Trophic niche overlap between sympatric harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) at their Southern European limit range (Eastern English Channel)

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Abstract

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15 Competition between the sympatric harbour (*Phoca vitulina*) and grey seals (*Halichoerus*

16 *grypus*) is thought to underlie some recent local declines of the former while the population of

17 the latter remains stable or increases. A better understanding of the interactions between these

18 two species is critical to elucidate current changes. This study aims at identifying and

19 quantifying the niche overlap between harbour and grey seals at their Southern European limit

20 range, in the *baie de Somme* (Eastern English Channel, France), in a context of exponential

21 increase in the number of resident harbour seals and visiting grey seals. Isotopic niche overlap

22 was quantified between both species using whisker $\delta^{13}C$ and $\delta^{15}N$ isotopic values, taking intra-

23 and interindividual variability into account. Dietary overlap was quantified from scat contents

24 using hierarchical clustering. A high degree of trophic niche overlap was identified between

25 both species. The narrower isotopic niche of harbour seals was nested within that of grey seals

26 (58.2% [CI95%: 22.7-100%] overlap). Six diet clusters were identified from scat content

27 analysis. Two of them gathered most of harbour seals' scats (85.5 % [80.3-90.2%]) and

28 around half of grey seals' ones (46.8% [35.1-58.4%]) that almost exclusively contained

29 benthic flatfish. Consumption of this type of prey was identified here to be the root cause of

30 trophic overlap. This highlighted the potential for competition between the two species at

31 their Southern European limit range, linked to foraging on benthic flatfish, in coastal waters

32 close to their haulout sites, especially during spring/summer. We suggest that (1) interspecific

33 competition for prey could occur/increase in the future if the number of grey and harbour

34 seals still increase and/or if flatfish supply decrease in this area, and (2) harbour seals would

35 be disadvantaged in such a case if they do not adapt, as being specialised on flatfish at the

36 colony scale.

1. Introduction

Detecting interspecific competition between sympatric species is a major objective in ecology as it structures niches and communities (Abrams, 1980; Alley, 1982; MacArthur and Levins, 1967). Competition is supposed to drive exclusion of the less fit species, especially when food resources are limited (Begon et al., 1986; Gause, 1932). Sympatric species sharing similar functional traits, dietary strategies and foraging grounds, can typically present a trophic overlap, and consequently co-exist or compete (e.g. Cupples et al., 2011; González-Solís et al., 1997; Jones and Barmuta, 1998). Since the niche of a species is conceptualised in the *n* dimensions defining the resources used in time and space (Hutchinson, 1957), parameters other than diet alone could underlie coexistence: foraging on the same prey but at a different period, and/or at different locations, and/or on different prey sizes / life stages (e.g. Brink et al., 2015). Describing trophic niches in multidimensions is therefore necessary for accurately identifying potential interactions (Costa-Pereira et al., 2019; Friedemann et al., 2016).

Identifying trophic interactions such as competition in the wild can be challenging, especially when studying mobile species. Some studies directly tested it in the field and succeeded in measuring the effects resulting from interspecific competition (e.g. Alatalo et al., 1985; Schoener, 1983). Alatalo et al. (1985) did so on four co-occurring bird species (*Parus montanus, P. critatus, P. ater and Regulus regulus*), and observed that the foraging niches of the two latter species spatially expanded in testing grounds where the number of *P. montanus* and *P. critatus* were artificially reduced for experimentation, in comparison to control grounds. However, it is complicated (or even impossible) to implement such a protocol in

61   many study cases, thus measuring trophic niche overlap provides an alternative indirect way

62   to investigate the potential for competition between co-occurring species (e.g. Ballejo et al.,

63   2018; Ogloff et al., 2019; Pianka, 1974). It is especially true for cryptic and mobile species

64   such as marine top predators that live and feed in a large 3-dimensional environment wherein

65   experimental setups on a scale commensurate with ecological realism are very limited.

66   The harbour seal (*Phoca vitulina*) and the grey seal (*Halichoerus grypus*) are two

67   sympatric species that are particularly interesting cases for studying trophic competition

68   among marine top predator species. Annual cycles of both species are asynchronous for

69   breeding and moulting – associated with an increase of time on land and a decrease of time at

70   sea – as it occurs successively and respectively in spring-summer for harbour seals (from June

71   to September) and in autumn-winter for grey seals (from October to April) in European

72   waters (Bonner, 1972). Conversely, they allocate most of their time at sea during the rest of

73   the year, supposedly exhibiting a higher foraging activity (Beck et al., 2003; Thompson et al.,

74   1994). Despite a partial trophic segregation in time, they can share a similar diet (Thompson

75   et al., 1996; Wilson and Hammond, 2019), diving behaviour (Baechler et al., 2002; Lesage et

76   al., 1999; Thompson et al., 1991) and potentially similar foraging grounds in coastal areas

77   (Planque et al., 2020; Thompson et al., 1996). Both species disperse in coastal waters on the

78   continental shelf and can use the same haulout sites (Thompson et al., 1996, Vincent et al.,

79   2017).

80   Harbour and grey seals are considered as generalist feeders at the species level, therefore

81   focusing on local prey availability (Kavanagh et al., 2010; Mohn and Bowen, 1996; Olsen and

82   Bjørge, 1995). Harbour seals restrict their foraging effort in narrower spatial areas generally

83   in the vicinity of their haulout sites (e.g. Thompson et al., 1996; Vincent et al., 2017),

84   suggesting they live at the scale of a breeding colony with more limited movements than grey

85   seals. The diet of harbour seals is characterised by high variations between sites (e.g. Olsen

86 and Bjørge, 1995; Spitz et al., 2010), supposed to reflect prey availability in the environment,

87 but by lower variations within a site (e.g. Spitz et al., 2015). Single dietary patterns observed

88 at the colony scale may be explained by "foraging traditions" due to parental and alloparental

89 investments in learning foraging strategies to pups (at sea), during lactation period (Spitz et

90 al., 2015). Thus, harbour seals could be more specialised at the colony scale rather than at the

91 individual scale. Higher specialisation for grey seals at the individual scale is shown by their

92 diet (Tucker et al., 2008), foraging patterns from carbon and nitrogen stable isotopes (Tucker

93 et al., 2007) and varying foraging areas between individuals (Austin et al., 2004). This

94 specialisation could arise from the ontogeny of foraging behaviour during early-life at-sea, in

95 the absence of parental post-weaning investment and teaching (Carter et al., 2017).

96   Drastic declines of harbour seals were locally observed these last decades along western

97 and eastern Atlantic coasts, and trophic competition with increasing number of grey seals was

98 suggested as one potential cause (Bowen et al., 2003; Hanson et al., 2013; Jones et al., 2015;

99 Sharples et al., 2012; Svensson, 2012; Thompson et al., 2019). Grey seal predation on harbour

100 seal was also recently observed (van Neer et al., 2015), but the extent of such direct

101 interactions and effects in populations are poorly documented. Understanding the potential

102 competitive interactions between the two species is therefore a key objective in the study of

103 their ecology (Bowen et al., 2003; Wilson and Hammond, 2019), and ultimately the

104 management of these populations. In their European core distribution, Wilson and Hammond

105 (2019) suggested a trophic effect of sandeels (Ammodytidae) stocks depletion in the North

106 Sea on interspecific competition. They highlighted that harbour seals declined in Great-

107 Britain where sandeels, previously identified as a key prey species, also declined. However,

108 sandeels were still abundant in grey seals' diet after these declines, thus Wilson and

109 Hammond (2019) suggested that both species might have competed for this type of prey that

110 could have caused deleterious effect on some harbour seal colonies sustainability. Recent

111   results in the North Sea now suggested that both species' trophic niches are mostly

112   segregating due to the continuing consumption of sandeels by grey seals and of a wider range

113   of other prey types by harbour seals (Damseaux et al. 2020).

114   Limit ranges of species are particularly interesting locations to study ecological processes

115   as they evolve in limitative environmental conditions compared to the core distribution

116   (Brown et al., 1996; Sexton et al., 2009). These processes, including trophic competition,

117   could therefore be exacerbated in such areas. The Southern limit of harbour and grey seals'

118   European range is located along the French coasts of the English Channel (Vincent et al.,

119   2017), where the main sympatric haulout site of both species is the *baie de Somme* BDS

120   (Eastern English Channel, EEC; location in Figure 1. A.). Harbour seals recolonised this area

121   from the 1990s and settled in a breeding colony (139 pups in 2018; Poncet et al., 2019).

122   Individual grey seals from the North Sea arrived in the EEC from the 2000s, but do not breed

123   in this area (Vincent et al., 2017). The number of individuals from both species is low in this

124   area (maximum yearly counts of 621 harbour seals and 269 grey seals in BDS in summer

125   2018; Poncet et al., 2019) compared to the core distribution (e.g. 45,100 [CI95%: 37,000-

126   60,400] harbour seals and 150,000 [131,000-171,600] grey seals in the nearby United

127   Kingdom in 2017; SCOS, 2018). Seal numbers still increase exponentially in the BDS for

128   both species, and especially faster for grey seals (+18.2%/year) than for harbour seals (+13%/

129   year) (Vincent et al., 2017). In this area, harbour seals' diet is essentially composed of small

130   flatfish from nurseries during summer period (Spitz et al., 2015), and their foraging areas are

131   very coastal and close to BDS haulout site (see Figure 1. B. modified from Planque et al.,

132   2020). Grey seals' foraging areas are both in these coastal areas as well as further (Figure 1.

133   B).

134   While harbour and grey seals' number still increase exponentially at their Southern

135   European limit range, we can assume that the level of interspecific competition (if there is

136   one) is still too low to impact seal population dynamics in this area. Resources used by seals

137   may not be currently limitative, however we cannot exclude that it could happen in the short-

138   or mid-term, if fish stock declines and reorganisation already observed in BDS these last three

139   decades continue (Auber et al., 2017; McLean et al., 2019). This study therefore aims at

140   identifying the potential for trophic competition between harbour and grey seals at their limit

141   range, in the BDS (France), by measuring trophic niche overlap. The analysis of carbon and

142   nitrogen stable isotopes in seal whiskers provided a tool to quantify trophic overlap.

143   Complementary analyses of seals' diet from scat contents also quantified the overlap, but

144   additionally documented seasonal variabilities and prey types implicated in this overlap. This

145   study therefore identified the potential for competition between sympatric harbour and grey

146   seals in assumed limitative conditions (limit range), and gave precisions on what could be the

147   nature of such interactions (i.e. implicated periods, prey types), prior to potential implications

148   on population dynamics in this area.

2. Material and Methods

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1. Study area

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151   This study was conducted in the *baie de Somme* (BDS) which is a macrotidal estuary

152   located on the French coasts of the Eastern English Channel (EEC) (Figure 1. A). EEC is

153   characterized by very shallow waters on the continental shelf (mostly shallower than 50 m

154   deep), strong tidal currents (e.g. Sentchev and Yaremchuk, 2007), and ecosystems strongly

155   structured by the presence of several high productive estuaries (*baie de Seine*, BDS, *baie

156   d'Authie*, *baie de Canche*; e.g. Carpentier et al., 2009; Girardin et al., 2018; Riou et al., 2001).

157   BDS estuary is one of the major fish nursery grounds in the EEC (the second, after *baie de

158   Seine*), especially important for commercial and flatfish species (mainly *Solea solea* and

159   *Pleuronectes platessa*; Carpentier et al., 2009; Riou et al., 2001; Selleslagh et al., 2009).

2. Stable isotopes analyses

Stable Isotopes Analyses (SIA) were performed on whisker samples collected on 8 harbour seals and 10 grey seals captured for telemetry studies from the BDS in 2008 and 2012 respectively (Table 1) (foraging areas already identified by Planque et al., 2020 for all harbour seals and for 7 on 10 grey seals; cf Figure 1. B.). Seals' whiskers are composed of inert keratinous tissue and provide a temporal integration of isotopic information during the period of whisker growth (Hirons et al., 2001; Hobson et al., 1996; Zhao and Schell, 2004). In this study, the longest whisker was sampled on each individual in order to provide the longest time integration in SIA.

All samples were cleaned before performing SIA in order to remove impurities which could bias isotopic measurements. Each whisker was individually soaked in a bath of 100% ethanol and impurities were removed by cleaning it manually. The samples were then set up in a beaker of milli-Q ultrapure quality water placed in an ultrasonic bath for 20 minutes. They were finally washed three times with mili-Q water and placed in an oven at 50 °C for 24 hours. After being washed and dried, each whisker was sectioned into approximately 10 mm sections from the proximal to the distal part. Each section was identified with a reference corresponding to the individual sampled and the distance from the whisker base (in mm), and was then sent for carbon and nitrogen stable isotopes analyses.

All whisker sections were analysed with an elemental analyser (Flash 2000, Thermo Scientific, Milan, Italy) coupled to an isotope-ratio mass spectrometer (Delta V Plus with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Results were expressed with the usual δ notation in parts per thousands (‰) relative to Vienna PeeDee Belemnite Standard for $\delta^{13}C$ and atmospheric N_2 for $\delta^{15}N$. Based on replicate measurements of internal laboratory standards, experimental precision is of $\pm$ 0.15 for both $\delta^{13}C$ and $\delta^{15}N$.

184   Harbour and grey seal isotopic niches in $\delta^{13}C$ and $\delta^{15}N$ were quantified with a

185   hierarchical model developed in a Bayesian framework. Jackson et al., (2011) pioneered

186   multivariate ellipse-based metrics to characterise isotopic niches (implemented in the *SIBER*

187   library in software R). Modelling isotopic standard ellipses in a Bayesian framework is

188   considered to be particularly accurate when aiming at identifying isotopic niche at colony

189   level with a small sample size, i.e. with few sampled individuals (Jackson et al., 2011). In the

190   present study, $\delta^{13}C$ and $\delta^{15}N$ stable isotopes analyses were performed at the level of whisker

191   segments, therefore providing intra-individual variability in isotopic composition during

192   several months (growth length of a seal whisker, Zhao and Schell, 2004). Standard isotopic

193   studies only consider interindividual variability to identify isotopic niche at the species level,

194   but we expanded this standard model to incorporate two levels of isotopic variability: intra-

195   individual level (characterized by several isotopic measurements along a whisker) and

196   interindividual one.

197   We assumed that isotopic data can be described by a bivariate normal distribution of

198   mean μ and covariance matrix Σ (Jackson et al., 2011). Let k denotes the k-th species and i

199   the i-th individual; n_{ik} is the number of isotopic measurements for individual i of species k.

200   Let $\mu_k = \{\mu_{1k}, \mu_{2k}\}$ be the mean isotopic values of species k, with subscript 1 corresponding to

201   carbon isotopic measurements, and 2 to nitrogen ones.

202   For each individual i of each species k,

203    $\qquad Y_{ik} \quad N_2\left(\alpha_{ik}, \Sigma_k\right)$ (1)

204   where N_2 denotes a bivariate Normal distribution of location parameters α_{ik} and

205   covariance matrix Σ_k. The correlation matrix Σ_k allows for a residual-level correlation

206   between carbon and nitrogen isotopic measurements. Parameters α_{ik} are individual-specific

207   mean isotopic values (so called 'random effects'):

$$208 \qquad \alpha_{ik} \sim S_2(n_{ik}, \mu_k, \Omega_k) \qquad\qquad (2)$$

209   where S_2 denotes a bivariate Student distribution of n_i degrees of freedom, with location

210   parameters μ_k and covariance matrix Ω_k. The Student distribution allows for potential outliers

211   (at the individual level): if there are few measurements for individual i, then the model allows

212   for the possibility that this individual may be an outlier. The correlation matrix Ω_k allows for

213   an individual-level correlation between carbon and nitrogen isotopic measurements.

214   Equations (1) and (2) define a hierarchical model that account for both intra- and

215   interindividual level correlation via the covariance matrices Σ_k and Ω_k respectively. For the

216   latter we used the prior of Huang and Wand, (2013) to ensure a marginal uniform distribution

217   on the correlation between carbon and nitrogen isotopic values:

$$218 \qquad \Omega_k \sim Wishart^{-1}\left(3, \begin{bmatrix} a_{1k} & 0 \\ 0 & a_{2k} \end{bmatrix}\right), \text{ and}$$

$$219 \qquad \Sigma_k \sim Wishart^{-1}\left(3, \begin{bmatrix} b_{1k} & 0 \\ 0 & b_{2k} \end{bmatrix}\right).$$

220   The priors for the variances parameters $\{a_{1k}, a_{2k}\}$ and $\{b_{1k}, b_{2k}\}$ were inverse gamma

221   distributions $\Gamma^{-1}(0.5, 1.0)$ which induce a marginal half-Student distribution with 2 degrees of

222   freedom on the scale (that is, the square-root of a variance) parameters (Huang and Wand,

223   2013). Weakly-informative priors were also used on location parameters $\mu_{1k}, \mu_{2k} \sim N(0.0, 20.0)$

224   . Parameter estimation was done using Hamilton Monte Carlo methods as implemented in

225   software Stan (Carpenter et al., 2017). Four chains were initialized using the default options in

226   package *rstan* (version 2.21.0, Stan Development Team, 2019), and run for a total of 2,000

227   iterations. The first 1,000 iterations served as warm-up, and the remaining 1,000 were thinned

228   to yield a sample of 4 draws per chain. Parameter convergence was assessed using the

229   Gelman-Rubin-Brooks $\hat{r}$ statistics ($\hat{r} < 1.05$).

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3. Isotopic niches identification and interspecific overlap

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231   Isotopic niches at the species level are operationalised as ellipses at 95% in $\delta^{13}C$ and $\delta^{15}N$

232   dimensions and can be estimated from the joint posterior distribution of parameters $\{\hat{\mu}_k, \hat{\Omega}_k\}$.

233   Individual-level variability is summarised by the covariance matrix $\hat{\Omega}_k$ and should be

234   included: otherwise, estimated isotopic niches will be too narrow if there is individual-level

235   variability, that is substantially differences in isotopic niches at the individual level within a

236   given species. Isotopic values for 100 new individuals i were drawn from $\alpha_{ik}^{new} \; N_2\left(\hat{\mu}_k^{(j)}, \hat{\Omega}_k^{(j)}\right)$,

237   where j denotes the j-th MCMC draw (iteration) from the joint posterior distribution; these

238   values then were used to estimate isotopic niches. This procedure was repeated by drawing

239   1,000 iterations j from the posterior distribution to account for estimation uncertainty: we

240   thus obtained a sample of 1,000 ellipses over which further inferences could be carried out. In

241   particular, interspecific overlap and its associated uncertainty can be easily assessed, and any

242   correlation between carbon and nitrogen isotopic values is automatically considered. We

243   additionally characterised the probability ranges belonging to the isotopic niches (i.e. to

244   model ellipses) as well as the probability of interspecific niche overlap (each step are

245   complementary illustrated in Appendix 1).

246   The overlap between harbour seal and grey seal isotopic niches was quantified using the

247   function 'maxLikOverlap' in the package *SIBER* (version 2.1.5; Jackson et al., 2011) in

248   software R (version 4.0.2, R Core Team, 2020) on the 1,000 ellipses generated for each

249   species from the model. It provides an estimate of the proportion of whole isotopic niche area

250   covered by both species that is overlapping, as well as the proportion of first species' isotopic

251   niche area in second species' one, and vice-versa.

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4. Diet analysis

Harbour and grey seal diets were assessed by analysing hard prey remains in scat samples. This study used an expanded dataset on harbour seals (e.g. Spitz et al., 2015) and grey seals. A total of 196 harbour seal scats and 126 grey seal scats were collected in the BDS from 2002 to 2019 and included at least one prey (3 harbour seal scats and 49 grey seal ones were removed from this study as they were empty of diagnostic hard parts) (Table 2). Scat samples were stored frozen at -20°C until laboratory analyses. We distinguished two seasonal periods for seal diet analyses: spring / summer (from April to September) and autumn / winter (October – March). The assignment of seal species that produced each scat sample was performed from a DNA analysis described by Spitz et al., (2015).

Diet analysis followed a procedure usually used for pinnipeds (Pierce and Boyle, 1991; Ridoux et al., 2007; Spitz et al., 2010). Scat samples were washed on a 0.2 mm mesh size sieve in order to analyse their content in diagnostic hard remains such as fish otoliths, fish bones and cephalopod beaks. These items were identified to the species level by using available keys and guides (Härkönen, 1986; Tuset et al., 2008) as well as our own reference material. Taxonomic identification of prey was performed at species, group of species pooled, or family levels.

Harbour and grey seals' diet were presented in this study in terms of proportion of reconstructed mass of ingested prey at the level of a seal species (level of all samples pooled for a species, sometimes during a specific season). We measured the length or width of fish otoliths, according to fish species or group of fish species, and the lower rostral length of cephalopod beaks. These measurements were then converted in individual body length and body mass by using available allometric relationships (Härkönen, 1986, Observatoire Pelagis unpublished data). We therefore reconstructed prey body mass associated with each measurable (i.e. not broken item) fish otolith or cephalopod beak (inferior part of the beak). A

277 prey was considered present in a sample when at least one diagnostic part was found. The

278 number of fish individuals in a scat sample was given by half the number of paired structures

279 (otoliths, operculum, dentary, premaxillary bones) rounded up to the integer or the number of

280 single structures (parasphenoid), and the number of cephalopods was given by the higher

281 number of upper or lower beaks. We finally calculated the reconstituted relative mass for each

282 prey taxon within each scat sample by multiplying the estimated number of individuals in this

283 taxon with the associated average individual body masses of prey in that sample. Possible

284 biases related to the digestive erosion of otoliths were not considered in this study. Prey body

285 size and mass calculated here are therefore relative values, underestimated from absolute/real

286 mass and size of prey ingested.

287 Results are presented here as functional groups of prey to characterize harbour and grey

288 seals' diet, rather than using classic taxonomic groups, considering that it is a more suitable

289 way to describe predator-prey interactions (Smith et al., 2015; Spitz et al., 2018) and to

290 identify the associated foraging strategies. Prey species (or group of prey species) –

291 taxonomically identified in seal diet – that shared similar functional traits were pooled in 6

292 different functional groups (Table 3): small benthic flatfish, large benthic flatfish, benthic

293 non-flatfish, demersal fish, pelagic fish, pelagic squids. Benthic flatfish were divided in two

294 different functional groups (small and large benthic flatfish) assuming that there may be

295 substantial ecological differences between more juvenile flatfish on nursery grounds close to

296 estuaries and more mature/adult flatfish even being taxonomically associated (Riou et al.,

297 2001). We therefore filtered individual prey with a relative body length threshold of 200 mm.

298 Diet data were set in a two-dimensional matrix of proportion of total reconstructed prey

299 mass summed by functional group (6 columns) for each seal scat sample (270 lines). It was

300 constructed on all non-empty scats without prior distinction between the two seal species. An

301 agglomerative hierarchical cluster analysis was applied on the diet matrix. This analysis

302   aimed at grouping seal scats that shared similar pattern in their composition in prey

303   (expressed here with functional groups). Hierarchical cluster analysis was performed using a

304   Euclidian distance procedure to estimate similarity between scats and employing the Ward.D2

305   algorithm to gather scats in groups (Murtagh and Legendre, 2014). The most relevant number

306   of clusters was determined using 'NbClust' function in *NbClust* package (version 3.0) in

307   software R (version 4.0.2, R Core Team, 2020) that run 30 differences indices usually used to

308   determine number of clusters (Charrad et al., 2014). The chosen number of clusters was the

309   one that was proposed by the highest number of indices. Cluster analysis was run using the

310   'eclust' function in *factoextra* package (version 1.0.7) in software R.

311   Functional composition of diet associated with each cluster was presented by calculating

312   the percentage of total prey mass of all scats, for each seal species separately, within this

313   cluster by functional group. Confidence intervals (CI95%) around these percentages by mass

314   were generated for each prey functional group with a bootstrap procedure (Reynolds and

315   Aebischer, 1991) written using software R. Random samples were drawn with replacement

316   and the clustering procedure described above was repeated 1,000 times. The lower and upper

317   bounds of the CI95% were defined as the quantile at 2.5% and 97.5% of the values generated.

318   **5. Dietary niches characteristics and interspecific overlap**

319   Interspecific dietary overlap between harbour and grey seals was quantified by

320   comparing the functional composition of their diet in prey mass, without consideration for

321   diet clusters, with the Pianka index (Pianka, 1974). It ranges from 0 to 1, where 0 indicates no

322   overlap and 1 indicates a complete overlap; segregation was considered substantial when

323   overlap values were <0.4 (Ross, 1986):

324    $$O = \frac{\sum PiA PiB}{\sqrt{\sum PiA^2 \sum PiB^2}}$$

325 Where *PiA* is the percentage by mass of prey in the functional group *i* found in harbour seals'

326 diet and *PiB* is the percentage by mass of prey in the functional group *i* found in grey seals'

327 diet. Confidence intervals (CI95%) around the Pianka value were estimated by randomly

328 comparing 10,000 times the diet generated with bootstrap procedures (with replacement) for

329 harbour and grey seals.

330 **6. Comparison of seal isotopic niche with isotopic values of potential prey**

331   Isotopic values of some fish and cephalopod species, identified in the present study as

332 preferential prey for harbour and grey seals (*cf* diet analysis), were available for the EEC

333 (Kopp et al., 2015). Kopp et al., (2015) measured isotopic values of fish and cephalopods

334 sampled at different depths in the EEC, and presented results for different depth strata and for

335 all depths pooled. We presented here the isotopic values of potential seal prey for all depths,

336 except for *Clupea harengus* for which we present values for the two sampled depth strata as

337 significant isotopic differences where identified between them (*e.g. C. harengus* in a benthic

338 pathway for 0-20 m, and in a pelagic pathway for 20-38 m). We compared harbour and grey

339 seal isotopic niches identified in this study with isotopic values of prey by applying a trophic

340 enrichment factor (TEF), i.e. the amount of increase of $\delta^{13}C$ and $\delta^{15}N$ values from prey to

341 consumer. Assuming that TEF vary depending on consumer species, prey and analysed

342 tissues (Crawford et al., 2008), we used TEFs values of + 2.4±1.3 ‰ for $\delta^{13}C$ and + 2.6±1.2

343 ‰ for $\delta^{15}N$ evaluated by Lerner et al., (2018) for grey seal whiskers using SIDER method

344 developed by Healy et al., (2018).

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3. Results

1. Isotopic niches overlap

Harbour and grey seals' isotopic niches (Figure 2. A) presented interspecific differences in width. Harbour seals' isotopic niche was characterized by an area of 3.88‰^{2} [CI95%: 1.09-8.17‰^{2}] and grey seals' one by an area of 5.93‰^{2} [2.32-10.82‰^{2}]. The probability of grey seals' isotopic niche to be larger than harbour seals' one was 0.78. Harbour and grey seals' isotopic niches were characterized by an interspecific overlap of 26.6% [8.8-45.3%] of total niche area covered by both species. Harbour seals' isotopic niche was more nested within the grey seals' one (58.2% [22.7-100%] of its area) than grey seals' isotopic niche was in the harbour seals' one (36.3% [11.1-63.5%] of its area). The associated probability of harbour seals' isotopic niche to be more nested within the grey seals' one than the opposite was 0.78.

Ranges of probability belonging to harbour and grey seals' isotopic niches were identified Figure 2. B), allowing the identification of probability ranges of interspecific overlap between both species (Figure 2. C).

Interindividual differences in δ^{13}C in isotopic niche were characterized by of the scale parameters (in matrix Ω) of 0.54‰ [0.24-0.94‰] for harbour seals and 0.41‰ [0.21-0.66‰] for grey seals, with a probability of 0.72 to be higher for harbour seals. The higher interindividual variability in isotopic niche was denoted in δ^{15}N for grey seals (0.83‰ [0.44-1.31‰]), while being much lower for harbour seals (0.41‰ [0.18-0.74‰]). The probability to have a higher interindividual variability in δ^{15}N in grey seals' isotopic niche than in harbour seals' one was 0.94. Most of the isotopic niche divergence observed between both species therefore resulted from the larger size of grey seals' isotopic niche that extended in δ^{15}N (Figure 2. B).

2. Diet composition and interspecific overlap

Harbour and grey seal diets in BDS resulted from a combination of six different diet clusters (Figure 3. A). These clusters were characterised by different patterns in functional prey compositions, reflecting different typologies of scat content (Figure 3. C). Scats from some clusters showed an almost exclusive composition in only one type of prey (clusters 3, 5, 6), while others showed a mixed content in different types of prey (clusters 1, 2, 4). Note that additional descriptive results on harbour and grey seal diets at taxonomic prey species level are available in supplementary materials (Appendices 2 and 3).

Scats in clusters 1 and 2 mostly contained small and large benthic flatfish with a minority of other prey types (benthic non-flatfish, demersal and pelagic fish). Proportion (in mass) of large benthic flatfish (≥200 mm) was more important than small ones (< 200 mm) in scats of cluster 1 (~50-75%), and, conversely, small benthic flatfish were more important than large ones in scats of cluster 2 (~50-75%). Scats in clusters 3 and 5 respectively included demersal and pelagic fish (almost) exclusively. Cluster 4 showed the prevalence of pelagic squids with additional demersal fish, benthic flatfish and pelagic fish in scats, and cluster 5 the prevalence of benthic non-flatfish with minor presence of demersal and benthic flatfish.

Harbour and grey seals' scats were unequally distributed in each detected diet cluster (Figure 3. B). Most of harbour seals' scats (85.5% [CI95%: 80.3-90.2%]) and around half of grey seals' ones (46.8% [35.1-58.4%]) were associated with clusters 1 and 2 characterised by a high prevalence of small and large benthic flatfish in content. These two diet clusters were the only ones that encompassed a high percentage of scats for both seal species, i.e. characterising most of the interspecific dietary overlap. Scats with prevalence of large flatfish (cluster 1) similarly accounted for around one quarter of harbour and grey seal samples (29.0% [22.8-35.8%] and 24.7% [14.3-33.8%] of scats respectively). However, scats with

prevalence of small flatfish (cluster 2) accounted for more than half of harbour seals' scats (56.5% [49.2-63.7%]), while being 2.5 times less for grey seals (22.1% [13.0-32.5%]).

Clusters 3 to 6 essentially characterised scat contents in other types of prey than benthic flatfish. They included half of grey seals' scats (53.2% [41.6-64.9%]) and few harbour seals' ones (14.5% [9.8-19.7%]). A substantial proportion of grey seals' scats showed an exclusive content in demersal fish (cluster 3; 14.3% [6.5-22.1%]) and pelagic fish (cluster 5; 27.3% [16.9-37.7%]), while very few harbour seals' ones were characterised by such a content (6.2% [3.1-9.8%] and 2.1% [0.5-4.1%] for both clusters respectively). Scats containing pelagic squids with additional fish (mostly demersal fish and flatfish) (cluster 4) were exclusively observed for grey seals and accounted for 11.7% [5.2-19.5%] of all species samples. Scats with a prevalence of benthic non-flatfish completed by minor other types of fish (cluster 6) were exclusively observed in a small proportion of harbour seal samples (6.2% [3.1-9.8%]).

A high degree of interspecific dietary overlap was identified using functional prey groups between harbour and grey seals from Pianka index (value when comparing all scat content data: 0.72 [0.53-0.81]).

Seasonal variation in diet between autumn/winter and spring/summer periods was identified for grey seals (Figure 4). Grey seal scats essentially containing large and small benthic flatfish (clusters 1 and 2) were in higher proportion during spring/summer (65.2% [47.8-82.6%]) than during autumn/winter (38.9% [25.9-51.9%]). Those with a prevalence of small benthic flatfish (cluster 2) were especially dominant during spring/summer (43.5% [26.0-60.9%]) while being in lower proportion during autumn/winter (13.0% [5.6-22.2%]). Grey seal scats mostly containing other types prey remains (i.e. scats of clusters 3, 4 and 5) were therefore dominant during autumn/winter period (61.1% [48.1-74.1%]). During this period, scats almost exclusively containing pelagic fish (cluster 5) were in higher proportion (33.3% [20.4-44.4%]) than those containing pelagic squids with additional pelagic and

417   demersal fish (cluster 4; 14.8% [5.6-24.1%]) or mostly containing demersal fish (cluster 3;

418   13.0% [5.6-22.2%]).

419   The content of harbour seal scats was less characterised by seasonal variations than for

420   grey seals (Figure 4). Harbour seal scats essentially containing small and large benthic flatfish

421   (clusters 1 and 2) were in similar proportions during autumn/winter and spring/summer

422   periods (81.8% [54.5-100%] and 85.7 [80.2-90.7%] respectively). Scats with a prevalence of

423   small benthic flatfish were dominant during both seasons (72.7% [45.5-100%] and 55.5%

424   [48.4-62.6%] of scats during autumn/winter and spring/summer respectively).

425   Seasonal variations in the composition of seals' diet implied differences in the

426   interspecific dietary overlap. The overlap between harbour and grey seals' diets was higher

427   during spring/summer (Pianka index: 0.78 [0.66-0.91]) than during autumn/winter (0.55

428   [0.29-0.8]) (probability to be higher during spring/summer: 0.96).

429   **3. Comparison of seal isotopic niche with isotopic values of potential prey**

430   Isotopic composition of potential seal prey, after application of trophic enrichment factor

431   (TEF) for δ^{13}C (+ 2.4±1.3 ‰) and δ^{15}N (+ 2.6±1.2‰) (assuming prey consumption), were

432   isotopically located in probability ranges belonging to harbour and grey seals' isotopic niches

433   (Figure 5). Five benthic flatfish species that constituted a large part of harbour seals' diet (see

434   section 3.2, Figure 3) had isotopic values (+TEF) in higher probability ranges belonging to

435   harbour seals' isotopic niche, except for *Microchirus variegatus* that were in lower probability

436   ranges. Similarly, these species, also identified as part of grey seals' diet, were isotopically

437   located in high probability ranges of grey seals' isotopic niche. Two demersal fish species had

438   isotopic values (+TEF) in higher probability ranges belonging to grey seals' isotopic niche.

439   However, these values were in lower probability ranges (*Trispterus luscus*) or almost entirely

440   out (*Merlangius merlangus*) of harbour seals' isotopic niche. The pelagic squid *Loligo*

vulgaris, identified here as a potential prey for grey seals (Figure 3), had isotopic values (+TEF) that exclusively range in grey seals' isotopic niche. While the benthic non-flafish *Callionymus lyra* was only identified here in harbour seals' diet (Figure 3) – therefore only considered as a potential prey for harbour seals – the isotopic value of this species was in the isotopic niche of both species.

Similarly, while the pelagic fish *Clupea harengus* was almost exclusively identified here in grey seals' diet (Figure 3), its isotopic value on the shallower strata (0-20 m, where this species was detected in a benthic pathway; cf Kopp et al., 2015) was in both seal species' niche. However, the isotopic value of *C. harengus* on the deeper strata (20-38 m, where this species was rather detected in a pelagic pathway) was almost in lower probability ranges of both seal species' niches.

4. Discussion

This study reveals a strong potential for trophic competition between sympatric harbour and grey seals at their Southern limit of their European range. Both species' trophic niches were overlapping, as measured with two complementary approaches (based on isotopic niches and diet composition), with the larger grey seals' niche covering most of the narrower harbour seals' niche. A specific foraging strategy was implicated in this overlap (feeding on benthic flatfish in coastal waters), that could imply potential competition. This study highlighted the context for interspecific competition, and a continuing increase in the number of grey and harbour seals and/or a decrease in flatfish supply in this area could imply/amplify effects on colonies.

1. Two complementary approaches

Two complementary analyses were used in this study to investigate the trophic niche overlap between sympatric harbour and grey seals. The identification of isotopic niches provided a first quantification of overlap that was strengthened and clarified by results from scat contents. In addition to documenting seasonal variations, diet analyses also specified the type of prey species implicated in this overlap (benthic flatfish). The final comparison of isotopic values of potential prey species – detected in scat samples – with seal isotopic niches confirmed the importance of benthic flatfish consumption in interspecific overlap, and stressed out the complementarity between all study results. We suggest that isotopic niches overlap may also result from consumption of prey species with isotopic values similar to benthic flatfish, but almost exclusively detected in harbour seals' diet (*Callionymus lyra*, benthic non-flatfish) or in grey seals' one (*Clupea harengus*, pelagic fish, on 0-20 m depth strata). These results could also give more prevision on the potential origin of *C. harengus* consumed by grey seals, here more likely in shallower waters (0-20 m) where this pelagic fish was detected in a more benthic pathway than in deeper waters (20-38 m, cf Figure 5). It therefore confirms the importance of multi-approaches focusing on various metrics to accurately characterise trophic niche overlap (e.g. Costa-Pereira et al., 2019).

Results from both methodologies imply limitations due to the nature of the data used, but their concomitance rather gives confidence in trophic niche identification. The two approaches provided information on seal foraging patterns at different yet complementary spatial and temporal scales, and with different sampling sizes in seal colonies / populations. Low numbers of individual whiskers sampled for isotopic niche determination classically led us to work in a Bayesian framework, considering interindividual variability (Jackson et al., 2011). The novelty aspect of isotopic niches was here to incorporate a medium temporal view of the trophic niche by including the intra-individual variability of the foraging patterns in the

487   model (time-integrated isotopic measures of several months along each whisker, according to

488   its growth; Zhao & Schell 2004). Isotopic niches could also incorporate a spatial dimension

489   by integrating several months of whisker growth i.e. several months of foraging. Working in a

490   probabilistic framework also gave more accuracy in the identification of isotopic niches and

491   overlap (i.e. with probability ranges). Diet contents additionally provided a qualitative

492   information on types of prey ingested to define seal trophic niche, that was not elucidated

493   from isotopic niches. Each seal scat is based on a restricted temporal view, giving a snapshot

494   of dietary events that could have occurred from several hours to several days before sampling.

495   However elapsed time from consumption could not be defined here as residence of prey

496   remains in the transit may vary depending on prey types and/or type of hard part (Harvey,

497   1989). Linking a precise time and location of these dietary events is almost impossible. While

498   one scat solely characterises dietary events at low spatial and temporal scales, the addition of

499   several samples collected at different times is assumed to provide a comparable (or higher)

500   temporal view of foraging patterns as for isotopic niches, but supposedly for more individuals.

501   We assumed that there were higher uncertainties in diet composition for some seasons and/or

502   species due to low sampling number (e.g. autumn / winter for harbour seals), therefore

503   incorporating less individual feeding events. Despite this, we detected seasonal tendencies in

504   diet overlap between harbour and grey seals that allowed for a best understanding in source of

505   potential competition.

506   **2. Niche overlap structured by strategies**

507   Grey and harbour seals' trophic niches were found to overlap at their Southern European

508   range, and consumption of benthic flatfish by both species was identified to be the root cause.

509   This finding is in sharp contrast with seals' European core distribution (North Sea) where

510   local harbour seal declines were already observed in the 2000's, as the diet overlap was

511   explained by sandeels consumption prior to these declines (Wilson and Hammond, 2019).

512 Recent results rather suggested a trophic segregation in the Scottish and German parts of the

513 North Sea with a continuing consumption of sandeels by grey seals in offshore waters, but

514 with an inshore consumption of a wider range of other prey types for harbour seals (Wilson

515 and Hammond, 2019; Damseaux et al., 2020). Variations in overlap patterns between seals'

516 European core distribution and limit range may arise from differing stages of population

517 context: established colonies at the core with potential effects from interspecific competition

518 already observed (one of the potential causes of harbour seal declines) VS. more recent seal

519 arrivals at the limit range where such interactions could currently implement but with no

520 visible effects in population dynamics for now.

521   In the present study, the trophic overlap is found to occur in coastal waters of the EEC, in

522 the vicinity of the BDS haulout site, where the harbour seals restricted their foraging effort

523 over months while grey seals also foraged further at a larger spatial scale (Figure 1. B,

524 modified from Planque et al., 2020). Our results and previous knowledge on foraging areas

525 highlighted that the narrow harbour seals' niche is almost nested in the larger grey seals' one,

526 and we suggested that it may be explained by differences in foraging strategies at the

527 individual and population levels between both species.

528   Harbour seals are usually considered as generalist feeders at species level (e.g. Damseaux

529 et al., 2020; Kavanagh et al., 2010; Olsen & Bjørge 1995), and can potentially forage on a

530 large number of different prey present in the environment. In the present study, we identified

531 that harbour seals from the BDS are specialised on benthic flatfish, especially small ones from

532 nurseries (Spitz et al., 2015), and that this specialisation seemed stable over time (narrow

533 time-integrated isotopic niche and stability of diet content over seasons). The presence of

534 large flatfish nurseries in the coastal estuaries of the EEC (Carpentier et al., 2009; Riou et al.,

535 2001; Selleslagh et al., 2009) must therefore drive the harbour seals' feeding strategies in this

536 area (Spitz et al., 2015). Spitz et al., (2015) also suggested that harbour seals' diet may reflect

537 "foraging traditions" at the colony level due to parental and alloparental investments during

538 their first weeks of life (lactation period), i.e. a pup will replicate the foraging strategy learned

539 with its mother during the lactation period. Restricted harbour seals' trophic niche and

540 foraging areas (as previously assessed from telemetry) in the BDS strengthened this

541 statement, with a single strategy illustrating most of the colony's foraging behaviour.

542　Grey seals are also generalist feeders at the species level consuming a high diversity of

543 prey (Beck et al., 2007; Mohn and Bowen, 1996; Ridoux et al., 2007), but they are rather

544 considered as specialist feeders at the individual level (Gosch et al., 2014; Tucker et al.,

545 2007). The broader trophic niche for grey seals and larger extent of their foraging areas may

546 reflect a higher specialisation at the individual level and/or a higher seasonal variability in

547 dietary preferences. The higher level of interindividual differences in $\delta^{15}N$ denoted for grey

548 seals illustrated why grey seals' niche was larger than harbour seals' one. It is also

549 characterised by isotopic values in the core of harbour seals' niche (where overlap occurred)

550 for three out of ten grey seal individuals, while being at the edge for the seven others (Figure

551 2). Trophic overlap may therefore be based on part of grey seal individuals that share similar

552 foraging strategies with harbour seals, while others would mostly segregate. Stronger seasonal

553 differences in the diet of grey seals could also explain the larger trophic niche for this species,

554 assuming that their feeding strategies may change according to prey availability in the

555 environment. Lower dietary overlap in autumn/winter could be explained by a higher

556 consumption of pelagic fish (especially *Clupea harengus*) by grey seals, regarding that this

557 prey species is known to migrate from the North Sea to the EEC during these seasons to

558 reproduce (e.g. Corten, 2013). We suggest that the larger trophic niche of grey seals could

559 result from a stronger diversity of foraging strategies, with individuals adapting their foraging

560 effort according to local prey availability. Grey seals foraging close to BDS and feeding on

561 benthic flatfish would therefore be potential competitors to harbour seals.

3. Ecological implications

A trophic competitive context between sympatric harbour and grey seals occurring at their limit range could ultimately have implications on harbour seals maintenance (e.g. Svensson, 2012; Wilson and Hammond, 2019). Our quantitative measurements of trophic niche overlap provided here a useful tool to identify the potential for interspecific competition, but do not provide the proof of effective competition. This study especially gave a first robust assessment of their niches and overlap in a period of exponential increase of both species' numbers in BDS with continuing implementation of a reproductive harbour seal colony and concomitant arrival of visitor grey seals from the North Sea (Vincent et al., 2017). It therefore reports the seals' foraging ecology prior to potential modifications in their populations in the EEC that could result from different causes, including resources availability and trophic interactions.

Regarding the population dynamic of harbour and grey seals in the EEC (exponential increase), we suggest that flatfish resources may currently be sufficient for both species' maintenance and growth in this area. However, the EEC is subject to strong and quick ecological shifts, most likely due to anthropogenic causes (e.g. climate change; Auber et al., 2017; McLean et al., 2019) with drastic declines in fish abundance observed these last decades in the BDS (decline by 80% for the last 30 years) and major changes in functional organisation of fish nurseries (McLean et al., 2019). Benthic flatfish in the EEC could therefore become a limitative resource for harbour and grey seals in the near future if the latter still increase exponentially and mostly focus their foraging effort on this prey type, and/ or if flatfish stocks continue to decrease. Similarly to the supposed effect that had sandeel declines in the North Sea on harbour seals maintenance, recently hypothesised by Wilson et al., (2019), we suggest that such a mechanism could similarly occur with flatfish in the BDS.

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An effective competition between these two species could induce the exclusion of the one that does not succeed to adapt (Gause, 1932), supposed to be harbour seals in this duo. Specialisation of harbour seals at colony level could make them more vulnerable to drastic changes in benthic flatfish nurseries in costal estuaries of the EEC if they do not adapt. Individual specialisation for grey seals, with larger interindividual differences within a larger trophic niche at population level, would rather be a major benefit for this species in a competitive context. Following this assumption, grey seals could therefore more easily adapt their foraging effort on prey available along different seasons, in different spatial areas. Ecological implications due to trophic interactions directly depend on the foraging behaviour plasticity of harbour and grey seals, and we hypothesised that this plasticity might be lower for harbour seal colony in BDS due to high specialisation on only one type of prey for the last decades. Monitoring harbour and grey seals' trophic niches, foraging areas and trends in number in the coming years is essential to identify potential changes that could results from competitive interactions for prey.

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857 **Figure and table legends**

858 **Figure 1** Location of the *baie de Somme* (along the French coasts of the Eastern English

859 Channel) used by harbour and grey seals as a haulout site (**A**) and foraging areas of nine

860 harbour seals and eight grey seals identified by Planque et al., (2020) using a vertical

861 approach (selection of faster U-shaped dives) (**B**). Bathymetry data was obtained from

862 SHOM, (2015). Foraging areas were identified from harbour and grey seal individuals

863 captured in the *baie de Somme*, respectively in 2008 and 2012 and tracked with GPS/GSM

864 tags (Sea Mammal Research Unit, University of StAndrews, UK). Likely foraging areas of

865 both species are characterised by spatial kernel densities (50%, 75%, 95%) of faster U-shaped

866 dives.

867

868 **Figure 2** Isotopic niches of harbour and grey seals estimated from Bayesian model ran on

869 δ^{13}C and δ^{15}N stable isotope ratios measured along a whisker of 8 harbour seal and 10 grey

870 seal individuals. **A** Isotopic niches characterised by standard ellipses at 95% confidence

871 interval for harbour seals (green) and grey seals (blue). **B** Ranges of probability belonging to

872 harbour and grey seals' isotopic niches. **C** Ranges of probability of interspecific isotopic

873 niche overlap. Each probability range in B and C were characterised by ellipses at 95%

874 around uniform points describing this probability (cf Appendix 1). Points in **A**, **B** and **C** are

875 averages of predicted isotopic values for observed harbour and grey seal individuals, and error

876 bars are confidence interval at 95%.

877

878 **Figure 3** Dietary clusters identified from 193 harbour seal and 77 grey seal scat samples. **A**

879 Identification of 6 diet clusters of scat samples according to their composition in prey

880 (functional groups) from hierarchical clustering. **B** Distribution of scat samples in percentage

881 in each diet cluster for both seal species with confidence interval at 95% (CI95%; error bars).

882 **C** Diet composition of all samples of harbour and grey seals associated with each cluster in

883 percentage by mass, with CI95% (error bars).

884

885 **Figure 4** Distribution of seal scat samples in percentage in each diet cluster during

886 autumn/winter (11 harbour seal scats and 54 grey seal ones) and spring/summer periods (182

887 harbour seal scats and 23 grey seal ones), with CI95% (error bars).

888

889 **Figure 5** Comparison of harbour and grey seals' isotopic niches (see Figure 4. B) with

890 isotopic values of potential prey in the Eastern English Channel. Considering a potential

891 consumption of prey by predator, we applied a trophic enrichment factor (TEF) of + 2.4±1.3

892 ‰ for $\delta^{13}C$ and + 2.6±1.2 ‰ for $\delta^{15}N$ on vales of prey isotopic composition. Isotopic data of

893 potential prey from Kopp et al., (2015).

894

895 **Table 1** Sampling of whiskers on 8 harbour seals and 10 grey seals to analyse $\delta^{13}C$ and $\delta^{15}N$

896 stable isotopes composition of 10 mm segments. Individual references are mentioned in

897 Planque et al., (2020).

898

899 **Table 2** Sampling of harbour and grey seal scat samples collected in the *baie de Somme* from

900 2002 to 2019. Only non-empty scat samples were presented here. The number of new scats

901 analysed, complementary to those presented in Spitz et al., (2015), are in brackets.

902

903 **Table 3** Measurable prey observed in harbour and grey seal scats in the present study, and

904 associated functional groups. Und.: undetermined species.

Data and scripts accessibility

The data used in this study are available on SEANOE repositories under the licence "Creative Commons BY-NC", and are freely downloadable: stable isotopes data from https://doi.org/10.17882/76528 and diet data from https://doi.org/10.17882/76780. The two scripts developed in this study to perform all presented analyses are freely available on GitHub repositories: isotopic niches analysis from https://github.com/YannPlanque/Isotopic_Niche_Overlap, and diet analysis from https://github.com/YannPlanque/Diet_Cluster_and_Overlap (written in R language).

Competing Interests Statement

The authors declare that they have no conflict of interest.

Author Contributions

This work was conducted by Yann Planque who conceptualised the manuscript, performed the analysis and wrote the original draft of the article, and by Dr Jérôme Spitz, Dr Matthieu Authier, Dr Cécile Vincent and Dr Florence Caurant who provided their support and expertise on manuscript conceptualisation, on data analysis, on the interpretation of results, and who reviewed and edited the manuscript. Dr Cécile Vincent and Dr Florence Caurant supervised this work during Yann Planque's PhD Degree, and are PIs of the underlying research projects (fundings).

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947 Ethical standards

948   All procedures performed in studies involving harbour and grey seals were in accordance

949 with the ethical standards of the French Ministry of the Environment as seals were caught and

950   instrumented under license numbers 08/346/DEROG and 11/874/DEROG, delivered by this

951   Ministry.