Revised estimates of harbour porpoise (*Phocoena phocoena*) bycatches in two Norwegian coastal gillnet fisheries

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ABSTRACT
Data from a monitored segment (18 vessels) of the fleet of about 6000 small vessels operating gillnets in the coastal zone were used to estimate the bycatch rate, and landings statistics of the target species for the whole fleet using same gear types were used to extrapolate to the entire fisheries. The estimated annual bycatch of about 6900 harbour porpoises in the period 2006-2008 (Bjørge *et al.* 2013) was based on incorrect landings statistics of the target species provided by the Directorate of Fisheries. Using the same model and correct landings statistics the revised estimate is 3541 (CV 0.10) porpoises annually.

The bycatch for the entire period 2006-2014 is estimated by two methods: ratio-based approaches and model-based approaches. In the ratio-based approaches, the data were stratified according to five different stratification schemes, by *month*, by *area*, by *region*, and by each possible combination of *area* × *month* and *region* × *month*. The stratified ratio-based bycatch estimates ranged from 2317 (CV 0.15) to 3375 (CV 0.16) porpoises.

In the model-based approaches, generalized additive models (GAMs) were used to estimate the bycatch rate and to extrapolate to entire fisheries. Poisson and negative binominal distributions and their zero-inflated counterparts were compared. The Poisson distribution performed best, and the best model based on Akaike's Information Criterion adjusted for small samples, AICc, yielded an annual bycatch of 2946 (CV 0.11) porpoises.

KEY WORDS: HARBOUR PORPOISE, BYCATCH, GILLNET FISHERIES.

INTRODUCTION

Throughout their range, harbour porpoises (*Phocoena phocoena*) are notoriously vulnerable to incidental catches in gillnets (Jefferson and Curry, 1994; Read *et al*., 2006; Vinther, 1999; Orphanides, 2009; IWC, 1992, 1996; ICES, 2008, 2011a). EU has introduced a regulation for monitoring and mitigating bycatches of small cetaceans in European Union fisheries (EU Regulation 812/2004). This regulation mandates that Acoustic Deterrent Devices (ADDs or pingers) should be used in gillnet fisheries in some areas and periods for vessels larger than 12m overall length, and obliges that observer programs should be established for vessels larger than 15m overall length. For small-sized fishing vessels less than 15m overall length, the EU regulation indicates that data on incidental catches of cetaceans should be collected through scientific studies or pilot projects. According to ICES (2011b), the measures of regulation 812/2004 have not been well implemented. A shortcoming of this regulation is that it does not address bycatch monitoring and mitigation for vessels smaller than 15m overall length, a segment of the gillnet fleet that may have substantial interactions with coastal harbour porpoises. Similar regulations to reduce bycatches of small cetaceans are not implemented in Norway, and currently no porpoise bycatch mitigation measures exist in Norway.

Based on data from a monitored segment of the Norwegian coastal fleet of gillnetters (15-22 vessels less than 15 m total length, named the Coastal Reference Fleet, CRF), the bycatch rate (number of bycaught porpoises per kg of the target species) was estimated in fisheries for cod (*Gadus morhua*) and monkfish (*Lophius piscatorius*). Landings statistics from the Directorate of Fisheries were used to extrapolate to entire fisheries (Bjørge *et al*., 2013). General additive models (GAMs) were used to derive bycatch rates and extrapolate to entire fisheries. The two best models estimated bycatches of 20,719 and 20,989 porpoises during the period 2006-2008, with CVs of 36% and 27%, respectively. Thus, about 6,900 porpoises were believed to have been taken annually in the gillnet fisheries for cod and monkfish.

The CRF has continued to collect data on porpoise bycatch, and in this paper we present bycatch estimates for the entire period 2006-2014. The Directorate of Fisheries again provided landings statistics for cod and monkfish taken with gillnets throughout this period. However, when comparing the recent submission of landing statistics with the statistics used by Bjørge *et al*. (2013) we found discrepancies. It turned out that the statistics first provided by the Directorate of Fisheries for 2006-2008 contained landings of cod and monkfish taken with all gear types utilized by the coastal fleet of commercial fishing vessels less than 15m total length. This included hand jigs, long lines, purse seine, Danish seine and demersal trawl. These are gear types with no or very low bycatches of harbour porpoises and applying the bycatch rate generated from gillnet fisheries for cod and monkfish to entire landings from all gear types severely overestimated the bycatch. Therefore, the estimated bycatch in Bjørge *et al*. (2013) was a substantial overestimate.

MATERIAL AND METHODS

The Coastal Reference Fleet

Norwegian landing statistics for target species are comprehensive and assumed to reflect the true catches, and fishing effort statistics are available for the larger vessels via their log books. However, for the fleet of small coastal vessels (less than 15m total length, where log books are not mandatory) improved information is needed on the sex, age, and size composition of all of the target species, on the relationship between fishing effort and catch of these target species, and on the species and size composition of the catches of all non-target species. Therefore, the Institute of Marine Research (IMR) contracted with two small (<15 m) fishing vessels in each of nine coastal statistical areas (Fig. 1) to provide detailed information on their fishing effort and their catches of all target and non-target species, including marine mammals and birds (Bjørge *et al*., 2006). These vessels were randomly selected among commercial vessels applying for the contract. The contracted vessels are referred to as the Coastal Reference Fleet (CRF), and each CRF vessel has a contact person at IMR. The contact persons visited the vessels regularly and remained onboard on day trips at sea. Any discrepancies in statistics between days with and without IMR staff onboard may lead to termination of a vessel's contract. The main task of the IMR staff onboard was to guide the fisher in correct reporting of effort, catch and bycatch.

Catch data from the monitored segment of the fleet, CRF

The CRF was contracted to target monkfish and cod using the same standard gillnet gear as used in the commercial coastal fleet, i.e., bottom-set gillnets with half mesh of 180 mm for monkfish, and bottom-set gillnets with half mesh of 75-105 mm for cod. The twin size was 0.7 mm in both gear types. The monkfish nets are 27.5 m long, 12.5 meshes high and 40-50 nets are typically set in a string. The cod nets are 27.5 m long and a varying numbers of nets (but far less than monkfish nets) are set in a string. In all the fisheries added together, a total of 841 harbour porpoises were taken by CRF over the nine years. In most cases, takes were of a single animal per trip, but takes of up to 13 harbour porpoises per trip were observed. A total of 317 harbour porpoises (37.7%) were caught in the cod fishery, and 392 harbour porpoises (46.6%) were caught in the monkfish fishery. Thus, a total of 84.3% of the CRF bycatch was taken in the cod and monkfish fisheries. The remaining 15.7% were caught by the CRF in other fisheries. The locations of the porpoises bycaught by CRF in the period 2006-2014 are depicted in Fig. 1. The total catches of monkfish and cod harvested by the CRF and the entire commercial fleet of vessels less than 15 m operating in the coastal zone in 2006-2014 are summarized, by coastal statistical area and month, in Fig. 2.

Defining fisheries in the CRF

The data shows that the CRF did not target cod and monkfish exclusively; other commercial species (such as saithe *Pollachius virens*, mackerel *Scomber scombrus*, herring *Clupea harengus*, haddock *Melanogrammus aeglefinus*, and many more) were frequently fished as well. In the period 2006 – 2014, cod catches constituted 45.6% of total landings, and monkfish a mere 2.9%. Therefore, to be able to extrapolate the CRF derived bycatch rates to the entire coastal fisheries, it was necessary to distinguish the cod and monkfish fisheries from other fisheries. We used a gear-based fisheries definition, according to the gear use stipulated in the CRF contracts. Thus, bottom set gillnets with mesh sizes between 75 and 105mm were defined as cod nets and bottom set gillnets with a mesh size of 180mm as monkfish nets. Additionally, gillnets of unspecified mesh size were included in the cod fishery. The CRF data was then aggregated by year, month, area and fishery, i.e. cod and monkfish catches and harbour porpoise takes were summed for every possible combination. The resulting data set consisted of 9 years × 12 months × 9 areas × 2 fisheries = 1944 data points.

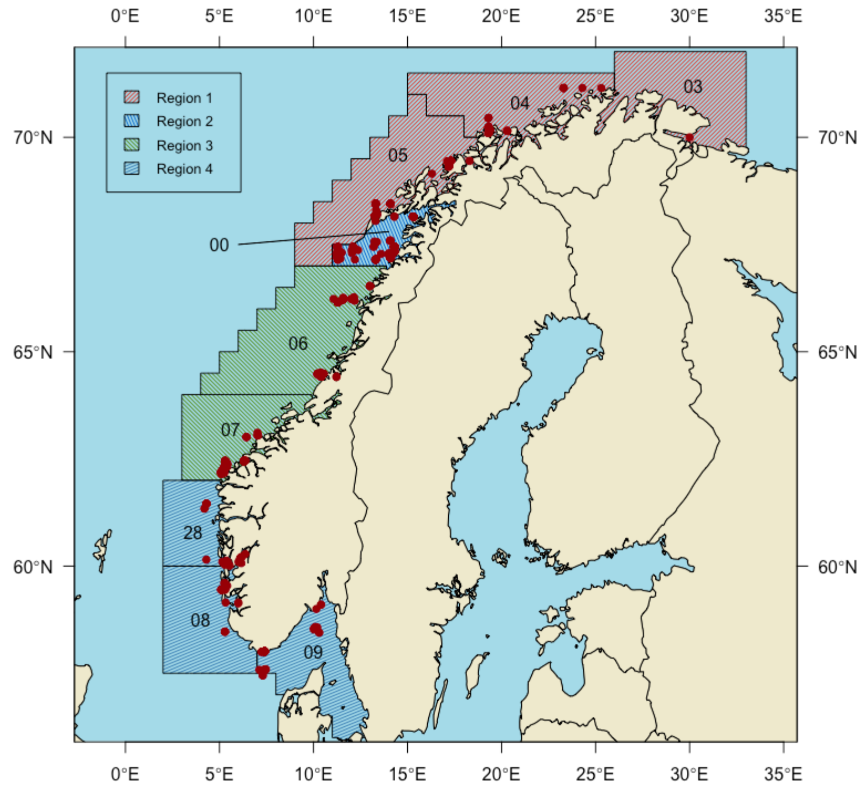

Figure 1: The nine fishery statistic areas along the Norwegian coastline. Shaded background lines represent the designation of areas into four different regions. Red dots represent bycatches of harbour porpoise taken by the CRF between 2006 and 2014.

Landings statistics from the entire commercial fleet less than 15 meters

Landings statistics for the entire commercial fleet of gillnetters less than 15 m were provided by the Directorate of Fisheries. These statistics are based on fish landed in harbours. The statistics are not specified by gillnet type, and therefore include fish taken by all types of bottom set gillnets. To account for this in our bycatch estimates, catch data from the commercial fleet was adjusted by the ratio of catch obtained in the cod/monkfish fisheries (as defined above) to the total catch for cod/monkfish, estimated from the CRF data.

$$C_{a,f} = C_{a,F} \times \frac{C_{b,f}}{C_{b,F}}$$

In this equation, C denotes catch, the subscripts a and b represent the commercial fleet and the reference fleet, respectively, while F and f indicates "all gears" and gears according to the above definitions, respectively. Thus, $C_{a,f}$ would represent the catch for fishery F in the commercial fleet, but corrected for only cod/monkfish gear use. The monkfish fishery primarily occurs in late summer and autumn, and is widely spread geographically (Fig. 2, right panels). Fishing effort in the coastal cod gillnet fishery is large, especially during the cod spawning season in February-April in northern statistical areas 00, 04, and 05 (Fig. 2 left panels). Nets of similar mesh size are used in multispecies gadoid fisheries that occur along the entire Norwegian coast throughout the year, but with smaller effort. Gillnet landings of cod are highest during February to April and lowest during July to January. The landing statistics were aggregated by year, month, and statistical area, in the same way as the CRF data.

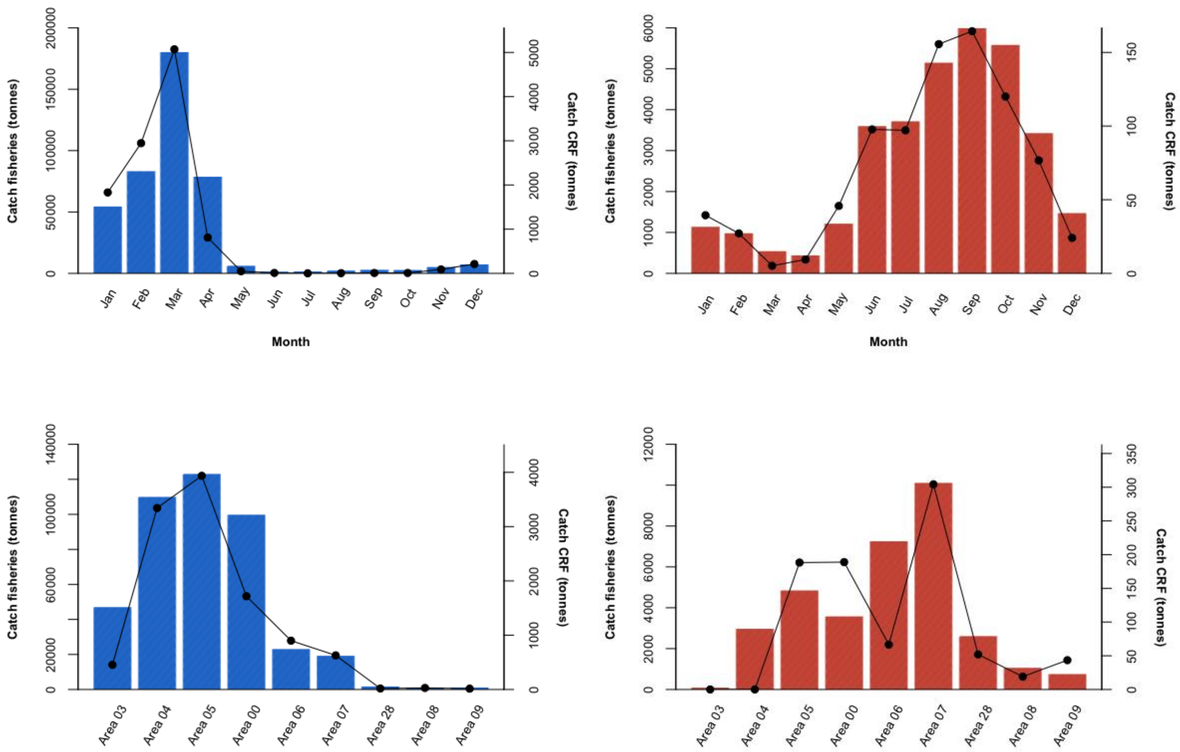

Figure 2: Cod (left panels, blue bars) and monkfish (right panels, red bars) landings in the nation wide coastal fleet (bars) and in the CRF (lines and dots), summed by month (top panels) and area (bottom panels).

Estimating bycatch rates by a ratio-based approach

Bycatch rates in the CRF were estimated using both ratio-based and model-based approaches. In the ratio-based approaches, the data were stratified according to five different stratification schemes, by *month*, by *area*, by *region*, and by each possible combination of *area* × *month* and *region* × *month*. The areas and regions used were the same ones as described previously. Two different measures of fishing effort were used: catch (tons of landed fish) and number of fishing trips. If we consider the $r_{i,j}$ as the ratio of bycatch to fishing effort, then a generalized ratio estimate can be expressed mathematically in the form:

$$r_{i,j} = \frac{t_{i,j}}{1 + e_{i,j}}$$

Where $t_{i,j}$ is the observed takes (bycatches) in stratum i for the fishery j and $e_{i,j}$ is the fishing effort in stratum i for fishery j. The constant 1 in the denominator was added because some stratification schemes yielded strata (such as the cod fishery in the latter half of the year) that had no bycatch, and division by zero is not defined. The bycatch ratios were then applied to the nation-wide fleet by multiplication with the unobserved effort. Letting B be the predicted number of takes in both fisheries across all strata and $E_{i,j}$ be the unobserved effort in stratum i for fishery j, we have:

$$B = \sum r_{i,j} \times E_{i,j}$$

This equation represents the final ratio-based bycatch estimate.

The CVs were calculated by bootstrapping. In each bootstrap iteration, a number of observations N equal to the number of strata in each stratification scheme were sampled at random with replacement from the CRF data. A bycatch estimate was calculated from the new sample, and extrapolated using data from the commercial fleet, as explained above. This procedure was replicated 1000 times, and the CV was calculated from the resulting distribution of B values (i.e. predicted bycatch).

Estimating bycatch rates by a model-based approach

In the model-based approach, generalized linear additive models (GAMs) were used. When fitting a GAM, the modeling function needs to make assumptions about the probability distribution of the data. It is therefore necessary to specify the family of statistical distribution that should be used. In their 2006 – 2008 analysis of the CRF data, Bjørge *et al*. (2013) assumed that the bycatch followed a Poisson distribution, an assumption which is often made for countable (e.g. bycatch) data. Usually, the choice of distribution incorporates information about the population which is being modeled, and in particular the expected distribution of that population based on biological and ecological knowledge. But in the case of the CRF data, the Poisson distribution may be a poor fit because the data may be over-dispersed and zero-inflated. Zero-inflation may violate distributional assumptions, and could possibly lead to uncertainty regarding parameter estimates (Martin *et al*., 2005). The same is true for over-dispersion. Therefore, it seemed prudent to test the Poisson assumption by exploring the extent of over-dispersion and zero-inflation in the fitted model, and examining results of models using other candidate distributions.

Over-inflation in the Poisson GAM was tested using the method outlined in Cameron and Trivedi (1990), using *overdispersion* from the R package *AER* (Kleiber and Zeileis 2008). In a Poisson model, we have the mean $E(Y) = \mu$ and $var(Y) = \mu$ (i.e. the mean and the variance are equal). The overdispersion test simply tests as a null hypothesis that $E(Y) = var(Y) = \mu$ against an alternative hypothesis, that $var(Y) = \mu + c \times f(\mu)$, where c is some constant, and $f(\mu)$ is some monotonic function. If the test results in a c value greater than one, this indicates over-dispersion and conversely, values less than one indicate under-dispersion. Since the negative binomial distribution is typically used in cases where the Poisson is not appropriate, the log-likelihood ratios of a negative binomial regression was also compared against a Poisson regression under the assumption that $Var(Y) = \mu$. This test was conducted with *odTest* from the R package *pscl* (Jackman, 2015).

The candidate distributions that were tested were the Poisson and the negative binomial (NB), as well as their zero-inflated counterparts, i.e. the zero-inflated Poisson (ziP) and the zero-inflated negative binomial (zinb). The best GAM (model 1.10) used in Bjørge *et al*. (2013) and associated nested models (models 1 – 13, listed in Table 1) were run using each of the statistical distribution families listed above. In all models, “number of harbour porpoises” was entered as the response variable and catch was specified as an offset. Nested models within each family were compared using AICc values (Aikake, 1974). The fit statistics of the best model candidates in terms of AICc within each family were then compared.

QQ-plots, or quantile-quantile plots, as in Augustin *et al*. (2012), of the best models within each family were used to evaluate the distributional assumptions of each model. Ordered theoretical quantiles based on the distribution selected were plotted against the ordered observed quantiles in the CRF data. If the distributional assumptions were correct, then the resulting points were expected to fall roughly on a line. The linearity of the resulting plots were used as a measure of the suitability of that distribution.

Table 1: The various GLM/GAM/GAMM models evaluated for modelling bycaught porpoises. "+" separates main effects, ":" denotes interactions and "*" indicates all main effects and interactions. REGION, FISHERY, SEASON and QUARTER are factor variables. Model 13 corresponds to model 1.10 in Bjørge et al. (2013).

#	Model formulation
	No smoothing terms (only factor variables):
1	offset(LOG.CATCH)
2	offset(LOG.CATCH) + REGION
3	offset(LOG.CATCH) + FISHERY
4	offset(LOG.CATCH) + SEASON
5	offset(LOG.CATCH) + FISHERY + SEASON
6	offset(LOG.CATCH) + FISHERY + REGION
7	offset(LOG.CATCH) + FISHERY + QUARTER
8	offset(LOG.CATCH) + SEASON + REGION
9	offset(LOG.CATCH) + QUARTER + REGION
10	offset(LOG.CATCH) + FISHERY + SEASON + REGION
11	offset(LOG.CATCH) + FISHERY + SEASON) + REGION + FISHERY : SEASON
12	offset(LOG.CATCH) + FISHERY + SEASON + REGION + FISHERY : REGION
13	offset(LOG.CATCH) + FISHERY + SEASON + REGION + FISHERY : REGION + FISHERY : SEASON

CVs for the GAM models were calculated by bootstrapping in the same manner described previously. In each bootstrap iteration, a number of observations n = 1944 (9 years × 12 months × 9 areas × 2 fisheries) were sampled at random with replacement from the CRF data. A bycatch estimate was calculated from the new sample, and extrapolated using data from the commercial fleet. This procedure was replicated 1000 times, and the CV was calculated from the resulting distribution of predicted values.

Analyses were conducted in RStudio version 0.99.887 with R version 3.1.1 (R Core Team, 2014), running on OS X El Capitan 10.11.3. Packages used include *mgcv* (Wood, 2006) and *nlme* (Pinheiro *et al*., 2016) for modelling, and *maps* (Becker *et al*., 2016), *maptools* (Bivand, 2016) and *rgdal* (Bivand *et al*., 2015) for map making.

RESULTS

Fig. 3 shows the frequency of strata with an associated bycatch $x \in \{0, 1, 2, \ldots, N\}$ animals, where N is the maximum number of animals taken in a single stratum, excluding values of x where the bycatch was 0. A stratum here refers to one of the 1944 possible combinations of year, month, area and fishery in the aggregated data set, as described previously. An examination of the frequency of takes revealed that the data were zero-inflated, but it is difficult to say what proportion of these zeroes were "true zeroes" and what proportion were "false zeroes", i.e. whether they were the result of there not being any harbour porpoises in the bycatch, or the fishermen's failure to record them. Some unknown proportion of true zeroes was expected due to the low fishing efforts in some areas and months (Fig. 2), but this proportion has not been estimated.

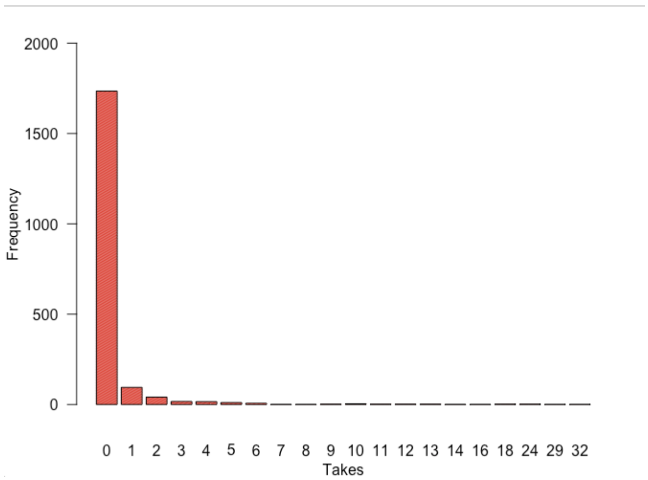

Figure 3: Frequency distribution of takes of harbour porpoise in the aggregated CRF data (n=1944).

The stratified ratio-based bycatch estimates ranged from 2317 (CV 0.15) to 3375 (CV 0.16) porpoises (Table 2). The various model formulations used in the model-based approach are shown in Table 1. The best model within each statistical distribution family, as determined by comparing AICc scores was model 13 for all families. This model included the factor variables *fishery*, *season* and *region*, and the interaction terms *fishery* × *region* and *fishery* × *season*. Model 13 explained 57-70% of the variation in bycatch, depending on the statistical family used. Fig. 4 provides diagnostic information about the three candidate models. If the model distributional assumptions are met, then the points on the QQ-plots (Fig. 4, left panels) should fall on the red lines. We can see that the deviance residuals of the Poisson (Fig. 4A) and the ziP models (Fig. 4C) deviate markedly from this line for low and large quantiles. The residuals of the NB model (Fig. 4E) on the other hand fall more neatly on the line, but deviate somewhat for quantiles > 1.75. The residual histograms show that the fittings of all three models result in a number of deviance residuals > 3, which contribute to skewing model predictions.

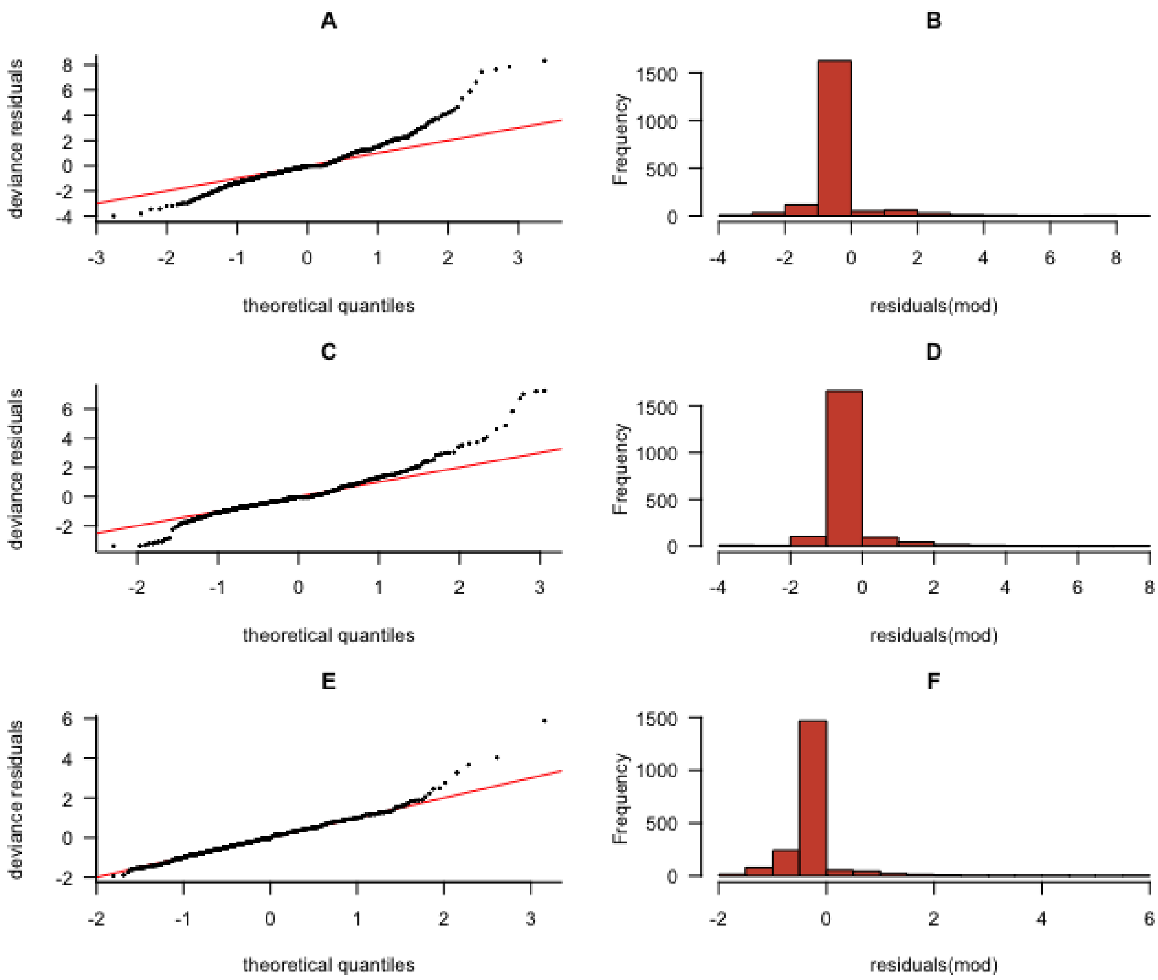

Figure 4: QQ-plots and deviance histograms for Poisson (A and B), zero-inflated Poisson (C and D) and negative binomial (E and F) models. Residuals refer to deviance residuals

The predicted bycatches with CVs and 95% confidence intervals for the best models are shown in Table 3. Taking the stratified ratio estimations of 2317 to 3375 porpoises as a ballpark range of the expected yearly bycatch, the predicted values from the Poisson and ziP models, ranging from 2857 to 4073 (Poisson) and 3963 to 6679 (ziP) seem reasonably close, with predictions from the latter model somewhat greater than expected.

Table 2: Stratified ratio-based bycatch estimates with associated CVs and 95% CIs for harbour porpoise in the combined cod and monkfish fisheries. All values represent averages over nine years of data, rather than a single year. Bycatch refers to average annual bycatch.

Data aggregation scheme	Predicted bycatch	CV	95% CI
Area × month	2317	0.15	1648 – 3012
Region × month	2483	0.12	1932 – 3125
Area	2459	0.28	1170 – 3877
Month	3375	0.16	2367 – 4569
Region	2476	0.16	1724 – 3227

Table 3: Model fit statistics for model #13 (specified in Table 1), with bycaught porpoises as the response variable. Predicted bycatch refers to the average yearly predicted bycatch for the nine years of data. R^2 refers to Pearson's correlation between the predicted response and the observed bycatch. CVs were bootstrap-generated.

Model #	DF	Deviance explained	Scale	AICc	Predicted bycatch	R^2	CV	95% CI
Poisson	10	0.57	0.78	2089	2946	0.66	0.11	2184 – 3707
Zero-inflated Poisson	10	0.64	0.55	1871	4199	0.64	0.11	2898 – 5498
Negative binomial	10	0.70	0.26	1565	6165	0.39	0.62	3567 – 10756

Fig. 5 compares observed data with the predicted bycatch per month and area using the best model (model 13) with different statistical distribution families. In all three cases, the models were able to capture the general variation in bycatch over months and areas, but the NB model greatly overestimated bycatch in the period February – April, and in areas 05, 00, and 06. Predicted bycatch derived from the Poisson and the ziP models was somewhat higher (than the observed bycatch) for the months February through April, but generally adhered much more closely to the observed bycatch than the NB model (Pearson's r = 0.66 and 0.64, respectively vs. 0.39 for the NB).

Applying the best model to the corrected landing statistics from the Directorate of Fisheries, the predicted yearly bycatch was 2946, 4199 and 6165 porpoises, for the Poisson, ziP and NB models, respectively. The stratified ratio estimates ranged from 2317 to 3375 porpoises. The predictions of the Poisson model seem to agree the most with the observed bycatch, and the stratified ratio estimates. The bootstrap-generated CV and the 95% confidence interval for the Poisson model was 0.11 and 2184 – 3707. Thus, the combined stratified ratio and model approaches suggest an annual bycatch of ~ 3000 harbour porpoises.

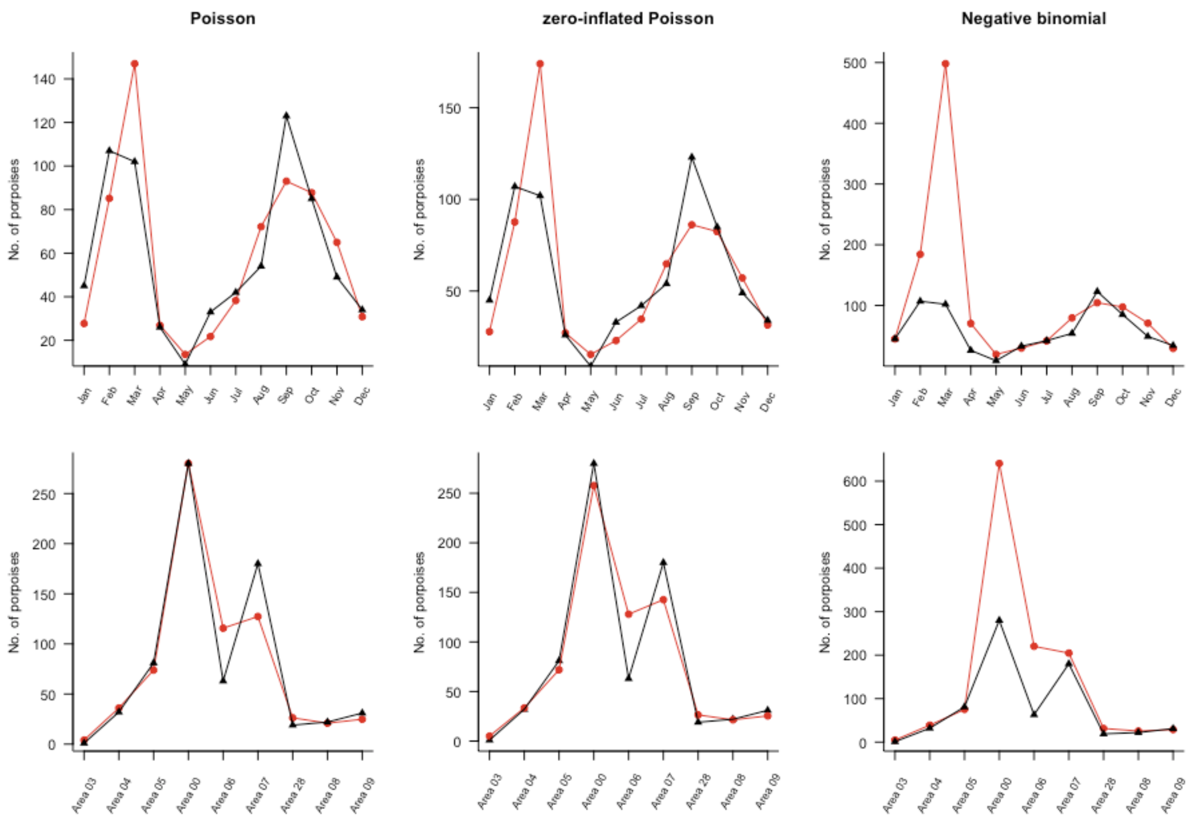

Figure 5: Predicted (red dots) and observed (black triangles) bycatch for month totals (above) and area totals (below), based on Poisson, NB and ziP GLM #13.

DISCUSSION

Our analysis has revealed that given the quality of the CRF data, a modelling approach for calculating harbour porpoise bycatch is problematic. Model diagnostic plots (Fig. 4) suggest that the NB model (rather than a Poisson/ziP model) may provide the best fit in terms of distributional assumptions, but there are considerable fitting difficulties associated with all three models. The deviance residuals associated with the NB model in particular greatly influences model predictions, causing a great positive bias in predicted bycatch for specific areas and months (Fig. 5). Bycatch predicted by the NB model in March, for instance, is quintupled compared to the actual observed bycatch. Extrapolations based on a model suffering from deviances of this magnitude cannot be considered to be reliable. This is reflected in the relatively high NB model CV of 0.62 (compared to 0.11 for Poisson/ziP models) and the wide 95% confidence interval, ranging from 3567 to 10756 porpoises. The size of the NB model confidence interval is thus 10756 – 3567 = 7189, compared to 1523 and 2600 for the Poisson and ziP models, respectively. The inappropriateness of the NB model was also apparent in the predictions based on model formulations 1 – 12, which were unreasonably high, ranging from 6165 to 23057 porpoises. Predictions for model formulations 1 – 8 were all greater than 10000 porpoises. Even though total model deviance for the Poisson and ziP models are greater in both cases than the NB model, model predictions of the former models are less influenced by the deviances, as evidenced by a closer correction with observed bycatch. It therefore seems that the CRF data do not wholly support this modelling approach and that it would be appropriate to defer to the traditional stratified ratio approach, or at least, consider the model predictions against the stratified ratio predictions. Among the three models evaluated, the predictions of the Poisson model most closely agree with the predictions of the stratified ratio approach. Thus, an annual bycatch of approximately 3000 harbour porpoises seems reasonable.

The current bycatch estimates are substantially smaller than the estimate in Bjørge *et al.* (2013) of 6,900 porpoises per year. Even the revised estimate using the best model in Bjørge *et al.* (2013) of 3541 porpoises CI 0.10 porpoises per year is about half the original estimate. The main reason for this difference is that the estimate in Bjørge *et al.* (2013) was extrapolated to entire fisheries based on incorrect statistics of landings of the target species. The landing statistics provided by the Directorate of Fisheries for the Bjørge *et al*. (2013) included landings taken with all gear types, including hand jigs, long line, purse seine, Danish seine and demersal trawl. These gear types have no or very little bycatch of harbour porpoise. And applying the bycatch rate generated by gillnet fisheries for cod and monkfish for extrapolating to entire fisheries with all gear types generated a substantial overestimate.

To evaluate if the bycatch is within sustainable limits, we need information on the abundance and population structure of the population or populations impacted. According to ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas) the bycatch of harbour porpoise should not exceed 1.7% of the best population estimate. The abundance of harbour porpoise in the North Sea and adjacent waters is known from the SCANS surveys (Hammond *et al.,* 2002), but there is currently no estimate of abundance of harbour porpoise in Norwegian coastal waters north of 62^{o}N. The plans for SCANS III include aerial survey of the near shore waters north to the Lofoten area (67.5^{o}N). This will contribute to the knowledge of abundance in Norwegian water. However, most of the bycatches, in particular in the fishery for monkfish, were in the complex waters among coastal archipelagos and fjords. These waters will only partly be covered by SCNS III, and given the complex nature of these waters, they are difficult to survey using distance sampling and conventional line transect methodology. We are therefore considering the possibility to use the allele-sharing method for estimating population size developed my Skaug (2001). This will include collecting genetic and age samples from bycaught porpoises.

The population structure of harbour porpoises in Norwegian waters is not well documented. Based on analyzing mtDNA samples from 45 porpoises from the North Sea and 38 porpoises from the Barents Sea, Tolley *et al*. (1999) concluded that porpoises along the entire Norwegian coast constituted a single population unit. In a review paper, Andersen (2003) supported the conclusion of Tolley *et al*. (1999), but noted that results from wider studies using mtDNA and nuclear DNA samples indicated that the Norwegian harbour porpoise population was distinct from populations in the rest of Scandinavian and European waters. However, within Norwegian waters, seasonal movements and the relationship between coastal and offshore porpoise groups are not known.

ACKNOWLEDGEMENTS

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