ARTICLE

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Food for thought: Harbor porpoise foraging behavior and diet inform vulnerability to disturbance

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Abstract

Research has shown that noise disturbance can disrupt the behavior of harbor porpoises. The significance of such disturbance is unclear. However, these animals may be vulnerable to starvation when disturbed due to their high energy requirements. Important parameters determining harbor porpoise energy balance are the size and energy content of prey, their foraging behavior and their energetic requirements for homeostasis, growth, and reproduction. Energy intake can be estimated using published data from tagged animals. Such analysis indicates a broad range of plausible levels of energy intake, in line with those from captive studies. Metabolizable energy intake estimates were most strongly affected by variations in target prey size and to a lesser extent, by the foraging intensity of porpoises. In all but the worst case scenarios, harbor porpoises are well equipped for their ecological niche due to their generalist diet, consisting of a range of moderate to high energy-density prey combined with ultra-high foraging rates and high capture success. If animals can find suitable prey, porpoises may be capable of recovering from some lost foraging opportunities. Minimizing disturbances is, however, important for their health. Further research into prey and the environment are required to fully test the assumption of vulnerability.

KEYWORDS
diet, disturbance, energetics, foraging, harbor porpoise, noise

1 | INTRODUCTION

The energy balance for any species is governed by the effort they expend to acquire food, the energetic value of that resource and how the energy acquired is utilized. This forms a cost–benefit equation, where the costs are represented by the energy expenditure involved in prey capture and that expended to maintain body processes, such as thermoregulation, growth, and reproduction. Marine mammals exhibit a wide range of life strategies, from large, long-lived species with long, interbirth intervals, to smaller species that reach sexual maturity early and produce a large number of offspring. Efficient foraging (maximizing benefits while minimizing costs) is, therefore, an essential element in the survival and reproduction of smaller species. Insights into energy acquisition and expenditure are therefore critical to developing an understanding of a species and its role in a changing ecosystem.

A number of studies have explored how energy budgets influence lifestyle (Kastelein, Hardeman, & Boer, 1997; Lockyer, 2007; McLellan et al., 2002). Harbor porpoises have short, stocky bodies, (females: length 160 cm and weight 60 kg; males: 145 cm and 50 kg) (Bjørge & Tolley, 2018). They are found throughout the cold, temperate waters of the Northern Hemisphere. In order to cope with relatively cold waters (and resulting thermoregulatory pressures) they require close proximity to food supplies and regular feeding due to their lack of major fat stores and their limited energy reserves (Lockyer, 2003). Heat loss is considered to be managed via cyclical shifts in energy intake to build up and then shed a blubber layer throughout the year (Rojano-Doñate et al., 2018). Female harbor porpoises are considered to be "income breeders" (Read, 2001; Read & Hohn, 1995), i.e., they balance the costs of pregnancy and lactation by increased food intake rather than depending on fat stores. These are evolutionary adaptations to a life that includes short-term periods of feast and famine.

A number of studies, using acoustic monitoring, have determined that harbor porpoises change their distribution and/or behavior following exposure to high-intensity, broadband noise sources (such as pile-driving, which is commonly used during the construction of offshore wind farms (Brandt et al., 2018; Dähne et al., 2013; Haelters, Dulière, Vigin, & Degraer, 2015) and lower intensity sources (Dyndo, Wiśniewska, Rojano-Doñate, & Madsen, 2015; Mikkelsen, Hermannsen, Beedholm, Madsen, & Tougaard, 2017). Reduced detection rates are often encountered during and following exposure to noise. It has been demonstrated that animals sometimes stop vocalizing in response to noise and therefore likely cease foraging (Wisniewska et al., 2018b). Near fasting has been shown to cause seasonally dependent variations in reduction of porpoise body mass of between 3.0% and 5.4% following 24 hr of near-fasting (Kastelein, Helder-Hoek, Jennings, van Kester, & Huisman, 2019). Whether porpoises can compensate following gaps in foraging requires further research on prey abundance, availability and the most limiting factors affecting porpoise health (assessed in this study). Kastelein et al. (2019) indicated that, following fasting, harbor porpoises can eat a large percentage (>90%; ~12–20 MJ) of their normal daily energy requirements in a 1 hr feeding bout and will then feed again shortly (without physical issues). What constitutes a significant disturbance (i.e., one that affects an animal's probability of survival or reproducing) remains a critical knowledge gap (King et al., 2015; Nabe-Nielsen et al., 2018).

Studies of porpoise diet in the North and Baltic Seas indicate that they ingest a wide range of prey types, typical of a generalist feeder, focusing on one or two prey species over short temporal scales (Andreasen et al., 2017; Börjesson, Berggren, & Ganning, 2003; Leopold, 2015; Ross, Andreasen, & Andersen, 2016; Santos & Pierce, 2003; Santos et al., 2004; Sveegaard et al., 2012). While there is significant temporal and spatial variation in the dominant prey species, the most commonly observed prey types include Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), sprat (*Sprattus sprattus*), and herring (*Clupea harengus*). Sandeels (*Family Ammodytidae*) and goby species (*Family Gobiidae*) also feature in their diet and may be important regionally (e.g., Andreasen et al., 2017; Santos et al., 2004). Diet varies with age and season with respect to both prey selection and prey size (Andreasen et al., 2017). Importantly, prey type differs in quality, with energy densities varying significantly from 4.2 kJ/g (wet mass) in whiting, to 7.6 kJ/g in sprat, parameters that also vary seasonally and with body length (Pedersen & Hislop, 2001; Wanless, Harris, Redman, & Speakman, 2005). Further, the lipid content, and therefore their seasonally dependent

value as food, of these fish vary. Overall, food intake and energy generation for porpoises is complex as they may forage on different species throughout the year.

Recent studies have deployed acoustic tags (DTAGs) on harbor porpoises and used the data collected to assess their vocalization and foraging behavior (Wisniewska et al., 2016, 2018a, 2018b). Acoustic click signatures, for males and females of different ages, in the audio recordings were used to estimate the number of foraging attempts made by tagged porpoises and to determine their success rates. The size of the targeted prey was also estimated. The majority of tagged animals foraged more during the night than during the day (as measured by daytime buzz-positive minutes [BPM] vs. night-time BPM) (Wisniewska, 2018b). Similarly, estimates of daily energy expenditure for tagged animals range from 7.8 to 31.0 MJ day^{-1} (corresponding to 0.25–0.59 MJ day^{-1} kg^{-1} of body mass). Further, it has been shown that exposure of animals to high levels of shipping noise can result in short-term disruptions in foraging (Wisniewska et al., 2018b). Despite these advances, our understanding of harbor porpoise vulnerability to disturbance is incomplete (summarized in Hoekendijk, Spitz, Read, Leopold, & Fontaine, 2018; Wisniewska et al., 2018a). Critical to understanding harbor porpoise vulnerability to missed foraging opportunities is an assessment of likely net energy gain at any time versus energy demands. The objective of this study was to utilize published studies to assess the effectiveness of harbor porpoises as foragers, what a bout of foraging might mean energetically for animals and how this learning informs how vulnerable harbor porpoises may be to disturbance. To achieve this, the data presented in (Wisniewska et al., 2016, 2018a) have been combined with our understanding of porpoise diet and the energy derived from different prey (e.g., Andreasen et al., 2017; Spitz, Mourocq, Schoen, & Ridoux, 2010; Wanless et al., 2005). These elements are used to estimate a plausible range of energy intake over the tag duration and, using the energy requirements of the same individuals (Rojano-Doñate et al., 2018), generate insights into the energy budget of harbor porpoises.

2 | MATERIALS AND METHODS

2.1 | Model development

Information on the individual tagged porpoises (ID, stage class, sex, standard length, month of tagging) and porpoise foraging parameter estimates (buzz rate, success rate of foraging attempt, size of prey targeted) were taken from recent papers (Wisniewska et al., 2016, 2018a) (Table 1). The animals were tagged between 2012 and 2016 in the Kattegat, at the mouth of the Baltic Sea (see Figure S1 in Wisniewska et al., 2018b). One tagged animal was referenced as "hp15_116a" in Wisniewska et al. (2018a), but as "hp15_117a" in Wisniewska et al. (2018b) and (Rojano-Doñate et al., 2018). These animals have the same tag date, length, tag deployment duration, and buzz count across the two studies and therefore are considered to be the same animal (with modified ID code) and have been treated as such in this study.

The total metabolizable energy intake for each tagged porpoise i (ME_i) was estimated using Equation 1.

$$ME_i = S_i \times C_i \times A \times \sum_{f=1}^{F} \sum_{p=1}^{P_f} \left(W_{f,p} \times d_{f,p} \times E_{f,q_i} \times k_{f,q_i,o_i} \right) \tag{1}$$

where S_i is the individual-specific rate of attempted captures that were successful; C_i is the number of capture attempts by that individual ("buzzes" as a proxy for capture attempts and success rate from Wisniewska et al., 2016, 2018a; summarized in Table 1 and Table S1); and A is assimilation efficiency (from Lockyer, 2007; Yasui & Gaskin, 1986). F is the main fish species recorded in porpoise diet by life stage and time of year (from Andreasen et al., 2017; summarized in Table 2 and Table S1). Each species f occurs in a number of 1 cm size bins/classes (P_f) in the range 3–20 cm. $W_{f,p}$ is the weight (in grams) of each fish species f given size class p and is equal to $a_f L_{f,p}{}^{b_f}$, where $L_{f,p}$ is the integer length (in centimeters) of fish in that size class, and a_f and b_f are constants that vary across different

TABLE 1 Information on tagged porpoises used in this study, derived from Wisniewska et al. (2016, 2018a).

| ID | Sex | Class | SL (cm) | Dur. (hr) | Month | Buzzes | Buzz hr^{-1} | SR % | Target prey size (cm) | | |
									<5	5–10	10–20
hp14_226b	M	J	126	20.0	Aug	3,234	153	91% (85–97)	53%	34%	13%
hp13_170a[a]	M	J	122	15.3	Jun	1,222	60	NA	NA	NA	NA
hp13_102a	M	J	114	22.7	Apr	3,405	162	99% (97–100)	95%	4%	1%
hp16_316a	M	J	113	39.1	Nov	5,715	146	NA	NA	NA	NA
hp12_272a	F	J	122	17.8	Sep	1,821	106	92% (87–97)	96%	3%	1%
hp12_293a[b]	F	A	163	16.4	Oct	1,346	86	97% (94–100)	75%	17%	8%
hp15_117a	F	A	170	12.4	Apr	906	73	NA	NA	NA	NA

Note: ID = code provided by Wisniewska et al. (2016, 2018a) in the form: [species][year]_[JulianDay]. Sex = the sex of the tagged animal, M = male, F = female. Class = the stage class of the animal, J = juvenile, A = adult. SL (centimeters) = the length of the tagged porpoise in centimers. Dur. (hr) = the duration in hours of the tag deployment in which data was collected on the animal (from start of foraging to tag release). Month = the month in which the animal was tagged. Buzzes = the total number of buzzes estimated for the tag duration. Buzz hr^{-1} = the total number of buzzes estimated divided by the tag duration. SR% = the estimated mean (and 95% confidence intervals) success rate of capture attempts by the tagged porpoises. Target prey size = prey size targeted by the tagged porpoises in Wisniewska et al. (2016, 2018a), derived from Figure 3C in Wisniewska et al. (2016). NA = data not available for that individual.
[a]Tag data only collected during daylight hours.
[b]This adult female was present with a calf.

TABLE 2 Seasonal prey mass composition derived from fig. 4 of Andreasen et al. (2017) for juveniles and adult porpoises (based on 339 stomach contents).

| | Seasonal prey mass composition (%) | | | | | | | |
| Stage class | Juveniles | | | | Adult | | | |
Prey species/group	Q1	Q2	Q3	Q4	Q1	Q2	Q3	Q4
Atlantic Cod	6%	18%	55%	29%	32%	18%	41%	55%
Whiting	1%	3%	17%	2%	4%	1%	1%	2%
Herring	38%	27%	9%	5%	9%	30%	17%	29%
Sprat	9%	10%	2%	5%	0%	7%	0%	1%
Sandeel family	0%	2%	1%	0%	0%	14%	6%	0%
Eelpout	10%	10%	0%	5%	0%	6%	24%	0%
Gobies family	30%	28%	10%	38%	1%	10%	4%	8%
Others	5%	2%	6%	15%	4%	14%	7%	5%

Note: Q1 = January–March; Q2 = April–June; Q3 = July–September; Q4 = October–December.

fish species (sources summarized in Table 3 and Table S1). $d_{f,p}$ is the estimated proportion of fish species f belonging to size class p from Wisniewska et al. (2016) (Table 1 and Table S1); E_{f,q_i} is the energy density (in kilojoules/gram wet weight) of each fish species f in the quarter during which each porpoise was tagged, q_i (Table 2); and is the proportion of fish species f in the porpoise diet in quarter q_i (from Anderson et al., 2017; summarized in Table 3 and Table S1), given the ontogenetic stage o_i of the tagged porpoise (juvenile or adult). Where foraging parameter estimates were not available for individual porpoises, the values provided for the most closely related individual were used. For example, no information on the success rate of foraging attempts was available for animal hp13_170a (a juvenile) and, therefore, the estimate for animal hp12_272a, (a similar sized juvenile) was used. The latter had the lowest success rate in the study and is, therefore, a conservative estimate. Similarly, the success rate for hp15_117a

TABLE 3 Weight-length relationships and energy density for prey species considered in this study. Gobies value taken as a proxy from grey gurnard and red mullet.

| Prey species | Weight-length parameters | | | Energy density | |
	a	b	Reference	Value (kJ/g)	Reference
Atlantic Cod	0.0143	2.9126	Silva et al. (2013)	4.2	Lawson et al. (1998)
Whiting	0.0166	2.7708	Silva, et al. (2013)	4.2[a]	Pedersen and Hislop (2001)
Herring	0.00603	3.0904	Coull et al. (1989)	6.0[a]	Pedersen and Hislop (2001)
Sprat	0.00211	3.4746	Coull et al. (1989)	7.6	Wanless et al. (2005)
Sandeel family	0.00124	3.32	Coull et al. (1989)	5.0[a]	Pedersen and Hislop (2001)
Eelpout	0.003	4.0957	Coull et al. (1989)	5.1	Spitz et al. (2010)
Gobies family	0.0056	3.3081	Silva et al. (2013)	4.4	Plimmer (1921)
Four-bearded rockling	0.0035	3.1062	Coull et al. (1989)	5.5	Spitz et al. (2010)
Horse mackerel	0.0034	3.2943	Coull et al. (1989)	6.0	Spitz et al. (2010)
Saithe	0.0085	3.0242	Silva et al. (2013)	4.2	Spitz et al. (2010)
Haddock	0.0092	3.1026	Silva et al. (2013)	4.4[a]	Pedersen & Hislop (2001)
Sole	0.0036	3.3133	Coull et al. (1989)	5.0	Spitz et al. (2010)
Flounder	0.0087	3.0978	Coull et al. (1989)	3.0	Plimmer (1921)

[a]Denotes where there was evidence of energetic density varying seasonally and with fish length, this was accounted for in analyses, but only an average value is presented here.

(an adult female) was not presented in Wisniewska et al. (2018a) so the foraging success data for animal hp12_293a (the only other adult female tagged) was used.

Estimates of the prey sizes targeted (derived from tailbeat frequency of fish detected on the DTAG) by the porpoises were presented for four of the individuals tagged (in Wisniewska et al., 2016). For the purposes of this study, the proportions of different prey sizes were digitally extracted using WebPlotDigitizer (version 4.0, https://automeris.io/WebPlotDigitizer/) (Table 1). In the published studies (Wisniewska et al., 2016, 2018a), porpoises primarily targeted fish that had body lengths of 3–10 cm and displayed proportions for prey sizes <5 cm, 5–10 cm, and 10–20 cm. Therefore, it was assumed that the smallest prey targeted was 3 cm and the largest was 20 cm corresponding to the minimum and maximum fish length targets specified. The lower value of this range is consistent with the size of the main prey items for Danish (Kattegat) harbor porpoises (Andreasen et al., 2017; Ross et al., 2016). Where data on targeted prey size were not available for individuals, the closest available estimate of target prey for a suitable proxy was used. For example, for animal hp13_170a, no estimates of target prey size were available, therefore the data from hp12_272a (a similar sized juvenile, see above) were used. Similarly for individuals hp16_316a (juvenile male) and hp15_117a (adult female) no target prey size estimates were available and so estimates from hp13_102a (juvenile male) and hp12_293a (adult female), respectively, were used in the calculations. These proxies also represent a minimum estimate, as they targeted predominantly small prey sizes (which have lower energy content than larger fish).

For this analysis the most likely target prey species, based on stomach contents of either stranded or bycaught animals, was considered. Data reported for 339 harbor porpoises (either bycaught or stranded) in the Western Baltic Sea and Kattegat between 1980 and 2011 has been utilized (Andreasen et al., 2017). Geographically, the study areas for diet and porpoise tagging overlap and so, this study focuses on these key prey species. In their analyses the samples comprised; males (n = 183), females (n = 156), juveniles (n = 228) and adults (n = 111). They determined that 91% of the stomach contents were comprised of: Atlantic cod (mean length = 23 cm, length range = 2.6–56.9 cm), whiting (mean = 14.9 cm, range = 2.9–46.6 cm), herring (mean = 17.7 cm, range = 2.6–30.6 cm), sprat (mean = 10.3 cm, range = 3.0–15.9 cm), sandeels spp. (mean = 15.1 cm, range = 4.1–21.0 cm), eelpout (or burbot,
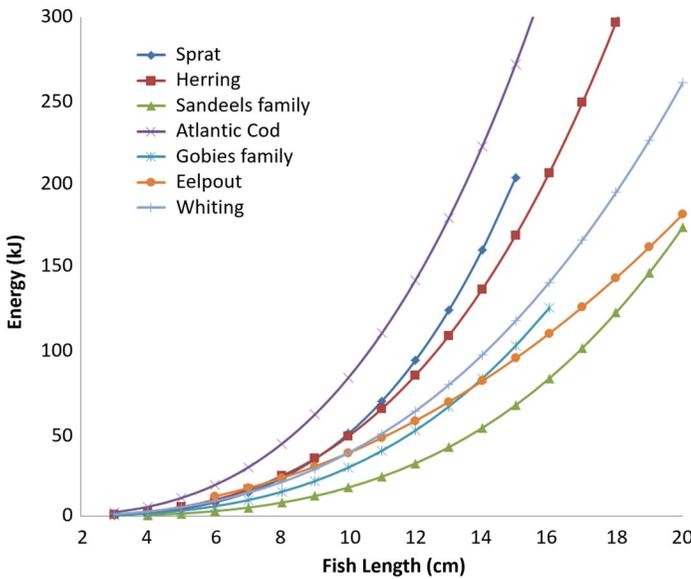
FIGURE 1 The relationship between average fish length (centimeters) and energy (kilojoules) for a range of harbor porpoise prey items (though seasonal and length-specific variations exist; see Equation 1). Fish length for each species is limited by the observed range of prey in stomach contents from Andreasen et al. (2017).

Zoarces viviparus) (mean = 19.6 cm, range = 6.0–28.7 cm), gobies spp. (mean = 4.9–5.8 cm, range = 2.5–12.7 cm), and the remaining diet items ("others") mostly comprised of sole (*Solea solea)*, flounder (*Platichthys flesus)*, gadoids (*Family Gadidae*, excluding cod and whiting), Atlantic horse mackerel (*Trachurus trachurus*), and four-bearded rockling (*Enchelyopus cimbrius*) (length range = 5.7–35.3 cm). Since mass is a cubic function of fish length (and the caloric value of a fish is a product of mass), larger prey offer substantially greater energy gains to the animal (Figure 1). Prey sizes used in analyses were based on the quoted size ranges (Andreasen et al., 2017); for example, eelpout <6 cm were not observed in the stomach contents of harbor porpoises, so it was assumed that any eelpout consumed were >6 cm. Metabolizable energy obtained for an animal was estimated from a range of values for assimilation efficiency values from the literature and were between 74% (Yasui & Gaskin, 1986) and 90%–95% (Lockyer, 2007). ME estimates were scaled by tag duration in (Table 1) and allometrically using mass estimates (Table S2).

2.2 | Sensitivity analysis of ME_i

To understand the sensitivities of calculations *ME*, the relative importance of each of the variables in Equation 1 was assessed. Some of the variables are nonindependent (i.e., a change in one results in a change in the other, for example, *d* the estimated proportion of fish in a size class) and so a classic sensitivity analysis was not possible. Collinearity between the variables was assessed using the *vif* and *GGally* packages. Energy density and proportions of different fish species in the diet *f* were found to be strongly correlated. Therefore a series of linear models with standardized *ME* estimates, variable combinations with interactions fitted across the nonindependent variables were assessed and the best model selected (determined by AIC). Model order was iteratively adjusted to ensure that results were not biased by the order of fitting of variables. To calculate the relative importance of each variable in the best model the contribution of each variable using the absolute value of the *t*-statistic for each model parameter was undertaken using *varImp* (in the *caret* package) (Kuhn, 2008). All relative importance assessment steps were implemented in R (version 3.4, https://cran.r-project.org/).

2.3 | Energy balance

Rojano-Doñate et al. (2018) estimated the field metabolic rates (FMR) for each of the tagged animals reported in previous studies (Wisniewska et al., 2018a, 2018b;). These FMR estimates were corrected in the current study using the reported tag durations to calculate the energy balance for these tag deployments (Table S2, Equation 2).

$$\text{Energy balance} = \frac{ME_i}{ER_i} \tag{2}$$

where ME_i is the metabolizable energy intake for each tagged porpoise i (from this study) and ER_i is the energy requirement estimate for the same tagged porpoise i from Rojano-Doñate et al. (2018) over the tag duration. Five short-term energy balance scenarios were assessed (detailed in Table S3). The first three scenarios dealt with the "average seasonal porpoise diet" (following dietary patterns observed in Andreasen et al., 2017), the "best case" (highest ME obtained and lowest ER estimates over the tag duration), "moderate case" (best estimate of ME obtained and ER), and "worst case" (lowest ME obtained and highest energy requirement estimates) scenarios were assessed. Finally, two scenarios investigated single species diet: the lowest and highest energy single prey species—defined as "single species–worst and best case" (see Table S3 for further details). For these single species analyses only prey that were a significant component of the relevant quarterly diet were considered (from Table 2). This avoided the inclusion of prey that were unlikely to be in the diet of the tagged porpoise. These scenarios provides a range of plausible values of ME ingested by the tagged animals and allow a better understanding of the role of prey caloric value in assessments of energy balance.

3 | RESULTS AND DISCUSSION

3.1 | Estimates of *ME* obtained by tagged porpoises

Estimates of potential metabolizable energy gained by seven different harbor porpoises were derived from published data (foraging records and diet studies) (Andreasen et al., 2017; Wisniewska et al., 2016, 2018a) under several different prey availability scenarios (Figure 2, Table S3). As expected there was considerable variance between the animals with two juvenile males providing the most extreme values: animal hp14_226b (juvenile male) was an outlier, as it
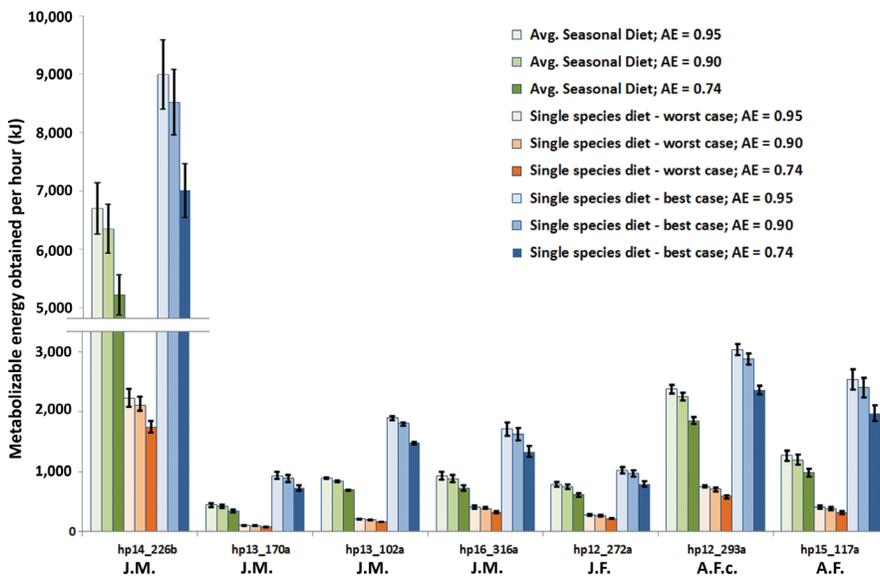

FIGURE 2 Estimates of average metabolizable energy obtained per hour (allometrically scaled) for each tagged porpoise from Wisniewska et al. (2016, 2018a). Note the broken *y*-axis. Error bars indicate the range of successful capture rates for each individual. The height of the main bars are a product of the total number of capture attempts, the prey species foraged on and the size of the prey. AE = assimilation efficiency. J.M. = juvenile male; J.F. = juvenile female; A.F.c = adult female with calf; A.F. = adult female (no calf).

TABLE 4 Sensitivity analysis of factors affecting *ME* intake estimates for the "average seasonal diet" scenarios. The relative importance of each variable was calculated using the absolute value of the *t*-statistic for each model parameter. Variables in italics denote variables fitted as interaction terms. Variables are ordered by *t*-statistic.

Variable	Symbol	*t*-statistic
Proportion of fish in each size class[a]	*d*	38.773
Number of successful captures[a]	*SC*	7.223
Assimilation efficiency[b]	*A*	3.999
Proportion of fish species in diet[c]	*k*	3.718

[a]Data sourced from Wisniewska et al. (2016).
[b]Data sourced from Lockyer (2007) and Yasui and Gaskin (1986).
[c]Data sourced from Andreasen et al. (2017) (see Table S1 for sources).

appeared to be targeting larger prey items and correspondingly had the highest *ME* values. Estimates for animal hp13_170a were lower, ranging between 2.6 and 3.3 kJ h^{-1} kg^{-1} and this fits with the observation that the animal was not tagged during hours of darkness. For the other animals, males and females, plus nursing females, most of the values of *ME* fitted between the two extremes described above. For all the animals, single species diets are predicted to give the highest *ME* values for the best case, whereas worst cases were calculated to fall below the values for average seasonal diet (derived from the stomach contents of bycatch and stranded animals (Figure 2).

To understand the drivers of the variance in ME described above, an assessment was made of the most important variables in Equation 1 (Table 4). The single most important factor was the size of prey item targeted, with fish of 5–10 cm and 10–20 cm resulting in the highest ME estimates (*t*-statistic: 37.77). The next most important variable was the number of successful captures by each tagged porpoise (a product of the total number of capture attempts—buzzes from the DTAG record and the estimated success rate—from Wisniewska et al. (2016) (*t*-statistic: 7.22). Finally, the assimilation efficiency of the ingested prey of the porpoises (*t*-statistic: 3.99) and the prey species (*t*-statistic: 3.72) were the least important variables.

3.2 | Energy balance assessment

To gain a better understanding of the *ME* estimates above, the energy requirements were incorporated into the assessment of energy balance for the tagged porpoises (using the same five scenarios) (Figure 3). Only in the worst case scenarios (both average seasonal and single species diets) did the energy capture fall below the calculated requirement (Figure 3). In most cases prey capture and energy intake were up to 1.5–two-fold greater than the calculated demand. This applied particularly to individual hp13_170a where tagging only covered the period (daytime) with the lowest foraging effort (Wisniewska et al., 2016). In nearly all examples the lowest energy yield came from the scenario that is least realistic—"single species diet-worst case" (Figure 3).

In the majority (>70%) of scenarios considered, animals obtained >100% of their energy requirements over the tag deployment. Among the juvenile animals hp14_226b, the animal obtained >100% in all scenarios and hp13_170a (only tagged during daylight hours) obtained >100% in all but the worst case scenarios (average and seasonal diets). All remaining juveniles obtained less than 100% of requirements only in a scenario with the "single species-worst case" prey species available. For the adults females tagged, the female without a calf only obtained >100% in 2 out of 5 scenarios, while the female accompanying a calf obtained >100% of required energy in 3 out of 10 scenarios.

3.3 | Model interpretation

This study predicts the energy intake and energy expenditure of tagged harbor porpoises, with the objective of gaining a better understanding of their vulnerability to disturbance. This is the first time that an energy balance has been estimated for harbor porpoises using data from field experiments on wild harbor porpoises and their prey. The analyses in
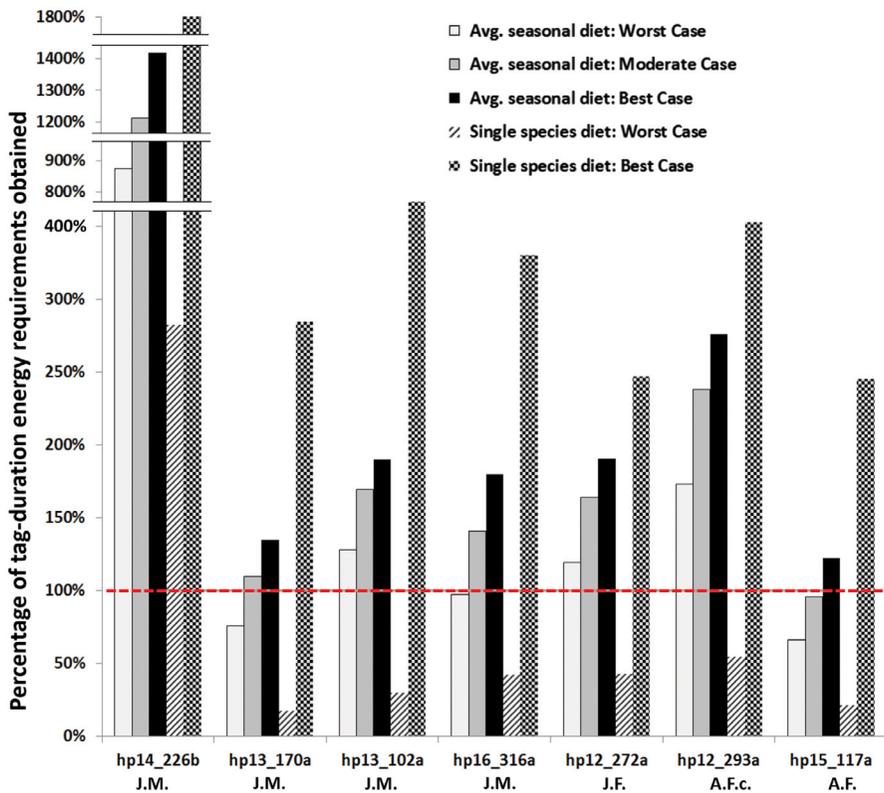
FIGURE 3 Best and worst case scenarios of obtained metabolizable energy for each of the tagged harbor porpoises relative to their estimated energy requirements over the tag duration (from Rojano-Doñate et al., 2018). Note the broken *y*-axis. The red dashed line shows the 100% energy requirement for each individual over the tag duration. J.M. = juvenile male; J.F. = juvenile female; A.F.c = adult female with calf; A.F. = adult female (no calf).

this study are built primarily on three previous studies; on the foraging behavior and energy requirements of seven tagged harbor porpoises. The animals tagged represent a very small sample size from which to draw conclusions.

Porpoises have been described to exist on an "energetic knife-edge" (e.g., Wisniewska et al., 2016) due to their life strategy. The estimates presented in this study indicate how inclusion of prey quality (specifically prey size distribution and energetic density) can meaningfully advance this research area. Critical, here, is the consideration of prey species, target size, and energy content when assessing how a species exists in its ecological niche. Ultra-high foraging rates can translate into ultra-high energetic intake when the energy density of potential prey species are considered. The range of metabolizable energy intake estimates generated in this study (Figure 2 and Figure 3) indicate a very broad range of plausible outcomes for the foraging observed in the tagged porpoises. However, the majority of case studies generating energy intake estimates >100% of energy requirements. Only under a worst-case scenario, were the tagged harbor porpoises predicted to only capture a small portion of their daily energy requirements. Such animals would indeed be vulnerable to disturbance via missed foraging opportunities. However, the worst case chosen is an extreme in which individuals are poor foragers (with low digestive efficiency) and with access only to atypical single species diet.

Some specific data sets do give further pause for thought. Animal hp14_226b, a juvenile male, was an outlier, with very high *ME* estimates, driven primarily by the animal targeting larger prey items (~47% of items >5 cm in length) and to a lesser extent, relatively high foraging rates (153 hr^{-1}) (from Wisniewska et al., 2016). Obviously it is possible that target prey size was overestimated. If the animal was feeding on the lowest energy prey available (or on a species not considered in this analysis) the ME values might fall back into the normal range for the other six

animals. Given the cube relationship between size and mass (i.e., size and energetic content) (Figure 1) overestimating the size of the prey would generate such high values of *ME*. It is also possible that the DTAG recorded buzzes from other porpoises in close proximity to the tagged animals (Stimpert et al., 2014). Animal hp13_170a exhibited low *ME* values but was only tagged during the day. The low buzz rate (60 hr^{-1}) may not have captured the peak foraging for that individual, as tagged animals in inner Danish waters appeared to increase foraging during the night (Wisniewska et al., 2018b) (discussed further below). Equally capture success rates may be overestimated. No other foraging success data exist for harbor porpoises by which to make more detailed comparisons. The intake estimates in this study are comparable with those for captive studies (both juvenile and adults: not adjusted for assimilation efficiency), which range between 646 and 1,304 kJ hr^{-1} (Rojano-Doñate et al., 2018); 333 and 1,042 kJ hr^{-1} (Kastelein et al., 1997); 681 and 1,479 kJ hr^{-1} (Lockyer, Desportes, Hansen, Labberté, & Siebert, 2003), and 375 and 1,083 kJ hr^{-1} (Kastelein, Helder-Hoek, & Jennings, 2018) (all estimates scaled to hours from daily estimates). The *ME* estimates in this stage mostly range from 323 to 996 kJ hr^{-1} in juveniles (hp14_226b was much higher), 921 to 1,350 kJ hr^{-1} for an adult with no calf (but potentially pregnant), and 1,795 to 2,452 kJ hr^{-1} for the female with a calf. Therefore the ME estimates in this study are in line with captive studies on harbor porpoises.

In the wild, it is likely that harbor porpoises are equipped to survive short periods (e.g., ~12 or more hours) with little energy intake. As generalists they exploit productive patches and the corollary to this is that they must also encounter less productive regions. Tagged animals were observed to forage more during periods of darkness (Wisniewska et al., 2016, 2018a, 2018b). It is implicit in this observation that harbor porpoises endure periods of 10–12 hr where foraging effort is greatly reduced (e.g., see Figure 2 in Wisniewska et al., 2016). The implication here is that the feeding overnight sustains the periods of nonfeeding behavior. Such behavior may reflect travel between foraging patches, periods of reduced activity to allow digestion of prey or a preference for foraging more during the night, when prey might be easier to catch. Kastelein et al. (2019) indicated that captive porpoises have a large extensible forestomach and, following a fasting period, are capable of ingesting >90% of their energy requirements (i.e., ~12–20 MJ) in a 1-hr period and were able to feed again shortly afterwards. How well this observation translates into free-living porpoises is not clear, but it is likely that food is less readily available in the wild than in captivity. In the specific context of disturbance, it is important to note that the location of tagged animals featured a high density of vessel traffic and offshore wind farm developments. These animals are likely to be regularly exposed to a range of anthropogenic noise sources, for example, see Figure S1 in Wisniewska et al. (2018b) and the data, therefore, reflect the foraging behavior, energy expenditure, and energy intake estimates in this study in an already perturbed environment.

Periodic "over-feeding" or *hyperphagia* has been established to be a key part of the lifestyle of a range of taxa. These include fish (e.g., Jobling & Johansen, 1999), reptiles (e.g., Castoe et al., 2013), birds (e.g., Guillemette, Richman, Portugal, & Butler, 2012) and both terrestrial (e.g., Wu & Storey, 2016) and marine mammals (e.g., Goldbogen & Madsen, 2018). It is also a strategy employed periodically by any predator with variable prey (e.g., migrating birds, hibernating mammals, central place foragers; e.g., Barnard & Brown, 1987). It has long been hypothesized that long-term energy intake over weeks to months is well-matched with energy expenditure (Kennedy, 1953). DTAG deployments provide a brief (hours), but important, snapshot of foraging behavior. Potentially they could capture periods of hyperphagia, but conversely, they may capture periods where expenditure cannot be balanced by intake. Therefore, hyperphagia is either indicative of some compensatory behavior or of some degree of building up reserves to support the animal between prey-dense patches. Harbor porpoises are known to exploit prey-rich patches over the short-term before engaging in larger scale movements over longer periods (Nielsen et al., 2018; Read & Westgate, 1997). Such a phenomenon could explain the extreme excesses in short-term energy intake relative to predicted expenditure in some cases (Figure 3).

Another possibility is that energy expenditure is underestimated. Tidal volume is increased following exercise (Fahlman et al., 2016; Ridgway, Scronce, & Kanwisher, 1969) and wild animals are considered to be exercising more than captive subjects (which were used to calibrate the respiration rates of wild animals in Rojano-Doñate et al., 2018). Consequently, the existing estimates of FMR for the tagged porpoises represent underestimates for foraging (and likely active) porpoises. If that is the case, the estimates of energy requirements obtained in Figure 3 would be reduced, but not sufficiently to change the conclusions of this analysis. Rojano-Doñate et al. (2018) highlighted the

FMR estimates from free-ranging porpoises indicated that porpoises required a minimum of 15 kJ of energy intake per minute. In over two thirds of the scenarios considered in this study, this minimum threshold was exceeded. The analyses presented here are for porpoises in inner Danish waters and therefore energy intake estimates may be different in other areas where other prey (with different energy content) are available.

The harbor porpoise diet suggests the species to be a generalist, with a wide range of prey available to the species (as observed in Andreasen et al., 2017; Santos & Pierce, 2003; Santos et al., 2004). Stomach contents data from Andreasen et al. (2017) suggest porpoises typically feed on larger prey than identified in acoustic targets by Wisniewska et al.(2016, 2018a), which might indicate the estimates of ME presented in this study could be underestimates. The assessment of viable prey types (upon which energetic calculations are based) is from stomach contents analysis of 339 harbor porpoises. Andreasen et al. (2017) corrected for residence time of stomach contents in their analyses and, therefore, they can be considered a robust assessment of the likely prey size targeted by porpoises in the region. However, the stomachs were collected between 1980 and 2011 and represent a generalist species diet over an extended period, but one that falls outside the tagging period, which may not be indicative of recent foraging trends in Kattegat harbor porpoises. One cannot rule out that the tagged animals were feeding on a species not documented or considered here and a number of studies have questioned the value of data derived from bycaught or stranded animals (e.g., Leopold, 2015; Ross et al., 2016).

One of the biggest sensitivities in this study are the estimates of the energy obtained per fish, which is driven primarily by fish length and to a lesser extent, the energetic content of prey. The assessment of the size of prey targets from Wisniewska et al. (2016) was limited to a subset of the animals tagged (0.9%–1.6% of available prey capture attempts in juveniles and 2.2% in adults) and thus potentially a large source of error in derived energy intake in this study. In the generation of prey length estimates, the tailbeat frequency of return echoes (converted to muscle contraction time) was used based on the previous analysis by Wardle (1975). This approach is sensitive to the values chosen for maximum swimming velocity, maximum stride length and the precision with which tailbeat frequency is measured. An example is presented in Wisniewska et al. (2016) for a fish of "body length <5 cm" (fig. 4D). This is derived from the values for maximum stride length of 0.8, maximum swimming velocity of 1.4 m/s, and tailbeat frequency of 36 Hz (measured from the echoes recorded on DTAGs) integrated using the equation from Wardle (1975). Repeating this analysis it can be determined that the fish length estimate in this example is 4.9 cm. Wardle and Videler (1980) provide a review of cases where observations show that fish species frequently exceed the theoretical maximum suggested in the earlier study (Wardle, 1975). Maximum stride length ranges between 0.6 and 0.8 (based on available empirical measures; Wardle, 1975), but using the lower stride length value suggests prey target size of 6.5 cm (an increase of 1.6 cm from the original estimate). Videler and Wardle (1991) indicate that strides lengths are low when fish are accelerating and so a value of 0.6 may be more appropriate for a prey item fleeing a predator over a short time period. The only prey species with a published stride length considered here is the Atlantic cod (0.6–0.62) (Videler & Wardle, 1991) and maximum burst swimming speeds (as would be observed during a predation event) are available for species such as herring (4.6 m/s), whiting (2.2 m/s) and Atlantic cod (1.9 m/s) (read from fig. 4 in He, 1993). Use of these swimming speeds in the prey size estimation (using the default of stride length of 0.8, tailbeat 36 Hz) would result in fish length estimates of 16.1 cm for herring (corresponding to an additional 67 kJ per fish) and 7.7 cm for whiting (an additional 11.8 kJ per fish). Use of the stride length and maximum burst velocity for cod (from the studies above) leads to an estimated fish target length of 8.9 cm (an additional 16.8 kJ per fish). In addition, even a small shift to larger prey can result in a significant increase in energy obtained, for example, from a 4 cm sandeel spp. (0.54 kJ) to a 5 cm sandeel spp. (1.14 kJ) represents a doubling of energy to the animal. When considering that tagged animals were observed making peak foraging attempts of between 200 and 500 hr^{-1}, such differences are critical in assessing the vulnerability of harbor porpoise as a species. We cannot say here if fish length estimates used are systematically underestimated, but if that is the case, then the estimates of metabolizable energy intake for each individual could be considered conservative (and size estimates would also better match estimates derived from stomach contents analyses). The intention here is to specifically highlight some of the sensitivities in this approach and the consequences for estimating energy—that is, the type and size of prey are critical to modeling energetic calculations and assessments of vulnerability. The studies by Rojano-Doñate et al. (2018), Wisniewska et al. (2016), and Wisniewska et al. (2018b) represent novel and exciting approaches to using acoustic tag data for studying

eco-physiology. Understanding the prey environment (and its quality) for harbor porpoises and other marine mammal species remains an important topic for which further field research is required. A greater knowledge of the abundance, distribution of harbor porpoise prey, their movements, and variations in porpoise metabolic costs is required to understand the ecology of this species and their susceptibility to perturbation.

3.4 | Conclusions

A holistic approach has been taken to understanding the energy balance for harbor porpoises. The results indicate a broad range of plausible levels of energy intake for tagged harbor porpoises indicating that these animals, in all but the worst case scenarios, are capable of exploiting the ecological niche into which they have evolved. This reflects their generalist diet and ultra-high foraging rates. These results may also inform the species susceptibility to disturbance and the drivers of capacity to cope with disrupted foraging (either via environmental variability or if caused by noise disturbance). Minimizing disturbances is important as other pathways may affect animal health but this study highlights porpoises may have some elasticity in recovering following short lost foraging opportunities (or the local absence of suitable prey), like any patch forager. Robust assessments of vulnerability to disturbance require consideration of the prey energy content and the size of prey being targeted as these are critical drivers of energy balance. Furthermore, an appreciation of the abundance, distribution and quality of prey is critical to understanding species ecology and the potential effects of disturbance.

AUTHOR CONTRIBUTIONS

Booth carried out all reviews, analysis, and writing in this manuscript.

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