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The early marine distribution of Atlantic salmon in the North-east Atlantic: A genetically informed stock-specific synthesis

John Gilbey[1] | Kjell Rong Utne[2] | Vidar Wennevik[2] | Alexander Christian Beck[2] | Kyrre Kausrud[3] | Kjetil Hindar[4] | Carlos Garcia de Leaniz[5] | Corrine Cherbonnel[6] | Jamie Coughlan[7] | Tom F. Cross[7] | Eileen Dillane[7] | Dennis Ensing[8] | Eva García-Vázquez[9] | Lars R. Hole[10] | Marianne Holm[2] | Jens Christian Holst[11] | Jan Arge Jacobsen[12] | Arne J. Jensen[4] | Sten Karlsson[4] | Niall Ó Maoiléidigh[13] | Kjell Arne Mork[2] | Einar Eg Nielsen[14] | Leif Nøttestad[2] | Craig R. Primmer[15] | Paulo Prodöhl[16] | Sergey Prusov[17] | Jamie R. Stevens[18] | Katie Thomas[13] | Ken Whelan[19,20] | Philip McGinnity[7,13] | Eric Verspoor[21]

[1]Marine Scotland Science, Freshwater Fisheries Laboratory, Faskally, Pitlochry, UK
[2]Institute of Marine Research, Bergen, Norway
[3]Norwegian Veterinary Institute, Oslo, Norway
[4]Norwegian Institute for Nature Research (NINA), Trondheim, Norway
[5]Department of Biosciences, Swansea University, Swansea, United Kingdom
[6]GENINDEXE, La Rochelle, France
[7]Aquaculture & Fisheries Development Centre, School of Biological, Earth and Environmental Sciences, University College, Cork, Ireland
[8]Fisheries and Aquatic Ecosystems Branch, Agri-Food and Biosciences Institute Northern Ireland, Belfast, UK
[9]Department of Functional Biology and Genetics, Universidad de Oviedo, Oviedo, Spain
[10]Division of Oceanography and Maritime Meteorology, Norwegian Meteorological Institute, Bergen, Norway
[11]Ecosystembased AS, Hosteland, Norway
[12]Faroe Marine Research Institute, Tórshavn, Faroe Islands
[13]Marine Institute, Mayo, Ireland
[14]Section for Marine Living Resources, National Institute of Aquatic Resources, Technical University of Denmark, Silkeborg, Denmark
[15]Organismal & Evolutionary Biology Research Program, University of Helsinki, Helsinki, Finland
[16]Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Belfast, Ireland
[17]Polar branch of "VNIRO" ("PINRO" named after N.M.Knipovich), Murmansk, Russia
[18]Hatherly Laboratories, Department of Biosciences, College of Life and Environmental Sciences, University of Exeter, Exeter, UK
[19]Atlantic Salmon Trust, Perth, UK
[20]School of Biology and Environmental Science, University College Dublin, Dublin, Ireland
[21]Rivers and Lochs Institute, Inverness College, University of the Highlands and Islands, Inverness, UK

Philip McGinnity and Eric Verspoor Joint senior authors.

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Correspondence
John Gilbey, Marine Scotland Science,
Freshwater Fisheries Laboratory, Faskally,
Pitlochry PH16 5LB, UK.
Email: John.Gilbey@gov.scot

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Abstract

The survival of Atlantic salmon (*Salmo salar*), an increasingly rare anadromous species, has declined dramatically during its marine phase, with disproportionate impacts on the poorly understood early post-smolt period. Logistical constraints on collecting oceanic data to inform this issue pose a formidable obstacle. To advance understanding of post-smolt distributional ecology in the North-east Atlantic, a comprehensive analysis of existing information was undertaken. Data were synthesized from 385 marine cruises, 10,202 individual trawls, and 9,269 captured post-smolts, spanning three decades and ~4.75 million km^2 of ocean, with 3,423 individuals genetically assigned to regional phylogeographic origin. The findings confirm major migrational post-smolt aggregations on the continental shelf-edge off Ireland, Scotland and Norway, and an important marine foraging area in the Norwegian Sea. Genetic analysis shows that aggregational stock composition does not simply reflect distance to natal rivers, with northern phylogeographic stock groups significantly under-represented in sampled high-seas aggregations. It identifies a key foraging habitat for southern European post-smolts located in international waters immediately west of the Vøring Plateau escarpment, potentially exposing them to a high by-catch mortality from extra-territorial pelagic fisheries. Evidence of the differential distribution of regional stocks points to fundamental differences in their migration behaviours and may lead to inter-stock variation in responses to environmental change and marine survival. The study shows that understanding of post-smolt marine ecology, as regards to stock-specific variations in habitat utilization, biological performance and exposure to mortality factors, can be significantly advanced by data integration across studies and exploiting genetic approaches.

KEYWORDS
genetic stock identification, marine distribution, migration behaviour, pelagic trawls, post-smolts, *Salmo salar*

1 | INTRODUCTION

Existing knowledge of the ecology of fish species in the marine environment remains insufficient for effective conservation management, particularly for small, rare, wide-ranging oceanic species or life-history stages (Appeltans et al., 2012; Powles et al., 2000), including the marine phases of anadromous salmonid fish (Drenner et al., 2012). However, the marine environment poses a formidable logistical and methodological challenge to gaining ecological knowledge, given its spatial scale, spatiotemporal heterogeneity and dynamism, and the vast distribution scales of many species. Furthermore, early life stages of many species are often effectively cryptic, being small, rare in occurrence, migratory and occurring within pelagic complexes of other more abundant species, all of which can make them difficult to locate and sample. Almost universally, these factors place practical, and often insurmountable, constraint on the quantity (e.g. locations and sample sizes) and quality (e.g. spatial–temporal representativeness) of primary as well as ancillary (e.g. environmental) data that can be collected. Yet, effective management requires understanding of the factors underlying changes in distribution, abundance and marine survival (Gattuso et al., 2018; Poloczanska et al., 2013).

These issues and challenges apply to studies of the marine phase of the Atlantic salmon (*Salmo salar*, Salmonidae), an anadromous salmonid. Though dominant in North Atlantic rivers, at least historically, during its marine phase it is a relatively rare species of the North Atlantic pelagic zone, both in terms of its numbers and biomass (Chaput, 2012). Moreover, it has become even rarer over the last three decades, with increasing marine mortality leading to major and progressive declines in numbers of adults returning to rivers (Chaput, 2012; ICES, 2021). Additionally, the species encompasses large numbers of reproductively and biologically distinct populations (Bourret et al., 2013; King et al., 2001, 2007), whose marine distributions may be variously distinct, such that river stock and population-level insight are essential for their effective conservation and management. Yet, though otherwise

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extensively studied, understanding of Atlantic salmon marine ecology remains limited and patchy (Thorstad et al., 2011). This is particularly true in respect to factors that underlie current declines in marine survival (Crozier et al., 2018), the impacts of climate change (Todd et al., 2011), and differences among regional stock groups in their marine ecology (Webb et al., 2007). To begin to address, these questions require a full understanding of where post-smolts do and do not occur, distributional differences among river and regional stock groups, and how their marine habitats are changing (Crozier et al., 2018).

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1.1 | Current understanding of Atlantic salmon marine ecology

After spending 1–8 years in freshwater, Atlantic salmon migrate into the North Atlantic from thousands of geographically dispersed rivers in western Europe and eastern North America, spanning 30° latitude (Thorstad et al., 2012), each river having its own genetically distinct stock and larger rivers encompassing multiple genetically distinct populations (King et al., 2007). Their migration starts with juveniles changing physiologically into smolts ready to cope with sea water, moving downstream and leaving natal rivers in the spring or early summer (Thorstad et al., 2011). In more southerly rivers, migration begins at a younger age and earlier in the season than those from more northerly populations (Jonsson & Jonsson, 2007; Otero et al., 2014), where the critical sea temperature (~8°C; Hvidsten et al., 1998) is reached later in the season (Thorstad et al., 2012).

Having left rivers they are referred to as post-smolts, a life-history phase typically defined as the period between the first entry into the marine environment and the middle of their first winter at sea; for stock assessment purposes, this is on the 31st of December of the same year (ICES, 2019a). During this phase, at least initially reflecting the geographical distribution of their rivers, they are distributed in the North Atlantic coastal zone such that there is considerable variability in the environments experienced by each river stock. What is known indicates that over time they become increasingly focussed in particular northern marine areas in the eastern and western Atlantic (Dadswell et al., 2010; Holm et al., 2004; Holst et al., 1993). However, some anadromous stocks have more restricted migrations such as those from rivers in Baltic Sea, in the eastern Atlantic, and in the Inner Bay of Fundy, in the western Atlantic (Webb et al., 2007). For salmon stocks from non-Baltic European rivers, in their first year at sea, it appears they migrate to feeding areas in the North-east Atlantic (Friedland, 1998; Holst et al., 2000), while those from North America are indicated to migrate to the Northwest Atlantic (Dadswell et al., 2010).

Marine survival of many river stocks has declined dramatically in recent decades, particularly in the southern parts of the species distribution, and is likely to be underpinned by multiple factors. These likely include changes in smolt size and time of sea entry, predation and parasites, distribution, aquaculture interactions, growth, age at maturity, by-catch, competition and climate—the so-called "likely suspects" (Crozier et al., 2019; Jonsson & Jonsson, 2004; Mills et al., 2013; Nicola et al., 2018). However, which factors are actually involved, to what extent, and where in the marine phase they operate, remains unclear and controversial (Crozier et al., 2018; Flávio et al., 2020; Limburg & Waldman, 2009; Parrish et al., 1998), with some studies suggesting that a large part of the increase in mortality is driven by inshore, estuarine and, even within river conditions (Crozier et al., 2018; Flávio et al., 2020; Limburg & Waldman, 2009; Parrish et al., 1998).

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Once in the marine environment, general considerations of life-history processes point to the early marine post-smolt phase being more susceptible to, and responsible for, a disproportionate share of marine mortality (Friedland, 1998; Thorstad et al., 2012). This stage starts with juveniles having undergone a profound physiological adjustment to a different osmoregulatory environment (Stefansson et al., 2008) and commencement of an oceanic feeding migration of one or more years (Youngson & Hay, 1996). In later marine stages, being fully physiologically adjusted to the marine environment, more experienced and larger relative to co-habiting species, they can be expected to be less vulnerable to typical mortality factors such as starvation and predation (Chaput, 2003; Peyronnet et al., 2007; Potter et al., 2003). However, relatively little is actually known about the extent that mortality at the post-smolt stage defines overall decreases in marine survival and the importance of different proximal factors (Crozier et al., 2018).

1.2 | Extending current understanding of post-smolt distributional ecology

Extending current understanding poses a major challenge. Oceanic studies are hindered by logistical difficulties of geographical scale and environment, and of sampling what at the post-smolt stage constitutes a small, rare species, with the latter now exacerbated by their decreasing marine abundance. As such, this makes it crucial to extract the maximal insight from existing data and archival material, including the exploitation of new and innovative analytical approaches.

Historically, insight into post-smolt distributional ecology has been largely gained by methods such as the recovery of physical tags at sea (Drenner et al., 2012; Maoiléidigh et al., 2018) and the reading of scales of returning adult fish caught in local coastal and in-river fisheries (Friedland, 1999; Friedland & Haas, 1996; Hubley et al., 2008; Peyronnet et al., 2007). However, the former is generally limited in the number of stocks and individuals that can practically be tagged, low recovery rates, and tags not providing information on the fish that die (Chaput, 2012), while scale reading provides no insight into where an individual has been in the ocean. Some insight into the latter question can be gained geolocation archival tags (e.g. Strøm et al., 2018) and for scales from stable isotope analysis (e.g. Hanson et al., 2013; MacKenzie et al., 2011). More recently, genetic stock identification (GSI) methods, which can quantify the contribution of different phylogeographic groups to fisheries (Bradbury et al., 2018; Layton et al., 2020; Shaklee et al., 1999), have begun to be used to characterize the spatial–temporal distribution of stocks at different marine stages, including the post-smolt stage (Jacobson et al., 2020).

Knowledge of marine distribution and ecology of salmon in the North-east Atlantic has been advanced significantly in the past by the investigation of the spatial patterns of post-smolt catches derived from trawl data (Haugland et al., 2006; Holm et al., 2000,2003; Holst et al., 1993,2000; Shelton et al., 1997), as well as diet analysis (Haugland et al., 2006; Jacobsen & Hansen, 2001; Utne et al., 2020) but no comprehensive, up-to-date analysis of general capture data exists that covers both research cruises and commercial fishing vessels. Neither do any existing studies encompass GSI methods to provide a large-scale stock-specific account of post-smolt distribution. This technique is now routinely used in commercial fishery management (e.g. Araujo et al., 2014; Beacham et al., 2004,2006,2012; Casey et al., 2016; Dahle et al., 2018; Gilbey et al., 2017; Ovenden et al., 2015; Ruzzante et al., 2000; VanDeHey et al., 2009) and has numerous applications in the conservation and management of Atlantic salmon (Verspoor et al., 2007 and references therein). However, the basis for undertaking such a study has been developed over recent years. Genetic baselines have been created and validated for the assignment of salmon to both continent of origin (Gilbey et al., 2017; Sheehan et al., 2010) as well as to regional phylogeographic groups, in both Europe (Ellis et al., 2011; Gilbey et al., 2018) as well as North America (Bradbury et al., 2018; Jeffery et al., 2018). These now make it possible to exploit GSI and the large collection of archived post-smolt tissues and provide the first stocks-specific account of post-smolt distributional ecology in the North-east Atlantic.

Distributional differences among North American and European post-smolt stocks at a trans-Atlantic level, with each restricted to their respective sides of the Atlantic, have been evidenced by tagging studies (Dadswell et al., 2010). However, little is known about how post-smolt distributions vary among regional stock groups within these regions (Bradbury, Hamilton, Chaput, et al., 2016; Bradbury, Hamilton, Sheehan, et al., 2016; Gilbey et al., 2017; Harvey et al., 2019; Jeffery et al., 2018; Olafsson et al., 2015). Tagging studies have revealed some variation among regional phylogeographic groups that goes beyond just differences in the geographical locations of their rivers of origin. The most striking examples are the Baltic Sea and Inner Bay of Fundy stocks (Webb et al., 2007), while smaller scale regional differences have been observed among regional stocks within the Baltic Sea (Jacobson et al., 2020) suggesting they are also likely to occur elsewhere.

Understanding the nature of these variations can be advanced by placing observed fish distributions into an ecological and evolutionary context and collecting data to test emergent distributional hypotheses. The marine distributions of Atlantic salmon stocks will reflect evolved behaviours that lead them to migrate to habitats that provide access to optimal feeding for growth and reproduction sufficient to allow populations to be self-sustaining. These may differ due to the historical exposure to different environmental conditions and involve two linked and potentially overlapping evolved behaviours—migration and foraging. Migration involves directed movement of individuals to a predictable historically favourable habitat for completion of its life-cycle, for example to feed or breed, and foraging is behaviour directed at finding food (Dingle & Drake, 2007). However, transient foraging may occur during migration and locational change during foraging.

The marine phase of most Atlantic salmon stocks appears to encompass a series of seasonal bouts of migration and feeding prior to

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their return migrations to natal rivers that dictate their marine distributions. These migrations will be conditioned by spatiotemporally variable (Friedland et al., 2005,2014; Mork et al., 2012) contemporary environmental factors (e.g. currents, temperature, prey and predator abundance). However, they will also be defined by evolved migration behaviours that are likely to differ among stocks due to their having geographically different evolutionary histories (e.g. Cauwelier, Verspoor, et al., 2018; Finnegan et al., 2013; Olafsson et al., 2014).

Many aspects of the ocean environment conditions are spatial and temporally variable. However, some key aspects will have been relatively temporally and spatially stable over evolutionary time frames, of hundreds to thousands of generations, and provide a basis for adaptive evolution of migratory behaviour, facilitated by, for example, magnetoreception (Naisbett-Jones et al., 2020; Putman et al., 2020) to target optimal marine habitat areas for migration and feeding. Furthermore, where such habitats occur in multiple areas, the potential exists for different phylogeographic groups to have different migratory pathways and destinations. One example of such a habitat area appears to be the system of currents in the Norwegian Sea (e.g. the system of currents in the Norwegian Sea, Mork et al., 2012) in which gyres mix warm Atlantic and cold Arctic waters, generating a hot-spot in marine productivity and to which the migratory behaviour of salmon could have evolved to bring fish from some areas, leading to the formation of both migrational and foraging aggregations. The former constitute groups of individuals that move along a common pathway towards a target habitat, and the latter co-located groups whose primary focus is foraging, and may also be conditioned by evolved congregational behaviour (the attraction of conspecifics to each other) driven, for example, by the advantage of shoaling for predator protection (Hoare et al., 2000; Pitcher, 1986; Szulkin et al., 2006; van Noordwijk et al., 2006). Due to their differing focus, migration or foraging aggregations will be fundamentally different in respect of where and when they occur and in the physical, chemical and biological nature of their environments.

1.3 | Study aims and objectives

The current study seeks to advance understanding of Atlantic salmon post-smolt ecology through its four specific objectives. The first was to synthesize and analyse available data from research and commercial trawling in the eastern part of the area covering the last three decades, excepting Icelandic marine areas and establish where post-smolts do and do not occur. The second was to exploit the genetic baseline of Gilbey et al. (2018) and archival tissues from post-smolts caught in the area during this period to provide an account of the spatial and temporal distribution of post-smolts for different identifiable phylogeographic stock groups. The third was to integrate the findings from these two analyses and consider them within a conceptual evolutionary migrational framework (Dingle & Drake, 2007) to gain insight into post-smolts distributional ecology in the study area and more generally. The fourth and final objective was to consider the management implications of the findings in respect of the oceanic habitat domains utilized by post-smolt salmon, and their environmental dynamics that are likely to condition post-smolt marine survival (Crozier et al., 2018).

2 | MATERIALS AND METHODS

2.1 | Cruise and trawl data

Information on post-smolt captures was compiled from pelagic research cruises and commercial catches from 1991 to 2019

TABLE 1 Overview of cruise and trawl numbers by country and organization

Organization	Country	Ship Type	Start	End	Cruises	Trawls
Faroe Marine Research Institute	Faroe Islands	Research Vessel	1995	2019	64	909
Fisheries Research Services (now Marine Scotland)	Scotland	Research Vessel	1996	1997	2	14
Marine Institute	Ireland	Research Vessel	2007	2009	7	61
University of Bergen/Institute of Marine Research	Norway	Research Vessel	2004	2016	15	627
Institute of Marine Research	Norway	Research Vessel	1993	2018	159	6,356
University of Tromso/Norwegian College of Fisheries Science	Norway	Research Vessel	2002	2009	7	87
Knipovich Polar Research Institute of Marine Fisheries and Oceanography	Russia	Research Vessel	1998	2014	14	110
Commercial (under research charter)	Russia	Fishing Vessel	2002	2017	21	
Commercial (under research charter)	Norway	Fishing Vessel	1991	2018	94	2,036
Commercial	Norway	Coastal nets	2017	2017	1	1
Commercial	Iceland	Fishing Vessel	2009	2009	1	1
Total			**1991**	**2019**	**385**	**10,202**

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encompassing 385 cruises carried out by institutions from Norway, Scotland, Russia, Faroe Islands, Ireland and Iceland totalling 10,202 separate trawls (Table 1). This comprised cruises carried out by both dedicated research vessels and commercial trawlers under charter for research purposes, including both targeted salmon research projects and annual systematic pelagic surveys, together with commercial by-catches. Full cruise information can be found in Supplementary Table S1. A variety of gear and trawl specifications were used, and most hauls were performed with the Åkra, Harstad or the Multpelt 832 trawls (Holm et al., 2000; ICES, 2013).

The survey data encompassed trawls carried out in the surface zone considered capable of catching post-smolt salmon since, on leaving their rivers, post-smolts are mainly found in the surface layers of the open sea (Guðjónsson et al., 2015; Holm et al., 2006). This consideration meant that trawls included in the present study had a maximum depth of the ground rope of 50 m (where depth data was available). The vertical openings of the trawls were up to 35 m, and setting a depth range of up to 50 m ensured that all surface trawls were included, even if they were below the surface in parts of the trawl haul. This limit prevented analysis of effort to be impacted by large numbers of deep trawls that were very unlikely to capture post-smolts. However, in a small number of cases smolts were captured at greater depths and so any reported trawl hauls catching salmon with a maximum trawl depth of more than 50 m were also included. For cruises which were targeted specifically to catch post-smolt salmon, data from all trawls were used, as was all data from data sets consisting of only salmon capture observations. All data were also used from trawls where salmon had been caught, but depth information was lacking, and/or salmon had been captured by any method by commercial fishing vessels. Where available, these data include both trawls which caught salmon and, just as importantly, trawls that did not. Full trawl information is detailed in Supplementary Table S2.

2.2 | Fish observations and samples

Salmon were identified after capture in trawls during haul inspections by expert observers. Numbers of salmon per trawl were recorded together with trawls with no captures. Recording of other fish data varied among the various cruises. In many cases, scales were taken and used to age fish, while sex was determined by dissection and visual observation. Fork lengths were also recorded and fin tissue samples were taken, primarily on research cruises, and stored in ethanol for later genetic analysis.

2.3 | Identification of post-smolts

The synthesis focussed on post-smolt salmon, a stage defined as starting when an individual enters the ocean and ends on the 31st of December of the same year (ICES, 2019a). In order to identify the post-smolts fish which had been aged by scale reading were used to create length frequency distributions of the different age classes of fish within each month of capture. These distributions were then used to assign ages to fish with no scale data. Upper length bounds for post-smolts, based on known scale-aged fish sizes, were determined by month over all years and larger fish excluded from the analysis.

2.4 | Assessment of overall distribution and its association with environmental variables

The overall distribution and distributions of post-smolts from different assignment units were assessed in relation to ocean currents, marine bathymetry and sea surface temperature (SST). The ocean current information used is described in Orvik and Niiler (2002) and Skagseth et al. (2008) and broader-scale currents in Dadswell et al. (2010). Sea surface temperature data were derived from European Centre for Medium-Range Weather Forecasts (ECMWF) and are focussed on monthly averages. For the period 1979-present (the satellite era), they are ECMWF ERA5 reanalysis of data for the area of interest in respect of ~30 km grid squares. For the period 1900–1978, we used the ERA20C reanalysis on a 125 km grid, produced with the Integrated Forecast System of the ECMWF. For convenience, the ERA20C data were interpolated to the ERA5 grid.

2.5 | Genetic stock identification (GSI)

GSI was used to determine the phylogeographic region of origin of post-smolts for which tissue was available. Genotyping was carried out at the Norwegian Institute of Marine Research, University College Cork (Ireland), Marine Scotland Freshwater Fisheries Laboratory, and Icelandic Fisheries Laboratories, and standardized among the laboratories (Ellis et al., 2011). Individual assignments were made using ONCOR (Kalinowski et al., 2007) with probabilities to reference baseline phylogeographic units calculated by the method of Rannala and Mountain (1997) using an assignment probability cut-off of 0.8. Fish not meeting this criterion were considered unassigned (Gilbey et al., 2018).

The continental origin of individual post-smolts was first determined using the North American/European six microsatellite reference baseline (Gilbey et al., 2017). European fish were then assigned to their phylogeographic group of origin by means of an inter-laboratory calibrated 14 microsatellite assignment panel (Ellis et al., 2011; Olafsson et al., 2010) and a comprehensive European baseline (Gilbey et al., 2018; Figure 1), including in the analysis only fish having at least 10 loci successfully genotyped. The baseline encompassed 26,822 individual salmon from 13 countries, 282 rivers and 467 sampling sites. Individual assignments were made at two levels of resolution. At Level 1, fish were assigned to one of three top genetically defined phylogenetic units: Iceland, Northern Europe

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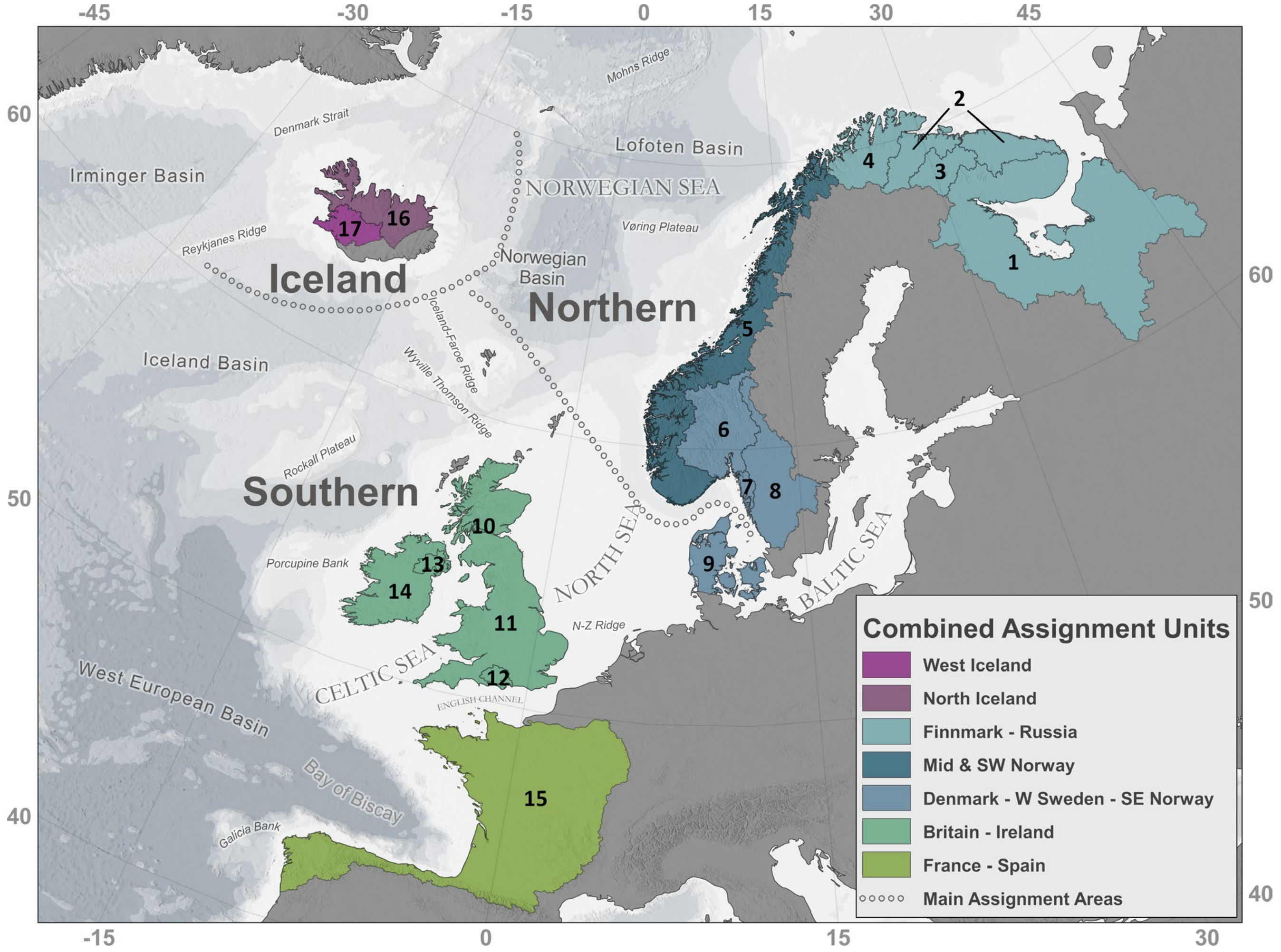

FIGURE 1 Phylogeographic assignment groups used for genetic assignment of European fish. Top level assignment units delineated by dotted lines. Assignment units used for individual assignment from Gilbey et al., (2018) denoted by numbers: 1 White Sea, 2 Kola, 3 Kola—Tuloma Basin, 4 Finnmark, 5 Mid & SW Norway, 6 SE Norway, 7 Enningdalselva, 8 W Sweden, 9 Denmark (non-Baltic), 10 Leven, 11 Britain, 12 English chalk streams, 13 Bann, 14 Ireland, 15 France & Spain, 16N Iceland, 17W Iceland. Combined regional assignment units used for mixed stock analysis denoted by colours

and Southern Europe. Level 2 assignments were then made to the 17 lower level phylogeographic units (Gilbey et al., 2018; Figure 1).

The 17 genetically based reporting groups from Gilbey et al. (2018) were further combined into seven broader regional phylogeographic groups (Figure 1) to assess stock distribution in relation to production. These groups were as follows: (1) France and Spain, (2) Britain and Ireland, (3) Denmark, West Sweden and Southeast Norway; (4) Mid and Southwest Norway, (5) Finnmark, Kola, and White Sea, (6) North Iceland and (7) West Iceland. These groups were based on direct or indirect phylogeographic/phylogenetic inferences outlined in a number of recently published reports. Groups 1 and 2—France/Spain and Britain/Ireland are based on the original assignment units of Gilbey et al. (2018); Group 3—Denmark/Sweden/SE Norway was supported by evidence from physical satellite tagging indicating that fish from this area move northward along the Atlantic coastline as post-spawning adults (Strøm et al., 2019); Group 4—Mid-SW Norway (Wennevik et al., 2019); Group 5—Finnmark/Kola/White Sea—Barents Sea (Tonteri et al., 2009; Wennevik et al., 2019); Group 6—North Iceland (Gilbey et al., 2018; Olafsson et al., 2014); Group 7—West Iceland (Gilbey et al., 2018; Olafsson et al., 2014).

Proportions of fish for each assignment unit overall, and in different marine areas, were estimated using Mixed Stock Analysis (MSA), for genotyped fish both at Level 1 (Iceland, Northern, Southern) and at the seven combined assignment units. A power analysis was performed using the R package *rubias* (Moran & Anderson, 2018) to test MSA assignment accuracy for the seven combined units (full details in Supplementary data—GSI). For each marine area, MSA proportions were determined using the conditional maximum likelihood method implemented in ONCOR and 95% confidence intervals estimated using 1,000 bootstraps. MSA was performed using all genotyped smolts across all years and also separately for the different aggregations of smolts observed. Marine aggregation boundaries were defined empirically as suggested by the data.

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2.6 | Estimates of North-east Atlantic smolt production

Stock proportions from the top phylogeographic Level 1 (Iceland, Northern, Southern) and seven combined regional groups were estimated using MSA, and compared to proportions expected based on the production of wild fish, to determine the nature and extent of deviations from expectations within aggregations. Expected relative salmon productivity of the seven regional groups was estimated using (1) rod catches for individual rivers reported by the national salmon management agencies and other bodies, and (2) pre-fisheries abundance (PFA) estimates of returning adult salmon from the Working Group for North Atlantic Salmon (ICES, 2017).

2.6.1 | Estimates based on individual in-river adult rod catches

Annual rod catches of one sea-winter (1SW) and multi-sea-winter (MSW) salmon for individual rivers were combined with counts of fish that were killed and those that were caught and subsequently released (detailed in Supplementary Table S3). Annual rod catches for 2008–2010 were averaged for rivers in Spain, France, Ireland, Northern Ireland, Scotland, England & Wales, Norway, Russia and Finland. These were considered to provide a good approximation of productivity from the different regions caught around the time of the main SALSEA-Merge surveys (Gilbey et al., 2018; Holst et al., 2000). These surveys provided the largest sample of post-smolts used in the genetic analysis.

2.6.2 | Estimates based on ICES pre-fisheries abundance (PFA) evaluations

PFA estimates are reported annually for different stock groups (Supplementary Data S4) by the ICES Working Group on North Atlantic Salmon (ICES, 2017). Reported 10-year average PFA estimates for the period 2007 to 2016 were used, combining counts for one sea-winter (maturing 1SW—i.e. potential 1SW returns) and older multi-sea-winter (non-maturing 1SW, i.e. potential MSW returns).

ICES PFA was allocated to the seven regional phylogeographic assignment groups. The ICES PFA estimate for France was used as a proxy for genetic Group 1, France & Spain. The genetic Group 2, Britain and Ireland, included ICES PFA estimates for Scotland, England, Wales, Ireland and Northern Ireland. The genetic Group 3 was based on estimates of PFA for Denmark and Sweden, and the PFA estimated by the Norwegian Scientific Advisory Committee for Atlantic Salmon (NSACAS) for Southern Norway (Anon, 2019). The Mid-Norway group, genetic Group 4, was estimated using the NSACAS PFA for mid-Norway. The Finnmark, Kola, White Sea area, genetic Group 5, was represented by the NSACAS estimated North Norway (including Tana) PFA combined with the ICES estimates of PFA for Finland and Russia. The proportions of fish that might be expected in the North Iceland genetic Group 6 were determined on the basis of the ICES PFA estimate for North and East Iceland. The South and West Iceland genetic Group 7 was based on the ICES PFA for South Iceland. Full details of the PFA allocation can be found in Supplementary Data S4.

2.6.3 | The relationship between production estimates

The two estimates of post-smolt production for the seven assignment units (Supplementary Data S5) show a strong positive correlation ($r = 0.986$), perhaps not unexpectedly given rod catch is an important data input into the PFA calculation (ICES, 2019a). The level of convergence between the two methods argues that relative post-smolt production is reasonably and accurately reflected by both metrics. However, the ICES PFA model incorporates quite robust computational adjustment to its data inputs and it was decided adjusted PFA would be used to assess differences in expected versus observed (genetically assigned groups of samples of post-smolts captured at sea at different periods and in different locations) proportions of phylogeographic groups in the analysis. This was evaluated using Fisher's exact tests carried out in R (R Core Team, 2015) with *p*-values based on 2000 permutations and the same approach used to assess temporal changes within areas.

3 | RESULTS

3.1 | Post-smolt distribution

The assembled data encompass 10,202 trawls carried out across ~4.7 million km^2 of the NE Atlantic (Figure 3, Supplementary Data S2). Trawl coverage extends latitudinally from 48.75° to 80.28° North and longitudinally from −24.55° West to 56.48° East. The intensity and distribution of the trawls and captures show marked variation, geographically (Figure 2) and temporally (years and months—Figure 3) and captured 10,636 Atlantic salmon across 1,505 of the trawl sets. Full details of trawl, post-smolt and assigned fish numbers are detailed in Supplementary data S6. Scale read ages, length data and month of capture were available for 4,377 fish, and age/length data of these fish used to define the monthly size boundaries for the remaining unaged post-smolts. This screening identified 9,269 post-smolts (Figure 4a, Supplementary Data S7). A detailed breakdown of all trawls and post-smolt captures by year and by month within years is provided in Supplementary Data S8 and S9, with proportional representations of post-smolt captures by month within years in S10.

The relationship between post-smolt numbers and fishing (trawl) catch per unit effort (CPUE) was assessed for each 1° latitude by 1° longitude map grid square containing at least one trawl (Figure 4b). Post-smolt capture distributions and densities were similar for the

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raw data (Figure 4a) and using CPUE (Figure 4b). Along the south-western Norwegian coast, because of the relatively higher intensity of trawls (Figure 2), the CPUE of post-smolt in this area is lower than suggested by numbers alone. However, the CPUE differences to a degree also reflect differences in the types of trawls used. The areas in which the two aggregations occur were predominantly sampled using the Salmon Trawl, including the focussed salmon surveys in the 1990s and 2000s. As it is a much more efficient trawl for post-smolts than the other trawl types, it yields much higher CPUEs all else being equal. Though this means CPUE differences between areas must be used cautiously, observed values probably reflect the broad relative spatiotemporal differences in post-smolts distribution and abundance in the sampled areas.

Across years, the data point to a seasonal spatial shift post-smolt distribution from May to September (Figures 4b and 5). In May, post-smolts occur in relatively large numbers along the shelf-edge off the coasts of Ireland and Scotland as well as along the south west Norwegian coast. In June, they are still seen in these areas but in relatively smaller numbers, particularly along the SW Norwegian coast. During June, despite sampling throughout the study area remaining relatively constant, post-smolt densities are highest in the southern Norwegian Sea around the Vøring Plateau area. Then, in July almost all occur in the Norwegian Sea concentrated in the Vøring Plateau area but also distributed more widely into the northern part of the Norwegian Sea. Additionally, a small number of post-smolts are for the first time also captured off the coast of Finnmark. By August, less fish are captured overall, but post-smolts are still concentrated around the Vøring Plateau area but distributed more broadly across the northern Norwegian Sea. In September, sampling effort shifts mostly to the north and east (Figure 5), making it difficult to establish if post-smolts are still in the central-southern Norwegian Sea but a few are caught in the surveyed area along the edge of the Barents Sea and Norwegian Sea. In October, November and December, effort is even lower but a small concentration of fish occurs just north of the Faroe Islands along the Iceland-Faroes Ridge.

The distribution of effort across areas and months for the different years is highly variable and biased (Supplementary Data S8,S9,S10), making it difficult to discern the true nature and extent

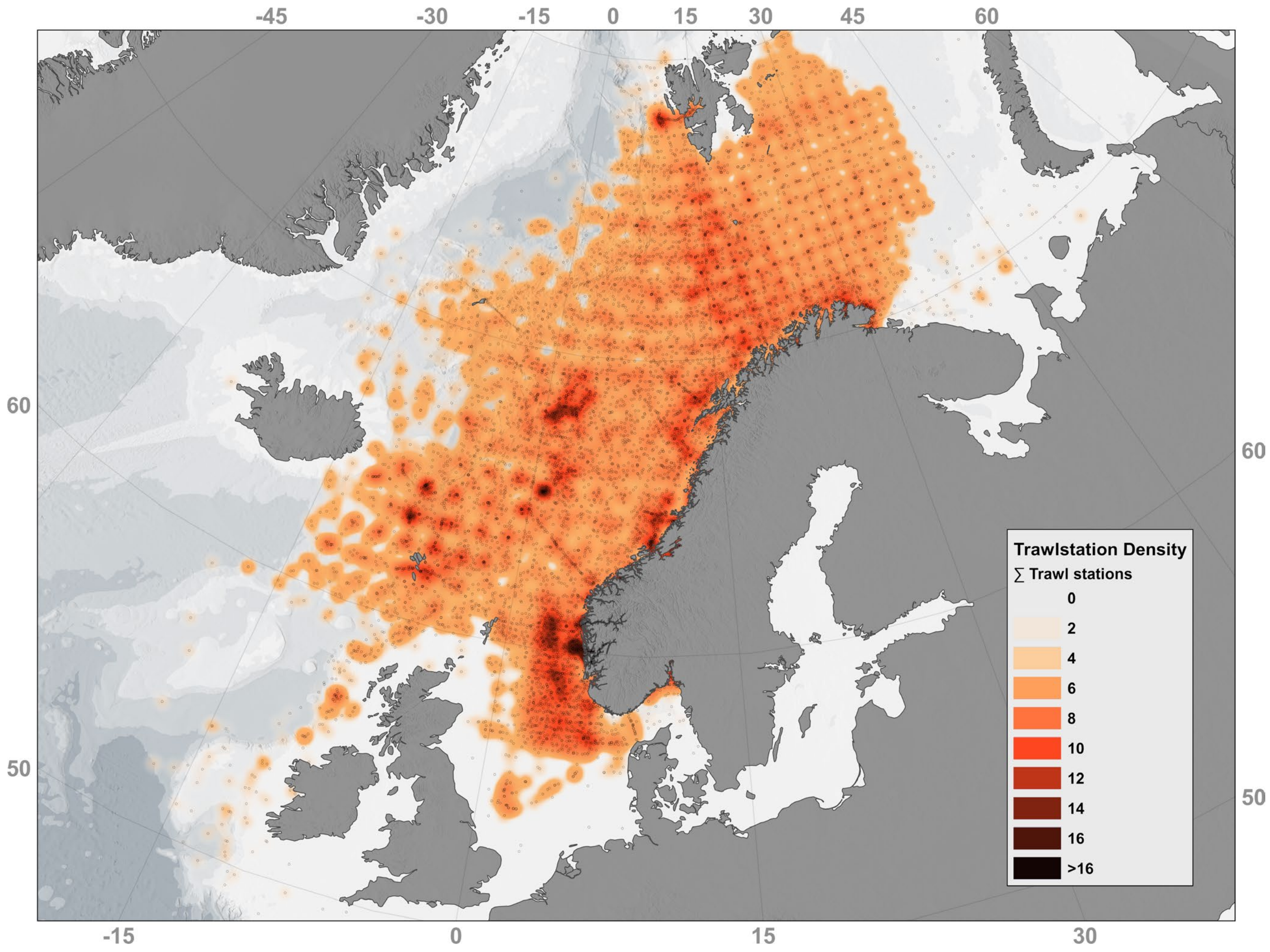

FIGURE 2 Extent and density of trawls included in the analysis. Each point represents a 1° latitude × 1° longitude grid square with densities calculated as mean number of trawls carried out in the grid over the whole data set

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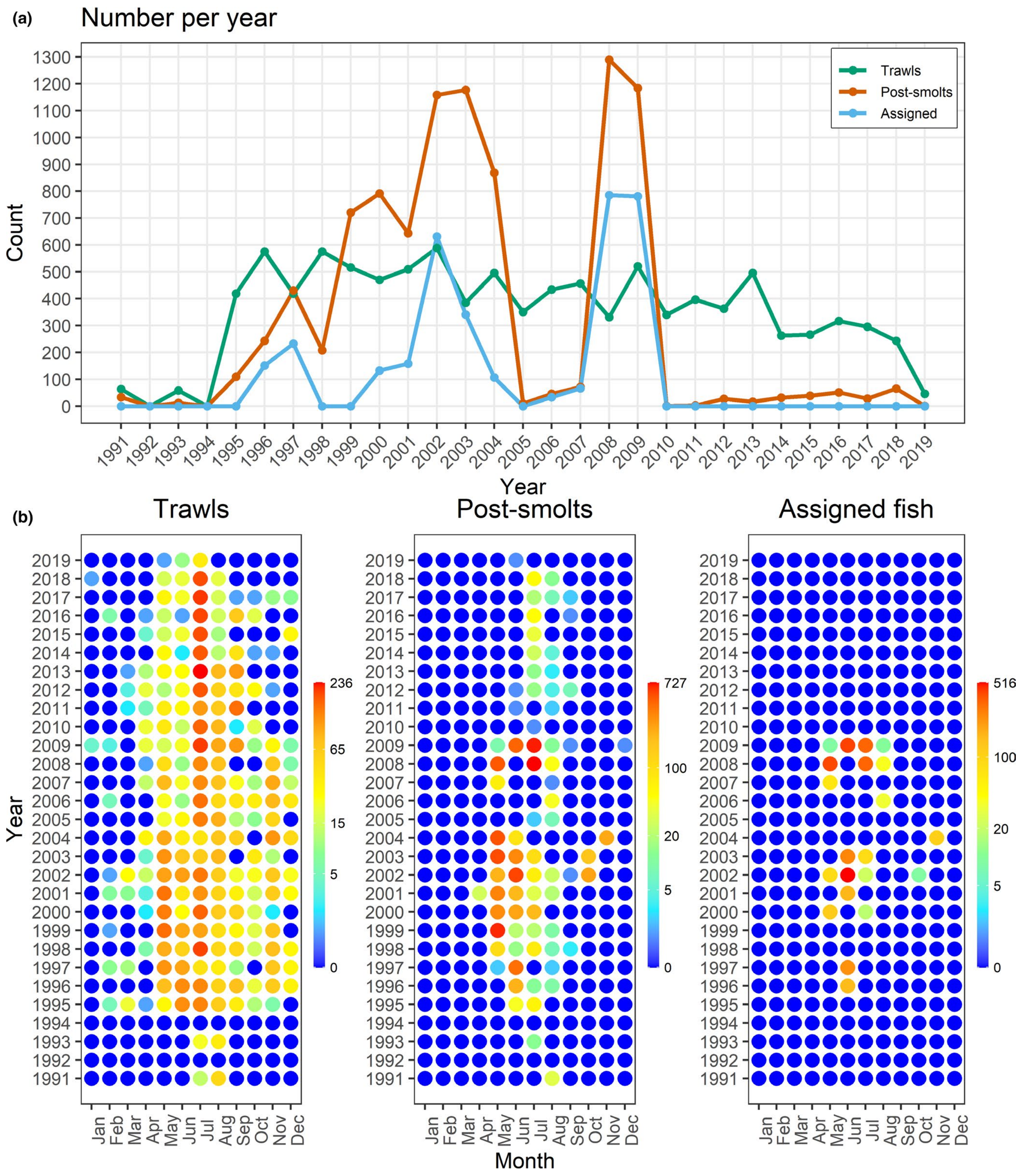

FIGURE 3 Trawl, smolt and assigned fish numbers per year and month. (a) Numbers of all fish by year; (b) Heat map plots of numbers of trawl, post-smolt and assigned fish by year and month

of inter-year distributional variation. In the earlier years, sampling was ad-hoc in nature with varying areas being covered including focus on areas west of the British Isles in May and on the western shelf-edge of the Vøring Plateau in July. While in later years, regular pelagic cruises were undertaken and sampling was more consistent. However again, apart from in July, areas covered across years were inconsistent. As such, and given the aim was to understand generalized patterns of migration and feeding rather than inter-annual changes, the further analysis focussed on monthly distributions using combined data from all years, with particular attention on

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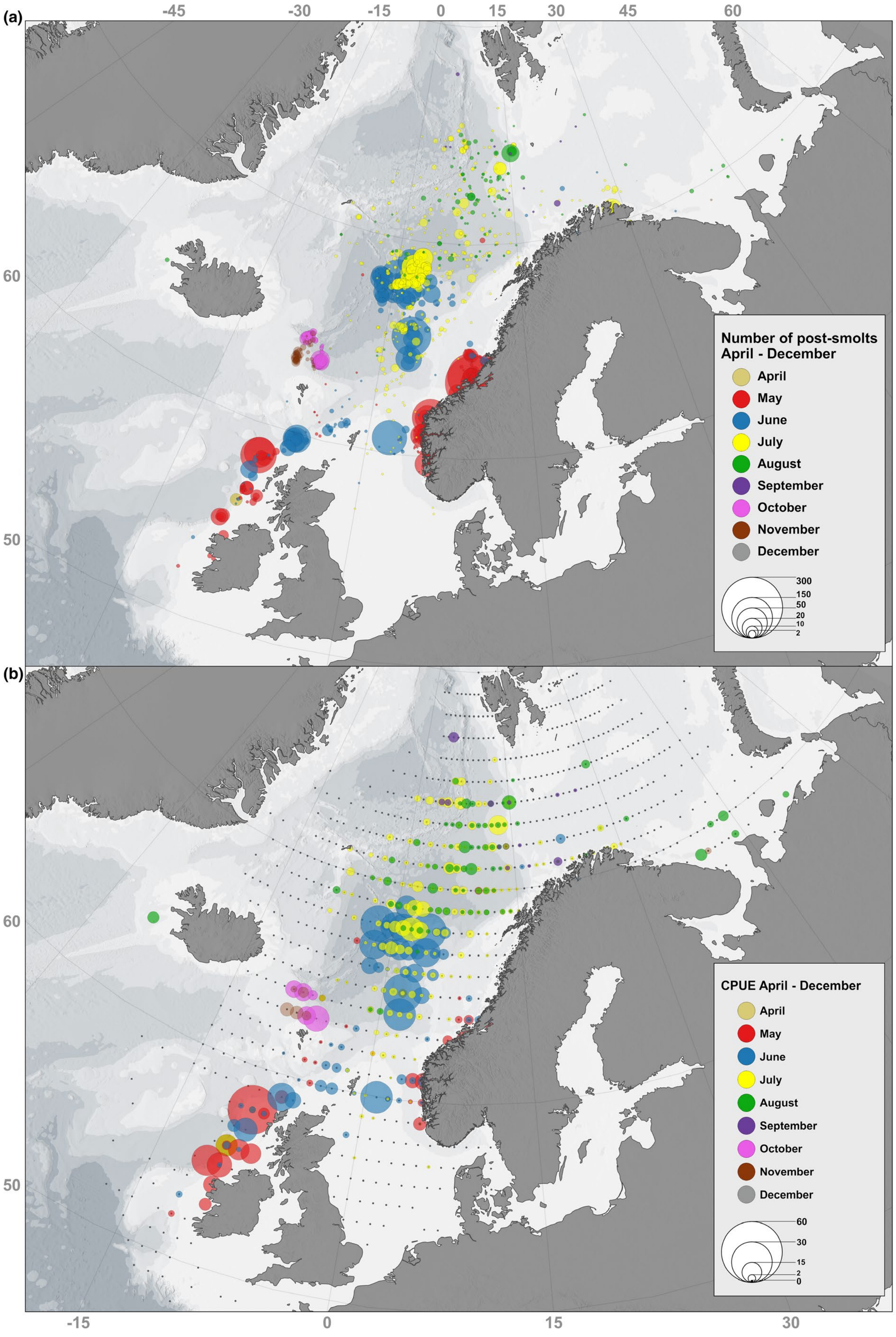

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FIGURE 4 Post-smolt captures over all months. Colours represent month of capture. (a) Number of post-smolt captures. Sizes of the points represent numbers of fish captured at each location. (b) Catch per unit effort (CPUE) for each 1° latitude × 1° longitude grid square containing at least one trawl. Points represent mean post-smolt captures per trawl within the grid unit. Small grey points represent grid squares with trawl coverage but no captures

months 5 to 8 (May to August) which contained the majority of both spatial coverage and fish observations (Figures 3 and 4).

3.2 | Association of aggregations with environmental factors

The study area is characterized by a complex set of warm and cold currents and gyre systems, as well as encompassing multiple continental shelf areas, ridges and basins and a NW-SE ridge running from Greenland, through Iceland, the Faroes to Scotland bathymetrically separates the North Atlantic from the Norwegian Sea to the NE (Figure 1). North-east of the Iceland-Faroe, to the north of the ridge, a major zone of mixing of Arctic and Atlantic waters occurs due to the northward Atlantic current and the East Icelandic Current, transporting cold Arctic waters from the Iceland Sea into the Norwegian Sea (Figure 6).

The southerly aggregation identified off the west of Ireland and Scotland was spatially coincident with an offshoot shelf-edge current that flows into the Norwegian Sea (Figures 1 and 6), an area with a relatively uniform sea surface temperature (SST- 6.5–7.5°C) during May and June (Supplementary Data S11), the time when the post-smolts are present. In contrast, the aggregations identified to the north of the Wyville-Thomson Ridge, present from June onwards, were concentrated around the escarpment on the western side of the Vøring Plateau. This area is dominated by the interfacing of two counter-clockwise circling gyres moving water around both the Norwegian basin and in the adjacent, northerly Lofoten Basin (Voet et al., 2010). The aggregations are also located in the area where the western branch of the northward Norwegian Atlantic Current, the Norwegian Atlantic Front Current (NwAFC), bifurcates into westward and eastward currents north of the Vøring Plateau (Figure 6; Orvik & Niiler, 2002). The NwAFC is associated with the Arctic front that separates cold Arctic and warm Atlantic waters and has very steep vertical thermocline and halocline gradients (Nilsen & Nilsen, 2007). These currents are involved in the mixing of cold Arctic and warm Atlantic waters (Raj et al., 2019), the intersection of gyre systems and are associated with marked spatial and seasonal changes in SST (Supplementary Data S11). The SST in this area spans the 5–8°C range.

The main distributional focus of post-smolts occurred off the Vøring Plateau escarpment but a northward shift in post-smolt distribution occurred from June to July, with a smaller secondary focus developing off the Barents Sea Plateau in concert with a northward shift in SST in August (Figure 6, Supplementary Data S11). At this time, post-smolts are also found in areas with 5–8°C SST. The only post-smolt aggregation seen later in the year, further south in October along the northern escarpment of the Iceland-Faroes Ridge, was also in an area characterized by the same general temperature and current conditions, as associated with the earlier, more northerly aggregations.

3.3 | Genetic assignments

Available tissue allowed 4,179 of the 9,269 post-smolt captures to be genotyped with 3,948 successfully scored using the quality cut-off of ≥10 genotypes across the 14 loci. Assignments to the Pan-Atlantic reference baseline (Gilbey et al., 2017) gave all fish an assignment probability of 1 as being European in origin. Regional assignment of the fish using the eastern Atlantic reference baseline (Gilbey et al., 2018) assigned 3,423 at Level 1 (Iceland, Northern Europe and Southern Europe) and 2,401 at Level 2 (the 17 lower level phylogeographic units) classified with an assignment probability of 0.8 or higher (Table 2, Supplementary Table S12). Application of the European baseline found no Baltic Sea-origin post-smolts. Individually assigned fish were dominated by fish of Southern origin with this group in turn being dominated by fish of British and Irish origin (Table 2; Supplementary Data S13). There were relatively low numbers of Icelandic and Northern fish identified, which is surprising given the study area's close geographical proximity to both Northern and Icelandic group rivers.

Power analysis of the accuracy of MSA using the 7 combined assignment units showed that MSA estimates were robust to these units (Supplementary data—GSI). Over the entire data set, proportions of fish estimates using MSA at Level 1 and at the seven combined assignment units were compared with proportions expected based on the estimated relative PFA, and at both assignment levels, observed proportions were found to differ and to depart significantly (Fisher's Exact Tests $p < .001$) from expectations (Figure 7). At Level 1, Icelandic (expected: 4.5%, observed 0.5%) and Northern (expected: 40.4%, observed 17.2%) regional groups were significantly under-represented. In contrast, the Southern group (expected: 55.0%, observed 82.4%) was highly overrepresented.

When looking at the seven combined units, the overrepresentation of Southern fish was seen to be due to an excess of fish of Britain/Ireland origin (expected: 53.8%, observed 81.0%). Within the remaining groups, under-representation is seen in the Mid/SW/Norway group (expected: 21.3%, observed 11.5%) and fish from the Finnmark/Russian group were massively under-represented (expected: 18.5%, observed 3.3%). Fish from the two Icelandic groups were almost entirely missing; West Iceland (expected: 3.1%, observed 0.1%) and North Iceland (expected: 1.4%, observed 0.4%). Fish from France/Spain, although in low numbers, were in proportions as expected (expected: 1.2%, observed 1.3%), while those from Denmark/W. Sweden/S. Norway, although again in low numbers,

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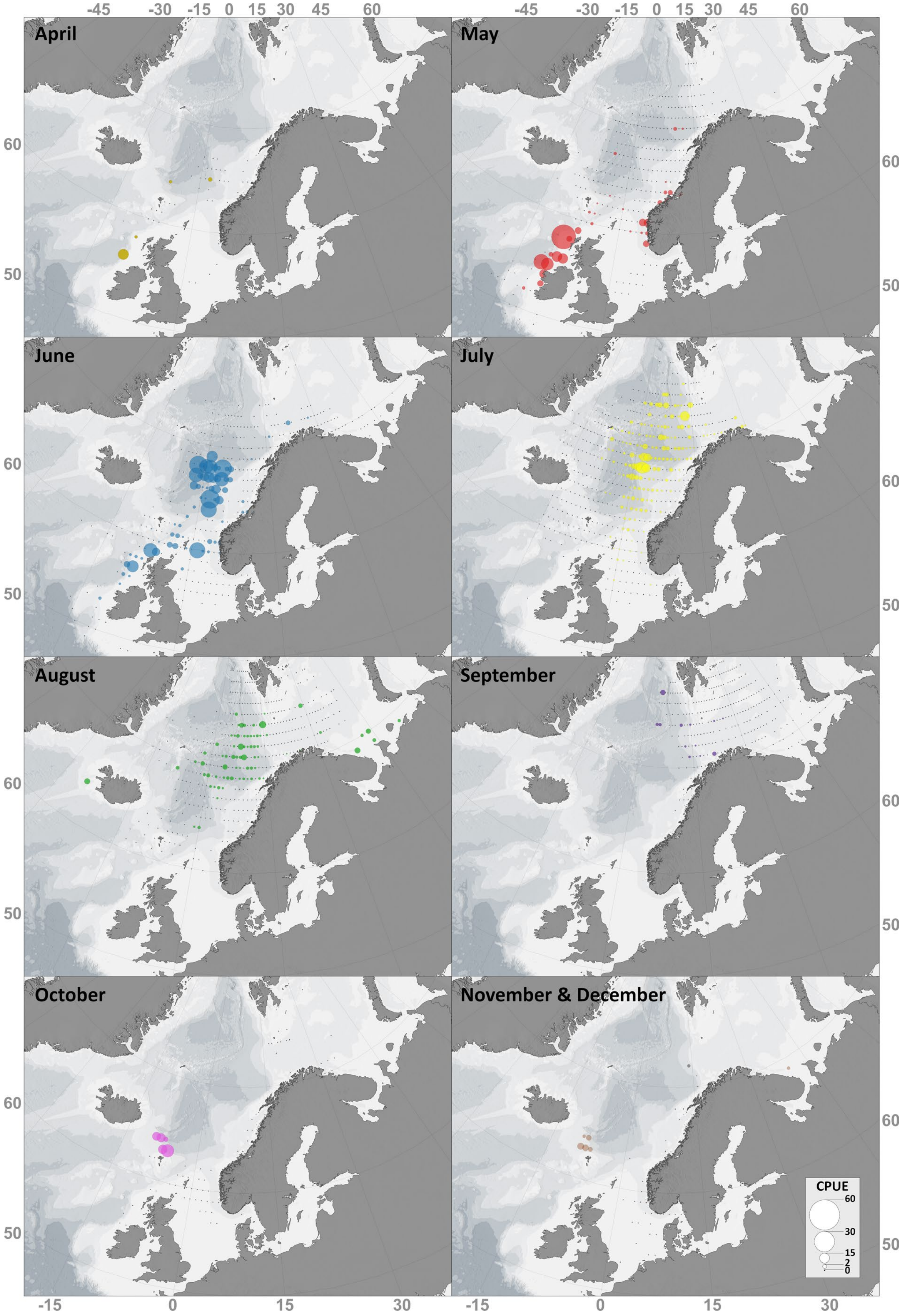

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FIGURE 5 Catch per unit effort by month (CPUE) for each 1° latitude × 1° longitude grid square containing at least one trawl. Points represent mean post-smolt captures per trawl within the grid unit. Small grey points represent grid squares with trawl coverage but no captures

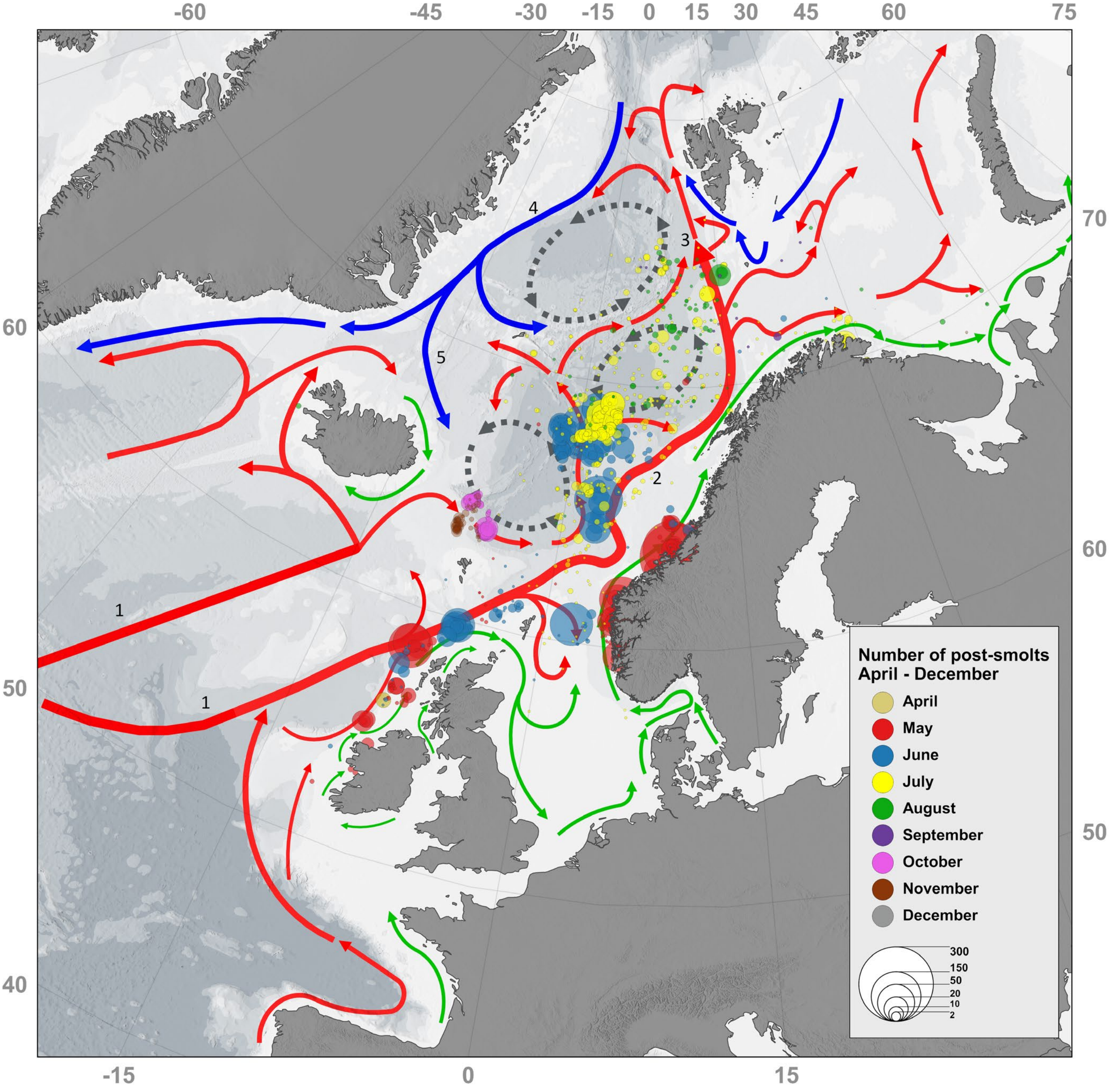

FIGURE 6 Post-smolt distribution, bathymetry, ocean currents and oceanic gyres in the study area. Red, green and blue arrows represent Atlantic, coastal, and Arctic currents, respectively. Oceanic gyres indicated by grey dashed arrows. Arrow sizes are proportional to current strengths. Major currents denoted by numbers: 1—North Atlantic Current; 2—Norwegian Atlantic Current; 3—West Spitsbergen Current; 4—East Greenland Current; 5—East Icelandic Current. Sources for current data: Norwegian Institute of Marine Research; OSPAR Commission (2000); Orvik and Niiler (2002); Skagseth et al. (2008); Trenkel et al. (2014); Reynolds et al. (2017)

were slightly overrepresented (expected: 0.6%, observed 2.6%). Observed versus expected comparisons of proportions of fish based on the entire data set could have been influenced by spatial (e.g. more fishing in the south) or temporal biases in sampling. In order to address this, the data set was examined in different regions and time periods.

Genotyped fish were mostly associated with six largely distinct spatial areas (Figure 8). These are: (A) on the shelf-edge

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TABLE 2 Numbers of Level 1 and 2 individually assigned fish per month over all years (see Figure 1 for assignment unit map)

Assignment	Month						Total	Total
Unit	5	6	7	8	10	11	(Numbers)	(Per cent)
Level 1								
Iceland	0	1	0	4	0	5	10	0.3
Northern	195	97	74	14	0	3	383	11.2
Southern	488	1644	726	64	9	99	3,030	88.5
Level 2								
Britain/Ireland								
Britain	220	935	509	46	6	57	1773	73.8
Ireland	73	171	34	4	0	8	290	12.1
River Bann	5	8	2	0	0	1	16	0.7
English Chalk[a]	0	1	1	0	0	1	3	0.1
River Leven	1	2	0	0	0	0	3	0.1
Mid/SW/Norway								
Mid-SW Norway	152	36	27	9	0	1	225	9.4
Finnmark/Russia								
Finnmark	2	4	7	0	0	0	13	0.5
Kola	0	0	1	0	0	0	1	0.0
White Sea	0	2	0	0	0	0	2	0.1
West Iceland								
West Iceland	0	0	0	2	0	0	2	0.1
North Iceland								
North Iceland	0	1	0	1	0	5	7	0.3
France/Spain								
France/Spain	4	17	6	0	0	0	27	1.1
Denmark/W. Swe/S. Nor								
South Norway	4	12	5	0	0	1	22	0.9
Denmark	0	5	4	0	0	0	9	0.4
Sweden	0	4	4	0	0	0	8	0.3

Note: Level 2 clustering is by assignment unit within the seven combined geographical groups as defined in the text.

[a] English Chalk refers to the southern English chalk stream rivers Avon, Itchen and Test.

off Ireland and Scotland, (B) the north-eastern North Sea, (C) the mid-Norwegian coastal shelf, (D) the south-central Norwegian Sea around the Vøring Plateau, (E) in the north Norwegian Sea and (F) north of the Faroes. Phylogeographic stock group proportions based on MSA among these aggregations across months and years were highly heterogeneous, for both Level 1 and combined Level 2 assignments (Figures 9 and 10).

In Area A (Figures 9a and 10a), Southern fish from Britain and Ireland dominated in the 2 months, May and June, with no significant difference in proportions between the months. In Area B (Figures 9b and 10b), near the southern Norwegian coast again, as likely considering the position of this aggregation, Northern fish from Mid/SW/Norway were found in greater numbers (although confidence intervals are large due to the small number of fish in this group). In May, these fish were almost entirely absent from Mid/SW/Norway, but in June, a small number of fish from Britain/Ireland appeared. In Area C (Figures 9c and 10c), on the central Norwegian coastal shelf the fish origins are dominated by fish from the Northern Mid/SW/Norway unit across both months, May and June, when captures were made. This time, the much higher numbers of fish provided a more robust confidence interval but there was no significant difference in proportions between the 2 months. Thus, the more coastal aggregations of post-smolts (A–C) reflected the phylogeographic stocks in the rivers closest to them.

Area D (Figures 9d and 10d) contained the largest and tightest aggregations of fish observed across any months (Figure 8) and had 2,195 assigned post-smolts. In both June and July, the area was dominated by fish from Britain/Ireland, with very few fish from the geographically much closer Norwegian assignment groups. Further north in Area E (Figures 9e and 10e), fish appeared in July and August and showed a high proportion of Southern fish, though post-smolts from the Mid/SW/Norway unit were also present in proportions

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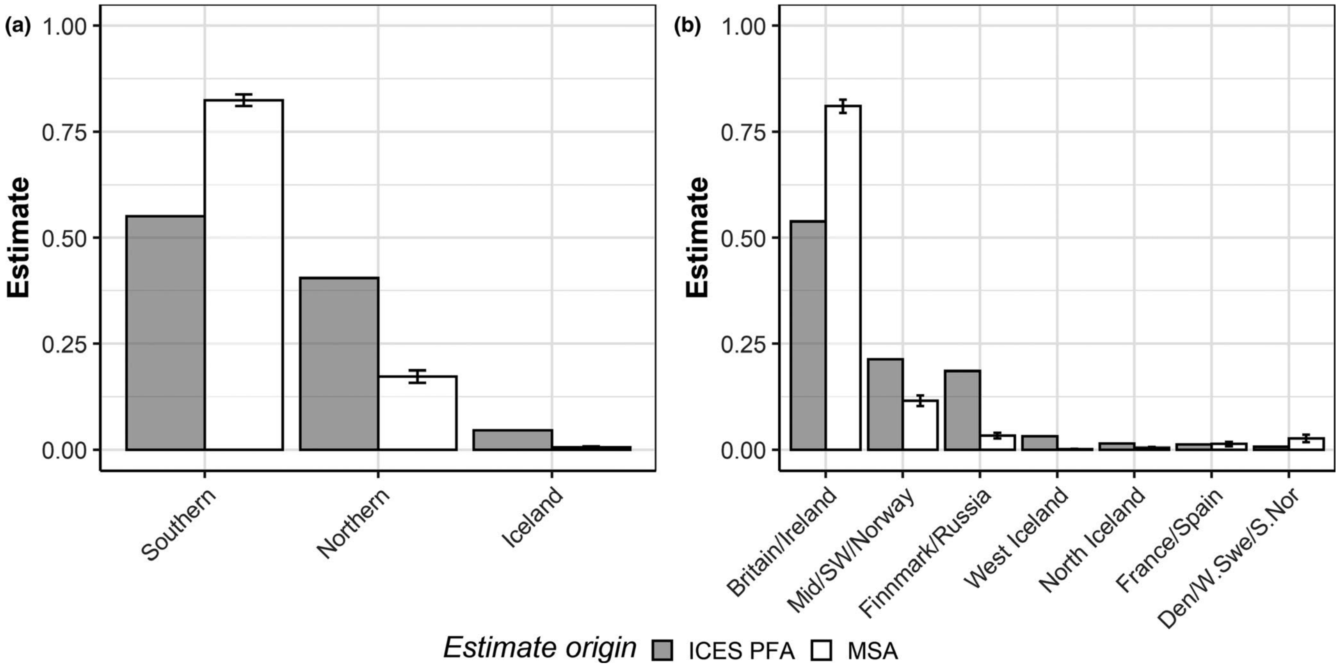

FIGURE 7 ICES pre-fishery abundance estimates (ICES PFA) compared with proportional representations of all genotyped post-smolts from 1996 to 2009 ($n = 3,948$) as determined by genetic mixed stock analysis (MSA) at (a) Level 1 and (b) the seven combined assignment groups. 95% CI based on 1,000 bootstraps and bars representing mid-point of CI estimates

which might be expected based on production. However, fish from the more northerly Finnmark/Russia unit were still absent. Area F north of the Faroes saw a small group of fish in October and a larger group in November, all of which were from Southern Britain/Ireland assignment units.

Area D on the Vøring plateau, and Area E, to the north, were examined in more detail by splitting them into three and two sub-areas, respectively (Figure 11). Sub-areas D1, D2 and D3 showed no differences in proportions of fish from the different assignment units across the three sub-units (Fishers $p = .745$), with all being dominated by southern assignment groups. In contrast, the two sub-areas to the north have significantly different stock proportions (Fishers $p < .05$). The eastern area E1 is the only area studied where proportions of fish from the Mid/SW/Norway assignment unit were at or close to expected proportions based on ICES PFA estimates. In contrast, the more westerly sub-area E2, as seen in the Vøring plateau area, shows an overrepresentation of southern British/Irish fish and an under-representation of northern Mid/SW/Norway, apart from in August when numbers involved are low.

4 | DISCUSSION

The reported analysis of three decades of historical trawl data and archival tissue samples undertaken is the most extensive and comprehensive, integrated spatial–temporal analysis of Atlantic salmon post-smolt distribution in the NE Atlantic Ocean carried out to date. At its most basic level, the assembled data base provides a foundation to which new data can be added as it is collected (see Supplemental material) and analyses revisited. However, as it stands, it provides the first spatial–temporal account, not only of post-smolt presence but, equally importantly, of their absence, giving a more robust perspective on where and when aggregations occur, the marine habitats post-smolts exploit, and the nature of seasonal changes in their distribution. This insight is essential to understand what factors underlie early marine phase mortality and the dramatic reduction in marine survival in recent decades (Holm et al., 2003). Furthermore, by exploiting genetic stock identification, it provides the first significant insight into the distribution of post-smolts from different regional phylogeographic stock groups and provides overwhelming evidence of heterogeneity among stock groups.

The study is constrained, to some extent, by the probabilistic nature of the assignment of individuals to phylogeographic groups as genetic assignment is based on frequency differences of variation among identified groups and hence probabilistic. As such, assignment accuracy depends on the quality of the baseline of genetic information, on the phylogeographic groups, and the degree of genetic differentiation among the identified groups at the marker loci used. However, these constraints are well understood and largely manageable and offset by allowing the origin of all fish to be assessed. In the current study, the individual assignment accuracy of the genetic baselines (Gilbey et al., 2017,2018) and mixed stock analysis (MSA) estimates of proportional stock contributions in spatial or temporal collections of samples (Supplementary data—GSI) are demonstrably robust and make it possible to assign with a high probability most post-smolts to regions of origin. Thus,

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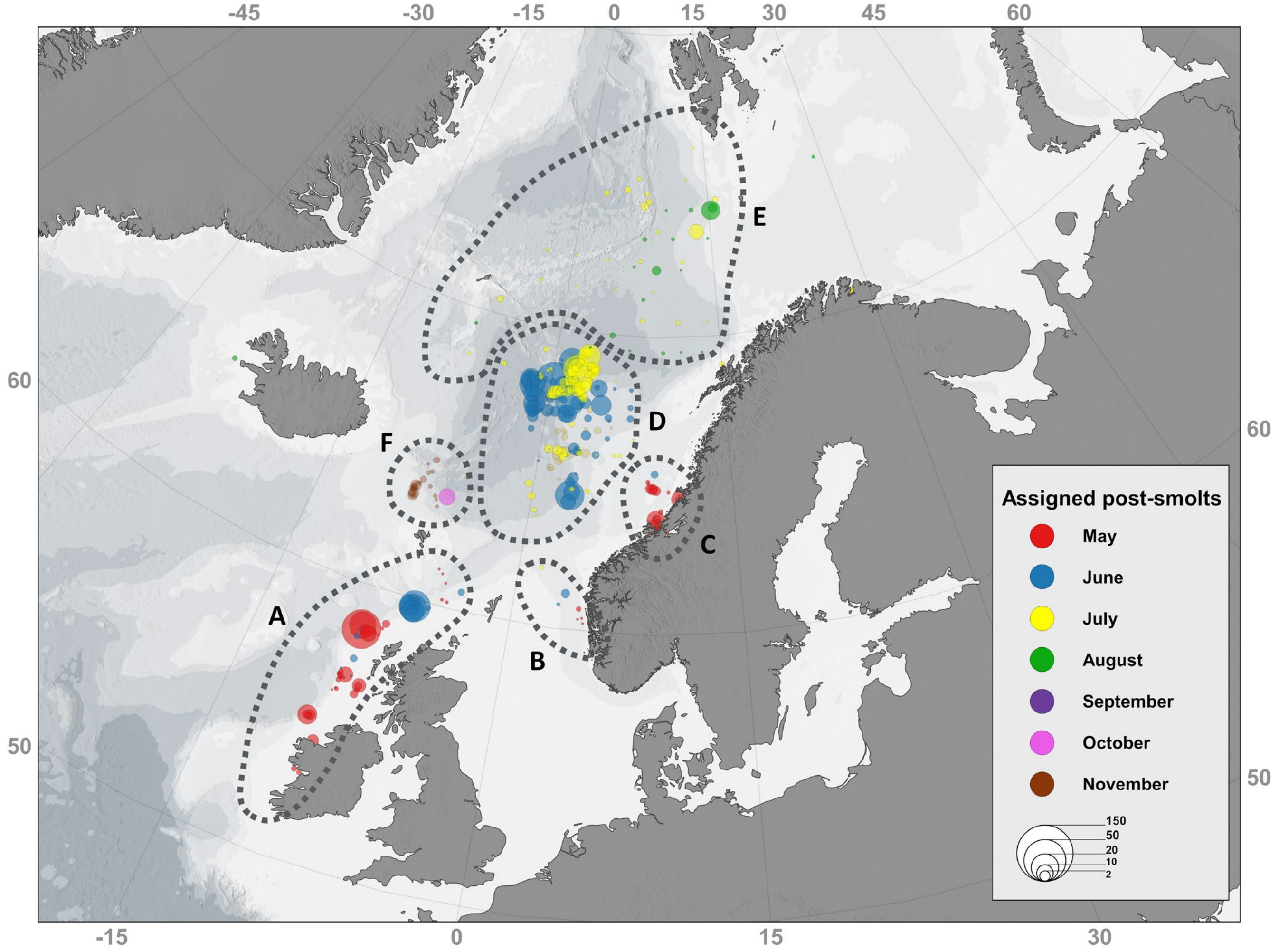

FIGURE 8 Aggregations of genetically assigned post-smolts across months. Dashed lines and letters A–E indicate identified aggregations examined separately in detail (see text)

considerable confidence can be placed in the accuracy of observed differences in stock proportions in the variously defined post-smolt aggregations, in which the origin of only a few fish was established from physical tags, though the latter provides valuable complementary information (ÓMaoiléidigh et al., 2018) and a further method of validating GSI assignments.

In contrast, less tractable limitations on the inferences that can be drawn from the study exist in relation to the ocean sampling associated with the trawl data and its derivation from multiple sources, using different trawling methods, and the uneven temporal and spatial coverage of the study area. These limitations are likely to persist in the future, given the logistic challenges of sampling the marine environment. The systematic collection of samples is almost impossible for many species that occur or migrate offshore over large geographic areas (Marris, 2007; Turvey et al., 2020). Such is the case for Atlantic salmon, and opportunistically collected data sets will often be the best, and even only ones available to advance understanding and guide management (Stewart et al., 2005; Thompson, 2013; Turvey et al., 2020). The findings from the data set analysed here reinforce, and significantly extend, previous insights gained from earlier studies in this region (Haugland et al., 2006; Holm et al., 2000,2003; Holst et al., 1993,2000; Shelton et al., 1997). However, the substantive sampling limitations mean that many inferences drawn from the data must be viewed as working hypotheses.

4.1 | General post-smolt distribution

Prior to 2000, accounts of Atlantic post-smolt distributions were sparse (Holm et al., 2000; Holst et al., 1993; Shelton et al., 1997) and initial studies focussed on searching for post-smolts where available knowledge suggested they would occur. However, Holst et al. (2000) recognized this provided a partial and biased assessment, and that non-targeted sampling would be essential to provide a fuller account. The present analysis to a significant degree addresses this limitation by synthesizing all trawl data, for presence and absence, across three decades of pelagic surveys for a large part of the potential NE Atlantic post-smolt distribution. By including absence data, the analysis also reveals more about where and when they do not occur, and more clearly defines areas of post-smolt abundance and distributional changes over time.

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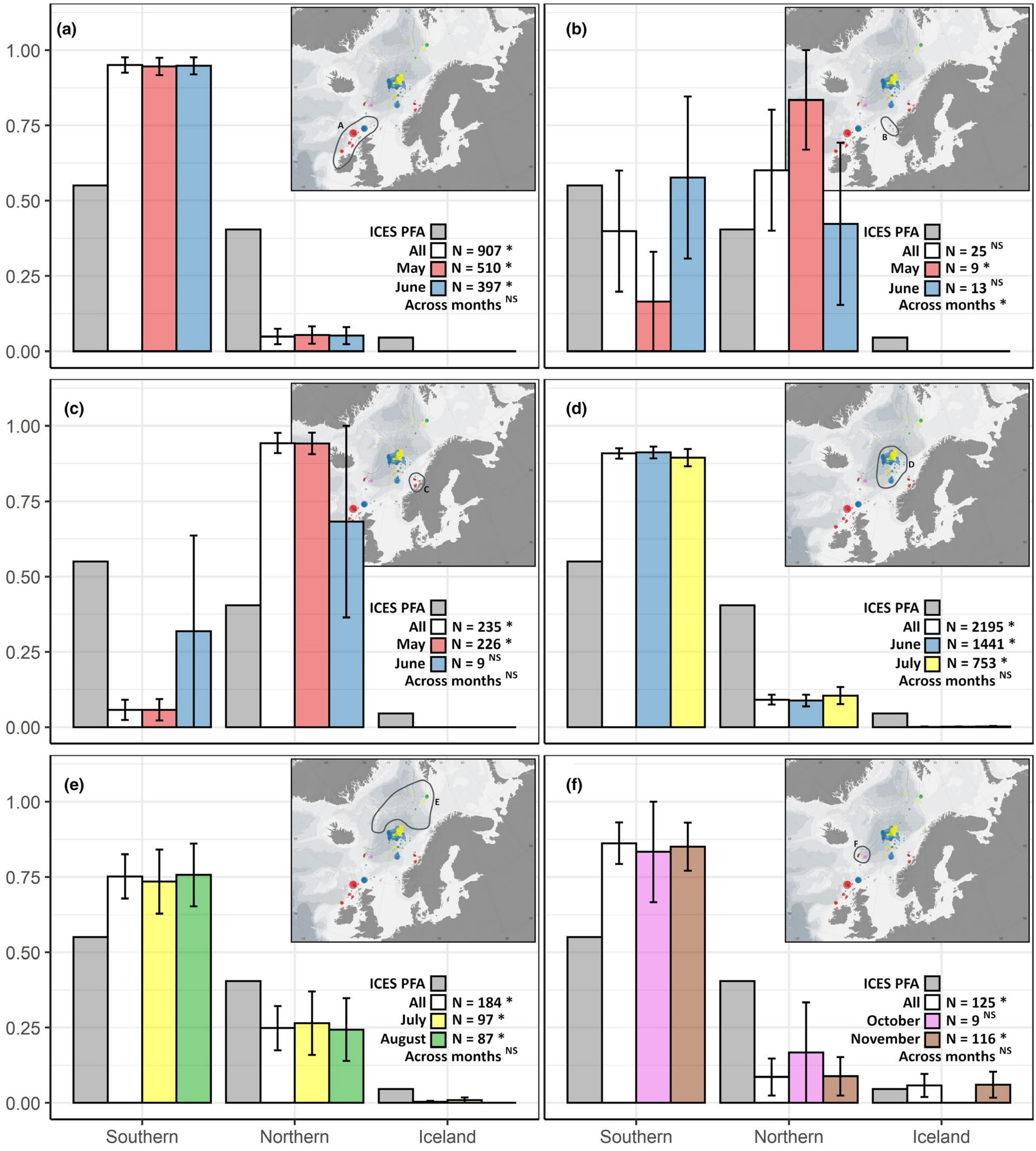

FIGURE 9 Proportional representation of Level 1 assigned post-smolts as determined by as determined by genetic mixed stock analysis (MSA). 95% CI based on 1,000 bootstraps and bars representing mid-point of CI estimates. Panels A–F represent proportions within the six identified aggregations (see Figure 8 and map inserts). Numbers of samples in each area/month are shown together with 0.05 significance (* or NS) of comparisons of observed proportions of stocks from different origins with ICES PFA estimates (grey bars) and changes across months

Despite data limitations, the results compellingly point to spatial concentrations of post-smolts across years that arguably represent seasonal migrational and foraging aggregations (Dingle & Drake, 2007). The earliest of these are in the southern coastal areas, with the clearest and largest concentration present in May and June moving northward in the continental shelf-edge current off the coast of Ireland and Scotland. A second aggregation, on the inshore coastal shelf area of Norway in June and July, and absent from the

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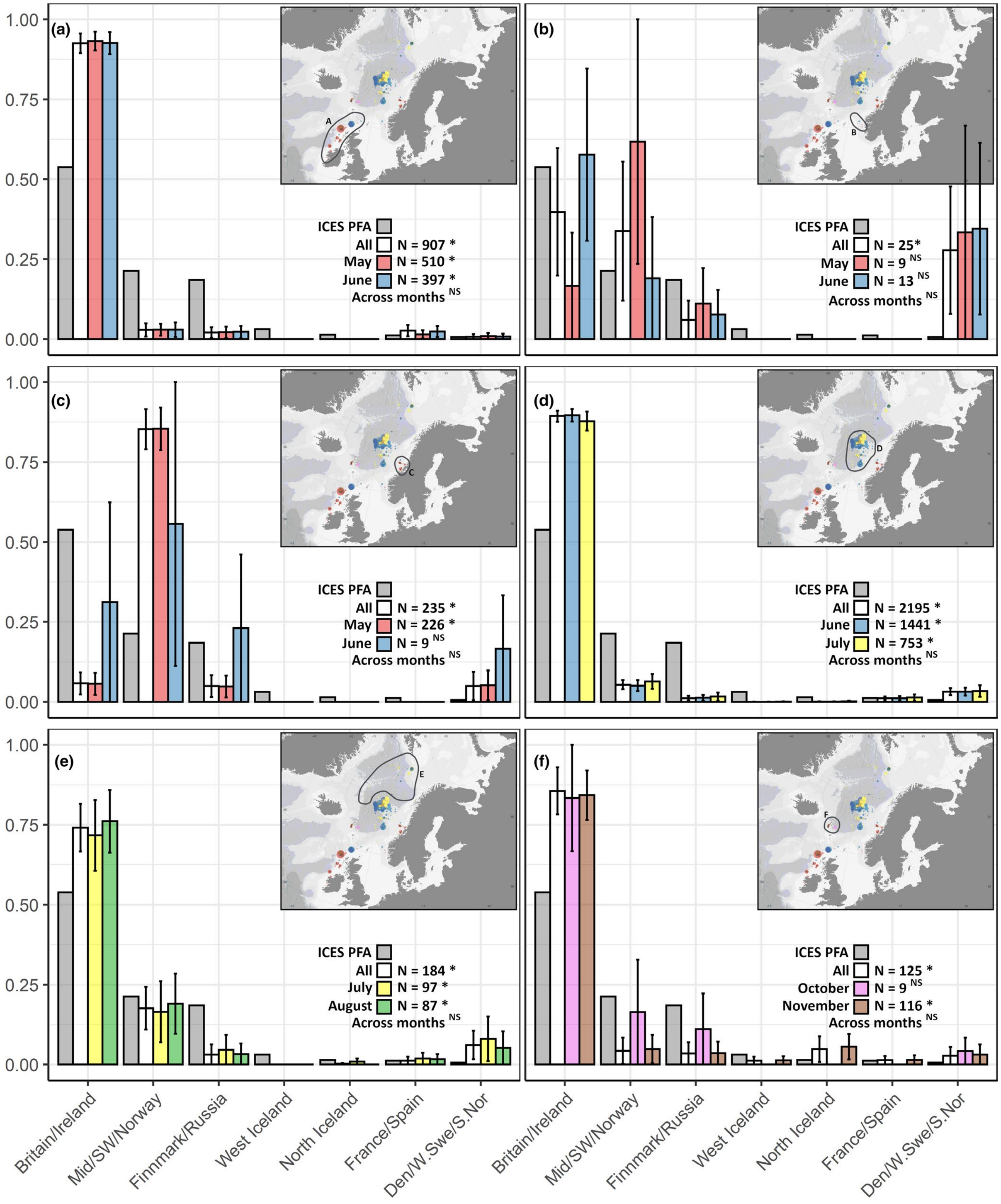

FIGURE 10 Proportional representation of combined Level 2 assigned post-smolts as determined by genetic mixed stock analysis (MSA). 95% CI based on 1,000 bootstraps and bars representing mid-point of CI estimates. Panels a–f represent proportions within the six identified aggregations (see Figure 8 and map inserts). Numbers of samples in each area/month are shown together with 0.05 significance (* or NS) of comparisons of observed proportions of stocks from different origins with ICES PFA estimates (grey bars) and changes across months

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coast by August, almost certainly are migrants from local rivers and moving north-westward towards the Norwegian Sea. Both these interpretations are supported by genetic data (see 4.2).

Other migrational aggregations are expected to occur in the study area, particularly in coastal areas near to salmon rivers. However, these have almost certainly been missed or are poorly defined due to sampling constraints. Further candidates are suggested by post-smolt captures at various points along the coast on the Norwegian shelf which most likely are groups of post-smolts departing local rivers, but in most parts of the study area, coastal sampling is poor or absent altogether including areas with substantive salmon stocks such as Iceland, the east coast of Scotland, and the Kola Peninsula at the times when post-smolts enter the sea (Otero et al., 2011) and start to migrate. A major offshore migrational aggregation likely to have been missed is in the northern North Sea, through which a large proportion of British post-smolts, from east coast rivers, have to migrate to reach their more northerly feeding areas, an area poorly sampled during the May to June period following smolt runs from North Sea rivers.

Further offshore, and later in the year, the analysis shows two concentrations of fish are likely to be feeding aggregations. The spatially and numerically largest of these occurs in the Norwegian Sea, off the continental shelf, focussed around the Vøring Plateau during the months of June to September and progressively expands its spatial extent northwards. No aggregation appears to be present in May, when none would be expected based on the timings of smolt runs in rivers (Otero et al., 2014) and migration speeds (Mork et al., 2012). Whether this aggregation continues beyond September is uncertain, given the lack of trawl surveys in the area after this time (Figure 2) as well as the decreased efficiency of trawls in catching larger fish. Information from commercial long-line fisheries targeting larger salmon in the general area, historically from November to the following April (Gilbey et al., 2017; Jacobsen et al., 2012), suggests the aggregation may persist and that its apparent absence might relate to sampling coverage and/or methods. Another smaller concentration seen later in the year to the south on the Iceland-Faroes Ridge appears to also be a foraging aggregation. However, as the sampling of the study area between these two foraging aggregations was sparse, whether they are distinct or different parts of a single, large entity is uncertain.

Sampling limitations may also account for the absence in the data of any spatial–temporal continuity between the migrational aggregation of the west coasts of Ireland and Scotland with the foraging aggregation around the Vøring Plateau escarpment. Sampling in the area between is sparse or absent altogether, particularly in June when post-smolts moving along the shelf-edge off Ireland and Scotland might be expected to reach these areas (Figures 2 and 5). Thus, the link between the identified aggregations in the two areas, while almost certain, remains to be directly demonstrated. This is also the case for the true magnitude of the relative differences in abundance observed between areas where different trawl types and approaches were used.

4.2 | Regional phylogeographic group distributions

Current regional stock group delineation used for salmon management in the NE Atlantic is based on a broad assessment of regional differences in demographic trends (ICES, 2011) and defines three stock complexes: North America, Northern Europe and Southern Europe, with recent work breaking the European complex into smaller regional groups (ICES, 2019a). This contrasts with the current study where, for the first time, post-smolts in the NE Atlantic are assigned to regional phylogeographic groups which provides a more precise, evolutionarily grounded and finer-scale account of differences in the marine distributions among stocks from different regions. In so doing, the analysis substantially advances existing understanding of this aspect of post-smolt distributional biology.

The results of this analysis strongly support, as has been postulated based on their geographic isolation, that post-smolts from North American, as well as Baltic Sea rivers, are not present in the NE Atlantic, at least in respect of the period/area covered by the study. This contrasts with later marine phases where North American salmon are found in the NE Atlantic (Gilbey et al., 2017) and European salmon in the NW Atlantic (Bradbury et al., 2021). However, while encompassing only Atlantic European fish, observed proportions of the regional Atlantic stock groups, both overall and in identified areas of aggregation, deviate from those expected from regional estimates of salmon numbers based on river returns. The earliest migrational aggregation, post-smolts migrating along the continental shelf off western Ireland and Scotland, is almost certainly composed entirely of wild Southern stock group fish, as expected from its southerly marine location and the historical view based on tagging data that the feeding habitats of all Eastern Atlantic stocks lie to the north of this area (Thorstad et al., 2011). The few post-smolts present in the May/June aggregation that assigned to the Northern stock group may be the small proportion of expected chance misclassifications, given the large number of fish genotyped. Alternatively, they may be escapes of juvenile Norwegian strain farm fish or wild hybrid progeny. Escaped Norwegian farm fish were widely recorded in Scottish and Irish rivers during the study period and to have interbred with wild fish (Ferguson et al., 2007; Munro, 2019). While overall captures are lower in June, the numbers observed in the two months are similar, with proportions higher in the latter month.

These individuals aside the finer geographic scale assignments (7 combined assignment units) for this aggregation in May and June show the same proportional contribution of Southern stock complex phylogeographic subgroups in the 2 months. This suggests a similar temporal pattern of arrival for the subgroups to this area. Furthermore, the proportions of fish from France/Spain, Britain and Ireland are broadly similar to expectations based on the estimated relative productivity of these areas, pointing to this being the primary migration route for these stocks and accords with the earlier departure of the post-smolts from the more southerly rivers in France and Spain than those further north in Ireland and Britain

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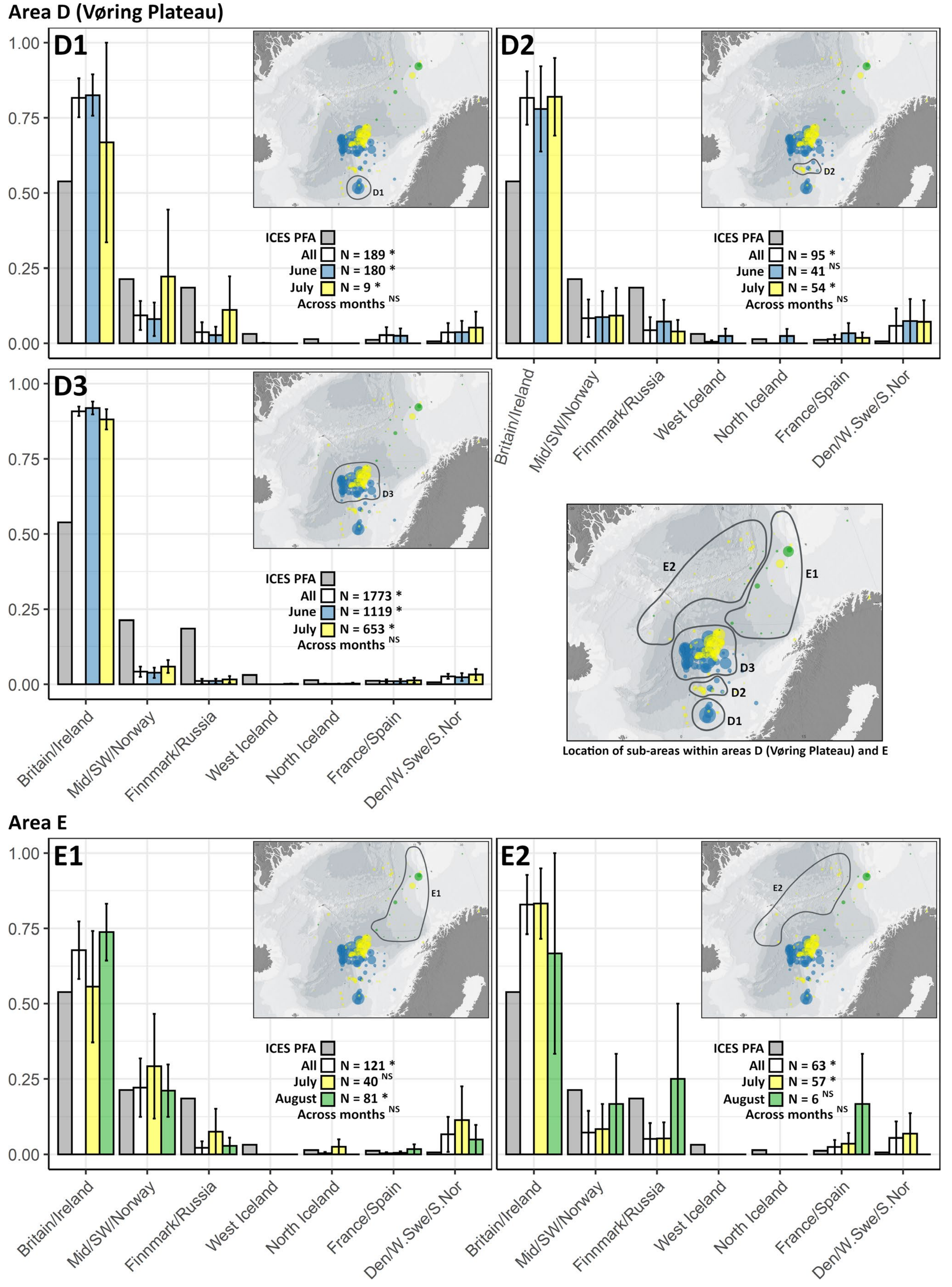

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FIGURE 11 Proportional representation of combined Level 2 assigned post-smolts as determined by genetic mixed stock analysis (MSA). 95% CI based on 1,000 bootstraps and bars representing mid-point of CI estimates. Panels D1–D3 and E1–E2 represent intra-aggregational sub-area proportions within the Vøring Plateau and northern E aggregations, respectively. Location of aggregation boundaries shown on map insert with individual boundaries shown as an insert within each plot. Numbers of samples in each area/month are shown together with 0.05 significance (* or NS) of comparisons of observed proportions of stocks from different origins with ICES PFA estimates (grey bars) and changes across months

(Otero et al., 2011). However, proportions of British fish would be predicted to be lower than expected, given much of the productivity from this region comes from rivers in eastern Britain, most of which would be expected to migrate northward out of the North Sea, rather than go south through the English Channel and northward along the Atlantic shelf-edge.

Post-smolts from Danish rivers were not found in the migrational aggregation to the west and north of Britain/Ireland but occur in June in the Norwegian Sea, consistent with their northward migration out of the North Sea. Conversely, post-smolts from the chalk streams in southern England, which could migrate north through North Sea, are evidenced to migrate westwards and join the shelf-edge aggregation, suggesting a migration divide associated with the now submerged Norfolk-Zeeland ridge and previously terrestrial divide. This difference between the two stocks, despite a relatively close geographical position, may reflect the fact that during much of evolutionary history of stocks in this area, this ridge was above sea level and would have necessitated different migrational routes (Cauwelier, Verspoor, et al., 2018).

The assignment of post-smolts in May aggregations along the Norwegian coast to the mid-Norwegian phylogeographic group, as well as the apparent absence of the aggregations in June, is consistent with those smolts being of recently emigrated local rivers (Otero et al., 2014). The absence in June is based on a lower sampling intensity but it does suggest that these early coastal concentrations are migrational rather than foraging, as expected. Potentially, they contribute to the Vøring Plateau aggregation where there is an increased proportion of this northern stock group. However, if they do, despite their geographical proximity, this does not result in anywhere near the expected proportions of this group in the aggregation based on river productivity estimates, suggesting that they may also move further north.

This discrepancy raises the important, and previously unanswered, question of the marine destination of most of the post-smolts from northern stock group rivers and, more specifically, those from Norway. That they do not occur in the Vøring Plateau aggregation in expected numbers has three potential explanations: (1) they migrate to the Barents Sea, (2) they go further north and west towards the Greenland Sea area and (3) they rapidly migrate to the area west of Svalbard. Observations of older fish (Gilbey et al., 2017; Jensen et al., 2014; Maoiléidigh et al., 2018; Strøm et al., 2018) and their presence further north in proportions expected from relative production estimates (Figure 11), point to the majority of Norwegian fish having migrated into the Barents Sea or west of Svalbard by late July. If so, this would explain why they were not captured in the extensive trawls carried out further south in Norwegian Sea in July. More generally, such major differences in migration patterns and foraging habitat among stock groups could account, at least in part, for differences in marine mortality rates between northern and southern river stocks in the NE Atlantic (ICES, 2019a).

Southern Complex post-smolts, found earlier in the aggregation off Ireland and Scotland, also dominate later in the Vøring Plateau aggregation further northward along the shelf-edge current. However, as expected with the addition of post-smolts from eastern British North Sea rivers, the ratio of British to Irish post-smolts more than doubles over that in the shelf-edge migrational aggregations off Ireland and Scotland. However, unexpectedly, the Vøring aggregation contains only a small component of Northern Complex fish, most of which are indicated to originate from rivers in southeast Norway and western Sweden, with only a few from Mid-southwest Norway and, few if any, from rivers in Finnmark/Kola/White Sea. The presence and higher proportion of the latter two northern groups further north point to their main marine foraging area being more northerly. At the same time, the small numbers of Southern post-smolts further north supports the view that the main foraging habitat for Southern post-smolts is focussed on the Vøring Plateau escarpment area in the Norwegian Sea.

In respect of Level 1 assignments, the composition of the Vøring Plateau aggregation remains unchanged from June to July, suggesting that most stocks that will migrate to this area have done so. However, in July, post-smolts appear less abundant around the Plateau and more post-smolt captures occur further north and the ratio of Southern to Northern Complex fish drops significantly. At the same time, among Northern Complex fish, there is an increasing proportion of more northern phylogeographic components from mid and northern Norway which suggests that as the year progresses, the various groups disperse from core foraging areas and become more spatially mixed. However, the observed proportions of Northern Complex post-smolts support the view that they do not migrate to central parts of the Norwegian Sea, but further north and that during the summer and autumn months the centre of their marine distribution remains further to the north.

The analysis shows an almost complete absence of Icelandic post-smolts in the study area. Though expected numbers are small, their phylogenetic distinctiveness (Gilbey et al., 2018) makes their misassignment highly unlikely, ruling out that they migrate into and forage in the Norwegian Sea. This almost total absence is unexpected given the close geographic proximity of Icelandic rivers, particularly in respect of stocks from North Iceland, and a lack of any obvious geographic barriers to their migration into the study area. This could in part reflect that Icelandic stocks represent only a small proportion of NE Atlantic stocks, linger longer in coastal areas, migrate to

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poorly sampled parts of the study area or leave their rivers later in the year. Certainly, in northern Icelandic rivers smolts may enter the sea as late as August (Antonsson & Gudjonsson, 2002). However, later in the year they were not even found among post-smolts captured in the area between Iceland and the Faroes despite this being very close to Icelandic rivers. Thus what seems more likely is their migratory pathways and destinations lie outside the study area. Tracking studies suggest that many, if not all, are likely to migrate to the Irminger Sea, northwest of Iceland (Guðjónsson et al., 2015).

4.3 | Biological implications

The aggregation off the Irish and Scottish west coasts in May and June is clearly migrational, with its northward movement facilitated by oceanic currents but also encompassing active swimming (e.g. Mork et al., 2012; Ounsley et al., 2019). Also, as the genetic analysis shows, this aggregation transitions into the aggregations of fish to the north found along the edge of the Vøring Plateau which is clearly focussed on foraging (Utne et al., 2020). Thus, there is a progressive temporal shift of the former into the latter from June to October (Figure 4), with the phylogeographic groups found in the migrational aggregations dominating in the foraging aggregations later in the year.

Though not directly evidenced by distributional data or modelling, it is possible to infer that other migrational aggregations almost certainly contribute to the Vøring aggregation such as those from the southern Norwegian Shelf and North Sea. This inference is supported by the presence of post-smolts from North Sea stock groups in the Vøring aggregation that are not observed in the aggregation off the coast of Ireland and Scotland, for example from Denmark. At the same time, the major under-representation or absence of post-smolts from other phylogeographic groups that might be expected to be present or dominate in the Vøring foraging aggregation, based on geographical proximity, implies the existence of other migrational and foraging aggregations. The lack of direct evidence for them reflects spatial and temporal sampling constraints underlying the assembled data within the study area, and that it does not encompass all of the NE Atlantic. Although this is a limitation of the study, the results do make clear that the use of ocean habitats is more complex than previously appreciated and involves differences among phylogeographic groups and river stocks.

The regional stock groups that dominate in the two main NE Atlantic migrational and foraging aggregations identified, those from southern Europe, Ireland and Britain, have apparently evolved a migratory syndrome distinct from other European phylogeographic groups, as have those in the Baltic as well as those in North America. This is the only plausible explanation for the notable absence, or major under-representation, of other regional stock groups in the study area. However, that stocks from southern France and Spain go first to the Norwegian Sea is at odds with Almodóvar et al. (2020) who, based on stable isotope analysis of scales, argue they head directly to West Greenland. Results here indicate they first go to the Vøring Plateau area before doing so.

The behaviour of the main migrational aggregation off the Atlantic coasts of Ireland and Scotland accords with the hypothesis of Dadswell et al. (2010) that post-smolt migration to foraging habitat is driven almost entirely by currents. This is consistent with the "drift" part of the migratory syndrome (Dingle & Drake, 2007), as currents can efficiently bring fish to the feeding habitats to which they have evolved. However, associations are likely to be more complex in some areas, such as the North Sea where current systems are more complex (Sündermann & Pohlmann, 2011) or in areas such as the English Channel or Irish Sea where currents are strongly associated with tides and reverse direction on a daily basis (Howarth, 2005; Idier et al., 2012).

4.4 | Association of aggregations with environmental factors

The observed post-smolt distribution is consistent with temperature and currents being key proximal environmental factors that attract and retain post-smolts, and define their optimal habitat niche (Pinsky et al., 2013). Such factors will also define habitats to which the populations or stock groups using them have adaptively evolved to target (Alerstam et al., 2003) and the idea of their having a specific thermal niche has been muted (Friedland et al., 2000; Reddin et al., 2006). Certainly, local temperature is a key variable related to sea entry time (Otero et al., 2014) and sea surface temperature (SST) is correlated with coastal post-smolt abundance and post-smolt mortality during the first month at sea (Friedland et al., 2003), though this relationship shows geographical variation (Friedland et al., 2005,2014). However, the environments of post-smolt in coastal areas will also vary in respect of other variables such as salinity, the nature, location, direction and strength of currents, and prey distribution (Beaugrand & Reid, 2003; Edwards et al., 2013; Thorstad et al., 2011,2012) and differ from areas where offshore migrational and foraging aggregations form.

The migrational aggregation off the west coast of Ireland and Scotland occurs in an area with a relatively uniform and warm temperatures both along the shelf-edge and over the migration time period, and a strong north-eastward flowing shelf current (Holm et al., 2003; Holst et al., 2000; Shelton et al., 1997), the latter exploited by post-smolts to move them northward into the Norwegian Sea (Mork et al., 2012). Temperature appears to show a lesser or, at least less obvious, proximal role in defining the location of offshore migrational aggregations, though some predisposition for colder, deeper waters may occur to reduce metabolic energy requirements. The SST off the coast of Ireland and Scotland during May and June when the migrational aggregation occurs is in the 7–9°C range (Supplementary Data S10), similar to the SST in the foraging area in the Norwegian Seas area. Responses to current speed and direction during migration are likely to be important but also variable depending on migration routes. Movement of this migrational aggregation associates strongly with the warm northward flowing regional current that facilitates movement to the more northerly foraging areas. In contrast, the Western Atlantic post-smolts, which

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also migrate northward to forage, must deal with a cold southward flowing Labrador Current but how they do so is not clear (Dadswell et al., 2010).

The environment around the Vøring Plateau escarpment to which the Ireland-Scotland shelf aggregation migrates contrasts with that along the shelf. Map-based sea surface temperatures in the area (Hindar et al., 2020) suggest waters in the region of approximately 7–9°C when the foraging aggregation occurs there. At the time, the area is also characterized by steep vertical and horizontal temperature gradients generated by the meeting of the warm Atlantic and cold Arctic currents in the area (Nilsen & Nilsen, 2007) which interact in two gyre-like systems that create the steep thermal gradients and mix the Arctic and Atlantic waters (Nilsen & Nilsen, 2007; Orvik et al., 2001; Skagseth et al., 2008). This habitat area shows a reverse L-shaped distribution from the Vøring Plateau area south and west to the east of Iceland along the northern Iceland-Faroes ridge escarpment (Figure 7). Though the relationship between oceanographic variables and fish productivity is complex (Friedland et al., 2012), in colder, higher latitude ecosystems, such habitats generally show high primary and secondary productivity (Mann & Lazier, 2006). Furthermore, they facilitate the passive energy-efficient physical entrainment of foraging fish with such areas and allow individuals to exploit different temperature zones to optimize growth energetics (Wilson et al., 2011). Thus, not surprisingly, such areas are also linked to observed aggregations of other pelagic fish species (ICES, 2019b).

Given the sampling limitations of the current distributional data set, it cannot be ruled out that the two observed aggregations in this area are actually part of a single, thermally focussed and, possibly, seasonally shifting foraging aggregation. Such habitat conditions also occur to the north of the aggregation and may be exploited later in the year as water temperatures to the north increase and move into the range preferred by the stocks in the aggregation. The importance of a specific thermal habitat for Atlantic salmon adults was shown by Jacobsen et al. (2012) in respect of the Iceland-Faroes Front and earlier by Jákupsstovu (1988). Using long-line survey data, Jákupsstovu (1988) showed older salmon aggregating into the eastern Norwegian Sea in the same thermal environment. Previous post-smolt studies across the Atlantic show them inhabiting a range of temperatures from 4–12°C (Holm et al., 2000; Reddin et al., 2006; Reddin & Friedland, 1993; Sheehan et al., 2012) but that post-smolt aggregations are most likely in a thermal habitat of ~8–10°C (Friedland, 1998,1999; Friedland et al., 1998,2003).

4.5 | Management and conservation implications

The analysis reported provides insight into the potential impact that natural and anthropogenic environmental change might have on post-smolt ecology and mortality. The evidence of preferred habitat areas and conditions raises concerns as climate-related changes in the North Atlantic Ocean are having major, and regionally varying, impacts on marine conditions (Delworth et al., 2016; Parsons & Lear, 2001), and these are accelerating due, for example, to increased melting of the Greenland Ice sheet (Kwiatkowski et al., 2019). However, its impact on future marine environments can be expected to be complex (Beaugrand & Kirby, 2018), though temperature change likely to be the dominant factor (Schuetz et al., 2019) as it underlies the distributional responses of most species and impacts their energetics and prey type and abundance.

Impacts of climate change on Atlantic salmon are likely to occur (Todd et al., 2010) and might be expected to be especially significant on the more biologically vulnerable post-smolt phase. Their extent will be conditioned by interactions between the evolved genetic behaviours of stock groups and the habitats they use, which show variation, and may lead to different impacts if migration routes differ, even where feeding areas are shared. The capacity to adapt can be expected to be variably constrained by genetic differences among stocks and be particularly problematic where environmental change exceeds historical rates under which stocks have evolved their particular migratory syndromes. Thus, there may be diverse fitness outcomes, with some positive and others negative, at least in the medium to long term. This mechanism will underlie the general process of historical adaptation to past climate change driven by glacial cycles and is likely to underlie differences seen historically among different, demographically defined regional stock groups (Secor, 1999). The difference is likely to be in the magnitude and direction of climate change and the extent to which seasonal timing of temperature changes has moved or will shift from historical norms. These will be highly informative indicators of potential climate niche displacement (Rijnsdorp et al., 2009).

The greater this niche displacement, the greater the level of maladaptation (Garcia de Leaniz et al., 2007) expected of species and species stocks that exploit the area, where moving to new areas with required conditions is not possible or energetically costly and further depresses fitness. Maladaptation is likely to be a particular issue in respect of marine adaptations as climate change velocities may be up to seven times higher in the sea than on land (Brito-Morales et al., 2020). If so, environmental change is even more likely to outstrip the capacity of the stocks involved to adapt to change, and may lead to an extinction vortex of increasing maladaptation (Cahill et al., 2013; Nogués-Bravo et al., 2018). The demise of the Inner Bay of Fundy salmon stocks whose foraging habitat was in southern waters in the Outer Bay and adjacent Gulf of Maine (Webb et al., 2007) may arguably be underpinned by such changes, as both marine areas having seen exceptional levels of environmental change over the last five or more decades (Mills et al., 2013). In contrast, while suffering depressed marine survival, stocks from the Outer Bay and elsewhere in the southern Western Atlantic migrate to the North Labrador Sea and off West Greenland (Bradbury, Hamilton, Sheehan, et al., 2016; Lacroix, 2008).

Mork et al. (2019), investigating contemporaneous climate variability in the Norwegian Sea, have shown significant warming and freshening over the last 10 years of waters adjacent to the Plateau in both the Norwegian and Lofoten Basins. Climate change will not just affect distributions of species such as the Atlantic salmon, but is also likely to lead to declines in biomass in middle latitude areas

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with increases in more northern areas (Lotze et al., 2019). Declines in biomass will result from increasing temperatures and decreasing primary productivity, with effects amplified at the higher trophic levels (Lotze et al., 2019). This will have a particularly negative impact on the growth of post-smolts along more southerly migration routes such as the Bay of Biscay and off Britain and Ireland. Alternatively, it will enhance growth on more northern migration routes, such as in the Barents Sea and foraging areas, with impacts in intermediate areas such as southern Norway and around Vøring Plateau area less clear.

Projections indicate increased primary productivity at higher latitudes (Lotze et al., 2019). However, the value of these new emerging areas in the high Arctic and Polar waters for replacing lost habitat for post-smolts production may be negligible for post-smolts from southern part of the range. Given strongly evolved migratory behaviour, populations in some phylogeographic groups, such as those from the southern part of the range, may well be unable to adapt their behaviour sufficiently to change their migration syndromes to deal with change, leading to increasing maladaptation. This may also be the situation faced by the Inner Bay of Fundy stock group, which historically only migrated to the now much warmer Outer Bay and Gulf of Maine (Webb et al., 2007).

Climate-induced changes in migrational environments in respect of temperature, salinity, current speeds and direction can be expected, as well as prey availability during migration. Long-term weakening of the Atlantic Meridional Overturning Circulation (AMOC), resulting in a reduction in the amount of heat transported into the Arctic and strength of ocean currents, has been reported (Caesar et al., 2018; Friedland et al., 2014; Thornalley et al., 2018). Ocean currents are a primary facilitating mechanism for delivering southern post-smolts into the Norwegian Sea foraging areas and climate changes may affect the timing or probability of arrival in this vital feeding area and increase overall rates of post-smolt mortality. Foraging success while migrating may also decline, particularly for southern stocks which undergo a longer migration through increasingly less optimal conditions.

Increasing insight into a species' distribution can be a double-edged sword. The discovery of foraging aggregations of larger salmon in the North Atlantic, off West Greenland and the Faroes Islands, led to the development of directed high-seas fisheries for the species in the mid-1960s (Jacobsen et al., 2012; Reddin & Friedland, 1999). Subsequently, insight from tagging studies, into the home rivers from which salmon come, combined with declines in rivers stocks, led to the establishment in 1984 of the North Atlantic Salmon Conservation Organization (NASCO) and regulations to ensure only sustainable marine fisheries are prosecuted. While there are no coastal or high-seas fisheries for the smaller salmon post-smolts and the development of such fisheries can be ruled out, by-catch mortality of post-smolts in other pelagic fisheries does occur (ICES, 2005,2019a; Olafsson et al., 2015).

Distributional insights can help to understand areas where by-catch may be a problem, such as foraging areas in international waters where fisheries are less restricted and only superficially monitored. This situation exists in respect of Vøring Plateau aggregational area, with the main concentrations of salmon indicated to be in international waters outside of exclusive economic zones (EEZs). It is also of concern in respect of the migrational aggregations on the shelf-edge off Ireland and Scotland and further north. Although within national EEZ zones, this migration route spans multiple national jurisdictions. By informing on the appropriate spatial and temporal control of high-seas pelagic fisheries, distribution insights gained from the study can be used to provide information to support the management of fisheries by-catches. It can also be used to target general ecosystem management measures in these areas such as the establishment of open water marine protected areas (Corrigan et al., 2014) based on a more robust comprehensive multi-species and ecosystem-based approach (Hyrenbach et al., 2000) to ensure that biological communities and food webs utilized are as healthy and productive as possible. Certainly, the protection of migration routes for marine species is not without precedent (Hays et al., 2014; Pomerleau et al., 2014).

Achieving the distributional understanding required to support effective management of Atlantic salmon post-smolts across its range will require significantly extending current understanding. In particular, it will be necessary to confirm the key aggregational areas for regional phylogeographic groups that are currently absent or under-represented in the study area, for example, the principal post-smolt feeding grounds for Norwegian and Icelandic smolts. The likely general areas where migrational and foraging aggregations of these latter phylogeographic groups appear likely to occur, respectively, to the north somewhere in the Svalbard/Barents Sea and in the East Greenland/Irminger Sea regions, based on what data are available, but it is critical their actual focal areas are accurately delineated. Understanding of the distribution of older post-smolts also needs to be improved and potentially more effective, methods for sampling older post-smolts later in the year, such as using experimental long-line fishing (Jákupsstovu, 1988); as the post-smolts grow older and are able to swim more quickly, and change their foraging behaviour, the effectiveness of sampling by trawling is likely to decrease. This will also give greater operational flexibility across weather and sea conditions and make it possible to temporally and spatially extend the scope of the surveys.

Combined with regular annual, temporal assessments of post-smolt abundance, and environmental (e.g. temperature) and biological parameters (e.g. post-smolt condition, prey availability, diet) in the identified key aggregational areas, this would lead to a better understanding of temporal distribution dynamics. This would help understand temporal trends in numbers and how they vary with habitat conditions, and how these differ among different phylogeographic stock groups. Such an approach can provide a more direct and reliable basis for explaining and predicting responses to change than studying the biology and ecology of the organism directly (Cheung et al., 2009; Pinsky et al., 2013). This should be integrated with assessments of longitudinal data on marine productivity changes, biodiversity alterations and changes in ecosystem functioning from "Essential Ocean Variables (EOVs)" collected by

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global ocean observation systems using remote sensing (Lindstrom et al., 2012; Muelbert et al., 2019) and of linked quantitative fishing of a strategic network of fixed sampling stations within migratory and foraging areas. This would provide insight into factors underlying the formation of aggregations, their size, timing of recruitment, and stock composition as well as stock status for fitness-related traits and parameters that could inform climate-mediated performance and survival.

Phylogeographic stock-specific phenotypic characterization, integrated with migrational information, for example, route and time at sea prior to capture, could provide greater insight into the relative roles of random oceanic conditions (e.g. flow, temperature, salinity, productivity, predation and competition) and non-random drivers (e.g. time of sea entry, inherent migratory behaviours) of fitness and dispersal. This would allow identification of areas with positive increases in fitness-related traits (e.g. growth, body condition, size at age, energy acquisition and energy use) and increase understanding of size-selective, behavioural and other drivers of marine mortality. This would in turn provide insight into the differential maladaptation of phylogeographic groups and its likely causes and how areas of positive and negative fitness change from year to year and underlie phenotypic diversification in fitness-related traits among populations. Insights gained would help understand the diversifying role of marine environmental heterogeneity and the evolutionary basis for different marine life-history strategies among populations, though variously having common or different marine feeding grounds.

In particular, analysis of stock-specific spatial–temporal post-smolt sex ratio information could be informative. A varying proportion of European salmon return to rivers to spawn as one or multi-sea-winter fish (ICES, 2019a) and the majority of the latter from southern European appear to have foraged off West Greenland (Jeffery et al., 2018; Reddin et al., 2012; Sheehan et al., 2010). Whether these fish generally migrate there directly from natal rivers or, as suggested by the current study, do so via the Norwegian Sea moving westwards later during the winter is unknown. Given the known bias towards females among multi-sea-winter fish in most river stocks of salmon (Chaput, 2003,2012), such information will help to understand the spatial and temporal associations of salmon in later phases of the marine cycle associated with different marine habitats and environment, and observed changes in proportional representation of one and multi-sea-winter salmon.

A fuller, finer-scale insight into stock-specific variations in marine distribution and performance would be realized by exploiting the higher resolution genetic stock identification methods (Jeffery et al., 2018; Layton et al., 2020) which have been developed since the SALSEA-Merge project (NASCO, 2012) to the assignment of captured post-smolts. While new baselines would need to be developed, the increased power and resolution of these newer markers would allow both a greater proportion of captured post-smolts to be accurately assigned to phylogeographic group of origin and their assignment to smaller phylogeographic units, including possibly even individual river stocks. This will require new screening panels and data baselines to be developed, ideally encompassing adaptively relevant and life-history markers (e.g. Cauwelier et al., 2018). Encompassing markers such as *Vgll3*, *six6*, *also* offers the possibility of comparing ocean migration and distribution patterns for different sea age phenotypes (Aykanat et al., 2020; Ayllon et al., 2015; Barson et al., 2015), enhancing understanding stock-specific responses to environmental change.

Though, in principle, the greatest insight into post-smolt migration biology can be gained by using telemetry to document individual behaviour (Dingle & Drake, 2007), population-based distributional studies can provide insights into post-smolt distributional biology that will be difficult if not impossible to gain from telemetry. Telemetric studies have to date been largely restricted to small numbers of larger salmon, and particularly to post-reproductive individuals (kelts) on their second or third migration (Hedger et al., 2017; Strøm et al., 2018) but less so for studies of post-smolts (e.g. Chaput et al., 2018; Daniels et al., 2019; Drenner et al., 2012; Guðjónsson et al., 2015; Holm et al., 2006; ICES, 1999; Lacroix, 2008; Reddin et al., 2006; Thorstad et al., 2012). As it stands, their ability to provide population-level information across the species marine phase is severely constrained by technical issues which make them difficult to use on smaller individuals, tag large numbers of fish across a representative set of river stocks and recover sufficient numbers of tags to build an accurate overall picture of population behaviour. Technological advances are increasingly overcoming issues of tag size, cost and battery life but the logistic challenges of studying post-smolts across a representative set of phylogeographic stocks are likely to remain for the foreseeable future. Thus, advances in understanding are most likely to be realized integrating insights from genetic-based distributional and telemetric studies and, given their respective limitations, using them to develop, parameterize and test migrational models such as those based on particle tracking (e.g. Mork et al., 2012). This integration will be the most powerful way to help define future conservation management challenges and priorities.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in both the journal online supplementary material of this article and in the Zendo data repository at http://doi.org/10.5281/zenodo.4605401

ORCID

John Gilbey https://orcid.org/0000-0002-5064-0589

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