

1 **Abstract**

- 2 1. Quantifying consumption and prey choice for marine predator species is key to understanding
3 their interaction with prey species, fisheries, and the ecosystem as a whole. However,
4 parameterising a functional response for large predators can be challenging because of the
5 difficulty in obtaining the required datasets on predator diet and the availability of multiple
6 prey species.
- 7 2. This study modelled a Multi-Species Functional Response (MSFR) to describe the
8 relationship between consumption by harbour porpoises (*Phocoena phocoena*) and the
9 availability of multiple prey species in the southern North Sea. Bayesian methodology was
10 employed to estimate MSFR parameters and to incorporate uncertainties in diet and prey
11 availability estimates. Prey consumption was estimated from stomach contents data of
12 stranded harbour porpoises. Prey availability to harbour porpoises was estimated based on the
13 spatial overlap between prey distributions, estimated from fish survey data, and porpoise
14 foraging range in the days prior to stranding predicted from telemetry data.
- 15 3. Results indicated a strong preference for sandeel in the study area. Prey switching behaviour
16 (change in preference dependent on prey abundance) was confirmed by the favoured Type III
17 functional response model. Variation in the size of the foraging range (estimated area where
18 harbour porpoises could have foraged prior to stranding) did not alter the overall pattern of
19 the results or conclusions.
- 20 4. Integrating datasets on prey consumption from strandings, predator foraging distribution
21 using telemetry and prey availability from fish surveys into the modelling approach provides
22 a methodological framework that may be appropriate for fitting MSFRs for other predators.

23
24 **Keywords:** Multi-species functional response, predator-prey interactions, *Phocoena phocoena*, North
25 Sea, prey switching, sandeels

26 1. Introduction

27 Prey populations are directly and indirectly affected by predation and their dynamics are influenced
28 by long-term and short-term responses of predators (Holling 1959, Murdoch & Oaten 1975). The
29 functional response helps to assess the potential impact that predators could have on their prey by
30 describing the response of predators to varying prey densities, providing insight into prey preference
31 and general predator-prey interactions (Dale et al. 1994). High consumption rates indicate strong
32 interactions between predators and prey, resulting from high encounter rates and/or active predator
33 choice. Switching between prey species may occur if predator preference changes with prey density,
34 for example when predators avoid scarce prey (Holling 1959).

35
36 Although the functional response has been subject to extensive empirical research, most studies have
37 been conducted within a laboratory setting or have described relationships among a small number of
38 species (Morozov & Petrovskii 2013). Modelling the multi-species functional responses (MSFR) for
39 wild animals is challenging because observing both consumption and prey availability outside a
40 controlled environment is difficult. Parametrising a MSFR requires substantial datasets on predator
41 diet and distribution, and the availability of multiple prey species covering a range of prey densities.
42 It is not surprising, therefore, that the ecological role of most large predators has not been quantified
43 and that we have an incomplete picture of their impacts in many ecosystems (Estes et al. 2011).
44 However, the use of Bayesian methods can overcome the problem of data sparsity, allowing MSFR
45 models to be fitted for top-predators (Smout et al. 2014, Suryawanshi et al. 2017).

46
47 In this study, we integrate long-term datasets on predator consumption, predator distribution and
48 prey abundance to model the MSFR of a marine high trophic level predator. We develop and apply
49 this framework using the harbour porpoise (*Phocoena phocoena*) in the southern North Sea as a case
50 study to examine the methodology, model performance, model output and the sensitivity of the
51 results to variation in assumptions.

52

53 The harbour porpoise is the most abundant large marine predator in the North Sea (Hammond et al.
54 2013). Its diet includes species that are also targeted by commercial fisheries (Santos & Pierce 2003),
55 such as whiting (*Merlangius merlangus*), Atlantic herring (*Clupea harengus*) and sandeels
56 (Ammodytidae). Results from three dedicated North Sea wide cetacean surveys showed a major
57 north to south shift in the summer distribution of harbour porpoise from 1994 to 2005 maintained in
58 2016 (Hammond et al. 2002, 2013, 2017). Changes in porpoise distribution are likely to be linked to
59 changes in prey distribution (Hammond et al. 2013). Harbour porpoises have a high metabolic rate
60 and only a limited energy storage capacity, which limits their ability to buffer against diminished
61 food availability/quality and makes them more susceptible to starvation if they fail to meet their high
62 metabolic demands (Spitz et al. 2012, Rojano-Doñate et al. 2018). Harbour porpoises are particularly
63 useful for this study, as they have high ingestion rates and probably must consume prey on a daily
64 basis (Wisniewska et al. 2016, Kastelein et al. 2019) unlike other cetaceans or pinnipeds that might
65 move through certain areas while not foraging.

66

67 Information on the relationship between harbour porpoise consumption and the availability of their
68 prey is lacking. However, there are data on prey consumption from the stomach contents of stranded
69 porpoises in the Netherlands (Leopold 2015), on the movement of porpoises in the North Sea from
70 satellite-linked telemetry (Sveegaard et al. 2011) and on prey abundance from the ICES International
71 Bottom Trawl Surveys (ICES 2018). Here, we aim to examine the use of MSFR models for a marine
72 high trophic level predator, and we choose the harbour porpoise as an interesting case study, the
73 framework for which could be useful for other species.

74

75 **2. Material and methods**

76 As a framework for analysis, the following sequence of steps was carried out to parameterize the
77 functional response (these steps are described in detail below): Step 1. Estimation of diet, Step 2.
78 Estimation of foraging range, Step 3. Estimation of prey availability, and Step 4. Fitting the Multi-
79 Species Functional Response. All data processing and modelling was performed in software R (R
80 Core Team 2018) and MSFR fitting was completed in WinBUGS (Lunn et al. 2000).

81

82 **2.1 Data preparation**

83 *2.1.1 Diet composition*

84 Harbour porpoise consumption was based on the hard remains of prey (fish otoliths) recovered from
85 the stomachs of individual animals stranded along the Dutch coastline between 2006 and 2015. For
86 sample collection and analysis, see Leopold (2015). Post-mortem examinations were carried out on
87 stranded animals documenting standard measurements (*e.g.* body length). Prey species were
88 identified to the lowest possible taxon. Otoliths were measured, paired when possible and graded for
89 wear and grade-specific correction factors were used to estimate undigested otolith size. Prey weight
90 was estimated by applying otolith size-fish mass relationships. Prey species that contributed $\geq 5\%$ of
91 the total estimated prey weight were selected as main prey species.

92

93 Uncertainty in diet composition arises from measurement (estimation of prey weight) and sampling
94 error (Hammond & Rothery 1996). Sampling error was estimated by non-parametric bootstrapping
95 using individual stranded porpoises as the sampling unit, stratified by season. To balance carcass
96 freshness and retain an adequate sample size only individuals with decomposition codes less than 4
97 were included in analysis (see Leopold 2015). Measurement effort was not estimated.

98

99 2.1.2 Foraging range

100 Estimating the foraging range of porpoises prior to stranding (i.e. the geographical range in which
101 the porpoise could have foraged) is difficult due to the unknown location of death. It is possible that
102 a stranded porpoise was alive and swimming until just before it stranded, or carcasses could have
103 drifted at sea for a considerable period of time (Peltier et al. 2013). This introduces uncertainty in
104 defining the area where porpoises likely foraged. The analysis aimed to take this uncertainty into
105 account by using realistic estimates of the rate at which porpoises could have moved prior to
106 stranding, to get informed estimates of their potential foraging range.

107

108 The foraging range was estimated using telemetry data from satellite-linked tags deployed on
109 harbour porpoises in Kattegat, the Belt Seas and the Western Baltic between 1997 and 2015 (see
110 Teilmann et al. (2007) and Sveegaard et al. (2011) for tagging procedures, tag settings, and data
111 filtering). The movements of harbour porpoises in Kattegat and the Belt Seas differ from those
112 further north in Skagerrak and in the North Sea (Sveegaard et al. 2011). To ensure the data were as
113 representative as possible for porpoises that stranded in the southern North Sea, data from the
114 southern Kattegat and further south (south of latitude 57.30 and east of 9.37) were excluded.

115

116 The use of stomach content data to estimate prey consumption depends on knowledge of the
117 temporal window within which porpoises could have obtained their last meal, which is dependent on
118 how long prey remains stay in the stomach. In the absence of information on passage rates of hard
119 prey remains for harbour porpoises, information for grey seals *Halichoerus grypus* and harbour seals
120 *Phoca vitulina*, which consume similar prey species, was used. Two days after consumption > 50%
121 of all otoliths were recovered in grey seal (Grellier & Hammond 2006) and > 85% in harbour seals
122 scats (Wilson et al. 2017). To estimate harbour porpoise foraging range, a minimum timeframe of 2

123 days was chosen. Additionally, timeframes of 4, 6, and 8 days were applied to explore how resilient
124 the results were to variation in the likely foraging area.

125

126 Prior to modelling the telemetry data, the track line of each tagged porpoise was processed to create
127 positions at regular intervals. These positions were used to generate minimal enclosing circles
128 (MECs) from sets of consecutive points for timeframes of 2, 4, 6, or 8 days (Fig. 1). Using a
129 generalized linear model (GLM) the MEC diameter (response variable assumed to follow a gamma
130 distribution with log link) was modelled as a function of timeframe and age, sex, season (quarter of
131 the year), and all two-way interactions. Model selection was based on AIC scores. The Variance
132 Inflation Factor (VIF) was used to detect multicollinearity using a threshold of 4 (Hair et al. 2010).

133

134 Tagged individuals are measured repeatedly, so a generalized linear mixed model (GLMM)
135 including a random effect for individual was investigated. However, the GLM was better supported
136 than the GLMM according to AIC scores and log-likelihoods.

137

138 Stranded porpoises are located on the coast, so the diameter of the MEC estimated from the GLM
139 was used to predict the radius of a circular buffer, centred on stranding location, to approximate the
140 foraging range (at sea) prior to stranding for each stranded individual (Fig. 2). Uncertainty about
141 foraging range was explored by fitting separate MSFR models for each timeframe (2, 4, 6, 8 days).

142

143 2.1.3 *Prey availability*

144 Relative fish abundances were estimated using data from the North Sea International Bottom Trawl
145 Survey (NS-IBTS), available from the International Council for the Exploration of the Sea (ICES)
146 (datras.ices.dk).

147 Only size classes determined to be consumable by harbour porpoises (< 40 cm - Aarefjord et al.
 148 1995) were selected. Catch per unit effort was transformed into biomass per unit effort (BPUE in g)
 149 by applying the length-weight relationship:

$$150 \quad BPUE = \sum_{\text{all } L < 400\text{mm}} a \left(\left(\frac{L}{10} \right) + (0.5e) \right)^b \times CPUE_L \text{ (eqn 1)}$$

151 where L is length class (in mm), indicated by the lower limit of that class, e is the resolution of the
 152 length, either 5 or 10mm (depending on species), $CPUE_L$ is the catch per unit effort for length class
 153 L , and a and b are length-weight conversion parameters the values of which were derived from
 154 Wilhelms (2013).

155

156 Prey datasets were subsetting according to season (either January-March or July-September). The
 157 porpoise diet data was categorised accordingly.

158

159 Generalised additive models (GAMs) were used to predict distribution for each species over the
 160 entire southern North Sea ($\leq 56^\circ$ latitude (Fig. 3)). Covariates considered were longitude, latitude,
 161 depth, and year. Within the GAMs with Gaussian error distribution the response variable BPUE was
 162 log-transformed to reduce the effects of relatively high/low catches. Smoothing parameter selection
 163 was performed by restricted maximum likelihood (REML) (Wood 2011). The model allowed the
 164 spatial pattern to change with time, by including a three-dimensional tensor product smooth for space
 165 and time:

$$166 \quad \text{Log}(BPUE_{it}) = s(\text{depth}_{it}) + \text{te}(\text{longitude}_i, \text{latitude}_i, \text{year}_t) \text{ (eqn 2)}$$

167 To avoid smoothing across land we applied a soap film smoother (Wood et al. 2008). In generating
 168 the soap film, knots were placed over the data and land was set to zero which ensured smoothing
 169 towards data points and avoided predicting over the boundary. Comparing the soap with a

170 conventionally used thin plate regression spline, showed that soap prevented predicting unrealistic
171 high fish densities in some areas (*e.g.* the Strait of Dover).

172

173 The predictions of the fitted model represent expected BPUE values. To estimate the true underlying
174 fish biomass, predictions would need to be scaled using gear efficiency and catchability estimates.
175 However, absolute estimates of abundance are not required for this study (see 2.2).

176

177 Sandeels are not well represented in the NS-IBTS due to catchability issues. Therefore, ICES
178 estimates sandeel spawning-stock biomass (used in this study) from other data sources such as
179 commercial catches and dredge surveys (ICES 2017). Gobies (Gobiidae) had to be excluded because
180 they are almost absent in the NS-IBTS due to their small sizes (Knijn et al. 1993) and there is no
181 other source of data.

182

183 The relative availability, and associated uncertainty, of each main prey species to each porpoise prior
184 to stranding was estimated as the relative amount of prey present within the area of sea within the
185 estimated circular buffer (see 2.1.2). For each buffer the total, mean, and SD of the availability of
186 each prey species were obtained by parametric re-sampling the estimated coefficients from the fitted
187 GAMs.

188

189 **2.2 Fitting the Multi-Species Functional Response**

190 A general equation for a single species functional response which allows the functional response to
191 take the form of a Type I, II or III is (Holling 1959):

$$192 \quad c = \frac{\alpha N^m}{1 + \alpha t N^m} \quad (\text{eqn 3})$$

193 where c is the predator consumption rate, a is the attack rate, N is prey availability, t is the
 194 consumption/handling time, and m is a shape parameter.

195

196 The equation can be re-written to include multiple prey species and in terms of diet composition
 197 because porpoise stomach contents do not provide information on consumption rates.

198
$$\frac{c_i}{\sum_j c_j} = \frac{\alpha_i N_i^m}{\sum_j \alpha_j N_j^m} \text{ (eqn 4)}$$

199 Here c_i is the consumption of prey species i and $\sum_j c_j$ is the sum of the consumptions of all prey
 200 species by the predator. Not all species in the diet need to be included for this relationship to hold,
 201 important in this study because gobies had to be excluded though they are important constituents of
 202 the diet. Catchability q_i relates the survey catch of each prey species B_i to the true abundance or
 203 biomass in the sea, N_i :

204
$$N_i = q_i \times B_i \text{ (eqn 5)}$$

205 so equation 5 can be rewritten as:

206
$$\frac{c_i}{\sum_j c_j} = \alpha_i \frac{(q_i B_i)^m}{\sum_j \alpha_j (q_j B_j)^m}$$

207 Then defining constant $a_i = \alpha_i q_i^{m_i}$ we can write:

208
$$\frac{c_i}{\sum_j c_j} = \frac{a_i B_i^m}{\sum_j a_j B_j^m} \text{ (eqn 7)}$$

209 Therefore, from consumption and CPUE data we can estimate the value of the a_i parameters.

210 Furthermore, for model fitting, all prey abundances were re-scaled so that the maximum observed
 211 value was 100 (assisting numerical performance and convergence) – similar arguments apply: the

212 estimated values of a_i are a measure of prey ‘preference’ or attack rate, but they relate to an index of

213 abundance and not to absolute estimates of biomass. m determines how sigmoidal the response is and

214 thus influences the form of the functional response. Two model types were compared. In model one,
215 the shape parameter $m=1$ represents a hyperbolic Type II functional response. In model two, $m=1.5$
216 allowed the functional response to take on the form of a Type III functional response.

217

218 The relationship between relative prey availability and consumption was estimated for each main
219 prey species in turn by setting the availability of all other prey to a specific constant level
220 (availability at minimum, mean, and maximum abundance).

221

222 Markov chain Monte Carlo (MCMC) methods used for model fitting enabled uncertainty in diet and
223 prey availability estimates to be incorporated. At each step in the Markov chain, for each prey
224 species, random values of prey availability were drawn from a zero-truncated Normal distribution.
225 For each model, the MCMC was run for 10,000 iterations after a burn-in of 1000 samples with two
226 parallel Markov chains.

227

228 Prey species that contributed $< 5\%$ to the diet of harbour porpoises were grouped into a single
229 category 'other prey'. All goby species were added to this category because no prey availability
230 estimates for these species could be calculated.

231

232 Examination of equation 7 indicates that diet composition data allow relative but not absolute values
233 of attack rate a_i to be estimated (equation 7 holds if all the a_i are multiplied by any arbitrary constant)
234 therefore it is difficult to create informative priors for absolute values of a_i . However, diet
235 composition can be calculated providing that relative values of a_i are known. Consequently, to
236 estimate relative values for a , a wide uniform prior $U(0,10)$ was used for all prey species except
237 sandeels, whose attack rate was fixed at a value of 1. This allowed for the relative values of attack
238 rate a for those other prey species to be substantially larger than the a value of sandeels, or to take

any smaller positive value. The marginal posterior distributions of a were checked after model fitting, to confirm that they had very low weights towards the prior's upper limit of 10, to ensure that the uniform priors were not over-constraining the exploration of parameter space. After fitting, models were compared using DIC scores (Spiegelhalter et al. 2002).

243

244 **3 Results**

245 **3.1 Prey consumption**

Stomach content data were available from 455 harbour porpoises. Juveniles of both sexes ($n = 344$ (74.8 %)) dominated the sample. The 'main' prey species included six different types of fish: whiting (27.1 % by biomass), gobies (20.8 %) and sandeels (18.5 %) were the most dominant species. Lesser contributions were made by herring (8.5 %), sprat (*Sprattus sprattus*) (6.9 %), cod (*Gadus morhua*) (6.0 %). Other species comprised 12.2 % of the diet.

251

252 **3.2 Foraging range**

In total, 2448 locations of 54 harbour porpoises were included in the telemetry analysis (females: 15 juveniles, 3 adults; males: 24 juveniles, 12 adults). The number of tracking days per individual ranged from 8 to 350 days (mean = 93.9 ± 87.3 SD).

256

All covariates had a VIF score lower than 1.4, therefore multicollinearity could be disregarded. GLM results are summarised in Table 1. Age, quarter, sex, and timeframe were all found to be significant predictors ($p < 0.01$) for the foraging range (MEC diameter) and explained 24.5% of the variation. Predicted foraging range was smaller for males than for females, and for juveniles in comparison to adults. Furthermore, the foraging range was significantly smaller in spring in comparison to the other seasons.

263

264 3.3 Prey availability

265 Correlograms of the final models indicated very weak autocorrelation and deviance residuals were
266 evenly spread. BPUE predictions in all grid cells, including unsurveyed cells, are shown in Fig. 3.
267 These broad scale predictions allowed examination of how abundance of each main prey species
268 varied spatially and temporally. The final GAM models explained between approximately one third
269 to two thirds of the total observed variation in the BPUE values (Table 2).

270

271 As described above, the availability of each prey species was predicted for each individual porpoise,
272 within the circular buffer that represented the foraging range for each timeframe. For illustration,
273 Fig. 4 displays the prediction of whiting availability for one porpoise for different timeframes.

274

275 3.4 Multi-species functional response

276 The best MSFR model in terms of timeframe according to DIC scores (Table 3) was the 4 days
277 model. Model two (DIC = 975701) with a Type III functional response was selected over model one
278 (DIC = 117216) with a Type II functional response. Consequently, predictions are only presented for
279 the 4 days Type III functional response model.

280

281 The posterior distributions for a were well defined given the wide uniform priors (Appendix S2).
282 The attack rate was considerably higher for sprat (mean = 0.238, 95% CI [0.226, 0.254]) in
283 comparison to whiting (mean = 0.120, 95% CI [0.114, 0.129]), herring (mean = 0.101, 95% CI
284 [0.095, 0.108]), 'other prey' (mean = 0.089, 95% CI [0.085, 0.095]), and cod (mean = 0.058, 95% CI
285 [0.055, 0.063]). Recall that the attack rate for sandeel was set at a fixed value of 1, indicating that it
286 was the highest: this is consistent with the generally high proportion of sandeels in the diet samples

287

288 Model predictions of diet composition captured the overall pattern in the observed diet composition
289 estimates (Table 4). The model predicted higher proportions of sandeels and cod, and lower
290 proportions of other species in comparison to the observed diet, but all predictions fell well within
291 the range of uncertainty indicating that the model predictions were robust.

292

293 The model predicted a strong relationship between relative prey availability and prey consumption
294 by harbour porpoises (Fig. 5). Overall, consumption of the selected prey species decreased as more
295 alternative prey (all other species) was available. In contrast, the consumption of sandeels remained
296 relatively high over all three levels of alternative prey availability (Fig. 5).

297

298 **4. Discussion**

299 Integrating disparate datasets to model the MSFR for harbour porpoises in the southern North Sea
300 provides a methodological framework that may be appropriate for other predators. The results
301 showed how the consumption of each of the harbour porpoise's 'main' prey species (except gobies)
302 varied with the availability of other prey.

303

304 **4.1 Methods evaluation and sensitivity**

305 Setting suitable spatial scales can be a major challenge in ecological studies and the accuracy of any
306 modelled relationship between prey consumption and availability relies profoundly on achieving
307 realistic spatio-temporal overlap. In this study, the foraging distributions of porpoises prior to
308 stranding are unknown, so it is crucial to explore whether assumptions made about the foraging
309 range of these stranded animals are reasonable. Our novel approach was to find the "most likely"
310 foraging area prior to stranding by predicting the range used as a function of time based on telemetry
311 data. Sensitivity of the results to this was explored by varying the timeframe used. The best fitting
312 MSFR model used a timeframe of 4 days. We conclude that the overall pattern of results is unlikely

313 to change much in response to changes in the predicted foraging range because there is little relative
314 difference in modelled prey distribution among prey species in the areas where porpoises could have
315 been foraging in the vicinity of the Dutch coast (Fig. 3). This is confirmed –by the result that
316 changing the foraging range did not alter the emerging patterns of estimated attack rates or the shape
317 of the functional response (Appendix S1). Our methodology thus appears rather robust to this aspect
318 of uncertainty.

319

320 **4.2 Ecological inference**

321 Different shapes of the predator functional response have different implications for prey populations,
322 especially at low prey densities. In our favoured model with a sigmoidal Type III functional
323 response, predation mortality decreases when a prey species becomes rare and is indicative of prey
324 switching when prey is at low abundance (that is, there is a change in preference dependent on prey
325 abundance). This may result in persistence and/or stabilizing effects on predator-prey dynamics
326 (Murdoch & Oaten 1975) because it may prevent one prey species from outcompeting others
327 (Roughgarden & Feldman 1975). A Type III response may result from a number of ecological
328 mechanisms, including prey refuge (McNair 1986), and learning time (Tinbergen 1960).

329

330 Classically, the attack rate parameter a in the functional response equation can be interpreted as a
331 form of relative preference of the predator for a certain prey type. Here we interpret these values
332 cautiously because of the nature of the prey abundance estimates we used. These were indices, scaled
333 in proportion to maximum values, and they were not estimates of overall total biomass (which is
334 difficult to calculate). Thus, for example the ‘maximum’ value of sandeel abundance was 100 and so
335 was the maximum value for whiting.

336

337 In this study, porpoises consumed a disproportionately larger proportion of the most abundant prey.
338 Sandeel consumption remained high even when other prey were abundant and was considerably
339 higher than the consumption of other prey at equal availability index values. At prey abundances
340 similar to those available to our study animals, harbour porpoise diets often have a high proportion of
341 sandeels, and it also implies that sandeel availability might have a particularly strong effect on the
342 consumption by porpoises of other prey species in this area. It has been shown that harbour porpoise
343 density increases with decreasing distance to sandeel grounds (Gilles et al. 2016), suggesting that
344 porpoises could be attracted to those areas.

345
346 Harbour porpoises in better body condition have been found to be more likely to have higher
347 amounts of fatty fish, such as sandeels in their diet (Leopold 2015). Our results add to the body of
348 evidence that sandeels are important to porpoises. Sandeels have high energy content and are
349 abundant in the southern North Sea, forming an important forage fish resource that supplies a
350 number of predator species including harbour porpoises, seabirds (Rindorf et al. 2000), and grey and
351 harbour seals (Wilson & Hammond 2019).

352

353 **4.3 Data limitations**

354 Foraging range was estimated from telemetry data collected in areas of the North Sea outside the
355 study area. By including data only from the area believed to be more similar to the study area, we
356 sought to minimise error in estimated foraging range. Estimates of foraging range using movement
357 data are uncertain and conservative. Active swimming is faster than drifting, so true foraging range
358 will be larger than that estimated from drifting alone. The fitted MSFRs gave similar results for
359 different reasonable assumptions about the foraging area available to porpoises before stranding, so
360 we conclude that the lack of telemetry data from the study area should not affect our conclusions

361 appreciably. ARGOS data from telemetry tags are subject to location error which was not quantified
362 in this study but is believed to be negligible in this context.

363

364 Our prey availability estimates do not represent the true amounts of fish in the area surveyed as a
365 trawl will not catch all the fish in its path and net efficiency will differ between various species. We
366 assume that these estimates reflect prey availability to predators, however, the link between prey
367 abundance and prey availability are relatively unknown since differences in prey behaviour (*e.g.*
368 diurnal and seasonal variation in schooling and burrowing behaviour) will affect this. Fortunately, the
369 methodology applied here requires relative spatio-temporal abundance trends, assuming that these
370 trends are proportional to the absolute abundance of prey, and thus incorporates some of these issues.

371

372 Current fisheries surveys sample at a coarse spatial resolution. Some species, especially sandeels and
373 gobies in this study, are poorly sampled. Given the importance of sandeels for many marine
374 predators and the lack of knowledge regarding spatio-temporal variability in their distribution and
375 abundance, improving effective sampling and modelling of sandeel distribution would improve the
376 quality of the inferences made from future studies. The inability to model sandeel and gobies
377 distributions spatially could have led to error in availability estimates, especially because sandeel
378 distribution is extremely patchy (Wright et al. 2000) and largely unknown for gobies. The
379 importance of gobies could have been underestimated because they were excluded from the prey
380 availability analysis. Although information on gobies distribution and abundance is largely lacking,
381 gobies are extremely abundant within Dutch coastal waters (Tulp et al. 2008). Therefore, it might be
382 justified having assumed that these species have a relatively consistent availability.

383

384 Care should be taken in making inferences from stranding data because they do not represent an
385 unbiased random sample of the population; there is likely an over-representation of individuals that

386 are inexperienced, old, and/or in poor health (Pierce et al. 2004). Indeed, a large proportion of the
387 stranded individuals in this study were juveniles so our results are biased towards this age class.
388 Despite these limitations stomach contents do provide valuable diet information that is otherwise
389 difficult to obtain. Nevertheless, we do not know to what extent our results reflect the functional
390 response of a ‘typical’ porpoise. Limiting the use of diet data from caught (by grey seals) bycaught
391 (in fishing nets) animals would be an alternative way to look at harbour porpoise diet (Leopold
392 2015).

393

394 **4.4 Context and applications**

395 Applying a Bayesian approach to model the MSFR appears to work well, allowing incorporation of
396 uncertainty in prey availability and consumption estimates. These features, together with the
397 resilience of the results, suggest that the modelled MSFR provides a strong methodological
398 framework that can be applied to a range of other species and might aid in quantifying the ecological
399 role of other predators that consume a variety of prey. For example, similar data exist for seabirds
400 (Wanless et al. 2005), grey seals, and harbour seals in the North Sea (SCOS 2017) and applying this
401 framework could provide valuable new insights into their population dynamics, especially in the
402 context of possible competition for prey between these two seal species (Wilson & Hammond 2019).
403 To take this further, the MSFR could be integrated into ecosystem models to predict and test how
404 prey and predator populations are expected to change under different fisheries management and
405 climatic scenarios that impact prey availability. This could also shed light on the extent of direct and
406 indirect competition between marine mammals, seabirds, and fisheries and possibly on the outcomes
407 of fisheries management and stock recovery programmes.

408

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412 part of the harbour porpoise tagging team.

413

414 **Ethics statement**

415 Porpoises were tagged by Aarhus University in collaboration with the DTU Aqua, National Institute
416 of Aquatic Resources, the Fjord and Belt Centre, University of Southern Denmark and the Institute
417 for Terrestrial and Aquatic Wildlife Research at University of Veterinary Medicine Hannover under
418 permissions from Danish Forest and Nature Agency (SN 343/SN-0008) and the Animal Welfare
419 Division (Ministry of Justice, 1995-101-62).

420

421 **Data Availability**

422 Data to estimate the relative availability of prey species is openly available from ICES webpage
423 (datras.ices.dk). A summary table of input data (prey availability and diet estimates with associated
424 uncertainties) for modelling the MSFR is provided.

425 **References**

- 426 Aarefjord, H. et al. 1995. Diet of harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. -
427 Report of the International Whaling Commission 16: 211-222.
- 428 Dale, B.W. et al. 1994. Functional response of wolves preying on barren-ground caribou in a
429 multiple-prey ecosystem. - Journal of Animal Ecology 63: 644-652.
- 430 Estes, J.A. et al. 2011. Trophic downgrading of planet Earth. – Science 333: 301-306.
- 431 Gilles, A. et al. 2016. Seasonal habitat-based density models for a marine top predator, the harbor
432 porpoise, in a dynamic environment. - Ecosphere 7: e01367.
- 433 Grellier, K. and Hammond, P.S. 2006. Robust digestion and passage rate estimates for hard parts of
434 grey seal (*Halichoerus grypus*) prey. - Canadian Journal of Fisheries and Aquatic Sciences 63:
435 1982-1998.
- 436 Hair, J. et al. 2010. Multivariate data analysis, 7th edn. - Pearson Education International
- 437 Hammond, P.S. and Rothery, P. 1996. Application of computer sampling in the estimation of seal
438 diet. - Journal of Applied Statistics 23: 525-533.
- 439 Hammond, P.S. et al. 2002. Abundance of harbour porpoise and other cetaceans in the North Sea and
440 adjacent waters. - Journal of Applied Ecology 3: 361-376.
- 441 Hammond, P.S. et al. 2013. Cetacean abundance and distribution in European Atlantic shelf waters
442 to inform conservation and management. - Biological Conservation 164: 107-122.
- 443 Hammond, P.S. et al. 2017. Estimates of cetacean abundance in European Atlantic waters in summer
444 2016 from the SCANS-III aerial and shipboard surveys. Sea Mammal Research Unite, University
445 of St Andrews, UK, 40 pp.
- 446 Holling, C.S. 1959. The components of predation as revealed by a study of small mammal predation
447 of the European pine sawfly. - Canadian Entomologist 91: 293-320.
- 448 ICES 2017. Report of the Benchmark on Sandeel (WKSand 2016), 31 October–4 November 2016,
449 Bergen, Norway. ICES CM 2016/ACOM:33. 301 pp.

450 ICES 2018. Report of the International Bottom Trawl Survey Working Group (IBTSWG), 19 - 23
 451 March 2018, Oranmore, Ireland. ICES CM 2018/EOSG:01. 233 pp.
 452 Kastelein, R.A. et al. 2019. Reduction in Body Mass and Blubber Thickness of Harbor Porpoises
 453 (*Phocoena phocoena*) Due to Near-Fasting for 24 Hours in Four Seasons. - Aquatic Mammals 45:
 454 37-47.
 455 Knijn, R.J. et al. 1993. Atlas of North Sea fishes: based on bottom-trawl survey data for the years
 456 1985-1987. - ICES Cooperative Research Report, 194, 268, ICES, Copenhagen.
 457 Leopold, M.F. 2015. Eat and be eaten, Porpoise diet studies. PhD thesis, Wageningen University,
 458 Wageningen.
 459 Lunn, D. et al. 2000. WinBUGS -a Bayesian modelling framework: concepts, structure, and
 460 extensibility. - Statistics and Computing 10: 325–337.
 461 McNair, J.N. 1986. The effects of refuges on predator-prey interactions: a reconsideration. -
 462 Theoretical population biology 29: 38-63.
 463 Morozov, A. and Petrovskii, S. 2013. Feeding on multiple sources: towards a universal
 464 parameterization of the functional response of a generalist predator allowing for switching. - PloS
 465 one 8: e74586.
 466 Murdoch, W.W. and Oaten, A. 1975. Predation and population stability. - Advances in ecological
 467 research 9: 1-131.
 468 Peltier, H. et al. 2013. The stranding anomaly as population indicator: the case of harbour porpoise
 469 *Phocoena phocoena* in North-Western Europe. - PloS one 8: e62180.
 470 Pierce, G.J. et al. 2004. Methods for dietary studies on marine mammals. Investigating the roles of
 471 cetaceans in marine ecosystems. CIESM Workshop Monographs, 25, 29-36, Monaco.
 472 R Development Core Team 2018. R: A Language and Environment for Statistical Computing. R
 473 Foundation for Statistical Computing, Vienna. URL <http://www.R-project.org> [accessed 07
 474 August 2018]

475 Rindorf, A. et al. 2000. Effects of changes in sandeel availability on the reproductive output of
 476 seabirds. - Marine Ecology Progress Series 202: 241-252.

477 Rojano-Doñate, L. et al. 2018. High field metabolic rates of wild harbour porpoises. - Journal of
 478 experimental biology 221: jeb185827.

479 Roughgarden, J. and Feldman, M. 1975. Species packing and predation pressure. - Ecology 56: 489-
 480 492.

481 Santos, M.B. and Pierce, G.J. 2003. The diet of harbour porpoise (*Phocoena phocoena*) in the
 482 northeast Atlantic. - Oceanography and Marine Biology: an Annual Review 41: 355-390.

483 Smout, S. et al. 2014. Modelling prey consumption and switching by UK grey seals. - ICES Journal
 484 of Marine Science 71: 81-89.

485 SCOS 2017. Scientific advice on matters related to the management of seal populations: 2017. St
 486 Andrews: SCOS, Sea Mammal Research Unit.

487 Spiegelhalter, D.J. et al. 2002. Bayesian measures of model complexity and fit. - Journal of the Royal
 488 Statistical Society: Series B (Statistical Methodology) 64: 583-639.

489 Spitz, J. et al. 2012. Cost of living dictates what whales, dolphins and porpoises eat: the importance
 490 of prey quality on predator foraging strategies. - PloS one 7: e50096.

491 Suryawanshi, K.R. et al. 2017. Impact of wild prey availability on livestock predation by snow
 492 leopards. - Royal Society open science 4: p.170026.

493 Sveegaard, S. et al. 2011. High-density areas for harbor porpoises (*Phocoena phocoena*) identified
 494 by satellite tracking. - Marine Mammal Science 27: 230-246.

495 Teilmann, J. et al. 2007. Time allocation and diving behaviour of harbour porpoises (*Phocoena*
 496 *phocoena*) in Danish and adjacent waters. - Journal of Cetacean Research and Management 9:
 497 201-210.

498 Tinbergen, L. 1960. The natural control of insects in pine-woods. 1. Factors influencing the intensity
 499 of predation by songbirds. - Archives Néerlandica Zoologica 13: 266-336.

500 Tulp, I. et al. 2008. Signals from the shallows: in search of common patterns in long-term trends in
 501 Dutch estuarine and coastal fish. - Journal of Sea Research 60: 54-73.

502 Wanless, S. et al. 2005. Low energy values of fish as a probable cause of a major seabird breeding
 503 failure in the North Sea. - Marine Ecology Progress Series 294: 1-8.

504 Wisniewska, D.M. et al. 2016. Ultra-high foraging rates of harbor porpoises make them vulnerable to
 505 anthropogenic disturbance. - Current Biology 26: 1441-1446.

506 Wilhelms, I. 2013. Atlas of length-weight relationships of 93 fish and crustacean species from the
 507 North Sea and the North-East Atlantic. *Thünen Working Paper*, 12, 1:552, Thünen Institute of Sea
 508 Fisheries, Hamburg.

509 Wilson, L.J. et al. 2017. Improved estimates of digestion correction factors and passage rates for
 510 harbor seal (*Phoca vitulina*) prey in the northeast Atlantic. - Marine Mammal Science 33: 1149-
 511 1169.

512 Wilson, L.J. and Hammond, P.S. 2019. The diet of harbour and grey seals around Britain: seeking
 513 evidence for the “ghost of competition past”. - Aquatic Conservation: Marine and Freshwater
 514 Ecosystems 29: 71-85.

515 Wood, S.N. et al. 2008. Soap film smoothing. - Journal of the Royal Statistical Society: Series B
 516 (Statistical Methodology) 70: 931-955.

517 Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of
 518 semiparametric generalized linear models. - Journal of the Royal Statistical Society: Series B
 519 (Statistical Methodology) 73: 3-36.

520 Wright, P.J. et al. 2000. The influence of sediment type on the distribution of the lesser sandeel,
 521 *Ammodytes marinus*. - Journal of Sea Research 44: 243-256.

522 **Tables**

523 **Table 1.** Summary of the generalized linear modelling to predict the foraging range of tagged
 524 harbour porpoises. Predicted mean diameter and SD (in parentheses) of minimum enclosing circle
 525 (MEC) in (km) for harbour porpoises according to time frame, quarter, age, and sex.

| Time Frame | Months | Adult | | Juvenile | |
|---------------|------------------|-------------|-------------|-------------|-------------|
| | | Female | Male | Female | Male |
| 2 days | January-March | 34.9 (1.3) | 32.6 (1.2) | 30.5 (1.3) | 28.2 (1.1) |
| 2 days | April-June | 42.3 (1.8) | 39.9 (1.7) | 37.9 (1.6) | 35.5 (1.4) |
| 2 days | July-September | 33.2 (1.3) | 30.8 (1.1) | 28.8 (1.0) | 26.4 (0.4) |
| 2 days | October-December | 33.5 (1.3) | 31.1 (1.1) | 29.1 (1.1) | 26.7 (0.9) |
| 4 days | January-March | 58.4 (1.2) | 56.0 (1.2) | 54.0 (1.2) | 51.6 (1.1) |
| 4 days | April-June | 65.8 (1.7) | 63.4 (1.6) | 61.4 (1.6) | 59.0 (1.4) |
| 4 days | July-September | 56.6 (1.3) | 54.2 (1.1) | 52.2 (1.0) | 49.9 (0.6) |
| 4 days | October-December | 57.0 (1.2) | 54.6 (1.1) | 52.6 (1.1) | 50.2 (0.9) |
| 6 days | January-March | 81.9 (1.4) | 79.5 (1.3) | 77.5 (1.4) | 75.1 (1.3) |
| 6 days | April-June | 89.2 (1.8) | 86.9 (1.7) | 84.8 (1.7) | 82.5 (1.6) |
| 6 days | July-September | 80.1 (1.5) | 77.7 (1.3) | 75.7 (1.3) | 73.3 (1.0) |
| 6 days | October-December | 80.4 (1.3) | 78.1 (1.3) | 76.0 (1.3) | 73.7 (1.1) |
| 8 days | January-March | 105.3 (1.6) | 102.9 (1.6) | 100.9 (1.7) | 98.6 (1.6) |
| 8 days | April-June | 112.7 (2.0) | 110.3 (2.0) | 108.3 (1.9) | 105.9 (1.8) |
| 8 days | July-September | 103.5 (1.8) | 101.2 (1.7) | 99.1 (1.6) | 96.8 (1.4) |
| 8 days | October-December | 103.9 (1.6) | 101.5 (1.6) | 99.5 (1.6) | 97.1 (1.5) |

543

544 **Table 2.** Percentage deviance explained values for the selected generalised additive models (GAMs)
545 per prey species and Quarter.

| | | | |
|-----|----------------|----------------------|----------------------|
| 546 | | Quarter one | Quarter Three |
| 547 | Species | (January-March) | (July-September) |
| 548 | | % deviance explained | % deviance explained |
| 549 | Cod | 28.3 | 25.3 |
| 550 | Herring | 43.1 | 30.3 |
| | Sprat | 32.9 | 32.8 |
| | Whiting | 60.7 | 54.0 |

551 **Table 3.** Deviance Information Criterion (DIC) scores of multi-species functional response (MSFR)
552 models according to different foraging range as determined by buffer sizes estimated from different
553 timeframes.

| Timeframe | 2 days | 4 days | 6 days | 8 days |
|-----------|--------|--------|--------|--------|
| DIC score | 113090 | 97202 | 133846 | 107295 |

554

555 **Table 4.** Predicted diet (for the 4 days MSFR model) of harbour porpoises and observed diet based
 556 on stomach content analysis of stranded animals. Expressed as mean and SD percentages of total
 557 prey mass.

| 558 | Prey species | Predicted | observed |
|-----|---------------------|------------------|-----------------|
| 559 | Cod | 5.0 (0.5) | 2.1 (10.0) |
| 560 | Herring | 6.4 (4.0) | 4.8 (10.0) |
| | Sandeel | 25.1 (8.2) | 17.2 (14.2) |
| 561 | Sprat | 7.0 (3.8) | 7.7 (14.2) |
| 562 | Whiting | 8.6 (1.8) | 12.7 (15.8) |
| 563 | Others | 47.6 (18.9) | 55.0 (12.2) |

