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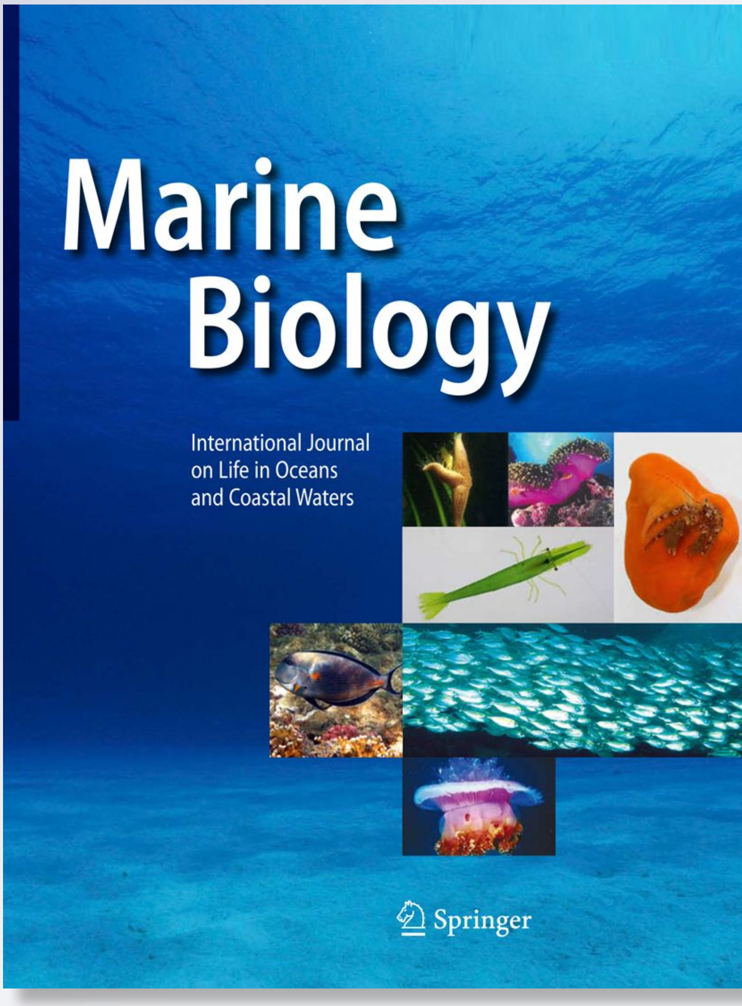

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ORIGINAL PAPER

Correlation between the seasonal distribution of harbour porpoises and their prey in the Sound, Baltic Sea

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Abstract Low densities of harbour porpoises in winter (November–March) and high densities in summer (April–October) were found in the Sound, connecting the Baltic Sea and Kattegat. Due to their high energy requirements, it is hypothesized that the density of harbour porpoises is related to local prey abundance. This was tested by examining the stomach content of 53 harbour porpoises collected between 1987 and 2010 in the Sound (high season, 34 porpoises; low season, 19 porpoises). A total of 1,442 individual fish specimens from thirteen species were identified. Twelve of these were present in the high–porpoise density season and seven in the low-density season. The distribution of occurrence and the distribution of number of fish species were different between seasons, indicating a shift in prey intake between seasons. Furthermore, during the high-density season, the mean and total prey weight per stomach as well as the prey species diversity was higher. However, no difference was found in the number of prey species between the two seasons, indicating a higher quality of prey in the high-density season. Atlantic cod was found to be the main prey species in terms of weight in the high-density season while Atlantic herring and Atlantic cod were equally important during the low-density season. Prey availability and predictability are suggested as the main drivers for harbour porpoise distribution, and this could be caused by the formation of frontal zones in spring in the northern part of the Sound, leading to prey concentrations in predictable areas.

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Introduction

Kattegat, Belt Seas, the Sound and the western Baltic are inhabited by a genetically distinct population of about 10,865 (CV = 0.32, 95% CI = 5,840–20,214) harbour porpoises *Phocoena phocoena* (SCANS-II 2008; Sveegaard 2011; Wiemann et al. 2010) (Fig. 1). Over the last two decades, our knowledge of its distribution has greatly improved due to the development of novel and application of well-established methods such as visual surveys from boat and plane (Hammond et al. 2002; Heide-Jørgensen et al. 1992, 1993; SCANS-II 2008), detections of incidental sightings and strandings (Kinze et al. 2003; Scheidat et al. 2006), passive acoustic monitoring (Kyhn et al. 2008; Verfuss et al. 2007), acoustic surveys (SCANS-II 2008;

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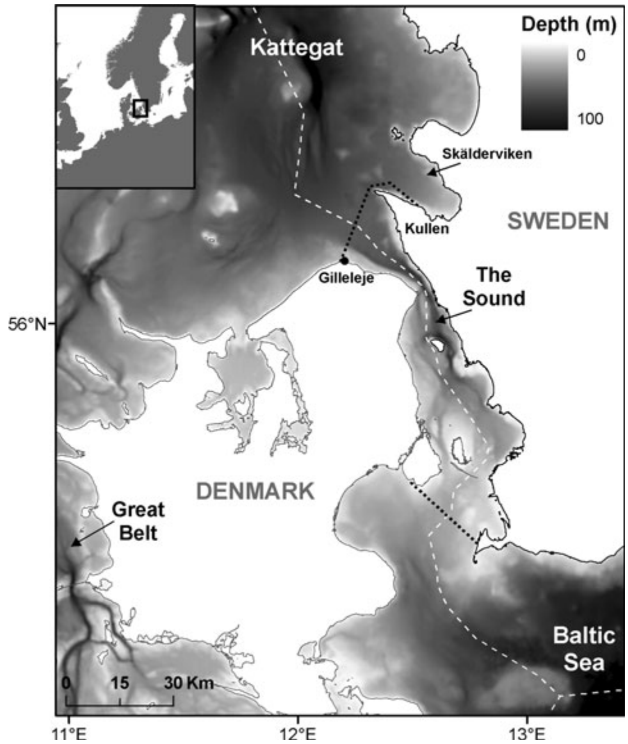

Fig. 1 Bathymetry map of the Sound and adjacent waters. The *black dashed lines* indicate the study area within which all harbour porpoise stomach samples were collected. The *white dashed line* indicates the exclusive economic zone (EEZ national borders)

Sveegaard et al. 2011b) and satellite tracking (Sveegaard et al. 2011a; Teilmann et al. 2007). These studies have shown that harbour porpoises within this region are not evenly distributed but aggregate in certain high-density areas, mainly in the narrow straits of Little Belt, Great Belt, the Sound and Fehmarn Belt. Furthermore, it has been found that the distribution changes over the year with harbour porpoises moving south in the winter. This change is not a coordinated migration but a gradual net movement of the population resulting in a very low winter abundance in some of the northern areas where summer density is high, for example the Sound and Kattegat (Sveegaard et al. 2011a, 2011b).

The environmental or biological factors governing harbour porpoise distribution are not well understood. However, as the harbour porpoise is one of the smallest cetaceans inhabiting a temperate environment, a high daily consumption rate must be achieved to maintain energy requirements (Koopman 1998; Lockyer and Kinze 2003; Lockyer 2007). The distribution of harbour porpoises is therefore expected to follow the distribution of its main prey species (Koopman 1998; Santos et al. 2004). In support of this, the harbour porpoise distribution has been found to correlate with the abundance of Atlantic herring (*Clupea harengus*) in Kattegat and Skagerrak (Sveegaard 2011) as well as environmental variables such as bathymetry, sediment type and temperature that are believed to affect the presence of prey (Bailey and Thompson 2009; Edrén et al. 2010; Embling et al. 2010; Marubini et al. 2009).

Although harbour porpoises consume a wide selection of prey species, analysis of stomach content suggests that preferences for certain prey species do exist (Santos et al. 2004). In the waters between the eastern North Sea (along the Danish west coast) and the western Baltic Sea, major prey species include Atlantic herring, sprat (*Sprattus sprattus*), Atlantic cod (*Gadus morhua*), whiting (*Merlangius merlangus*), gobies (Gobiidae) and sandeels (Ammodytidae) (Aarefjord et al. 1995; Benke et al. 1998; Börjesson et al. 2003). The relative importance of these species to harbour porpoise varies between regions (Benke et al. 1998; Santos and Pierce 2003) and possibly over time, but little is known about changes in diet on a smaller spatial and temporal scale and how these changes may affect porpoise movements and distribution.

The Sound is a narrow strait connecting the Baltic Sea and Kattegat (Fig. 1). In this strait, thirteen years of harbour porpoise satellite tracking ($n = 62$, 1997–2010) (Sveegaard et al. 2011a) as well as acoustic surveys throughout the year (2007) (Sveegaard et al. 2011b) has illustrated harbour porpoise presence to vary seasonally with considerably higher densities in the spring and summer (April–October, 7 month) as compared to autumn and winter (November–March, 5 month). Due to the constant high-energy requirement of harbour porpoises, we hypothesize that this seasonal variation is related to a shift in food quantity and/or quality. In this study, we examine this theory by analysing the stomach content of stranded and bycaught harbour porpoises in the Sound across the year, focussing on the differences between the two seasons with high and low porpoise density, respectively.

Methods

Study area

The Sound (ICES Subdivision 23) is a transition zone between the brackish water from the Baltic Sea and the more saline water from Skagerrak/Kattegat (Jakobsen 1980). The Sound is about 100 km long, 5–25 km wide and has a maximum depth of 40 m. Its southern border is defined by the Drogden sill with shallow waters of approximately 7–8 m depth (Jakobsen and Castejon 1995). The northern boundary is defined as a straight line between Gilleleje, Denmark and the northern tip of Kullen, Sweden. In this study, we included the north-western part of Skälderviken in order to increase sample size as satellite tracking has shown this part of Skälderviken to be part of the porpoise

Table 1 Summary of sampled harbour porpoises in each year by season (high: Apr–Oct, low: Nov–Mar), sex, size class (L: length of porpoise) and cause of death

Year	*n*	By season		By sex		By size		By cause of death		Unknown
		High	Low	F	M	A (L ≤120 cm)	B (L >120 cm)	Bycatch	Stranded	
1987	5		5	3	2	3	2	5		
1988	9	3	6	5	4	2	7	2		7
1989	5	4	1	3	2	2	3	1		4
1990	3	2	1	2	1		3	3		
1991	1		1		1	1			1	
1996	1		1	1		1		1		
1997	3	1	2		3	2	1	2	1	
1998	4	2	2		4	3	1	4		
2000	4	2	2	3	1	2	2	3	1	
2009	2	2		1	1	1	1	1	1	
2010	16	3	13	4	12	10	6	16		
	53	19	34	22	31	27	26	38	4	11

foraging area in the northern Sound (Sveegaard et al. 2011a). The Sound is subjected to heavy ship traffic, with about 59,000 vessels passing in 2008 (~70% of the traffic between Kattegat and the Baltic Sea; www.helcom.fi). Due to ship safety, the use of trawl or any type of towed fishing device has been banned in the Sound since 1932 (Svedang 2010). This makes the Sound unique to any other part of the adjacent seas by providing an environment of undisturbed benthic flora and fauna, which allows for rich and varied fish populations (Svedang 2010).

Porpoise diet

Fifty-three harbour porpoise stomachs (22 females, 31 males; mean length, 120 ± 16 cm; range, 91–170 cm) were sampled within the Sound between 1987 and 2010. Of these, 38 were incidentally bycaught in fishing gear, four were found stranded and eleven were of unknown origin, that is, either stranded or bycaught (Table 1).

The porpoise stomach samples were not distributed evenly throughout the year, but peaked in April with 18 samples (Fig. 2). According to local fishermen, harbour porpoises are more frequently incidentally bycaught during this particular month due to the extensive use of large-masked fishing nets for lumpsucker (*Cyclopterus lumpus*).

The method of analysis was similar for all stomachs and follow the description in Aarefjord et al. (1995): First, the stomach and the lower part of the oesophagus were rinsed with running water and the content separated through a stable of sieves with mesh sizes of 2, 1 and 0.5 mm, respectively. Retained whole or partly digested prey items, fish bones and otoliths were counted, identified and measured. The number of prey consumed by each porpoise was then calculated by summing the number of intact prey items and

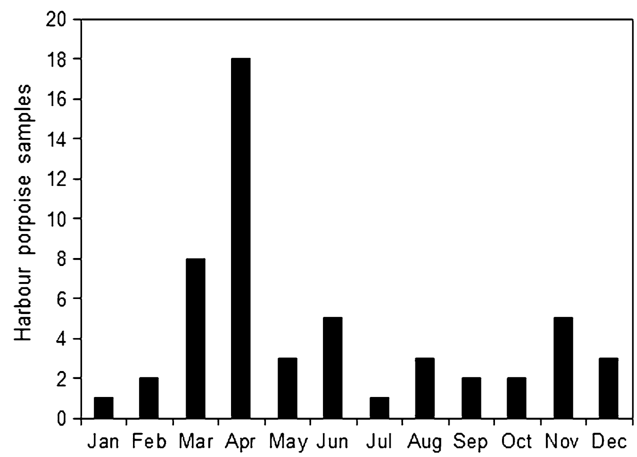

Fig. 2 Monthly distribution of stomach samples from bycaught or stranded harbour porpoises in the Sound 1987–2010

the number of prey estimated from remains for each species. For fish, this was estimated as the number of otoliths divided by two.

The weight of each fish was estimated from the measured length and width of otoliths according to the regressions by Härkönen (1986). Although other fish size/otolith size relationships are available, Härkönen (1986) was chosen because it is based on data collected in close proximity of the Sound (Skagerrak and Kattegat). Some otoliths were degraded to an extent only allowing identification to family level: for fish weight estimations of *Clupeidae* spp. and *Gadidae* spp., an average weight of all measured species within each family was estimated: separately for the high- and low-density period. For gobies (*Gobiidae* spp.) and sandeel (*Ammodytidae* ssp.), regressions from *Pomatoschistus minutus* and *Ammodytes marinus* were used, respectively. Regarding fish length estimates, however, Leopold

(2001) was used rather than Härkönen (1986) because the latter provided an insufficient otolith size range for some species.

The harbour porpoise stomachs were collected over two intervals, 1987–2000 ($n = 35$) and 2009–2010 ($n = 18$) (Table 1). If a shift had occurred in prey preferences of harbour porpoises between these periods, it could potentially have biased the results. Consequently, the two groups of porpoises (1987–2000 and 2009–2010) were tested using a Student's *t* test for differences in the number of species within each stomach, the total weight of prey within each stomach and the total number of fish within each stomach. Prior to analysis, the data were tested for equality of variance (Levene's test for equality of variance) to meet the assumptions of *t* tests.

The harbour porpoise stomach samples were assigned to either the low-density (November–March) or the high-density months (April–October) according to the porpoise density in the Sound. The two groups were analysed for differences in sex ratios, mean porpoise length and the total prey mass per stomach.

The data were tested for an overall correlation between porpoise length and the mean prey length consumed. To further examine the potential influence of porpoise size and choice of prey, the 53 porpoises were grouped into young porpoises of less than two years of age with length ≤120 cm (group A, $n = 27$) and porpoises older than two years with length >120 cm (group B, $n = 26$). To obtain homogeneity in variance, the data were rank-transformed and a two-way ANOVA used to conduct a multivariate comparison between total prey weight per stomach in high and low seasons in relation to size groups A and B.

Three measures of prey importance were calculated (as defined by Börjesson et al. 2003): (1) the percentage frequency of occurrence, %O (the number of stomachs found to contain a particular prey species divided by the total number of stomachs with identifiable remains, multiplied by 100), (2) the percentage by numbers, %N (the number of individuals of the particular prey species divided by the total number of prey individuals found, multiplied by 100) and (3) the percentage by mass of each species, %W (the total weight of the particular prey species divided by the total weight of all prey species, multiplied by 100). These measurements were calculated for the period of high and low harbour porpoise density. For between-season comparison of distribution of %O, %N and %W, we used Kendall's coefficient of concordance (Siegel 1957). This is a nonparametric statistic test that does not assume normal distributed data and may be used for assessing agreement among probability distributions. Comparison of number of prey per stomach was tested using a Mann–Whitney *U* test.

Species richness and Simpson's reciprocal diversity index (InvD) (Magurran 1988, Simpson 1949) was calculated for each stomach, and the results were compared between high and low seasons. Species richness is the number of species present within each stomach. Simpson's diversity index provide additional information about community composition as it includes evenness (frequency of species) as well as species richness in the calculations. Simpson's reciprocal diversity index is calculated as: $\mathrm{InvD} = 1/(\sum(n/N)^2)$, where n is the total number of organisms of a particular species and N is the total number of organisms of all species. In this form (also named Hill's N2), the unit is 'species' and is interpreted as the number of equally frequent species necessary to obtain the diversity observed in the sample in focus (Krebs 1999).

Results

Porpoise diet

The comparison of the two sampling periods (1987–2000 and 2009–2010) showed no significant differences in the number of species, the total weight of prey and the total number of fish within each porpoise stomach (Table 2), and the two groups were consequently pooled in the subsequent analyses.

The dividing of stomach samples in high-density (April–October) and low-density season (November–March) resulted in 34 samples in the high-density season and 19 samples in the low-density month. Sex ratios and body lengths of the porpoises in the high and the low seasons, respectively, were not statistically different (Table 2). The multivariate comparison showed that porpoise group A (≤120 cm) did not consume smaller prey items than

Table 2 Summary statistics results for harbour porpoise sample comparisons

	Parameters	Test	Test value	*P*
1987–2000 ($n = 35$) versus 2009–2010 ($n = 18$)	Number of prey species within each stomach	Student's *t* test	$t_{51} = 1.466$	0.149
	Total weight of prey	Student's *t* test	$t_{50.2} = 1.387$	0.171
	Total number of prey	Student's *t* test	$t_{51} = 0.553$	0.590
Low-density months (Nov–Mar, $n = 19$) versus high-density months (Apr–Oct, $n = 34$)	Differences in sex ratios	Fisher's exact test		0.570
	Lengths of porpoises	Student's *t* test	$t_{30} = 1.829$	0.077

porpoise group B (>120 cm) in any season (two-way ANOVA, $F_{1, 49} = 1.013$, $P = 0.319$), but the porpoises in the high-density season consumed larger total prey mass per porpoise than porpoises in the low-density season (two-way ANOVA, $F_{1, 49} = 5.225$, $P = 0.027$). Also, we found no correlation between length of the porpoise and the mean length of prey it had consumed across all samples (Linear regression, $F_{1,51} = 0.151$, $P = 0.669$). Hence, the influence of porpoise sex and length on choice of prey is not further considered in the analysis.

The 53 stomachs analysed contained fish remains of a total of 1,442 individual fish representing eight families and thirteen species. The longest fish eaten was a European eel, *Anguilla anguilla*, 59 cm long and undigested in the stomach of a 138-cm-long female porpoise. The mean fish length was 16.6 ± 9.0 cm across all samples. We found a significant difference in mean fish length between seasons (Fig. 3; Table 3), and when testing the individual species separately, Atlantic cod was significantly longer in the high-density season (Student's *t* test, mean length, $t_{19}=3.567$,

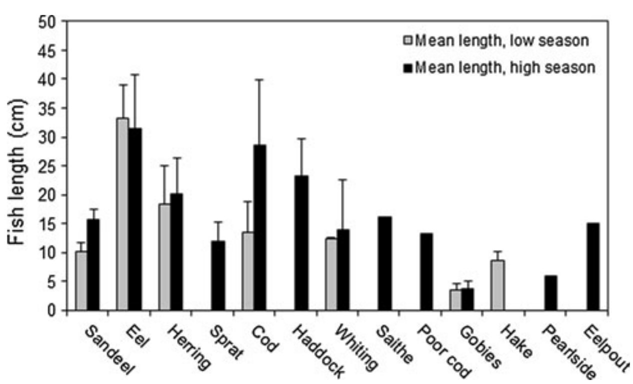

Fig. 3 Mean length of individual fish species per stomach found in harbour porpoises in high (Apr–Oct, $N_{fish} = 458$) and low (Nov–Mar, $N_{fish} = 984$) seasons in the Sound. *Error bars* represent standard deviation of mean fish length. Species include sandeel ($n = 30$), eel ($n = 17$), herring ($n = 118$), sprat ($n = 42$), cod ($n = 81$), haddock (Melanogrammus aeglefinus, $n = 8$), whiting ($n = 35$), saithe (*Pollachius virens*, $n = 1$), poor cod (*Trisopterus minutus*, $n = 1$), gobies ($n = 1034$), hake (*Merluccius merluccius*, $n = 3$), pearlside (*Maurolicus muelleri*, $n = 1$) and eelpout (*Zoarces viviparous*, $n = 7$). Otoliths not identified on species level are excluded (family level or unidentified, $n = 64$)

$P = 0.002$). The total prey mass per stomach was significantly larger in the high season (mean, 1,518.8 ± 357.2 g) than in the low season (mean, 430.9 ± 122.6), but the number of prey species per stomach did not differ between seasons (Table 3), indicating that individual prey size was larger in the high season.

In terms of occurrence, herring, cod and gobies dominated as prey in both high and low seasons (30–44%) (Fig. 4a). No difference was found between seasons in the frequency of occurrence for the individual species, but the distribution of occurrence across fish species differed between high- and low-density seasons (Table 3). The latter was due especially to contributions from sandeel, sprat and a range of gadoids.

Regarding the numerical occurrence (%N), we found that the distribution across fish species differed significantly between high and low seasons (Table 3); (Fig. 4b). Particularly more gobies are consumed during the low season compared to the high season, whereas sandeel, herring, sprat and gadoids (especially cod and whiting) are consumed more frequently in the high season.

For weight (%W) of the consumed species, the most noticeable difference was the equal importance of cod in both seasons while herring was only important in the low-density season (Fig. 4c). As opposed to %O and %N, the distribution of fish weight across species did not differ significantly between high and low seasons (Table 3). This suggests that it is the same prey species that contribute to the majority of prey weight found in the porpoise stomachs in both seasons.

Overall, herring and cod are the most important prey species in terms of occurrence and weight and may therefore potentially influence the spatio-temporal distribution of harbour porpoises. Consequently, the length distribution of these two species was further analysed for both seasons (Fig. 5). There was no apparent difference between the length distributions in the two seasons for herring, but the majority of cod was <20 cm long in the low season and >30 cm long in the high season.

The porpoise diet contained more species in the high-density season compared to the low-density season. Of the

Table 3 Summary statistics for comparison of consumed prey of porpoises between low-density months (Nov–Mar, $n = 19$) and high-density months (Apr–Oct, $n = 34$)

Test parameters	Test	Test value	P
Mean prey length per stomach	Student's *t* test	$t_{48.5} = 3.452$	**0.001**
Total prey weight per stomach	Student's *t* test	$t_{40.2} = 2.875$	**0.006**
Number of prey per stomach	Mann–Whitney *U* test	U = 338.5	0.773
Distribution of O%	Kendall's coefficient of concordance		**0.029**
Distribution of N%	Kendall's coefficient of concordance		**0.029**
Distribution of W%	Kendall's coefficient of concordance		0.134
Simpson's reciprocal diversity index	Student's *t* test	$t_{49.1} = 2.724$	**0.009**
Species richness	Student's *t* test	$t_{48.6} = 1.942$	0.058

Significant *P* values ($\alpha < 0.05$) are marked in *bold*

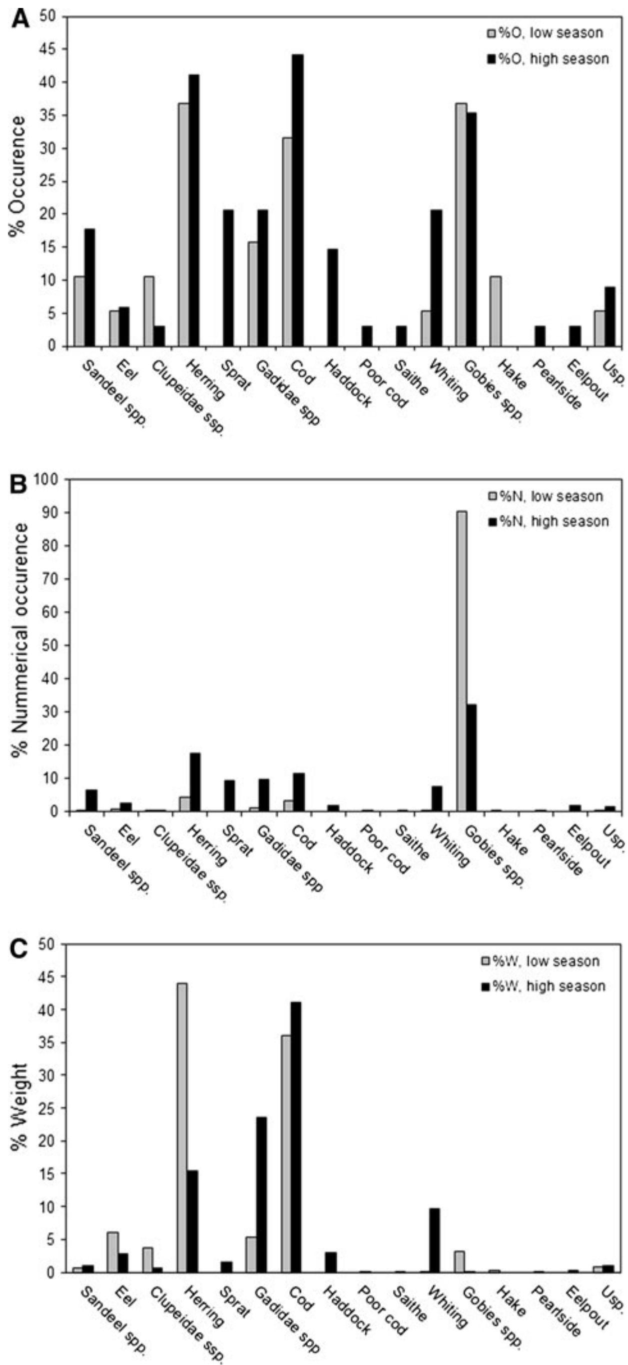

Fig. 4 Distribution of **a** frequency of occurrence, **b** percentage by numbers and **c** percentage by mass of each fish species in stomachs of harbour porpoises in high-density (Apr–Oct, $n_{fish} = 458$) and low-density (Nov–Mar, $n_{fish} = 984$) seasons, respectively. *Sandeel* spp., *Clupeidae* spp., *Gadidae* spp. and *Gobies* spp. refer to unidentified species of each family. Usp. denotes unspecified fish species. For scientific names of species, see Fig. 3 and text

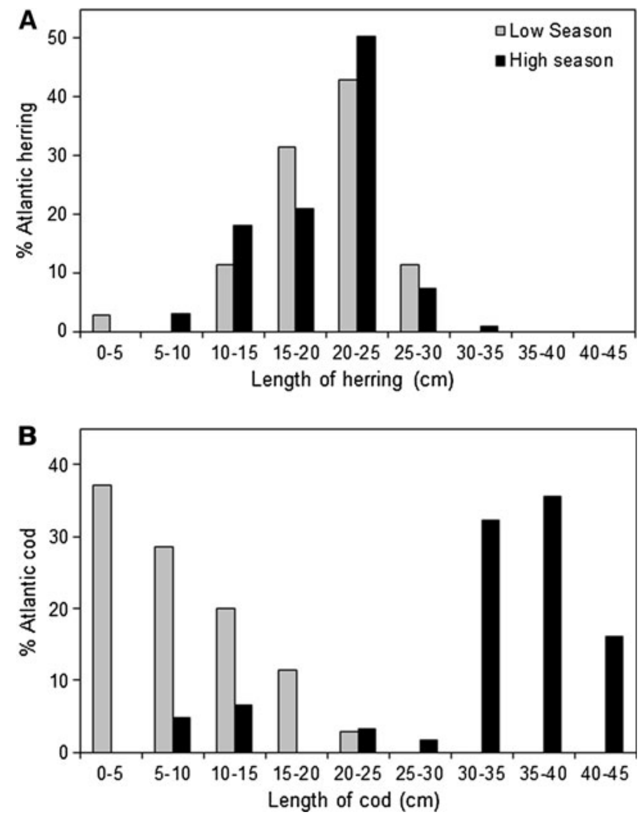

Fig. 5 Length distribution of **a** herring and **b** cod consumed by harbour porpoise (across stomachs) in the Sound divided in high-density (Apr–Oct, $n_{herring} = 79$, $n_{cod} = 52$) and low-density (Nov–Mar, $n_{herring} = 39$, $n_{cod} = 29$) harbour porpoise density period

13 species found, 12 were present in the summer and 7 in the winter. Furthermore, in the low-density season, 47% of all porpoises had consumed only one prey species and the maximum number of species found in a stomach was three. In the high-density season, 32% had consumed one species while 35% had consumed 3–5 species. The mean Simpson's reciprocal diversity index—obtained for the prey community of each porpoise stomach—was significantly higher in the high season (InvD = 1.71 ± 0.11) than in the low season (InvD = 1.29 ± 0.10) (Table 3). Since Simpson's reciprocal diversity index includes evenness (frequency of species) as well as species richness in the calculations, higher index values represent generally more varied diet and not merely that a few individuals of a new species are included. We found a marginally significant difference between the two seasons in species richness (Table 3). Consequently, the increase in Simpson diversity index in high season is mainly caused by a higher frequency of species in prey intake.

Discussion

Harbour porpoise density in the Sound varies across the year with high densities during summer (April to October) and low densities during winter (November–March). When comparing the consumed prey of harbour porpoise stomach samples from the winter season with samples from the summer, we found both quantitative and qualitative differences in consumed prey, which may explain the observed seasonal difference in harbour porpoise presence. In the high season, mean and total prey weight per stomach was larger, the distribution of occurrence and number of fish species were different, and a higher diversity of prey species was found compared to the low season. Furthermore, cod was found to be the main prey species in terms of weight in the high season, while herring and cod were the main prey species in the low season. No difference was found in the number of prey species between the two seasons, but the relative distribution of numbers was different. That the number of fish individuals did not differ between seasons, as opposed to the mean prey weight per stomach, indicates that the quality, that is, weight of prey, is enhanced in the high season.

Cod, herring and gobies were the most frequently occurring species in both seasons, whereas sprat, whiting, haddock and sandeel mainly or only occurred in the high season. Overall, cod was found to be the most important prey species in the high season in terms of both occurrence and prey mass. Furthermore, although the occurrence of cod was high all year, we found a significant difference in the size of cod in the high and the low seasons, with cod being longer in the high-density season and shorter in the low-density season. Cod is an important commercial species, which has caused several stocks to the point of extinction (Cardinale and Svedang 2004). However, the Sound includes a demographically separate cod subpopulation (Angantyr et al. 2007; Cardinale and Svedang 2004), which are more abundant and have higher age diversity than cod in the adjacent Kattegat (Svedang 2010). This may be an important factor influencing the presence of porpoise in the Sound.

Herring was an important prey source in the winter, but not in the summer. This corresponds well with the fact that the southern part of the Sound constitutes an important autumn and winter habitat for the Rügen spring-spawning herring stock, and in this period (September to February), the abundance of herring may be up to three times greater than in the rest of the year (Nielsen et al. 2001). It is unknown why this large aggregation of herring does not attract more porpoises to the Sound in the winter, but perhaps the herring are less available due to a seasonal change in behaviour. In the summer, herring occupy large foraging areas, whereas the main driver for overwintering herring is predator avoidance and energy conservation (Huse and Ona 1996). In Norwegian waters, herring do so by schooling and moving to deeper waters (>400 m) during the day. The Sound is much shallower, and although the overwintering herring display similar schooling behaviour (Nielsen et al. 2001), the effect of seasonal herring behaviour on harbour porpoise distribution needs further research.

Gobies constitute a major prey group in terms of occurrence and number of individual fish, however, not in terms of weight. The Sound has been found to hold several species of gobies in large quantities (e.g. two-spotted goby, *Coryphopterus flavescens*, and black goby, *Gobius niger*) (Angantyr et al. 2007). This may suggest gobies to constitute a supplementary 'back up' prey, when larger, more energy-efficient prey species are less available.

The porpoise diet was more varied during high-density season compared to the low-density season. The sample size of 53 stomachs used in this study is comparable to the sample size in other studies in adjacent areas. Aarefjord et al. (1995) also found thirteen species during the examination of forty porpoise stomachs in Kattegat, Lick (1991, 1994, 1995) found eight species in the German Baltic (62 porpoise stomachs), whereas Börjesson et al. (2003) found twenty species in Kattegat and Skagerrak (112 porpoise stomachs). This indicates a decline in species diversity from the North Sea and Skagerrak to the Baltic Sea possibly following the gradient in salinity. Since the Sound is in the southern end of this area, thirteen species are consistent with previous studies. However, our sample size was reduced by the stratification into seasons, and the sample size for the high season is nearly twice as high as during the low season. Börjesson et al. (2003) estimated that approximately 35 stomach samples were the minimum sample size in Skagerrak and Kattegat needed to obtain all prey species with relative frequencies $\geq$10% with 95% confidence. Consequently, our 34 samples from the high-density season are sufficient, but the 19 samples in the low density may result in species being underrepresented or missing. However, as we did not merely test species richness but also species diversity that includes evenness, we advocate that the results are legitimate. This is further supported by the fact that the porpoises in the high-density season had more different species per stomach than in the low-density season. Finally, the low sample size in the winter does not affect the result of a larger prey size in summer and the switch from cod in the summer to herring and small cod in the winter, as cod and herring are both found in relative frequencies $\geq$10%.

Energy density of prey species greatly influences their nutritional value to predators, and it is an established foraging theory that predators should prefer prey that yield more energy than the cost of foraging (Sih and Christensen 2001). Mature herring (25–30 cm) may contain up to twice the energy density ($\sim$10 kJ g^{-1}) of cod of similar size (Lawson et al. 1998, Spitz et al. 2010), indicating that if porpoises had the choice, we would expect herring to be more important than cod in the Sound. However, since energy density of all fish species changes across seasons and for herring with up to 250% (Pedersen and Hislop 2001), it is impossible to calculate an exact total energy budget for the harbour porpoise diet in the Sound. Furthermore, the behaviour of the different fish species may change between seasons, making them more or less available as prey to the porpoises.

A known bias in otolith studies is the faster degradation of small otoliths (e.g. gobies, herring or juvenile cod) compared to larger otoliths (e.g. mature cod), and consequently the estimated weight and length of small fish may tend to be underestimated. Correction for this potential bias was not included in the study because information on otolith degradation was unavailable for some of the early porpoise samples. Regardless, in this study, we compare species with similar-size otoliths in the different seasons, and thus the otolith erosion can be regarded as a constant within species and are therefore of less importance.

Frontal zones have been suggested to affect prey availability for harbour porpoises (Skov and Thomsen 2008) and are correlated with enhanced primary production due to upwelling of nutrients (Pingree et al. 1975), making an area attractive for fish species and consequently for larger marine predators like the harbour porpoise. In the northern part of the Sound, frontal zones are formed each spring due to strong easterly winds generating a water outflow from the Baltic Sea (Cappelen and Jørgensen 1999; Gustafsson 1997; 2000; Jakobsen and Castejon 1995; Nielsen 2005; Pedersen 1993). Consequently, the prey may be more easily available for the porpoises in the spring.

Conclusion

This study found a significant difference in several aspects of diet between high- and low–harbour porpoise density seasons. Prey availability and eventually predictability of prey may be the most important factors driving harbour porpoise distribution. These measures are, however, very difficult to study and could be influenced by many variables in the marine environment.

The combined effect of higher mean weight of prey, higher diversity and the apparently high availability of the primary prey, cod as well as presence of frontal zones during spring is believed to cause the observed shift in seasonal porpoise abundance in the Sound. The low density of harbour porpoises in November–March that corresponds poorly with the high abundance of herring in this season may be caused by lower availability of prey due to a lack of fronts and dense schooling in deeper waters. Our result indicates that porpoise movements may be influenced not only by availability of prey but also by an oceanographic complexity.

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