Vol. 54: 105–122, 2024
https://doi.org/10.3354/esr01328

ENDANGERED SPECIES RESEARCH
Endang Species Res

Published May 30

Feeding ecology of harbour porpoises *Phocoena phocoena* stranded on the Galician coast (NW Spain) between 1990 and 2018

Alberto Hernandez-Gonzalez[1,2,3,*], Camilo Saavedra[1], Fiona L. Read[3,4], Alfredo López[5,6], Anabela Gouveia[7], Pablo Covelo[5], Alexandre Alonso-Fernández[3], Francisco Velasco[8], M. Begoña Santos[1], Graham J. Pierce[3,4,6]

[1]Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Vigo, 36390 Vigo, Spain
[2]Universidade de Vigo, Campus Do Mar, Facultad de Ciencias del Mar, 36310 Vigo, Spain
[3]Instituto de Investigaciones Marinas (IIM-CSIC), 36208 Vigo, Spain
[4]School of Biological and Environmental Sciences, Zoology Building, University of Aberdeen, Aberdeen AB24 2TZ, UK
[5]Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA), 36380 Gondomar, Spain
[6]Centro de Estudos do Ambiente e do Mar (CESAM), Universidade de Aveiro, 3810-193 Aveiro, Portugal
[7]Universidade do Algarve, Campus da Penha, Faculdade de Ciências e Tecnologia, 8005-139 Faro, Portugal
[8]Instituto Español de Oceanografía (IEO-CSIC), Centro Oceanográfico de Santander, 39004 Santander, Spain

ABSTRACT: Diet studies on the endangered and genetically distinct Iberian population of the southern harbour porpoise *Phocoena phocoena* are scarce. The present study provides updated information on the feeding ecology of this cetacean along the Galician coast (NW Spain) over the last 3 decades (1990–2018). The stomach contents of 72 stranded harbour porpoises were analysed to determine diet composition, to study which factors affect dietary variability and to estimate overlap between harbour porpoise diet and the target species of the fisheries in the study area, one of the most important fishing regions in Europe. Results showed that harbour porpoises are mainly piscivorous. We identified 33 prey taxa, but only 4 were important in the diet: fish of the genus *Trisopterus*, blue whiting *Micromesistius poutassou*, Atlantic horse mackerel *Trachurus trachurus* and European hake *Merluccius merluccius*. Interannual and ontogenetic variability in the diet were statistically significant, although differences in diet between sexes or between seasons were not detected. The diet of harbour porpoises from the Galician coast shows a partial overlap with fisheries catches in the area in terms of commercial fish species (≈61%) and size classes (≈45%), confirming the potential vulnerability of the Iberian population to interactions with fishing activities (i.e. bycatch in fishing gear and/or reduced prey availability).

KEY WORDS: Diet analysis · Endangered cetacean species · Marine top predator · Western Iberian Peninsula

1. INTRODUCTION

Conventional studies on the feeding ecology of marine mammals, investigated from stomach contents, are especially relevant to determine the composition of the diet, its variation over time, and also to describe the trophic relationships between them and the dynamic ecosystem which they inhabit (Pierce & Boyle 1991, Trites et al. 1997). Therefore, studies on feeding ecology are essential to understand the interactions between fisheries and wild marine mammal populations, as well as the competition for resources

*Corresponding author: ahernandez@iim.csic.es

Publisher: Inter-Research · www.int-res.com

and its repercussions (e.g. Lassalle et al. 2012, Giralt Paradell et al. 2021).

In European waters, the diet of harbour porpoises *Phocoena phocoena* includes a wide diversity of prey species (Santos & Pierce 2003), with some authors suggesting that the species is an opportunistic feeder since its diet composition is related to prey availability (Martin 1995, Teilmann & Dietz 1998). However, several studies concur that a small number of prey species normally dominates the diet of harbour porpoises, with fish species of the family Gadidae often being the most important prey (e.g. Víkingsson et al. 2003, Santos et al. 2004, Jansen et al. 2013). Previous studies on the diet of harbour porpoises have also found that they feed on both demersal and pelagic prey species in shallow waters, while in deeper waters they are also able to exploit deep-sea species that migrate vertically in the water column (e.g. lanternfish *Myctophum punctatum*, herring *Clupea harengus*, pearlside *Maurolicus muelleri*, sprat *Sprattus sprattus*) (Bjørge & Tolley 2002, Schaffeld et al. 2016, Arndt & Evans 2022).

There are geographical differences in the diet composition of harbour porpoises. In Scandinavian waters (i.e. Baltic Sea and North Sea), energy-rich fish species of the family Clupeidae are predominant in the diet (Aarefjord et al. 1996, Koschinski 2001, Mahfouz et al. 2017). However, in Scotland, they fed mainly on herring until the stock of this prey species crashed (Santos & Pierce 2003). The depleted state of some key fish stocks might also be an issue for harbour porpoise populations given that this cetacean needs to feed near continuously to maintain its high metabolic rate and to avoid loss of body condition in cold waters (Leopold et al. 2015, Wisniewska et al. 2016). It has been estimated that harbour porpoises need to consume up to 2–5 kg of prey daily, which represents 4–10% of their total body weight (Fontaine et al. 1994, Kastelein et al. 1997, Santos et al. 2014). These high energy requirements imply that the porpoises must maintain close contact with their prey resources (Koopman 1994), especially energy-rich prey, to decrease the likelihood of starvation (MacLeod et al. 2007).

The Iberian population of the southern harbour porpoise is distributed along the Atlantic coast of the Iberian Peninsula, approximately between Cabo de São Vicente in Portugal northwards to Cape Finisterre in Spain (Hammond et al. 2021). This population has some particular characteristics, e.g. it is genetically isolated from the northern European population (Fontaine et al. 2007, 2010, Llavona 2018), and it has also been noted that Iberian individuals are morphologically larger (Lens 1997, López 2003, Read 2016). As a result, it has been proposed to consider the southern harbour porpoises, i.e. the Iberian population together with the NW African population, as a subspecies, namely *P. p. meridionalis* (Fontaine et al. 2014).

Galicia (NW Spain) is one of the most fishery-dependent communities in EU waters (Natale et al. 2013, Surís-Regueiro & Santiago 2014), with more than 4000 registered fishing vessels (https://www.pescadegalicia.gal/rexbuque/), representing a potential threat to the conservation of harbour porpoises. Although harbour porpoises comprise only 7% of all stranding records in Galicia (López et al. 2002), between 1990 and 2018, over 40% of diagnosed deaths amongst stranded harbour porpoises were the result of fisheries interactions (Covelo et al. 2018, Read et al. 2020). Furthermore, Vingada et al. (2011) referred to evidence of around 200 animals from this population dying annually due to fishery bycatch in Portuguese waters. The high bycatch mortality rates in the polyvalent fleet are almost certainly unsustainable for the small size of the Iberian population (Read 2016, Pierce et al. 2020, Read et al. 2020) since mortality also causes a loss of genetic diversity in a declining population (ICES 2019b, NAMMCO & IMR 2019, Chehida et al. 2023).

Only 5 previous studies have examined the feeding ecology of southern harbour porpoises: 1 in France (Spitz et al. 2006), 3 in Galicia (González et al. 1994, Santos 1998, Read et al. 2013) and 1 in Portugal (Aguiar 2013). These authors concluded that southern harbour porpoises mainly feed close to the seafloor on demersal fish species, although some pelagic (commercially important) fish species were also found in their diet. It should be noted that Spitz et al. (2006) examined harbour porpoises from all along the French coast of the Bay of Biscay and most likely included a mixture of harbour porpoises from southern and northern populations, while González et al. (1994) referred to the presence of fish otoliths in the stomach of 1 specimen, and Read et al. (2013) provided an update of the results reported by Santos (1998). This limited knowledge of southern harbour porpoise feeding ecology (in terms of diet composition and, in particular, long-term trends or changes in diet composition), together with its restricted distribution and the fisheries impact, has contributed to increase the concern about the conservation status of this species over the last years. Indeed, in the Spanish Catalogue of Threatened Species the status of the harbour porpoise changed from 'vulnerable' in 2011 to 'in danger of extinction' in 2020 (BOE 2020).

The present study includes all past information on Galician samples; a total of 56 stomach contents were analysed from 1991 to 2010 and the sampling was extended to 2018 through the analysis of 16 new non-empty stomach contents, assembling a time series of almost 3 decades. The aims of the present study were to (1) re-characterise the diet of the Iberian population of the southern harbour porpoise that inhabits the Galician coasts; (2) re-analyse potential drivers of dietary variation; (3) estimate the consumption of the main prey species; (4) compare the overlap between the diet of harbour porpoises and catches of fisheries operating in the area; and (5) estimate the energy intake represented by food remains in the stomachs (diet quality) in relation to harbour porpoise sex (males vs. females), body length and cause of death (bycaught vs. not bycaught).

2. MATERIALS AND METHODS

2.1. Sample collection

Since 1990, members and volunteers of the non-governmental organisation Coordinadora para o Estudio dos Mamíferos Mariños (CEMMA) have routinely attended cetacean strandings in Galicia and carried out post-mortem examinations following the standard protocol of the European Cetacean Society (Kuiken & García-Hartmann 1991). During necropsies, information such as the species, body length, sex, blubber thickness, decomposition status, date of stranding and location is collected along with various biological samples (e.g. teeth, gonads, stomach contents). In addition, the cause of death was only classified as 'evidence of bycatch' or 'no evidence of bycatch' for animals with decomposition state 2 (mild) and 3 (moderate), per Kuiken & García-Hartmann (1991). Because the assumptions of normality (Shapiro—Wilk test) and homoscedasticity (equal variance test) were fulfilled, differences in length between male and female harbour porpoises were compared with the parametric Student's *t*-test using the software R version 3.6.1 (R Core Team 2019). Results of statistical tests were considered to indicate significant differences or effects when $p < 0.05$.

From 1991 to 2018, the stomach contents of 80 harbour porpoises stranded on the Galician coast were collected (Fig. 1). The stomach contents were obtained by either opening the 3 stomach compartments (forestomach, main stomach and pyloric stomach)

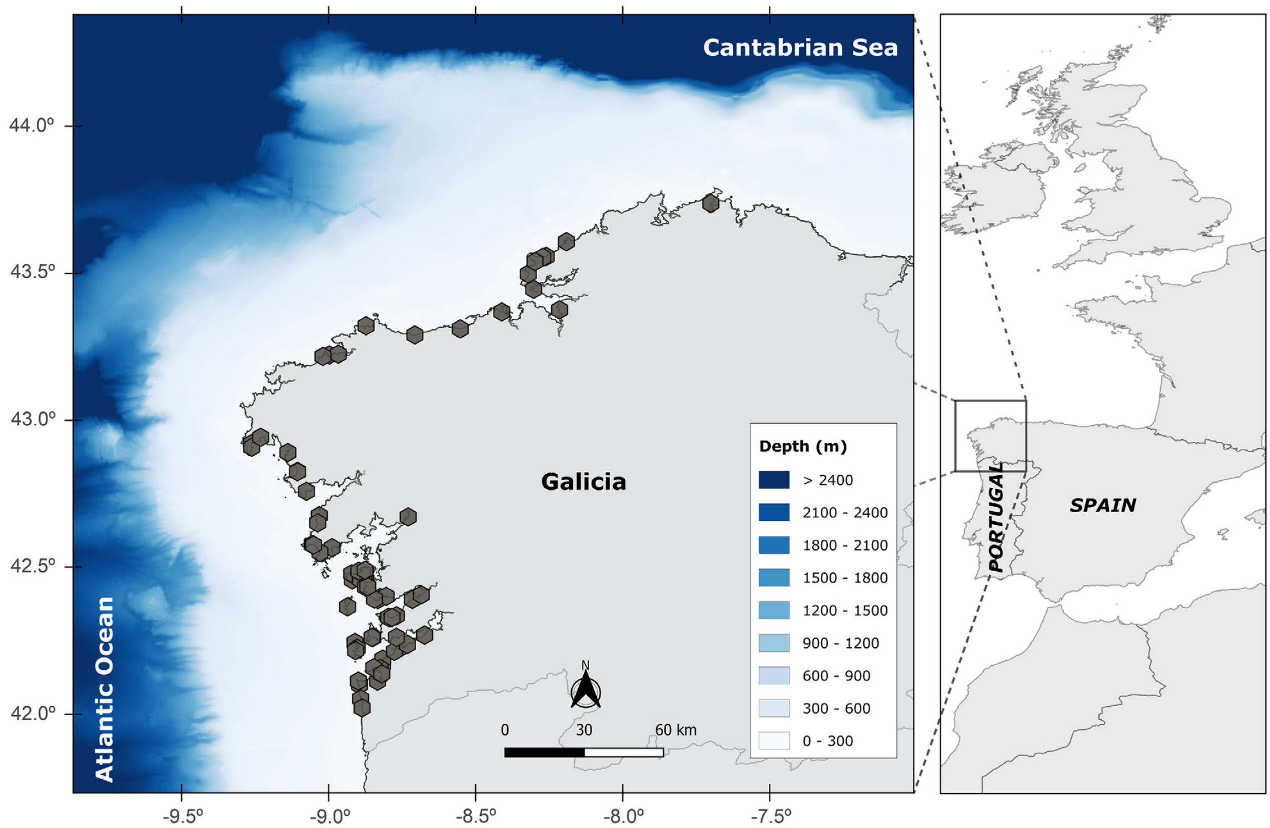

Fig. 1. Galician coast (NW Spain), showing the stranding locations of the 72 harbour porpoises whose stomach contents were analysed in the present study (1990—2018)

during the necropsy and storing the food remains in glass jars with 70% ethanol (n = 70), or by removing all 3 stomach compartments together and freezing them until further analysis in the laboratory (n = 10). Since 8 of the 10 frozen stomachs sampled did not contain any identifiable food remains, they were not included in the final diet analysis. Here we present the results from the analysis of the 72 non-empty stomachs.

In the laboratory, analysis was conducted following a standard protocol whereby all stomach contents were washed under tap water and rinsed through a set of 3 nested sieves with decreasing mesh sizes (1.0, 0.5 and 0.3 mm) to allow the separation of prey remains and to avoid clogging of the sieves. Diagnostic hard prey remains such as fish sagittal otoliths and bones, cephalopod beaks, crustacean exoskeletons and mollusc shells were transferred to 70% ethanol in labelled glass vials for sterilization. All prey hard structures were then dried at room temperature except for cephalopod beaks and crustacean remains, which were kept in 70% ethanol.

2.2. Prey identification and diet characterisation

The identification of fish was carried out to the lowest possible taxonomic level based on examination of sagittal otoliths, jaw bones and other diagnostic bones, using published guides (e.g. Härkönen 1986, Watt et al. 1997). We also had access to a reference collection held at the Spanish Institute of Oceanography. Since the diagnostic remains are generally paired structures, the minimum number of fish was estimated as half the highest number of sagittal otoliths or specific bones (premaxilla, maxilla, dentary, posttemporal, otic bulla and pharyngeal arch), rounded up. Cephalopods were identified from their hard remains (lower and upper beaks) using both published guides (e.g. Clarke 1986) and reference material. The number of cephalopods was estimated from the number of upper or lower beaks, whichever was higher.

Crustacean exoskeletons and mollusc shells were also recorded in a few stomachs and were identified whenever possible, but they were generally found broken, eroded or in an advanced stage of digestion. Some of these remains could originate as part of secondary ingestion, i.e. having been eaten by the prey of the harbour porpoises (although technically this could apply to any smaller prey remains). Their importance (either in number or weight) was minimal when compared with the other remains, and it was often not possible to determine the number of individuals involved. We have therefore listed them but not included them in further analysis.

Prey remains were photographed with a Leica S8 APO stereoscopic microscope (Leica Microsystems) fitted with a camera (Carl Zeiss Axiocam ERc5s). Measurements were taken using image analysis software (ZEN 2012). When more than 30 hard prey remains of the same type (i.e. the same diagnostic structure from the same species) were present in a sample, a random subsample of at least 30 items was measured and extrapolated to the total.

Standard sagittal otolith measurements were used to reconstruct original fish size using published regressions (e.g. Härkönen 1986). Fish weight was derived either from fish length or from sagittal otolith size, also using published regressions (e.g. Bedford et al. 1986. Similarly, mantle length and body weight of the cephalopod prey were reconstructed based on standard measurements from either the upper or the lower beak (rostral length for squids and hood length for octopods and sepiolids) using published regressions (e.g. Clarke 1986), or from our own unpublished regressions. The regressions used in this study to obtain prey lengths and weights are shown in Table S1 in the Supplement at www.int-res.com/articles/suppl/n054p105_supp.pdf. No corrections were made for digestive reduction in sagittal otolith size.

For each stomach, we recorded the presence/absence, number and summed (reconstructed) weight of each prey taxon. For describing the overall diet, 4 indices were used to determine the relative importance of each prey taxon:

(a) Frequency of occurrence (%F):

$$\%F = \left(\frac{F_i}{F_t}\right) \times 100 \tag{1}$$

where F_i is the number of stomach contents with the prey taxon i and F_t is the total number of stomach contents analysed.

(b) Percentage of prey number (%N):

$$\%N = \left(\frac{N_i}{N_t}\right) \times 100 \tag{2}$$

where N_i is the total number of individuals of prey taxon i in all the stomachs and N_t is the total number of individuals of all prey in all stomachs.

(c) Percentage of prey biomass (%W):

$$\%W = \left(\frac{W_i}{W_t}\right) \times 100 \tag{3}$$

where W_i is the total reconstructed biomass of prey taxon i in all the stomachs and W_t is the total reconstructed biomass of all prey items in all stomachs.

To compare these results with other harbour porpoise diet studies carried out in European Atlantic waters, we also calculated:

(d) Percentage index of relative importance (%IRI):

$$\%\mathrm{IRI} = \left(\frac{\mathrm{IRI}_i}{\mathrm{IRI}_t}\right) \times 100 \quad (4)$$

where IRI_i is the index of relative importance of prey taxon i (Hart et al. 2002), calculated as:

$$\mathrm{IRI}_i = (\%N_i + \%W_i) \times \%F_i \quad (5)$$

and IRI_t is the sum of IRI_i values across all prey taxa.

To determine the effects of sampling error, a nonparametric bootstrap method, following the methodology described by Santos et al. (2014), was used to obtain the median and the 95% confidence interval (CI) of diet composition (i.e. %F, %N, %W and %IRI) for the prey taxa identified in the diet. The bootstrap calculation process replicates the original calculations 1000 times, each time resampling the stomach samples with random replacement from the original set of samples (n = 72). Thus, each replicate consists of selecting a new sample (at random) and adding the data on presence, total number and total weights of each prey taxon in the sample to the running totals for each of the 38 prey taxa, finally expressing results for each prey taxon following the formulae listed above. The 1000 results for each index and each taxon were then sorted to allow the lower and upper 95% CI and median value to be extracted. The bootstrapping routine was run with the software R version 3.6.1 (R Core Team 2019) using the package 'boot' version 1.3.20 (Canty & Ripley 2019).

Several studies in the Northeast Atlantic have observed differences in the diet between adult and juvenile harbour porpoises (see Santos & Pierce 2003). However, as no information was available on the maturity of the harbour porpoise individuals in our sample, we used Spearman's rank correlation coefficient to determine whether the number of prey taxa in the stomachs increased with increasing harbour porpoise length. This was necessary because the preliminary examination of the data suggested a monotonic but non-linear relationship between the variables.

2.3. Drivers of diet variability

Generalised additive models (GAMs) were applied to model the diet composition of harbour porpoises using the R package 'mgcv', version 1.8.28 (Wood 2017). To choose the best approach, data series were firstly explored for outliers, collinearity and interactions. Then, 4 different binomial GAMs with logit link function were run for each key prey taxon to investigate factors affecting prey occurrence:

$$\begin{aligned}\mathrm{logit}(\mathrm{Occurrence}_i) &= \alpha + f_1(\mathrm{PorpL}_i) + f_2(\mathrm{Lat}_i)\\ &+ f_3(\mathrm{Year}_i) + f_4(\mathrm{Day}_i) + f_5(\mathrm{AbunP}_i)\\ &+ \beta_1(\mathrm{Sex}_i) + \beta_2(\mathrm{DecomS}_i) + \varepsilon_i\end{aligned} \quad (6)$$

where α is the intercept, the f_{ns} are the dimensional nonparametric smoothing functions, β_{ns} are the linear coefficients and ε is the error term.

The response variable was the occurrence (presence/absence), in each harbour porpoise i, of each main prey taxon: genus *Trisopterus* (hereafter '*Trisopterus*' but probably consisting mainly or entirely of pouting *T. luscus*, a benthopelagic species characteristic of coastal waters of the Iberian Peninsula), blue whiting *Micromesistius poutassou*, Atlantic horse mackerel *Trachurus trachurus* and European hake *Merluccius merluccius*. Continuous explanatory variables were harbour porpoise length (PorpL), stranding location (latitude, Lat), year of stranding (Year), day of year (Day) and an annual index of abundance for each main prey taxon (AbunP). Categorical explanatory variables were harbour porpoise sex (male/female, Sex) and carcass decomposition state (DecomS, a factor with 3 possible levels: mildly decomposed, moderately decomposed and highly decomposed).

The annual index of abundance for each main prey taxon was included in the models to investigate the effect of prey abundance on harbour porpoise diet variability. Depending on the prey taxon and data availability for the study area, different sources of information were used to provide the index of prey abundance. For European hake and Atlantic horse mackerel, we used the annual estimates of spawning-stock biomass of the southern stocks (Cantabrian Sea and Atlantic Iberian waters, ICES divisions 8.c and 9.a) of these 2 species, as published in the advice provided in 2019 by the International Council for the Exploration of the Sea (ICES) (ICES 2019a). For blue whiting, ICES assesses a single stock that is widely distributed, from Gibraltar to Norway. To obtain more local indices of abundance, we used the catch per unit effort data obtained by the northern Spanish shelf groundfish survey 'DEMERSALES' (Instituto Español de Oceanografía). This survey is part of the ICES programme of International Bottom Trawl Surveys (IBTS) that take place annually in autumn and cover the north and north-western shelf waters of the Iberian Peninsula (ICES divisions 8.c and 9.a). For species of the genus *Trisopterus*, ICES only assesses Norway pout *T. esmarkii*, which is a species that is absent from Iberian Peninsula waters (Svetovidov 1996), hence we used the abundance index of pouting estimated from the 'DEMERSALES' survey.

To avoid overfitting in GAMs, all continuous explanatory variables, except year of stranding, were fitted using smoothers with the maximum number of degrees of freedom restricted to 3 (k = 4). When the value for the effective degrees of freedom of a smoother was 1 in the optimal GAM (i.e. a linear fit), we replaced the smoother with a linear term. Since day of year is a cyclic variable, we applied a cyclic cubic spline. To identify the optimal GAMs, we used a backward selection procedure in which, at each step, one non-significant variable was removed from the model. The final models were the ones with the lowest values of Akaike's information criterion (AIC; Akaike 1974).

Generalised additive mixed models (GAMMs) were also applied to test for relationships between prey length (PreyL, as the response variable) and harbour porpoise length (PorpL) and prey taxon (both as explanatory variables). Harbour porpoise individuals were added as a random effect to GAMMs on the assumption that individuals of a given prey taxon within a single stomach may be of similar size (i.e. because it is assumed that the harbour porpoise fed on a single shoal of fish). Since the response variable (prey length) is a continuous variable with only positive values, GAMMs were run using a Gamma distribution with a logarithmic link function:

$$\text{logit}(\text{Occurrence}_i) = \alpha + f\,(\text{PorpL}_i) + \beta\,(\text{Taxa}) + a + \varepsilon_i \quad (7)$$

where α is the intercept, f is the dimensional nonparametric smoothing function, β is the linear coefficient and ε is the error term. The random effect a was included in the model to allow variation within the same individual harbour porpoise. Random effects were assumed to be normally distributed with mean 0 and variance σ_a^2.

2.4. Consumption rates and competition with fisheries

The annual food consumption (I_i, tonnes) by the Iberian population of the southern harbour porpoise in Atlantic waters of the Iberian Peninsula was estimated for the main prey species following the equation used by Santos et al. (2014):

$$I_i = \frac{\text{N} \times P_i \times \text{IB} \times T}{1000} \quad (8)$$

where N is the harbour porpoise population size inhabiting the Iberian Peninsula shelf waters, estimated to be 2898 individuals (95% CI 1386–5122), a figure obtained from the results of the SCANS III survey that took place in the summer of 2016 (Hammond et al. 2021). This estimate refers to the entire population of the Iberian Peninsula, not only that of the study region. However, it should be noted that the aerial survey found the highest density (animals km^{-2}) of this species in the Atlantic shelf waters off Galicia and north-central Portugal. For the purpose of this study, N was assumed to remain constant during the study period since the previous abundance estimation obtained by the SCANS II survey in 2005 was quite similar (2880 harbour porpoises) (Hammond et al. 2013).

P_i is the calculated proportion by weight of prey taxon i in the diet obtained from the analysis of the stomach contents. IB is the average daily food ingestion by an individual harbour porpoise (in kg). T is the number of days when prey and predator are in contact during a year (assumed to be 365 d).

To obtain the average daily food ingestion (IB) by harbour porpoises, we used the equation of Innes et al. (1987):

$$\text{IB} = 0.258 \times \text{BW}^{\,0.69} \quad (9)$$

where BW is the harbour porpoise body weight (in kg). The BW value was derived from the length–weight regression obtained by González-Fernández (2020) from harbour porpoises stranded in the study area (n = 37, r^2 = 0.96):

$$\text{BW} = -62.586 + 0.782 \times \text{BL} \quad (10)$$

where BL is the body length (in cm). The body length of the 72 harbour porpoises in the present study were known (measured during necropsies). Note that this approach assumes that the overall diet recorded in Galicia during 1990–2018 can be applied to the whole area, and that the animals studied for the diet are representative of the whole Iberian population.

To assess the effects of variability in harbour porpoise body weights and hence in daily food consumption, a non-parametric bootstrap method (with 1000 replicates), following the procedure described above, was also applied to generate 95% CI and to calculate the mean. To determine the relative amounts of fish taken by fisheries and harbour porpoises in Atlantic Iberian Peninsula waters, we compared the estimated annual consumption by the Iberian population with the reported annual fishery catches on their main prey species in the area during the time-period 1990–2018.

Annual catches (landings and discards) for the main harbour porpoise prey species (i.e. blue whiting, Atlantic horse mackerel and European hake) in ICES divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian Waters), fished by Spanish and Portuguese fleets, were obtained from the ICES data set collections (ICES 2019c). For pouting, official data on annual landings were obtained from the published figures provided on the webpage of the regional governments of Galicia and Asturias (Xunta de Galicia 2019, Principado de Asturias 2019). In Portugal, annual landings of pouting at the different ports of mainland Portugal were obtained from the Direção-Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM 2019). The 95% CIs of the landings values, expressed as a percentage of average landings, were calculated by resampling from the data set of annual landings using the same bootstrap procedure described above.

2.5. Prey energy content

The estimated biomass (%W) of the prey taxa found in the stomachs of harbour porpoises was converted into energy values (kJ g^{-1}), using the energy density (ED) data provided by Spitz et al. (2010) on different species, to determine the energetic content of harbour porpoise diet. The 95% CIs of the energy values obtained from the prey species in the stomachs were calculated using the same bootstrap procedure described above. Differences in dietary energy content between male and female harbour porpoises were evaluated using Student's t-test (n = 72) because the assumptions of normality (Shapiro–Wilk test) and homoscedasticity (equal variance test) were fulfilled. However, for those harbour porpoises whose decomposition state was 2 (mild) or 3 (moderate) and the evidence of bycatch could be determined during necropsies, a Mann–Whitney test was used to analyse differences in dietary energy content between bycaught and non-bycaught individuals (n = 37). This was necessary because, in this case, the assumptions of normality (Shapiro–Wilk test) and homoscedasticity (equal variance test) were not fulfilled. Results of statistical tests were considered to indicate significant differences or effects when $p < 0.05$. We also used a Gaussian GAM to depict the possible relationship between dietary energy content and harbour porpoise body length. In this GAM, the response variable was the log-transformed estimated prey energy density of the stomach contents, while the continuous explanatory variable was harbour porpoise length (fitted with degrees of freedom restricted to 3):

$$\log(\text{PreyE}_i) = \alpha + f\,(\text{PorpL}_i) + \varepsilon_i \qquad (11)$$

where α is the intercept, f is the dimensional nonparametric smoothing function and ε is the error term.

3. RESULTS

3.1. Sample composition

Harbour porpoise stomachs (n = 72) with food remains were analysed. Information on the samples (year of stranding, area, season, sex) is summarized in Table 1. Of these 72 samples examined, 10 animals showed evidence of having died as a result of bycatch in fishing gear, while 27 did not show evidence of interaction with fisheries. For the remaining 35 individuals, cause of death could not be determined due to their advanced state of decomposition. Nearly half of the strandings (43.1%, n = 31) occurred in winter; i.e. from 21 December to 20 March. Less than half of the samples (47.2%, n = 34) were females. Furthermore, most harbour porpoise strandings were concentrated in the southern part of Galicia, correspond-

Table 1. Summary of sampled harbour porpoises by period, area, season and sex

Years	N	Area		Season				Sex	
		Western (Pontevedra)	Northern (La Coruña and Lugo)	Winter (21 December to 20 March)	Spring (21 March to 20 June)	Summer (21 June to 20 September)	Autumn (21 September to 20 December)	Female	Male
1991–1999	28	21	7	7	10	5	6	10	18
2000–2008	19	13	6	10	5	2	2	14	5
2009–2018	25	13	12	15	4	4	2	10	15
Total	72	47	25	32	19	11	10	34	38

ing to the high number of sightings in this area during coastal surveys (Pierce et al. 2010).

Total length of sampled harbour porpoises ranged from 104 to 193 cm in females and 110 to 180 cm in males. Mean ± SD estimated length was 147.1 ± 24.2 cm for females and 144.3 ± 17.2 cm for males. The average length of all individuals was 145.6 ± 20.7 cm, with no significant difference between males and females (Student's *t*-test: $t_{58.7} = 0.6$, p = 0.559). Estimated weights ranged from 19 to 88 kg in females (mean 50.7 ± 15.7 kg) and from 23 to 78 kg in males (mean 50.2 ± 15.9 kg). Mean weight of all individuals was 50.5 ± 15.8 kg.

3.2. Prey identification and diet characterisation

In total, 6411 diagnostic hard prey items (i.e. fish sagittal otoliths and bones, and cephalopod beaks) were identified, which corresponded to the remains of 2455 individual fish and 85 individual cephalopods. These individuals belonged to 23 families, including 20 fish and 6 cephalopod taxa, respectively. Of the diagnostic hard prey items, 55.9% (n = 3583) were identified to species level, 20.6% (n = 1320) to genus level and 17.6% (n = 1131) to family level; the remaining 5.9% (n = 377) could not be identified due to erosion or fragmentation of the prey remains.

Overall, the diet of harbour porpoises consisted mainly of fish, in terms of all measures of importance (%*F* = 86.1, %*N* = 96.7, %*W* = 99.1, %IRI = 98.9). Cephalopods were also present in 13.9% of the stomachs, but they represented only 3.3% of the total number (%*N*), and even less by reconstructed prey weight (%*W* = 0.9) and index of relative importance (%IRI = 1.1) (see Table S2). The number of different prey taxa present in each stomach varied between 1 and 10. Most frequently (in 63.9% of cases), stomachs contained between 1 and 3 different prey taxa, while 95.8% of harbour porpoises contained 7 or fewer different prey taxa (Fig. 2). There was no significant correlation between harbour porpoise length and number of prey taxa in the stomachs (Spearman test: *S* = 46 766, p = 0.2; n = 72).

The total reconstructed prey mass was 118.6 kg (a mean of 1.6 kg per stomach). The estimated mean lengths were 16.6 cm (range: 2.1–45.0 cm) for fish, 4.6 cm (range: 1.2–20.2 cm) for squids and 2.9 cm for octopuses. For all prey taxonomic groups eaten by harbour porpoises, the mean length was 16.2 cm, with 27.2% of prey under 10 cm, 42.2% between 10 and 20 cm, 24.6% between 20 and 30 cm and 6% >30 cm in length (Fig. 3). The mean weight was 72.4 g (range: 0.04–1020.6 g) for fish, 12.7 g (range: 0.1–235.9 g) for squids and 4.8 g for octopuses. Across all prey taxa, the estimated mean weight was 53.6 g, with 83.8% of prey under 100 g, 10.49% between 100 and 200 g and 5.7% >300 g.

Specifically, *Trisopterus*, blue whiting, Atlantic horse mackerel and European hake were the main prey taxa in terms of occurrence (%*F* = 43.1, 36.1, 36.1 and 31.9, respectively), biomass (%*W* = 23.9, 19.2, 20.1 and 15.4, respectively) and importance (%IRI = 28.4, 23.1, 16.8 and 11.2, respectively). By weight, these 4 prey taxa together made up about 78.7% of the overall reconstructed prey weight (%*W*). However, according to overall numerical importance, blue whiting was the most important prey species (%*N* = 19.9), followed by *Trisopterus* (%*N* = 16.5), silvery pout (%*N* = 10.7) and gobies (%*N* = 8.8). The average estimated sizes of these 4 main fish taxa in harbour porpoise diet were 16.9 ± 8.6 cm for *Trisopterus* (range: 2–37.9 cm; n = 435), 18.2 ± 4.1 cm for blue whiting (range: 7–31.5 cm; n = 404), 21.1 ± 7.2 cm for Atlantic horse mackerel (range: 6.1–39 cm; n = 271) and 24.0 ± 10.5 cm for European hake (range: 3.3–44.9 cm; n = 198).

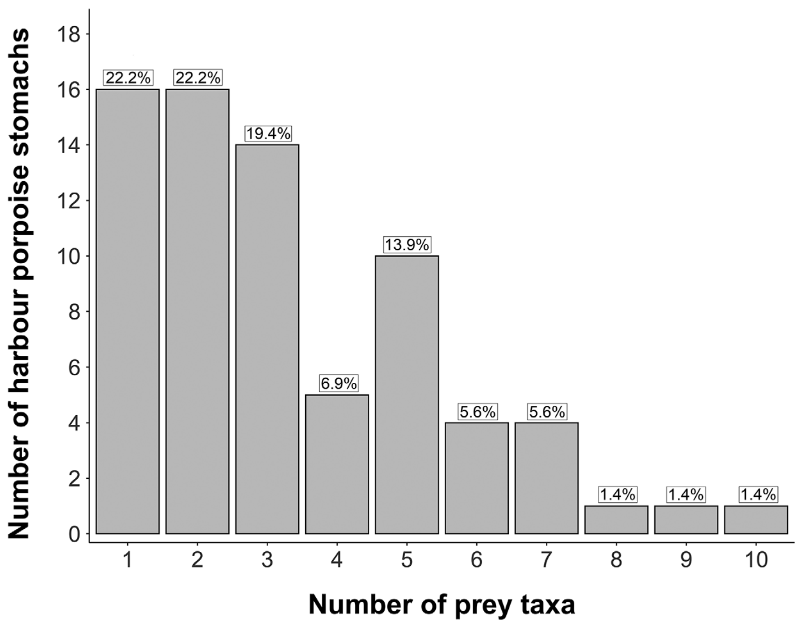

Fig. 2. Relative frequencies of the presence of different prey taxa found in the stomachs (n = 72) of harbour porpoises stranded in Galicia (NW Spain), reflecting the variety of prey in the stomach contents

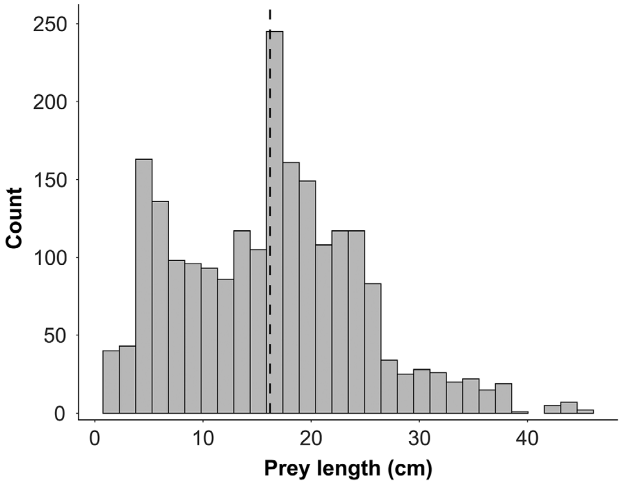

Fig. 3. Frequency distribution of the estimated sizes of all prey eaten by the 72 harbour porpoises stranded in Galicia (NW Spain), from 1990 to 2018. Dashed line represents the mean length of prey (16.2 cm), including both cephalopods and fish taxa

3.3. Drivers of diet variability

Table 2 summarizes the final GAMs, indicating which explanatory variables significantly affected the presence of each main prey taxon in harbour porpoise stomach contents. The smallest porpoises were more likely to have eaten *Trisopterus* (Fig. 4A). The occurrence of blue whiting increased with increasing porpoise length (Fig. 4B), and they were most often present in the stomachs of animals stranded between 2000 and 2006 (Fig. 5A). Atlantic horse mackerel was eaten more frequently by the largest porpoises (Fig. 4C). The occurrence of European hake in the stomachs increased over the time series (Fig. 5B). GAMM results showed that prey length increased with porpoise length, with maximum prey lengths (30−45 cm) found in porpoises of around 160 cm of total length (Fig. 6). However, the relationship was rather weak, as shown by low values of R^2 and deviance explained (0.27, and 38%, respectively).

3.4. Consumption rates and competition with fisheries

The average daily food consumption by a harbour porpoise on the Galician coast is estimated to be 3.9 ± 0.8 kg (95% CI = 3.7−4.1 kg), or 1.4 t of food per year (95% CI = 1.4−1.5 t). Using these average values and assuming a population size of 2898 individuals (95% CI = 1386−5122) (Hammond et al. 2021), the Iberian population would consume 11.3 t of food daily (95% CI = 5.1−21.0 t). Scaling up, it is thus estimated that the Iberian population would consume a total of 4125 t of food per year (95% CI = 1862−7665 t) (Table 3).

Between 1990 and 2018, the average annual weights of catches (landings and discards) of the main prey species of harbour porpoises, by the Portuguese and Spanish fleets operating in Atlantic Iberian waters and Cantabrian Sea (ICES divisions 8.c and 9.a) were 27580 t of blue whiting (95% CI = 24 080−30 687 t), 11 573 t of Atlantic horse mackerel (95% CI = 7370−16 389 t), 5704 t of European hake (95% CI = 4716−6658 t) (ICES 2019c) and (from 1998 to 2018) 2776 t of pouting (95% CI = 2100−3450 t) (DGRM 2019, Principado de Asturias 2019, Xunta de Galicia 2019). Using our estimates of prey biomass consumed, the amount of fish eaten by the Iberian population corresponds to around 34.2% of the *Trisopterus* catches (95% CI = 7.0−86.8%), 2.6% of the blue whiting catches (95% CI = 0.9−6.7%), 7.3% of the Atlantic horse mackerel catches (95% CI = 2.0−16.0%) and 10.9% of the hake catches (95% CI = 2.3−30.7%) declared by the Portuguese and Spanish fleets operating in the Iberian Peninsula Atlantic waters (Fig. 7).

Table 2. Results of the optimal generalised additive models (GAMs) for presence/absence of the 4 main prey taxa in the stomachs of harbour porpoises stranded in Galicia (NW Spain). Data set comprises those porpoises for which all of the information was available (n = 72); for all models, the distribution family selected was binomial. edf: effective degrees of freedom; AIC: Akaike's information criterion

GAM response variables	Significant explanatory variables	edf	p	Deviance explained (%)	AIC
Trisopterus occurrence	s(Harbour porpoise length, k = 4)	1	0.048	4.3	98.2
Blue whiting occurrence	s(Harbour porpoise length, k = 4)	1.9	0.009	31.9	78.8
	s(Year)	3.3	0.009		
Horse mackerel occurrence	s(Harbour porpoise length, k = 4)	2.8	0.010	15.4	87.6
European hake occurrence	s(Year)	2.5	0.001	26.6	74.4

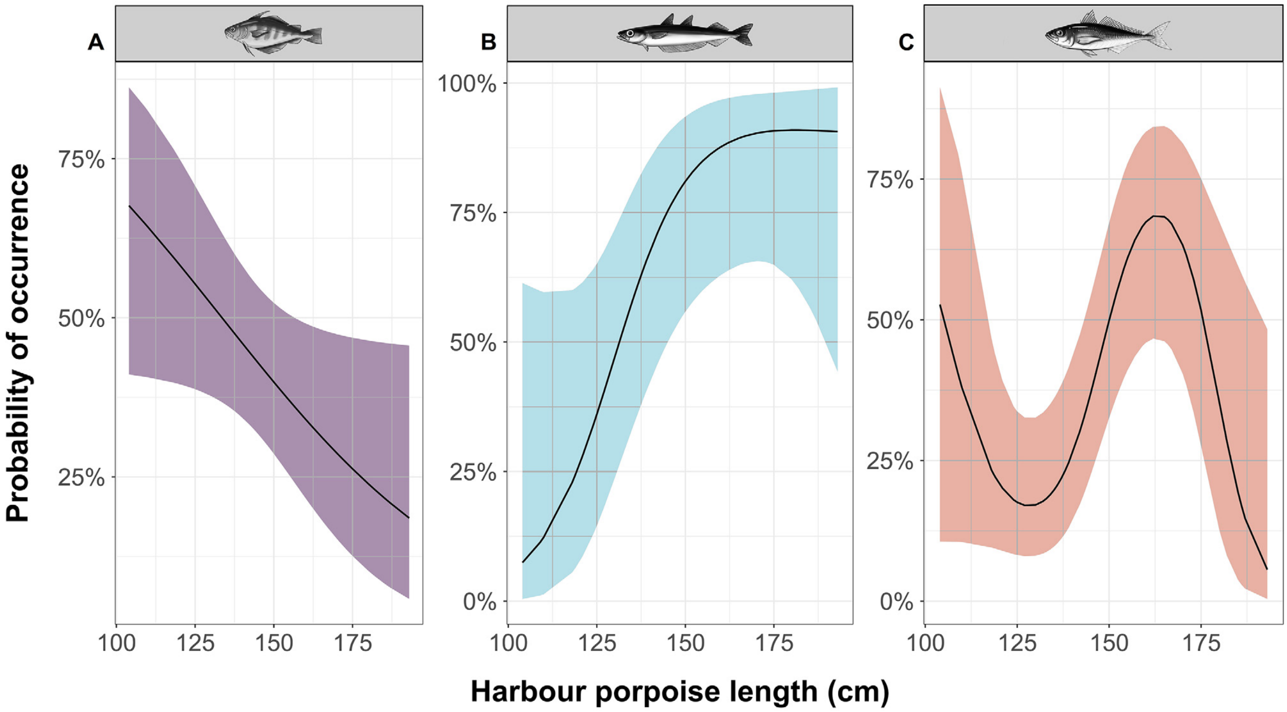

Fig. 4. Predicted values from optimal generalised additive models (GAMs) showing the relationship between the selected explanatory variable (harbour porpoise length) and the occurrence of (A) *Trisopterus*, (B) blue whiting and (C) Atlantic horse mackerel in their stomachs (n = 72). The black line is the predicted trend and the shaded area represents the 95% CI

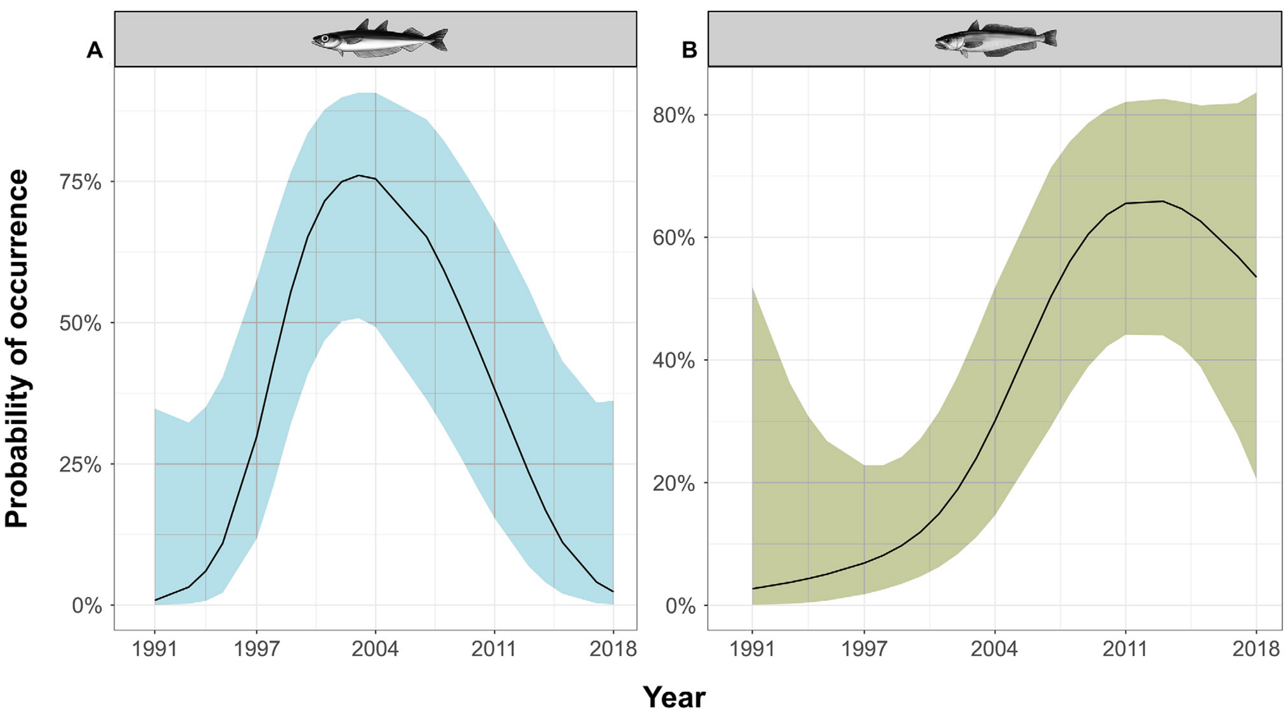

Fig. 5. Predicted values from optimal GAMs showing the relationship between the selected explanatory variable (year) and the occurrence of (A) blue whiting and (B) European hake in harbour porpoise stomachs (n = 72). The black line is the predicted trend and the shaded area represents the 95% CI

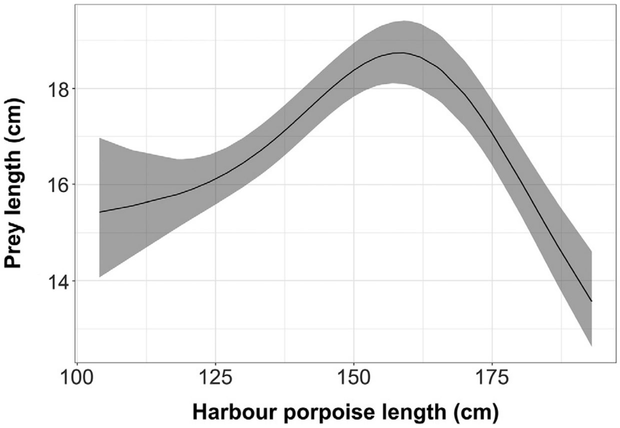

Fig. 6. Predicted values from the optimal generalised additive mixed model showing the relationship between harbour porpoise length and prey length. The black line is the predicted trend and the shaded area represents the 95% CI

3.5. Prey energy content

The total energy represented by the prey consumed by all harbour porpoises in our sample was close to 600 000 kJ, with an average energetic content of 5066 kJ per kg of food. The estimated energy content per harbour porpoise stomach ranged from 7 to 64 569 kJ, with an average of 8296 ± 12 555 kJ (95% CI = 5671–11 464 kJ). We found no differences in dietary energy content between male and female harbour porpoises (Student's *t*-test: $t_{58.9} = 0.6$, $p = 0.566$), nor between bycaught and non-bycaught individuals (Mann–Whitney test: $W = 140$, $p = 0.877$). In addition, there was no relationship (optimal GAM: adjusted $R^2 = 0.1$, $p = 0.05$; $n = 72$) between body length and dietary energy content.

4. DISCUSSION

Studies on the diet of cetaceans are important to help understand their feeding ecology and their foraging behaviour. In addition, when the diet is reconstructed using a direct procedure, as in this case, it also allows us to assess the possible overlap between harbour porpoise prey and fishery catches, in terms of the species, the numbers removed and their size distributions, which can indicate the potential for competition for food resources as well as the associated risk of bycatch mortality. Certainly, there are drawbacks in describing cetacean diet using stomach content analysis, since various errors and biases can arise, such as underestimation of original prey size due to otolith erosion by digestion, measurement errors and errors in the estimation of the biomass represented by the hard remains of prey (see Pierce & Boyle 1991). Nevertheless, stomach content analysis arguably still offers the best available solution to determining prey species and the number and sizes of each that are eaten (e.g. Santos et al. 2013). Thus while molecular techniques can identify more prey species, they are much less effective for determining the quantitative contribution of each prey to the diet.

4.1. Prey identification and diet characterisation

Although our sample size is relatively small (n = 72), this study collates all information from all the stomach contents that have been collected from the Iberian population of the southern harbour porpoises stranded in Galicia from 1990 to 2018. Results of our analysis indicate that the diet of southern harbour porpoises is largely made up of *Trisopterus*, blue whiting, Atlantic horse mackerel and European hake. A similar piscivorous diet was described for harbour porpoises in the Bay of Biscay, where the analysis of 29 stomachs collected from individuals stranded along the French coast between 1988 and 2003 showed that harbour porpoises mainly feed on Atlantic horse mackerel, sardine, blue whiting and whiting *Merlangius merlangus* (Spitz et al. 2006). In the north and central areas of Portugal, Aguiar (2013) identified coastal fish species such as dragonet *Callionymus*

Table 3. Estimated daily and annual consumption rates of southern harbour porpoises, both at the individual and the population level; 95% confidence intervals are in brackets

Prey	Individual		Population	
	Daily consumption (kg)	Annual consumption (kg)	Daily consumption (t)	Annual consumption (t)
Trisopterus	0.9 (0.3–1.6)	329 (110–584)	2.6 (0.4–8.2)	949 (146–2993)
Horse mackerel	0.8 (0.3–1.4)	292 (110–511)	2.3 (0.4–7.2)	840 (146–2628)
Blue whiting	0.7 (0.4–1.1)	256 (146–402)	2.0 (0.6–5.6)	730 (219–2044)
European hake	0.6 (0.2–1.1)	219 (73–402)	1.7 (0.3–5.6)	621 (110–2044)
Other prey	0.8 (0.0–2.5)	304 (0–901)	2.4 (0.0–3.4)	880 (0–1248)

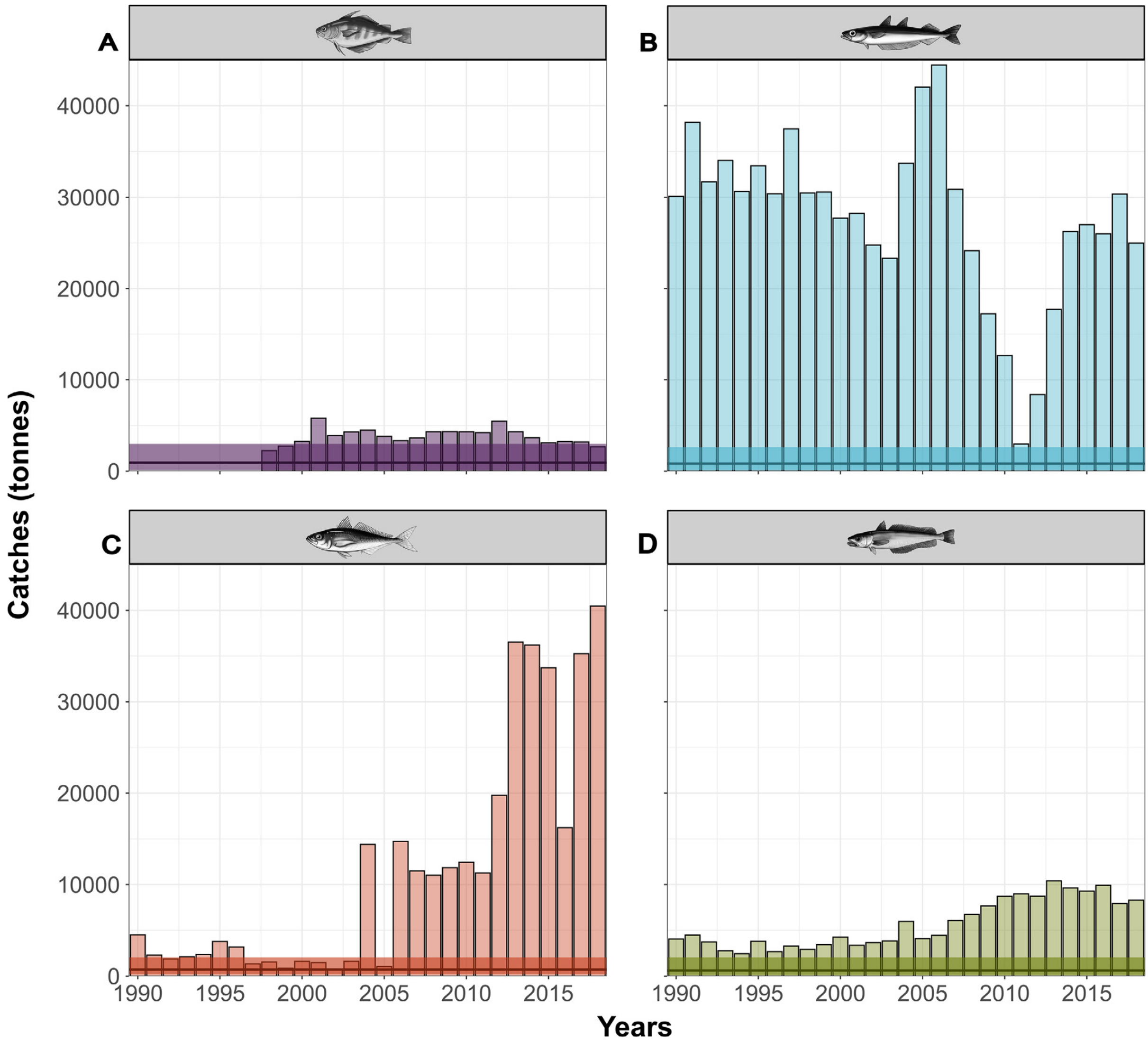

Fig. 7. Comparison between biomass eaten by the Iberian population of southern harbour porpoises (solid horizontal line; shaded area is the 95% CI) and the biomass removed by fisheries in ICES divisions 8.c and 9.a (Cantabrian Sea and Atlantic Iberian Peninsula waters) from 1990 to 2018 (vertical bars), for (A) *Trisopterus*, (B) blue whiting, (C) Atlantic horse mackerel and (D) European hake. Years without bars indicate those years for which catch data were not available

lyra, *Trisopterus*, *Liza* sp., sardine and European hake as the most important prey species in the diet of 54 harbour porpoises bycaught between 1998 and 2013. In these 2 nearby regions (France and Portugal), and also in the present study (Galicia), harbour porpoises feed on a wide variety of prey taxa and their relative importance in the diet composition varies geographically, seasonally and between years, probably due largely to differences in prey availability. For example, in the stomach contents of the Portuguese harbour porpoises, blue whiting appeared only in 1 out of 54 stomachs, while in Galicia, it was one of the main prey species. Concerning 'high-quality' (more energy-rich) prey species, the occurrence of sardine was higher in the diet of harbour porpoises from Portugal, while Atlantic horse mackerel was more frequent in the stomachs of harbour porpoises stranded in Galicia. Furthermore, when comparing the mean lengths of the main prey between harbour porpoises from Galicia and Portugal, we also found similarities for *Trisopterus* (16.9 vs. 17.3 cm), Atlantic horse mackerel (21.1 vs. 17.5 cm) and European hake (24 vs. 20.8 cm).

4.2. Drivers of diet variability

Final GAMs revealed significant variation in the diet related to harbour porpoise size and study year.

None of the other explanatory variables tested (i.e. sex, month or latitude) had a significant effect; however, the relatively small sample size limited the statistical power of the analysis, and the existence of such effects cannot be ruled out. GAM results indicated that European hake have become more prevalent in the diet since 1990, while blue whiting showed a peak of occurrence around 2000−2006. These trends in the diet do not seem to be related to the abundance of these species in the study area. This may be explained in part because we have used very broad (at the stock level and with an annual resolution) indices of prey abundance while, ideally, it would have been more appropriate to consider the effects of fish abundance on harbour porpoise diet at smaller spatial and temporal scales. However, such prey abundance indices are not currently available. Results of the GAMs also showed that *Trisopterus* occurred more often in the later years of the available series and more frequently in the stomachs of smaller harbour porpoises. In addition, since fish of the genus *Trisopterus* inhabit shallow inshore coastal waters (<100 m depth; Svetovidov 1996), and pelagic prey species (blue whiting and Atlantic horse mackerel) tend to occur more frequently in the stomachs of larger harbour porpoises, these results may indicate that smaller harbour porpoises live closer to the coast.

We analysed the stomach contents of stranded harbour porpoises and, therefore, the exact location where a porpoise might have been feeding prior to its death is not known. Although harbour porpoises can be found in offshore waters (Aguilar et al. 1983, Nielsen et al. 2018), the species is commonly distributed in nearshore coastal waters (Gaskin et al. 1974, Read 1999) and, in Galicia, it is the third most frequently observed cetacean from shore-based watches (Pierce et al. 2010). The assemblage of inshore prey species that are prevalent in the diet, together with the identity of the main prey species found in harbour porpoise stomachs (i.e. *Trisopterus*) supports this coastal distribution. Certainly, stranded carcasses can arrive from offshore waters or from Portuguese waters due to the complex current system of the northwest Iberian Peninsula (e.g. the upwelling system) (Fiúza 1983, Peliz et al. 2002, Relvas et al. 2007). However, carcasses of coastal animals are more likely to reach the coast as the stranding event is highly dependent on the likelihood of a carcass having positive buoyancy (i.e. drifting with wind and currents and not sinking) and also of being discovered in a good state of preservation (which increases the possibility of it being reported to the authorities). Therefore, the stranding location can be considered as the best available proxy for the feeding area.

4.3. Consumption rates and competition with fisheries

The stomach content data set includes a small percentage of bycaught individuals (10 out of 72). It has been argued that bycaught animals, which were probably feeding on the target species of the fishery, could provide a misleading view of the normal diet and lead to overestimation of the overlap between harbour porpoise diet and fisheries catches (Santos et al. 2004, Aguiar 2013). While this does not mean that feeding on commercial fish species is unnatural, it could lead to such a diet being overrepresented among strandings. Equally, however, harbour porpoises dying from infectious diseases could have stopped feeding normally prior to their death. In practice, as occurred in other studies performed in the northeast Atlantic on harbour porpoise diet (see Santos & Pierce 2003), we did not find any significant difference in diet composition between bycaught and non-bycaught individuals.

We have estimated that the Iberian population could remove, on average, around 6.9% of what the Portuguese and Spanish fishing fleets, operating in the Atlantic waters of the Iberian Peninsula (ICES divisions 8.c and 9.a), have been reporting annually as total landings of blue whiting, Atlantic horse mackerel and European hake from 1997 to 2018. In the case of fish of the genus *Trisopterus*, this figure is higher (around 34.2%), probably because these fish are mainly the target of artisanal fisheries that only operate in coastal areas very close to shore (Alonso-Fernández et al. 2019). In addition, this high overlap is expected, since harbour porpoises are usually distributed along the coastal area (ICES 2018, 2019b) and also because catches of artisanal fisheries are lower than those of commercial fisheries.

Estimates of food consumption by the endangered Iberian population inhabiting Galician waters were calculated based on dead stranded animals, some of which may not have been feeding normally before they died (e.g. due to disease, ageing or injury). While we cannot eliminate these biases, we can at least estimate the degree of variability which can arise due to sampling error. For this reason, we have accounted for the uncertainty associated with the estimates of food consumption using a bootstrap procedure (i.e. confidence intervals in estimates include sampling error in our calculations). This uncertainty could be reduced by using larger sample sizes; however, this will likely take some time due to the opportunistic nature of strandings data. In the future, our calculations and estimates could be revisited as new information becomes available for the study area.

The original sizes of harbour porpoise prey species could have been underestimated in the present study since we did not correct for the effect of sagittal otolith erosion caused by the acid pH of the stomachs. Nevertheless, a comparison of the mean sizes of the main prey species eaten by harbour porpoises with those legally taken by fisheries (i.e. above the minimum landing size [MLS] established for each fish species: DOG 2012) indicate that both size distributions partially overlap. In length, around 28% (n = 121) of pouting were over the MLS (22 cm), 51% (n = 206) of blue whiting were over the MLS (18 cm), 79% (n = 214) of Atlantic horse mackerel were over the MLS (15 cm) and 35% (n = 69) of European hake were over the MLS (27 cm). However, although these commercial species (*Trisopterus*, blue whiting, Atlantic horse mackerel and European hake) represent an important component of the diet of harbour porpoises, our calculations indicate that the Iberian population is consuming a relatively small amount compared to official commercial catches of the fisheries operating in the area.

Studies on harbour porpoise diet in the northeast Atlantic (e.g. North Sea, Baltic Sea) have also shown a significant overlap with fishery landings (see Santos & Pierce 2003). Indeed, marine mammals have always been perceived as competitors by fishers, being considered to be responsible for diminishing catches in addition to damaging nets (e.g. Dacosta et al. 1997, Kaschner & Pauly 2005). However, the existence of resource competition between marine mammals and fishers cannot be proven without demonstrating negative impacts of one over the other (e.g. Trites et al. 2006, Chasco et al. 2017, Ohlberger et al. 2019). In the present study, as in many others, in relation to resource competition, no such determination can be made; we can only speak of potential resource competition. Santos et al. (2004) pointed out that fish removed by marine mammals are not necessarily fish that would become available to fishers, since other factors (e.g. predator–prey interactions between different fish species) also play a role in the complex marine food web. However, the existence of significant bycatch mortality among Iberian harbour porpoises (e.g. Torres Pereira et al. 2023) is a clear indicator of interference competition, as indeed would be any reduction of fishery catches (albeit self-imposed) due to limits imposed on fishing activity to reduce bycatch mortality of protected species.

4.4. Prey energy content

The trophic position of the Iberian population of southern harbour porpoises has been determined through the analysis of their carbon and nitrogen stable isotope signatures (see Méndez-Fernández et al. 2012, 2013, 2017). Results from these studies indicated that harbour porpoises occupy one of the highest trophic positions in Galicia, above other odontocetes (toothed whales) such as bottlenose dolphins *Tursiops truncatus* and striped dolphins *Stenella coeruleoalba*. This is probably because the consumption of benthic animals is related to high trophic levels, and harbour porpoises made a greater use of benthic resources (e.g. *Trisopterus*).

Optimal foraging theory proposes that diet selection is driven by the energetic costs and benefits of feeding on each prey species. Therefore, the diet depends on prey abundance and availability, catchability and energy density (Pulliam 1974), such that the species and size-classes of prey eaten will be those resulting in the highest net rate of energy intake. Our results indicate that harbour porpoises in Galicia feed mainly on moderate-quality prey (with energy density [ED] ranging from 4 to 6 kJ g^{-1}). Although high-quality prey species such as sardine (ED = 8.7 kJ g^{-1}; Spitz et al. 2010) are also present in the stomachs throughout the year, they represent a minor component of the diet, possibly due to their relatively low abundance (ICES 2020).

Harbour porpoises show sexual dimorphism, with females reaching larger sizes than males (Read 1999, López 2003, Read 2016). This means that females have lower body surface area to body volume ratio, and therefore, their exposure to the environment is lower compared to males (i.e. less energy is lost through radiation so that they need less energy intake to maintain their internal temperature). On the other hand, females have a relatively quick reproductive output since they are able to be simultaneously lactating and pregnant each year (Bjørge & Tolley 2002), so that they need more energy intake during those periods of time. All of these conditions influence the energy requirements of harbour porpoises and thus may have important consequences on their feeding behaviour (e.g. diet composition, consumption rates). However, our results are consistent with those obtained by Spitz et al. (2012) and did not indicate a clear relationship between ED and harbour porpoise body length. We also found no relationship between ED and harbour porpoise sex. These results are likely due to the fact that it was not possible to test all factors that could be playing a role in prey selection by harbour porpoises (i.e. our sample was composed of males and females of similar lengths, and no pregnant or lactating females were identified during necropsies).

5. CONCLUSIONS

In this study, we provide a fully quantitative description of the diet of southern harbour porpoises, based on all stomach contents available to date from stranded individuals in Galicia. In addition, we evaluated the diet variability in relation to a series of factors that can influence diet choice. Our results indicate that harbour porpoises inhabiting Galician waters feed on both demersal and pelagic prey species with an average of around 16 cm in length and of moderate energetic quality. Ontogenetic variation in the diet was also confirmed, with the smallest porpoises feeding on more coastal prey species such as *Trisopterus*. No differences in diet between sexes could be detected. Interannual variability in the diet over the 3 decades considered was observed, with European hake increasing in the diet over the time series and more blue whiting being consumed during part of the period (from 1990 to 2004). However, no clear relationship between diet and annual prey abundance was found, probably due to the low resolution of the prey abundance indexes used.

Some of the porpoises' prey species are also target species of the fisheries in the area. We found partial overlap between the sizes of prey species targeted by the fisheries and those consumed by the porpoises. Sharing some resources might increase the vulnerability of the Iberian porpoise population to bycatch in fishing gears. On the other hand, except for the genus *Trisopterus*, our estimates of fish consumption by the Iberian population are relatively small when compared with catches of the fisheries in the distribution area (Atlantic waters off the Iberian Peninsula), which does not seem to have a significant impact on the fishing fleet, but could cause a reduction in the availability of resources for harbour porpoises.

Acknowledgements. We thank all volunteers of CEMMA who collaborated in the field work collecting the samples analysed in this study. A.H.G. received a pre-doctoral grant from the Xunta de Galicia co-financed with funds from the operational program FSE-Galicia 2014–2020. Continuation and completion of the work was funded by the European Recovery Funds Next Generation EU within the Spanish Government's Resilience Plan (MERMA CIFRA project), in the framework of the Agreement between the Ministry of Agriculture, Fisheries and Food (MAPA) and the State Agency Spanish Council for Scientific Research (CSIC) to promote fisheries research as a basis for sustainable fisheries management. The Galician stranding network was funded by the regional government Xunta de Galicia co-financed with European Regional Development Funds (ERDF/FEDER). We also acknowledge the anonymous reviewers, whose comments contributed to improving the quality of this manuscript. Species drawings for *T. luscus, M. poutassou, T. trachurus* and *M. merluccius* were kindly provided by artist ©Tokio (tokioilustracion@gmail.com).

LITERATURE CITED

Aarefjord H, Bjorge AJ, Kinze CC, Lindstedt I (1995) Diet of the harbour porpoise (*Phocoena phocoena*) in Scandinavian waters. Rep Int Whal Comm Spec Iss 16:211–222

Aguiar ZVP (2013) Ecologia alimentar do bôto (*Phocoena phocoena*) ao longo da costa continental portuguesa. MSc thesis, Universidade do Porto

Aguilar A, Grau E, Sanpera C, Jover L, Donovan G (1983) Report of the 'Ballena 1' whale marking and sighting cruise in the waters off western Spain. Rep Int Whaling Comm 33:649–655

Akaike H (1974) A new look at the statistical model identification. IEEE Trans Automat Contr 19:716–723

Alonso-Fernández A, Otero J, Bañón R, Campelos JM and others (2019) Inferring abundance trends of key species from a highly developed small-scale fishery off NE Atlantic. Fish Res 209:101–116

Arndt E, Evans J (2022) Diel activity of littoral and epipelagic teleost fishes in the Mediterranean Sea. Rev Fish Biol Fish 32:497–519

Bedford BC, Woolner LE, Jones BW (1986) Length–weight relationships for commercial fish species and conversion factors for various presentations. Fish Res Data Rep 10. MAFF Directorate of Fisheries Research, Lowestoft

Bjørge A, Tolley KA (2002) Harbour porpoise *Phocoena phocoena*. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of marine mammals, 2nd edn. Academic Press, Amsterdam, p 549–551

BOE (2020) Orden TED/1126/2020 de 24 de noviembre de 2020, por la que se modifica el Anexo del Real Decreto 139/2011, de 4 de febrero, para el desarrollo del Listado de Especies Silvestres en Régimen de Protección Especial y del Catálogo Español de Especies Amenazadas, y el Anexo del Real Decreto 630/2013, de 2 de agosto, por el que se regula el Catálogo Español de Especies Exóticas Invasoras. Boletín Oficial del Estado 314:108167–108171. https://www.boe.es/boe/dias/2020/12/01/pdfs/BOE-A-2020-15296.pdf

Canty A, Ripley BD (2019) Boot: bootstrap R (S-Plus) functions. R package version 1.3-23. https://CRAN.R-project.org/package=boot

Chasco BE, Kaplan IC, Thomas AC, Acevedo-Gutiérrez A and others (2017) Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. Sci Rep 7:15439

Chehida YB, Stelwagen T, Hoekendijk JPA, Ferreira M and others (2023) Harbor porpoise losing its edge: Genetic time series suggests a rapid population decline in Iberian waters over the last 30 years. Ecol Evol 13:e10819

Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford

Covelo P, Llavona A, López A (2018) Marsopa en Galicia,

¿qué ha cambiado en 20 años? XI Congreso Sociedad Española de Cetáceos, Bilbao
Dacosta M, Benavente P, López A (1997) Revisión histórica e cultural do arroás en Galicia. Eubalaena 10:13–19
DGRM (Direção Geral de Recursos Naturais, Segurança e Serviços Marítimos) (2019) Publicações Datapescas — DGRM. https://www.dgrm.mm.gov.pt/web/guest/datapescas-dgrm (accessed 28 February 2019)
DOG (2012) Orden de 27 de julio de 2012, por la que se regulan los tamaños mínimos de diversos productos pesqueros en la Comunidad Autónoma de Galicia. Diario Oficial de Galicia 226:44545–44563. https://www.xunta.gal/dog/Publicados/2012/20121127/AnuncioG0165-191112-0006_es.pdf
Fiúza AF (1983) Upwelling patterns off Portugal. In: Suess E, Thiede J (eds) Coastal upwelling: its sediment record. Plenum, New York, NY, p 85–98
Fontaine MC, Baird SJE, Piry S, Ray N and others (2007) Rise of oceanographic barriers in continuous populations of a cetacean: the genetic structure of harbour porpoises in Old World waters. BMC Biol 5:30
Fontaine MC, Tolley KA, Michaux JR, Birkun A and others (2010) Genetic and historic evidence for climate-driven population fragmentation in a top cetacean predator: the harbour porpoises in European waters. Proc R Soc B Biol Sci 277:2829–2837
Fontaine MC, Roland K, Calves I, Austerlitz F and others (2014) Postglacial climate changes and rise of three ecotypes of harbour porpoises, *Phocoena phocoena*, in western Palearctic waters. Mol Ecol 23:3306–3321
Fontaine PM, Hammill MO, Barrette C, Kingsley MC (1994) Summer diet of the harbour porpoise (*Phocoena phocoena*) in the estuary and the northern Gulf of St. Lawrence. Can J Fish Aquat Sci 51:172–178
Gaskin DE, Arnold PW, Blair BA (1974) *Phocoena phocoena*. Mamm Species 42:1–8
Giralt Paradell OG, Methion S, Rogan E, López BD (2021) Modelling ecosystem dynamics to assess the effect of coastal fisheries on cetacean species. J Environ Manag 285:112175
González AF, López A, Guerra A, Barreiro A (1994) Diets of marine mammals stranded on the northwestern Spanish Atlantic coast with special reference to Cephalopoda. Fish Res 21:179–191
González-Fernández M (2020) Estudio biométrico comparativo de Delphinidae y Phocoenidae en Galicia. BSc thesis, Universidade de Vigo
Hammond PS, Macleod K, Berggren P, Borchers DL and others (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Conserv 164:107–122
Hammond PS, Lacey C, Gilles A, Viquerat S and others (2021) Estimates of cetacean abundance in European Atlantic waters in summer 2016 from the SCANS-III aerial and shipboard surveys. Wageningen Marine Research. https://library.wur.nl/WebQuery/wurpubs/fulltext/414756
Härkönen TJ (1986) Guide to the otoliths of the bony fishes of the Northeast Atlantic. Danbiu ApS Biological Consultants, Hellerup
Hart RK, Calver MC, Dickman CR (2002) The index of relative importance: an alternative approach to reducing bias in descriptive studies of animal diets. Wildl Res 29:415–421
ICES (2018) Report of the Working Group on Bycatch of Protected Species (WGBYC), 1–4 May 2018, Reykjavik, Iceland. ICES CM 2018/ACOM:25
ICES (2019a) Working Group on Marine Mammal Ecology (WGMME). ICES Sci Rep 1:22
ICES (2019b) Report of the ICES Advisory Committee on blue whiting (*Micromesistius poutassou*), hake (*Merluccius merluccius*) and horse mackerel (*Trachurus trachurus*) of southern stock. ICES Advice 2019. ICES, Copenhagen
ICES (2019c) Official historical and nominal catches 1990–2018. Version 26-06-2019. ICES, Copenhagen. http://ices.dk/data/dataset-collections/Pages/Fish-catch-and-stock-assessment.aspx
ICES (2020) Bay of Biscay and Iberian Coast ecoregion. ICES Fisheries overviews. ICES, Copenhagen. https://doi.org/10.17895/ices.advice.7604
Innes S, Lavigne DM, Earle WM, Kovacs KM (1987) Feeding rates of seals and whales. J Anim Ecol 56:115–130
Jansen OE, Michel L, Lepoint G, Das K, Couperus AS, Reijnders PJH (2013) Diet of harbour porpoises along the Dutch coast: a combined stable isotope and stomach contents approach. Mar Mamm Sci 29:E295–E311
Kaschner K, Pauly D (2005) Competition between marine mammals and fisheries: food for thought. In: Salem DJ, Rowann AN (eds) The state of the animals III. Humane Society Press, Washington, DC, p 95–117
Kastelein RA, Hardeman J, Boer H (1997) Food consumption and body weight of harbour porpoises (*Phocoena phocoena*). In: Read AJ, Wiepkema PR, Nachtigall PE (eds) The biology of the harbour porpoise. De Spil Publishers, Woerden, p 217–233
Koopman NH (1994) Topographical distribution and fatty acid composition of blubber in the harbour porpoise, *Phocoena phocoena*. PhD dissertation, University of Guelph
Koschinski S (2001) Current knowledge on harbour porpoises (*Phocoena phocoena*) in the Baltic Sea. Ophelia 55: 167–197
Kuiken T, García-Hartmann M (eds) (1991) Proc 1st European Cetacean Society workshop on cetacean pathology: dissection techniques and tissue sampling, Leiden, The Netherlands, 13–14 September. Eur Cetacean Soc Newsl 17 (Spec Issue):1–39
Lassalle G, Gascuel D, Le Loc'h F, Lobry J and others (2012) An ecosystem approach for the assessment of fisheries impacts on marine top predators: the Bay of Biscay case study. ICES J Mar Sci 69:925–938
Lens S (1997) A note on the harbour porpoise (*Phocoena phocoena*) in the coastal waters of Spain. Rep Int Whaling Comm 47:841–849
Leopold MF, Begeman L, Heße E, van der Hiele J and others (2015) Porpoises: from predators to prey. J Sea Res 97: 14–23
Llavona A (2018) Population parameters and genetic structure of the harbour porpoise (*Phocoena phocoena*, L. 1758) in the Northwest Iberian Peninsula. PhD dissertation, Universidade de Aveiro
López A (2003) Estatus dos pequenos cetáceos da plataforma de Galicia. PhD dissertation, Universidade de Santiago de Compostela
López A, Santos MB, Pierce GJ, González AF, Valeiras X, Guerra A (2002) Trends in strandings and by-catch of marine mammals in north-west Spain during the 1990s. J Mar Biol Assoc UK 82:513–521
MacLeod CD, Santos MB, Reid RJ, Scott BE, Pierce GJ (2007) Linking sandeel consumption and the likelihood of starvation in harbour porpoises in the Scottish North Sea: Could climate change mean more starving porpoises? Biol Lett 3:185–188

Mahfouz C, Méziane T, Henry F, Abi-Ghanem C and others (2017) Multi-approach analysis to assess diet of harbour porpoises *Phocoena phocoena* in the southern North Sea. Mar Ecol Prog Ser 563:249–259

Martin AR (1995) The diet of harbour porpoises (*Phocoena phocoena*) in British waters. Paper SC 47(SM48):6. Scientific Committee of the International Whaling Commission, Dublin

Méndez-Fernández P, Bustamante P, Bode A, Chouvelon T and others (2012) Foraging ecology of five toothed whale species in the Northwest Iberian Peninsula, inferred using carbon and nitrogen isotope ratios. J Exp Mar Biol Ecol 413:150–158

Méndez-Fernández P, Pierce GJ, Bustamante P, Chouvelon T and others (2013) Ecological niche segregation among five toothed whale species off the NW Iberian Peninsula using ecological tracers as multi-approach. Mar Biol 160: 2825–2840

Méndez-Fernández P, Simon-Bohuet B, Bustamante P, Chouvelon T and others (2017) Inter-species differences in polychlorinated biphenyls patterns from five sympatric species of odontocetes: Can PCBs be used as tracers of feeding ecology? Ecol Indic 74:98–108

NAMMCO (North Atlantic Marine Mammal Commission), IMR (Norwegian Institute of Marine Research) (2019) Report of Joint IMR/NAMMCO International Workshop on the Status of Harbour Porpoises in the North Atlantic, Tromsø, Norway

Natale F, Carvalho N, Harrop M, Guillen J, Frangoudes K (2013) Identifying fisheries dependent communities in EU coastal areas. Mar Policy 42:245–252

Nielsen NH, Teilmann J, Sveegaard S, Hansen RG, Sinding MHS, Dietz R, Heide-Jørgensen MP (2018) Oceanic movements, site fidelity and deep diving in harbour porpoises from Greenland show limited similarities to animals from the North Sea. Mar Ecol Prog Ser 597: 259–272

Ohlberger J, Schindler DE, Ward EJ, Walsworth TE, Essington TE (2019) Resurgence of an apex marine predator and the decline in prey body size. Proc Natl Acad Sci USA 116:26682–26689

Peliz Á, Rosa TL, Santos AMP, Pissarra JL (2002) Fronts, jets, and counter-flows in the Western Iberian upwelling system. J Mar Syst 35:61–77

Pierce GJ, Boyle PR (1991) A review of methods for diet analysis in piscivorous marine mammals. Oceanogr Mar Biol Annu Rev 29:409–486

Pierce GJ, Caldas M, Cedeira J, Santos MB and others (2010) Trends in cetacean sightings along the Galician coast, north-western Spain, 2003–2007, and inferences about cetacean habitat preferences. J Mar Biol Assoc UK 90: 1547–1560

Pierce GJ, Weir C, Gutierrez P, Verutes G and others (2020) Is Iberian harbour porpoise (*Phocoena phocoena*) threatened by interactions with fisheries? IWC Scientific Committee Document SC/68B/SM/04 Rev2

Principado de Asturias (2019) Dirección general de pesca marítima. https://pesca.asturias.es/pesca-subastada-en-lonjas?p_p_id=com_liferay_document_library_web_portlet_DLPortlet_INSTANCE_ot0uH304wWwn&p_p_lifecycle=0&p_p_state=normal&p_p_mode=view&_com_liferay_document_library_web_portlet_DLPortlet_INSTANCE_ot0uH304wWwn_mvcRenderCommandName=%2Fdocument_library%2Fview (accessed 28 February 2019)

Pulliam HR (1974) On the theory of optimal diets. Am Nat 108:59–74

R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Read AJ (1999) Harbour porpoise (*Phocoena phocoena*). In: Ridgway S, Harrison R (eds) Handbook of marine mammals. Academic Press, London, p 323–350

Read FL (2016) Understanding cetacean and fisheries interactions in the north-west Iberian Peninsula. PhD dissertation, Universidade de Vigo

Read FL, Santos MB, González AF, López A, Ferreira M, Vingada J, Pierce GJ (2013) Understanding harbour porpoise (*Phocoena phocoena*) and fishery interactions in the north-west Iberian Peninsula. Document AC20/Doc.6.1.b (S), 20th ASCOBANS Advisory Committee Meeting, Warsaw, Poland, 27–29 August 2013. SSFA/ASCOBANS/2010/4

Read FL, Santos MB, Ferreira M, López A, Pierce GJ (2020) Harbour porpoise (*Phocoena phocoena*) and fisheries interactions in the north-west Iberian Peninsula. IWC Scientific Committee Document SC/68B/SM/06 Rev1

Relvas P, Barton ED, Dubert J, Oliveira PB, Peliz A, Da Silva JCB, Santos AMP (2007) Physical oceanography of the western Iberia ecosystem: latest views and challenges. Prog Oceanogr 74:149–173

Santos MB (1998) Feeding ecology of harbour porpoise, common dolphin, bottlenose dolphin and sperm whale in Northeast Atlantic. PhD dissertation, University of Aberdeen

Santos MB, Pierce GJ (2003) The diet of harbour porpoise (*Phocoena phocoena*) in the Northeast Atlantic. Oceanogr Mar Biol Annu Rev 41:355–390

Santos MB, Pierce GJ, Learmonth JA, Reid RJ and others (2004) Variability in the diet of harbour porpoises (*Phocoena phocoena*) in Scottish waters 1992–2003. Mar Mamm Sci 20:1–27

Santos MB, German I, Correia D, Read FL and others (2013) Long-term variation in common dolphin diet in relation to prey abundance. Mar Ecol Prog Ser 481:249–268

Santos MB, Saavedra C, Pierce GP (2014) Quantifying the predation on sardine and hake by cetaceans in the Atlantic waters of the Iberian Peninsula. Deep Sea Res II 106: 232–244

Schaffeld T, Bräger S, Gallus A, Dähne M and others (2016) Diel and seasonal patterns in acoustic presence and foraging behaviour of free-ranging harbour porpoises. Mar Ecol Prog Ser 547:257–272

Spitz J, Rousseau Y, Ridoux V (2006) Diet overlap between harbour porpoise and bottlenose dolphin: an argument in favour of interference competition for food? Estuar Coast Shelf Sci 70:259–270

Spitz J, Mourocq E, Schoen V, Ridoux V (2010) Proximate composition and energy content of forage species from the Bay of Biscay: high- or low-quality food? ICES J Mar Sci 67:909–915

Spitz J, Trites AW, Becquet V, Brind'Amour A, Cherel Y, Galois R, Ridoux V (2012) Cost of living dictates what whales, dolphins and porpoises eat: the importance of prey quality on predator foraging strategies. PLOS ONE 7:e50096

Surís-Regueiro JC, Santiago JL (2014) Characterization of fisheries dependence in Galicia (Spain). Mar Policy 47: 99–109

Svetovidov AN (1996) Gadidae. In: Whitehead PJP, Bauchot

ML, Hureau JC, Nielsen J, Tortonese E (eds) Fishes of the north-eastern Atlantic and the Mediterranean, Vol III. UNESCO, Paris, p 680–710

Teilmann J, Dietz R (1998) Status of the harbour porpoise in Greenland. Polar Biol 19:211–220

Torres-Pereira A, Araújo H, Monteiro SS, Ferreira M and others (2023) Assessment of harbour porpoise bycatch along the Portuguese and Galician coast: insights from Strandings over two decades. Animals 13:2632

Trites AW, Christensen V, Pauly D (1997) Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean. J Northwest Atl Fish Sci 22:173–187

Trites AW, Christensen V, Pauly D (2006) Effects of fisheries on ecosystems: just another top predator? In: Boyd IL, Wanless S, Camphyusen CJ (eds) Top predators in marine ecosystems. Cambridge University Press, Cambridge, p 11–27

Víkingsson GA, Ólafsdóttir D, Sigurjónsson J (2003) Geographical, and seasonal variation in the diet of harbour porpoises (*Phocoena phocoena*) in Icelandic coastal waters. NAMMCO Sci Publ 5:243–270

Vingada J, Ferreira M, Marçalo A, Santos J and others (2011) SafeSea — Manual de apoio para a promoção de uma pesca mais sustentável e de um mar seguro para cetáceos. Programa EEAGrants, EEA Financial Mechanism 2004–2009 (Projecto 0039), Braga

Watt J, Pierce GJ, Boyle PR (1997) Guide to the identification of North Sea fishes using premaxillae and vertebrae. ICES Coop Res Rep 220. ICES, Copenhagen

Wisniewska DM, Johnson M, Teilmann J, Rojano-Doñate L and others (2016) Ultra-high foraging rates of harbour porpoises make them vulnerable to anthropogenic disturbance. Curr Biol 26:1441–1446

Wood SN (2017) Generalized additive models: an introduction with R, 2nd edn. Chapman and Hall/CRC, New York, NY

Xunta de Galicia (2019) Consellería do Mar. https://mar.xunta.gal (accessed 28 February 2019)

ZEN (2012) Blue Edition Software 2.3 lite. Carl Zeiss Microscopy, Jena

Editorial responsibility: Robert Harcourt, Sydney, New South Wales, Australia
Reviewed by: D. Tollit and 1 anonymous referee

Submitted: September 4, 2023
Accepted: March 12, 2024
Proofs received from author(s): May 7, 2024