

Establishing good pelagic habitat conditions for planktivorous fish

Cefas report for Putting it Together: Plankton and Fisheries (PIT PAF)

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Date in format: March 2024



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Cefas Document Control

Submitted to:	Defra via the Environment Agency
Date submitted:	26/03/2024
Project Manager:	Tim Marjoram
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Executive sign-off (approval for submission) by:	Michelle Devlin
Version:	1.0
Recommended citation for this report:	Thompson, M.S.A., Greig, L., Scott, J., Griffin, K., Tett, P (2024) Establishing good pelagic habitat conditions for planktivorous fish. Final report for Defra project C8421D. Centre for Environment, Fisheries & Aquaculture Science (Cefas), Lowestoft, UK.

Version control history

Version	Author	Date	Comment
0.1	Murray Thompson, Lily Greig, James Scott, Kate Griffin	07/02/2024	Initial version
0.2	Marcelo Gomes	26/02/2024	QC
0.3	Murray Thompson	28/02/2024	QC comments addressed, sent for exec sign off
0.4	Michelle Devlin	29/02/2024	Exec sign off checks
1	Tim Marjoram	26/03/2024	Non-science QC and finalised

Contents

1. Key messages.....	2
2. Executive summary.....	2
3. Introduction	3
4. The PELTIC: spatial relationships between copepods and planktivorous fish	5
4.1. Methods.....	5
4.1.1. Data	5
4.1.2. Statistical analysis.....	6
4.2. Results	7
4.2.1. Spatial patterns in zooplankton and planktivorous fish responses	7
4.2.2. Scale dependence of the relationships between copepods and planktivorous fish ...	9
5. Macroecological trends in the Northeast Atlantic	10
5.1. Methods.....	10
5.1.1. Data.....	10
5.1.2. Statistical analyses	13
5.2. Results	14
6. Discussion.....	22
7. References.....	24
8. Appendix	28

1. Key messages

- The aim of this work was to identify areas and times when pelagic habitat conditions, including the quantity and composition of plankton, were good for planktivorous fish.
- In addition to improving biodiversity assessments under OSPAR and UK Marine Strategy, this work aligns strongly with Defra-funded [Pelagic Natural Capital project](#) (PELCAP) to explore how plankton functional diversity, and healthy plankton communities provide essential ecosystem services, upon which we all depend.
- Two studies are presented: the first uses highly spatially resolved information that has been collected in a coordinated way across zooplankton and fish assemblages in the Celtic Sea and western English Channel; the second is a study across the northeast Atlantic to reveal large scale spatial and temporal trends in fish body condition relevant to OSPAR biodiversity assessments.
- Both studies are geared towards improving understanding of how change in the zooplankton and planktivorous fish assemblages are affecting one-another and thus the status of marine food webs.
- In general, at larger spatial scales, zooplankton abundance and the proportion of large copepods related positively with planktivorous fish body condition. Decreases in the abundance and changes in the composition of zooplankton, coupled with climate change, which have been reported for the northeast Atlantic, are indicative of widespread deteriorating habitat conditions for planktivorous fish.

2. Executive summary

In 2018 it was concluded that the extent to which Good Environmental Status (GES) has been achieved in respect of food webs in UK waters was uncertain: “It is known that components of the marine food web are changing, but it is not clear how they are affecting each other.” This study synthesises information on biodiversity indicators for plankton ([Changes in Phytoplankton and Zooplankton Communities](#)) and planktivorous fish ([Pilot Assessment of Feeding Guilds](#)) for UK waters and surrounding marine ecosystems which contribute to the UK Marine Strategy D1 (biodiversity), and D4 (food webs) and are relevant to D6 (benthos). It is a collaboration between pelagic biodiversity, food web and fisheries experts brought together in The UK Pelagic Habitats Expert Group (PHEG). Our aim was to identify areas and times when pelagic habitat conditions, including the quantity and composition of plankton, were good for planktivorous fish. Such information will help determine environmental status for pelagic habitats to support The Convention for the Protection of the Marine Environment of the North-East Atlantic (the ‘OSPAR Convention’; henceforth OSPAR) Quality Status Reporting process and assessments of Good Environmental Status (GES) under the EU Marine Strategy Framework Directive (MSFD) and subsequently to meet the needs of the UK Marine Strategy and Defra’s 25 Year Environment Plan.

Detecting quantitative relationships between highly dynamic planktivorous fish and zooplankton populations empirically has been remarkably elusive. This is, in part, because of the high uncertainty in the spatial distribution of small planktivorous fish biomass estimates using standard otter and beam trawl surveys which represent the only long-term and extensive source of information on fish species populations beyond catches (the latter of which do not follow consistent survey methods). Coordination across surveys of zooplankton and fish is also not yet commonplace, nor is measuring zooplankton size which is a key determinant of resource quality.

We present two studies here, the first a study in the Celtic Sea and western English Channel with highly spatially resolved information that has been collected in a coordinated way across zooplankton and fish assemblages; the second a macroecological study across the northeast Atlantic to reveal large scale spatial and temporal trends in fish body condition relevant to OSPAR. Both studies are geared towards improving understanding of how change in the zooplankton and planktivorous fish assemblages are affecting one-another and thus the status of marine food webs. We present evidence of quantitative links between zooplankton populations and fish body condition over different spatial and scales. In general, at larger spatial scales, zooplankton abundance and the proportion of large copepods related positively with planktivorous fish body condition. Temperature was also often an important predictor, relating negatively to fish body condition and which interacted with other predictors. Our results suggest that decreases in the abundance and changes in the composition of zooplankton, coupled with climate change, which have been reported for the northeast Atlantic, are indicative of widespread deteriorating habitat conditions for planktivorous fish.

3. Introduction

Achieving environmental ambitions such as The United Nations Sustainable Development Goal to “*Conserve and sustainably use the oceans, seas and marine resources for sustainable development*” and effective application of ecosystem-based management (OSPAR Commission, 2010) will depend on understanding the causes and consequences of change across food webs. Yet, the majority of indicators used to assess the status of marine ecosystems focus on change within component parts of food webs, rather than understanding the links between them. In the northeast Atlantic, evidence shows that climate change is a key driver of both plankton and planktivorous fish biodiversity and size composition, with widespread compositional change in both assemblages favouring smaller organisms (Holland et al., 2023; Pitois & Fox, 2006; Thompson, Couce, et al., 2023). Plankton are the main source of marine production on which many species depend, either directly as a resource, or indirectly since planktivores are key prey for many predators including humans via wild-capture fisheries (Capuzzo et al., 2017; Engelhard et al., 2014; Lynam et al., 2017). A key knowledge gap, therefore, is what impact changes in the quantity and quality of plankton (i.e., the composition of lifeforms; McQuatters-Gollop et al., 2019) are having on the wider ecosystem. The extent to which Good Environmental Status (GES) has been achieved in respect of food webs in UK waters is therefore uncertain (OSPAR, 2023).

A key assumption of many marine ecosystem models is that decreases in the quantity and quality of zooplankton populations resulting from climate change will negatively affect higher trophic levels because of reductions in the flow and efficiency of energy transfer from plankton to fish (Atkinson et al., 2024; du Pontavice et al., 2021; Heneghan et al., 2023; Kwiatkowski et al., 2019). Plankton communities have been changing across the Northwest European shelf on decadal timescales, with widespread decreases in abundance and body size in offshore waters where the bulk of the commercially exploited planktivorous stocks reside, primarily linked to climate change drivers (Holland et al., 2023; Pitois & Fox, 2006). Positive spatial correlations between plankton and planktivorous fish biomass has been shown empirically, while direct temporally dynamic relationships evident in models (e.g., Lynam et al., 2017) have been more elusive (Pitois et al., 2012; Thompson et al., 2020). There are a few key constraints in the way observations are made and assessed that may be contributing to this mismatch. Quantitatively linking large-scale and long-term change between plankton and fish assemblages has been hampered by: a lack of

coordination between surveys across their assemblages; plankton body size is not routinely surveyed due to the lack of in-situ size data, yet organismal size determines many ecological processes in food webs (Brose et al., 2006; Petchey et al., 2008; Woodward et al., 2005); planktivores have relatively low catchability using standard otter or beam trawl survey gears meaning population biomass estimates can have high uncertainty (Nnanatu et al., 2020; Walker et al., 2017); and, despite the advantages of acoustic surveys for fish (Egan et al., 2020; ICES, 2015a; van der Kooij et al., 2016), they do not yet provide sufficiently long-term and spatially extensive information across many species to gauge the effects of climate change on plankton and planktivorous fish interactions.

Fish body condition estimated from age, length and weight data (e.g., Engelhard et al., 2013) offers an alternative and novel means to assess pelagic habitat conditions. There are a few key reasons why fish body condition could offer valuable insight into pelagic habitat conditions: it is not susceptible to catchability issues that affect planktivorous fish biomass estimates; the spatial and temporal extent of observations corresponds with observations of plankton lifeforms (i.e. the quantity and composition of planktivorous fish prey) from the Continuous Plankton Recorder survey (CPR, <https://www.cprssurvey.org/data/our-data/>; Batten et al., 2003; Holland et al., 2023); body condition provides a short-term (weeks-months) insight into pelagic habitat conditions which are highly temporally dynamic.

We draw together two studies to help establish when and where planktivorous fish body condition varied, and whether zooplankton quantity and quality were important determinants of favourable habitat conditions. First, we use the PELTIC survey which has simultaneous, highly spatially resolved observations from across plankton and pelagic fish assemblages in the Celtic Sea and western English Channel. The aim of this study was to determine the spatial scale of the relationships between copepod size, copepod abundance and planktivorous fish body condition. Second, we use a post-hoc data sampling design across the northeast Atlantic to exploit macroecological information from the Continuous Plankton Recorder survey and otter trawl surveys based on when and where observations from each were made. The aim of the second study was to reveal large scale spatial and temporal trends in fish body condition relevant to OSPAR, and better understand how plankton contribute to these trends. Both studies are geared towards improving understanding of how change in the plankton and planktivorous fish assemblages are affecting one-another and thus the status of marine food webs. We test the following hypotheses: i) there is spatial and temporal structure in fish body condition; ii) the spatial relationship between zooplankton and fish is scale-dependent; iii) variability in planktivorous fish body condition is related to change in the zooplankton assemblage, temperature, and the density of planktivorous fish. Our aim being to establish good habitat conditions for planktivorous fish in terms of the quantity and quality of their plankton prey while also accounting for large variability in temperature and potential competition from populations of fish in the same feeding guild.

4. The PELTIC: spatial relationships between copepods and planktivorous fish

4.1. Methods

4.1.1. Data

Data are collected as part of the Cefas PELTIC Survey (PELagic ecosystem in the western and eastern ceLTIC seas) over the last 11 years aboard the RV Cefas Endeavour (ICES, 2015b). The survey occurs in the Celtic Sea and western English Channel during October to coincide with pelagic fish spawning. The principal aim of the survey is to inform ICES fish stock assessments although the survey captures an end-to-end description of the ecosystem from physical variables (e.g. salinity, nutrient concentrations), phytoplankton, zooplankton, pelagic fish (which are typically planktivorous (Thompson, Lynam, et al., 2023) up to the apex predators, marine mammals and birds. The key strength of the survey for our assessment is the simultaneous collection of highly spatially resolved observations from across plankton and fish assemblages. The time-series where data are available for both plankton and fish is still relatively short (9 years), hence we focus primarily on the spatial relationships between copepods and planktivorous fish.

A series of daytime acoustic transects are run to assess the abundance of pelagic fish for ICES stock assessments. To validate the acoustics, ad hoc pelagic trawls are undertaken sporadically based on acoustic signals (van der Kooij et al., 2016). Trawl monitoring, trawl door type and dimensions and rigging are described in ICES (ICES, 2015b; Pitois et al., 2021). For each trawl (Fig. 1), all fish were sorted or a representative subsample where the catch was too large to be manually sorted to provide a true length representation of the species. Fish were measured (mm, rounded to nearest half centimetre), weighed (grams), aged (to years) and identified to species level. Of the species measured Anchovy (ANE), Horse Mackerel (HOM), Mackerel (MAC), Pilchard (PIL) and Sprat (SPR) are analysed in this report. The three-letter code in brackets after represents the ICES species code. These data can be used to convert the acoustic trawls to fish abundance and biomass. These data are then stored in a Cefas based SQL repository from where they were downloaded for analysis. For the current study only individual fish weight and length were used. Fish data were available from 2012 to 2021.

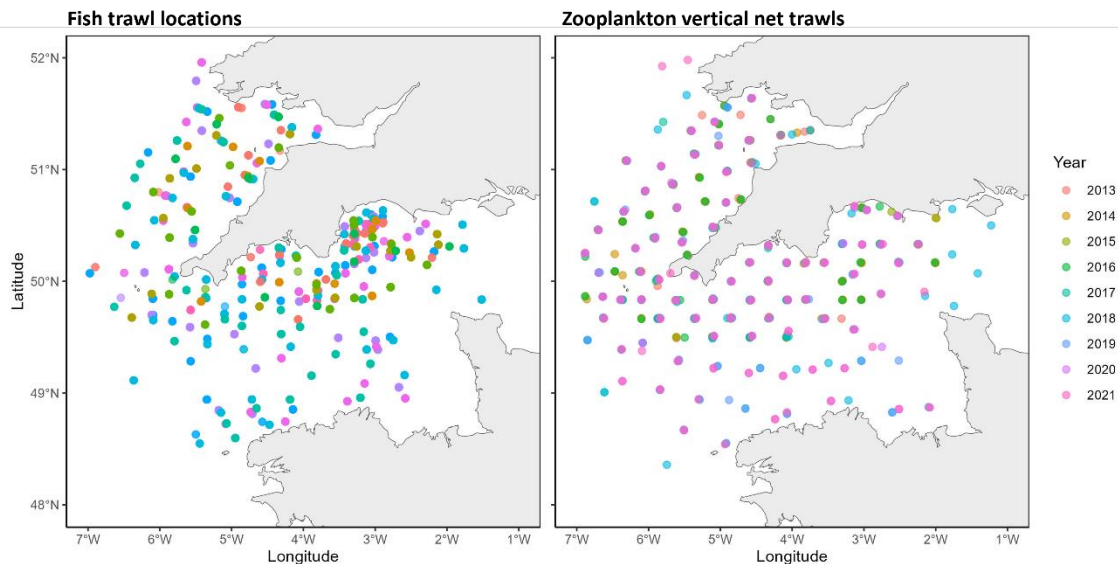


Figure 1. Study map for both fish trawl locations and zooplankton vertical trawls over the last 11 years as part of the PELTIC survey. Colour indicates year surveyed.

Zooplankton are collected by vertical trawl using an 80 UM ring net and stored for analysis post survey in preservation fluid (70% Industrial Methylated Spirit) to be analysed back on land (see Figure 1 for the spatial and temporal distribution of samples). Subsequent was later undertaken using a Hydroptic v3 ZooScan (Gorsky et al., 2010). Here, samples are reduced using a folsom splitter and the subsample is then poured into a flatbed scanner. After arranging objects to ensure even spacing and best orientation as possible, the subsample is scanned. Images and size metrics are returned which are subsequently uploaded to the EcoTaxa platform (Picheral et al., 2017). This allows a user to quickly sort images into taxonomic classes using manual validation. Size metrics are not typically collected by traditional light microscopy. Although more detailed taxonomic resolution is available, only copepods were selected. This was primarily because they are a key prey for pelagic fish (Pitois et al., 2021; Turner, 2004) and the techniques used in obtaining *in situ* size from copepods is reliable (Edvardsen et al., 2002; Scott et al., 2023). For each vertical trawl, the geometric mean size (mm) of the copepods was taken as well as the mean abundance of copepods (individuals per m^{-3}). The geometric mean was found to be a more representative description of the community size than the arithmetic mean to take account for the non-normal distribution of copepod sizes (Pitois et al., 2021). Copepod data were available for years 2013 to 2021.

4.1.2. Statistical analysis

Initial analysis aimed to investigate the relation of space independent of time on fish body condition, copepod abundance and geomean size. Fish body condition was assessed using species-specific \log_{10} transformed length-weight linear relationships in the R package *glmmTMB* (Magnusson et al., 2017). Generalized Linear Mixed Model (GLMM) is an extension of the Generalized Linear Model (GLM). It combines both fixed effects (like in a regular regression) and random effects (which account for variability between groups, in this case the year the data were collected). The GLMM model has a series of assumptions and criteria for performing a successful model run. All fish met these assumptions. Fish with a positive or negative residual from the linear

model is indicative of an individual that is above or below the average weight for their length, respectively (i.e. a measure of individual fish body condition).

We used the sdmTMB R package which fits generalised linear mixed effects models (GLMMs) using stochastic partial differential equations (Anderson et al., 2022) to test for effects of copepod abundance and size on fish body condition. Using sdmTMB allowed us to plot change in the responses over space. The 'spatial effect' is the effect of space on the response variable in the unit of the response. For example, where we assess spatial patterns in fish body condition, our spatial random field captures change in fish weight at length in grams on a log₁₀ scale, with positive and negative values showing areas with higher and lower than average values, respectively, and independent of time. This allowed us to explore spatial gradients in fish body condition. Temporal change was not of primary interest here because the survey time-series is relatively short. The sdmTMB has a series of model assumptions and criteria and assumptions that must be met for a successful model run. All species met assumptions apart from Anchovy whose results are not reported. The same analysis was undertaken for copepod abundance and size to obtain an understanding of their typical spatial patterns, independent of time.

For each location and time where fish length and weight data were collected, we collated information on their potential zooplankton prey across multiple spatial scales using an increasing radius. The radius was increased from 10 km to 250 km in increments of 10 km. For each radius tested, the following GLMM model was fit to test the response of body condition to predictors of copepod abundance and copepod size: *body condition* ~ *log₁₀(copepod mean abundance)* + *log₁₀(copepod geomean) size* + (1|year). The `(1|Year)` syntax specifies `year` as a random effect. Using the GLMM, for each fish species, the 'best' radius was determined by having the highest marginal *R*² value and both the predictors being highly significant (*p* < 0.001), thus revealing the spatial scale at which interactions between copepods and planktivorous fish populations are best explained (i.e., we test whether fish body condition is explained by local or more regional patterns in copepod size and abundance).

4.2. Results

4.2.1. Spatial patterns in zooplankton and planktivorous fish responses

Copepod abundance increased towards the centre of the study region, whereas size increased moving south (Fig. 2). Spatial gradients in body condition were evident for all species but varied in strength and distribution (Fig. 3; model assumptions were not met for anchovy so those results are not reported here). Sprat and mackerel had more consistent spatial patterns over the study period, indicated by the increased range in spatial effect values. Pilchard had the weakest spatial patterns with spatial effect values $< \pm 0.01$. Weight at length increased moving southeast across the study region for pilchard, increased moving southwest for sprat, was highest in the centre of the study area for horse mackerel, and was highest to the north and west for mackerel (Fig. 3).

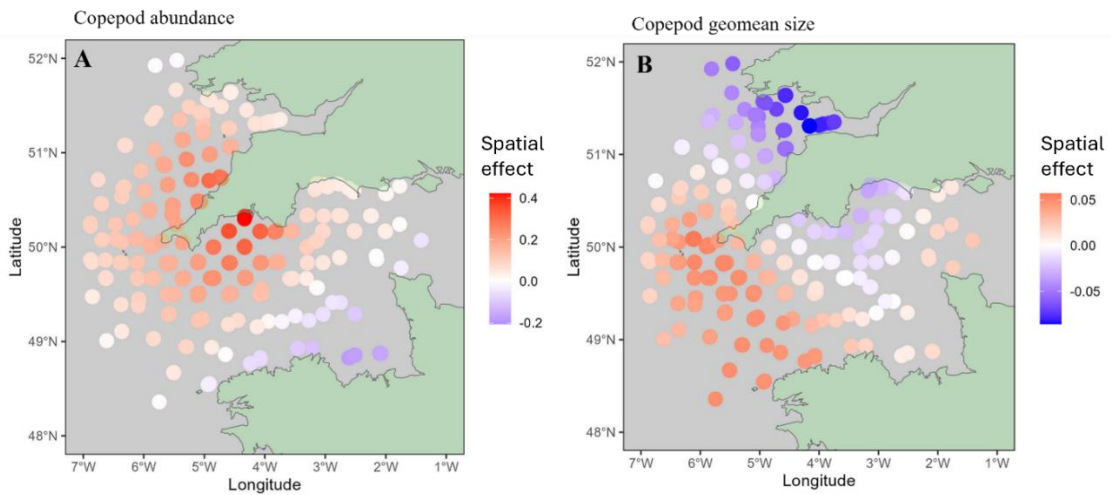


Fig. 2. Spatial gradients in (A) copepod abundance and (B) copepod geomean size. Spatial effect represents change in the response variable (A = indiv. per m³ and B = geomean size in mm). Positive and negative values show areas with higher and lower than average values, respectively, independent of time.

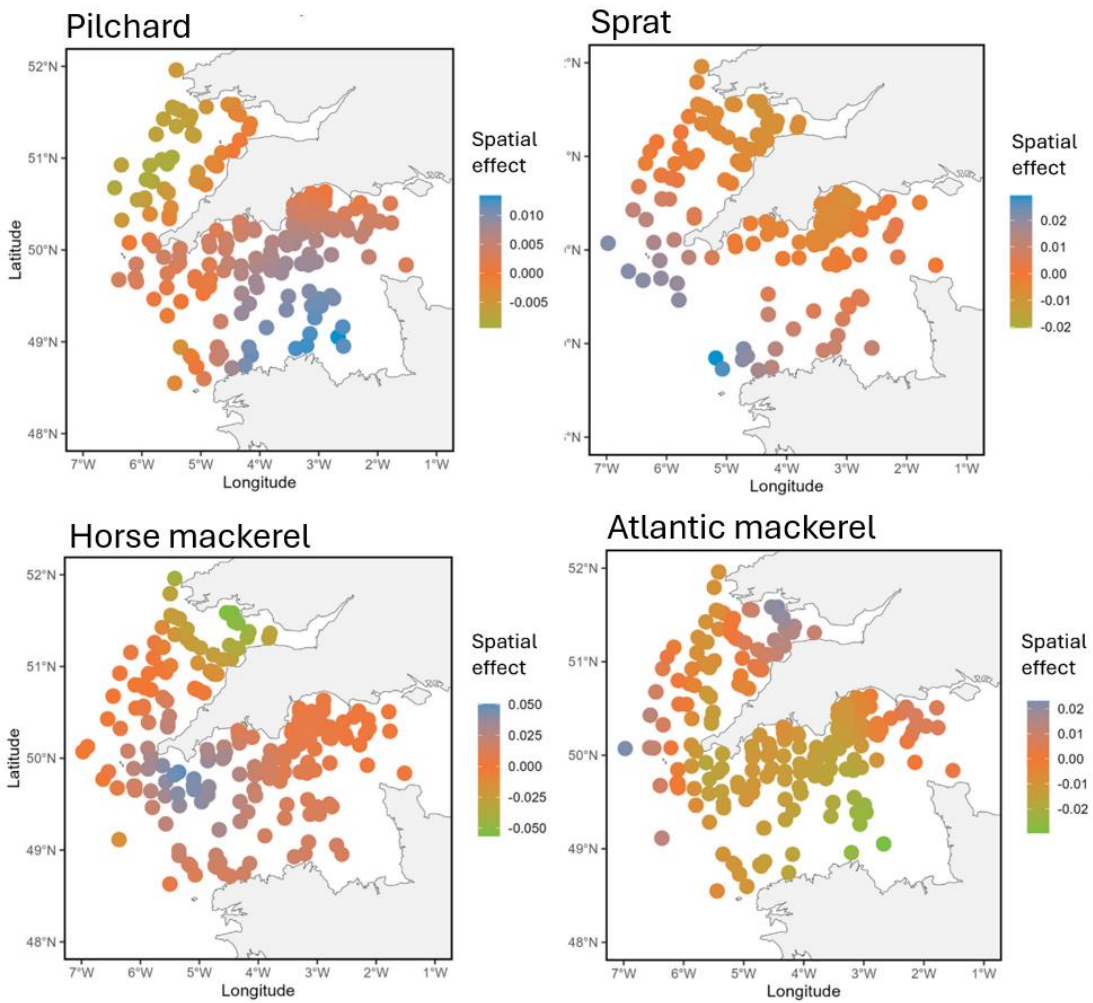


Fig. 3. Spatial gradients in fish body condition. Spatial effect represents change in the response variable (residuals in g on a \log_{10} scale from species-specific length-weight linear relationships). Positive and negative values show areas with higher and lower than average fish weight at length, respectively, independent of time.

4.2.2. Scale dependence of the relationships between copepods and planktivorous fish

The direction of the relationship between fish body condition, copepod size and abundance was spatially scale dependent (Fig. 4). Effect sizes and model marginal R^2 values were generally strongest at the smallest and largest radii (Fig. 4A, B). At the smallest radius, all species had a significant positive relationship with copepod abundance but for anchovy, whose estimate was not significant and close to 0 (Fig. 4C). For radii between 20 – 40 km, the relationship tended to be negative, whereas at the largest radius (200 km), all species had a significant positive relationship but for horse mackerel whose estimate was not significant and close to 0. Overall, copepod size was a more consistently significant predictor of fish body condition than abundance (Fig. 4). However, only sprat had a consistently positive relationship with copepod size, horse mackerel showed negative relationships at small and large radii, and the direction of the relationship for other species was more varied (Fig. 4D).

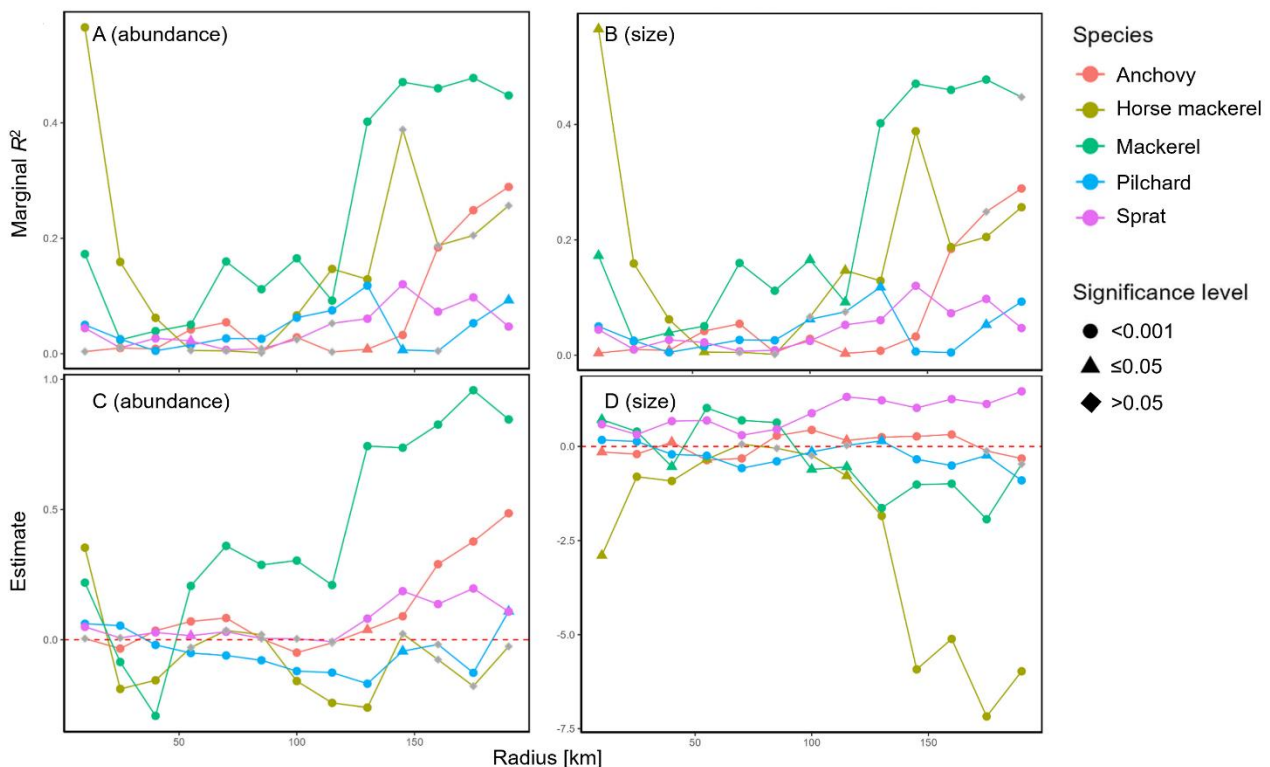


Figure 4. GLMM model fit and estimates for fish body condition (response variable) and copepod abundance and size as fixed effects. The marginal R^2 of the full model with the significance of copepod abundance (A) and size (B) displayed. The estimates of copepod abundance (C) and size (D) on fish body condition. The red dashed line in plots C-D distinguish between negative (<0) and positive relationships (>0).

5. Macroecological trends in the Northeast Atlantic

5.1. Methods

5.1.1. Data

Temperature is a key variable affecting pelagic habitat conditions. For example, it has been shown to be the primary driver of change in offshore plankton assemblages (Holland et al., 2023), it reduces fish weight at length (Gomes et al. in prep), affects how species richness is distributed across the food web (Thompson, Couce, et al., 2023), and alters top-down and bottom-up food web processes between plankton and fish (Capuzzo et al., 2017; Lynam et al., 2017). We collate annual and six-monthly means of temperature data at 5km resolution using E.U. Copernicus Marine Service Information (NWSHELF_MULTIYEAR_PHY_004_009; <https://doi.org/10.48670/moi-00059>) to generate short- to mid-term measures of environmental conditions for each haul (i.e., where and when we have observations of fish age, length and weight). These data were generated by the Forecasting Ocean Assimilation Model 7 km Atlantic Margin model (FOAM AMM7) which uses version 3.6 of the Nucleus for European Modelling of the Ocean (NEMO) ocean model (Madec, 2016) with observations assimilated using version 6 of NEMOVar (Mogensen et al., 2012).

Fish age, length and weight information were derived from ICES' Database of Trawl Surveys (DATRAS; <https://datras.ices.dk>) and Cefas' Fishing Survey System (FSS) database (<https://data.cefas.co.uk/#/View/3233>; Morris et al., 2016). We select herring (*Clupea harengus*), sprat (*Sprattus sprattus*), mackerel (*Scomber scombrus*), and Norway pout (*Trisopterus esmarkii*) to assess variability in pelagic habitat conditions across OSPAR regions because they are known to be planktivorous and occupy much of the northeast Atlantic (Thompson, Lynam, et al., 2023). There were 67373, 18554, 28311 and 14546, individual fish samples for herring, mackerel, sprat and Norway pout, respectively, spanning years 1997 – 2020 (see Figs S1-S12 for the spatial and spatiotemporal distribution of observations for each species). For planktivorous fish prey, we use the relative abundance of large copepods (i.e. a measure of zooplankton prey quality; Van Deurs et al., 2014, 2015) and the total abundance of zooplankton derived from the Continuous Plankton Recorder survey (CPR, <https://www.cprsurvey.org/data/our-data/>; Batten et al., 2003).

Large scale and long-term surveys across plankton and fish have not been designed in a coordinated way. This has hampered quantitatively linking change across plankton and fish assemblages because observations cannot be readily linked in time or space. We employ a post-hoc data sampling approach that uses information on when and where observations were made across the different surveys to exploit information from both. For each haul location, we collate all plankton observations from the CPR survey within 75 km and from the preceding six months (short-term) to generate regional abundances (a median of m³ abundance estimates across samples) of potential planktivorous fish prey (Fig. 5). We were also interested to test whether variation in the abundance of planktivorous fish affected fish body condition, e.g., negatively via

competition for resources or positively as schooling fish follow their resources. Planktivore abundance was estimated from internationally coordinated fish surveys that include information on fish species, size and numbers that can be used to assess change in planktivore populations (Lynam & Ribeiro, 2022). The density-dependent effects of planktivores was tested by estimating the median abundance of planktivorous fish (i.e., classified following Thompson, Lynam, et al., 2023) observed in research otter trawls within a 75 km radius and 45 days (Fig. 5). We use different temporal ranges for estimating the effects of prey (preceding 6 months) and density-dependence (within 45 days) on fish body condition because CPR surveys have higher temporal resolution (multiple observations through the year) compared to fish surveys (typically repeated annually). CPR observations thus afford assessment of prey conditions in the months preceding when the fish was observed (i.e., likely when body condition was being determined), whereas fish surveys provide annual snapshots of planktivorous fish populations.

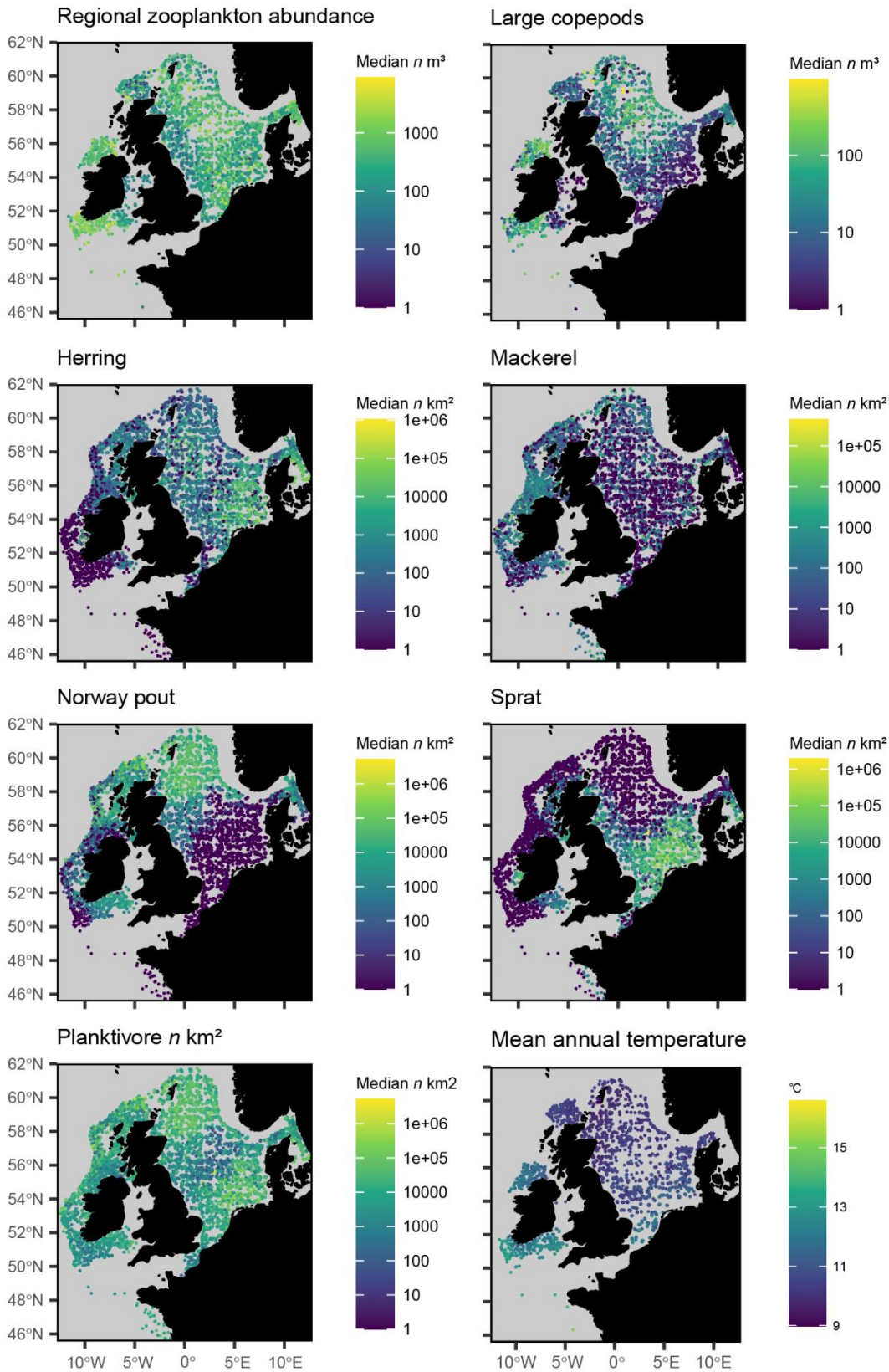


Fig. 5. Regional zooplankton and planktivorous fish abundances in relation to all haul locations (i.e. median $n \text{ m}^3$ in the preceding 6 months within 75 km and median n per km^2 within 45 days and 75 km for zooplankton and fish, respectively).

5.1.2. Statistical analyses

“COMP4 assessment units” (Common Procedure for the Identification of the Eutrophication Status of the OSPAR Maritime Area, 4th application) are a geographical representation of the environmental conditions most likely to drive plankton distribution, dynamics, and community composition (Enserink et al., 2019). Fish body condition was assessed using species-specific \log_{10} transformed length-weight linear relationships in the R package *glmmTMB* (Magnusson et al., 2017). Fish with a positive or negative residual from the linear model is indicative of an individual that has high, low or mid (i.e. closer to average) weight for their length, respectively (Fig. 6 helps illustrate this).

Spatial and temporal change in fish body condition was assessed across COMP4 assessment units. We can expect small effect sizes of other predictors given there is relatively little residual variation in the length-weight relationships but, in biological terms, that variation is critically important. Kendall's τ trend analysis was used to identify areas of significant temporal trends in fish species responses based on the relationship between mean values for individual fish across each Comp4 assessment unit and year. Kendall's τ scores of -1 to $+1$ represent a 100% probability of a decreasing or increasing trend, respectively. By using Kendall's τ , which is rank-based and non-parametric, we can detect correlations which may be non-linear.

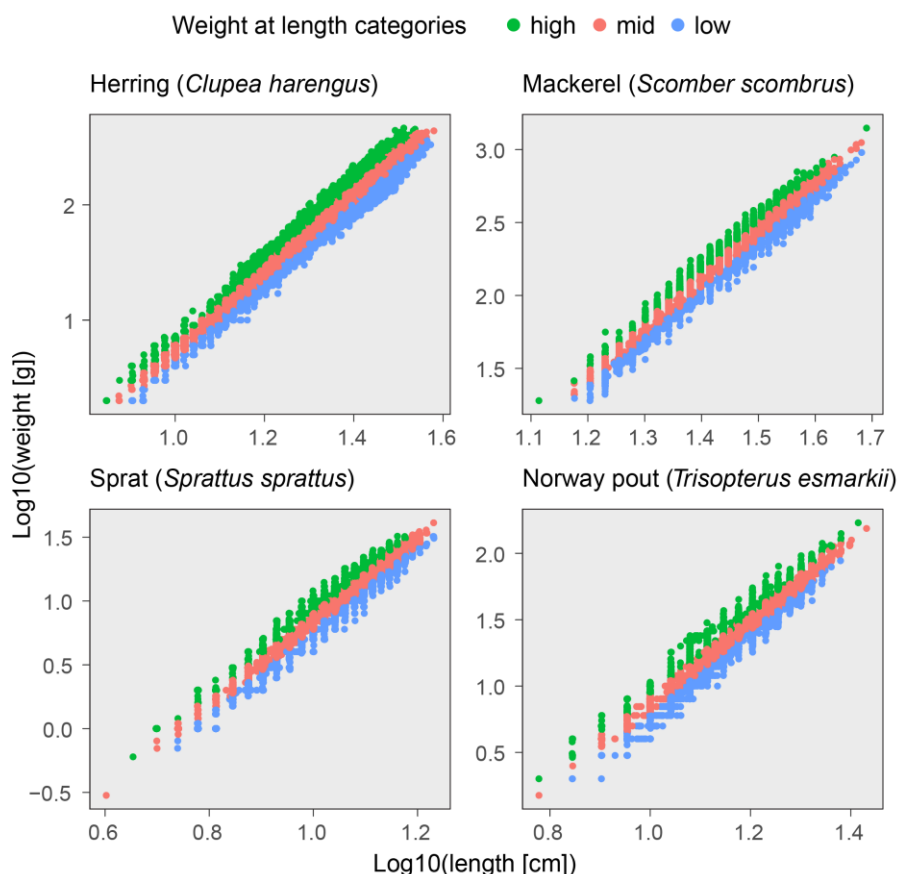


Fig. 6. Fish length-weight relationships, with weight at length categories identified for illustrative purposes defined based on standard deviation (SD) from the mean as high (>1 SD, positive residual) or low (>1 SD, negative residual) or those 'mid' closer to average (<1 SD).

We use the sdmTMB R package which fits generalised linear mixed effects models (GLMMs) using stochastic partial differential equations (Anderson et al., 2022) to test for effects of zooplankton abundance and composition, planktivore abundance and temperature on fish length-weight relationships. This package allows one to use linear models whilst also accounting for spatial and spatiotemporal autocorrelations in the data. Fish weight (g) was modelled as the response and fish length (cm), sea surface temperature, the regional proportion of large copepods, regional zooplankton abundance and regional planktivore abundance as fixed predictors (Fig. 5), with interaction terms between each. Weight, length, regional zooplankton abundance and regional planktivore abundance were all \log_{10} transformed. The key advantage of the sdmTMB approach is its ability to account for unmeasured variables which are not included in the fixed effects, and which can lead to the spatial and spatiotemporal autocorrelation within the data. Consistent spatial deviations through time in fish weight may occur due to physical or biological factors, such as missing environmental or genetic predictors that could help explain systematic spatial difference in fish species length-weight relationships. Similarly, spatiotemporal deviations (months and years in time) in fish weight may occur due to unmeasured factors such as seasonal differences caused by spawning or large-scale annual variation caused by the North Atlantic Oscillation. By identifying and accounting for these autocorrelations, the sdmTMB package can improve predictions of the impacts of measured variables as well as uncover revealing patterns caused by unmeasured variables.

As sdmTMB does not currently have capacity for randomly varying slopes across a subcategory of the data (e.g., different species), a separate model was fit for each species. The time slices used to estimate the spatial deviations in weight were month and year, and the time slices were set to be independent and identically distributed. The ggeffects package in R was used to estimate and visualise the marginal effects of individual predictors on the response variables (Lüdecke, 2018). Predictions were made on the dataset used to generate the model, and the spatial and spatiotemporal fields were plotted to show the variability in the data not captured by the fixed effects. The R^2 values of the sdmTMB models were found using the recently developed r2.sdmTMB function in R (sdmTMB/scratch/r2-glmm.qmd at main · pbs-assess/sdmTMB (github.com)). We report the total value including the fixed and random effects (the conditional R^2) as well as that due only to the fixed effects (the marginal R^2), and that due to the spatiotemporal random effects (partial spatiotemporal R^2) to provide information on model fit.

5.2. Results

There was spatial structure in fish body condition across the study area for all species (Fig. 7). Compared with the wider Atlantic, fish weight at length in the North Sea was typically higher than the average (positive residuals), with the most positive residuals for herring in the northern North Sea, mackerel and sprat in the southern North Sea, and Norway pout to the northeast of the study region. At the Comp4 assessment unit scale, there were few areas with significant change in body condition over time (Fig. 8). Herring weight at length increased in the south and western North Sea, whereas sprat weight at length reduced around Scotland and in the Kattegat and Norway pout weight at length reduced in the Skagerrak and in the central North Sea (change is at the fringe of the distribution of Norway pout where only few observations were made and so should be interpreted with caution).

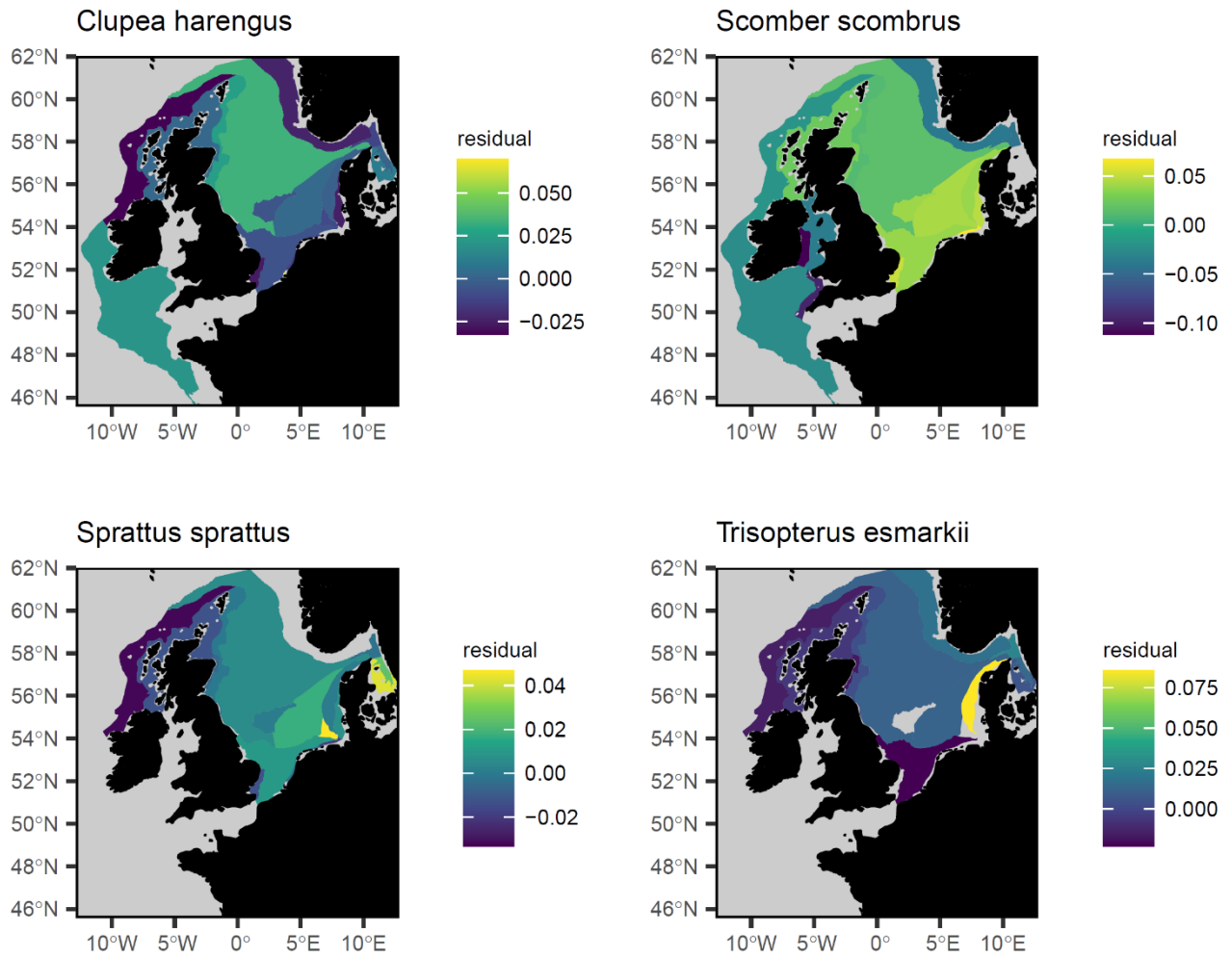


Fig 7. Mean residuals from \log_{10} transformed length-weight relationships for fish species plotted across Comp4 assessment units. Positive and negative residuals indicate where fish weight at length was higher or lower than the average, respectively.

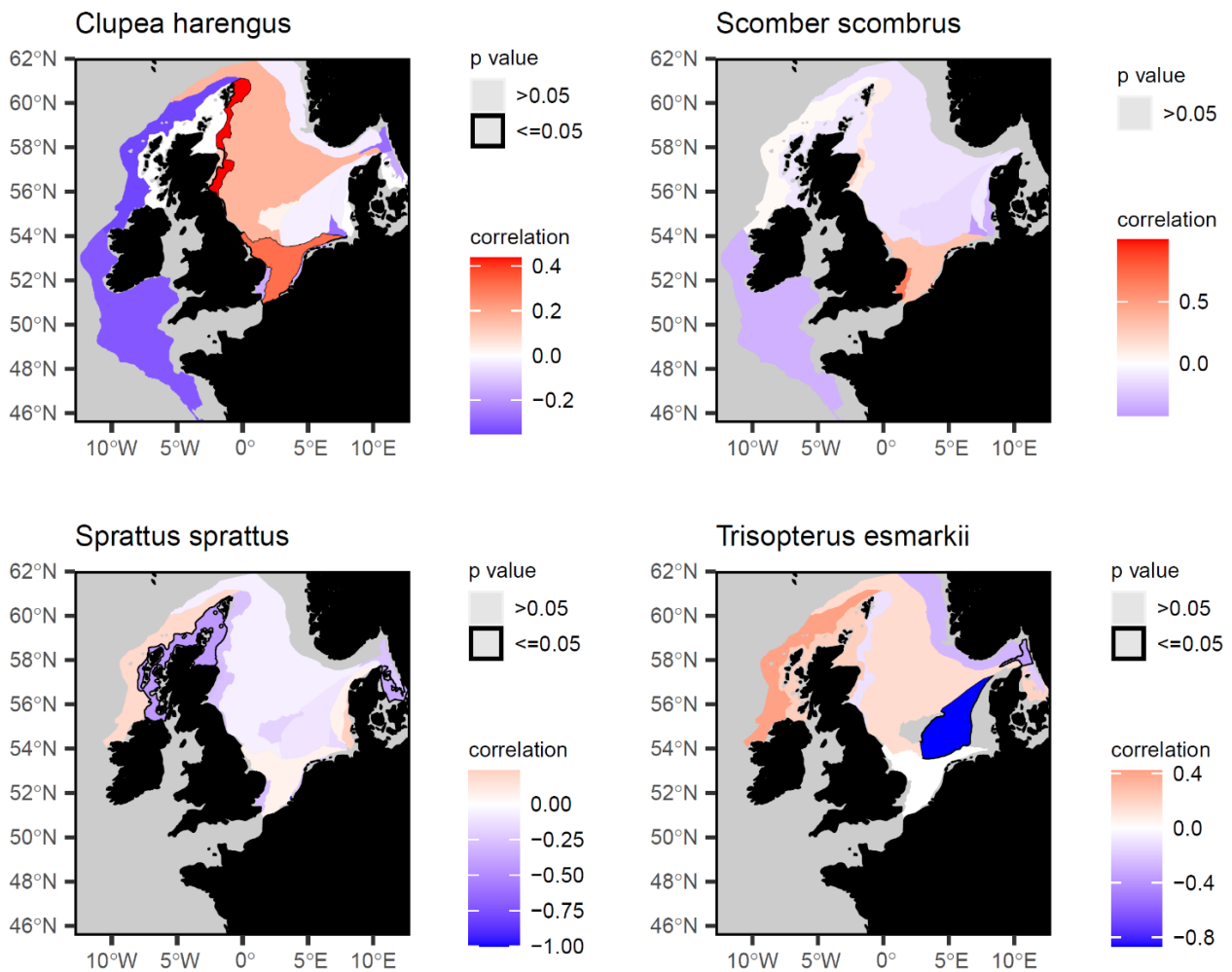


Fig 8. Temporal change in annual mean residuals from log₁₀ transformed length-weight relationships for fish species plotted across Comp4 assessment units. Temporal increases are shown by red cells (correlation values between 0 and +1) and declines in blue cells (correlation values between 0 and -1). Comp4 assessment units where the temporal change is significant are highlighted with black borders.

Conditional R^2 for our sdmTMB models were 0.992 (marginal = 0.979, partial spatiotemporal = 0.0125), 0.975 (marginal = 0.946, partial spatiotemporal = 0.0282), 0.977 (marginal = 0.96, partial spatiotemporal = 0.0177), and 0.964 (conditional = 0.939, partial spatiotemporal = 0.0243), for herring, mackerel, sprat and Norway pout, respectively. All our sdmTMB models showed that length was the best predictor of weight (Tables 1-4). Temperature also came out either highly significant on its own (for mackerel, sprat and Norway pout) or via significant interactions with other predictors (herring), and related negatively with fish weight across all models (i.e., fish weight at length decreased as temperature increased; Figs. 9-12). Both total zooplankton and the proportion of large copepods were also generally either significant predictors on their own or had significant interactions with other predictors, and both related positively with fish weight across all models (i.e., fish weight at length increased as zooplankton and the proportion of large copepods increased; Figs. 9-12), albeit with high uncertainty in some cases. The abundance of planktivores had mixed effects across species, negatively relating to the weight of herring, positively relating to the weight of mackerel, interacting with the length for sprat, with no significant effects or interactions for Norway pout. Our spatial and spatiotemporal random fields captured important

autocorrelation in the data (Figs. S1-S12) that helped improve predictions of the impacts of measured variables while also revealing other important areas and times of variation in those species length-weight relationships.

Table 1. sdmTMB model results for herring, including slopes for the various predictors, their interactions, associated standard error, and *p* values.

Term	Estimate	S. error	<i>p</i>
Intercept	-2.3	0.083	<0.001
Log10(length)	3.3	0.027	<0.001
Surface temperature	-0.012	0.0063	0.058
Log10(total zooplankton count)	-0.065	0.024	0.0062
Fraction of large copepods	0.01	0.053	0.85
Log10(number of planktivores)	0.056	0.015	<0.001
Log10(length): Surface temperature	-0.0055	0.0014	<0.001
Log10(length): Log(total zooplankton count)	0.029	0.0064	<0.001
Log10(length): Fraction of large copepods	0.066	0.015	<0.001
Log10(length): Log10(number of planktivores)	-0.026	0.0033	<0.001
Surface temperature: Log10(total zooplankton count)	0.0028	0.0017	0.091
Surface temperature: Fraction of large copepods	-0.0067	0.0037	0.071
Surface temperature: Log10(number of planktivores)	-0.0022	0.001	0.032
Log10(total zooplankton count): Fraction of large copepods	0.0032	0.0084	0.71
Log10(total zooplankton count): Log10(number of planktivores)	-0.00029	0.0031	0.92
Fraction of large copepods: Log10(number of planktivores)	-0.0045	0.0058	0.44

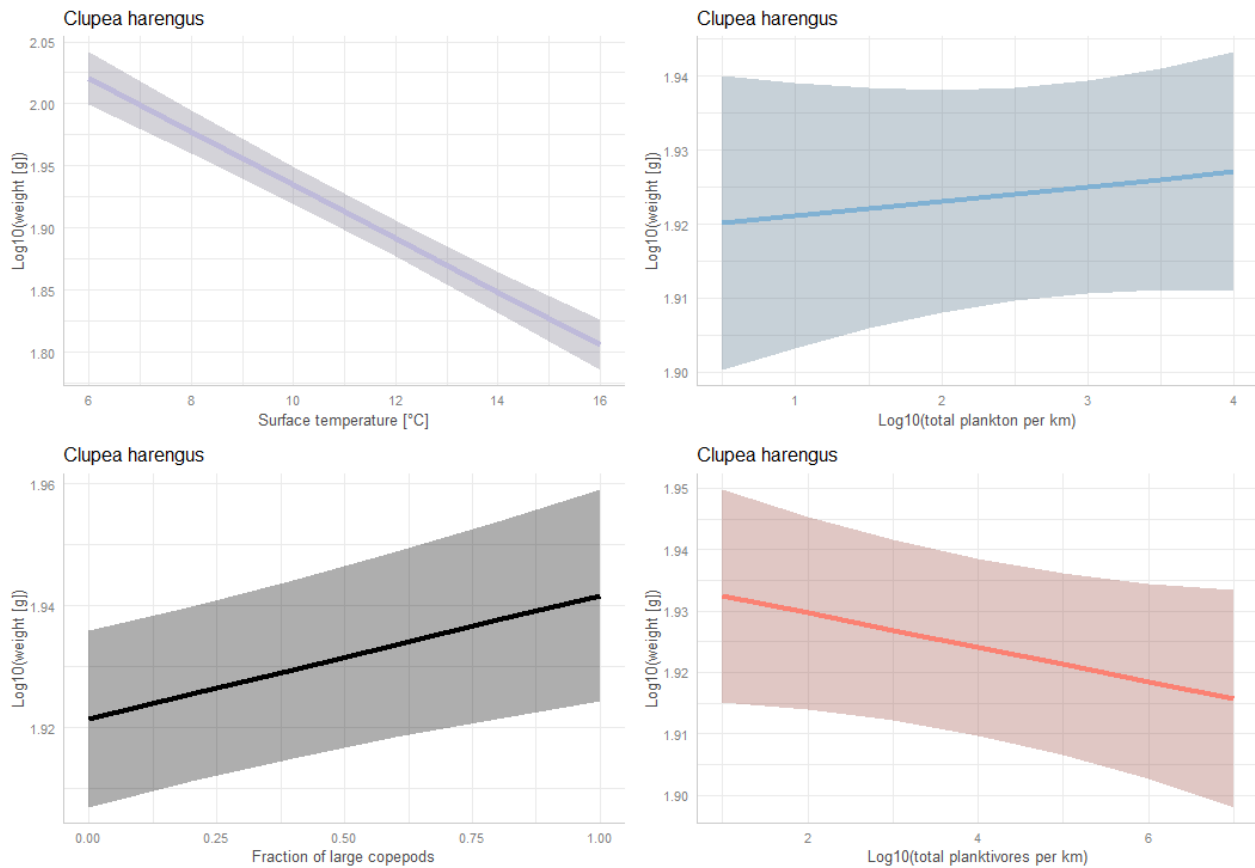


Figure 9. The effect of surface temperature, zooplankton abundance, proportion of large copepods, and abundance of planktivores on the weight at length of herring.

Table 2. sdmTMB model results for mackerel, including slopes for the various predictors, their interactions, associated standard error, and *p* values.

Term	Estimate	S. error	<i>p</i>
Intercept	-1.2	0.12	<0.001
Log10(length)	2.4	0.06	<0.001
Surface temperature	-0.094	0.0079	<0.001
Log10(total zooplankton count)	-0.0085	0.032	0.79
Fraction of large copepods	0.34	0.067	<0.001
Log10(number of planktivores)	-0.053	0.017	0.0022
Log10(length): Surface temperature	0.06	0.0034	<0.001
Log10(length): Log(total zooplankton count)	0.0077	0.015	0.61
Log10(length): Fraction of large copepods	-0.093	0.031	0.0031
Log10(length): Log10(number of planktivores)	0.026	0.0075	<0.001
Surface temperature: Log10(total zooplankton count)	-0.00089	0.0017	0.6

Surface temperature: Fraction of large copepods	-0.014	0.0041	<0.001
Surface temperature: Log10(number of planktivores)	0.00095	0.001	0.35
Log10(total zooplankton count): Fraction of large copepods	0.012	0.014	0.4
Log10(total zooplankton count): Log10(number of planktivores)	0.0034	0.0035	0.34
Fraction of large copepods: Log10(number of planktivores)	-0.015	0.008	0.067

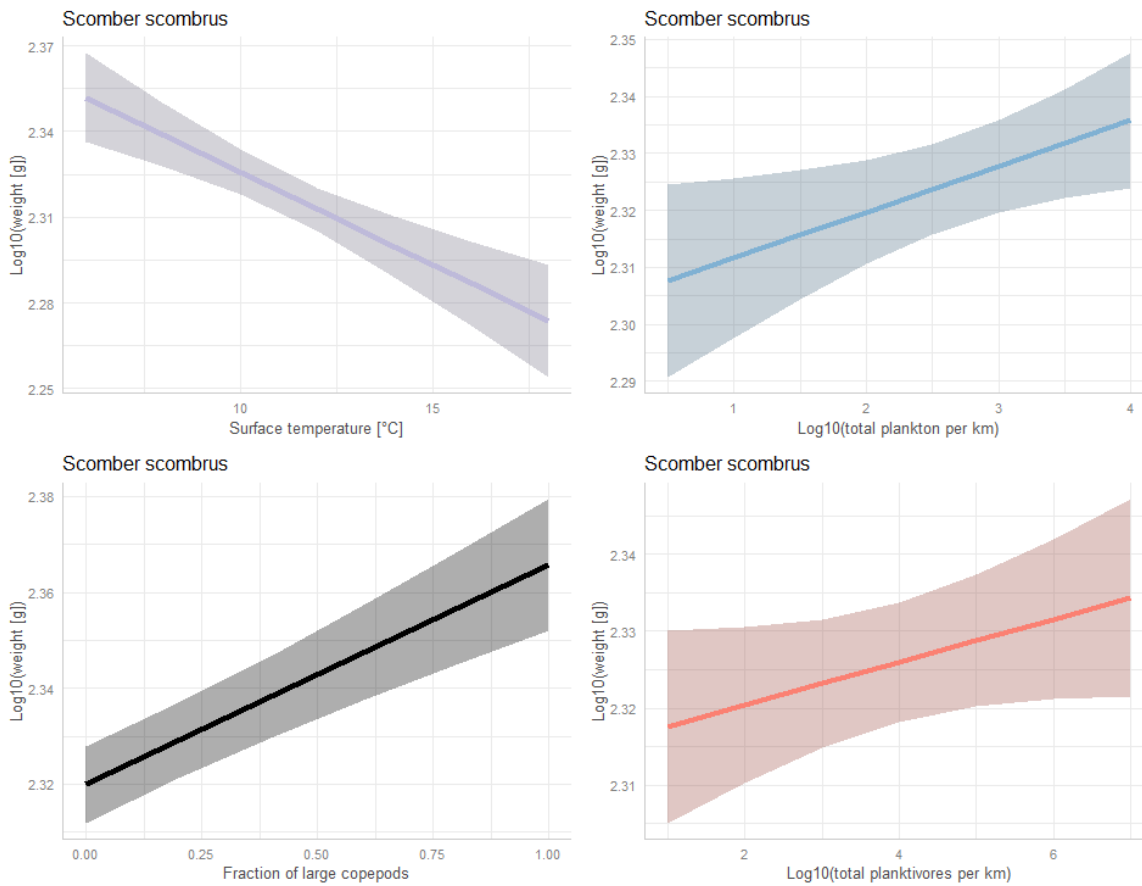


Figure 10. The effect of surface temperature, zooplankton abundance, proportion of large copepods, and abundance of planktivores on the weight at length of mackerel.

Table 3. sdmTMB model results for sprat, including slopes for the various predictors, their interactions, associated standard error, and *p* values.

Term	Estimate	S. error	<i>p</i>
Intercept	-2.1	0.15	<0.001
Log10(length)	3.1	0.071	<0.001
Surface temperature	-0.078	0.01	<0.001
Log10(total zooplankton count)	0.19	0.043	<0.001
Fraction of large copepods	0.086	0.12	0.48

Log10(number of planktivores)	0.034	0.028	0.22
Log10(length): Surface temperature	0.054	0.0031	<0.001
Log10(length): Log(total zooplankton count)	-0.17	0.018	<0.001
Log10(length): Fraction of large copepods	-0.039	0.041	0.34
Log10(length): Log10(number of planktivores)	-0.039	0.0077	<0.001
Surface temperature: Log10(total zooplankton count)	8e-04	0.0026	0.76
Surface temperature: Fraction of large copepods	-0.0034	0.0087	0.7
Surface temperature: Log10(number of planktivores)	0.0014	0.0016	0.41
Log10(total zooplankton count): Fraction of large copepods	0.01	0.018	0.56
Log10(total zooplankton count): Log10(number of planktivores)	-0.0035	0.0058	0.55
Fraction of large copepods: Log10(number of planktivores)	-0.0039	0.014	0.77

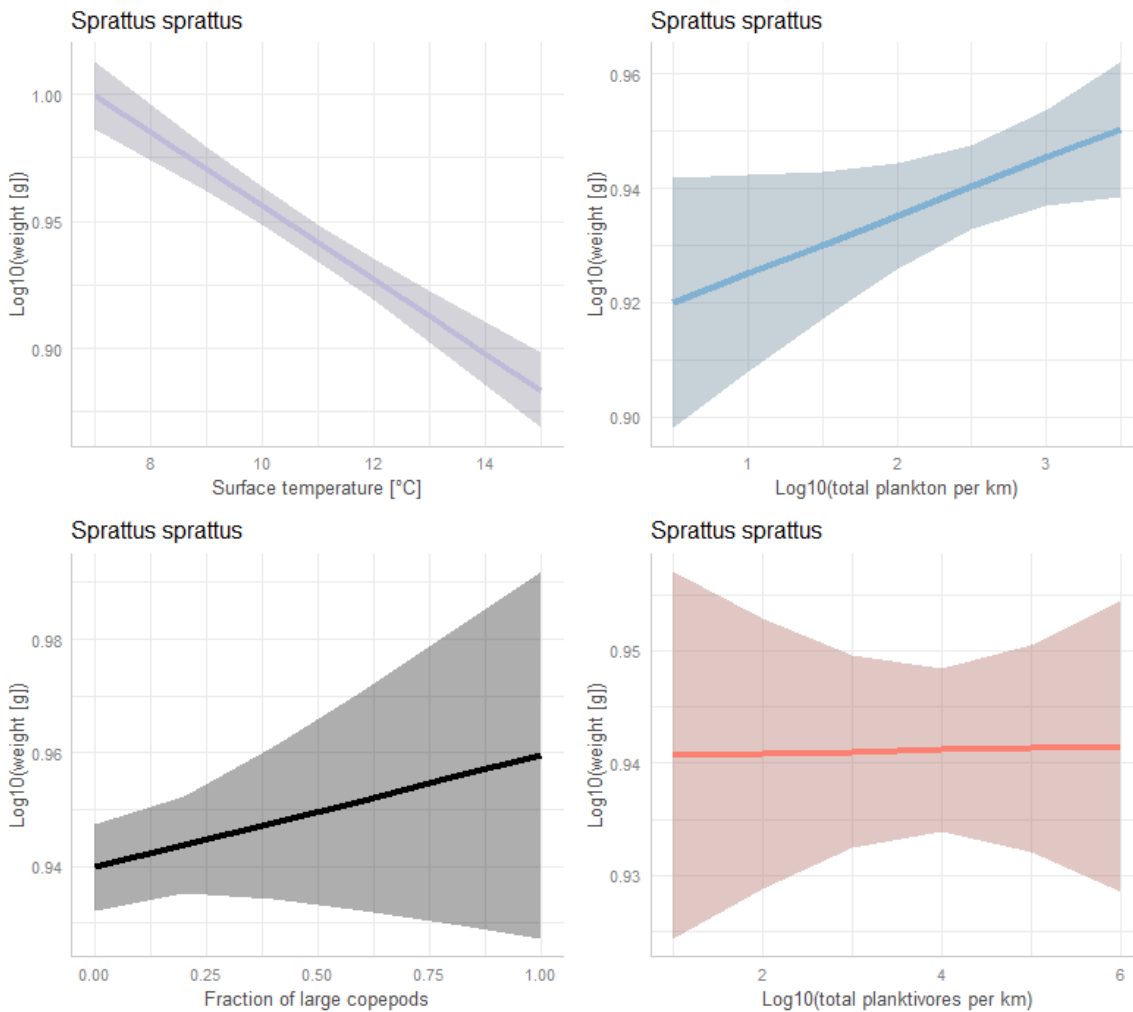


Figure 11. The effect of surface temperature, zooplankton abundance, proportion of large copepods, and abundance of planktivores on the weight at length of sprat.

Table 4. sdmTMB model results for Norway pout, including slopes for the various predictors, their interactions, associated standard error, and *p* values.

Term	Estimate	S. error	p
Intercept	-1.4	0.19	<0.001
Log10(length)	2.4	0.097	<0.001
Surface temperature	-0.077	0.014	<0.001
Log10(total zooplankton count)	0.062	0.05	0.21
Fraction of large copepods	-0.12	0.12	0.29
Log10(number of planktivores)	0.0074	0.031	0.81
Log10(length): Surface temperature	0.062	0.0053	<0.001
Log10(length): Log(total zooplankton count)	-0.052	0.017	0.0026
Log10(length): Fraction of large copepods	0.021	0.036	0.56
Log10(length): Log10(number of planktivores)	-0.013	0.0094	0.17
Surface temperature: Log10(total zooplankton count)	-0.0011	0.0033	0.74
Surface temperature: Fraction of large copepods	0.0038	0.007	0.58
Surface temperature: Log10(number of planktivores)	7.3e-05	0.0021	0.97
Log10(total zooplankton count): Fraction of large copepods	0.022	0.017	0.19
Log10(total zooplankton count): Log10(number of planktivores)	0.0024	0.0054	0.66
Fraction of large copepods: Log10(number of planktivores)	0.0018	0.01	0.86

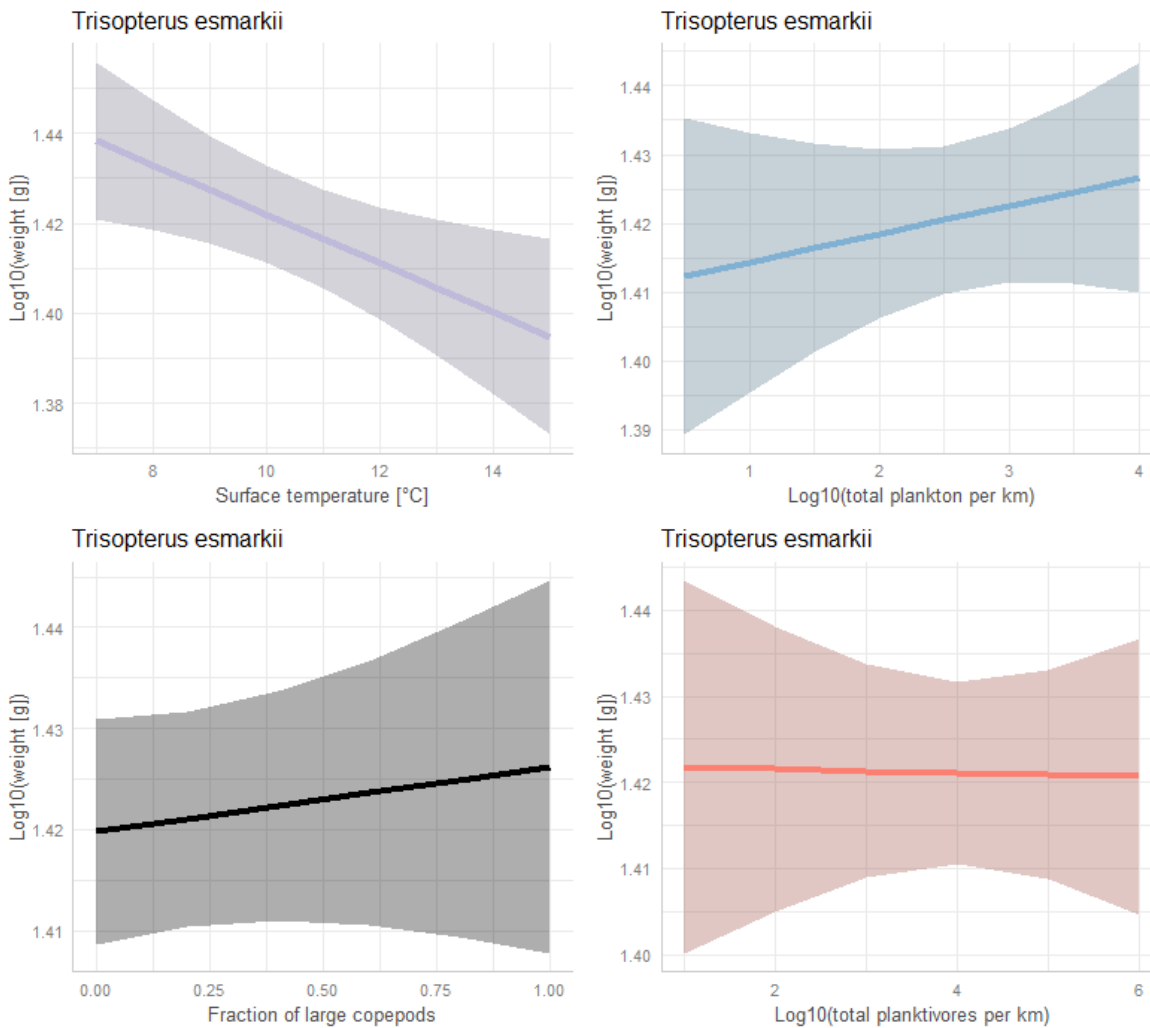


Figure 12. The effect of surface temperature, zooplankton abundance, proportion of large copepods, and abundance of planktivores on the weight at length of Norway pout.

6. Discussion

Detecting quantitative relationships between highly dynamic planktivorous fish and zooplankton populations empirically has been remarkably elusive. We present compelling evidence that quantitatively links changes in zooplankton abundance and size with fish body condition over different spatial scales and different studies across the northeast Atlantic (Figs 4, 9-12). In general, at larger spatial scales (75 km and above), zooplankton abundance and the proportion of large copepods related positively with planktivorous fish body condition. Temperature was also often an important predictor, relating negatively to fish body condition and which interacted with other predictors. This suggests that decreases in the abundance and size of plankton, as has been detected over large areas of the northeast Atlantic (Holland et al., 2023; Pitois & Fox, 2006), and warming through climate change, represent deteriorating pelagic habitat conditions for planktivorous fish (Thompson, Couce, et al., 2023). Our study adds to existing evidence that demonstrates information on both plankton size and abundance is critical to improve our understanding of how human pressures (e.g., climate) may affect the capacity of marine

ecosystems to perform critical ecosystem functions (seafood, climate regulation; Atkinson et al., 2024; Pitois & Fox, 2006).

Much marine ecosystem research assumes that decreases in the quantity and quality of zooplankton populations resulting from climate change will negatively affect higher trophic levels because of reductions in the flow and efficiency of energy transfer from plankton to fish (Atkinson et al., 2024; du Pontavice et al., 2021; Heneghan et al., 2023; Kwiatkowski et al., 2019). Despite this, empirical evidence of the direct links between changes in plankton and planktivorous fish populations have been challenging to identify (Pitois et al., 2012, 2021; Thompson et al., 2020). Key limitations here have been high uncertainty in planktivorous fish biomass estimates (Nnanatu et al., 2020; Walker et al., 2017), the lack of routine plankton body size data collection, and technical challenges of linking observations across surveys of plankton and fish assemblages. Estimates of fish body condition help circumvent these challenges because they are not so susceptible to catchability issues as biomass estimates, they can be derived from long-term and extensive data collected across the northeast Atlantic and provide insights on relatively short-term (weeks-months) pelagic habitat conditions which are highly temporally dynamic. In addition, our post-hoc data sampling approach enabled us to draw on temporally and spatially relevant observations from across surveys to measure the effect of zooplankton assemblage structure and the density-dependence from potential planktivorous competitors on fish body condition. We also account for unmeasured variables via spatial and spatiotemporal random fields that could otherwise confound interpretation of the relationship between zooplankton and planktivorous fish. The results we present demonstrate that we have developed the capability to predict planktivorous fish species body condition using pelagic habitat conditions and quantitatively link changes across the food web that could be applied to determine environmental status.

We did not detect systematic temporal declines in fish body condition across species at the Comp4 assessment scale (Fig. 8). This could be because interactions between plankton and fish are not determined at the scale of Comp4 areas, or at annual scales, or that the observations of fish body condition we make use of are largely from the North Sea where plankton assemblages have been more stable over the study period. The direction of the relationship between fish body condition and measures of zooplankton abundance and size were spatially scale-dependent. This could be indicative of the scale at which top-down and bottom-up processes manifest. For instance, evidence of top-down effects, where planktivores with higher weight at length (potentially indicative of recent feeding) have depleted zooplankton populations, appear to be relatively local (under 50 km) and weak (Fig. 4). At larger scales, however, bottom-up processes where higher zooplankton populations act to increase fish weight at length appear to become more prominent and stronger (Fig. 4).

In future, drawing on longer-term and more spatially extensive observations of fish body condition to better interrogate the possible mechanisms underlying the scale dependent effects we report could be fruitful. This was not possible in the time because many data stored on DATRAS that were missing key information on where and when observations were made (likely due to issue with merging information on hauls and biology) will require significant post-processing to make them fit for use. If these data could be sufficiently processed, an analysis of fish body condition could be extended in time, space and across the food web to include benthivores and piscivores (Thompson et al., 2020; Thompson, Lynam, et al., 2023), for instance. Such an approach could reveal areas, times, and specific ecosystem components that are healthy, stressed, or undergoing change. Fish growth rates could be estimated empirically from such data and used to test more rigorously what 'good' body condition is for given environmental conditions, because having weight at length that

deviates from the average (Fig. 6) may be advantageous in specific environments, e.g., where prey availability fluctuates and there is a need to store energy. Development of routine *in situ* size measurements in future could also dramatically improve capability to assess and predict trends in plankton size and abundance that is currently not possible for the study region (Pitois et al., 2021).

We use change in fish body condition to determine how changing pelagic habitat conditions has affected fish, based on the quantity and composition of plankton, temperature and fish with similar foraging strategies. Decreases in the abundance and changes in the composition of zooplankton, coupled with climate change, point to widespread deteriorating habitat conditions for planktivorous fish in the northeast Atlantic. Such information will help determine environmental status for pelagic habitats to support The Convention for the Protection of the Marine Environment of the North-East Atlantic (the 'OSPAR Convention'; henceforth OSPAR) Quality Status Reporting process and assessments of Good Environmental Status (GES) under the EU Marine Strategy Framework Directive (MSFD) and subsequently to meet the needs of the UK Marine Strategy and Defra's 25 Year Environment Plan.

7. References

- Anderson, S. C., Ward, E. J., English, P. A., & Barnett, L. A. K. (2022). sdmTMB: an R package for fast, flexible, and user-friendly generalized linear mixed effects models with spatial and spatiotemporal random fields. *BioRxiv*, 2022–2023. <https://doi.org/10.1101/2022.03.24.485545>
- Atkinson, A., Rossberg, A. G., Gaedke, U., Sprules, G., Heneghan, R. F., Batziakas, S., Grigoratou, M., Fileman, E., Schmidt, K., & Frangoulis, C. (2024). Steeper size spectra with decreasing phytoplankton biomass indicate strong trophic amplification and future fish declines. *Nature Communications*, 15(1), 381. <https://doi.org/10.1038/s41467-023-44406-5>
- Batten, S. D., Clark, R., Flinkman, J., Hays, G., John, E., John, A. W. G., Jonas, T., Lindley, J. A., Stevens, D. P., & Walne, A. (2003). CPR sampling: the technical background, materials and methods, consistency and comparability. *Progress in Oceanography*, 58(2–4), 193–215. <https://doi.org/10.1016/J.POCEAN.2003.08.004>
- Brose, U., Jonsson, T., Berlow, E. L., Warren, P., Banasek-Richter, C., Bersier, L.-F., Blanchard, J. L., Brey, T., Carpenter, S. R., Blandenier, M.-F. C., Cushing, L., Dawah, H. A., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M. E., Martinez, N. D., Memmott, J., ... Cohen, J. E. (2006). CONSUMER–RESOURCE BODY-SIZE RELATIONSHIPS IN NATURAL FOOD WEBS. *Ecology*, 87(10), 2411–2417. [https://doi.org/https://doi.org/10.1890/0012-9658\(2006\)87\[2411:CBRINF\]2.0.CO;2](https://doi.org/https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2)
- Capuzzo, E., Lynam, C. P., Barry, J., Stephens, D., Forster, R. M., Greenwood, N., McQuatters-Gollop, A., Silva, T., van Leeuwen, S. M., & Engelhard, G. H. (2017). A decline in primary production in the North Sea over 25 years, associated with reductions in zooplankton abundance and fish stock recruitment. *Global Change Biology*, 24(1), e352–e364. <https://doi.org/10.1111/gcb.13916>

- du Pontavice, H., Gascuel, D., Reygondeau, G., Stock, C., & Cheung, W. W. L. (2021). Climate-induced decrease in biomass flow in marine food webs may severely affect predators and ecosystem production. *Global Change Biology*, 27(11), 2608–2622. <https://doi.org/10.1111/gcb.15576>
- Edvardsen, A., Zhou, M., Tande, K. S., & Zhu, Y. (2002). Zooplankton population dynamics: measuring in situ growth and mortality rates using an Optical Plankton Counter. *Marine Ecology Progress Series*, 227, 205–219. <http://www.jstor.org/stable/24864953>
- Egan, A., Rindorf, A., Berges, B., Kvamme, C., Loots, C., van Damme, C., Sparrevohn, C. R., Johnsen, E., Berg, F., & Mosegaard, H. (2020). *Herring assessment working group for the area south of 62° N (HAWG)*. <http://doi.org/10.17895/ices.pub.6105>
- Engelhard, G. H., Blanchard, J. L., Pinnegar, J. K., van der Kooij, J., Bell, E. D., Mackinson, S., & Righton, D. A. (2013). Body condition of predatory fishes linked to the availability of sandeels. *Marine Biology*, 160(2), 299–308. <https://doi.org/10.1007/s00227-012-2088-1>
- Engelhard, G. H., Peck, M. A., Rindorf, A., C. Smout, S., Van Deurs, M., Raab, K., Andersen, K. H., Garthe, S., Lauerburg, R. A. M., Scott, F., Brunel, T., Aarts, G., Van Kooten, T., & Dickey-Collas, M. (2014). Forage fish, their fisheries, and their predators: Who drives whom? *ICES Journal of Marine Science*, 71(1), 90–104. <https://doi.org/10.1093/icesjms/fst087>
- Enserink, L., Blauw, A., van der Zande, D., & Markager, S. (2019). Summary report of the EU project 'Joint monitoring programme of the eutrophication of the north Sea with satellite data'(Ref: DG ENV/MSFD second Cycle/2016). *Belgium: REMSEM*, 21.
- Gorsky, G., Ohman, M. D., Picheral, M., Gasparini, S., Stemmann, L., Romagnan, J.-B., Cawood, A., Pesant, S., García-Comas, C., & Prejger, F. (2010). Digital zooplankton image analysis using the ZooScan integrated system. *Journal of Plankton Research*, 32(3), 285–303. <https://doi.org/10.1093/plankt/fbp124>
- Gurvan Madec, & the NEMO team. (2016). Nemo Ocean Engine. *Note Du Pôle de Modélisation de l'Institut Pierre-Simon Laplace No 27*. ISSN No 1288-1619
- Heneghan, R. F., Everett, J. D., Blanchard, J. L., Sykes, P., & Richardson, A. J. (2023). Climate-driven zooplankton shifts cause large-scale declines in food quality for fish. *Nature Climate Change*, 13(5), 470–477. <https://doi.org/10.1038/s41558-023-01630-7>
- Holland, M., Louchart, A., Artigas, L. F., & McQuatters-Gollop, A. (2023). Changes in Phytoplankton and Zooplankton Communities Common Indicator Assessment Changes in Phytoplankton and Zooplankton Communities. *OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic*. OSPAR Commission, London. <https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/changes-plankton-communities/>
- Holland, M. M., Louchart, A., Artigas, L. F., Ostle, C., Atkinson, A., Rombouts, I., Graves, C. A., Devlin, M., Heyden, B., Machairopoulou, M., Bresnan, E., Schilder, J., Jakobsen, H. H., Lloyd-Hartley, H., Tett, P., Best, M., Goberville, E., & McQuatters-Gollop, A. (2023). Major declines in NE Atlantic plankton contrast with more stable populations in the rapidly warming North

Sea. *Science of The Total Environment*, 898, 165505.
<https://doi.org/https://doi.org/10.1016/j.scitotenv.2023.165505>

ICES. (2015a). Manual for international pelagic surveys (IPS). *Series of ICES Survey Protocols SISP 9–IPS*, 92. <http://doi.org/10.17895/ices.pub/7582>

ICES. (2015b). Manual for international pelagic surveys (IPS). *Series of ICES Survey Protocols SISP 9–IPS*, 92. <https://doi.org/10.17895/ices.pub.7582>

Kwiatkowski, L., Aumont, O., & Bopp, L. (2019). Consistent trophic amplification of marine biomass declines under climate change. *Global Change Biology*, 25(1), 218–229.
<https://doi.org/https://doi.org/10.1111/gcb.14468>

Lüdecke, D. (2018). ggffects: Tidy data frames of marginal effects from regression models. *Journal of Open Source Software*, 3(26), 772. [10.21105/joss.00772](https://doi.org/10.21105/joss.00772)

Lynam, C. P., Llope, M., Möllmann, C., Helaouët, P., Bayliss-Brown, G. A., & Stenseth, N. C. (2017). Interaction between top-down and bottom-up control in marine food webs. *Proceedings of the National Academy of Sciences*, 114(8), 1952–1957.
<https://doi.org/10.1073/pnas.1621037114>

Lynam, C. P., & Ribeiro, J. (2022). A data product derived from Northeast Atlantic groundfish data from scientific trawl surveys 1983-2020.
<https://doi.org/https://doi.org/10.14466/CefasDataHub.126>

Magnusson, A., Skaug, H., Nielsen, A., Berg, C., Kristensen, K., Maechler, M., van Benthem, K., Bolker, B., Brooks, M., & Brooks, M. M. (2017). Package ‘glmmTMB.’ *R Package Version 0.2.0*, 25. <https://doi.org/10.32614/RJ-2017-066>

McQuatters-Gollop, A., Atkinson, A., Aubert, A., Bedford, J., Best, M., Bresnan, E., Cook, K., Devlin, M., Gowen, R., Johns, D. G., Machairopoulou, M., McKinney, A., Mellor, A., Ostle, C., Scherer, C., & Tett, P. (2019). Plankton lifeforms as a biodiversity indicator for regional-scale assessment of pelagic habitats for policy. *Ecological Indicators*, 101, 913–925.
<https://doi.org/10.1016/j.ecolind.2019.02.010>

Mogensen, K., Balmaseda, M. A., & Weaver, A. (2012). *The NEMOVAR ocean data assimilation system as implemented in the ECMWF ocean analysis for System 4*, ECMWF Tech. Memo. 668

Morris, D., Andres, O., Ayers, R., Brown, A., Capuzzo, E., Cooper, K., Dye, S., Fernand, L., Flatman, S., Greenwood, N., Haverson, D., Hull, T., Hyder, K., Jennings, S., Jolliffe, R., Metcalfe, J., Meadows, B., Pearce, D., Pinnegar, J., ... Wright, S. (2016). *Cefas Fishing Survey System*. Cefas, UK. V1. doi: <https://doi.org/10.14466/CefasDataHub.6>

Nnanatu, C. C., Thompson, M. S. A., Spence, M. A., Couce, E., van der Kooij, J., & Lynam, C. P. (2020). Bayesian hierarchical space-time models to improve multispecies assessment by combining observations from disparate fish surveys. *ArXiv*. <http://arxiv.org/abs/2012.02196>

- OSPAR. (2023). *Food webs Thematic Assessment*. In: OSPAR, 2023: Quality Status Report 2023. OSPAR Commission, London. Available at: <https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/thematic-assessments/food-webs/>
- Ospar Commission. (2010). The North-East Atlantic Environment Strategy. *Strategy of the OSPAR Commission for the Protection of the Marine Environment of the North-East Atlantic, 2020, 2010–2013*.
- Petchey, O. L., Beckerman, A. P., Riede, J. O., & Warren, P. H. (2008). Size, foraging, and food web structure. *Proceedings of the National Academy of Sciences*. <https://doi.org/10.1073/pnas.0710672105>
- Picheral, M., Colin, S., & Irisson, J.-O. (2017). *EcoTaxa, a tool for the taxonomic classification of images*. <https://ecotaxa.obs-vlfr.fr>. <https://ecotaxa.obs-vlfr.fr>
- Pitois, S. G., & Fox, C. J. (2006). Long-term changes in zooplankton biomass concentration and mean size over the Northwest European shelf inferred from Continuous Plankton Recorder data. *ICES Journal of Marine Science*, 63(5), 785–798. <https://doi.org/10.1016/j.icesjms.2006.03.009>
- Pitois, S. G., Graves, C. A., Close, H., Lynam, C., Scott, J., Tilbury, J., van der Kooij, J., & Culverhouse, P. (2021). A first approach to build and test the Copepod Mean Size and Total Abundance (CMSTA) ecological indicator using in-situ size measurements from the Plankton Imager (PI). *Ecological Indicators*, 123, 107307. <https://doi.org/https://doi.org/10.1016/j.ecolind.2020.107307>
- Pitois, S. G., Lynam, C. P., Jansen, T., Halliday, N., & Edwards, M. (2012). Bottom-up effects of climate on fish populations: data from the Continuous Plankton Recorder. *Marine Ecology Progress Series*, 456, 169–186. <https://www.int-res.com/abstracts/meps/v456/p169-186/>
- Scott, J., Pitois, S., Creach, V., Malin, G., Culverhouse, P., & Tilbury, J. (2023). Resolution changes relationships: Optimizing sampling design using small scale zooplankton data. *Progress in Oceanography*, 210, 102946. <https://doi.org/https://doi.org/10.1016/j.pocean.2022.102946>
- Thompson, M. S. A., Couce, E., Schratzberger, M., & Lynam, C. P. (2023). Climate change affects the distribution of diversity across marine food webs. *Global Change Biology*, 29(23), 6606–6619. <https://doi.org/https://doi.org/10.1111/gcb.16881>
- Thompson, M. S. A., Lynam, C. P., & Preciado, I. (2023). *Pilot Assessment of Feeding Guilds*. In: *OSPAR, 2023: The 2023 Quality Status Report for the Northeast Atlantic*. <https://oap.ospar.org/en/ospar-assessments/quality-status-reports/qsr-2023/indicator-assessments/feeding-guild-pilot-assessment/>
- Thompson, M. S. A., Pontalier, H., Spence, M. A., Pinnegar, J. K., Greenstreet, S. P. R., Moriarty, M., Hélaouët, P., & Lynam, C. P. (2020). A feeding guild indicator to assess environmental change impacts on marine ecosystem structure and functioning. *Journal of Applied Ecology*, 57(9), 1769–1781. <https://doi.org/10.1111/1365-2664.13662>

- Turner, J. T. (2004). The importance of small planktonic copepods and their roles in pelagic marine food webs. *Zool. Stud*, 43(2), 255–266.
- van der Kooij, J., Fässler, S. M. M., Stephens, D., Readdy, L., Scott, B. E., & Roel, B. A. (2016). Opportunistically recorded acoustic data support Northeast Atlantic mackerel expansion theory. *ICES Journal of Marine Science*, 73(4), 1115–1126. <https://doi.org/10.1093/icesjms/fsv243>
- Van Deurs, M., Jorgensen, C., & Fiksen, O. (2015). Effects of copepod size on fish growth: A model based on data for North Sea sandeel. *Marine Ecology Progress Series*, 520, 235–243. <https://doi.org/10.3354/meps11092>
- Van Deurs, M., Koski, M., & Rindorf, A. (2014). Does copepod size determine food consumption of particulate feeding fish? *ICES Journal of Marine Science*. <https://doi.org/10.1093/icesjms/fst090>
- Walker, N. D., Maxwell, D. L., Le Quesne, W. J. F., & Jennings, S. (2017). Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, 74(5), 1448–1457. <https://doi.org/10.1093/icesjms/fsw250>
- Woodward, G., Ebenman, B., Emmerson, M., Montoya, J. M., Olesen, J. M., Valido, A., & Warren, P. H. (2005). Body size in ecological networks. *Trends in Ecology and Evolution*, 20(7), 402–409. <https://doi.org/10.1016/j.tree.2005.04.005>

8. Appendix

Data availability and consistent spatial deviations in $\log_{10}(\text{weight})$
Clupea harengus

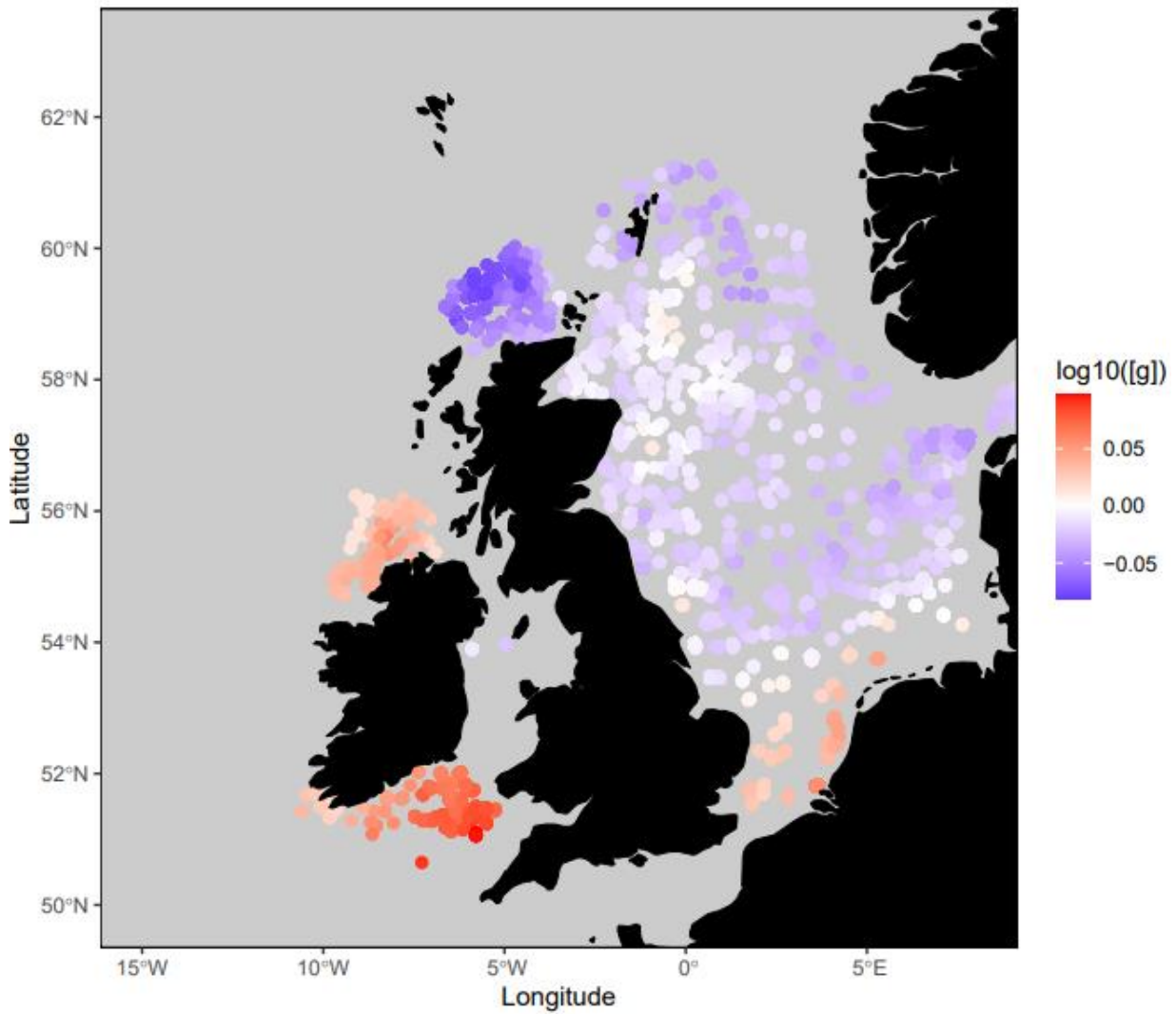


Fig. S1. The residual spatial variation in herring body condition (g on \log_{10} scale), independent of time, captured by the spatial random field.

Data availability and monthly deviations in $\log_{10}(\text{weight})$

Clupea harengus

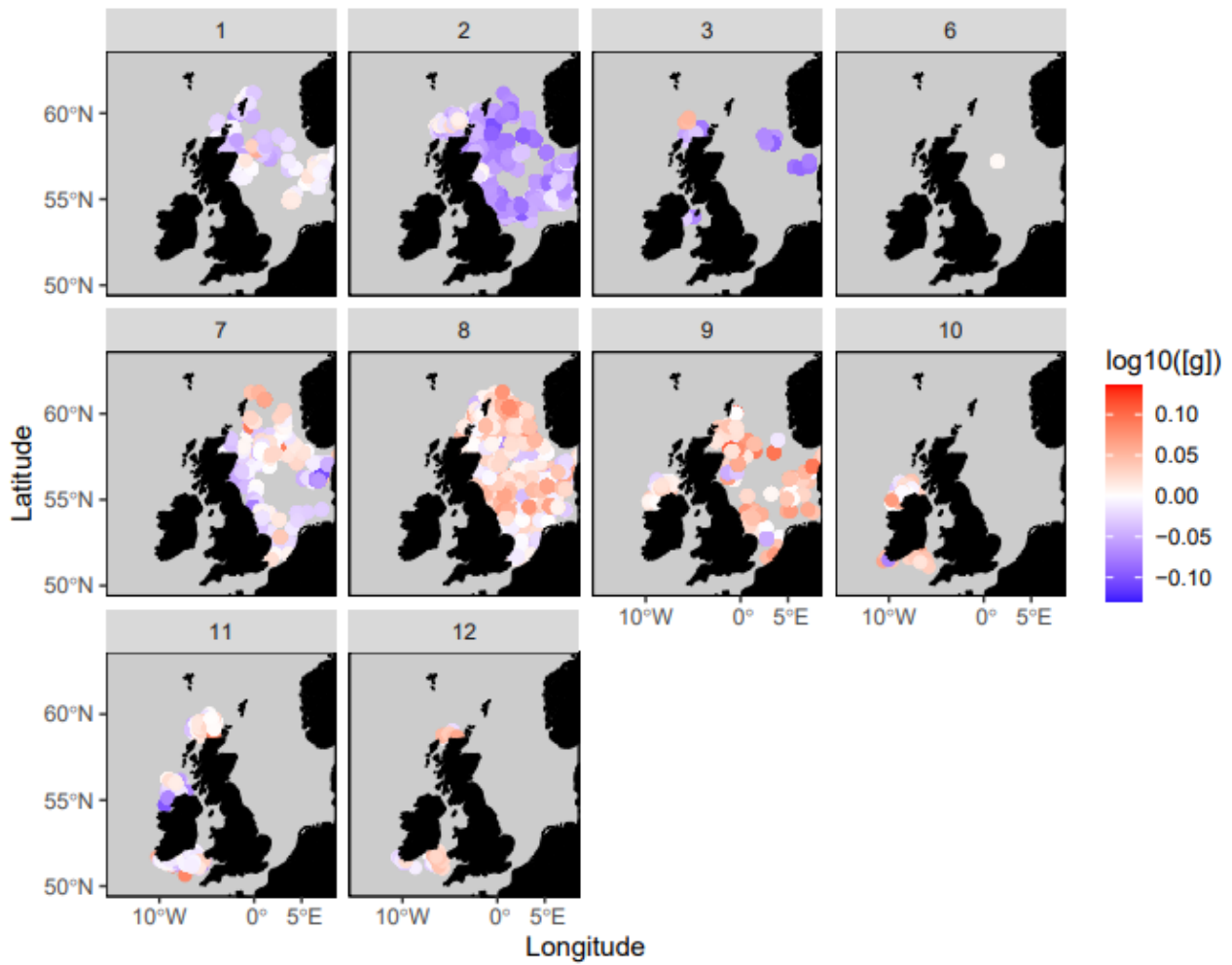


Fig. S2. The residual seasonal spatiotemporal variation in herring body condition (g on \log_{10} scale), independent of time, captured by a random field for month.

Data availability and annual deviations in $\log_{10}(\text{weight})$
Clupea harengus

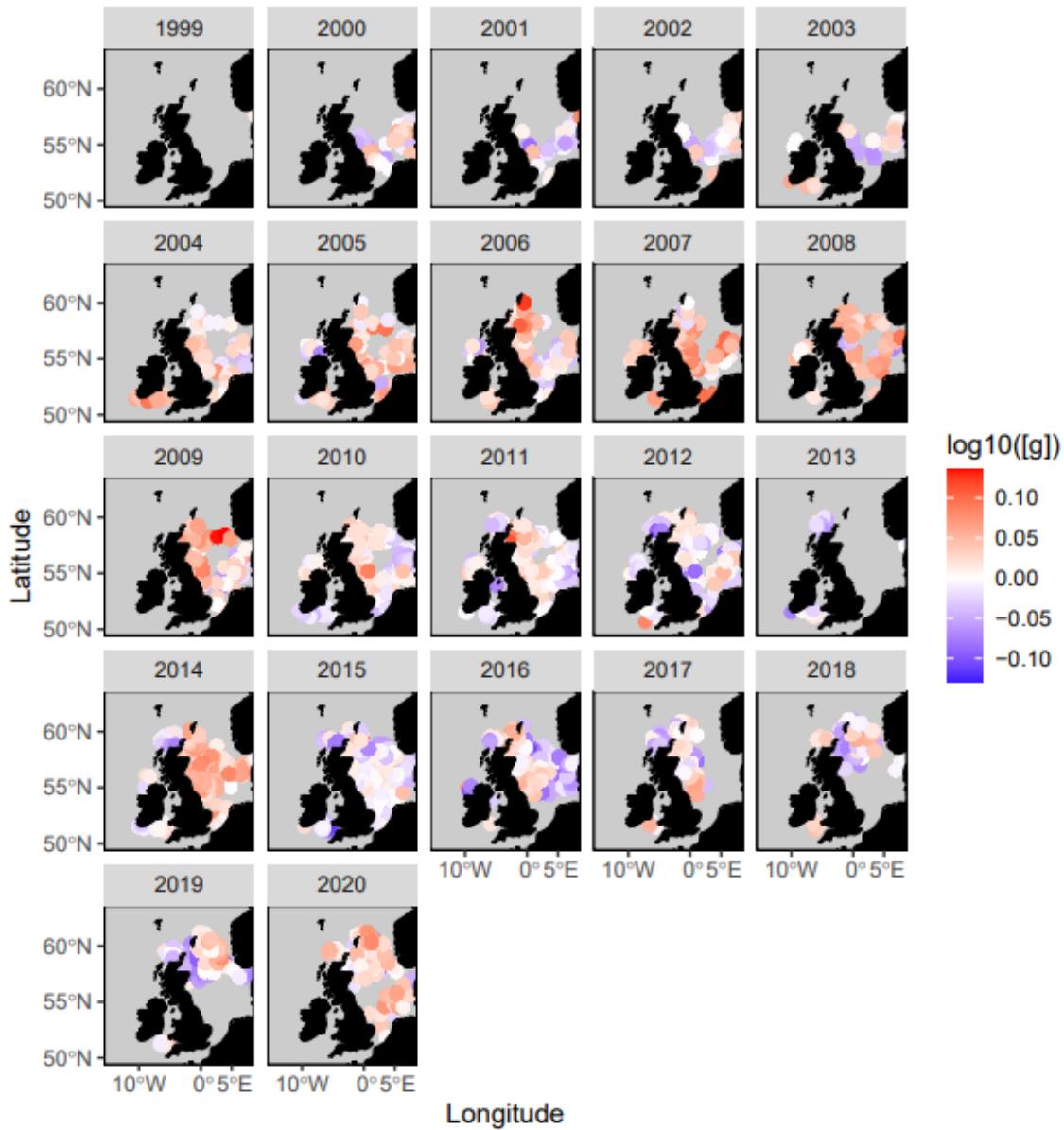


Fig. S3. The residual annual spatiotemporal variation in herring body condition (g on \log_{10} scale), independent of time, captured by a random field for year.

Data availability and consistent spatial deviations in $\log_{10}(\text{weight})$
Scomber scombrus

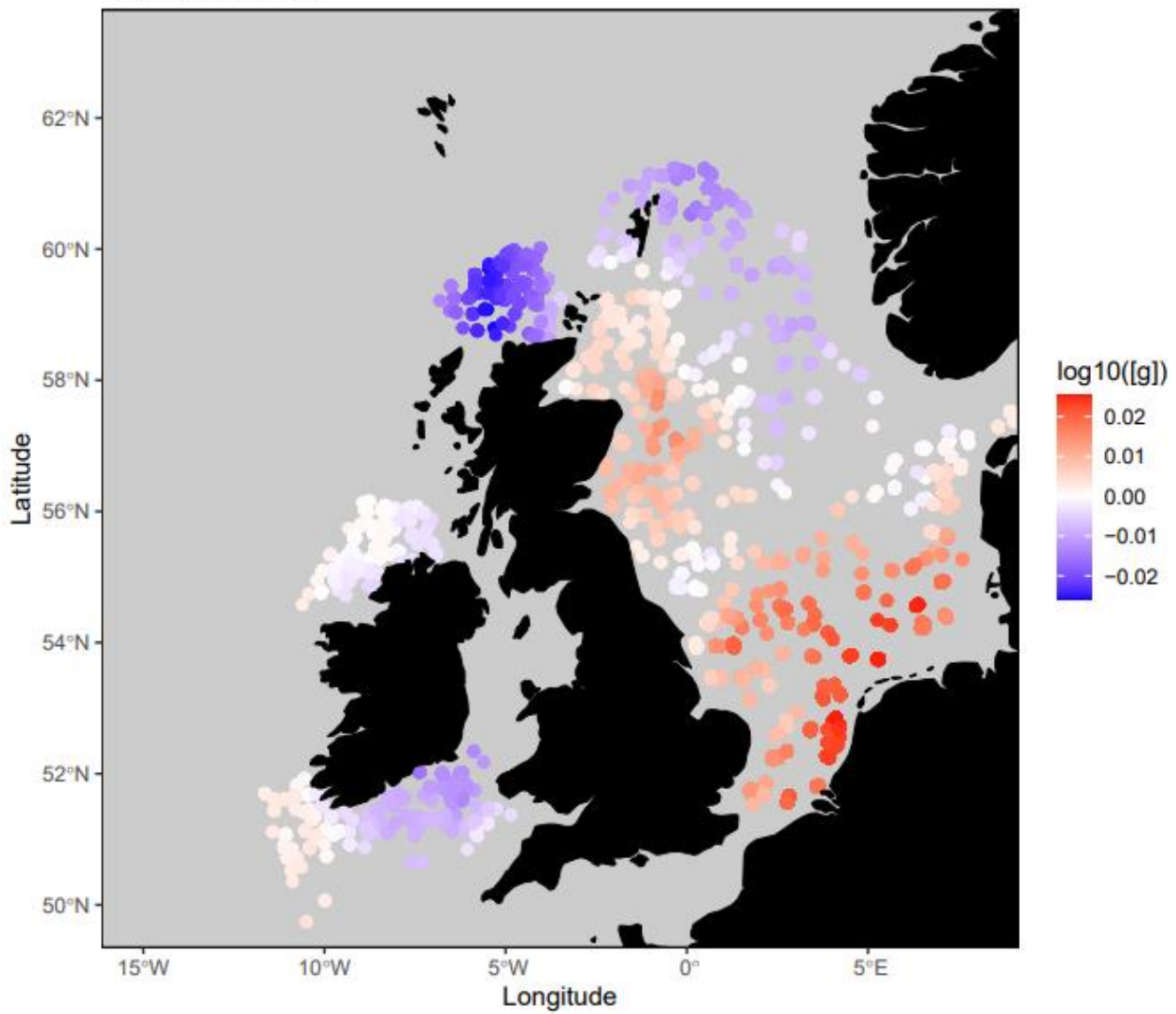


Fig. S4. The residual spatial variation in mackerel body condition (g on \log_{10} scale), independent of time, captured by the spatial random field.

Data availability and monthly deviations in $\log_{10}(\text{weight})$

Scomber scombrus

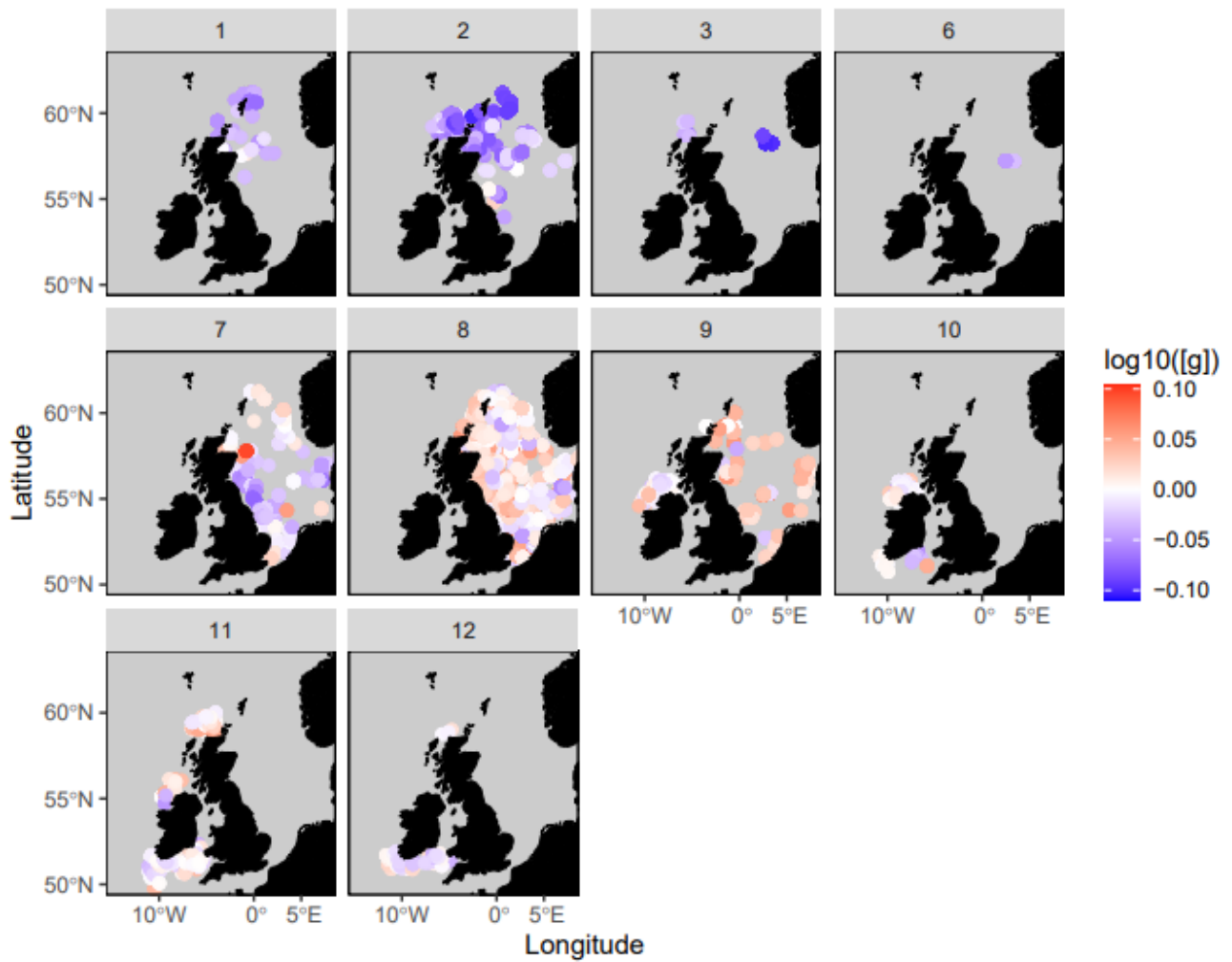


Fig. S5. The residual seasonal spatiotemporal variation in mackerel body condition (g on \log_{10} scale), independent of time, captured by a random field for month.

Data availability and annual deviations in $\log_{10}(\text{weight})$
Scomber scombrus

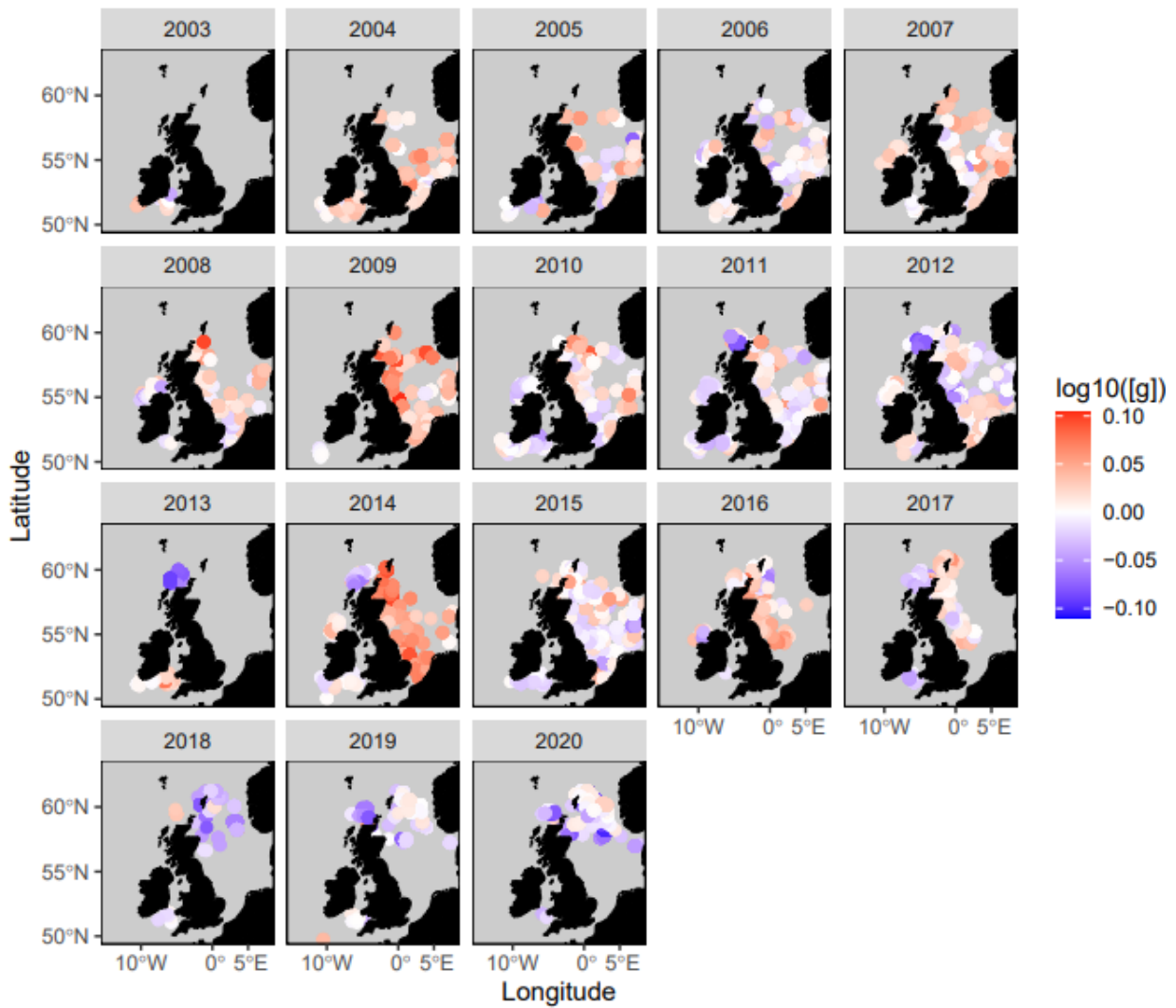


Fig. S6. The residual annual spatiotemporal variation in mackerel body condition (g on \log_{10} scale), independent of time, captured by a random field for year.

Data availability and consistent spatial deviations in $\log_{10}(\text{weight})$
Sprattus sprattus

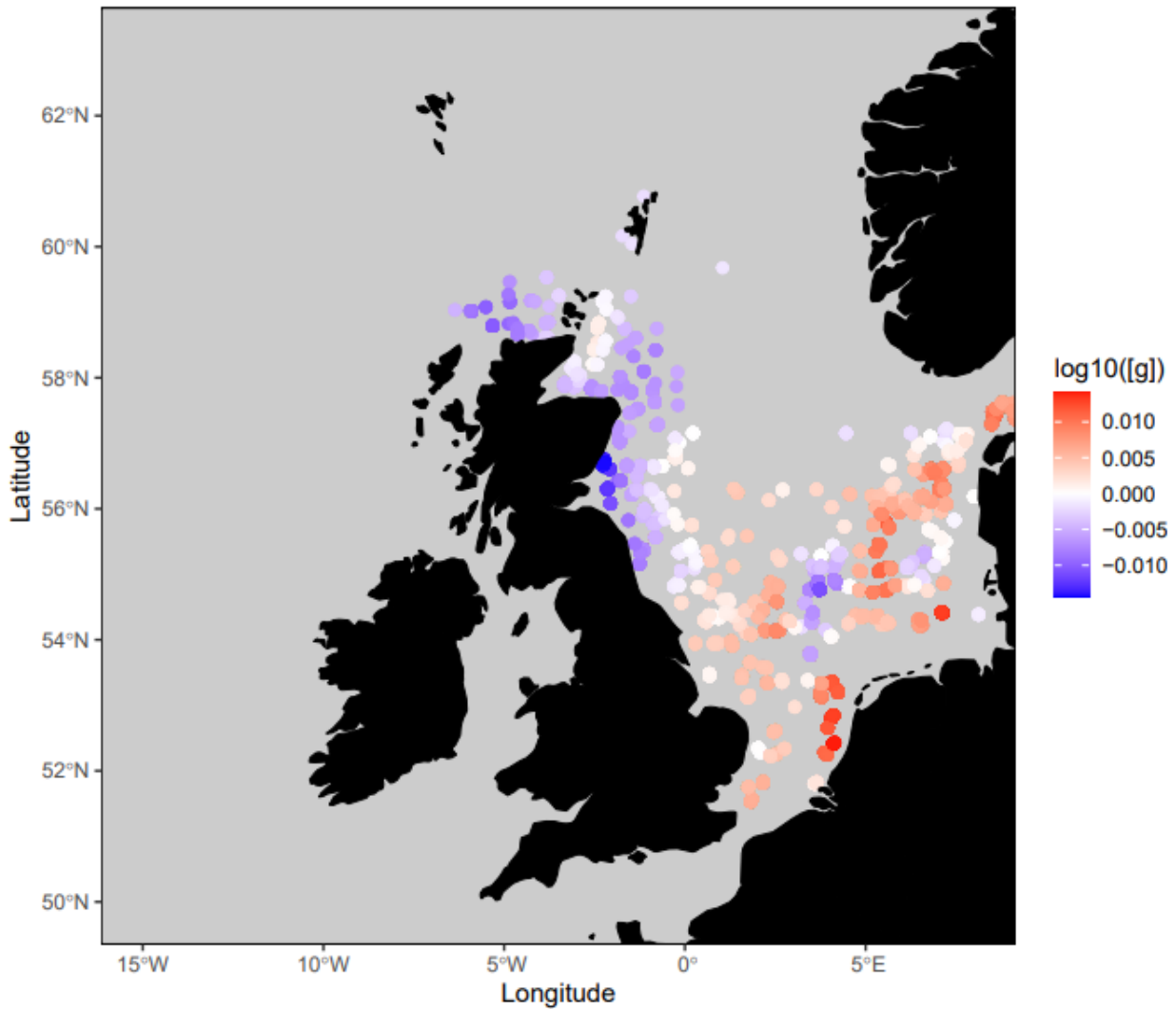


Fig. S7. The residual spatial variation in sprat body condition (g on \log_{10} scale), independent of time, captured by the spatial random field.

Data availability and monthly deviations in $\log_{10}(\text{weight})$
Sprattus sprattus

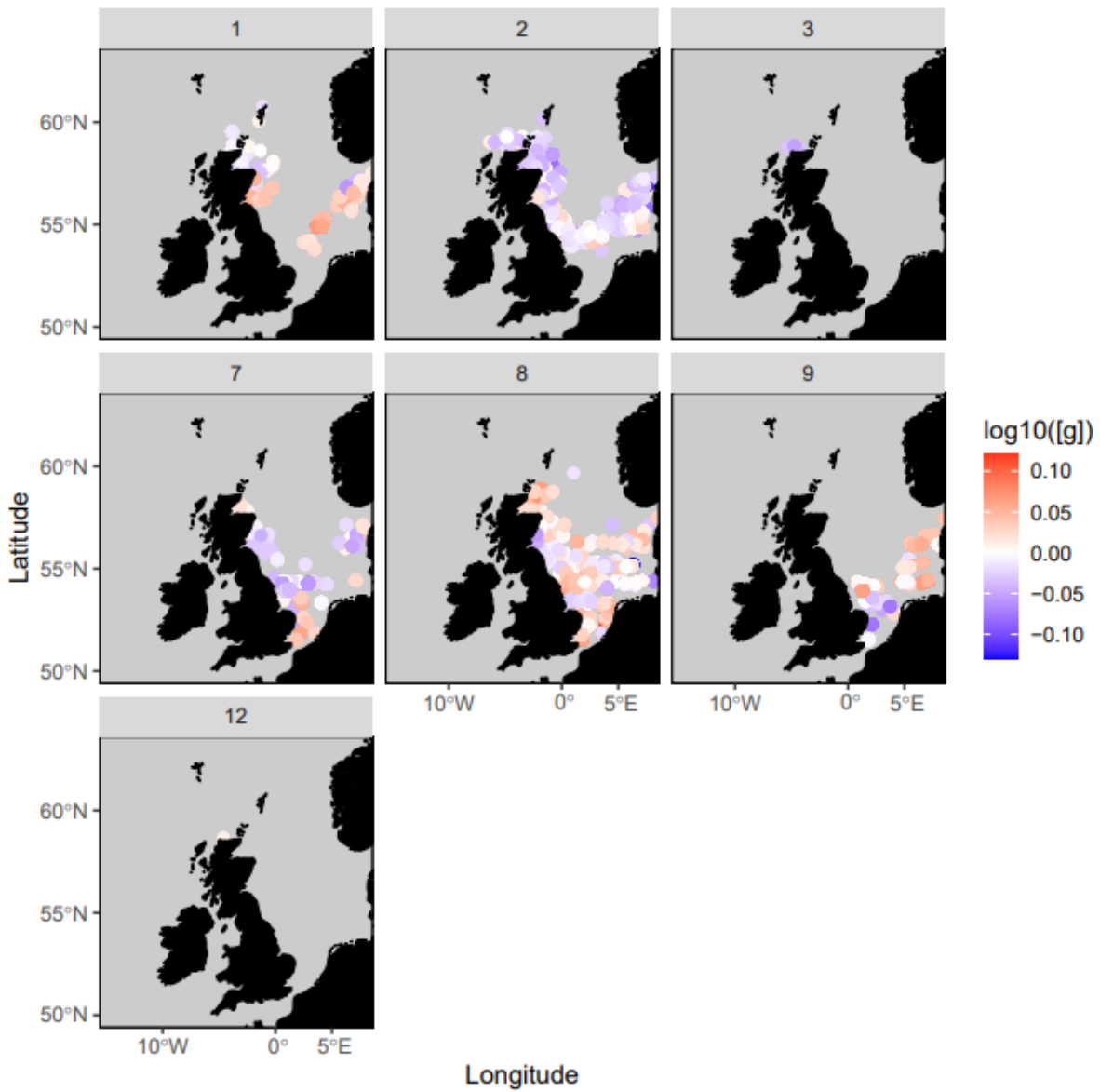


Fig. S8. The residual seasonal spatiotemporal variation in sprat body condition (g on \log_{10} scale), independent of time, captured by a random field for month.

Data availability and annual deviations in $\log_{10}(\text{weight})$
Sprattus sprattus

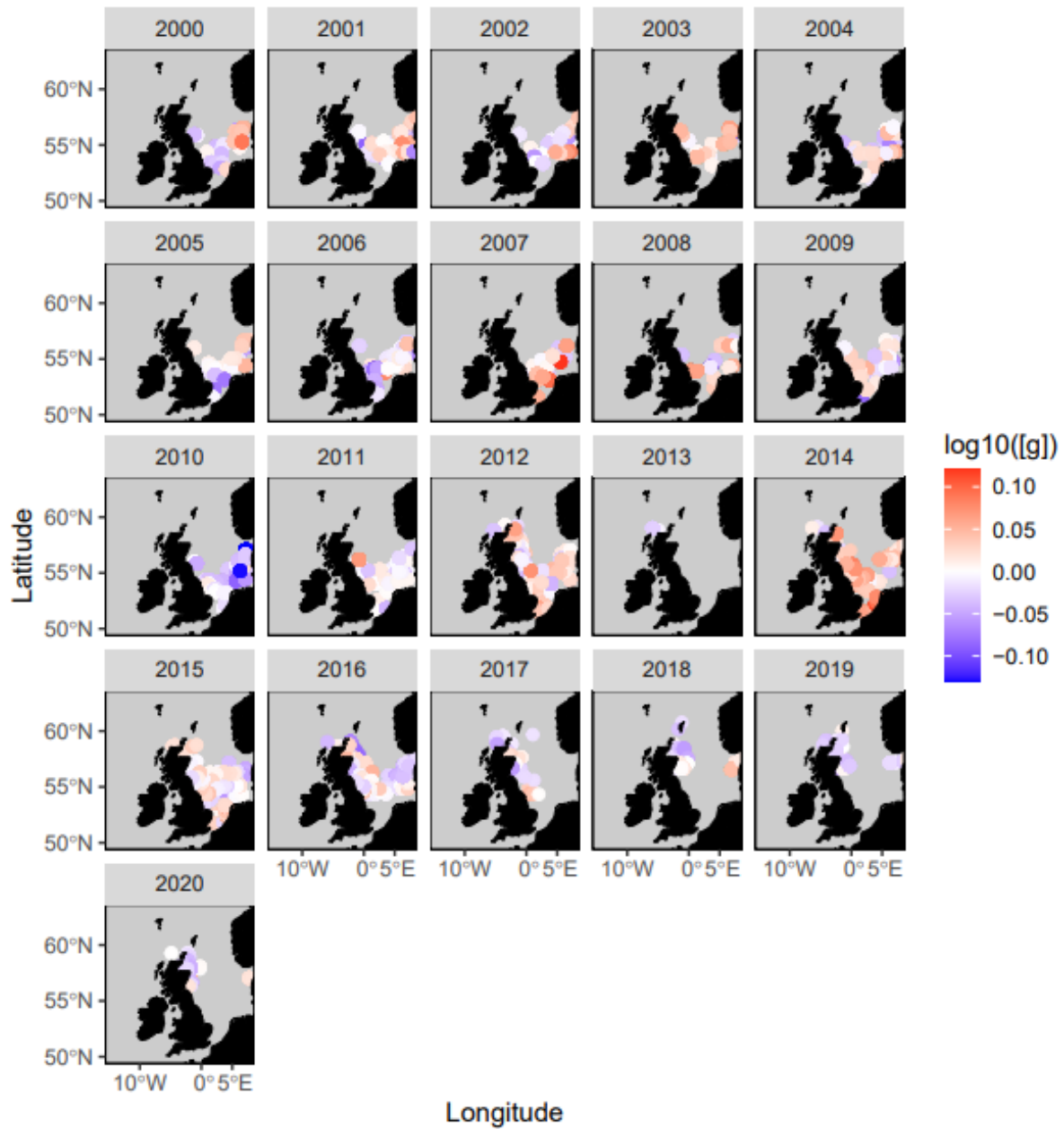


Fig. S9. The residual annual spatiotemporal variation in sprat body condition (g on \log_{10} scale), independent of time, captured by a random field for year.

Data availability and consistent spatial deviations in $\log_{10}(\text{weight})$
Trisopterus esmarkii

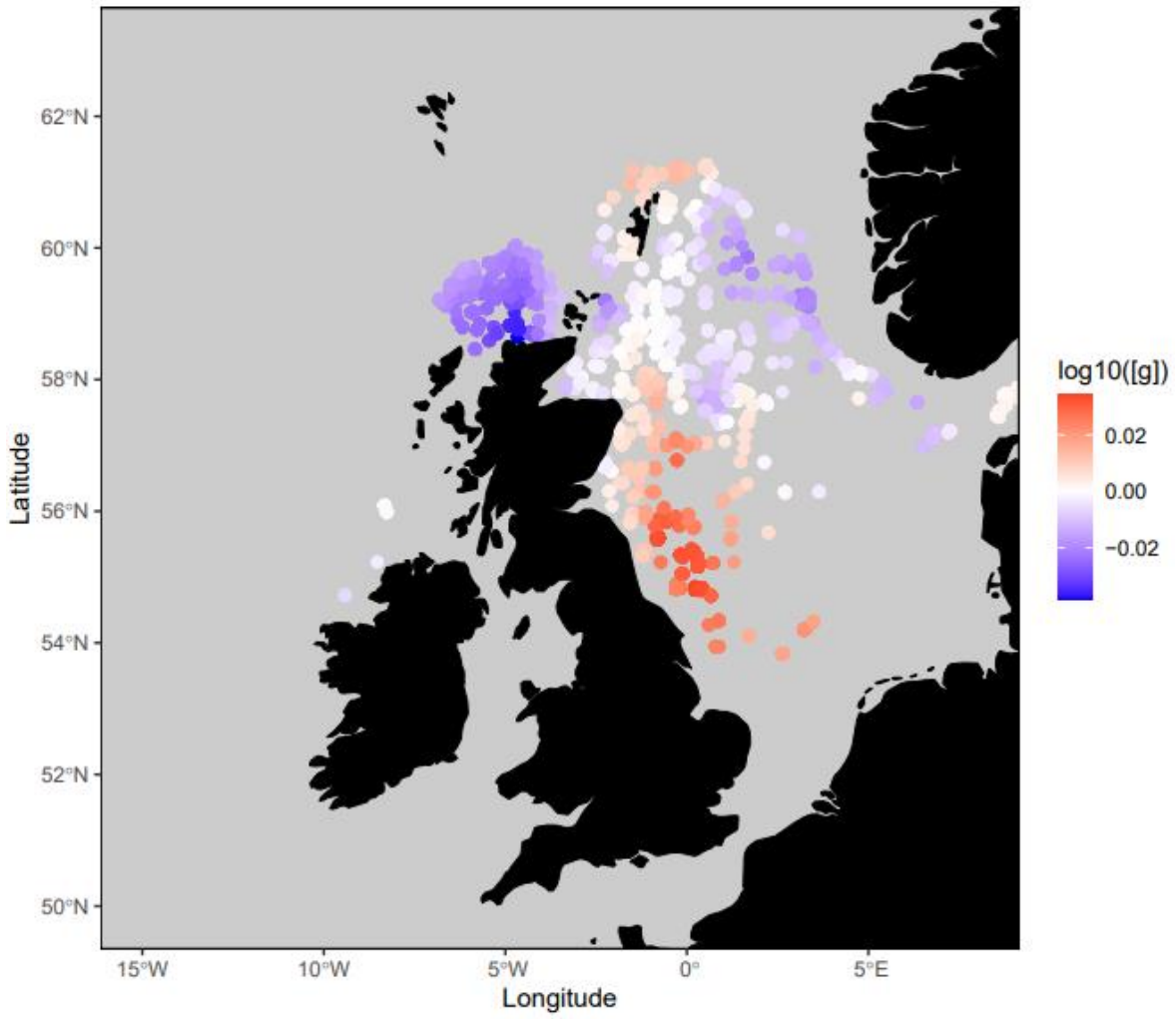


Fig. S10. The residual spatial variation in Norway pout body condition (g on \log_{10} scale), independent of time, captured by the spatial random field.

Data availability and monthly deviations in $\log_{10}(\text{weight})$

Trisopterus esmarkii

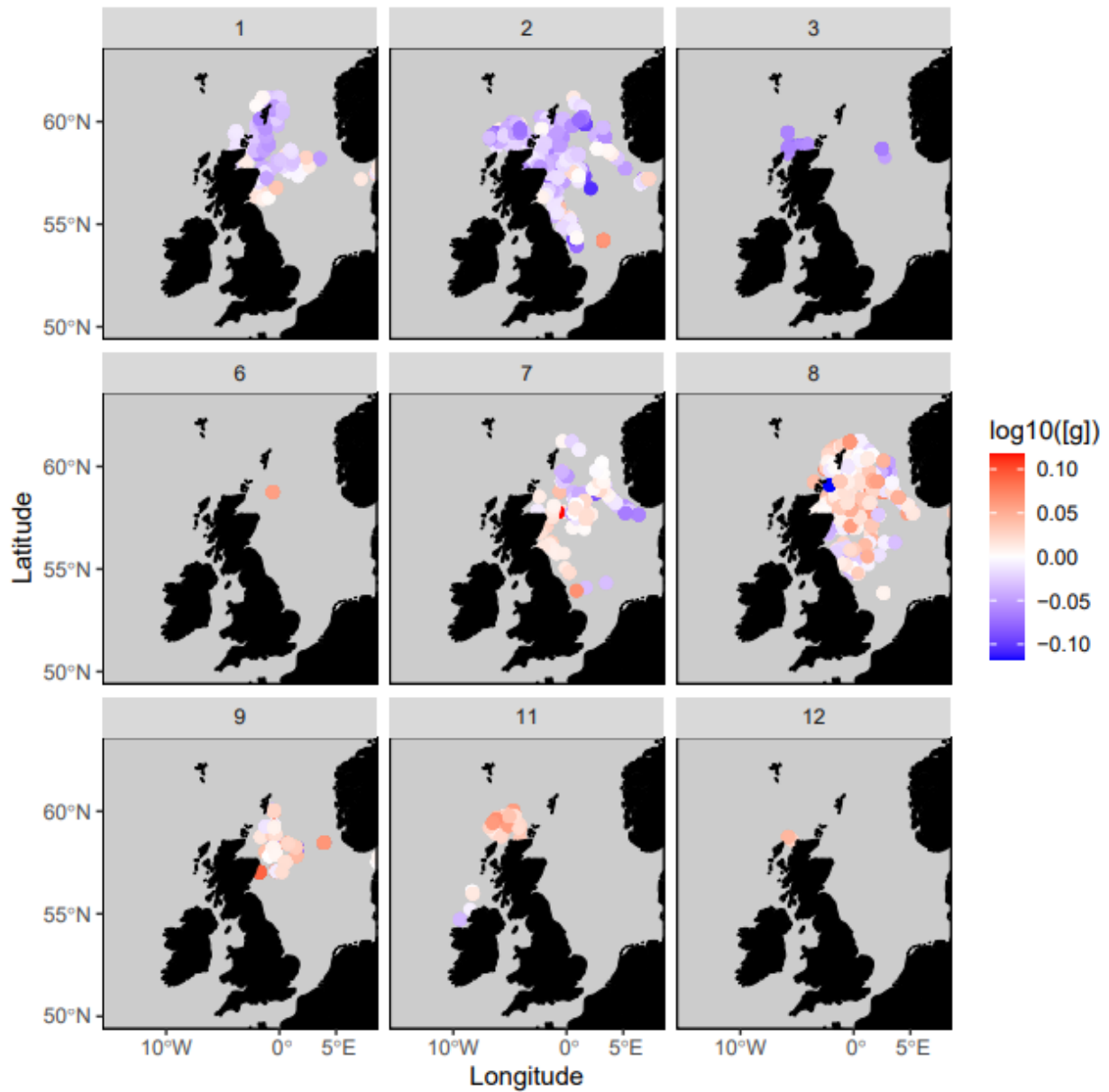


Fig. S11. The residual seasonal spatiotemporal variation in Norway pout body condition (g on \log_{10} scale), independent of time, captured by a random field for month.

Data availability and annual deviations in $\log_{10}(\text{weight})$
Trisopterus esmarkii

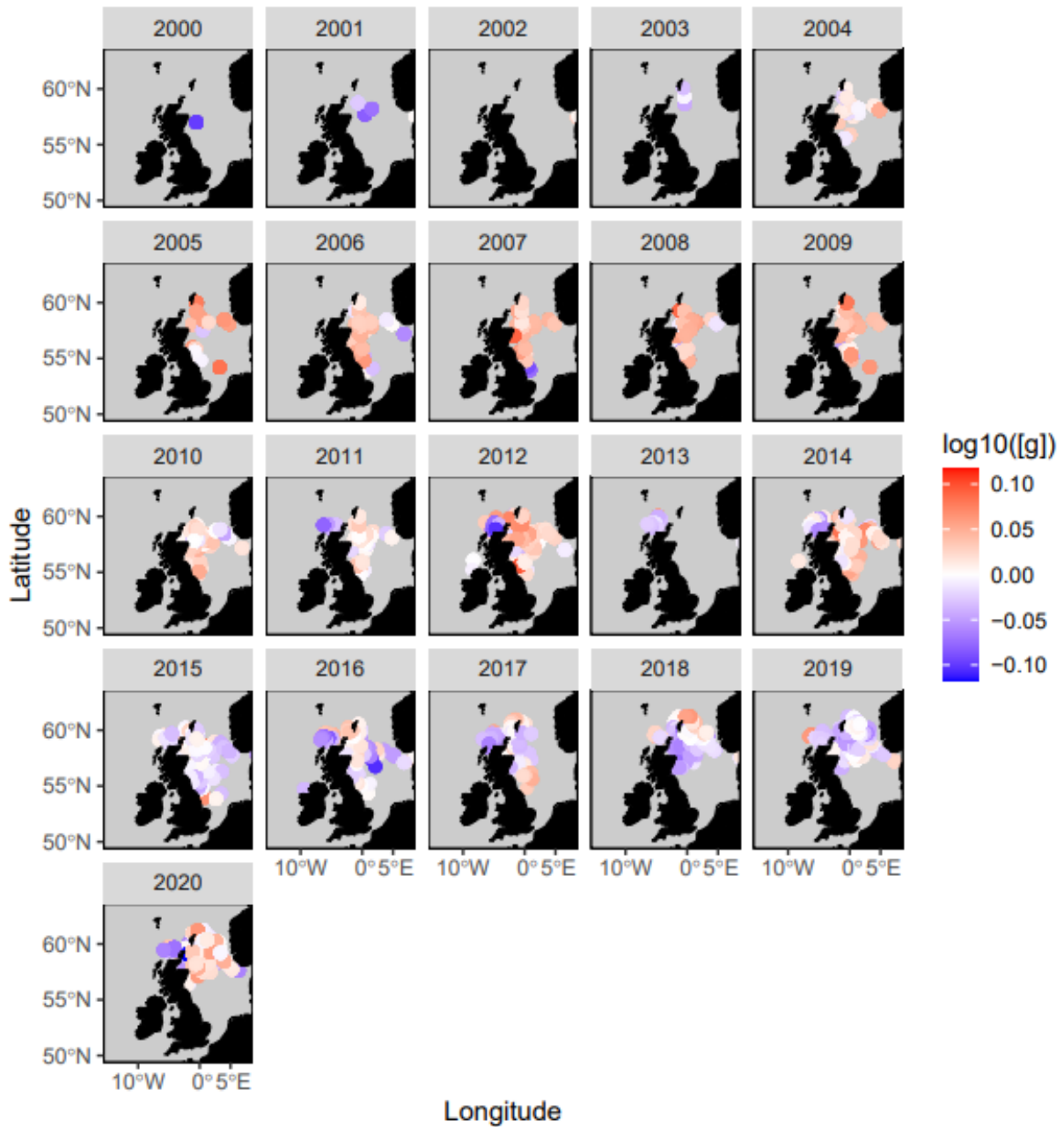


Fig. S12. The residual annual spatiotemporal variation in Norway pout body condition (g on \log_{10} scale), independent of time, captured by a random field for year.

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