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A calorific map of harbour porpoise prey in the North Sea

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Summary

This project provides a first attempt to describe the spatiotemporal energetic availability of different prey species to harbour porpoises (*Phocoena phocoena*) in the North Sea. Harbour porpoises are very abundant in the North Sea and their diet consists of a variety of prey species. Harbour porpoises are listed on Annex II of the EU Habitats Directive and accordingly Special Areas of Conservation (SAC) are designated for this species, one of them being in the southern North Sea. The distribution of porpoises is thought to be prey driven but our understanding of prey availability, particularly in the context of the Southern North Sea SAC, is currently limited. The need to assess and potentially manage activities within the SAC is the context for initiating this work.

To compare our prey estimates with knowledge of porpoise distribution we predicted prey availability for the most recent two years that North Sea-wide cetacean surveys were carried out (2005 and 2016). A cleaned dataset of the International Bottom Trawl Survey (NS-IBTS) was used to create density surface models using Generalised Additive Models for the different prey species. Soap filters were used to avoid smoothing across boundary features. Relative gear efficiency factors per prey species and size class data were used to correct for catchability and biomass values were converted to energetic content using energy density values from the literature. Energy maps were produced for Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), European sprat (*Sprattus sprattus*), Atlantic herring (*Clupea harengus)* and sandeels (Family *Ammodytidae*).

The modelled prey distribution maps fit well with previously described spatial patterns for the fish species. Overall, it appears that the energy available was higher in summer and was also higher in 2016 in comparison to 2005, especially in the southern and north-western North Sea. For both the Southern North Sea SAC and in the wider North Sea, the main energetic contributions to the overall energy density were from whiting and sandeels. During the winter, European sprat also added considerably to the overall energy density while in summer, Atlantic herring added a substantial amount of energy.

Overall, large amounts of prey energy are predicted to be available both within and outside the SAC boundary. Based on five of the reported main prey species of harbour porpoise overall mean estimates of total energy available in the North Sea ranged between 21,610 (winter) - 30,764 megajoule (MJ) per km^2 (summer) in 2005 and 34,661 (winter) - 76,938 MJ per km^2 (summer) in 2016. Reviews of harbour porpoise daily energy requirements varied between 9 - 31 MJ per day. However, the energy predicted may not correlate to the actual available energy for porpoises given the role of other marine predators and the fishing industry present in the North Sea.

Contents

1   Introduction

Harbour porpoises are wide-ranging highly mobile animals (Read & Westgate 1997) and the most abundant cetacean species in the North Sea (Hammond *et al.* 2002, 2013, 2017). The diet of harbour porpoises consists of a wide variety of fish and cephalopod species and varies regionally; however, only a few prey types dominate the diet in any one area (Santos & Pierce 2003; Santos *et al.* 2004). In Scottish waters, historical studies have indicated whiting and sandeels dominate porpoise diets (Santos & Pierce 2003). In Dutch coastal waters, porpoises tend to consume predominantly gadoids such as cod and whiting, gobies (Family *Gobiidae*), sandeels, and clupeids like European sprat and Atlantic herring (Leopold 2015).

Harbour porpoises are considered to feed at high rates, (*e.g.* pursuing up to 200-550 prey items an hour at peak times with high capture success rates) (Wisniewska *et al.* 2016, 2018). It has been suggested that Wisniewska *et al.* (2016) might show an extreme view of porpoise biology (Hoekendijk *et al.* 2018). Still, harbour porpoises have a high metabolic rate and only a limited energy storage capacity (Bjørge 2003). Consequently, there is concern porpoises could be vulnerable to starvation due to their limited ability to buffer against diminished food availability.

Different prey types have a range of energy densities and therefore represent different values to the predator (Booth, in review). Given that there are estimates of foraging effort (Wisniewska *et al.* 2016, 2018) and energy requirements (for the same individuals) (Rojano-Donates *et al.* 2018), it is now possible to assess the potential for porpoises to meet their energy demands. Estimates from Booth (in review) indicate a broad range of energy intake rates for tagged harbour porpoises between 0.57 - 0.99 MJ per hour for juveniles and 0.92 - 2.45 MJ per hour for adults (prey type and prey target size were key drivers of energy intake estimates). The energy requirements for the same tagged individuals ranged from 0.39 - 1.29 MJ per hour (Rojano-Donates *et al.* 2018) (these correspond well to estimates of the daily energy intake for captive porpoises ranges between 8 - 35.5 MJ per day (Kastelein *et al.* 1997; Lockyer *et al.* 2003)). From a model developed for wild adult harbour porpoises, Gallagher *et al.* (2018) estimated minimum daily energy intake requirements to range from 6.7 (±2.1) MJ per day for males and 16 (±5.3) MJ per day for pregnant and lactating females.

Harbour porpoise limited energy storage, high foraging and metabolic rate, may mean that porpoise distribution is more tightly linked to higher prey abundance and/or prey quality than for other marine mammal species (*e.g.* bottlenose dolphins and seals which have larger energy stores and therefore are more likely to be able to cope with periods with limited prey availability). For harbour porpoises, this highlights that understanding prey quality and considering the energetic content of prey is critical to our understanding of porpoise ecology.

Results from two dedicated North Sea-wide surveys showed a major summer distribution shift of harbour porpoises from northern to the southern areas (Hammond *et al.* 2002, 2013). In 2016 SCANS III, the large-scale ship and aerial survey to study the distribution and abundance of cetaceans was carried out, full results are not yet published. The drivers of this distributional shift are not yet identified but are likely to be linked to changes in prey distribution (Sveegaard *et al.* 2012; Hammond *et al.* 2013). However, the spatiotemporal relationship between these predators and their prey is poorly understood. Defining important areas for harbour porpoises is therefore difficult due to their high mobility and probable prey-driven distribution.

The identification and designation of Special Areas of Conservation (SAC) in the UK under the Habitat's Directive has used environmental variables as proxies for prey distribution. One of these SACs lies within the southern North Sea. The selection process for this site was

based on predictions of persistent high-density areas of harbour porpoise (Heinänen & Skov 2015). The resulting Southern North Sea SAC is located off the east coast of England covering an area of 36,951km^2 and includes distinct key winter (October-March) and summer (April-September) areas thought to be preferred due to prey availability (JNCC 2017). The majority of the northern part of the site represents the summer area while the southern part is considered an important winter region (Figure 1).

To more fully understand the extent to which the SAC contributes to achievement of the Favourable Conservation Status (FCS) for harbour porpoises within UK waters it is crucial to better understand the relationship between porpoises and their prey.
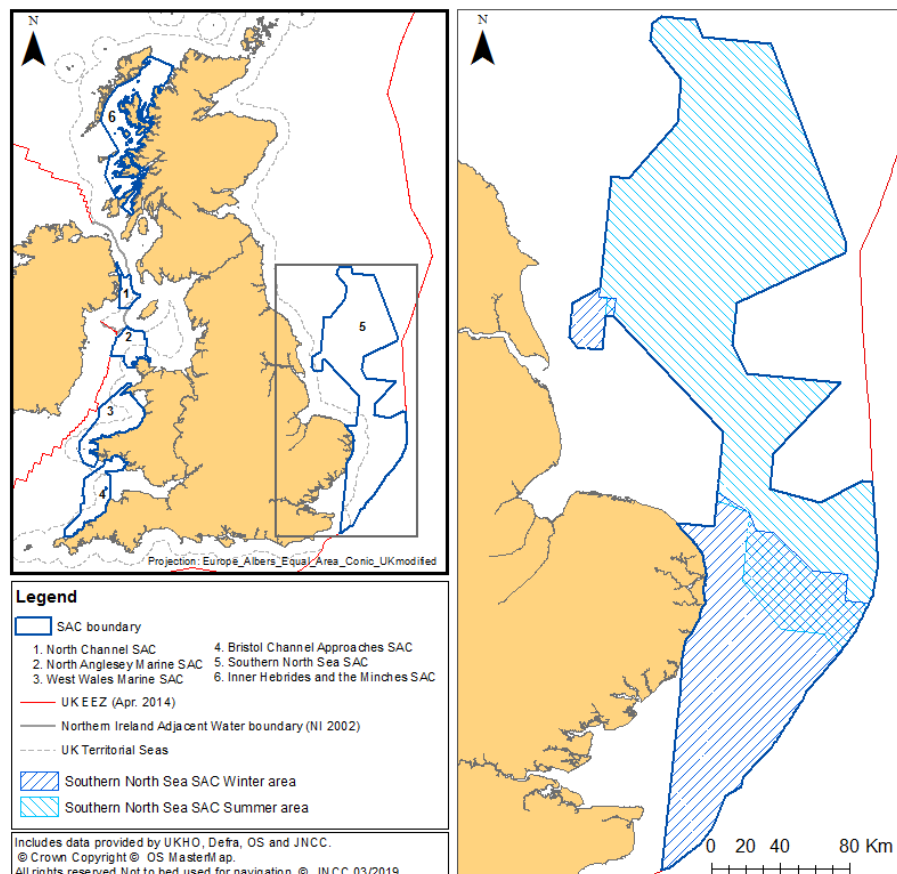
Figure 1. Sites designated for harbour porpoise in UK waters. Site 6 (six) is the Southern North Sea SAC and is the primary focus of this project.

1.1 Project objectives

The overall goal of this project was to better understand the spatial and temporal variations in prey abundance and to map the calorific value of prey that might impact porpoise distribution. The project can be broken down into the following specific objectives:

- Review published literature to summarize harbour porpoise diet and identify 'main' prey species along with a range of energy density values for the 'main' prey species (by season and size class where available).
- Generate seasonal maps of the energetic value of the 'main' prey species in the North Sea and seasonal maps showing the total calorific value of all the 'main' prey species combined.

2 Methods

2.1 Identification of important prey species

The importance of prey species for harbour porpoises was assessed through the estimated proportion (by reconstructed biomass) that prey species contributed to the diet. This was done by examining different studies that used stomach content analysis to determine the diet of harbour porpoises in the western North Sea (see the overview in section 1 and below). This method derives the estimated diet composition of undigested hard prey remains (*e.g.* otoliths) in stomach contents of stranded and bycaught individuals. Prey species that contributed ≥5% of the total prey weight (regardless of season or year) were selected as main prey species.

Important prey species for harbour porpoises in the western North Sea included: gobies, whiting, Atlantic herring, sandeels and European sprat (Table 1). In Scottish waters; the north-western North Sea, whiting and sandeels dominated the diet (Santos 1998; Santos *et al.* 2004). In Dutch waters in the southwestern North Sea, the most important prey species included six different types of fish: gobies, whiting, sandeels, European sprat, Atlantic herring, and Atlantic cod (Jansen 2013; Leopold *et al.* 2011; Leopold 2015; Santos 1998). The same species groups were also identified as most important for harbour porpoises that stranded along the Dutch coastline by Leopold (2015) according to an Index of Relative Importance (IRI). However, the recovery rate of large otoliths is higher due to longer digestion times compared to smaller ones (Ross *et al.* 2016). This may introduce bias as the contribution of larger fish species (*i.e.* cod, whiting) in the diet could be overestimated, while smaller species are underestimated (*i.e.* Atlantic herring, European sprat, gobies, sandeels).

Table 1. The main diet composition of harbour porpoises in different areas of the North Sea. Calculated according to the estimated proportion (by reconstructed biomass) that each prey contributed to the diet. The sample size of each study is reported as n. Numbers are not always reported to species level, in such instances, values are reported by species group. Grey highlighted numbers represent prey groups and species that contributed more than 5% of the total prey weight.

Species group and species	Dutch North Sea				Scottish North Sea	
	1989-1995[1] n=62	2003-2010[2] n=76	2003-2010[3] n=229	2006-2014[4] n=826	1992-1996[1] n=72	1992-2003[5] n=188
Gobies	6.4%	36.6%	22.1%	20.5%		
Gadidae	85.9%			36.5%	54.2%	
whiting	78.7%	25.4%	42.3%		43.6%	53.0%
haddock						
saithe						5.6%
pollock						
Atlantic cod	3.3%	5.2%	4.4%			3.8%
Clupeidae	1.9%			10.9%		
Atlantic herring		5.9%	4.6%		3.0%	1.3%
European sprat		4.1%	5.8%			
Sandeels	2.8%		11.1%	18.1%	41.1%	25.6%
Lesser sandeel		13.2%				

[1] (Santos 1998) [2] (Jansen 2013) [3] (Leopold *et al.* 2011) [4] (Leopold 2015) [5] (Santos *et al.* 2004)

2.2   Fish biomass estimation

2.2.1   Trawl survey data

The generation of calorific maps for harbour porpoise, prey species in the North Sea were based on fish survey data. Within the North Sea, the International Council for the Exploration of the Sea (ICES) coordinates the International Bottom Trawl Survey (NS-IBTS). This survey aims to monitor the abundances of commercial and non-commercial fish species. The NS-IBTS started in the 1960s but in 1983 surveying expanded to the entire North Sea within the 200m depth contour from January-March. From 1991 these surveys were carried out in each season (known as quarters) to provide information on the seasonal distribution of stocks sampled. However, it was impossible to maintain such high levels of research vessel effort (ICES 2012) and therefore, since 1996 most countries carry out surveys only twice a year, in quarter one (January-March) and quarter three (July-September). This therefore dictates the resolution available for exploring seasonality in prey availability for harbour porpoises.

Data from these surveys are reported as Catch Per Unit Effort (CPUE), measured as the number of individuals caught per half an hour trawling. However, here we would like to estimate fish density per unit area and thus have to correct for the area swept during the trawl. This also reduces the high variation in CPUE that is due to differences in area swept (largely linked to trawl duration and tow speed but also related to door- and wing-spread). Furthermore, although the data that are available from ICES[1] have passed quality control routines there are still quality issues (Daan 2001; ICES 2018a). Fortunately, Marine Scotland Science has produced publicly available quality assured monitoring and assessment datasets that are derived from the NS-IBTS (Moriarty *et al.* 2017) and these have been used for this project. The catch data for all species are expressed as biomass per km^2 at length classes (cm). Biomass per km^2 was calculated as:

$$D_{biomass,S,L,H} = \frac{(N_{S,L,H} * W_{S,L})}{A_{H,Wing}}$$
(1)

Where $D_{biomass,S,L,H}$ is the biomass of fish of species (S) and length (L) per km^2 estimated at the spatial location of trawl sample (H), $N_{S,L,H}$ is the total number of fish of specified species and length in the catch at a location, $W_{S,L}$ is the estimated weight of individual fish of specified species and length, and $A_{H,Wing}$ is the area of seabed swept by the net.

2.2.2   Sandeels and gobies

Due to catchability issues and the vertical distribution pattern of sandeels the NS-IBTS data are not representative for this species and therefore another approach had to be adopted. Annual total stock biomass (TSB) estimates from ICES for sandeel area 1-4 (excluding the northern North Sea Figure 5) and sandeel habitat areas were used (ICES 2018b; Jensen *et al.* 2011). Annual TSB per sandeel area was converted to energetic content using the energy density from Table 2. The estimated energetic content was then divided by the total area of the sandeel habitat in the ICES area resulting in an energy per km^2 for each sandeel area.

Gobies are also not well represented in the NS-IBTS data due to their small size and occurrence in untrawlable areas close to the coast (Knijn *et al.* 1993). Therefore, gobies had to be excluded from the analysis.

2.2.3   Data selection

Data from 2003-2017 were used to make predictions for the years (2005 and 2016) for which estimates of harbour porpoise abundance in the North Sea are available (Hammond *et al.* 2013, 2017). Survey coverage across the North Sea for the NS-IBTS is displayed in Appendix 1. For this project both the quarter 1 (January-March) and quarter 3 (July-September) datasets were used (Moriarty & Greenstreet 2017a, 2017b). These quarters were taken to represent the winter (October-March) and summer (April-September) seasons identified within the SAC. Only size classes determined to be readily consumable by harbour porpoises (<40cm - Aarefjord *et al.* 1995) were selected.

2.2.4   Catchability

As bottom trawl gear does not catch all fish in the path of the net, survey catches do not represent true amounts of fish in the area surveyed. To account for this relative gear efficiency factors per species and size class from Walker *et al.* (2017) were used. These factors were estimated using a method that firstly estimated catch-ratios between different gear types that were then rescaled to estimate gear efficiency by comparing abundance estimates with the estimates from stock assessments (Fraser *et al.* 2007; Walker *et al.* 2017).

2.3   Energy conversion

Estimates of biomass for each prey species were converted to energetic content using energy density values from the literature. Where available, energy densities per season and length class for the study area were used. However, there are only limited published data records and therefore this could only be done for Atlantic herring and whiting. When data for a given size class was missing, the value of the closest size class was assigned. When such data were not available, a single energy density value was used for all size classes (*i.e.* cod, European sprat and sandeels). The energetic conversion factors are shown in Table 2.

Table 2. Prey species energy content.

Species	Size class (cm)	Quarter	Energy Density (kJ per g)	Reference
Cod	all	all	4.2	1
Whiting	1.0-11.9	1	4.1	2
	12.0-14.9	1	4.0	2
	15.0-19.9	1	4.3	2
	20.0-24.9	1	4.8	2
	25.0-39.9	1	5.0	2
	1.0-5.9	3	3.8	2
	6.0-7.9	3	3.7	2
	8.0-9.9	3	3.6	2
	10.0-11.9	3	3.8	2
	12.0-14.9	3	3.9	2
	15.0-19.9	3	4.7	2
	20.0-24.9	3	5.3	2
	25.0-39.9	3	5.4	2
Atlantic Herring	1.0-9.9	1	4.6	3
	10.0-11.9	1	4.7	2
	12.0-14.9	1	4.4	2
	15.0-19.9	1	4.4	2
	20.0-24.9	1	6.5	2
	25.0-39.9	1	8.5	3
	1.0-4.9	3	4.1	2
	5.0-5.9	3	4.2	2

	6.0-7.9	3	3.9	2
	8.0-9.9	3	4.5	2
	10.0-11.9	3	4.4	2
	12.0-14.9	3	5.2	2
	15.0-19.9	3	10.1	2
	20.0-24.9	3	11	2
	25.0-39.9	3	11.9	2
Sandeel	all	all	5.8	3
European Sprat	all	all	7.6	3

[1](Lawson *et al.* 1998) [2](Pederson & Hislop 2001) [3] (Wanless *et al.* 2005)

2.4 Estimation of spatial distribution of energy

The spatial energy distribution represented by each prey species and season (quarter 1 and 3) over the entire North Sea was modelled as a function of a number of covariates using a Generalised Additive Modelling (GAM) framework. Covariates considered included depth, year, latitude, and longitude. All analysis was performed in R version 3.5.1 (R Development Core Team 2018).

The GAMs included a three-dimensional tensor product smooth for space (longitude, latitude) and time (year). Furthermore, to increase confidence in predictions close to land and to avoid smoothing across boundary features, soap film smoothers were used (Wood *et al.* 2008). This approach avoids the assumption that densities are similar in neighbouring areas that are separated by land. In generating the soap film, knots were placed over the data and land was set to zero which ensured smoothing towards data points and avoided predicting over the land boundary.

In preliminary analyses, we considered a variety of error distributions for the response variable (energy density (in MJ) per km^2): Gaussian, negative binomial, quasi-Poisson, and Tweedie distribution. Additionally, a log-transformation of the response variable was considered for all error distributions. The appropriate distribution and/or transformation was selected by visual inspection of Normal Q-Q plots and Residuals vs Fitted plots.

Smoothing parameter selection was performed by restricted maximum likelihood (REML) (Wood 2011). Model selection was based on a mixture of measures (*i.e.* Akaike information criterion (AIC), REML, percentage deviance explained) and a visual inspection of predicted versus observed spatial distributions. Additionally, the need of the complex full soap model with a smooth interaction of space and time was checked. The full soap 3D model (equation 2) was compared with a soap 2D model that replaced the three-dimensional space-time effect by an additive space-time effect. Furthermore, we compared the three-dimensional space-time model with the soap filter against fitting the model with a conventionally used thin-plate regression spline (TPRS) basis. Year was included as a cubic regression spline (CRS) and depth was modelled as a smoothing spline.

Three-dimensional space-time effect model:
$$\left(Energy_{it}\right) = s\left(depth_{it}\right) + te\left(longitude_i, latitude_i, year_t\right) \qquad (2)$$

Additive space-time effect model:
$$\left(Energy_{it}\right) = s\left(depth_{it}\right) + te\left(longitude_i, latitude_i\right) + s\left(year_t\right) \qquad (3)$$

Within the three-dimensional space-time effect model the spatial pattern could change with time. In the additive space-time effect model the spatial pattern was fixed, but the intensity could change with time.

Temporal autocorrelation of the residuals was checked using autocorrelation function (ACF) plots and spatial autocorrelation was investigated using variograms and bubble plots.

2.5   Prediction maps

Prediction surfaces showing the spatial variation in energy represented by each prey species were generated over a regular bathymetry grid available from the European Marine Observation Data Network (EMODnet) Seabed Habitats project[2]. This raster with a resolution of 115m x 115m was re-gridded to a resolution of 1km^2.

The prediction grid was restricted to the area that was covered by the data for each season. The prediction grid for winter covered an area of 469,145km^2 and in summer the grid was slightly smaller (463,010km^2).

First, a distribution map for each prey species per year (2005, 2016) and season (winter – January-March, summer – July-September) was generated. Second, surfaces for each species were summed to produce a map of combined energy represented by all prey species combined (maps separated by season and year). This process was done with and without the inclusion of sandeels because the approach to generate the energy surfaces for sandeels was different from the other species.

Third, the total energy represented by each species over the entire North Sea was calculated by summing energy values over all grid cells in the prediction grid. The mean energy density was estimated, as well as the % of the total energy that lay within the entire SAC and the seasonal component of the SAC that matched the season of the distribution map. Furthermore, the interquartile range (IQR) and median values for energy surfaces for each species by year and season for the entire North Sea were calculated. To compare the amount of energy in the SAC in comparison to the North Sea relative to the area size, a Ratio Energy SAC (RES) score was calculated per species. RES values of 1 would indicate that the SAC has similar average energy (MJ per km^2) to the wider North Sea while values >1 would suggest that the SAC has higher average energy values. RES was calculated both for the entire SAC and for the seasonal component of the SAC as:

$$RES = \frac{(total\ energy\ SAC : total\ energy\ North\ Sea)}{(total\ area\ size\ SAC : total\ area\ size\ North\ Sea)} \tag{4}$$

3   Results

3.1   Model

The assumption of normality and homogeneity of variances was most appropriately satisfied by a log-transformation and Gaussian distribution of the response variable. The log-transformation reduces the effects of relatively high/low catches. Correlograms, variograms, and bubble plots of the final models indicated very weak autocorrelation and deviance residuals were evenly spread.

The most adequate model for all prey species was the full soap 3D model explaining between approximately 26% to 79% of the total observed variation in the data (Table 3). Although, the TPRS model always (except for sprat in winter) had a better fit in terms of AIC and other measure (Table 3) the full soap 3D model improved the performance of the model by avoiding leakage across land. Furthermore, the soap filter seemed to perform better in

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[2] emodnet-seabedhabitats.eu.

the visual comparison between predicted and observed distributions and used considerably fewer degrees of freedom. The variation explained was considerably higher for European sprat probably due to the distinct distributional pattern.

Table 3. For all models (*i.e.* full soap 3D (three-dimensional space-time effect model with soap filter) TPRS (three-dimensional space-time effect model with a TPRS base) and the soap 2D (additive space-time effect model with soap filter)) the AIC score, REML score, percentage deviance explained, and degrees of freedom (DF) per prey species and season. Winter represents January-March and summer represents July-September.

Species	Season	Model	AIC	REML	deviance explained	DF
Cod	*Winter*	**full soap 3D**	**18525**	**9325**	**26.1**	**109**
		TPRS	18482	9312	29.3	198
		soap 2D	18644	9367	21.9	57
	Summer	**full soap 3D**	**14926**	**7540**	**41.5**	**111**
		TPRS	14858	9321	45.7	198
		soap 2D	15000	7553	38.4	62
Atlantic Herring	*Winter*	**full soap 3D**	**19721**	**9972**	**41.5**	**159**
		TPRS	19596	7528	42.8	278
		soap 2D	19983	10053	29.9	62
	Summer	**full soap 3D**	**17638**	**8879**	**40.2**	**106**
		TPRS	17578	9943	43.9	182
		soap 2D	17689	8894	37.5	59
European Sprat	*Winter*	**full soap 3D**	**17461**	**8851**	**78.8**	**172**
		TPRS	17762	8868	81.0	297
		soap 2D	17770	8958	75.8	64
	Summer	**full soap 3D**	**16021**	**8134**	**60.9**	**144**
		TPRS	15854	8793	65.8	279
		soap 2D	16059	8125	58.7	73
Whiting	*Winter*	**full soap 3D**	**16042**	**8156**	**50.1**	**151**
		TPRS	15907	8090	54.3	267
		soap 2D	16212	8189	45.6	67
	Summer	**full soap 3D**	**14235**	**7265**	**49.9**	**161**
		TPRS	14009	8101	55.1	230
		soap 2D	14212	7232	47.7	81

3.2 Depth

For each prey species, energy increased with increasing depth until reaching a maximum after which the trend either plateaued or decreased (Figure 2).

The density of Atlantic herring reached an optimum around 145m depth in winter and 105m depth in summer. The optimum density distribution for cod seemed to lie around 100m depth in both seasons. In winter the trend plateaued while in summer the trend declined sharply at depths greater than 100m. Regardless of season, the optimum density distribution of European sprat was around 60m. The optimum density distribution of whiting lay between 75m and 150m depth.
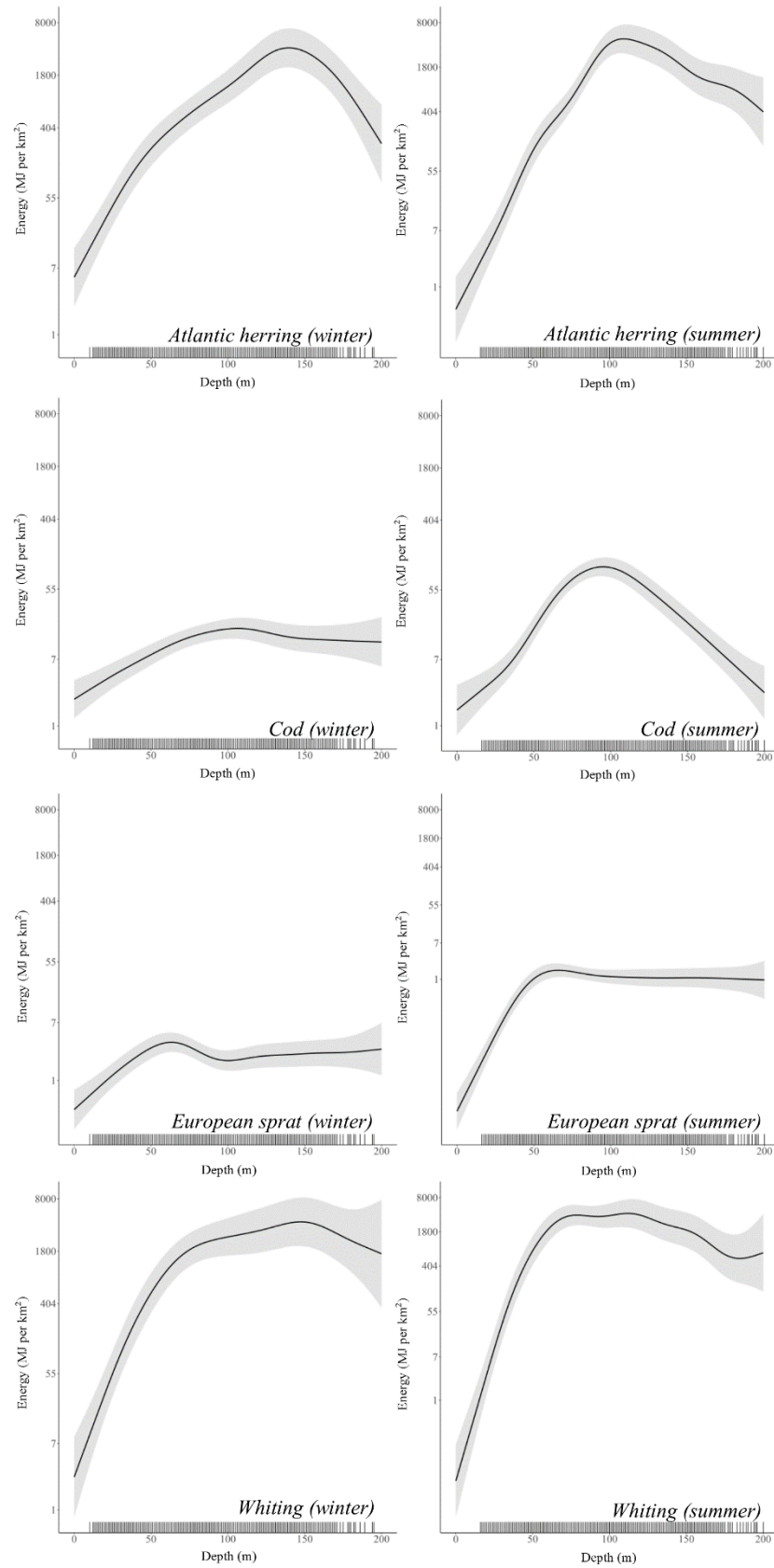
Figure 2. Effect of depth (m) on the energy (MJ) per km^2 according to final generalised additive models. Created by fixing all other parameters in the model (*i.e.* x, y, year) to median values. Note y-axis is at similar scale but plots are not aligned.

3.3   Spatiotemporal distribution pattern and trend by species

Distribution maps of energy represented by each prey species (except sandeels) are shown in Figure 3 for winter and Figure 4 for summer. Predicted energy availability was greater in 2016 than in 2005 for all species except cod. The annual distribution of energy represented by sandeels in 2005 and 2016 is shown in Figure 5. Median energy values along with the IQR for each species and overall are summarized in Table 4.

3.3.1   Atlantic herring

Atlantic herring energy was mainly distributed in the south-eastern and north-eastern North Sea in winter and in the north-western North Sea during summer. During both seasons, high energy density areas shifted southwards from 2005 to 2016. The lowest overall amount of energy was observed in the summer of 2005 with median energy values of 601.8 MJ per km^2 (IQR = 54.6 - 4914.8) and the highest in the summer of 2016 (median = 812.4 MJ per km^2 (IQR = 134.3 - 6634.2)).

3.3.2   Cod

The available energy represented by cod (<40cm - see methods) was relatively low in comparison to the other prey species and was especially low in the summer of 2016 (median (IQR) = 7.4 (1.1 - 54.6) MJ per km^2). Median energy in winter 2016 was estimated to be 13.5 (IQR = 5.0 - 73.7) MJ per km^2. Energy available was higher in 2005 in both summer and winter (medians of 30.0 and 18.2 MJ per km^2 respectively). The available energy from cod was mainly distributed in the northern part of the North Sea with high values on the north-eastern edge of the predicted surface (close to the Norwegian trench). In winter, cod energy values were greater in 2016 than in 2005, especially in the northern North Sea. In the northern North Sea, energy represented by cod in summer was higher in 2016 than 2005. However, in winter energy was lower in 2016 compared to 2005 and shifted more to the north.

3.3.3   European sprat

Energy represented by European sprat was mainly distributed in the southern and north-western part of the North Sea. Relatively low values were observed in the north-eastern North Sea. In summer, energy was concentrated south of the Dogger Bank and north of the Southern Bight. The entire spatial pattern shifted slightly more north in 2016 in comparison to 2005. Energy estimates were higher in 2016 than 2005 in both the winter (medians: 2005 - 37 MJ per km^2; 2016 - 224 MJ per km^2) and summer (medians: 2005 - 109 MJ per km^2; 2016 - 543 MJ per km^2).

### 3.3.4   Whiting

Whiting energy was widely distributed throughout the North Sea except over the Dogger Bank and in the eastern part of the German Bight. These lower energy areas were more profound in 2005 than in 2016. In summer and in 2016 the energy was higher in the Southern Bight. Overall, the energy from whiting was the highest among all species modelled in this study (Figure 3 & 4, Table 4 & 5). As with other species, the energy available was higher in 2016 than 2005 in both winter (medians: 2005 - 1339 MJ per km^2; 2016 - 2441 MJ per km^2) and summer (medians: 2005 - 4447 MJ per km^2; 2016 - 8955 MJ per km^2).

3.3.5   Sandeels

Sandeel energy values (for the whole year) were higher in the north-western North Sea and relatively very low in the eastern part. Overall, the energy represented by sandeels was higher in 2016 than 2005 and the difference between low and high values was amplified in 2016. The IQR and median values of sandeels are zero (Table 4) indicating that the distribution of sandeels is patchy. But the mean energy estimates (Table 4) indicate that where they are present, large amounts of energy are available (mean 2005: winter - 9,577 MJ per km^2; summer - 9,452 MJ per km^2), especially so in 2016 (mean 2016: winter - 16,772 MJ per km^2; summer - 16,553 MJ per km^2).

A calorific map of harbour porpoise prey in the North Sea
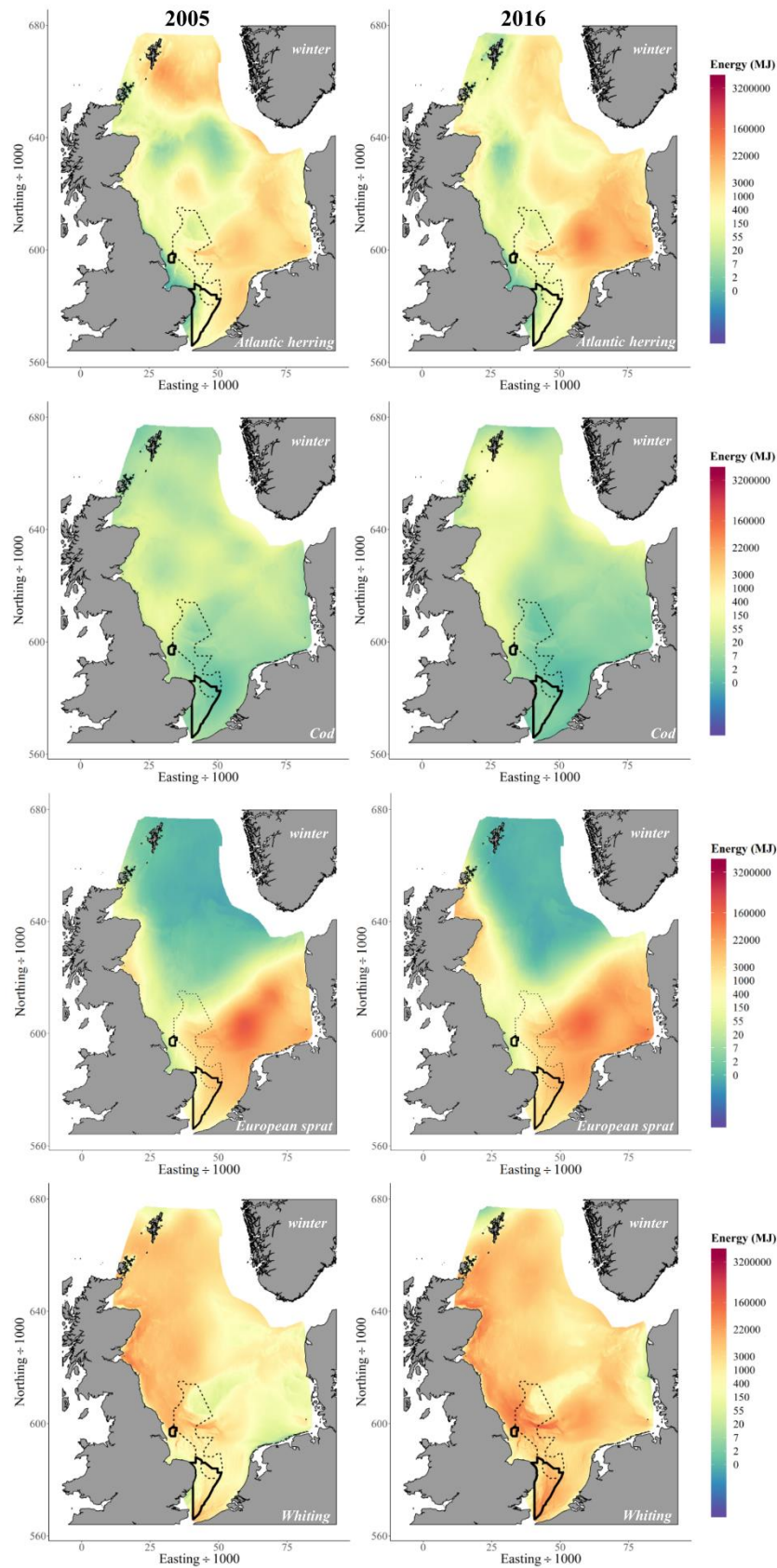
Figure 3. Spatiotemporal winter distribution (January-March) of porpoise prey species energy per km^2 for the North Sea, illustrated for 2005 in left panels and 2016 in right panels. Bold outlines represent the winter part of the SAC and the dotted lines represent the summer part of the SAC.

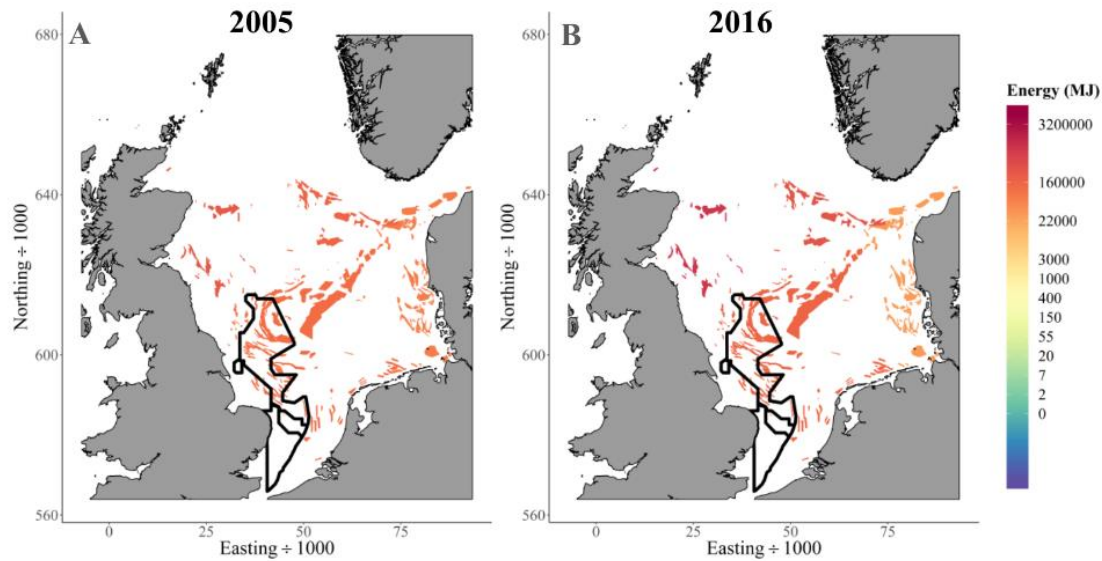A calorific map of harbour porpoise prey in the North Sea
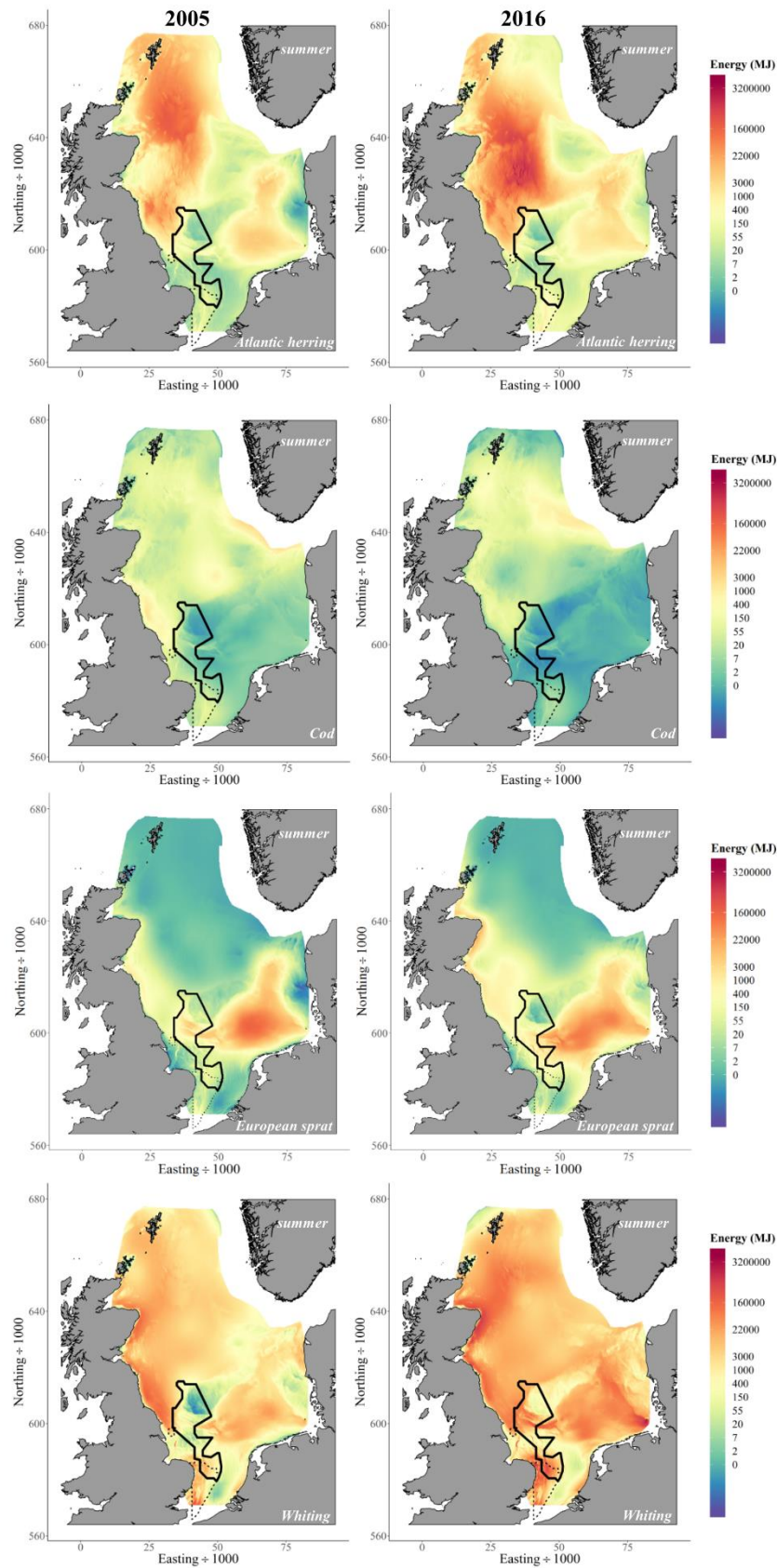
Figure 4. Spatiotemporal summer (July-September) distribution of porpoise prey species energy per km² for the North Sea, illustrated for 2005 in left panels and 2016 in right panels. Bold outlines represent the summer part of the SAC and the dotted lines represent the winter part of the SAC.

Figure 5. Distribution of sandeels per km² for the North Sea in 2005 (left) and 2016 (right). Energetic values are based on ICES sandeel stock assessments and locations are based on sandeel fishing grounds. The bold outlines represent the entire extent of the SAC.

3.3.6   Overall energy maps by season and year

Maps of the energy across all species analysed for each year (2005, 2016) and season (winter, summer) are shown in Figure 6. Energy contribution by species is shown in Table 4.

In Appendix 2 there are also combined maps for all species that could be modelled using GAMs, thus excluding sandeels. Appendix 3 shows maps of available energy resolved to the scale of the SAC boundary.

Overall, there are extremely high levels of energy available to harbour porpoises (and other predators) (relative to the population density and daily energy requirements of harbour porpoises in the North Sea). Total estimates (including sandeels) indicate mean energy available per unit area between 21,610 - 34,661 MJ per km² in 2005 and 30,763 - 76,937 MJ per km² in 2016 (Table 4). The higher values in 2016 are mainly in the southern and north-western North Sea. Of the five prey species considered here over the predicted two years, whiting and sandeels were the main contributors in terms of energy over the entire North Sea (Table 4). During winter, the contribution of European sprat to the overall pattern was also considerable. Atlantic herring is a main contributor in summer.
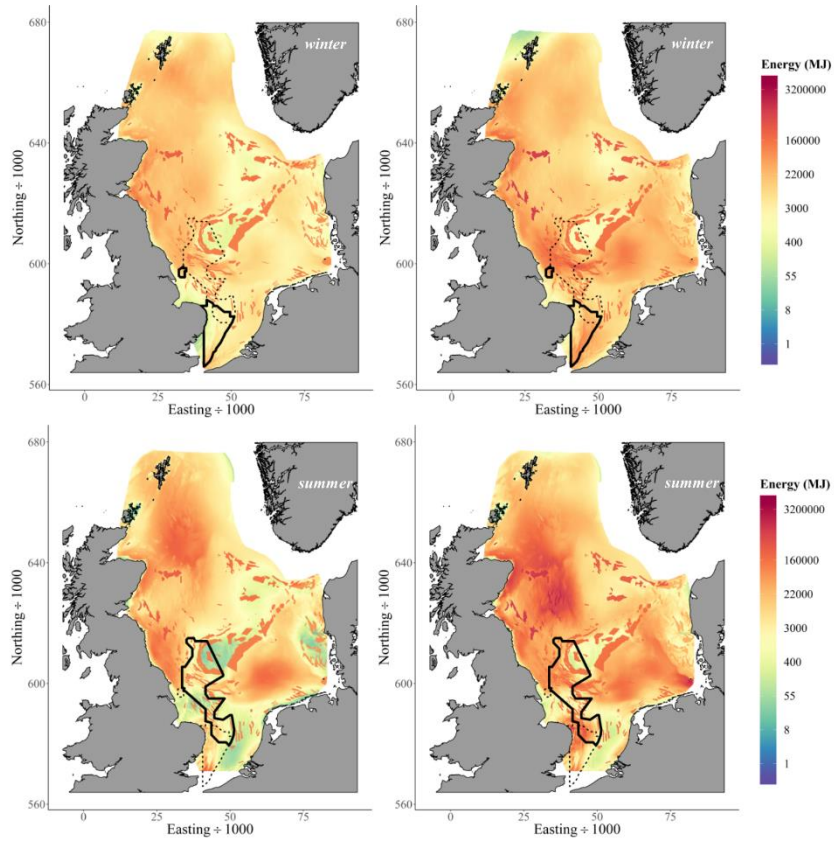
Figure 6. Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species energy per km² for the North Sea, illustrated for 2005 on the left and 2016 on the right. Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.

A calorific map of harbour porpoise prey in the North Sea

Table 4. Mean, median, and Interquartile range (IQR) values for energy (MJ per km^2) surfaces for each species and all species combined by year and season for the entire North Sea. Species contribution illustrates the contribution of each species to the energy in the total North Sea (for the species considered here). Note that the area of the North Sea that was predicted over is different by season, slightly smaller in summer (for winter the North Sea area is 469,145km^2 and in summer this area is 463,010km^2). Furthermore, to compare the amount of energy in the SAC in comparison to the North Sea relative to the area size a Ratio Energy SAC (RES) was calculated. RES was calculated as: (total energy in SAC / total energy in the North Sea) / (total area size SAC / total area size of the North Sea). RES SAC season represents the RES score using the seasonal SAC boundary and RES SAC total represents the RES score using the full SAC boundary. RES values >1 would suggest that the SAC has higher average energy values (MJ per km^2) than the wider North Sea.

Species	Year	Season	Mean energy (MJ per km^2)	Median (MJ per km^2)	IQR (MJ per km^2)	Species contribution	RES SAC season	RES SAC total
Cod	2005	*Winter*	26	18	9 - 33	0.1	0.22	0.40
		Summer	93	30	6 - 90	0.3	0.10	0.19
	2016	*Winter*	54	14	5 - 74	0.2	0.07	0.08
		Summer	65	7	1 - 55	0.1	0.07	0.07
Atlantic herring	2005	*Winter*	1,668	602	148 - 2,208	7.7	0.19	0.23
		Summer	11,035	625	55 - 4,915	35.8	0.02	0.01
	2016	*Winter*	3,060	665	164 - 2,441	8.8	0.04	0.10
		Summer	31,409	812	134 - 6,634	40.8	0.02	0.01
European sprat	2005	*Winter*	6,668	37	2 - 2,981	30.8	0.41	0.40
		Summer	3,023	5	1 - 110	9.8	0.16	0.12
	2016	*Winter*	6,929	221	1 - 6,003	20.0	0.63	0.58
		Summer	2,617	33	2 - 545	3.4	0.17	0.13
Whiting	2005	*Winter*	3,797	1,339	493 - 6,003	17.5	0.44	0.65
		Summer	7,037	2,441	602 - 6,634	22.8	0.16	0.69
	2016	*Winter*	8,065	4,447	1,998 - 8,103	23.3	**1.81**	**1.94**
		Summer	26,073	8,955	3,641 - 24,343	33.9	**1.10**	**1.60**
Overall without sandeel	**2005**	***Winter***	**12,159**	**4,915**	**2,208 - 13,360**		0.30	0.44
		Summer	**21,187**	**4,447**	**1,097 - 19,930**		0.09	0.25
	2016	***Winter***	**18,108**	**9,897**	**5,432 - 22,027**		**1.63**	**1.74**
		Summer	**60,165**	**14,765**	**4,447 - 59,874**		0.50	0.71
Sandeel	2005	*Winter*	9,577	0	0-0	43.8	0.04	**1.88**
		Summer	9,452	0	0-0	31.2	**2.71**	**1.90**
	2016	Winter	16,772	0	0-0	47.8	0.04	**1.43**
		Summer	16,553	0	0-0	21.8	**2.05**	**1.45**
Overall with sandeel	**2005**	***Winter***	**21,611**	**6,634**	**2,697 - 16,318**		0.19	**1.07**
		Summer	**34,661**	**6,634**	**1,636 - 36,316**		1.00	0.83
	2016	***Winter***	**30,764**	**13,360**	**6,634 - 26,903**		0.85	**1.60**
		Summer	**76,937**	**22,027**	**5,432 - 80,822**		0.88	0.90

3.3.7 The SAC region relative to the wider North Sea

To assess the value of the SAC area relative to the North Sea, RES scores were calculated. In general, with the inclusion of sandeels to the energy surfaces, the RES values were close to 1 indicating the SAC area was as, or slightly less 'valuable' compared to the wider North Sea region on average. In winter 2005, the seasonal SAC region appeared to be below average (RES = 0.19) but the full SAC boundary had a score of 1.07 indicating the area was slightly above average overall. In general in 2016, the RES scores indicated the SNS SAC was very slightly below average (RES = 0.85 - 0.88 for the seasonal SAC regions) and above average during the winter period (for the full SAC boundary; RES = 1.60)

These results also demonstrate the importance of the role of sandeels in the SAC region as the species was a key driver of the RES scores (see 'Overall without sandeel' in Table 4). Without the inclusion of the sandeel data, the value of the SAC relative to the wider North Sea is greatly diminished with RES scores ranging from 0.30-0.71. The exception is winter 2016 where the distribution of whiting is important to the overall energy in the SAC.

As noted above, while there are relative spatial variations in energy available, the absolute values mean and median energy (MJ per km^2) indicate there are very high levels (relative to porpoise densities and known energy requirements in the North Sea) of energy available to porpoises via the five prey species considered here.

4 Discussion

This project provides a first attempt to describe the spatiotemporal distribution of energetic availability of harbour porpoise prey species in the North Sea.

4.1 Model evaluation

The results of the GAM-based spatiotemporal modelling indicate that this approach was capable of creating realistic distribution maps of energy density of prey species. The inclusion of a three-dimensional tensor product and the use of soap film smoothers allowed the spatial distribution pattern to change with time and avoided smoothing across boundary features. The final models captured an adequate amount of the variation in the data (Table 3) suggesting a good model fit.

The spatial covariates (longitude and latitude) did well in modelling the distributional pattern. However, biologically these variables are hard to interpret and are proxies for environmental covariates. To better understand why prey species are distributed in certain places the spatial covariates should be substituted or accompanied by more biologically meaningful parameters (*e.g.* temperature, salinity, primary productivity, and vertical mixing (Munk *et al.* 1995)). Covariate data could for instance be obtained from The Copernicus Marine Environment Monitoring Service[3]. This could provide insight into how prey availability might alter due to environmental change and might be particularly interesting to explore in the North Sea as it is an area were temperature rise is faster than the global average (Dulvey *et al.* 2008).

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[3] marine.copernicus.eu.

4.2 Implications of the results

4.2.1 Distribution maps

Although there are species-specific spatiotemporal variations there are several overall patterns that can be drawn from the results. The modelled distributional maps and overall trends of the prey species fit well with previously described spatial patterns and population trends from ICES stock assessment and other sources (*e.g.* ICES 2017, 2018b; Milner 2016; Teal *et al.* 2009). However, there might be some discrepancies due to recent alterations in distribution or due to the size class restriction in this study (only selected fish <40cm) which would only really affect cod and to a lesser extent whiting.

Overall, the predicted energy density was higher in summer and in 2016 compared to 2005 especially in the southern and north-western North Sea. During winter the highest energy values were observed in the southern North Sea an additional high area in the north-western North Sea was apparent in summer. The contribution of Atlantic herring and European sprat to the overall energy availability was distinct by season. It should be noted that there are likely to be variations in fish biomass and recruitment across different fish species, regions and years. It is unclear how porpoises would respond to such variations in prey density.

In general, the SAC region does not seem to cover the very highest energy areas identified by the spatial models in the North Sea, but nonetheless comprises a significant energy resource. Whiting and sandeels increase the relative average energy availability within the overall SAC to above the average of the North Sea in winter (RES score Table 4). The RES score for whiting is indicative of the value of the species in the SAC region. For sandeels, their patchy distribution in the North Sea drives the patterns observed and the SAC covers a couple of sandeel grounds. Furthermore, the results indicate that the summer component of the SAC encompasses an area with relative high amounts of sandeel energy. It is important to note, that although the energy values in some areas in the North Sea, including the SAC, are relatively low compared to very high energy areas, these 'colder spots' might not necessarily represent "bad" foraging areas. Overall, large amounts of energy are predicted to be available both within and outside the SAC region. Overall mean estimates of total energy available ranged between 21,610 (winter) - 30,764 MJ per km^2 (summer) in 2005 and 34,661 (winter) - 76,938 MJ per km^2 (summer) in 2016 (for five of the main harbour porpoise prey species). Wild harbour porpoise daily energy requirements vary between 9 - 31MJ (Rojano-Donates *et al.* 2018). This suggests that within "low" energy areas there would still be plenty of energy available to sustain porpoises in the area.

However, this estimation is overlooking the fact that there are other sources of energy "loss" such as competition with other predators (*i.e.* sea birds, other marine mammals, foraging fish as well as fisheries). Therefore, the energy predicted here may not correlate to the actual available energy for porpoises given the role of other predators and fishing industry present in the North Sea. This may vary significantly across the North Sea region and without this we cannot assess whether areas mapped as "high" energy represent high energy available to porpoises. This highlights the difficulty in assessing predator-prey relationships within a complex ecosystem with many different trophic interactions. Furthermore, by not considering these multi-species interactions the results might become counterintuitive.

4.2.2 Diet and prey quality

Given the relative importance of whiting and sandeels in the diet of harbour porpoises (Table 1) it was tentatively postulated that these species might be more abundant. Correspondingly, the energy availability of these species is higher compared to the other species. Logically, regardless of prey preference one would assume that when a prey species is more abundant

it would also be more consumed. However, this might be very dependent on the availability of other prey within the system. Furthermore, this result does not indicate if these species might be important for harbour porpoise distribution or if porpoises might prefer certain prey. Prey preference might be dependent on multiple factors such as predictability and catchability. To get a better idea what porpoises prefer the relationship between prey availability and consumption, a multi-species functional response, could be modelled (Ransijn *et al.* in prep).

The energetic balance for any species is governed by the effort expended to acquire resources, the energy available in resources acquired and how the energy acquired is allocated. Marine mammals exhibit a wide range of life history strategies, from large, long lived species with long inter-birth intervals, to smaller species, like the harbour porpoise which reach sexual maturity quickly and reproduce frequently. For harbour porpoises, efficient foraging (maximising intake whilst minimising expenditure) is therefore an essential element in such organism's survival and reproduction. Therefore, understanding the energy available in an ecosystem is critical to understand the ecology of the species, identifying important areas and in understanding the potential drivers of change for populations. Foraging behaviour should eventually, according to optimal foraging theory, maximize the fitness of individuals (Pyke *et al.* 1984) by maximizing the energy obtained per unit of energy spent. To target the most abundant and/or profitable prey, predators might switch between prey species, foraging tactics, or feeding grounds (Schenk & Bacher 2002). For a species like the harbour porpoise that feeds on multiple prey species, this could imply that the diet of harbour porpoises or their feeding areas may change as the availability of their prey changes.

Another consideration in the interpretation of the energy available maps is that porpoises will not be able to assimilate 100% of the energy available in any prey item. There are limited data on the assimilation efficiency (*i.e.* the percentage of energy from an item that is usable by the animal) in porpoises, but published estimates range from 0.74 (Yasui & Gaskin 1986) to 0.95 (Locker 2007) (*i.e.* 74%-95%). There are likely to be prey-specific assimilation rates as observed in studies with captive seals (Lawson *et al.* 1997).

Harbour porpoise life history suggests that proximity to suitable prey species is important for their survival. As a generalist species, this study suggests that the North Sea represents a suitable habitat for harbour porpoises with a range of energy sources available which might inform species distribution. However, it is important to consider that a number of other drivers affect a species distribution: including (real or perceived) risk of predation or injury from marine mammal interactions (*e.g.* grey seals, bottlenose dolphins or killer whales), competition, and potentially exposure to anthropogenic stressors.

4.3 Assumptions and uncertainty

At this stage we have no means of assessing how biased our estimates are and the uncertainty in the results are due to a variety of factors. However, the three main sources that could be explored in the future are catchability, energetic content, and spatiotemporal model predictions. It is not trivial to robustly estimate the uncertainty that results from combining these different sources of error.

4.3.1 Explorable uncertainty

To estimate absolute fish abundance the survey densities were scaled using relative gear efficiency correction factors from Walker *et al.* (2017). However, the uncertainty associated with these estimates were not incorporated. The catchability uncertainty is probably the largest source of error; both the extent to which main prey species are represented in survey

trawls (*e.g.* gobies, and depth distribution of different prey species) and because different assumptions could lead to quite significant alterations in the estimated numbers of fish (Aarts 2019). Nevertheless, the spatial pattern is not believed to change considerably unless catchability also varies on quite a high spatial resolution scale and/or the size classes of a particular species are distinct in their spatial distribution.

Where possible, we transformed biomass to energy density according to fish length and season. However, for some species this information is not available and therefore we used a single conversion estimate that thus ignored the variation according to length and season. Furthermore, uncertainty in these estimates due to sampling error was not accounted for. Therefore, we might over or underestimate the energy available to porpoises.

Uncertainty in the predictions of the spatiotemporal model can be explored using different methods such as parametric or nonparametric re-sampling, jackknife, and others.

4.3.2   Assumptions

The selection of "important" prey species for harbour porpoises was based on studies that used data from stranded and bycaught animals. There was no data from the UK for the southern North Sea region and the studies that were carried out in the UK (Scotland) span 1992-2003 and there may have been changes in the importance of prey species since then. As such, we could have missed important prey species for porpoises within the SAC area. However, when comparing studies from the North Sea, the proportion of prey species might change but we believe we have covered the "main" species with the exception of gobies. While there is no published energy density value for a goby species, Booth (in review) indicates that the energy content of Family Gobiidae species is likely to be similar to grey gurnard and red mullet (estimated as 4.4 kJ per gram following Plimmer 1921).

Biases due to stomach content methodology could have led to an underestimation of potential "important" prey species as it only provides information on the most recent meal (Leopold *et al.* 2015; Jansen 2013). Although, as previously mentioned the importance of cod could have been overestimated their inclusion is unlikely to considerably alter the overall conclusions of this study as their energy availability is relatively low. Biases could also have been induced by variation in sample size and composition according to sex, age and origin of the sample (bycaught or stranded). Despite these limitations, stomach contents analysis gives valuable information on the harbour porpoise prey-spectrum and the contribution of prey to the diet.

As previously mentioned, the data used does not allow for a similar approach for other "important" prey species (sandeels and gobies) due to catchability issues in the survey design. Gobies had to be excluded and therefore our results underestimate the energy available to porpoises (because this and other foraged prey species are not accounted for in this five species analysis). This is especially the case in the southern North Sea were gobies are more abundant (Knijn *et al.* 1995; Tulp *et al.* 2008).

For sandeels another approach was applied. The coarse analysis for sandeels that precluded seasonal variations and only rough spatial variation to be modelled could have led to error in the availability estimates. This might have crucial implications as sandeels are an important prey species for harbour porpoises and contribute markedly to the energy available (Gilles *et al.* 2016; Leopold 2015).

By selecting size classes that are smaller than 40cm the results show estimation for consumable prey. However, porpoises might have a particular preference for certain lengths. Therefore, it would be interesting to compare the length distribution of different prey types in

the trawl data with the distribution that are consumed by porpoises from stomach content analysis.

5   Recommendations

In this study, we have generated available energy maps for harbour porpoises based on modelling approaches and we have outlined notes on interpretation and the assumptions made in deriving the outputs. Below we present recommendations for future work, both to extend this effort to better understand the role of the Southern North Sea SAC in harbour porpoise ecology, but also to improve and refine predictions of energy available.

To increase the reliability and understanding in the predicted energy estimates of different prey species we recommend the following additional work:

- The relationship between harbour porpoise density and prey availability can now be explored. We would recommend doing this by having different prey species availabilities as covariates in a porpoise distribution model. For instance, this could be based on SCANS II (2005) and III (2016) survey data. This would allow the exploration of a more detailed and direct overlap between the distribution of porpoise and their prey. Furthermore, this might indicate which prey species might relate the most with the distribution of porpoises in the North Sea.

Other areas of potential advancement or refinement are described below:

- **Sandeel habitat-based model**
  Develop a seasonal habitat-based density model for sandeels based on grab samples data to increase the spatiotemporal resolution of the distribution models.

- **Gobies**
  Explore other data or approaches (*e.g.* habitat-based modelling) to model gobies an important prey that had to be excluded for this analysis.

- **Porpoise prey size "preference"**
  Compare the length distribution for each prey species that are deemed consumable (<40cm) for porpoises according to the NS-IBTS data against consumed size classes based on stomach content data. This will provide insight into porpoise prey size class "preference".

- **Uncertainty**
  Come up with an approach to explore the three different sources of uncertainty (relative gear efficiency factors, energy conversion, model predictions) without overestimating the total degree of uncertainty.

- **Energetic content of prey**
  To improve the seasonal energetic value of prey one should first explore if this information is available (*e.g.* CEFAS and others). If not, one could inquire if there would be interest to collaborate on a project to carry out some bomb calorimeter measurements.

This study represents a multidisciplinary effort to inform spatial management via the integration of knowledge across taxa, principally the critical functional linkage between a marine mammal and some of their prey species. Future assessments will be improved by inclusion of more recent data available on stomach contents from stranded and bycaught porpoises from English/Scottish datasets (if they exist) and considerations of additional data

sources (*e.g.* from CEFAS or Marine Scotland or other organisations that carry out fish surveys) that might have more information on seasonal energetic value of prey. Therefore, to better understand this subject for harbour porpoises and other marine mammals, a multidisciplinary work of marine mammal scientists, environmental scientists and fish biologists would be extremely valuable to guide research to address fundamental questions in marine spatial planning, marine ecology and assessment of anthropogenic impacts.

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Appendix 1
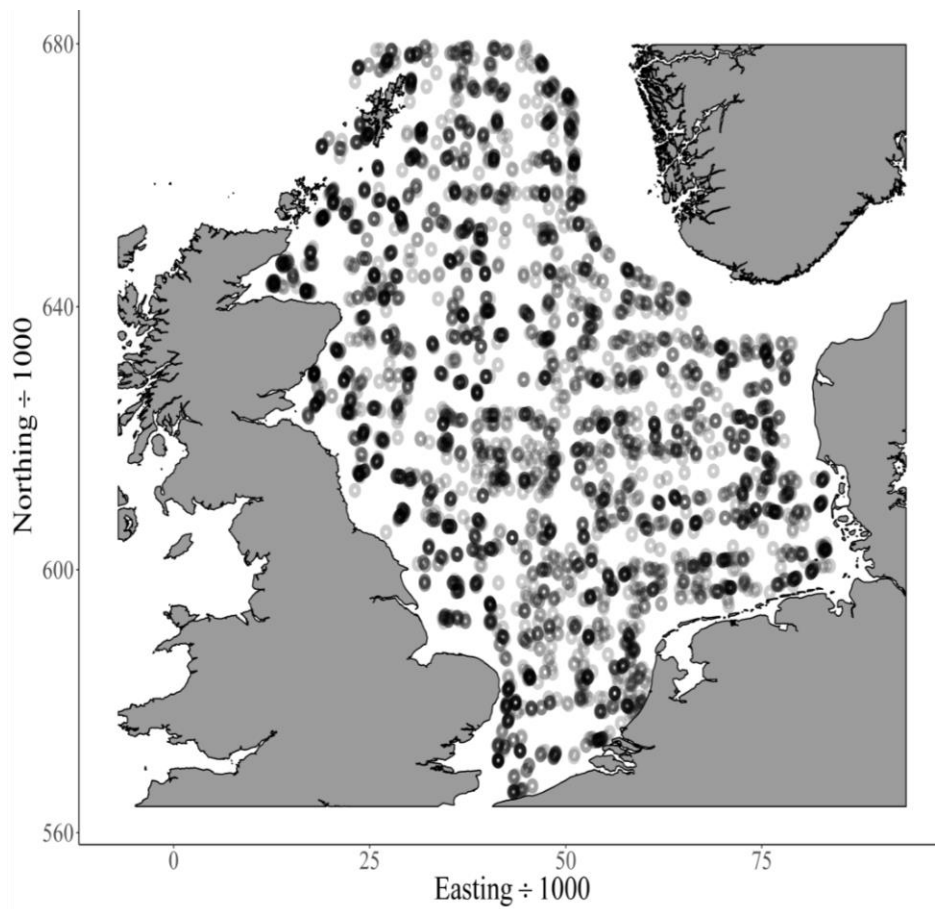
Figure A1. Survey coverage of the NS-IBTS across the North Sea (2003-2017). Darker coloured circles represent locations that were more frequently sampled.

Appendix 2
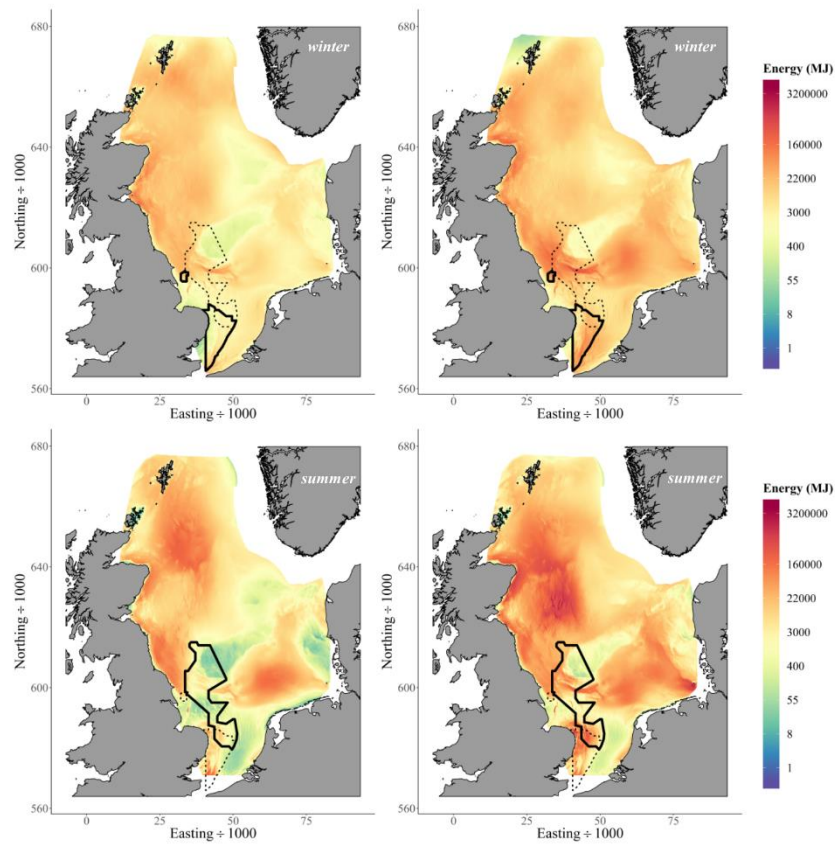
Figure A2. Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species excluding sandeels energy per km^2 for the North Sea, illustrated for 2005 on the left and 2016 on the right. Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.

Appendix 3
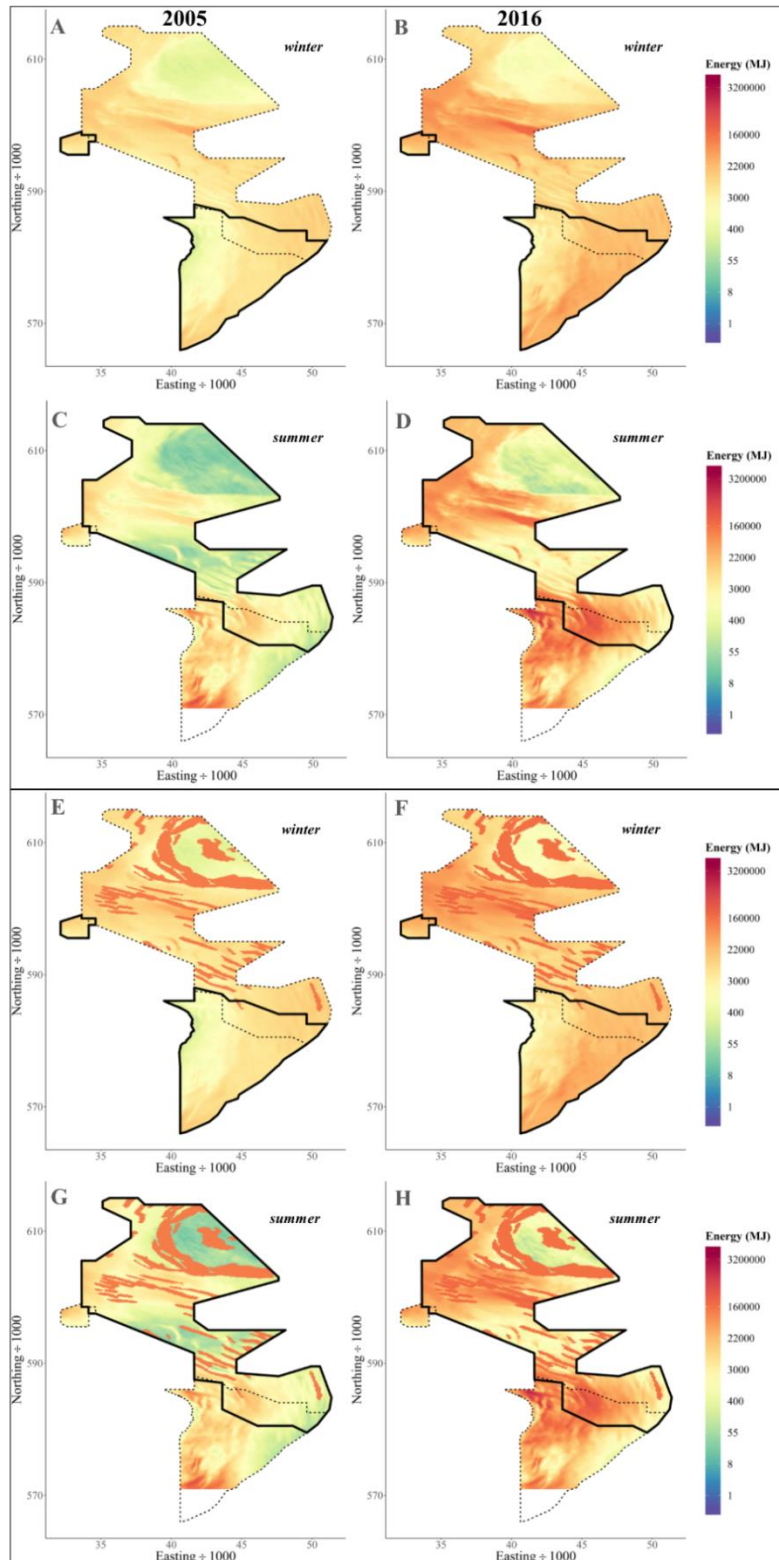
Figure A3. Spatiotemporal winter (January-March) and summer (July-September) distribution of all porpoise prey species energy per km² for the SAC, illustrated for 2005 on the left and 2016 on the right. A distinguish is made for total maps that included sandeels (bottom panels (E-H)) or not (top panels (A-D)). Bold outlines represent the corresponding seasonal part of the SAC while the dotted lines represent the other part of the SAC.