

A spatial statistical approach for identifying population structuring of marine fish species: European sprat as a case study

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Many marine fish species are widely distributed over large areas. Failing to acknowledge that such species may be composed of distinct populations may result in overestimation of the stock's true harvest potential. To avoid overexploitation, ways to identify population structuring are therefore needed. In this study, we developed and applied a statistical approach to identify biologically relevant population boundaries for a widely distributed marine fish species, European sprat (*Sprattus sprattus*). Specifically, we compiled and standardized multiple trawl-survey data sets and used a range of statistical tools to assess whether the current management boundaries adequately account for potential population structuring. Our results demonstrate regional differences in spatial abundance patterns, temporal dynamics and population demographics. These findings are in line with recent genetic studies of sprat, indicating reproductive isolation between the Baltic Sea/Kattegat and a larger cluster containing the North-, Irish-, Celtic Sea, and Bay of Biscay. Since relying on routinely collected survey data, our statistical approach can be a cost-effective complement to population genetic methods for detecting population structuring. These can be used to guide spatial management efforts and ensure sustainable exploitation, especially under climate change and the expected changes in species distributions across current management borders.

Keywords: fisheries management, population structuring, spatial population dynamics, spatial statistics.

Introduction

Many marine and terrestrial species are widely distributed over large areas, often spanning across boundaries of different jurisdiction (Lascelles *et al.*, 2014; Gervasi *et al.*, 2019; Nandintsetseg *et al.*, 2019). The large distribution ranges are, at least in part, due to their ability to actively migrate and/or passively disperse over large distances (i.e. as seeds, eggs or larvae) in pursuit of suitable habitats for feeding, survival and reproduction. Despite their seemingly continuous distribution across their range, many wide-ranging species are comprised of discrete populations, genetically separated from each other by means of various physical, morphological, and behavioural barriers. However, many wide-ranging and commercially exploited species are managed without considering the existence of such population structuring. For example, traditional fisheries management often relies on management units (i.e. stocks) and stock assessments that assume large and homogeneously distributed populations, where management units are usually defined by administrative or political boundaries, rather than by biological processes (Stephenson, 1999; Reiss *et al.*, 2009; Randon *et al.*, 2018; Cadrin, 2020). Failing to acknowledge that fish stocks may be composed of distinct populations with independent dynamics and productivity may result in overestimation of the stocks' true harvest potential (Frank and Brickman, 2000; Sterner, 2007; Randon *et al.*, 2018; Cadrin, 2020). This may lead to unsustainable

exploitation patterns, particularly on smaller, less productive stock components, eventually causing stock collapse (Svedang *et al.*, 2010; Ciannelli *et al.*, 2013; Kerr *et al.*, 2017). Ways to identify population structuring are therefore critically needed to inform spatially explicit management actions to ensure a sustainable exploitation of distinct stock components.

The rapid development of molecular techniques to detect genetic differentiation has shown great promise in identifying signs of reproductive isolation between and within populations. Such population structuring seem to occur even in widely distributed marine fish species with large effective population sizes, high fecundity and few physical barriers hindering their migration or dispersal (Gaggiotti *et al.*, 2009; Dalongeville *et al.*, 2018; Knutsen *et al.*, 2018; Spies *et al.*, 2018; Hemmer-Hansen *et al.*, 2019). However, detailed maps of the spatial distributions of populations and the boundaries between them, as well as their seasonal and inter-annual variability, is currently only supported by the availability of genetic data. The collection and analysis of genetic data have until recently been considered too costly to undertake at high spatial or temporal resolutions, despite the management importance of characterising potential population structuring (Martinsohn *et al.*, 2019). Hence, developing complementary approaches that rely on already available and routinely collected monitoring data (used as standard input to existing stock assessments) to identify population structuring and de-

Received: April 22, 2021. Revised: December 17, 2021. Accepted: January 12, 2022

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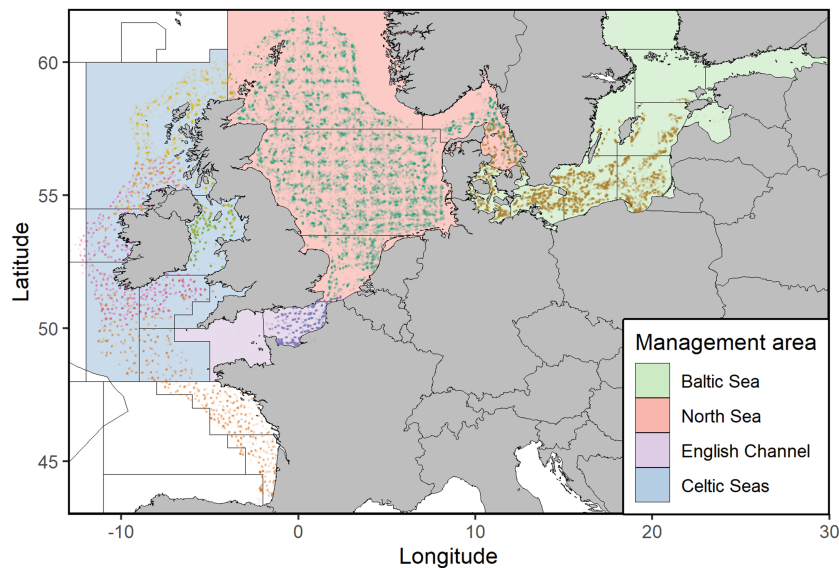


Figure 1. Map of the ICES management areas (polygons) and the current sprat management units (shaded polygons), as well as the positions of sampling locations based on available long-term trawl-surveys (coloured sampled locations) throughout the area (see Table S1 for more details).

fine ecologically relevant management units is therefore of general interest.

In this study, we demonstrate a statistical approach, based on standard trawl-survey data used to generate abundance indices applied in stock assessments, to identify and define population structuring within a widely distributed marine fish species, European sprat (*Sprattus sprattus*). Sprat is a fast-growing, short-lived, small pelagic species with a large commercial interest and a wide distribution range throughout European seas. Large-scale genetic studies indicate the existence of reproductively isolated populations, broadly separated along a pronounced environmental gradient spanning from the Baltic Sea to the western entrance of the Mediterranean (Berlow *et al.*, 2004; Limborg *et al.*, 2012; McKeown *et al.*, 2020; Quintela *et al.*, 2020). However, the actual boundaries between populations are poorly defined, at least at the finer spatial resolution needed for stock management. Within the large geographic area covered by the *International Council for the Exploration of the Seas* (ICES), sprat has traditionally been considered as belonging to five discrete management units (i.e. stocks), comprising the Baltic Sea, Skagerrak/Kattegat, North Sea, the English Channel, and the Celtic Seas (Figure 1). These units primarily reflect historic centres of operation for main fisheries, rather than actual population boundaries. To assess whether the current management units adequately account for potential population structuring, we aim to define ecologically relevant distributions and boundaries between populations by investigating spatial patterns in: (i) abundance distributions, (ii) temporal population dynamics and (iii) population demographics. On the basis of these three criteria, we pursue the following research questions:

- (i) Is there evidence for spatial structure in sprat abundances that could indicate limited spatial overlap between potential populations?
- (ii) Do sprat show spatially varying temporal trends and trajectories in abundances that could indicate different population processes?

- (iii) Does sprat size distribution vary spatially, indicating different population demographics and/or phenology of growth and recruitment?

Material and methods

Data collection

Scientific monitoring data of sprat abundances and distribution from seven bottom-trawl surveys covering the North Sea, the Baltic Sea, the eastern English Channel, the Scottish west coast, the Irish Sea, the Celtic Sea and the Bay of Biscay (Figure 1) were extracted from the publically accessible data base “DATRAS” hosted by ICES (<https://datras.ices.dk>; Table S1). To ensure the best available spatio-temporal coverage, we included all hauls sampled during the autumn-winter surveys (i.e. carried out during the 1st and 4th quarter of the calendar year) for which monitoring is conducted throughout the entire area. However, to account for potential seasonal changes in spatial abundance distributions, particularly during the primary spawning season in spring and summer (Alheit, 1987), we complemented the autumn-winter survey data with a separate analysis on the available spring and summer samples obtained during cruises carried out in the 2nd and 3rd quarter. After data extraction, the raw data (so-called “exchange data” in DATRAS) was exposed to formal data quality checks in order to omit invalid or erroneous records, as well as to ensure comparable units (see section 1.1 in the supplementary material for more details). We further corrected the abundance at length for differences in swept area (see section 1.2 in the supplementary material for more details) following the approach by Maureaud *et al.* (2019). This resulted in catch-per-unit effort (CPUE) data expressed as number of individuals per km² of a given length class per haul.

Data processing and standardization

We then standardized the CPUE data across surveys to correct for differences in sampling intensity and coverage in space and time. This was done by fitting a spatio-temporal index standardization model to the CPUE-at-length data from all sur-

veys using the R-package VAST (Thorson and Barnett, 2017) release number 3.5.1. This model has the advantage of predicting (interpolating and extrapolating where necessary) density across time and space within the entire survey domain. We performed data standardization across surveys following the current “best practice” guidelines for VAST (Thorson, 2019). Specifically, we defined the spatial domain for this analysis by overlaying a 10 km by 10 km square grid over the entire domain covered by the surveys and then retained any grid cell that was within 30 km of the nearest sample. Visual inspection confirmed that this set of grid cells had continuous coverage in spatial areas that contained samples while not extending beyond the range of data or onto land, and this was used as the extent for interpolating and extrapolating modelled densities for subsequent use. We then applied a k-means algorithm to distribute 2000 “extrapolation cells” in proportion to these grid cells and fitted a Poisson-link delta model using a gamma distribution for positive catch rates (Thorson, 2018). This model involves estimating two log-linked linear predictors $p_1(i)$ and $p_2(i)$ for each sample i occurring in year t_i for length class c_i at location s_i . The first linear predictor is specified as:

$$p_1(i) = \underbrace{\beta_1(c_i, t_i)}_{\text{Temporal variation}} + \underbrace{\omega_1^*(s_i, c_i)}_{\text{Spatial variation}} + \underbrace{\varepsilon_1^*(s_i, c_i, t_i)}_{\text{Spatio-temporal variation}}$$

where $\beta_1(c_i, t_i)$ is a matrix of fixed-effect intercepts for each combination of length-class and year, $\omega_1^*(s_i, c_i)$ is the value of Gaussian markov random field (GMRF) $\omega_1^*(c)$ representing the average spatial distribution for each length-class, and $\varepsilon_1^*(s_i, c_i, t_i)$ is the value of GMRFs $\varepsilon_1^*(c, t)$ representing annual deviations from this spatial distribution (termed “spatio-temporal variation”) for each length-class and year. The second linear predictor $p_2(i)$ is defined similarly but involves additional fixed and random effects. The predictors are then back transformed to calculate the likelihood of encounters and the expected number for each length group given that it is encountered (see section 1.3 in the supplementary material for more information regarding computational details and interpretation).

We estimated spatial and spatio-temporal random fields for both linear predictors at each of 200 “knots” that are selected by applying a k-means algorithm to the 2000 extrapolation cells. We subsequently used bilinear interpolation to predict the value of random fields at the 2000 extrapolation-cells or the location of each sample given their estimated values at the 200 knots. Although VAST has been shown to be robust to the choice of the number of knots (Thorson *et al.*, 2021), we performed an additional sensitivity analysis by re-running the entire analysis based also on 300 knots. Please note that we do not estimate any correlation in spatial or spatio-temporal terms among length classes, and also do not estimate any temporal smoothing. This specification ensures that the model does not induce any estimation covariance in predicted density among classes for a given year, or among years for a given class.

VAST uses R-INLA to calculate the triangulated mesh used in the stochastic partial differential equation (SPDE) approach to approximate the probability of random fields (Lindgren *et al.*, 2011), and also to calculate matrices implementing bilinear interpolation (Lindgren, 2012). VAST then uses the Template Model Builder (TMB) package (Kristensen *et al.*, 2016) to implement Laplace approximation (Skaug and Fournier,

2006) to approximate the marginal likelihood of fixed-effects when integrating across random effects (in this case, spatial and spatio-temporal random fields). TMB also provides the gradient of this marginal likelihood with respect to fixed effects (e.g. intercepts and variance parameters), and VAST then uses a conventional nonlinear minimizer to identify the values that maximize the log-marginal likelihood. We check convergence by confirming that the gradient of the log-marginal likelihood with respect to each fixed effect is low (<0.0001 for base and sensitivity runs), and that the Hessian matrix is positive definite. The estimation performance of VAST has been extensively tested elsewhere when fitted to independent operating models (i.e. “cross-tested”) and compared with alternative regression frameworks (Grüss *et al.*, 2019; Brodie *et al.*, 2020). Using this framework, we separately model density for 14 length classes across the entire area, including each interval from 4 to 16 cm, as well as two length classes encompassing the few individuals caught that were smaller or larger than 4 and 16 cm, respectively. Finally, the predicted numerical density by length class derived from VAST were aggregated across a regularly spaced spatial grid with a cell resolution of 0.5° . We then sum numerical density estimates across length classes to calculate the estimate of total abundance in each grid cell and year (hereafter called “standardized abundance”). To test for potential spatial differences in population demographics throughout the area, we also calculated the mean length (in units cm) in each grid cell across years, weighted by the numerical density in each length class.

We acknowledge that even after performing a proper data standardization across surveys and years, the bottom trawling gears are not adequately sampling pelagic species, including sprat. Hence, the estimated numerical densities are likely underestimating the true densities due to the effects of gear catchability and selectivity (Walker *et al.*, 2017). However, bottom trawl surveys are routinely used as tuning fleets in the formal stock assessments for sprat and have shown to perform equally well compared to hydroacoustic surveys (ICES, 2018; ICES, 2021). Furthermore, spatial distribution patterns of sprat based on bottom-trawl surveys (ICES, 2005) are similar to commercial catches from pelagic trawlers (ICES, 2021) and available ichthyoplankton surveys (Taylor *et al.*, 2007). To that end, we are confident that our model estimates derived from VAST provide standardized relative abundance measures across the entire area and time frame suitable for the purpose of this study.

Differences in spatial distributions of abundance

To investigate and characterize potential population structuring based on spatio-temporal abundance distributions, we calculated the median and coefficient of variation (CV) in standardized abundances for each grid cell across all years ranging from 1997 to 2019. We interpret grid cells with high median abundance and low interannual CV as representing a core area for a population. Conversely, grid cells with other combinations of medians and CVs represent areas outside the core distribution; for example, areas outside the distribution range (low median, low CV) or transition areas with occasional occupancy (low median, high CV). To account for potential seasonal changes in migration and distributions, the analysis was performed on both the autumn-winter and spring-summer abundances predicted from VAST. The abundances were log transformed prior to the analysis to stabilize the variance and

to avoid potential biases originating from hauls with extreme values.

Differences in temporal population dynamics

In addition to showing discrete spatial abundance distributions, distinct populations should demonstrate independent dynamics, caused by limited immigration and emigration between populations, i.e. indicating a lack of meta-population dynamics (Kritzer and Sale, 2004). However, discrete populations may show correlated abundance trends simply resulting from similar responses to some underlying large-scale driver, as previously shown for discrete sardine and anchovy populations across upwelling areas of the world (Schwartzlose *et al.*, 1999; Lindegren *et al.*, 2013). Consequently, one should be cautious against correlated population dynamics resulting from such external forcing as it may mask the existence of reproductively isolated stock components. To investigate potential differences in population dynamics across the area, we extracted the main modes of variability in time series of log-abundances for each grid cell from 1997 to 2019. To do so, we calculated the covariance matrix containing the covariance between the log-abundance across time for each pair of grid cells, then applied Principal Component Analysis (PCA) to this covariance matrix, and mapped the resulting loadings (i.e. eigenvector values) per grid cell on the Principal Components (PCs) that explained the largest part of the total variability. The resulting maps show grid cells with correlated or uncorrelated trends and temporal trajectories for each PC axis included. Because the abundance trajectories are highly variable, particularly in areas outside the main distribution range that are infrequently occupied by sprat, the derived PC scores and loadings are rather prone to such variability and noise. Therefore, we additionally investigated the long-term abundance trends in each grid cell by fitting linear regression models with log-abundance as a response and year as a single predictor and extracted the corresponding slopes as an alternative metric of temporal changes across the area. As in the previous analysis on abundance distributions, the PCA and linear trend analysis were performed and estimated on both the autumn–winter and spring–summer abundances derived from VAST.

Differences in population demographics

We calculated a time-series of mean length for each grid cell to compare temporal trends and changes in size throughout the area from 1997 to 2019. As in the previous analysis on abundance trends, we extracted the main modes of variability in mean length using PCA and mapped the resulting loadings per grid cell on the main PCs explaining the largest part of the total variability. Likewise, we investigated temporal trends by fitting linear regression models with mean length as a response and year as a single predictor and extracted the corresponding slopes for each grid cell. As in the previous analysis, the PCA and linear trends were performed and estimated on both the autumn–winter and spring–summer abundances derived from VAST.

Detecting potential sub-stock structuring through spatial clustering

To detect potential signals of population structuring throughout the area, we finally performed hierarchical clustering based on six variables representing each of the three criteria defined earlier: differences in abundance distributions (median

and CV of log-abundance), temporal dynamics (trend and first mode of variability in log-abundance), and demographics (trend and first mode of variability in average length). To test the robustness of results to the choice of input variables, while avoiding bias caused by the inclusion of multiple variables representing similar characteristics, we performed two separate analyses. Both use the median and CV of abundances and weighted mean length as input, but alternatively include either (i) the PC loadings or (ii) the linear slopes of abundances and length trajectories by grid cell as proxies for temporal developments. To account for spatial distances (and to limit the extent to which geographically far apart grid cells are being clustered together), we also included pair-wise spatial distances between grid cells, estimated as the shortest path through the water between grid cell midpoints (using the *costDistance* function in the R package “gdistance”). However, since we are primarily interested in patterns arising from ecological differences, we decreased the importance of spatial distances in the clustering analysis relative to the ecological variables by down weighting its contribution in the overall dissimilarity matrix calculation (by applying a weighting factor of 0.05 using the *fuse* function in the R package “analogue,” Simpson and Oksanen, 2021). Despite the minor importance given to the spatial distances, we also performed an additional analysis excluding spatial distances to formally test the sensitivity of clustering results to the inclusion or excluding of spatial distances.

The optimal number of clusters for each analysis was determined using the elbow criteria (a.k.a. a “skree plot”): the number of clusters where the degree of unexplained variation changes only marginally if increasing the number of clusters. Additionally, we also cut the resulting dendrograms into two or four groups and plotted the resulting clusters to illustrate and present the results of clustering and potential population structuring across a range of clusters. We illustrated differences between clusters for each of the three criteria of population structuring by comparing the mean and standard deviation for all variables across grid cells belonging to the same cluster. Finally, we also performed an additional clustering analysis on the available spring–summer data, albeit on a much more narrow area (due to the lack of survey), to demonstrate potential differences and similarities of population structuring between seasons. All statistical analyses were conducted in the R software, version 4.0.2 (R core Team, 2020).

Results

Differences in spatial abundance distributions

The derived spatial abundance distributions show that sprat is found in high median numbers throughout most of the surveyed area (Figure 2a). Specifically, the Irish Sea, the central part of the southern North Sea, the Kattegat and the Baltic Sea (particularly the southern and the western part bordering Sweden) demonstrate high median abundance and low CVs, indicating that these are areas with consistently high numbers of individuals. Places where median abundance was lower include the deeper and offshore parts of the northern North Sea, West of Scotland, and Ireland, as well as the Celtic Sea and Bay of Biscay. These areas, especially the northern North Sea, are also characterized by a high CV (Figure 2b), indicating that the presence and abundance of sprat in these waters is both low and highly infrequent. The modelled abun-

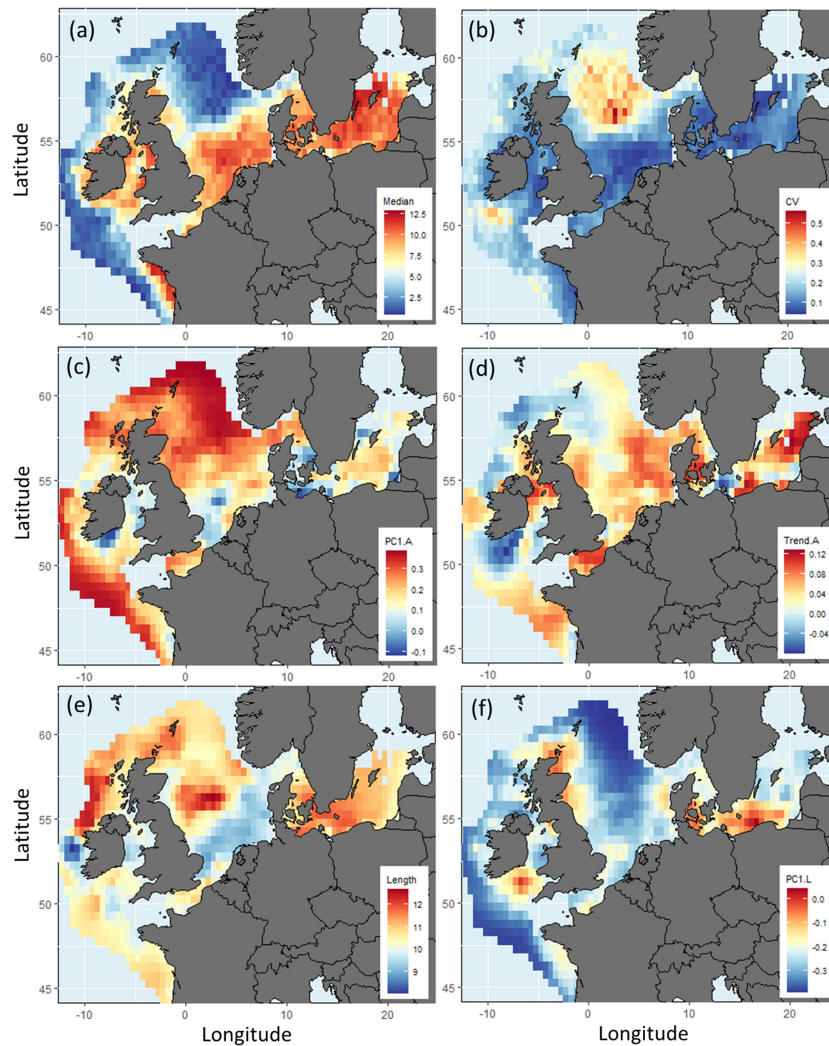


Figure 2. Spatial distribution of median (a) and coefficient of variation, CV (b) of log(abundance) across years in each 0.5° grid cell based on available autumn-winter data. Likewise, loadings on PC1 (c) and fitted linear trends (d) based on time-series of log(abundance) in each grid cell, as well as the abundance-weighted mean length (e) and loadings on PC1 (f) based on time series of mean length are shown in each grid cell. (See Figure S1 for similar maps based on available spring-summer data).

dance estimates show similar spatial patterns for the spring-summer (spawning season), indicated by high median abundances and low CVs in the central southern North Sea and Kattegat (Figure S1a, b), but with a somewhat more contracted distribution relative to the estimated autumn-winter distribution. However, the fewer surveys and samples available during the spring-summer (spawning) season preclude a full comparison of spatial abundance patterns throughout the entire area.

Differences in temporal population dynamics

The PCA analysis of abundance trajectories shows a high degree of the total variance in log-abundance ($\sim 40\%$) explained solely by PC1 (Figure S2a), which demonstrates highly variable dynamics with a marked increasing trend from the mid-2000s onwards (Figure S2b). The corresponding loadings, demonstrating the correlation between PC1 and the individual abundance trajectories in each grid cell, show primarily positive values throughout the area (Figure 2c). However, restricted areas in the Kattegat, western Baltic Sea, the south-

western North Sea as well as coastal areas in the Celtic Sea and Bay of Biscay, demonstrate weak or only slightly negative loadings, indicating abundance trajectories largely different from PC1. The linear trend analysis shows primarily positive slopes, indicating long-term increasing abundances throughout the area (Figure 2d), except for restricted areas in the southern Baltic Sea, North of Scotland and the southern coast of Ireland. Although limited in spatial extent, the PCA carried out on the available abundance estimates from spring-summer surveys show a similar high degree of explained variance ($\sim 60\%$) solely by PC1 (Figure S2c). The corresponding loadings on PC1, characterized by pronounced inter-annual variability and a slightly increasing trend from 2010 onwards (Figure S2d), show positive values primarily in the northern North Sea, while the Kattegat and the central parts of the southern North Sea demonstrate no or weakly negative loadings (Figure S1c). Furthermore, the trend analysis shows weak or moderately positive values throughout most of the area (Figure S1d), except for the southern part of Kattegat and south-western North Sea showing a more pronounced long-term increase.

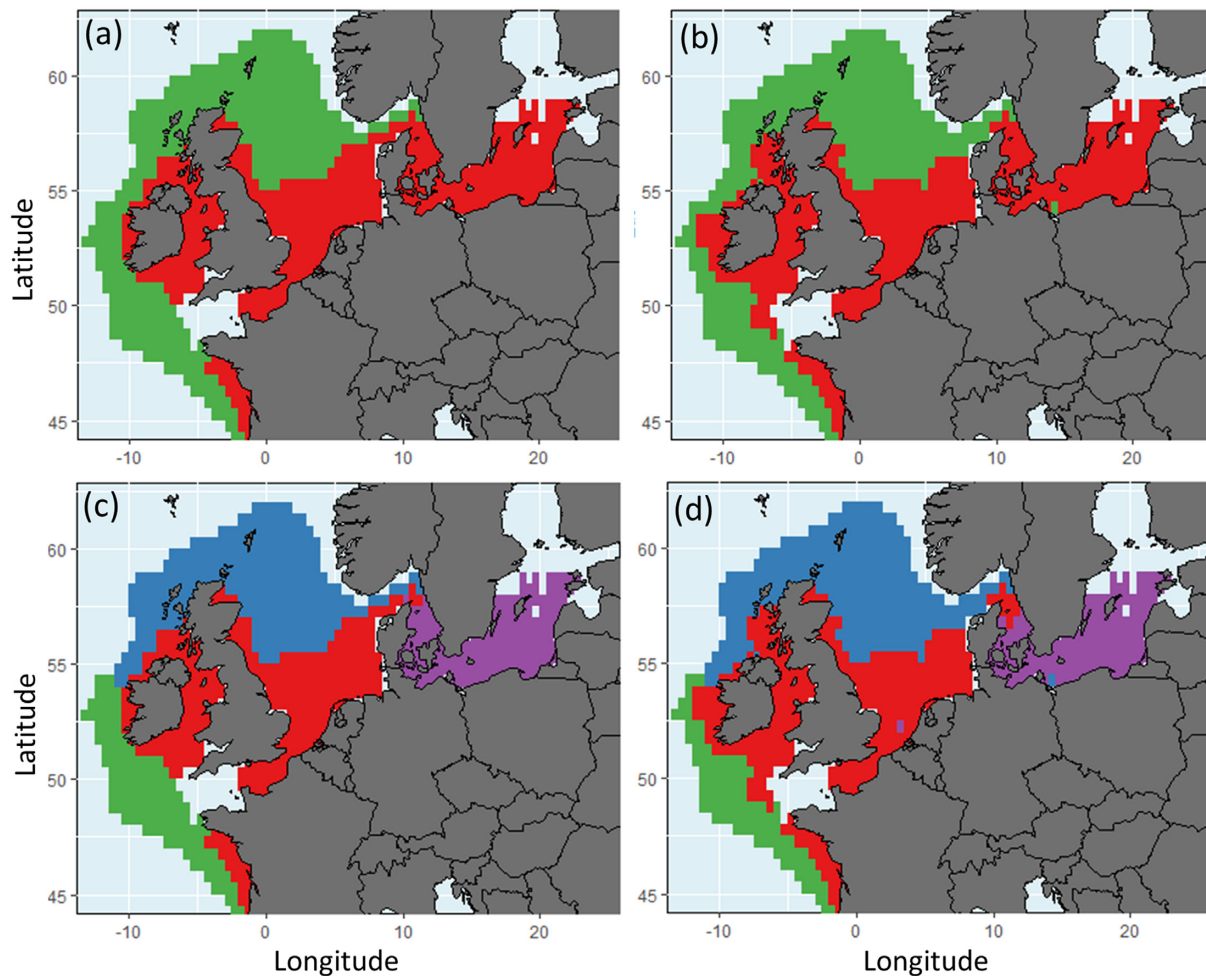


Figure 3. Results of hierarchical clustering illustrating potential population structuring across a range of clusters when cutting the resulting dendrograms into 2 (a, b) or 4 (c, d) groups. Both analyses use the median and coefficient of variation (CV) of abundances and weighted mean length as input, but alternatively include the PC loadings (left column) or the linear slopes of abundances and length trajectories (right column) by grid cell as proxies for temporal trends. Please note that the optimal number of clusters were four (c, d) regardless of the choice of input variables (e.g. comparing with Figure S5).

Differences in population demographics

Spatial patterns in mean abundance-weighted length show smaller average sizes (~ 9 cm) in the southern North Sea, the Irish Sea and west coast of Ireland compared to other areas (Figure 2e) where values are higher (~ 11 cm). The spatial differences in mean length are also manifested during spring-summer, where estimates show higher values in the Kattegat compared to the southern North Sea (Figure S1e). The PCA analysis of length trajectories show a rather high degree of the total variance in average-length explained ($\sim 50\%$) solely by PC1 (Figure S3a), demonstrating highly variable dynamics with no apparent long-term trend in length (Figure S3b). The corresponding loadings on PC1 show primarily negative values throughout the area (Figure 2f), with the southern Baltic Sea, the south coast of Ireland and the northeast coast of Scotland showing loadings closer to zero. The lack of a temporal trend is also evident from the trend analysis demonstrating fitted regression coefficients close to, or slightly less than zero across grid cells (Figure S4a). The PCA performed on the available spring-summer data show a high degree of explained variance ($\sim 90\%$) explained by PC1 (Figure S3c), characterized by highly variable dynamics without a long-term trend

(Figure S3d). The corresponding loadings on PC1 show primarily positive values throughout the area, especially in the northern North Sea. Finally, the lack of a temporal trend in PC1 is also evident from the trend analysis demonstrating fitted regression coefficients close to zero, except for Kattegat showing weakly positive values (Figure S4b).

Hierarchical clustering

Hierarchical clustering distinguished four primary clusters, representing potential population structuring, regardless of the choice of input variables. This was determined by the elbow criteria and illustrated by a sharp drop in the residual sum of squares up until four groups using either PC loadings or the fitted regression coefficients from the trend analysis as input (Figure S5a, b). The primary classification (i.e. the first split in the dendrograms in both analyses) separate the northern North Sea, north-western Scotland and Ireland and the offshore areas of the Celtic Sea and Bay of Biscay from the Baltic Sea, southern North Sea, Irish Sea and the coastal waters around UK, Ireland and the Bay of Biscay (Figure 3a, b). In the second classification the latter group mentioned above is further sub-divided by separating the Baltic Sea and Kattegat

from the other areas (Figure 3c, d). There is good agreement in terms of the spatial divide between clusters in both analyses, as well as the additional clustering analysis using the available spring-summer data (Figure S6). Finally, the clustering results were insensitive to the inclusion of spatial distances (i.e. the shortest path through the water), or the choice of the number of knots since the primary and secondary classifications into two or four overall clusters were almost identical if based on only ecological distances (Figure S7), or using 300 knots as a basis for the data processing and analysis (Figure S8).

Discussion

The rapid development of genetic techniques for identifying signs of reproductive isolation have proven effective to detect population structuring, even among widely distributed marine fish species (Dalongeville *et al.*, 2018; Knutsen *et al.*, 2018; Spies *et al.*, 2018; Hemmer-Hansen *et al.*, 2019). However, using these techniques for several species to conduct detailed mapping of the actual boundaries between populations, as well as their seasonal and inter-annual variability would be time consuming and costly (Martinson *et al.*, 2019). Hence, a complementary and cost-effective approach used alongside genetics is needed to identify population structuring and to inform appropriate spatial management measures. In this study, we demonstrate a statistical approach that relies on routinely collected monitoring data to assess and identify potential population structuring for widely distributed marine fish species, using European sprat as a case study. Our results indicate potential signs of population structuring of sprat within northern European seas based on our three criteria: spatial patterns of relative abundances, temporal dynamics, and demographics. Although investigating the underlying drivers and processes responsible for such regional differences are beyond the scope of our study, we discuss our findings in relation to existing literature and evidence from population genetics, and discuss the broader implications of our results and approach for management and advice.

The four overall spatial clusters identified by our analysis largely distinguish between shallow and coastal areas where sprat is numerous and consistently occurs (i.e. Baltic Sea, Kattegat, southern North Sea, Irish Sea, and the coastal areas of the Celtic Sea and Bay of Biscay), and offshore areas where occurrence is sporadic and highly variable in terms of numbers of individuals between years. For the sake of clarity, we henceforth refer to these clusters (including their corresponding colours in Figures 3 and 4) as follows: the northern North Sea/Scotland (“NSS”; blue), the Celtic Sea offshore (“CSO”; green), the Baltic Sea/Kattegat (“BSK”; purple), and the Irish/Celtic/North Sea (“ICN”; red). The differences between these clusters is clearly illustrated by the pronounced differences in median abundances and CVs between clusters situated largely within (BSK and ICN) or outside (NSS and CSO) the primary distribution area of sprat (Figure 4a and b). These differences in turn reflect the habitat requirements of sprat, which prefer coastal areas with strong tidal mixing and freshwater input (Munk, 1993; Valenzuela and Vargas, 2002; Daewel *et al.*, 2008). The spatial heterogeneity is likely due to a combination of external and internal factors affecting the reproduction, growth, and survival of individuals. These factors include both environmental constraints (e.g. in terms of temperature, salinity and oxygen), biotic factors (e.g. availability of food, predators and competitors) and human im-

pacts from fishing, that all vary in both space and time. We therefore encourage future studies to make use of the available data and statistical tools, including species distribution models (Melo-Merino *et al.*, 2020) to investigate the spatio-temporal variability of occurrence and abundance and their underlying drivers.

The heterogeneous abundance distributions presented here illustrate several centres of distribution with limited or no spatial overlap. However, such aggregations may, on their own, not necessarily evidence the existence of population structuring. This is because dispersal, either due to the passive advection of early life stages (i.e. eggs and larvae) or through active migration of adults, can lead to population mixing. The outcome of such mixing across habitats and areas will inevitably serve to harmonize population dynamics and demographic structure (i.e. size distribution, age distribution and growth), especially if accompanied by reproductive mixing (i.e. gene flow). Such dispersal and mixing, even between seemingly separate aggregations, may therefore lead to the formation of meta-population structuring (Kritzer and Sale, 2004; Lindegren *et al.*, 2014). Consequently, exploring these other population properties, as well as potential signs of genetic differentiation, is needed to robustly identify population structuring.

In terms of population dynamics, the four spatially explicit clusters identified in our analysis all demonstrate positive loadings on PC1, yet the strength of loadings differ between clusters (Figure 4c). This is particularly evident between clusters situated within the main distribution area identified in this study (i.e. BSK and ICN clusters) that show generally weaker loadings compared to areas outside (i.e. NSS and CSO clusters). This means that while the abundance trajectories of grid cells are correlated, albeit weakly to the dominant mode of variability (i.e. PC1), the actual temporal dynamics differ. This is illustrated by pronounced differences in the mean abundance time-series between clusters (Figure 4d), where the clusters within or outside the main distribution area (i.e. BSK/ICN vs NSS/CSO, respectively) show different trajectories. This is also the case between the two clusters within the main distribution area (NSS and CSO) that both demonstrate similar loadings and long-term increasing trends but largely different inter-annual variability. The similar trends are likely due to the same positive direct or indirect response of sprat recruitment (i.e. in terms of increased egg production and early life survival) to temperature (MacKenzie and Koster, 2004; Nissling, 2004; Baumann *et al.*, 2006), which has increased throughout the area (Belkin, 2009). Such correlated dynamics arising from similar responses to climate have previously been shown for discrete sardine and anchovy populations across upwelling areas of the world (Schwartzlose *et al.*, 1999). Conversely, the different inter-annual variability between clusters may arise from regional differences in other underlying processes directly or indirectly influencing reproduction, growth, and survival. These processes likely encompass a combination of top-down and bottom-up forces known to affect the dynamics of small pelagic fish, including regional differences in: (i) prey composition and availability (Last, 1987); (ii) the presence of predators and strength of predation (Lindegren *et al.*, 2011; Bartolino *et al.*, 2014); (iii) spatio-temporal differences in fishing effort (Essington *et al.*, 2015); and (iv) differences in the degree of density-dependence (Casini *et al.*, 2011; Hunter *et al.*, 2019; Lindegren *et al.*, 2020) and inter-specific competition from other small pelagic fish (Casini *et al.*, 2004; Lindegren *et al.*,

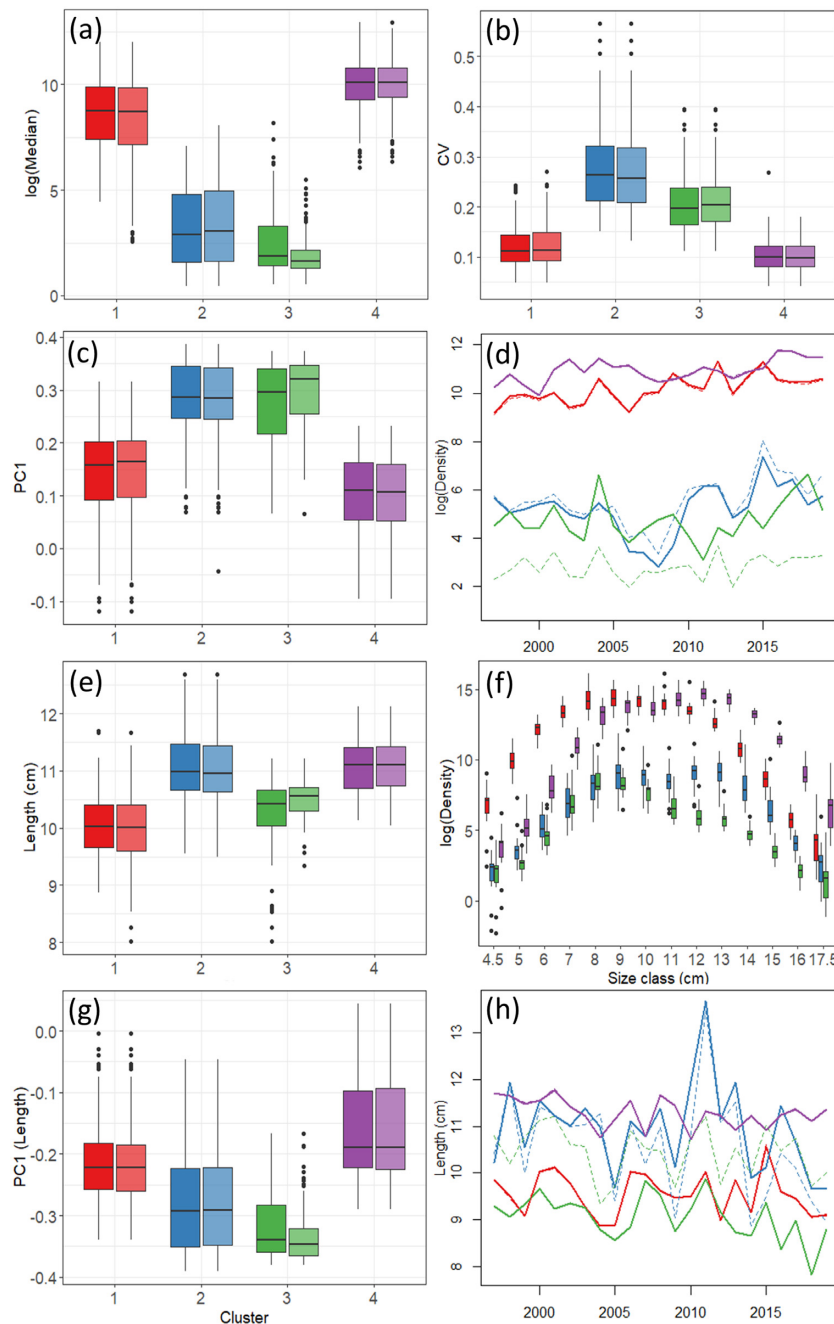


Figure 4. Boxplots showing median (a) and CVs (b) of log(abundances) across grid cells belonging to each of the four optimal clusters identified in both analyses. The colours correspond to clusters shown in Figure 3c, d where the lighter and darker shades reflect the analysis using PC1 loadings or temporal trends as input, respectively. Likewise, loadings on PC1 based on log(abundance) time-series (c), mean long-term abundance trends (d), mean lengths (e), the size distribution (f), as well as the PC1 loadings of length time-series (g) and the mean temporal developments in length (h) are shown for each cluster and analysis.

2011; Raab *et al.*, 2012). Consequently, future studies should strive to better understand the effect and relative importance of these factors underpinning the variation in sprat population dynamics throughout European seas.

Finally, the regional differences in underlying processes affecting recruitment, growth and survival may also explain the observed spatial differences in terms of population demography; our third criteria of population structuring. This is illustrated by different weighted mean length, as well as length distributions between clusters (Figure 4e, f), especially between the two clusters in the main distribution area of sprat, where

grid cells within the Baltic Sea/Kattegat cluster show a significantly higher mean length and a size distribution shifted towards larger individuals. Whether these patterns are primarily due to differences in growth (e.g. size at age) or size-dependent survival caused by regional differences in predation and commercial fishing is unclear, partly due to the limited availability of age data across all surveys. Nevertheless, some regional differences in length-at-age have previously been documented between the southern and northern North Sea, as well as waters West of Scotland (Hunter *et al.*, 2019), supporting regional differences in growth as a plausible explanation.

Alternatively, potential differences in survey catchability by length group may bias the length distribution and consequently our perception of the true population demography and its spatial variability (Walker *et al.*, 2017). Such differences should primarily bias the abundance of smaller-sized individuals since juveniles are poorly sampled both due to their small size and prevalence in shallow and coastal nursery areas that are poorly covered by the surveys. Hence, if a consistent bias between surveys or areas exist (all else being equal), it should mainly be reflected in the shape of the lower tail of the length distribution (e.g. left-hand side of Figure 4f), while the upper tail should be unaffected and similar between areas and surveys. Since differences in the length distribution between the Baltic Sea/Kattegat versus the North-Irish/Celtic Sea/Bay of Biscay cluster are occurring in both the lower and upper tail (i.e. reflecting a consistent shift towards larger sizes), the differences are unlikely due to such a potential survey bias. Nevertheless, we call for further studies examining the influence of key life-history characteristics (i.e. growth, reproduction, maturation, and survival) and their underlying drivers on population demography, as well as potential differences in survey catchability of sprat and small pelagic fish in general caused by differences in gears, habitats and fish behaviour, notably diel vertical migrations (Cardinale *et al.*, 2003).

From a methodological point of view, we also recommend future research and developments of statistical approaches that can simultaneously standardize data and apply PCA or estimate spatially varying temporal trends (Barnett *et al.*, 2021; Grüss *et al.*, 2021), while properly accounting for the propagation of uncertainty. In our case, model uncertainty may primarily underestimate the reported CVs of abundances (Figure 2b), while the other metrics that rely on median abundances (summed over length groups), trends or PCA loadings (based on annual average abundances summed over length groups), or lengths (weighted by abundances) should be only marginally affected by the underlying model uncertainty, especially at the rather coarse spatial resolution used in our study. Nevertheless, we encourage future comparisons between the present approach to spatial clustering and previously applied approaches including the “Regions of Common Profile” (RCP; Hill *et al.*, 2017), Hierarchical Modelling of Species Communities, HMSC (Ovaskainen *et al.*, 2017) or tensor decomposition (Frelat *et al.*, 2017). To the best of our knowledge, RCP has been applied to identify biogeographic classifications using multivariate information, but it has not been applied to identify areas with similar temporal dynamics. Similarly, HMSC has previously been used to emphasize spatial differences in species traits rather than temporal dynamics as emphasized here. In any case, we anticipate there to be many fruitful avenues exploring and comparing multiple methods and their utility in studying the patterns and underlying processes leading to population structuring.

In summary, our approach has identified potential signs of population structuring of sprat in European waters, illustrated by differences in spatial abundance patterns, temporal dynamics, and population demographics between regional clusters. Our findings are well in line with the most recent population genetic studies of sprat (McKeown *et al.*, 2020; Quintela *et al.*, 2020), indicating reproductive isolation between the Baltic Sea and a larger cluster containing the North Sea, Celtic Sea, and Bay of Biscay (hence corresponding to the BSK and ICN clusters identified here). The

similarity in the overall clusters and signs of population structuring defined also by genetics supports the robustness of our results, as well as the complementary use and added value of our statistical approach alongside population genetics to detect the existence of discrete populations and their associated boundaries. This is particularly relevant in areas and species where monitoring data are in place but where genetic data are lacking or have inadequate sampling and spatio-temporal coverage.

Our findings largely support the recent revision of management units of sprat within ICES (ICES, 2018), particularly merging previously separate assessment units in the North Sea and Skagerrak/Kattegat. However, we recommend that future scientific research and evaluation of population boundaries pay attention to the occurrence and potential mixing with the Baltic Sea sprat component, especially in the southern and central parts of the Kattegat. This should be done to avoid spatial allocation of catches leading to an unsustainable level of exploitation affecting the Baltic Sea population in this area. The same degree of caution (when deciding on the spatial allocation of quotas) is generally applicable throughout the ICES domain and beyond, where mixing between reproductively isolated populations takes place. Notably, specific consideration should be given to the sprat management units in the English Channel and Celtic Sea. These units are currently assessed and managed separately, but according to our analysis and recent population genetics (McKeown *et al.*, 2020; Quintela *et al.*, 2020), likely belong to a large, demographically connected cluster that also includes the North Sea and Bay of Biscay. If these units are to be merged and assessed jointly together with the North Sea and Bay of Biscay, spatial management and advice should account for the occurrence of potential population structuring within this large area. Even if finer population structuring in the North Sea–Channel–Biscay area was not detectable (or deemed statistically optimal) in our broad-scale analysis, it is still possible that fine-scale demographic structures exist within the area. Consequently, increasing efforts to increase the coverage and intensity of sampling, as well as reporting of all key parameters (including swept area estimates) within this area is needed, particularly in the western English Channel where comparable surveys are entirely missing.

Population structuring is common among marine fish stocks worldwide (Dalongeville *et al.*, 2018; Knutsen *et al.*, 2018; Spies *et al.*, 2018; Hemmer-Hansen *et al.*, 2019), but is often overlooked within traditional fisheries management (Stephenson, 1999; Reiss *et al.*, 2009; Svedäng *et al.*, 2010; Randon *et al.*, 2018; Cadrin, 2020). Such reproductively isolated local populations do exist for sprat and for other widespread small pelagic fish species (Wright *et al.*, 2019; Huret *et al.*, 2020; McKeown *et al.*, 2020; Quintela *et al.*, 2020). Evidence of population structuring should therefore be given due consideration to ensure sustainable exploitation and management approaches, especially under the looming threat of climate change causing shifts in distributions across current management boundaries (Baudron *et al.*, 2020; Maureaud *et al.*, 2021).

Supplementary Data

Supplementary material is available at the ICESJMS online version of the manuscript.

Data availability statement

The raw data used in this study is derived from publicly available sources (see Table S1 and links mentioned in the “Material and Methods” section). Likewise, the method used for data standardization is based on open access R scripts (<https://github.com/James-Thorson-NOAA/VAST>). The data and code can also be shared on request to the corresponding author.

Funding

The study was supported by the European Maritime and Fisheries Foundation and the Ministry of Environment and Food of Denmark (grant ID: 33113-B-17-091; project: Maintaining a sustainable sprat fishery in the North Sea, BEBRIS).

Author contribution and competing interest statement

ML designed research with input from MvD and DB; JT, AM, and ML performed data processing and standardization; ML performed statistical analysis with input from all authors; ML drafted the first version of the ms and all authors took part in writing and revising subsequent versions throughout the peer review process. The authors declare no competing interests.

Acknowledgments

We would like to thank all people involved in the recent sprat benchmark workshop for their valuable comments and feedback on the project. We would also like to thank N. Maginnis for providing assistance estimating pair-wise distances as the shortest path through the water. The manuscript was improved by comments from K. Johnson and G. Carroll prior to submission, as well as constructive comments from two anonymous reviewers during peer review. Please note that the scientific results and conclusions, as well as any views or opinions expressed herein, are those of the author(s) and do not necessarily reflect those of NOAA or the Department of Commerce.

References

- Alheit, J. 1987. Variation of batch fecundity of sprat, *sprattus sprattus*, during the spawning season. ICES Council Meeting, H/44, <https://epic.awi.de/id/eprint/49/>.
- Barnett, L.A.K., Ward, E.J., and Anderson, S.C. 2021. Improving estimates of species distribution change by incorporating local trends. *Ecography*, 44: 427–439.
- Bartolino, V., Margonski, P., Lindegren, M., Linderholm, H.W., Cardinale, M., Rayner, D., Wennhage, H. *et al.* 2014. Forecasting fish stock dynamics under climate change: baltic herring (*Clupea harengus*) as a case study. *Fisheries Oceanography*, 23: 258–269.
- Baudron, A. R., Brunel, T., Blanchet, M.A., Hidalgo, M., Chust, G., Brown, E. J., Kleisner, K. M. *et al.* 2020. Changing fish distributions challenge the effective management of european fisheries. *Ecography*, 43: 494–505.
- Baumann, H., Hinrichsen, H.H., Mollmann, C., Koster, F.W., Malzahn, A.M., and Temming, A., 2006. Recruitment variability in baltic sea sprat (*Sprattus sprattus*) is tightly coupled to temperature and transport patterns affecting the larval and early juvenile stages. *Canadian Journal of Fisheries and Aquatic Sciences*, 63: 2191–2201.
- Belkin, I.M., 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography*, 81: 207–213.
- Berlow, E.L., Neutel, A.M., Cohen, J.E., de Ruiter, P.C., Ebenman, B., Emmerson, M., Fox, J.W. *et al.* 2004. Interaction strengths in food webs: issues and opportunities. *Journal of Animal Ecology*, 73: 585–598.
- Brodie, S.J., Thorson, J.T., Carroll, G., Hazen, E.L., Bograd, S., Haltuch, M.A., Holsman, K.K. *et al.* 2020. Trade-offs in covariate selection for species distribution models: a methodological comparison. *Ecography*, 43: 11–24.
- Cadrin, S.X., 2020. Defining spatial structure for fishery stock assessment. *Fisheries Research*, 221: 105397.
- Ciannelli, L., Fisher, J. A. D., Skern-Mauritzen, M., Hunsicker, M. E., Hidalgo, M., Frank, K. T., and Bailey, K. M. 2013. Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. *Marine Ecology Progress Series*, 480: 227–243.
- Cardinale, M., Casini, M., Arrhenius, F., and Hakansson, N. 2003. Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the baltic sea. *Aquatic Living Resources*, 16: 283–292.
- Casini, M., Cardinale, M., and Arrhenius, F., 2004. Feeding preferences of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the southern baltic sea. *ICES Journal of Marine Science*, 61: 1267–1277.
- Casini, M., Kornilovs, G., Cardinale, M., Möllmann, C., Grygiel, W., Jonsson, P., Raid, T. *et al.* 2011. Spatial and temporal density dependence regulates the condition of central baltic sea clupeids: compelling evidence using an extensive international acoustic survey. *Population Ecology*, 53: 511–523.
- Daewel, U., Peck, M.A., Kühn, W., John, M.A.S.T., Alekseeva, I., and Schrum, C. 2008. Coupling ecosystem and individual-based models to simulate the influence of environmental variability on potential growth and survival of larval sprat (*Sprattus sprattus*) in the north sea. *Fisheries Oceanography*, 17: 333–351.
- Dalongeville, A., Andreello, M., Mouillot, D., Lobreaux, S., Fortin, M.J., Lasram, F., Belmaker, J. *et al.* 2018. Geographic isolation and larval dispersal shape seascape genetic patterns differently according to spatial scale. *Evolutionary Applications*, 11: 1437–1447.
- Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., Siple, M. C. *et al.* 2015. Fishing amplifies forage fish population collapses. *Proceedings of the National Academy of Sciences*, 112: 6648.
- Frank, K.T., and Brickman, D., 2000. Allee effects and compensatory population dynamics within a stock complex. *Canadian Journal of Fisheries and Aquatic Sciences*, 57: 513–517.
- Frelat, R., Lindegren, M., Denker, T.S., Floeter, J., Fock, H.O., Sguotti, C., Stäbler, M. *et al.* 2017. Community ecology in 3D: tensor decomposition reveals spatio-temporal dynamics of large ecological communities. *Plos One*, 13(4): e0196353
- Gaggiotti, O.E., Bekkevold, D., Jørgensen, H.B.H., Foll, M., Carvalho, G.R., Andre, C., and Ruzzante, D.E., 2009. Disentangling the effects of evolutionary, demographic, and environmental factors influencing genetic structure of natural populations: atlantic herring as a case study. *Evolution; International Journal of Organic Evolution*, 63: 2939–2951.
- Gervasi, V., Linnell, J.D.C., Brøseth, H., and Gimenez, O., 2019. Failure to coordinate management in transboundary populations hinders the achievement of national management goals: the case of wolverines in scandinavia. *Journal of Applied Ecology*, 56: 1905–1915.
- Grüss, A., Thorson, J.T., Stawitz, C.C., Reum, J.C.P., Rohan, S.K., and Barnes, C.L., 2021. Synthesis of interannual variability in spatial demographic processes supports the strong influence of cold-pool extent on eastern bering sea walleye pollock (*Gadus chalcogrammus*). *Progress in Oceanography*, 194: 102569.
- Grüss, A., Walter, J.F., Babcock, E.A., Forrestal, F.C., Thorson, J.T., Laueretta, M.V., and Schirripa, M.J., 2019. Evaluation of the impacts of different treatments of spatio-temporal variation in catch-per-unit-effort standardization models. *Fisheries Research*, 213: 75–93.
- Hemmer-Hansen, J., Hüsey, K., Baktoft, H., Huwer, B., Bekkevold, D., Haslob, H., Herrmann, J.P. *et al.* 2019. Genetic analyses reveal complex dynamics within a marine fish management area. *Evolutionary Applications*, 12: 830–844.

- Hill, N.I., Foster, S.D., Duhame, G., Welsford, D., Koubbi, P., and Johnson, C.R. 2017. Model-based mapping of assemblages for ecology and conservation management: a case study of demersal fish on the kerguelen plateau. *Diversity and Distributions*, 23: 1216–1230.
- Hunter, A., Speirs, D.C., and Heath, M.R., 2019. Population density and temperature correlate with long-term trends in somatic growth rates and maturation schedules of herring and sprat. *Plos One*, 14(3): e0212176.
- Huret, M., Lebigre, C., Iriondo, M., Montes, I., and Estonba, A., 2020. Genetic population structure of anchovy (*Engraulis encrasicolus*) in North-western europe and variability in the seasonal distribution of the stocks. *Fisheries Research*, 229: 105619. h
- ICES. 2018. Benchmark Workshop on Sprat (WKSPRAT 2018). ICES WKSPRAT Report 2018, 5–9 November 2018. ICES HQ, Copenhagen, Denmark. ICES CM 2018/ACOM:35. 60pp.
- ICES. 2021. Herring assessment working group for the area south of 62° n (HAWG). ICES Scientific Reports, 3: 12. 779 pp.
- ICES, 2005. <https://www.ices.dk/about-ICES/projects/EU-RFP/EU%20Repository/ICES%20FishMap/ICES%20FishMap%20species%20factsheet-sprat.pdf>
- Kerr, L. A., Hintzen, N. T., Cadrin, S. X., Clausen, L., Worsøe Dickey-Collas, M., Goethel, D. R., Hatfield, E. M.C. *et al.* 2017. Lessons learned from practical approaches to reconcile mismatches between biological population structure and stock units of marine fish. *ICES Journal of Marine Science*, 74: 1708–1722.
- Knutsen, H., Jorde, P.E., Hutchings, J.A., Hemmer-Hansen, J., Grønkjær, P., Jørgensen, K.E.M., André, C. *et al.* 2018. Stable coexistence of genetically divergent atlantic cod ecotypes at multiple spatial scales. *Evolutionary Applications*, 11: 1527–1539.
- Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M., 2016. TMB: automatic differentiation and laplace approximation. *Journal of Statistical Software*, 70: 1–21.
- Kritzer, J.P., and Sale, P.F., 2004. Metapopulation ecology in the sea: from levins' model to marine ecology and fisheries science. *Fish and Fisheries*. 5: 131–140.
- Lascelles, B., Notarbartolo Di Sciara, G., Agardy, T., Cuttelod, A., Eckert, S., Glowka, L., Hoyt, E. *et al.* 2014. Migratory marine species: their status, threats and conservation management needs. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24: 111–127.
- Last, J.M., 1987. The food of immature sprat (*Sprattus sprattus* (L.)) and herring (*Clupea harengus* L.) in coastal waters of the north sea. *ICES Journal of Marine Science*, 44: 73–79.
- Limborg, M.T., Hanel, R., Debes, P. V., Ring, A.K., André, C., Tsigenopoulos, C.S., and Bekkevold, D., 2012. Imprints from genetic drift and mutation imply relative divergence times across marine transition zones in a pan-European small pelagic fish (*Sprattus sprattus*). *Heredity*, 109: 96–107.
- Lindgren, M., Rindorf, A., Norin, T., Johns, D., and van Deurs, M. 2020. Climate- and density-dependent regulation of fish growth throughout ontogeny: north sea sprat as a case study. *ICES Journal of Marine Science*, 77: 3138–3152
- Lindgren, M., Andersen, K.H., Casini, M., and Neuenfeldt, S., 2014. A metacommunity perspective on source-sink dynamics and management: the baltic sea as a case study. *Ecological Applications*, 24: 1820–1832.
- Lindgren, Martin, Checkley, D.M., Rouyer, T., MacCall, A.D., and Stenseth, N.C., 2013. Climate, fishing, and fluctuations of sardine and anchovy in the california current. *Proceedings of the National Academy of Sciences*, 110: 13672–13677.
- Lindgren, M., Östman, Ö., and Gårdmark, A., 2011. Interacting trophic forcing and the population dynamics of herring. *Ecology*, 92: 1407–1413.
- Lindgren, 2012. Continuous domain spatial models in R-INLA. *ISBA Bull*, 19: 14–20.
- Lindgren, F., Rue, H., and Lindström, J., 2011. An explicit link between gaussian fields and gaussian markov random fields: the stochastic partial differential equation approach. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*, 73: 423–498.
- MacKenzie, B.R., and Koster, F.W., 2004. Fish production and climate: sprat in the baltic sea. *Ecology*, 85: 784–794.
- Martinson, J.T., Raymond, P., Knott, T., Glover, K.A., Nielsen, E.E., Eriksen, L.B., Ogden, R. *et al.* 2019. DNA-analysis to monitor fisheries and aquaculture: too costly? *Fish and Fisheries*, 20: 391–401.
- Maureaud, A., Hodapp, D., van Denderen, P.D., Hillebrand, H., Gislason, H., Spaanheden Dencker, Tim., Beukhof, E. *et al.* 2019. Biodiversity – ecosystem functioning relationships in fish communities : biomass is related to evenness and the environment, not to species richness. *Proceedings of the Royal Society B: Biological Sciences*, 286: 20191189.
- Maureaud, A., Frelat, R., Pécuchet, L., Shackell, N., Mérigot, B., Pinsky, M. L., Amador, K. *et al.* 2021. Are we ready to track climate-driven shifts in marine species across international boundaries? – A global survey of scientific bottom trawl data. *Global Change Biology*, 27: 220–236
- McKeown, N.J., Carpi, P., Silva, J.F., Healey, A.J.E., Shaw, P.W., and van der Kooij, J., 2020. Genetic population structure and tools for the management of european sprat (*Sprattus sprattus*). *ICES Journal of Marine Science*, 77: 2134–2143
- Melo-Merino, S.M., Reyes-Bonilla, H., and Lira-Noriega, A., 2020. Ecological niche models and species distribution models in marine environments: a literature review and spatial analysis of evidence. *Ecological Modelling*, 415: 108837
- Munk, P., 1993. Differential growth of larval sprat *sprattus sprattus* across a tidal front in the eastern north sea. *Marine Ecology Progress Series*, 99: 17–27.
- Nandintsetseg, D., Bracis, C., Olson, K.A., Böhning-Gaese, K., Calabrese, J.M., Chimeddorj, B., Fagan, W.F. *et al.* 2019. Challenges in the conservation of wide-ranging nomadic species. *Journal of Applied Ecology*, 56: 1916–1926.
- Nissling, A., 2004. Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the baltic sea – implications for stock development. *Hydrobiologia*, 514: 115–123.
- Ovaskainen, O., Tikhonov, G., Norberg, A., Blanchet, F. G., Duan, L., Dunson, D., Roslin, T., and Abrego, N. 2017. How to make more out of community data? A conceptual framework and its implementation as models and software. *Ecology Letters*, 20: 561–576.
- Quintela, M., Kvamme, C., Bekkevold, D., Nash, R.D.M., Jansson, E., Sørvik, A.G., Taggart, J.B. *et al.* 2020. Genetic analysis redraws the management boundaries for the european sprat. *Evolutionary Applications*, 13: 1906–1922.
- R Core Team(2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Raab, K., Nagelkerke, L.A.J., Boerée, C., Rijnsdorp, A.D., Temming, A., and Dickey-Collas, M., 2012. Dietary overlap between the potential competitors herring, sprat and anchovy in the north sea. *Marine Ecology Progress Series*, 470: 101–111.
- Randon, M., Réveillac, E., Rivot, E., Du Pontavice, H., and Le Pape, O., 2018. Could we consider a single stock when spatial sub-units present lasting patterns in growth and asynchrony in cohort densities? A flatfish case study. *Journal of Sea Research*, 142: 91–100.
- Reiss, H., Hoarau, G., Dickey-Collas, M., and Wolff, W.J., 2009. Genetic population structure of marine fish: mismatch between biological and fisheries management units. *Fish and Fisheries*, 10: 361–395.
- Schwartzlose, R.A., Alheit, J., Bakun, A., Baumgartner, T.R., Cloete, R., Crawford, R.J.M., Fletcher, W.J. *et al.* 1999. Worldwide large-scale fluctuations of sardine and anchovy populations. *South African Journal of Marine Science*, 21: 289–347.
- Simpson, G.L., and Oksanen, J. 2021. analogue: analogue matching and modern analogue technique transfer function models. (R package version 0.17–6).
- Skaug, H., and Fournier, D., 2006. Automatic approximation of the marginal likelihood in non-Gaussian hierarchical models. *Computational Statistics & Data Analysis*, 51: 699–709.

- Spies, I., Hauser, L., Jorde, P.E., Knutsen, H., Punt, A.E., Rogers, L.A., and Stenseth, N.C., 2018. Inferring genetic connectivity in real populations, exemplified by coastal and oceanic atlantic cod. *Proceedings of the National Academy of Sciences*, 115: 4945–4950.
- Stephenson, R.L., 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fisheries Research*, 43: 247–249.
- Sterner, T., 2007. Unobserved diversity, depletion and irreversibility the importance of subpopulations for management of cod stocks. *Ecological Economics*, 61: 566–574.
- Svedang, H., Stal, J., Sterner, T., and Cardinale, M., 2010. Consequences of subpopulation structure on fisheries management: cod (*Gadus morhua*) in the kattegat and oresund (North sea). *Reviews in Fisheries Science*, 18: 139–150.
- Taylor, N., Fox, C.J., Bolle, L., Dickey-Collas, M., Fossum, P., Kraus, G., Munk, P. *et al.* 2007. Results of the spring 2004 north sea ichthyoplankton surveys. The distribution of fish eggs and larvae from international ichthyoplankton survey, ICES Cooperative Research Report.
- Thorson, J. T., Cunningham, C. J., Jorgensen, E., Havron, A., Hulson, P. J. F., Monnahan, C. C., and von Szalay, P. 2021. The surprising sensitivity of index scale to delta-model assumptions: recommendations for model-based index standardization. *Fisheries Research*, 233: 105745.
- Thorson, J.T., 2019. Guidance for decisions using the vector autoregressive spatio-temporal (VAST) package in stock, ecosystem, habitat and climate assessments. *Fisheries Research*, 210: 143–161.
- Thorson, J.T., 2018. Three problems with the conventional delta-model for biomass sampling data, and a computationally efficient alternative. *Canadian Journal of Fisheries and Aquatic Sciences*, 75: 1369–1382.
- Thorson, J.T., and Barnett, L.A.K., 2017. Comparing estimates of abundance trends and distribution shifts using single- and multispecies models of fishes and biogenic habitat. *ICES Journal of Marine Science*, 74: 1311–1321.
- Valenzuela, G.S., and Vargas, C.A., 2002. Comparative larval growth rate of *sprattus sprattus* in relation to physical and biological oceanographic features in the north sea. *Arch. Fish. Mar. Res.*, 49: 213–230.
- Walker, N.D., Maxwell, D.L., Le Quesne, W.J.F., and Jennings, S., 2017. Estimating efficiency of survey and commercial trawl gears from comparisons of catch-ratios. *ICES Journal of Marine Science*, 74: 1448–1457.
- Wright, P. J., Christensen, A., Regnier, T., Rindorf, A., and van Deurs, M. 2019. Integrating the scale of population processes into fisheries management, as illustrated in the sandeel, *ammodytes marinus*. *ICES Journal of Marine Science*, 76: 1453–1463.

Handling Editor: Ernesto Jardim