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Diet composition and food consumption rate of harbor porpoises (*Phocoena phocoena*) in the western Baltic Sea

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ABSTRACT

Stomach content composition and prey-specific consumption rates of juvenile and adult harbor porpoises (*Phocoena phocoena*) were estimated from a data set including 339 stomachs collected over a 32 yr period (1980–2011) in the western Baltic Sea. The stomach contents were mainly hard parts of fish prey and in particular otoliths. The bias originating from differential residence time of otoliths in the stomachs was addressed by use of a recently developed approach. Atlantic cod and herring were the main prey of adults, constituting on average 70% of the diet mass. Juvenile porpoises also frequently consumed gobies. Here, the mass contribution by gobies was on average 25%, which was as much as cod. Other species such as whiting, sprat, eelpout, and sandeels were of minor importance for both juveniles and adults. The diet composition differed between years, quarters, and porpoise acquisition method. Yearly consumption rates for porpoises in the western Baltic Sea were obtained in three scenarios on the daily energy requirements of a porpoise in combination with an estimate including the 95% CLs of the porpoise population size. Cod of age groups 1 and 2 and intermediate-sized herring suffered the highest predation from porpoises.

Key words: Atlantic cod, Baltic Sea, food rations, gobies, harbor porpoise, herring, stomach contents, stomach residence time of otoliths.

The harbor porpoise (*Phocoena phocoena*) is among the most common cetacean species in the Northeast Atlantic, and as such an important top predator and indicator species (Santos and Pierce 2003, Hammond *et al.* 2013). Its prey comprise a wide range of fish including commercially valuable species such as Atlantic cod (*Gadus morhua*) and greater sandeel (*Ammodytes marinus*) (Santos and Pierce 2003, Víkingsson *et al.* 2003, Heide-Jørgensen *et al*. 2011). In the European Union, porpoises hold a high conservation status under several directives and conventions (*e.g.*, Bern and Bonn Convention, Oslo and Paris Convention OSPAR). According to the EU Habitats Directive a favorable conservation status has to be secured, whereas the Marine Strategy Framework Directive (MSFD) (2008/56/EC)[2] requires that Member States achieve (or maintain) a good environmental status (GES) across all European waters in an ecosystem-based approach. Like many marine mammals, porpoises are threatened by anthropogenic activities such as pollution, habitat degradation, underwater noise, incidental bycatch in fisheries, and depletion of prey (*e.g*., Kock and Benke 1996; DeMaster *et al.* 2001; ASCOBANS 2002, 2012; Vinther and Larsen 2004; Siebert *et al.* 2012; Dähne *et al.* 2013). Conflicts between fisheries and porpoises are common, yet the magnitude of the problem is often unknown and difficult to assess (Northridge 1991, DeMaster *et al.* 2001, Bearzi *et al.* 2008, Morissette *et al.* 2012, Santos *et al*. 2014). Knowledge about the diet composition and food consumption rates of harbor porpoises is important for the protection of porpoises and for fisheries management. Ensuring adequate availability of the main prey species through fishing quotas or real-time moratoria helps sustain a healthy porpoise population (ASCOBANS 2012). On the other hand, assessing the predation mortality by porpoises on commercially valuable fish species using multispecies or ecosystem-based models contributes to more accurate population estimates, which in effect improves fish stock assessment and fisheries management.

The harbor porpoise is the only cetacean species that occurs year-round and reproduces in the western Baltic Sea (Hasselmeier *et al.* 2004, Siebert *et al.* 2006, Scheidat *et al.* 2008, Viquerat *et al.* 2014, Sveegaard *et al*. 2015). The ecosystem is species-poor compared to the North Sea (Link *et al*. 2009, Narayanaswamy *et al*. 2013) to which it is connected through the Sound and the inner Danish Belts (Leppäkoski *et al.* 2002, Johannesson and André 2006). The main prey species of porpoises in the western Baltic Sea are Atlantic cod, whiting (*Merlangius merlangus*), Atlantic herring (*Clupea harengus*), sprat (*Sprattus sprattus*), and gobies (*Gobiidae*) (Aarefjord *et al.* 1995, Benke *et al.* 1998, Lockyer and Kinze 2003, Sveegaard *et al.* 2012). Despite knowledge about the general diet of porpoises here and in nearby areas, no previous studies have attempted to quantify the food consumption rates for the local porpoise population.

Diet studies on porpoises are based on the prey composition in the forestomach, which is primarily determined by hard parts, in particular fish otoliths (Pierce and Boyle 1991, Bowen and Iverson 2013). Otoliths are used for species identification and to estimate the fish body length and mass from known body length and mass–otolith length relationships (*e.g.*, Härkönen 1986, Leopold *et al.* 2001). They wear down during the digestive processes in the forestomach until they reach a critical point and disintegrate. Both the reduction in otolith size and the difference in otolith residence time give rise to severe biases in the estimated diet composition and thus the species-specific consumption rates (Jobling and Breiby 1986, Jobling 1987, Pierce and Boyle 1991, Bowen and Iverson 2013). Correction for otolith size reduction to estimate prey size is common practice (*e.g.*, Recchia and Read 1989, Börjesson *et al.* 2003, Víkingsson *et al.* 2003, Leopold *et al.* 2015), but until now no studies have accounted for the differential residence time of otoliths in the forestomach of porpoises (Ross *et al.* 2016).

The aim of this study is to estimate diet composition and consumption rate of harbor porpoises in the western Baltic Sea by accounting for the differential residence time of otoliths. The data set comprises 339 nonempty stomachs of bycaught or stranded animals collected over a 32 yr period (1980–2011). Differences in the composition of stomach contents between years, quarters, sexes, juveniles/adults, and bycaught/stranded animals were analyzed and quarterly diet compositions were estimated for juveniles and adults. Total yearly consumption rates for harbor porpoises in the western Baltic Sea were estimated based on porpoise abundance estimates nested in three scenarios of low, medium and high daily energy requirements of a porpoise. Furthermore, the consumed numbers by age and length group, respectively, of the commercially important species cod and herring were calculated. The results are relevant for both protection of harbor porpoises and for fisheries management and therefore discussed in both contexts.

Materials and Methods

Stomach Sampling

In total, 339 nonempty stomachs (Table 1) were sampled as part of the postmortem examination of stranded or bycaught harbor porpoises collected through dedicated stranding networks in the western Baltic Sea in the period 1980–2011 (Benke *et al.* 1998; Harwood *et al.* 1999; Siebert *et al.* 2001, 2006). The majority of the samples were collected within the ICES Subdivisions (SD) 22–24, but a few samples originated from the southern part of the Kattegat, ICES SD 21 (Fig. 1).

Total body length, body mass, and sex (Table 2) were recorded according to standard procedures (Siebert *et al.* 2001). If possible, teeth were collected for age estimation (Lockyer 1995). Samples of reproductive organs were used to determine maturity status (juvenile/adult). In cases where this was not possible, the maturity status was assessed from body length (Siebert *et al.* 2001) or age (Lockyer 1995), and animals between 0 and 4 yr old or less than 125 cm long were classified as juveniles (Siebert *et al.* 2006). The forestomach was removed and frozen for later analysis in the laboratory.

Laboratory Analysis of Stomach Contents

The contents in the forestomach were analyzed according to the standard procedure for marine mammals (Pierce and Boyle 1991). Prey items were separated using a series of sieves with mesh sizes of 0.5–2.0 mm and identified to the lowest taxonomic level possible. The material was flushed through the sieves into a small bucket, the content of which was examined to make sure that even the smallest otoliths were found. Very few otoliths <0.5 mm were retrieved. The intact and partially digested food items were identified. Slowly digestible objects such as fish otoliths and skeletal remains were identified using a selection of species identification literature (Härkönen 1986, ICES 1997, Leopold *et al.* 2001) as well as a personal otolith collection containing samples from 50 species each of different length groups (Andreasen 2009, Gilles 2009). Total length of intact fish prey was measured to the nearest millimeter. The vast number of remains in the stomachs used for species- and size-specification was, however, made up by otoliths (>99%).

To estimate the total number of fish in each stomach, the few intact fish prey were added to the number of identified otoliths. A fish has three pairs of otoliths and only the sagittal otoliths were identified and measured with two otoliths representing one fish (Pierce and Boyle 1991). If more than 100 otoliths were present for a single species in a stomach, a random subsample of 100 otoliths was taken for length measurements.

The otoliths were viewed with sulcus facing upwards under a stereo microscope (Leica MZ12) at a 1.25–2.50× magnification corresponding to 2.56–5.12 μm/pixel using reflected light in a standardized set-up. The images were digitized (Leica camera DFL290) and used to measure otolith length and width to nearest mm below in IMAGE PRO (vs. 5.0). Individual prey total lengths were calculated from the length or width of the otoliths based on otolith-fish length relationships reported in the literature (Härkönen 1986, Leopold *et al.* 2001). In cases where otoliths could be identified only to family or genus, the otolith-fish length relationship for closely related species were used in agreement with Leopold *et al.* (2001).

Each retrieved otolith was classified by stage of digestion on a scale from 0 to 5 on which stage 0 was assigned to pristine otoliths removed from the fish skull and stages 1–5 to otoliths recovered directly from the porpoise forestomach: (1) the otolith has a well-defined surface structure; (2) the otolith has smooth edges and margins, but the surface structure is less visible; (3) the otolith has increasingly concave lobes and the surface structure is degraded; (4) the otolith has concave lobes and has lost most of its surface structure; (5) the otolith is severely degraded or broken. This classification is in accordance with other porpoise diet studies (Recchia and Read 1989, Börjesson *et al.* 2003, Víkingsson *et al.* 2003).

In line with our own observations and previous studies (*e.g.*, Börjesson *et al*. 2003, Pinnegar *et al*. 2005), exclusively otoliths of digestion stages 0–2, for which the length reduction is negligible, were used to establish species-specific size distributions in analyses of diet composition and estimation of food consumption rates.

Fish prey accounted for the vast majority of the stomach contents by number (Table 3), while remains of invertebrates, like polychaete jaws and crustacean exoskeletons, accounted for less than 0.02%, and were therefore not included in the estimation of diet composition and consumption rates. The identified invertebrates are listed in Table S1. Crustacean exoskeletons were identified in accordance with Køie *et al.* (2000).

Statistical Analyses of Stomach Content Data

The stomach contents of porpoises of different ages and sexes, collected in different years and quarters and acquired either as bycaught or stranded were examined statistically to test for differences in prey mass composition and frequency of occurrence of individual prey species/categories. The levels of the five predictor variables were year (Y) = 1980–2011 (continuous); quarter of the year (Q) = Q1, Q2, Q3, Q4; age (A) = juvenile, adult; bycaught (B) = yes, no (stranded); sex (S) = female, male. All statistical analyses were run in the statistical programming environment R 3.1.2. (R core Team 2014).

A PERMANOVA (Anderson 2001) using Bray-Curtis dissimilarity matrix (Bray and Curtis 1957) on prey mass composition of the stomach contents was applied to test whether the variation could be attributed to any of the five predictor variables. Individual prey masses were estimated from the lengths of the otoliths based on known otolith-fish size relationships (Härkönen 1986, Leopold *et al.* 2001). A total of 23 dependent variables (prey categories) were used (see Table 3): the major prey were grouped by species (15 variables) or family (7 variables), and the rest of the prey were lumped together in one group (1 variable). The prey mass composition in stomach contents was based on otoliths of all digestion stages. Each model was run for 999 iterations. PERMANOVAs were run in the R package "vegan" (Oksanen *et al*. 2014).

The five predictor variables were further investigated by use of univariate tests, GAMs, to examine how the variables affected the eight main prey categories of which seven accounted for 91% of the total prey mass in the PERMANOVA and the remaining species were grouped into the last category; cod, herring, gobies, whiting, sprat, sandeel, eelpout (*Zoarces viviparus*), and "other fish prey." The PERMANOVA also showed that juvenile porpoises generally had fewer species in the stomach. To avoid introducing a bias in the GAMs due to the higher relative prey masses of specific species in juveniles, presence/absence data were used. The frequency of occurrence of each of the main prey categories in the porpoise stomachs was therefore examined by univariate tests to quantify the contributions of the five predictor variables (*Y*, *Q*, *A*, *B*, *S*,) to the observed variation (*i.e*., using the binomial error distribution). Only main effects were included since testing for interactions would not be supported by the data. Porpoise population trends and potentially also stomach contents may behave nonlinearly, and therefore generalized additive models (GAMs, Hastie and Tibshirani 1990) were used to test for the effect of year as a cubic spline smoother. The models were run in the R package “gamlss” (version 4.3-6) and model selection was based on the function “stepGAIC” (Rigby and Stasinopoulos 2005). Models were run separately for each of the prey categories. The frequency of occurrence *P* of a prey category was described by

$$P = f(Y) + Q + A + B + S \tag{1}$$

where *f* indicates a nonparametric additive smooth function.

Reconstruction of Prey Mass Composition in the Diet

The diet composition was estimated by accounting for biases related to the digestive processes in the forestomach as described by Ross *et al.* (2016). Prey-specific length distributions were established based on otoliths of digestion stages 0–2. In a second step, differential residence time of otoliths in the stomachs was accounted for by use of the weighting factor to each sagittal otolith to correct the length distribution of the otoliths as recommended by Ross *et al.* (2016). They found the relationship between original sagitta length l_S and elapsed time *T* until disintegration in a hydrochloric solution based on the results in Christiansen *et al.* (2005), who performed *in vitro* experiments on degradation of otoliths of different sizes belonging to the three different species, *i.e.*, capelin (*Mallotus villosus*), herring, and polar cod (*Boreogadus saida*). The estimated numbers of prey were pooled by species into 10 mm length groups for prey <100 mm and 50 mm length groups for prey >100 mm. The number of otoliths of digestion stage 3 was subsequently included to scale each prey-specific length distribution to total number of individuals of a fish species in the samples. Finally, total mass M_{il} of prey *i* by length group *l* was estimated by use of known length-mass relationships (Leopold *et al.* 2001).

The diet composition was estimated separately for juveniles and adults to examine for diet differences.

Population Consumption Rates

Yearly population consumption rates were estimated directly from the obtained quarterly diet compositions for juveniles and adults. Due to lack of knowledge about the ratio between juveniles and adults in the western Baltic Sea population, a ratio of 1:1 was assumed based on strandings and bycatches reported in the Baltic Sea (Siebert *et al.* 2006). The diet composition was scaled by values of the *per capita* energy requirements in three scenarios and estimates of the porpoise population size.

The porpoise abundance estimate was based on dedicated line-transect surveys that (1) covered the complete study area and (2) were conducted during the study period where the stomach samples were collected. The only surveys that fulfilled these requirements were the SCANS (Small Cetacean Abundance in the North Sea and adjacent waters; July 1994; Hammond *et al*. 2002) and the SCANS-II surveys (July 2005; Hammond *et al*. 2013). Both surveys covered the shelf waters of the European Atlantic in a synoptic survey effort involving several ships and aircrafts, also targeting the western Baltic Sea. The published abundances were rescaled to fit with the ICES regions of interest. In 1994 three smaller strata covered the study region; *i.e*., the area where the stomach samples were collected. However, one of the blocks had a very low sighting rate, which led to a high CV (Hammond *et al.* 2002). In 2005 only one large stratum covered the complete area in the western Baltic Sea, the inner Danish waters, the Kattegat and the Skagerrak, leading to a more straight-forward rescaling of the abundance and variance estimates as well as a more robust estimate (low CV). Thus, only the SCANS-II survey results were used for estimating the population consumption rates. For scaling of abundances, it was assumed that the density of animals within a given stratum was constant throughout. This way, the number of porpoises in the western Baltic Sea was estimated to be 8,847 (95% CI = 4,463–17,537). Estimation of population numbers is associated with a substantial degree of uncertainty and to account for this the estimate as well as the upper and lower 95% CLs were used to estimate the total yearly consumption rates.

Two approaches have previously been used to acquire the daily energy requirements R_E of harbor porpoises. One way is to multiply the basal metabolic rate by factors that account for assimilation efficiency and locomotion (*e.g.*, Kleiber 1975). Kenney *et al*. (1997) estimated a value of 14.6 MJ/d for a 40 kg porpoise based on conservative values of the multiplicative factors. Yasui and Gaskin (1986) obtained a daily feeding rate of wild nonlactating harbor porpoises of 10.3 MJ/d. The other way is to estimate feeding rates of animals kept in human care. Kastelein *et al*. (1997) estimated a daily energy intake of 8–25 MJ/d for porpoises in an indoor pool, whereas Lockyer (2007) estimated an intake of 21–42 MJ/d based on porpoises held in an outdoor enclosure. Energy requirements of porpoises vary with season and maturity stage (Lockyer *et al.* 2003, Santos *et al.* 2014), but due to lack of sufficient information on seasonal differences and population demography (age structure and sex ratios), inclusion of this variation was omitted. Based on the above-mentioned case studies, three estimates for R_E (10, 20, and 30 MJ/d) were used to mimic low, medium, and high energy requirements scenarios.

Quarterly, prey species- and length-specific energy densities E_{il} acquired from Pedersen and Hislop (2001) and Temming and Herrmann (2003) in conjunction with R_E of an average harbor porpoise were used to scale to total prey numbers in the daily food intake of the porpoise population by quarter of the year following the methodology described in Ross *et al.* (2016):

The daily consumption of energy in prey species i of length group l is expressed by

$$C_{E,il} = M_{il}E_{il}(\sum_{il}M_{il}E_{il})^{-1}R_EN \quad (2)$$

Here, M_{il} is the body mass of this prey category and N the number of porpoises in the western Baltic Sea. Consequently, the total consumed mass of this prey per day is

$$C_{M,il} = M_{il}(\sum_{il}M_{il}E_{il})^{-1}R_EN \quad (3)$$

Finally, given that

$$C_{M,il} = n_{il}m_{il} \quad (4)$$

where m_{il} is the mean body mass, the number n_{il} of consumed prey i in length group l is obtained by insertion of equation (3) into equation (4):

$$n_{il} = C_{M,il}(m_{il})^{-1} = M_{il}(m_{il}\sum_{il}M_{il}E_{il})^{-1}R_EN \quad (5)$$

In multispecies stock assessment, the consumption rate of fish prey is typically estimated by prey age class. For the present purpose, quarterly age-length keys (ALKs) were used to estimate age from length of the commercially important cod. ALKs were generated from ICES Baltic International Trawl Survey (BITS) data, retrieved from the online available Database of Trawl Surveys (DATRAS).[3] The number n_a of individuals in age class *a* consumed daily in each quarter of the year by the harbor porpoise population in the western Baltic Sea is

$$n_a = \sum_l n_l p_{la} \quad (6)$$

where p_{la} is the proportion of cod in length group *l* allocated to age class *a*. The yearly consumption rates were then calculated from the quarterly values of n_a and compared with the age-specific population numbers of cod to assess the predation by harbor porpoises on the western Baltic cod population. The population numbers for cod in ICES SDs 22–24 were derived from the ICES Baltic Fisheries Assessment Working Group (WGBFAS) Report (ICES 2014*a*), and averaged over the period 1980–2011.

Results

Stomach Content Composition

The stomachs contained a wide range of prey species. Remains of more than 32 fish species were identified (Table 3). A small number of invertebrates were also found and identified, mainly crabs, shrimps, and polychaetes (Table S1).

The PERMANOVA of prey mass composition in the stomach contents showed that all effects were significant except for sex (Table 4). Nevertheless, each predictor variable explained very little of the data variation, and the residual variance accounted for almost 93% of the variation.

Seven main prey categories, accounting for 91% of the total prey mass were identified: cod, whiting, herring, sprat, sandeels, eelpout, and gobies (Table 3). The rest of the fish were lumped into the category “other fish prey.” Gobies comprised black goby (*Gobius niger*), sand goby (*Pomatoschistus minutus*) and a large number of individuals, which could not be identified to species level due to advanced stages of otolith digestion. The category “other fish prey” included a mixture of flatfishes (sole, *Solea solea*, and flounder, *Platichthys flesus*), gadoids (other than cod and whiting or only identifiable to family level), salmonids and other taxa, all of which were present in low numbers.

The prey-specific patterns based on frequency of occurrence showed different trends. Results of the GAMs are shown in Table 5. Furthermore, the functional plots of the main effects for the three main prey species (cod, herring, and gobies) are shown in Figures 2 and 3.

Overall, the effect of year was significant for all prey categories except for sandeel. The frequency of occurrence of gobies, herring, sprat, whiting, and “other fish prey” generally increased during the time period investigated. Cod decreased markedly in the 1980s and then started to increase in 1990 (Fig. 2a). Eelpout decreased throughout the period. The changes between the species were intercorrelated, *i.e.*, periods with high consumption of cod coincided with low consumption of other main species such as herring.

Quarterly (seasonal) differences were seen for cod, gobies and sandeel. Higher frequency of occurrence of cod occurred in autumn and winter (3rd and 4th quarters of the year) (Fig. 2c), while for sandeel the highest frequency of occurrence was seen in spring (2nd quarter). The frequency of occurrence of gobies in harbor porpoise stomachs was significantly lower in autumn (3rd quarter) compared to the other quarters (Fig. 3d).

Differences between porpoise age groups were seen with higher frequency of occurrence of cod (Fig. 2b), eelpout and “other fish prey” in the stomachs of adults, whereas the frequency of occurrence of gobies (Fig. 3b) and sprat was higher in the stomachs of juveniles. The frequency of occurrence of herring, whiting and sandeel did not differ between age groups.

In general, the frequency of occurrence of the individual prey categories was similar among bycaught and stranded porpoises. The exception was herring for which the occurrence in the stomachs of the bycaught animals was significantly higher as compared to the stranded individuals (Fig. 2e)

Sex-related differences were found with higher frequency of occurrence of gobies (Fig. 3c), herring (Fig. 2f) and whiting in males and of sandeel and “other fish prey” in females.

Diet Composition

The results from the PERMANOVA and GAM analyses on stomach contents showed that the effects of most of the predictor variables were significant, which suggests that the diet composition would differ. Due to the limited number of porpoise stomachs, it was, however, not possible to disaggregate the data accordingly. Thus, it was decided to focus exclusively on quarterly differences in diet composition of juveniles and adults.

Cod, herring, and gobies were the main prey of harbor porpoises in the western Baltic Sea (Table 6). The share of cod and herring in the diet of adults was 36% and 34%, respectively. In juveniles, cod and gobies constituted 26% and 25% each, while herring was the third most common prey with a contribution of 18%. Sprat and whiting were less important in the diet of adults, while for juvenile porpoises these prey species made up 6% and 7% with whiting being particularly important in the 3rd quarter of the year (21%). Few sandeels were eaten by juveniles, whereas adults consumed them more frequently (5%), especially in the 2nd quarter.

Substantial seasonal variation in the diet was observed (Fig. 4). Juveniles generally had a more uniform diet composition throughout the year with the most pronounced differences in the 3rd quarter, where cod and whiting constituted more than 70% of the diet. The proportion of gobies was relatively constant (28%–38%) throughout the year except for the 3rd quarter, where it was lower (10%). Herring was mainly eaten in the first two quarters of the year. For adults, the seasonal diet composition was more variable. In the first and last quarters of the year, cod and herring made up the majority of the diet (>80%). Eelpout was important in the 3rd quarter, where it formed almost 25%, while the rest of the year its contribution was insignificant. Similarly, sandeels were eaten in the 2nd quarter and to a lesser extent in the 3rd quarter (Fig. 4).

Population Consumption Rates

The total yearly consumption rates estimates were based on the diet composition, the estimated population abundance (including 95% CLs) and the *per capita* energy requirements. Due to lack of knowledge about seasonal and individual variation in energy requirements, the potential variation was mimicked by three scenarios: (1) low (10 MJ/d), (2) medium (20 MJ/d), and (3) high (30 MJ/d).

Using the population size and the energy requirements for each of the three scenarios resulted in a large range of consumption rates (Table 7). The low scenario predicted a daily consumption rate of 1.8 kg, while the high scenario predicted 5.6 kg/d (see Table S2 for the low and high scenarios).

The daily prey mass requirements estimated from the daily energy requirements and the diet composition varied between quarters from 3.7 kg to 3.8 kg and from 3.4 kg to 3.8 kg for juveniles and adults, respectively (medium scenario). The low variation of the estimates for juveniles was supported by the more uniform diet composition throughout the year. For adults, the lowest mass consumption was seen in the 3rd quarter and the highest in the 1st quarter reflecting lower prey energy densities, particularly for herring and sprat. The differences in daily consumption rates between juveniles and adults were due to differences in the diet composition, *i.e.*, the energy content of the prey. It should also be kept in mind that porpoise size was ignored and the daily energy requirements were assumed to be the same for juveniles and adults.

Cod of age groups 1 and 2 were most heavily preyed upon by the porpoises (Table 8). The medium scenario suggested that 14%–18% of these age groups were removed annually. The low and high scenarios predicted <5% and between 40% and 50%, respectively. Cod older than 4 yr were only consumed infrequently. Age groups 0, 2, and 3 were mainly eaten the last two quarters of the year, while for age group 1, the highest predation was in the 1st quarter.

More than 50% of the annual intake of herring was consumed in the 1st quarter (Table 9). The intermediate size class was mainly targeted in this quarter, whereas the consumption of the large size class was more equally distributed over the year. The small herring were mostly consumed in winter although in modest numbers compared to the two larger length classes.

Discussion

The main findings of this study that cod, herring, and gobies are the main prey of harbor porpoises in the western

Baltic Sea are supported by previous studies (Aarefjord *et al.* 1995, Benke *et al.* 1998, Lockyer and Kinze 2003, Sveegaard *et al.* 2012). Moreover, the diet resembles that observed for porpoises in the North Sea and adjacent areas except that sandeels and whiting were only consumed in small quantities (Benke *et al.* 1998, Santos and Pierce 2003, Jansen *et al*. 2013, Leopold 2015).

The diet differed between years, quarters, juveniles and adults, and between bycaught and stranded porpoises. Cod and herring constituted on average 70% of the diet mass for adults, while gobies were also important for juveniles. Differences between juveniles and adults have been reported from other areas as well (Smith and Gaskin 1983, Víkingsson *et al*. 2003, Leopold 2015). The total number of prey species in the diets was the same, but the average number was lower in juveniles pointing to a higher degree of individual specialization. However, at the same time adults seemed to be more specialized by a more uneven distribution of prey proportions in the diet as mainly cod and herring were preyed upon. The latter contrasts the more generalized diet of adults found in studies on other sea areas (Víkingsson *et al*. 2003). This may, however, simply be a consequence of low availability of appropriate prey items, considering that the Baltic Sea has a much lower species diversity compared to the North Sea (Link *et al.* 2009, Leppäkoski *et al*. 2002, Narayanaswamy *et al*. 2013).

The fish sizes consumed by harbor porpoises in the present study ranged from 2.5 cm to 63 cm. Highest predation was exerted on 1–2 yr old cod and herring of 10–19 cm. These results are in agreement with the prey sizes reported in other studies from the same area (*e.g.*, Börjesson *et al*. 2003). A more recent case study based on echo recording tags from one adult and three subadult porpoises tagged over a short time period found that most of the targeted prey were in the size range of 3–10 cm (Wisniewska *et al*. 2016). Though the method employed by Wisniewska *et al*. (2016) offers an interesting new way of investigating the diet of cetaceans, studies encompassing more porpoises tagged over much longer time spans are needed to acquire a more complete description of the general diet.

As expected, seasonal changes in diet occurred, although these were less pronounced for juveniles. In the 3rd quarter, juveniles consumed large amounts of cod and whiting, likely linked to the arrival of recruits hatched in the spring. For both juveniles and adults, the highest diet share of cod was in the last two quarters of the year. Herring was primarily eaten in first two quarters, coinciding with the migration of spring-spawning herring from the feeding grounds in the Skagerrak and North Sea to the Rügen area in the western Baltic Sea (Parmanne *et al.* 1994, Guse *et al.* 2009, ICES 2013).

The difference in diet composition between stranded and bycaught porpoises with higher proportions of herring in the diet of bycaught porpoises could simply be due to the majority of the porpoise bycatch originating from the herring fisheries. The current knowledge about the diet of sick *vs.* healthy and stranded *vs.* bycaught porpoises is too limited to conclude on the observed differences.

The four main issues when estimating diet composition and consumption rates of cetaceans are sampling, reconstruction of diet based on stomach contents, abundance estimates, and energy requirements. These together with the assumptions during each step of analysis are discussed below.

Sampling

The acquisition of harbor porpoise stomachs for diet analyses is restricted to stranded or bycaught animals. Therefore, sampling of stomachs is inherently opportunistic and often biased (Lockyer and Kinze 2003, Víkingsson *et al.* 2003, Pierce *et al.* 2007, Santos *et al.* 2014). However, at least in the geographically narrow western Baltic Sea the sampling might be more representative than in other areas given the higher chances of stranding as well as the dedicated German stranding scheme involving beach patrols (Siebert *et al.* 2006).

The diet is likely to differ between age groups, sexes, as well as between bycaught and stranded animals as seen here and in other studies (*e.g.*, Smith and Gaskin 1983, Aarefjord *et al*. 1995, Börjesson *et al.* 2003, Víkingsson *et al.* 2003). In the present study, the ratios of bycaught to stranded and males to females were close to one for both juveniles and adults. However, the ratio of juveniles to adults was significantly skewed towards juveniles (2:1). A ratio of 1:1 was assumed for the western Baltic porpoise population age structure based on the ratio derived from reported strandings and bycatches for the German part of the western Baltic Sea (Siebert *et al.* 2006). When estimating the population consumption rates, the juveniles and adults were thus down and up-weighed, respectively.

The biased age-structure was particularly pronounced in the 1st quarter of the year, where the ratio of juveniles to adults was 6:1. Scaling up from only seven adults gives rise to large uncertainty. It is therefore highly recommended to collect and analyze more stomachs from adults in the 1st quarter prior to application of estimated consumption rates in multispecies or ecosystem-based assessment models.

The stomachs in the present study were collected over a long time period (1980–2011) and the statistical analyses showed significant temporal differences. Aggregation into smaller time periods was considered inappropriate since it would have reduced the sample sizes considerably and, thus, increased uncertainty dramatically. The present findings can therefore only be regarded as average figures over the examined time period.

Reconstruction of Diet

No previous studies on porpoise diet composition have attempted to correct for the differential residence time of otoliths in the stomach. Here, differential residence time was accounted for by the method presented in Ross *et al.* (2016) to reduce the bias related to large otoliths having a higher probability of recovery due to their longer stay in the stomach. The functional relationship was based on otoliths of different sizes from three fish species and further supported by the large body of literature on evacuation of prey from the stomachs of piscivorous fish (*e.g.*, Andersen 1998, Koed 2001, Temming and Herrmann 2003, Krog and Andersen 2009) as well as a mechanistic gastric evacuation model (Andersen and Beyer 2005). However, the description of residence time can probably be improved and refined by inclusion of other otolith features such as shape and resistance to digestion. Hence, as suggested in Ross *et al.* (2016), experiments on *in vitro* degradation rates of otoliths from a representative suite of prey fish should be performed to refine the description of differential residence time of otoliths in cetacean stomachs.

Most studies on diet and prey-specific food intake of porpoises are based on mass and do not take into account the energy density of prey species. The exception is Pinnegar *et al.*

(2005), who did not use season- and size-specific variation in energy density. In this study, the daily prey mass requirements varied by up to 10% over the seasons as a result of the seasonal differences in diet composition. This is especially important for herring and sprat where the energy content varies significantly over the year and between size classes (Pedersen and Hislop 2001). Although the seasonal and size-based dynamics of energy densities were not known for all prey species, the main prey were covered. Using mean energy densities on exclusively the less frequent prey species limits the bias related to differences in energy densities. Energy densities of prey fishes in the North Sea were considered representative of prey in the western Baltic Sea.

Population Abundance Estimates

Robust abundance estimates are needed to provide reliable estimates of the total yearly consumption rates of the harbor porpoise population in the western Baltic Sea. The SCANS small cetacean surveys (Hammond *et al*. 2002, 2013) were the only dedicated surveys covering the complete area of the western Baltic Sea during the stomach sampling period. Since the most recent survey in 2005 yielded a more precise estimate (lower CV for the western Baltic Sea), it was decided to use this survey's results to estimate the population abundance.

In order to include potential biases related to sampling errors, the 95% confidence interval of the abundance estimate was used to provide upper and lower limits in all three daily energy requirements scenarios. More information about demography (age structure and sex ratio) and geographical distribution of the porpoise population is needed to improve the accuracy of the estimated total yearly consumption rates (Pierce *et al.* 2007, Santos *et al.* 2014).

Energy Requirements

Lack of knowledge about energy requirements in the wild is considered one of the major barriers in the quantification of the ecological role of cetaceans (Pierce *et al.* 2007, Santos *et al.* 2014). Energy requirements depend on several biological and environmental variables such as activity level, reproductive and maturity status, and water temperature. Juveniles have increased energy demands due to their high growth rates and female adults due to pregnancy and lactation (Yasui and Gaskin 1986, Recchia and Read 1989, Lockyer *et al.* 2003). The monitored females in human care were neither pregnant nor lactating (Kastelein *et al.* 1997, Lockyer *et al.* 2003, Lockyer 2007), whereas mature females in the wild often are pregnant and lactating at the same time (Read and Hohn 1995, Read *et al.* 1997). Due to lack of knowledge about both the differences in energy requirements and the population demography in the western Baltic Sea, it was not attempted to implement age- or sex-specific values for energy requirements.

The average energy requirements value of 20 MJ/d used here in the medium scenario was based partly on results from feeding studies on porpoises in the Baltic Sea and nearby areas, partly on energetically founded considerations including basal metabolic rates for mammals (*e.g.*, Kleiber 1975, Yasui and Gaskin 1986, Innes *et al*. 1986, Kenney *et al.* 1997, Reed *et al.* 2000, Lockyer 2007). Mean daily consumption rates of 3.6–3.7 kg (medium scenario) are higher than most literature values based on body mass–metabolism relationships (*e.g.*, Yasui and Gaskin 1986, Innes *et al.* 1987, Kenney *et al.* 1997, Santos *et al.* 2014). In contrast, they are in the lower range of those reported for porpoises in human care under temperature conditions, which are similar to those in the western Baltic Sea (*e.g.*, Kastelein *et al.* 1997, Lockyer *et al.* 2003, Lockyer 2007). They are, however, similar to the average value of 3.5 kg used for porpoises in the North Sea Stochastic Multispecies (SMS) model (Pinnegar *et al.* 2005).

Ecosystem Perspectives

Cetaceans have already been included in multispecies and ecosystem-based models to investigate topics such as competition between cetaceans and the fisheries in the Pacific Ocean and the Bay of Biscay (Trites *et al*. 1997, Bearzi *et al.* 2008, Lassalle *et al*. 2012), predation mortality on cod, herring, and capelin in the Barents Sea (Tjelmeland and Bogstad 1998, Lindstrøm *et al.* 2009), trophic impacts along the north eastern coast of the United States. (Kenney *et al.* 1997, Morissette *et al*. 2006) and off Northwest Africa (Morissette *et al.* 2010), and ecosystem dynamics in the California Current (Brand *et al.* 2007).

Conflicts between fisheries and marine mammals are also important when considering management as well as protection of mammal populations with a critically endangered status such as the harbor porpoise subpopulation in the Baltic Sea (Vinther and Larsen 2004, Herr *et al.* 2009, ASCOBANS 2012, Siebert *et al*. 2012, Santos *et al.* 2014). Availability of good quality prey is critical for the survival of any population. Although it is hypothesized that harbor porpoises are opportunistic feeders, they have a high energy demand, especially as mature females are pregnant and lactating during most of the year (Read and Hohn 1995, Read *et al.* 1997). Therefore, proper management of the main prey species of porpoises is an important prerequisite for achieving good environmental status in the framework of the

Marine Strategy Framework Directive. In addition, recommendations of ASCOBANS and HELCOM also imply the protection of prey to ensure a habitat quality favorable to the conservation of the harbor porpoise in the Baltic Sea (HELCOM 1996, ASCOBANS 2012).

Currently, porpoises are not included directly in the SMS model for the Baltic Sea, which is used to assess the status of the cod, herring, and sprat stocks based on fishing and natural mortality (Lewy and Vinther 2004, ICES 2014*b*). Their predation is considered to be of minor importance due to the low abundance of porpoises compared to the North Sea (ICES 2014*b*). In the North Sea, harbor porpoises are assumed to exert high predation mortality on cod (Pinnegar *et al.* 2005, ICES 2014*b*). In line with this, the present study suggests that porpoises in the western Baltic Sea consume large quantities of cod, which are commercially important in the Baltic fisheries. The younger age groups of cod suffered the highest predation. It should, however, be stressed that although the present study addresses the bias originating from differential residence time of fish prey otoliths, it has not been able to incorporate the statistical uncertainty associated with estimating diet composition because of the relatively small sampling size. The associated variance is probably considerable and the confidence intervals around the consumption estimates are correspondingly underestimated, which points to the need for sampling of further stomach content data. The predation on cod is affected by other factors as well such as interactions between fish species and changes in fish population dynamics, which was also indicated by the intercorrelations between the consumption of the different fish species shown in the multivariate analyses.

The consumption rates of juvenile and adult harbor porpoises presented here can easily be scaled up or down depending on the population size and the energy requirements. By incorporating information about demography and seasonal and age-based variation in energy demands more accurate food consumption rate estimates can be achieved.

This study provides a framework for estimating prey-specific consumption rates by harbor porpoises that could inform the western Baltic Sea multispecies and ecosystem-based models. For more accurate estimates, the consumption rates should preferably be based on more recently collected stomachs with adequate spatial and temporal coverage. Moreover, the uncertainties derived from the different steps in the estimation of diet composition and population consumption rates should be incorporated into the multispecies and ecosystem-based models.

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Figure 1. Locations of the collected harbor porpoise stomach samples in the western Baltic Sea.

Figure 2. Graphical presentation of results from the GAM analyses. The significant effects of individual variables on frequency of occurrence of cod (a–c) and herring (d–f) in the stomachs of 339 harbor porpoises in the western Baltic Sea in the period 1980–2011. The variables are: year (a, d), age (b), quarter (c), bycaught (e) and sex (f).

Figure 3. Graphical presentation of results from the GAM analyses. The significant effects of individual variables on

frequency of occurrence of gobies in the stomachs of 339 harbor porpoises in the western Baltic Sea in the period 1980-2011. The variables are: year (a), age (b), sex (c), and quarter (d).

Figure 4. Quarterly prey mass composition (%) in the diet of juvenile (a) and adult (b) harbor porpoises in the western Baltic Sea in the period 1980–2011.

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[3]Available at https://datras.ices.dk/Data_products/Download/Download_Data _public.aspx.

Supporting Information

The following supporting information is available for this article online at http://

Table S1. Invertebrate prey observed in 339 harbor porpoise stomachs in the western Baltic Sea in each quarter Q of the year for the period 1980–2011. Numbers of individuals by prey category and quarter of the year.

Table S2. Estimated yearly food consumption rates (tons) by prey category and *per capita* daily food intake (kg) of the populations of juvenile and adult harbor porpoises in the western Baltic Sea in 1980–2011. The porpoise abundance estimate of 8,847 (95% CI = 4,463–17,537) and the ratio 1:1 of juveniles to adults are assumed. Two scenarios are presented: low and high daily energy requirements of 10 MJ/d and 30 MJ/d, respectively, combined with abundance estimates including lower and upper 95% CLs.

Table 1. Numbers of harbor porpoises collected for diet analyses in the western Baltic Sea in the period 1980–2011 with information about sex, maturity status (juvenile or adult) and how the animals were acquired (bycaught or stranded).

	Quarter of the year					Acquisition			Sex		Total
	1	2	3	4	Unspecified	Bycaught	Stranded	Unspecified	F	M	
Juvenile	35	62	76	54	1	105	108	15	103	125	228
Adult	7	24	48	31	1	41	59	11	53	58	111

Table 2. Mean total length (L_T) and weight (W) (± SD) of harbor porpoises by sex and maturity status (juvenile or adult) sampled in the western Baltic Sea in the period 1980–2011. N_L is the numbers of animals length measured and N_W the number of animals weighed.

	Sex	L_T (cm)	N_L	W (kg)	N_W
Juveniles	F	117 ± 10	102	28 ± 7	80
	M	114 ± 10	123	26 ± 7	100
Adults	F	153 ± 13	51	52 ± 14	41
	M	141 ± 8	57	42 ± 6	42

Table 3. Fish prey taxa observed in 339 harbor porpoise stomachs in the western Baltic Sea in the period 1980–2011. N_T is total number of otoliths, N_M is number of otoliths measured, *%F* is frequency of occurrence, and *l* is total prey length.

Family	Species	N_T	N_M	% F	l (cm) Mean	Range
Agonidae	Pogge (*Agonus cataphractus*)	2	0	0.3	—	—
*Ammodytidae***	Unspecified	1,400	667	11	15.1	4.1–21.0
Anarhichadidae	Atlantic wolffish (*Anarhichas lupus*)	7	0	0.6	—	—
Anguillidae	European eel (*Anguilla anguilla*)*	64	33	3.2	37.7	10.0–63.0
Belonidae	Garfish (*Belone belone*)	2	0	0.3	—	—
*Callionymidae***	Common dragonet (*Callionymus lyra*)	8	8	0.3	4.3	3.0– 6.6
	Reticulated dragonet (*Callionymus reticulatus*)	6	3	0.3	11.4	11.0–11.7
	Unspecified	2	0	0.3	—	—
Carangidae	Atlantic horse mackerel (*Trachurus trachurus*)*	101	92	0.6	11.1	5.7–13.0
Cottidae	Shorthorn sculpin (*Myoxocephalus scorpius*)	4	2	0.6	10.3	10.3–10.4
*Clupeidae***	Herring (*Clupea harengus*)*	1,130	756	28	17.7	2.6–30.6
	Sprat (*Sprattus sprattus*)*	541	457	11	10.3	3.0–15.9
	Unspec.	27	0	2	—	—
*Gadidae***	Atlantic cod (*Gadus morhua*)*	3,235	2,467	54	23	2.6–56.9
	Whiting (*Merlangius merlangus*)*	3,481	1,117	53	14.9	2.9–46.6
	Four-bearded rockling (*Enchelyopus cimbrius*)*	65	61	1.5	19.8	10.0–30.5
	Haddock (*Melanogrammus aeglefinus*)*	22	13	1.5	25.5	14.2–35.3

	Common ling (*Molva molva*)	4	0	0.6	—	—
	Saithe (*Pollachius virens*)	3	3	0.6	9.2	7.5–10.0
	Norway pout (*Trisopterus esmarkii*)*	253	65	1.8	8.2	4.2–10.2
	Poor cod (*Trisopterus minutus*)	6	3	0.6	9.4	9.1–10.0
	Unspecified Gadoid	58	30	4.7	10.5	10.0–26.1
	Unspecified *Trisopterus*	3	3	0.6	6.3	3.5–11.6
Gasterosteidae	Sea stickleback (*Spinachia spinachia*)	1	0	0.3	—	—
*Gobiidae***	Black goby (*Gobius niger*)*	1,430	496	4	5.8	2.6–14.6
	Sand goby (*Pomatoschistus minutus*)	255	243	1.2	4.9	2.5–12.6
	Unspecified	28,047	2,468	42	3.7	2.5–11.1
Merlucciidae	European hake (*Merluccius merluccius*)*	32	32	0.9	11.9	10.0–26.9
Osmeridae	European smelt (*Osmerus eperlanus*)*	62	0	0.9	—	—
*Pleuronectidae***	Dab (*Limanda limanda*)	1	0	0.3	—	—
	Flounder (*Platichthys flesus*)*	14	14	0.3	10.1	7.7–11.9
	European plaice (*Pleuronectes platessa*)	1	1	0.3	8.4	—
	Common sole (*Solea solea*)*	31	16	0.6	18.4	14.0–24.1
	Unspecified	71	32	1.8	14.2	7.7–24.1
*Salmonidae***	Common whitefish (*Coregonus lavaretus*)	6	1	0.9	10	—
	Unspecified	38	0	1.2	—	—

Sternoptychidae	Silvery lightfish (*Maurolicus muelleri*)	2	1	0.3	10	—
Syngnathidae	Unspecified pipefish	22	1	2.6	10	—
Zoarcidae	Viviparous eelpout (*Zoarces viviparus*)*	334	135	7	19.6	6.0–28.7
Unspecified		375	1	16	10	—

Note: In the PERMANOVA, 23 prey categories were included as dependent variables; the major prey were grouped by *species (15 variables) or **family (7 variables), and the rest of the prey were lumped together in one group (1 variable).

Table 4. Results of minimum adequate model of the PERMANOVA using Bray-Curtis dissimilarity matrix and 999 iterations on prey composition data for harbor porpoises in the western Baltic Sea in the period 1980–2011. Significant effects are in bold.

	df	Sums of squares	Mean squares	F	R^2	P (>F)
Year	1	2.137	2.1366	5.5786	0.016	**0.001**
Quarter	3	3.867	1.2891	3.3658	0.0289	**0.001**
Age group	1	2.017	2.0172	5.2667	0.015	**0.001**
Bycatch	1	1.382	1.3822	3.6088	0.0103	**0.002**
Sex	1	0.492	0.492	1.2845	0.0037	0.211
Residuals	324	124.094	0.383		0.9262	
Total	331	133.99	1			

Table 5. Results of the GAMs for each of the eight prey categories observed in the stomachs of 339 harbor porpoises in the western Baltic Sea in the period 1980–2011. Estimates indicate positive or negative regression coefficients for the intercept and the factor variables, and estimated number of knots for the cubic spline smoothers over the years, *i.e.*, cs(year). Significant effects are in bold.

	Estimates	SE	*t*	*P* (>|*t*|)
Cod				
(Intercept)	−101.7	0.585	−173.846	**<2e-16**
cs(year)	0.05	0	190.079	**<2e-16**
Adult	0.638	0.257	2.484	**0.014**
Q2	0.444	0.452	0.981	0.327
Q3	0.989	0.425	2.325	**0.021**
Q4	1.054	0.454	2.322	**0.021**
Whiting				

			[4279]-46	
(Intercept)	−111.4	5.746	−19.387	**<0.001**
cs(year)	0.055	0.003	18.214	**<0.001**
Male	0.471	0.57	0.825	0.41
Herring				
(Intercept)	−27.360	0.841	−32.52	**<0.001**
cs(year)	0.013	0	29.026	**<0.001**
stranded	−0.615	0.257	−2.388	**0.018**
Male	0.499	0.267	1.869	0.063
Sprat				
(Intercept)	−153.455	53.965	−2.844	**0.005**
cs(year)	0.076	0.027	2.811	**0.005**
Adult	−0.91	0.424	−2.146	**0.033**
Sandeels				

[4279]-47

(Intercept)	−0.843	0.309	−2.733	**0.007**
Male	−0.563	0.348	−1.619	0.106
Q3	−0.921	0.377	−2.443	**0.015**
Q4	−1.438	0.503	−2.861	**0.005**
Gobies				
(Intercept)	−55.910	0.563	−99.241	**<0.001**
cs(year)	0.028	0	107.544	**<0.001**
Adult	−0.523	0.257	−2.033	**0.043**
Male	0.395	0.239	1.656	0.099
Q2	−0.259	0.427	−0.607	0.544
Q3	−1.078	0.406	−2.656	**0.008**
Q4	0.192	0.432	0.444	0.658
Eelpout				

(Intercept)	191.406	50.645	3.779	**<0.001**
cs(year)	−0.097	0.025	−3.832	**<0.001**
Adult	1.176	0.451	2.606	**0.01**
Other fish prey				
(Intercept)	−44.090	0.398	−110.668	**<0.001**
cs(year)	0.022	0	100.722	**<0.001**
Adult	0.363	0.242	1.503	0.134
Male	−0.407	0.229	−1.777	0.077

Table 6. Relative prey mass composition (%) in the diet of juvenile and adult harbor porpoises in the western Baltic Sea in the period 1980–2011.

	Atlantic cod	Whiting	Herring	Sprat	Sandeels	Eelpout	Gobies	Other fish
Juveniles	0.26	0.07	0.18	0.06	0.01	0.06	0.25	0.11

Adults	0.36	0.02	0.34	0.02	0.05	0.07	0.06	0.08

Table 7. Estimated yearly food consumption rates (tons) by prey category and *per capita* daily food intake (kg) of the populations of juvenile and adult harbor porpoises in the western Baltic Sea in 1980–2011. The porpoise abundance estimate of 8,847 (95% CI = 4,463–17,537) and the ratio 1:1 of juveniles to adults are assumed. The “medium” *per capita* energy requirement scenario (20 MJ/d) combined with abundance estimates including lower and upper 95% CLs is presented. The “low” and “high” scenarios are available in Table S2.

Prey type	Juveniles			Adults		
	Mean	95% CLs		Mean	95% CLs	
		Lower	Upper		Lower	Upper
Atlantic cod	1,591	803	3,153	2,124	1,072	4,211
Whiting	408	206	809	113	57	225
Herring	1,101	555	2,183	1,996	1,007	3,957
Sprat	367	185	728	110	55	217
Sandeels	44	22	88	297	149	587
Eelpout	348	175	690	420	212	833
Gobies	1,523	768	3,019	324	164	642
Other fishes	678	342	1,344	440	222	872

Total	6,060	3,056	12,014	5,824	2,938	11,544
Daily *per capita*	3.8			3.6		

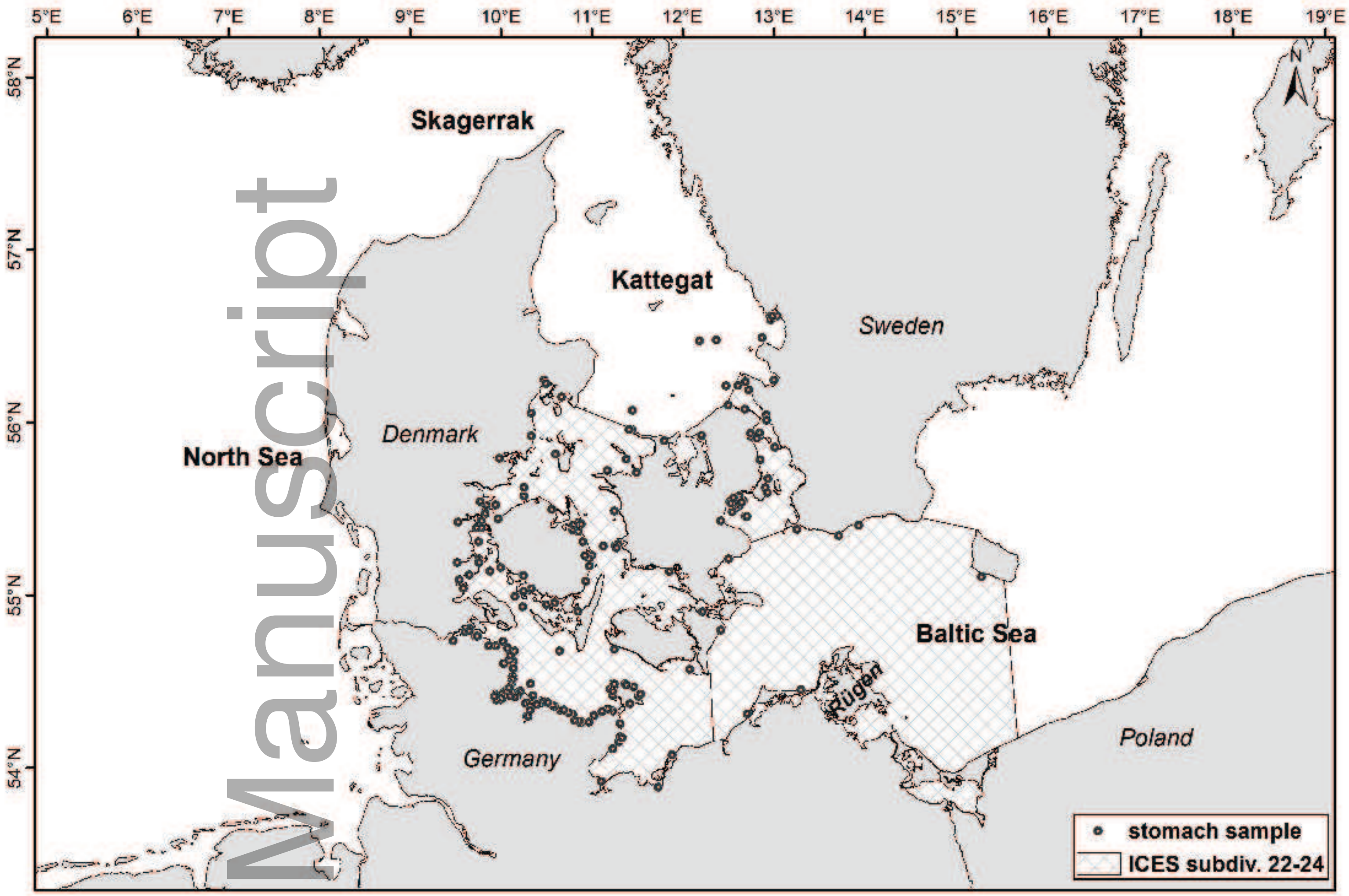
Table 8. Estimated mean number (×10^3) by age class of cod consumed each quarter by the population of harbor porpoise in the western Baltic Sea in 1980–2011. The abundance estimate of 8,847 (95% CI = 4,463–17,537) and the ratio of 1 of juveniles to adults is assumed. The numbers in brackets show the consumption rates based on the 95% confidence interval of the abundance estimate. The “medium” *per capita* energy requirement scenario (20 MJ/d) is presented. N_{pop} is the estimated mean population size (×10^3) of cod by age class averaged over the period 1980–2011 (ICES 2014*a*) and *P* is the proportion of a given age class consumed by harbor porpoises.

Age class	0	1	2	3	4	5	6+
Q1	684	4,365	761	343	70	17	2
	(345–1,356)	(2,202–8,653)	(384–1,508)	(173–680)	(35–139)	(9–34)	(1–4)
Q2	1,021	715	999	272	59	11	2
	(515–2,024)	(361–1,417)	(504–1,980)	(137–539)	(30–117)	(6–22)	(1–4)
Q3	3,725	2,954	2,688	451	13	0	0
	(1,879–7,384)	(1,490–5,856)	(1,356–5,328)	(228–894)	(7–26)	0	0
Q4	4,039	3,520	1,375	385	91	16	1
	(2,038–8,006)	(1,886–6,978)	(694–2,726)	(194–763)	(46–180)	(8–32)	(1–2)
Yearly	9,469	11,554	5,822	1450	233	44	6

	(4,777–18,770)	(5,829–22,903)	(2,937–11,541)	(731–2,874)	(118–462)	(22–87)	(3–12)
N_{pop}	13,3714	64,393	42,756	19656	5990	1690	680
P	0.07	0.18	0.14	0.07	0.04	0.03	0.01
	(0.04–0.14)	(0.09–0.36)	(0.07–0.27)	(0.04–0.15)	(0.02–0.08)	(0.01–0.05)	(0–0.02)

Table 9. Estimated mean number (×10^3) by length-class (cm) of herring consumed each quarter (Q) by the harbor porpoise population in the western Baltic Sea in 1980–2011 using the “medium” *per capita* energy requirements scenario (20 MJ/d). The abundance estimate of 8,847 (95% CI = 4,463–17,537) and the ratio 1:1 of juveniles to adults is assumed. The numbers in brackets show the consumption rates based on the 95% confidence interval of the abundance estimate.

Length class	Q1	Q2	Q3	Q4
1–9	497 (251–985)	77 (39–153)	0	202 (102–400)
10–19	8,231 (4,152–16,316)	1,362 (687–2,700)	778 (392–1,542)	1,065 (537–2,111)
≥20	1,434 (723–2,843)	2,182 (1,101–4,325)	891 (449–1,766)	1,108 (559–2,191)
Total	10,162 (5,126–20,143)	3,621 (1,827–7,178)	1,668 (841–3,306)	2,375 (1,198–4,708)



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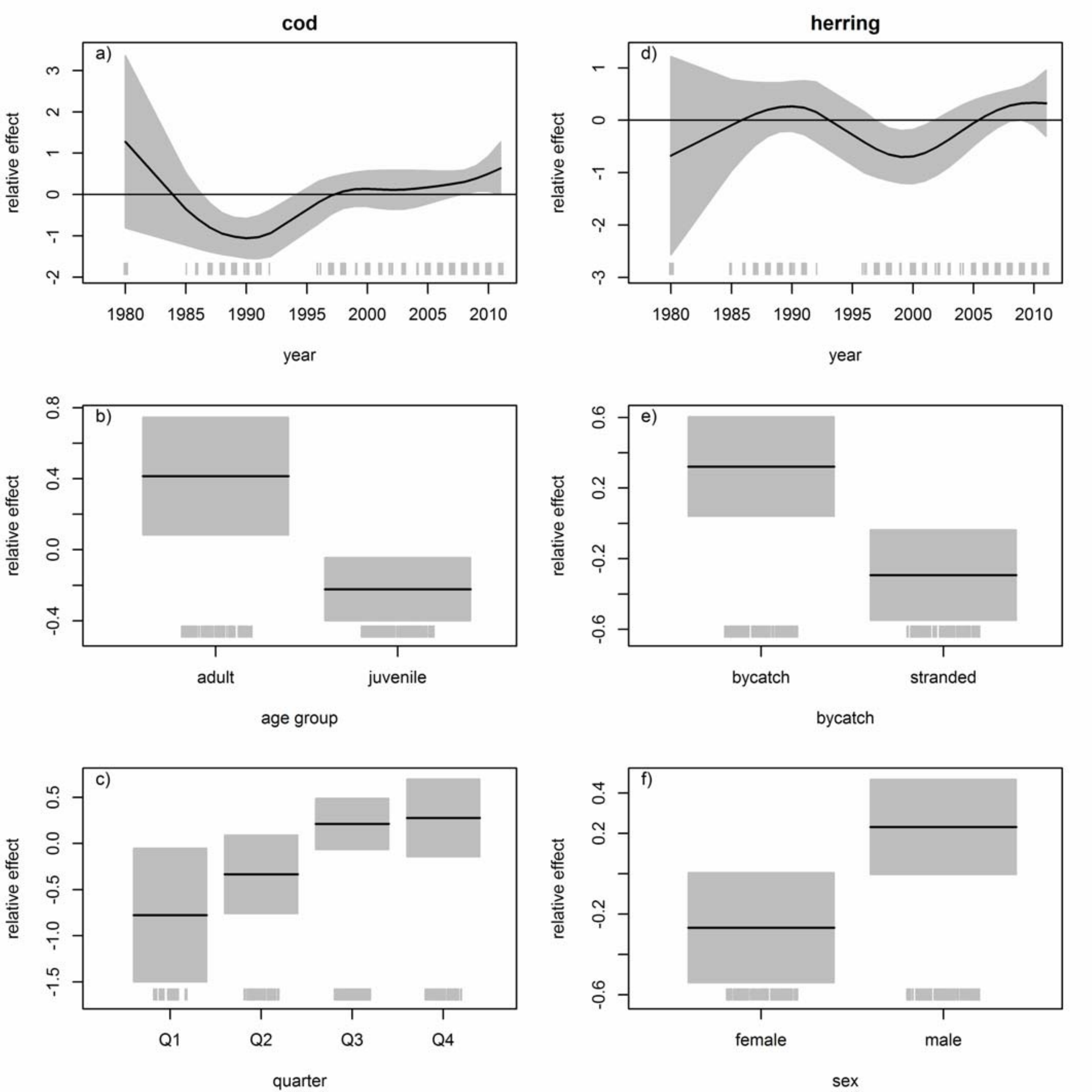
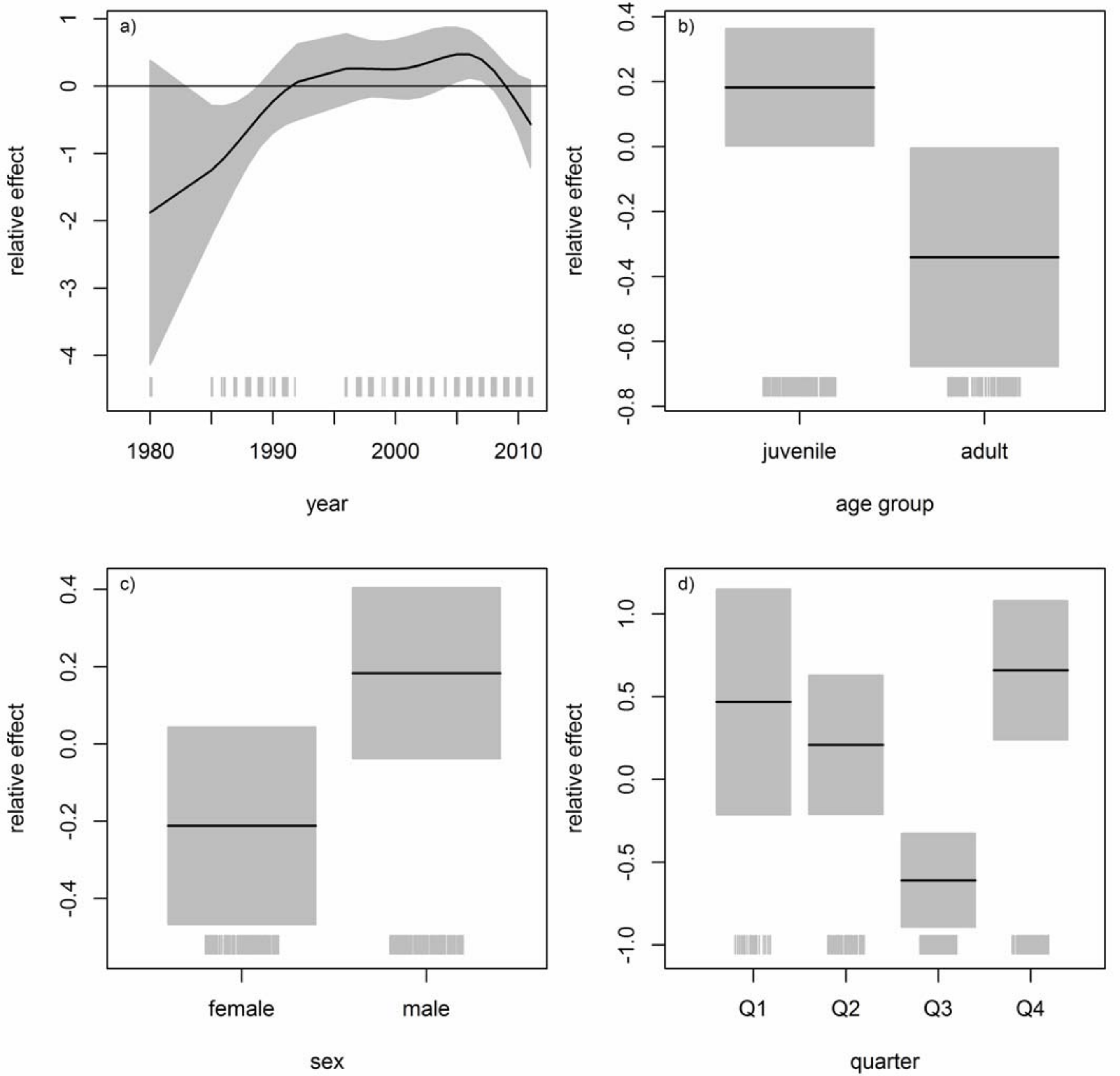


cod
herring
a)
b)
c)
d)
e)
f)
relative effect
year
age group
quarter
bycatch
sex
adult
juvenile
Q1
Q2
Q3
Q4
bycatch
stranded
female
male
1980
1985
1990
1995
2000
2005
2010


a)
relative effect
1
0
-1
-2
-3
-4
1980
1990
2000
2010
year
b)
relative effect
0.4
0.2
0.0
-0.2
-0.4
-0.6
-0.8
juvenile
adult
age group
c)
relative effect
0.4
0.2
0.0
-0.2
-0.4
female
male
sex
d)
relative effect
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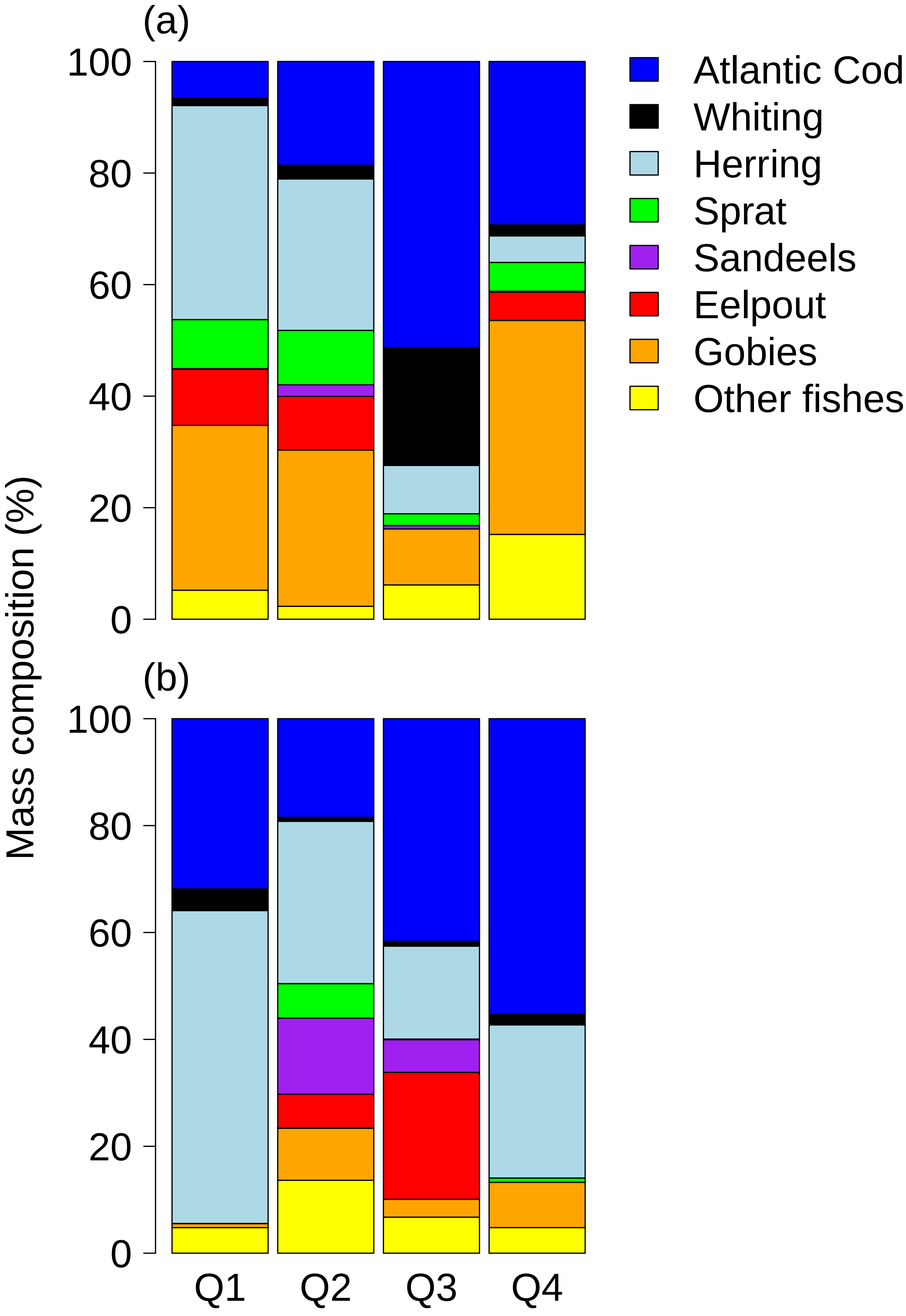
0.5
0.0
-0.5
-1.0
Q1
Q2
Q3
Q4
quarter



(a)
(b)
Mass composition (%)
0
20
40
60
80
100
Q1
Q2
Q3
Q4
Atlantic Cod
Whiting
Herring
Sprat
Sandeels
Eelpout
Gobies
Other fishes