Integrated modelling of Atlantic mackerel distribution patterns and movements: a template for dynamic impact assessments

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ABSTRACT

Modelling is important for impact assessments of anthropogenic pressures on wildlife. Models are particularly useful when dealing with complex dynamic systems (as pelagic ecosystems) where data are limited and if various ‘what if’ scenarios should be tested. The aim of this study was to produce and implement an integrated modelling approach, linking high resolution hydrodynamic models (HDM) of the marine environment with correlative species distribution models (SDM) and agent-based models (ABM), for describing the spatio-temporal distribution and movements of Atlantic mackerel (*Scomber scombrus*) in the Norwegian Sea. The SDM was fitted with scientific mackerel trawl data as response variables (collected in July and August 2006-2014) and temperature (from the HDM), water depth and time period as predictors of spatial distributions. The SDM was able to produce dynamic predictions of a similar order of magnitude as observed catch per unit effort (CPUE) as well as realistic large-scale distribution patterns, when tested on independent data (not included in the modelling). The ABM was calibrated, with normalized SDM predictions (habitat suitability as a proxy for food availability) and hydrodynamics as input and simulated on a single year (2013) for the period May-October, when the migratory mackerel is present in the study area. A pattern-oriented modelling (POM) approach was used to verify if the model reproduced multiple observed real-world patterns. The ABM produced similar patterns as observed regarding migration timing, growth and large scale geographic distribution. Fine scaled information on mackerel movement and behaviour is limited, which is also reflected in the results. More data and knowledge are therefore required to improve the patterns emerging from fine scaled processes. The potential of the model for assessing an impact of a single seismic survey (mimicking a real survey) was finally evaluated. The exercise allowed estimating the number of affected fish (within 50 km from the sound source) and potential changes in local migrations, with the specific assumed minimum sound pressure thresholds (resulting in a fleeing reaction by the mackerel) set to 165 dB re 1 µPa. The model framework was shown to be useful by allowing simulations of impact scenarios in a realistic and dynamic environment. The model can be further updated when data on fine scale movements of mackerel and most importantly when improved data on response behaviour to impacts of sound become available.

Key words: Agent based model, species distribution model, Atlantic mackerel, migration, movement, underwater sound

1. INTRODUCTION

To manage the consequences of anthropogenic disturbance on changes in animal behaviour and ultimately on population dynamics, it is often essential to analyse and predict distributions and movements (or dispersal) of animals. Predictive modelling is often the only available approach for quantifying complex large-scale distribution and movement patterns to inform environmental impact and risk assessments and other types of conservation decisions (Grimm and Railsback, 2012; Guisan et al., 2013). Marine animals, particularly at higher levels of the trophic hierarchy, such as pelagic fish, seabirds and marine mammals, are good examples of highly mobile animals living in a dynamic environment. Scarce and potentially biased biological data are typical for these animals, as it can be difficult to collect extensive data sets offshore on their movements and distributions. These animals are also increasingly encountering anthropogenic disturbances like offshore constructions, shipping, pile driving, seismic surveys, fishing and bycatch (Bolt et al., 2014). Many of the anthropogenic pressures are mobile, similar to the pelagic animals, and a dynamic modelling framework making most out of the available data and knowledge is therefore needed to be able to assess potential impacts. Integrating different modelling techniques can be a useful way of analysing complex questions, combining patterns with processes (see e.g. Baveco et al., 2017; Johnston et al., 2017).

Ecological models used for predictions are usually either statistical correlative models or to a lesser degree numerical processed based models (Palacio et al., 2013). Correlative species distribution models (SDMs, also called habitat models) are widely used for quantifying relationships between species and the environment (Elith and Leathwick, 2009). However, SDMs are generally not able to describe movement patterns and migration, as individual behaviour cannot be readily incorporated into a “traditional” SDM framework. Therefore, when movement factors are included in SDMs it is usually in a non-dynamic fashion describing a species’ ability to access a suitable habitat (Miller and Holloway, 2015). A benefit of SDM is that it is a data driven approach, that does not require previous knowledge about the underlying processes. Conversely, this also limits the model to only describe relationships from the available data (Palacio et al., 2013).

Processed based modelling, as agent-based models (ABMs, also called individual based models, IBMs), on the other hand, requires good knowledge of the underlying processes as emergent behaviours of agents or individuals are modelled and simulated, based on describing essential processes by equations (Grimm, 1999; Grimm and Railsback, 2005). One essential difference to SDMs is that an ABM can better incorporate movements and any other potential important process such as for example bioenergetics, life histories, inter- and intra-specific interaction and interactions between the species and its environment. An ABM can therefore be considered as a bottom up modelling approach (DeAngelis and Grimm, 2014).

Both modelling approaches (correlative and process based) have strengths and weaknesses, and benefits of combining the two approaches have been recognized and also successfully applied (Dorman et al., 2012; Latombe et al., 2014; Evans et al., 2016). However, there are still rather few published examples. An integrated modelling approach implies that strengths of both model types can be used in the same modelling framework. Statistical modelling can be helpful for utilization of available data without the requirement of a full understanding of the important processes. Statistical models can also speed up the tedious calibration process of an ABM and allow for cross-validation (Latome et al., 2014). An ABM can be used for introducing stochasticity, together with any kind of relevant known important and dynamic process (DeAngelis and Grimm, 2014).

Integrated modelling was applied in this study with Atlantic mackerel (*Scomber scombrus*) in the Norwegian Sea as a case study species and underwater noise as a potential anthropogenic pressure. Atlantic mackerel is a highly mobile migratory species living in a dynamic environment (Nøttestad et al., 2016b). It is an abundant pelagic planktivorous species entering the Norwegian Sea and adjacent areas during summer for feeding on primarily *Calanus* spp. (Bachiller et al., 2015). The mackerel spawning stock has doubled since 2003 and was in 2016 estimated to be around 4 million tonnes (ICES, 2017). Mackerel has expanded its feeding area during the last decade (Nøttestad et al., 2016a), and is now abundant in new areas such as along the northern Norwegian and southern Icelandic coasts. The reason for the expansion is not fully known, and more knowledge about the migration dynamics is needed to improve the understanding of trophic interactions as well as for integrated assessment (ICES, 2017). Disturbance from impulsive sounds such as those from seismic explorations or pile driving can potentially have a negative impact on marine organisms (e.g. Carroll et al., 2017; Slabbekoorn et al., 2010; Gill et al., 2012), including the Atlantic mackerel. Although fish species without a swim bladder (e.g. Atlantic Mackerel) are considered to be less sensitive to noise disturbance in comparison to fish species which possess a swim bladder (e.g. herring and cod) (Whalberg and Westerberg, 2005). Fish in close vicinity to the sound source may experience physical damage, such as tissue injury (McCauley et al., 2003) and permanent or temporary hearing loss (Popper et al., 2005). However, due to the short distance between the source and the fish required for this to occur, such effects are usually limited to only few individuals (Popper et al., 2005). At larger distances from the source, but within hearing range, behavioural changes may occur. Behavioural effects and masking are less acute and dramatic but apply to many more individual fish (Slabbekoorn et al., 2010; Hawkins et al., 2014). The latter is not very well understood, although some case studies exist, indicating behavioural responses such as avoidance (Engås et al., 1996), changes in swimming speed (Thomsen et al., 2012), reduced feeding motivation (Løkkeborg et al., 2012) and changes in depth distribution (Pearson et al., 1992; Hawkins et al., 2014).

An ABM describing mackerel migration patterns has previously been constructed by Utne and Huse (2012) and an ABM focusing on estimating consumption of zooplankton (*Calanus finmarchicus*) by Utne et al. (2012). The present study builds on the findings of these two modelling exercises with the aim to construct an integrated template for modelling and simulations of realistic distributions, movements and migration of Atlantic Mackerel. To achieve this, we combine hydrodynamic modelling, species distribution modelling and agent-based modelling. We also assessed the potential of using the model template for an assessment of potential impacts of a "real" seismic surveys. The modelling framework outlined in this study can be useful for other species and pressures as well, making it possible to assess dynamic impacts on mobile species.

2. METHODS

2.1 Integrated modelling concept and time period

Three types of models are integrated in this study, hydrodynamic modelling (HDM, describing the environment), species distribution modelling (SDM, producing horizontal CPUE predictions and after normalization a habitat suitability index, HSI, as a proxy for food resources) by relating scientific mackerel trawl data to environmental predictors and agent-based modelling (ABM) introducing movement rules and bioenergetics with HSI and hydrodynamics as forcings. Each modelling level is feeding into the next (Figure 1). The modelling period extends from beginning of May to end of October, the period when Atlantic mackerel is present in the Norwegian Sea. The SDM is fitted on data from surveys conducted each year in July and August between 2006 and 2014. However, the spatial patterns of the ABM are calibrated on data from 2013. An overview of each modelling step is described below.

Figure 1. General overview of the integrated modelling approach.

2.2 Hydrodynamic model (HDM) and environmental data

The study area/model domain covers the Norwegian Sea and parts of the Barents Sea between 59-82° N and 5° E-34° W (Figure 2). The model domain is extracted from a larger DHI MIKE 3 3D FM model (DHI, 2016) covering the North Sea, the Norwegian Sea and the Barents Sea during the period 2006-2014. The 3D numerical model is calibrated based on a range of input data, including bathymetry, initial water levels, current velocities, boundary conditions and other driving forces including wind speed, direction and tides (see full list and source in Appendix A, Table A1). The model is used for simulating the dynamic environmental variables (Table 1) within the study domain during the above-mentioned period at one-hour temporal resolution. The simulation results are used as input for the species distribution model and agent-based model. The spatial resolution varies between 500 m and 8 km (approximate widths of flexible triangular grid elements, see DHI, 2016) with a maximum grid area of 100 km^2, the coastal area having the finest resolution. The vertical discretization has 33 levels with a 1.5 m resolution at the surface, decreasing to 750 m at the bottom, and 13 levels within the upper 61 m. See Appendix A for further description and validation of the HDM.

Post-processing of the 3D HDM data was required to be useful in species distribution modelling, for integration with the mackerel survey data. The 3D-model data were summarized into a horizontal 2D-grid (5x5 km) and the average of approximately the top 30 m of the water column was calculated for the variables listed in Table 1. This is the general depth distribution of mackerel during summer in the Norwegian Sea (Nøttestad et al., 2016b). The variables are either direct output (e.g. temperature and salinity) of the HDM or post-processed variables (e.g. salinity gradient and current gradient), potentially describing features aggregating mackerel prey. The HDM data were further extracted to (intersected with) the mackerel survey data "instantaneously" (temporal interpolation between 1-hour time-steps) based on both position and time. Daily means around each trawl were also extracted as well as mean values for the entire annual survey period from 10 July to 10 August.

Figure 2. Model domain. Black and red lines show agent release site, southern and western, respectively. Yellow polygon shows the area of sound disturbance simulation.

2.3 Atlantic Mackerel data

Data on mackerel distribution and abundance were obtained from scientific trawl catches conducted in July-August during the years 2006-2014 as part of the coordinated ecosystem surveys in the Norwegian Sea and adjacent areas (IESSNS). Standardized trawl hauls were taken at the surface at predetermined locations, with roughly 60 nmi between each trawl haul. The geographic coverage of the surveys varied (Figure 3). A detailed description of the gear, rigging and fishing operation is given in ICES (2013). The trawl has a vertical opening of 30-35 m and a horizontal opening of 65-70 m. Catch per unit effort (CPUE) from mackerel trawl hauls (kg nmi^{-1}) was used as input to the species distribution model. CPUE is calculated as total catch (kg) divided by the area covered by the trawl (nmi^{-2}). See Nøttestad et al. (2016a) for a full description of CPUE calculations. All surveys included in the analyses are visualized in Figure 3.

In addition to the scientific trawling data, data on commercial landings were made available for the study from the Norwegian directorate of fisheries (Figure A5, Appendix A). These data were provided with a daily resolution and a spatial resolution varying with geographic area. In coastal areas, the resolution is 0.5 degree latitude and 1 degree longitude. The spatial distribution of the fishery data was considered to be biased, particularly with distance to coast because the small vessels only operate close to the shore. Therefore, the fishery data were not included in the SDM. The fishery data were, however, assumed to be representative for describing the temporal advancement in terms of latitude and were therefore used in the temporal calibration of the ABM (section 2.5).

Figure 3. Mackerel trawl locations used in species distribution modelling. Scientific trawls were conducted in July-August 2006-2014 as part of the coordinated ecosystem surveys in the Norwegian Sea and adjacent areas (IESSNS).

2.4 Species distribution modelling

The mackerel data were related to the hydrodynamic variables using a generalized additive mixed model (GAMM). The analyses were conducted in R (R core team, 2016) and the mgcv package (Wood, 2006). The mixed model was used to account for potential non-independency within surveys (i.e. survey trawls closer to each other in time and space can be considered not to be independent of each other, potentially violating the assumption of independence of model residuals, see e.g. Zuur et al., 2009). The GAMM was fitted with mackerel CPUE as the response variables and the hydrodynamic variables (Table 1), water depth and time periods as predictor variables. We tested the influence of all the listed environmental variables in Table 1, but we did not include uninfluential variables in our final model. Model selection was guided by the approximate p-values and model AIC and also by inspecting the response curves (unrealistic responses, i.e. if the model was fitting "noise" the variable was not included, or the response was simplified). We used the Tweedie error distribution for model fitting and included a correlation structure (ARMA) within surveys to account for the non-independency. The p-factor in the Tweedie error distribution as well as the p-factor in the ARMA correlation structure (Zuur et al., 2009) were selected by fitting a range of different models and selecting the best one based on AIC. In the model we included an interaction between temperature and a factor defining three periods (1 = 2006-2008, 2 = 2009-2011 and 3 = 2012-2014) to account for a potential spatial expansion during the 9 years of modelling (as indicated by e.g. Nøttestad et al., 2016a). The reason for not including a factor variable defining each year is that by using a group of three years we achieve a more equal spatial distribution (in 2008 and 2009 surveys were only conducted in the north with a very low catch and if the model would be fitted with a yearly factor, the CPUE in the whole model domain would be under-predicted). We fitted models on all three temporal scales (hourly data, daily means and survey period mean) to assess potential differences.

The GAMM was checked for meeting model assumptions regarding autocorrelation by inspecting a variogram and an autocorrelation function plot (acf) of model residuals, and the assumption of residual homogeneity was visually assessed. The predictive accuracy of the model was validated by leaving out one year at a time, fitting the model on the remaining years and testing the model on the left-out year. The agreement between "observed" and predicted CPUE was assessed using Spearman's correlation (Potts and Elith, 2006) and visually by plotting observed values on top of the predicted ones.

The model was finally used for predicting CPUE on each hourly time-step during the whole model period May-October; which means extensive extrapolation in time with the assumption that the modelled relationships (between CPUE and environmental variable) are the same throughout the model period. The predicted CPUE was further converted into a Habitat Suitability Index (HSI) by normalizing the CPUE into a scale ranging between 0-1. Prior to normalization, extreme values (due to extrapolations) were re-scaled. For each time-step, the mean value in the study area and the standard deviation were calculated and the allowable minimum and maximum values were defined as the average ± 3 times the standard deviation. If a value was higher it was set to the minimum or maximum allowable value, respectively. The global maximum and minimum values used for normalization were defined as the calculated 99th and 1st percentile value across all time steps and model elements. Any habitat suitability value exceeding the 99th percentile or below the 1st percentile was set to the 99th and 1st percentile value, respectively. The normalization was calculated by using the formula:

$$y = \frac{x - \min(x)}{\max(x) - \min(x)}$$

Table 1. Environmental variables assessed for inclusion in SDM, all variables except water depth are either direct or post-processed HDM variables.

Variable	**Unit**	**Direct model output/post-processed**
Current speed	m/s	Direct
Current direction	radians	Direct
Current gradient	m/s/m	Post-processed
Upwelling (vertical current velocity)	m/s	Direct

Vorticity (eddy activity)	m/s/m	Post-processed
Salinity	Psu	Direct
Salinity gradient (adjacent grid cells)	Δ psu	Post-processed
Temperature	ºC	Post-processed
Vertical density gradient (Brunt Vaisala frequency)	N^2	Post-processed
Water depth (etopo downloaded from NOAA)	M	https://maps.ngdc.noaa.gov/viewers/wcs-client/

2.5 Agent-based modelling

A complete model description of the ABM, following the “Overview, Design concepts and Details” protocol (ODD, Grimm et al., 2010), is included in Appendix A. A condensed model description is given here. The model was built in MIKE Zero 2016 ABM Lab (https://www.mikepoweredbydhi.com/products/abm-lab). The purpose of the ABM is to construct a realistic physiology-based migration model for mackerel in the Norwegian Sea covering the time period of May-October 2013, with an equidistant time step of 5 minutes. The ABM model domain is resolved using a triangular flexible mesh, with a maximum model element area of 100 km^2. Within the model simulation period, mackerel undertakes seasonal migration and during this period the mackerel agents will try to optimise their movement according to a kinesis walk description (Humston et al., 2000) linked to HSI (habitat suitability index), distance to land and ambient temperature. While moving, the bioenergetics of the agents (which is body weight relative to the energy balance), are dependent on HSI, temperature and swimming speed. The body weight gain rate further determines the direction and timing of mackerel migration. The bioenergetics module, adapted from Utne et al. (2012), is directly coupled to the dynamic predictions of sea surface temperature and HSI, with the model assumption that the consumption rate scales with predicted HSI. Respiration costs are furthermore dependent on the realized swimming velocity of simulated mackerel, which in turn depends on which movement decisions they make relative to environmental stimuli

(Figure 4). The predicted net gain in wet weight over the feeding season relative to the initial weight of simulated mackerel will determine when they will decide to turn back and migrate towards their wintering grounds outside of the model domain (SEASONAL MIGRATION, see below). If mackerel agents are located within the area of seismic survey, they react to sound disturbance if the sound crosses a pre-defined level.

At each time step the simulated mackerel makes movement decisions in relation to distance and sound pressure level (SPL) of the sound source (SOUND DISTURBANCE), land (LAND AVOIDANCE), temperature (TEMPERATURE AVOIDANCE), season (SEASONAL MIGRATION related to bioenergetics and date) and habitat suitability (KINESIS MOVEMENT). The sound response module is introduced below (chapter 2.6). The response to land is implemented as a minimum distance of 10 km, if closer the mackerel agents move in the opposite direction for 6 hours (which has been calibrated). The response to temperature is defined based on a minimum temperature threshold of 7 degrees (Iversen, 2004), if in colder water the agent moves towards warmer water and if in warm waters the direction is dependent on the season (northwards during spring and southwards during autumn). The seasonal migration is implemented so that mackerel agents try to optimise body weight in spring; if in very good habitat (HSI index) the directional migration is turned off (defined based on a habitat index threshold value of 0.7). If the habitat index is below the threshold the mackerel migrates towards north in spring according to a migration probability which is defined based on time of year and HSI. In autumn, when they have reached an optimal weight gain (optWG) or based on time of year (sampled Julian day 213±7) the mackerel agents migrate in a southerly direction towards (a sampled direction including stochasticity) their place of origin. The kinesis movement is implemented as a combination of the Kinesis movement as described by Humston et al. (2000) and a correlated random walk where the HSI is the external stimulus determining the mackerel movements.

After a movement decision has been made, all state variables are updated at the end of each time step. The state variables are saved for each time step which allows for post-assessments of for example body weight and location (or any other state variable) at any time during a model simulation. The state variables are: location (x, y coordinates), speed (relative to prevailing currents, land and sound), body length, initial body weight, total body weight, origin (migrating from Atlantic or North Sea), cumulative duration of exposure to temperatures below minimum temperature, duration of land avoidance, cumulative instantaneous sound pressure, time of sound exposure, optimal weight gain and turn date of the seasonal migration. Values of dynamic Euler variables (temperature, currents, HSI) at the new agent location for evaluation and calculation are updated at the beginning of the next time step. Figure 4 shows a flow diagram describing the general movement decisions of fish. Model simulation is based on 40 000 agents, each agent consists of 175 000 individuals corresponding to 7 billion individuals observed in the whole study area (assuming that our model extent is 45% of the swept-area surveys and catchability index = 2 ICES, 2016, 2014; Nøttestad et al., 2016a).

Figure 4. Flow diagram describing general decisions of mackerel. Boxes with white background depict model evaluations made by each agent and grey boxes depict resultant movement decisions.

2.5.1 ABM calibration

The ABM includes 61 model parameters of which 19 were subject to calibration, while the rest were retrieved from literature. The parameters are listed in Appendix A, Table A2, and it is indicated whether they needed to be calibrated or were retrieved from literature. The pattern-oriented modelling (POM, Grimm and Railsback, 2012) concept was used for calibrating the parameters, to identify the combination of parameters that was best in reproducing the observed patterns (Appendix B). POM is a widely used strategy for making ABMs structurally realistic, more general and accurate and accepted by the scientific community. This is done by simultaneously comparing multiple observed “real world” patterns to model outcomes and thereby achieving the most parsimonious model that captures the key mechanisms and behaviour of the real system (Grimm and Railsback, 2012). The POM strategy is based on the assumption that patterns are good descriptors or indicators of the underlying essential structures and processes in a system. (MacLane et al., 2011). We used the following patterns:

1. Changes in fish total body mass during migration for 34 cm (see figure Figure 2 in Bachiller et al., 2018) and 36 cm fish (see Figure 2b in Olafsdottir et al., 2016). In order to compare modelled and observed values from literature we calculated the

correlation coefficient; index of agreement (IOA) (Wilmott, 1981); mean absolute error and root mean square error (Appendix B).

2. Speed of migration derived from commercial mackerel landings for years 2012-14. We defined three check zones (60-62° N, 65-75° N and 70-72° N) and compared median day and distribution of number of fish passing through these zones during spring and autumn migration separately.
3. Spatial distribution in July in comparison to data obtained during scientific trawls.

2.5.2 Sensitivity testing of ABM

We tested model sensitivity to seven parameters for which there were no available values measured in the field or reported in literature: average sustained swimming velocity, average spring migration direction, average autumn migration direction, average day number when autumn migration starts, minimum HSI required to stop active migration, minimum temperature for mackerel tolerance and a constant defining relationship between HSI and consumption rate – functional response (KL). We varied one parameter at a time with ±25% from the values used in the final simulations or within a range reported in literature (Appendix C, Table C1). We ran one simulation for each parameter combination (sensitivity analysis index) with 20 000 agents each (20 000 agents were used to save simulation time because there was no obvious difference between using 20 000 or 40 000 as in the final simulations). We used five patterns to compare changes in model performance in between sensitivity analysis indices in relation to results of the parameter settings for the final simulation: three POM patterns as described above, as well as the proportion of fish commencing autumn migration due to achievement of the desired body weight and mean mackerel body weight before starting autumn migration. In order to compare sensitivity analysis indices reproducing changes in mackerel mean body weight over model duration we calculated an index of agreement (Wilmott, 1981) and correlation coefficient between modelled and empirical values for each index (Appendix B). Speed of migration was compared by calculating median day of fish crossing three check lines: 60-62N, 65-67N and 70-72N. Comparison between spatial distributions in July between models with various parameter settings (sensitivity analysis indices) was based on changes in 25, 50, 75 and 95% kernel utilisation distribution. Estimation of kernel home range was done in adehabitatHR R package (Calenge, 2006) with smoothing factor (h) = 1 and grid = 120.

2.6 Sound disturbance module

A sound disturbance module was implemented as part of the ABM to enable an assessment of potential impact on fish due to sound. The sound source in the model is a moving source (survey vessel) with vessel sailing speed and sailing distance mimicking a real seismic survey (survey conducted in June - July 2013 (Figure 2, A6 in Appendix A). The exact positions along the track and timing of airgun blasts are not known and the positions of blasts were, therefore, created assuming that the vessel was moving with a speed of 4 knots and no blasting was conducted during the 4 hours when the vessel was turning. At each time step the direction, distance, sound pressure level (SPL in dB re 1 μPa, hence after referred to as dB) and sound exposure level (SEL, cumulative SEL in dB re 1 $\mu Pa^2 \cdot s$, hence after referred to as dB) to the active airgun are saved to each agent. Sound attenuation at the distance between source and fish, SPL, is calculated based on spherical and cylindrical spreading as suggested by Weston et al., (1971). SEL is calculated based on method suggested by Southall et al., (2007) taking into account changes in fish location every time step and the actual frequency, pressure and duration of pulses (see detailed description in the ODD, Appendix A).

Forcing information regarding sound disturbance includes: geographic coordinates of airgun, source sound pressure level (230 dB) of airgun (if at a given time step there is no blast SPL = 0) and water depth at the airgun (6 m) and is given every time step. Mackerel reacts to disturbance based on model-predicted SPL relative to vessel location (taking attenuation into account). If this SPL gets over any of four pre-defined thresholds (lowest threshold = 165 dB; based on experience gained by Sivle et al., 2016), a triggering mechanism is established, and fish change their speed and direction in relation to the sound source and do not forage while fleeing. The larger the threshold crossed, the more pronounced changes in speed and direction (increase in correlation of turning angle in correlated random walk). This threshold is based on levels obtained in a study where captive mackerel reacted to playback of sound with partly similar frequency range as seismic pulses from air guns, and does not necessarily represent the true reaction thresholds of free ranging mackerel to this type of sound exposure. Indeed, later experience indicates that reaction thresholds of mackerel will also depend on the suddenness of the signal (Sivle et al. 2017). In the current model settings, fish do not react based on cumulative SEL, but this parameter is saved and presented in the results as well.

3. RESULTS

3.1 Species distribution modelling results

According to the SDM, higher mackerel CPUE is described by increasing water temperature, increasing water depth and time period (Table 2, Figure 5). The temporal resolution (hourly, daily, and monthly) was assessed and there was no clear improvement of aggregating data into coarser temporal resolution, and therefore the hourly resolution was used. No spatial correlation was found in model residuals and residual patterns did not show any clear patterns of violation of the homogeneity assumption. The validation of the model on independent data indicated that the model is fit for purpose. The mean Spearman's correlation for all years was 0.42, ranging from 0.14 in 2006 and 0.62 in 2009, the validation results for 2013 were mapped as well (Table 3, Figure 6). The results indicate predictions of the right order of magnitude, i.e. smaller observed values are predicted as smaller and higher observed values predicted as higher. The general distribution patterns, based on visual inspection, were also similar (Figure 6), with peak CPUE in the central parts of the Norwegian Sea and lower values closer to the coast, in the north as well as farthest to the east. This corresponds also well with the described distribution patterns of their main prey species, *Calanus finmarchicus* (Broms et al., 2009; Head et al., 2013). The model was finally predicted on hourly time steps during the whole model period and converted into a habitat suitability index, normalized to range between 0 and 1 (Video 1). We also predicted the mean geographic distribution for the survey periods for three years, one from each period in 2007, 2010 and 2013 (Figure 7).

Table 2. Fix-effect GAMM model results. The parametric coefficients (estimate), standard error, t value and approximate significance (p-value) are shown for the parametric terms and degree of freedom (edf), f-values and approximate p-value for the smooth terms. Period 1 = 2006-2008, period 2 = 2009-2011 and period 3 = 2012-2014.

		Estimate/edf.	Std. error	t/f value	p-value
Parametric terms	Intercept	3.8784	0.3365	11.526	<0.001
	Period 2	1.1691	0.3833	3.051	<0.01

	Period 3	2.2017	0.3546	6.209	<0.001
Smooth terms	Temp: period 1	1.841	-	14.29	<0.001
	Temp: period 2	1.517	-	6.469	<0.01
	Temp: period 3	1	-	6.808	<0.01
	Water depth	1.87	-	17.503	<0.001
n	743				

Figure 5. Response curves of the GAMM. The response is indicated on the Y-axis in the scale of the linear predictor (log), and the range of the predictors is indicated on the x-axis. The degree of smoothing of the continuous variables is displayed in the title of the Y-axis. The grey area and dotted lines indicate 95% confidence intervals. Period 1 = 2006-2008, period 2 = 2009-2011, and period 3 = 2012-2014.

Table 3. “Leave-one-year out” validation, the SDM was fitted on data excluding one whole year at a time for testing. The agreement between observed and predicted CPUE was assessed using Spearman’s correlation.

Year	Spearman's correlation
2006	0.14
2007	0.47
2008	0.41
2009	0.62
2010	0.52
2011	0.21
2012	0.29
2013	0.49
2014	0.60
Average	0.42

Figure 6. Observed CPUE in 2013 vs predicted CPUE for visual assessment. When only one colour appears in a circle the same class interval is both observed and predicted. The 2013 data were not included in the model (for validation) and can therefore be regarded as independent data.

Figure 7. Predicted CPUE by the SDM (GAMM) on one year from each period used as a factor in the model (period 1 = 2007, period 2 = 2010 and period 3 = 2013), illustrating the increase end expansion of the mackerel during the model period (all data included in fitting the final model).

3.2 Agent based modelling results

The ABM was simulated for the whole period May-October (Video 2). The model was calibrated to reproduce three POM-patterns (Figures 8-10). Median dates when modelled fish crossed latitudinal check points corresponded well with the observed values in the fisheries data. Modelled fish migrated 13 days faster and 14 days later through the mid check point (65-67° N) during spring and autumn migration, respectively, in comparison to observed speed of mackerel migration (Figure 8). The modelled fish growth reproduced the observed weight-at length pattern throughout the feeding period. The index of agreement between modelled and observed weights was 0.84 and 0.85 and the correlation coefficients were 0.78 – 0.88 for 34- and 36 cm fish, respectively (Figure 9). The ABM underestimated density of mackerel along the Norwegian coast south of Lofoten islands (Figure 10) but reproduced densities well in the central part of the study area.

Figure 8. Comparison of speed of spring (northwards) and autumn (southern) migration between modelled (sim) and observed (obs) North Atlantic mackerel at three ‘check points’:

60-62° N, 65-67° N and 70-72° N. Observed and modelled median dates when fish crossed 60-62° N check point on their southwards migration are equal.

Figure 9. Observed and modelled changes in mean body weights of 34 cm and 36 cm fish over model duration and their statistical comparison.

Figure 10. Mean predicted density of agents (km^2) for July 2013 in comparison to observed values represented by catch per unit effort (CPUE, [kg nmi^{-1}]) for the same period. Model simulation is based on 40 000 agents, each representing 175 000 fish. The depicted densities are not corrected for number of fish represented by each agent. Note different and, therefore, not directly comparable units of CPUE and predicted density.

3.2.1 Sensitivity analysis of ABM

Mean mackerel body weight was most sensitive to average sustained swimming velocity, average spring migration direction and functional response between HSI and consumption rate (KL) out of the parameters chosen for the sensitivity analysis (Figures C1-C2, Appendix C). The parameters average day number when autumn migration begins, or minimum habitat suitability index required to stop the migration had little effect on average body weight and on model outputs in general (Figures C1-C7). Speed of migration showed little variation with changes of the sensitivity analysis parameters (Figure C3, Appendix C), although average sustained swimming velocity and average spring migration direction were most influential. The extent of spatial distribution in July was most sensitive to changes in KL (Figure C4). Changes in proportion of mackerel migrating due to increase in body weight and changes in mackerel mean body weight at the end of spring migration were most sensitive to KL, average sustained swimming velocity, and average spring migration direction (Figures C6-C7).

3.3 Sound disturbance scenarios

There was no effect of the seismic survey on any of the POM patterns (Figures D1-3 in Appendix D) for the mackerel agents during the model simulation based on the assumed sound disturbance parameters (Table A2). During the survey, 376 agents, representing 65.8 million mackerel, were “affected” by sound disturbance and therefore exposed to SPL level above the pre-defined threshold of 165 dB. The majority (75%) of the affected agents experience disturbance (>165 dB SPL), less than 30 times during the survey, considering that the airgun was fired every 10 seconds during the 10-day survey (excluding the four hours every time the ship was turning). On average, fish agents reacted to sound at a distance of 3.9 ± 1.4 km (mean ± sd) from the source location. Fish agents, which reacted to sound, experienced a cumulative SEL of maximum 197 dB, and the mean ± sd of maximum values for each agent was 175.5 ± 5.2 dB. Mean ± sd SPL for these fish was 168.1 ± 3.1 dB and duration of exposure over SPL threshold was 35.1 ± 21.2 min (Figure 11, Video 3).

Figure 11. Distribution of SPL (grey bars) and cumulative SEL (red bars) (left panel) and time of exposure to sound [min] over reaction threshold (right panel) for fish reacting to sound disturbance in a model simulation. Vertical lines with corresponding colours depict mean values.

There were no significant changes in mean total body weight over duration of seismic survey for disturbed and non-disturbed fish within the seismic area and the 50 km buffer zone around it (Figure D4, Appendix D; Welch Two Sample t-test: t = -1.0, df = 15.5, p = 0.3). Nor were there any significant changes in mean total body weight between fish exposed to disturbance and the same individuals from the simulation when sound disturbance module was off (Figure D4, Appendix D; Welch Two Sample t-test: t = -0.6, df = 13.7, p = 0.6).

4. DISCUSSION

Study of long-term and large-scale impacts of anthropogenic pressures on marine animals can best be evaluated by modelling. The modelling approach should be able to describe dynamic distributions and movement patterns of species and also be able to incorporate the dynamic pressure in the same modelling framework. In this paper we have successfully implemented such an approach, where we calibrated and validated the model based on the best available knowledge and which can be improved further when better data become available. However, as with all modelling approaches it is important to assess the performance of the model and outline important assumptions and limitations. We discuss these aspects in more detail below.

4.1 The model's ability to reproduce observed patterns

If a model is to be useful it should be able to reproduce the pattern observed in nature (Grimm and Railsback, 2012). There is, however, often a lack of data for calibration and validation on independent data (on completely new data). In this study we validated the SDM separately using a cross-validation approach leaving out a whole year at a time for testing, which can be regarded as independent data. The SDM was able to predict CPUE of similar order of magnitude as in the independent data set (Table 3). The model is rather simple, including only temperature (grouped by period) and water depth as spatial predictors, which can be considered as describing generic large-scale patterns. Mackerel is generally found in warmer water and the highest abundance of the main prey species *Calanus finmarchicus* has been described to be found in in the deeper Atlantic water mass in the Norwegian Sea (Broms et al., 2009), which corresponds well with our model results. The small-scaled variation in CPUE in the scientific trawls was not captured very well by the SDM; however, somewhat closer to the coast a high number of mackerel were caught but not predicted (Figure 6).

The ability of the ABM to reproduce reality was tested using the POM approach. The ABM was calibrated with all available data (no independent validation set was available). However, the POM approach is designed to test for the predictive ability of the model (Grimm and Railsback, 2012) and therefore independent data are not a necessity. The model was successful in reproducing the timing of migration (Figure 8) and the observed bodyweight (Figure 9). This indicated that the bioenergetics model module works well and simulated large scale migration movements correspond with observations. The resulting distribution patterns were further assessed visually during calibration to match the patterns observed in the mackerel trawl data. However, the resulting patterns are quite similar to the SDM and not very patchy (Figure 10), which indicates that fine-scaled processes are potentially not fully reflected in the final model simulations.

The ABM includes a range of parameters for which there is no published information or existing knowledge. The sensitivity analyses showed that certain parameters may influence model performance considerably and therefore our model should be updated once data are available (Appendix C). However, it is worth noting that we varied sensitivity parameters quite substantially (25%) and therefore a relatively high proportional effect on the output should be expected.

In summary, the integrated modelling approach is able to predict realistic large-scaled distribution and movement patterns. However, fine-scale processes are not well described in the model. If the model is applied, it is therefore important to recognize the limitations and consider how it could influence the results.

4.2 Model assumptions and limitation

With the purpose of identifying what type of information is most needed for improving the models (i.e. defining knowledge gaps), and for applying the models, we discuss here the main limitations and assumptions of the models. One of the most important limitations of the SDM is that it is fitted on data from July and early August only and it is assumed that the relationships and processes driving the patterns are the same throughout the study period. However, the consequences of the extensive extrapolation are impossible to assess accurately. Data from other periods during the study would therefore improve the model. However, the available data are from the middle of the model period and as the model produces realistic patterns for this period it can be regarded as an indication that the predictions during other periods also are reasonable. Or, at least, it would be more problematic if data would only be available from the beginning or end of the study period.

Another important model limitation is that the distribution of zooplankton was not included in the model and the food availability is assumed to be reflected by the habitat suitability index. The reason for not including actual food as a predictor is that the distribution of zooplankton would also need to be modelled, and as high quality spatial information on food is also scarce, it would introduce another source of uncertainty but not necessarily improve the predictions. There might also be a miss-match between high prey abundance and predator abundance. If high quality information on food resources during different times of the study period would be available, it could nevertheless potentially improve the habitat suitability index predicted by the SDM or used directly in the ABM as a forcing.

Other important limitations of the ABM are that potentially important fine-scaled behavioural processes are omitted from the model due to lack of knowledge. Predator interactions as well as other types of inter-specific and intra-specific interaction are not included in the model. There is no schooling behaviour included in the model, since each agent is effectively representing 175 000 mackerel. Currently it is not computationally feasible to attempt to model 7 billion mackerel 1:1 at a large spatiotemporal scale. However, it might be possible to use outputs from the regional ABM model to force the boundary conditions of a localized model around a survey area where the scale allows for modelling mackerel 1:1 with more advanced fine-scale behaviours in the future. Inclusion of these processes would make the model more realistic in terms of fine-scaled patterns. Another key element in the ABM model setup is the temporal introduction of mackerel along the western and southern boundaries. The current magnitude and timing of the introduction rate of each mackerel sub-population into the model domain were found through a reiterative calibration process relative to replicating POM-patterns. Monitoring data that would allow us to more accurately estimate the boundary conditions of the ABM would be of high value for further model development. Similar to the SDM model, the ABM model would also greatly benefit from detailed distribution data for other months than just July, in order to better understand the model's ability to replicate spatiotemporal distribution patterns. One of the main underlying assumptions in the ABM model is that we assume unlimited food resources, and that HSI is directly proportional to food availability (leading to higher mackerel consumption rate). While the established model was able to predict observed weight-at-length gains to a very satisfactory degree, an event like food depletion due to very high densities of mackerel might be a driver for local movements as well.

4.3 Model utilization for impact assessment of noise

In this study we have shown an example of how a sound disturbance module could function in terms of assessing the number of impacted fish and their potential behavioural and physiological reaction. Actual consequences of the exposure in our defined scenario are highly uncertain, as very little information about the responses of mackerel to sound disturbance is available. The presented module is therefore an example and eventually when more information becomes available it may be possible to assess the consequences of sound disturbance on the bioenergetics and consequently on local and regional dynamics of mackerel. Due to lack of data for the studied species the modelled fish agents react only to experienced SPL; however, a range of other possible triggering mechanisms is possible, for example SEL (e.g. Slabbekoorn et al., 2010; Hawkins et al., 2014; Sivle et al., 2016; 2017), although no data on SEL is available for mackerel at the moment (field experiments are however currently being conducted). We therefore included several options in the model for mackerel to respond: 1) mackerel reacts to pre-calculated and user-defined distance thresholds to vessel location; 2) mackerel reacts to the model-predicted SEL relative to vessel location; 3) mackerel reacts to calculated SEL from user-defined distances and corresponding SPL at those distances. Further, each of these options can be extended by habituation and changes in mackerel behaviour dependant on ambient background noise (see details in Appendix A). Additionally, in our model scenario we included exposure to only one seismic survey, of which affected agents experienced a disturbance with a duration of 35 minutes on average, resulting in no effect on fish condition. However, in a real-life scenario, several seismic surveys may take place along the migration path in the Norwegian Sea, as well as simultaneously within a larger area such as the Barents Sea. Hence, an agent may experience a higher degree of disturbance than accounted for here, and such accumulated effects could be included in future versions of model simulations. Our model may, therefore, have a widespread application in the future.

CONCLUSION

The pelagic marine system is dynamic and complex and empirical data are sparse. In recent years the anthropogenic activity offshore has increased and consequently also the risk of conflicts with wildlife. The integrated modelling approach is aiming at utilizing different modelling approaches for making the most out of our data and knowledge. The approach is capable of reproducing observed natural distribution and movement patterns at larger scales and it is further possible to improve the predictive ability of fine-scaled patterns when such information becomes available. Currently very little fine-scaled information on mackerel behaviour is available. The integrated sound disturbance module allows assessing potential impacts of a mobile disturbance source on mobile fish species in a dynamic environment. To our knowledge this has not been done before for a fish species. The natural system is highly complex, and the model results should, due to their limitations discussed above, be used with care. However, the only way of assessing impacts at population level is by using different modelling techniques. This study and the modelling approach contribute with another building block in the quest for improving our ability to assess anthropogenic disturbance on pelagic fish species or marine species in general.

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