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Habitat and resource segregation of two sympatric seals in the North Sea

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ABSTRACT

In the North Sea, sympatric grey and harbour seals may compete for food resources impacted by intense fishing activities and a recent increase of seal populations. In order to reduce inter-specific competition, sympatric species must segregate at least one aspect of their ecological niches: temporal, spatial or resource segregation. Using isotopes and Se and Hg concentrations, the foraging resources of grey seals and harbour seals and the potential competition between these species in the North Sea was studied. $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were combined with the concentrations of Hg and Se in blood samples of harbour and grey seals from the North Sea. Blood samples were collected on 45 grey seals and 37 harbour seals sampled along German and Scottish coasts. This multi-tracer approach showed spatial and resource partitioning within grey and harbour seals. Data indicated the offshore foraging distribution of grey seals as reflected by the lower $\delta^{15}N$ values and T-Hg concentrations and higher Se concentrations, and the inshore foraging distribution of harbour seals because of higher $\delta^{15}N$ values and T-Hg concentrations and lower Se concentrations. The SIAR mixing model revealed a more selective diet of grey seals compared to harbour seals, and the importance of sandeels in grey seal diet reflected by their high $\delta^{34}S$ values. Lastly, diet ellipse overlaps between grey seals and harbour seals sampled along the German coasts suggested a potential sharing of food resources, possibly due to the increase number of grey seals number in this area during the foraging season – all year except breeding and moulting periods. The multi-tracer approach provided a more robust discrimination among diet resources and spatial foraging distributions of grey seals and harbour seals in the North Sea.

Key words: seals, North Sea, stable isotopes, sulphur, mercury, selenium

1. INTRODUCTION

In the North Sea, grey seals (*Halichoerus grypus*) (Fabricius 1791), and harbour seals (*Phoca vitulina*) (Linnaeus, 1758) are considered as sympatric species because of their overlapping habitats and space use (Jones *et al.* 2015). In order to coexist and reduce inter-specific competition, sympatric species must segregate at least one aspect of their ecological niches: temporal, spatial or resource segregation (Schoener 1974). Grey seals and harbour seals in the North Sea use the same areas on land and at sea, are mainly piscivorous, and have comparable life cycles (McConnell *et al.* 1999; Brown *et al.* 2012). Nevertheless, the annual breeding and moulting cycles of grey seals and harbour seals in the North Sea are asynchronous (Hall and Thompson 2009; Burns 2009) but their at-sea distributions during foraging trips may overlap and foraging occurs at the same time for a large part of the year (McConnell *et al.* 1999; Das *et al.* 2003; Herr *et al.* 2009; Sharples *et al.* 2012; Vincent *et al.* 2017). They may therefore be expected to display spatial and/or resource partitioning to some extent. To determine the potential for resource partitioning of the grey seals and harbour seals, and the potential competition between these species in the changing environment of the North Sea was investigated. Inadequate knowledge of the spatial and trophic ecology of grey and harbour seals compromises our understanding when using them as environmental bioindicators of the changing environment of the North Sea. For example, an unusual dietary behaviour has been described recently on several grey seal males in the North Sea. These individuals fed on other marine mammals such as harbour seals and harbour porpoises (*Phocoena phocoena*) (Haelters *et al.* 2012; Bouveroux *et al.* 2014; Jauniaux *et al.* 2014; van Neer *et al.* 2015; Leopold *et al.* 2015) or presented some case of cannibalism (Bishop *et al.* 2016; Onoufriou *et al.* 2016; Brownlow *et al.* 2016; van Neer *et al.* 2019). This particular behaviour has been hypothesized to be a consequence of (**i**) increased competition for food resources as grey seal population size has increased (Lotze 2005; Brasseur *et al.* 2015; Russell 2016) and (**ii**) of fishing intensity in the North Sea. Various tracers (e.g. stable isotope ratios, trace elements, fatty acids) have been useful in feeding and trophic ecology but previous work on grey and harbour seals has focused on understanding how each varies (Walton *et al.* 2000; Walton and Pomeroy 2003; Herr *et al.* 2009; de la Vega *et al.* 2016). Some ecological studies have successfully combined stable isotopes with trace elements, or fatty acids or direct knowledge of spatial use through satellite telemetry to study other marine mammal species (Waite *et al.* 2012; Pinzone, Damseaux *et al.* 2019).

Stable isotope ratios of carbon (C) and nitrogen (N) have been widely used for more than 25 years in ecological and trophic studies on fish and marine mammals (Newsome *et al.* 2010). Few research has been conducted on combining those with stable isotope ratio of sulphur (S) (Jardine *et al.* 2006; Tucker, Bowen, and Iverson 2007; Newsome *et al.* 2010; Fry and Chumchal 2011; Jansen *et al.* 2013). Sulphur stable isotopes allow for discrimination between freshwater or marine environments, and between marine benthic or pelagic producers, depending on their source of S (Connolly *et al.* 2004; Wilson *et al.* 2012). Primary producers that use predominantly seawater sulphates, such as pelagic microalgae and phytoplankton, tend to be enriched in ^{34}S (~18‰) (Connolly *et al.* 2004). Those using sedimentary sulphides such as marsh plants on the coasts or anaerobic bacteria found in the sea bottom, are instead more depleted in ^{34}S (-10 to +5‰) (Connolly *et al.* 2004). The δ^{34}S value may discriminate between marine benthic and pelagic food chains and provide information about foraging resources and foraging distributions of seals. The δ^{13}C and the δ^{34}S values do not vary a lot from one trophic level to another and so give information about the source of primary production on which the consumer depends (Connolly *et al.* 2004; Newsome *et al.* 2010). δ^{15}N values show a sequential and predictable enrichment from one trophic level to the next, and is a good indicator of the trophic position of the animal (Minagawa and Wada 1984; Newsome *et al.* 2010). Moreover, the δ^{13}C and δ^{15}N values may give an indication on the foraging distributions of seals as their values decreased from coastal and open sea areas in German and Scottish parts of the North Sea (MacKenzie *et al.* 2014; Glew *et al.* 2019). In addition, isotopic ratios allow identification of the food resources on which a predator depends with the use of mixing models (SIAR). Moreover, the Stable Isotope Bayesian Ellipses (SIBER) approach - a newly developed technique - allows the use of stable isotope ratios to build geometric spaces (or “isospaces”). These can be used as proxies (variables that serve in place of an unobservable or immeasurable variable) of species' or populations' ecological niches commonly referred to “isotopic niches” (Newsome *et al.* 2007). Each dimension is linked with environmental and/or food resource requirements at both intra- and inter-individual level (Bearhop *et al.* 2004; Layman and Allgeier 2012). For this reason, it can be used as a proxy of the habitat and resources most commonly used by the species or the population (Layman and Allgeier 2012), and allows for quantification of the overlap of the isotopic or ecological niches of the species, and as such, allows a better understanding of the competition between them and the intensity (Parnell *et al.* 2010; Jackson *et al.* 2011).

Trace elements have been used extensively in ecotoxicology and pollution monitoring, and elements such as Hg and Se represent powerful tools in the study of feeding and trophic ecology of marine mammals (Bustamante *et al.* 1998; Becker *et al.* 2002; Stewart *et al.* 2004; Croteau, Luoma, and Stewart 2005; Lahaye *et al.* 2007; Ramos and Gonzalez-Solis 2012). Indeed, the biomagnification of Hg reflects the trophic position of the animal in the food web as previously described in different aquatic species (Kidd *et al.* 1995; Atwell, Hobson, and Welch 1998; Bearhop *et al.* 2000; Aubail *et al.* 2011). Hg and Se concentrations may also vary among habitats: higher Hg levels were recorded in coastal waters (1.6 – 69 ng.L^{-1}) compared to offshore waters (0.25-41 ng.L^{-1}) of the southern North Sea (Borchardt *et al.* 1988; Sheahan *et al.* 2001; Baeyens *et al.* 2003) as sediments act as a sink for decontamination of coastal areas in the North Sea (Huafang *et al.* 2012). The Se content of the algae/plants is a major factor controlling the Se status of herbivores and carnivores (Schomburg and Arnér 2017). The nutritional intake of Se by herbivores may differ considerably, depending on their geographical area and their spatial distribution (Schomburg and Arnér 2017). Thus, Se intake of carnivores differs considerably depending on their own food preferences and of those of lower trophic levels and local Se availability.

The objectives of the present study were 1) to define the foraging niches of sympatric grey and harbour seals sampled alive along German and Scottish coasts using a multi-tracer approach (δ^{13}C, δ^{15}N and δ^{34}S values and Hg and Se concentrations). Then, we will 2) compare their ecological niches and 3) assess potential competition for food resources.

2. MATERIAL AND METHODS

2.1 Sampling of grey seals, harbour seals and fish

This study used samples collected from grey seals and harbour seals from Scottish and German coasts (**Map 1**). In Scotland, grey seals were sampled on the Isle of May (56°11’N, 2°33’W) in October – November 2016 and harbour seals were sampled on Orkney (59°05’N, 2°97’W) in April – May in 2017 (**Map 1**). Both sites presented similar environmental characteristics such as sea surface and bottom temperatures and similar isotopic baseline values (MacKenzie *et al.* 2014; Glew *et al.* 2019). All Scottish seals were adults. All grey seals were females forming part of a wider demographic study. Scottish seals were immobilized with a mass dependent injection of Zoletil® 100, Virbac (Pomeroy *et al.* 1999) before collecting morphometric data and samples. All Scottish captures and sampling were performed under the UK Home Office licence (permit: # 60/3303). In Germany, grey seals were sampled on Helgoland (54°18’N, 7°88’E) in May 2015, and harbour seals were sampled on Lorenzenplate (54°38’N, 8°53’E) in April 2017 (**Map 1**). Seals sampled in Germany were caught with a net (3 m × 200 m), transferred into individual tube nets, and restrained manually for 45 minutes for sampling collection and measurements. Captures always occurred around noon, according to low tide. All German captures and sampling were performed under the National Park Office Schleswig - Holstein permit: AZ 312-72241.121-19.

Whole blood samples were collected from the extradural vein in (**i**) *Vacutainer^{TM} red top serum tubes* including a silicone-coated interior and increasing silica act clot activator and in (**ii**) *Vacutainer^{TM} royal blue tubes* indicated for trace metal analyses. Within 3 hours of collection, blood collected in *Vacutainer^{TM} red top serum tubes* were centrifuged for 10 minutes at 2000g. Serum was extracted, keeping only the red blood cells for stable isotope analysis. Samples were stored at -20°C until analysis.

Fish muscles were sampled from catches landed in the port of St Monans (east coast, Scotland) in June 2016. Fish were caught in the along the Scottish coasts in the North Sea. We sampled 10 Atlantic herring (*Clupea harengus*), 4 Atlantic cod - juveniles - (*Gadus morhua*), 6 European hake (*Merluccius merluccius*), 6 haddock (*Melanogrammus aeglefinus*), 6 monkfish (*Lophius piscatorius*), 6 European plaice (*Pleuronectes platessa*) and 6 common sole (*Solea solea*). Stable isotope data on sandeels (*Ammodytes marinus*) sampled in Scotland were extracted from Käkelä *et al.* (2007).

Prior to analysis, blood and fish muscle samples were freeze-dried, ground with a mortar and pestle into powder. Whole blood (containing red blood cells) does not require lipid extraction because it contains only low levels of lipids. The major carrier of fatty acids in this tissue is serum albumin, meaning that the serum contains higher levels of lipids than the red blood cells (Habran, Damseaux *et al.* 2019).

2.2 Stable isotope ratio analysis

Approximately 2-2.5 mg of each sample was weighed and loaded into tin boats. All dried masses were measured to the nearest 0.01 mg. Stable isotope measurements were performed with an isotope ratio mass spectrometer (IsoPrime100) coupled to an N-C-S elemental analyser (Vario MICRO cube, Elementar) for automated analyses. Stable isotope abundances were expressed in delta (δ) notation as the deviation from standards in parts per thousand (‰) according to the following equation:

$$\delta X = \left(\frac{R_{sample} - R_{standard}}{R_{standard}}\right)$$

where X is ^{13}C, ^{15}N or ^{34}S and R is the corresponding ratio $^{13}C/^{12}C$, $^{15}N/^{14}N$ or $^{34}S/^{32}S$. The δ values are multiplied by 1000 for easier understanding. The isotopic ratios were estimated relative to the international standards of Vienna Pee Dee Belemnite (vPBD) for carbon, Atmospheric Air for nitrogen and Vienna Canyon Diablo Troilite (vCDT) for sulphur. International Atomic Energy Agency certified reference materials (IAEA, Vienna, Austria) were used as analytical standard calibrated against the international isotopic references sucrose (IAEA-C_6, $\delta^{13}C = -10.8 \pm 0.5$ ‰; mean ± SD), ammonium sulfate (IAEA-N_2, $\delta^{15}N = 20.3 \pm 0.2$ ‰; mean ± SD), and silver sulfide (IAEA-S_1, mean $\delta^{34}S = -0.3$ ‰) as primary standards, and sulfanilic acid ($\delta^{13}C = -25.6 \pm 0.4$ ‰; $\delta^{15}N = -0.1 \pm 0.5$ ‰ ; $\delta^{34}S = 5.9 \pm 0.5$ ‰ ; mean ± SD in each case) as secondary analytical standard.

2.3 Total mercury analysis

Approximately 10mg of freeze-dried whole blood and 2-2.5mg of freeze-dried muscle were weighed (0.01mg precision) and loaded into quartz boats (preheated to 450°C for 5min to remove any impurity of Hg (Damseaux *et al.* 2017)). T-Hg concentrations were determined by atomic absorption spectroscopy at 254nm (Direct Mercury Analyzer - DMA-80- Milestone) according to the US EPA standard method 7473. This method has been in-house validated for solid samples by measuring blanks (HCl 1%) levels and internal standardized solution (T-Hg 100 ppb) before every analysis. Quality control and quality assurance was checked by Certified Reference Materials (CRMs) (DORM-2 Dogfish muscle = 4.64 ± 0.14 µg g^{-1} dw, and Seronorm L-3 whole blood = 17.9 ± 1.8µg l^{-1}). These were analysed at the beginning and the end of the analysis to monitor the drift of the instrument (Damseaux *et al.* 2017). The percentage recovery for DORM-2 ranged between 101% and 105% and for Seronorm L-3 from 90% to 100% showing optimal run of the analyses. Concentrations are expressed as nanograms per gram of dry weight (ng g^{-1} dw).

2.4 Selenium analysis

Approximately 0.2-0.25g of freeze-dried whole blood and 0.18-0.22g of freeze-dried muscle were weighed. Samples were subjected to microwave assisted digestion in $\text{Teflon}_{\text{TM}}$ vessels with 2 ml HNO_3 (65%), 1 ml H_2O_2 (30%) and 5 ml of 18.2 MΩ-cm deionized water. After, samples were diluted to 50 ml with 18.2MΩ-cm deionized water. Se concentrations were determined by inductively coupled plasma mass spectroscopy (ICP-MS, PerkinElmer, Sciex, DCR 2). Internal standards (CertiPUR®, Merck) were added to each sample and calibration standard solutions. Quality control and quality assurance for ICP-MS included field blanks, method blanks, Certified Reference Materials (CRMs) – DOLT-3 and Seronorm L-3 (DOLT-3 Dogfish liver = 7.06 ± 0.48 µg g^{-1} dw, and Seronorm L-3 whole blood = 17.9 ± 1.8µg l^{-1}). The percentage recovery for DOLT-3 ranged between 97% and 99% and for Seronorm L-3 from 98% to 110% showing optimal run of the analyses. Concentrations are expressed in nanograms per gram of dry weight (ng g^{-1} dw).

2.5 Data transformation

In order to minimize the effect of the different isotopic baselines because of the different areas and sampling years of grey seals and harbour seals, we decided to standardized the isotopic and trace element values in order to decrease the data variation and so decrease the impact of year, place and therefore baseline variations on the data. We transformed our isotopic and trace element data following the Cucherousset and Villéger method (2015). This method creates a standardized multidimensional space where each axis is unitless and scaled to have the same range (0 to 1). Therefore, we corrected the δ values (δk_{st}, equation 1) and trace element concentrations ($[C]_{st}$, equation 2) for both species in the same area following 2 equations:

Equation 1 $$\delta k_{st} = \frac{(\delta k - \min(\delta k))}{(\max(\delta k) - \min(\delta k))}$$

(Cucherousset and Villéger 2015)

Equation 2 $$[C]_{st} = \frac{([C] - \min([C]))}{(\max([C]) - \min([C]))}$$

(Pinzone, Damseaux *et al.* 2019)

2.6 Isotopic and ecological niches using SIBER

Following Jackson *et al.* (2011) we used the Stable Isotopes Bayesian Ellipses (SIBER) package (version 2.1.4) in R (version 3.6.0; R Core Team 2017) to explore variations in δ^{13}C, δ^{15}N, δ^{34}S values and T-Hg, Se concentrations of grey seals and harbour seals of the North Sea. The isotopic niches of δ^{13}C *vs.* δ^{15}N and δ^{15}N *vs.* δ^{34}S and the ecological niches of δ^{13}C *vs.* T-Hg, T-Hg *vs.* δ^{15}N, δ^{34}S *vs.* T-Hg, δ^{13}C *vs.* Se, Se *vs.* δ^{15}N and δ^{34}S *vs.* Se were determined for each species at each site. SIBER was used to generate bivariate standard ellipses that represent the core range of values (a proxy of the trophic and habitat resources on which the consumer depends; Layman *et al.* 2007; Layman and Allgeier 2012). The geometric representation of a niche in SIBER is the standard ellipse area (SEA). It encompasses 40% of studied individuals and represents a bivariate equivalent of standard deviation. As such, it contains only the "typical" members of a population without being influenced by outlier individuals in the considered space (Newsome, Martinez del Rio, *et al.* 2007). For this reason, it can be used as a proxy of the spatial foraging distribution and resources most commonly used by the population (Layman and Allgeier 2012). To limit calculation biases when comparing small and/or unbalanced samples, standard ellipse areas were corrected for small sample size (SEA$_C$) when the analysed groups contained less than 30 individuals (Syväranta *et al.* 2013). This choice does not cause bias in standard ellipse areas estimation for larger sample sizes, as SEA and SEA$_C$ tend to converge when sample size increases (Jackson *et al.* 2011). Then, standard ellipse areas of each species were also estimated using Bayesian modelling (SEA$_B$). SEA$_B$ involves the use of an iterative model based on Bayesian inference to estimate the covariance matrix from the data, with iterations set to 10^6. SEA$_B$ is more effective at taking into account both natural and analytical variability in the data and provides a distribution of solutions rather than a single value - as for SEA and SEA$_C$-, providing error estimates.. Model solutions were presented using percentages of model runs for pairwise comparisons

2.7 Mixing models

Bayesian stable isotope mixing models were applied to calculate the relative contributions of potential food resources to the diets of harbour seals and grey seals sampled along the Scottish coasts. Different potential food resources were sampled and used in the model based on general knowledge about the feeding preferences of the consumers (Hall *et al.* 1998; Walton *et al.* 2000; Walton and Pomeroy 2003; Sharples *et al.* 2009; Hammond and Rothery 2010; Brown *et al.* 2012). To reach the methodological requirements of the model, the potential food resources were grouped according to stable isotope composition similarity (Group 1: juvenile cod; Group 2: plaice and sole; Group 3: monkfish, European hake, haddock; Group 4: herring; Group 5: sandeel). Fractionation factors of 0.8 ± 0.1‰ and 3.3 ± 0.1‰ obtained from hooded seal red blood cells were applied for $\delta^{13}C$ and $\delta^{15}N$, respectively (Pinzone *et al.* 2017). The model was run using SIAR (Parnell and Jackson 2015) on R version 3.6.0. Model was run for 10^6 iterations, with no resource contribution data defined *a priori* (uninformative prior). Model outputs (percentages of contribution of each food resource to consumer diet) were presented using modes and 95% credibility interval of the posterior solution distribution function.

2.8 Data analysis

Because only female grey seals were sampled on the Isle of May, we restricted comparisons for Scottish samples to results from female harbour seals.

The normality of residuals was assessed using a Shapiro test (Shapiro *et al.* 1968) and the homoscedasticity using a Bartlett test. Because most of the values deviated from a normal distribution and did not present homogeneity of variances, the non-parametric Mann-Whitney U test (Whitney 1951) was used for species comparisons and the Spearman's rank correlation ρ was used for correlations between trace element concentrations and stable isotope ratios. Moreover, log transformation of the data followed by parametric tests showed the same results as the non-parametric tests. Therefore, we decided to keep the non-parametric tests and more important the raw data making the link between **Table 1** and linear regression results easier.

For all tests, rejection of the null hypothesis was set at *p-value* < 0.05. Statistical analyses were conducted with Past software (PAleontological STatistics - Version 3.25).

3. RESULTS

Scottish harbour seals displayed significantly higher $\delta^{13}C$ values than grey seals (**Table 1**). For both locations, harbour seals displayed significantly higher $\delta^{15}N$ values and T-Hg concentrations and lower $\delta^{34}S$ values and Se concentrations than grey seals (**Table 1**).

3.1 Stable isotopes and trace elements

For both species and in both locations, $\delta^{13}C$ and $\delta^{15}N$ values were significantly correlated to T-Hg (for all, Spearman's coefficient correlation. T-Hg-$\delta^{13}C$: grey seals: r = 0.260, *p-value* = 0.019; harbour seals: r = 0.346, *p-value* < 0.001; T-Hg-$\delta^{15}N$: grey seals: r = 0.251, *p-value* = 0.025; harbour seals: r = 0.634, *p-value* < 0.001; **Fig. 1**) and Se (for all, Spearman's coefficient correlation. Se-$\delta^{13}C$: grey seals: r = -0.258, *p-value* = 0.021; harbour seals: r = -0.150, *p-value* = 0.044; Se-$\delta^{15}N$: grey seals: r = -0.751, *p-value* < 0.001; harbour seals: r = -0.234, *p-value* = 0.001; **Fig. 1**) concentrations in blood. No significant difference was found between $\delta^{34}S$ and T-Hg or Se concentrations (for all, Spearman's coefficient correlation, *p-value* > 0.05).

3.2 Isotopic niches

The $\delta^{13}C$ *vs.* $\delta^{15}N$ plots did not display overlap between Scottish grey seal and harbour seal ellipses (**Fig. 2A**). In contrast, overlap between German seals represented 11% of the grey seal ellipse area and 24% of the harbour seal ellipse area (**Fig. 2D**). Scottish harbour seals presented larger $\delta^{13}C$ *vs.* $\delta^{15}N$ SEA (SEAc: 0.123‰^{2}) than Scottish grey seals (SEA: 0.091‰^{2}) in 79% of model runs (**Table 2**). In contrast, German grey seals presented larger $\delta^{13}C$ *vs.* $\delta^{15}N$ SEA (SEAc: 0.187‰^{2}), than German harbour seals (SEAc: 0.085‰^{2}) in 98% of model runs (**Table 2**).

The $\delta^{34}S$ *vs.* $\delta^{15}N$ plots did not display any overlap between grey seal and harbour seal ellipses in both areas (**Fig. 2B-3B**). Scottish harbour seals presented larger $\delta^{34}S$ *vs.* $\delta^{15}N$ SEA (SEAc: 0.083‰^{2}) than Scottish grey seals (SEA: 0.048‰^{2}) in 95% of model runs (**Table 2**). In contrast, German grey seals presented larger $\delta^{34}S$ *vs.* $\delta^{15}N$ SEA (SEAc: 0.057‰^{2}) than German harbour seals (SEAc: 0.041‰^{2}) in 81% of model runs (**Table 2**).

3.3 Ecological niches

The $\delta^{13}C$ *vs.* T-Hg plots displayed overlap between Scottish seals that represented 93% of the grey seal ellipse area and 53% of the harbour seal ellipse area (**Fig. 2C**). Ellipse overlap between German seals represented 4.4% of grey seal ellipse area and 4.9% of harbour seal ellipse area (**Fig. 2F**). Scottish harbour seals presented larger T-Hg *vs.* δ^{13}C SEA (SEAc: 0.178‰^{2}) than Scottish grey seals (SEA: 0.098‰^{2}) in 97% of model runs (**Table 2**). In contrast, German grey seals presented larger δ^{13}C *vs.* T-Hg SEA (SEAc: 0.140‰^{2}) than German harbour seals (SEAc: 0.126‰^{2}) in 57% of model runs (**Table 2**).

The T-Hg *vs.* δ^{15}N plots did not display overlap between grey seal and harbour seal ellipses in both areas (**Fig. S1A-F**, **Table 2**). Scottish and German grey seals presented larger T-Hg *vs.* δ^{15}N SEA (SEA: 0.104‰^{2}; SEAc: 0.141‰^{2}; respectively) than Scottish and German harbour seals (SEAc: 0.082‰^{2}; SEAc: 0.078‰^{2}; respectively) in 72% and 93% of model runs, respectively (**Table 2**).

The δ^{34}S *vs.* T-Hg plots did not display overlap between grey seal and harbour seal ellipses in both areas (**Fig. S1B-G**, **Table 2**). Scottish and German harbour seals presented larger δ^{34}S *vs.* T-Hg SEA (SEAc: 0.1127‰^{2}; SEAc: 0.0575‰^{2}; respectively) than Scottish and German grey seals (SEA: 0.0497‰^{2}; SEA: 0.0289‰^{2}) in 100% and 96% of model runs, respectively (**Table 2**).

The Se *vs.* δ^{13}C plots display overlap between Scottish seals that represented 2% of the grey seal ellipse area and 1.5% of the harbour seal ellipse area (**Fig. S1C**). Ellipse overlap between German seals represented 40% of grey seal ellipse area and 58% of harbour seal ellipse area (**Fig. S1H**). Scottish harbour seals presented larger δ^{13}C *vs.* Se SEA (SEAc: 0.146‰^{2}) than Scottish grey seals (SEA: 0.135‰^{2}) in 57% of model runs (**Table 2**). In contrast, German grey seals presented larger δ^{13}C *vs.* Se SEA (SEAc: 0.197‰^{2}) than German harbour seals (SEA: 0.136‰^{2}) in 81% of model runs (**Table 2**).

The Se *vs.* δ^{15}N plots did not display overlap between Scottish grey seals and harbour seal ellipses (**Fig. S1D**). In contrast, ellipse overlap between German seals represented shown16% of the grey seal ellipse area and 34.5% of the harbour seal ellipse area (**Fig. S1I**). Scottish and German grey seals presented larger Se *vs.* δ^{15}N SEA (SEA: 0.133‰^{2}; SEAc: 0.154‰^{2}; respectively) than Scottish and German harbour seals (SEAc: 0.065‰^{2}; SEAc: 0.071‰^{2}; respectively) in 99% and 98% of model runs, respectively (**Table 2**).

The δ^{34}S *vs.* Se plots did not display overlap between grey seal and harbour seal ellipses in both areas (**Fig. S1E-J**). Scottish and German harbour seals presented larger δ^{34}S *vs.* Se SEA (SEAc: 0.0927‰^{2}; SEAc: 0.0666‰^{2}; respectively) than Scottish and German grey seals (SEA: 0.0544‰^{2}; SEAc: 0.0426‰^{2}; respectively) in 95% and 88% of model runs, respectively (**Table 2**).

3.4 Mixing models

The bi-plot of $\delta^{13}C$ and $\delta^{15}N$ values shows Scottish harbour and grey seals in the middle of the mixing space together with the potential prey values adjusted for trophic enrichment (**Fig. 3**). The SIAR mixing model suggests that the diet of the grey seals was represented by a high proportion of plaice and sole (mode: 50% of diet; Bayesian 95% credibility interval: 29–64%) followed by sandeels (mode: 46% of diet; Bayesian 95% credibility interval: 26–67%). Harbour seal diet was more diversified. Juvenile cod represented the most important food resource for harbour seals (mode: 30% of diet; Bayesian 95% credibility interval: 17–52%), followed by plaice and soles (mode: 29% of diet; Bayesian 95% credibility interval: 4–41%), and monkfish, European hake and haddock (mode: 23% of diet; Bayesian 95% credibility interval: 1–38%) (**Fig. 4**).

4. DISCUSSION

Grey seals and harbour seals are considered as sympatric species in the North Sea. Therefore, they might be expected to show spatial and/or resource partitioning to some extent to reduce direct competition for prey (Brown *et al.* 2012). We found evidence of such partitioning based on stable isotope and trace element content of tissue samples obtained from seals in the North Sea, representing long term integrated dietary intake rather than short term stomach content analysis.

4.1 Stable isotopes and trace elements

δ^{13}C, δ^{15}N and δ^{34}S values combined with Hg and Se concentrations in blood revealed spatial and resource partitioning for harbour seals and grey seals sampled in Germany and in Scotland.

The δ^{13}C values generally reflect the inshore *vs.* offshore foraging distribution of species (Newsome *et al.* 2010). In the North Sea, δ^{13}C values decreased from coastal to open sea areas as previously shown by isoscape - model prediction of spatial distribution of stable isotope values along German and Scottish coasts (MacKenzie *et al.* 2014; Glew *et al.* 2019). Differences in water Hg concentrations between coastal and offshore areas are less frequent in the northern North Sea (Coquery and Cossa 1995) compared to the southern bay where higher Hg concentrations are always detected in coastal waters (1.6 – 69 ng.L^{-1}) compared to offshore waters (0.25-41 ng.L^{-1}) (Borchardt *et al.* 1988; Sheahan *et al.* 2001; Baeyens *et al.* 2003). Positive correlation between δ^{13}C values and T-Hg concentrations (**Fig. 1**) may be explained by a closer habitat to anthropogenic activities and so a more coastal foraging distribution of seals.

The δ^{15}N values show a sequential and predictable enrichment from one trophic level to the next one and so are widely used as an indicator of the trophic position of an animal (Minagawa and Wada 1984; Newsome *et al.* 2010). The positive correlation we found between δ^{15}N values and T-Hg concentrations in blood reflects a biomagnification of T-Hg in grey seals and in harbour seals (**Fig. 1**). Such positive correlations between δ^{15}N values and T-Hg concentrations have previously been described in different species such as birds, fish and marine mammals in marine and fresh water ecosystems (Kidd *et al.* 1995; Atwell *et al.* 1998; Bearhop *et al.* 2000; Aubail *et al.* 2011).

Correlation between the δ^{13}C and δ^{15}N values and Se concentrations also support offshore *vs.* inshore habitats for grey seals and harbour seals respectively. Se is an essential element and its content in algae/plants is a major factor controlling the Se status of herbivores and carnivorous (Schomburg and Arnér 2017). These photosynthetic organisms reflect Se availability of a specific area which depends on environmental deposition, pH, mineral pattern and other soil-specific characteristics. This interaction highlights that the nutritional intake of Se by herbivores may differ considerably, depending on their geographical area and so their spatial distribution (Schomburg and Arnér 2017). δ^{13}C and δ^{15}N values are lower in offshore areas compared to coastal areas in the North Sea (MacKenzie *et al.* 2014; Glew *et al.* 2019). This negative correlation between δ^{13}C and Se was also found in blood of northern elephant seals (*Mirounga angustirostris*) that feed on epi- and mesopelagic prey in various offshore areas in the Northern Pacific (Habran *et al.* 2011) and in different tissues (muscle, liver, kidney and epidermis) of the bowhead whales (*Balaena mysticetus*) (Dehn *et al.* 2006). Bowhead whales feed on euphausids and copepods in pelagic areas (Lowry 1993) and so display offshore isotope composition in δ^{13}C and δ^{15}N (Dehn *et al.* 2006). Our results reveal that that depending on their foraging distribution, seals may undergo different Se exposure.

The marine environment is presumed to be a major source of Se (between 45% - 77% of global emissions (Mosher *et al.* 1987)) which is dispersed by the atmosphere to the land (Mosher *et al.* 1987; Amouroux *et al.* 2001). Significant concentrations of Se occur in surface ocean waters. Biotransformation of dissolved Se by phytoplankton produces different compounds of gaseous Se as DMSe, DMDSe and DMSeS that will be dispersed by the atmosphere (Amouroux *et al.* 2001). Moreover, volatile Se compounds are dependent on plankton biomass and therefore on primary productivity. Total volatile selenide concentrations are linearly dependent on the primary productivity (Amouroux and Donard 1996). We hypothesise that natural Se maritime emissions decrease from inshore to offshore waters in the North Sea as primary productivity decrease in offshore and deeper waters (Richardson and Pedersen 1998; Škaloud *et al.* 2006; MacKenzie *et al.* 2014; Glew *et al.* 2019). Thus, Se biotransformation by phytoplankton and therefore Se emissions will be less important in offshore areas compared to inshore areas. This has been shown in the Mediterranean Sea that is considered as 42% of offshore waters and 58% of coastal waters (Amouroux and Donard, 1996). Primary productivity is 3 times higher in coastal waters and therefore shown a Se air flux 3 times higher in coastal waters compared to offshore waters assuming Se depleted coastal zones (Amouroux and Donard 1996). We hypothesize that offshore waters and food webs should present higher Se concentrations than inshore waters in the North Sea environment, because of the negative correlations we found. This has been shown (**i**) in the north Pacific with a decrease of selenate (SeO$_4^{2-}$) concentrations along an offshore-inshore transect (Cutter and Bruland 1984); (**ii**) in the south Atlantic where total dissolved Se concentrations drop in coastal zones suggesting additional Se removal perhaps by enhanced phytoplankton growth and release into the atmosphere (Cutter and Cutter 2001); (**iii**) in the eastern Canadian Arctic with sandeel that presented higher Se concentrations (1.15 ± 0.16 µg g^{-1} ww) than all other fish species, such as cod, (0.30-0.69 µg g^{-1} ww), which is explained by the more pelagic feeding of sandeel (Pedro *et al.* 2019).

Further studies are needed to add support to this hypothesis. First, transects in the North Sea will be useful to determined Se concentrations in different areas (inshore *vs.* offshore). Secondly, the composition of the plankton in these areas will be important to determine as cocolithophorids (e.g. *E. huxleyi*) are strongly related to DMSe emissions (Amouroux *et al.* 2001). Se could be valuable to obtain information about the food resources on which grey seals and harbour seals in the present case depend, and their foraging distribution (offshore *vs.* inshore areas). Inter-individual variability in Se concentrations could be related to sedentarily or travelling movements of grey seals and harbour seals.

4.2 Spatial and resource segregation between sympatric grey seals and harbour seals

As shown previously, the $\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$ values and T-Hg and Se concentrations may discriminate between marine inshore or offshore areas in the North Sea (Connolly *et al.* 2004; Newsome *et al.* 2010; MacKenzie *et al.* 2014; Glew *et al.* 2019).

4.2.1 Scotland

Grey seals sampled along the Scottish coasts shown lower $\delta^{13}C$ and $\delta^{15}N$ values and higher $\delta^{34}S$ values and Se concentrations than harbour seals (**Table 1**). All these ecological tracer values indicate a more offshore foraging behaviour of grey seals compared to harbour seals along Scottish coasts and therefore a spatial segregation between both species.

Significantly higher $\delta^{15}N$ values were observed in harbour seal than in grey seal blood sampled along Scottish coasts (**Table 1**, **Fig. 2A**). Seal diet depends of distance from the seals' haul out sites and of prey's biomass densities. Therefore, seal diet is also time dependent because of changing abundance of some prey at different areas and times. SIAR modelling revealed that grey seals sampled in Scotland presented a more selective diet as their diet is mostly comprised of flatfish and sandeels compared to harbour seals that have a generalist diet (**Fig. 3-6**). Our results showed that their diet is composed of 50% of plaice and sole but also 46% of sandeels against 30% of juvenile cod, 29% of plaice and sole and 23% of monkfish, European hake and haddock for harbour seals. In addition, several studies compared the sandeel diet proportion in seal species and shown that sandeels constitute the primary part of grey seal diet (~78.5% for Scottish grey seals) compared to harbour seals (3-19%) in various areas (Behrends 1985; Thompson *et al.* 1991, 1996; Bowen and Harrison 1994; Hall *et al.* 1998; Das *et al.* 2003; Beck *et al.* 2007; Gilles *et al.* 2008; Breed *et al.* 2009; Hall and Thompson 2009; Hammond and Rothery 2010; Hammond and Wilson 2016; Hanson *et al.* 2017; Scharff-Olsen *et al.* 2018; ICES 2018). During the interpretation of these results, we have keep in mind that fish were sampled near Orkney as fish sampling along the Isle of May was not possible during grey seal sampling phase. Therefore, these results are carefully interpreted for grey seals from the Isle of May according to the literature (Hammond and Wilson 2016; Hanson *et al.* 2017). Stable isotope ratios were checked with the results obtained by Hanson *et al.* in 2017 for grey seal prey sampled along the Isle of May. The stable isotope ratios for our fish and those sampled for Hanson *et al.* 2017 were similar despite the different areas of sampling (Hanson *et al.* 2017).

Grey seals may adapt their prey selection according to resource pulses and their foraging areas (Hall 1999; Walton and Pomeroy 2003; Beck *et al.* 2007; Thomas *et al.* 2011; Brown *et al.* 2012; Ramasco *et al.* 2017; Scharff-Olsen *et al.* 2018). For example, grey seals sampled at the Isle of May eat more sandeels in autumn and more cod in spring (Hammond and Rothery 2010). This is also the case for harbour seals which eat more sandeels during winter (Sharples *et al.* 2009). This may, in part, explained the difference in δ^{15}N values observed between grey seals and harbour seals sampled along the Scottish coasts. These species were sampled at different season and therefore at different resource pulses. Even if both species present seasonal variations, the diet stay quite different as grey seal may eat larger cods than harbour seals and prefer sandeels mostly present in offshore areas less frequented by harbour seals (Hall *et al.* 1998; Rindorf *et al.* 2019). As sandeels present lower δ^{15}N values this may explain the lower δ^{15}N values of grey seals compared to harbour seals in the present study (**Table 1**, **Fig. 2A**) (Minagawa and Wada 1984; Newsome *et al.* 2010). This also explained the lower T-Hg concentrations in blood of grey seal compared to harbour seal (**Table 1**). The higher proportion of larger fish as cod, monkfish, European hake and haddock compared to sandeel explained the higher T-Hg concentrations in harbour seals compared to grey seals as Hg biomagnified (Kidd *et al.* 1995; Atwell *et al.* 1998; Bearhop *et al.* 2000; Aubail *et al.* 2011). The T-Hg *vs.* δ^{13}C plot (**Fig. 2C**) of Scotland shown a significantly bigger SEA for harbour seals (**Table 2**). This shows how the feeding strategy (generalist *vs.* specialist) influences T-Hg patterns of contamination in seals. Indeed, the generalist foraging diet of harbour seals may lead to higher variability of T-Hg concentrations, while the more specialised foraging diet of grey seals lead to a very narrow range of T-Hg concentrations.

The importance of sandeels in grey seal diet is fully supported by the δ^{34}S *vs.* δ^{15}N, δ^{34}S *vs.* T-Hg and δ^{34}S *vs.* Se plots (**Fig. 2A, S2A, S5A**). These figures shown clear separations between grey seal and harbour seal ellipses sampled along Scottish coasts (**Table 2**). Harbour seals are known to forage on the seabed even if prey are less available but do not select specific prey (Tollit *et al.* 1998; Scharff-olsen *et al.* 2018). This was confirmed by the SIAR model that shown the more generalist diet of harbour seals compared to grey seals (**Fig. 3-6**). McConnell *et al.* shown that grey seals spend 40% of their dives near to the seabed in offshore waters (McConnell *et al.* 1999). Unfortunately, they were not able to determine if that specific time was related to foraging activities but supposed it because they were always diving in the presence of seabirds and always on a specific seabed type, a mix of gravel and sand; the favourite of sandeels (McConnell *et al.* 1999). Sandeels, representing 46% of grey seal diet and less than 10% of the harbour seal diet, mostly live in the sand in offshore waters and emerge into the water column for limited times (Hall *et al.* 1998; Rindorf *et al.* 2019).
The δ^{34}S values differed significantly between grey seals and harbour seals sampled along the Scottish coasts (**Table 1**, **Fig. 2A**). This apparent discrepancy may be linked to the source of S on which the primary producers depend (Connolly *et al.* 2004). Sandeels feed on copepods and fish larvae living in the water column and therefore depending of the water column sulphates (Christensen 2010). This explains the high δ^{34}S values characteristic of pelagic resources we observed for grey seals. The δ^{34}S values of harbour seals are explained by their diet composed of 30% of juvenile cods and 29% of plaices and soles, as suggested by the SIAR model. These fish feed on polychaetes, crustaceans and bivalves that depend on the seabed sulphides. This explained the lower δ^{34}S values characteristic of benthic sources. Briefly, grey seal blood presents a pelagic isotopic composition and harbour seal blood a benthic isotopic composition along Scottish coasts.

Along Scottish coasts, our results shown larger SEA_B for the δ^{34}S *vs.* δ^{15}N, δ^{34}S *vs.* T-Hg and δ^{34}S *vs.* Se plots for harbour seals than for grey seals (**Table 2**). Orkney harbour seal numbers have decreased by 85% between 1996 and 2017 (SCOS 2018). A possible cause of decline could be competition for prey resources with other predators or commercial fishing (Russell *et al.* 2015). In 2014, Scottish government increased quotas for mackerel (*Scomber scombrus),* herring (*Clupea harengus*), cod (*Gadus marhua*) and haddock (*Melanogrammarus aeglefinus*), in inshore waters around Orkney (Duncan 2018). Sharples *et al.* (2012) shown that harbour seals from Orkney had short duration trips at sea (~24-36h) in April and May (the sampling time of this study) therefore direct competition between inshore foraging seals and fisheries is likely. Other current hypotheses to explain the harbour seal decline include interactions with grey seals(Haelters *et al.* 2012; Bouveroux *et al.* 2014; Jauniaux *et al.* 2014; van Neer *et al.* 2015; Leopold *et al.* 2015), killer whales (*Orcinus orca*) and infection by *Brucella* and exposure to harmful algae toxins (Kershaw *et al.* 2017; SCOS 2018). Algal toxins may decrease prey quality of harbour seals such as plaice, whiting, and cod if these are contaminated (Jensen *et al.* 2015). Where prey quality decreases, harbour seals may switch foraging patterns in response. Thus the higher SEA_B of Orkney harbour seals may be related to their foraging plasticity in response to increase of fishery activities and/or decrease of prey quality in this area.

4.2.2 Germany

Along the German coasts, we also observed significantly higher $\delta^{15}N$ values in harbour seal compared to grey seal blood (**Fig. 2D-B**). This may be related to the important proportion of benthic resources such as flatfish (e.g. plaice and sole) (Behrends 1985; Das *et al.* 2003; Gilles *et al.* 2008; de la Vega *et al.* 2016; ICES 2018; Aarts *et al.* 2019) according to different stomach content and stable isotope studies in southeast bay of the North Sea. The lower $\delta^{15}N$ values of German grey seals may also be related to the high proportion of sandeels in their diet mostly present in offshore areas less frequented by harbour seals (Hall *et al.* 1998; Rindorf *et al.* 2019). As sandeels present lower $\delta^{15}N$ values (**Fig. 3**) this may also explain the lower $\delta^{15}N$ values of German grey seals as in Scottish grey seals (**Fig. 3**, **Table 1**) (Minagawa and Wada 1984; Newsome *et al.* 2010). Moreover, the important proportion of pelagic sandeels in German grey seal diet and of benthic resources in German harbour seal diet (Behrends 1985; Das *et al.* 2003; Gilles *et al.* 2008; de la Vega *et al.* 2016; ICES 2018; Aarts *et al.* 2019) is confirmed by the $\delta^{34}S$ *vs.* $\delta^{15}N$, $\delta^{34}S$ *vs.* T-Hg and $\delta^{34}S$ *vs.* Se plots (**Fig. 2E, S2B, S5B**) that shown clear separations between grey seals and harbour seals sampled along German coasts (**Table 2**).

Russell *et al.* showed that 58% of grey seal females breeding in the UK did foraging in the southern North Sea (Russell *et al.* 2013; Russell 2016). Moreover, an important proportion of grey seals (50%) and harbour seals (80%) breeding and moulting in the Wadden Sea forage in the southern North Sea (Brasseur *et al.* 2014, 2015, 2018; Jensen *et al.* 2018). According to de la Vega *et al.*, harbour seals breeding in the Wadden Sea might well depend on benthic food resources during the foraging season (de la Vega *et al.* 2016). The $\delta^{13}C$ *vs.* $\delta^{15}N$, $\delta^{13}C$ *vs.* Se and Se *vs.* δ^{15}N plots in blood show more important overlap between grey seals and harbour seals sampled along the German coasts compared to the Scottish coasts (**Fig. 2D, S3B, S4B**). As the ellipses are proxies of the trophic niches, these overlaps indicate that both seal species may share more of their resource in this area.The important increase of grey seals and harbour seals in the southern waters for foraging season may explain the greater overlap we found between both species sampled along the German coasts compared to those sampled along the Scottish coasts.

Grey seals sampled along the German coasts also show a higher SEA$_B$ for δ^{13}C *vs.* δ^{15}N (**Fig. 2D**, **Table 2**) and Se *vs.* δ^{15}N plots (**Fig. S1I**, **Table 2**). If the number of seals increased along the German coasts during the foraging season, this may lead to wider foraging distributions of grey seals to find their preferred prey in response to the intra- and inter-specific sharing of food resources and in order to avoid competition for food resources. Many studies show the philopatric aspect and the coastal distribution of harbour seals in the Wadden Sea and around the North Sea basin (Tougaard *et al.* 2008; Cunningham *et al.* 2009; Herr *et al.* 2009; Dietz *et al.* 2012; Sharples *et al.* 2012; Aarts *et al.* 2016; Vincent *et al.* 2017; Jensen *et al.* 2018; Aarts *et al.* 2019) contrasting with long trip durations and mostly offshore movements of grey seals (Bowen and Harrison 1994; Hall *et al.* 1998; McConnell *et al.* 1999; Herr *et al.* 2009; McClintock *et al.* 2012; Brasseur *et al.* 2015; Huon *et al.* 2015; Aarts *et al.* 2016; Vincent *et al.* 2017; Scharff-Olsen *et al.* 2018). Moreover, grey seals sampled along German coasts shown lower δ^{15}N values and higher δ^{34}S values and Se concentrations than harbour seals (**Table 1**). All these ecological tracer values indicate a more offshore foraging behaviour of grey seals compared to harbour seals along German coasts such as those sampled along the Scottish coasts.

In both δ^{13}C *vs.* T-Hg and T-Hg *vs.* δ^{15}N plots of Germany (**Fig. 2F, S4B**), ellipses of harbour seals and grey seals aligned differently along axes. Grey seals ellipses aligned along the δ^{13}C and the δ^{15}N axes showing their wider foraging distributions. Indeed, the δ^{13}C and the δ^{15}N values decreased between coastal and open sea areas in the southern bay of the North Sea (MacKenzie *et al.* 2014; Glew *et al.* 2019).In contrast, harbour seals shown important variations in T-Hg concentrations (**Fig. 2F**). We can hypothesize that harbour seals sampled along the German coasts consume larger prey items (Grandjean *et al.* 1992; Hong *et al.* 2012). This could contribute to the wide range of Hg concentrations in harbour seal blood and be explained by the increase of harbour and grey seals in the southern bay of the North Sea during the foraging season (Russell *et al.* 2013; Brasseur *et al.* 2014, 2015, 2018; Russell 2016; Jensen *et al.* 2018).

The δ^{13}C *vs.* T-Hg plot (**Fig. 2F**) allows a good distinction of grey seals and harbour seals living along the German coasts. The coastal distribution of harbour seals in the southeastern North Sea compared to grey seals may explain the higher Hg concentrations we found (**Table 1**) (Tougaard *et al.* 2008; Cunningham *et al.* 2009; Herr *et al.* 2009; Dietz *et al.* 2012; Sharples *et al.* 2012; Aarts *et al.* 2016; Vincent *et al.* 2017; Jensen *et al.* 2018; Aarts *et al.* 2019). In general, mercury contamination appears to reflect the known inputs into coastal waters suggesting the addition of mercury of industrial origin at coastal sites (Sergeant and Armstrong 1973). Coastal areas are more influenced by the Hg anthropogenic pollution than offshore areas. Indeed, total dissolved Hg concentrations in coastal waters (1.6 – 69 ng L^{-1}) are significantly higher than those in offshore waters (0.25 – 41 ng L^{-1}) in the southern bay of the North Sea (Borchardt *et al.* 1988; Sheahan *et al.* 2001; Baeyens *et al.* 2003). Coquery and Cossa shown that offshore waters of the southern North Sea, as well as Scottish waters, showed lower total dissolved and particulate Hg concentrations than coastal waters and Hg concentrations more than four times higher in German coastal waters compared to those of Scotland (Coquery and Cossa 1995). This is potentially due to the demography of southern bay countries compared to Scotland. Moreover, the Meuse, the Scheldt, the Elbe and the Rhine flow into the southern bay of the North Sea. As European rivers they cross a lot of countries (e.g. the Netherlands, Germany, France and Belgium) and industrial and intensive agricultural zones. A lot of chemical compounds accumulated by these rivers during their trips are released into the North Sea. Studies shown the high concentrations of Hg in the Rhine (Pieters and Geuke 1994), the Meuse (van Vliet and Zwolsman 2008), the Scheldt (Coquery and Cossa 1995; Baeyens and Leermakers 1998; Leermakers *et al.* 2001; Baeyens *et al.* 2003) and the Elbe (Coquery and Cossa 1995). Indeed, the Elbe presented total Hg concentrations (512 µg L^{-1}) higher than German coastal zone (12 µg L^{-1}) and than open North Sea (3 µg L^{-1}) (Coquery and Cossa 1995). The difference in Hg concentrations between coastal and offshore waters supports the influence of the foraging distribution on the T-Hg concentrations of seals sampled along the German coasts. In contrast Hg concentrations of Scottish seals are probably related to their diet - the most important route of exposure for Hg (Das *et al.* 2003; Lahaye *et al.* 2007) - and less to extrinsic factors because of less anthropogenic releases of Hg in the Scottish waters.

CONCLUSION

The multi-tracer approach combining Hg, Se, $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values successfully discriminated among diet resources and spatial foraging distributions of grey seals and harbour seals in the North Sea. This approach indicates offshore foraging distribution and more selective diet of grey seals compared to inshore foraging distribution and more generalist diet of harbour seals along both Scottish and German coasts. Our results suggested some partitioning between theses sympatric species in order to avoid competition for food resources. Nevertheless, ellipses overlaps suggested potential sharing of food resources in German seals.

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In the North Sea, sympatric grey and harbour seals may compete for food resources impacted by intense fishing activities and a recent increase of seal populations. In order to reduce inter-specific competition, sympatric species must segregate at least one aspect of their ecological niches: temporal, spatial or resource segregation. Using isotopes and Se and Hg concentrations, the foraging resources of grey seals and harbour seals and the potential competition between these species in the North Sea was studied. δ^{13}C, δ^{15}N and δ^{34}S values were combined with the concentrations of Hg and Se in blood samples of harbour and grey seals from the North Sea. Blood samples were collected on 45 grey seals and 37 harbour seals sampled along German and Scottish coasts. This multi-tracer approach showed spatial and resource partitioning within grey and harbour seals. Data indicated the offshore foraging distribution of grey seals as reflected by the lower δ^{15}N values and T-Hg concentrations and higher Se concentrations, and the inshore foraging distribution of harbour seals because of higher δ^{15}N values and T-Hg concentrations and lower Se concentrations. The SIAR mixing model revealed a more selective diet of grey seals compared to harbour seals, and the importance of sandeels in grey seal diet reflected by their high δ^{34}S values. Lastly, diet ellipse overlaps between grey seals and harbour seals sampled along the German coasts suggested a potential sharing of food resources, possibly due to the increase number of grey seals number in this area during the foraging season - all year except breeding and moulting periods. The multi-tracer approach provided a more robust discrimination among diet resources and spatial foraging distributions of grey seals and harbour seals in the North Sea.

Credit author statement

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Declaration of interests

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Map 1 – Sampling sites of grey seals (GS) and harbour seals (HS) in the North Sea; Helgoland and Lorenzenplate in the German Wadden Sea and Orkney and Isle of May along the Scottish coasts. Data are expressed as sampled species and year of sampling. Number of females and males and adults and juveniles sampled are giving for both species for all sampling sites. NO COLOR

Fig. 2 - Relationship between $\delta^{13}C$ and $\delta^{15}N$ values (‰) in red blood cells and T-Hg and Se concentrations (ng g^{-1} dry weight) in whole blood of grey seals (grey) and harbour seals (black) from the North Sea. Spearman's rank correlation ρ (for all, *p-value < 0.05*) was used for correlations between trace element concentrations and stable isotope ratios. NO COLOR

Fig. 3 - $\delta^{13}C$ *vs.* $\delta^{15}N$ (A and D), $\delta^{34}S$ *vs.* $\delta^{15}N$ (B and E) and $\delta^{13}C$ *vs.* T-Hg (C and F) biplots represented the potential overlap and the $SEA_{(C)}$ of harbour seal (black triangles) and grey seal (grey points) blood sampled along the Scottish (solid lines) and German (dotted lines) coasts. Isotopic and trace element data were transformed following the Cucherousset and Villéger method (2015). NO COLOR

Fig. 3 - Bi-plot of carbon and nitrogen isotope composition (mean ± SD) of food sources and consumers species (grey seals and harbour seals) sampled along the Scottish coasts. Fractionation factors of 0.8 ± 0.1‰ and 3.3 ± 0.1‰ were applied for $\delta^{13}C$ and $\delta^{15}N$ values, respectively (Pinzone *et al.* 2017). COLOR

Fig. 4 - Estimates of relative contribution of each potential food resource to Scottish grey seal (A) and harbour seal (B) diet calculated by SIAR model. Boxplots are posterior probability distributions of model estimations of proportions. The dark, intermediate and light boxes are the 50%, 75% and 95% credibility intervals. Sandeels values are extracted from Käkelä *et al.* 2007. COLOR

Table 1 – Stable isotope values of $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ (‰) in red blood cells and T-Hg and Se concentrations (ng g^{-1} of dry weight) in whole blood of grey seals and harbour seals (both sexes; adults and juveniles) sampled along the German coast, and of grey seals and harbour seals (adult females) sampled along the Scottish coast in the North Sea. Data are expressed as mean (median) ± SD (min – max). n = number of samples. Mann-Whitney test (*p-value* < 0.05) was used for species comparison; U and *p-value* are expressed in the table and significant *p-values* are in bold. NO COLOR

	German coast		Scottish coast	
	Grey seals	Harbour seals	Grey seals	Harbour seals
$\delta^{13}C$	-17.2 (-17.3) ± 0.8 (-18.3 to -15.8) n = 11	-17.4 (-17.3) ± 0.6 (-18.6 to -16.7) n = 20	-17.8 (-17.9) ± 0.4 (-18.8 to -17.0) n = 34	-17.5 (-17.5) ± 0.4 (-18.6 to -16.9) n = 17
	Mann-Whitney, U = 101, *p-value* = 0.726		**Mann-Whitney, U = 163, *p-value* = 0.012**	
$\delta^{15}N$	17.3 (17.8) ± 1.2 (15.1 to 18.8) n = 11	18.5 (18.6) ± 0.5 (16.6 to 19.1) n = 20	13.4 (13.2) ± 0.7 (12.7 to 15.7) n = 34	15.8 (15.9) ± 0.5 (14.6 to 16.5) n = 17
	Mann-Whitney, U = 31, *p-value* = 0.001		**Mann-Whitney, U = 10, *p-value* < 0.001**	
$\delta^{34}S$	17.4 (17.3) ± 0.9 (15.9 to 19.3) n = 11	8.8 (8.7) ± 1.2 (6.7 to 10.5) n = 20	14.6 (14.6) ± 0.9 (13.2 to 16.9) n = 33	9.6 (9.8) ± 2.0 (6.5 to 12.4) n = 17
	Mann-Whitney, U = 0, *p-value* < 0.001		**Mann-Whitney, U = 2, *p-value* < 0.001**	
T-Hg	794.9 (733.8) ± 283.2 (370.1 to 1285.1) n = 11	1376.9 (1338.2) ± 376.1 (808.0 to 2430.2) n = 20	300.7 (271.5) ± 147.5 (122.4 to 944.5) n = 34	364.6 (347.2) ± 108.4 (179.3 to 544.4) n = 17
	Mann-Whitney, U = 19, *p-value* < 0.001		**Mann-Whitney, U = 172, *p-value* = 0.020**	
Se	5164.0 (4670.0) ± 2097.8 (3014.2 to 9175.4) n = 11	3749.3 (3270.0) ± 2216.8 (1476.9 to 11800.0) n = 19	11636.1 (11455.9) ± 3736.6 (3052.7 to 17948.1) n = 31	4705.9 (4000.0) ± 2054.4 (2000.0 to 10000.0) n = 17
	Mann-Withney, U = 50, *p-value* = 0.02		**Mann-Withney, U = 27, *p-value* < 0.001**	

Table 2 – Summary of ellipse overlapping and SEA_B of isotopic ($\delta^{13}C$ *vs.* $\delta^{15}N$, $\delta^{15}N$ *vs.* $\delta^{34}S$) and ecological niches ($\delta^{13}C$ *vs.* T-Hg, T-Hg *vs.* $\delta^{15}N$, $\delta^{34}S$ *vs.* T-Hg, $\delta^{13}C$ *vs.* Se, Se *vs.* $\delta^{15}N$, $\delta^{34}S$ *vs.* Se) of grey seal (GS) and harbour seal (HS) blood sampled along German and Scottish coasts. Presence of overlap between GS and HS SEA (standard ellipse area) is indicated by the "✓" symbol (✓ = 0-5% of GS and HS ellipse overlap, ✓✓ = 5-40% GS and HS ellipse overlap, ✓✓✓ = 40-100% GS and HS ellipse overlap), absence of overlap is indicated by the "X" symbol. Significantly higher SEA_B for GS is indicated by the ">" symbol, significantly higher SEA_B for HS is indicated by the "<" symbol, and no significant difference in SEA_B between both species is indicated by the "=" symbol. COLOR

	Ellipse overlap Grey seals *vs.* Harbour seals		**SEA_B** Grey seals *vs.* Harbour seals	
	German coast	Scottish coast	German coast	Scottish coast
$\delta^{13}C$ *vs.* $\delta^{15}N$	✓✓	**X**	**>**	**=**
$\delta^{34}S$ *vs.* $\delta^{15}N$	**X**	**X**	**=**	**<**
$\delta^{13}C$ *vs.* T-Hg	✓	✓✓✓	**=**	**<**
T-Hg *vs.* $\delta^{15}N$	**X**	**X**	**=**	**=**
$\delta^{34}S$ *vs.* T-Hg	**X**	**X**	**<**	**<**
$\delta^{13}C$ *vs.* Se	✓✓✓	✓	**=**	**=**
Se *vs.* $\delta^{15}N$	✓✓	**X**	**>**	**>**
$\delta^{34}S$ *vs.* Se	**X**	**X**	**=**	**<**

Graphical abstract

Highlights

- Foraging niches of sympatric grey and harbour seals were studied.
- $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values and Hg and Se concentrations were used.
- This approach allowed for better understanding resources utilized.
- Grey seals exhibited a less complex diet and sandeels were an important component
- SIAR and SIBER analyses provided information on specific diets