Identification of high-risk areas for harbour porpoise Phocoena phocoena bycatch using remote electronic monitoring and satellite telemetry data

Article *in* Marine Ecology Progress Series · August 2016

DOI: 10.3354/meps11806

Vol. 555: 261–271, 2016
doi: 10.3354/meps11806

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published August 18

Identification of high-risk areas for harbour porpoise *Phocoena phocoena* bycatch using remote electronic monitoring and satellite telemetry data

Lotte Kindt-Larsen[1,*], Casper Willestofte Berg[1], Jakob Tougaard[2], Thomas Kirk Sørensen[1], Kerstin Geitner[1], Simon Northridge[3], Signe Sveegaard[2], Finn Larsen[1]

[1]National Institute of Aquatic Resources, Technical University of Denmark, 2920 Charlottenlund, Denmark
[2]Department for Bioscience, Aarhus University, 4000 Roskilde, Denmark
[3]Sea Mammal Research Unit, University of St Andrews, St Andrews, Fife KY16 8LB, UK

ABSTRACT: The bycatch of harbour porpoise *Phocoena phocoena* is an issue of major concern for fisheries management and for porpoise conservation. We used high-resolution spatial and temporal data on porpoise abundance and fishing effort from the Danish Skagerrak Sea to identify areas with potentially higher and lower risk of porpoise bycatch. From May 2010 to April 2011, 4 commercial gillnet vessels were equipped with remote electronic monitoring (REM) systems. The REM system recorded time, GPS position and closed-circuit television (CCTV) footage of all gillnet hauls. REM data were used to identify fishing grounds, quantify fishing effort and document harbour porpoise bycatch. Movement data from 66 harbour porpoises equipped with satellite transmitters from 1997 to 2012 were used to model population density. A simple model was constructed to investigate the relationship between the response (number of individuals caught) and porpoise density and fishing effort described by net soak time, net string length and target species. Results showed that a model including both porpoise density and fishing effort data predicted bycatch better than models containing only one factor. We therefore conclude that porpoise telemetry or REM data allow for identification of areas of potential high and low bycatch risk, and better predictions are obtained when combining the 2 sources of data. The final model can thus be used as a tool to identify areas of bycatch risk.

KEY WORDS: Harbour porpoise · Bycatch mitigation · REM · Natura 2000 · Fisheries management

INTRODUCTION

Harbour porpoises *Phocoena phocoena* and commercial fisheries interact in various ways. Some are direct, in which marine mammals come into physical contact with fishing gear and are bycaught incidentally. Others are indirect, e.g. through resource competition (DeMaster et al. 2001). Bycatch in gillnets has been documented in many gillnet fisheries and is usually regarded as the main anthropogenic impact on porpoises (Vinther 1999, Read et al. 2006).

In order to minimize fisheries impacts on the species, porpoises in European Union (EU) waters are protected under both the Habitats Directive (EC 1992) and Council Regulation 812/2004 (EC 2004). In the Habitats Directive, the harbour porpoise is listed in Annexes II and IV, which means that special areas should be established for the conservation of the species, and that the deliberate actions of killing, disturbance and habitat deterioration are prohibited throughout its range (EC 1992). EU Council Regulation 812/2004 (EC 2004) lays

*Corresponding author: lol@aqua.dtu.dk

down measures on the use of acoustic deterrent devices on static nets used at certain times and in certain areas, phasing out driftnets and monitoring bycatch in certain fisheries.

Bycatch monitoring can be conducted using a number of different methods, although on-board observers are recommended as providing the most accurate data (IWC 1994). More recently, remote electronic monitoring (REM) systems have shown great potential in documenting porpoise bycatch (Kindt-Larsen et al. 2012). Both types of observer programmes are, however, expensive and can be challenging to implement. Limited financial resources often lead to common questions from environmental and fisheries managers as to where bycatch monitoring should be focused, and in which areas and seasons porpoises are particularly exposed to high risk of entanglement in fishing gears. A tool to identify such areas and seasons would therefore be valuable.

This study aimed to examine whether data on harbour porpoise density and gillnet fishing could be used to identify high risk areas for porpoise bycatches in the Danish Skagerrak Sea over the course of 4 seasons. Porpoise density data were obtained from satellite-tracked harbour porpoises, while fishing effort data and records of porpoise bycatch events were obtained from vessels monitored by REM systems.

MATERIALS AND METHODS

Study area

The study was conducted in the Danish part of the Skagerrak Sea (see Fig. 1). Both trawling and gillnet fishing are carried out in the area (Sørensen & Kindt-Larsen 2016), which also contains high densities of harbour porpoises (Sveegaard et al. 2011a). Three areas in the Skagerrak have been designated as Danish Natura 2000 sites under the Habitats Directive for the protection of porpoises: 'Skagens Gren og Skagerrak' (2691 km^2), 'Store Rev' (109 km^2) and 'Gule Rev' (471 km^2) (see Fig. 3). 'Skagens Gren og Skagerrak' was designated due to its high porpoise densities (Sveegaard et al. 2011a) while the other 2 areas were initially designated because of the presence of reef structures. Harbour porpoises were added subsequent to the initial designation of these 2 sites due to the generally high occurrence of the species in the Skagerrak (M. Krawack pers. comm.).

Fishing effort data

Data on fishing effort were collected from 4 gillnet vessels from 1 May 2010 to 30 April 2011 using REM systems from Archipelago Marine Research. The REM systems recorded time, position and closed-circuit television (CCTV) footage of all trips (port to port), and thus represent a full census of fishing effort by these 4 vessels. Video footage of all net string hauls was analysed using EMI software v.1.1.3.11189 (Archipelago Marine Research). Since all net strings were set in almost straight lines, their lengths were calculated as the distances between the GPS position of the start and end buoy of a net string. Soak time was determined as the mean time the net string had been in the water by subtracting the mean time of setting from the mean time of hauling. Fishing effort was determined as the product of net string length and soak time. Data from May 2010 were lost from one vessel; data from the same vessel in May 2011 were therefore used to fill this information gap on the assumption of predictable seasonal fishing patterns.

REM fishing effort data were divided into seasons and fisheries categories. The seasons were winter (December, January, February), spring (March, April, May), summer (June, July, August) and autumn (September, October, November) (Fig. 1). The fishery categories were plaice *Pleuronectes platessa*, cod *Gadus morhua* and hake *Merluccius merluccius*. Participating fishermen filled in a daily log with information on the gear used, including mesh sizes. These data were added to the REM data on a haul basis during analysis.

The cod fishery by the 4 vessels was conducted in all 4 seasons, with the greatest number of hauls conducted in autumn and winter (68%) and the least in summer (6%). The plaice fishery had most hauls in spring and summer, while the hake fishery took place only during the summer (Table 1). The 3 fisheries differed with respect to mesh size, soak time and net string length. The cod fishery used the largest mean mesh size (154 mm) and the hake fishery the smallest (130 mm). Mean soak time was shortest for the hake fishery (6 h) and longest for plaice (12 h). The shortest mean net string length (671 m) was found in the cod fishery and the longest in the plaice fishery (1974 m). However, both fisheries exhibited large variability in soak time and net string lengths (Table 2).

Based on fishing effort data and seabed topography, 3 areas with homogeneous bottom types were identified for analysis: Area A, containing a sandbank and sandy/small stone sea bed; Area B, interspersed boulder reefs and reef structures created by leaking

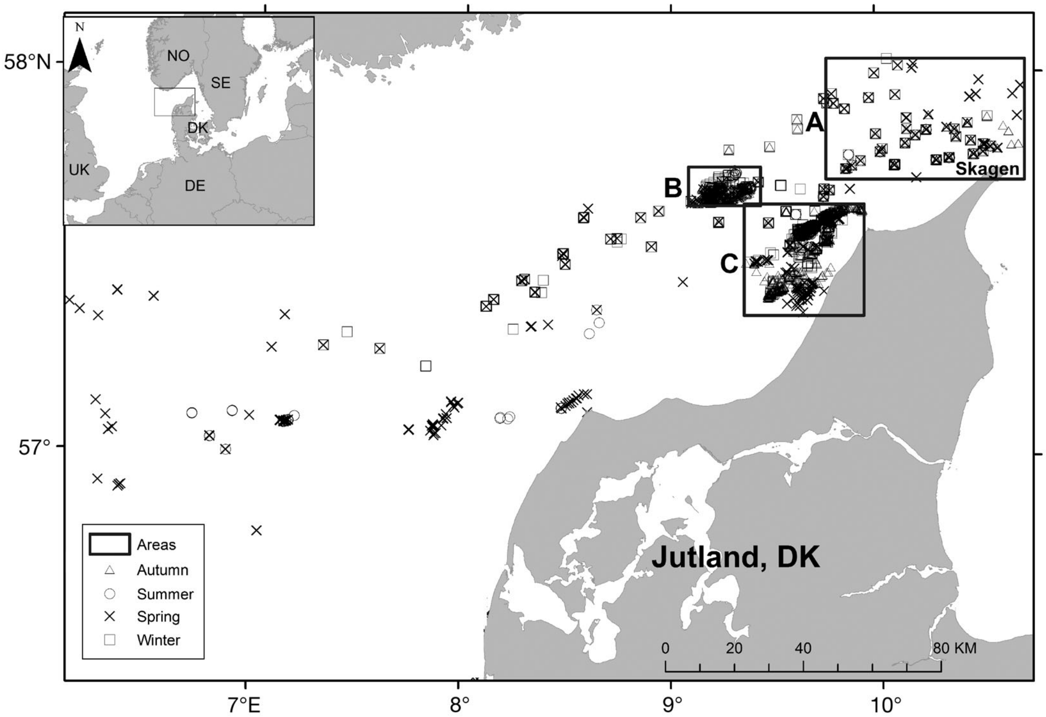

Fig. 1. The 3 areas in the Danish Skagerrak Sea in which harbour porpoise bycatch was examined over 4 seasons, and the respective gillnet effort of the 4 remote electronic monitoring (REM) vessels. A total of 524 hauls were observed in Area A, 381 hauls in Area B and 1136 hauls in Area C; each symbol represents a single gillnet haul

Table 1. Recorded harbour porpoise bycatch events and hauls for the 3 types of fisheries (cod, plaice and hake) in the Danish Skagerrak Sea ('All', Fig. 1), including the 3 areas (A, B and C; see Fig. 1) during 4 seasons (all seasons, winter [Dec–Feb], spring [Mar–May], summer [Jun–Aug] and autumn [Sep–Nov]). (–) no data

Fishery and area	All seasons		Winter		Spring		Summer		Autumn	
	Hauls	Bycatch	Hauls	Bycatch	Hauls	Bycatch	Hauls	Bycatch	Hauls	Bycatch
Cod All	2178	18	796	12	559	0	122	2	701	4
A	524	5	87	2	199	0	72	2	166	1
B	296	5	145	3	55	0	4	0	92	2
C	844	8	365	7	51	0	4	0	424	1
Plaice All	401	14	–	–	179	14	191	0	31	0
A	–	–	–	–	–	–	–	–	–	–
B	38	0	–	–	–	–	7	0	31	0
C	276	1	–	–	99	1	177	0	–	–
Hake All	65	1	–	–	–	–	65	1	–	–
A	–	–	–	–	–	–	–	–	–	–
B	47	1	–	–	–	–	47	1	–	–
C	16	0	–	–	–	–	16	0	–	–
Total	2644	33	796	12	738	14	378	3	732	4

gas and Area C, mixed stone bottom (Fig. 1). Areas B and C were used by all 3 fisheries while area A was used only for cod and plaice. A total of 528, 381 and 1136 hauls were observed in Areas A, B and C, respectively (Table 1). The 4 vessels landed 23 % of the total gillnet landings in the area (AgriFish 2010) and were responsible for 22 % of the total catch value.

Table 2. Mean mesh size, soak time and net string length for the different fisheries

Fishery	Mesh size (mm)		Soak time (h)				Net string length (m)			
	Mean	CV	Mean	Min.	Max.	CV	Mean	Min.	Max.	CV
Cod	154	10	8	2	29	70	671	19	7705	130
Plaice	136	3	12	3.5	45	61	1974	242	6157	61
Hake	130	0	6	3	9	26	1059	108	1244	17

Harbour porpoise density data

From 1997 to 2012, 88 harbour porpoises were tagged with satellite transmitters in Danish inshore waters near Skagen. Of these, 66 swam into the study area during the period of tag transmission, where they transmitted a total of 4590 locations (1 location d^{-1} porpoise^{-1}, average individual^{-1}: 85, range: 1 to 395). For information on tagging sites, sex, age, length, weight and transmission period see Supplement 1 at www.int-res.com/articles/suppl/m555p261_supp.pdf, and for tagging procedure and types of transmitters used, see Sveegaard et al. (2011a).

The transmitters were positioned by System Argos, and the data provided detailed information on individual porpoise movements. Locations obtained through System Argos are less precise than those of GPS and may deviate from the actual location of the animal by several km. During processing by System Argos, individual positions were classified into 1 of 6 location classes according to precise latitude and longitude estimates. Locations were filtered using the Douglas Argos filter (Douglas 2006), which removes the most unlikely positions, i.e. those that either require unrealistically high swimming speeds or sharp turning angles by the porpoises. Even so, inaccuracies remained, and these were dealt with by the method described in Tougaard et al. (2008). In short, the study area was divided into a regular, rectangular grid consisting of 1 × 1 km cells. Assuming errors of longitude and latitude are distributed normally with a mean of zero and a standard deviation specific for each location class (Vincent et al. 2002), the most likely number of true positions within each grid cell can be computed from the positions inside it and the adjacent cells. The values assigned to the grid cells therefore reflect the likelihood that they were visited by porpoises equipped with satellite transmitters. By assuming that the behaviours of the tagged animals are representative of the porpoises in the area in general, these grid values can be used as a proxy for density. This method differs from kernel density estimators often used on the same type of data (e.g. by Sveegaard et al. 2011a) in that results are local (i.e. do not change by extension or reduction of the total study area) and do not rely on arbitrarily selected smoothing factors. The satellite tracking data converted into the density grid are shown in Fig. 2.

Porpoise densities were calculated for each season. In all seasons, several of the 1 × 1 km grid cells had a value of zero. The zero values do not necessarily represent areas with no individuals, but may be caused by a low number of tagged porpoises in those seasons. Thus, in order not to over-interpret porpoise density data, the densities were aggregated from the 1 × 1 km grid into 3 larger areas (A, B and C), and by season.

The porpoise distribution data were collected over a relatively long time frame compared to the fishing effort. We therefore conducted a variogram analysis to determine whether or not the observed spatial patterns were stable over time (see Supplement 2 at www.int-res.com/articles/suppl/m555p261_supp.pdf).

Bycatch data

Data on harbour porpoise bycatch were obtained from the CCTV video footage of the 4 REM gillnet vessels. All videos of net hauls were examined by trained staff recording the number of bycatch events. For each event, the time and position were logged using EMI software. In total, 33 by-caught porpoises were observed in the video footage (Fig. 3). Of these,

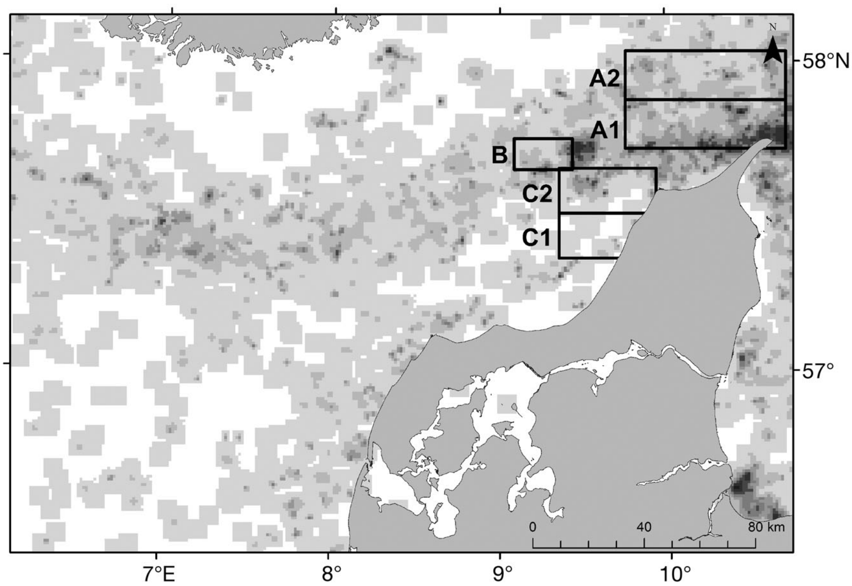

Fig. 2. Harbour porpoise density data estimated from satellite-derived positions from the 66 porpoises tagged during the period 1997 to 2012, and locations of Areas A, B and C; Areas A and C were further subdivided into Areas A1, A2 and C1, C2 based on large differences in porpoise density within the larger zones

18 were caught in the cod, 14 in the plaice and 1 in the hake fishery, and 26 (79%) of these bycatches occurred in the winter and spring (Table 1).

Bycatch model

Fishing effort, porpoise bycatch and density data were separated into seasons. Areas A and C were each divided into 2 sub-areas (A1, A2, C1, C2; Fig. 2) since large differences in densities were observed within them.

In our model, we assume the following general relationship between the response (which is the expected number of porpoise bycatches, $E(N_i)$, caught in the i^{th} haul) and porpoise density (P_i) (within the area where the i^{th} haul occurred, along with the effort pertaining to the i^{th} haul described by soak time (ST_i), net string length (NL_i), and target species, s_i (which is used as a proxy for additional differences in gear characteristics, such as mesh size and net height):

$$E(N_i) = \alpha(s_i)\mathrm{ST}_i^{\beta(s_i)}\mathrm{NL}_i^{\phi(s_i)}P_i^{\gamma(s_i)} \tag{1}$$

where $\alpha(s_i)$ is a coefficient of proportionality, while the exponents $\beta(s_i)$, $\phi(s_i)$ and $\gamma(s_i)$ allow for a non-linear relationship. This is equivalent to the formula for a chemical reaction, where the risk of reaction (bycatch) is proportional to the product of the concentration of each reactant (porpoises and fishing). Exponents equal to 1 correspond to first-order reactions (Chang 2005). In our general relationship, we do not assume that the exponents β, γ and ϕ are equal to 1, which would imply a linear relationship, although removal of the exponents was tested as a possible model reduction.

A Poisson generalized linear model (GLM) with a log link was used:

$$\log(E(N_i)) = \log(\alpha(s_i)) + \beta(s_i)\log(\mathrm{ST}_i) + \phi(s_i)\log(\mathrm{NL}_i) + \gamma\log(P_i) \tag{2}$$

A Poisson distribution is a natural choice as we are dealing with count data in the dataset {0,1,2} where the maximum number of bycaught porpoises per haul was 2. Note that the log link implies the predictors should also be log transformed when a multiplicative structure in the natural domain can be assumed. This simply means that we take log on both sides of the equation. The main purpose of the model was to test whether γ was significantly greater than 0, i.e. whether there was a positive correlation between porpoise density and the number of individuals caught in the gillnet fishery. The model selection strategy was initially the full model, in which insignificant terms were removed successively and tests performed to determine if any of the regression coefficients could be replaced by an offset, i.e. assuming direct proportionality in fishing effort and/or porpoise density (β = 1, ϕ = 1). The model selection was based on Akaike's information criterion (AIC; Akaike 1974) and was run using the function 'glm' in R (R Core Team 2012).

An alternative model (Hypothesis 3 below) with porpoise density, P, replaced with a free parameter for each combination of area and season (denoted AS), was also tested. In other words, the following 3 hypotheses were tested:

(1) Porpoise bycatch is best explained by fishing effort alone and hence the species' true underlying density can be considered equal in all areas and all seasons;

(2) porpoise bycatch is best explained by a combination of fishing effort and observed densities (P) from independent satellite tracking data; and

(3) porpoise bycatch is best explained by a combination of fishing effort and estimates of the species' true underly-

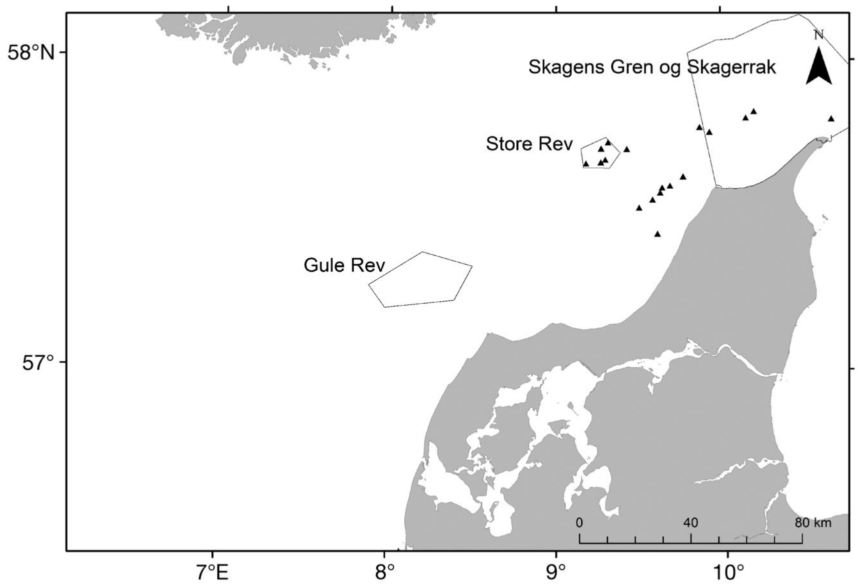

Fig. 3. Harbour porpoise bycatch events (triangles) from the 4 monitored fishing vessels. The polygons represent Natura 2000 sites 'Skagens Gren og Skagerrak', 'Store Rev' and 'Gule Rev'

ing densities, where the latter are estimated as free parameters for each AS, rather than using the satellite data.

Hypothesis 1 versus 2 was tested by comparing the AIC of models with and without inclusion of P as an explanatory variable. Hypothesis 3 was tested by replacing $\gamma \log(P_i)$ (or simply $\log(P_i)$ if γ was not significantly different from 1) with $\delta(\mathrm{AS}_i)$ in Eq. (2), where δ maps the i^{th} haul to the corresponding AS.

The final model was validated using residual deviance as a measure of goodness of fit (Madsen & Thyregod 2010). In addition, the assumption of linearity between the predictors and log-intensity was tested by replacing the linear terms with splines (replacing GLM with generalized additive model, GAM), both with and without log transformation of the predictors.

RESULTS

Bycatch model

The model results are listed in Table 3. Model III had a lower AIC score than Models I and II, indicating that the inclusion of target fish species (s_i) did not improve the model fit; the same was true for net string length (NL_i) (Models IV versus III). When comparing Models IV and V, β was not significantly different from 1. This implies that the number of porpoises caught was directly proportional to the soak time (ST_i). When reducing from Model V to VI, γ was not significantly different from 1. This means that the number of bycaught porpoises was proportional to their densities. Models VII and VIII contained either soak time or porpoise densities, but both resulted in higher AIC values compared to Model VI. The alternative, where porpoise density was replaced with a free parameter for each combination of area and season (Model VI A), also provided a higher AIC score compared to Model VI. The best model in terms of AIC was thus Model VI. The GAM equivalents of the models revealed no evidence against the assumption of linearity (Model VI had a lower AIC value than all the GAMs). Model VI can therefore be written as:

$$E(N_i) = \alpha\, \mathrm{ST}_i P_i.$$

The estimate of log(á) was −3.67 with a standard deviation of 0.22. The goodness of fit test had a p-value close to 1, which means that the Poisson distribution assumptions in the final model could not be rejected. The AIC differences revealed evidence against Hypotheses 1 (a constant true underlying porpoise abundance) and 3 (the true underlying densities could be estimated by free parameters). We can therefore conclude that the observed porpoise density was indeed useful for predicting bycatches. Hypothesis 2, i.e. 'Porpoise bycatch is best explained by a combination of fishing effort and observed porpoise densities (P) from independent satellite tracking data', was therefore accepted (Table 3).

In Fig. 4, the predicted number of bycatches (from Model VI) was plotted against the total number of observed bycatches within each area and season. Fig. 5 maps the spatial bycatch risk per 1000 hauls in the different areas and seasons predicted by Model VI, while Fig. 6 plots the predicted bycatch in relation to season and area including uncertainties. The 2 plots reveal great differences in porpoise bycatch rate, depending on area and season (Fig. 5 & 6). In winter, Area A1 had the highest bycatch rate followed by Areas A2, C2, B and C1. In spring, Area A1 had the highest bycatch rate, followed by Areas B, A2, C2 and C1. The bycatch rate was generally lower in summer compared to the other seasons and the largest value was again in Area A1 followed by B, C1, C2 and A2. The bycatch rate in autumn was high in Area A1, followed by C2, B, A2 and C1.

Table 3. Formulas, Akaike's information criterion (AIC) score and number of parameters of the 8 different models; the model with the lowest AIC value is shown in **bold**. Formula parameters are as follows: $E(N_i)$ = number of porpoise bycatches caught in the i^{th} haul, P_i = porpoise density, ST_i = soak time, NL_i = net string length, AS_i = area and season. $\alpha(s_i)$ is a coefficient of proportionality, while the exponents $\beta(s_i)$, $\pi(s_i)$ and $\gamma(s_i)$ allow for a non-linear relationship

Model	Formula	AIC	No. of parameters
I	$\log(E(N_i)) = \log(\alpha(s_i)) + \beta\,(s_i)\log(\mathrm{ST}_i) + \phi(s_i)\log(\mathrm{NL}_i) + \gamma \log(P_i)$	230.7	10
II	$\log(E(N_i)) = \log(\alpha(s_i)) + \beta \log(\mathrm{ST}_i) + \phi\log(\mathrm{NL}_i) + \gamma \log(P_i)$	225.2	6
III	$\log(E(N_i)) = \log(\alpha) + \beta \log(\mathrm{ST}_i) + \phi\log(\mathrm{NL}_i) + \gamma \log(P_i)$	222.2	4
IV	$\log(E(N_i)) = \log(\alpha) + \beta \log(\mathrm{ST}_i) + \gamma \log(P_i)$	221.2	3
V	$\log(E(N_i)) = \log(\alpha) + \log(\mathrm{ST}_i) + \gamma \log(P_i)$	219.2	2
VI	$\log(E(N_i)) = \log(\alpha) + \log(\mathrm{ST}_i) + \log(P_i)$	**218.7**	**1**
VI A	$\log(E(N_i)) = \log(\alpha) + \log(\mathrm{ST}_i) + \delta(\mathrm{AS}_i)$	235.7	19
VII	$\log(E(N_i)) = \log(\alpha) + \log(\mathrm{ST}_i)$	225.1	1
VIII	$\log(E(N_i)) = \log(\alpha) + \log(P_i)$	228.7	1

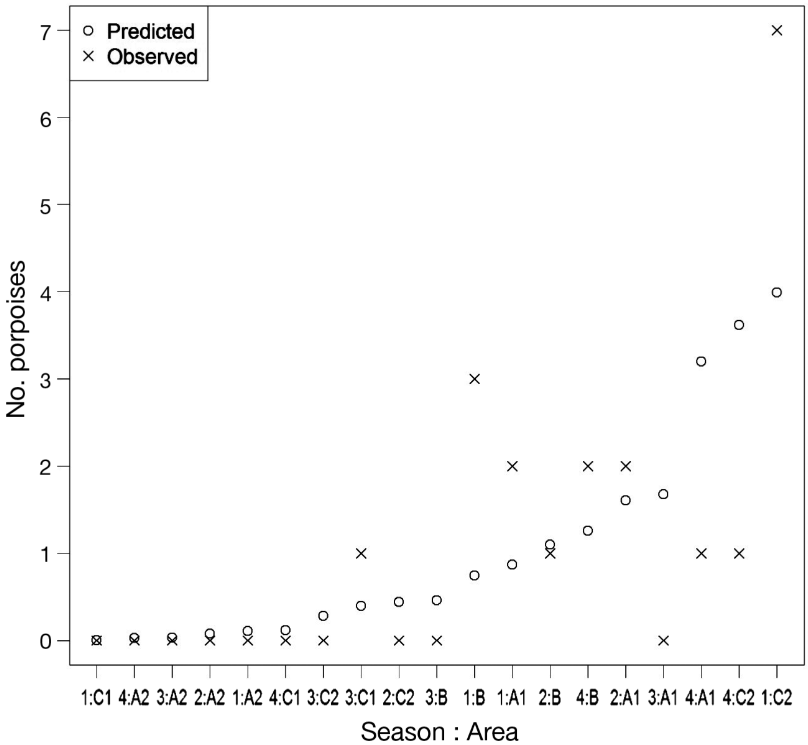

Fig. 4. Harbour porpoise bycatches, predicted from Model VI and observed in the 5 different areas (A1, A2, B, C1, C2; see Fig. 2) over 4 seasons (1: winter; 2: spring; 3: summer; 4: autumn)

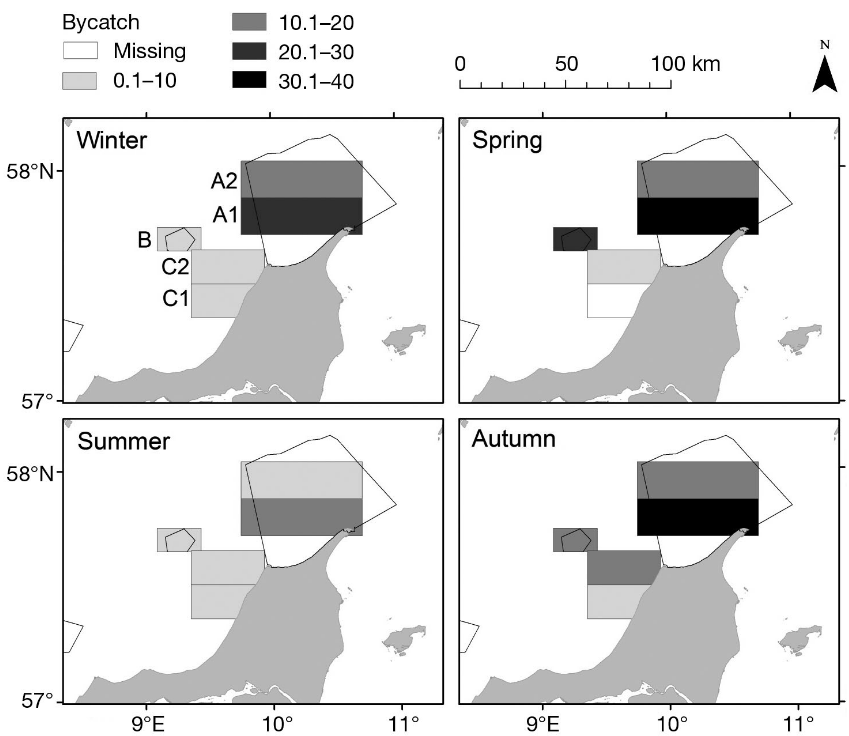

Fig. 5. Predicted harbour porpoise bycatch in 5 areas (A1, A2, B, C1, C2; see Fig. 2) and 4 seasons. Polygons represent Natura 2000 sites (see Fig. 3). The unit of the bycatch legend is number of bycaught porpoises per 1000 hauls

DISCUSSION

In this study, we had a unique dataset to investigate fishing effort and porpoise densities as factors predicting porpoise bycatch risk in relation to area and season. Our best-fitting model showed that a simple 2-stage procedure using porpoise densities and fishing effort in terms of soak time could predict bycatch risk, since a clear correlation between this and the products of porpoise densities and soak time was identified. In addition, the results of the model revealed large differences in bycatch risk predictions in terms of area and season. Our results, nevertheless, indicate in which area and season porpoise bycatch risks are highest for the 4 representative vessels. Our final model can be used as a tool to identify the areas of high and low porpoise bycatch risk if representative porpoise density and fishing effort data are available for a particular area. Furthermore, the model may be used as a tool to discover changes in bycatch risk by area and season, and monitor if changes over time are due to either shifts in fishing grounds and effort or changes in porpoise distribution. The modelled risk maps can thus support development of sampling plans for bycatch monitoring and assist managers in the development of spatially explicit mitigation strategies. The direct dependence of bycatch on both porpoise density and fishing effort highlights the importance of obtaining good density data in areas of high fishing effort and the documentation of this information (and preferably direct bycatch statistics) for areas known to have high densities of porpoises.

Our model rests on a number of assumptions. The first is that satellite-tagged porpoises are representative of the general distribution of individuals in the area. Ideally, tracking data from animals tagged in 2010 only should have been used, but only 4

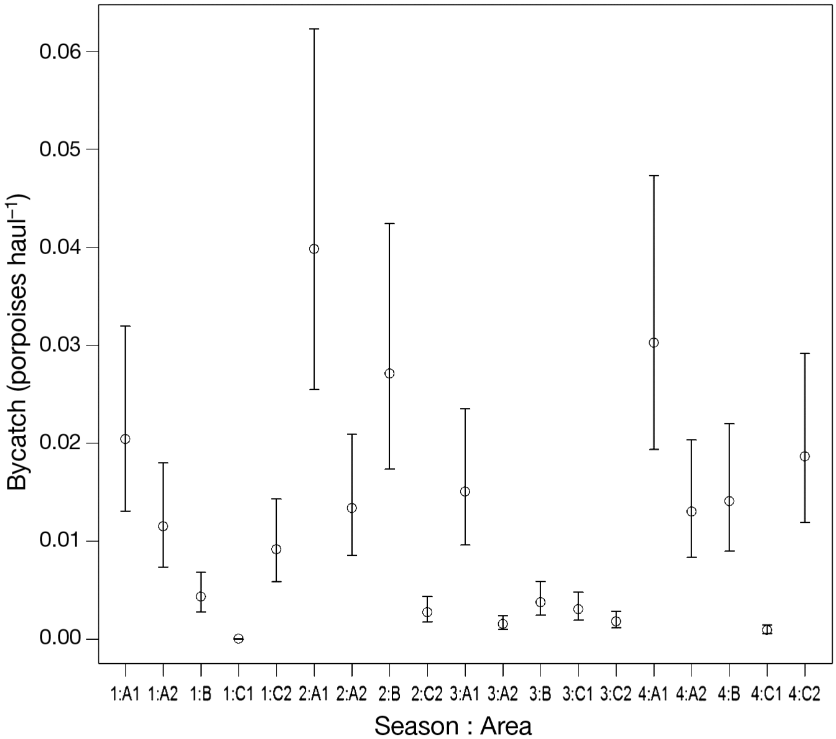

Fig. 6. Bycatch of harbour porpoises in relation to area (A1, A2, B, C1, C2; see Fig. 2) and season (1: winter; 2: spring; 3: summer; 4: autumn). Error bars are 95% confidence intervals

porpoises were tagged in 2010. Using data from only 4 animals as a proxy for all the animals in the area could lead to severe biases of the results. Consequently, we used porpoise tracking data over a longer time period. Whether the porpoise density data collected over this longer period of time are representative of the density distribution in 2010 can, however, be questioned. Especially since porpoise densities in other areas have shown changes over time (Hammond et al. 2002, 2013). This depends on whether there are large differences in movements and preferred areas between individual porpoises and whether a sufficient number of porpoises have been tagged. This is difficult to examine, but a variogram analysis of the satellite data suggested that the spatial patterns were stable over time (Fig. S3 in Supplement 2 at www.int-res.com/articles/suppl/m555p261_supp.pdf). The porpoise density map was also validated by using free parameters i.e. estimating the true underlying densities (Model VI A; Table 3). If the porpoise density map was not representative of the general population in 2010, Model VI A would have shown a lower AIC score. This would indicate that the bycatch could be better predicted by using the free parameters instead of the porpoise density map. This, however, was not the case, since Model VI had the lowest AIC. Porpoise densities in areas neighbouring the Skagerrak Sea, i.e. the southeastern Skagerrak Sea and Kattegat, have also been shown to be constant over time. The use of satellite tracking data from 64 porpoises to identify areas of high density was confirmed by comparison with densities obtained from acoustic surveys (Sveegaard et al. 2011b). The porpoise density map furthermore shows that porpoise densities are very high along the Norwegian Trench, a conspicuous topographic feature of the Skagerrak that follows the coast of southern Norway. Here, steep bottom topography results in high biological productivity compared to the rest of the Skagerrak Sea. This area of high productivity is stable and could be the reason for the observed stability of porpoise densities (Sveegaard et al. 2012). Therefore, we believe that the porpoise density distribution has not changed over time in ways that would invalidate our results.

Despite stability over time, porpoise densities could be biased if tagged individuals were different from the overall population. Earlier studies have shown no differences in home range size between males and females, but immature harbour porpoises have larger home ranges than mature individuals (Sveegaard et al. 2011a). Since the dataset used in this study contained a mixture of both juvenile and adult males and females, we do not believe that any important bias is present due to demographic differences between the tagged and overall populations.

Although we used satellite tagging data, porpoise densities could be assessed by other methods, e.g. repeated acoustic or visual surveys with high spatial coverages (Hammond et al. 2013, SAMBAH 2016). In some cases, these types of density data might even be preferred since they depict total density and are not influenced by tagging position or the small number of individuals tagged. Sighting surveys, however, only represent porpoise density at the time of the survey, while passive acoustic monitoring could be used to explore seasonal variations.

Furthermore, the stratification of the porpoise telemetry data by area and season requires a selective selection of strata by the modeler. If the strata chosen are too small, random noise will dominate and the variance of the porpoise density estimate will be large, resulting in uncertain (but unbiased) predictions. Conversely, if larger strata are chosen, the variance will be reduced but bias may be introduced since porpoise densities are not in reality constant over large areas and time spans.

The second assumption is that the fishing effort estimations truly represent those of the 4 gillnet vessels. Net string length was calculated as the distance between the start and end setting positions, meaning that unless nets were set in a straight line, string length was underestimated. Due to the high resolution of GPS data (every 10 s) it was possible to verify that most net strings were indeed set in a straight line. Short net string lengths were, however, identified in the dataset (19 m; Table 2) indicating that some inaccuracies were present, since most net panels are ~50 m and a string length of only 19 m is unlikely. We believe that these are due to variations in determining the positions of the start and end of the net string and are unlikely to have biased our results. A systematic underestimation of the string length will influence the parameter, but since we are not interested in this value it does not influence our primary conclusions. Most important is that the fishing effort was calculated by the same method for all 4 vessels.

The third assumption is that recorded porpoise bycatches are representative of the true number of such events in the monitored fishing operations. As described by Kindt-Larsen et al. (2012), detections of bycatch on video footage can be influenced by video quality, positioning of the camera and viewer experience. In our study, cameras were positioned for optimal detections, only trained staff was used and video recordings were never of such a poor quality that porpoise bycatch would not have been detectable. If, however, porpoise carcasses fell from the net before reaching the surface, they would not be recorded. The bycatches recorded on the video footage will therefore always be a minimum estimate. However, since good video quality was obtained from all vessels and the bycatches were almost evenly distributed between them, there is no reason to believe that any particular overriding bias should be present in any undetected bycatches.

The results of the modelling showed that bycatches were not distributed evenly but depended on porpoise density and fishing intensity (soak time) in the area. Other studies have likewise shown that longer soak times have a positive correlation with bycatch (Palka et al. 2008, Orphanides 2009). It was, however, surprising that net string length was not identified as a significant factor in the final model, since logically the longer the net, the higher the chance of catching a porpoise. The reason for such non-significance in the full model elaborated in this study is most likely that the differences in net string lengths were too small to be detectable in the model. Since the model parameters were based on only 33 bycatches, it seems highly likely that if more bycatch events were added to the model, net string lengths would become a significant factor. The lack of an effect of net length could also be due to the fact that one of the vessels occasionally used very short net strings to catch cod on highly productive wrecks. The wreck net fishery has been shown to be associated with high bycatch rates (Vinther 1999), and is known for using short net strings (<400 m). Net lengths from this fishery could therefore influence the results in such a way that this factor did not emerge as significant factor overall. It was not possible, however, to delete these sets from the analysis as wreck net sets were not independently identified, and short nets were also used in other contexts.

Harbour porpoise bycatch was observed in all 3 fisheries monitored in this study, but target species was rejected from the best-fitting model. Earlier studies in the North Sea also reported porpoise bycatches in cod, plaice and hake fisheries, but bycatch rates were found to vary in relation to the target species (Vinther 1999). It seems likely that the lack of significance of target species in our models is also due to the relative small dataset (33 bycatches). Most notably, our results in relation to bycatches in the hake fishery should be interpreted with caution due to the relatively limited number of observations from this fishery. In our study, only 1 porpoise was bycaught during 65 hauls for the hake fishery. Other programmes collecting porpoise bycatch data in hake gillnet fisheries have identified higher rates (Tregenza et al. 1997, Larsen et al. 2013). Based on the experiences gained from these other studies, we believe that both net string length and target species could become significant factors if more data were included in the model. We recommend that more REM monitoring trials be conducted on porpoise bycatch, and that these data are incorporated into the model to reveal the full effects of net string length and target species.

In relation to coverage of the gillnet fleet, the 4 REM vessels landed 23% of total gillnet landings in the area and were responsible for 22% of the total catch value. Vessel monitoring system (VMS) locations from the Danish gillnet fleet show that vessels >15 m length overall (loa) were also active in Areas B and C. Not a single VMS point was, however, recorded in Area A. The most likely reason for this is that Areas B and C are better gillnet fishing grounds, while Area A serves as an important fishing ground for the trawl fishery, which may deter netting as it poses a risk of losing gillnets (Sørensen & Kindt-Larsen 2016). Vessels <15 m loa would, however, favour the use Area A and take the risk of losing gear, since they have limited scope for fishing further from land. During 2010, vessels <15 m loa did not carry VMS and their positioning data were therefore not available. It is unnecessary to sample the entire fishing fleet to validate the model. Because bycatch is proportional to fishing effort, only data on porpoise density are required to map the relative risk. To determine whether some gear types are responsible for more bycatch than others will, however, require the combined data of fishing effort and bycatch.

The simple relationship identified by our model is logical, but to our knowledge this study is the first to demonstrate that bycatch risk can be predicted by such a simple relationship. The model of a 2-factor product to detect risk was initially proposed in the Lotka-Volterra model of predator–prey relationships (Lotka 1910). This model states that a prey item can only be caught by a predator if there is an area and time overlap between the 2. Transferring this into porpoise bycatch, we state that such an incident can only occur if fisheries and porpoises overlap in space and time. Other authors have incorporated fishing effort and species density data using similar methods to reveal areas of bycatch risk (e.g. Goldsworthy & Page 2007, Herr et al. 2009, Hamer et al. 2013, Murray & Orphanides 2013). In South Australian shelf waters, overlays between distributions of demersal gillnet effort and Australian sea lions *Neophoca cinerea* and New Zealand fur seals *Arctocephalus forsteri* were made to identify areas of possible interactions (Goldsworthy & Page 2007, Hamer et al. 2013). Herr et al. (2009) mapped the spatial and temporal overlap between porpoises and fisheries in the German Bight. These authors could not, however, correlate their predicted high risk areas with observed bycatch rates due to a lack of monitoring of the latter in the relevant fisheries. Our main advantage over other studies of bycatch risk was that we were able to verify predicted bycatches with observed bycatches.

CONCLUSIONS

This study presented a unique dataset involving high-resolution information on fishing effort, porpoise densities and bycatches, which allowed for fine-scale analyses that identified and verified a relationship. This relationship has resulted in a method to predict potential areas of bycatch risk when spatial data on porpoise densities are available. The model predictions can act as a starting point for investigations of harbour porpoise bycatches and should be of considerable interest for fisheries management and bycatch mitigation in general, and in relation to the design and implementation of effective conservation measures for protected areas in particular.

Acknowledgements. The authors thank the 4 fishers for access to their REM data and for their committed collaboration. Additionally, we thank Archipelago Marine Research for technical support with the REM system and data analysis. We also thank everyone who assisted with the porpoise tagging, especially the pound net fishermen, without whom no tagging would have been possible. The tagging was carried out under permission from the Danish Forest and Nature Agency (SN 343/SN-0008) and the Animal Welfare Division (Ministry of Justice, 1995-101-62). Some of the satellite-tagged porpoises were tagged as part of a joint project between the Danish Institute for Fisheries Research, the Fjord and Belt Centre, Aarhus University (AU) and University of Southern Denmark in the years 1998 to 2002, and others were tagged as part of a cooperation between AU and U. Siebert at the University of Kiel, Research and Technology Centre (FTZ) in 2003 to 2009. We finally thank the Danish Ministry for Food, Agriculture and Fisheries, the European Fisheries Fund, MESMA (EU-FP7 project on monitoring and evaluation of spatially managed marine areas) and MYFISH (EU-FP7 project on monitoring and evaluation of spatially managed marine areas) for funding the project.

LITERATURE CITED

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

ArgriFish (2010) Yearbook of fishery statistics 2010. Ministry of Food, Agriculture and Fisheries, Copenhagen. http://webfd.fd.dk/info/sjle3/fsa_bog2010/Fiskeristatistisk.pdf

Chang R (2005) Physical chemistry for the biosciences. University Science Books, Sausalito, CA

DeMaster DP, Fowler CW, Perry SL, Richlen ME (2001) Predation and competition: the impact of fisheries on marine-mammal populations over the next one hundred years. J Mammal 82:641–651

Douglas D (2006) The Douglas Argos-filter algorithm, version 7.03. US Geological Survey, Anchorage, AK. http://alaska.usgs.gov/science/biology/spatial/pdfs/argosfilterv703_manual.pdf

EC (European Commission) (1992) Habitats Directive: Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora. Off J Eur Union L 206:7–50

EC (2004) Council Regulation (EC) No. 812/2004 of 26 April 2004 laying down measures concerning incidental catches of cetaceans in fisheries and amending Regulation (EC) No. 88/98. Off J Eur Union L 150:12–31

Goldsworthy SD, Page B (2007) A risk-assessment approach to evaluating the significance of seal bycatch in two Australian fisheries. Biol Conserv 139:269–285

Hamer DJ, Goldsworthy SD, Costa DP, Fowler SL, Page B, Sumner MD (2013) The endangered Australian sea lion extensively overlaps with and regularly becomes bycatch in demersal shark gill-nets in South Australian shelf waters. Biol Conserv 157:386–400

Hammond PS, Berggren P, Benke H, Borchers DL and others (2002) Abundance of harbour porpoise and other cetaceans in the North Sea and adjacent waters. J Appl Ecol 39:361–376

Hammond PS, Macleod K, Berggren P, Borchers DL and others (2013) Cetacean abundance and distribution in European Atlantic shelf waters to inform conservation and management. Biol Conserv 164:107–122

Herr H, Fock HO, Siebert U (2009) Spatio-temporal associations between harbour porpoise *Phocoena phocoena* and specific fisheries in the German Bight. Biol Conserv 142: 2962–2972

IWC (International Whaling Commission) (1994) Report of the workshop on mortality of cetaceans in passive fishing nets and traps. In: Perrin WF, Donovan GP, Barlow J (eds) Gillnets and cetaceans. Report International Whaling Commission, Special Issue 15, IWC, Cambridge, p 1–72

Kindt-Larsen L, Dalskov J, Stage B, Larsen F (2012) Observing incidental harbour porpoise *Phocoena phocoena* bycatch by remote electronic monitoring. Endang Species Res 19:75–83

Larsen F, Krog C, Eigaard OR (2013) Determining optimal pinger spacing for harbour porpoise bycatch mitigation. Endang Species Res 20:147–152

Lotka AJ (1910) Contribution to the theory of periodic reactions. J Phys Chem 14:271–274

Madsen H, Thyregod P (2010) Introduction to general and generalized linear models. Chapman & Hall, London

Murray KT, Orphanides CD (2013) Estimating the risk of loggerhead turtle *Caretta caretta* bycatch in the US mid-Atlantic using fishery-independent and -dependent data. Mar Ecol Prog Ser 477:259–270

Orphanides CD (2009) Protected species bycatch estimating approaches: estimating harbour porpoise bycatch in US northwestern Atlantic gillnet fisheries. J Northwest Atl Fish Sci 42:55–76

Palka DL, Rosmann MC, Vanatten A, Orphanides CD (2008) Effect of pingers on harbour porpoise (*Phocoena phocoena*) bycatch in the US Northeast gillnet fishery. J Cetacean Res Manag 10:217–226

R Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Read AJ, Drinker P, Northridge S (2006) Bycatch of marine mammals in US and global fisheries. Conserv Biol 20: 163–169

SAMBAH (2016) Static Acoustic Monitoring of the Baltic Sea Harbour Porpoise (SAMBAH). Final report under the LIFE+ project LIFE08 NAT/S/000261. Kolmårdens Djurpark AB, Kolmården

Sørensen TK, Kindt-Larsen L (2016) Uncovering governance mechanisms surrounding harbour porpoise conservation in the Danish Skagerrak Sea. Mar Pol 71:318–324

Sveegaard S, Teilmann J, Tougaard J, Dietz R, Mouritsen KN, Desportes G, Siebert U (2011a) High-density areas for harbor porpoises (*Phocoena phocoena*) identified by satellite tracking. Mar Mamm Sci 27:230–246

Sveegaard S, Teilmann J, Berggren P, Mouritsen KN, Gillespie D, Tougaard J (2011b) Acoustic surveys confirm the high-density areas of harbour porpoises found by satellite tracking. ICES J Mar Sci 68:929–936

Sveegaard S, Nabe-Nielsen J, Stæhr KJ, Jensen TF, Mouritsen KN, Teilmann J (2012) Spatial interactions between marine predators and their prey: herring abundance as a driver for the distributions of mackerel and harbour porpoise. Mar Ecol Prog Ser 468:245–253

Tougaard J, Teilmann J, Tougaard S (2008) Harbour seal spatial distribution estimated from Argos satellite telemetry: overcoming positioning errors. Endang Species Res 4:113–122

Tregenza N, Berrow SD, Hammond PS, Leaper R (1997) Harbour porpoise (*Phocoena phocoena* L.) by-catch in set gillnets in the Celtic Sea. ICES J Mar Sci 54:896–904

Vincent C, McConnell BJ, Ridoux V, Fedak MA (2002) Assessment of Argos location accuracy from satellite tags deployed on captive grey seals. Mar Mamm Sci 18:156–166

Vinther M (1999) Bycatches of harbour porpoises (*Phocoena phocoena* L.) in Danish set-net fisheries. J Cetacean Res Manag 1:123–135

Editorial responsibility: Per Palsbøll, Groningen, The Netherlands

Submitted: February 23, 2015; Accepted: June 15, 2016
Proofs received from author(s): August 8, 2016