Contents lists available at ScienceDirect



Ecological Modelling



Insights on integrating habitat preferences in process-oriented ecological models – a case study of the southern North Sea



ECOLOGICAI MODELLING

Miriam Püts^{a,*}, Marc Taylor^a, Ismael Núñez-Riboni^a, Jeroen Steenbeek^b, Moritz Stäbler^c, Christian Möllmann^d, Alexander Kempf^a

^a Thünen Institute of Sea Fisheries, Herwigstraße 31, 27572 Bremerhaven, Germany

^b Ecopath International Initiative Research Association, Barcelona, Spain

^c Leibniz Centre for Tropical Marine Research, Fahrenheitstr. 6, 28359 Bremen, Germany

^d Institute of Marine Ecosystems and Fishery Science, Center for Earth System Research and Sustainability (CEN), Große Elbstraße 133, 22767 Hamburg, Germany

ARTICLE INFO

Keywords: Ecospace Spatial-temporal framework Habitat capacity Species distribution model Food web model Ecopath with Ecosim

ABSTRACT

One of the most applied tools to create ecosystem models to support management decisions in the light of ecosystem-based fisheries management is Ecopath with Ecosim (EwE). Recently, its spatial routine Ecospace has evolved due to the addition of the Habitat Foraging Capacity Model (HFCM), a spatial-temporal dynamic niche model to drive the foraging capacity to distribute biomass over model grid cells. The HFCM allows for continuous implementation of externally derived habitat preference maps based on single species distribution models. So far, guidelines are lacking on how to best define habitat preferences for inclusion in process-oriented trophic modeling studies. As one of the first studies, we applied the newest Ecospace development to an existing EwE model of the southern North Sea with the aim to identify which definition of habitat preference leads to the best model fit. Another key aim of our study was to test for the sensitivity of implementing externally derived habitat preference maps within Ecospace to different time-scales (seasonal, yearly, multi-year, and static). For this purpose, generalized additive models (GAM) were fit to scientific survey data using either presence/absence or abundance as differing criteria of habitat preference. Our results show that Ecospace runs using habitat preference maps based on presence/absence data compared best to empirical data. The optimal time-scale for habitat updating differed for biomass and catch, but implementing variable habitats was generally superior to a static habitat representation. Our study hence highlights the importance of a sigmoidal representation of habitat (e.g. presence/absence) and variable habitat preferences (e.g. multi-year) when combining species distribution models with an ecosystem model. It demonstrates that the interpretation of habitat preference can have a major influence on the model fit and outcome.

1. Introduction

Habitat preference of species is a widely known concept in ecology; first defined as the tendency of a species to choose one resource over another if both are equally available (Johnson et al., 1980). Since then, multiple definitions and extensions of the concept have been suggested (e.g. Rosenzweig and Abramsky, 1986; Hall et al., 1997; Aarts et al., 2008), next to numerous definitions of habitat itself and whether it comprises only abiotic factors or biotic relationships as well (e.g. Darwin, 1859; Allee et al., 2000; Valentine et al., 2005). These different interpretations of habitat and habitat preferences or lack of a common definition might lead to miscommunication between and misinterpretations by scientists (Hall et al., 1997). Additionally, there are still ongoing discussions about how to quantify habitat preferences in the light of their use and availability (Beyer et al., 2010). modeling these preferences faces certain problems, such as an unequal access of individuals to all habitats and areas as well as variations of habitat availability and quality over time (Garshelis, 2000). Combining a spatially resolved trophic ecosystem model with habitat preference maps based on single species distribution models (SDM) can be a solution to better account for habitat preferences within the ecosystem model.

In the recent years, spatially explicit ecosystem models are increasingly being applied to study the effects of climate change, spatial fisheries management or to support marine spatial planning (e.g. Romagnoni et al., 2015; Alexander et al., 2016; Bossier et al., 2018). Therefore, it is necessary to establish best practices when it comes to

* Corresponding author.

E-mail address: miriam.puets@thuenen.de (M. Püts).

https://doi.org/10.1016/j.ecolmodel.2020.109189

Received 26 November 2019; Received in revised form 20 June 2020; Accepted 22 June 2020 Available online 29 June 2020

0304-3800/ © 2020 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/BY-NC-ND/4.0/).

working with spatially explicit ecosystem models as well as protocols on how to best combine these ecosystem models with SDMs. A popular ecosystem modeling approach with an increasing number of models worldwide is implemented in the Ecopath with Ecosim software (EwE, Christensen et al., 2004; Colleter et al., 2015; Heymans et al., 2016). EwE encompasses three modeling components: the static, mass-balanced Ecopath that is used to construct a 'snapshot' of the trophic food web of individual species or functional groups (FGs), originally proposed by Polovina (1984) and further developed since (Christensen and Pauly, 1992). The temporal simulation module Ecosim uses the Ecopath parameterization as a baseline to assess ecosystem dynamics over time. with the main goal to evaluate the impact of environmental stressors and fisheries on the ecosystem (Walters et al., 1997, 2000). Ecospace adds the spatial dimension to the model (Walters et al., 1999; Christensen et al., 2014), providing a routine which allows for impact analysis of spatial management measures such as marine protected areas and physical structures like wind farms (Christensen and Walters, 2004). Many Ecopath and Ecosim models have been published in the past, while publications applying Ecospace are comparably rare, but increase in appearance recently (Colleter et al., 2015).

In recent releases of the EwE software, the options to inform Ecospace about habitat preferences have become very flexible. One of the first possibilities was to assign absence/presence preferences connected to static habitat layers implemented in the basemap. To include multiple environmental stressors, a new habitat foraging capacity model (HFCM) was implemented that allowed the user to implement continuous rather than binary habitat preferences (Christensen et al., 2014). The foraging capacity of a cell is based on the foraging arena theory implemented in Ecosim, defining the capacity of a cell for a predator to forage on a prey (Ahrens et al., 2012). It is used as a multiplier to the search area (A) in the foraging arena equation (Christensen et al., 2014). From here on, multiple, cumulative environmental drivers could also affect the computed foraging capacity of the FGs in a given cell, implemented via environmental preference functions. This increased the variation between the cells to distribute the FGs over the map where they are most likely to occur (Christensen et al., 2014). Furthermore, it opened the opportunity to close the gap between SDMs and ecosystem models, by allowing the user to implement environmental response functions derived from SDMs (Grüss et al., 2016). One of the most recent improvements to relate FGs' distributions in Ecospace directly to scientific surveys, is the possibility to implement scaled habitat preferences predicted by external SDMs directly as foraging capacity maps into Ecospace (Fig. 1). This increases the interchangeability between different model types further.

Thus far, temporal abundance changes of each FG in Ecosim are reproduced in each grid cell of Ecospace. The new spatial-temporal data framework allows for time-dynamic inclusion of geospatial data such as habitat maps during each Ecospace run (Steenbeek et al., 2013). Including dynamically changing environmental driver maps, and a dynamic redistribution of biomass based on species environmental preferences allows for a better representation of changes in the physical habitat (Christensen et al., 2014). This also allows implementing timedynamic foraging capacity maps based on external SDMs during the Ecospace run. This enables the modeler to bypass the necessity to enter environmental preference functions in Ecospace. Implementing these maps can be done, just like the environmental driver maps, in different temporal frequencies, e.g. seasonally, annually or once every few years. To integrate them with the computed foraging capacity and to account for shifts in habitat preferences over the period of the model run increases the realism in distributing the biomass of FGs over the grid cells.

Combining the single species distribution modeling approach with a trophic ecosystem model in this way bears potentials to increase our knowledge on impacts of changes in biotic and abiotic factors on species and fisheries yield. This increases Ecospace usefulness as a support tool for spatial management decisions. The application of this approach to many FGs simultaneously in a strongly exploited ecosystem like the North Sea has so far not been reported. Neither has the test for the sensitivity of different implementation frequencies of external foraging capacity maps, which might show how inertia and sensitivity of the ecosystem model differs with forcing frequencies.

Therefore, this study aims to analyze which representation of habitat preference best serves to create foraging capacity maps and is capable to interact with the information contributed by the trophodynamic model. Furthermore, the sensitivity of the updating frequency of foraging capacity maps (e.g. seasonal, annual, multiannual) on Ecospace's biomass and catch predictions compared to the empirical data is being evaluated.

2. Material and methods

2.1. Ecopath with Ecosim model of the southern North Sea

Our Ecospace model is based on a previously published EwE model (Stäbler et al., 2016), representing the ecosystem of the southern North Sea in the base year 1991 up to 2010 (statistical areas IVb and IVc, defined by the International Council for the Exploration of the Sea (ICES)). The southern North Sea model has a focus on commercially important species and higher trophic levels, and comprises 68 groups of which 35 represent multi-species groups and 30 single species. Particulate organic matter, dissolved organic matter and discards are represented in three additional groups. Life history changes are implemented for seven commercially important species, cod (Gadus morhua), whiting (Merlangius merlangus), haddock (Melanogrammus aeglefinus), herring (Clupea harengus), sole (Solea solea), plaice (Pleuronectes platessa) and brown shrimp (Crangon crangon) through the multi-stanza approach (Walters et al., 2010). These stanzas characterize juvenile and adult life stages of the fish species, while brown shrimp was split according to the body size they need to reach to be targeted by the fishery. Fishery exploitation is implemented in the model through twelve fleets, representing the diversity of the fishing sector in this region.

There have been several adaptations to the original Ecopath and Ecosim model of the southern North Sea. These were changes in the diet matrix and the addition of off-vessel prices in Ecopath, as well as some changes to the reference time series in Ecosim. For more detail, see Appendix A. To account for these alterations in Ecopath and Ecosim, we used the new stepwise fitting routine to fit predator/prey vulnerabilities and primary production anomaly splines that resulted in the lowest discrepancies between the model and the observed time series (Scott et al., 2016). The fitting routine automatically repeats the sensitivity search and Ecosim runs with an increasing number of vulnerability parameters. These different parameterizations towards reference time series were fitted; the resulting measures of fit include residual sum of squares (SS, log-scaled biomass, catches) and Akaike information criterion (AIC; Akaike, 1974). The Ecosim settings with the lowest AICs (AICs that differed more than 2 compared to the lowest AIC were excluded) were then tested for their model efficiency (see Table 2, Stow et al., 2009) in reproducing the reference time series of biomass and catch. For further information on this Ecopath and Ecosim model of the southern North Sea, see Stäbler et al., 2016, 2018, 2019 and Appendix A.

2.2. Ecospace of the southern North Sea

The software used to construct the Ecospace model is EwE version 6.6, professional edition, and fit to time series for the period 1991 - 2010 and run in monthly time steps. As a basis for distributing biomasses simulated by Ecosim in space, a basemap of the study area was constructed as a georeferenced Esri American Standard Code for Information Interchange map (Esri ASCII), with a resolution of 0.125° per edge length of each grid cell. The bounding box for the study area



Fig. 1. Biomass maps created within the southern North Sea Ecospace model for all FGs. Colors depict high (red) to low (blue) relative biomass. Thirty-two of these functional groups were driven via external foraging capacity maps based on habitat preferences derived from species distribution models (SDMs), indicated by the white star.

ranged from -4° to 9° longitude and from 51° to 57.25° latitude. We assigned static habitats to the basemap encompassing various sediment structures, a distance to coast measure and fishing habitats. All habitat maps were binary, defined by 1 = present and 0 = not present. Sediment types were derived from the European Marine Observation and Data Network (EMODnet, 2017) using a seabed substrate map that includes five substrate classes (mud to muddy sand, sand, coarse sediment, mixed sediment, rock and boulders). To account for seabirds living close to the coast to breed on land, the habitats "near coast" and "marine" were added. The 12 nautical mile zone representing territorial waters of each surrounding country was used as a proxy to separate coastal from offshore areas. Additionally, depth was included as an environmental driver, ranging from 0 to 100 m. Data used to reproduce the bathymetry of the study area was retrieved from the General Bathymetric Chart of the Oceans (General Bathymetric Chart of the Oceans (GEBCO), 2019). These have a higher resolution than Ecospace; therefore, within each grid cell the mean depth was taken and then classified into ten discrete depth categories in ten meter intervals, starting with 5 m.

Fishing effort allocation across the grid implements the effect of spatially explicit exploitation (Christensen et al., 2008; Christensen and Walters, 2004; Walters et al., 1999). Usually, fishing fleets are assigned simply to the same habitats as FGs targeted in order to distribute fishing effort on the basemap. We attempted a more realistic representation of the spatial dynamics of the fisheries using spatially resolved effective fishing effort data (Scientific, Technical and Economic Committee For Fisheries, 2017). However, for a few fleets that have very specific target FGs (like sandeel and nephrops trawlers) the fleets follow the distribution of these FGs, while all others were assigned to the before mentioned habitat structures. Mean annual primary production was

added to the basemap as a static layer, based on Moderate Resolution Imaging Spectroradiometer (MODIS) ocean color data; from 2002 to the present (Behrenfeld and Falkowski, 1997; http://www.science.oregonstate.edu/ocean.productivity/index.php) and was kept constant over time to solely examine the influence of varying foraging capacity.

Ecospace takes a habitat preference approach and allocates Ecosim's biomass dynamically over a basemap of grid cells with respective preferred and non-preferred habitats. The spatial allocation of the biomass is based on the foraging capacity for each FG within a cell. Within cells with preferred habitats, FGs have increased feeding rates (allowing for increased growth rate) and survival rates. Outside of these cells, dispersal rates, which depict random movement within the model area, may be higher to escape the non-preferred habitats (Christensen et al., 2008). In the HFCM, the computed foraging capacity within Ecospace can be overwritten by external foraging capacity or multiplied by cell specific habitat capacity and environmental capacity. As external foraging capacity, scaled habitat preference maps predicted by SDMs can be integrated into Ecospace directly. These maps have the same spatial extent and resolution as the Ecospace basemap and each grid cell has a specific foraging capacity between 0 and 1 assigned to. From here on, habitat preferences refers to the predicted results of the SDMs, while they are referred to as external foraging capacity as soon as they enter Ecospace to overwrite the computed foraging capacity. In addition, Ecospace can calculate foraging capacity from FGs affinity for given habitats and from FGs functional responses to environmental conditions. Habitat capacity is based on the habitat layers implemented in the basemap (here sediment and distance to coast). Each habitat type gets a proportion assigned of how suitable the habitat is for a certain FG. Environmental capacity is based on environmental driver maps (here depth). It is being ascertained by applying an environmental



Fig. 2. Foraging capacity options in Ecospace.

response function specific to each FG to the environmental driver map. All aforementioned possibilities within Ecospace can be applied individually or combined (Fig. 2).

In this study, foraging capacity for most FGs was pre-defined by external foraging capacity maps, while for some FGs the foraging capacity was calculated from affinity for habitats and/or environmental preferences. Distributions for six FGs were affected though habitat affinities, while for eleven FGs an environmental response function depending on depth was implemented. Foraging capacity maps for 32 FGs were driven from external habitat preferences through the spatialtemporal data framework (see Fig. 1). The multi-stanza modus of Ecospace computes the distributions of multi-stanza groups to be highly correlated within each group, which sometimes leads to a better fit if only one of the stanzas is distributed by temporarily changing the foraging capacity. We followed this approach for the FG plaice, where only the distribution of the juvenile stanza was driven by its foraging capacity. The adult stanzas distribution was a result of the distribution of juveniles as well as presence of predators and prey. For crangon, the stanza smaller than commercial catch size followed the distribution of the stanza targeted by fisheries.

In Ecospace, biomass is time-variant within a cell even if no external forcing occurred since a fraction of biomass is always dispersing randomly around the basemap, represented by the dispersal rate (km/ year). The base dispersal rate set as default within Ecospace is 300 km/ year, except for detritus (Christensen et al., 2008). For our model, we chose five different dispersal rates to represent the mobility of FGs based on their life form, i.e. 1000 km/year for fast top predators, 600 km/year for pelagic FGs, 300 km/year for faster moving demersal fish FGs, 30 km/year for mainly flat fish and zooplankton FGs, 3 km/ year for nearly stationary or sessile groups (primarily benthic FGs). These dispersal rates were chosen based on the general "300–30–3" rule (similar to Chen et al., 2009), expanding the classes for more differentiation in speed. Using a custom built plug-in for EwE, each Ecospace run was started with a 10-year spin-up (or burn-in) period to stabilize FG distributions. For more details about the Ecospace structure, see the Appendix A.

2.3. Species distribution models

The new spatial temporal data framework within Ecospace allows for the implementation of time dynamic foraging capacity maps. These are habitat preferences generated by SDMs prior to implementation and then applied directly as foraging capacity, with a range of 0-1. This method was applied for thirty-two FGs, representing most single species FGs, including six multi-stanza groups, and eleven multi-species FGs (see Appendix A). These groups represent mainly commercially important species and also groups that were well represented within the scientific surveys that sampled the data used for the SDMs. Data on species abundance for this analysis was gathered from two different surveys, due to the different catchability of the surveys for certain groups. Catch-per-unit-effort data (CPUE, number_per_hour) from quarter 3 (Q3, only sampled quarter) of the ICES Beam Trawl Survey (BTS) from 1991 to 2010 was used for juvenile and adult sole (Solea solea), brill (Scophthalmus rhombus) and turbot (Scophthalmus maximus), long-rough dab (Hippoglossoides platessoides) and monkfish (Lophius piscatorius). For the remaining 25 FGs, CPUE data was used for quarter 1 (Q1) and Q3 of the ICES International Bottom Trawl Survey (IBTS) from 1991 to 2010 (see Appendix A). For the chosen timeframe, Q1 and O3 are the only two quarters that were sampled continuously.

One of the major aims of this study is to identify the best representation of habitat preference when combining an SDM with a trophic food web model. We tested two representations in this study: a more general representation based on binary data (presence/absence model) versus one that accounts for gradations in quality by considering abundance (hurdle model). The idea is to identify if a sigmoidal or an exponential response is best suited when combined with the trophic model. The hurdle model contains binary (presence/absence) and continuous response (abundance) sub models that are applied to the data separately and the predicted distribution resulting them are being multiplied at the end (Cragg, 1971; Maunder and Punt, 2004). A hurdle model approach is widely used in SDMs due to its ability to deal with data sets that contain a high number of zeros (i.e. 'zero-inflated').

In their recent published paper, Coll et al. (2019) used Bayesian models (integrated nested laplace approximation; INLA) to create single FG distribution maps. We tested the applicability of INLA for our study against the fitting method commonly used for generalized additive models (GAM;Hastie and Tibshirani, 1986), i.e., PIRLS (Penalized Iteratively Re-weighted Least Squares). The GAMs were created using the 'mgcv' package (Wood, 2009), while INLA was applied with the 'R-INLA' package (Rue et al., 2009). Due to high computational costs, we modelled only key groups with either high commercial importance or a small sample size (cod (adult), whiting (adult), starry ray & others, sole (adult) and plaice (adult)). Both modeling approaches were fitted to presence/absence (PA) data and a combined hurdle model. For the hurdle model, a GAM was fitted to CPUE (with CPUE>0) data using the classical approach (PIRLS) and using INLA and the resulting predictions were subsequently multiplied with the results of the PA model. To consider time dependency, both the GAM and R-INLA were run for each year separately. A k-fold cross-validation approach with 4 folds was applied to compare the predictive skill of the different model types. The fit was assessed with the area under the response curve (AUC;

Swets, 1988) for the presence/absence and with the root mean squared error (RMSE) for the hurdle model. The results of this assessment showed that for this study, INLA does not outperform the less time-consuming fitting method used in a GAM. Therefore, GAM was chosen and will be described in more detail in the following paragraph. For more information about the comparison of these two SDMs, see Appendix 1.

Presence/absence data were modelled using a GAM with the canonical link logit. For the hurdle model, also CPUE data was modelled with a non-zero abundance GAM (CPUE = CPUE > 0) using the gamma distribution with a log link to assess the abundance:

$$logit(\vec{PA}) = s(lat, lon, k = 10), \tag{1}$$

and

Λ

$$log(CPUE) = s(lat, lon, k = 10),$$
(2)

with *lat* and *lon* representing sampling locations, \hat{PA} and $C\hat{PUE}$ being the modelled dependent variables, respectively. The s(lat, lon) smoother is a thin plate regression spline (Wood, 2003), using the basis dimensions k (Wood, 2017). The results were then used to predict the occurrence and the presence in survey catches on a spatial grid implemented in Ecospace (i.e., $0.125^{\circ} \times 0.125^{\circ}$). Consequently, the hurdle model (*hurd*) was applied, combining the resulting predictions of the two models, \hat{PA} and $C\hat{PUE}$:

$$hurd = \stackrel{\frown}{PA} \times \stackrel{\frown}{CPUE}.$$
(3)

Finally, all model predictions were standardized between 0 and 1, dividing all predictions by their annual maximum for the later use in Ecospace. In some cases the annual CPUE was n < = 10 and could not be modelled for these specific years (pertains six FGs) even though over all the species were well represented within the data. In these cases, maps from the previous year were taken (see Appendix B).

2.4. Ecospace scenarios

Eight scenarios were tested to evaluate the influence of the different habitat preferences representations (PA versus hurdle) and to address the second aim of the paper, the analysis of the best input frequency. Each representation was applied at each frequency (Table 1). The baseline scenario was used to compare the originally static version of Ecospace to the time dynamic foraging capacity.

For each scenario, skill assessments for the model predictions of biomass and catch have been conducted for all FGs that have been fitted to time series in the underlying Ecosim (Table 2, see Appendix B for a list of FGs used for the skill assessment). Before calculating fit statistics, these biomass and catch time series were smoothed by applying a GAM to represent general trends. Furthermore, since the reference time series of biomass and catch are relative measures only, they were scaled to the absolute values resulting from Ecospace (for more information see Appendix B). We used a set of measures for the skill assessment. They inform about either the temporal, the spatial or the spatial-temporal fit of Ecospace. The root mean square error (RMSE) describes the distance between simulated and observed time series. Model efficiency (MEF) is a measure of model skill with respect to the range of natural variations. A value >0 indicates a close match between the time series, while values <0 indicate that a constant value would be a better predictor than the simulations (Stow et al., 2009). In this study, for biomass and catch the MEF was calculated in relation to the biomass or catch value of the base year 1991. To assess the spatial fit of the different scenarios, the Schoener's D index was used. It serves as a metric to calculate spatial niche overlap, and therefore enabling the spatial comparison between the SDMs and Ecospace. It is based on the probability of occurrence, ranging from 0 (no match) to 1 (maps are identical; Schoener, 1968; Warren et al., 2008). Here we applied the hurdle-based habitat preference maps from the SDM models a second time. Not as

Table 1

Scenarios of implementing habitat preference maps at different temporal frequencies. Each frequency was tested twice, once with habitat preference maps based on the presence/absence model, once with maps based on the hurdle model.

SDM	Scenario name	Frequency	Data Input
presence/absence	Seasonal	Every 6 month, implemented in January and July	IBTS FGs: maps for Q1 and Q3
presence/absence	Annual	Annually, implemented in January	BTS FGs: maps only for Q3, starting map for the first half of 1991 IBTS: Mean map of Q1 and Q3 BTS: map of Q3
presence/absence	Multi-years	Every 5 years (1991, 1996, 2001, 2006)	IBTS and BTS: Mean map for 5 years (1991–1995, 1996–2000, 2001–2005, 2006–2010)
presence/absence	Baseline	Once before the run	IBTS: Mean map of 1991
			BTS: Q3 map of 1991
hurdle	Seasonal	Every 6 month, implemented in January and July	IBTS FGs: maps for Q1 and Q3
			BTS FGs: maps only for Q3, starting map for the first half of 1991
hurdle	Annual	Annually, implemented in January	IBTS: Mean map of Q1 and Q3
			BTS: map of Q3
hurdle	Multi-years	Every 5 years (1991, 1996, 2001, 2006)	IBTS and BTS: Mean map for 5 years (1991–1995, 1996–2000, 2001–2005, 2006–2010)
hurdle	Baseline	Once before the run	IBTS: Mean map of 1991
			BTS: Q3 map of 1991

Table 2

Skill assessment metrics. Thresholds mark the breaking point above which the results were classified as satisfying. Sim represents the smoothed mean biomass or catch results of Ecospace extracted at the end of each year; obs refers to the equivalent time series implemented in Ecosim. Except for Schoener's D, all values were log-transformed. psim represents probability values in the annually extracted Ecospace results for each cell and pobs probability values in each cell of the reference maps.

Metric	Formula	Threshold
Root mean squared error (RMSE)	$\sqrt{\frac{\sum_{i=1}^{N}(\text{sim}-obs)^2}{N}}$	RMSE < = 0.25
Model efficiency 1991 (MEF)	$\frac{(\sum_{i=1}^{n}(obs - obs1991)^2 - \sum_{i=1}^{n}(sim - obs)^2}{\sum_{i=1}^{n}(obs - obs1991)^2}$	MEF>0
Pearson correlation (PEAR) Schoener's D	$\frac{Cov(sim, obs)}{\sqrt{Var(sim)} * \sqrt{Var(obs)}}$ $1 - \frac{1}{2} \sum_{i} psim - pobs $	PEAR > = 0.75 $PEAR < = -0.75$ Schoener's $D > = 0.5$

input maps into Ecospace, but as a reference of observed habitat preferences. We used the hurdle maps rather than the PA maps, because they include species abundance (here: survey-based CPUE) and not just presence/absence and the resulting maps in Ecospace are representing biomass rather than just presence/absence distributions. To avoid confusion with the hurdle scenarios, it will be called *abundance reference* from here on. The overlap was therefore calculated between the Ecospace biomass distributions at the end of every year and the abundance reference.

Spatially resolved catch data for the entire time period in this study was not available. Therefore, a comparison between observed fishing distribution and spatially disaggregated Ecospace catch results was not an option. We calculated the Pearson correlation (PEAR) between reference time series used in Ecosim for catch and catch results derived from Ecospace as an additional metric to evaluate the fit of the model in terms of spatially aggregated catch.

Thresholds were applied to assess the number of FGs that achieve a good fit in relation to a satisfactory threshold. Some of the thresholds were chosen ad hoc, others were defined based on their general range (like Schoener's D index). Additionally, a Taylor diagram (Taylor, 2001) was created between the abundance reference and the scenario outputs, to directly evaluate the spatial-temporal fit. Each grid cell of each year for each FG was compared between observation and scenario output to account for differences in space and time.

3. Results

3.1. Comparison of Ecospace scenarios - Biomass

The model fit of Ecospace was evaluated for three aspects (temporal, spatial and spatial-temporal fit) and for two variables (catch and biomass). Results for the skill assessment metrics evaluating the temporal fit of the mean biomass revealed, that scenarios forced with capacity maps from PA GAMs provide better fits than the scenarios that were forced with capacity maps from the hurdle model (Table 3). Among the PA forced scenarios, the multi-year scenario achieved the best results for MEF and RMSE, while the static baseline scenario performed worst in terms of RMSE. In contrast to the PA scenarios, the temporally variable hurdle scenarios performed worse than the static baseline scenario in the case of metrics that evaluate the temporal fit. The seasonal hurdle scenario had to be excluded from all following skill assessments, since it resulted in the depletion of the FG mature herring, implying a bad fit already within the Ecospace run.

When comparing the spatial distribution of the abundance reference with the Ecospace maps, the Schoener's D index showed the best results for the temporally variable hurdle scenarios. All PA scenarios followed this and the worst fit was achieved with the static hurdle baseline scenario. Evaluating individual Schoener's D indices on FG level revealed only small differences within the PA or hurdle scenarios. Therefore, in the following, only the example of the PA annual scenario is discussed in detail (see Appendix B for the other individual results). Only two of the thirty-two FGs with foraging capacity maps displayed medians below the threshold of 0.5 for the individual Schoener's D indices (Fig. 3). Gurnards and herring (adult) had the worst fits in all PA scenarios with time dynamic maps. Some FGs showed a large range of

Table 3

Model efficiency (MEF) and root mean squared error (RMSE) were used to assess the temporal fit, and Schoener's D index was applied to evaluate the spatial fit. All metrics show the skill assessment based on biomass averaged over all FGs for each scenario. Results marked with * represent the best results in terms of the overall mean. The numbers within the brackets display percentage of functional groups that exceeded the thresholds (MEF threshold = 0, RMSE threshold = 0.25, Schoener's D index = 0.5).

PA Seasonal 0.497 (92.2) 0.4123 (33.3) 0.6695 (96.9) PA Annual 0.5358 (94.1) 0.4065 (33.3) 0.6734 (93.8) PA Multi-years 0.5719 (92.2)* 0.3986 (37.3)* 0.6587 (93.8) PA Baseline 0.5421 (96.1) 0.4145 (29.4) 0.6214 (87.5)	Scenario\Skill	MEF biomass	RMSE biomass	Schoener's D biomass
Hurdle Annual -0.2413 (70.6) 0.5466 (17.6) 0.7503 (93.8)* Hurdle Multi-years 0.0518 (70.6) 0.5198 (19.6) 0.7182 (93.8) Hurdle Reguling 0.5518 (70.6) 0.423 (14.4) 0.5424 (58.8)	PA Seasonal PA Annual PA Multi-years PA Baseline Hurdle Annual Hurdle Multi-years Hurdle Baseling	0.497 (92.2) 0.5358 (94.1) 0.5719 (92.2)* 0.5421 (96.1) - 0.2413 (70.6) 0.0518 (70.6) 0.551 (04.1)	0.4123 (33.3) 0.4065 (33.3) 0.3986 (37.3)* 0.4145 (29.4) 0.5466 (17.6) 0.5198 (19.6) 0.412 (21.4)	0.6695 (96.9) 0.6734 (93.8) 0.6587 (93.8) 0.6214 (87.5) 0.7503 (93.8)* 0.7182 (93.8)

Schoeners' D index PA Annual



Fig. 3. Schoener's D index as a measure of niche overlap from 1991 to 2010 for each functional group forced with annually changing PA habitat capacity maps. Thick black line marks 0.5, the threshold above which the fit was considered acceptable. The boxplot indicate median, upper, and lower quartile for each group. Lines below and above the boxes indicate values outside the middle 50% range while dots represent outliers.

values in between years (e.g. monkfish, norway pout, thornback and spotted ray), while others showed 'outliers', identified by the boxplot. There was no evident correlation between the trophic level and the fit of the model. In addition, there was no evident difference between FGs for which the foraging capacity was forced by habitat preference maps based on data of the IBTS and the BTS survey. Due to sampling design, the former were forced by a mean map between Q1 and Q3, while maps based on data collected in Q3 only forced the latter. Multi-stanza FGs displayed no pattern within these results.

Ranking MEF of all scenarios (1 – best to 7 – worst) for the different FGs individually revealed differences in the best fitting scenarios (Fig. 4). The PA multi-years scenario showed the worst fit for only two FGs, which also reflected the general trend towards the multi-year scenario as the one with the best fit for biomass. FGs for which this scenario had the worst fit were nephrops and sandeels. For most FGs, the temporally variable hurdle scenarios ranked lowest among the MEF, as expected based on the summarized results over all FGs. Nevertheless, some FGs seemed to benefit from these scenarios, the majority being mostly FGs with quite low trophic levels. The PA baseline scenario also showed fifteen ranks five and higher, while the hurdle baseline scenario shows twenty-three ranks five and higher. This indicates that adding

variability in the foraging capacity during the run by updating the habitat maps increases the MEF. Overall, the preference for scenarios between the different FGs was quite diverse. There was no evident pattern or clustering based on trophic levels or ecological niches. What became apparent was the dominance of the PA scenarios over the hurdle scenarios when condensing the FGs into larger groups and calculating the mean rank for the MEFs of the scenarios. The hurdle baseline or the hurdle multi-year scenario have a positive effect only on other demersal fish and crustaceans, the latter being the only group where solely a hurdle scenario is beneficial.

Mean biomass over time evaluated for four commercially important FGs (mature cod, whiting, sole and plaice) as examples, revealed distinctive patterns for each scenario (Fig. 5). These displayed FGs were subjected to different kinds of spatial-temporal forcing. The foraging capacity of cod (adult) and whiting (adult) was based on the IBTS survey; thus, the maps varied for Q1 and Q3. They were therefore the class of FGs that were directly influenced by changing foraging capacity within the seasonal scenario. For sole (adult) on the other hand the distribution was based on the BTS survey, so solely on Q3. Plaice (adult) is shown as an example of FGs, which was only forced by the distribution of the connected stanza plaice (juvenile) and a static basemap.



Ranked biomass MEF per functional group

ranks 1234567

Fig. 4. Ranked model efficiency for biomass per functional group per scenario with the best (1) to worst (7) fit, from dark to light blue. Scenarios from left to right: S = Seasonal, A = Annual, M = Multi-years, B = Baseline. Functional groups are sorted by trophic level. Species silhouettes represent different ecological groups, colors represent the scenario with the best fit (mean rank over all functional groups within the group). From top to bottom: marine mammals & birds, elasmo-branches, gadoids, forage fish, other demersal fish, flatfish, crustacean (commercially important), zooplankton and benthos. If a group has multiple colors, it points to multiple best fits.

Therefore, within these four FGs there was an increase in complexity of forcing. All four revealed that the hurdle scenarios, which represented the abundance-based maps, underestimated the biomass for these FGs in most cases, especially in the beginning of the run. Only in the case of cod (adult) the annual and multi-years hurdle biomass exceeded the reference time series after 2000. In most cases for the PA scenarios, the trend depicted in the Ecospace scenarios matched those of the time series and with increased periodicity of map input, the peaks of the reference time series were being matched. What did become apparent, especially in the case of PA scenarios, was that steep and abrupt changes in biomass were not accounted for in all Ecospace scenarios. The steep decrease of cod (adult) biomass beginning in 1998 was not represented. Additionally, there was a lack of biomass decrease for plaice (adult) and sole (adult) in the beginning of the time series.

To evaluate the temporal and spatial fit in combination, the correlation and the centered root mean squared error (RMSE) between Ecospace biomass layers and the abundance reference for all scenarios were evaluated with a Taylor diagram (Fig. 6). Within this diagram, the abundance reference is represented by the circle labeled "observation". Therefore, the closer a symbol for the scenario is to the observation, the better the fit. For this analysis, the variation between the standard deviation of the Ecospace output and the observed abundance reference was smaller for the hurdle scenarios. This was to be expected, since the abundance reference is the output of the hurdle SDM. Therefore, the spatial overlap is closely related. Yet, the PA scenarios result in better RMSE and correlation than the hurdle scenarios. Within the hurdle scenarios, the annual scenario had the best correlation and RMSE, which were quite similar for the other two scenarios. Yet these two



Fig. 5. Mean biomass [t/km²] over all cells per year for selected commercially important functional groups. Left: PA scenarios, right: Hurdle scenarios. Different colors represent the different scenarios, while the black line represents the observations scaled by the FGs biomass entered in Ecopath.

scenarios (hurdle multi-years and hurdle baseline) perform better in terms of standard deviation. For PA, the three temporally variable scenarios reached quite similar results, while the static baseline scenario had a better standard deviation but a worse correlation and RMSE.

3.2. Comparison of Ecospace scenarios - Catch

Since the distribution of catch was not based on a GAM and has therefore no spatially resolved maps to compare to, the catch skill assessment only evaluates the temporal fit. It is based on a comparison between the observed relative time series included in Ecosim and the mean catch values obtained from the different Ecospace scenarios (Table 4). The metrics used to distinguish between the fits of the models shown here were MEF, RMSE and PEAR. Similar to biomass, the time dynamic hurdle scenarios showed the worst fit in all metrics, while the hurdle baseline scenario comes close to the results achieved with the PA scenarios. Overall, the seasonal as well as the multi-years PA scenario showed the best fit, supporting once more the decision towards a multiyear PA scenario.

A more concise picture emerged based on the ranked MEF for the single FGs (Fig. 7). Similar to biomass and expected based on the skill assessment metrics table, the temporally variable hurdle scenarios showed the worst fit for most of the FGs. Only for a few foraging fish, demersal fish and flatfish the fit was better for these scenarios. Especially for the higher trophic levels, the annual hurdle scenario almost

always resulted in the worst overall MEF. This was also reflected in the grouped MEF ranks displayed by the FG silhouette in different colors. The PA seasonal and the PA multi-years scenario showed the best fit for most of the ecological groups (three times red (PA seasonal) and four times orange (PA multi-years)). The hurdle baseline scenario had a good fit for three of the ecological groups, but also received the lowest rank seven times. This shows a high variation in model fit for the different scenarios among the ecological groups, especially when it comes to the hurdle scenario. The two annual scenarios and the hurdle multiyears scenario did not achieve the best grouped MEF for any ecological group.

Mean catch over time was analyzed for the same FGs as for biomass in Section 3.1, they therefore underlie the same foraging capacity forcing (Fig. 8). The increasing variability over time was visible here as well, but not quite as apparent as for biomass. The PA based scenarios matched the time series especially in trend and in most cases, they matched the observations. Yet, here again the southern North Sea Ecospace model failed to account for strong changes in the catch time series, as it was visible for biomass time series comparison of cod (adult). The hurdle scenario on the other hand completely underestimated the catch for cod, plaice and sole, especially in the beginning of the time series. In most cases, even the trend was not that precise within the hurdle scenarios.

Overall, the results showed, that the fit of these scenarios differed between the different metrics applied and that each aspect had to be taken into account, temporal, spatial and spatial-temporal. Even

Ecospace vs. abundance reference scaled with q



Fig. 6. Ecospace-simulated biomass vs. observed abundance (CPUE) by scenario in terms of correlation (right arch), RMSE (green arch) and Standard Deviation (x and y axis). Both biomass and abundance data are log-transformed, and log-abundance values were re-scaled with a parameter q, derived for each unique scenario and FG. Comparisons were made per cell per year per functional group.

Table 4

Model efficiency (MEF), root mean squared error (RMSE) and Pearson correlation (PEAR) based on catch assessment for each scenario displaying the mean over all functional groups. Results marked with * represent the best results in terms of the overall mean. The numbers within the brackets display percentage of functional groups that exceeded the thresholds (MEF threshold = 0, RMSE threshold = 0.25, Schoener's D index = 0.5).

Scenario/Skill	MEF catch	RMSE catch	PEAR catch
PA Seasonal	0.4829 (89.7)*	0.5016 (28.2)	0.478 (64.1)*
PA Annual	0.4664 (89.7)	0.4931 (33.3)	0.4289 (64.1)
PA Multi-years	0.4489 (89.7)	0.4885 (33.3)*	0.4393 (61.5)
PA Baseline Hurdle Annual	0.4469 (39.7) 0.4065 (92.3) 0.1385 (76.9)	0.4937 (30.8) 0.6043 (12.8)	0.4393 (01.3) 0.4141 (61.5) 0.2364 (38.5)
Hurdle Multi-years	0.3182 (79.5)	0.5557 (15.4)	0.2287 (53.8)
Hurdle Baseline	0.428 (89.7)	0.5024 (30.8)	0.4572 (59.0)

between catch and biomass, the scenarios with the best fit differed. Yet, one concise result was the dominance of varying foraging capacity over time and the necessity of a broader definition of this capacity by applying maps based on presence/absence (Table 5).

4. Discussion

4.1. Goals, insights and uncertainties

Within the spatial-temporal framework of EwE, it is now possible to combine habitat preference maps based on SDMs with Ecospace and update these maps during its execution. One of the main goals of this study was to analyze the effect of implementing either presence/absence or abundance-based maps as habitat preferences into a mechanistic trophic food web model. Our study showed that the interpretation of habitat preference could largely affect model's outcomes and fits. We demonstrate that it is necessary to select SDM settings that can inform habitat preference maps without overly constraining trophic or other processes to be addressed by the food web model. This can be achieved by choosing a model with a sigmoidal response (for instance, the logistic model), which leads to a spatial distribution allowing a broader foraging capacity than with a model with exponential response (as the hurdle model). Furthermore, the aim was to evaluate and illustrate the benefits of accounting for changes in habitat preferences over time. All modeling performance metrics employed showed that accounting for changes over time leads to better fits than static maps. Additionally, we displayed a way of how to assess the performance of an Ecospace model outside of EwE.

This Ecospace model is also subject to structural and parameter uncertainties. Building on two other components, Ecopath and Ecosim, Ecospace already inherits uncertainties introduced by these, like data on diets that stem from a single year only (Stäbler et al., 2016) or missing processes as encountered for the stock dynamics of cod (Fig. 5). These uncertainties may increase when combining SDMs and models with trophic interactions. There is a wide range of species distribution models (Guisan and Zimmermann, 2000), of which we tested two approaches to find the best model for our purposes.

Furthermore, it is an important issue that there is no standard routine to optimize Ecospace parameterizations. While for Ecopath and Ecosim there are implemented routines to evaluate the model fit and uncertainties (Steenbeek et al., 2018), Ecospace models have to be assessed outside of EwE. We tried to overcome this shortcoming by creating a routine outside of EwE to evaluate the fitting performance of different scenarios by temporal and spatial comparisons to empirical data. We were able to give insight into problems and pitfalls when combining SDM based distribution maps with trophodynamic modeling in Ecospace, which is quite a new approach. Therefore, this work may serve as basis for further case studies and developments in this field.

4.2. Defining habitat capacity in combination with trophodynamic modeling

Implementing SDMs into Ecospace can be a good asset to make food web modeling more robust. A recently published approach by Coll et al. (2019) implemented results from a Bayesian SDM model, either as foraging capacity maps or as environmental forcing function. For their data-poor case study, the combination of both modeling techniques increased the fit compared to an Ecospace that is not informed via SDM. Before the possibility of implementing foraging capacity maps, SDMs could only be incorporated by applying a response curve to environmental layers based on the SDM results (Chagaris, 2013). For these it has to be decided on which factors to include and all chosen drivers have to be incorporated into Ecospace separately (Grüss et al., 2018). This envelope approach expects a certain mechanistic understanding of the different abiotic drivers that influence habitat preferences, which brings about the possibility that certain influencing factors might be missed by this method. Nevertheless, one advantage of this method is the flexibility of changing abiotic driver maps to existing preference functions to test, for example, climate change scenarios. Also it poses a good approach for models in populations and areas that are data poor (Coll et al., 2019).

For areas with good data availability, like the southern North Sea, the need for previous knowledge about mechanistic processes can be overcome by applying SDMs with latitude and longitude as predictors, bypassing the necessity to include other abiotic factors that drive the distribution. This may be sufficient to evaluate e.g., the impact of a closed area under the assumption of non-changing foraging capacity. However, the way the single species GAMs were built for this study does not allow to test the influence of different environmental parameters in predictions and forecasts based on varying environmental factors (e.g. analysis of the influence of climate change). However, other environmental factors can easily be incorporated into the GAMs for future endeavors (e.g. Nuñez et al., 2019).

Compared to Coll et al. (2019), we used the spatial-temporal framework to update the habitat preferences derived from SDMs directly as foraging capacity maps during the execution of Ecospace, rather than inducing changes in the abiotic driver maps connected to forcing functions. Implementing habitat preference maps within the spatial-



Ranked catch MEF per functional group

ranks 1234567

Fig. 7. Ranked model efficiency for biomass per functional group per scenario with the best (1) to worst (7) fit, from dark to light blue. Scenarios from left to right: S = Seasonal, A = Annual, M = Multi-years, B = Baseline. Functional groups are sorted by trophic level. Species silhouettes represent different ecological groups, colors represent the scenario with the best fit (mean rank over all functional groups within the group). From top to bottom: elasmobranches, gadoids, forage fish, other demersal fish, flatfish, squid and cuttlefish, crustacean (commercially important) and benthos. If a group has multiple colors, it points to multiple best fits.

temporal framework opens the possibility to account for different influences and their strength over time (Steenbeek et al., 2013). Yet there is no common agreement on what habitat preferences to incorporate (e.g. which abiotic and biotic factors) and there are no clear guidelines on how to include these preferences into a complex ecosystem model where trophic interactions and fishing pressure have to be accounted for. It was demonstrated that presence/absence based habitat preferences overall performed better than the abundance weighted hurdle model based preferences. This might be an effect of the data used, as survey data constitute a representation of spatial abundance distributions in a single point of time, but we would argue that it is rather a general effect of the mathematical profile underlying the models.

The presence/absence model was fitted with a logit link, resulting in a sigmoidal profile, while the presence only model was fitted with a log link, which results in an exponential profile. Combining these two models leads to an exponential profile for the final hurdle model. While the sigmoidal profile allows a more general representation of distribution, the exponential profile highlights the areas with high abundances. Both profiles come with benefits but also restrictions. Combining the sigmoidal profile with a trophodynamic model allows for enough flexibility for further interactions that might influence the habitat preference of a species. Moreover, even though the hurdle scenarios yielded better results for the Schoener's D index, it showed that the more general approach of implementing the presence/absence maps was able to represent the distribution of the single FGs as well when combined with the ecosystem model. Yet this profile lacks the opportunity to include known hot spots with high interests for the species and good foraging opportunities (example maps in Fig. 9). The skill assessment of the hurdle model on the other hand showed, that the implementation of maps based on an exponential profile creates too much



Fig. 8. Mean catch [t/km²] over all cells per year for selected commercially important FGs. Left: PA scenarios, right: Hurdle scenarios. Different colors represent the different scenarios, while the black line represents the observations.

Table 5

Summary of the best fitting scenarios under the different dimensions (temporal, spatial, spatial-temporal). Displayed for biomass and for catch.

Dimension	Biomass	Catch
temporal	PA multi-years	PA seasonal
Spatial	hurdle annual	–
spatial-temporal	PA seasonal, annual, multi-years	–

spatial restriction. This constraint can have multiple effects within a spatial food web model. It can induce perfect overlap with the predator and fleets, which leads to high pressure on the FG and not much space to escape. Alternatively, as opposed to this, there can be no or hardly any overlap with predators and fleets, which in turn leads to an uncontrolled increase in biomass. Furthermore, there can be no or just minimal overlap with the own prey, which can lead to starvation.

Implementing these habitat preferences into Ecospace during the run raised the question on the best periodicity. Our results show that accounting for changes in distribution of species over time increases the overall fit of the model to spatial-temporal data. It could be argued, that the hurdle scenarios with the generally inferior fit implied a different conclusion. Here the static baseline scenario had the best fit. But this was only the case when concentrating on the metrics evaluating the temporal fit. The spatial metric Schoener's D index revealed that the static baseline scenario had the worst fit among all hurdle scenarios. This implies, that even though this scenario is good in reproducing temporal trends, it does so on the cost of spatial redistribution and thus becoming more unrealistic compared to the other scenarios.

For catch, the multi-years scenario and the seasonal scenario displayed the best results. Most fishing habitats were created based on known fishing areas, wide enough to redistribute the effort in case of shifts in habitat preferences. Therefore, adapting to more rapid changes over time might not be as crucial as for biomass. This is in line with findings by Romagnoni et al. (2015) who also found that changes in different parameters for their Ecospace of the entire North Sea (IV a, b and c) affected biomass and catch differently. This can be justified by the way effort is distributed in Ecospace. Each fleet's effort is proportionally distributed over the cells by a "gravity model", dependent on the sum over the FGs biomass caught by the fleet times the off-vessel prices and the catchability for each FG (Walters et al., 1999). If the fishing area covers enough ground to react to shifts in distribution, it follows the redistribution.

Considering all results, it reveals that in terms of periodicity the multi-years scenario performs best. Yet, the periodicity should support the time period one would like to study (e.g. short period: seasonal might work better, long period: seasonal may not be necessary, annual or even multi-years can suffice) and the research questions the model was built for (e.g. long-term changes in the ecosystem vs. effects of rapid increase of fishing mortality in the distribution of species). Furthermore, changes within the ecosystem during the run were only represented by the changes in foraging capacity. Including monthly, seasonal or annual changes of the chlorophyll-a maps or accounting for changes in water temperature might be necessary to adequately represent the changes over time and to reach a better model fit.



Fig. 9. GAM based distribution maps (left) and how they are incorporated in Ecospace (right). The top row represents presence/absence maps with the sigmoidal profile, while the lower row represents hurdle maps with the exponential profile. Here on the example of plaice (juvenile). The size of the circles in the hurdle map display the different CPUE values.

4.3. Best practice suggestions for applying a spatial-temporal framework to foraging capacity and shortcomings identified

There are several key best practice suggestions arising from this study for forcing the foraging capacity via the new Ecospace spatialtemporal capabilities. First, when applying scaled habitat preferences predicted with SDMs as foraging capacity, the best performing SDM may not be the best to use in an ecosystem model context. Although the exponential profile of the hurdle model has a better representation of the CPUE data, Ecospace performed worse when fed with its output. This is likely because the sigmoidal profile of the presence/absence maps is more informative as overall habitat capacity measure and additionally more flexible towards further mechanistic structures within the ecosystem model and therefore improving our knowledge on habitat preferences. Implementing time dynamic maps is the preferred option over a constant base map. Time dynamic maps are an important improvement in Ecospace especially in times of climate change; where in future work the temporal shift in temperature can be accounted for within the foraging capacity maps.

The study also identifies a few caveats. First, there is still no automated routine to evaluate the fit of Ecospace. We chose to test the fits using a set of skill assessment metrics and it has proven a good way to find the settings with the best fit. It is important to apply a wide set of different metrics to assess the fit of an ecosystem model, to account for the temporal and spatial fit (Olsen et al., 2016). Model efficiency with the value for the base year 1991, as well as the Pearson correlation (for catch) and root mean squared error served as metrics that informed about the mean temporal fit over the years. Nevertheless, these metrics did not account for spatial dynamics in habitat preference maps over time when compared to the empirical time series. This could be accomplished with the Schoener's D index, which measures the niche overlap, and therefore allows the spatial comparison between the Ecospace output maps and the abundance reference. The combination of the spatial and temporal fit could be achieved with the Taylor diagram, comparing Ecospace and abundance reference standardized maps for all years per grid cell.

One major issue within Ecospace is the current inability to react to situations like partial spatial mismatch between predator and prey by changing vulnerabilities based on occurrences in space. Vulnerabilities are only fitted to Ecosim time series, not taking the amount of spatial overlap into account. As done with this model for brown shrimp, changing single vulnerabilities within Ecosim is possible and justifiable (too much pressure of the adult stanza on the juvenile, while they are both common within a narrow area at the coast). Nevertheless, there is no other way than visibly checking the fit and using skill metrics as done here, to validate the changes. An automated routine, like the automated fitting routine for vulnerabilities and primary production splines applicable to Ecosim (Mackinson et al., 2009; Scott et al., 2016) would be a necessary improvement to account for species overlap in narrow areas. Additionally, as seen in Fig. 5, most sharp changes of biomass compared to the observation are hard to meet in this complex ecosystem model. Especially steep downward trends within the time series (as seen for cod, sole and plaice) have proven to be a challenge. There is a need for additional spatial processes, for example by implementing mediation functions or account for biomass accumulation based on spatial conditions, to match these trends and to force a steeper biomass trend in Ecospace.

When fitting Ecospace, multi-stanza groups have to be fitted with caution, as seen in this study for plaice. Distributions of juveniles and adults of the same species are linked through the implementation of multi-stanza group settings (Walters et al., 2010), so it may improve the fit if forcing of stanzas distributions separately were possible. Therefore, the distribution of plaice was driven by forcing the foraging capacity of only the juvenile life history stage over time to avoid overfitting the model. In agreement with the Schoener's D index, the results showed a good niche overlap for the spatial distribution of plaice juvenile and adults, confirming that forcing the foraging capacity of only one of the two multi-stanza was sufficient to drive spatial distributions

of both stages. For highly cannibalistic groups however, it might be necessary to force one part of the multi-stanza, e.g. by migration to spawning grounds, to account for changes that only apply to one species life stage. This would be particular relevant when using multi-stanza for species that have very different ecological and trophic ontogenetic changes across their life stages (e.g. eggs, larvae, juveniles and adults).

Even though the Schoener's D index of most FGs surpassed the threshold, there is a difference in variability (Fig. 3). The highest variabilities are displayed in pelagic FGs and FGs where the survey coverage might not have been extensive enough. This has two implications. First, it is important to carefully select FGs and the corresponding data when applying SDMs to Ecospace. The smaller the data coverage for the SDM the more variability in the spatial fit. Second, Ecospace seems to perform better when reproducing spatial distributions of more spatially bound FGs than for the fast moving pelagic FGs.

5. Conclusion

In our study, the new capabilities of Ecospace have proven to be a beneficial asset when reconstructing species' spatial distributions and their shifts over time. It also showed that in an ecosystem model like the one for the southern North Sea, implementing temporally changing habitat preferences maps based on PA on a sigmoidal profile generate better results than an exponential profile based on CPUE. Furthermore, combining SDMs with this trophic model has the potential to further inform about habitat preferences that include biotic interactions introduced by Ecospace. Nevertheless, our knowledge about the best practice in the new spatial-temporal external foraging capacity implementation could benefit from testing further strategies of fitting. In the future, the new capabilities inside Ecospace can be applied to assess changes in ecological indicators over time as well as to test different management strategies within the framework of marine spatial planning. In the light of climate change, it is possible to test how ecosystems react to temperature driven foraging capacities. Finally, there is not one best practice how to construct an ecosystem model. As with all models, the best model is always the one that best answers your research question in your part of the world's oceans and the best periodicity might differ between models and research questions. However, our study adds insights on the impact of habitat capacity maps on Ecospace results and helps to identify the issues that need to be taken into account when using SDMs as input for ecosystem models like Ecospace.

CRediT authorship contribution statement

Miriam Püts: Conceptualization, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. Marc Taylor: Conceptualization, Methodology, Writing - original draft, Writing - review & editing. Ismael Núñez-Riboni: Methodology, Writing - original draft, Writing - review & editing. Jeroen Steenbeek: Methodology, Writing - original draft, Writing - review & editing. Moritz Stäbler: Writing - original draft, Writing - review & editing. Christian Möllmann: Writing - original draft. Alexander Kempf: Supervision, Conceptualization, Methodology, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

None

Acknowledgement

We thank the participants of WKEWEIA for their input and comments on this work and Dr. Kathryn Morrison (McGill University) for enriching discussions about INLA. Furthermore, sincere gratitude to Dr. Natalia Serpetti (SAMS) for her thoughts on the paper draft and her support and discussions about the automated fitting routine. We are grateful for the feedback of Sandra Rybicki (TI-SF) on a draft of this paper. Comments given by the two anonymous reviewers greatly improved the manuscript. This research did not receive any specific grant from funding agencies in the public, commercial, or not-for-profit sectors.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecolmodel.2020.109189.

References

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., Matthiopoulos, J., 2008. Estimating space-use and habitat preference from wildlife telemetry data. Ecography 31, 140–160. https://doi.org/10.1111/j.20070906-7590.05236.x.
- Ahrens, R.N.M., Walters, C.J., Christensen, V., 2012. Foraging arena theory. Fish Fish 13, 41–59. https://doi.org/10.1111/j.1467-2979.2011.00432.x.
- Akaike, H., 1974. A new look at the statistical model identification. IEEE Trans Automat Contr 19 (6), 716–723.
- Alexander, K.A., Meyjes, S.A., Heymans, J.J., 2016. Spatial ecosystem modelling of marine renewable energy installations: gauging the utility of Ecospace. Ecol. Modell. 331, 115–128. https://doi.org/10.1016/j.ecolmodel.2016.01.016.
- Allee, R.J., Dethier, M., Brown, D., Deegan, L., Ford, R.G., Hourigan, T.F., Maragos, J., Schoch, C., Sealey, K., Twilley, R., Weinstein, M.P., Yoklavich, M.M., 2000. Marine and Estuarine Ecosystem and Habitat Classification. NOAA Technical Memorandum NMFS-F/SPO-43. National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Behrenfeld, M.J., Falkowski, P.G., 1997. Photosynthetic rates derived from satellite-based chlorophyll concentration. Limnol. Oceanogr. 42, 1–20. data accessed on: http:// www.science.oregonstate.edu/ocean.productivity/index.php last accessed: Jan. 2018.
- Beyer, H.L., Haydon, D.T., Morales, J.M., Frair, J.L., Hebblewhite, M., Mitchell, M., Matthiopoulos, J., 2010. The interpretation of habitat preference metrics under useavailability desians. Philos. Trans. R. Soc. B Biol. Sci. 365, 2245–2254. https://doi. org/10.1098/rstb.2010.0083.
- Bossier, S., Palacz, A.P., Nielsen, J.R., Christensen, A., Hoff, A., Maar, M., Gislason, H., Bastardie, F., Gorton, R., Fulton, E.A., 2018a. The Baltic sea Atlantis: an integrated end-to-end modelling framework evaluating ecosystem-wide effects of human-induced pressures. PLoS ONE. https://doi.org/10.1371/journal.pone.0199168.
- Chagaris, D.D., 2013. Ecosystem-based evaluation of fishery policies and tradeoffs on the West Florida Shelf. University of Florida.
- Chen, Z., Xu, S., Qiu, Y., Lin, Z., Jia, X., 2009. Modeling the effects of fishery management and marine protected areas on the Beibu Gulf using spatial ecosystem simulation. Fish. Res. 100 (3), 222–229. https://doi.org/10.1016/j.fishres.2009.08.001.
- Christensen, V., Pauly, D., 1992. ECOPATH II A software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Modell. 61, 169–185
- Christensen, V., Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecol. Modell. 172, 109–139. https://doi.org/10.1016/j.ecolmodel.2003. 09.003.
- Christensen, V., Walters, C.J., Pauly, D., Forrest, R., 2008. Ecopath With Ecosim Version 6 User Guide 281. Fish. Centre, Univ. Br. Columbia, Vancouver, Canada, pp. 1–235.
- Christensen, V., Coll, M., Steenbeek, J., Buszowski, J., Chagaris, D., Walters, C.J., 2014. Representing Variable Habitat Quality in a Spatial Food Web Model. Ecosystems 17. https://doi.org/10.1007/s10021-014-9803-3.
- Coll, M., Pennino, M.G., Steenbeek, J., Sole, J., Bellido, J.M., 2019. Predicting marine species distributions: complementarity of food-web and Bayesian hierarchical modelling approaches. Ecol. Modell. 405, 86–101. https://doi.org/10.1016/j.ecolmodel. 2019.05.005.
- Colleter, M., Valls, A., Guitton, J., Gascuel, D., Pauly, D., Christensen, V., 2015. Global overview of the applications of the Ecopath with Ecosim modeling approach using the EcoBase models repository. Ecol. Modell. 302, 42–53. https://doi.org/10.1016/j. ecoImodel.2015.01.025.
- Cragg, J.G., 1971. Some statistical models for limited dependent variables with applications to the demand for durable goods. Econometrica 39, 829–844.
- Darwin, C., 1859. On the Origin of Species by Means of Natural Selection, 6th Edition. John Murray, London.
- EMODnet_Substrate_1M_6October2016_singlepart, downloaded from:https://www.emodnet-geology.eu/, last accessed: May 2017.
- Garshelis, D.L., 2000. Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani, L., Fuller, T.K. (Eds.), Research Techniques in Animal ecology: Controversies and Consequences. Columbia University Press, New York, NY, pp. 111–164.
- General Bathymetric Chart of the Oceans (GEBCO), downloaded from:https://www.gebco.net/data_and_products/gridded_bathymetry_data/, last accessed: Feburary, 2019.
- Grüss, A., Babcock, E.A., Sagarese, S.R., Drexler, M., Chagaris, D.D., Ainsworth, C.H., Penta, B., De Rada, S., Sutton, T.T., 2016. Improving the spatial allocation of functional group biomasses in spatially-explicit ecosystem models: insights from three

M. Püts, et al.

Gulf of Mexico models. Bull. Mar. Sci. 92, 473–496. https://doi.org/10.5343/bms. 2016.1057.

- Grüss, A., Chagaris, D.D., Babcock, E.A., Tarnecki, J.H., 2018. Assisting Ecosystem-Based Fisheries Management Efforts Using a Comprehensive Survey Database, a Large Environmental Database, and Generalized Additive Models. Mar. Coast. Fish. 10, 40–70. https://doi.org/10.1002/mcf2.10002.
- Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecol. Modell. 135, 147–186.
- Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25, 173–182.

Hastie, T., Tibshirani, R., 1986. Generalized additive models. Statistical Science 1, 297–318.

Heymans, J.J., Coll, M., Link, J.S., Mackinson, S., Steenbeek, J., Walters, C., Christensen, V., 2016. Best practice in Ecopath with Ecosim food-web models for ecosystem-based management. Ecol. Modell. 331, 173–184. https://doi.org/10.1016/j.ecolmodel. 2015.12.007.

Johnson, D.H., 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61, 65–71. https://doi.org/10.2307/1937156.

- Mackinson, S., Daskalov, G., Heymans, J.J., Neira, S., Arancibia, H., Zetina-Rejón, M., Jiang, H., Cheng, H.Q., Coll, M., Arreguin-Sanchez, F., Keeble, K., Shannon, L., 2009.
 Which forcing factors fit? Using ecosystem models to investigate the relative influence of fishing and changes in primary productivity on the dynamics of marine ecosystems. Ecol. Modell. 220, 2972–2987. https://doi.org/10.1016/j.ecolmodel. 2008.10.021.
- Maunder, M.N., Punt, A.E., 2004. Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70, 141–159. https://doi.org/10.1016/j.fishres.2004.08.002.
- Núñez-Riboni, I., Taylor, M.H., Kempf, A., Püts, M., Mathis, M., 2019. Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (Gadus morhua) under climate change. ICES Journal of Marine Science fsz132. https://doi. org/10.1093/icesjms/fsz132.
- Olsen, E., Fay, G., Gaichas, S., Gamble, R., Lucey, S., Link, J.S., 2016. Ecosystem model skill assessment. Yes We Can! PLoS One 11, 1–24. https://doi.org/10.1371/journal. pone.0146467.
- Polovina, J.J., 1984. Model of a coral-reef ecosystem .1. The Ecopath model and its application to French frigate shoals. Coral Reefs 3, 1–11.

Rosenzweig, M.L., Abramsky, Z., 1986. Centrifugal community organization. Oikos 46, 339–348.

- Romagnoni, G., Mackinson, S., Hong, J., Eikeset, A.M., 2015a. The Ecospace model applied to the North Sea: evaluating spatial predictions with fish biomass and fishing effort data. Ecol. Modell. 300, 50–60. https://doi.org/10.1016/j.ecolmodel.2014.12. 016.
- Rue, H., Martino, S., Chopin, N., 2009. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. J. R. Stat. Soc. Ser. B Stat. Methodol. 71, 319–392. https://doi.org/10.1111/j.1467-9868.2008. 00700.x.
- Schoener, T.W., 1968. Anolis lizards of Bimini: resource partitioning in a complex fauna. Ecology 49, 704–726.
- Scientific, Technical and Economic Committee For Fisheries, 2017. The 2017 Annual Economic Report on the EU Fishing Fleet (STECF-17-12). Publications Office of the European Union, Luxembourg ISBN 978-92-79-73426-7, doi:10.2760/36154, PUBSY No. JRC107883.
- Scott, E., Serpetti, N., Steenbeek, J., Heymans, J.J., 2016. A Stepwise Fitting Procedure for automated fitting of Ecopath with Ecosim models. SoftwareX 5, 25–30. https://

doi.org/10.1016/j.softx.2016.02.002.

- Stäbler, M., Kempf, A., Mackinson, S., Poos, J.J., Garcia, C., Temming, A., 2016. Combining efforts to make maximum sustainable yields and good environmental status match in a food-web model of the southern North Sea. Ecol. Modell. 331, 17–30. https://doi.org/10.1016/j.ecolmodel.2016.01.020.
- Stäbler, M., Kempf, A., Smout, S., Temming, A., 2019. Sensitivity of multispecies maximum sustainable yields to trends in the top (marine mammals) and bottom (primary production) compartments of the southern North Sea food - web. PLoS ONE 14, 1–18. https://doi.org/10.1371/journal.pone.0210882.
- Stäbler, M., Kempf, A., Temming, A., 2018. Assessing the structure and functioning of the southern North Sea ecosystem with a food-web model. Ocean and Coastal Management 165, 280–297. https://doi.org/10.1016/j.ocecoaman.2018.08.017.
- Steenbeek, J., Coll, M., Gurney, L., Mélin, F., Hoepffner, N., Buszowski, J., Christensen, V., 2013. Bridging the gap (Chong et al., 2019)between ecosystem modeling tools and geographic information systems: driving a food web model with external spatialtemporal data. Ecol. Modell. 263, 139–151. https://doi.org/10.1016/j.ecolmodel. 2013.04.027.
- Steenbeek, J., Corrales, X., Platts, M., Coll, M., 2018. Ecosampler: a new approach to assessing parameter uncertainty in Ecopath with Ecosim. SoftwareX 7, 198–204. https://doi.org/10.1016/j.softx.2018.06.004.
- Stow, C., Jolliff, J., Jr, D.M., 2009. Skill assessment for coupled biological / physical models of marine systems. Mar. Syst. 76 (1–2), 4. https://doi.org/10.1016/j.jmarsys. 2008.03.011.
- Swets, J.A., 1988. Measuring the accuracy of diagnostic systems. Science 240 (4857), 1285–1293. https://doi.org/10.1126/science.3287615.
- Taylor, K., 2001. Summarizing multiple aspects of model performance in a single diagram, J. Geophys. Res 106 (D7), 7183–7192.
- Ed. byValentine, P.C., Todd, B.J., Kostylev, V.E., 2005. Classification of marine sublittoral habitats with application to the northeastern North America region. In: Barnes, P.W., Thomas, J.P. (Eds.), Benthic Habitats and the Effects of Fishing. American Fisheries Society Symposium, 41. American Fisheries Society, Bethesda, Maryland, pp. 183–200.
- Walters, C., Christensen, V., Pauly, D., 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7, 139–172. https://doi.org/10.1023/A:1018479526149.
- Walters, C., Pauly, D., Christensen, V., 1999. ECOSPACE: prediction of mesoscale spatial patterns in trophic relationships of exploited ecosystems, with particular reference to impacts of marine protected areas. Ecosystems 2, 539–554.
- Walters, C., Pauly, D., Christensen, V., Kitchell, J.F., 2000. Representing density dependent consequences of life history strategies in aquatic ecosystems: ecoSim II. Ecosystems 3, 70–83. https://doi.org/10.1007/s100210000011.
- Walters, C., Christensen, V., Walters, W., Rose, K., 2010. Representation of Multistanza Life Histories in Ecospace Models for Spatial Organization. Bull. Mar. Sci. 86, 439–459 https://doi.org/papers3://publication/uuid/F835554D-9C95-4A26-AA0B-31166058CC5B.
- Warren, D.L., Glor, R.E., Turelli, M., 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution (N. Y). 62, 2868–2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x.
- Wood, S., 2003. Thin Plate Regression Splines 65, 95-114.
- Wood, S.N., 2009, mgcv, R Package Version 1.6-0.
- Wood, S.N., 2017. Generalized Additive Models: An Introduction With R (Wnd Edition). Chapman and Hall/CRC.