

Spatio-temporal variation in the zooplankton prey of lesser sandeels: species and community trait patterns from the Continuous Plankton Recorder

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The phenology, distribution, and size composition of plankton communities are changing rapidly in response to warming. This may lead to shifts in the prey fields of planktivorous fish, which play a key role in transferring energy up marine food chains. Here, we use 60 + years of Continuous Plankton Recorder data to explore temporal trends in key taxa and community traits in the prey field of planktivorous lesser sandeels (*Ammodytes marinus*) in the North Sea, the Faroes and southern Iceland. We found marked spatial variation in the prey field, with *Calanus* copepods generally being much more common in the northern part of the study area. In the western North Sea, the estimated amount of available energy in the prey field has decreased by more than 50% since the 1960s. This decrease was accompanied by declining abundances of small copepods, and shifts in the timing of peak annual prey abundances. Further, the estimated average prey community body size has increased in several of the locations considered. Overall, our results point to the importance of regional studies of prey fields, and caution against inferring ecological consequences based only on large-scale trends in key taxa or mean community traits.

Keywords: *Calanus finmarchicus*, forage fish, north-east Atlantic, sand eel, sand lance, zooplankton.

Introduction

In most marine ecosystems, planktivorous forage fish play a crucial role as prey for top predators (Engelhard *et al.*, 2014; Pikitch *et al.*, 2014). The growth, survival, and recruitment of these forage fish have often been found to be linked to food conditions (e.g. Ayón *et al.*, 2008; Engelhard *et al.*, 2014; Boldt *et al.*, 2019), suggesting that understanding the dynamics of their plankton prey is important. In addition to prey abundances, aspects of the prey field such as prey size, taxonomic composition and temporal patterns of prey availability may play a key role in determining forage fish ingestion and growth rates (e.g. Boldt *et al.*, 2019; Ljungström *et al.*, 2020). Many of these prey field characteristics have changed, or will change, as global warming is driving the plankton community to, generally, become smaller in size and exhibit shifts in both distribution and phenology (Richardson, 2008; Daufresne *et al.*, 2009; Poloczanska *et al.*, 2013). Exploring temporal trends in their prey field is thus an important component of understanding the effects of changing environmental conditions on forage fish.

One species of forage fish with dynamics closely linked to those of their zooplankton prey is the lesser sandeel (*Ammodytes marinus*, hereafter: “sandeel”), a lipid-rich, shoaling species inhabiting the north-east Atlantic where it is an important prey for several species of piscivorous fish, seabirds and marine mammals (Engelhard *et al.*, 2014). It spends most of

the year inactive, burrowed into sandy sediments, but emerges in spring to feed (Wright *et al.*, 2000; Rindorf *et al.*, 2016). The diet consists mainly of copepods, including both smaller species (e.g. *Acartia*, *Pseudocalanus*, *Paracalanus* and *Temora* spp.) and larger copepods of the genus *Calanus* (Macer, 1966; Godiksen *et al.*, 2006; Eliassen, 2013; van Deurs *et al.*, 2013). However, in samples from some locations and time points, other taxa such as appendicularians (Gómez García *et al.*, 2012) or fish larvae (Rankine and Morrison, 1989) may dominate. Other prey types repeatedly found in sandeel stomachs include fish eggs (Macer, 1966; Rankine and Morrison, 1989), crustacean larvae (Macer, 1966; Eliassen, 2013), polychaetes (Macer, 1966; Eliassen, 2013) and amphipods (Macer, 1966; Eigaard *et al.*, 2014). The diet seems to generally reflect what is available in the water column but may differ in composition, reflecting some degree of selectivity (Godiksen *et al.*, 2006; Gómez García *et al.*, 2012; Eliassen, 2013).

Several studies have explored links between sandeel ingestion and/or growth rates and aspects of their prey field. Sandeel size has been found to correlate with total prey biomass (Eliassen, 2013; MacDonald *et al.*, 2019), and modelling studies of sandeel energetics suggest that the degree of temporal match between the sandeel foraging window and peak abundances of zooplankton is also a key determinant of fitness (van Deurs *et al.*, 2010). In addition, prey size has been put forward as an important driver of sandeel ingestion

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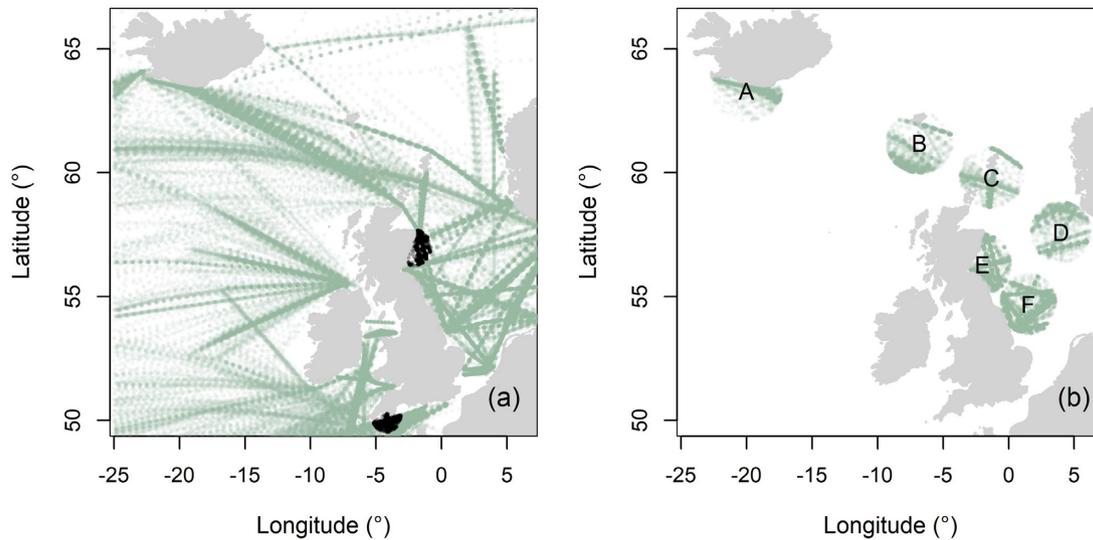


Figure 1. (a) CPR samples collected in study area 1958–2018. Black points indicate samples used to calculate correction factors, centred around the Stonehaven (north) and L4 (south) sampling sites. (b) Samples used to create time series of sandeel food conditions (A = southern Iceland, B = the Faroes, C = Shetland, D = East Central Grounds, E = Firth of Forth, F = Dogger Bank). Coastline shapefile was obtained from the European Environment Agency (2017).

rates, with a modelling study suggesting that a prey field comprised of larger species results in faster ingestion rates, mainly because larger prey are easier to spot by the visually foraging sandeel (van Deurs *et al.*, 2015). The study thus concluded, as others have before (Bergstad *et al.*, 2002; van Deurs *et al.*, 2014), that high abundances of large, lipid-rich *Calanus* copepods are likely to provide particularly good foraging conditions for sandeels.

Based on these identified links between the prey field and sandeel growth, it may be expected that variation in the available prey plays a large role in driving the marked spatio-temporal variation that has been observed in sandeel growth rates (see Boulcott *et al.*, 2007; van Deurs *et al.*, 2014; Rindorf *et al.*, 2016; Wanless *et al.*, 2018). This variation in growth rates in turn has knock-on effects on maturation, fecundity and survival (Boulcott *et al.*, 2007; Boulcott and Wright, 2011; MacDonald *et al.*, 2018). In addition, it would also be expected that observed trends in the north-east Atlantic zooplankton community, including shifts in phenology (Richardson, 2008) and trends in size and community composition (Pitois and Fox, 2006), will have knock-on effects on sandeel populations. However, as no systematic investigation into temporal trends in the sandeel prey field across multiple feeding grounds has been conducted, our understanding of the extent to which observed large-scale trends translate into changes in the sandeel prey field is limited. A few studies have looked at site-specific data of prey abundances (based on local prey samples or ecosystem model outputs) and linked these to variation in sandeel size, both at large spatial scales (Rindorf *et al.*, 2016) and at the single-site short-term temporal scale (Eliassen, 2013; MacDonald *et al.*, 2019). However, these studies do not provide any information on long-term trends and how these may vary over space.

This study thus fills a gap in our knowledge by characterising temporal trends in sandeel prey fields in six aggregations of sandeel grounds in the north-east Atlantic, over a latitudinal range from the southern North Sea to Iceland. To do so, we make use of long-term (ca. 60 years) transect data on

zooplankton densities collected by the Continuous Plankton Recorder. Based on existing knowledge of which aspects of the sandeel prey field drive variation in ingestion rates and growth, as described above, we examine temporal trends in (i) the total amount of energy available, (ii) prey community phenology, (iii) median prey size and (iv) abundances of individual key prey taxa, with a particular focus on copepods. The study provides insight into how rapid changes in zooplankton abundances, phenology as well as size composition in the north-east Atlantic translate into changes in the sandeel prey field, which is key for understanding subsequent effects on sandeel growth and transfer of energy up the food chain.

Methods

Continuous Plankton Recorder data

The Continuous Plankton Recorder (CPR) survey is a large-scale marine plankton sampling scheme (see Richardson *et al.*, 2006 for details). The CPR, which collects plankton on continuously moving bands of silk, is towed behind commercial vessels at a depth of around 7 m, generating a large dataset of monthly transects from 1958 to the present day. The coverage is particularly good in the north-east Atlantic (Figure 1a). After transportation to laboratory facilities, the silk is divided into samples corresponding to 10 nautical miles (ca. 3 m³ filtered seawater), and zooplankton caught on the silk are identified and counted. We expressed the counts of each taxon as abundance m⁻³ by dividing the counts by the estimated volume of water filtered (calculated based on greenness index to account for clogging, see John *et al.*, 2002).

Our dataset (Johns, 2020) included taxa which have previously been found to occur repeatedly in sandeel stomachs in the north-east Atlantic (see Supplement 1 for details on diet and how taxa were selected). However, for simplicity, the list of relevant CPR taxonomic groups was then subset so that only groups that were present in at least 5% of CPR samples in the time period and locations of interest were included. The final list of taxa, following the taxonomic groupings used

by the CPR, included: *Acartia* spp., Appendicularia, *Calanus finmarchicus* (V–VI), *Calanus helgolandicus* (V–VI), *Calanus* spp. (V–VI), *Calanus* spp. (I–IV), *Centropages hamatus*, *Centropages typicus*, *Centropages* spp., cirripede larvae, copepod nauplii, Decapoda larvae, fish eggs, fish larvae, Hyperidea spp., *Metridia lucens*, *Oithona* spp., *Para-Pseudocalanus* spp., and *Temora longicornis*. Unless otherwise noted, the copepod categories refer to adult copepods (V–VI), except for in the case of *Para-Pseudocalanus* spp., which includes adults of *Paracalanus* and *Pseudocalanus* spp., but may also include other unidentifiable small copepods, including juveniles (Richardson *et al.*, 2006).

Abundance correction factors

The efficiency with which the CPR samples the plankton varies between taxa (Clark, 2001; Kane, 2009). Accounting for inter-taxon variation in sampling efficiencies is important as it will impact composite metrics such as average zooplankton size. To, at least partly, address this issue, we derived taxon-specific abundance correction factors. These were obtained by using data from two multi-decade single-location plankton time series: Stonehaven on the Scottish east coast (57°N 2.1°W, 1997–2016; see Bresnan *et al.*, 2015; Marine Scotland Science, 2018) and the L4 station on the southern coast of England (4.2°W 50.25°N, 1988–2017; see Atkinson *et al.*, 2015). These schemes use nets with a smaller mesh size and a larger opening than the CPR, thus increasing the sampling efficiency for at least some taxa. Further, the nets are hauled from close to the sea bed to the surface, meaning that variation in the vertical distribution of the plankton does not impact the estimates. Details on how correction factors were calculated and applied can be found in Supplement 1.

Zooplankton trait values

For each taxonomic group as listed above, we collated information on wet weight (mg), prey energy density (J g wet weight⁻¹) and prey size (total length, mm). The latter combined with the shape of each prey type was used to calculate the prey image area (area of the prey item as viewed by predators). The square root of the image area is expected to be directly proportional to detection rates in visual foragers (Aksnes and Utne, 1997). Values were sourced from the literature (see Table S4 in Supplement 1) and were chosen to be as representative for the area and the season as possible.

Spatial aggregation

To generate prey field time series, the CPR data were aggregated over space. This was done in six locations of relatively dense aggregations of sandeel grounds (Figure 1b): Dogger Bank (54.7°N 1.5°E, roughly at North-West Rough, see Boulcott *et al.*, 2007), Firth of Forth (56.3°N 2°W, roughly at Wee Bankie, see Greenstreet *et al.*, 2006), East Central Grounds (ECG, 57.6°N 4°E, see Bergstad *et al.*, 2002), Shetland (59.8°N 1.3°W, close to aggregation of sandeel grounds in southern Shetland, see Wright and Bailey, 1996), southern Faroes (61.2°N 6.8°W, see area of high sandeel densities in Jacobsen *et al.*, 2019) and southern Iceland (63.3°N 20°W, close to grounds sampled in Lilliendahl *et al.*, 2013).

For each location, we aggregated data in a circular area centred on the coordinates above, using a radius of 135 km. This radius was chosen based on a trade-off between sample size and homogeneity of the sample, and also ensured that

there was no overlap in the areas used for data aggregation (Figure 1b; see also Figures S1–S2 in Supplement 1). The radius is well within those used previously for spatial aggregation of CPR data (e.g. 463 km, Beaugrand *et al.*, 2000; 277.8 km, Pitois and Fox, 2006).

Generating daily abundance estimates

As CPR transects are generally covered on a monthly basis (Richardson *et al.*, 2006), samples were sorted into 12 equally sized sampling intervals for each year-location combination. For each interval, the arithmetic mean was calculated. This mean was then associated with the midpoint of the sampling interval and values between each midpoint were obtained through piece-wise cubic Hermite interpolation (Fritsch and Carlson, 1980; Figure S3 in Supplement 1). Two subsets of daily interpolated abundances were created, one for the 1 + group feeding season (day 80–165, van Deurs *et al.*, 2013; see also Henriksen *et al.*, 2021), and one for the 0 group feeding season (day 150–250, van Deurs *et al.*, 2013; see also Reeves, 1994; Wright and Bailey, 1996; Jensen, 2000; Régner *et al.*, 2017). We also investigated the sensitivity to the exact choice of dates for the feeding windows by advancing and delaying the feeding windows by up to 30 days, keeping the length constant. Values for a given year-location combination are only reported if there were at least three samples per month during the feeding season (March–August). On average, 9.8 samples were available per month (SD = 5.3).

Spatio-temporal variation in the sandeel prey field

Using the two subsets, we explored long-term trends in sandeel food conditions (1958–2018). We looked at three prey field-level aspects of sandeel food conditions: (i) the total amount of energy available, (ii) prey community phenology and (iii) median prey size. For the total amount of energy available, we multiplied the daily abundances of each taxon by the taxon-specific energy content of an individual, added them up for all taxa and calculated the daily average over the feeding season. For prey field-level phenology, we calculated the total amount of energy within each feeding season (1 + and 0 group) for each year and location (interpolated daily total energy summed across all days of each feeding season), and divided that by the total amount of energy available in each year (interpolated daily total energy summed across all days of the year). This captures the extent to which the feeding season aligns with prey availability; a higher value suggests a greater overlap with the peak availability of prey. For this metric, we restricted the analysis to years with at least 3 CPR samples in each of the 12 monthly sampling periods (rather than just applying this criterion to the months within the feeding season, as in the other analyses). Finally, median prey size was represented by the square root of the median prey image area, calculated by replicating the square root of the taxon-specific image area in proportion with the daily abundance of the taxon and calculating the median of these values for each day, before calculating the average over the feeding season.

To look at temporal variation in total available energy, proportion of energy available within the feeding season as well as median prey size, we used Generalised Additive Models (GAMs). We also used GAMs to explore changes in the abundances of individual taxa. As we were particularly interested

Table 1. *P*-values from GAMs relating to long term smooths (1958–2018) for each feeding season (1 + = 1 + group [day 80–165] and 0 = 0 group [day 150–250]), for each considered aspect of the prey field and each location. For direction of relationships, see Figures 2–4. Note that these *p*-values are approximate (see Wood, 2017).

| Response variable | Smooth | Location | | | |
|-----------------------------------|--------|-------------|----------------|---------|----------|
| | | Dogger Bank | Firth of Forth | ECG | Shetland |
| Available energy | 0 | <0.0001 | <0.0001 | 0.19 | 0.23 |
| | 1 + | 0.45 | <0.0001 | 0.27 | 0.022 |
| Energy inside/outside time window | 0 | <0.0001 | <0.0001 | 0.21 | 0.031 |
| | 1 + | 0.36 | 0.059 | 0.096 | 0.48 |
| Prey size | 0 | <0.0001 | 0.0002 | 0.26 | 0.023 |
| | 1 + | <0.0001 | <0.0001 | 0.07 | 0.0013 |
| <i>Calanus finmarchicus</i> | 0 | 0.0002 | 0.0007 | 0.085 | 0.0032 |
| | 1 + | 0.10 | 0.0011 | 0.48 | 0.032 |
| <i>Calanus helgolandicus</i> | 0 | 0.79 | 0.0004 | 0.028 | 0.0006 |
| | 1 + | <0.0001 | <0.0001 | <0.0001 | <0.0001 |
| Small copepods | 0 | <0.0001 | <0.0001 | 0.003 | 0.92 |
| | 1 + | <0.0001 | <0.0001 | 0.0001 | 0.094 |

in copepods, we used abundances of *Calanus finmarchicus*, *Calanus helgolandicus* and small copepods (<1.3 mm; see van Deurs *et al.*, 2014; this included *Acartia* spp., *Oithona* spp., *Para-Pseudocalanus* spp. and *Temora longicornis*) as response variables. The models were fitted using the package mgcv (Wood, 2017) in R 4.0.3 (R Core Team, 2020, used for all analyses and graphics). All models, apart from the model of proportion of energy available within the feeding season, were fitted as follows:

$$\log \{E(\text{response}_i)\} = \beta_0 + \beta_1 \text{season}_{1i} + f(\text{year}_i) \text{season}_{0i} + f(\text{year}_i) \text{season}_{1i}, \quad \text{response}_i \sim \text{gamma} \quad (1)$$

where *f* indicates a smoothing function, which in our case was always a thin plate spline, and *season_i* represents indicator variables for the feeding season (0 or 1+), taking on values of 0 or 1. The model of proportion of energy available within the feeding season was instead fitted as:

$$\text{logit} \{E(\text{proportion in window}_i)\} = \beta_0 + \beta_1 \text{season}_{1i} + f(\text{year}_i) \text{season}_{0i} + f(\text{year}_i) \text{season}_{1i}, \quad \text{proportion in window}_i \sim \text{beta} \quad (2)$$

Each location was considered separately. The smoothing parameters were estimated using restricted maximum likelihood. As sufficient data were only available for a limited number of years in the Faroes and Iceland, no models were fitted to these data. Diagnostic plots that were used to evaluate model fit are available in Supplement 2 (Figures S4–S9), *p*-values in Table 1.

While available time series do not indicate any temporal trends in sandeel phenology, timing is variable and likely responds to environmental conditions (Lynam *et al.*, 2013; Régner *et al.*, 2017; Henriksen *et al.*, 2021). To explore the extent to which the sandeels may be able to counteract any changes in available energy by adjusting the timing of the feeding window, we also looked at the trend in available energy when, instead of a fixed window, we used an optimised window of a fixed length based on maximum available energy.

Finally, we explored patterns in the different taxonomic groups in more detail. First, we visualised trends in each taxon within each location by plotting the average abundance during the feeding season (from beginning of 1 + group to end of the 0 group feeding season) across years, scaled by the

maximum average abundance during the time period. Second, we quantified the contribution of each taxonomic group to total available energy by, for each given location-year combination, multiplying taxon-specific average daily abundances by taxon-specific energy content and dividing this by the average total daily available energy in the prey field. We visualised both how the contribution changed across years and the contribution averaged over all years.

Results

The long-term trends in estimated average total daily available energy varied between locations. There was strong evidence for sharp declines in the available energy in both the Firth of Forth and Dogger Bank (Table 1), with declines in the Firth of Forth corresponding to an 80% and an 85% reduction from 1958 to 2018 for the 1 + group and the 0 group feeding seasons, respectively, and a parallel decline of roughly 60% in Dogger Bank during the 0 group feeding season (Figure 2g; j). There were no clear trends in the ECG or Shetland, apart from some evidence of a positive trend during the 1 + group feeding season in Shetland (Figure 2a; d; Table 1). Estimated average total daily available energy in the Faroes and Iceland was towards the lower end of values observed in the other locations (mean ± SE kJ m⁻³: Faroes 1+ group = 0.95 ± 0.03, 0 group = 1.9 ± 0.04, N = 15; S Iceland 1+ group = 0.92 ± 0.04, 0 group = 2.0 ± 0.06, N = 5; Supplement 3 Figures S10a–b).

The negative trends observed in Dogger Bank and the Firth of Forth were generally robust towards different assumptions regarding the timing of the feeding window (Supplement 3 Figure S11), although the decline in available energy in the Firth of Forth during the 1 + group feeding window was not evident under all assumptions (Figures S11e). While flexibility in the timing of the feeding window did not seem to allow the sandeels to fully counteract the decline in available energy for the Dogger Bank and Firth of Forth 0 group sandeels (Supplement 3 Figure S16e–f; h), the possibility to extend the feeding season provides some opportunity to maintain similar levels of energy availability, although less so in recent years (Supplement 3 Figure S17).

In both the Firth of Forth and Dogger Bank, there was strong evidence for trends towards a smaller proportion of

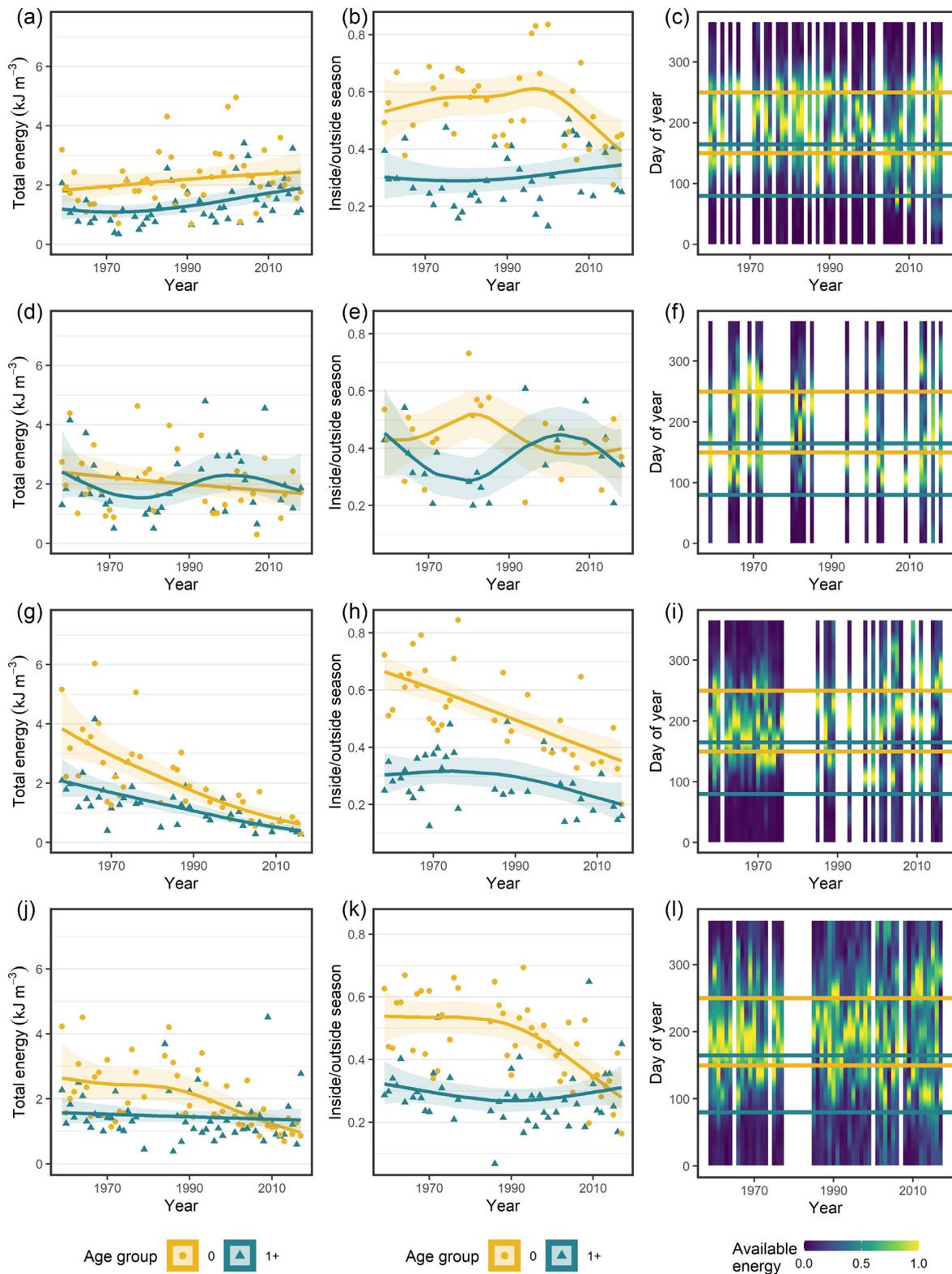


Figure 2. Temporal trends in available energy for (a–c) Shetland, (d–f) East Central Grounds, (g–i) Firth of Forth and (j–l) Dogger Bank. (a; d; g; j) Average daily total available energy (kJ m^{-3}) over time. Blue and yellow markers denote averages during the 1 + group (day 80–165) and 0 group (day 150–250) feeding seasons, respectively. Lines show GAM predictions, with shaded 95% confidence intervals. (b; e; h; k) Proportion of total available energy over the year that is available within the 1 + group and the 0 group feeding season, respectively. Lines show GAM predictions, with shaded 95% confidence intervals. (c; f; i; l) Distribution of available energy over the year, for each year within each location (scale from maximum to minimum available energy). Blue and yellow lines indicate location of 1 + group and 0 group feeding seasons, respectively.

energy being available during the 0 group feeding season (Figure 2h; k; Table 1). This seemed to result from community-level phenological shifts in both directions (i.e. peaks occurring before and/or after the feeding season, Figure 2i; l).

As for the estimated median prey size, increases of around 25%–60% have occurred in the Firth of Forth, Dogger Bank and Shetland (in Shetland only during the 1 + group feeding season), while there was no evidence for such a trend in the ECG (Figure 3; Table 1). The increases were generally robust to different assumptions regarding phenology, although less so in Shetland (Figure S12 in Supplement 3). Only the increase in median prey size in Shetland was driven by an increase in absolute abundances of taxa with large body sizes (Figure S18a–b in Supplement 3). In the Firth of Forth and Dogger Bank the increases were instead related to declines in the abundances of small prey types (Figure S18e–l in Supplement 3). In the Faroes and S Iceland, median prey sizes fell towards the higher end of values observed in the other locations (mean \pm SE mm: Faroes 1+ group = 0.56 ± 0.007 , 0 group = 0.48 ± 0.004 , N = 15; S Iceland 1+ group = 0.59 ± 0.008 , 0 group = 0.50 ± 0.007 , N = 5; Supplement 3 Figures S10c–d).

Abundances of individual taxa exhibited some clear spatio-temporal patterns. *Calanus finmarchicus* abundances were higher in the ECG, the Faroes and S Iceland than in the other locations, and there was strong evidence for a decline between the 1960s and the 1980s in Shetland, the Firth of Forth and Dogger Bank (only during 0 group feeding season in Dogger Bank; Figure 4a; d; g; j; Figures S10e–f in Supplement 3; Table 1). *Calanus helgolandicus* was instead comparatively rare throughout the study area prior to the late 1990s, when there was strong evidence for clear increases in Dogger Bank (only 1 + group season), the ECG and Shetland, and more modestly so in the Firth of Forth (Figure 4b; e; h; k; Table 1). In the Faroes and S Iceland, *Calanus helgolandicus* was close to absent in samples (Figures S10g–h in Supplement 3). There was also strong evidence for marked declines in the abundance of small copepods in both Dogger Bank and the Firth of Forth throughout the study period, with a decline also visible in the ECG from the 1960s to the 1970s (Figure 4c; f; i; l; Table 1). The overall patterns were generally robust to different assumptions regarding phenology (Figures S13–S15 in Supplement 3).

Small taxa such as appendicularians, and in particular small copepods, all made up a large proportion of the available energy in the Firth of Forth, Dogger Bank, Shetland and the ECG (Figure 5). However, the relative contribution from small copepods follows the negative trend in abundances seen in several locations. Further north, *Calanus finmarchicus* adults and earlier stages of *Calanus* copepods also made a substantial contribution to the total available energy during the feeding season: 37% in the ECG, 44% in the Faroes and 52% in S Iceland, as compared to 12% in Dogger Bank, 10% in the Firth of Forth, and 18% in Shetland, in an average year.

Discussion

The aim of this study was to characterise spatio-temporal variation in the sandeel prey field in the north-east Atlantic in the context of a rapidly reorganising plankton community. We found some clear temporal trends, including dramatic declines in the estimated available energy in the western North

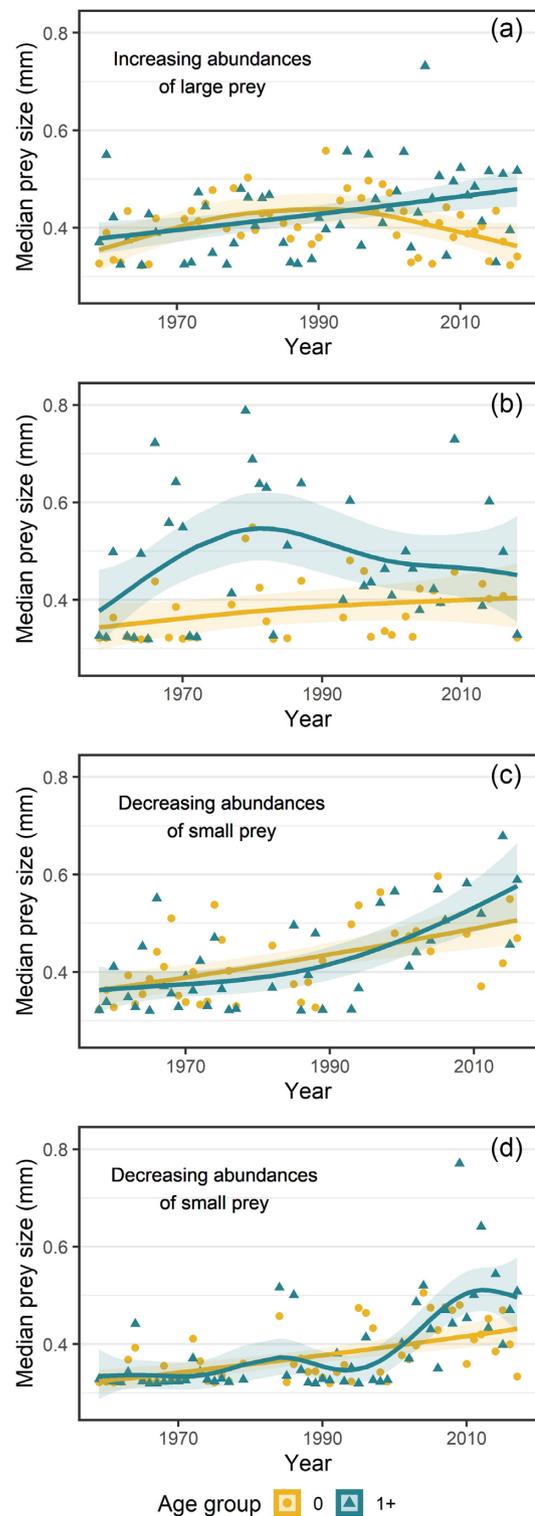


Figure 3. Temporal trends in average daily median prey size (mm) for (a) Shetland, (b) East Central Grounds, (c) Firth of Forth and (d) Dogger Bank. Blue and yellow markers denote averages during 1 + group (day 80–165) and 0 group (day 150–250) feeding seasons, respectively. Lines show GAM predictions, with shaded 95% confidence intervals. Text indicates drivers of observed trends (Figure S18 in Supplement 3).

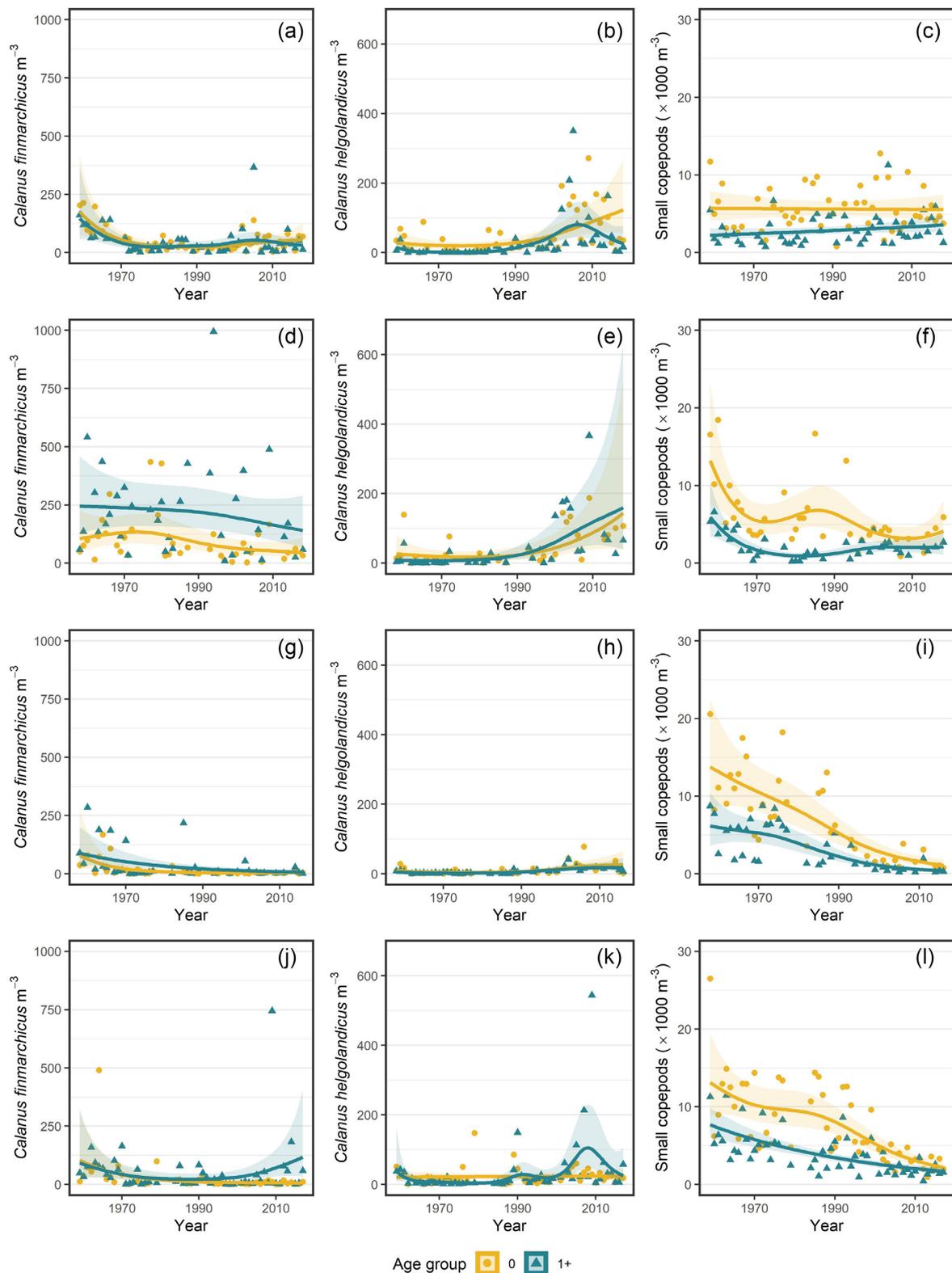


Figure 4. Temporal trends in abundances of *Calanus finmarchicus* (a; d; g; j), *Calanus helgolandicus* (b; e; h; k) and small copepods (c; f; i; l) for (a–c) Shetland, (d–f) East Central Grounds, (g–i) Firth of Forth and (j–l) Dogger Bank. Blue and yellow markers denote averages during 1 + group (day 80–165) and 0 group (day 150–250) feeding seasons, respectively. Lines show GAM predictions, with shaded 95% confidence intervals.

Sea, which were accompanied by marked declines in the abundance of small copepods, increases in estimated average prey size and a temporal shift of peak food availability out of the sandeel feeding season. The prey field also varied markedly

over space, with *Calanus* copepods generally being more common in the northern part of the study area (agreeing with previous studies, e.g. Planque and Fromentin, 1996). The key patterns are summarised in Figure 6.

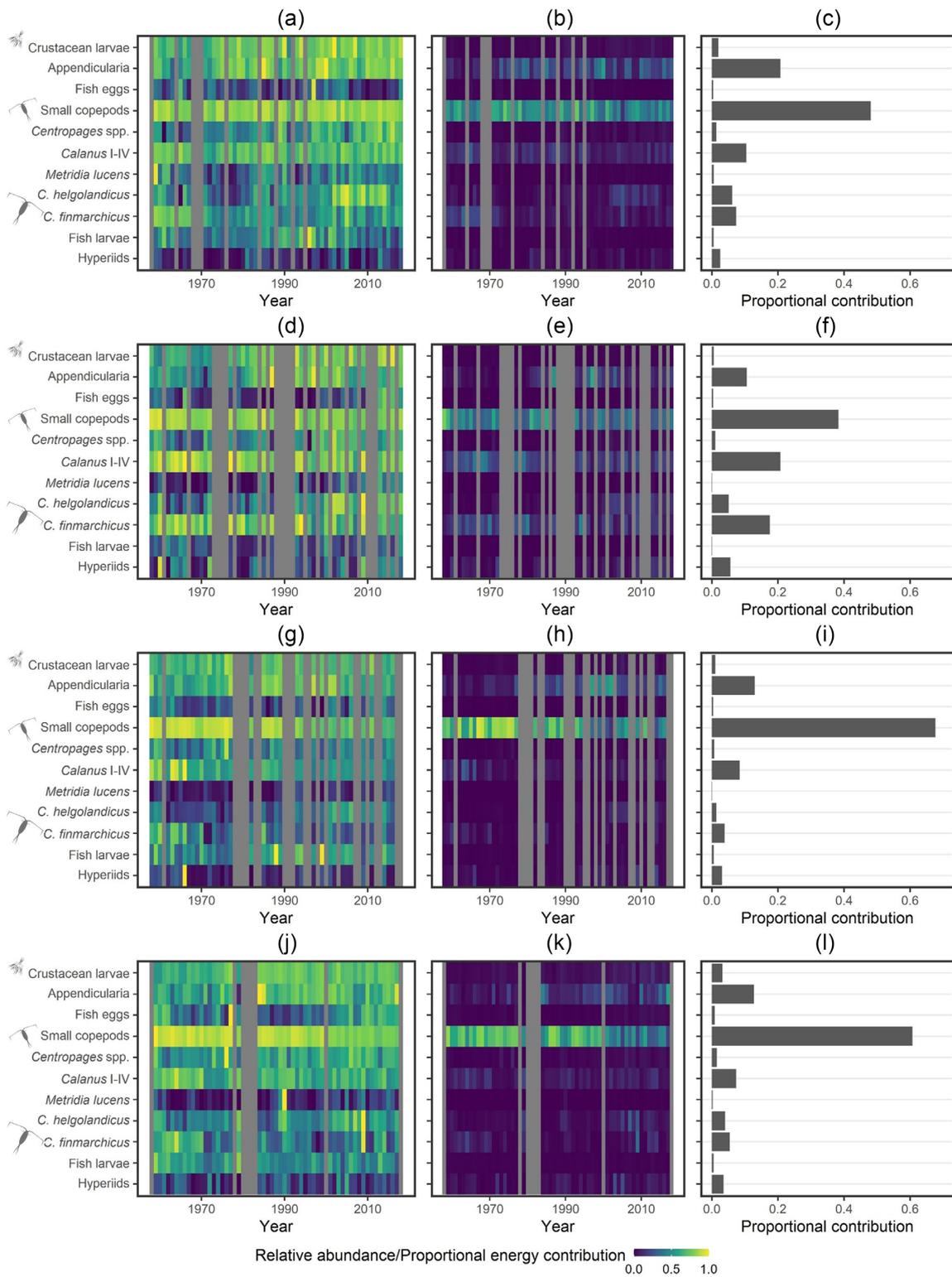


Figure 5. Relative abundances and contributions to total available energy from individual taxa from beginning of 1 + group feeding season to end of 0 group feeding season (day 80–250) for (a–c) Shetland, (d–f) East Central Grounds, (g–i) Firth of Forth and (j–l) Dogger Bank. Some taxa are grouped: crustacean larvae (copepod nauplii, Decapoda and cirripede larvae), small copepods (*Acartia* spp., *Oithona* spp., *Para-Pseudocalanus* spp. and *Temora longicornis*) and *Centropages* spp. (*C. hamatus*, *C. typicus* and *Centropages* spp.). Taxa roughly sorted by size. (a; d; g; j) Average abundances (individuals m⁻³) for given location-year combination averaged over the whole season and divided by maximum value across all location-year combinations (all abundances considered as log₁₀(x + 1)). Can be compared across years and space but not taxa. (b; e; h; k) Relative contribution to total energy within each location-year. Can be compared across taxa within year and location, but not across space—along time within location it shows how the relative contribution to total energy changes. (c; f; i; l) Relative contribution summed over all years.

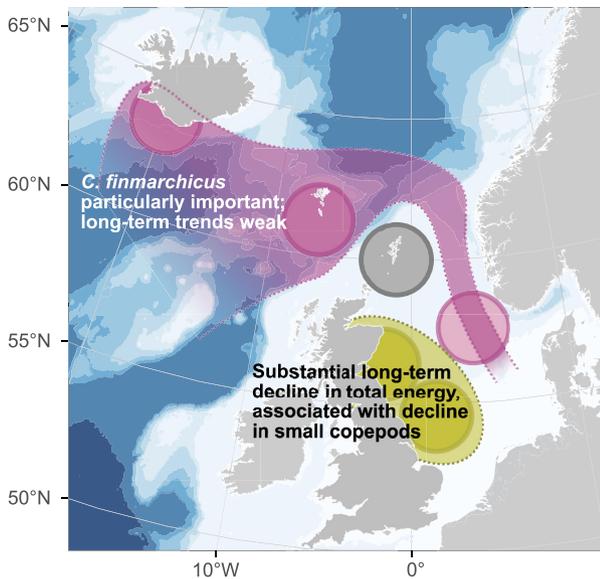


Figure 6. Summary of the main patterns identified in the sandeel prey field. Map was produced using the R-package ggOceanMaps (Vihtakari, 2022).

How do observed patterns relate to general plankton community trends?

In general, the mean body size of aquatic organisms in a given location is expected to decrease over time in response to global warming (Daufresne *et al.*, 2009). This may result from a decline in length-at-age, a greater proportion of younger individuals and/or a higher proportion of small-bodied species. However, in contrast with this, we found median sandeel prey size to increase in Dogger Bank, the Firth of Forth and Shetland. The increase in Dogger Bank lines up with the results from a previous study finding an increase in average zooplankton size from 1960 to 2000 in the southern North Sea (Pitois and Fox, 2006). However, we also saw increases in the more northerly locations of the Firth of Forth and Shetland, whereas, in contrast, Pitois and Fox (2006) identified a decrease in average prey size in the northern North Sea. This discrepancy might stem from a difference in the extent of the area aggregated, the time period covered and the taxa included. In the Firth of Forth and Dogger Bank, the increase appeared to be driven by a decline in the abundance of small prey types, in particular small copepods, which exhibited declines of over 70% and 80% during the 1 + group and 0 group feeding seasons, respectively (Figure 4i; l). This trend in small copepods has been noted previously in the North Sea and has been attributed to declines in food availability and quality, resulting from changes in phytoplankton biomass and composition (Capuzzo *et al.*, 2018; Schmidt *et al.*, 2020). These changes in turn have been attributed to reduced nutrient input and indirect effects of temperature (e.g. reduced nutrient availability as a result of stronger stratification), going against the general expectation of a positive impact of temperature on primary productivity (Capuzzo *et al.*, 2018). Taken together, our findings highlight that one cannot necessarily assume that large-scale, general trends, such as decreases in average body size within a community, come through at a local scale. In addition, they show that trends at the community level (increasing average prey size) can mask a more complex picture (environmentally driven declines of a set of small prey taxa).

As also seems to be the case elsewhere (Poloczanska *et al.*, 2013), there is a clear trend for a poleward distributional shift in the north-east Atlantic zooplankton community, progressing with a speed of around 200–250 km per decade (Edwards *et al.*, 2020). This shift includes a northward expansion of *Calanus helgolandicus*, resulting in abundance increases clearly visible in all considered locations except for the Faroes and S Iceland. The increase of *Calanus helgolandicus* in the North Sea has been accompanied by a decrease in the abundances of *Calanus finmarchicus* (Planque and Fromentin, 1996; Edwards *et al.*, 2020). However, in this study, we only saw modest declines of *Calanus finmarchicus* in the early part of the time series (1960s–1980s) in Shetland, the Firth of Forth and Dogger Bank. The disparity between this study and previous studies may be the result of the study region of previous studies showing a much greater overlap with areas of peak *Calanus finmarchicus* abundances close to the Norwegian coast. This suggests that one should be cautious when inferring local conditions from observations from a much larger area.

In addition to shifts in size composition and distributions, shifts in zooplankton phenology are also occurring in response to warming temperatures, generally in the form of advanced spring phenology (Richardson, 2008). In contrast with this, it does not seem as if a clear advancement in phenology has occurred in the sandeel prey field, at least not at the community-level. We did, however, see that the amount of energy available within the 0 group sandeel foraging window has decreased substantially in both Dogger Bank and the Firth of Forth. Instead, food availability for sandeels now appears to often peak before or after the 0 group feeding season. The observed pattern may to a large extent be the result of the decline in the abundance of small copepods, which show a seasonal peak that aligns well with the 0 group feeding season (Figure 7). It may be that for many planktivores, changes in zooplankton composition have a larger impact on the phenology of the prey field as compared to shifts exhibited by individual taxa.

Sources of uncertainty

The identified patterns are subject to multiple sources of uncertainty. The composite metrics, total energy available and median size, will have been impacted by choices of taxon-specific trait values and correction factors. Both can show considerable spatial and temporal variation (both within and across seasons). For example, the size-corrected dry weight of *Calanus helgolandicus* may roughly double over the 1 + group feeding window (see Bottrell and Robins, 1984); and the age structure (and thus also size structure) of each species will also change over the course of the season (see e.g. Jónasdóttir *et al.*, 2021). This variability in trait values may introduce some directional bias, for example if the size of a given taxon shows a latitudinal, temperature-dependent gradient (e.g. Wilson *et al.*, 2015). However, the relative size and energy content of the different taxa are likely to be broadly correct, which suggests that the direction of observed spatio-temporal patterns in size and energy availability are robust. For example, *Calanus finmarchicus* female prosome length in the study area may vary from ca. 2.2 to 2.9 mm depending on location and time of year (Wilson *et al.*, 2015; Jónasdóttir *et al.*, 2021), which still clearly distinguishes it from small copepods (prosoma length ca. 0.7–1.3 mm; Table S4 in Supplement 1). Still, we encourage future studies exploring the role of within- and

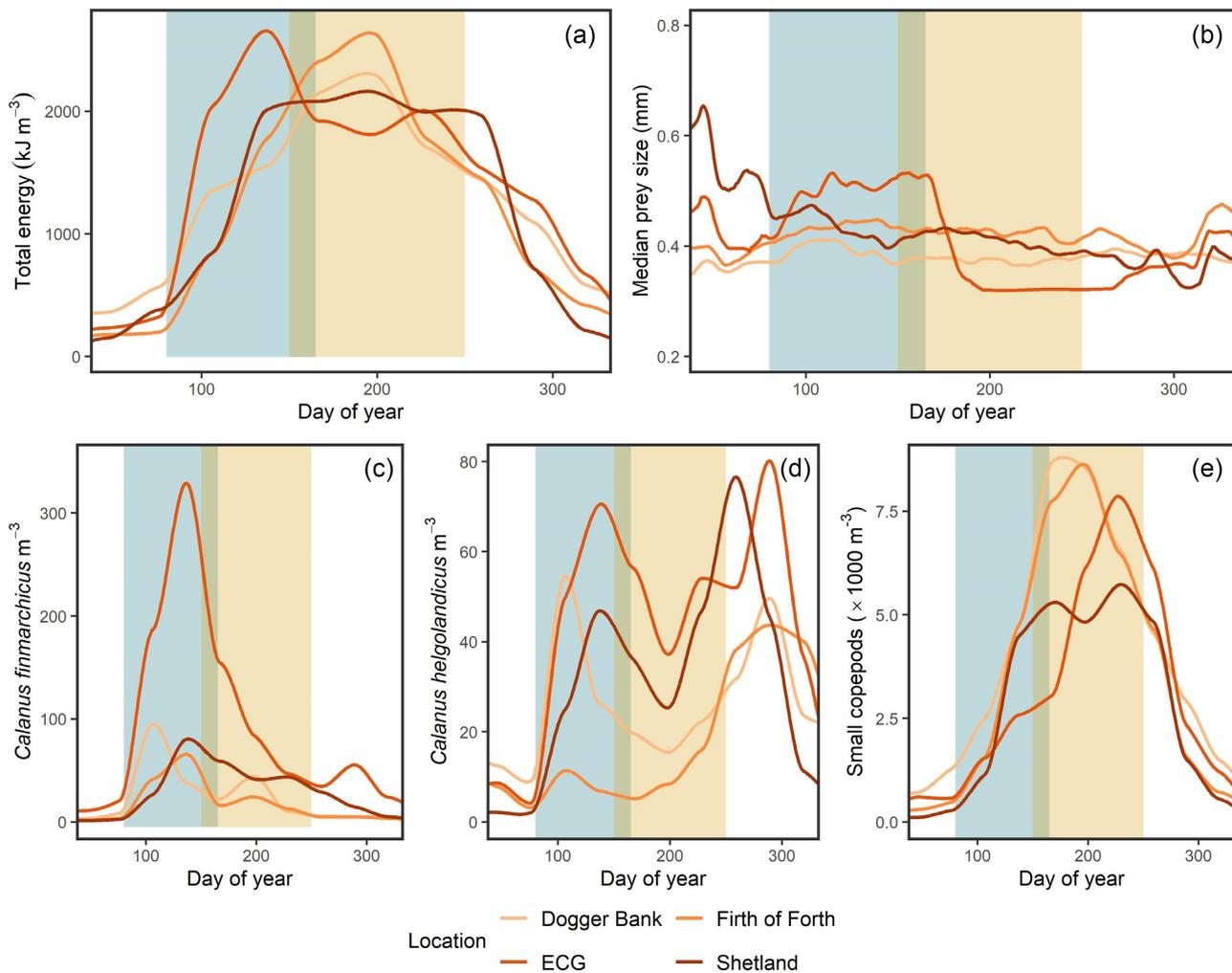


Figure 7. Total available energy (a), median prey size (b) and total abundances (individuals m⁻³) of (c) *Calanus finmarchicus*, (d) *Calanus helgolandicus*, and (e) small copepods (*Acartia* spp., *Oithona* spp., *Para-Pseudocalanus* spp. and *Temora longicornis*) per day, averaged across all years with sufficient data. Blue and yellow boxes denote the extent of the 1 + group (day 80–165) and 0 group (day 150–250) feeding seasons, respectively, and each line represent a location.

between-season variation in individual prey traits (energy density, size) in driving ingestion rates and growth in sandeels and other planktivores, in particular in comparison with the role of taxonomic composition and abundances.

Similar arguments apply to the correction factors. It is clear that estimated correction factors are variable and depend on where and how these were estimated (see Table S3 in Supplement 1). This could result from, for example, variation in thermocline depth, which can strongly impact the vertical distribution of some taxa (e.g. Jónasdóttir and Koski, 2011). This could introduce systematic bias, in particular over space. However, persistent taxonomic patterns are still evident across estimates (for example, poorer catchability of small copepods such as *Oithona* spp.), which suggests that applying correction factors contribute to a more representative view of community composition.

The fact that our key results mainly relied on changes in a few key taxa—in particular small copepods—makes us confident that our overall conclusions regarding spatio-temporal variation in sandeel food conditions do not depend on methodological choices. However, the focus should be on

trends rather than absolute values, which are highly uncertain, especially since they are also sensitive to whether CPR transects happen to go through high-density patches or not. Further, it should be noted that while we focused on *available food*, the *actual ingested food* will be partly modified based on what prey is selected (see e.g. Godiksen *et al.*, 2006). Still, the available food of course provides a key constraint on what is actually consumed.

Finally, as sandeel phenology depends on growth rates, timing of hatching and spawning, and possibly also active behavioural responses (Wright and Bailey, 1996; Régnier *et al.*, 2017; MacDonald *et al.*, 2018; Henriksen *et al.*, 2021), the extent and length of the feeding window likely varies between years and across space. There is insufficient knowledge to account for this variation, but our sensitivity analyses suggested that the main trends were largely robust to uncertainties in sandeel phenology (Figures S11–S15 in Supplement 3). Further, there did not seem to be much scope for sandeels to counteract declines in available energy through adaptive changes in the extent and length of the feeding window (Figures S16–S17 in Supplement 3). Still, the extent to which the sandeels can

and do adapt their behaviour warrants further investigation (see e.g. Henriksen *et al.*, 2021). This should also include studies of possible limitations, such as the trade-off with predation risk (van Deurs *et al.*, 2010), and the lack of behavioural control of the start of the 0 group feeding season, which depends on timing of hatching and growth rates (Wright and Bailey, 1996).

Spatio-temporal variation in the prey field vs sandeel growth rates

Based on previous studies, we would expect prey fields with a greater amount of available energy, larger median prey size and greater abundances of *Calanus* copepods to be associated with better sandeel growth conditions (Bergstad *et al.*, 2002; Eliassen, 2013; van Deurs *et al.*, 2014; van Deurs *et al.*, 2015; MacDonald *et al.*, 2018; MacDonald *et al.*, 2019). In line with this, declines in available energy in the Firth of Forth and Dogger Bank, mainly driven by declines in the abundances of small copepods, took place alongside observed declines in sandeel size in these locations (see van Deurs *et al.*, 2014; Wanless *et al.*, 2018). The declines in available energy were particularly marked during the 0 group feeding season, which suggests that observed declines in sandeel size may to a large part be driven by poor growth conditions during the sandeels' first year of life. This is supported by bioenergetic modelling, which further suggests that the poor food conditions could be exacerbated by warm temperatures, although the direct effect of temperature on growth is small in comparison with the effect of food (MacDonald *et al.*, 2018). Further, in recent decades, observed spatial differences in sandeel growth in the North Sea (ECG > Dogger Bank > Firth of Forth, Boulcott *et al.*, 2007) largely corresponded to spatial differences in available energy, median prey size and abundances of *Calanus* copepods in the expected direction.

However, in contrast with our expectations, the declines in sandeel size in the western North Sea were also paralleled by increases in median prey size. That increases in median prey size did not seem to have a positive effect on growth rates via, for example, larger prey being easier to spot (van Deurs *et al.*, 2015) can be explained by the change being driven by a decline in abundances of small taxa, rather than an increase in abundances of large taxa. Further, there were no clear declines in abundances of *Calanus* copepods, apart from a modest decline in abundances of *Calanus finmarchicus* in the first 20 years of the time series. This does not line up in time with the declines in sandeel size, where sandeels in the Firth of Forth have displayed a gradual decline in size since the start of the time series in 1975 (Wanless *et al.*, 2018) and the Dogger Bank sandeels increased in size from the mid-1970s to the late 1980s, to then show a gradual decline. Thus, we found no evidence to support that a decline in the abundance of *Calanus finmarchicus* is responsible for the decline in sandeel size in Dogger Bank, as has been suggested previously (van Deurs *et al.*, 2014), at least not in the part of Dogger Bank considered here. Still, considering that *Calanus* copepods may be a preferred and actively targeted prey (van Deurs *et al.*, 2015; MacDonald *et al.*, 2018), the sandeels have likely been affected by both the declines in *Calanus finmarchicus* densities early in the time series, and the increase of *Calanus helgolandicus* in recent years. While the *Calanus helgolandicus* increase may provide a boost in food availability in locations such as Dogger Bank and the Firth of Forth where *Calanus finmarchicus* has been

comparatively rare in recent years, a continued shift in dominance (see Edwards *et al.*, 2020) could hit hard in areas such as the ECG due to the poor alignment in timing of sandeel and *Calanus helgolandicus* (see Planque and Fromentin, 1996; Wilson *et al.*, 2015; Figure 7).

In Shetland, available energy and median prey size both increased and only a small decline in *Calanus finmarchicus* abundances was observed, while at the same time, data from the diet of Atlantic puffin chicks (*Fratercula arctica*) on Fair Isle (south of Shetland) point to a decline in sandeel size (Miles *et al.*, 2015). The discrepancy between observations and expectations in Shetland could potentially be explained either by the fact that we cannot capture zooplankton dynamics very well in this area, which includes several routes of transport of Atlantic water into the North Sea (Turrell *et al.*, 1992), or by the observed sandeel size variation being driven primarily by other mechanisms, such as, for example, reduced pre-metamorphic growth rates as a result of temperature-driven trophic mismatch (see e.g. Régnier *et al.*, 2017).

Conclusions

Our findings thus suggest that the key role that *Calanus finmarchicus* has been assumed to play in sandeel dynamics may need to be re-evaluated in parts of the North Sea (see also Régnier *et al.*, 2017). The results instead point towards the key role played by small prey types. This lines up with previous sandeel diet studies (Macer, 1966; Gómez García *et al.*, 2012), and a bioenergetic modelling study finding that most energy ingested by Firth of Forth sandeels comes from small copepods and non-copepod prey, rather than from large copepods (MacDonald *et al.*, 2018). The results also support the idea that the observed declines in small copepods in the north-east Atlantic, which appear to mainly be the result of shifts in the biomass and composition of phytoplankton, could have important knock-on effects on upper trophic levels (see also Capuzzo *et al.*, 2018; Schmidt *et al.*, 2020).

More broadly, our results suggest that one needs to be careful when interpreting the information from indicators of food conditions developed based on theoretical considerations (e.g. average prey size), or previously identified "key taxa." Further, it is also clear that we cannot assume that broad trends, such as declines in zooplankton body sizes or advanced zooplankton phenology, translate neatly into corresponding changes in forage fish prey fields at a local scale. As such, a more complete understanding of relevant changes in forage fish food conditions requires considering multiple aspects of the prey field at a spatial resolution that matches that of the species' population dynamics. In the north-east Atlantic, and other areas where there are sufficient CPR transects, the approach outlined here can be adapted to suit other planktivores by adjusting the seasonal extent, taxon list and geographical area, and can serve as a useful starting point.

Supplementary Data

Supplementary material is available at the ICESJMS online version of the manuscript. Supplementary materials contain details of the data processing (Supplement 1), diagnostic plots for the GAMs (Supplement 2), as well as additional results (Supplement 3), as described in the text.

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Author contributions

Conceptualization: N.S.B., R.G.N. and A.B.O.; Data curation: D.G.J.; Formal analysis: A.B.O.; Funding acquisition: N.S.B. and R.G.N.; Supervision: N.S.B., R.G.N., M.R.H. and P.J.W.; Visualization: A.B.O. and N.S.B.; Writing—original draft: A.B.O.; Writing—review & editing: all authors

Data availability

The CPR dataset can be found at <https://doi.org/10.17031/1673>, the Stonehaven dataset can be acquired from Marine Scotland Science (<https://doi.org/10.7489/610-1>) and the L4 dataset is held by the Plymouth Marine Laboratory. Code can be found at <https://github.com/agnesolin/CPRsandeel>.

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