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Original Article

Spatially explicit stock assessment uncovers sequential depletion of northern shrimp stock components in the North Sea

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Space is a critical component of fisheries management. Despite this, very few of the world's fish and shellfish stocks are currently assessed using methods that are spatially structured. In the Northeast Atlantic, northern shrimp in the North Sea and Skagerrak, is currently assessed using a spatially structured assessment model. This metapopulation model includes two spatial units (the Norwegian Deep and the Skagerrak), however, in the recent past, the fishery on northern shrimp in the North Sea also occurred in a third neighbouring fishing area, the Fladen Ground. Here, we have reconstructed the dynamics of northern shrimp in the Fladen Ground using historic landings, a standardized commercial index of abundance and fragmented survey data and integrated this third spatial unit into the assessment model of the stock. In doing so, we find evidence of sequential spatial depletion, whereby high rates of fishing mortality have successively eroded stock components in a west to east pattern of overexploitation and produced cryptic collapses. This finding is the first documented case of sequential spatial depletion in the Northeast Atlantic, a phenomenon that could be common and largely overlooked by stock assessment methods that are inherently non-spatial.

Keywords: cryptic collapses, Northeast Atlantic, Northern shrimp, spatially structured stock assessment..

Introduction

Detailed considerations of spatially structured population dynamics have increasingly been shown to play a crucial role in understanding ecological processes. This is based on the principle that every key ecological process takes place in a spatial context and may encompass a spatial structure that affects or determines the detail of the outcome (Dale and Fortin, 2014). In metapopulations, (i.e. plant or animal populations connected through dispersal) it is well recognized that the dynamics of individual subpopulations can diverge considerably from the dynamics of the aggregated metapopulation (e.g. Melbourne and Chesson, 2006). This implies that for exploited metapopulations, such as commercial fish stocks, harvest strategies that appear appropriately prescribed at large spatial scales can, at local scales, lead to declines or even the effective extirpation of local subpopulations (Okamoto *et al.*, 2020). Okamoto *et al.* (2020) call these local-scale declines "cryptic collapses."

Increased knowledge of the spatial distribution and dynamics of marine resources is crucial for fisheries management and the conservation of marine organisms. The interaction of biological and environmental processes and spatial exploitation patterns, can cause demographic rates to vary across space, causing detectable spatial patterns in fish populations and yields (Kapur *et al.*, 2021). Despite this, the spatial dimension is the most neglected dimension in stock assessment (Berger *et al.*, 2017) and this absence can lead to biases in estimated management quantities, such as Total Allowable Catches (TAC; e.g. Punt *et al.*, 2019).

With few exceptions (e.g. tropical tunas in the Indian Ocean), most stock assessments around the globe lack a spatially explicit dimension. In Northeast Atlantic waters, almost all stocks are considered homogenous units within their area of distribution, and only the northern shrimp stock (*Pandalus borealis*) in the Skagerrak, Kattegat and northern North Sea is assessed by a spatially explicit model (https://www.ices.dk/advice/Pages/Latest-Advice.aspx). It has been demonstrated that several stocks that occupy one broad region might consist of several spawning components (e.g. Ruzzante *et al.*, 1999; Bekkevold *et al.*, 2005; Cardinale *et al.*, 2011a). Simulation studies have shown that an ignorance of spatial structuring in stock assessments may result in (i) biases in estimated population parameters; (ii) biases in estimated stock status; (iii) inappropriate management targets; (iv) recommendations of inappropriate harvest levels; and (v) the depletion of local populations, which in turn will lead to higher risks of depleted fish stocks (e.g. Yiping *et al.*, 2011; Goethel *et al.*, 2016, but see also recent reviews of Cadrin *et al.*, 2023 and Goethel *et al.*, 2023). In fact, Morse *et al.* (2020) found that using single-area models separately for each of two connected stocks in a simulation framework (i.e. ignoring spatial mixing) resulted in biased estimates of recruitment and spawning biomass for both stocks (i.e. area-specific bias in terms of local depletion). Thus, a failure to account for spatial complexity might lead to the serial extirpation of stock components (e.g. Hutchinson *et al.*, 2003). However, data-driven examples of the "serial depletion phenomenon" in harvesting marine resources, where the harvesters successively exploit, deplete, and finally

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abandon fishing grounds, are rare (e.g. Orensanz *et al.*, 1998; Cardinale *et al.*, 2011b).

In the Northeast Atlantic, stocks of fish and shellfish have been exploited for hundreds of years (Thurstan *et al.*, 2010; Cardinale *et al.*, 2015). A recent reconstruction of the historical dynamics of northern shrimp in ICES (International Council for the Exploration of the Sea) divisions 3.a and 4.a East (Skagerrak and Kattegat and northern North Sea in the Norwegian Deep) showed that sub-areas of the putative stock distribution have been sequentially depleted (ICES, 2022a), where the western component (Norwegian Deep) was depleted first, followed by a decline of the eastern component (Skagerak and Kattegat) (Figure 1). However, there are two additional shrimp fishing grounds in the North Sea, the Fladen Ground (division 4.a West; northern North Sea) and the Farn Deeps (division 4.b West, central North Sea). The Fladen Ground (currently considered inhabited by a separate stock and managed accordingly) was exploited from the beginning of the 1960 s to the beginning of the 2000 s, when the fisheries and the stock collapsed (Eigaard and Søvik, 2021; ICES, 2021). The Farn Deeps was also considered a separate stock; here, the fisheries ceased in the late 1990 s, with only 5 tonnes landed in 1998 (ICES, 2004). The spatial structuring of shrimp in the North Sea and Skagerrak area has been the subject of scientific discussion for many years (e.g. ICES, 2013). Knutsen *et al.* (2015), based on the lack of genetic divergence between shrimp in the Skagerrak and the Norwegian Deep, concluded that the present assessment and management regime of northern shrimp in this area, which defines the entire Skagerrak and Norwegian Deep as one single management unit, is appropriate. On the other hand, they suggested the existence of a separate genetic population in the Fladen Ground (Knutsen *et al.*, 2015). However, the spatial genetic structure in the sampled area was weak, and there were several non-significant pairwise estimates (F_{ST}) between samples from the Fladen Ground and the Norwegian Deep and Skagerrak.

The Farn Deeps shrimp stock, with annual landings varying between zero and 500 tonnes in 1977–1998 (mean 125 tonnes) (ICES, 2004), has never been assessed by ICES, or been regulated by total allowable quotas (TAC) (ICES, 2001a). For the Fladen Ground stock, a TAC has been in place since 1992 (ICES, 2001b), but ICES only started providing advice on fishing opportunities in 2006 (ICES, 2021). The Skagerrak, Kattegat and Norwegian Deep stock, shared between Norway, Sweden and Denmark, has been exploited since the end of the 19th century (ICES, 2022a). Between 1985 and 2009, total catches fluctuated between 10 500 and 16 000 tonnes, while catches have declined in the last decade due to lower recruitment and declines in the spawning stock biomass (ICES, 2022b). The shrimp in the Skagerrak, Kattegat and Norwegian Deep has been managed using TACs since 1992 (ICES, 2022b), and currently ICES provides one quota advice for the whole management unit, which is subsequently split between Skagerrak-Kattegat and the Norwegian Deep (Norwegian waters of the North Sea). Denmark and Sweden are allocated destined quotas by Norway in the Norwegian Deep, while the Norwegian shrimp fleet may fish its quotas interchangeably between the two areas.

Northern shrimp is a cold-water species living on soft mud or sand/silt on the continental shelves in the North Atlantic, usually at depths between 50 and 500 m (Shumway *et al.*, 1985). The North Sea constitutes the southernmost part of the species' distribution in the Northeast Atlantic, where it lives at temperatures from 6 to 9 °C (Schluter and Jerosch, 2009). Northern shrimp has a pelagic larval phase lasting for 2–3 months depending on the temperature (Shumway *et al.*, 1985), which enables drift over long distances (Pedersen *et al.*, 2003; Jorde *et al.*, 2015; Le Corre *et al.*, 2020). Oceanographic features, such as bathymetry, temperature, salinity, and habitat heterogeneity could all act as barriers to population connectivity in marine species, but there are no indications of such barriers between the Fladen Ground and the Norwegian Deep-Skagerrak-Kattegat areas. The strong, northward current out of the Skagerak [the Norwegian Coastal Current (NCC)] (Albretsen *et al.*, 2012; Sundby *et al.*, 2017) suggests that shrimp in Skagerrak and the Norwegian Deep may be connected by larval drift. Surface currents in the central parts of the North Sea are less strong and more wind driven (Winther and Johannessen, 2006), but connectivity through larval dispersal between the Fladen Ground and the Norwegian Deep cannot be ruled out.

In this paper, we first (i) reconstruct the historical dynamics of the northern shrimp fishery in the Fladen Ground in terms of landings from 1958, which is considered the start of the exploitation of this stock and (ii) estimated a standardized commercial index of abundance of northern shrimp in the Fladen Ground from 1989 and an additional survey biomass index and associated length compositions of the Fladen Ground stock. We then integrated collated data in the current assessment model of northern shrimp in divisions 3.a and 4.a East by assuming that the Fladen Ground is part of the northern shrimp metapopulation in the North Sea and Skagerrak area, whereby the Fladen Ground is treated as the third component of the northern shrimp stock complex. Our results provide evidence of sequential spatial depletion in the Northeast Atlantic and illustrate that by ignoring this spatial dimension and likely metapopulation dynamics in the shrimp stock complex in the North Sea and Skagerrak area may have had long term negative consequences for both the stock and the fisheries. The result of this study calls, once again, for the urgent and explicit integration of space into stock assessment and fisheries management.

Materials and methods

Reconstructing historical landings of northern shrimp in the fladen ground

Historical landings from the Fladen Ground were reconstructed by combining data obtained from the ICES historical database and those reported by ICES in the biennial assessment of the stock (ICES, 2021). This produced a continuous time series of landings from 1959 to 2020. Landings data were available by country (Denmark, United Kingdom, Sweden and Norway) from 1970. For the period 1959–1969, the aggregated data were split by country using the average proportion as estimated between 1970 and 1972, where Danish landings represented 92% of the total landings.

Index of northern shrimp biomass from the danish norway pout trawl fishery in the fladen ground

The fishery for Norway pout (*Trisopterus esmarkii*) in the North Sea is nearly exclusively performed by Danish and Norwegian vessels using small mesh demersal trawls, especially in the Fladen Ground and along the edge of the Norwegian Trench in the northeastern part of the North Sea. The main

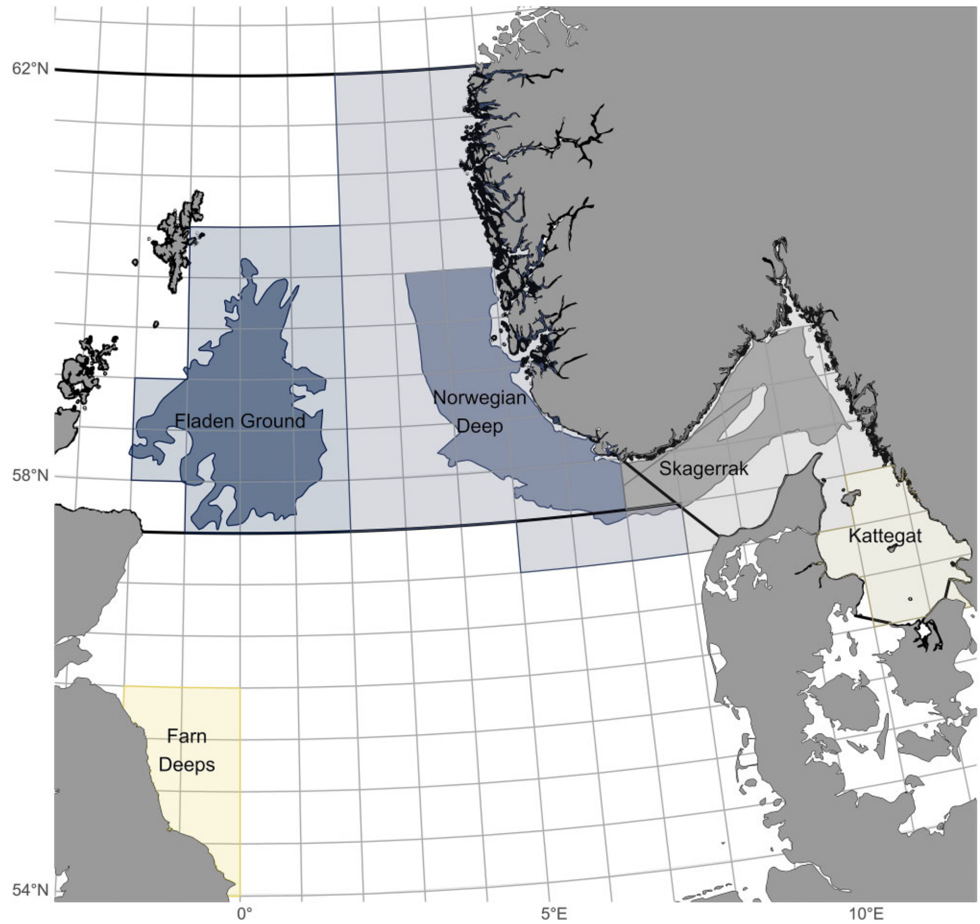

Figure 1. Spatial distribution of the northern shrimp stock complex in the North Sea and Skagerrak area as defined by ICES. The lighter shaded polygons show the extent of the stock distribution as defined by ICES statistical rectangles, darker shaded areas represent stock areas as delineated by bathymetry and bottom substrate; grey grid cells represent the rectangles in the ICES statistical grid. Skagerrak and Kattegat correspond to ICES division 3.a, Norwegian Deep to division 4.a East, Fladen Ground to division 4.a West, and Farn Deeps to division 4.b West.

fishing seasons are the 3rd (July–Sept) and 4th (Oct–Dec) quarters of the year, with high catches also in the 1st quarter (Jan–Mar), especially before 1999. The international Norway pout fishery was reviewed by Nielsen *et al.* (2016), including a detailed analysis of the Danish commercial fishery. A description of the Norwegian fishery segment can be found in Johnsen *et al.* (2016). These papers include analyses of quarterly and spatial distributions of the Norway pout fishery and catches, by-catches and discards, quota uptake and fishery regulations in the area. Recently, Paoletti *et al.* (2021) analysed the spatial and temporal dynamics of the Danish large vessel pelagic fleet, including the Norway pout fishery conducted by this fleet in 2015–2020.

Here, we developed a standardized catch per unit effort (CPUE) index for relative shrimp biomass based on data from a Danish harbour sampling scheme for the Norway pout fishery. The Danish Norway pout landings from the Fladen Ground have been sampled in harbours by the Danish Control Agency since 1989. The data cover the period from 1989 to 2021, except for 2005 and 2007 when there was no quota and therefore no fishery. The main purpose of the harbour sampling has been to estimate total species composition in weight. Catches of northern shrimp were only available aggregated by month and ICES rectangle. Therefore, a generalized linear mixed model (GLMM) was used to standardize the data to account for spatial variations of CPUE and within-year differences and extract the year-effect as an index for annual changes in relative biomass. Specifically, to estimate the expected CPUE, northern shrimp catches in tonnes were modelled with a Gamma distribution with a log-link function and effort (in kilowatt hours) was treated as a known offset, using year and month as categorical variables and ICES statistical rectangles as random intercept terms. Only catch and effort data from those four statistical rectangles (45F0, 46F0, 45E9, and 45F1) that were overlapping with the core northern shrimp distribution on the Fladen Ground (see below) were included in the standardisation.

Catch efficiency is positively related to increases in skipper skills, improvements in gear technology, investment in auxiliary equipment, replacement of old vessels by new ones and, to a lesser extent, to upgraded engines (Hilborn, 1985; Squires and Kirkley, 1999; Rijnsdorp *et al.*, 2006; Palomares and Pauly, 2019). Such factors are usually defined as "technological creep," which is expected to increase over time through continuous development and improvements in the fishing industry (Pascoe *et al.*, 2001; Marchal *et al.*, 2002; O'Neill *et al.*, 2003). This is particularly important in our case because of the limited resolution of the effort data. Thus, CPUE in the year y were corrected for technological creep as:

$$\mathrm{CPUE}_y = \mathrm{CPUE}_y \cdot (1.023)^{(1989-y)},$$

where the assumed value of a 2.3% annual increase in catching efficiency was taken from Palomares and Pauly (2019). It is also well aligned with the value estimated by Eigaard *et al.* (2014; 2.4%) and to an estimated annual 3% increase in effective harvesting capacity suggested by the European Commission (EC, 2008). In addition, we ran a sensitivity analysis on the effect of this technological creep on the model results, with three additional levels of creeping, i.e. no creeping (nominal CPUE), 3% (as suggested by EC (2008)) and 4% as upper limit suggested by Palomares and Pauly (2019).

Norwegian shrimp survey in the fladen ground

Covering the northern shrimp distribution in the Fladen Ground has been a secondary objective of a demersal trawl survey for northern shrimp conducted annually since 1984 by the Norwegian Institute of Marine Research (IMR) in Skagerrak and the Norwegian Deep. The survey has a fixed station design. Samples of up to 300 shrimp are taken from each trawl haul for sex determination and carapace length measurements (in mm). All age groups, except the 0-group, are well captured by the survey trawl (20 mm mesh size in codend). A detailed description can be found in Søvik and Thangstad (2021). However, because of limited time and difficult weather conditions, coverage of the Fladen Ground has not been achieved regularly. Despite this, there is an almost consistent time series from 1987 until 1994 (with 1990 and 1992 missing), the survey then returned to the Fladen Ground only in 2021. In total, there are observations from 67 stations in the Fladen Ground from 7 years in the period 1987–2021.

The survey data were used to delineate the northern shrimp distribution on the Fladen Ground and to select the relevant ICES rectangles for the commercial CPUE standardisation (see above). Stock indices based on the survey data as well as length compositions were used as input in the stock assessment model. Stock indices were estimated using the same approach as applied for the Norwegian Deep and Skagerrak area (ICES, 2022a), using GLMMs including Gaussian Markov random fields with total catch (biomass) and abundance per length group standardized to distance as response, assuming a Tweedie and a Poisson distribution, respectively. Both models included year as categorical effect and bottom depth as continuous fixed effect with a smooth spline. In contrast to the Norwegian Deep-Skagerrak area, spatial correlation was estimated as one spatial random field without any temporal correlation due to the disjointed time series and limited number of observations. The models were implemented using the R packages sdmTMB (Anderson *et al.*, 2022) and spatioTemporal (Breivik *et al.*, 2021).

Integration of the fladen ground component as a separate area in the northern shrimp assessment model

Assessment of northern shrimp in ICES divisions 3.a and 4.a East is conducted using the Stock Synthesis (SS) model (Methot and Wetzel, 2013; Methot *et al.*, 2021; ICES, 2022a). SS is programmed in the ADMB C++ software and searches for the set of parameter values that maximizes the goodness-of-fit, then calculates the variance of these parameters using inverse Hessian and MCMC methods. The assessment including the Fladen Ground stock component was conducted using the 3.30.20 version of the SS software under the Windows platform.

Assessment model configuration

The assessment model of northern shrimp in ICES divisions 3.a and 4.a East was developed by ICES in 2022 (ICES, 2022a) as a two area model with a population of 8+ age classes (with age 8 representing a plus group) fitted to length composition data (Table 1). Northern shrimp cannot be aged, therefore age is derived using a Von Bertalanffy growth curve through which observed lengths are translated into estimated ages internally in the model. The population is split into two sexes, with hermaphroditic individuals being born as males and changing to females later in life (protandrous hermaphroditism) (Berkeley, 1930). The model has a quarterly time step to account for differences in individual growth throughout the year. The original model developed by ICES in 2022 is hereafter defined as the "benchmark model." The two areas considered in the benchmark model were the Skagerrak-Kattegat area (hereafter defined also as area 1) and the Norwegian Deep (hereafter defined also as area 2) (Figure 1).

In this study, we added a third area, the Fladen Ground (area 3), so that the model developed here (hereafter defined as the "3-areas model") has three areas (Figure 1). As for the benchmark model, that is currently used for management advice, the 3-areas model developed in this study assumes no movement between areas after settlement of the pelagic larvae. The two models have the same inherent structure and parametrisation except for the addition of a thirds area (i.e. the Fladen Ground) in the 3-areas model as well as catch and survey data of that area.

The 3-areas model starts in 1970 (as does the benchmark model), although landings data from the Norwegian Deep and Skagerrak-Kattegat are available since 1908 (ICES, 2022a). The benchmark model starting in 1908 and the same model commencing in 1970 provided practically the same results in recent years, as shown by ICES (2022a).

The benchmark model considers six different fleets, one for each area and country (Norway, Sweden, and Denmark). In the 3-areas model, Fladen Ground landings were assumed to be derived by a single fleet as fleet specific data were not available for all years and because most of the landings in the Fladen Ground are taken by the Danish fleet (average 72% over 1970–2020; ICES, 2021). The stock index from the Norway pout fisheries carried out by the Danish fleet in the Fladen Ground since 1989 was used as a biomass index for the Fladen Ground stock. Length frequency distributions of Fladen Ground catches were not available except for 2021, and thus selectivity of the Fladen Ground fleet was assumed to be the same as for the Danish fleet targeting northern shrimp in the Norwegian Deep. In the absence of a time series of length composition data, we consider that the best option was to assume that selectivity of the Danish fleet in the Fladen Ground to be the same as the Danish fleet operating in the neighbouring area, the Norwegian Deep, for which data are available. Moreover, the selectivity of all fleets is very similar (ICES, 2022a), so we consider this assumption to be the most reasonable in this case. Finally, stock indices and length compositions for the Fladen Ground stock based on the Norwegian survey data were used as input in the 3-areas model.

As in the benchmark model, spawning stock biomass in the 3-areas model was estimated at the beginning of the year (1st January) and was considered proportional to fecundity. Recruitment was assumed to be a single event occurring at the beginning of the year. Recruitment was derived from a

Table 1. Northern shrimp in divisions 3.a and 4.a. Input data used in the "3-areas model" SS model.

Type	Name	Year range	Range
Catches	Total annual catches in tonnes by area and fleet	1970–2021	
Discards	Total annual discards in tonnes by area and fleet (except the Fladen Ground fleet)	Danish fleet 2013–2021 in areas 1 and 2	
		Norwegian fleet 2009–2021 in areas 1 and 2 Swedish fleet 2008–2021 in areas 1 and 2	
Length compositions	Commercial catch in numbers per length class, fleet and area; Survey catch in numbers per length class, sex and area	Danish fleet 2013–2021 in areas 1 and 2	0.2–3.5 cm
		Norwegian fleet 2006–2021 in areas 1 and 2 Swedish fleet 1990–2021 in areas 1 and 2 Norwegian survey: 1984–2021 in areas 1 and 2 Norwegian survey: 1987–1994 and 2021 in area 3	
Maturity ogives	Empirical female maturity at length estimated from survey data assumed to be constant for the entire time series and all areas		
Natural mortality	Natural mortality by age class assumed to be constant for the entire time series and all areas		0–8+
Stock indices	Biomass and length-based abundance indices from Norwegian survey for Norwegian Deep, Skagerrak-Kattegat and Fladen Ground;	Survey: Norwegian survey for Norwegian Deep and Skagerrak-Kattegat 1985–2021;	
	Standardized commercial CPUE index for the Fladen Ground	Norwegian survey for Fladen Ground 1987–1994 (except 1990, 1992), 2021 Standardized commercial CPUE index for the Fladen Ground 1989–2021	
SSB index	SSB proportional to fecundity		

Beverton-Holt (BH) stock recruitment relationship (SRR) and variation in recruitment was estimated as deviations from the SRR. Recruitments are defined as lognormal deviates around a log-bias adjusted spawner-recruitment curve. The magnitude of the log-bias adjustment is calculated from the level of which is the *SD* of the recruitment deviations (in log-space). Recruitment deviates were estimated for 1984–2020 as main recruitment deviations (37 annual deviations) and for 1978–1983 as early recruitment deviations (6 annual deviations). Recruitment deviates were assumed to have a *SD* (σR), which is estimated within the model. Main recruitment deviations have several options for how they are implemented in SS, including zero-centred deviations. Early recruitment deviations instead are not zero-centred. The intended usage of the early recruitment deviations is only to provide variance for the early population abundance. Therefore, early recruitment deviations typically are used for years before there is no data to inform the model about the specific year-to-year fluctuations in recruitment. This is the early part of the time series where the only data typically are landed catch. For further details see Methot *et al.*, 2021.

The allocation of recruitment to each area was estimated within the model for each year from 1984 to 2020, and it was thus time varying and based on the data. The model does not have an explicit time period to account for a larval phase, but the estimation of time-varying annual recruitment allocation implicitly accounts for the larval dispersal process. Additionally, high flexibility was allowed on the two estimated recruitment allocation parameters via high fixed sigma values for the deviation parameters. There was no movement after settlement included in the model. The steepness (h) for the SRR and the autocorrelation of recruitment are also estimated within the model.

As in the benchmark model, growth parameters were estimated internally by the 3-areas model and were assumed to be the same for both females and males, and for the three areas. Weight was estimated from a time-invariant and fixed length-weight relationship ($a = 0.0016$, $b = 2.7532$), while female length at maturity (Lm50%) was described by a sigmoidal function with Lm50% set at 1.974 cm for the entire time series and for all areas. Length-weight and length at maturity (for females) parameters were fixed and derived externally

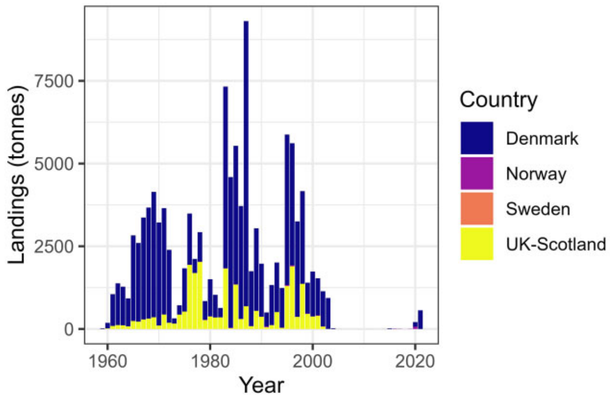

Figure 2. Reconstructed historical landings of northern shrimp in the Fladen Ground by country, 1959–2021. For the years 1959–1969, aggregated data were split by country using the average proportions from 1970–1972.

using survey data. Details on how weight and length at maturity were derived are described in the stock annex for the shrimp stock in divisions 3.a and 4.a East (ICES, 2022c).

Age dependent natural mortality (*M)* for the benchmark model was estimated based on life history traits and assumed to be time-invariant and the same for both sexes. The benchmark model that is used for providing annual advice is an ensemble of three models, which differ only in the assumed *M*. Here we used the so-called "reference model" as a basis for parameterizing the 3-areas model, which is the model that uses the median *M* (ICES, 2022a).

As for the benchmark model, fishery selectivity in the 3-areas model is assumed to be length-specific and time-invariant. For both the commercial fleets and the survey, a logistic selectivity function was used. The commercial fleets also have a retention selectivity for discards, which is assumed to be time varying from 2017. For further details on the assessment model and benchmark model results see ICES (2022a).

Results

Historical landings of northern shrimp in the fladen ground

Reconstructed historical landings of northern shrimp in the Fladen Ground by country are shown in Figure 2. Landings have fluctuated between zero and around 9000 tonnes, with a typical trend of rapidly increasing landings as the fishery developed in the 1960 s. Landings peaked in 1987, and in 1995, and drastically declined thereafter (Figure 2). Since 2004, the Fladen Ground shrimp fishery has been virtually non-existent. The Danish fleet accounted for the greatest share of the landings, while the Scottish fleet landed a smaller proportion. The Norwegian and Swedish fleets landed negligible amounts. The fishery took place mainly during the first half of the year, with the highest activity in the second quarter. Interview information from the fishing industry obtained in 2004 indicated that the decline in landings was caused by a combination of high fuel prices, low shrimp abundance, and low prices on the small shrimp typically found on Fladen Ground (ICES, 2023). Since 2012, there have been minor Danish and Norwegian landings of northern shrimp from the Fladen Ground, mainly taken as bycatch (landed for industrial purposes) in the Norway pout fisheries. Denmark landed 13 and 24 tonnes in a targeted shrimp fishery in 2015 and 2021, respectively.

Indices of northern shrimp biomass in the fladen ground

Bycatch of shrimp in the Danish Norway pout fishery indicates that the distribution of northern shrimp is concentrated in specific areas on Fladen Ground, notably ICES rectangles 45F0 and 46F0 (Figure 3). Shrimp catches contracted spatially over time despite a stable distribution of the Norway pout fishery. Shrimp catches moved from minor bycatch found throughout most of the Fladen Ground in the 1990 s to registrations only in a sandy mud area (Søvik and Thangstad, 2021) in southern Fladen Ground since 2000.

The GLMM used to standardize CPUE performed reasonably well (adjusted pseudo-R squared = 0.59 (compared to a null model with random effects only) and deviance explained = 53.8%, based on 470 observations with 425 residual degrees of freedom). However, there was a slight underestimation of observed northern shrimp catches that could not be resolved with available covariates (Figure S1). All year effects were found to be statistically significant ($p < 0.05$), as well as months, notably a significant decrease in northern shrimp catches was estimated during June and July. ICES rectangles modelled as random intercepts, on the other hand, did not explain any observed variation.

The effect of technological creep on the commercial index of biomass of northern shrimp in the Fladen Ground as derived from the Danish Norway pout fishery is shown in Figure S2. The commercial index of biomass of northern shrimp in the Fladen Ground showed highest values in the middle of the 1990 s and lowest in the last part of the time series, with an increase since around 2010 (Figures 4 and Figure S2). The general trend is rather similar between time series with different assumptions of technological creep and only exhibited large differences in 2013 and 2021 (Figure S2).

The index time series may potentially be biased by the introduction of a mandatory sorting grid in the Norway pout fishery in 2012 but given the small size of shrimp compared to Norway pout, it is unlikely that the grid has sorted out a significant amount of shrimp.

The substantial variation among the few observations per year in the Norwegian survey on the Fladen Ground were reflected by substantial uncertainty in the estimated stock indices (Figure 4, upper right panel). Because of the large uncertainty and the large gap in observations between 1994 and 2021, no clear trend could be determined. Despite the limited data, the models used to estimate the stock indices (biomass and length compositions) performed well and passed model diagnostics based on residual distributions.

Integration of the fladen component as a separate area in the northern shrimp assessment model

The 3-areas model converged (convergence < 0.0001) and the Hessian matrix was inverted, which provides uncertainty estimates of the model. The trend of the fraction unfished and fishing mortality (F) from the 3-areas model is similar to the original benchmark model (ICES, 2022a; Figure S3). The fit of the data of the Skagerrak-Kattegat and Norwegian Deep (i.e. length compositions, landings, discards and area specific survey indices) is practically indistinguishable from the benchmark model (ICES, 2022a; Figure 4 and Figures S4–S6).

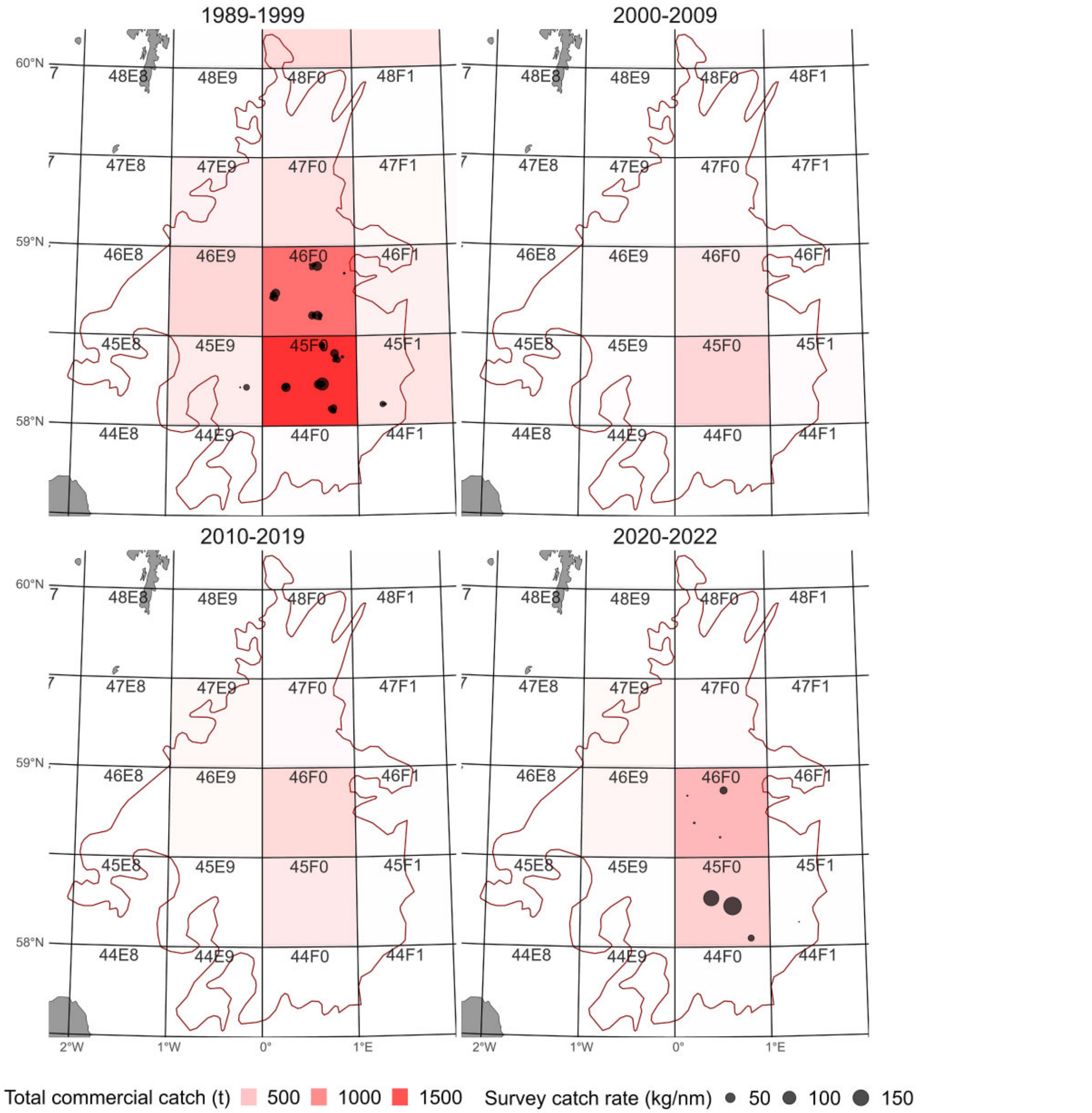

Figure 3. Total northern shrimp bycatch in the Danish Norway pout fishery by decade and statistical rectangle (red colour gradient) and observations during the Norwegian survey (black dots, scaled to catch rate). Bycatches were summed over period and statistical rectangle. Observations from the scientific survey are plotted at the start position of each demersal trawl haul. The extent of the Fladen Ground is indicated with a solid line, the ICES statistical grid with dark grey lines (the code for each rectangle is included), and land masses as grey polygons.

Estimated key parameters from the “3-areas model” are very similar to those of the original benchmark model (Table 2). Fitting of the Fladen Ground CPUE index from the 3-areas model is good (Figure 4, upper left panel).

The assumption of technological creep is found to have a limited effect on the estimates of both spawning stock biomass and fishing mortality for the Fladen Ground stock component (Figure S7) and thus only detailed results from the 3-areas model that assumes 2.3% of technological creeping annually are presented.

Fishing mortality by area shows sequential depletion of the different stock components. Fladen Ground was reduced to less than 20% of carrying capacity (i.e. B_0) in the end of the 1990 s, most likely caused by extremely high yearly landings, particularly in 1983, 1987, and 1995, when between 6000 and 9300 tonnes were landed only from the Fladen Ground. The high fishing pressure practically mined this subcomponent of the stock complex, resulting in very low biomasses in the early 2000 s (Figure 5 and Figure S8). The model estimates recruitment in the Fladen Ground to have been extremely low after the collapse (Figure 5 and Figure S8). Soon after the collapse of the Fladen Ground stock component, recruitment in the Norwegian Deep started to dwindle, with this component also falling below 20% of B_0 in the beginning of the 2010 s. The Skagerrak-Kattegat component also declined but remains the healthiest of the three, although recruitment has deteriorated also in this area in recent years, except for two good year classes (2013 and 2021). The 2021 value of the Fladen Ground CPUE index and the 2021 Norwegian survey biomass index together with increased catches suggest a recent increase in the biomass of the Fladen Ground component. However, the 3-areas model also estimates an increase in fishing

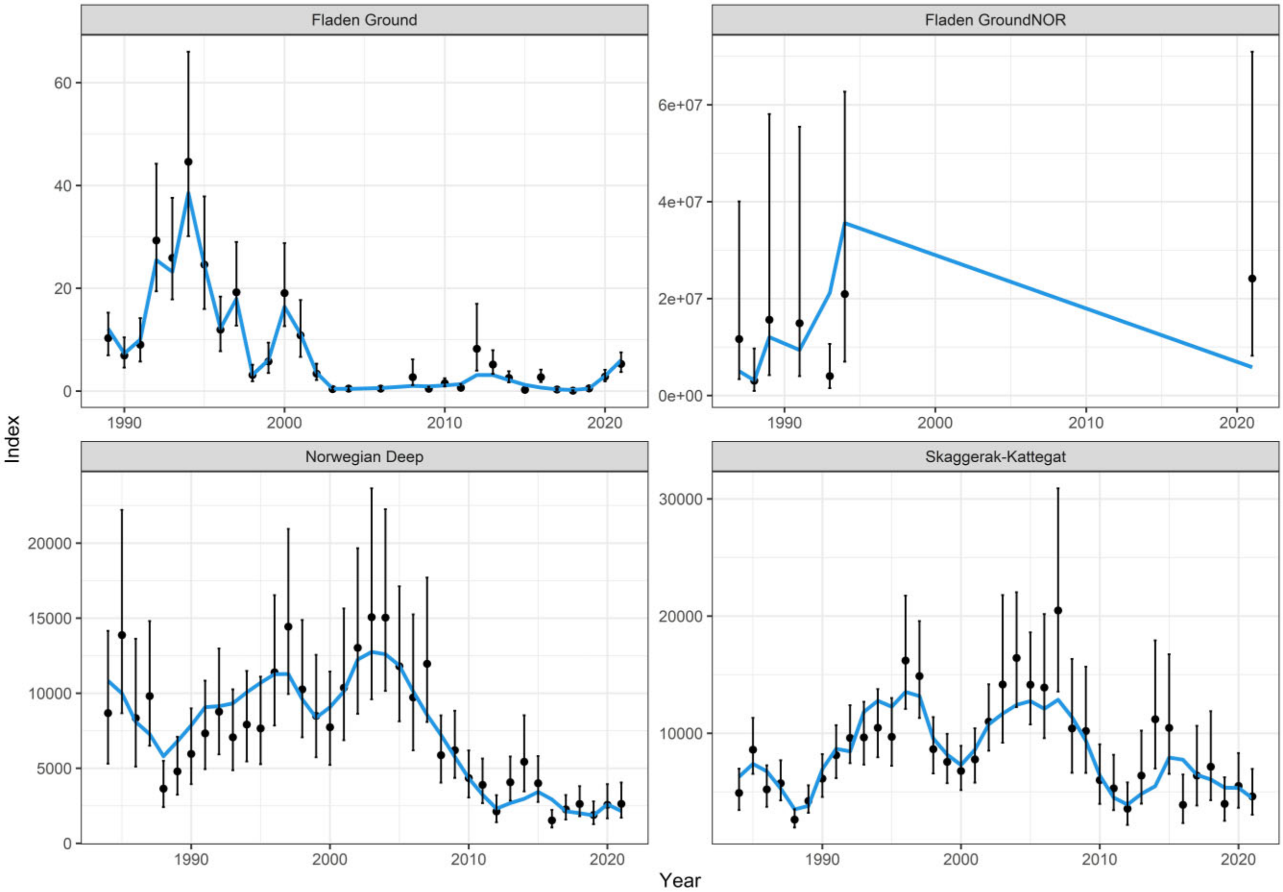

Figure 4. Model fit (blue line) of all indices (median and estimated standard error) used in the 3-areas model. Upper left: Standardized CPUE (kg/kwh) (Fladen Ground) of northern shrimp caught as bycatch in the Danish Norway pout fishery operating in the Fladen Ground, 1989–2021. The CPUE time series used in the assessment model assumes a technological creep of 2.3% annually. The standardized index is assumed to be estimated in October of each year of the time series. Upper right: standardized biomass index (Fladen GroundNOR) of the Norwegian survey carried out in the Fladen Ground. Lower left: standardized biomass index (Norwegian Deep) of the Norwegian survey carried out in the Norwegian Deep. Lower right: standardized biomass index (Skagerrak-Kattegat) of the Norwegian survey carried out in the Skagerrak-Kattegat.

Table 2. Comparison between the key model parameters estimated by the two-areas benchmark model and the 3-areas model including the Fladen Ground. L_{inf} and *k* are the estimated Von Bertalanffy growth parameters, R_0 is the recruitment (on the log scale) at B_0 (carrying capacity) and *h* is the steepness of the BH SRR, Std.dev is the estimated *SD*.

	Three-areas model		Benchmark model	
Variable	**Value**	**Std.dev**		**Std.dev**
Total likelihood	1559.4		1442.4	
L_{inf} *(cm)*	2.68	0.040	2.69	0.041
k	0.46	0.017	0.46	0.017
R_0	18.1	0.180	17.95	0.188
h	0.68	0.095	0.71	0.124

mortality in recent years (Figure 5 and Figure S8). It is important to note that the 2021 survey index value is not well fitted by the model, which is due to the large coefficient of variation and the limited number of hauls conducted in 2021 (Figure 4) as well as no adjacent (time series) survey estimates.

Discussion

Moving towards an ecosystem approach to fisheries management requires spatially explicit stock assessment and management. Yet in the Northeast Atlantic, fish and shellfish resources are typically assumed to be homogenous within their defined management units. With few exceptions, not accounting for possible differences in key biological characteristics and/or fishing patterns within the distribution area of a stock is common practice for assessing and managing fisheries resources in the ICES area. Here, we showed that the lack of an explicit and scientifically informed management before 1992 (ICES, 2001b), possibly in combination with a neglect of spatial stock dynamics, caused a fisheries collapse following the spatial depletion of the Fladen Ground stock component in the northern shrimp stock complex of the North Sea. We also showed that the spatial depletion phenomenon is occurring at present, despite the availability of a spatial stock assessment, as

Figure 5. Summary of stock trajectories of the three components of the northern shrimp stock complex in the North Sea and Skagerrak-Kattegat, 1970–2021. Shown is recruitment (in thousands of individuals of age 0 shrimp), spawning stock biomass (in tonnes), catches (in tonnes) and fishing mortality. Fishing mortality is expressed as the average F-at-age classes 1 to 3, which constitutes the bulk of the biomass.

illustrated by the depletion of one of the stock components in the northern shrimp stock in divisions 3.a and 4.a East. We therefore argue that the lack of the spatial dimension in assessment combined with a spatially relevant management system are the most important causes of the observed decline.

Sequential exploitation refers to the movement of harvesters to new grounds as the traditional ones become unprofitable (Grima and Berkes, 1989). To our knowledge this study is the first data driven example in the ICES area of this phenomena when harvesting marine resources, where harvesters sequentially exploit, deplete and finally abandon traditional fishing grounds (Cardinale *et al*., 2011b). In the Gulf of Alaska, the expansion of the area fished and the associated serial depletion as fisheries develop, coupled with the spatial structure of the stock was hypothesized to be the cause of the collapse of the Kodiak's red king crab stock in the 1960 to the 1980 s (Orens, anz *et al*., 1998). Serial depletion generates the conditions for local extinctions that compromize the productivity of fish stocks (Svedäng *et al*., 2010) and the structure of the ecosystem, and those are often the conditions that trigger the collapse of fish stocks. This calls for assessment and management which are inherently spatial, in order to minimize the risk of local extinctions (Cardinale *et al*., 2011a). Kapur *et al*. (2021) consider that it is often better to explicitly include spatial structure in assessments and Punt *et al*. (2019) found that accounting for spatial structure improves hindcast performance and short-term forecasting when there is post-recruitment dispersal among sub-stocks. Explicitly considering the spatial structure has the capability to provide a greater degree of biological realism in stock assessment models by (1) allowing for spatial variation in demographic parameters, (2) reducing the variance of fixed effect parameter estimates, and (3) more accurately reflecting the spatial dynamics of the fishing fleet(s), which likely differ from those of fish population dynamics (Punt *et al*., 2019).

The Fladen Ground was exploited and depleted between the beginning of the 1980 s and the beginning of the 2000 s. A TAC system was in place in 1992, but prior to 2006, the TAC was set by EC/EU without being based on an actual assessment and never restricted the fishery (ICES, 2001b). In the 1980 s, ICES noted that the fishing mortality on the adult females was very high, and that the fishery to a large extent depended on the recruiting year classes (ICES, 1987). Non-restrictive quotas and the lack of an assessment of this stock component, together with recruitment failure, probably caused the depletion of the Fladen Ground stock. Some years earlier, the Farn Deeps shrimp fisheries, and likely also the stock, collapsed (ICES, 2001a). However, our results show that, notwithstanding a stock assessment and management, spatial depletion is still occurring, and it is exacerbated nowadays for the remaining components of the stock complex, i.e. the Norwegian Deep and the Skagerrak-Kattegat. The decline of the Norwegian Deep component has previously been noticed by ICES (Søvik and Thangstad, 2021), but the full extent was not documented until 2022, when the first spatially explicit assessment model was developed by ICES (ICES, 2022a). Similar to the Fladen Ground component (Figure 3), the distribution of the Norwegian Deep stock component has shown a spatial contraction; since the beginning of the 2010 s, shrimp density as observed on the Norwegian survey has been very low in the northwestern part of the area (Søvik and Thangstad, 2021). A continuation of the serial depletion of the northern shrimp stock complex in the North Sea area has recently been demonstrated along the western Norwegian coast, where scientific surveys have shown that the species has declined or disappeared entirely in fjords (Zimmermann *et al.*, 2021).

One limitation of our study is that we assume global recruitment (i.e. steepness and thus density-dependence is the same for the three areas). Assuming global recruitment in the presence of source-sink dynamics or when biology (e.g. steepness, natural mortality and weight at age) might differ between areas can make stocks vulnerable to local depletion. In the shrimp stock complex in the North Sea and Skagerrak-Kattegat, there are indications of differences in biology between areas as Skagerrak might constitute a source area. Presently, recruitment is higher in Skagerrak compared with the Norwegian Deep but this was also the case in earlier decades when the Norwegian Deep stock component was the largest (Figure 5). The two areas seem to constitute a source-sink system where larvae and/or juveniles drift west into the Norwegian Deep, while larvae hatched here drift north and out of the area (discussed further below). Recruitment in Skagerrak has since 2008 been at a lower level compared with the 1990 s and the 2000 s (Figure 5), which probably partly explains the lower stock in this area, and to some extent the decline of the Norwegian Deep stock component. Furthermore, we cannot exclude that the Norwegian Deep also received larvae and juveniles from the Fladen Ground in earlier years. The rapid decline in recruitment in the Norwegian Deep following the collapse of the Fladen Ground, might indicate that, to some extent, also these two areas represent a source-sink system (Figure S8). This implies that, if the Fladen Ground was sourcing the Norwegian Deep, the collapse of the Fladen Ground triggered a domino effect on the other two components of the stock complex. Further data and drift studies would be needed to verify this hypothesis.

In addition to the factors discussed above, warmer conditions might have contributed to the sub-stock collapses and shift in the centre of biomass eastwards. Environmental conditions may have become unfavourable for larvae and/or adults in the shallower parts of the stock distribution in the North Sea. As such, the deeper parts of Skagerrak could constitute a climate change refugium for the species. Climatic changes and overfishing were hypothesized to be the two main causes for the collapse of many crustacean stocks in the Gulf of Alaska in the period 1960–1990 (Orensanz *et al.*, 1998). Shrimp larvae need to feed rapidly after hatching to avoid starvation (Wienberg, 1982). Any phenological shifts in the timing of hatching that are not matched by shifts in the timing of the spring phytoplankton bloom could have important consequences for the survival of new recruits (Koeller *et al.*, 2009). Warmer conditions might also shift the distribution of predators and pathogens, causing increases in natural mortality. In the Gulf of Maine, a temperature mediated expansion of the distribution of longfin squid was linked to the 2012 collapse of the northern shrimp stock (Richards and Hunter, 2021). Two pathogenic parasites, causing egg mortality (Chang *et al.*, 2020) and black spot gill syndrome (Lee *et al.*, 2019), are known to cause mortality in northern shrimp and infection rates have been shown to be higher under warmer conditions (Apollonio *et al.*, 1986).

The delimitation of fish stocks, i.e. management units, are often defined based on historical or practical considerations that do not adequately account for metapopulation dynamics such as migration or larval drift. Larval drift is a complex process driven by a combination of behaviour (e.g. spawning location and timing, and larval vertical movement), developmental biology (e.g. duration from spawning to larval settling) and oceanography. Large-scale gyres and currents play an important role for recruitment as drivers of ecosystem productivity and larval advection/retention (see e.g. Hátún *et al.*, 2016; Zimmermann *et al.*, 2019), but they can also transport eggs and larvae over large distances and connect seemingly independent areas and stocks. As a shelf sea, the circulation of water masses in the North Sea is dominated by the inflow of saline Atlantic water from the north, and European shelf water inflow through the English Channel in the south (Eisma *et al.*, 1987; Winther and Johannessen, 2006; Sündermann and Pohlmann, 2011; Sundby *et al.*, 2017). The Atlantic water masses split into two branches. The eastern branch flows along the western slope of the Norwegian Trench into Skagerrak. The western branch has its inflow in the shallower area above the shelf east of Shetland, and is partly creating an anticlockwise circular current around the Fladen Ground and partly reuniting with the eastern branch to enter the Norwegian Deep and Skagerrak areas (Sundby *et al.*, 2017). In the opposite direction to the saline Atlantic water, low-saline outflow from the Kattegat and the Jutland Current creates the NCC that follows the Norwegian coast in a western and northern direction (Albretsen *et al.*, 2012; Sundby *et al.*, 2017). The NCC is known as a key driver of connectivity and recruitment dynamics of many important fish stocks that spawn along the Norwegian coast, such as Northeast Arctic and coastal cod (*Gadus morhua*) stocks (Opdal *et al.*, 2011; Myksvoll et al., 2013; Ottersen *et al.*, 2014) and Norwegian spring-spawning herring (*Clupea harengus*) (Skagseth *et al.*, 2015; Zimmermann *et al.*, 2019). This applies also for northern shrimp where the NCC likely supplies larvae from Skagerrak to the Norwegian Deep, and further ensures gene flow along the whole Norwegian coast (Jorde *et al.*, 2015; Hansen *et al.*, 2021), although a large-scale surface gyre in Skagerrak (Gustafsson and Stigebrandt, 1996) may contribute to larval retention in this area. While a connection between northern shrimp on the Fladen Ground, the Norwegian Deep and Skagerrak has not been explored, it seems likely that larvae can drift from the Fladen Ground with the Atlantic water masses in the southeastern direction to the Norwegian Deep. The inflow from the north, its intra- and interannual variation linked to climate, and the resulting complex current dynamics have been established as important recruitment drivers for multiple fish stocks in the North Sea, such as cod (Knutsen *et al.*, 2004; Stenseth *et al.*, 2006: Huserbråten *et al.*, 2018), herring (Bartsch, 1993) and sandeel (*Ammodytes spp.*) (Berntsen *et al.*, 1994). Our results suggest a possible source-sink connection between the Fladen Ground and the Norwegian Deep that should be further investigated with larval drift and genetic studies.

Examples of spatial depletion in the ICES area are rare (but see North Sea cod, ICES, 2022d). However, we expect that spatial depletion of stock components in the Northeast Atlantic may be a common phenomenon and might be overlooked by stock assessments and management that are inherently non-spatial. Such issues are related to a lack of a spatial dimension combined with short time series of landings, notwithstanding a multi-centurial history of exploitation in the North Sea (Thurstan *et al.*, 2010; Cardinale *et al.*, 2015; Kleiven *et al.*, 2022; Melaa *et al.*, 2022), most likely have obscured past disappearances of stock components and produced cryptic collapses *sensu* Okamoto *et al.* (2020). Therefore, the results of this study once again call for the urgent integration of space into stock assessment and fisheries management.

There are recent signs of an increase in biomass of northern shrimp in the Fladen Ground both from the Norwegian survey and the CPUE index of the Danish Norway pout fisheries. However, the extent of this increase is uncertain as the number of hauls of the 2021 Norwegian survey was small and the increase in 2021 of the CPUE of the Danish Norway pout fisheries is relatively large only when no technological creep is assumed, which is unlikely to be the case (Eigaard *et al.*, 2014; Palomares and Pauly, 2019). This also coincides with a further increase in the percentage of northern shrimp bycatch in the Norway pout landings from the Fladen Ground (ICES, 2023) (data not included in this study). Nevertheless, assessment forecasts indicate that it could take more than 20 years to rebuild the Fladen Ground component. The most likely scenario is that one or several relatively large year class(es) in very recent years combined with limited fishing effort, has allowed the Fladen Ground component to recover. If this is the case, there is an urgent need to protect the Fladen Ground component through explicit spatial management.

Supplementary data

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

Conflict of interest

The authors have no conflicts of interest to declare.

Author contributions

MC conceiving the idea, MC, FZ and HW carried out the analyses. All authors discussed and interpreted the results. All authors drafted the manuscript and approved the final version prior submission.

Data availability statement

Data are available on request to the corresponding author.

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