A review of marine stressors impacting Atlantic salmon *Salmo salar*, with an assessment of the major threats to English stocks

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Abstract Atlantic salmon *Salmo salar* is a socio-economically important anadromous fish species that has suffered synchronous population declines around the North Atlantic over the last five decades. Reduced marine survival has been implicated as a key driver of the declines, yet the relative importance of different stressors causing mortality at sea is not well understood. This review presents a synopsis of the principal stressors impacting Atlantic salmon in estuarine and marine environments. It also applies a semi-quantitative 2-D classification system to assess the relative effects of these stressors on English salmon stocks and their likely development over the next decade. Climate change and predation were identified as the biggest threats at present and over the next decade. Poor water quality and bycatch were classified as relatively high impact stressors, but with a lower likelihood of becoming more prevalent in the future due to available mitigation measures. Other, less influential, stressors included tidal barrages, artificial light at night, impingement in power-station cooling waters and thermal discharges, pile-driving noise pollution, invasive non-native species, electromagnetic fields, salmon mariculture, and tidal lagoons. Salmon fisheries exploitation was not regarded as an important stressor currently because effective exploitation rate controls have been implemented to substantially reduce fishing pressure. Future research priorities include addressing knowledge gaps on expanding stressor impacts from climate change, predation, renewable energy developments, and artificial light at night. Local management actions directed towards improving freshwater and estuarine habitats to maximise ecosystem resilience to stressors and minimise their cumulative impacts are recommended.

Keywords Salmonid population declines · Marine survival · Stressors · Threat classification · Management actions

Introduction

Atlantic salmon *Salmo salar* (hereafter salmon) is a socio-economically important anadromous fish species exploited in commercial, subsistence, and recreational fisheries (ICES 2019). After hatching in spring,
juveniles remain in fresh water for 1–8 years, with an increase in age-at-smoltification with increasing latitude, before migrating to sea to feed and grow prior to returning as adults to reproduce in rivers (Hansen and Quinn 1998; Klemetsen et al. 2003). This species is genetically structured into reproductively isolated populations of European and North American origin that diverged over 600,000 years ago (King et al. 2007). Today, more than 2000 genetically distinct salmon populations are distributed in water courses flowing towards the North Atlantic Ocean (Verspoor et al. 2007).

Despite marked improvements in freshwater habitats and substantial reductions in fisheries exploitation (Friedland et al. 2003; Jonsson and Jonsson 2004; ICES 2020a), salmon have suffered synchronised population declines around the North Atlantic over the last five decades (Parrish et al. 1998; Limburg et al. 2009; Lehnert et al. 2019; Olmos et al. 2019). The temporal coherence observed in the population declines across large geographic areas implies common factors operating simultaneously on the freshwater and marine phases of the life cycle (Parrish et al. 1998; Potter and Crozier 2000; Friedland et al. 2009).

Salmon suffer the highest numbers of mortalities in fresh water (Smialek et al. 2021), where the biggest threats to population persistence are climate change, modified river discharge, overexploitation, pollution, land-use change, and invasive non-native species (Dudgeon 2019). Freshwater conditions affect the physiological development of juvenile salmon, subsequently influencing the growth and survival of older life stages in the marine environment (Russell et al. 2012a). However, increased marine mortality has been a key driver of the observed population declines in recent decades (Chaput 2012; Olmos et al. 2019; Thorstad et al. 2021). Marine return rates, commonly defined as the proportion of emigrating juvenile salmon (smolts) that survive to return to rivers as adults, have fallen to record lows since the 1980s (Chaput 2012), with typically <5% of smolts now surviving (ICES 2020b).

Juvenile salmon are generally growing faster and migrating to sea at younger ages and smaller sizes (Jonsson and Jonsson 2004; Russell et al. 2012a), and smaller fish can have a lower probability of marine survival (Gregory et al. 2019). Differences in juvenile growth can arise from varying environmental conditions and maternal effects in fresh water (Einum and Flemming 2000; Kennedy et al. 2008; Burton et al. 2013), subsequently influencing the age and size of smolts migrating to sea (Russell et al. 2012a). Most mortality between smolt and adult stages is generally considered to take place during the first year of life at sea when survival, maturation, and migration trajectories are being defined (Hansen and Quinn 1998; Potter and Crozier 2000; Friedland et al. 2009).

Fluctuations in the sea age composition of adult salmon have been reported for more than 100 years, with periods where stocks were dominated by fish maturing after one-sea-winter or multi-sea-winters (Bielak and Power 1986; Summers 1995; Heddell-Cowie 2005). In the North East Atlantic, the annual proportion of one-sea-winter salmon increased from the 1980s to the late-1990s and then decreased after 2000 (ICES 2020b). In contrast, the annual proportion of one-sea-winter salmon in the North West Atlantic has increased steadily since the 1970s, but the underlying mechanisms remain unclear. Adult salmon are now tending to return to rivers (hereafter adult returns) in the North East Atlantic at older ages and in poorer condition due to reductions in marine feeding opportunities limiting the growth and maturation potential of the fish (Bacon et al. 2009; Jonsson et al. 2016; Bal et al. 2017).

Reduced marine survival is widely accepted to be an important contributory factor to the observed salmon population declines in recent decades (Chaput 2012; Olmos et al. 2019; Thorstad et al. 2021). Identifying which biotic and abiotic stressors have the biggest impacts on marine survival has therefore been subject to a substantial research effort over the last 30 years (Friedland et al. 1993; Cairns 2001; Jonsson and Jonsson 2004). Multiple stressors have been implicated, including, *inter alia*, climate change, predation, pollution, broad-scale oceanographic changes, overexploitation, and salmon mariculture (Parrish et al. 1998; Cairns 2001; Forseth et al. 2017). However, incomplete knowledge of the nature, severity, and extent of the different stressors impacting marine survival has hindered salmon conservation efforts (Jonsson and Jonsson 2004). To remedy this situation, several multidisciplinary efforts have been made to explore marine survival issues, identify knowledge gaps, and prioritise research directions (Mills 2000; Crozier et al. 2018; ICES 2020a). Understanding the relative importance of different stressors impacting marine survival has never been more important to
prioritise research and management initiatives to protect and restore salmon stocks.

Many of the freshwater stressors impacting salmon are known, and management actions are available to mitigate them (Thorstad et al. 2021). In contrast, the marine stressors impacting salmon remain poorly understood, and management actions are being sought to lessen their impacts and improve the marine survival of salmon (Crozier et al. 2018). Accordingly, the present review had two objectives: 1) present a synopsis of the principal marine stressors impacting salmon survival between the time juveniles leave fresh water and return to rivers as adults prior to reproducing; and (2) apply a semi-quantitative classification system based on the approach devised by Forseth et al. (2017) to assess the major threats to English salmon stocks in the marine environment and prioritise management actions.

Methods

An extensive literature review on the marine stressors impacting salmon survival was undertaken by scrutinising peer-reviewed articles and grey literature. A marine stressor was defined as an activity that impacts salmon in estuaries, nearshore waters, and/or the open ocean; these stressors were primarily human generated.

Study areas

The study areas included all 42 ‘principal salmon rivers’ in England, which were selected to assess the effects of different marine stressors on salmon and their likely development over the next decade (Fig. 1). Each river was grouped into one of four ‘regional marine plan areas’ designated by the UK’s Marine Management Organisation (MMO). These regional marine plan areas were the North East, South, South West, and North West.

The classification system

A semi-quantitative 2-D classification system based on the approach developed by Forseth et al. (2017) for Norwegian rivers was applied to determine the relative impact of marine stressors on salmon originating from English rivers at present and projected over the next decade. Thus, the first dimension, the effects axis, describes the assessed effect of each stressor on salmon, and the second dimension, the development axis, represents the likelihood of development over the next decade. Combined, the effects and development axes form a 2-D classification system that can be used to categorise stressors into four major impact groups (Fig. 2a):

1. Expanding high impact stressors included factors affecting salmon to a relatively high extent at present and with the potential to become more prevalent over the next decade. Mitigation measures implemented are unable to limit expansion of negative effects in the future.
2. Stabilised high impact stressors were factors that negatively affect salmon at present but are expected to be less detrimental over the next decade. Mitigation measures implemented are expected to limit expansion of negative impacts in the future.
3. Expanding low impact stressors represented factors that have low effects on salmon at present but are likely to expand over the next decade. Mitigation measures implemented are unable to limit expansion of negative impacts in the future.
4. Stabilised low impact stressors were factors with low impacts on salmon at present and over the next decade. Mitigation measures implemented are expected to limit expansion of negative impacts in the future.

Five major modifications were made to the original classification system devised by Forseth et al. (2017) to ensure effective application to English salmon stocks given that different marine stressors with varying severity and extent of impact were expected. First, the classification system in the present assessment focused solely on marine stressors rather than those operating across aquatic systems. Second, evidence from the literature review and expert local knowledge were combined to assess the effects and future development of the stressors instead of relying only on expert judgement. Third, the habitat zone where each stressor occurs was evaluated. Fourth, separate scores were provided for salmon in the early stages of their marine phase (smolt/post-smolt) when the fish were relatively small and migrating through estuarine and nearshore waters and for adults in the oceanic phase.
of the life cycle and on their return migration, as opposed to scoring the percentage reduction in adult returns and the number of lost or critically endangered populations. Lastly, the nomenclature for the four major impact groups was revised.

Stressors considered

To identify stressors with the potential to impact salmon during their marine phase, the literature review was complemented by consultations with England’s Environment Agency fisheries officers responsible for the management of river stocks. The information was compiled into the semi-quantitative classification system (Table 1), which identified thirteen stressors: climate change, predation, water quality, bycatch, artificial light at night, tidal barrages, power station impingement and thermal discharge, noise pollution from pile-driving, invasive non-native species, electromagnetic fields, fisheries exploitation, salmon mariculture, and tidal lagoons. Although this review focuses on the impacts of these stressors on salmon in estuarine and marine environments, freshwater literature was drawn upon where necessary to

![Map of 42 rivers and neighbouring regional marine plan areas](image1)

**Fig. 1** A map showing the location of 42 rivers (Environment Agency 2020) and neighbouring regional marine plan areas (MMO 2017) selected to assess the impacts of marine stressors on Atlantic salmon that originate from England (inset map; Ordnance Survey 2021a, b). Rivers include: 1 = Coquet; 2 = Tyne; 3 = Wear; 4 = Tees; 5 = Yorkshire Esk (NE: North East); 6 = Itchen; 7 = Test; 8 = Hampshire Avon; 9 = Stour; 10 = Piddle; 11 = Frome; 12 = Axe; 13 = Exe; 14 = Teign; 15 = Dart (S: South); 16 = Devon Avon; 17 = Erme; 18 = Yealm; 19 = Plym; 20 = Tavy; 21 = Tamar; 22 = Lynher; 23 = Fowey; 24 = Camel; 25 = Torridge; 26 = Taw; 27 = Lyn; 28 = Severn (SW: South West); 29 = Ribble; 30 = Wyre; 31 = Lune; 32 = Kent; 33 = Leven; 34 = Crake; 35 = Duddon; 36 = Cumbria Esk; 37 = Ir; 38 = Calder; 39 = Ehen; 40 = Derwent; 41 = Eden; and 42 = Border Esk (NW: North West). All the rivers were designated ‘principal salmon rivers’ by the Environment Agency on the basis of the prospect of annual rod catches of at least 50 fish around the time of the development of Salmon Action Plans (SAPs) for stock management (Cefas et al. 2019b)
illustrate important issues. National experts were consulted to check the accuracy and comprehensiveness of the literature review and the assessment of individual stressors.

Scoring approach

Different metrics were used to describe each stressor along the effects and development axes. The scores allocated to each metric were based on a range of semi-quantitative or qualitative criteria, each operating on a four-point scale, in accordance with Forseth et al. (2017). Unlike Forseth et al. (2017), however, impact and development metrics were scored from zero (no impact or development) to three (high impact or development potential) because not all the stressors considered in the present assessment were deemed to have impact or development potential. Habitat zone and mitigation metrics were scored on a scale of one to four because the origin of a stressor impact could not be zero and the application of extensive measures does not guarantee the complete alleviation of a stressor impact. Assuming a stressor was considered appropriate for inclusion in an assessment (i.e., it was considered to apply in a particular region), then all scores were summed and expressed as a proportion of the potential maximum score. If a stressor was
**Table 1** Classification of the different marine stressors along the (a) effects and (b) development axes for English Atlantic salmon stocks in 2018 averaged across the four regional marine plan areas

| Criteria and scoring | Climate change | Predation | Water quality | Bycatch | ALAN | Tidal barrages | Power stations | Noise pollution | Invasive species | EMF | Fisheries exploitation | Salmon mariculture | Tidal lagoons |
|----------------------|----------------|-----------|---------------|---------|------|----------------|----------------|---------------|-----------------|-----|-----------------------|------------------|--------------|
| (a) Effects axis characteristics considered | 2.5 | 2.5 | 2.0 | 2.3 | 1.0 | 0.3 | 0.5 | 1.0 | 0.3 | 0.3 | 2.5 | 0.0 | 0.0 |
| 1. Percentage of affected river stocks | 0: 0%, 1: 1–25%, 2: 26–50%, 3: > 50% | 4.0 | 3.0 | 3.0 | 2.0 | 3.0 | 3.0 | 3.0 | 3.0 | 2.0 | 3.0 | 2.0 | 2.0 |
| 2. Habitat zone | 1: Offshore | 2: Nearshore | 3: Estuarine | 4: All | 3.0 | 2.5 | 3.0 | 2.3 | 1.0 | 0.3 | 1.5 | 1.5 | 1.0 | 2.0 | 1.3 | 0.3 | 0.0 |
| 3. Spatial extent of stressor | 0: None | 1: Small | 2: Moderate | 3: Large | 3.0 | 3.0 | 2.0 | 1.0 | 1.0 | 2.0 | 2.0 | 1.0 | 0.0 | 1.0 | 0.0 | 3.0 | 1.0 |
| 4. Impact on smolts Evidence from literature review | 0: None | 1: Low | 2: Moderate | 3: High | 3.0 | 2.0 | 2.0 | 1.0 | 1.0 | 2.0 | 1.0 | 1.0 | 0.0 | 1.0 | 2.0 | 2.0 | 1.0 |
| 5. Impact on adults Evidence from literature review | 0: None | 1: Low | 2: Moderate | 3: High | 3.0 | 2.0 | 2.0 | 1.0 | 1.0 | 2.0 | 1.0 | 1.0 | 0.0 | 1.0 | 2.0 | 2.0 | 1.0 |
| 6. Impact on smolts Local knowledge | 0: No impact | 1: Low | 2: Moderate | 3: High | 1.8 | 1.8 | 1.3 | 1.0 | 1.0 | 0.5 | 0.5 | 0.3 | 0.3 | 0.3 | 1.0 | 0.0 | 0.0 |
| 7. Impact on adults Local knowledge | 0: No impact | 1: Low | 2: Moderate | 3: High | 1.5 | 1.3 | 1.3 | 1.8 | 0.5 | 0.3 | 0.5 | 0.3 | 0.0 | 0.0 | 1.5 | 0.0 | 0.0 |
Table 1 (continued)

| Criteria and scoring | Climate change | Predation | Water quality | Bycatch | ALAN | Tidal barrages | Power stations | Noise pollution | Invasive species | EMF | Fisheries exploitation | Salmon mariculture | Tidal lagoons |
|----------------------|----------------|-----------|---------------|---------|------|----------------|----------------|----------------|-----------------|-----|------------------------|------------------|--------------|
| 8. Implemented mitigation measures That have reduced the effects or likelihood of losing populations | 1: Extensive, with large effects | 3.0 | 3.0 | 2.0 | 3.0 | 3.5 | 3.0 | 2.0 | 2.0 | 3.0 | 1.0 | 1.0 | 3.0 | 3.0 |
| Sum (maximum 26) | 21.8 | 19.0 | 16.5 | 14.3 | 12.0 | 11.3 | 11.0 | 10.0 | 7.5 | 7.5 | 12.3 | 10.3 | 0.0 |
| Compiled relative effect (0–1) | 0.8 | 0.7 | 0.6 | 0.5 | 0.5 | 0.4 | 0.4 | 0.3 | 0.3 | 0.5 | 0.4 | 0.0 |
| Knowledge | 1: Extensive, 2: Moderate, 3: Poor | 1.5 | 1.5 | 1.0 | 2.3 | 3.0 | 2.8 | 3.0 | 2.0 | 3.0 | 2.0 | 1.0 | 3.0 | 3.0 |
| (b) Development axis characteristics considered | | | | | | | | | | | | | |
| 1. Main area for likely development | 1: Offshore | 4.0 | 3.0 | 3.0 | 2.0 | 3.0 | 3.0 | 2.8 | 3.0 | 3.0 | 3.0 | 3.0 | 2.0 | 2.0 |
| 2. Likelihood of stressor becoming more prevalent in the next 10 years | 0: Nil | 3.0 | 2.5 | 2.0 | 2.0 | 2.8 | 1.8 | 2.0 | 3.0 | 2.0 | 2.5 | 1.0 | 1.3 | 1.0 |
Table 1 (continued)

| Criteria and scoring | Climate change | Predation | Water quality | Bycatch | ALAN | Tidal barrages | Power stations | Noise pollution | Invasive species | EMF | Fisheries exploitation | Salmon mariculture | Tidal lagoons |
|----------------------|----------------|-----------|---------------|---------|------|----------------|----------------|----------------|----------------|------|------------------------|------------------|-------------|
| 3. Potential for effective measures | 3.0 | 3.0 | 2.0 | 3.0 | 3.0 | 2.0 | 1.0 | 2.0 | 1.0 | 1.0 | 2.0 | 2.0 |
| Projection of present situation | | | | | | | | | | | | |
| 1: Extensive and very effective measures planned | | | | | | | | | | | | |
| 2: Several and effective measures planned | | | | | | | | | | | | |
| 3: Some effective measures, all measures with small effects planned | | | | | | | | | | | | |
| 4: Few/no effective measures planned | | | | | | | | | | | | |
| Sum (maximum 11) | 10.0 | 8.5 | 7.0 | 7.0 | 8.8 | 7.8 | 6.8 | 7.0 | 7.0 | 6.5 | 5.0 | 5.3 | 5.0 |
| Compiled development (0–1) | 0.9 | 0.8 | 0.6 | 0.6 | 0.8 | 0.7 | 0.6 | 0.6 | 0.6 | 0.5 | 0.5 | 0.5 |
| Uncertainty of projected development | 3.0 | 3.0 | 1.0 | 2.0 | 2.0 | 2.8 | 1.0 | 1.5 | 3.0 | 1.5 | 1.0 | 2.0 | 2.0 |

Stressors include modified oceanic conditions linked to the changing climate (climate change), mortality due to consumption by predators (predation), poor water quality in the marine environment (water quality), incidental capture in non-target fisheries (bycatch), noise pollution from pile-driving (noise pollution), emissions of artificial light at night (ALAN), tidal barrages for renewable energy generation (tidal barrages), power station impingement and thermal discharge (power stations), invasive non-native species (invasive species), electromagnetic fields (EMF) from subsea cables, commercial and recreational exploitation by targeted salmon fisheries and illegal, unreported and unregulated fishing (fisheries exploitation), salmon mariculture in nearshore waters (salmon mariculture), and tidal lagoons for renewable energy generation (tidal lagoons).
absent from a region, then the effects and development scores were zero.

Several metrics adapted from Forseth et al. (2017) were considered for each stressor on the effects axis. First, the percentage of affected river stocks measured the severity of the stressor impact, which is analogous to the number of affected populations considered by Forseth et al. (2017). Assessments of the percentage of affected river stocks were based on local knowledge compiled following consultation with the respective Environment Agency fisheries officer responsible for the management of each river stock. The criteria ranged from zero to > 50% of river stocks affected to account for instances where a stressor effect was absent to prevalent amongst river stocks. Second, unlike Forseth et al. (2017), the habitat zone where the stressor effect occurs was assessed using information from the literature review combined with local knowledge. Effects were assumed to diminish with increasing distance offshore for most of the stressors because encounter probability was generally considered lower in offshore waters than in shallower estuarine or nearshore waters. Climate change was the exception to this assumption given that this stressor could not be assigned to a specific habitat zone due to its broad spatial extent. The four habitat zones were defined as offshore, nearshore, estuarine, and all marine habitats. Third, the spatial extent of each stressor was assessed by evaluating the geographic distribution from published articles and online sources (Fig. S1–S9), matching the approach taken by Forseth et al. (2017). If geographic distribution maps were unavailable for a particular stressor, then alternative data sources (e.g., documented occurrence) were obtained to provide an indication of the spatial extent. Each stressor was classed as either point source or diffuse, with its spatial extent ranging from absent to small, moderate, or large. Finally, the existence, scope, and utility of mitigation measures were evaluated to determine the capacity to alleviate stressor effects on salmon, in line with Forseth et al. (2017). Assessments were based on documented effects in published articles, reports, and online sources. Mitigation scores ranged from extensive measures with large beneficial effects to very few or no measures with apparent effects.

Three metrics modified from Forseth et al. (2017) were considered for each stressor on the development axis. First, the main area for likely development was assessed based on evidence from the literature review combined with local knowledge, and ranged from offshore to nearshore, estuarine, or all marine habitats. In line with the habitat zone assessment, the likely development of all the stressors considered, except climate change, were assumed to diminish with increasing distance offshore. Second, the likelihood of each stressor becoming more prevalent over the next decade was based on a combination of evidence from the literature review, supporting information from UK government documents and planning websites, and local knowledge. The likelihood of increasing stressor prevalence over the next decade was ranked from no change to a high probability of increase. This differed from the approach taken by Forseth et al. (2017), where the likelihoods of future losses in adult returns and additional populations becoming critically endangered or lost were considered, because this assessment focused on stressor rather than impact development. Third, the potential for effective mitigation was based on a projection of the present situation and the scope for implementing measures to alleviate stressor impacts, which matched the Forseth et al. (2017) approach. This was primarily derived from expert judgement of public information, including UK government white papers, regulations, and guidelines from relevant management bodies. Classification of mitigation measures ranged from the availability and likely development of extensive and very effective measures to very few or no effective measures.

In line with Forseth et al. (2017), each stressor was also classified based on the extent of the knowledge informing the assessment of its effect and the uncertainty related to its projected development. In relation to the former, the extent of knowledge for the different stressors was classified as extensive, moderate, or poor. This classification was based on the evidence from published sources and local information from Environment Agency fisheries officers. The uncertainty of the projected development was classified as small, moderate, or large using published evidence and expert opinion. These knowledge and uncertainty scores were subsequently combined to categorise each stressor assessment as having extensive knowledge and small uncertainty, moderate knowledge and moderate uncertainty, or poor knowledge and high uncertainty.
Initial scoring was undertaken by the expert who completed the evidence review for each stressor, taking account of the separate regional information in each case. The scores were then extensively discussed and reviewed by all the experts before reaching consensus. Final scores were averaged across all four regional marine plan areas in England to provide an overall stressor ranking at the national level.

Results

The results are presented in order of the highest to lowest overall stressor ranking, giving an indication of their relative importance for English salmon stocks.

Climate change

Anthropogenic greenhouse gas emissions have increased the global average surface temperature by about 0.85 °C over the twentieth century (IPCC 2014), with many regions of the world already experiencing warming in excess of 1.5 °C in at least one season (IPCC 2018). Warmer temperatures in the North Atlantic have modified oceanic conditions, reducing the growth and survival of salmon by decreasing marine feeding opportunities (Peyronnet et al. 2007; Todd et al. 2008; Friedland et al. 2009). Salmon forage in marine feeding areas that experienced climate-driven regime shifts in biophysical conditions during the late-1980s (Friedland et al. 2012; Mills et al. 2013; Almodóvar et al. 2019). Several studies have postulated that a climate-driven shift in zooplankton community composition towards more temperature tolerant species might be associated with reductions in the marine growth and survival of salmon due to decreases in food abundance and nutritional content (Beaugrand and Reid 2003; Todd et al. 2008; Jons-son et al. 2016). The marine survival of post-smolts is strongly influenced by 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 (Olmos et al. 2020). Increased ocean acidification due to higher levels of CO2 caused by climate change may have diminished the capacity of salmonids to detect olfactory cues used to find prey, avoid predators, and locate natal rivers during homing migrations (Ou et al. 2015; Williams et al. 2019). Little doubt therefore remains that broad-scale, climate-induced changes in oceanic conditions have contributed significantly to recent salmon population declines (Beaugrand and Reid 2012; Friedland et al. 2014; Nicola et al. 2018).

The relative proportion of one-sea-winter to multi-sea-winter adult returns has fluctuated over time (Bielak and Power 1986; Summers 1995; Heddel-Cowie 2005). Since the 2000s, the trend in the North East Atlantic has generally been towards an increasing proportion of older, later maturing individuals (ICES 2019). Salmon are believed to be delaying sexual maturity in response to reduced marine feeding opportunities, thereby limiting the growth and maturation potential of the fish (Bacon et al. 2009; Otero et al. 2012; Jonsson et al. 2016; Bal et al. 2017). Age-at-maturity in salmon is a classic evolutionary trade-off to optimise lifetime fitness (Flem-ming 1996). Larger, later-maturing individuals, which spend more time at sea, have higher fecundity but also run a greater risk of mortality before first reproduction (Fleming and Einum 2011). In contrast, smaller, earlier-maturing individuals, which spend less time at sea, have lower fecundity but a higher probability of surviving to reproduce. Declines in growth during the first summer at sea have been linked to changes in the sex composition of adult returns (Tréhin et al. 2021), because females may need to spend more years at sea than males to achieve the minimum body size required to attain sexual maturity (Barson et al. 2015; Mobley et al. 2020) and therefore might be subject to higher mortality rates.

Increased temperatures resulting from climate change have modified salmon migration timing. Smolts are understood to synchronise the timing of their seaward migration to coincide with the arrival of optimal thermal conditions at sea to maximise survival (McCormick et al. 1998; Hvidsten et al. 1998, 2009). Otero et al. (2014) found that, on average, smolts are initiating their seaward migration 2.5 days earlier per decade in response to increased temperatures in fresh water. Earlier seaward migration can result in a mismatch with optimal conditions for post-smolt growth and survival at sea (Kennedy and Crozier 2010; Russell et al. 2012a; Simmons et al. 2021). Climate change is also believed to affect the timing of adult returns, although the mechanisms remain unclear. Adult salmon are generally returning to
rivers earlier in the North West Atlantic (Huntington et al. 2003; Juanes et al. 2004; Dempson et al. 2017) and later in the North East Atlantic (Solomon and Sambrook 2004; Valiente et al. 2011; Bal et al. 2017), with potentially detrimental effects on reproductive success (Jonsson and Jonsson 2009).

Knowledge about climate change impacts on the marine migration routes of salmon is limited. Salmon migrate northwards towards marine feeding areas that are geographically segregated among populations (Mackenzie et al. 2012; Soto et al. 2018; Glibey et al. 2021). Local movements in estuaries and nearshore waters are influenced by tidal currents (Holm et al. 2003; Lacroix and Knox 2005; Lacroix et al. 2005), while movements in offshore waters are governed by surface currents (Dadswell et al. 2010; Mork et al. 2012; Strom et al. 2018). Interannual variation in climatic conditions shapes marine migration routes by changing surface currents, surface temperatures, and salinities that guide salmon towards feeding areas with different environmental conditions and prey availability (Friedland et al. 2012; Mork et al. 2012; Byron et al. 2014). Over the next century, climate models predict a global weakening of surface currents, reducing nutrient availability, and primary production, with negative effects on fish stocks in the North Atlantic (Gröger et al. 2013). Climate change is not expected to result in the extinction of salmon across the North Atlantic because projected future temperatures are unlikely to exceed their thermal optimum in all areas (Jonsson and Jonsson 2009; ICES 2017a). However, the distribution of salmon is projected to contract by the end of the twenty-first century due to climate change reducing the availability of suitable thermal habitat (Lassalle and Rochard 2009). Suitable thermal habitat for salmon is expected to extend northwards with the invasion of new spawning, nursery, and feeding areas north of the species’ present distributional range but with the extirpation of southern populations (Todd et al. 2011; Hedger et al. 2013; Hastings et al. 2020). Salmon are already responding to warmer temperatures by expanding their range northwards into the Arctic Ocean (Jensen et al. 2014; Bilous and Dunmall 2020), and disappearing from the southern edge of their distribution area (Parrish et al. 1998; Jonsson and Jonsson 2009).

Exactly how salmon will respond to future climate change is highly uncertain because oceanic conditions in the North Atlantic are now beyond a historical context (ICES 2017a). Furthermore, it is likely that climate change will interact with other stressors (e.g., predation, water quality, and invasive non-native species) to have synergistic negative impacts on salmon (Graham and Harrod 2009).

Predation

Salmon are vulnerable to predatory mammals, birds, and fish (Ward and Hvidsten 2011). Direct predation effects are usually less obvious during the early freshwater life stages, when most losses of salmon occur, and density-dependent processes are more likely to regulate recruitment and compensate for impacts at the population-level (Jonsson et al. 1998; Milner et al. 2003). However, the potential for such compensatory processes typically weakens through the early life stages, and older life stages (smolts, post-smolts, and adults) are not thought to be regulated by density-dependent processes nor subject to compensation (Ward and Hvidsten 2011). Losses of smolts and post-smolts are thus expected to have a direct proportional impact on adult returns (Thorstad et al. 2012a).
Predation on smolts during the first months at sea is a major source of natural mortality impacting salmon abundance (Hansen et al. 2003). Smolts leaving fresh water and entering the sea are particularly vulnerable to predation due to their relatively small body size and naivety with regards to predator avoidance (Friedland et al. 2012; Flávio et al. 2020). For example, on average 49% (23–79%) of smolts are estimated to be lost to predation each year in the lower reaches of rivers and estuaries in Denmark (Jepsen et al. 2019). Furthermore, 59% of smolts have been estimated to suffer predation-related mortality in the Miramichi River estuary and Bay in Canada (Daniels et al. 2019). The extent and location of losses of post-smolts and pre-spawning adults to predators is largely unknown beyond estuaries. Recent developments in archival tag technology have shed some light on the mortality of post-spawning adult salmon returning to the sea (known as kelts). Strøm et al. (2019) reported 22 predation events (14%) and 38 undetermined mortalities (24%) from 156 tagged kelts released from 12 rivers around the North Atlantic, with 59% of the predation events attributed to endothermic fishes.

Marine mammals including seals and cetaceans have been reported aggregating in river mouths, estuaries, and nearshore waters to prey on emigrating smolts and returning adult salmon (Thorstad et al. 2012a; Civil et al. 2019). Adult salmon are most at risk of predation by marine mammals when returning from sea to reproduce (Butler et al. 2008). Smaller salmon stocks and population units, such as early-running spring salmon, are particularly vulnerable to seal predation (Butler et al. 2006). Seals are perceived to have contributed to some local salmon population declines, leading to calls from fisheries stakeholders for seal populations to be controlled in the vicinity of salmon fisheries (Butler et al. 2006, 2008, 2011; Graham et al. 2009). However, seal predation on salmon may be limited to a relatively small proportion of individuals that specialise in targeting salmonids (Hammill and Stenson 2000; Bowen et al. 2002; Graham et al. 2011), or fishing in particular areas around nets (Graham et al. 2011; Harris et al. 2014), and predation levels can be exacerbated when the fish aggregate below migration barriers (Bendall and Moore 2008).

Piscivorous birds are known to consume salmon in estuaries and nearshore waters (Dieperink et al. 2002; Harris et al. 2008). Cormorants Phalacrocorax spp. have been observed aggregating in estuaries during smolt runs, when they may represent a major mortality source (Jepsen et al. 2019; Flávio et al. 2020). For example, salmon smolts have been shown to comprise a large percentage of the diet of cormorants in Northern Ireland (66%) and Scotland (18%) (Kennedy and Greer 1988; Marquiss et al. 1998). Harris et al. (2008) reported that goosander Mergus merganser predation removes a moderate percentage of total annual smolt production on the rivers North Esk (3–16%) and Spey (3–5%) in Scotland. Other investigations in Scotland indicate latitudinal trends in the diet of goosanders and cormorants, with salmon comprising a larger percentage of the prey items in northern (41% and 18%, respectively) than southern (9% and <1%, respectively) rivers (Marquiss et al. 1998), consistent with the relative abundance of different fish species. Avian predation is potentially exacerbated at migration barriers, where other bird species (e.g., herons and gulls) could also aggregate to prey on smolts. Gulls have been identified as a potentially important predator on Pacific salmonids around North American dams (Ruggerone et al. 1986; Collis et al. 2002), but this has been little studied in the context of Atlantic salmon (Jepsen et al. 2006).

Piscivorous fish predate on salmon in the marine environment (Friedland et al. 2012). However, this remains poorly understood because it is not readily observable. Salmon are known to be consumed by sharks and large pelagic fish (Lacroix 2014; Daniels et al. 2018; Strøm et al. 2019). Predation could occur in nearshore waters from a range of fish species, such as Atlantic cod Gadus morhua and saithe Pollachius virens, which have been identified as important predators of salmon smolts and post-smolts in some areas (Jepsen et al. 2006; Thorstad et al. 2012b; Friedland et al. 2017). Sea bass Dicentrarchus labrax is another notable predator of salmon smolts that has expanded its geographical distribution range in the North Sea since the 1980s (Colman et al. 2008), and thus it is conceivable that this might have increased predation pressure on salmon smolts. A study carried out in the tidal reaches of the River Frome in South England postulated that 5% of total annual smolt production could be lost to sea bass predation (Riley et al. 2011). The creation of sea bass nursery areas in estuaries (Anon, 1990) could therefore negatively affect smolt production from rivers, whilst affording some protection against bycatches of returning adult salmon.
by prohibiting the operation of bass fisheries. Similarly, it has been inferred that 1.9–17.5% of smolts are lost to striped bass *Morone saxatilis* predation in the Miramichi River estuary in Canada, thus it is plausible that the observed increase in the abundance of this predator might have contributed to salmon population declines over the last two decades (Daniels et al. 2018).

Predation is a natural process regulating salmon stock size in balance with predator levels. However, the evidence indicates that predation is a relatively major source of mortality for salmon (Hansen et al. 2003), which can have disproportionate negative impacts on depleted stocks (Ward and Hvidsten 2011).

**Water quality**

The water quality characteristics with the greatest potential to have sublethal and lethal effects on salmon in marine waters were broadly categorised into dissolved oxygen, suspended sediment, and contaminants. All three characteristics have been shown to be important regulatory factors, with the potential to interact synergistically to impact salmon, often exacerbated by other stressors such as increased temperature (Alabaster and Lloyd 1982; Cabral et al. 2019).

Dissolved oxygen governs the development, growth, and survival of salmon (Brett 1972). The behavioural responses of salmon to dissolved oxygen fluctuations include changes in movement and activity, increased use of surface respiration and air breathing, and altered habitat use (Kramer et al. 1987). Salmon consume more oxygen at higher temperatures due to an increased metabolic rate (Beamish 1964). Interactions between temperature and dissolved oxygen concentrations influence migration success by modifying the aerobic scope of salmon during muscular exercise (Alabaster and Gough 1986; Farrell 2009). High temperatures lower dissolved oxygen concentrations in estuaries delaying the upstream migration of adult salmon into rivers, thereby increasing estuarine residency time (Solomon and Sambrook 2004; Bendall et al. 2012). Adult salmon avoid entering estuaries when dissolved oxygen levels are below 5.5 mg L\(^{-1}\) (Priede et al. 1988). If dissolved oxygen falls below the lethal limit of 1.5 mg L\(^{-1}\), then salmon mortality due to asphyxiation can occur (Kazakov and Khalyapina 1981). For example, exposure to dissolved oxygen below the lethal limit was identified as a major contributory factor to salmon mortality in the River Tamar estuary in South West England between 1975 and 1995 (Solomon and Sambrook 2004). For smolts, the lethal dissolved oxygen concentration that produces 50% mortality over a 3-day period is 2.5 mg L\(^{-1}\) (Alabaster et al. 1979).

Fine sediment entering the marine environment from land drainage, erosion, and construction activities can become mobilised and suspended in the water column by turbulence (Winterwerp and Kranenburg 2002). Salmon exhibit behavioural and physiological responses to changes in suspended sediment (Newcombe and Jensen 1996; Robertson et al. 2007; Kemp et al. 2011). Most investigations into the effects of suspended sediment have focussed on freshwater life stages, during which sediment size and loading rates influence spawning habitat availability, egg and embryo survival, fry emergence timing, juvenile growth, and smoltification age (MacCrimmon and Gots 1986; Lisle and Lewis 1992; Armstrong et al. 2003; Suttle et al. 2004). In contrast, limited information exists on the impacts of suspended sediment in estuarine or nearshore waters, where salmon would most likely encounter high suspended sediment levels during the smolt migration or as returning adults. Possible impacts could range from a temporary behavioural avoidance reaction to more serious physiological effects, potentially resulting in impaired migration and, in extreme conditions, mortality. However, salmon successfully migrate through estuaries that have naturally high suspended sediment levels to enter rivers, up to several thousand mg L\(^{-1}\) in the case of the Severn Estuary in South West England (Gibson 1933), and increased turbidity can improve salmon survival by lowering predation rates (Gregory and Levings 1998). Extrapolating to population-level impacts is difficult because limited attention has been given to the long-term effects of increased suspended sediment (Kjelland et al. 2015).

Water-borne contaminants, including pesticides, heavy metals, and synthetic hydrocarbons, can adversely affect salmon (Giattina and Garton 1983). Salmonids can bioaccumulate contaminants from their prey (Burreau et al. 2006). For example, juvenile chinook salmon *Oncorhynchus tshawytscha* accumulate synthetic hydrocarbons from their prey along estuarine migration routes (Johnson et al. 2007).
In the open ocean, Atlantic salmon are potentially at similar risk of accumulating contaminants. For instance, the historically polluted River Tees in North East England is a source for polybrominated diphenylethers in the North Sea food web, with biomagnification occurring from invertebrates through fish to seals (Boon et al. 2002). Adult returns to the River Tees accumulate polybrominated diphenylethers, polychlorinated biphenyls, and hexachlorobenzene over an unknown portion of their lifetime (Assunção et al. 2020). Multiple contamination events can cumulatively affect salmon, particularly in smolts prior to seawater entry (Russell et al. 2012a). Smolts exposed to atrazine pesticides in fresh water, and then exposed to oestrogenic chemicals in estuaries, exhibit reduced growth and survival during marine residency (Moore et al. 2003; Waring and Moore 2004). Physiological effects of sublethal contaminant exposure on smolts include reduced salinity tolerance when entering marine waters (Kroglund and Finstad 2003; Moore et al. 2008), with the effects of some contaminants such as aluminium increasing with higher water acidity (Kroglund et al. 2007; McCormick et al. 2012; Thorstad et al. 2013). Adult returns may also be impacted by sublethal contaminant levels modifying olfactory cues required for successful homing to spawning grounds (Saunders and Sprague 1967).

Over the last 50 years, improvements in water quality have been an important contributory factor to the recovery of many salmon stocks (Kroglund et al. 2001; Doughty and Gardiner 2003; Mawle and Milner 2003; Saltveit et al. 2014). A striking example of improved water quality aiding stock recovery has been provided by the River Tyne in North East England (Mawle and Milner 2003). After being almost lost in the twentieth century, the Tyne salmon stock has undergone a remarkable recovery following de-industrialisation and better sewage treatment, which ameliorated low dissolved oxygen and high ammonia concentrations resulting in improved estuarine water quality (Milner et al. 2008). Improvements in estuarine water quality have also led to the recovery of other salmon stocks in England, such as those on the rivers Wear, Mersey, and Tamar (Nuttall and Purves 1974; Mawle and Milner 2003; Jones 2006). Nonetheless, just 50 out of 166 (≈30%) estuaries and nearshore waters in England had acceptable water quality in 2018 according to the standards set out in the EU’s Water Framework Directive (Defra 2020), with sewage effluent, agricultural run-off, and industrial waste identified as key pollution sources. Indeed, good chemical status in 2018 was only achieved in 2441 out of 6537 (≈37%) European estuaries and nearshore waters, where the main pressures included atmospheric deposition of contaminants and discharges from urban wastewater treatment plants (EEA 2018). Restoring and maintaining water quality has and will continue to be challenging because many pollutants remain dormant in benthic substrate and aquifers for extended periods of time before being mobilised into aquatic systems. Further remediation work is therefore necessary to ensure that the quality of estuarine and nearshore waters is suitable to sustain salmon populations.

Poor water quality is a concern for salmon in riverine, estuarine, and nearshore habitats (Solomon and Sambrook 2004; Thorstad et al. 2008). Low dissolved oxygen concentrations can have severe impacts on salmon over relatively large spatial and temporal scales in rivers, estuaries, and nearshore waters. In contrast, high suspended sediment levels typically have localised, short duration, and low severity impacts on salmon. Contaminant exposure is an important perturbation due to the widespread occurrence and persistence of chemical compounds along migration routes.

Bycatch

Salmon are at risk of incidental capture by marine fisheries targeting other species. Bycatches of salmon are taken in marine fisheries targeting pelagic species in estuarine and nearshore waters, which can result in the mortality of injured fish (ICES 2005). For example, marine fisheries exploiting mullet (Mugilidae) and sea bass are known to take bycatches of salmon in England’s nearshore waters (Sumner 2015). Emigrating smolts are less at risk of bycatch than returning adult salmon because their small size, surface-swimming behaviour, and peak spring emigration render them less likely to be intercepted by most fishing gears operating in nearshore waters. In contrast, adult salmon reach larger sizes and return to rivers over a large part of the year (Thorstad et al. 2008), which makes them more vulnerable to being taken as bycatch in a wider range of marine fisheries than smolts. The greatest risk comes from marine fisheries targeting pelagic species of similar size.
High seas pelagic fisheries in the North Atlantic, particularly those targeting mackerel and herring, are known to take bycatches of salmon (ICES 2014). Annual bycatch estimates for salmon from European countries range from 300 to 800 fish in Icelandic mackerel fisheries, representing a very small percentage (0.01–0.03%) of the estimated total salmon abundance in the North East Atlantic. Other fishery-independent bycatch estimates from summer surveys of the Nordic Seas between 2010 and 2013 indicated that less than 2% of the total salmon abundance in the North East Atlantic was taken as bycatch. ICES (2014) recognised that catches in North Atlantic pelagic fisheries, potentially overlapping geographically with the movements of salmon, had increased in recent years. For example, concerns were raised over the northward expansion of the blue whiting Micromesistius poutassou fishery in the North East Atlantic. However, much of the catch in this fishery is taken prior to smolts emigrating into the ocean and at a depth greater than generally occupied by salmon. Therefore, the blue whiting fishery is likely to have little impact on salmon stocks, but uncertainties remain (ICES 2017b).

The severity and extent of salmon bycatch by marine fisheries is of concern but remains difficult to quantify accurately. Losses of adult returns to bycatch will have a greater impact on stock sustainability than losses of emigrating smolts, given that returning adults are emigrated smolts that have survived to maturity.

Artificial light at night

Emissions of artificial light at night (ALAN) are estimated to be increasing globally by 6% per annum (Hölker et al. 2010), raising concerns about potential environmental impacts. More than 20% of the world’s nearshore regions (excluding Antarctica) experience some form of artificial light pollution (Davies et al. 2014), and some of the largest urban conurbations are located adjacent to the tidal reaches, estuaries, and ports of rivers that support salmon stocks.

Light perception by salmon depends not only on the intensity and wavelength of the light source, but also the light-transmitting qualities of the water and the depth at which the fish is located. Visual sensitivity in salmon alters during development (Cheng et al. 2006), with major changes occurring during smoltification (Beatty 1966; Folmar and Dickhoff 1981; Alexander et al. 1994), which render smolts and post-smolts sensitive to the blue-green end of the visible spectrum (Migaud et al. 2007; Vera et al. 2010). Experimental studies focusing on the effects of ALAN on salmon have demonstrated significant disruption to the diel migratory pattern of smolts leaving fresh water, as well as to fry dispersing from spawning redds (Riley et al. 2012, 2013, 2015). As these patterns are believed to have evolved primarily as anti-predation measures, any disruption caused by ALAN is speculated to decrease recruitment success to the adult population.

Little research has been undertaken into the effects of ALAN on salmon in estuaries and nearshore waters. In recent years, interest on the effects of ALAN on marine life has increased (Davies et al. 2014; Alter et al. 2021). Behavioural effects have been observed in marine fish, including increased activity levels and a cessation of normal circadian and circatidal activity patterns in intertidal rockfish Girella laevis (Pulgar et al. 2019), as well as changes in swimming behaviour and susceptibility to nocturnal predation resulting in increased overall mortality in coral reef fish larvae (O’Connor et al. 2019). Lighting from ships has been shown to modify fish behaviour to depths of at least 200 m (Berge et al. 2020). No studies of the effects of ALAN on wild salmon in the marine environment have been published, but artificial lighting at fish farms increases the swimming depth of salmon in sea cages (Juell et al. 2003; Hansen et al. 2017).

Given the difficulty of extrapolating experimental evidence from aquaria or streams, the potential effects of ALAN on wild smolts and adults migrating through estuaries or marine waters are unclear. This potential stressor is widespread across many estuaries, and emissions of ALAN are likely to increase in the future. However, impacts may be minor in estuaries, where turbid water limits light penetration, and in areas where salmon can descend into deep water beyond the light penetration depth. Light emissions from oil and gas platforms may have a pronounced local impact on salmon behaviour at sea, particularly in the North Sea, which contains over 500 of such installations (OSPAR 2015), but the probability or likely severity of the impact is poorly understood. Salmon that have adapted to detect and respond to extremely low levels of natural light during the polar
night might be susceptible to artificial light in Arctic seas (Berge et al. 2020).

Tidal barrages

Barrages have been constructed across rivers, bays, and estuaries for renewable energy generation, the provision of recreational facilities, freshwater storage, flood protection, and urban regeneration (Sitharam et al. 2020). Tidal barrages are quite rare, with relatively few examples in the world. Detrimental impacts have been attributed to their construction and operation, including but not limited to loss of intertidal habitats and associated biota due to modified flow patterns and sediment dynamics (Drinkwater and Frank 1994; Wolf et al. 2009; Frid et al. 2012; Hooper and Austen 2013; Kidd et al. 2015). For example, tidal barrages at La Rance in North West France and on the River Wansbeck in North East England decreased tidal ranges by 40% and 80%, respectively, causing changes to flow and sediment regimes, thus affecting the quality and quantity of suitable habitat available for wading birds and fish (Worrall and McIntyre 1998; Hooper and Austen 2013). Changes in fish species composition can occur following the construction of a tidal barrage, such as in the case of the Geum estuary barrage in South Korea, where freshwater species increased and diadromous species decreased upstream of the barrage (Yoon et al. 2017).

Salmon can be directly impacted by tidal barrages creating a physical barrier that disrupts migrations, and therefore these structures have the potential to cause local extirpation of stocks if fish passage is severely compromised (Drinkwater and Frank 1994; Gough 1996; Russell et al. 1998; Moore and Potter 2014). Barrier operations can indirectly impact salmon through modifications of the river’s natural discharge regime, thereby affecting migration cues and fish passage (Gillson 2011). Modified discharge regimes can impose additional energetic costs for migrating salmon in their attempt to negotiate the physical barrier, with potentially deleterious impacts at the population-level (Gough 1996; Russell et al. 1998). In addition, tidal barrages will alter hydrological conditions by reducing the tidal range upstream of the structure, resulting in a loss of suitable estuarine habitats for salmon (Frid et al. 2012; Hooper and Austen 2013; Kidd et al. 2015). Reduced tidal ranges can alter migratory cues crucial for initiating and orientating salmon during their upstream and downstream migrations. Aside from these issues, salmon can be susceptible to mechanical injuries due to turbine passage in power generating barrages, increased predation pressure and higher stress levels, with lesser effects posed by factors such as noise, habitat fragmentation, and water quality (Dadswell and Rulifson 1994; Dadswell et al. 2018).

The evidence indicates that tidal barrages can negatively impact salmon stocks. However, given that there are only few operating tidal barrages in the world, the severity and extent of their impact on salmon stocks are regarded as low at present but there is high potential for development over the next decade.

Power station impingement and thermal discharge

Power stations dispose of waste heat created in the electricity generation process typically using a water supply for cooling (Sarkar 2015). During this process, water is abstracted from a nearby water body to dissipate the produced heat, and the thermal effluent (usually 8–12.5 °C above ambient water temperature) is discharged into the same water body (Langford 2001) or into a heated-water effluent reservoir. Detrimental ecological impacts resulting from water intake and disposal include the trapping of organisms against screens that prevent debris entering water intakes in a process known as impingement (Turnpenny 1988), and the mechanical and thermal stresses imposed on organisms drawn through cooling systems in a phenomenon known as entrainment (Briand 1975; Bamber et al. 1994; Bamber and Seaby 2004). Thermal and chemically altered effluents can also have ecological impacts on receiving waters and adjacent biota (Bamber 1990; Langford 1990; Pawson and Eaton 1999). Increased temperatures from thermal discharge will rarely cause the mortality of fish species in isolation but can affect their performance as temperatures often surpass optimal conditions for growth and development (Coutant and Brook 1970; Wither et al. 2012). High chlorine levels in thermal discharges can also negatively affect fish, with increased avoidance behaviour or mortality detected in salmon at levels as low as 0.01 mg L⁻¹ (Brungs 1973). The severity of the ecological effect depends on the location of the power plant (Turnpenny et al. 2010), with confined water bodies such as estuaries
more prone to long-term effects than offshore waters (Wither et al. 2012). In addition, the position of the intake influences fish entrapment rates and the design of the outlet determines the velocity, quantity, and the temperature of the effluent released into the recipient water body (Turnpenny et al. 2010).

Salmon is a cold-water species that has among the lowest temperature threshold of any teleost fish in temperate regions (Jobling 1981), and therefore is expected to be highly sensitive to thermal effluents. Exposure to water temperatures above 22 °C can impede salmon migration (Alabaster and Gough 1986; Alabaster 1991; Alabaster et al. 1991). Delays in the upstream migration of adult salmon have been correlated with low river discharge, high temperatures, and reduced oxygen content (Solomon and Sambrook 2004), with oxygen content postulated as the main factor governing migration success (Roston et al. 2010). Increased temperatures from thermal discharges can affect the reproductive success of salmon, particularly if exposure occurs in late autumn or early winter when ovulation and spermatogenesis takes place in adults (Taranger and Hansen 1993; Vikingstad et al. 2008; Pankhurst and King 2010). Interactions between water temperature, river discharge, and oxygen content are complex, resulting in high levels of uncertainty about the potential impacts of thermal discharges on salmon migration. Limited information is available on the impacts of increased temperatures on the downstream migration of smolts, but it is expected to be severe if the transition from fresh to ‘heated’ salt water was abrupt.

Power station impingement and thermal discharge impacts on salmon will be location and time specific. Detrimental impacts are expected during seaward migration in areas where the power station outlet and/or thermal plume intersects with salmon migration routes.

Noise pollution from pile-driving

Underwater noise pollution is a growing concern, with detrimental effects on marine life noted from both continuous noise sources such as shipping and impulsive noise sources such as seismic surveys and pile-driving (Merchant et al. 2016; Faulkner et al. 2018). Despite this, there is a paucity of information on the effects of underwater noise on fish in the marine environment (Popper et al. 2020). Concern has been expressed about the ecological impacts of underwater pile-driving sounds on salmon (reviewed by Hawkins et al. 2015). Salmon have been classified as ‘hearing generalists’ with low sensitivity to sound pressure under a narrow range of frequencies and limited auditory response thresholds compared to other fish species (Hawkins and Johnstone 1978; Popper and Fay 1999; Hawkins and Popper 2014). Hearing in salmon is restricted to frequencies ranging from 32 to 380 Hz and the species lacks specialist auditory apparatus, indicating sensitivity for particle motion rather than sound pressure (Hawkins and Johnstone 1978).

Fishes generally avoid harmful pile-driving sounds to minimise adverse physiological responses and physical damage (Putland et al. 2019). Behavioural responses to pile-driving sounds include short-term directional movement away from the noise source and long-term avoidance reactions resulting in potential changes to migration patterns and access to feeding areas (Hawkins 2006; Gill et al. 2012; Hawkins et al. 2015). However, the behavioural responses of salmon to pile-driving sounds remain poorly understood. During the construction of a liquefied natural gas terminal in the Baltic Sea, pile-driving sounds above the lowest hearing threshold of salmon by 122 dB were postulated to have the potential to impede spawner passage and damage the hearing of fish at a distance less or equal to 40 m from the source (Bagočius 2015). Another study found that pile-driving sounds within the hearing range of juvenile pink Oncorhynchus gorbuscha and chum salmon O. keta, which were emitted over a radius of at least 600 m in the Snohomish River (Washington State, USA), modified the abundance and distribution of both species by producing avoidance reactions that reduced schooling behaviour (Feist et al. 1996). Nonetheless, salmon have also been found to lack behavioural responses to pile-driving sounds ranging from 160 to 194 dB (Nedwell et al. 2003; Harding et al. 2016). For example, a tagging study indicated that the behaviour of salmon migrating through the River Tyne estuary was similar irrespective of whether they were exposed to pile-driving sounds (Moore and Bendall 2011). However, individuals entering the river to spawn might have been delayed by pile-driving operations, potentially negatively affecting the salmon stock.

Despite recent advancements, information gaps are too substantial to draw firm conclusions about the impacts of underwater pile-driving sounds on salmon.
Although salmon have been shown to exhibit behavioural and physiological responses to pile-driving sounds, impacts are likely to be restricted to periods when smolts and adults move through estuaries and nearshore waters where construction schemes are mostly situated.

Invasive non-native species

Introductions of invasive non-native species in the marine environment are increasing globally, with detrimental ecological consequences being reported (Molnar et al. 2008). Non-native species are classed as invasive if they establish, spread, and cause a significant change in species communities or ecosystem processes, or cause severe economic losses to human activities (Copp et al. 2005). Invasive non-native species can affect native taxa and ecosystems through alteration of trophic pathways (Mooney and Cleland 2001), habitat modification (Bax et al. 2003), competition and predation, and the spread of pathogens and parasites (Bax et al. 2003; Eno et al. 1997; Tidbury et al. 2014). However, little is known about the possible impacts of invasive non-native species on salmon in estuarine and marine environments.

Concerns have been expressed about the potential ecological impacts of invading pink salmon on indigenous Atlantic salmon stocks due to competition and predation (ICES 2018). Pink salmon is a Pacific salmonid species that had been deliberately introduced to Russian rivers discharging into the Barents Sea before spreading to other rivers in the North Atlantic, in particular those of Norway (Sandlund et al. 2019). Occasional pink salmon captures have been reported in rivers outside Russia since the early-1960s, but unprecedented numbers were caught in 2017 across a wide geographic area (ICES 2018). In Norway, record numbers of pink salmon were captured in 2017 (Mo et al. 2018; Sandlund et al. 2019), with reports of 6594 individuals caught in 262 rivers (Berntsen et al. 2020). Similarly, the reported numbers of pink salmon caught in the UK (341), Sweden (80), Iceland (66), and Ireland (36) in 2017 were unparalleled (Armstrong et al. 2018; ICES 2018; Millane et al. 2019). The pink salmon invasion of rivers in the North Atlantic is in its early stages and characterised by considerable inter-annual variation in the numbers of captured individuals mainly due to spawning runs occurring on a two-year cycle. Recent unpublished data on pink salmon captures in 2019 and 2021 indicate an emerging increasing trend in the species’ prevalence across the North East Atlantic (NINA 2021). Although competition with Atlantic salmon in fresh water might be limited by pink salmon’s use of different spawning habitats, an earlier spawning season, and short juvenile residency before seaward migration (Copp 2017), there is evidence of competition between adults and overwintered autumn-run salmon in Russian rivers (ICES 2013). With colonisation in its early stages, there is no evidence for marine competition, but this could occur if the abundance of pink salmon increases, and a European-funded study to address this knowledge gap will commence in 2021 (University of Gdańsk 2021). A recent study has found that pink salmon eggs and carcasses can increase the amount of marine-derived nutrients and energy available to juvenile Atlantic salmon in rivers, but little is known about the potential population-level effects at present (Dunlop et al. 2021).

Other invasive non-native species could potentially affect the marine life stages of salmon via changes to food supply, with these likely to operate in conjunction with other stressors such as climate change. One species of note is the invasive ctenophore Mnemiopsis leidyi, which has caused trophic cascades in plankton communities in the Mediterranean and Black Seas (Tiselius and Møller 2017). Hamer et al. (2011) warn of the possibility of this ctenophore affecting fish recruitment in the North Sea through zooplankton predation and competition with larval fish, and such effects could, if on a large enough scale, affect salmon.

Invasive non-native species in the marine environment are not presently considered a prominent stressor for salmon stocks. However, climate change could increase the likelihood of a wider range of non-native species impacting salmon stocks over the next decade.

Electromagnetic fields

Rapid development of ‘green’ energy from renewable energy installations and increases in subsea cable networks have increased the range of sources of artificial electromagnetic fields (EMF) in the marine environment (Gill et al. 2014). Interest in the potential effects of artificial EMF on salmonids has consequently grown in recent years (Formicki et al. 2019; Gill...
and Desender 2020). Salmonids are electromagnetically sensitive due to the presence of magnetic receptors, containing microscopic crystals of magnetite, which may facilitate behavioural and physiological responses to fluctuations in EMF (Walker et al. 1985; Moore et al. 1990). They use EMF to navigate during long-distance migrations to marine feeding areas and direction-find when returning to their natal rivers (Putman et al. 2013; Scanlan et al. 2018; Minkoff et al. 2020). Artificial EMF emitted from subsea cables could therefore have marked effects on salmonids that rely on the Earth’s natural geo-magnetic fields for spatial navigation and orientation at sea (Gill et al. 2012).

Exposure to EMF can generate behavioural and physiological responses in salmonids (Walker et al. 1997), but most of the available information is limited to Pacific salmonids (Yano et al. 1997; Klimley et al. 2017; Fey et al. 2019; Jakubowska et al. 2021). For example, Wyman et al. (2018) demonstrated that artificial EMF emanating from a high-voltage (200 kV) subsea cable in the field did not significantly alter the migration success of juvenile Chinook salmon through the San Francisco Bay in California, USA. After activation, however, higher proportions of juveniles crossed the cable location, and fish were more likely to be detected south of their normal migration route, suggesting that artificial EMF could influence migratory cues. The limited information available for Atlantic salmon shows a lack of detectable behavioural or physiological responses to artificial EMF under laboratory conditions (Armstrong et al. 2015), particularly at low frequencies (Richardson et al. 1976).

Salmon may encounter artificial EMF from marine renewable energy installations along their nearshore migration routes, where these overlap with subsea cable networks, particularly in shallow waters <20 m deep (Gill et al. 2012). As both smolts and adults primarily use the surface layers of the water column, this preferred habitat, combined with diminishing EMF with distance from the cable, is expected to reduce the likelihood of interactions with artificial EMF from buried cables. However, the advent of floating offshore renewable energy installations will require consideration of interactions with migratory fish in surface waters (Hutchison et al. 2020). In the context of existing subsea cables, the risk of exposure to artificial EMF will be greatest when salmon undertake periodic deep dives to the seabed in estuaries and nearshore waters. Depending on dive frequency and the magnitude and persistence of any artificial EMF encountered, the effects on salmon could range from short-term behavioural responses (e.g. a change in swimming speed or direction) to a more serious, long-term response including disruption or delay to migration (Öhman et al. 2007).

Drawing firm conclusions on the impacts of artificial EMF from subsea cables on salmon is challenging due to the scarcity of available information on population-level effects (Boehlert and Gill 2010; Hutchison et al. 2020). However, the potential impacts are considered to be relatively low at present, with possible greater effects confined to the shallow waters of estuaries and nearshore areas, noting that this evaluation has large uncertainty and will require revisiting as more extensive cable networks and new renewable energy technologies increase in prevalence.

Fisheries exploitation

Concerns have been expressed over the population impacts of fisheries exploiting salmon in the North Atlantic (Parrish et al. 1998; Jonsson and Jonsson 2004). Mean annual exploitation rates have decreased for one-sea-winter and multi-sea-winter salmon retained in commercial and recreational fisheries from Europe and North America since the early-1970s (ICES 2019). However, these reductions in exploitation rates have not produced the expected gains in adult returns, indicating that factors other than fishing are responsible for increased levels of marine mortality (Klemetsen et al. 2003; ICES 2019). It has been speculated that illegal fishing at sea might account for the shortfall in adult returns (Dadswell et al. 2021), but evidence to support this hypothesis is lacking. For many years, surveillance flights provided no evidence of illegal fishing for salmon on the high seas (e.g. ICES 2013), and there have been no reports of such activity more recently.

Salmon have been exploited in home-water and distant-water fisheries (ICES 2019). Mean annual exploitation rates for one-sea-winter and multi-sea-winter salmon in home-water fisheries operating in most countries throughout Europe and North America have declined to the lowest levels over the last 50 years. This reflects the closure of many fisheries and increasingly restrictive measures to reduce levels
of exploitation in most countries. For example, mean annual exploitation rates in home-water net and rod fisheries in England and Wales have decreased substantially for one-sea-winter (57–10%) and multi-sea-winter (42–5%) salmon since the early-1970s (Cefas et al. 2019a). Various fisheries regulations have been introduced to ensure that the exploitation of English salmon stocks in home-water fisheries is at low levels (Cefas et al. 2019b), with no exploitation by commercial fisheries permitted since 2019 (Cefas et al. 2020). Mixed-stock fisheries at sea in the Republic of Ireland closed in 2007. Furthermore, the exploitation of salmon stocks in distant-water, high-seas fisheries off West Greenland and the Faroes has decreased markedly since the late-1980s (ICES 2019). The West Greenland salmon fishery has been restricted to an internal-use subsistence fishery, with the commercial export of salmon prohibited since 1998 (NASCO 2014). No commercial salmon fishery has operated at the Faroes since 1991 and the research fishery was closed in 2001 (NASCO 2020).

Fisheries exploitation has the potential to impact the marine feeding, growth, and survival of salmon indirectly through bottom-up processes modifying the abundance of other fish species they interact with as competitors, predators, or prey, such as sandeels Ammodytes spp. and herring (Jacobsen and Hansen 2000; Haugland et al. 2006; Rikardsen and Dempson 2011). The North Sea herring stock has recovered from overfishing to reach the highest abundance levels since the 1970s (ICES 2020c). High abundances of herring within the feeding areas of salmon might act as a ‘double-edged sword’, being both an important prey as juveniles and a competitor with post-smolts for food resources as adults (Rikardsen and Dempson 2011). In contrast, the relationship between salmon and sandeels is considered a more straightforward predator–prey relationship, although the impact of fishing pressure on sandeel stock dynamics is less clear than with herring. Therefore, the degree to which fisheries exploitation may impact the growth and survival of salmon at sea by altering marine feeding conditions remains unclear.

Exploitation in home-water and distant-water fisheries is regarded as less of a threat to salmon stocks than in the past because effective controls have been implemented to substantially reduce fishing pressure in the North Atlantic.

Salmon mariculture

Farmed salmon production has increased rapidly since the early-1980s, with over 1.5 million tonnes of salmon farmed in the North Atlantic in 2018 (ICES 2019). Most farmed salmon are produced in Norway (81%) and Scotland (10%). In contrast, farmed salmon production is considerably smaller in the Faroes (4%), Canada (2%), Republic of Ireland (1%), Iceland (1%), Russia (1%), the USA and Northern Ireland (data unavailable, but production understood to be very small in both countries). No farmed salmon are produced in mariculture facilities elsewhere in the North Atlantic.

Salmon farming can impact the productivity of wild salmon populations by transferring diseases, but the most pronounced effects on wild salmon stocks are believed to result from sea lice Lepeophtheirus salmonis infestations and genetic introgression between escaped farmed fish and wild conspecifics (ICES 2016). Sea lice are an ectoparasitic crustacean that occurs naturally in low levels on wild salmon (Torrissen et al. 2013; Serra-Llinares et al. 2014). However, higher levels of sea lice on wild salmon have been observed near mariculture facilities (Serra-Llinares et al. 2014; Helland et al. 2015). Infestations of sea lice on salmon can increase their marine mortality (Ford and Myers 2008; Vollset et al. 2018), sensitivity to ocean warming (Shephard and Gargan 2020), and susceptibility to viruses (Barker et al. 2019). Mortality of post-smolts due to sea lice infestations can cause sizeable (0.6–39%) reductions in adult returns (Gargan et al. 2012; Krkošek et al. 2013; Skilbrei et al. 2013). Lice-induced mortality is higher in years of low marine survival, suggesting an additive effect of lice infestation with other stressors (Connors et al. 2012; Jackson et al. 2013; Godwin et al. 2015). Salmon mariculture has been identified as a major stressor for wild salmon stocks in Norway (Forseth et al. 2017).

Escapees from salmon farms pose a genetic threat to the fitness and viability of wild salmon stocks (McGinnity et al. 2003). The numbers of farmed salmon escaping mariculture facilities can be high, with 2.86 million escapes reported in Scotland between 1999 and 2014 (Ellis et al. 2016), and more than 26,000 escaped farmed salmon confirmed by scale reading in Norway between 1989 and 2013 (Diserud et al. 2019). Genetic introgression between
wild and farmed salmon is known to occur extensively in Norwegian rivers (Karlsson et al. 2016) and has also been demonstrated elsewhere, such as in Canada (Wringe et al. 2018). In rivers where the density of wild spawning fish is low, the spawning success of escapees is likely to increase and therefore stressed populations are likely to suffer a greater level of introgression (Glover et al. 2012, 2013; Heino et al. 2015). Such introgression can lead to phenotypic changes in the wild population, reducing fitness due to loss of local adaptations (Fraser et al. 2010; Bolstad et al. 2017), and over the longer-term reducing population resilience to environmental perturbations (Lande and Shannon 1996; McGinnity et al. 2009; ICES 2016). Genetic introgression is unlikely to occur at a significant magnitude in areas away from mariculture facilities, such as English rivers where numbers of escaped fish are in general comparatively low (Milner and Evans 2003; Walker et al. 2006). It is possible that escaped farmed salmon from neighbouring facilities on the west coast of Scotland impact wild salmon stocks in North West England, but these impacts are likely to be small given that post-smolts are believed to move offshore rapidly to pick up the shelf edge current and migrate northwards towards marine feeding areas (Shelton et al. 1997; Holm et al. 2000, 2003).

The severity and extent of the impacts of salmon mariculture on wild salmon stocks are location specific depending on the size of the production facilities. Impacts on salmon stocks in Norway and Scotland are considered to be high because most of the world’s salmon mariculture facilities exist in these areas (Forseth et al. 2017; Tett et al. 2018). In contrast, salmon mariculture is likely to have low, if any, impacts on English salmon stocks at present given the lack of production facilities in the country. However, salmon mariculture is expected to expand in Scotland and Norway over the next decade (Norwegian Ministry of Trade, Industry and Fisheries 2015; Scotland Food and Drink 2016), and the potential risks for English salmon stocks remain under review.

Tidal lagoons

Growing interest in marine renewable energy installations has led to the proposed development of tidal lagoons that convert kinetic energy from tidal currents into electricity (Chowdhury et al. 2021). A high degree of uncertainty exists over the ecological impacts of tidal lagoons because few such developments exist globally (Roche et al. 2016), but concerns have been expressed over their potential effects on salmon (Dadswell and Rulifson 1994). The principal risks of tidal lagoons for salmon would be physical injury and/or mortality due to turbine passage rather than as an impediment to migration (Davies 1988; Wilson et al. 2006). Salmon from rivers in the vicinity of tidal lagoons may encounter these structures during the smolt migration and when adults return to rivers to spawn. Losses of salmon due to turbine entrainment depend upon the probability of individuals: (a) moving or being drawn into the vicinity of the turbine intake; (b) failing to take avoidance action; and (c) being killed or mortally wounded as they pass through. Aside from turbine-related mortality, tidal lagoons could impact salmon by modifying water quality in the surrounding region (Xia et al. 2010; Cornett et al. 2013) and attracting predators. Potential impacts may be location-specific depending on factors such as device design, volume of water impounded, tidal range, current speeds, turbine approach velocities, the proximity of rivers and key migration routes, and the status of local salmon stocks.

Little information exists on the ecological impacts of tidal lagoons on salmon. Many of the risks have been too poorly quantified to draw firm conclusions on the behavioural and physiological responses of salmon to tidal lagoons and any subsequent population-level effects. Given that few of these developments exist in the world, the present impacts on salmon stocks are considered to be low or non-existent. However, there is a growing interest in generating renewable energy from tidal lagoons, which might pose a threat to salmon over the next decade.

Overview of the ranking of marine stressor impacts on English salmon stocks

At the national level, climate change and predation were classified as expanding high impact stressors (Fig. 2; Table 1), with implemented or planned mitigation measures having small effects. Climate change ranked highest on the effects and development axes, representing the stressor with the greatest overall impact. However, the knowledge supporting the effects and future development of both these stressors was poor with high levels of uncertainty. Other
stressors with relatively high effects scores included poor water quality and bycatch, although these all had lower development scores due to the availability of effective mitigation measures. In contrast, ALAN and tidal barrages were classified as expanding low impact stressors, attracting relatively low effects scores but representing a high likelihood of further development over the next decade given that planned mitigation measures are expected to have limited effects. Fisheries exploitation of salmon stocks and salmon mariculture represented stabilised low impact stressors with relatively low scores on both axes. The fisheries exploitation score reflected the major reductions in fishing mortality resulting from the implementation of extensive management measures, while salmon mariculture had a low score given its absence around the nearshore waters of England. Other factors with relatively low effects scores, but slightly higher development scores, included power station impingement and thermal discharge, noise pollution from pile-driving, invasive non-native species, and EMF. Tidal lagoons scored zero on the effects axis because no such structures exist in England, although there is a potential for future development.

Spatial variation in the proportion of votes by local fisheries officers for each stressor impacting salmon stocks was evident among the four marine plan areas in England (Fig. 3). Differences therefore existed in the regional stressor rankings (Fig. 4; Tables S1–S4). Climate change scored highest on the effects and development axes with the largest impact in all regions except the North West, where predation ranked highest on the effects axis. In the South and South West regions, climate change had markedly higher scores along both axes than any other stressor due to the absence of effective mitigation measures. Other stressors with relatively high effects scores included poor water quality and bycatch. Invasive non-native species and EMF had among the lowest effects scores across regions. Stressors with relatively low effects scores among regions included power station impingement and thermal discharge, ALAN, noise pollution from pile-driving, and fisheries exploitation. However, ALAN was the stressor considered to have the greatest potential to expand over the next decade, along with predation and climate change because planned mitigation measures are anticipated to have small effects. Salmon mariculture scored zero on the effects axis in all regions, except the North West region where there are concerns about the potential impact on English salmon stocks of fish emanating from Scottish salmon farms. Tidal barrages also scored zero on the effects axis in all regions, except the North East region due to the presence of a tidal barrage on the River Tees estuary, but there is potential for future development elsewhere.

Discussion

Salmon are vulnerable to stressors operating across life stages and environments, which makes their conservation challenging (McDowall 1999). Management prioritisation of key stressors is therefore crucial. While it is more feasible to address stressor impacts in fresh water, marine environmental issues must not be overlooked, where density-dependent effects are nominal, resulting in proportional losses of adult returns. The present assessment identified climate change and predation to exert the biggest impacts on English salmon stocks in the marine environment both currently and over the next decade. Regional differences in both climate change and predation prevalence were evident across England. Specifically, greater climate change impacts were expected in the South due to higher temperatures projected under future climatic scenarios (Lowe et al. 2019), while predation ranked highest in the North West given local concerns about rising levels of bird and seal predation on salmon stocks in estuaries. As knowledge on the effects and projected development of both stressors was poor, careful monitoring, assessment, and mitigation is required to inform management decisions to protect and restore salmon stocks. Climate change and predation are challenging issues to address given that both stressors have a high uncertainty of projected development, low mitigation potential due to their large spatial extent and many predator species have protected status, and they interact with other factors to generate synergistic and additive effects. However, targeted management actions to address specific stressors are possible in some circumstances.

Efforts to limit climate change impacts on salmon stocks depend on international actions to reduce greenhouse gas emissions, with legally binding targets set at national (HMSO 2008) and international (UNFCCC 2015) levels. While such actions are
necessary to tackle climate change globally, alleviating locally operating stressors will be more practical to implement than addressing broad-scale environmental changes. This is crucial to maximise ecosystem resilience to stressors and minimise their cumulative impacts (Falkenberg et al. 2013; Schef-fer et al. 2015; Ramírez et al. 2018). Priority should be given to protecting and improving estuaries due to the high likelihood of future anthropogenic development (Kennish 2002), which might threaten salmon stocks, especially in heavily modified environments where multiple stressors operate concurrently (Toft et al. 2018; Hodgson et al. 2020). However, it must be recognised that fully improving and protecting the resilience of estuaries will also require the rehabilitation and restoration of whole catchments from headwaters to the river mouth (Riley et al. 2018). Given that stressor exposure during one life stage can affect subsequent survival (Fenkes et al. 2016), effective management of freshwater habitats is equally important to the maintenance and enhancement of salmon stocks (Mainstone et al. 2012), especially as fisheries managers have a limited ability to control factors that influence salmon survival at sea (Russell et al. 2012a), particularly beyond territorial waters. Improvements in salmon stock status, predominantly in North East England (e.g., the Rivers Tyne, Tees, and Wear), have occurred against wide-scale population declines in many areas of the North Atlantic (Mawle and Milner 2003), indicating that freshwater effects on spawners and recruits can be dominant controls of stock size. Management actions in freshwater habitats should endeavour to maximise the number of smolts entering the ocean in the best condition and minimise stressor impacts that compromise marine survival (Russell et al. 2012a; Gregory et al. 2019). Local actions to combat the impacts of climate change on salmon in freshwater habitats should focus on ensuring access

**Fig. 3** A map of England with bar charts inset within the North East (NE), South (S), South West (SW), and North West (NW) marine plan areas showing the proportion of votes by local fisheries officers for each marine stressor impacting salmon stocks
to cold-water refugia, improving habitat connectivity, and maintaining natural discharge regimes in rivers (Smialek et al. 2021; Thorstad et al. 2021).

Losses to predators can be ameliorated through compensatory processes, especially for the earliest freshwater life stages, but these losses are also dependent on the timing and extent of predation, stock size, and other human-generated stressors (Ward and Hvidsten 2011). Most salmon stocks in England are in a depleted state (Cefas et. al 2019a), therefore the population-level impacts of predation will be proportionally greater than for stocks at full reproductive capacity. Addressing predation will be more pragmatic than tackling climate change in the short-term and at local management scales. The key will be to identify potential predation ‘bottlenecks’ in rivers and estuaries, and where seasonal concentrations of migrating salmon are particularly vulnerable to predators (Halfyard et al. 2012; Thorstad et al. 2012b; Lothian et al. 2018). This vulnerability is exacerbated when salmon are exposed to other stressors such as migration barriers (Moore et al. 1996) and poor water quality (Moore et al. 2007, 2008). Alleviating other stressors could mitigate predation impacts on salmon, but more coordinated actions will typically be required to deter predators at key life stages and identified bottlenecks. Given that predation is probably the most important source of mortality when salmon leave fresh water and enter the marine phase of their life cycle (Hansen et al. 2003), regulation of avian and mammal predation is likely to be beneficial at those times using harassment techniques (e.g., non-lethal acoustic/visual deterrents), local population reductions where necessary, justified, and legally approved (Russell et al. 1996; Butler et al. 2008), and habitat improvement (e.g., barrier removal) as an integrated control strategy (Russell et al. 2012b; Harris et al. 2014; Götz and Janik 2015).

Stressors with relatively high effects scores and moderate likelihoods of increasing in prevalence over the next decade included poor water quality and bycatch. Although improved water quality has enhanced salmon stock status in many English rivers over the last 50 years (Mawle and Milner 2003), concerns about the impacts of poor water quality on the passage of smolts and adult salmon through...
estuaries exist (Hugman et al. 1984), especially given the potential for synergistic effects in combination with other stressors including climate change (Teichert et al. 2016). Measures to alleviate poor water quality impacts have been implemented under the EU’s Water Framework and Marine Strategy Framework Directives, which aim to safeguard the good ecological status of aquatic ecosystems (EC 2000, 2008, 2017). Maintaining established water quality standards and ensuring that adequate controls are placed on construction schemes (e.g., timing restrictions and regular water quality monitoring; DECC 2011) is essential to minimise impacts on salmon stocks in estuaries and nearshore waters in the future. Salmon are taken as bycatch in high-seas pelagic fisheries targeting other species (ICES 2006, 2014), but these losses are considered nominal at present (ICES 2017b). Nevertheless, bycatch rates could increase over the next decade because of climate-related geographic shifts in pelagic fish distribution. Less is known about the bycatch of returning adults in estuarine and nearshore fisheries, and local concerns were expressed over possible impacts on salmon. Some mitigation measures have been established to restrict salmon bycatch (e.g., seasonal fishing restrictions and mesh size limits), but enhanced monitoring and regulation are required to minimise incidental captures in non-target fisheries.

All the other stressors considered were assessed to have relatively low effects on English salmon stocks at present, but differences existed in their potential prevalence over the next decade. These included marine renewable energy installations (tidal barrages and lagoons) that have become the focus for ‘green’ energy generation and EMF closely related to their development (EC 2009; DECC 2009). Tidal barrages were assessed to pose a larger risk to salmon than tidal lagoons due to their higher future development and lower mitigation potentials. Electromagnetic fields appeared to be a relative minor issue for salmon due to effective measures and transient nature of possible impacts. Given the growing interest in marine renewable energy installations, the effects of impingement and thermal discharge from power stations on salmon were expected to increase less rapidly in the future than in the past. Invasive non-native species and ALAN both had low impacts on salmon given the lack of documented effects in the marine environment, with a moderate-to-high likelihood of becoming more prevalent over the next decade. Noise pollution from pile-driving had a high likelihood of increasing in prevalence over the next decade. Impacts are, however, likely to be low because of the poor hearing sensitivity of salmon (Hawkins and Popper 2014), transient nature of their migration (Klemetsen et al. 2003), and the wide range of mitigation measures available (e.g., noise free periods, soft-start procedures, and acoustic barriers; JNCC 2010). Fisheries exploitation and salmon mariculture were considered to pose a relatively small threat to English salmon stocks at present, with salmon mariculture having a greater likelihood of development over the next decade. However, it is expected that mitigation measures to control fisheries exploitation and salmon mariculture will continue to emerge (Cefas et al. 2019b; Lekang et al. 2016). Identifying the impacts of salmon mariculture on wild salmon stocks is an area of ongoing investigation (NASCO 2021), which requires further progress towards achieving the international goals of effective sea lice management and the containment of farmed fish in production facilities (ICES 2016; NASCO 2016).

Stressor impacts vary depending on salmon life stage (Smialek et al. 2021; Thorstad et al. 2021). As autumn migrating parr can reside in the lower reaches of rivers and estuaries for extended periods of time (October–April) before migrating to sea as smolts in the spring (Pinder et al. 2007; Riley et al. 2009), they will likely be exposed to some potential stressor effects for longer durations than life stages undertaking more transient migrations. Autumn migrating parr have been found to be important stock components in some rivers on both sides of the North Atlantic (Cunjak et al. 1989; Pinder et al. 2007; Riley et al. 2009), but their significance is unknown in others where it has not been assessed. Smolts transiting through the tidal reaches of rivers and estuaries for one day to several weeks during spring and early summer could be subject to potential stressor effects for relatively short durations (Thorstad et al. 2012a). In contrast, post-smolts and adult salmon moving over large geographic areas through estuaries, nearshore waters, and the open ocean for one or more years are likely to be exposed to potential stressor effects for comparatively long durations (Hansen et al. 2003; Klemetsen et al. 2003).

Differences existed in the stressors considered and the scoring approach used to assess their impacts.
on salmon stocks in England and Norway. The present assessment focused solely on marine stressors impacting English salmon stocks, whereas Forseth et al. (2017) considered stressors operating across freshwater and marine environments in Norway. In terms of the scoring approach, the present assessment combined evidence from the literature review and expert local knowledge instead of only relying on expert judgement. Nevertheless, a broad comparison of stressor impacts is possible because both assessments were informed by a 2-D classification system with similar principles. Escaped farmed salmon and sea lice were assessed to have the biggest impacts on Norwegian salmon stocks at present and in the future given the scale of the mariculture industry there. In contrast, no salmon mariculture facilities exist in England, and therefore the risks from escaped farmed salmon and sea lice were considered low. In Norway, climate change and predation were assessed as having relatively low impacts on salmon stocks compared to the results of the present assessment. This could be due to latitudinal effects and the presence of strong evidence on the key stressors in Norway, thereby lowering climate change and predation scores in the overall ranking, as well as high uncertainty on their projected development. However, both assessments agreed that fisheries exploitation at present rates posed a relatively small threat to salmon stocks given the effective controls imposed.

Six caveats should be noted in relation to the present review. First, not all the marine stressors potentially impacting salmon were considered. For example, trophic cascades, disease outbreaks, parasites, marine plastics, and pharmaceuticals were not considered because they were not deemed to be important anthropogenic factors impacting salmon survival at sea. Second, stressor impacts were broadly scored for smolts and adult salmon. Partitioning these scores into finer time intervals during the migratory phase might have provided better insight into stressor impacts. Third, determining stressor impacts at the population-level was challenging because studies tend to focus on the biological responses of individuals or groups rather than entire populations. Fourth, knowledge on the effects of seven out of thirteen stressors was classified as poor and the uncertainty of the future development high, therefore it is inevitably difficult to draw firm conclusions about the impacts of these stressors. Fifth, stressor scores were semi-quantitative based on evidence from the literature review, local fisheries officers, and expert judgement. Although a more quantitative classification would be preferable, the limited amount of data available for all salmon stocks makes this an unrealistic aspiration. Sixth, evaluation of synergistic and additive stressor effects was beyond the scope of the present review, but this remains an important consideration in the long-term sustainability of salmon stocks (Russell et al. 2012a; Wright et al. 2017; Hodgson et al. 2019). Despite these caveats, the present review identified climate change and predation as the most important threats to English salmon stocks in the marine environment, thereby contributing to a growing body of evidence that suggests broad-scale environmental factors are key drivers of the reductions in the marine survival of salmon.

An important next step for research is to understand better how the synergistic and additive effects of multiple stressors impact salmon across aquatic ecosystems (Sobocinski et al. 2018; Hodgson et al. 2019). Salmon are subjected to multiple stressors at differing spatial and temporal scales, and stressor exposure at one life stage can have subsequent implications later in life and can have inter-generational effects, thereby altering life-history traits and population-level processes (Cline et al. 2019). It is well established that stressors acting in fresh water, including altered temperature regimes, migration obstacles, and contaminants, can have ‘carry-over’ effects on smolt physiological development, post-smolt behaviour, sea survival, growth, and homing ability (McCormick et al. 2009). A reduction in stressor impacts throughout the salmon life cycle is therefore crucial. A priority for the future is to develop an integrated management approach that addresses both anthropogenic and natural drivers of change, including complex interactions and cumulative effects, at the ecosystem level (Wells et al. 2020). Knowledge gaps and uncertainties are evident for all the stressors considered in this review. The prioritisation of evidence needs to address these stressors is challenging, not least because the scale and extent of the stressors varies over time. New evidence is constantly emerging, so it will be essential to maintain a watching brief of future developments. Research should focus both on how better to address and mitigate prominent stressors at present and on those stressors for which
knowledge is limited and are likely to expand in severity and/or extent in the future.

Conclusion

The findings from this review can aid in the prioritisation of management actions and to direct future research to protect and restore salmon stocks. It is clear that the nature, severity, and extent of the stressors impacting the marine survival of salmon are location and time specific. Management actions should therefore focus on alleviating locally operating stressors that reduce the number and condition of smolts entering the ocean. In England, the stressors assessed to have the largest impacts on salmon stocks in the marine environment are climate change and predation. Although tackling both these stressors is and will remain challenging, targeted management actions to alleviate the highest-impact stressors in estuaries and to ensure freshwater habitats remain suitable to sustain salmon stocks are possible. Salmon have persisted for millennia by adapting to environmental change, but the present rate of environmental change is unprecedented (ICES 2017b). Safeguarding as many returning adults as possible to provide more time for salmon populations to adapt to environmental change has therefore never been more important. Future research should address knowledge gaps on expanding stressor impacts from climate change, predation, renewable energy developments, and artificial light at night, as well as possible synergistic effects. The findings from this review are relevant to other diadromous species of fish and lamprey, given that these have similar life traits involving migrations through aquatic ecosystems and exposure to multiple anthropogenic pressures. The semi-quantitative 2-D classification system used in the present review to rank stressor impacts on salmon represents a useful tool with which to prioritise research and management initiatives, and it is an approach that can be readily transferred to other species and systems (Forseth et al. 2017). To provide a more detailed overview of different threats and help prioritise conservation efforts at appropriate spatial and temporal scales, it is recommended that a dynamic ecosystem-based assessment be developed with which to evaluate regularly, as new evidence emerges, the cumulative risks across ecosystem components and salmon life stages.

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Availability of data and material Raw data presented at regional scale are available in the Supplementary Information.

Declarations

Conflict of interest There are no conflicts of interest to report.

Consent to participate All the authors agree with the contents of the manuscript and give their consent to submit.

Consent for publication This work is original research carried out by the authors and all of us agree with its submission in the present form to the journal. The manuscript is not currently under consideration in another journal. The consent has also been obtained from the responsible authorities at Cefas, where the work has been carried out (internal QA).

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