Atlantic Salmon: Changing Survival Patterns and Shifting Populations

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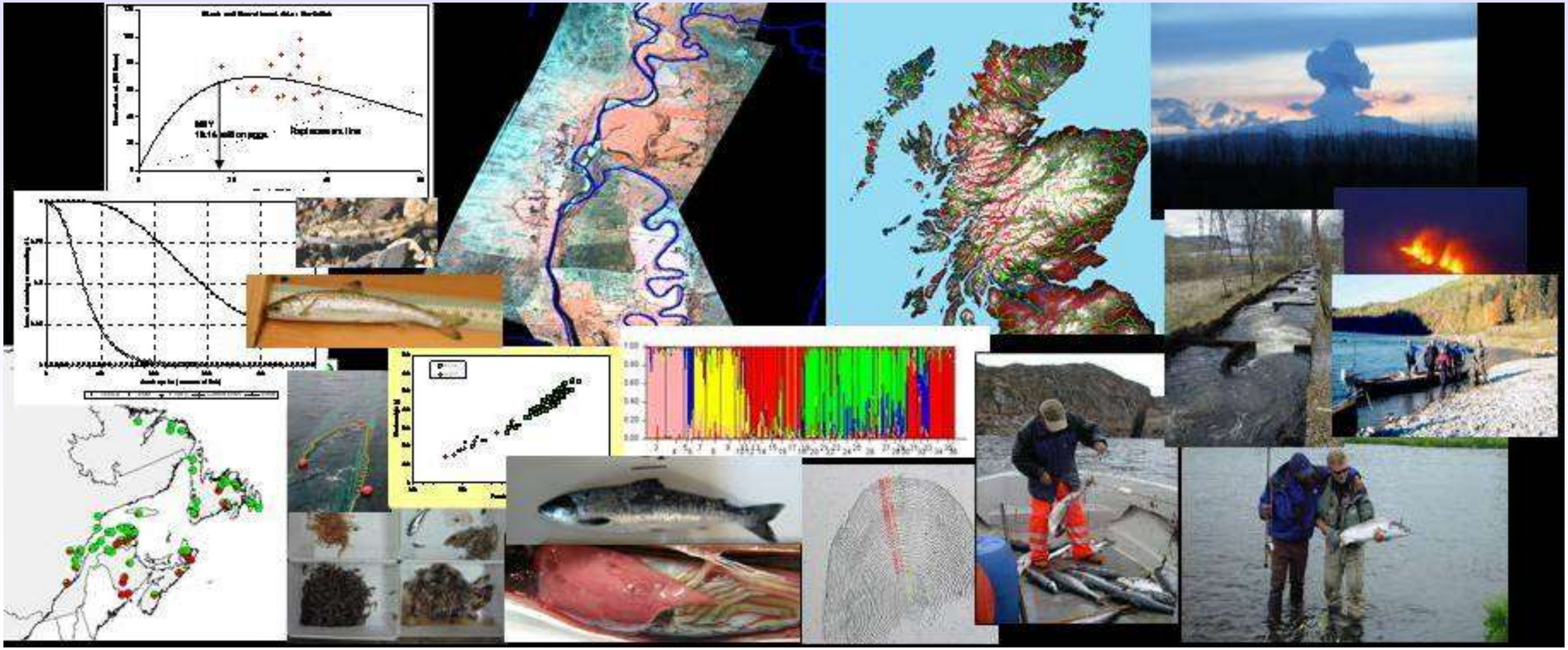


Atlantic Salmon: Changing Survival Patterns and Shifting Populations

1) Evolutionary history and biology of the species: an iconic marine migrant that maintained a mandatory freshwater phase

2) Variations in life history, flexible population responses to climatic and environmental variations.

3) Sequential trade-offs to fitness beginning in freshwater.

4) Levels and changes in marine survival and salmon abundance.

4) Challenges to understanding how salmon respond to changing environments

5) Survival of populations is not a random process, so can we change the odds of winning in the future?

Acknowledgements

- The numerous members of the ICES Working Group on North Atlantic Salmon from more than 13 countries over the past five decades.
- Countless individuals involved in the monitoring of stocks, compilation of catch data and biological characteristics from national governments, NGOs and aboriginal communities.
- The large and diverse scientific community (we all stand on the shoulders of giants)

Atlantic Salmon Background

- Obligate freshwater spawner, with anadromous (going to sea) life history as an option (land-locked, ouananiche populations)
- Can be repeat spawner (unlike Pacific salmon that die after spawning)

Some definitions:

10 – 18 cm

Smolt: juvenile life stage that transitions from freshwater to marine (anadromous component)

45 – 65 cm; 1.5 – 3 kg

Small salmon (1SW): also called grilse, composed mostly of one-sea-winter anadromous salmon, in regulations, measures < 63 cm fork length, < 2.7 kg in commercial and Labrador FSC fisheries

70 – 100+ cm; 4 – 12+ kg

Large salmon (MSW): also called salmon, multi-sea-winter salmon, composed mostly of maiden 2SW and 3SW salmon, and repeat spawners, in regulations >= 63 cm, fork length, >= 2.7 kg in commercial and Labrador FSC fisheries

Atlantic Salmon evolutionary history: an iconic marine migrant that maintained a mandatory freshwater phase

Family Salmonidae
Subfamily Salmoninae
Salmo salar **Linneaus**

- Pacific vs Atlantic salmonine divergence ~ 20 million years before present (BP)
- Atlantic Salmon shares common ancestor with Brown Trout (*Salmo trutta*) (< 5 million years BP)

Two phylogenetic groups (600K – 700K years BP)

- Northwest Atlantic (54 chromosone pairs)
- Northeast Atlantic (58 chromosone pairs)

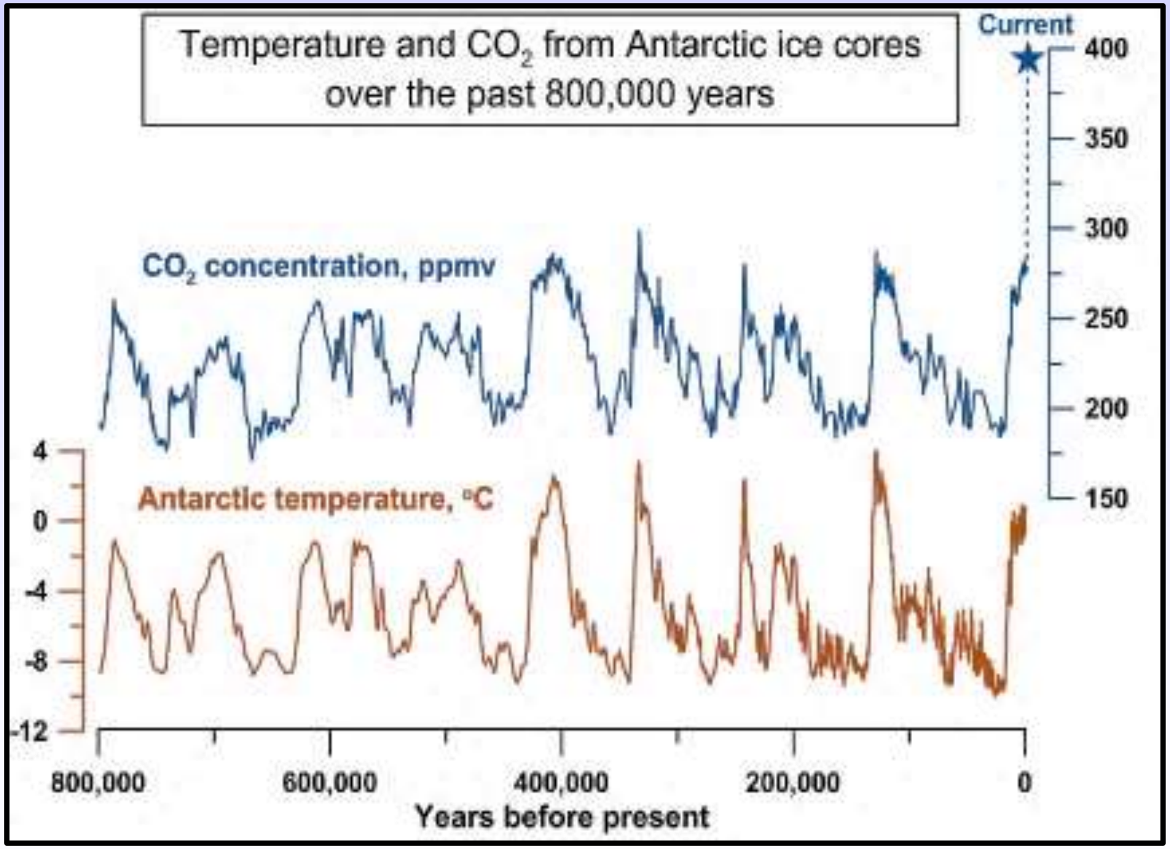
Within Northeast Atlantic, two subgroups (< 18K years BP)

- Atlantic (susceptible to *Gyrodactylus salaris*)
- Baltic (resistant to *G. salaris*)

Ref: King, et al. 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.

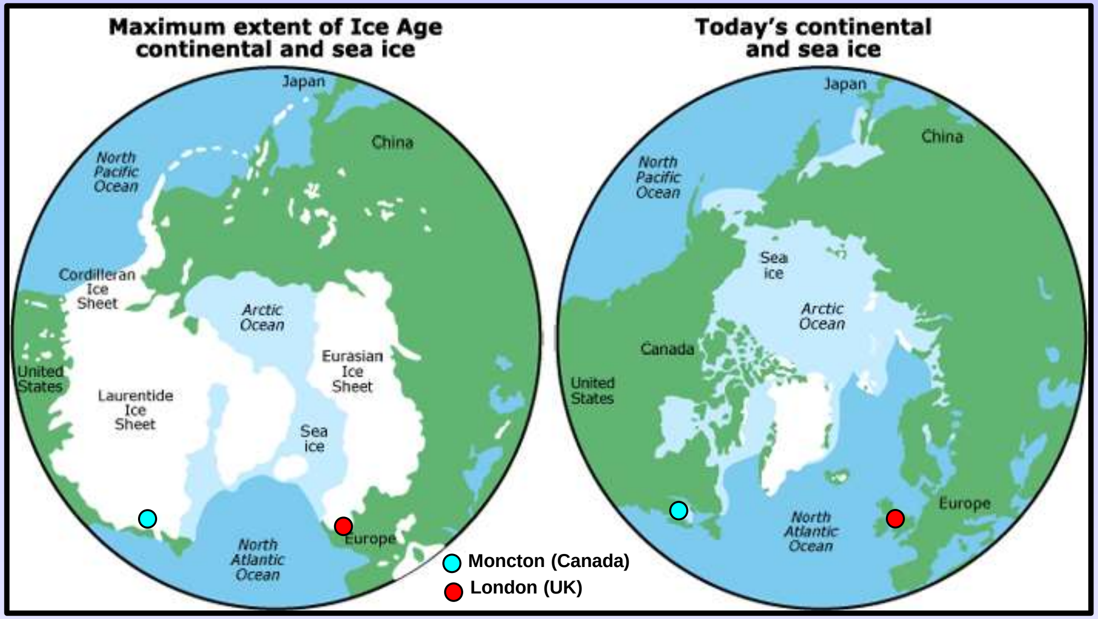
- Over the 700,000 years of Northwest/Northeast Atlantic Salmon evolution, climatic and geophysical conditions have been extremely variable.

- Late Quaternary period (the past one million years of *S. salar* evolutionary history) is punctuated by a series of large glacial–interglacial conditions with cycles that last about 100,000 years.
- Climate has almost always been in a state of variation within maximum and minimum values (range of 10ºC average global temperature).



- During the most recent glacial period (~18-75 k years BP), sea level was as much as 120 m lower than present and there was substantial loss and creation of freshwater habitat and marine habitat.

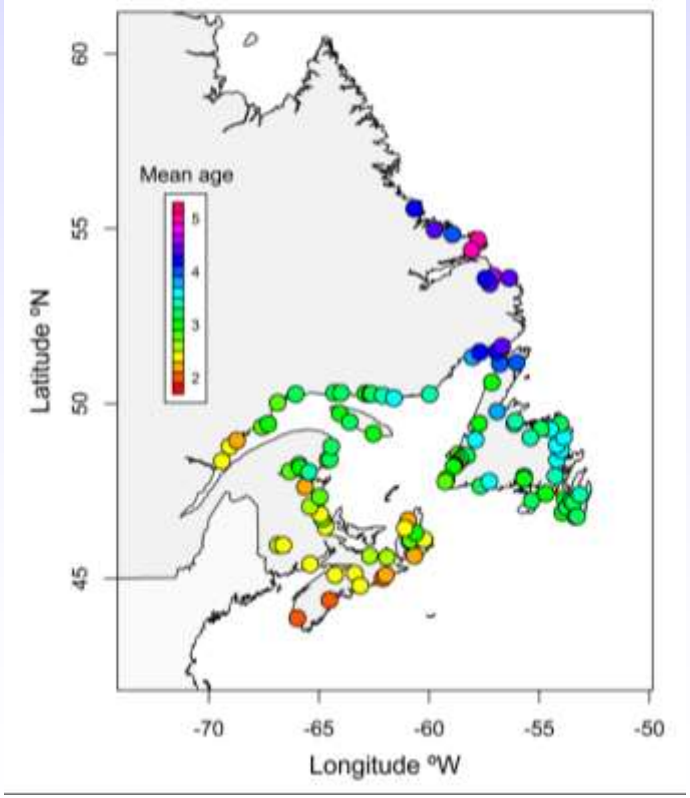
- The most recent expansion of Atlantic Salmon occurred during the Holocene period (11 k years), from primarily southern refugia to its contemporary distribution in over 2000 rivers in the North Atlantic and evolution of diverse life history characteristics.



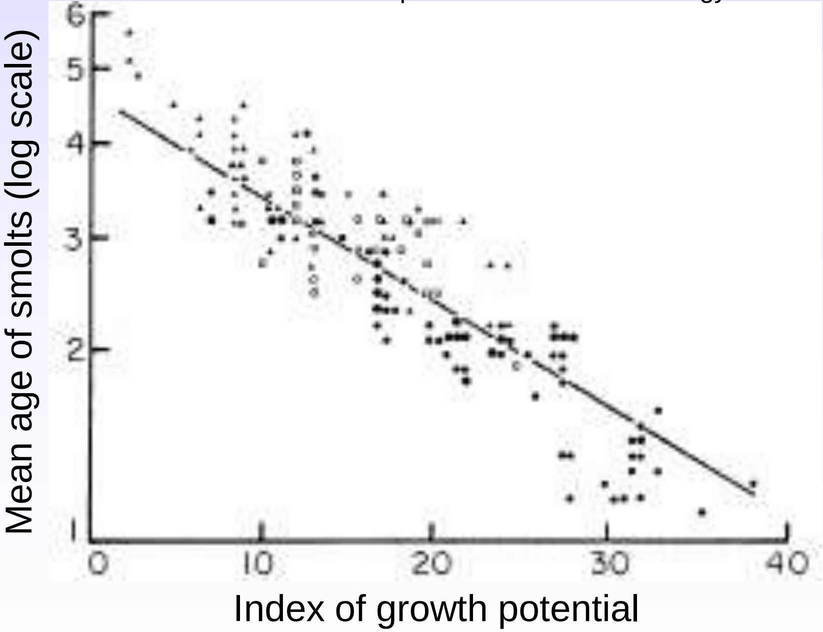
Some examples of plastic responses in life history characteristics

- Life history characteristics (age at smoltification, growth rates, sea age at maturity, size at age, ...) are in large part flexible responses to climatic and environmental variations (phenotypic plasticity).

- River age at smoltification is related to growth potential, with older ages in northern (colder) latitudes, and the relationship is consistent across the species range in the North Atlantic.

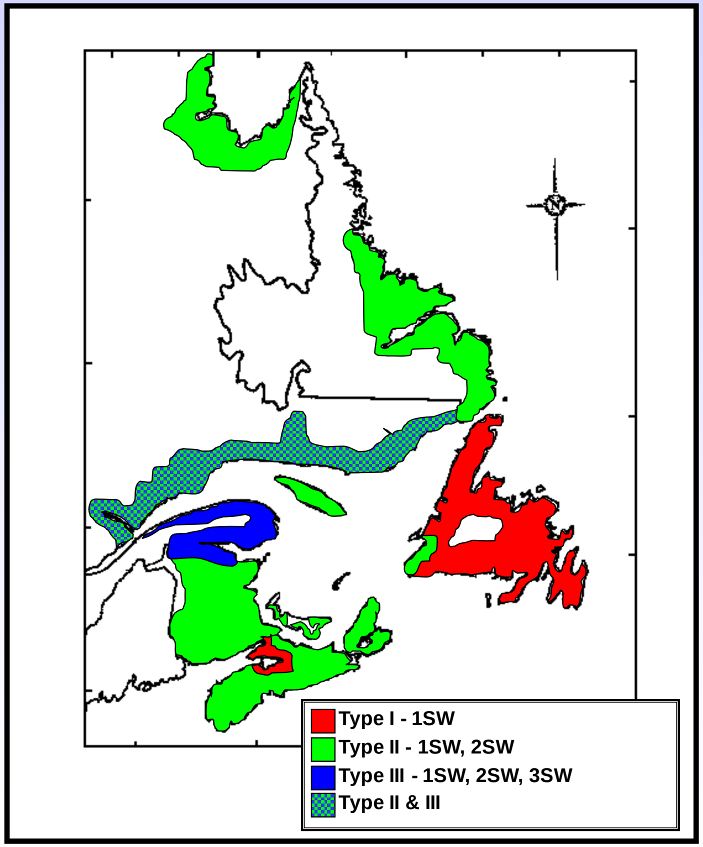


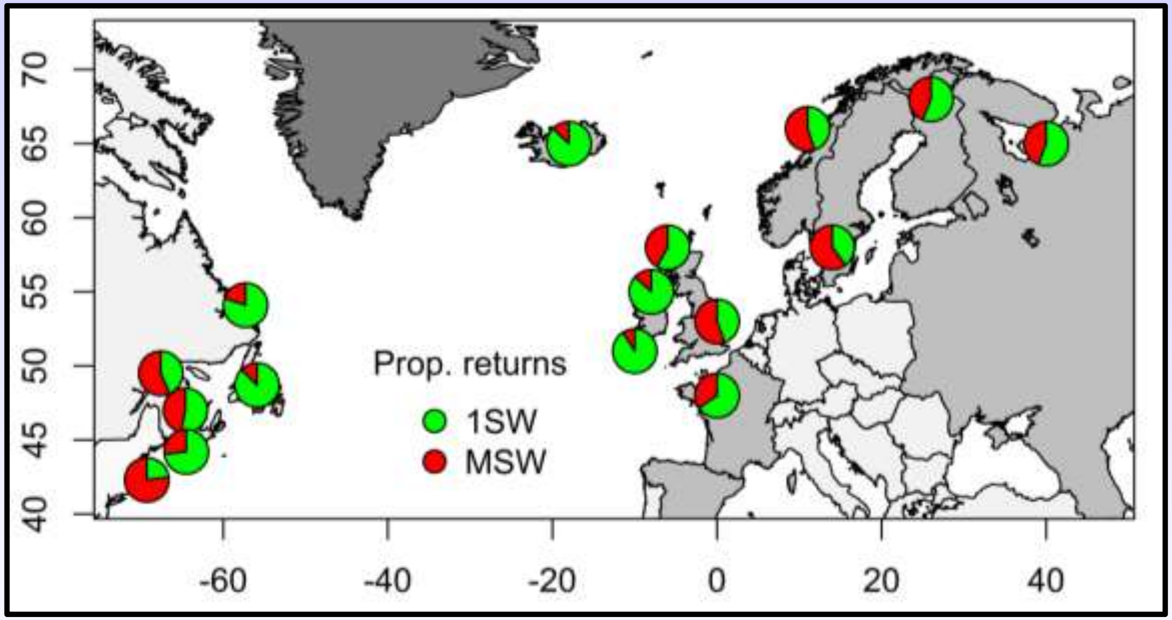
Ref.: Metcalfe and Thorpe. 1990. J. Animal Ecology 59.



Plasticity in sea age at maturity

- Important geographic variation in proportions at sea age of return.
- Some populations are dominated by 1SW maturing adults (Newfoundland in Canada; Iceland, Ireland, Northern Ireland in the Northeast Atlantic).

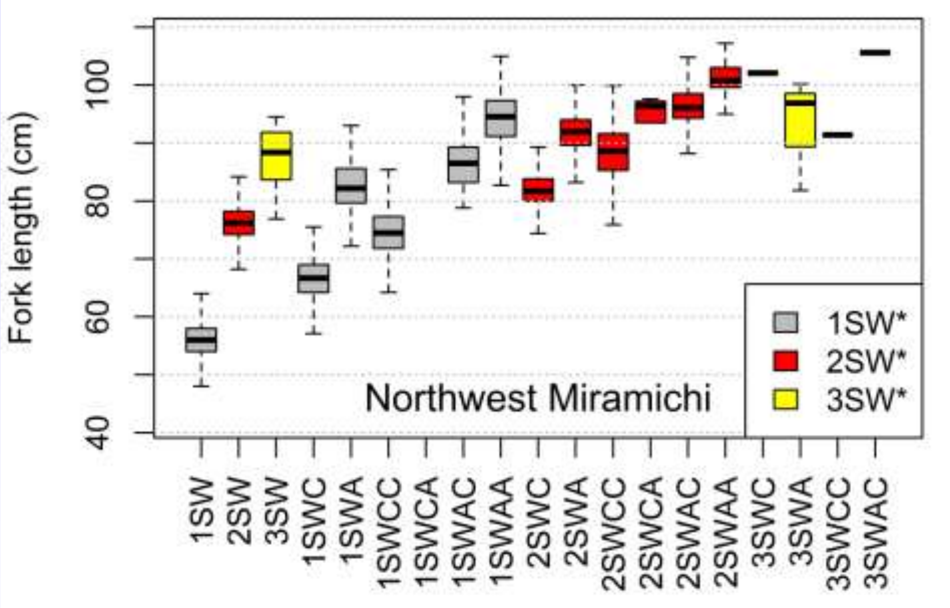




Source: ICES Working Group Report North Atlantic Salmon

Plasticity in size at maturity

- Maturing after one-sea-winter (1SW; ~ 18 months at sea), 2SW to 5SW (MSW).
- Body sizes ranging from 45-70 cm for 1SW, to > 100 cm for 3-5SW.
- Repeat spawners can be common, and grow with each spawning event.



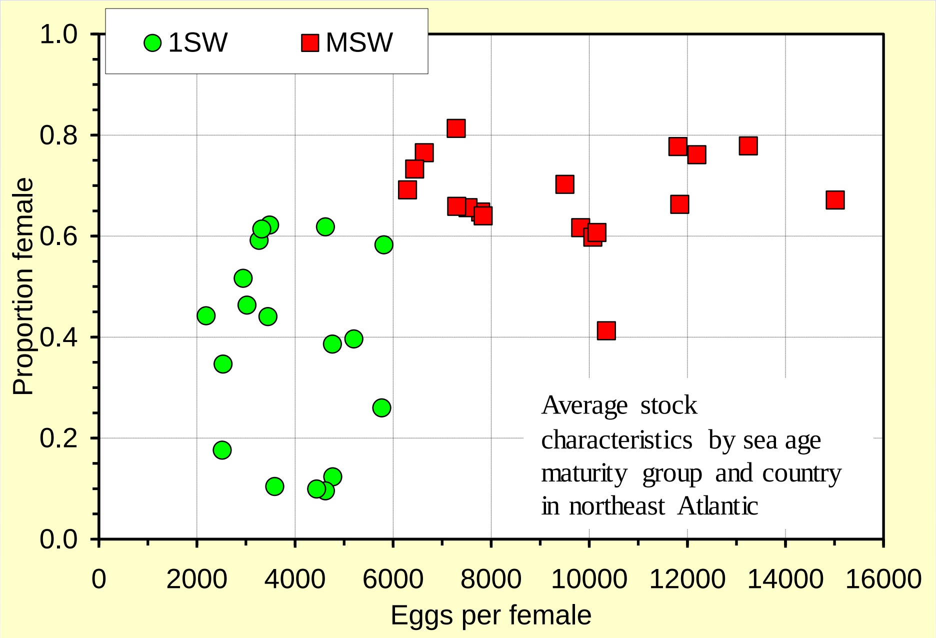
Credit: F. Butruille

Credit: A. McNeill

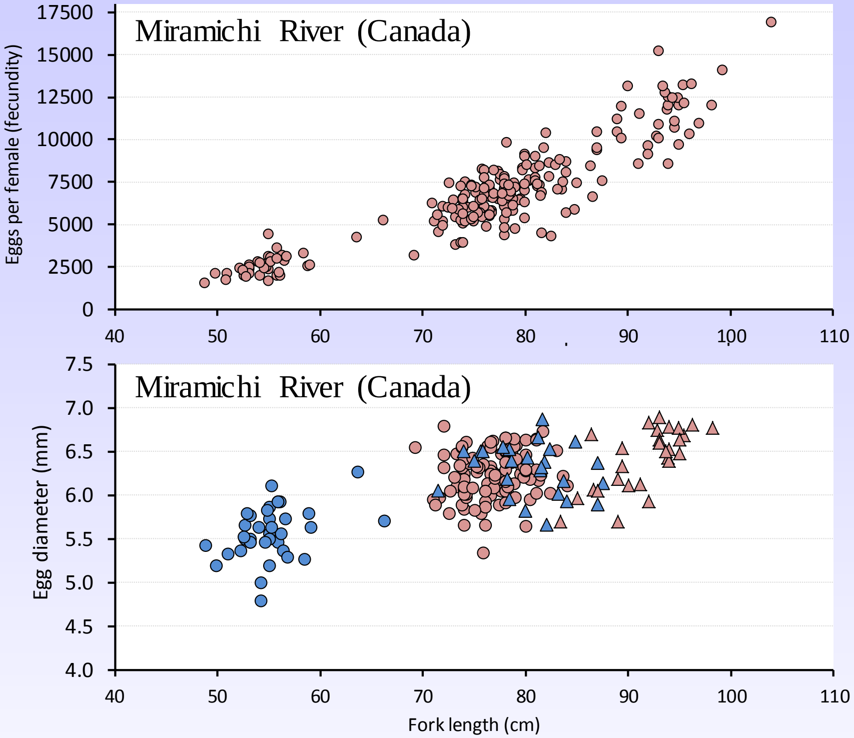
Credit: H. Sparholt

Plasticity in reproductive characteristics

- Sex ratio differs by sea age-at-maturity, fecundity increases with body size.



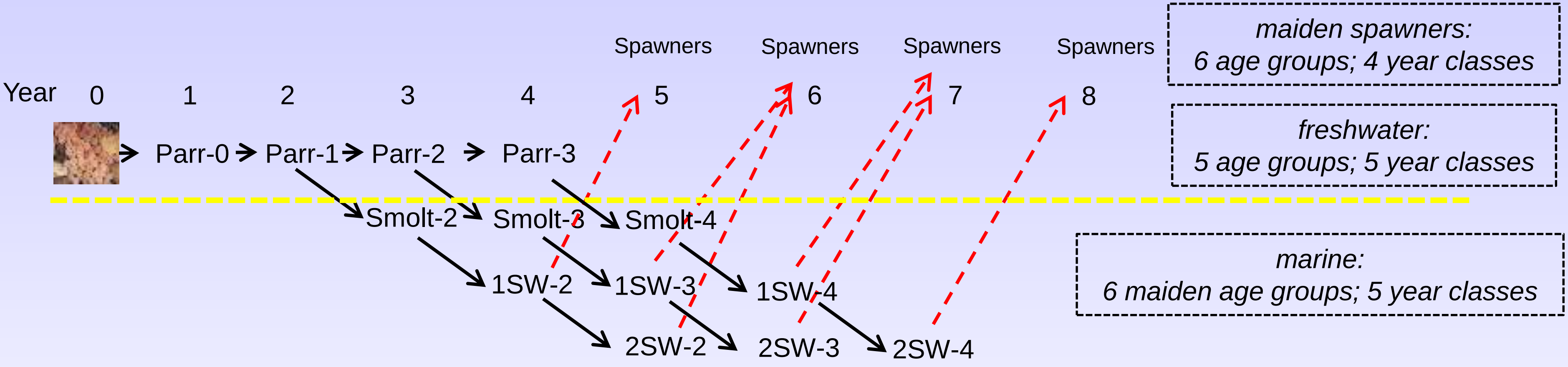
Average stock characteristics by sea age maturity group and country in northeast Atlantic



- Salmon spawn a moderate number (2,000 to 18,000 per female) but large (4.5 to 7 mm diameter) eggs.

Diversity in life history characteristics is important in the resilience and persistence of populations (portfolio effect)

Life history example, 3 smolt ages, 2 sea ages, no repeat spawners



Spawners Spawners Spawners Spawners

Year 0 1 2 3 4 5 6 7 8

Parr-0 Parr-1 Parr-2 Parr-3

Smolt-2 Smolt-3 Smolt-4

1SW-2 1SW-3 1SW-4

2SW-2 2SW-3 2SW-4

maiden spawners:
6 age groups; 4 year classes

freshwater:
5 age groups; 5 year classes

marine:
6 maiden age groups; 5 year classes

Including repeat spawning life histories:

- a single year class can contribute spawners in eight years or more
- annual spawning run can comprise 8+ yearclasses (ex. Miramichi)

Repeat spawning diversity

- Miramichi River (Canada) – 52 sea age spawning histories (excluding smolt age) with 7th spawning migration
- River Teno (Finland) – 120 combinations of freshwater and sea age spawning histories (smolt ages 2-8; maiden sea age 1-5; previous spawners)

Northern populations with a large range of smolt ages and multi-sea-winter life histories are more resilient than southern populations with minimal smolt age diversity and singular sea age at maturity.

Why anadromy?

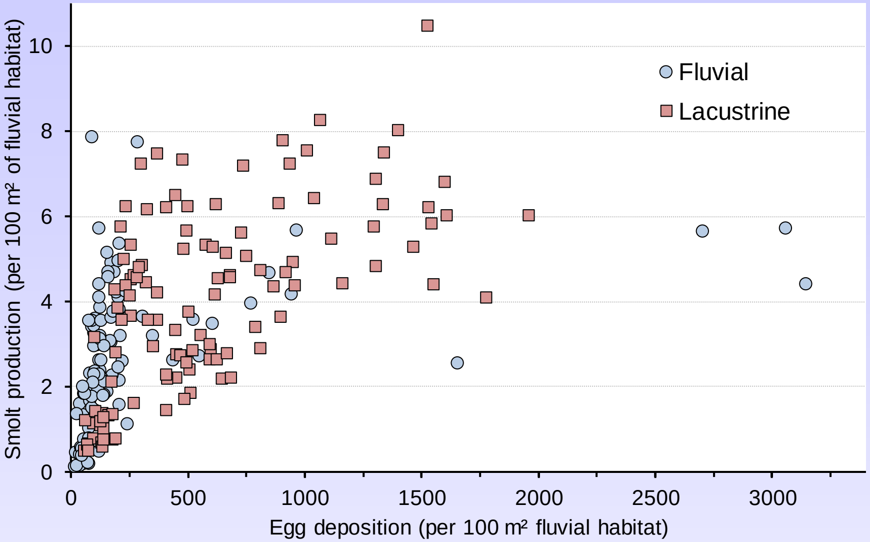
- Anadromy evolved as a tradeoff between survival to reproduction and reproductive capacity (eggs per fish):
  - production in the marine environment is considered to be density independent
  - salmon grow rapidly at sea (one of the fastest growing fish)

	Atlantic Salmon	Sockeye Salmon	Chinook Salmon	Bluefin Tuna
Smolts	10 – 20 cm (1-6 yrs)	6 – 13 cm (1-2 yrs)	6 – 13 cm (0 – 1 yr)	
One year at sea	45 – 65 cm	35 – 40 cm	30 – 45 cm	45 – 60 cm
2 years at sea	60 – 90 cm	45 – 55 cm	50 – 65 cm	65 – 90 cm
3 years at sea	80 – 100 cm	50 – 60 cm	65 – 80 cm	85 – 120 cm
4 years at sea			80 – 95 cm	100 -150 cm

- larger body size results in greater reproductive products (eggs, sperm) with demonstrated benefits of larger body size to spawning success
- marine mortality rates are very high compared to other species (>90% of the animals may die in one year) because they are risk takers; in order to grow rapidly, they must eat which increases the risk of being eaten

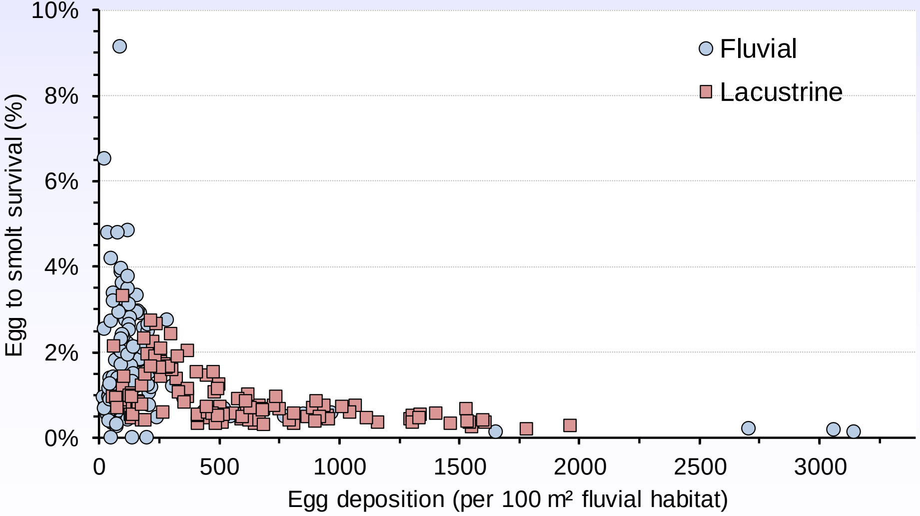
What are the main drivers of Atlantic Salmon abundance and diversity?

- Atlantic Salmon is an obligate freshwater spawner.
- Density dependent regulation occurs in freshwater, with constraints to production primarily a consequence of the quantity of available habitat (competition for shelter, territories, food,...).



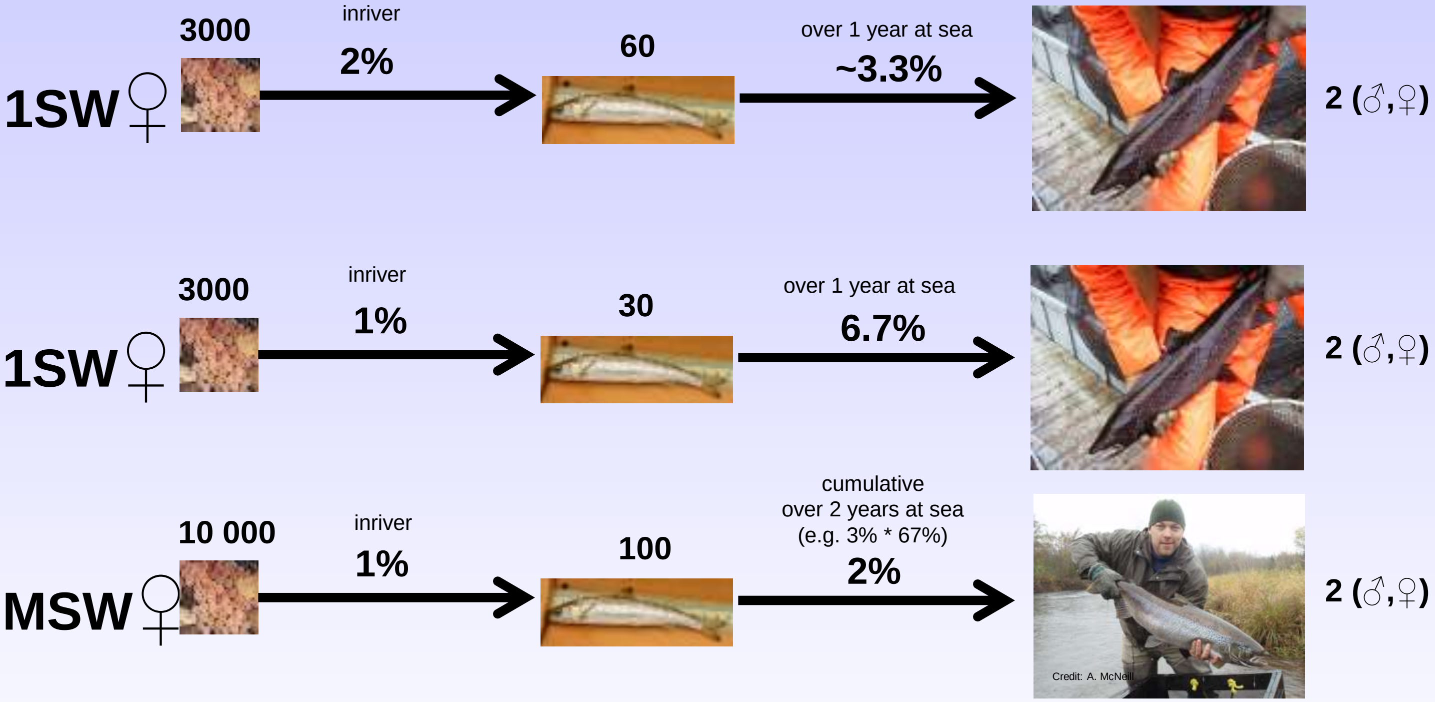
data from 14 monitored rivers of eastern Canada (Chaput et al. 2016)

- Relatively high survival rate in freshwater; egg to smolt survival rates can exceed 3% at low egg deposition densities but highly variable among rivers.
- Survival rates generally <1% at egg depositions > 500 eggs 100 m^{-2}.
- Estimated maximum egg to smolt survival at the origin of a Beverton-Holt stock and recruitment relationship: 5.3% (0.5% to 25.3%; 95% BCI).



Sequential trade-offs that begin in freshwater

- Relatively high survival rate in freshwater can offset low survival rates at sea.
- Examples of survival tradeoffs for a female spawner to replace herself.

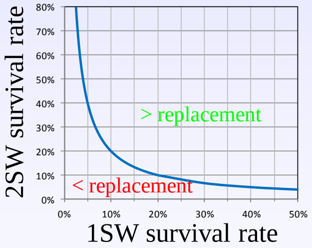


1SW♀ **3000** inriver **2%** → **60** over 1 year at sea **~3.3%** → **2 (♂,♀)**

1SW♀ **3000** inriver **1%** → **30** over 1 year at sea **6.7%** → **2 (♂,♀)**

MSW♀ **10 000** inriver **1%** → **100** cumulative over 2 years at sea (e.g. 3% * 67%) **2%** → **2 (♂,♀)**

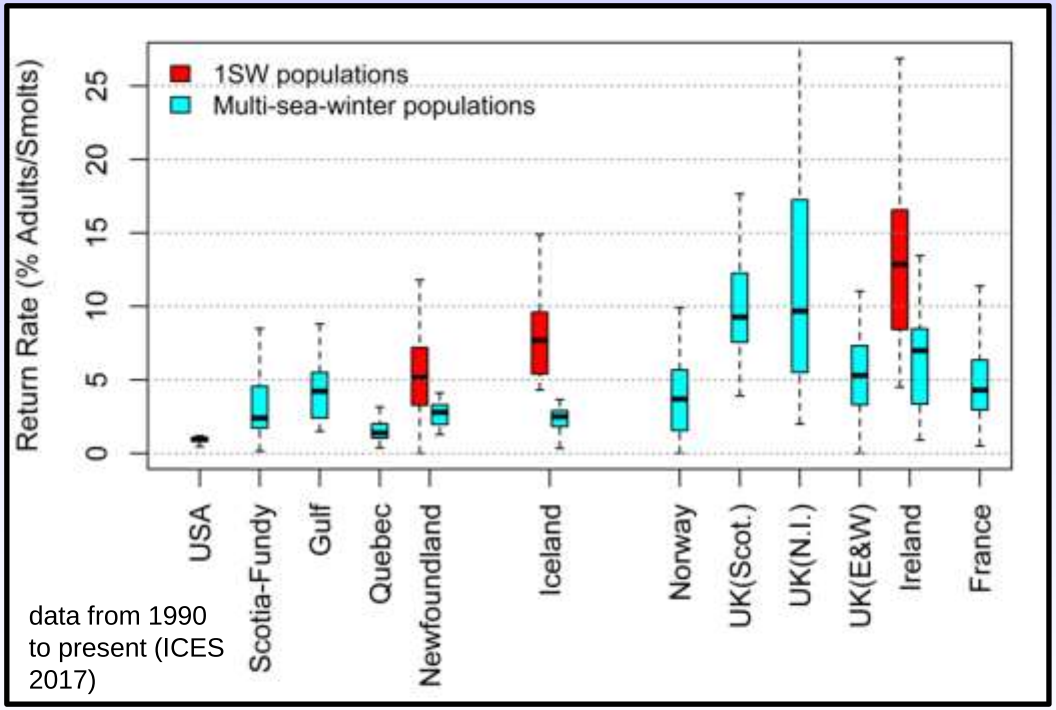
Credit: A. McNeill



- These are spawner replacement rates.
- For a population to grow in abundance, higher (fw or marine) corresponding survival rates are required.

What are the realized marine return rates for Atlantic Salmon?

- Return rates (adults/smolts) are proxies of marine survival.
  - 1SW stocks: return rate = sea survival
  - MSW stocks: return rate ≠ sea survival
    - return rate = 1SW.Surv * Prop. maturing as 1SW +
      1SW.Surv * (1 - Prop. maturing as 1SW) * Surv.2SW

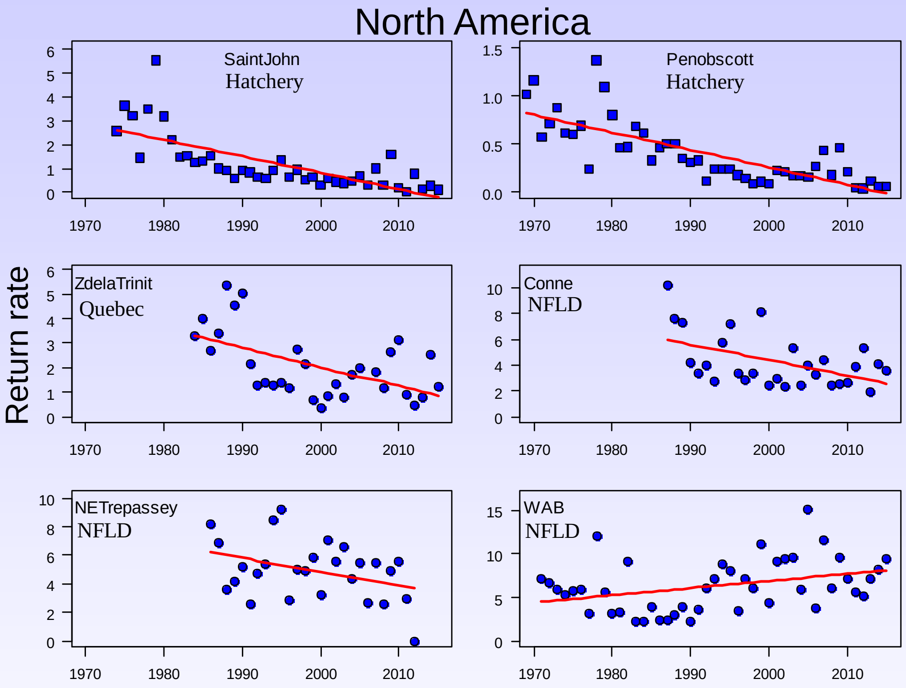


data from 1990 to present (ICES 2017)

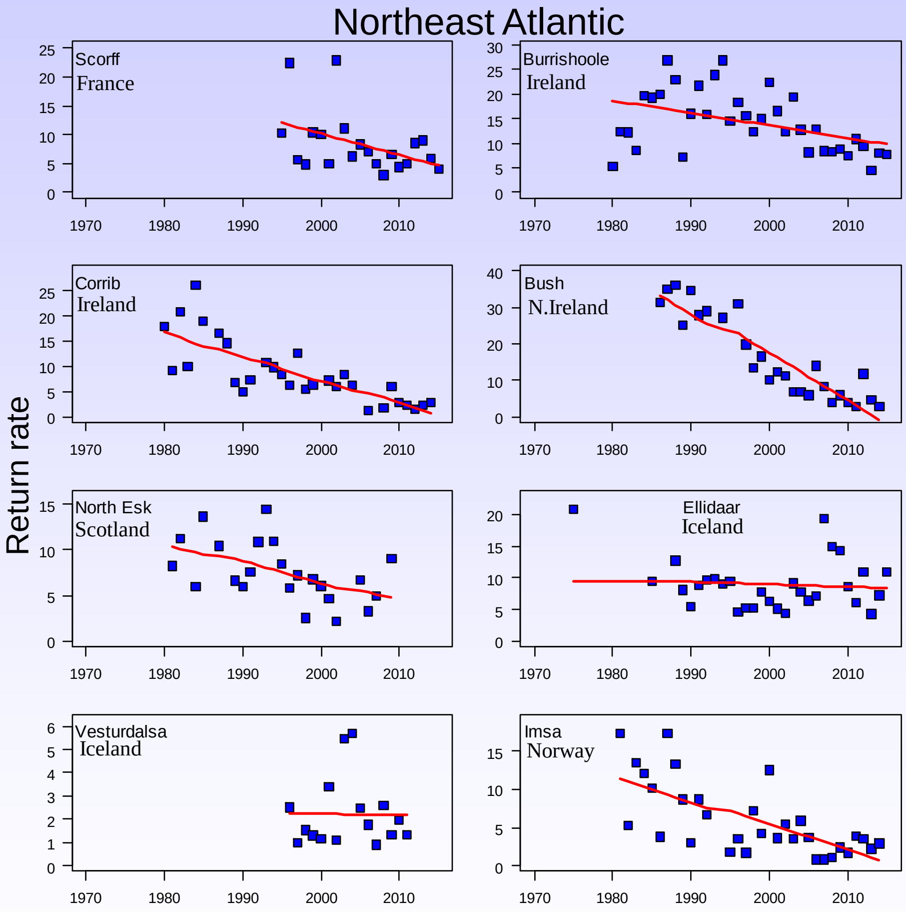
- Return rates for 1SW stocks are higher than for MSW stocks.
- Return rates for salmon stocks in Iceland and Europe > in eastern North America.
- Have they changed over time?

Trends in return rates

- Return rates in monitored rivers show declines over the past four decades in southern regions of North America and in most regions of the Northeast Atlantic.



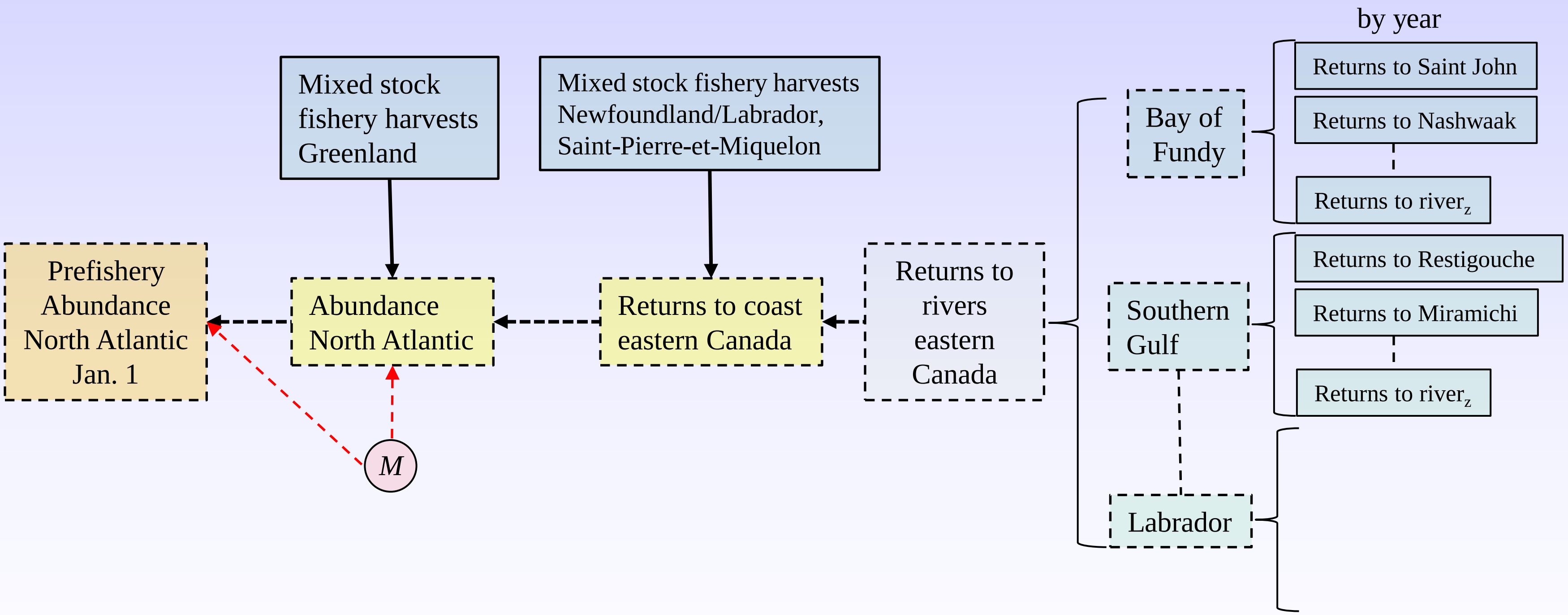
not corrected for marine fisheries in Newfoundland, Labrador, SPM, Greenland



not corrected for marine fisheries in Faroes, Greenland (but corrected for coastal fisheries)

Evidence of reduced abundance of salmon in the North Atlantic

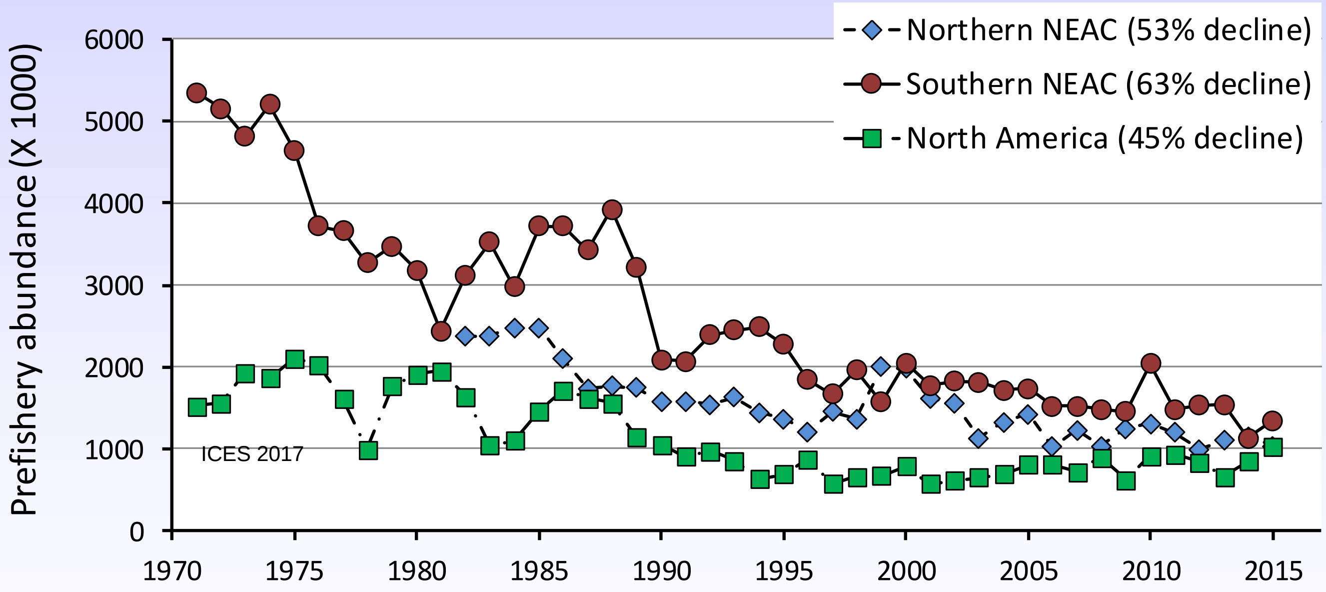
- Bookkeeping exercise (run reconstruction) to estimate the abundance of salmon at different points in the life cycle (focus on adult salmon in the marine phase).
- Cumulate backwards from returns to rivers, adding marine fisheries removals, and adjusting for estimates of survival (M = 0.03 per month) in later stages of marine phase.
- Estimate abundance as of January 1 of the first winter at sea.

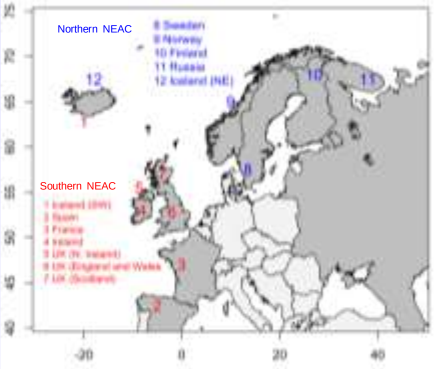


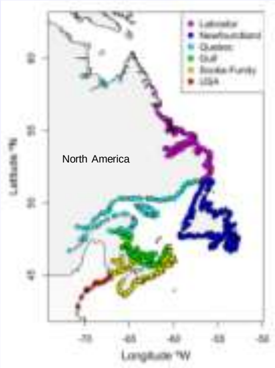
- Do this for small salmon (< 63 cm; 1SW) and large salmon (>= 63 cm; MSW).
- Do this for eastern North America, south Northeast Atlantic, north Northeast Atlantic.
- Beginning in 1971 (1982 for north Northeast Atlantic).

Evidence of reduced abundance of salmon in the North Atlantic

- Important declines in estimated pre-fishery abundance (as of Jan. 1 of first winter at sea) of Atlantic Salmon in three major stock complexes of the North Atlantic.
- Peak estimated abundance that likely exceeded 10 million fish at sea in the 1970s to an average less than 3.5 million fish in past ten years.

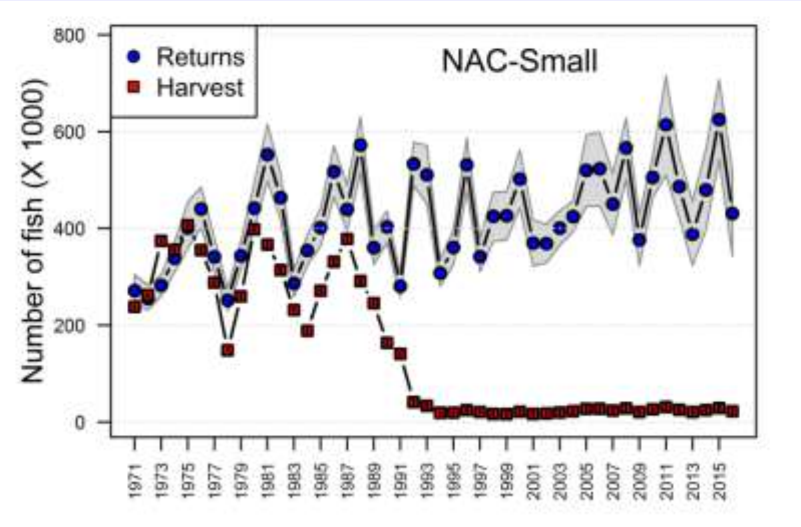


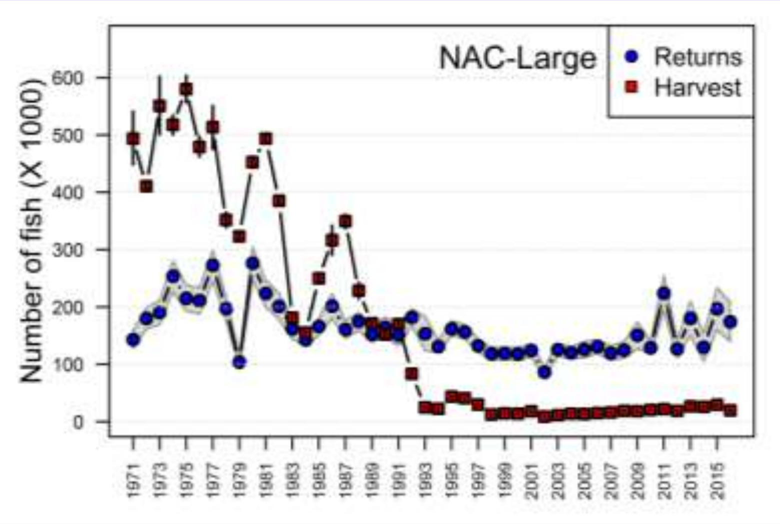




Contrasting trends in returns (post marine fisheries) to regions

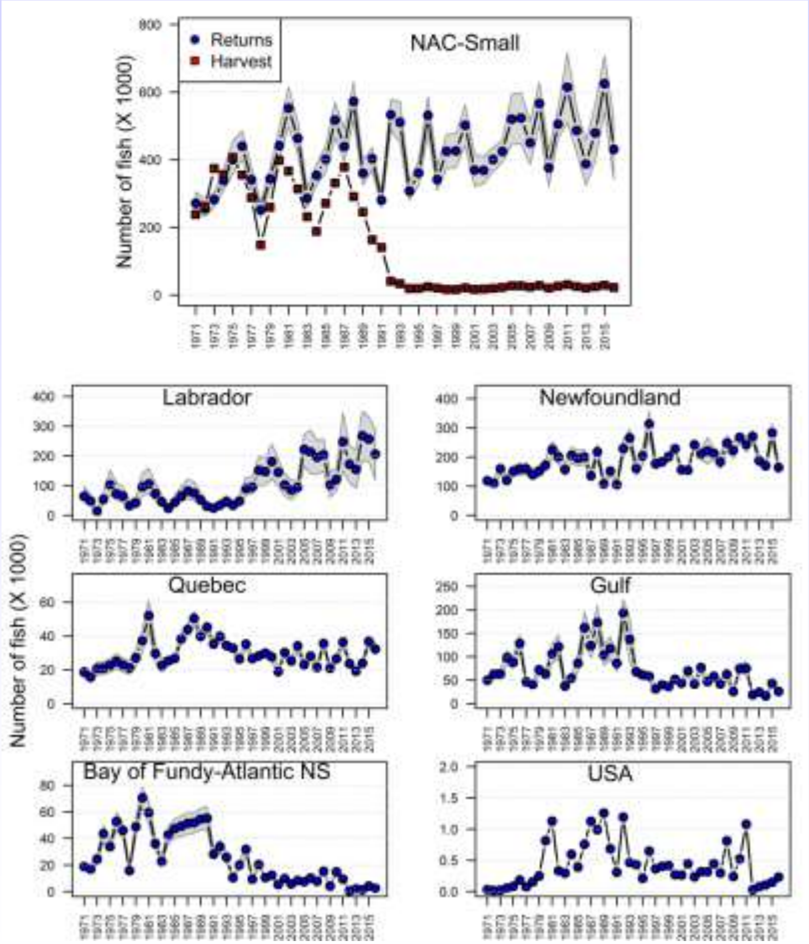
- Small salmon returns to NAC show annually oscillating and generally increasing trend in returns to rivers but marine fishery harvests (Newfoundland, Labrador, SPM) were as high as 400 thousand fish in the 1970s, currently about 20 to 30 thousand.
- Large salmon returns for NAC show flat trend but marine harvests (Greenland, Newfoundland, Labrador, SPM) were just under 600 thousand in the early 1970s, currently 15 to 30 thousand.

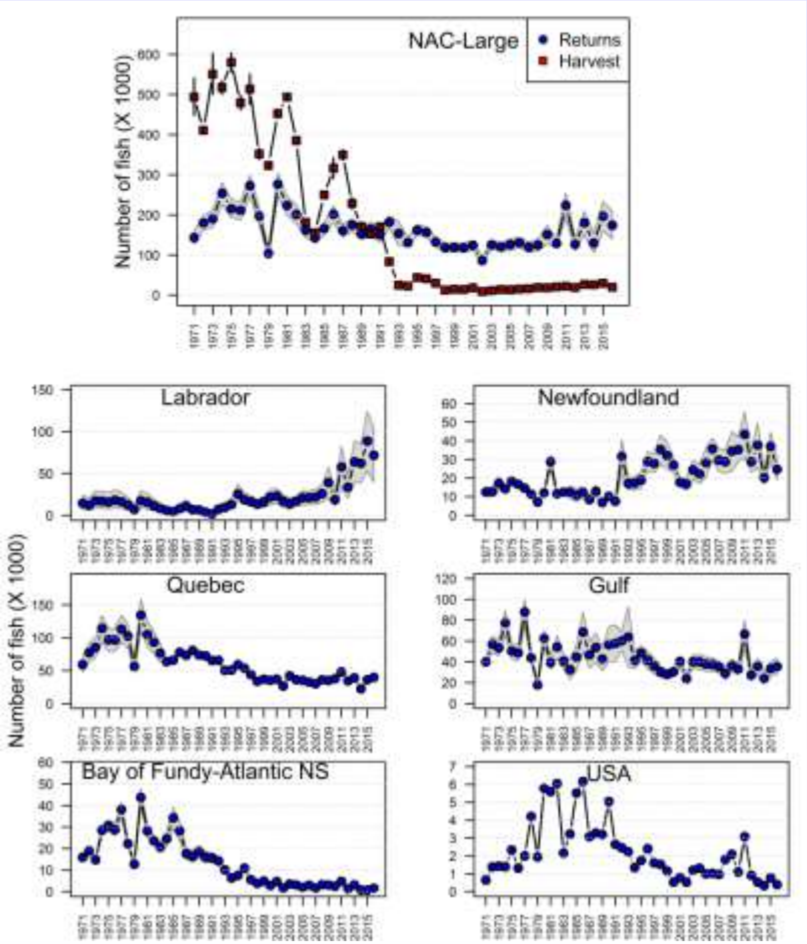




Contrasting trends in returns (post marine fisheries) to regions

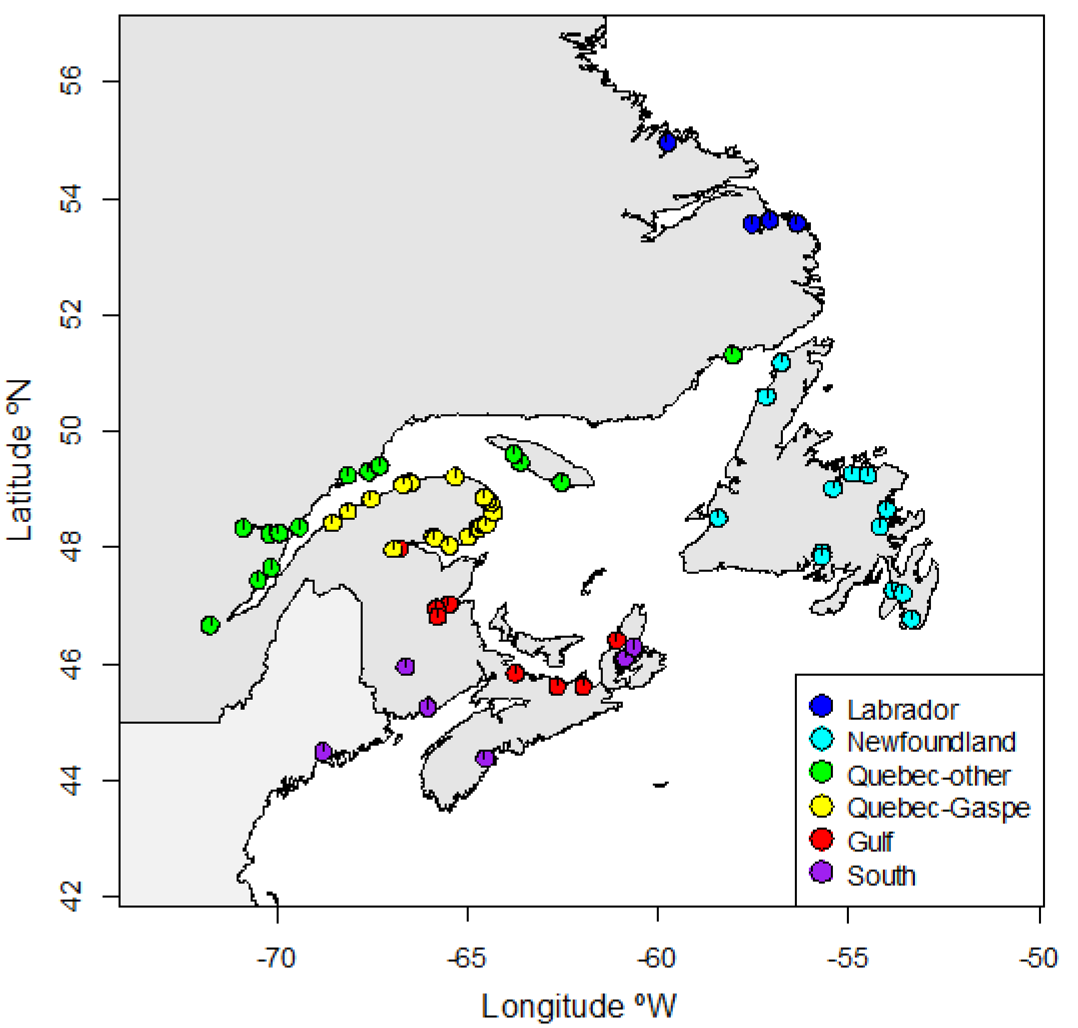
- Increasing returns of small and large salmon to Labrador and Newfoundland (northern regions).
- Decreased returns of large salmon in the other regions of eastern Canada, severe declines in the two most southern regions, despite reductions in mixed stock marine fisheries harvests.
- Decreased returns of small salmon in the Maritime provinces (Gulf and Bay of Fundy-Atlantic NS), no noted decline for Quebec, despite reductions in mixed stock marine fisheries harvests.





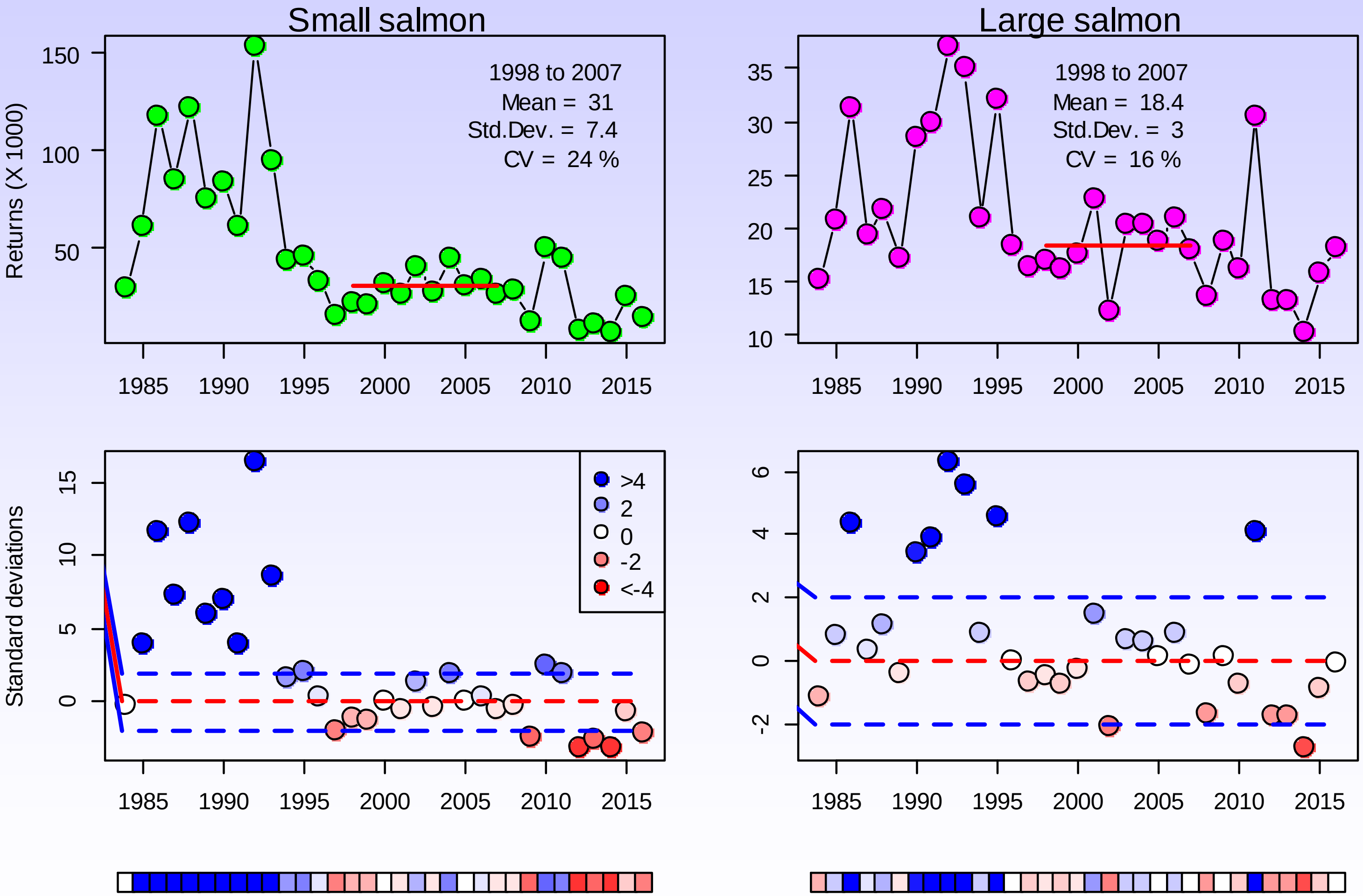
Contrasting patterns of returns to individual rivers

- Returns or indices to individual rivers of small salmon and large salmon are available for 61 rivers, with a large number of data series back to 1984.



Contrasting patterns of returns to individual rivers

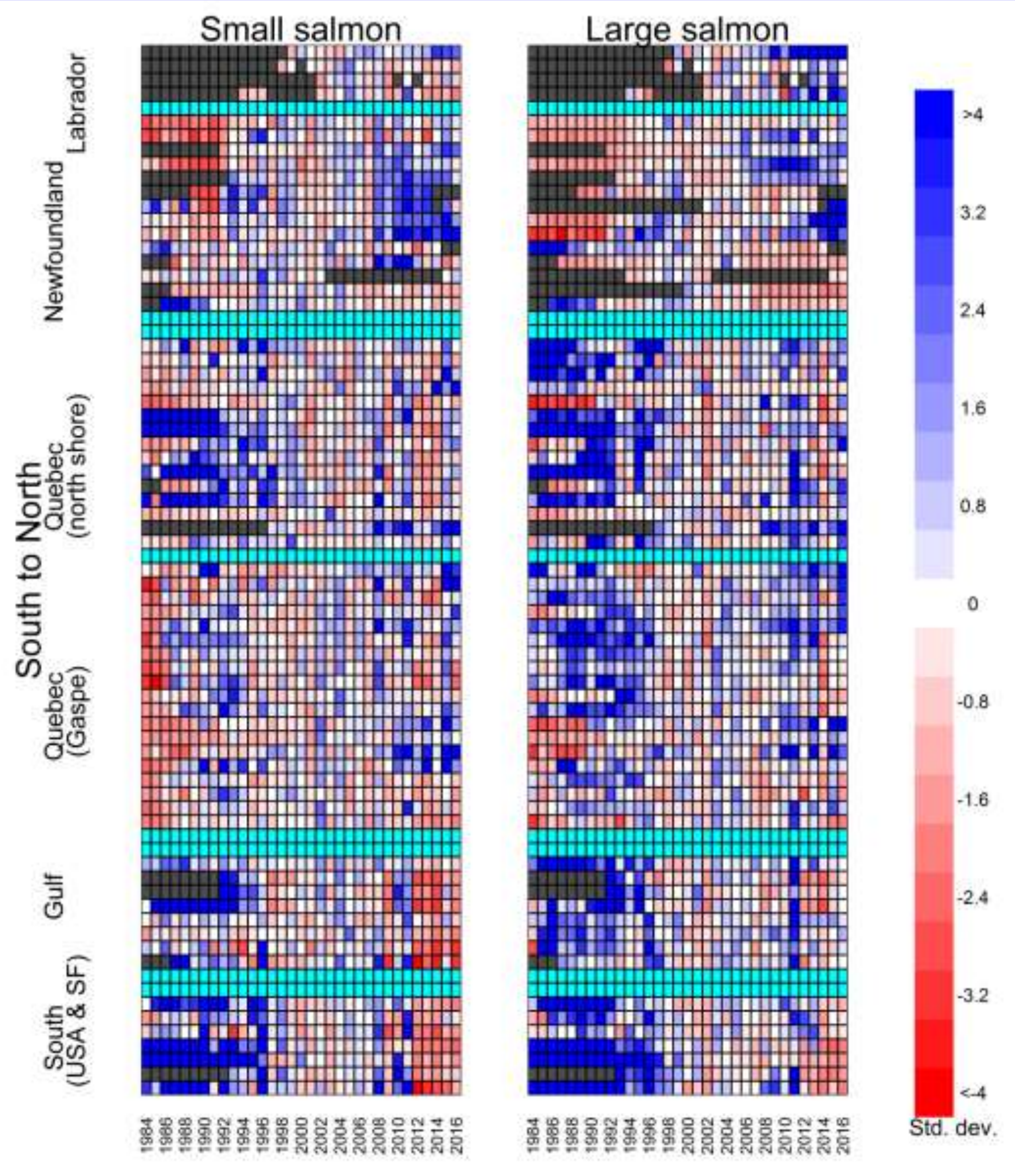
- Annual returns to each river are standardized to their river specific mean and standard deviation of the 1998 to 2007 return years (removes scale of returns size, adjusts for within river variability).
- Anomalies ([return – mean] / stddev) are shown by region for each monitored river.



- annual returns of small salmon are more variable than for large salmon

- blue is positive anomaly, red is negative anomaly
- values within ±2 std. dev. (light blue to light red) are within the “norm” of the standard period (i.e. not unusual)

Contrasting patterns of returns to individual rivers



- each row is an individual river standardized time series
- dark grey = no data
- teal = break between regions
- overall large geographic contrasts with some areas having reds at the beginning of the time series and blues at the end of the time series, others have blues at beginning and reds at the end
- southern areas (South, Gulf)
  - strong positive anomalies to mid 1990s, strong negative anomalies since 2010+
- Newfoundland
  - positive anomalies since 2010+ with exception of the southern NFLD rivers (bottom rows of that area) which are reversed, positive anomalies to negative anomalies over the time series
- large scale effects in some years: for large salmon positive anomaly in 2011 from south to Quebec in contrast to 2014 with negative anomaly over same large area, 2012 to 2016 for small salmon

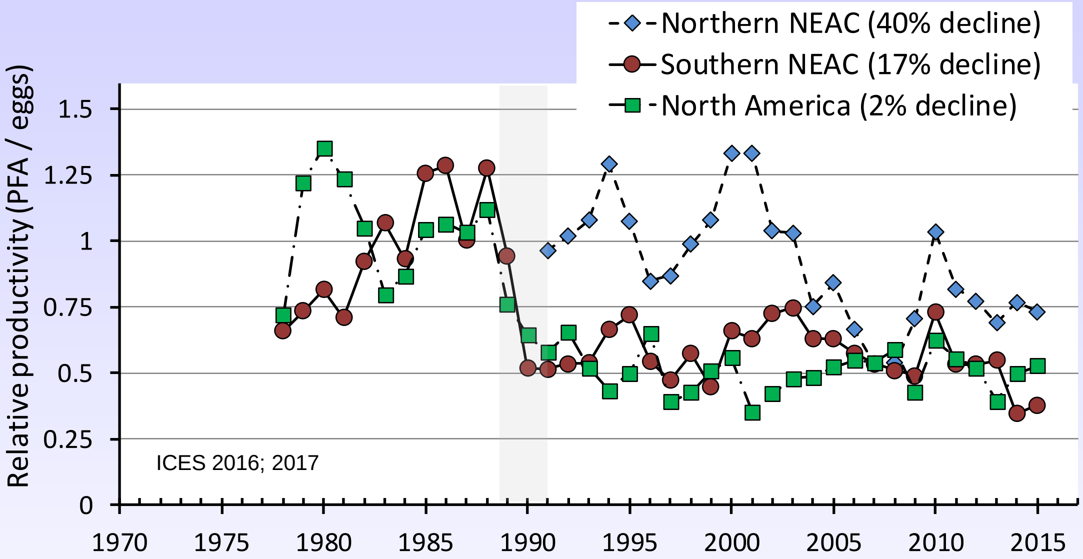
Local scale versus large scale effects

Abundance of adult Atlantic Salmon in individual rivers and overall for eastern North America can be affected by local factors initially (as juveniles in freshwater and in the initial stage of migration of smolts) and by broad spatial scale factors in the later stages of marine life when salmon from stocks from eastern North America are found in a common area at sea (for ex. Labrador Sea).

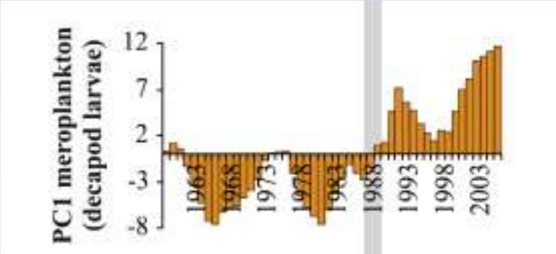
- There is evidence of more regional scale factors acting on Atlantic Salmon. Declines in abundance have been more important in the southern areas of Canada than in the northern areas.
- There is evidence of broad spatial scale shifts in the marine ecosystem that affected Atlantic Salmon stocks in North America as well as in Europe.

Evidence of large spatial scale effects

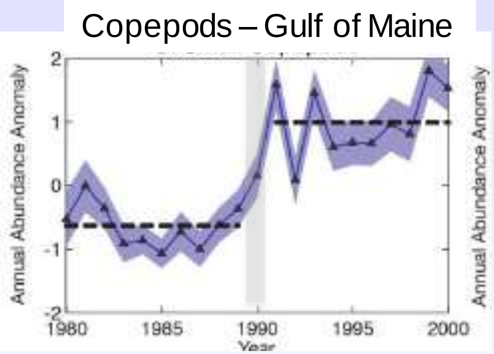
- Relative productivity (PFA abundance / eggs) is annually highly variable, and shows sharp almost step decline over 1989 to 1991 for North America and Southern NEAC.



Plankton index North Sea



Copepods – Gulf of Maine



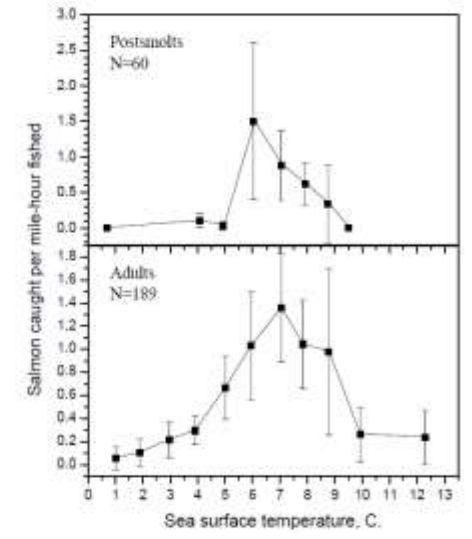
- Regime shift characterized by a break in phytoplankton community structure and a corresponding decline in salmon productivity occurred in the late 1980s early 1990s and has persisted.

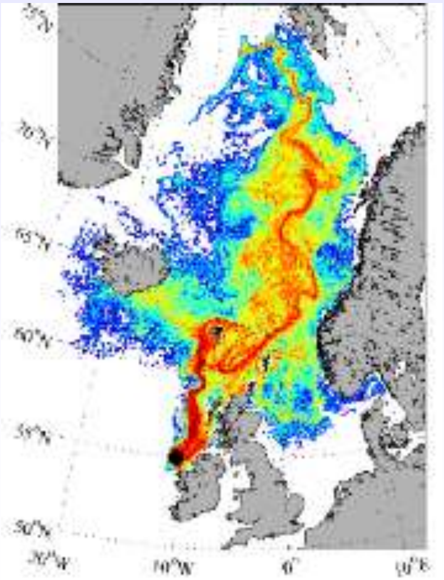
Largest gains in abundance can be achieved by improved marine survival

Understanding of marine ecology of salmon is improving but limited

(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.)

- Salmon spend much of their time in the surface waters but also dive deeper in the water column, probably in search of prey.
- Salmon are found closer to the surface at night then during the day.
- Migration routes are still generally inferred.
- Food and feeding at sea remains generally descriptive.





Largest gains in abundance can be achieved by improved marine survival

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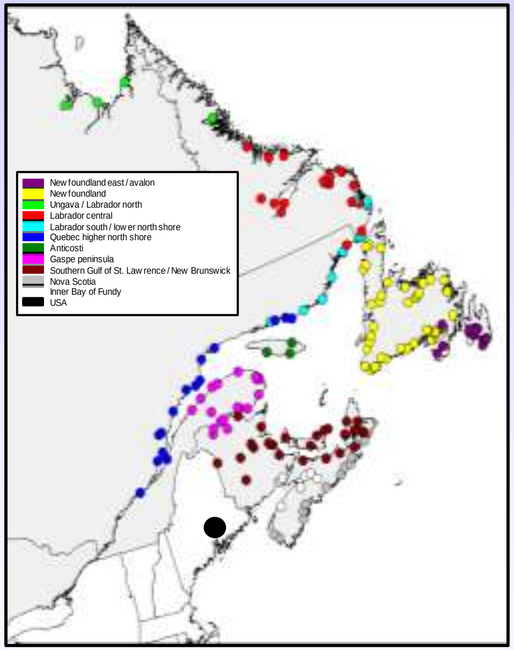
(Reddin, D.G. 2006. Perspectives on the marine ecology of Atlantic salmon (*Salmo salar*) in the Northwest Atlantic. DFO Can. Sci. Advis. Sec. Res. Doc. 2006/018.)

- Many studies show correlations between marine climate and salmon growth and survival at sea.
- The North Atlantic Oscillation Index seems to be related to salmon abundance in the Northeast Atlantic but not in the Northwest.
- Identifying salmon captured at sea to region of origin is now possible, but river-specific origin is still a work in progress.



- Why is our knowledge still so limited?

Challenges to understanding salmon responses to changing environments and why marine survival has declined

Salmon and people interactions, empirical observations, and scientific knowledge gained during a fraction of a percent of the species evolutionary history.

- Atlantic salmon remains recovered from archaeological sites in the Iberian Peninsula (Spain) dating to 40,000 BP (observation on distribution of salmon, refugium for Atlantic salmon during the most recent ice age).
- Sustained interactions between peoples and salmon dates to ~ 12,000 years BP, associated with retreating ice sheet and warmer conditions (**0.2%** of species evolutionary legacy; **2%** of NW / NE salmon evolutionary history).
- First written records (Saint Bede, 8th century), in fishing regulations of 1030 (King Malcolm II), and in the Magna Carta of 1215 (**10%** post-range expansion history).
- Overfishing concerns and control of poaching in the 1500s, artificial propagation of salmon early 1700s (**6%** post-range expansion).
- Reliable data on fisheries landings from the mid 1800s (in some areas) (**2%** post-range expansion).
- Quantitative assessments of abundance of adults began < 60 years ago (**0.6%** post-range expansion).

Challenges to Studying Marine Ecology

- Low abundance overall of Atlantic Salmon in the North Atlantic (currently less than 4 million fish of pre-adult size).
- Marine phase dispersed over the broad North Atlantic.
- Very small river-specific population sizes for the majority of salmon rivers.
- High mortality at sea; in order to study migration and distribution of salmon over their extended life at sea extensive sampling effort including marking a large number of animals as they leave rivers is required.

These factors, among others, make studying Atlantic Salmon at sea by capturing, tracking, testing hypotheses particularly difficult.

If the question of Atlantic Salmon population dynamics, persistence, and interactions with the ecosystems (including humans) was easy, it would already have been answered.

Survival of salmon : can we change the odds of winning?

- Survival is not a random process (even if it sometimes appears to be).
  - lower return rates of hatchery smolts relative to wild smolts (consistent)
- **Atlantic Salmon is an obligate freshwater spawner.**
- Conditions during rearing in freshwater carry over and have fitness consequences at sea.
  - effects of contaminants on behaviour, adaptability to seawater (pH effects)
  - mismatch between freshwater and marine conditions at smolt migration
  - larger smolts generally survive better than smaller smolts
- Reproductive capability of returning adults can be compromised.
  - M74 syndrome that affects egg viability in Baltic salmon due to prey consumed
  - inadequate energy stores or size to successfully migrate to headwater spawning areas, dig redds in appropriate substrate
- Aggressive / risk taking behaviour for feeding which enhances probability of becoming prey, can be consequence of genetics, rearing environment (natural and artificial).
- Survival is a process of selection for the fittest individuals under encountered conditions (Darwinian principle) and if we intervene in any part of the salmon life cycle, we could be doing more harm than good.

What do we want for *Salmo salar*?

- *Salmo salar* will not likely persist over its contemporary distribution. Over its evolutionary history, its range and abundance have contracted and expanded. We can expect the same to occur again. Salmon will not be everywhere we are.
    - But that is not what we aspire to.
- *Salmo salar* will not go extinct. There has never been more *S. salar* on the planet than there is now (2.3 million tonnes of aquaculture production in 2016; @ 3 kg per fish ~ 700 million salmon)
    - But that is not what we aspire to.
- We should aspire to have salmon in the areas and in rivers, and in quantities that have occurred over the brief period of time of interaction between *S. salar* and *H. sapiens* (the Holocene period? < 100 years of empirical studies?)
- To do so, we should ensure that the rate of change in conditions encountered by *S. salar* due to anthropogenic causes is at the same pace as the change in conditions during its evolutionary history; it should occur at glacial pace.

And next?

- Continued efforts to improve the capacity of rivers to produce healthy / uncompromised wild juveniles (the freshwater and marine environments are linked).
    - the best environment for producing juveniles is in the wild
- Maintain monitoring capacity to track long term performance of salmon populations (index rivers), in response to human interventions, and test hypotheses over the entire geographic range.

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- The large and diverse scientific community (we are all building on our predecessors' work and knowledge).

Thank you for the invitation to present this afternoon. I would be happy to take any comments or questions now or later. I welcome the exchange.

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