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Spatio-temporal variability of *Nephrops norvegicus* density distribution on the Aran grounds and its implications for ecosystem-based fishery management

Hocine A. Benchikh[1], **Edward A. Codling**[2], **Colm Lordan**[3], **Emer Rogan**[1,*]

[1]School of Biological, Earth and Environmental Sciences, University College Cork, Distillery Fields, North Mall, Cork T23 N73K, Ireland
[2]School of Mathematics, Statistics and Actuarial Science, University of Essex, Colchester CO4 3SQ, United Kingdom
[3]Marine Institute, Fisheries Science Services (FEAS), Oranmore, Co. Galway, H91 R673, Ireland

*Corresponding author. School of Biological Earth and Environmental Sciences, Distillery Fields, North Mall, University College Cork,Cork T23 N73K, Ireland. E-mail: E.Rogan@ucc.ie

Abstract

Under the EU biodiversity strategy, changes in fishery management are expected to move fishing activity in Europe towards an ecosystem-based approach by 2030 and to achieve this goal it is essential to identify the spatial distribution of the most valuable commercial fisheries. Using geo-referenced census data of *Nephrops norvegicus* burrows from underwater TV surveys, the spatio-temporal distribution patterns on the Aran grounds (west of Ireland) from 2002 to 2018 was investigated in relation to habitat and fishing exploitation. A geostatistical approach revealed a patchy distribution, varying in size and intensity over the years. The mud content of the seabed was not influential in explaining spatial variability of burrow distribution. Spatio-temporal analysis showed an overall depletion of burrow abundance over the central area of the study contrasting with its margins and leading to an increase in vessel search activity towards the periphery. This study of the Aran ground stock revealed a decreasing trend in *N. norvegicus* density from 2002 to 2018, despite increasing landings. It also highlighted spatially variable adverse effects of fishing pressure across different areas. These findings may inform habitat conservation planning in line with EU regulations on fishing impacts.

Keywords: geostatistics; empirical orthogonal function analysis; maximum covariance analysis; underwater TV surveys; burrow density

Introduction

The EU Biodiversity Strategy for 2030 (COM 380 final 2020), aims to strengthen the protection of marine ecosystems and to restore them to achieve "good environmental status." Accordingly, marine resources must be harvested sustainably "by maintaining or reducing fishing mortality to or under maximum sustainable yield levels," "by eliminating the by-catch or reducing it to a level that allows species recovery" and "by promoting the conservation and restoration of natural habitats against the damaging effect of fishery activity on the seabed." This necessitates an interdisciplinary integrative approach, that accounts for different attributes including biological and physiological characteristics, species interactions (*e.g.* food chain), environmental and climatic variables (*e.g.* geology, wind, temperature, ocean circulation). However, these data generating processes "operate at different spatial and temporal scales which generate discontinuous distributions of features in the ecosystem" (Holling 1992), increasing (or complementing) the difficulty of integrating such disparate sources of information for use in this new approach to fisheries management. In fact, any differences between the areas that ecologists observe and the areas their observations are intended to represent have implications for ecological understanding, as the unobserved portions of space and time may contain important patterns and processes that are not captured (Estes et al. 2018). In this respect, mapping the evolving spatial pattern of *Nephrops norvegicus* abundance is an important first step for evaluating the relevant temporal and spatial distributional dimensions. Understanding how marine ecosystems respond to changing climate patterns (IPCC 2013, 2014, 2019) underscores the importance of examining ecological processes across multiple temporal and spatial scales. The heterogeneity of ecological data, combined with the mismatch between observational data and ecological processes, complicates such analyses (Dungan et al. 2002).

Although identifying population density at different locations and how these change over time at different spatial and temporal scales is challenging both for fisheries management and for maritime spatial planning (Buckland et al. 2000, Rapacciuolo and Blois 2019) it is of benefit. For instance, in Morfin *et al.* (2012) the spatio-temporal analysis of abundance and distribution of 12 key exploited species in Gulf of Lion (Northwestern Mediterranean Sea) from 1994 to 2010 enabled the detection of sub-areas where the species persisted the most and showed that these species never saturated their habitats, suggesting that they fluctuate below their carrying capacity, consistent with the overexploitation of several of these species. Based on the analysis of how species and fishery catches are distributed in space and time, spatio-temporal modelling of the seasonal dynamics of Pacific Dover sole (*Microstomus pacificus*) population of the US west coast, between 2004 and 2011, helped to differentiate potential causes such as fishing, movement and environmental covariates (Ono et al. 2016). For long-lived marine species such as cetaceans inhabiting dynamic nearshore and offshore areas, understanding the environmental factors associated with changes in spatial and temporal distribution patterns, abundance and habitat use (Barlow et al. 2024) is crucial for monitoring in a context of climate changes (IPCC 2013, IPCC SM 2019) and can inform management efforts to address threats from multiple human activities (e.g. bycatch, pollutant spills, ship strikes, Roberts et al. 2016).

N. norvegicus is one of Ireland's most valuable species, ranked third in terms of value of the exported fish species (approx. 28€43 M) equivalent to 3 700 tonnes (BIM 2020) and the Aran grounds is the second most important fishing mud patch in terms of size, supporting an important indigenous processing industry (Meredith 1999, Foley et al. 2016). Unfortunately, determination of population status by means of integrated age- or length-structured stock assessment models or trawl surveys is impractical for *N. norvegicus* in the Aran fields. This is due to difficulties in ageing the species (ICES 2006, 2009) and the high variability in the length-class structure, lacking multimodality, thus making it difficult to separate year classes (Haynes et al. 2016). In addition, commercial landings are marked by important diel (dawn and dusk) variations (Chapman, 1972; Aguzzi et al. 2003, Chiesa, 2010) and seasonal contrasts (Aguzzi et al. 2004, Aguzzi and Sardà 2008), where sex bias in catches markedly increase and peak in spring and (to a lesser extent) in autumn. This is associated with females leaving their burrows for hatching over several successive evenings, breaking off approximately 8 to 10 months of burrow living that commenced soon after egg laying (spawning) in autumn (Farmer 1975, Smith and Papadopoulo 2008, Powell and Eriksson 2013). Under controlled circumstances trawl surveys may provide useful indices of local abundance (Tuck et al. 1997a, Tuck et al. 1997b), but they are influenced by confounding factors in the case of *N. norvegicus* in the Aran fields, such as weather conditions, sea state, neap tides and its strong diurnal pattern, making this type of survey problematic since catch rates are not necessarily indicative of abundance (ICES 2009) and hence not deemed a satisfactory method for measuring stock trends (e.g. Bailey et al. 1993, Briggs 2000). In addition, in the Aran grounds, demographic information collected from trawl surveys exhibit a high degree of variability in biological parameters between sampled sites of the same stock unit (ICES 2016), also reported elsewhere (Tuck et al. 1994, Briggs 1995, Tully and Hillis 1995), making an optimal management strategy troublesome. In fact, the spatial component also appears to have an important role in the definition of the species population structure. Within the same stock unit, its distribution can be very heterogeneous and a stock may thus be divided into a (large) number of smaller "stocklets" with differences in population density (Maynou et al. 1998a, Maynou 1998b), morphometrical traits like size, growth rate, sex composition, female maturity (Farmer 1975, Bailey 1986, Tully and Hillis 1995, Eriksson 1999, Tuck et al. 2000, Ulmestrand and Eggert 2001, Tuck et al. 1997a, McQuaid et al. 2006; Haynes et al. 2016) and behaviour (Merder et al. 2020).

These difficulties in applying traditional stock assessment approaches to *N. norvegicus* stocks led to the rapid conversion to the underwater TV (UWTV) survey fishery-independent method for estimating burrow density and informing harvest strategies. On the assumption that one animal inhabits one burrow complex (Rice and Chapman 1971, Farmer 1975, ICES 2009), abundance is determined using video footage of the seabed collected at each station derived from a grid design and converted into burrow density per m^2.

To provide quantitative advice based on the UWTV surveys, a "harvest ratio" defined as the ratio of total removals to total abundance in number is used as part of the calculation. Thus, in compliance with the ICES requirement for an MSY approach, an MSY proxy harvest rate is defined. An option table is created based on a range of harvest ratios from 0 to those associated with candidate reference points $F_{0.1}$ and F_{max} that have been used as F_{MSY} proxy. These reference points are derived from two methods (separable cohort analysis and separable length cohort analysis) that depend on length, but with slightly different model structure. The first utilizes an underlying age-structured population model and the second uses a length-structured model. As both model outputs appear to be reasonable estimates and there is no *a priori* reason to believe that either model is more correct than the other, it was decided (ICES 2009) that for each candidate reference points, the mean harvest ratio between the two modelling approaches is taken for the point estimate of the MSY harvest rate (ICES 2016, Bell et al. 2018).

N. norvegicus is a benthic species with specific habitat requirements at different stages of its life-cycle; the seafloor is one of the determinant factors for recruitment (Farmer 1975, Campbell et al. 2009) and juvenile recruitment usually relies on the successful settlement of larvae on suitable habitat comprising silt, clay and eventually a proportion of sand (Chapman et al. 1971, Smith 1987, Powell and Eriksson 2013). Adults shelter inside burrows built beneath the seabed extending between 20–30 cm below the mud surface (Marrs et al. 1996). Adults probably only undertake very small-scale movements (a few 100 metres) although Merder et al. (2020) reported 21–500 m distance travelled by recaptured individuals. Thus, the catchability of *N. norvegicus* is strongly influenced by the behaviour of the animal on the seabed. In Aran grounds, adults are caught, primarily by otter trawls, when they emerge to forage (Aguzzi et al. 2003, Aguzzi et al. 2004, Aguzzi and Sardà 2008, Aguzzi et al. 2009). Its habitat is readily accessible to trawling and the fishing impact is obvious. High-density areas may be targeted very effectively by fishers and fishing location choice has a significant effect on catch (Gerritsen and Lordan 2011), as fishers routinely consider in their decision making their tacit knowledge of good fishing locations. Over the years, the proportion of vessels with higher powered engines and overall vessel length has increased and have become more efficient at catching *N. norvegicus* (Benchikh 2022).

In patchily structured populations, where density of animals is spatially differentiated, a sedentary species like *N. norvegicus* is easily targeted and susceptible to varying geographical levels of fishing pressure and, hence, if temporal changes in the population occurred locally, it is probably masked by these spatial variabilities (Briggs 1995, Tully and Hillis 1995). Thus, a spatio-temporal approach identifying such local impact can be crucial to adaptive fishery management (Rijnsdorp et al. 2011, Kraak et al. 2012, Dolder et al. 2018, Izquierdo et al. 2021, Kim et al. 2022) and to evaluate ecological impacts on habitat. Therefore, provided there is adequate data resolution (Mills et al. 2007, Hinz et al. 2012, Jennings and Lee 2012), analysing fluctuations of the *N. norvegicus* population distribution struc-

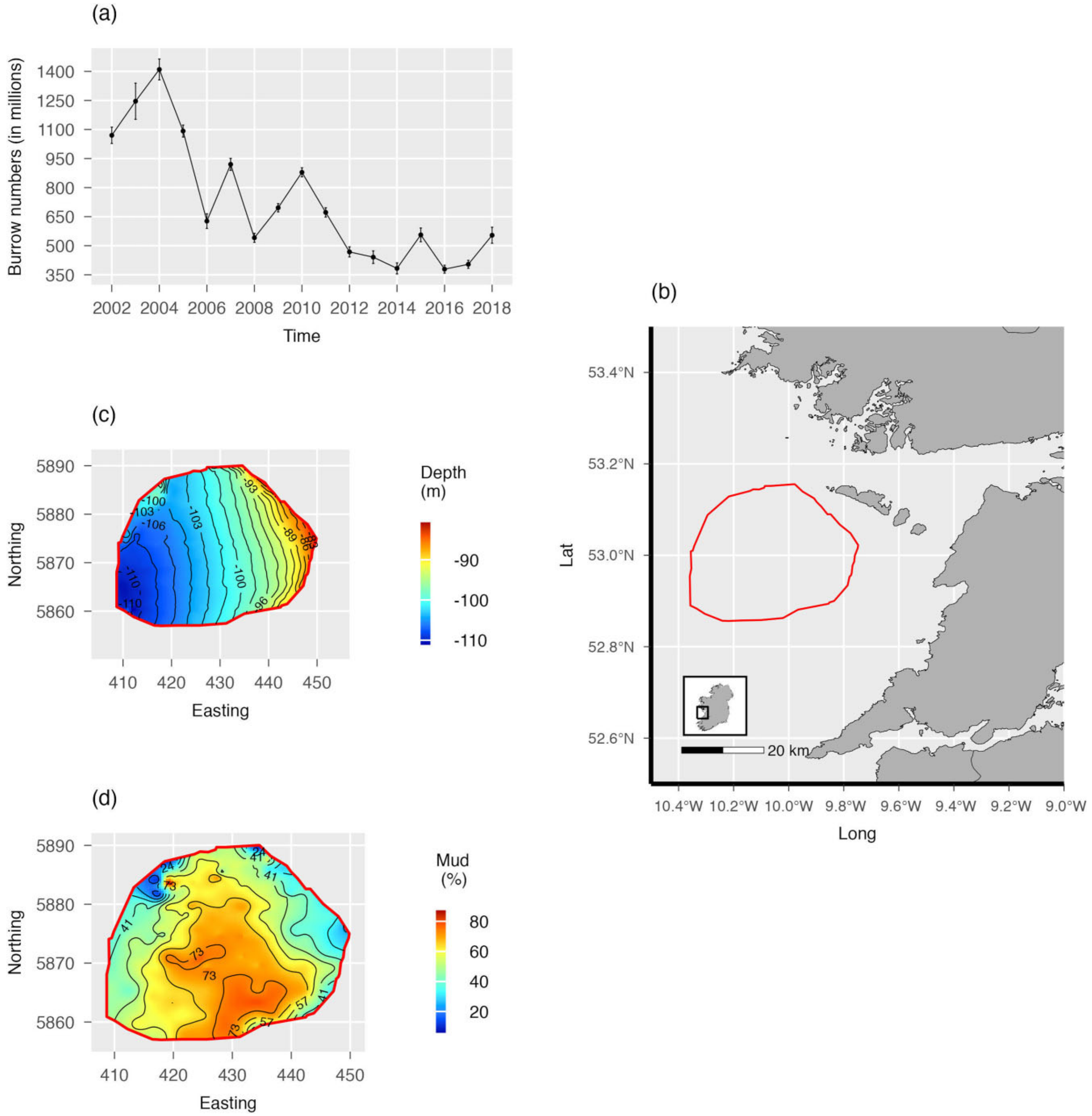

Figure 1. (**a**) Under water TV (UWTV) estimates of Aran grounds population abundance of *Nephrops norvegicus* from 2002 to 2018. (**b**) Aran grounds study area (red line). (**c**) Bathymetry over the area of study approximated with multilevel *B-splines* using R software (R Core 2020, version 3.6.3); (**d**) Cartography of mud seabed content over the area of the study generated by *B-splines* interpolation of year surveys 2002, 2003, 2004 and 2006. The mud fraction in the sediment is composed of silt and clay according to Folk classification. Easting/northing coordinates in UTM zone 29, WGS84.

tures in space and time, is a useful step toward a better understanding of the species-environment relationships, particularly in the context of a hot spot fishing ground like Aran grounds.

Given the species' sedentary nature and habitat specificity, understanding spatio-temporal variability in distribution is critical for effective management. This study investigates the influence of habitat characteristics—especially mud content—on burrow distribution, examines long-term trends in abundance, and evaluates the impact of fishing intensity over a 17-year period. The findings aim to support adaptive fisheries management and contribute to the EU Marine Strategy Framework Directive's objectives.

Materials and methods

Area of study: Aran grounds

Accounting for about 90% of the burrow abundance in this functional unit (FU17), *N. norvegicus* in Aran grounds occupy an extensive area of muddy sediment which lies to the west and southwest of the Aran Islands (Fig. 1b) where the eastern flank of the ground shallows up but the majority of the ground is gradually deepening to around 100–110 m with the deepest parts to the southwest (Fig. 1c). The seabed area features a relatively wide homogeneous central zone of sediment (Fig. 1d) with more than 60% mud content while areas with less than 40% are located mostly in the northern half of the study area (beyond 5875 Northing).

The prevailing local hydrological conditions are weak currents occurring throughout the water column and the presence of a seasonal bottom dominant fronts on its eastern flank (Nolan and Lyons 2006) established in May and remaining until Autumn causing a persistent jet like flow from south to north close to the seabed. The longitudinal position of this frontal gradient varies from year to year (20–48 km), being relatively close to the Irish coast to being far offshore (Nolan and Lyons 2006) and may influence the recruitment and settlement success of post-larval *Nephrops* since it could potentially advect larvae from the suitable seabed area (ICES 2007).

UWTV sampling and counts

The area of study has been regularly surveyed since 2002. The initial design was based on a grid of 3∗3 nautical miles (nm) with two random stations selected within each square. Since 2003, a randomized fixed grid design was used, where a point (or a station) is picked at random and the subsequent stations are sampled at a fixed distance of 2.5 nm north-south and east-west. From 2003 to 2010 the survey distance between stations was 2.25 nm and every 3.5 nm (or 6.5 km) since 2012 (Lordan et al. 2017, Doyle et al. 2020). The grid has been extended in an adaptive way until the boundaries (the perimeter of the ground) are established, i.e. until the burrow densities are at, or close to, zero. A sensitivity analysis for the years 2005, 2010 and 2011 (ICES SGNEPS 2012) showed that the overall abundance estimate remains reasonably precise and that the spatial variability in burrow density observed are comparable with spacing at 2.25 nm.

At each station, an underwater camera mounted on a sledge is deployed. Once stable on the seabed, a 10 minute tow records footage of an area of the seabed corresponding with a field of view of 75 cm (72 cm between 2002–2006) over which burrow complexes are identified, counted manually by trained counters, and finally converted into density per m^2 after selecting the appropriate distance over ground from various positional signals. Surveys generally take place in early June, however, in 2003, due to poor weather and technical problems the coverage was poor compared with the other years. In 2004, meteorological conditions delayed the completion of the survey, and consequently, approximately 50% of the remaining stations were carried out one month later, in July (ICES 2007). The TV samples are translated into abundance of burrows through geostatistical approximation with an assumed occupancy ratio of 1 animal per burrow and the method is counting animals of a size not available to the fishery, enabling settlement patterns and habitat use to be examined in detail, and further to delineate the spatial management units in line with the ecosystem approach to fisheries management.

Cartography of N. norvegicus distribution

Seventeen years of geo-localised burrow counting (2002–2018) were utilised to compute annual variograms and estimate the spatial variability of the burrow density values and variances using ordinary kriging (Krige 1951, Matheron 1963). Indicator kriging was used to determine if variable versus constant spatial structure(s) was present. It was obtained by transforming the response variable and converting burrow sample density to a binary term (presence/absence or 0/1). We selected the 20th percentile value from the samples as a threshold to binarize the density values, assigning 0 to those below and 1 to those above. For each year, the resulting variogram model was fitted leading to a presence/absence annual map with its associated probabilities (Pebesma 2004, Ribeiro and Diggle 2018).

Spatio-temporal approach of N. norvegicus density distribution

Spatio-temporal trend

To describe the changes in the spatial structure(s) of the burrow distribution over the 2002–2018 period and outline the main features, empirical orthogonal function (EOF) analysis was used. The EOF analysis aims at finding structures that explain the maximum amount of variance in a two-dimensional data. In our case, we are seeking to find characteristic spatial structures of density distribution that vary within time. Here, the first dimension is space and the second dimension is time, also called the sampling dimension. The analysis produces a set of structures in the first dimension (space), called EOF's which we can think of as being the structures in the spatial dimension. The complementary set of structures in the sampling dimension (here, time) are called the principal components (PC's). PC's relate one-to-one to the EOF's. PC's time series indicate how each EOF varies in amplitude with time. Each EOF conveys as much of the original information as possible without redundancy due to the orthogonal property ($EOF_1 \perp EOF_2 \perp EOF_3 \ldots$) In our case, the EOF analysis is performed over 17 years (time sampling dimension) of gridded density fields resulting from ordinary kriging estimates of burrow density (Pebesma 2004, Taylor et al. 2013, Gräler et al. 2016).

N. norvegicus settlement: influence of mud content

The putative relationship of the *N. norvegicus* stock to its direct habitat was investigated. The mud (silt + clay) proportion of the seabed sediment was selected to gauge the influence on animal density distribution. Particle size analysis of sediment samples collected in 2002 ($n = 60$), 2003 ($n = 29$), 2004 ($n = 30$) and 2006 ($n = 74$) during under water TV surveys was carried out using a Low Angle Lazer Light Scattering (LALLS) method using a Malvern Instrument (ICES 2007) and compiled for mapping. Mud (silt + clay) content of the seabed was then interpolated over the area of interest (Fig. 1d) with the *B-cubic splines* (Finley et al. 2017) using R computing language (R Core 2020, version 3.6.3). Within a linear regression framework, we tested different combinations of burrow density against mud proportion involving presence or absence of intercept, varying in time or not, plus the "mud proportion" variable with its slope varying in time or not. The relevant results retained are summarised by equations $M1: density_t = \beta_t * rateMud + residuals_t$ and $M2: (density)_{pooled} = \beta * rateMud + residuals$ for years $t = 2002, 2003, \ldots, 2018$ (Fig. A1). This analysis of the relationship between burrow density (*density*) and mud proportion (*rateMud*) led us to select the linear regression model ($M1: density_t = \beta_t * rateMud + residuals_t$) for the geostatistics universal kriging (Matheron 1969) of burrow density (Fig. A3). We also considered the Loess regression approach of the Easting direction (Fig. 3) and the generalized additive modelling (Wood 2004) of the mud-density relationship (Fig. 5) as reliable fits for visual inspection.

Detecting relationship between annual N. norvegicus abundance (cross variograms)

So far, we have estimated unknown values of burrow density using the modelling of a single variable (*e.g.* ordinary kriging estimates). However, a data set will often contain not only the primary variable of interest, but also one or more secondary variables. These secondary variables are usually spatially cross-correlated with the primary variable and thus contain useful information about the primary variable. In theory, the addition of the cross-correlated information contained in the secondary variable should help to reduce the variance of the estimation error. In this regard, cokriging as a method of estimation using the primary variable as well as the secondary variable by exploiting the cross-correlation between the pair of (primary and secondary) variables was used.

Under this framework, *N. norvegicus* density estimates, for instance, in year 2005 are no longer derived using only the available data of the current year, but incorporate the useful information brought by the cross variogram of the pair variables: that is to say, the primary variable (year 2005) and the secondary variable associated to year 2002 or 2003 or 2004.

To perform co-kriging, the spatial structure of the covariable (or secondary variable) and its covariance with the target (or primary) variable is modelled. Called coregionalisation, it consists in fitting the model (*i.e.* here our pooled variogram) to both the direct and cross-variograms simultaneously, and these models must lead to a positive definite cokriging system. Purposively, the annual burrow density over these 17 years have been pooled leading to the choice of the following exponential model of variogram:

$$\gamma_{fit}^{\mathrm{Exp}}(h) = \begin{bmatrix} c_o\ if\ |h| = 0 \\ c_0 + c_1\left(1 - \exp\left(-\frac{h}{a}\right)\right)\ if\ |h| > 0 \end{bmatrix}$$

with nugget effect $c_0 = 0$, partial sill $c_1 = 0.23$ and practical range $3a = 12.54\ km$.

Thus, for the co-kriging, the fitted direct (or auto) variograms are set to $\gamma_{fit}^{\mathrm{Exp}}(h)$ and the cross variograms $r_{ij} * \gamma_{fit}^{\mathrm{Exp}}(h)$ are "proportional" where r_{ij} is the point-wise correlation between years (i) and (j). For each observation point in year (i) the spatial nearest neighbour observation in year (j) is obtained, and a correlation r_{ij} is calculated. Notice that the variogram models fitted this way have the same shape (exponential model) and range whereas the nugget and partial sill parameters are adjusted with the correlation coefficient values r_{ij}. Finally, for the solution of the cokriging equations to exist and be unique, a linear model of co-regionalisation is found which requires a single range and structure (Isaaks and Srivastava 1989, Pebesma 2004, Pebesma and Duin 2005, Bivand et al. 2013, Rossister 2018).

Fishing pressure

The spatial distribution of *N. norvegicus* density was investigated by examining its relationship with the fishing effort using vessel monitoring system (VMS) covering the period 2005–2018. All European Community vessels > 10 m are required to record the retained catch weight by species, gear type and effort (in hours fished) in logbooks on a daily basis (Commission Regulation 1983), and from 2005, fishing vessel length > 15 m are required to transmit their positions at least every 2 hours, and since 2006, vessel speed and course information are also included. In the case of the Aran grounds, using the instantaneous speed, Gerritsen and Lordan (2011) determined the speed range that optimally identify the VMS records that correspond to fishing activity to link the VMS data to the catch data of the logbooks.

Thus, using the Maximum Covariance Analysis (MCA) approach we examine the covariance of the two data fields of interest, namely, the ordinary kriging map estimates of burrow density distribution and the aforementioned rasterised vessel monitoring system data. Since UWTV surveys are standardised to take place early in June, therefore, for instance, 2006 ordinary kriging estimates map is associated with the VMS data subset period from June 2005 to May 2006, noted 2005(6) and 2006(5) respectively, and so on for the following years.

Once the scaled covariance matrix between *N. norvegicus* burrow density and fishing pressure is built, a singular value decomposition (SVD) of it yields two matrices of singular vectors (often termed left and right matrices of singular vectors in the SVD analysis) and the associated singular value set (analogous to eigenvalue of EOF analysis). The left singular vectors are the column of the left matrix that represent the structures in the covariance field of density and are spatially orthogonal. Similarly, the right singular vectors express the structures in the covariance field of the fishing pressure. These left and right singular vectors are spatial patterns analogous to the EOFs, but one for each variable (density and fishing pressure).

Each pair of spatial patterns (left and right singular vectors) is called a mode and describes co-variability between structures in the data set that are best correlated with structures in the other data set. They are structures that explain the maximum amount of covariance between the two variables or fields. Each of these coupled spatial patterns (or modes) explain a fraction (%) of the square covariance (SCF) between the two fields of interest (*N. norvegicus* density vs fishing pressure). The largest fraction of SCF is brought by the first pair of patterns (mode 1) associated to the higher singular value, while the successive pair (mode 2) represents the maximum SCF that is unexplained by the previous one and associated to the 2nd lower singular value, etc. Moreover, for a parsimonious description of the essential co-variability between data fields, a few significant modes are selected by means of the singular value spectrum and the North *et al.* (1982) criteria.

The expansion coefficient time series (analogous of the PC's in the EOF analysis) describe how each mode of variability oscillates. The k-th expansion coefficients for each variable are computed by projecting the k-th singular vector onto the corresponding original data. In contrast to the PC's in the EOF analysis, the expansion coefficient time series in MCA are not mutually orthogonal. Instead, the correlation coefficient value between the k-th expansion coefficients time series of the two variable is a measure of the strength of the coupling spatial structures between the two fields (*Nephrops* burrow density and fishing pressure) within the k-th mode.

Now, two types of maps can be derived from the MCA outputs. On the one hand, the homogeneous correlation map corresponding to the k-th mode is obtained by projecting the k-th

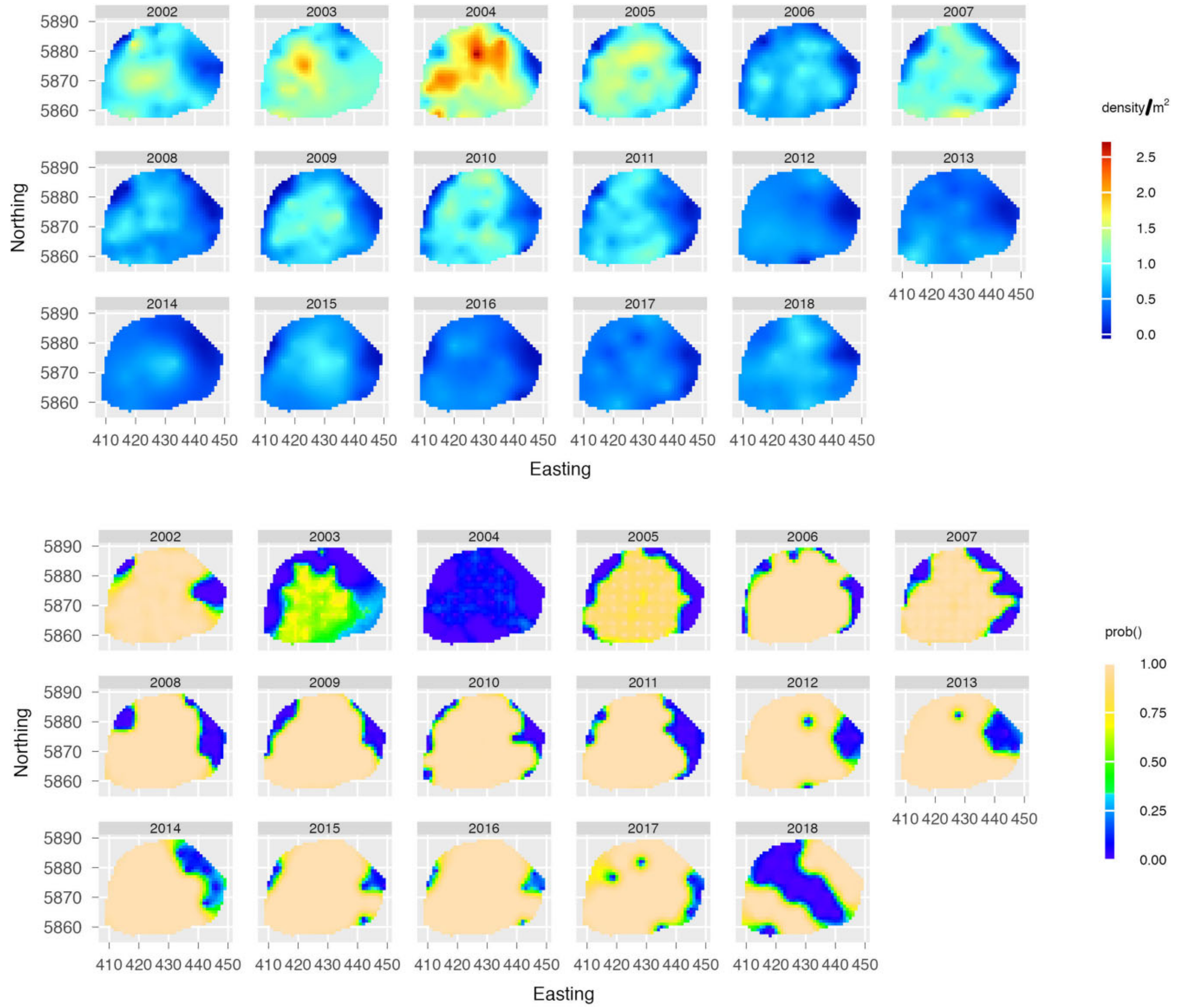

Figure 2. (**a**) Ordinary kriging estimates of *Nephrops norvegicus* burrow density distributions for 2002–2018. (**b**) Indicative kriging map estimates of probability distributions of burrow density > 20% first quantile threshold. Easting/northing coordinates in UTM zone 29, WGS84.

expansion coefficient time series of the left field with the input data for the left field (and vice versa). In this case, the map shows how the singular vector does in explaining the variance of their own data set and indicates the spatial localization of the co-varying parts. On the other hand, the heterogeneous correlation map of the k-th mode exhibits correlation values constructed by projecting the k-th expansion coefficients of the right (or left) field with the data grid point values of the other field (and vice versa). In this study, the contour lines of these correlation coefficient values are used to examine the influence of fishing pressure on the local variability of the density field (Björnsson and Venegas 1997, Hartmann 2003, Taylor et al. 2013).

Results

Edges versus midfield occupation

Spatial estimates of burrow distribution from ordinary kriging, based on variogram models fitted to annual samples of underwater TV surveys, display patchiness in the distribution of *N. norvegicus* density fluctuating in their form and intensity with lower density of population patches at some edges in contrast with a central zone recording higher density (Fig. 2a). Indicative kriging map estimates (Fig. 2b) of probability distribution of burrow densities > 20% first quantile threshold confirms this spatial regional organisation. In addition, scatterplots of the response variable against the spatial coordinates indicate a decrease in the density values in the eastern direction (Fig. 3) in line with the lowest proportion of mud localised at the eastern sides of the area (Fig. 1d). The high level of variance, observed in 2002, resulted in the stratified random survey design used at that time which arises with gaps in the spatial cover leading to an increase in the kriging predicted variances. In 2003 and 2004, relatively high variance values stemmed from the poor weather conditions faced during the surveys resulting in a decrease in the number of sampled sites (Fig. A2).

Spatio-temporal trend

Based on empirical orthogonal function analysis, 87% of all the variability in the burrow density distribution data from 2002 to 2018 is explained by two leading eigenvectors (or-

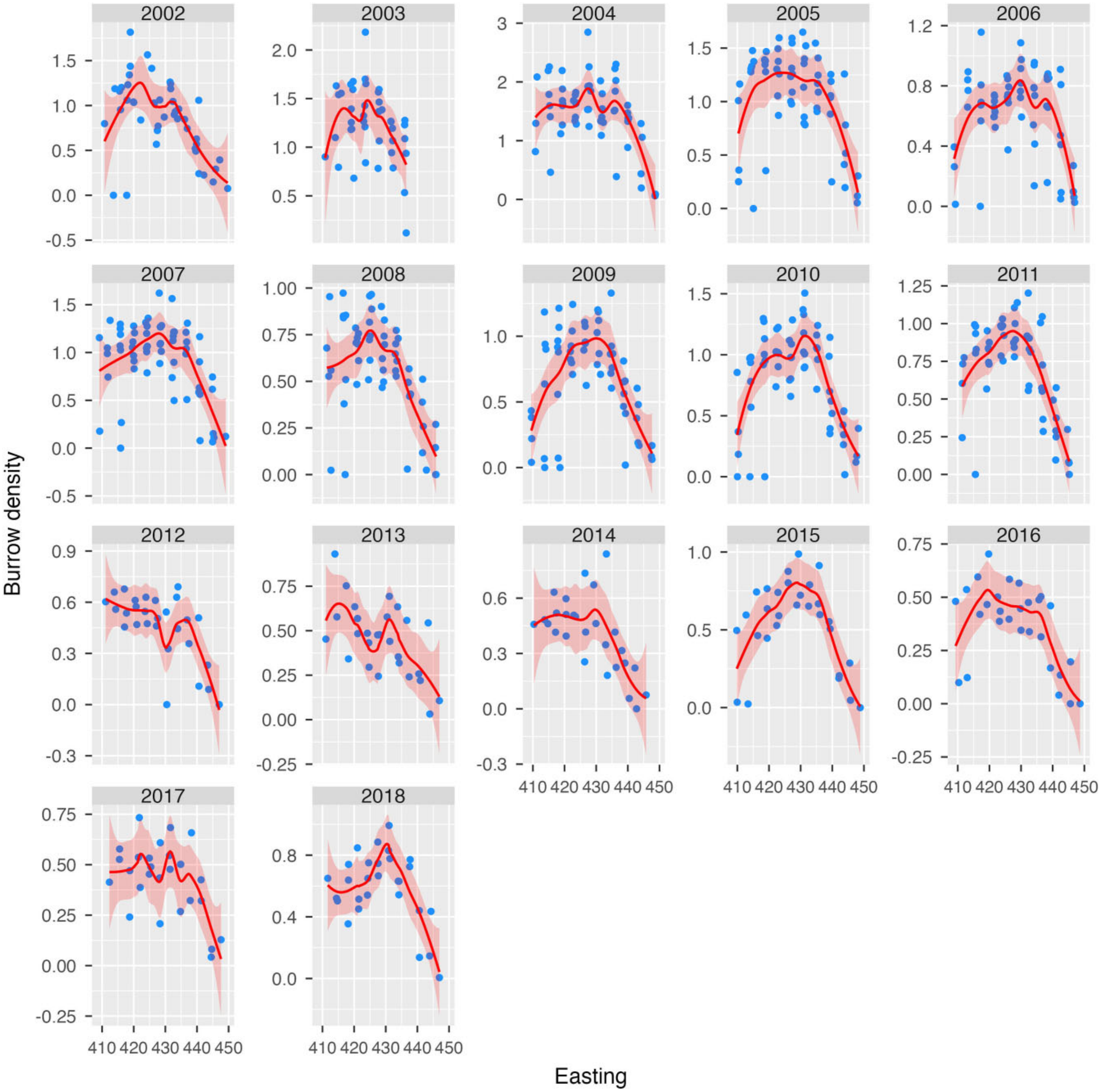

Figure 3. *Loess* regression of the burrow density level in relation to easting direction (with span = 0.5). Easting/northing coordinates in UTM zone 29, WGS84.

thogonal factors EOF_1 and EOF_2) accounting for 82% and 5%, respectively (Figs. 4a-b), assuming that the remaining EOF's contributions are negligible since all other eigenvalues are smaller than < 4%.

The EOF method takes all the variability in the time evolving field of burrow density and breaks it into a few standing patterns (EOFs) and a time series (PCs or loadings) to go with each EOFs which informs how the amplitude of each EOF varies with time.

The spatial pattern associated with EOF_1 (Fig. 4a) is the pattern on which the data projects most strongly (82%) and that explains the largest amount of variance in the data. It illustrates the general decreasing trend in *Nephrops* density over 17 years. The EOF_1 map (Fig. 4a) highlights a depletion of *Nephrops* density over the whole area of interest with a decreasing trend towards the periphery. The PC_1 time series (Fig. 4c) exhibits two dominant sets of relatively high values of loading coefficients, between 2002–2005 and 2012–2018, underlining the relative importance of the EOF_1 spatial structure. Meanwhile, the loading signs indicate the direction of the link with this general pattern. In between, an unsettled succession of coefficients goes from 2006 to 2011 that could illustrate a shifting period. In this respect, 2006–2011 estimates of UWTV survey abundance (in millions of burrows) is characterised by an intermediate averaged level of 722 million compared with the upper and lower averaged burrow number of 1204 and 455 million for the periods 2002–2005 and 2012–2018, respectively (Fig. 1a).

The EOF_2 expresses only 5% of the variance of the data (Fig. 4b) and since the EOF's eigenvectors are orthogonal to

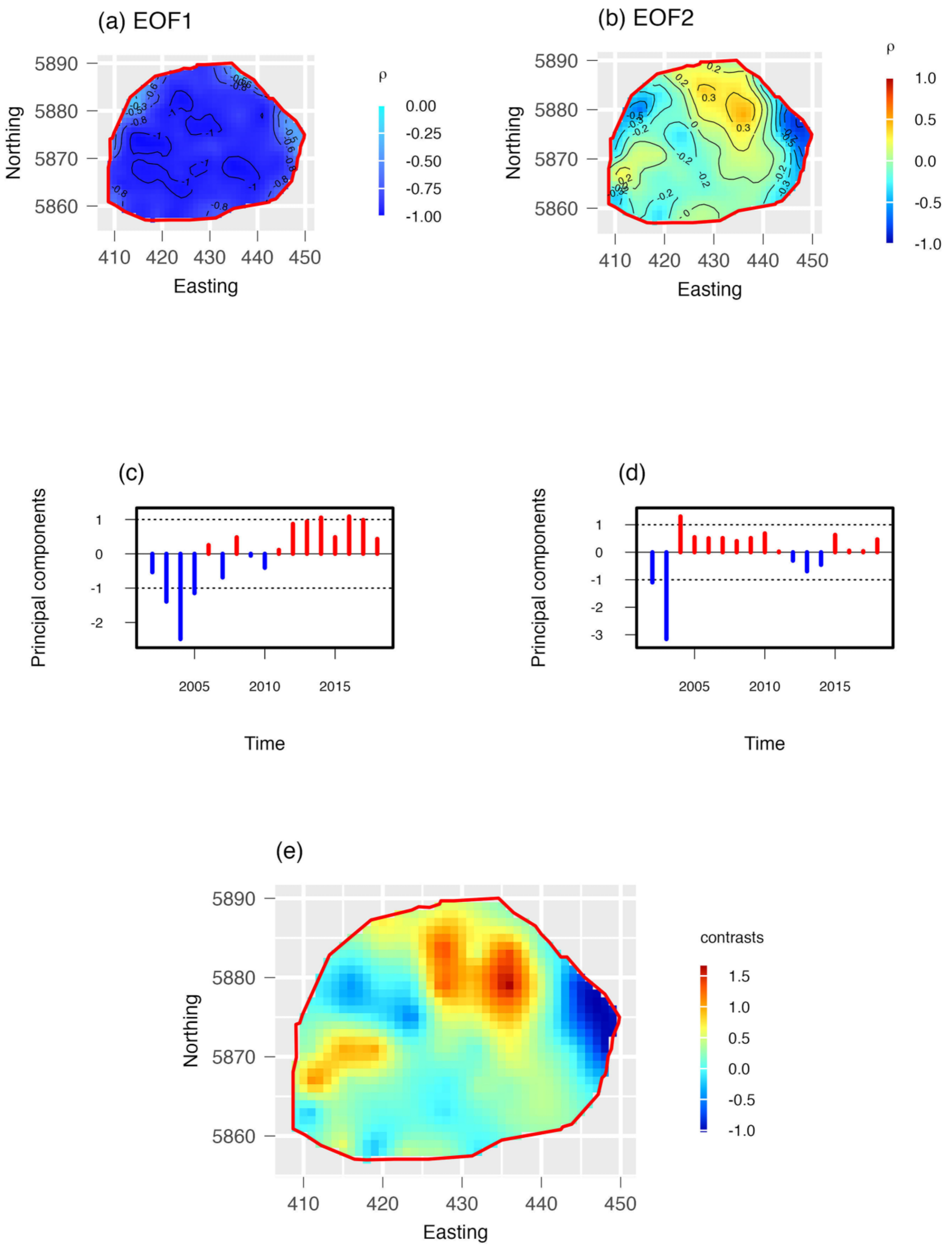

Figure 4. (**a-c**) Homogeneous correlation maps of the first (EOF_1) and second (EOF_2) empirical orthogonal factors derived from the empirical orthogonal function analysis of ordinary kriging map estimates of burrow density distribution for years 2002 to 2018. (**b–d**) Principal components time series of the first (EOF_1) and second (EOF_2) empirical orthogonal factors. EOF_1 and EOF_2 spatial patterns respectively account for 82% and 5% of the variance in the data cloud. Isoline values indicate how strongly related are the original data to the regional spatial structures (*Pearson* correlationρ). (**e**) Spatial structures resulting from the difference between ordinary kriging maps estimates of years 2003 and 2004. Easting/northing coordinates in UTM zone 29, WGS84.

each other, each conveys as much of the original information as possible without redundancy ensuring independence of the resulting associated maps. With respect to the PC_1 series (Fig. 4d), EOF_2 spatial structure mainly illustrates a strong antagonism or shift between 2003 and 2004. In fact, mapping the difference between the prediction maps of 2004 and 2003 (Fig. 4e) led to notable regional similarities with the EOF_2 spatial patterns (Fig. 4b). And hence, we consider that, very likely, EOF_2 map depicts a strong and short time departure from the general trend as represented by EOF_1 spatial structures.

The correlation values displayed in the homogeneous correlation maps (Fig. 4a-b) indicate how strongly the real data are associated to the spatial structures. Since the square of the correlation values represents the variance explained locally, the contours lines of the EOF_1 homogeneous correlation map account for up to 100% of the variability in the data in some areas, with lowest fractions of local variance situated at the north-west and north-east margins of the study area (Fig. 4a). The EOF2 homogeneous correlation map (Fig. 4b) displays a dipole pattern (that is, distribution of positive and negative values) with the largest local variance recorded in regions of negative values and accounting for up to 50% of the variance. EOF2 allows us to identify geographically the abrupt burrow density change occurring between years 2003 and 2004 (PC2 time series, Fig. 4d).

Seabed habitat: mud content

The density of burrows was seen to increase with the proportion of mud in the sediment (Fig. 5) up to a certain threshold. In fact, the flat segment of the Generalised Additive Model (GAM) curve suggests that beyond ∼ 55%–60% of mud content this positive relationship ceases. Visual examination reveals a minimum of about 20% mud is typical to maintain a burrow, with one outlier value of 7.55% from the 766 coordinates selected for this spatial analysis approach (Table 1). Thus, in the Aran grounds, burrow density records correspond to a minimum of 14.4% and a maximum of 82.8% of mud content of the seabed and it is difficult to infer an optimal percentage. The EOF analysis of the universal kriging map estimates of burrow abundance (that is to say, incorporating mud as covariate) shows striking resemblance of $EOF_{1\&2}$ regional spatial structures and $PC_{1\&2}$ time series patterns and did not improve the total variance explained (+5%, Fig. A3).

Inter-annual relationship of burrow abundance

An exponential variogram model was fitted to the pooled burrow densities (Fig. 6a). Within the cokriging framework, the inter-annual relationship between these 17 years of burrow densities are evaluated by the cross-variogram fits (Fig. 6c) relying on this exponential model of which the nugget and partial sill parameters are adjusted by the associated coefficient values$r_{ij}$of the matrix of correlation (Fig. 6b).

Despite the presence of pair of years exhibiting under- and over-estimates of the sill, as summarised for instance by the cases involving 2002 (Fig. 6c), the large number of coupled outputs indicate strong inter-annual relationship in density. In fact, not considering this relationship led to poor model performance (Fig. 6d) underlying the influence of the relationship of burrow abundance between years. The correlation coefficient values (r_{ij}) involving the year 2003 are among the lowest during the 17-year time period (Fig. 6b) likely related to poor weather and technical problems during the survey compared with the other years.

Sensitivity to fishing pressure

The influence of the fishing pressure on this *N. norvegicus* population distribution was investigated using maximum covariance analysis (MCA) of ordinary kriging estimates of burrow density and vessel monitoring system data (VMS). Notable changes in *N. norvegicus* distribution and fishing behaviour took place over the period 2006–2018. The first pair of patterns (*i.e.* mode 1) describes the largest fraction of the square covariance ($SCF_1 = 62\%$) and each succeeding pair pattern (*i.e.* mode 2 and mode 3) describes the maximum fraction of square covariance ($SCF_2 = 10\%$ and $SCF3 = 9\%$, respectively) that is unexplained by the previous pairs. However, singular values 2 (85) and 3 (78) are close enough to raise questions. There is no definite way to select the number of significant modes. Here was examined the singular value spectrum (of the SVD analysis of the data matrix) ordered from largest to smallest, augmented by a 95% significance error estimation of each singular value. Thus, according to the North *et al.* (1982) rule of thumb, only the mode 1 is significant since the first neighbouring singular values that are closer together than this standard error are singular value 2 and 3 (with overlapping lower and upper limits of 81 and 82, respectively).

Thus, singular values 2 and 3 are said to be "indistinguishable" within the statistical uncertainty, meaning that any linear combination of the two modes is just as significant as the modes individually, necessitating a cautious approach to interpreting their structures.

Nonetheless, mode 2 and mode 3 are also orthogonal in space and time as required by the MCA approach. Although retaining them may challenge our capacity to monitor spatio-temporal shifts in *N. norvegicus* population density, their inclusion is justified given the broader research objectives. Homogeneous correlation maps (Figs. 7a-d-g) allow us to evaluate the local correlation between the spatial density patterns displayed by each mode and the original data values at each grid point and shows that the leading MCA mode 1 spatial structures explained up to 81% (0.9 × 0.9) of the local variance. The heterogeneous correlation maps (Figs. 7b-e-h) emphasise the strength of the regional relationship between the density distribution and fishing intensity.

Thus, in the case of mode 1 (Fig. 7b) the correlation is strong and negative [-0.4—0.8] over almost the entire area and gradually decreasing towards the periphery. It illustrates the negative influence of the fishing pressure on the local variability of the *N. norvegicus* density, with up to more than 60% in the central area. The variability of *N. norvegicus* density data in relation to the fishing activity falls to 16% (0.4 × 0.4) at best, for a delimited zone located at the north-west and south-east margins. These areas are historically less prone to *Nephrops* harvesting (Fig. 8a-b). The mode 2 ($SCF_2 = 10\%$) heterogeneous map (Fig. 7e) discloses a regional distribution of positive and negative coefficient values delimiting the mid-field and peripheral areas with quite similar ranges of correlation values in either region (up to ± 0.4). The spatial patterns of the mode 3 ($SCF_3 = 9\%$) appear less obvious (Fig. 7h) with a fading aspect of the mode 2 spatial patterns whereas correlation values varying between (±0.1) are more widely distributed. Therefore, the structures exhibited here do not outline a notable and readable contribution of the fishing pressure to the

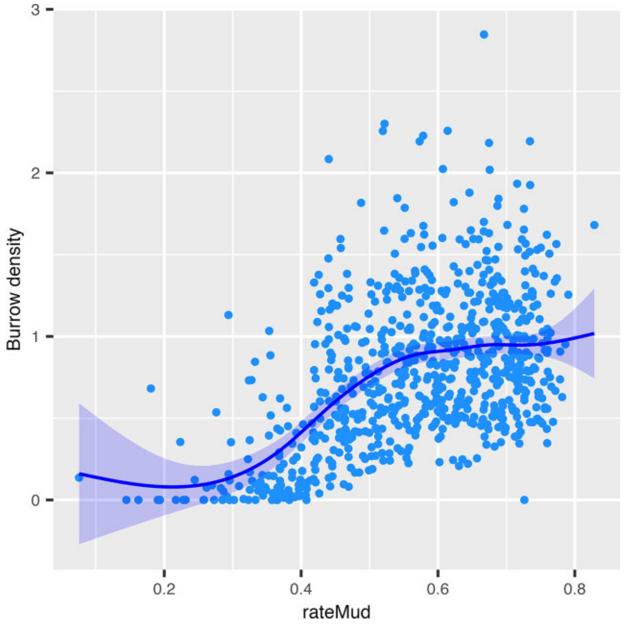

Figure 5. Generalized additive model fit of burrow density-mud covariate relationship from 2002 to 2018. Estimation using cubic regression spline function of the proportion of the mud content of the seabed (rateMud) and the generalized cross validation (GCV) smoothing parameter selection method (Wood 2004). The deviance explained is ∼28%, the intercept estimate is 0.77 with *P*-value < 2e-16, the effective degree of freedom of the smooth term is 5.11 with *P*-value < 2e-16. The basis dimension is k = 11, with k-index = 0.94 and *P*-value = 0.045.

local variability of the *N. norvegicus* density. Moreover, according to the homogeneous maps, the strength of the relationship between the original data values at each grid point and the spatial patterns picked up by MCA approach, drop to 16% and 4% for the mode 2 (Fig. 7d) and the mode 3 (Fig. 7g) compared to the standing 81% of the mode 1 (Fig. 7a). The explanatory potential of the spatial structures set out by modes 2 & 3 is weakened and, as already mentioned, undermined by the "statistical proximity" of the singular values 2 and 3.

Nonetheless, the MCA capability to link space and time information is conveyed by the expansion coefficient time series oscillations (Fig. 7c-f-i) associated with spatial patterns of the mode. Therefore, the expansion coefficients time series of mode 2 (Fig. 7f) consists of a mixture of 2–3 years fluctuations superimposed over a dominant rise and fall dynamic trend accounting for more than half of the time period (2009–2015). The expansion coefficients time series of mode 3 (Fig. 7i) shows no obvious differences in the general pattern depicted by the mode 2 (Fig. 7f). In both cases, the (density and fishing) pair fields are tightly fluctuating despite differences in the successive series of peaks and troughs (e.g. 2010, 2011, 2012, 2014) and a noticeable phase opposition between density field and fishing pressure in year 2018 for mode 3 (Fig. 7i). These discrepancies could likely be associated with differences in both signs (±) and spatial location of the correlation values observed at the periphery area of the heterogeneous correlation maps between mode 2 and 3 (Figs. 7e-h).

Thus, with the MCA summary map (Fig. 7b) of the significant regional co-variability between *Nephrops* density and VMS data from 2005 to 2018 and the information conveyed by the EOF$_1$ map (Fig. 4a) reflecting the spatio temporal decreasing trend of the stock abundance over the same area, we were able to delineate the area subject to the most adverse effects of fishing pressure on the stock, that is mainly occurring mid-field. In addition, visual inspection of rasterised VMS data maps from 2006 to 2018 (Figs. 8a-b-c) reveals an abandonment of the central zone in favour of the peripheral areas for vessels with > 15 hours fishing effort (Fig. 8b). This is associated with an abrupt decline in the mean area fished that took place in 2014, regardless of the effort range classes (Fig. 8c).

Discussion

Efforts to assess and mitigate environmental impacts, such as from fishing, require a good understanding of habitat use, distribution and abundance and species responses to changes. In addition, understanding how fishers react to changes in relative abundance and species re-distribution is an important management consideration. Here, we specifically focused on examining the spatial and temporal trends in an economically important fishery for *N. norvegicus* in the northeast Atlantic. These data highlight spatial and temporal changes in burrow abundance over a 17-year period, revealing a downward trend in density. Examining the relationship in density level between years with the cokriging approach pinpointed the influence of past abundance on the current one. In addition, co-variation analysis between *N. norvegicus* population density and vessel monitoring system data using an MCA approach shows the impact of fishing intensity and the resulting spatial changes in the fishing behaviours.

Spatio-temporal trend

The influence of the mud proportion of the seabed in shaping *N. norvegicus* burrow spread on the Aran grounds was found to be limited. Indeed, despite being crucial for the recruitment of the species (Farmer 1975, Smith 1987, Campbell et al. 2009, Powell and Eriksson 2013), we see that burrow densities between years can vary from 1 to 10 for the same mud proportion (Fig. 5), limiting de facto the explanatory power of the mud covariate. However, the surface extent and forms of (ordinary) kriging predictions of burrow density have fluctuated over the study period with lower densities (< 20% of first quantile threshold) likely located at the edges of the Aran grounds study area corresponding to the lower mud proportion of the seabed and burrows are rarely recorded in substrates with less than 20% mud. This spatial structure of *N. norvegicus* species has also been described for Mediterranean areas (Fariña et al. 1994, Maynou et al. 1998a,

Table 1. Easting/northing coordinates of locations with less than 20% mud content in the seabed. Estimates obtained using the B-cubic splines interpolation (Finley et al. 2017) of sampling data (see Materials & Methods).

Coords	417E–5884N	419E–5887N	434E–5889N	415E–5884N	418E–5886N	418E–5886N
Mud %	19.0	18.0	7.5	16.2	14.4	19.3

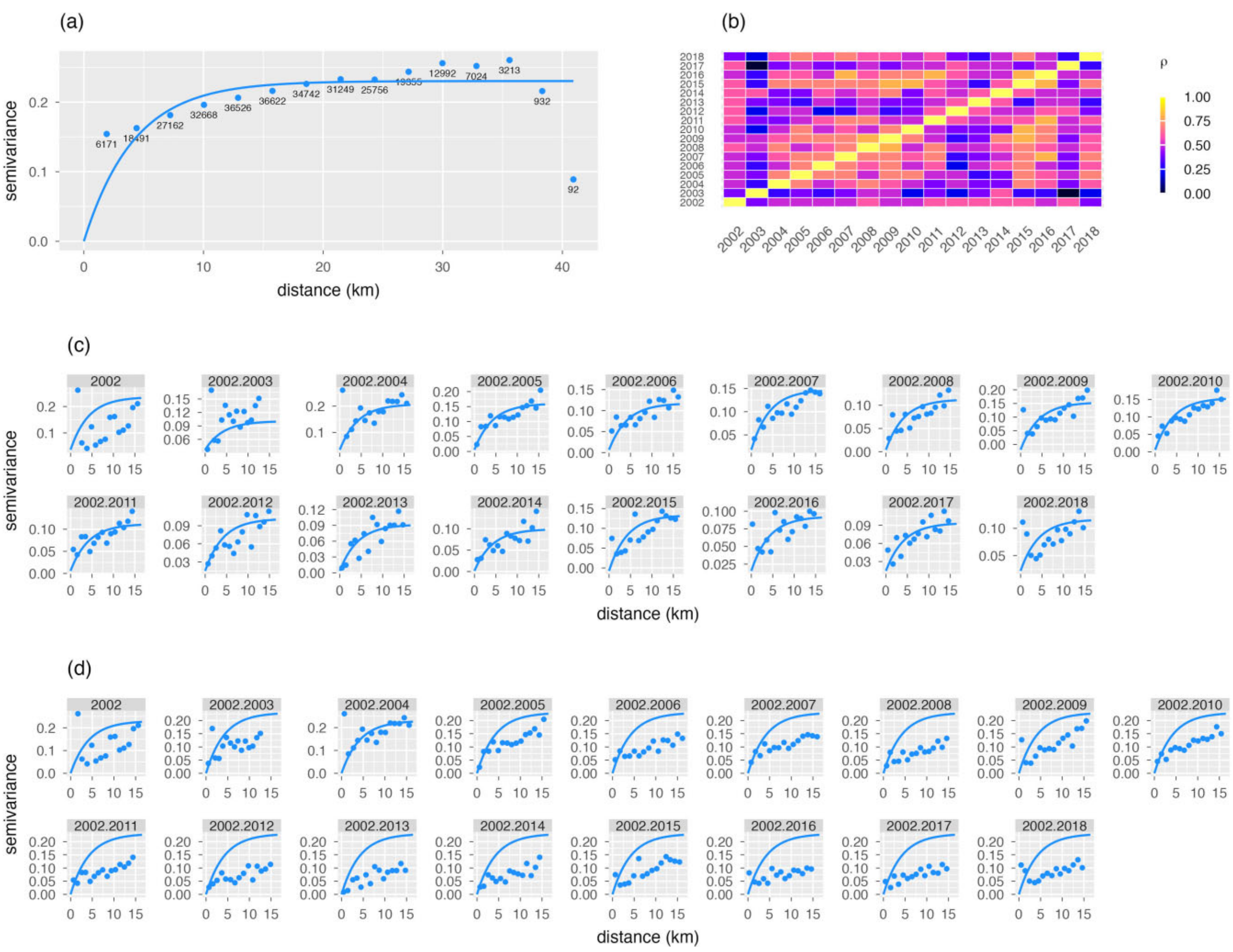

Figure 6. (**a**) Omnidirectional variogram fit using aggregated (pooled) burrow density data of 2002–2018 period. The point pairs data involved in sample variogram estimates are indicated and the fitted exponential model parameters are nugget $c_0 = 0$, partial sill $c_1 = 0.23$ and practical range (3a) $= 12.54$ *km*. (**b**) *Pearson* correlation (ρ) matrix entries ($\boldsymbol{r_{ij}}$) obtained by inverse distance weight using sample site values. (**c**) Linear model of coregionalisation fits ensuring a positive definite cokriging system. The fitted models for all direct variograms (*e.g.* 2002) were set to the pooled exponential model while the cross variogram model fits (*e.g.* 2002.2001, 2002.2003, etc…) are adjusted versions of it (that is, scaled in sill and nugget) using correlation coefficients $\boldsymbol{r_{ij}}$. (**d**) Direct and cross sample variogram fits using the non adjusted pooled exponential model for pairwise years involving 2002.

Maynou 1998b, Morfin et al. 2012). The ordinary kriging map estimates used here rely on spherical variogram models which appear to be the most satisfactory choices. The theoretical model has a linear behaviour at small separation distances near the origin and maintains a quasi-linear behaviour up to the sill (Isaaks and Srivastava 1989, Wackernagel 2003, Chiles and Delfiner 2012) in agreement with what was observed: an almost linear growth in burrow density up to a certain distance then a stabilization. Occasionally, the experimental variograms showed linear trends at particular directions and this appears after the range is passed indicating that within this range (radius) density distribution patterns are safely modelled (Clark 1979). In addition, within this geostatistical framework, major changes in density distribution patterns were found providing important information on the stock status. Empirical orthogonal function analysis revealed a decrease in the global abundance of burrows over the area of study for the period 2002–2018 and the relative amplitudes of changes are now spatially illustrated, highlighting an acute depletion in density in the central zone. In addition, the EOF$_2$ map showed the sensitivity of this approach to highlight a significant departure from the general decreasing trend, detected from the principal components time series (PC$_2$ time series) which corresponds to the highest increase in burrow records between 2002 and 2018. The variability of loading values over time (PCs times series) illustrates the natural stochastic variability component of the population dynamics.

Fishing pressure

Space and time changes in density distribution are also explained by the sensitivity of the stock to the fishing pressure. In fact, MCA unravelled the influence of fishing activity on burrow density and captured the salient components embedded in this strongly coupled relationship. Mapping of fishing effort distribution using VMS data highlights the movements between fishing areas to maintain a high catch rate (Hilborn 1985, Hilborn and Walters 1987), and the relatively homogeneous spread of (-) correlation values over the entire area (Bell et al. 2005) illustrates this effective targeting in the Aran grounds, one of the most important fishing patches in terms

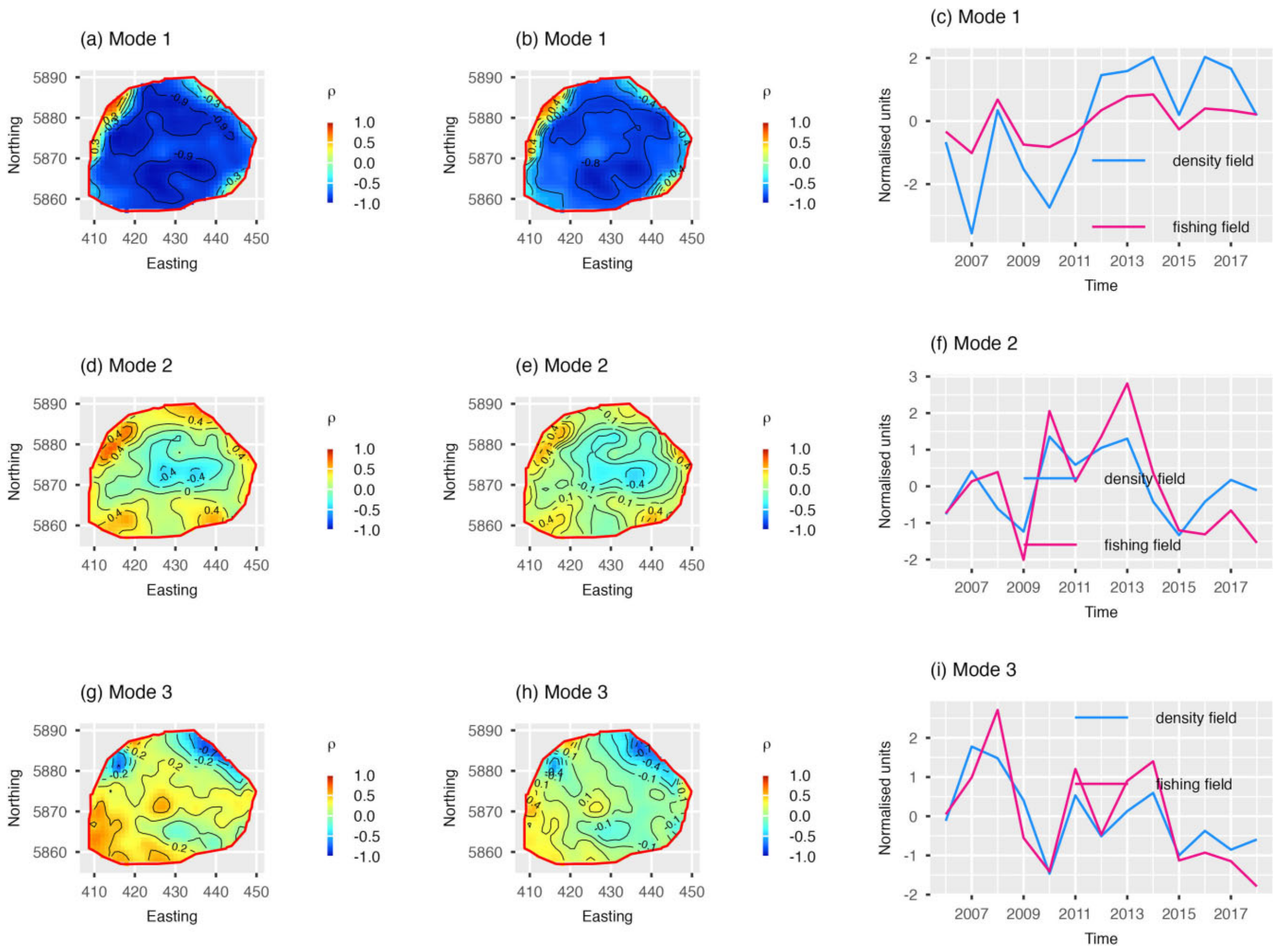

Figure 7. (**a-d-g**) Homogeneous correlation maps of the spatial burrow density patterns for the first 3 modes of the maximum covariance analysis (*MCA*). Each mode counting respectively for 63%, 12% and 9% of the *square covariance fraction* (*SFC*). Isoline values indicate how strongly related (*Pearson* correlationρ) are the original data to the regional spatial structures. (**b-e-h**) Heterogeneous correlation maps of the first 3 *MCA* modes showing locally (*Pearson*) correlation (ρ) between burrow density distribution and fishing pressure using VMS data proxy. (**c-f-i**) Expansion coefficient time series describing variability over time of the coupled fields (*i.e.* burrow density and fishing effort data) for each mode. VMS data cover the period 2005(6)–2018(5). Easting/northing coordinates are in UTM zone 29, WGS84.

of size and yield for the Republic of Ireland (Meredith 1999, Foley et al. 2016, BIM 2020). MCA mapping outputs provided a means to detect area differences over time and space of fishing behaviour and its impact. Historically, the higher fishing effort was in the central zone of Aran grounds and was likely related to the larger body size of *Nephrops* in this area, while the peripheral areas with lower density, linked with low mud content, are relatively neglected. The MCA coupling approach allowed us to differentiate spatially the relative strength of this link and, potentially, help in our understanding of the variability in *N. norvegicus* biological parameters observed between survey samples within the same stock (ICES 2016). In this regard, in Clew Bay, further north of the Aran grounds, Merder et al. (2020) observed a density-dependent suppression of growth (in body size) for males with a disproportionate effect on slower growing males; meanwhile, the spatial distributions of smoothed growth appeared to differ between sexes where male growth was higher in peripheral areas compared to the central area where catches were higher and females with higher growth tended to be in the central fished area. According to our MCA and EOF results, the midfield area is subject to the higher fishing pressure and a decreasing trend in the number of burrows. Nevertheless, despite, the precautions already mentioned concerning the consequences of adjacent singular values 2 & 3, preventing any reliable use of the strength (correlation values) and dynamic (signs ±) information provided by the associated coupled density-fishing fields, we can discern potential changes outside the central zone and towards the periphery (Fig. 7e and Fig. 7h).

In this respect, the rasterised VMS maps from 2006 to 2018 show that this area is no longer preferred. Very likely, this change in fishery strategy is attributable to a decline in *Nephrops* abundance and compelled fishers to alter their spatial fishing strategy (Fig. 8c) by considering other patches to balance the effect of the diminishing resource. However, it should also be noted that this new fishing strategy did not result in a lack of activity and as a result, the fishing pressure continued on the central sub-population.

Past influences

Under the cokriging framework, we highlighted the interannual correlations between variogram modelling (Fig. 6), which summarises “the spatial” behaviour of the burrow den-

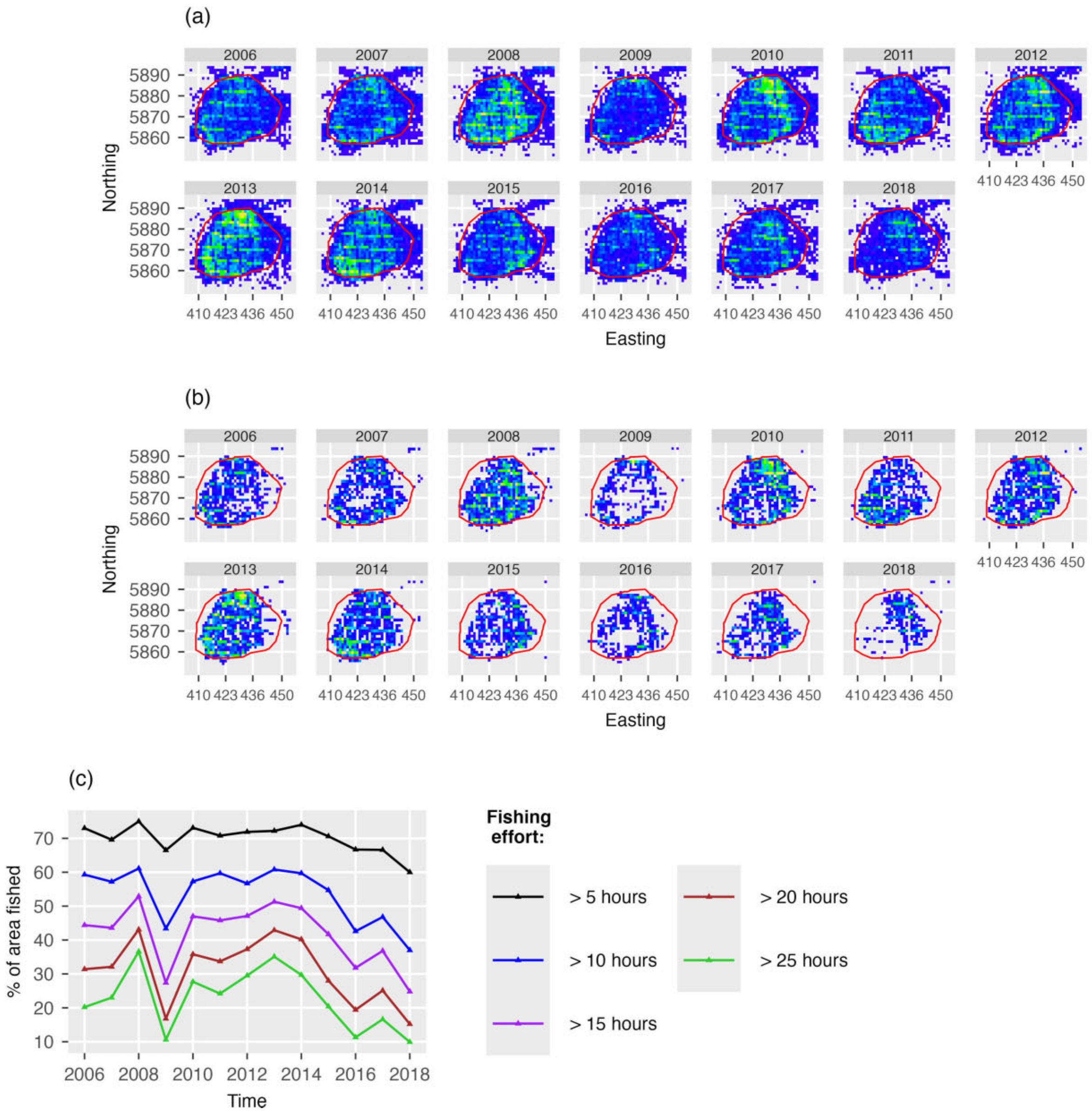

Figure 8. (**a**) Rasterised maps of fishing effort distribution from 2005(6)–2018(5) vessel monitoring data. (**b**) Rasterised maps of the fishing effort distribution higher than 15 hours in Aran grounds from 2005(6)–2018(5) vessel monitoring data. (**c**) Evolution of the relative percentage area covered by *Nephrops* fishing activity between 2005(6)–2018(5) in Aran grounds (computed from vessel monitoring system data). Easting/northing coordinates in UTM zone 29, WGS84.

sity distribution over the area of study, suggesting the influence of past abundance on the level of current burrow density. These spatio-temporal correlations for many years (Fig. 6c) are consistent with evaluations of *N. norvegicus* larval dispersal from 2002–2019 in the Aran grounds using biophysical larval transport models (O'Sullivan et al. 2015, McGeady et al. 2022) indicating that recruitment levels appear to be reliant on retention of native larvae because imports from other areas are low. That is to say, the quantity of larvae mostly originates from the Aran grounds spawning stock biomass, hence strengthening the potential relationship between burrow abundance over years. In addition, regional structures delimiting sub-areas with probability of density < 20% first quantile (Fig. 2b) are also subject to a certain annual variability attributable to recruitment success which also relies on the local hydrodynamic regime prevailing over the area (White et al. 1988, Hill 1990, Hill and White 1990, Nolan and Lyons 2006). In this regard, the year 2018 seems to illustrate this departure from the general spatial structures of the density distribution. Larval trajectory modelling (O'Sullivan et al. 2015, McGeady et al. 2019) provides a means to investigate and evaluate the annual fluctuations between potential recruitment and UWTV records ascribed to ocean circulation conditions. Although a linear model of co-regionalisation was found, ensuring a positive definite cokriging system (Fig. 6), this approach led to high predicting error variances (up to 30%, not shown in this paper) in comparison to the ordinary kriging predictions (Fig. 2a) based on annual sample variogram modelling, rendering it unsuitable for management purposes.

Limitations

The numerical outputs of EOF and MCA analysis do not indicate the underlying mechanisms that led to the spatial ($EOF_{1\&2}$ or mode 1) and associated temporal structures ($PC_{1\&2}$ or expansion coefficients) identified. Both methods provide measures of the variability in the data set and therefore their interpretation is a matter of interpretation. Also, once a pattern or a signal is identified it must be recognised/detected elsewhere in the data. For instance, the general trend of a decrease inburrow density in Aran grounds (EOF_1) is clearly in line with the dramatic decline of UWTV abundance records (Fig. 1a) while contrasting with the increasing landings during the same period (not shown here). Hence, it is wise to re-examine EOF and MCA signal(s) to ascertain whether EOFs produced in an analysis are a reflection of scientifically meaningful structures in the data. Are the spatial and temporal structures explainable in terms of our knowledge? What kind of relationship exists between the data sets under consideration using MCA analysis and does it make sense scientifically?

As mentioned previously, there are caveats regarding the space and time scales of the data ('Dungan et al. 2002; Estes et al. 2018). This is particularly important in the case of the MCA where two type of data sets of different structures are computationally forced by the scientist to share a common sampling dimension. In our case, the aggregated daily records of the VMS lends itself to this kind of manipulation but this will not always be the case. Similarly, in the EOF analysis we defined the structure dimension of Aran grounds as space, and, the year sampling dimension as time. Consequently, the structures obtained ($EOF_{1\&2}$, and $PC_{1\&2}$, or mode 1and expansion coefficients) will depend on the particular spatial and temporal slice of data that was used to compute them. Thus, caution should be used when trying to interpret these statistically derived measures and their significance (Dommenget, D. and Latif, M. 2001, Hartmann, D. L. 2003).

Perspectives

Under the EU fisheries management framework, the fundamental scale for implementing the total allowable catch or quota for any fish stock is the area of management divided into functional units. In the case of the Aran grounds, the results presented here confirm that the size of the functional unit is appropriate, since the fishery ground matches the corresponding mud patch habitat (Begg et al. 1999).

Such a clear geographical delimitation of the population coupled with the sedentary behaviour of the species, provides an initial framework for *N. norvegicus* stock management to comply explicitly with EU regulations on conservation status of a species and habitat. In other words, the "sum of the influences acting on the abundance and the long-term distribution of the species concerned" [and] "on the natural habitat and its typical species that may affect the long-term natural distribution, structure and functions as well as the long-term survival of its typical species" (Regulation EU 2019) must be acknowledged. Translating these requirements into quantitative and qualitative measures for resource management represents one of the most exciting and challenging tasks for marine ecologists. Implementing such a spatial management system requires key information on the species including habitat requirements. We see that translating the current management of the Aran grounds *N. norvegicus* fishery into a more spatially explicit management regime (*e.g.* Kraak et al. 2012) would require not only a real time track of each vessel (*i.e.* fishing effort) along with targeted catches (*e.g.* Dolder et al. 2018) at high resolution, but also, a better understanding of the *N. norvegicus* habitat requirements and the mechanisms involved in the density dependence effects. From this perspective, vessel monitoring system data implemented in Aran grounds since 2005 for vessels > 15 metres (Gerritsen and Lordan 2011) and more recently for vessels > 12 metres, provides an explicit spatial overview of this fishery activity. It also broadens the opportunity to implement indicator tools for integrated fishery management for instance by measuring the occurrence of suitable *N. norvegicus* habitat (Eastwood et al. 2007, Stelzenmüller et al. 2008), as well as, for example, the frequency of trawling, or trawled versus un-trawled areas, allowing the status of impacted seabed biota on fishing grounds to be measured (*e.g.* community biomass removal, time of recovery, Hiddink et al. 2017). Bottom trawling intensity has been reported to influence the diet of *N. norvegicus* shifting from benthic food towards a more planktonic based food target (Hinz et al. 2017). Thus, for Aran grounds, already available VMS data could be translated into a bottom trawling intensity index and such cartography examined in conjunction with *N. norvegicus* diet analysis from areas subject to different fishing intensity and evaluate its effect on landing traits (*e.g.* weight). The spatial approaches used here show that the UWTV survey method can be used to track changes in abundance and highlights the decrease in the stock despite the fisher's alternative fishing strategy. The spatial dimensions allow us to map yield onto the gridded habitat and provides a suitable framework to build a bridge between habitat requirements and the management of a stock.

Under the current "ecosystem approach" paradigm enshrined in the EU marine strategy framework (COM 380 final 2020) or, at global scale, in the United Nations plan for a decade of ocean science for sustainable development (UNESCO 2021), we are engaged to design a science that we need to monitor, protect, manage and restore ecosystems and their biodiversity under changing environmental, social and climate conditions. Such a pathway requires us to generate knowledge on the effects of multiple environmental stressors on ocean living resources with particular attention towards key species that sustain global populations. In this respect we have seen that spatiotemporal approaches provided a suitable framework. Ono *et al.* (2016) identified depth, latitude, and the presence of rock outcrops as factors potentially influencing the spatial dynamic of Dover sole (*Microstomus pacificus*) along the US coast in relation to the seasonal coastal upwelling that brings nutrient-rich water from the deep to the shallow waters off the west coast of the USA, increasing its primary productivity and creating favourable conditions for juvenile Dover sole. While assessing drivers of trait variation in space and time of North Sea fishes from 1983 to 2014, Beukhof *et al.* (2019) found that the majority of spatio-temporal changes were explained by variations in biotic (phytoplankton colour index) and abiotic (winter bottom temperature and salinity) environmental conditions, which were themselves influenced by large-scale ocean-atmospheric forcing in the late 1980s. In their analysis of 30 years of gray whale distribution along the nearshore Californian coast, Barlow *et al.* (2024) underscored the role of upwelling dynamics—particularly the pulse and relaxation phases—and the influence of habitat features like benthic substrate, shelf width and estuaries, which are used differently for foraging. These spatio-temporal examples not only highlight the value of integrating spatial and temporal dimensions to investigate interactions between species and the abiotic components of their environment but also provide scientific insights for diagnosing the impacts of global climate change and anthropogenic activities on ocean ecosystems—and ultimately, for informing adaptive strategies.

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Author contributions

Hocine A. Benchikh (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Writing - original draft [equal], Writing - review & editing [equal]), Edward A. Codling (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Writing - original draft [equal], Writing - review & editing [equal]), Colm Lordan (Conceptualization [equal], Funding acquisition [equal], Supervision [equal], Writing - original draft [equal], Writing - review & editing [equal]), and Emer Rogan (Conceptualization [equal], Funding acquisition [equal], Project administration [equal], Supervision [equal], Writing - original draft [equal], Writing - review & editing [equal]).

Supplementary data

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

Conflict of interest : The authors have no conflict of interest to declare.

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Data availability

The data underlying this article were provided by the Marine Institute under a data sharing agreement or through publicly available repositories such as Marine Institute (2025). The VMS linked logbook data is not publicly available but aggregate views used in the analysis will be shared on request to the corresponding author with permission of the Marine Institute.

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