotopes reveal linkages between ocean climate, plankton community dynamics, and survival of two populations of Atlantic salmon (*Salmo salar*). *ICES J. Mar. Sci.* 69: 784–794.
- Trueman, C.N., MacKenzie, K.M., and Palmer, M.R. 2012b. Identifying migrations in marine fishes through stable-isotope analysis. *J. Fish Biol.* 81: 826–847.
- Tucker, S., Bowen, W.D., Iverson, S.J., Blanchard, W., and Stenson, G.B. 2009. Sources of variation in diets of harp and hooded seals estimated from quantitative fatty acid signature analysis (QFASA). *Mar. Ecol. Prog. Ser.* 384: 287–302.
- Ugarte, F., Simon, M., Laidre, K., and Rosing-Asvid, A. 2013. Recent increase of catches of killer whales in Southeast Greenland - Is there a need for NAMMCO advice? NAMMCO SC/20/20, 13–16 November 2013, Reykjavik, Iceland, pp. 5.
- Valiente, A.G., Juanes, F., and Garcia-Vazquez, E. 2011. Increasing regional temperatures associated with delays in Atlantic salmon sea-run timing at the southern edge of the European distribution. *Trans. Amer. Fish. Soc.* 140: 367–373.

- Vester, H., and Hammerschmidt, K. 2013. First record of killer whales (*Orcinus orca*) feeding on Atlantic salmon (*Salmo salar*) in northern Norway suggest a multi-prey feeding type. *Mar. Biodiversity Records*, 6:e9.
- Víkingsson, G.A., Ólafsdóttir, D., and Sigurjónsson, J. 2003. Geographical, and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. *NAMMCO Scientific Publications*, 5: 243–270.
- Vilhjálmsón, H. 2002. Capelin (*Mallotus villosus*) in the Iceland–East Greenland–Jan Mayen ecosystem. *ICES J. Mar. Sci.* 59: 870–883.
- Vongraven, D. and Bisther, A. 2014. Prey switching by killer whales in the North-east Atlantic: observational evidence and experimental insights. *Journal of the Marine Biological Association of the United Kingdom*, 94(6): 1357–1365.
- Waggitt, J.J., Evans, P.G.H., Andrade, J., Banks, A.N., Boisseau, O., Bolton, M., Bradbury, G., Brereton, T., Camphuysen, C.J., Durinck, J., Felce, t., Fijn, R.c., Garcia-Baron, I., Garthe, s., Geelhoed, S.C.V., Gilles, A., Goodall, M., Haelters, J., Hamilton, S., Hartny-Mills, L., Hodgins, N., James, K., Jessopp, M., Kavanagh, A.S., Leopold, M., Lohrengel, K., Louzao, M., Markones, N., Martínez-Cedeira, J., Ó Cadhla, O., Perry, S.L., Pierce, G.J., Ridoux, V., Robinson, K.P., Santos, M.B., Saavedra, C., Skov, H., Stienen, E.W.M., Sveegaard, S., Thompson, P., Vanermen, N., Wall, d., Webb, A., Wilson, J., Wanless, S., and Hiddink, J.G. 2020. Distribution maps of cetacean and seabird populations in the North-East Atlantic. *J. Appl. Ecol.* 57: 253–269.
- Walker, J.L., Potter, C.W., and Macko, S.A. 1999. The diets of modern and historic bottlenose dolphin populations reflected through stable isotopes. *Mar. Mammal Sci.* 15: 335–350.
- Wallace, S.D., and Lawson, J.W. 1997. A review of stomach contents of Harp Seals (*Phoca groenlandica*) from the Northwest Atlantic: an update. Tech Rep 97-01. International Marine Mammal Association, Guelph, Ontario, Technical Report 97-01:1–99.
- Weir, C.R., and Stockin, K.A. 2001. The occurrence and distribution of bottlenose dolphins (*Tursiops truncatus*) and other cetacean species in the coastal waters of Aberdeenshire, Scotland. Sea Watch Foundation Report. Oxford, UK: Sea Watch Foundation, pp. 68.
- Wells, R.S., and Scot, M.D. 2018. Bottlenose dolphin, *Tursiops truncates*, common bottlenose dolphin. In: Würsig, B., Thewissen, J.G.M., and Kovacs, K.M. (Eds.). *Encyclopedia of Marine Mammals*. Third Edition. Amsterdam; Elsevier-Academic Press, pp. 118–125.
- Went, A.E.J. 1964. Irish salmon – a review of investigations up to 1963. *Scientific Proceedings of the Royal Dublin Society Series A*, 1(15): 365–412.
- West, J.B., Bowen, G.J., Cerling, T.E., and Ehleringer, J.R. 2006. Stable isotopes as one of nature's ecological recorders. *Trends Ecol. Evol.* 21: 408–414.
- West, J.B., Bowen, G.J., Dawson, T.E., and Tu, K.P. 2010. *Isoscapes: understanding movement, pattern, and process on Earth through isotope mapping*. Springer, New York, New York, USA.
- Wilson, B., Arnold, H., Bearzi, G., Fortuna, C.M., Gaspar, R., Ingram, S., Liret, C., Pribanic, S., Read, A.J., Ridoux, V., and Schneider, K. 1999. Epidermal diseases in bottlenose dolphins: impacts of natural and anthropogenic factors. *Proc. Royal Soc. London. Series B: Biol. Sci.* 266: 1077–1083.
- Wood, S.A., Brault, S., and Gilbert, J.R. 2007. 2002 aerial surveys of grey seals in the Northeastern United States. *NAMMCO Scientific Publications*, 6: 117–121.
- Yano, A., Nicol, B., Jouanno, E., Quillet, E., Fostier, A., Guyomard, R., and Guiguen, Y. 2013. The sexually dimorphic on the Y-chromosome gene (sdY) is a conserved male-specific Y-chromosome sequence in many salmonids. *Evol. Appl.* 6: 486–496.

Annex 1: WKSalmn list of participants

Name	Institute	Country	E-mail
Hlynur Bardarson	Marine and Freshwater Research Institute	Iceland	hlynur.bardarson@hafogvatn.is
Mark Bilsby	Atlantic Salmon Trust	UK	mark@atlanticsalmontrust.org
Geir Bolstad	Norwegian Institute for Nature Research	Norway	Geir.bolstad@nina.no
Richard Brenner	Alaska Department of Fish and Game	USA	Richard.brenner@alaska.gov
Colin Bull	University of Stirling	UK	c.d.bull@stir.ac.uk
Jonathan Carr	Atlantic Salmon Federation	Canada	jcarr@asf.ca
Gérald Chaput	Fisheries and Oceans Canada, Moncton (NB)	Canada	Gerald.Chaput@dfo-mpo.gc.ca
Dennis Ensing	Agri-food and Biosciences Institute (AFBI)	UK	dennis.ensing@afbini.gov.uk
Jonathan Gillson	Cefas, Lowestoft Laboratory	UK	jonathan.gillson@cefass.co.uk
Stephen Gregory	Game and Wildlife Conservation Trust Salmon and Trout Research Centre	UK	sgregory@gwct.org.uk
Erica Head	Bedford Institute of Oceanography	Canada	Erica.Head@mar.dfo-mpo.gc.ca
Jan Arge Jacobsen	Faroese Marine Research Institute	Faroese	janarge@hav.fo
Priscilla Licandro	Plymouth Marine Laboratory	UK	Priscilla.licandro@outlook.com
David Meerburg	Atlantic Salmon Federation	Canada	dmeerburg@asf.ca
Niall Ó Maoiléidigh	Marine Institute, Fisheries Ecosystem Advisory Services	Ireland	niall.omaoleidigh@marine.ie
Mark Payne	DTU Aqua-National Institute of Aquatic Resources	Denmark	mpa@aqua.dtu.dk
Etienne Prévost	UMR INRA/UPPA Ecobiop	France	Etienne.prevost@inra.fr
Ana Ribeiro Santos	Cefas, Lowestoft Laboratory	UK	Ana.ribeirosantos@cefass.co.uk
Mark Saunders	North Pacific Anadromous Fish Commission	Canada	msaunders@yearofthesalmon.org
John Peter Strøm	The Arctic University of Norway	Norway	John.f.strom@uit.no
Mike Tillotson	Gulf of Maine Research Institute	US	mtillotson@Gmri.org
Kjell Rong Utne	Institute of Marine Research	Norway	Kjell.rong.utne@hi.no
Vidar Wennevik	Institute of Marine Research	Norway	Vidar.Wennevik@hi.no
Ken Whelan	Atlantic Salmon Trust	UK	ken.whelan@hotmail.com

Annex 2: List of presentations at WKSAlmon

<u>Presenter and co-authors</u>	<u>Subject / title</u>
W. Crozier and <u>K. Whelan</u>	The Likely Suspects Framework
<u>M. Saunders</u>	The International Year of Salmon – Overview of Activities in Pacific
<u>R. Brenner</u>	State of Alaska’s Salmon and People (SASAP)
<u>M. Tillotson</u> , L. Carlson, M. Barajas, K. Mills, and T. Sheehan	USA and West Greenland Marine Survival Data
<u>G. Chaput</u>	North American Atlantic Salmon perspective
<u>H. Bardarson</u>	Marine and Freshwater Research Institute Iceland
<u>J.A. Jacobsen</u>	Aspects of the marine ecology of Atlantic salmon
<u>E. Prévost</u>	Salmon ecology at sea: France
<u>N. O’Maoileidigh</u>	Wild Salmon Stock Assessment and Research - Ireland
<u>J. Gilson</u> , I. Russell, and S. Gregory	Available data for Atlantic salmon from England and Wales that could be used to explore hypotheses on mechanisms driving population dynamics at sea
<u>D. Ensing</u> and R. Kennedy	UK- Northern Ireland Data
<u>G. Bolstad</u>	SeaSalar and some of the relevant data from Norway
<u>K.R. Utne</u>	Contribution from Institute of Marine Research Norway: salmon datasets
<u>N. O’Maoileidigh</u>	CRR 343 – Fifty years of marine tag recoveries
<u>J. Carr</u> , J.F. Strøm, J. Daniels, G. Chafe, E. Brunsdon, M. Robertson, and T. Sheehan	Using Telemetry to Map the Spatial and Temporal Distribution of Atlantic Salmon in the Ocean
<u>J.F. Strøm</u>	Sea Salar - Atlantic Salmon At Sea Factors Affecting Their Growth And Survival
<u>Erica Head</u>	The Northwest Atlantic Ecosystem: observations of physical and biological conditions from the DFO Atlantic Zone inshore and offshore monitoring programmes (AZMP and AZOMP)
<u>P. Licandro</u>	Overview of oceanographic conditions in the Northeast Atlantic
<u>J.A. Jacobsen</u>	Pelagic fish complex – Northeast Atlantic
<u>A.R. Santos</u>	(ICES InterCatch; DATRAS; STECF; RDB)
<u>J.A. Jacobsen</u>	By-catch estimates of salmon in the Faroese pelagic fisheries in 2011
<u>K.R. Utne</u>	Contribution from Institute of Marine Research Norway: ecological datasets
I. Russell, <u>J. Gillson</u> , T. Bašić, B. Riley and L. Talks	Prioritising the management of Atlantic salmon based on the relative impacts of stressors in the marine environment around England

Presenter and co-authors	Subject / title
<u>K.R. Utne</u>	Overview of biotic and environmental conditions potentially influencing salmon growth and survival – data from the Northeast Atlantic
<u>M. Payne</u>	WGS2D – Working Group on Seasonal-to-Decadal Prediction of Marine Ecosystems
<u>S. Gregory</u> and E. Rivot	Project SAMARCH 2017 – 2022
<u>D. Ensing</u>	EU DCF/DC-MAP and Data Calls

Annex 3: ICES resolution

A **Workshop for North Atlantic Salmon At-Sea Mortality** (WKSALMON), chaired by Gerald Chaput and Niall O'Maoiléidigh will meet at ICES HQ, Copenhagen, Denmark on 24–28 June 2019 for a 5-day scoping meeting; then in autumn 2019 for a 3-day data evaluation meeting; and then for a 5-day modelling meeting in 2020/2021 to:

- a) Identify data sources that could inform estimates of at-sea salmon mortality and the associated available data, including data from North Atlantic salmon as well as ecosystem data (such as oceanographic time series, plankton surveys, International Ecosystem Summer Survey in the Nordic Seas (IESSNS), pelagic or demersal fish surveys);
- b) Develop a data call that will integrate these sources with existing ICES databases;
- c) Evaluate the appropriateness of data and methods used to estimate at-sea salmon mortality;
- d) Identify data gaps and develop recommendations for future data acquisition;
- e) Evaluate modelling approaches to integrate marine data fully to cover the whole life-cycle of Atlantic salmon in the context of the 'Likely Suspects' Framework (see http://www.nasco.int/sas/pdf/archive/papers/2018/SAG_18_04_AST%20Likely%20Suspects%20Framework%20Update.pdf);

The workshop will report by **tbd** for the attention of ACOM.

Supporting Information

Priority	High
Scientific justification	<p>The goal is to improve the scientific assessments and advice for the conservation of wild Atlantic salmon through a series of workshops that explore how best to integrate available data on salmon, specifically data on marine survival, within the appropriate ICES database(s) for use in models to advance the conservation of wild salmon at sea. Parallel initiatives are being planned elsewhere to refine and integrate freshwater and inshore marine data, particularly on the survival of migrating smolts and post-smolts, so as to provide a comprehensive understanding of the key mortality factors affecting the whole lives of Atlantic salmon. These data will be used to populate the Likely Suspect Framework, which will link patterns in at-sea mortality of Atlantic salmon to appropriate geographic and temporal scales.</p> <p>Ultimately these workshops will result in an improvement in the ICES advice for Atlantic salmon through enabling the provision, collation and standardisation of salmon data that are currently unavailable to ICES.</p>
Resource requirements	-
Participants	Data providers, diadromous experts, scientists and experts involved in salmon research, stock assessments, and ecosystem approaches
Secretariat facilities	Meeting rooms, secretariat staff
Financial	-
Linkages to advisory committees	ACOM
Linkages to other committees or groups	WGNAS; EPDSG; WGOOFE; WGZE; WGSPEC; WGMEDS
Linkages to other organizations	NASCO