Transient demographic dynamics of recovering fish stocks shaped by past climate, harvest, and management

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Abstract

Large-scale commercial harvesting and climate-induced fluctuations in ocean properties shape the dynamics of marine populations as interdependent drivers at varied timescales. Selective removals of larger, older members of a population can distort its demographic structure, eroding resilience to fluctuations in habitat conditions and thus amplifying volatility in transient population dynamics. Through the implementation of stricter management measures since the 1990s, many historically depleted fish stocks began showing signs of recovery. But these interventions coincided with accelerated changes in the oceans triggered by increasingly warmer and more variable climates. Applying multilevel models to annual estimates of demographic metrics of 38 stocks comprising 11 species across seven ecoregions in the Atlantic Ocean, this study explores how time-varying local and regional climate conditions contributed to the transient dynamics of recovering populations exposed to variable fishing pressures moderated by management actions. Analyses reveal that progressive reductions in fishing pressure and shifting climate conditions shaped rebuilding patterns of the stocks through restorations of maternal demographic structure (reversing age truncation) and reproductive capacity. As the survival rates and demographic structures of reproductive fish improved, transient growths became less

sensitive to variability in recruitment and juvenile survival and more to that in adult survival. As the biomass of reproductive fish rose, recruitment success rates also became increasingly regulated by density-dependent intrinsic processes involving higher numbers of older fish. When reductions in fishing pressure were insufficient or delayed, however, stocks became further depleted, with more eroded demographic structures. Although warmer climates in spawning seasons promoted recruitment success in some ecoregions, changing climate conditions over the past decades began adversely affecting reproductive performance overall. These shared patterns underscore the value of demographic transients in developing robust strategies for managing marine resources sustainably. Such strategies could form the foundation for effective applications of adaptive measures resilient to future environmental changes.

Keywords: age truncation, stock assessment, meta-analysis, demographic buffering, climate change, fisheries management, matrix population model, life history trait, life table response experiment, hierarchical modeling

Introduction

Excessive human exploitation continued through the twentieth century has depleted marine living resources worldwide, threatening biodiversity, food and nutrient security, and other ecosystem services that the oceans provide (Pauly, Watson & Alder 2005; Crowder *et al.* 2008; Worm *et al.* 2009). Long-lived, late-maturing vertebrate predators are disproportionately depleted by industrial fishing as target or incidental catch (Christensen *et al.* 2003; Juan-Jordá *et al.* 2022). As part of the efforts to halt and reverse the losses, national government and intergovernmental organizations began applying the precautionary principle to the management of marine fisheries (Hilborn *et al.* 2001; Punt 2006), following international agreements, including the Code of Conduct for Responsible Fisheries adopted by the Food and Agriculture

Organization of the United Nations (FAO 1995; Melnychuk *et al.* 2021). Since the implementation of stricter management measures to regulate fishing operations in the early 1990s, an increasing number of historically overexploited fish stocks began showing signs of recovery (Hilborn *et al.* 2020; Juan-Jordá *et al.* 2022). These management interventions, however, coincided with accelerated changes in the oceans (Barange *et al.* 2018). Global climate is becoming increasingly warmer and more variable, modifying regional and local habitat conditions that support the biomass production of fish stocks, possibly shifting biologically sustainable levels of harvesting (Chassot *et al.* 2010; Free *et al.* 2019).

The dynamics of marine resource populations in many systems are shaped by drivers operating interactively at varied timescales, including high-frequency perturbations like fishing and low-frequency variability in ocean properties forced by climate (Rouyer *et al.* 2012; Goto *et al.* 2022b). When exposed to such persistent, nonstationary perturbations, near-term (transient) dynamics of an exploited population, which depend on both variable vital rates (survival, growth, and fecundity) and demographic (age and stage) structures, may deviate from asymptotic (equilibrium) dynamics (Hastings 2004; Koons *et al.* 2016). Past research instructs us that large-scale shifts in ecosystem productivity under alternative climate regimes can be propagated through the system to influence fluctuations in fisheries catches (Chassot *et al.* 2010; Cheung, Watson & Pauly 2013). Climate effects on marine species are often integrated over a series of oceanic, ecological, and biological processes over time and space (Ottersen *et al.* 2001; Stenseth *et al.* 2003). Fluctuations in population structure and size can, for example, emerge with some time lag from age (or stage)-dependent demographic processes like birth and death (Jenouvrier *et al.* 2022) modulated by seasonal and interannual variations in weather and habitat conditions (Hutchings & Reynolds 2004; Lindegren *et al.* 2013). These transient fluctuations in the

population could sustain over generations through delayed feedbacks (Hastings 2004). In contrast, fishing operations and management actions that regulate the operations can directly modify short-term trends and variability in population structure and demographic rates, and thus the transient dynamics of exploited species (Gamelon, Sandercock & Sæther 2019). Large-scale commercial fishing often selectively removes larger, older members of the population, truncating age (and size) structure, modifying life history traits, reducing the capacity to absorb the effects of perturbations, and thus amplifying year-to-year variation in population size in variable environments (Hsieh *et al.* 2006; Rouyer *et al.* 2012). Fishing-induced age truncations (juvenescence) are widely reported for harvested marine populations (Hsieh *et al.* 2010; Rouyer *et al.* 2012), many of which suffer from reduced reproductive capacity (Hixon, Johnson & Sogard 2014). Climate-induced changes in the variability of ocean habitat conditions thus may indirectly promote or impede the recovery of depleted populations with weakened demographic resilience to perturbations (Lindegren *et al.* 2013; Harris *et al.* 2018).

In commercial fisheries, a harvested population is commonly managed through regulation of fishing pressure based on its population status (Beddington, Agnew & Clark 2007). Because of high socioeconomic values, exploitation of marine resource populations is regularly monitored through scientific surveys and assessed based on population size estimates (Hilborn & Walters 1992). These population assessments form the scientific basis for the implementation of management measures like catch limits. When population size declines below a predefined threshold (a reference point set under the precautionary principle, ICES 2021; Goto *et al.* 2022a), for example, fishing pressure may be adjusted to mitigate the risk of overharvesting. This adaptive management cycle (human–natural system feedbacks through monitoring, assessment, and management action) thus can be considered as natural experiment (Hilborn & Walters 1992;

Jensen, Branch & Hilborn 2012), providing opportunities to gain insights into the transient dynamics of managed populations in variable environments. Understanding what drives these transients would help develop robust strategies to sustainably manage human exploitation of marine resource populations as we face increasingly uncertain conditions in the oceans.

This article reports a study that empirically explores how past fishing, management action, and climate variability have influenced the transient dynamics of recovering fish populations in the northeast Atlantic Ocean (FAO Major Fishing Area 27, Fig. 1a). These populations experienced wide ranges of fishing pressure, climate, and management action in recent decades (Hidalgo *et al.* 2011; Rouyer *et al.* 2011; Zimmermann & Werner 2019). Annual fishing pressures applied to many northeast Atlantic stocks began to be eased in the late 1990s to rebuild biomass that support sustainable harvesting (Sparholt, Bertelsen & Lassen 2007; Lassen, Kelly & Sissenwine 2014). As a result, these stocks experienced considerable changes in population size, demographic structure, and productivity following the reductions in fishing pressure (Hidalgo *et al.* 2012; Rouyer *et al.* 2012; Britten, Dowd & Worm 2016). During these periods the regional climate also became increasingly warmer and more variable as greenhouse gas emissions rose, which was reflected particularly in upper ocean heat content and transport (Delworth *et al.* 2016; Zanna *et al.* 2019). Warming patterns, however, highly varied among geographic subregions (ecoregions) owing to local air–sea feedbacks (Roemmich *et al.* 2015; Delworth *et al.* 2016), triggering a series of oceanographic and ecological responses at variable rates (Beaugrand 2009; Delworth *et al.* 2016). To glean insights into the recovery patterns of historically depleted fish stocks, this study specifically asks how local and regional climate variability may contribute to variations in the reproductive performance and transient growth of marine species exposed to variable fishing pressures moderated by management actions.

Materials and Methods

Data

Time series (1946–2016) of annual estimates of age-specific information (mean body mass, abundance, maturity rate, and natural and fishing mortality rates) and management measures (reference points) of marine fishes in the northeast Atlantic Ocean were extracted from the 2017 stock assessment reports by the International Council of Exploration of the Sea (ICES) (Table 1). In the assessment of each stock (defined here as a population in a management unit area defined by the ICES) the demographic rates and life history traits were estimated using data from commercial catch and scientific monitoring surveys. Stock sizes and fishing mortality rates then were estimated annually using age-structured population models fitted to time series data of abundance indices (ICES 2017e; ICES 2017a; ICES 2017b; ICES 2017c; ICES 2017f; ICES 2017d). The reliability of the models and data had been evaluated by experts prior to assessments and extensively documented (e.g., ICES 2016). For analysis I excluded stocks with missing age-specific information, rejected assessments, or shorter time series (less than 15 years). The final dataset consists of 38 stocks comprising 11 species (cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, saithe *Pollachius virens*, herring *Clupea harengus*, plaice *Pleuronectes platessa*, turbot *Scophthalmus maximus*, sole *Solea solea*, whiting *Merlangius merlangus*, sprat *Sprattus sprattus*, megrim *Lepidorhombus spp*., and four-spot megrim *Lepidorhombus boscii*) across seven ecoregions in the northeast Atlantic Ocean defined by the ICES: the Norwegian and Barents Seas (combined as a single ecoregion for analysis), the Greater North Sea, the Baltic Sea, Faroes, Icelandic waters, the Bay of Biscay and the Iberian Coast (hereafter the Bay of Biscay), and the Celtic Seas (Table 1 and Fig. 1a). These stocks

support some of the largest fisheries in the region, collectively yielding 1.9 to 2.6 million tonnes of commercial landings annually in the recent decades (1997–2016).

Climate indices and sea surface temperatures (SST) were used as proxies for regional (North Atlantic) and local (ecoregion) climate conditions (1946–2016). Monthly time series of three regional climate indices were downloaded and averaged over winter (most active) months for analysis (Fig. 1b): the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO) indices (both computed from the Hadley Centre Sea Ice and Sea Surface Temperature data set [HadISST1, https://www.metoffice.gov.uk] and the extended reconstructed SST [ERSSTv5, NOAA Physical Sciences Laboratory; https://psl.noaa.gov] and averaged over the sources), and upper (0–700 m) ocean heat content (OHC) anomaly in the North Atlantic (NOAA National Centers for Environmental Information; https://www.ncei.noaa.gov/). The NAO index reflects the dominant mode of atmospheric variability between the Azores and Iceland, linked with a range of large-scale oceanic features (such as surface temperature and heat content) in the North Atlantic that regulate biological and ecosystem processes (Stenseth *et al.* 2003). The AMO index, computed by averaging SSTs over the North Atlantic (25°–60°N at 7°–70°W) using the method by van Oldenborgh *et al.* (2009), also reflects large-scale climate variability that may influence the movement and migration of marine species (Faillettaz *et al.* 2019). OHC measures the amount of excess heat (from increasing greenhouse gases) trapped in the ocean, integrating basin-wide heat storage and transport (Zanna *et al.* 2019). Because of high signal-to-noise ratio, OHC reflects more consistent decadal trends (less influenced by natural variability) than other climate indices (Roemmich *et al.* 2015).

Reconstructed gridded monthly SST data were downloaded from and averaged over three sources to account for systematic uncertainties in each source: HadISST1, COBE Sea Surface

Temperature SST (NOAA Physical Sciences Laboratory), and ERSSTv5. I first averaged the SST data over ecoregion and for each ecoregion I computed SST anomalies by subtracting the mean across years and dividing by the standard deviation for each season (Fig. 1c); winter (December in the previous year–February, $wSST_{anom}$), spring (March–May, $spSST_{anom}$), summer (June–July, $smSST_{anom}$), and autumn (September–November, $aSST_{anom}$).

Transient population growth and elasticity

I used transient population growth rate as an integrated measure that captures time-varying demographic rates and age structures responding to non-stationary extrinsic factors (fishing pressure, management action, and climate) and estimated the growth rates for each stock using an age-structured matrix projection model (Caswell 2001). Leslie (state-transition) matrices (A) were first constructed with annual estimates of age-specific survival and reproductive rates. Survival rates ($S_{a,y}$) were estimated as $S_{a,y} = \exp(-Z_{a,y})$, where $Z_{a,y} = F_{a,y} + M_{a,y}$, and $F_{a,y}$ and $M_{a,y}$ are fishing and natural mortality (non-fishing like predation and starvation) rates for a-year olds in year y. Egg production rates are often not estimated in the assessments of marine fish stocks, and here I estimated recruitment success (integrating over reproduction and early life stage survival) rate per spawner (reproductive fish) for a-year olds in year y ($RS_{a,y}$) (Rouyer *et al.* 2011) as a proxy for per capita fecundity rate as

$$RS_{a,y} = \frac{R_y m_{a,y-a_R}}{\sum_{a=a_{min}}^{a=a_{max}} m_{a,y-a_R} N_{a,y-a_R}} \quad (1)$$

where R_y is the recruit number in year y, $m_{a,y-a_R}$ and $N_{a,y-a_R}$ are the maturity rate (fraction of juveniles becoming adults) and abundance of a-year olds in year y-a_R (spawning year), a_R is the age of recruits, which accounts for variations in age at recruitment (0–3 years old) among stocks reported in the assessments. a_{min} and a_{max} are the youngest and oldest ages in the stock. I then numerically estimated deterministic transient growth rates (λ_{trans}) by projecting age-specific

abundances using the annual state-transition matrices and the annual estimates of age-specific numbers taken from the assessments as

$$\lambda_{\text{trans,y}} = \frac{n_{\text{y+T}gen,y}}{n_y}$$

$$\boldsymbol{n}_{\text{y+Tgen}} = \boldsymbol{n}_{\text{y}}\boldsymbol{A}_{\text{y}} \quad (2)$$

where $\boldsymbol{n}_{\text{y}}$ and $\boldsymbol{A}_{\text{y}}$ are a vector of initial age-specific numbers and an $a \times a$ state-transition matrix in year y, and T_{gen} is the generation time (years) in year y. To account for variations in life-history strategy among stocks, the transient growth rates of each stock were estimated over its generation time, which is defined as the mean age of parents of a cohort (Caswell 2001),

$$T_{\text{gen},y} = \frac{\sum_a a(\prod_{j=1}^{a-1} S_{j,y})R_{a,y}}{\sum_a(\prod_{j=1}^{a-1} S_{j,y})R_{a,y}} \quad (3)$$

The transient growth rates here were thus defined in the timescales of 2.6 to 6.7 years (Fig. S1), relevant for fisheries management.

To evaluate the contributions of demographic variations I performed transient life table response experiments (LTRE) by numerically estimating transient elasticities (e_y) to survival and fecundity rates through matrix projections (Koons *et al.* 2016); demographic parameters (fecundity or survival) of all ages were first perturbed by a small amount (1%), and stock numbers were projected to re-compute $\lambda_{\text{trans},y}$ (Durant *et al.* 2013). Elasticity (relative sensitivity), defined as the proportional change in λ_{trans} relative to a proportional change in a demographic rate (Caswell 2001), was computed as $e_{\text{y}} = \frac{\Delta \log \lambda_{trans,y}}{\Delta \log \alpha_y}$, where α_{y} is the survival or fecundity rates in year y that are perturbed (Coulson *et al.* 2004). Age-specific elasticities were then summed for analysis; changes in elasticities to juvenile and adult survival rates were evaluated separately by summing age-specific elasticities weighted by maturity rates. To quantify how the transient dynamics deviate from expected long-term equilibriums (asymptotic dynamics assuming stable

environments and age structures) across years I also computed asymptotic (geometric) growth rates and stable age distributions from the logarithms of the dominant (largest) eigenvalues and the right eigenvectors (respectively) of the annual state-transition matrices (Caswell 2001).

To evaluate how variations in demographic structure have contributed to the recovery patterns of fish stocks, I used mean age and age diversity of spawners as indices for demographic structures. Mean age (SA_{mean}) is the weighted (by abundance) average of spawner age as

$$AS_{mean,y} = \frac{\sum_{a=a_{min}}^{a=a_{max}} a m_{a,y} N_{a,y}}{\sum_{a=a_{min}}^{a=a_{max}} m_{a,y} N_{a,y}} \quad (4)$$

The Shannon diversity index was used as an indicator of age diversity ($SA_{diversity}$) and computed as $SA_{diversity,y} = -\sum_{a=a_{min}}^{n} p_{a,y} \ln(p_{a,y})$, where $p_{a,y}$ is the proportion of a-year-old spawner number in year y (Marteinsdottir & Thorarinsson 1998).

Management actions (here adjustment of fishing pressures) are based on perceived current stock status and harvest control rules set by the ICES (which are designed to achieve sustainable harvesting without compromising the reproductive capacity of the stock). The current status is assessed using scientific monitoring and catch data before the provision of annual catch advice (total allowable catch). Under the control rules, when the estimated SB remains above a fixed threshold (B_{pa}) at the start of the year following the assessment, the catch limit is computed based on target exploitation rate (F_{msy}). These two parameters (B_{pa} and F_{msy}) are designed to prevent overharvesting by accounting for uncertainty in population and harvest dynamics (ICES 2019). When the SB falls below B_{pa}, exploitation rate is adjusted to F_{msy} scaled to the proportion of SB relative to B_{pa}, thereby allowing the population to rebuild (adaptive management). For analysis here fishing pressure and SB relative to stock-specific reference points ($\bar{F}/F_{msy}$ and SB/B_{pa}) were used as proxies to evaluate the influence of the management measures on the transient dynamics of fish stocks. Fishing pressure is defined as the instantaneous rate of fishing mortality ($\bar{F}$),

which is commonly estimated by averaging age-specific fishing mortality rates over dominant ages in fishery catch (Table 1).

Data analysis

To explore how management-guided changes in fishing pressure and climate change have influenced the transient dynamics and recovery patterns of the northeast Atlantic fish stocks, I applied multilevel (hierarchical) modeling to derived demographic metrics to account for nonindependence in data structure (Gelman & Hill 2006) with stock, ecoregion, and year as grouping factors (random intercepts). Data exploration including identification of collinearity (through visual inspection correlation plots and variance inflation factors) and outliners (>three standard deviations) was performed before analysis (Zuur *et al.* 2009). The data exploration revealed two groups of stocks with diverging (increasing and declining) patterns in stock status based on relative spawner biomass (SB/B_{pa}). To explore mechanisms underlying the differences I applied generalized additive mixed effects models (GAMMs, Wood 2017) to these groups separately. In the following analyses the stocks were grouped based on stock status in the last 15 years of the time series (2002–2016); if spawner biomass is larger than 80% of a biological threshold (B_{pa}) for at least 50% of the period (eight years) a stock is classified as 'recovering', otherwise 'non-recovering'. This classification resulted in 27 recovering and 10 non-recovering stocks (Table 1). Trend analyses were first performed with year as a covariate to capture shared long-term historical patterns in relative spawner biomass, spawner demographic structure (mean age and age diversity), relative fishing pressure ($\bar{F}/F_{\mathrm{msy}}$), and transient growth. The response variables were assumed to follow a Gamma distribution with continuous, positive expected values μ and a logarithmic link function as

$$Y_{jk} \sim \mathrm{Gamma}(\mu_{ijk},\ \tau)$$

$$E(Y_{ijk}) = \mu_{ijk}$$

$$\text{var}(Y_{ijk}) = \mu_{ijk}^2/\tau$$

$$\log(\mu_{ijk}) = \beta_0 + f_1(\text{Year}_{ij}) + \text{stock}_i + \text{ecoregion}_j + \text{year}_{jk}$$

$$\text{stock}_i \sim N(0, \sigma^2_{stock}),\ \text{ecoregion}_j \sim N(0, \sigma^2_{ecoregion}),\ \text{year}_{jk} \sim N(0, \sigma^2_{year}) \quad (5)$$

where Y_{jik} is the response of stock i in ecoregion j in year k, τ is a Gamma distributed parameter, β_0 is the intercept, and f_1 is a smoother function (thin-plate cubic splines with ten maximum degrees of freedom or knots) for year; $stock_k$, $ecoregion_i$, and $year_{jk}$ are normally distributed random intercepts with mean zero and standard distribution σ for stock, ecoregion, and year nested within ecoregion. The structure of random effects was selected based on likelihood ratio tests applied to ten structures fitted with a restricted maximum likelihood method (REML) (Table S1). Further, I assessed direct effects of fishing on spawner biomass and age structure by evaluating relationships between relative fishing pressure and relative biomass and age structure of spawners as

$$Y_{jk} \sim \text{Gamma}(\mu_{ijk},\ \tau)$$

$$E(Y_{ijk}) = \mu_{ijk}$$

$$\text{var}(Y_{ijk}) = \mu_{ijk}^2/\tau$$

$$\log(\mu_{ijk}) = \beta_0 + f_1(\text{Fishing}_{ij}) + \text{stock}_i + \text{ecoregion}_j + \text{year}_{jk}$$

$$\text{stock}_i \sim N(0, \sigma^2_{stock}),\ \text{ecoregion}_j \sim N(0, \sigma^2_{ecoregion}),\ \text{year}_{jk} \sim N(0, \sigma^2_{year}) \quad (6)$$

where Y_{jik}, τ, β_0, σ_{stock}, $\sigma_{ecoregion}$, and σ_{year} are the same as above. f_1 is a smoother function for relative fishing pressure.

The contributions of fishing, management action, and climate to the transient dynamics of fish stocks with variable age structures were evaluated in two steps. I first tested for time-varying

contributions of these extrinsic factors to variations in vital rates and then evaluated how these factors influenced the elasticities of transient population growth:

Covariates of recruitment variability. Because natural mortality rates were assumed time-invariant in most of the assessments, variations in survival rates are in effect driven by fishing. Here, RS was thus selected as a demographic response variable (which integrates probabilities of survival (and maturation) to adult and spawning) for analysis. Further, because RS can vary with variations in spawner age structure and biomass (intrinsic factors), these intrinsic factors were also tested. To test for the time-varying contributions of the extrinsic and intrinsic factors, the following model was fitted to the data:

$$\mathrm{RS}_{\mathrm{total}ijk} \sim \mathrm{Gamma}(\mu_{ijk},\ \tau)$$

$$E(\mathrm{RS}_{\mathrm{total},ijk}) = \mu_{ijk}$$

$$\mathrm{var}(\mathrm{RS}_{\mathrm{total},ijk}) = \mu_{ijk}^2/\tau$$

$$\log(\mu_{ijk}) = \beta_0 + f_1(\mathrm{Year}_{ij}) + f_2(\mathrm{Year}_{ij}, \mathrm{Biomass}_{ijk}) + f_3(\mathrm{Year}_{ij}, \mathrm{Demography}_{ijk}) +$$

$$f_4(\mathrm{Year}_{ij}, \mathrm{Fishing}_{(i-1)jk}) + f_5(\mathrm{Year}_{ij}, \mathrm{Climate}_{ij}) + \mathrm{stock}_i + \mathrm{ecoregion}_j + \mathrm{year}_{jk}$$

$$\mathrm{stock}_i \sim N(0, \sigma^2_{stock}),\ \mathrm{ecoregion}_j \sim N(0, \sigma^2_{ecoregion}),\ \mathrm{year}_{jk} \sim N(0, \sigma^2_{year}) \qquad (7)$$

where $\mathrm{RS}_{\mathrm{total,y}}$ is the total per capita recruitment success rate of stock i in ecoregion j in year k, β_0 is the intercept, f_1–f_5 are smoother functions for covariates: year, year × density, year × demographics (spawner mean age and age diversity), year × climate, and year × fishing. *Climate*, *Biomass*, and *Demography* were lagged 0–3 years (depending on stock) to align with climate conditions and spawner status (biomass and age structure) in spawning year, whereas *Fishing* was lagged by an additional year (spawning year–1) to reflect indirect effects of fishing on recruitment success that are not accounted for by variations in spawners. Regional climate covariates were also lagged an additional year ($Climate_{(i-1)j}$) to reflect indirect effects through

regulation of local climate and ecosystem processes. Time (year)-varying covariate smoothers were tested as tensor product construction. For interpretability and model convergence one covariate of each type was tested at a time; one local or regional climate index (see above) for climate, SB or SB/B_{pa} for spawner density, $\bar{F}$ or $\bar{F}/F_{\mathrm{msy}}$ for fishing pressure, and $\mathrm{SA}_{\mathrm{mean}}$ or $\mathrm{SA}_{\mathrm{diversity}}$ for demographics.

Covariates of elasticity to recruitment variability. The transient dynamics of depleted fish stocks with age truncation often become recruitment-dependent and thus sensitive to variations in climate and habitat conditions. As the stocks recover (increases in abundance and age diversity), the transient dynamics are expected to become less sensitive to recruitment variability. To test for time-varying contributions of the extrinsic and intrinsic factors to variations in elasticity to RS (e_{rec}), the following model was fitted to the data, assuming e_{rec} follows a Beta distribution with expected values μ ($0 < \mu < 1$) and a logistic link function as

$$e_{\mathrm{rec},ijk} \sim \mathrm{Beta}(\mu_{ijk}, \phi)$$

$$E(e_{\mathrm{rec},ijk}) = \mu_{ijk}$$

$$\mathrm{var}(e_{\mathrm{rec},ijk}) = \mu_i (1 - \mu_i)/(\phi + 1)$$

$$\mathrm{logit}(\mu_{ijk}) = \beta_0 + f_1(\mathrm{Year}_{ij}) + f_2(\mathrm{Year}_{ij}, \mathrm{Biomass}_{ijk}) + f_3(\mathrm{Year}_{ij}, \mathrm{Demography}_{ijk}) + f_4(\mathrm{Year}_{ij}, \mathrm{Fishing}_{(i-1)jk}) + f_5(\mathrm{Year}_{ij}, \mathrm{Climate}_{ij}) + \mathrm{stock}_i + \mathrm{ecoregion}_j + \mathrm{year}_{jk}$$

$$\mathrm{stock}_i \sim N(0, \sigma^2_{stock}),\ \mathrm{ecoregion}_j \sim N(0, \sigma^2_{ecoregion}),\ \mathrm{year}_{jk} \sim N(0, \sigma^2_{year}) \qquad (8)$$

where ϕ is a parameter (> 0), and β_0, f_1–f_5, σ_{stock}, $\sigma_{ecoregion}$, and σ_{year}, are the same as above.

All numeric covariates were standardized by subtracting the mean and dividing by the standard deviation (z-scores). In model selection, intrinsic covariates were first added, followed by indirect fishing, and then climate. With the random effect structure selected (above) the models were tested sequentially for covariates by fitting with a maximum likelihood method,

followed by parameter (re)estimation with REML (Zuur *et al.* 2009) for the model with the lowest Akaike information criterion (AIC) score and highest model weight (w). AIC is computed as AIC = $-2\ln(L) + 2k$, where L is the likelihood of the model and k is the number of parameters, and the model weight of model i (w_i) is computed as

$$w_i = \frac{\exp(-\Delta AIC_i/2)}{\sum_j \exp(-\Delta AIC_i/2)} \quad (9)$$

As diagnostics, model residuals were checked for homogeneity and regressed against covariates that were both included and not included in the selected models (Zuur *et al.* 2009). All analyses were performed in R (version 4.2.1, R Development Core Team 2022) with the R packages of *gamm4* (v.0.2-6, Wood & Scheipl 2020) and *mgcv* (v.1.8-40, Wood 2022) for model-fitting, *mgcv* and *gratia* (v.0.7.3, Simpson & Singmann 2022) for model diagnostics, and *popbio* (v.2.7, Stubben, Milligan & Nantel 2020) for computations of demographic parameters and projections of population dynamics.

Because fish populations in different ecoregions experience a wide range of climate conditions and often have adapted to local environments, fish–covariate patterns may deviate from shared patterns captured by the regional models. To test this hypothesis, ecoregion-scale analyses were also performed using the same model structures for RS_{total} and e_{rec} and the model selection steps as above except for random effects. Because random effect estimates become less stable when the number of groups is fewer than eight (Bolker 2015), the random effect of the ecoregion-scale models consisted of year only, with stock being a fixed effect, except for Celtic Seas; the random effects of the Celtic Seas model consisted of year and stock.

Results

Regionwide analyses showed that relative fishing pressures on the recovering stocks on average peaked in the early 1990s ($\bar{F}/F_{msy}$ = ~2.2) and near-linearly declined since (~2.1% per

year; ΔAIC = 88.4), followed by increasing mean age (ΔAIC = 35.7), relative spawner biomass (ΔAIC = 17.2), and age diversity (ΔAIC = 21.1) (Fig. 2a). In contrast, relative fishing pressures on the non-recovering stocks kept rinsing until the late 1990s (to $\bar{F}/F_{\mathrm{msy}}$ = ~3.7 on average) before declining (~3.0% per year, ΔAIC = 63.3), but their relative spawner biomass continued to decline (ΔAIC = 92.7 and 31.5; Fig. 2a). Although the mean spawner age of the non-recovering stocks began rising with declining relative fishing pressures, no change in age diversity was detected (Fig. 2a). Direct effects of selective fishing consistently emerged as negative correlations between relative fishing pressure and spawner biomass and age structure in both stock groups (ΔAIC = 15.1–165.0, Fig. 2b). Contrasting temporal patterns between relative fishing pressure and spawner features were more pronounced in some ecoregions captured in year-specific (nested within ecoregion) random effect (variance) estimates, especially the Norwegian–Barents Seas, which showed abrupt shifts in the early 1990s (Fig. S2).

The time series of transient population growth rates reflected the contrasting patterns between the recovering and the non-recovering stocks, and variations among ecoregions (Fig. 3 and S3). The regional average growth rates of the recovering stocks linearly increased over the study period (ΔAIC = 15.0, Fig. 3). Although the relative spawner biomass of the non-recovering stocks continued to decline, their average growth rates began rising in the late 1990s (ΔAIC = 2.8, Fig. 3) when the relative fishing pressures began declining (Fig. 2a). These transient dynamics differed from asymptotic dynamics; the transient growth rates were lower than asymptotic growth rates in most stocks, and the deviations varied over years, with ~50% (19) of the stocks showing increasingly less differences in the last decade (Fig. S4). The observed age distributions of many of these stocks also differed from theoretical stable age distributions and

skewed toward younger ages (Fig. S5) owing to disproportionately higher annual mortality rates of older fish by fishing (Fig. S6).

Regionwide analyses detected declining trends in per capita recruitment success rate in both recovering and non-recovering stocks (ΔAIC = 2.1 and 2.7, Fig. 4a), with high among-stock variances (σ^2_{stock} = 0.31 and 0.48). Ecoregion-specific random intercepts also revealed generally higher year-to-year fluctuations in the non-recovering than in the recovering stocks (Fig. S3). After accounting for variations among stocks, ecoregions, and years, the recruitment rates of both stock groups declined with increasing relative spawner biomass (Fig. 4c and Table 2), which was more supported by data than absolute biomass (Table S2). But the temporal patterns of density dependency differed between the groups; the density dependent effect in the recovering stocks increased as the biomass rose, whereas that in the non-recovering stocks emerged in the last two decades but declined over time (Fig. 4c). Likewise, the contribution of spawner age structure to recruitment variability differed between the stock groups; the relationship between recruitment success and mean age in the recovering stocks shifted from positive to negative in the early 1990s, whereas that in the non-recovering stocks remained largely positive (Fig. 4b). An indirect positive fishing effect on recruitment rate was detected in the recovering stocks until the late 1980s but gradually diminished since (Fig. 4d). The models for both stock groups showed weak support for climate effects (Table S2). Of the climate indices tested for the non-recovering stocks (whose model had slightly more support than the recovering stocks), the model with ocean heat content anomaly in the year of spawning showed shifting (positive to negative) climate effects in the recent decades (Fig. 4e).

Ecoregion-scale analyses on recruitment success revealed patterns largely consistent with the regional analyses with some system-specific deviations (Fig. 5). In ecoregions with non-

recovering stocks like the Baltic, Celtic, and North Seas the density-dependent effect on recruitment on average became weakened over time; in contrast, the effect in the Norwegian–Barents Seas (with only recovering stocks) became strengthened (Fig. 5c). Correlations with spawner age structure metrics were detected in all but the Bay of Biscay and Faroes (Fig. 5b); in the Baltic Sea a positive correlation with age diversity became detectable in the early 1990s when fishing pressures began declining (Fig. 2). The time-varying effect of spawner age was especially pronounced in the Norwegian–Barents Seas stocks, showing a shift from positive to negative in the 1990s (Fig. 5b). An indirect fishing effect was (weakly) supported only in the North Sea stocks (Table S3 and Fig. 5d). Climate anomalies (in the year of spawning) contributed to variability in recruitment success in all ecoregions except the North Sea but the indices with the most statistical support varied among ecoregions (Fig. 5e and Table S3) despite high correlations among climate indices (Fig. S7). The ways climate anomalies contributed to recruitment variability also differed (Fig. 5e). In the Baltic Sea and Faroes correlations with climate anomalies remained largely positive during the past few decades. In contrast, the positive effect in the Norwegian–Barents Seas began declining in the recent decades. In the Bay of Biscay and Icelandic waters the climate effect shifted from positive to negative.

Trend analyses revealed consistent temporal patterns in elasticities to vital rates for the recovering and non-recovering stocks. Both showed declining elasticities to (post-recruitment) juvenile survival rate (ΔAIC = 15.6 and 18.9) and increasing elasticities to adult survival rate over time (ΔAIC = 17.0 and 6.7) (Fig. S8). But the regionwide analyses detected a declining trend in elasticities to recruitment success rate in the recovering stocks only (ΔAIC = 3.6, Fig. 6a). Ecoregion-specific variances in all the models fluctuated over years, but on average

elasticities to adult survival showed higher deviations from the regional trends than the other vital rates (Fig. S8).

Regionwide analyses on elasticities to recruitment success largely reflected the time-varying responses in recruitment to intrinsic and extrinsic drivers. For the recovering stocks the model indicated that more diverse ages increasingly contributed to elasticities in more recent years, whereas the contributions of mean ages gradually increased in the non-recovering stocks (Fig. 6b). Elasticities to recruitment declined with higher spawner biomass in both stock groups, but the density-dependent effect in the non-recovering stocks diminished over time (Fig 6c). The model with an indirect fishing effect in both stock groups showed a declining contribution to variations in the elasticities after the reductions in fishing pressure (Fig. 6d). In contrast, the models for both stock groups indicated an increasingly more positive climate effect (with the AMO index and winter sea temperature anomaly) over time (Fig. 6e).

Ecoregion-scale analyses on elasticities to recruitment success detected declining trends in all but the Bay of Biscay and the Norwegian–Barents Seas (Fig 7a), which showed little change in trends. The analyses also indicated spatial heterogeneity in the ways time-varying intrinsic and extrinsic drivers contributed to variations in the elasticities. For example, shifting contributions of spawner age structure were detected in most ecoregions, showing both diminishing (e.g., Faroes and North Sea) and increasing (e.g., Baltic Sea and Icelandic waters) trends (Fig. 7b). Negative correlations with spawner biomass were consistently detected except in the Baltic Sea (Fig. 7c). This maternal effect increased over time except in the Norwegian–Barents Seas, which showed the opposite trend (Fig. 7c). The models with an indirect fishing effect had statistical support for Faroes, and the Celtic, North, and Norwegian–Barents Seas; the fishing effect declined and/shifted over time except the Norwegian–Brents Sea, which showed an increasing

contribution of fishing since the 1990s (Fig. 7d). In the Baltic Sea and the Bay of Biscay a positive climate effect emerged in the 2000s (Fig. 7e), reflecting the temporal patterns of shifting local climate effects on recruitment success (Fig. 5e). In Faroes and Icelandic waters, where climate anomalies (the NAO index and spring sea temperature) had a positive effect on recruitment, the elasticities were inversely correlated with the indices, but this effect shifted to the opposite in the 2000s (Fig. 7e).

Discussion

Analyses on the transient dynamics of northeast Atlantic fish stocks reveal that management-aided reductions in fishing pressure and shifting climate conditions nonlinearly shaped rebuilding patterns of these historically depleted stocks through restorations of demographic structure (reversing age truncation) and reproductive capacity in recent decades. As the survival rates and demographic structures of reproductive fish improved with declining fishing pressures, transient population growth rates became less sensitive to variability in recruitment and juvenile survival and more to that in adult survival, allowing the stocks to rebuild biomass despite declining recruitment success. As the biomass of reproductive fish rebuilt, recruitment success rates also became increasingly regulated by density-dependent intrinsic processes involving increasingly higher numbers of older reproductive fish. Although warmer than average climates promoted recruitment success through the early 2000s in some ecoregions, warming trends over the past decades began adversely affecting reproductive performance. Variations in regulation of fishing pressure among stocks also led to diverging trends in recoveries of the stocks exposed to a range of local climate conditions. Insufficient or delayed reductions in fishing pressure can further deplete a stock and erode reproductive fish demographic structure, thereby diminishing fecundity and thus recovery potential, while also remaining sensitive to climate variability.

Rebuilding biomass by accounting for demographic structure through management are thus not only key to sustainable use of marine resource populations but also the foundation for effective applications of adaptive measures resilient to future environmental changes.

Transient dynamics of recovering populations from intense fishing pressures

Fishing-induced changes in the demography and reproductive capacity of an exploited population can be reversible when management measures are effectively applied to regulate fishing pressures. This pattern is displayed particularly in the Norwegian–Barents Seas, where fishing pressures were reduced by more than 60% (compared to the regional average of ~50%) since the early 1990s, followed by sharp rises in the average age and biomass of reproductive fish. But when a population experiences long-term intensive harvesting, recovery time can become longer (Hutchings 2015) and more uncertain (Neubauer *et al.* 2013), with the population remaining in long transient states (Hastings *et al.* 2018). Although fishing pressures on many northeast Atlantic fish stocks precipitously declined through stricter management measures applied since the late 1990s, demographic restorations and stock recoveries on average progressed gradually. Reducing fishing pressures can allow more adults to survive and contribute to the production of new recruits but the restoration of the demographic structure takes place over generations and may take longer (a decade or more) for severely depleted stocks. Further, although the declining trends in reproductive fish biomass halted in the early 2000s in most ecoregions, reduction levels in fishing pressure varied among ecoregions and stocks and were reflected in recovery patterns. When reductions in fishing pressure were not sufficient or delayed, the declining trends in reproductive capacity and deterioration of demographic structure in some stocks continued. Slow recoveries of severely depleted fish stocks are reportedly widespread (Hutchings 2000). Regionwide analyses on the non-recovering stocks in the

northeast Atlantic reveal that sustaining high fishing pressures for even a few more years can result in vastly different recovery patterns, with further age truncations and reductions in reproductive capacity, which could further diminish fishery yields (Hilborn *et al.* 2020).

Removal of some biomass from a population by harvesting can promote its productivity (Neubauer *et al.* 2013) by attenuating density-dependent effects on early life stage processes (competition for food and space for example, Anderson *et al.* 2008). Intense fishing pressures before the implementation of stricter management measures–mediated through reproductive fish–may have led to higher recruitment rates in depleted stocks in the northeast Atlantic Ocean. Fishing not only truncates age structure but induces changes in life-history traits that may influence recovery (Neubauer *et al.* 2013; Hutchings & Kuparinen 2020). The generation times of these depleted northeast Atlantic stocks were shortened (by 14 to 50%), which is often associated with high year-to-year variability in recruitment (Minto, Myers & Blanchard 2008) and high average recruitment rates (Bjørkvoll *et al.* 2012). Higher growth rates of depleted (and age-truncated) fish populations also likely benefited during the early stages of recovery as more reproductive fish contributed to spawning events, thereby increasing the probability of recruitment success. These indirect effects, however, diminished over time following the reductions of fishing pressures. Despite the signs of recovery in reproductive fish, per capita recruitment success rates on average declined in the northeast Atlantic stocks, as also reported in other Atlantic ecoregions (Britten, Dowd & Worm 2016). But these apparent patterns were shaped by different processes among stocks. In the recovering stocks density dependency remained present in recruitment success throughout the past decades and its strength increased as reproductive fish biomass rose, likely slowing recoveries as fishing pressures declined. In contrast, in the non-recovering stocks density dependency in recruitment success emerged only

502 after the reductions in fishing pressure but its strength continued to decline with reproductive fish
503 biomass, suggesting contributions of other (extrinsic) drivers.
504 Density dependency in early life stages also perhaps explains nonlinear relationships (shifting
505 from positive to negative) between reproductive fish age and per capita recruitment success in
506 the recovering stocks (especially in the Norwegian–Barents Seas) following the reductions in
507 fishing pressure. Higher mean age and age diversity in reproductive fish are expected to promote
508 recruitment success (Rogers & Dougherty 2019). Age-dependent variations in spawning pattern
509 can influence egg viability and larval survival; older spawners tend to produce more viable
510 offspring (Hixon, Johnson & Sogard 2014). But the analyses on the northeast Atlantic fishes
511 show that only the non-recovering (age-truncated) stocks kept positive relationships between
512 reproductive fish age structure and recruitment success. In the recovering stocks, density
513 dependency may have played a larger role than maternal effects, revealing a shift in
514 compensatory processes. As adult survival improves and population density increases, pre-recruit
515 survival may decline (owing to competition for food and other resources including cannibalism
516 by adults), contributing to apparent increases in average ages of reproductive fish.
517 Short-term (year-to-year) fluctuations in recruitment can propagate through transient dynamics
518 of a population when its (demographic) buffering capacity is compromised by age truncation
519 (Anderson *et al.* 2008). Truncated age distributions in reproductive fish may produce volatile
520 population behaviors that reflect recruitment pulses (Anderson *et al.* 2008). As adult survival
521 improved and stock biomass rebuilt in many northeast Atlantic fish stocks, the transient growth
522 rates became less sensitive to recruitment variability and more sensitive to adult survival. The
523 regionwide analyses show that increases in transient growth rate and biomass during the past few
524 decades resulted largely from improved survival rates of older fish. Greater sensitivities to adult

525 survival also may make harvested populations more manageable. Nonlinear responses to age
526 structure in reproductive fish is however also evident in sensitivity to recruitment variability.
527 Although the buffering effect of increasingly age-diverse reproductive fish emerged in many
528 ecoregions especially in the early stages of recovery, this relationship also shifted as the
529 recoveries further progressed (e.g., the Norwegian–Barents Seas), likely responding to other
530 intrinsic dynamics.

531 *Climate regulation of demographic variations*

532 Fish populations experiencing persistent selective depletions of older adults often become
533 sensitive to variations in early life stage processes that reflect signals in environmental
534 conditions like climate variability (Ottersen, Hjermann & Stenseth 2006; Rouyer *et al.* 2011).
535 Warmer than average climate conditions in the northeast Atlantic Ocean increasingly contributed
536 to observed patterns in fish recruitment success, reflecting shifting climate effects on recruitment
537 processes. For example, stratification may become intensified as climate warms, limiting nutrient
538 movement to deeper waters and food accessibility for the early life stages of demersal and
539 benthic species (Moore *et al.* 2018). At the region scale, however, the models captured only
540 weak responses in recruitment by the fish stocks to regional climate signals likely because of
541 heterogeneous warming patterns among ecoregions, as also seen in other parts of the world
542 (Barange *et al.* 2018). Region-scale analyses may mask differential effects of local climate and
543 oceanographic features (climate-induced shifts in ocean heat content and primary productivity
544 for example) that marine species are adapted to and experience (Conover 1992).

545 Ecoregion-scale variability in recruitment success may better reflect how fish reproductive
546 behavior responds to regional climate mediated by local habitat conditions, as hypothesized in
547 past research (Myers 1998; Ottersen & Stenseth 2001). For stocks in high latitude systems like

548 the Norwegian–Barents Seas and Icelandic waters, for example, climate conditions in winter–
549 spring (December–May) that regulate phonologies like timings of spawning migration (Sundby
550 & Nakken 2008) contributed to recruitment variability. Warming-induced reductions in sea ice
551 extent in these ecoregions promoted ecosystem productivity in the late 1990s and early 2000s
552 and may have benefited upper trophic animals like fish (Stenevik & Sundby 2007), likely
553 through changes in growth rate and life stage duration (Houde 2016). When spawning times
554 coincide with the period of high prey abundance, pre-recruit fish can grow more and experience
555 less size-dependent mortalities (like predation), contributing to greater recruitment success
556 (Peck, Huebert & Llopiz 2012). In contrast, in semi-enclosed systems like the Baltic Sea
557 warming-induced changes in nearshore habitat conditions in summer (June–August) (lower
558 salinity caused by higher precipitation and freshwater inflows for example, MacKenzie *et al.*
559 2007) may have played a greater role in regulating recruitment success through biophysical
560 processes during early life-stages.
561 Demographic responses by fish populations to changing climate conditions also may vary
562 discontinuously (Brander 2007). Local and regional climate conditions (both favorable and
563 unfavorable) that early life stage fish experience can persist through time (Ottersen *et al.* 2001)
564 and may emerge as delayed effects on transient population dynamics. In some northeast Atlantic
565 ecoregions the ways that climate affects fish recruitment success shifted from positive to
566 negative and may have slowed their recoveries. These shifts suggest that even in the ecoregions
567 where warming climate promoted stock productivity in the early twentieth century, fish began to
568 experience adverse (direct and indirect) effects. Mobile species can adjust their movement
569 (deeper and poleward) to mitigate physiological stress from warming upper water columns
570 (Pinsky *et al.* 2013; Engelhard, Righton & Pinnegar 2014). But asynchronous shifts in spatial

571 distribution by spawning fish and seasonal events in lower trophic groups like plankton booms
572 (phenological mismatches) also could trigger a series of events unfavorable for early life fish
573 (Asch & Erisman 2018), shrinking the probability of recruitment success.

574 Climate variability that regulates local ocean conditions may propagate through vital rates to
575 shape transient population dynamics of marine species (Jenouvrier *et al.* 2018). Depleted
576 populations in particular may have heightened sensitivities to adverse environmental conditions
577 (Hidalgo *et al.* 2011; Rouyer *et al.* 2011), which are becoming increasingly more variable in
578 recent decades (Rathore *et al.* 2020). Although the sensitivities of transient growth to recruitment
579 variability in the northeast Atlantic fish stocks declined as they recovered in the recent decades,
580 the analyses reveal that increasingly warmer than average climate began influencing how
581 recruitment variability propagates through transient dynamics. For example, in high-latitude
582 systems like Faroes, where the sensitivity to recruitment variability negatively covaried with
583 climate, this stabilizing effect diminished (and shifted to the opposite) as the climate warmed. In
584 contrast, in the Baltic Sea, where the sensitivity to recruitment variability positively covaried
585 with climate, this amplifying effect became strengthened as the climate warmed. Climate effects
586 on transient population dynamics also may, however, depend on the status (including
587 demographic structure) of fish stocks. In the Norwegian–Barents Seas, where fish stocks
588 experienced higher reductions in fishing pressure early and thus higher biomass rebuilding rates
589 than other stocks, changes in climate conditions had little influence on the sensitivities of
590 transient growth.

591 *Transients as an integrated measure of effects of fishing, management, and climate*

592 Analysis of transient population dynamics can reveal how time-varying demographic structures
593 and vital rates contribute to recovery patterns of managed resource populations when also

exposed to low-frequency, nonstationary drivers like climate. Declined sensitivities to highly variable demographic parameters like recruitment, as displayed by the northeast Atlantic fish stocks, can provide a buffer against rising environmental variability. Increasing sensitivities to adult survival further suggest that the stocks also are expected to become more responsive to management actions through regulation of fishing pressure (enforcing positive feedback), and future management plans would benefit from maintaining healthy (age-diverse) reproductive populations of exploited species (Pinsky & Byler 2015). Combined with other management measures (like use of marine protected areas and fish size limits, White *et al.* 2013; Hixon, Johnson & Sogard 2014), restoring and maintaining the demographic structure of an exploited species thus may enhance resilience against destabilizing effects of environmental variability amplified by climate change.

Emerging non-negligible changes in demographic responses to rising climate variability nevertheless may influence the efficacy of fisheries management. Although historical climate conditions promoted the productivity of fish stocks in the northeast Atlantic Ocean, some stocks in this region and elsewhere in the Northern Hemisphere already are experiencing adverse effects of changing climate (Pershing *et al.* 2015; Free *et al.* 2019). As many biological responses to climate-driven changes in surface temperature and other ocean properties are often nonlinear, we would expect continued shifts in how climate influences marine resource populations and management (Britten, Dowd & Worm 2016). Accounting for these climate-induced changes thus may not only reduce uncertainties in assessment but also improve the performance of management measures (Rouyer et al. 2011; Bahri et al. 2021).

Exploited marine fish species are an integral part of an ecosystem and changes in their abundances and demographic structures may propagate through community and ecosystem

dynamics (Jennings & Kaiser 1998), triggering a series of changes in ecologically connected species (Goto *et al.* 2020). As adult survival improves in historically overharvested populations, ecological processes including resource competition and predation also may indirectly modify vital rates and demographic structures of non-target species (van Gemert & Andersen 2018). Improving our understanding of how warming and more variable climates continue to reshape the transient dynamics (through changes in life history traits and demographics) would help develop management plans to mitigate the risk of overexploitation and safeguard ecosystem services against rising environmental variability.

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Data Availability Statement

The data that support the findings of this study are openly available in ICES Scientific Reports at https://ices-library.figshare.com/, reference number ICES CM 2017/ACOM:06, ICES CM 2017/ACOM:08, ICES CM 2017/ACOM:11, ICES CM 2017/ACOM:12, ICES CM 2017/ACOM:13, and ICES CM 2017/ACOM:21, and in the data archives of Met Office Hadley Centre, and NOAA Physical Sciences Laboratory and National Centers for Environmental Information at https://www.metoffice.gov.uk, https://psl.noaa.gov, and https://www.ncei.noaa.gov.

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Tables

Table 1. Stock-specific information and management measures used in assessments for 38 fish stocks in the northeast Atlantic Ocean included in the study. Stock ID indicates a unique ID for each stock assigned by the International Council of Exploration of the Sea (ICES); period and years indicate the years and the total number of years that stock data are available; age indicates the age classes included in the assessments; *F* range indicates the age range used to compute mean fishing mortality rates for assessment; F_{msy} and B_{pa} indicate the management reference points set for each stock as target fishing mortality rates that produce maximum sustainable yields and biomasses that satisfy the precautionary approach; and status indicates recovery status assigned based on spawner biomass relative to B_{pa} for analysis (R: recovering and NR: non-recovering) in this study.

common name	scientific name	ecoregion	stock ID	period	years	age	*F* range	F_{msy}	B_{pa}	status	source¶
cod	*Gadus morhua*	Norwegian–Barents Seas	cod.27.12	1946-2016	71	3-15+	5 -10	0.40	460000	R	a
cod	*Gadus morhua*	North Sea	cod.27.47d20	1963-2016	54	1-6+	2-4	0.31	150000	NR	b
cod	*Gadus morhua*	Baltic Sea	cod.27.22-24	1994-2016	23	1-5+	3-5	0.26	38400	NR	c
cod	*Gadus morhua*	Icelandic Waters	cod-farp	1959-2016	58	1-10+	3-7	0.23	29226	NR	d
cod	*Gadus morhua*	Icelandic Waters	cod.27.5a	1955-2016	62	3-14+	5-10	0.20	160000	R	d
cod	*Gadus morhua*	Celtic Seas	cod.27.6a	1981-2016	36	1-7+	2-5	0.17	22000	NR	e
cod	*Gadus morhua*	Celtic Seas	cod.27.7a	1968-2016	49	0-6+	2-4	0.31	8161	NR	e
cod	*Gadus morhua*	Celtic Seas	cod.27.7e-k	1971-2016	46	1-7+	2-5	0.35	10300	NR	e
four-spot megrim	*Lepidorhombus boscii*	Bay of Biscay and Iberian Coast	ldb.27.8c9a	1986-2017	31	1-7+	2-5	0.19	4600	R	f
haddock	*Melanogrammus aeglefinus*	Norwegian–Barents Seas	had-arct	1950-2016	67	3-13+	4-7	0.35	80000	R	a
haddock	*Melanogrammus aeglefinus*	North Sea	had.27.46a20	1972-2016	45	0-8+	2-4	0.19	132000	R	b
haddock	*Melanogrammus aeglefinus*	Icelandic Waters	had-faro	1957-2016	60	1-10+	3-8	0.13	22843	R	d
haddock	*Melanogrammus aeglefinus*	Icelandic Waters	had.27.5a	1979-2016	38	2-11+	4-7	0.52	59000	R	d
haddock	*Melanogrammus aeglefinus*	Celtic Seas	had-rock	1991-2016	26	1-7+	2-5	0.20	10200	R	e
haddock	*Melanogrammus aeglefinus*	Celtic Seas	had.27.7b-k	1993-2016	24	0-8+	3-5	0.40	10000	R	e
herring	*Clupea harengus*	Baltic Sea	her.27.25-2932	1974-2016	43	1-8+	3-6	0.22	600000	R	c
herring	*Clupea harengus*	Baltic Sea	her.27.28	1977-2016	40	1-8+	3-7	0.32	57100	R	c
megrim	*Lepidorhombus whiffiagonis and L. boscii*	Bay of Biscay and Iberian Coast	meg.27.8c9a	1986-2016	31	1-7+	2-4	0.19	980	R	f
plaice	*Pleuronectes platessa*	North Sea	ple.27.7d	1980-2016	37	1-7+	3-6	0.25	25826	R	b
plaice	*Pleuronectes platessa*	North Sea	ple.27.420	1957-2016	60	1-10+	2-6	0.21	230000	R	b
plaice	*Pleuronectes platessa*	Baltic Sea	ple.27.7e	1999-2016	18	1-5+	3-5	0.37	5550	R	c
plaice	*Pleuronectes platessa*	Celtic Seas	ple.27.7a	1981-2016	36	1-8+	3-6	0.16	5825	R	e
plaice	*Pleuronectes platessa*	Celtic Seas	ple-echw	1980-2016	36	2-10+	3-6	0.24	2443	NR	e
saithe	*Pollachius virens*	North Sea	pok.27.3a46	1967-2016	50	3-9+	4-7	0.36	150000	R	b
saithe	*Pollachius virens*	Icelandic Waters	pok.27.5b	1961-2016	56	3-11+	4-8	0.30	41400	R	d
saithe	*Pollachius virens*	Icelandic Waters	pok.27.5a	1980-2016	37	3-14+	4-9	0.20	61000	R	d
saithe	*Pollachius virens*	Norwegian–Barents Seas	pok.27.1-2	1960-2016	57	3-8+	4-7	0.32†	220000	R	a
sole	*Solea solea*	Baltic Sea	sol.27.20-24	1984-2016	33	2-6+	3-5	0.23	2600	R	c
sole	*Solea solea*	Bay of Biscay and Iberian Coast	sol-bisc	1984-2016	33	2-8+	3-6	0.33	10600	R	f
sole	*Solea solea*	Celtic Seas	sol.27.7a	1970-2016	47	2-8+	4-7	0.20	3100	NR	e
sole	*Solea solea*	Celtic Seas	sol.27.7e	1969-2016	48	2-12+	3-9	0.29	2900	R	e
sole	*Solea solea*	Celtic Seas	sol.27.7fg	1971-2016	46	1-10+	4-8	0.27	2380	R	e
sprat	*Sprattus sprattus*	Baltic Sea	spr.27.22-32	1974-2016	43	1-8+	3-5	0.26	574000	R	c
summer-spawning herring	*Clupea harengus*	Icelandic Waters	her-vasu	1987-2016	30	3-13+	5-10	0.22	273000	R	e
turbot	*Scophthalmus maximus*	North Sea	tur.27.3a	1981-2016	36	1-8+	2-6	0.36*	4163*	R	b
whiting	*Merlangius merlangus*	North Sea	whg.27.47d	1990-2016	27	1-8+	2-7	0.15	166708	R	b

whiting	*Merlangius merlangus*	Celtic Seas	whg.27.6a	1981-2016	36	1-7+	2-4	0.23	44600	NR	e
whiting	*Merlangius merlangus*	Celtic Seas	whg-iris	1980-2016	37	0-6+	1-3	0.22	16300	NR	e

†F_{msy} was not defined for Barents Sea Saithe in 2017 and an alternative reference point applied (F_{mp}) were used for analysis in the study.
*The reference points for North Sea turbot were not defined until 2018 and the stock was excluded from multilevel modeling analysis.
¶Stock information is taken from ICES Scientific Reports: (a) ICES (2017a), (b) ICES (2017e), (c) ICES (2017b), (d) ICES (2017c) (e) ICES (2017f), (f) ICES (2017d).

Table 2. Parameter estimates and test statistics for the generalized additive mixed effects models selected for the northeast Atlantic fish stocks with per capita recruitment success (RS_{total}) as a response variable (Table S2). EDF, *F*, CI, *t*, and SD indicate the effective degrees of freedom, F-statistic, confidence intervals, t-value, and standard deviation.

model structure and parameter	smoother		fixed effect			random effect	
	EDF	*F*	estimate	95% CI	*t*	variance	SD
recovering							
$RS_{total} \sim f(\text{Year}) + f(\text{Year}, SA_{mean}) + f(\text{Year}, SB/B_{pa}) + f(\text{Year}, \bar{F}_{lag1})$							
$f(\text{Year})$	1.00	7.75					
$f(\text{Year}, SA_{mean})$	4.49	3.12					
$f(\text{Year}, SB/B_{pa})$	5.43	19.58					
$f(\text{Year}, \bar{F}_{lag1})$	2.00	5.73					
β_0			2.26	(1.81, 2.7)	9.97		
β_{Year}			-0.15	(-0.26, -0.03)	-2.51		
$\beta_{Year \times SAmean1}$			-0.34	(-0.51, -0.17)	-3.99		
$\beta_{Year \times SAmean2}$			-0.04	(-0.14, 0.07)	-0.71		
$\beta_{Year \times SSB/Bpa1}$			0.43	(0.26, 0.61)	4.83		
$\beta_{Year \times SSB/Bpa2}$			-0.05	(-0.17, 0.07)	-0.81		
$\beta_{Year \times \bar{F}lag1,1}$			-0.06	(-0.18, 0.06)	-1.00		
$\beta_{Year \times \bar{F}lag1,2}$			0.16	(0.06, 0.26)	3.07		
stock						0.20	0.45
ecoregion/year						0.13	0.36
ecoregion						0.06	0.25
residual						0.34	0.58
non-recovering							
$RS_{total} \sim f(\text{Year}) + f(\text{Year}, SA_{mean}) + f(\text{Year}, SSB/B_{pa}) + f(\text{Year}, OHC)$							
$f(\text{Year})$	1.00	7.95					
$f(\text{Year}, SA_{mean})$	4.47	0.58					
$f(\text{Year}, SB/B_{pa})$	3.51	17.8					
$f(\text{Year}, OHC)$	2.19	187.8					
β_0			2.40	(1.58, 3.22)	5.75		
β_{Year}			-0.26	(-0.48, -0.03)	-2.22		
$\beta_{Year \times SAmean1}$			-0.18	(-0.47, 0.11)	-1.20		
$\beta_{Year \times SAmean2}$			0.82	(0.6, 1.05)	7.15		
$\beta_{Year \times SSB/Bpa1}$			-0.40	(-0.63, -0.16)	-3.28		
$\beta_{Year \times SSB/Bpa2}$			0.05	(-0.15, 0.25)	0.46		
stock						0.42	0.64
ecoregion/year						0.17	0.41
ecoregion						1.81×10^{-5}	4.26×10^{-3}
residual						0.27	0.52

Table 3. Parameter estimates and test statistics for the generalized additive mixed effects models selected for the northeast Atlantic fish stocks with elasticity to recruitment success (e_{RS}) as a response variable (Table S2). EDF, F, 95% CI, t, and SD indicate the effective degrees of freedom, F-statistic, confidence intervals, t-value, and standard deviation.

model structure and parameter	smoother		fixed effect			random effect	
	EDF	F	estimate	95% CI	t	variance	SD
recovering							
$e_{RS} \sim f(\text{Year}) + f(\text{Year, SA}_{mean}) + f(\text{Year, SB}/B_{pa}) + f(\text{Year, } \bar{F}_{lag1}/F_{msy}) + f(\text{Year, AMO}_{lag1})$							
f(Year)	1.00	0.60					
f(Year, SA_{mean})	3.51	1.61					
f(Year, SB/B_{pa})	7.61	39.16					
f(Year, $\bar{F}_{lag1}/F_{msy}$)	5.06	3.71					
f(Year, AMO_{lag1})	7.15	3.09					
β_0			-5.16	(-5.25, -5.07)	-118.0		
stock						0.02	0.16
ecoregion/year						0.01	0.11
ecoregion						0.01	0.08
non-recovering							
$e_{RS} \sim f(\text{Year}) + f(\text{Year, SA}_{mean}) + f(\text{Year, SB}/B_{pa}) + f(\text{Year, } \bar{F}_{lag1}/F_{msy}) + f(\text{Year, wSST}_{anom})$							
f(Year)	1.00	2.10					
f(Year, SA_{mean})	7.01	141.36					
f(Year, SB/B_{pa})	6.65	4.88					
f(Year, $\bar{F}_{lag1}/F_{msy}$)	3.60	1.96					
f(Year, $wSST_{anom}$)	3.02	1.52					
β_0			-5.16	(-5.36, -4.96)	-50.2		
stock						0.09	0.31
ecoregion/year						0.008	0.088
ecoregion						3.4×10^{-7}	5.8×10^{-4}

Figure legends

Figure 1. Study systems and climate conditions in the northeast Atlantic Ocean. (a) Geographic locations of the ecoregions, which are defined by the International Council of Exploration of the Sea (ICES): Norwegian and Barents Seas (62°0'N–82°0'N at 11°0'W–68°30'E), Greater North Sea (56°0'N at 2°55'E), Baltic Sea (53°35'N–65°54'N at 11°57'E–30°14'E), Faroes (60°0'N–63°0'N at 15°0'W–4°0'W), Icelandic waters (64°38'N at 18°55'W), the Bay of Biscay and the Iberian Coast (42°39'N at 8°53'W), and Celtic Seas (48°0'N–60°30'N at 18°0'W–1°21'W). (b) Regional climate indices (North Atlantic Oscillation (NAO) index, Atlantic Meridional Oscillation index, and upper (0–400m) ocean heat content (OHC) anomaly) during the study period (1946–2016). (c) Seasonal sea surface temperature anomalies in each ecoregion. The time series of temperature anomalies in each ecoregion are truncated to show only the years that the fish stock data and assessments included in the study are available.

Figure 2. Regional patterns in fishing pressure and reproductive metrics of the recovering and non-recovering northeast Atlantic fish stocks during the study period (1946–2016). (a) Temporal trends in relative fishing pressure, relative spawner biomass, mean spawner age, and spawner age diversity. Vertical dashed lines indicate the reference year (2002) used to define the recovery status of fish stocks based on relative spawner biomass in analysis. (b) Relationships between relative fishing pressure and relative spawner biomass and age structure metrics. Solid lines and ribbons indicate regional average trends in time (a) or relative fishing pressure (b) and 95% confidence intervals estimated by generalized additive mixed effects modeling with year (a) or relative fishing pressure (b) as a fixed effect, and ecoregion, year within ecoregion, and stock as random effects. Circles indicate partial residuals estimated from the models. Relative fishing pressure and relative spawner biomass are defined as estimated fishing mortality rate and

spawner biomass relative to management reference points (F_{msy} and B_{pa}) defined by the International Council of Exploration of the Sea (ICES).

Figure 3. Regional trends in transient population growths of the recovering and non-recovering northeast Atlantic fish stocks during the study period (1946–2016). Solid lines and ribbons indicate temporal trends and 95% confidence intervals estimated by generalized additive mixed effects modeling with year as a fixed effect, and ecoregion, year within ecoregion, and stock as random effects. Circles indicate partial residuals estimated from the models.

Figure 4. Regional trends in and covariates of per capita recruitment success (fecundity) of the recovering and non-recovering northeast Atlantic fish stocks during the study period (1946–2016). (a) Temporal trends. Solid lines and ribbons indicate temporal trends and 95% confidence intervals estimated by generalized additive mixed effects modeling with year as a fixed effect, and ecoregion, year within ecoregion, and stock as random effects. Red circles indicate partial residuals estimated by the models. (b–e) Time-varying effects of spawner age structure, spawner biomass, fishing pressure. and climate condition. Covariates selected for each type in the models are indicated in the y-axis labels. Color gradients and contour lines indicate the partial effects of covariates estimated (as tensor interaction terms) in the models (only the covariate types that are supported by data are shown). Warmer colors indicate higher values, and the ranges of the partial effects differ among the covariates and are indicated as values on the contour lines. Gray circles indicate back-transformed input data.

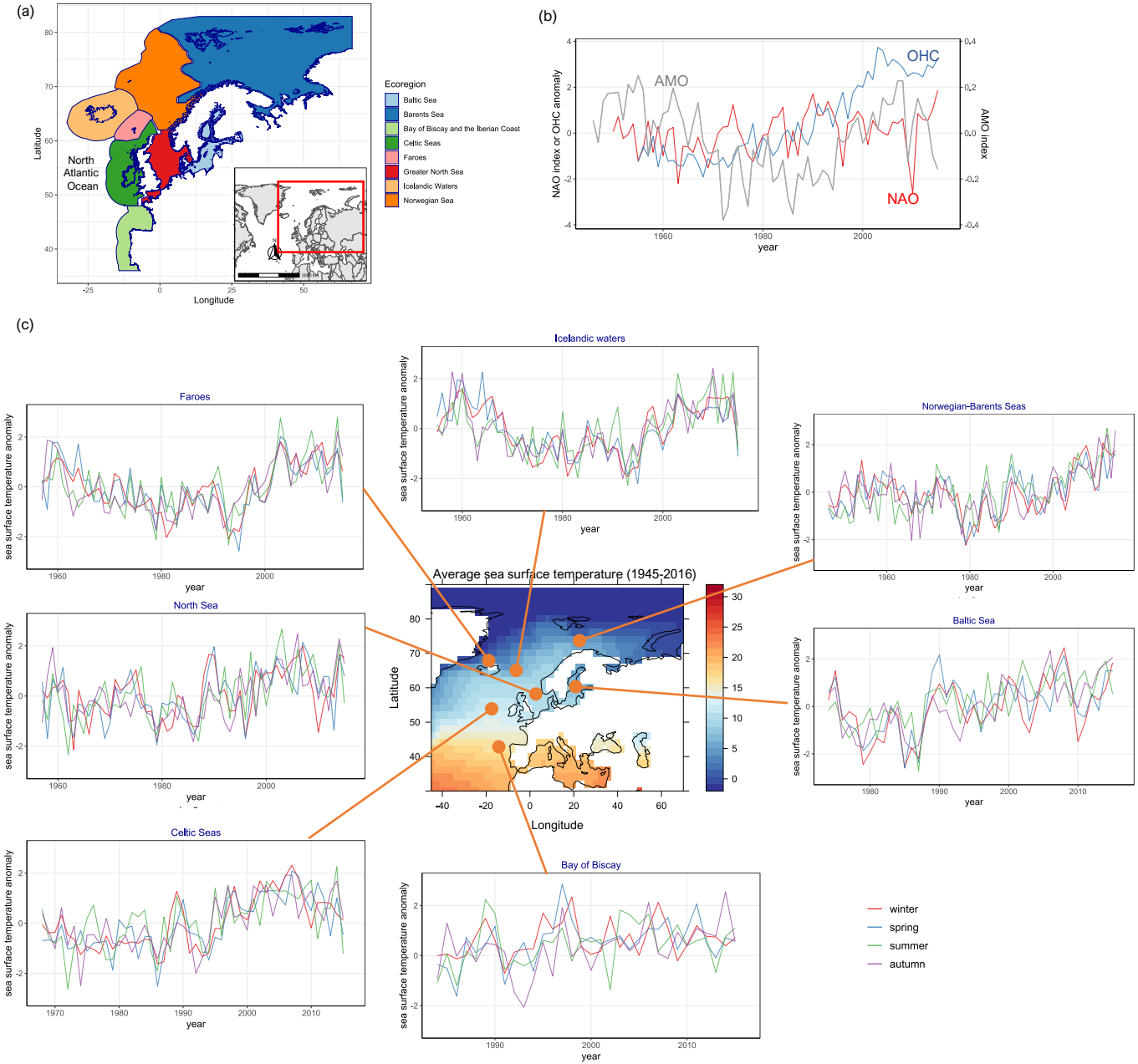
Figure 5. Ecoregion-scale trends and covariates of per capita recruitment success (fecundity) of the northeast Atlantic fish stocks during the study period (1946–2016). (a) Temporal trends. Solid lines and ribbons indicate temporal trends and 95% confidence intervals estimated by generalized additive mixed effects modeling with year as a fixed effect, and ecoregion, year

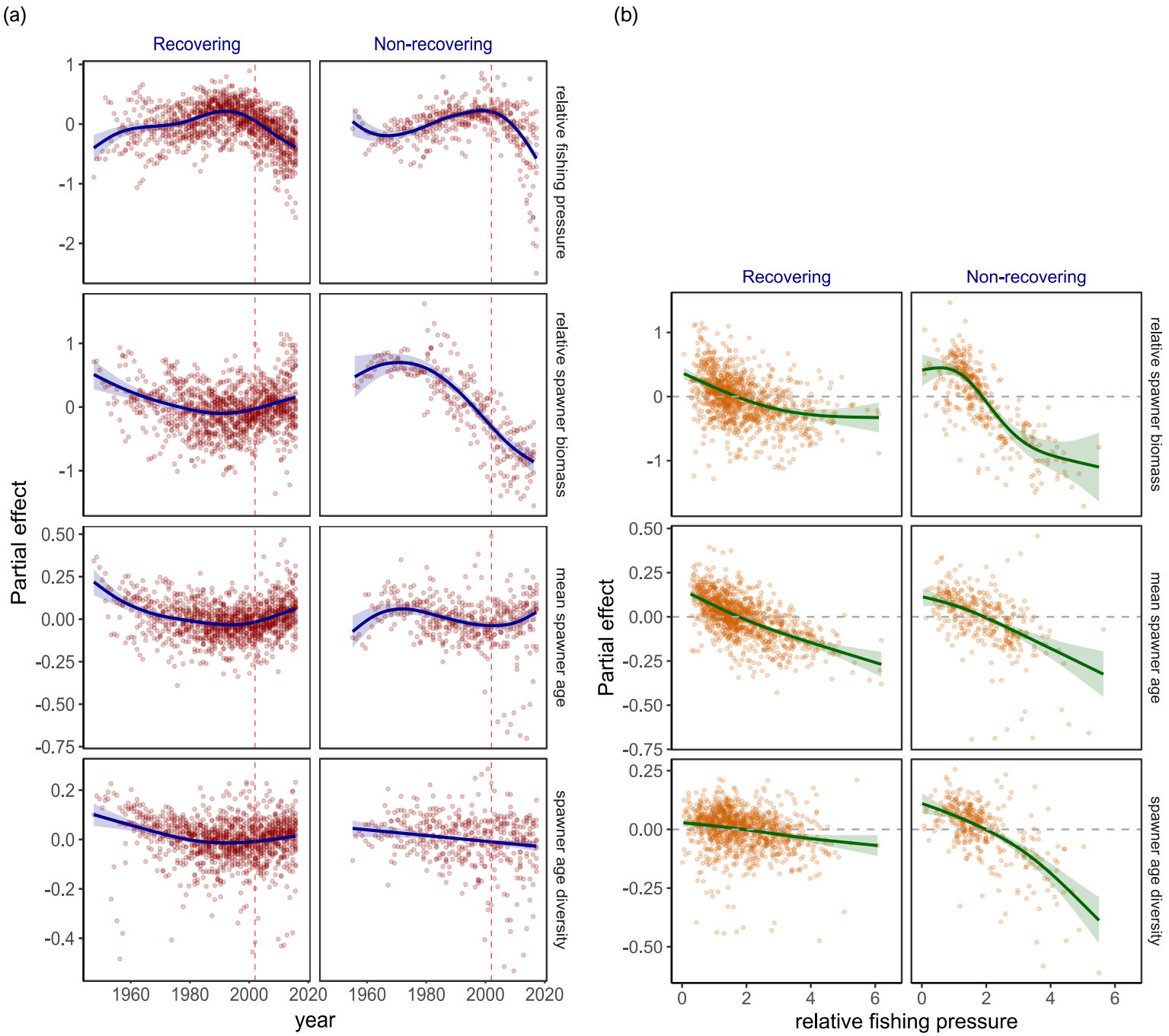
within ecoregion, and stock as random effects. Circles indicate partial residuals estimated by the models. (b–e) Time-varying effects of spawner age structure, spawner biomass, fishing pressure. and climate condition. Covariates selected in the models are indicated in the y-axis labels. Color gradients and contour lines indicate the partial effects of covariates estimated (as tensor interaction terms) in the models. Warmer colors indicate higher values, and the ranges of the partial effects differ among the covariates and are indicated as values on the contour lines. Gray circles indicate back-transformed input data.

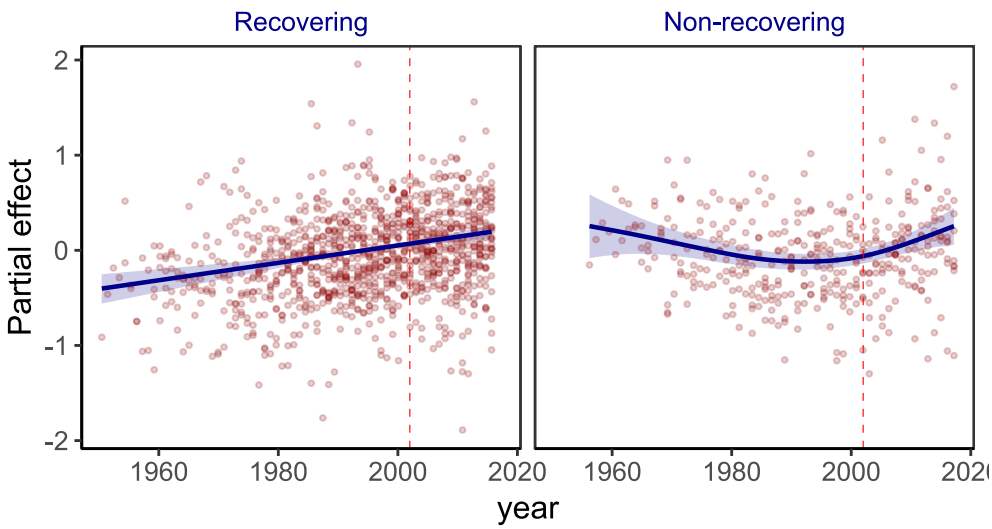
Figure 6. Regional trends in and covariates of elasticity to per capita recruitment success of the recovering and non-recovering northeast Atlantic fish stocks during the study period (1946–2016). (a) Temporal trends. Solid lines and ribbons indicate temporal trends and 95% confidence intervals estimated by generalized additive mixed effects modeling with year as a fixed effect, and ecoregion, year within ecoregion, and stock as random effects. Circles indicate partial residuals estimated by the models. (b–e) Time-varying effects of spawner age structure, spawner biomass, fishing pressure, and climate condition. Covariates selected in the models are indicated in the y-axis labels. Color gradients and contour lines indicate the partial effects of covariates estimated (as tensor interaction terms) in the models. Warmer colors indicate higher values, and the ranges of the partial effects differ among the covariates and are indicated as values on the contour lines. Gray circles indicate back-transformed input data.

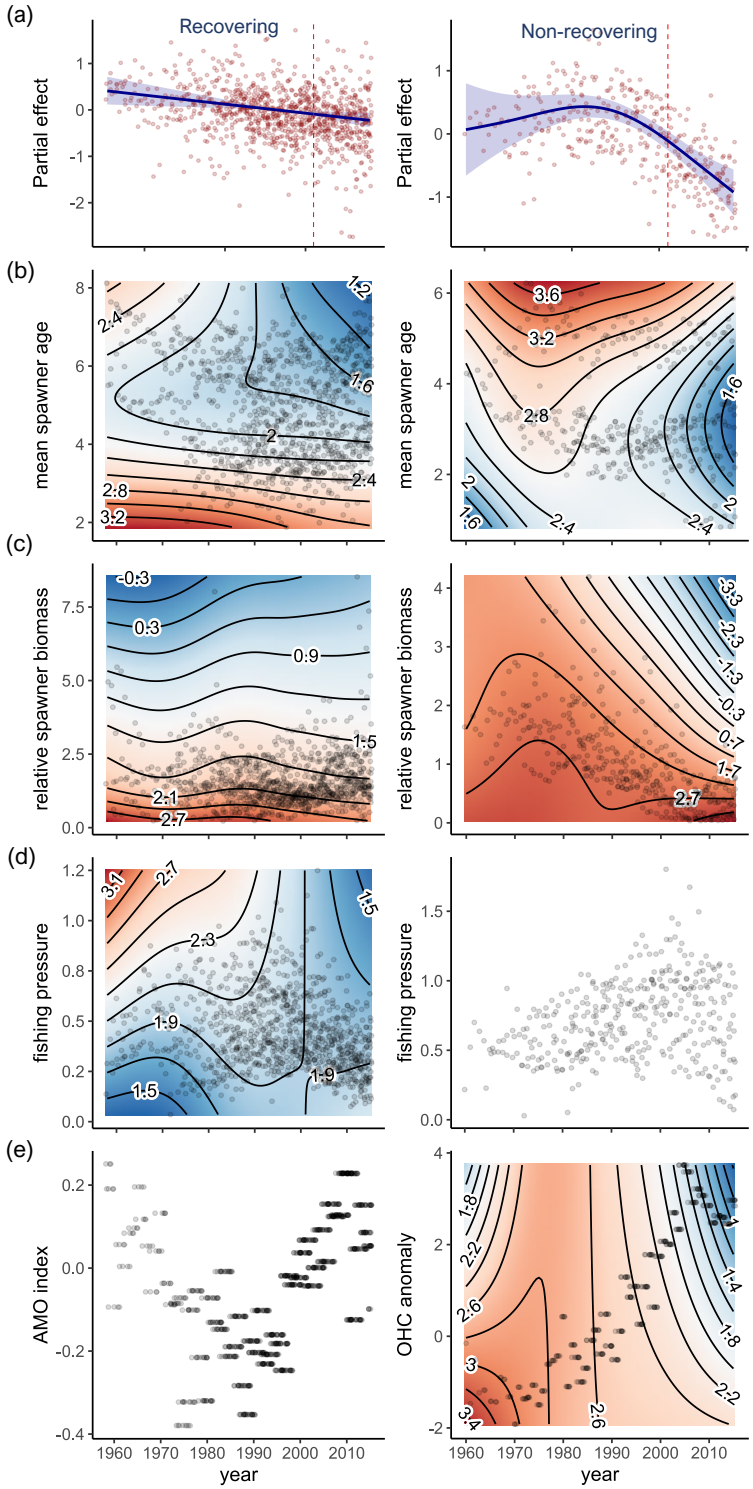
Figure 7. Ecoregion-scale trends and covariates of elasticity to per capita recruitment success of the northeast Atlantic fish stocks during the study period (1946–2016). (a) Temporal trends. Solid lines and ribbons indicate temporal trends and 95% confidence intervals estimated by generalized additive mixed effects modeling with year as a fixed effect, and ecoregion, year within ecoregion, and stock as random effects. Circles indicate partial residuals estimated by the

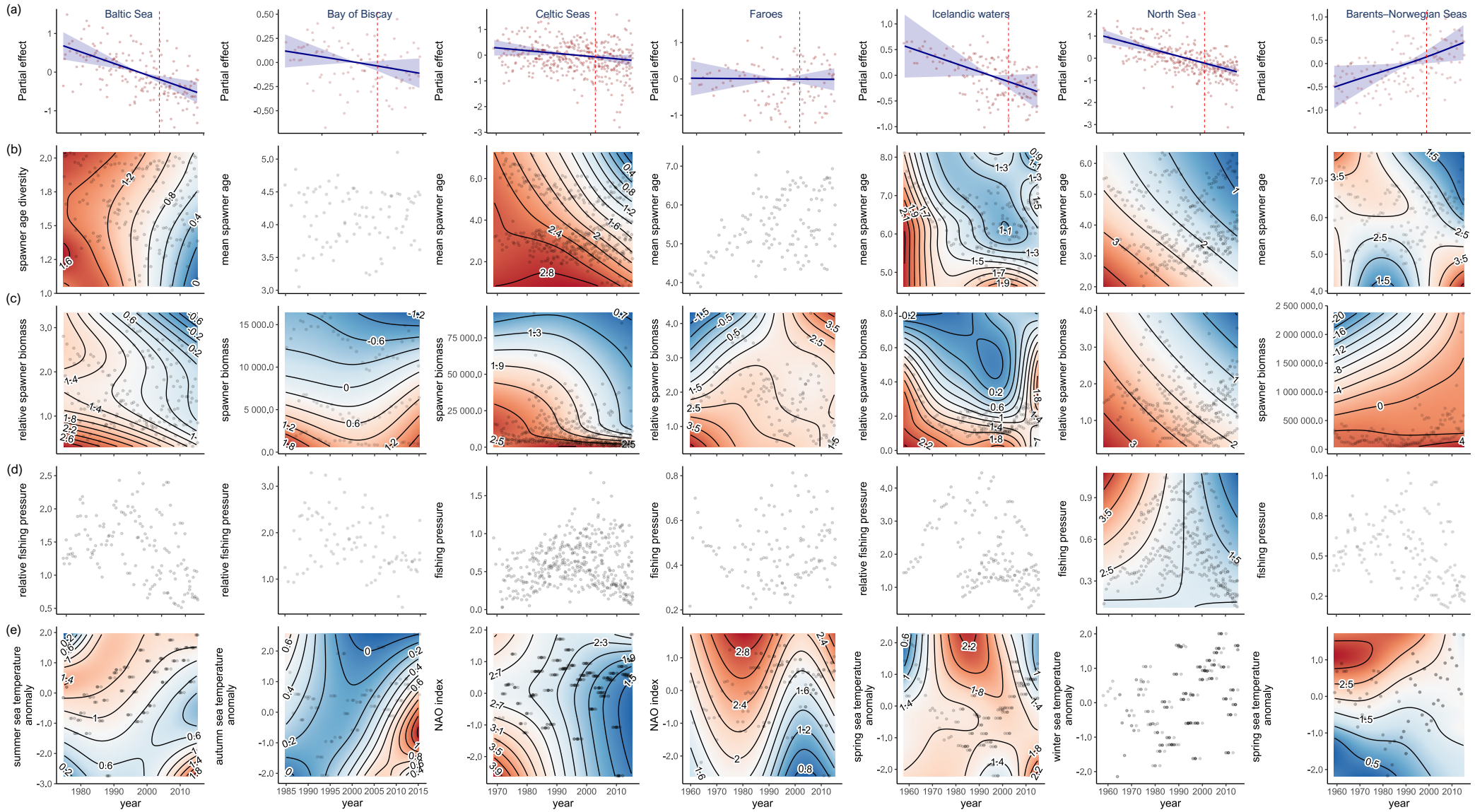
models. (b–e) Time-varying effects of spawner age structure, spawner biomass, fishing pressure. and climate condition. Covariates selected in the models are indicated in the y-axis labels. Color gradients and contour lines indicate the partial effects of covariates estimated (as tensor interaction terms) in the models. Warmer colors indicate higher values, and the ranges of the partial effects differ among the covariates and are indicated as values on the contour lines. Gray circles indicate back-transformed input data.

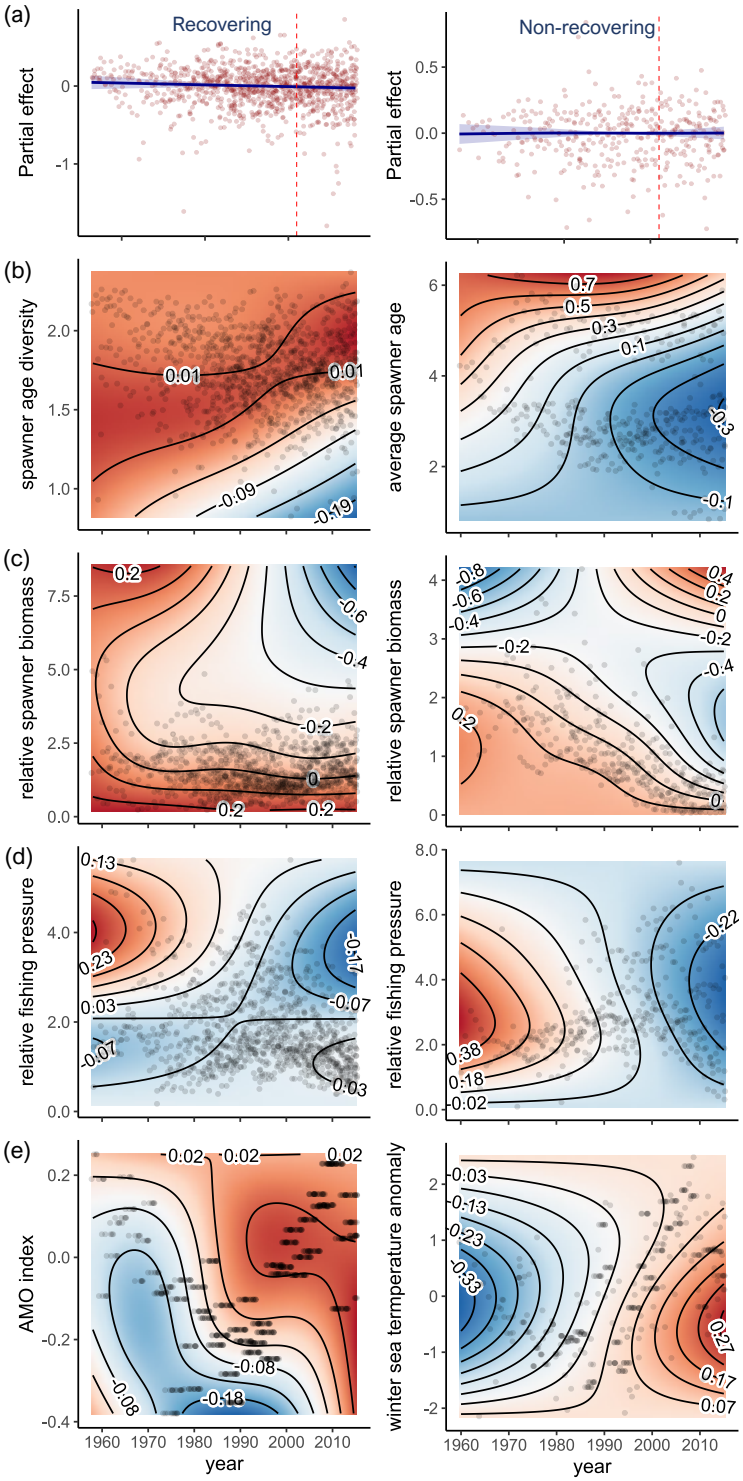

(a)
North Atlantic Ocean
Latitude
Longitude
Ecoregion
Baltic Sea
Barents Sea
Bay of Biscay and the Iberian Coast
Celtic Seas
Faroes
Greater North Sea
Icelandic Waters
Norwegian Sea
(b)
AMO
OHC
NAO
NAO index or OHC anomaly
AMO index
year
(c)
Faroes
Icelandic waters
Norwegian-Barents Seas
North Sea
Baltic Sea
Celtic Seas
Bay of Biscay
Average sea surface temperature (1945-2016)
sea surface temperature anomaly
year
Latitude
Longitude
winter
spring
summer
autumn

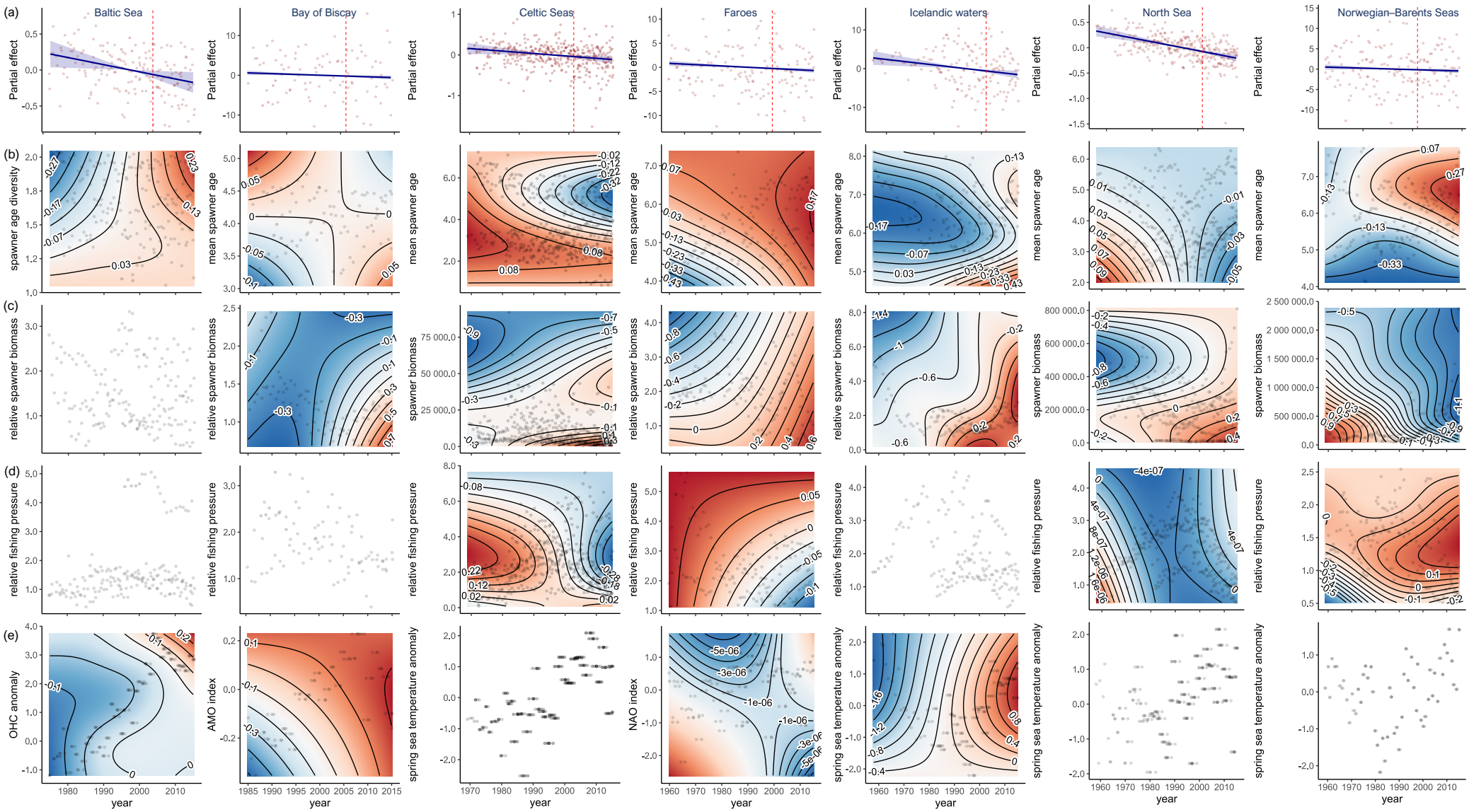

(a)
Recovering
Non-recovering
relative fishing pressure
relative spawner biomass
mean spawner age
spawner age diversity
Partial effect
year
(b)
Recovering
Non-recovering
relative spawner biomass
mean spawner age
spawner age diversity
Partial effect
relative fishing pressure


Recovering
Non-recovering
Partial effect
2
1
0
-1
-2
1960
1980
2000
2020
year


(a)
Recovering
Non-recovering
Partial effect
(b)
mean spawner age
(c)
relative spawner biomass
(d)
fishing pressure
(e)
AMO index
OHC anomaly
year


(a)
Baltic Sea
Bay of Biscay
Celtic Seas
Faroes
Icelandic waters
North Sea
Barents–Norwegian Seas
Partial effect
(b)
spawner age diversity
mean spawner age
(c)
relative spawner biomass
spawner biomass
(d)
relative fishing pressure
fishing pressure
(e)
summer sea temperature anomaly
autumn sea temperature anomaly
NAO index
spring sea temperature anomaly
winter sea temperature anomaly
year


(a)
Recovering
Non-recovering
Partial effect
(b)
spawner age diversity
average spawner age
(c)
relative spawner biomass
(d)
relative fishing pressure
(e)
AMO index
winter sea termperature anomaly
year
year


(a)
Baltic Sea
Bay of Biscay
Celtic Seas
Faroes
Icelandic waters
North Sea
Norwegian–Barents Seas
Partial effect
(b)
spawner age diversity
mean spawner age
(c)
relative spawner biomass
spawner biomass
(d)
relative fishing pressure
(e)
OHC anomaly
AMO index
NAO index
spring sea temperature anomaly
year