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Overview of the status of Atlantic salmon (*Salmo salar*) in the North Atlantic and trends in marine mortality

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Since the early 1980s, the ICES Working Group on North Atlantic Salmon has collated and interpreted catch data, exchanged information on research initiatives, and provided advice to managers in support of conservation efforts for Atlantic salmon. During the past three decades, the annual production of anadromous Atlantic salmon from more than 2000 rivers draining into the North Atlantic has been less than 10 million adult-sized salmon. This represents a minor component, by number and biomass, of the pelagic ecosystem in the North Atlantic Ocean. Ideally, Atlantic salmon would be assessed and managed based on river-specific stock units, the scale that best corresponds to the spawner to recruitment dynamic. In reality, comparatively few river-specific assessments are available for either the Northwest or the Northeast Atlantic. The marine survival of Atlantic salmon is low and, based on return rates of smolts to adults from monitored rivers, has declined since the mid- to late 1980s. Abundance has declined more severely for the multi-sea-winter components, and especially in the southern areas of the species' range. Common patterns in abundance, inferred at the level of stock complex in the North Atlantic, suggest that broad-scale factors are affecting productivity and abundance and that they are acting throughout the salmon's time at sea.

Keywords: Atlantic salmon, marine mortality, North Atlantic, productivity.

Introduction

The Atlantic salmon (*Salmo salar*) is an obligate freshwater, relatively short-lived fish species. Landlocked and anadromous forms of Atlantic salmon are found throughout its range in the North Atlantic (Webb *et al.*, 2007); only the anadromous form is considered in this overview. More than 2000 rivers draining into the North Atlantic support populations of Atlantic salmon. The distribution of the species has large spatial overlap with areas of high human population density, and its freshwater spawning means that it is vulnerable to human activities over most of its range (Parrish *et al.*, 1998).

Age of anadromous Atlantic salmon at first spawning can be as young as 3 years and as old as 14 years (Niemelä *et al.*, 2006; Webb *et al.*, 2007). The most common river age for salmon is 2–4 years, with the most common sea age at first spawning being 1–3 years (Webb *et al.*, 2007). The species is iteroparous and repeat spawning has been extensively documented (Moore *et al.*, 1995; Klemetsen *et al.*, 2003; Niemelä *et al.*, 2006).

Growth is slow in freshwater, but rapid in the marine environment (O'Connell *et al.*, 2006). The size of smolts (the juvenile stage that migrates from rivers to the sea) is variable, but is in the range ~10 to <20 cm average fork length (FL). After a year at sea, adult salmon returning to spawn range in FL from ~50 to 65 cm and in whole weight from 1.5 to 3+ kg. After two years at sea, salmon measure 65–80 cm FL and weigh 6 to >10 kg (Klemetsen *et al.*, 2003; O'Connell *et al.*, 2006). This fast growth at sea results in distinct, generally non-overlapping sizes at maturity. Maturation schedules vary by sex and geographically, some regions being dominated by fish that mature after one year at sea (1SW, commonly referred to as grilse), and others by multi-sea-winter (MSW) salmon (Porter *et al.*, 1986; ICES, 2010). Sex ratios can differ among regions, with a large proportion of females in grilse-dominated stocks, but with mostly male grilse and mostly MSW females in MSW-dominated stocks (O'Connell *et al.*, 2006).

The Atlantic salmon can be highly migratory in the ocean, undertaking feeding migrations and aggregating in a broad range of geographic areas, including around Greenland and the Faroe Islands (Hansen and Jacobsen, 2003; ICES, 2008). These feeding aggregations result in fisheries on mixed stocks (many individual river populations) during the first and second years of the fish at sea.

This overview presents a summary of information on the abundance of Atlantic salmon in the North Atlantic, but excludes Baltic salmon, which have an ancestral lineage and marine ecology that differ from salmon in the North Atlantic (King *et al.*, 2007), are assessed separately by ICES, and are managed in a different international forum. The most recent information on the production of Atlantic salmon and on mortality rates at sea is presented, based on the assessments of the ICES Working Group on North Atlantic Salmon (ICES, 2011). Those assessments form the basis of the ICES advice used by the North Atlantic Salmon Conservation Organization (NASCO) in establishing regulatory measures for the distant-water fisheries at the Faroes and off West Greenland.

Survival rates of Atlantic salmon

Anadromous Atlantic salmon occupy both freshwater and marine environments during their life. The natural mortality (M) at sea is of particular interest for management of the fisheries. Estimates of M during the marine phase are difficult to obtain because the adults enumerated back to the river are the survivors of both natural and fishing mortality at sea, and they can return to spawn at several sea ages (Chadwick, 1987; Ritter, 1989; Crozier and Kennedy, 1994; Potter and Crozier, 2000).

Theoretical approaches can provide indications of integrated rates of lifetime and life-stage specific survival (Chaput, 2003). Rates of egg-to-smolt survival decrease with increasing egg deposition, and values $<0.5\%$ have frequently been observed in some populations in eastern Canada, particularly at high rates of egg deposition (Chaput *et al.*, 1998). For an egg-to-smolt survival rate of 0.5%, a 1SW salmon population with an average female fecundity of 3000 eggs would replace itself if the return rate from smolt to spawning adult was 13%, whereas a 2SW salmon population with an average female fecundity of 6000 eggs would require a return rate of 6.7%. A 2SW salmon population that spends 24 months at sea could replace itself at a marine mortality rate of 74% per year ($M = 1.35$; almost 11% per month). The rate of survival at sea required for replacement decreases with increasing egg-to-smolt survival (Chaput, 2003).

Chaput *et al.* (2003) revised and applied a maturity-schedule method to estimate a value of M at sea for Atlantic salmon stocks that mature at two different ages. Solutions for survival in the first and second years at sea can be obtained if survival rates are assumed to be similar for males and females and if survival rates in the first year at sea are similar for maturing and non-maturing salmon. Estimates derived from the maturity-schedule model support the widely held view that most of the mortality in the ocean is during the first year but that mortality rates in the second year can also be high. Monthly mortality rates of 10–15% in the second year at sea were estimated for a wild salmon population (Chaput *et al.*, 2003). High rates of mortality in the second year at sea were also estimated for Icelandic stocks (Jonasson *et al.*, 1994). Salmon have unusually high annual rates of mortality at sea compared with other marine fish species for which annual mortalities of 18% ($M = 0.2$) are frequently assumed, in contrast to the 65–95% mortality estimated for Atlantic salmon.

Perspectives on salmon abundance

The longest historical indicator of Atlantic salmon abundance is the time-series of reported catches. Dunfield (1985) provides a historical interpretation of Atlantic salmon abundance in North America dating back to precolonial times. A number of “back of the envelope” estimates suggest that the abundance of Atlantic salmon pre-European colonization was in the range 10–12 million fish (65 000 t), although an alternative value of about 5 million fish (23 000–27 000 t) was also inferred.

Catch statistics became more reliable in Canada from 1910, and detailed reported catches by region for North America and the Northeast Atlantic from 1960 are provided in ICES (2011). For North America, the catches are predominantly from Canada, and peaked in 1930 at 6000 t (Figure 1) following the introduction of improved fishing technologies. Catches subsequently declined, were <3000 t from 1965 to 1980 (Figure 1), and have declined markedly since 1980. Since 1960, total catch in the North Atlantic peaked between 1965 and 1975 at just under 12 000 t (Figure 1). Based on the trend in catches in Canada in the 1930s (Figure 1), perhaps the catch before 1960 in the North Atlantic exceeded 12 000 t. However, the time-series from Norway, one of the largest salmon-fishing countries in the Northeast Atlantic, indicates landings of 500–1200 t between 1876 and 1950, rising to just 2000 t in 1960, although the sea-catch over that period is incomplete (Hansen, 1988). The mixed-stock distant-water fisheries at the Faroes and Greenland developed in the late 1960s, with peak combined annual catches generally <2000 t (Figure 1). Contemporary catches in the Northeast Atlantic have been about three times the values reported for North America (Figure 1).

Declared catch data are insufficient as an index of abundance because they are frequently incomplete (ICES, 2011), are reported by jurisdiction, which may include multiple stocks, and are closely related to variations in fisheries management measures, including quotas and closures.

Moving from catches to estimates of total adult abundance

Ideally, Atlantic salmon would be assessed and managed based on river-specific stock units, the scale corresponding best to the spawner to recruitment dynamic. In reality, $<25\%$ of the more than 2000 rivers with salmon populations in the North Atlantic area are assessed (Crozier *et al.*, 2003; ICES, 2011). For 2010, a total of just more than 500 river assessments were presented to the ICES Working Group on North Atlantic salmon.

Alternatively, stock status is assessed at broader national and subcontinental scales. The grouping of salmon rivers into these broader geographic categories reflects, in part, the common biology and ecology of neighbouring salmon stocks (Crozier *et al.*, 2003) as well as the jurisdictional structure of fisheries management. For managing the mixed-stock distant-water fisheries at Greenland and the Faroes, assessing stock status at this broader scale was considered appropriate.

Run-reconstruction methods were developed to estimate the total abundance of a salmon cohort at a stage before the distant-water fisheries (Figure 2). In this case, the cohort refers to the smolt cohort. This was done for NASCO’s North American Commission (NAC) and North-East Atlantic Commission (NEAC) areas. The idea was first presented at ICES in 1992 and was subsequently adopted for stocks on both sides of the Atlantic (Rago *et al.*, 1993; Potter *et al.*, 2004). The starting point is a river- or region-specific estimate of abundance generally based on catches and estimates of exploitation rates, the latter most often derived from expert opinion. Uncertainties are treated using minimum and maximum ranges of exploitation rates. The challenge in identifying the stock origin in mixed-stock fisheries is circumvented by tabulating abundance by stock complexes, consisting of stocks that are exploited collectively in the mixed-stock fisheries. This facilitates working back in time to an earlier period of the salmon’s life cycle by estimating abundance at

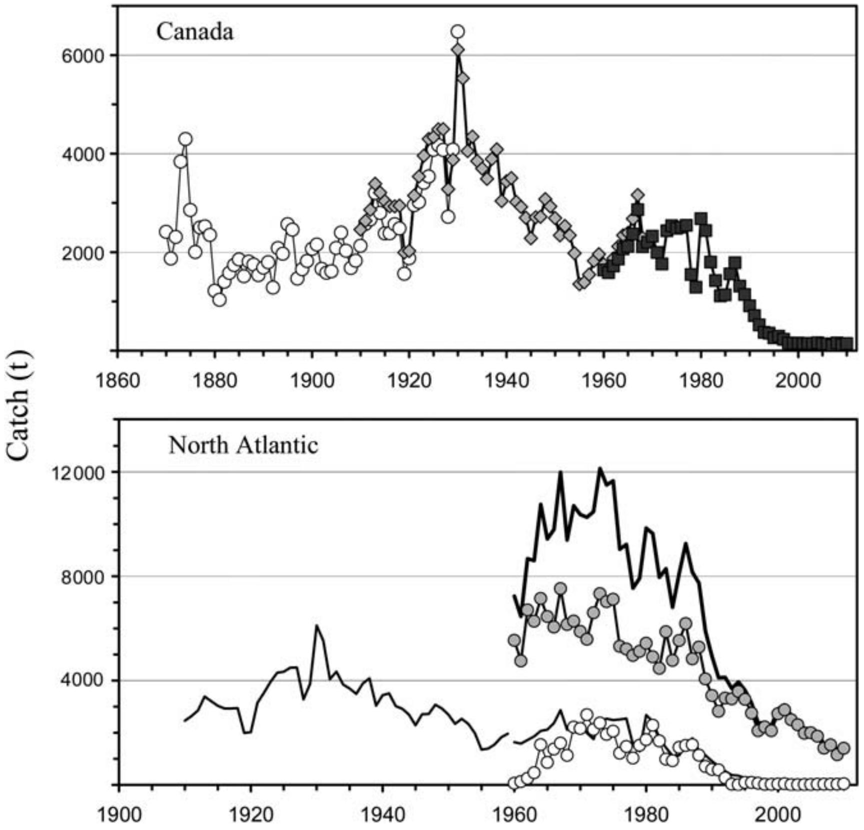

Figure 1. Catches (t) of Atlantic salmon in fisheries in the North Atlantic. In the top panel, catches in Canadian fisheries from different sources are shown [open circles, 1870–1930 from Huntsman (1931) and Taylor (1985); grey diamonds, 1910–1969 from May and Lear (1971); black squares, 1960–2010 from ICES (2011)]. The lower panel summarizes catches from the North Atlantic (bold line; ICES, 2011), by Canada [line; May and Lear (1971) and ICES (2011)], for the Northeast Atlantic [grey circles; ICES (2011)], and for Greenland and the Faroes [open circles; ICES (2011)].

successive periods corrected for survival, adding in catches at the appropriate time, to arrive at an estimate of prefishery abundance (PFA) before any mixed-stock, distant-water exploitation. The value of M for salmon at sea in the post-PFA period has to be inferred from auxiliary information. ICES now sets M at 0.03 per month in the second year at sea, based on inverse-weight and maturity-schedule models, and it is assumed to have been constant over the time-series (ICES, 2002; Crozier *et al.*, 2003).

Estimates of PFA and stock and recruitment dynamics have been modelled for three stock complexes in the North Atlantic based on NASCO's NAC and NEAC areas, with the latter subdivided into northern (N-NEAC) and southern (S-NEAC) stock complexes (Table 1). ICES (2011) estimated the PFA for NAC to 1 August of the second summer at sea, before exploitation at West Greenland and at the point when 1SW maturing salmon return to rivers. For the present analysis, the NAC PFA is estimated back to 1 January of the first winter at sea, corresponding to the date of PFA reconstruction of both NEAC stock complexes. For completeness, information on catches and returns to Norway for the period 1971–1983, previously documented in ICES (2001) but excluded in recent assessments by ICES (2011) owing to questions on age composition, were included. The PFA is estimated for two maturity age groups of salmon; 1SW maturing salmon, and MSW salmon, the latter group comprising mainly 2SW salmon with some 3SW and older salmon, plus repeat spawners.

The estimated PFA of Atlantic salmon in the North Atlantic on 1 January of the first winter at sea was highest in the early 1970s at some 10 million fish, and consisted of about equal numbers of 1SW (or small) salmon and MSW (or large) salmon (Figure 3). The abundance was greatest in the S-NEAC area at about 5 million fish (Figure 3b), followed by N-NEAC at about 2.5 million fish (Figure 3a), and NAC at 2.3 million fish (Figure 3c). By the mid-1990s, abundance had declined to the lowest levels in the time-series in all stock complexes, and in the most recent 5-year period, total PFA continued to decline to ∼1.5 million fish in S-NEAC, 1.2 million fish in N-NEAC, and <900 000 fish in NAC.

Based on the median values of the estimated PFA in the period 1971–2009, the abundance of MSW salmon declined by 54% for the N-NEAC area, by 81% for the S-NEAC area, and by 88% for the NAC area (Table 1; right panels of Figure 3). The abundance of 1SW salmon declined less than that of MSW salmon, but between 1971 and 2010, the declines were 49, 66, and 40% for N-NEAC, S-NEAC, and NAC, respectively (Table 1; right panels of Figure 3). Equally importantly, declines in returns to coastal waters (after distant-water fisheries at Greenland and Faroes) were observed in all three areas (Table 1; Figure 3 centre panels). This contrasts with estimates of spawning escapement. In the NAC area, spawning escapements increased for both sea-age groups, but particularly for 1SW salmon; in the N-NEAC area,

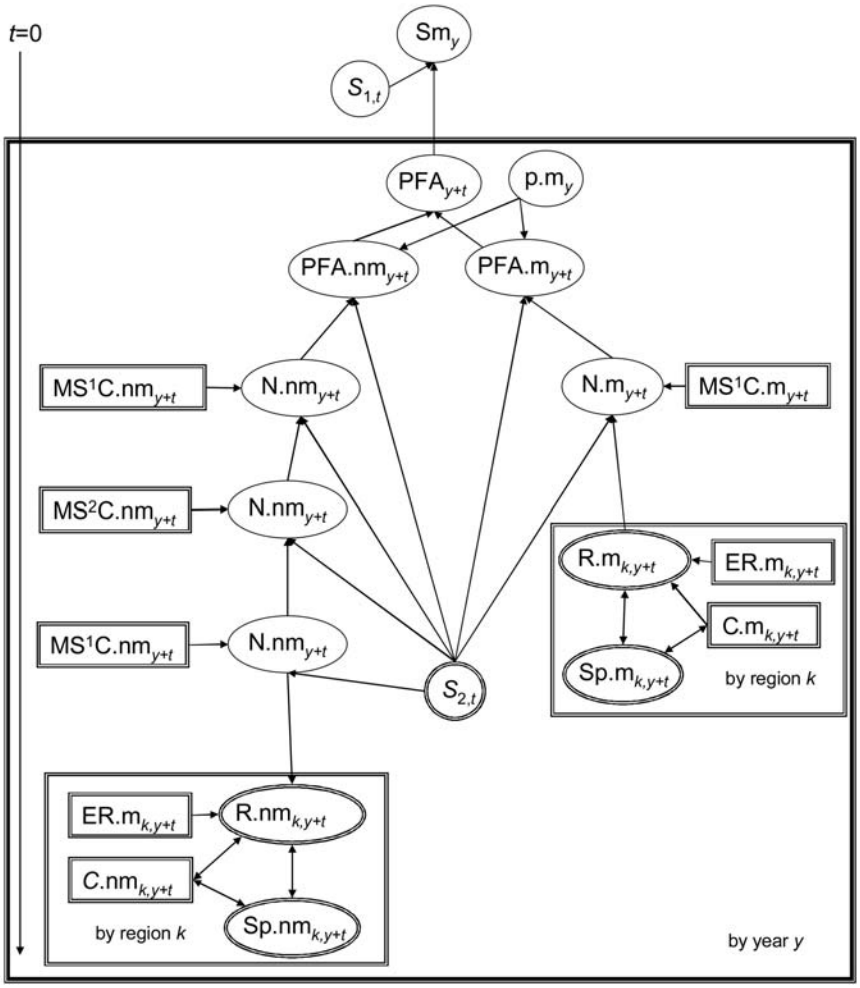

Figure 2. Simplified flow diagram of the PFA reconstruction of abundance of Atlantic salmon at previous lifestages. $C.*_{k,y+t}$ is the catch (in numbers) of 1SW (m) and MSW (nm) maturing age groups (*) in region *k* in year *y* and at time *t* (months); ER.* is the exploitation rate, R.* is the returns at the point in time and location of C.*, and Sp.* is the spawning escapement. $MS^jC.*$ is the catch of salmon in the marine mixed-stock fishery *j*; mixed-stock fisheries at sea include the Newfoundland and Labrador commercial fisheries in Canada, the Faroes fishery, and the fishery at Greenland. $S_{i,t}$ is the rate of natural survival in period *i* (first year at sea, second year at sea) for year *y*. N.* is the abundance of salmon before the mixed-stock fishery, and PFA.* is the abundance of salmon destined to become 1SW or MSW before any exploitation. The value $p.m_y$ is the proportion of the overall PFA that matures at 1SW, and Sm_y is the abundance of smolts leaving rivers in year *y*. The rectangles are inputs observed or measured, and the ellipses are states not measured but inferred from the reconstruction. The arrows indicate how the information flows in the run-reconstruction.

spawning escapements increased for 1SW salmon; and in the S-NEAC area, spawning escapements declined by 51% for MSW salmon and by 13% for 1SW salmon (Table 1; left panels of Figure 3).

The trends in abundance at the stock-complex level average out trends in abundance at national and regional scales (Table 1). Declines in the returns of 1SW salmon and MSW salmon were more severe relative to the stock-complex trends in the southern region of NAC (Scotia–Fundy), in southern countries in S-NEAC (France, Ireland), and in Norway in N-NEAC.

Variation in abundance attributable to variations in spawner numbers

Except the S-NEAC complex, the estimated declines in PFA and returns are in opposing sign to the trends in spawning escapements. Spawning escapements have been maintained at the complex level by reductions in exploitation in the distant-water fisheries and in homewaters (ICES, 2011). Based on the assumptions for the PFA modelling, specifically that *M* has been constant over the time-series, the declines in PFA are attributed to decreased productivity between the spawning stage and the PFA stage, i.e. effects in freshwater and during the first year at sea.

PFA dynamics by complex were modelled using the estimates of adult spawners, adjusted to the number of eggs per fish based on life-history characteristics of the age groups within each region of the stock complexes (ICES, 2011). The spawner to PFA dynamic was modelled as

$$\mathrm{PFA}_y = \mathrm{e}^{\alpha_y}\mathrm{LE}_y\mathrm{e}^{\varepsilon}, \qquad (1)$$

where α_y is the productivity parameter from eggs ($\times 1000$) to PFA (number of fish) for PFA year *y* (on a log-scale), LE_y the estimated

Table 1. Percentage change over the period (1971–2009 for MSW PFA; 1971–2010 for all others) by maturity group in PFA, returns, and spawners within and overall by stock complex.

Stock complex and country	PFA (%)		Returns (%)		Spawners (%)	
	1SW	MSW	1SW	MSW	1SW	MSW
N-NEAC	−49	−54	−56	−52	+19	0
Russia			+14	−41	+132	−12
Finland			0	−26	−7	−21
Norway			−73	−59	−31	+8
Iceland (north and east)			+154	−68	+194	−39
S-NEAC	−66	−81	−65	−73	−13	−51
UK (Scotland)			−52	−70	+86	−42
UK (Northern Ireland)			−51	−67	+153	−47
UK (England and Wales)			−49	−65	−18	−47
Ireland			−78	−86	−51	−78
France			−67	−91	−93	−66
Iceland (south and west)			+18	−96	+25	−88
NAC	−40	−88	−40[a]	−81[a]	+71	+1
NAC (rivers)[b]			+43	−47		
Labrador			+263	+87	+325	+96
Newfoundland			+64	+157	+93	+193
Quebec			+26	−69	+37	−40
Gulf			−42	−44	−45	+24
Scotia–Fundy			−84	−95	−75	−89
United States			+443	−58	+624	−15

[a] Returns to the coast include mixed-stock marine fishery catches in Newfoundland and Labrador and Saint-Pierre and Miquelon.
[b] Returns to rivers are after mixed-stock marine fishery catches in Newfoundland and Labrador and Saint-Pierre and Miquelon.

lagged eggs ($\times 1000$) corresponding to the PFA cohort in year y, and $\epsilon \sim N(0,\sigma^2)$. Productivity is modelled as an integration of survival in freshwater and during the first year at sea. An important assumption is the absence of heritability of age at maturity, i.e. that all eggs are considered equivalent regardless of the age of the spawners. Lagged eggs refer to the adjustment of the egg depositions to correspond to the expected age at smoltification. At the stock-complex level, lagged eggs are the sum of the eggs from the spawners in year $y-(s+2)$ weighted by the proportion of the smolts produced at age s in region k summed over regions in the complex. Two years are added to the smolt age, for the spawning year and smolt migration year, to lag the eggs to the corresponding year of PFA:

$$\mathrm{LE}_y = \sum_k \sum_s Eggs_{y-(s+2),k} \times prop_{s,k}. \qquad (2)$$

The total lagged eggs for NAC increased by ~10% during the period 1978–2009 (Figure 4a), with an increasing proportion since 2004 contributed by 1SW spawners (Figure 4b). Lagged eggs declined in S-NEAC by ~33% during the period 1978–2009 and, as in NAC, an increased proportion of the eggs was contributed by 1SW spawners, particularly since 2001. For the shorter time-series from N-NEAC, lagged eggs increased by 35% over the period 1990–2009, and the proportion of lagged eggs from 1SW salmon also increased (Figure 4a and b).

The proportion of the total PFA made up of 1SW salmon (the proportion maturing in Figure 4c) in both NAC and S-NEAC increased to the highest levels by 1995 (Figure 4c). This contrasts with the dynamic in N-NEAC, where the proportion of the total PFA consisting of 1SW salmon fluctuated between 0.5 and 0.6 over the short time-series, but then fell to 0.4 and remained at that level from 2007 to 2009 (Figure 4c).

Productivity was highest for NAC between 1979 and 1988, as high as 1.7 fish per 1000 eggs ($\alpha = 0.50$), but it has declined continually since, reaching its lowest value of 0.45 fish per 1000 eggs in 2001 ($\alpha = -0.80$; Figure 4d). The maximum estimated productivity for the S-NEAC complex was about 1 fish per 1000 eggs ($\alpha = 0$) from 1982 to 1989, but it fell abruptly in 1990 and remained at a level of 0.45–0.74 fish per 1000 eggs ($\alpha = -0.3$ to -0.8). For the N-NEAC complex, productivity varied around 1 fish per 1000 eggs, but it has declined from 2004 to reach its lowest level in 2007 and 2008 at 0.5 fish per 1000 eggs ($\alpha = -0.6$). Over the past 5 years, therefore, productivity has been strikingly similar among the three stock complexes, at about 0.6 fish per 1000 eggs (Figure 4d). The decline in productivity in the S-NEAC and NAC areas began in 1989, but the decline was abrupt over a single year for S-NEAC, though more gradual and over almost a decade for NAC. The recent decline in productivity of the N-NEAC stock complex was over a period of about 5 years.

Disentangling freshwater effects from marine effects

There is ample evidence from river-specific studies that spawning stock is an important conditioning variable of recruitment abundance expressed as a density-dependent response during the freshwater stages (Chaput *et al.*, 1998; Jonsson *et al.*, 1998; Elliott, 2001; Gibson, 2006), which manifests itself in adult production (Prévost *et al.*, 2003; Michielsens and McAllister, 2004). Such a compensatory relationship is the basis for the setting of conservation limits (Chaput *et al.*, 1998; Crozier *et al.*, 2003; Prévost *et al.*, 2003). There is no evidence of density-dependent survival at sea and, often, returns of adults are poorly predicted from estimates of smolts going to sea, survival at sea seemingly being annually random (Hansen and Quinn, 1998; Gibson 2006).

Other than estimates of spawners, there are no estimates of freshwater production for the stock complexes in the North Atlantic, and in the few monitored stocks, there are no consistent trends in smolt production (ICES, 2011). For the NAC and N-NEAC areas, smolt production would not be expected to have decreased (i.e. it has increased or remained stable), because egg depositions have increased. For S-NEAC, lagged eggs have declined, although there is no information on whether or not smolt production followed the same trend.

There are a limited number of stocks for which the return rates of smolts to adults have been measured. In a few instances, the return rates can be inferred to represent survival rates at sea, because the adults are almost entirely 1SW maturing salmon. In all other cases, where there are two or more ages at maturity, the return rates of smolts to 1SW are the product of the proportion of the smolts destined to mature as 1SW salmon and the first year survival at sea. The return rates to 2SW salmon (or large salmon as proxy) are the products of the proportion (p) of the

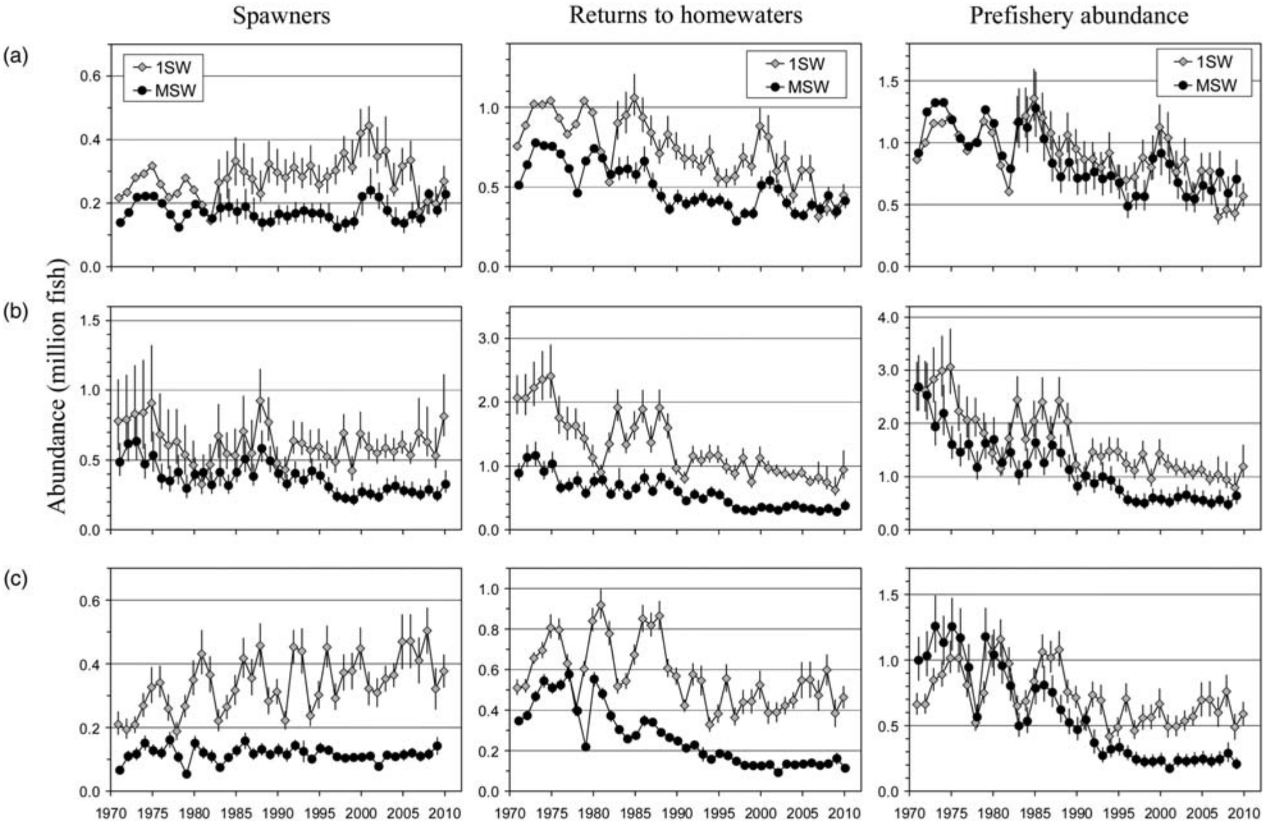

Figure 3. Estimated abundance (number of fish, median, and 95% percentile range) of Atlantic salmon by age at maturity, as spawners (left column), returning to the coast (centre column), and before any exploitation on the high seas (PFA; right column) for (a) N-NEAC, (b) S-NEAC, and (c) NAC. Spawners and returns to the coast are for the year of assessment and PFA for the year of the first winter at sea (smolt year + 1).

smolts not maturing as 1SW salmon, first year survival, and second year survival.

$$\mathrm{Return.rate}_{y+1}^{1\mathrm{SW}} = \frac{\mathrm{Return}_{y+1}^{1\mathrm{SW}}}{\mathrm{Smolts}_y} = \mathrm{p.mat}_y^{1\mathrm{SW}} S_y^1, \qquad (3)$$

$$\mathrm{Return.rate}_{y+2}^{2\mathrm{SW}} = \frac{\mathrm{Return}_{y+2}^{2\mathrm{SW}}}{\mathrm{Smolts}_y} = (1 - \mathrm{p.mat}_y^{1\mathrm{SW}}) S_y^1 S_{y+1}^2,$$

where S is the survival. This confusion between the proportion maturing and survival rates means that it is not possible to determine absolute measures of survival from return rates of smolts. However, the trends in return rates may be informative of trends in marine survival if it is assumed that the probability of maturing has been constant.

In the North Atlantic, return rates of 1SW salmon are generally higher than those of 2SW salmon, and return rates of wild smolts are higher than those of hatchery-reared smolts (Figure 5). The highest measured return rates of 1SW salmon in predominantly 1SW stocks (rivers with only 1SW symbols in Figure 5) are generally in the range 6–12%, whereas in MSW salmon stocks, return rates of 1SW salmon are in the range <1–6% and for 2SW salmon, in the range <1–3%. The return rates of European stocks are generally higher than for North American stocks, with return rates to the coast for smolts from the River Bush (1SW stock) being as high as 35% (Crozier and Kennedy, 1994) and return rates to the coast for other stocks generally being >10%. These return rates are for 1SW fish. True rates of survival in the first and second years at sea are higher than return-rate values. In the few cases where estimates of survival rates at sea for MSW stocks were derived using the maturity-schedule method, survival in the first year at sea was <10%, and survival in the second year at sea was often <50% for wild fish and <20% for a hatchery stock (Chaput *et al.*, 2003).

For both NAC and NEAC stocks, return rates in the recent decade have been below rates observed before the 1990s (Figure 6). The only exception to this pattern appears to be for the Western Arm Brook time-series (NAC; Figure 6a), for which return rates to the river since the early 1990s are better than during the 1970s. When corrected for exploitation rate in marine fisheries before 1992 (Dempson *et al.*, 2001), return rates in the 1990s are less than those during the 1970s. This pattern of decreased return rates is consistent with reduced productivity (lagged eggs to PFA), as noted for the NAC and S-NEAC stock complexes.

Consequences for management and challenges for the future

The stock status of Atlantic salmon on a broad ocean scale has only been assessed in the past two decades, motivated by the challenge of managing mixed-stock, distant-water fisheries at Greenland and the Faroes. The assessments are based on estimates of overall and region-specific stock abundance to a prefishery life stage derived

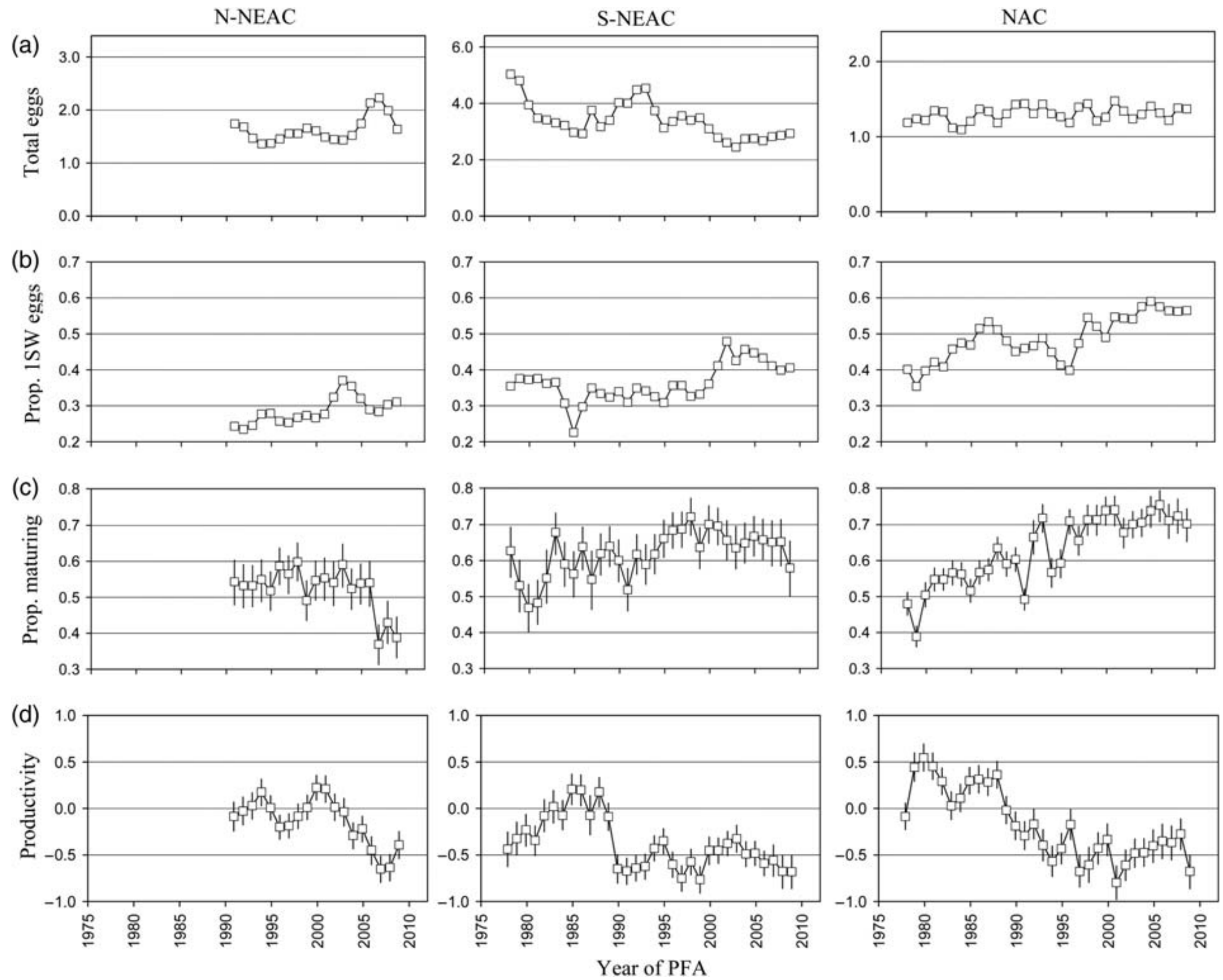

Figure 4. Trends in (a) total lagged eggs ($\times 10^9$), (b) the proportion of lagged eggs from 1SW salmon, (c) the proportion of the reconstructed PFA that is 1SW maturing salmon (median and 95 percentile range), and (d) the productivity (α on a log-scale; median and 95 percentile range) for the N-NEAC (left), S-NEAC (middle), and NAC (right) stock complexes by year of PFA.

using run-reconstruction models. The assessments conducted by ICES consist of estimates of abundance of adult salmon at two maturing stages at sea, but are still only performed reliably at the large stock-complex level. The information content of run-reconstruction models is constrained by the assumptions that need to be made concerning natural mortality, both in terms of its absolute level and trend, and concerning the mixed-stock composition of the fisheries. The ability to identify stock origin in mixed-stock fisheries has progressed from recaptures of tagged animals, through growth characteristics from scales to distinguish continent of origin, to genetic tools for assigning continent and subcontinent of origin, and in some cases, to river origin, but these are still incomplete (Reddin and Friedland, 1999).

Reconstruction of PFA depends most importantly on the assumptions of *M* from the PFA stage to returns to homewaters. *M* is assumed to be 0.03 per month in the second year at sea, equivalent to about 30% mortality per year (ICES, 2002). Stock-specific analyses indicate, however, that this value may be too low for the second year at sea, at least in recent years (Chaput *et al.*, 2003). Of equal concern is the assumption in the run-reconstruction models that M is constant over time, because this does not appear to be a reasonable assumption given the observed trend of declining return rates of 1SW salmon, and the severe decline in the MSW salmon component, particularly in the NAC area (Table 1). If abundance was determined largely by survival in the first year at sea and not in the second year, then MSW returns would also have declined, but the rate of decline would have been of the same order as for 1SW salmon, and less severe than observed. The more marked decline in MSW abundance compared with that of 1SW fish may also be explained by a change in the age at maturity, with a greater proportion of the smolt cohort maturing as 1SW fish since the 1980s. Based on the documented sex ratios by age at maturity, there is no evidence of such a change being real.

The ratio of fishing exploitation rate to *M* determines the potential benefits of fisheries reductions to improved returns to rivers and to spawning escapement. Immediate benefits of improved spawning escapements are greater in management of river fisheries of adults where *M* is considered to be very low in contrast to management of marine fisheries several months removed from returns to rivers where *M* is much higher.

The total population of Atlantic salmon in the North Atlantic is derived from more than 2000 salmon-producing rivers in the Northeast and Northwest Atlantic (Crozier *et al.*, 2003). Each

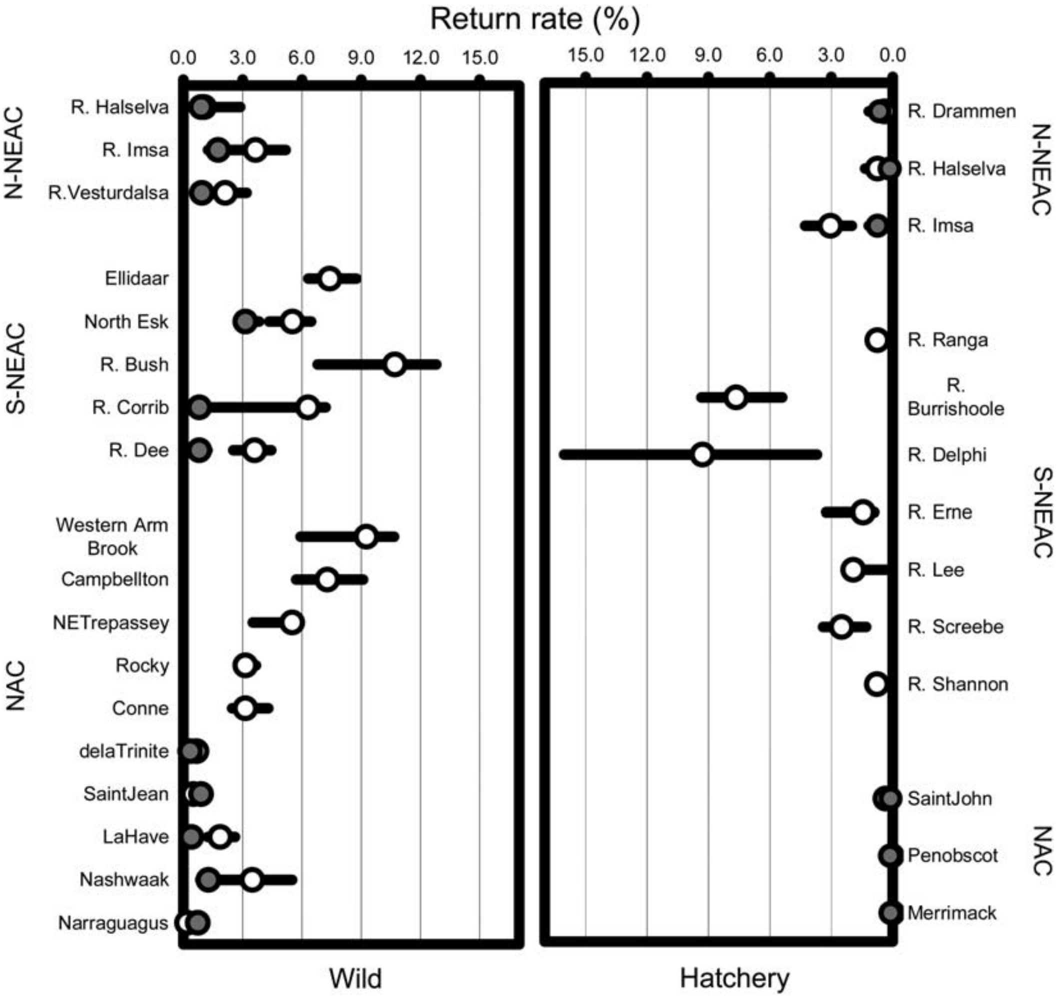

Figure 5. Comparison of the return rate (%; median, interquartile range) of 1SW (white symbols) and 2SW (or MSW for North Esk; grey symbols) of wild (left) and hatchery (right) salmon smolts to rivers from the N-NEAC, S-NEAC, and NAC areas for the 1999–2008 smolt migration years. Only populations with observations in at least nine of the years are included (ICES, 2011).

river represents a potentially discrete population with highly refined homing abilities and stock fidelity (Webb *et al*., 2007). Ideally, stock assessments would be conducted for every stock based on management requirements. The reality, however, is that annual river-specific stock assessments are only available for some 25% of the river populations, although the number of stocks assessed has increased over time (ICES, 2011).

Stock-complex assessments form the basis for catch advice for mixed-stock fisheries, but they mask the regional and river-specific situations of Atlantic salmon populations. In some parts of the NAC and NEAC areas, the abundance of Atlantic salmon has declined by much greater amounts, and the abundance of spawners is much lower than interpreted based on stock-complex trends (ICES, 2011). This poses particular threats to stocks that are at low abundance and subject to other threats unrelated to fishing, such as freshwater habitat degradation.

Interpretation of what constitutes a healthy population is based on the abundance of salmon over the past half century at most, because quantitative data only became available in the final few decades of the 20th century. In some parts of its range, Atlantic salmon were extirpated as early as the late 1800s (MacCrimmon and Gots, 1979). Inferences of abundance before industrialization and the colonization of North America are at best just guesses of what might have been reality. In the past four decades, the abundance of adult-sized anadromous Atlantic salmon has been fewer than 10 million fish annually, which is a minor component, by number and biomass, of the pelagic ecosystem in the North Atlantic Ocean (Sparholt, 1990).

Changes in the marine ecosystem of the North Atlantic have been noted (Beaugrand, 2003), and these are reported to be having consequences for Atlantic salmon (Dickson and Turrell, 2000; Beaugrand and Reid, 2003; Friedland *et al*., 2009), possibly indicating (a) factor(s) on the scale of the whole North Atlantic that is (are) constraining productivity at sea at the stock-complex level in both the Northwest and Northeast Atlantic. Reduced productivity is expressed in terms of increased mortality rather than reduced growth at age, or other changes in biological characteristics (Chaput *et al*., 2005; ICES, 2010). Productivity declined first in the late 1980s for the NAC and S-NEAC stock complexes, the two complexes migrate to feed at West Greenland in the second year at sea. The productivity of the N-NEAC stock complex declined in 2007 and, in contrast to the other areas, is reflected in the reduced production of the maturing 1SW component.

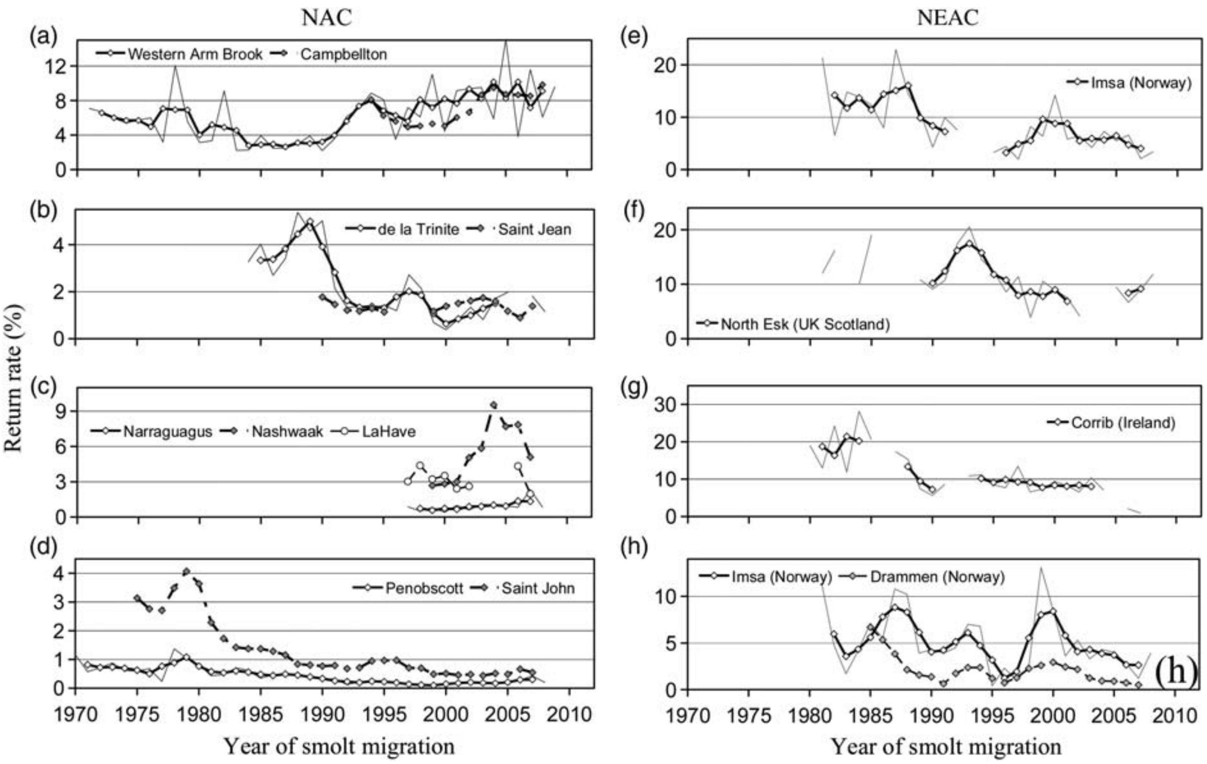

Figure 6. Trends in return rates of smolts to adult salmon (adult age groups combined) by year of smolt migration. The light lines without symbols are annual values for selected rivers, and the solid lines with symbols are the 3-year running mean values by river. (a)–(c) for NAC and (e)–(g) for NEAC are for wild salmon, arranged approximately north to south. (d) for NAC and (h) for NEAC are for hatchery-origin salmon.

Now, more than ever, maintenance and expansion of diverse river-specific monitoring and assessment programmes are required. Monitoring abundance is not a scientifically glamorous activity, and it requires long-term engagement and investment of resources. The availability of many river-specific assessments is crucial to improving knowledge, because such assessments would provide the foundation for testing hypotheses of factors that define salmon population abundance and regulation and for rational management.

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