Predicting harbour porpoise strandings based on near shore sightings indicate elevated temporal mortality rates

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Summary

The increase in anthropogenic activities and their potential impact on wildlife requires the establishment of monitoring programs and identification of indicator species. Within marine habitats, marine mammals are often used as ecosystem sentinels because of high public interest, international legislation, and their role as top-predators in marine ecosystems. This has led to investigations into their abundance, distribution, health and vital rates informing conservationists and managers who aim for their protection. In the North Sea, the harbour porpoise (*Phocoena phocoena*) is the most frequently encountered cetacean, both in terms of sightings and strandings. Large-scale abundance surveys in the North Sea revealed a redistribution of porpoises from north to south between the 1994 and 2005 surveys. The increase in local abundance in the southern North Sea corresponds to an increase in strandings in this region. However, since 2004 higher temporal stranding rates on the Dutch coast have been documented, which might not solely be the result of higher abundance of porpoises, but may reflect elevated mortality levels. Elevated mortality can be caused by anthropogenic or natural pressures. It is therefore vital to be able to differentiate between changes in strandings due to changes in the regional population size or elevated mortality as a direct consequence of anthropogenic activities.

The main goal of this study was to assess if stranding frequencies along the Dutch coast can be explained by local population density. We use 29 years of sighting and stranding data (1990-2018) to try to assess which coastal sighting months best explaining the observed variation in stranding numbers. In addition, we estimate discrepancies between the observed strandings and predicted strandings based on sightings, which may indicate temporal excessive high or low mortalities.

Both the number of stranded porpoises and the coastal sighting rate has increased rapidly up to around the mid 2000's, after which they remained high, but with large inter-annual fluctuations. On an annual basis there is a strong correlation between porpoise strandings and sighting rate. However, there is a strong seasonal miss-match. The highest stranding rate occurs in late summer (July - August), while the highest sighting rate is in early spring (February - March). Despite low absolute sighting rates in late summer, the sighting rates in those months is the best predictor for the monthly variability in the number of stranded porpoises, even for those found ashore in late winter and early spring. A possible explanation is that sightings in late-summer might reflect dispersing individuals from the breeding population. The size of this reproductive breeding population might determine the number of juveniles dying in the following year. In contrast, porpoises sighted in February and March might reflect a larger segment of the North Sea population that in some years reside closer to the Dutch shore compared to other years. The number of stranded porpoises classified as fresh are more closely related to the seasonal and annual variability in coastal sightings, suggesting that the carcasses that wash up in advanced state of decomposition might have died further offshore and therefore out of sight.

When accounting the stranding for the sighting rate, the temporal patterns in the residuals show that in the early 1990's (when porpoise sightings were still rare) and after 2010, the number of stranded porpoises exceeded the number expected based on the sightings. Especially in the summer of 2011, the number of dead porpoises found ashore was excessively high. The possible cause for the perceived elevated mortality rate in the last decade might be natural, like redistribution of porpoises relative to the coast or increased mortality due to increased density dependent competition of a population near carrying capacity. Alternatively, the cause of the perceived elevated mortalities might be human-related, like increased anthropogenic activities at sea, and warrants further in-depth investigations into the causes of mortality. Through these analyses we show the ability to indicate temporal unusual mortality events, demonstrating how stranding records could serve a valuable indicator for wildlife monitoring.

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1 Introduction

Monitoring wildlife populations has gained significant interest since the rise in human activities and the responsibility to monitor wild animals and their habitats effectively (Tyne et al. 2016, Tablado and Jenni 2017). A successful monitoring program should detect changes in population parameters, which can be used to define and assess conservation objectives (Bubb et al. 2005). Ecological relevance, statistical credibility and cost-effectiveness are the three expected performances of an efficient wildlife monitoring plan (Elzinga et al. 2001). In the marine environment, marine mammals are often used as indicator species. Specifically, cetaceans are relatively long-lived animals which feed at or near the top of the food chain, making them suitable sentinels for ecosystem health (Moore 2008, Bossart 2011). In Europe, cetaceans are protected by a range of international and national regulations, e.g. EU Habitat Directives, the Marine Strategy Framework Directive, the Agreement on the Conservation of Small Cetaceans in the Baltic, North East Atlantic, Irish and North Seas and the Dutch Nature Protection Act. These conventions require the assessment of cetacean abundance and distribution, which is mainly done through ship- or aerial based surveys (Hammond et al. 2002, Scheidat et al. 2012, Geelhoed and Scheidat 2018). These surveys are costly and logistically challenging since cetaceans spend most of their time well below the surface, and are highly mobile species that use large areas of space, only a small area can be covered by the survey. Consequently, this results in temporal restrictiveness and low-resolution estimates, and therefore they cannot detect precipitous declines or local and smaller-scale changes (Taylor et al. 2007, Peltier et al. 2013, Ten Doeschate et al. 2018). This demonstrates a need for additional indicators that can be used as early warning signals of population change.

Due to the statutory requirement of several international conventions, stranding networks have been implemented in numerous European countries for decades. Spatiotemporal changes in stranding frequencies have been used as an indicator of at-sea mortality (Hart et al. 2006, Pyenson 2011, Williams et al. 2011, IJsseldijk et al. 2019, Betty et al. 2020), however it is currently unknown how representative these strandings are for the at-sea population. This is caused by the complexity in quantifying the several components that influences the stranding process (Hart et al. 2006, Peltier et al. 2013, Ten Doeschate et al. 2018).

In North-western Europe, the North Sea basin is inhabited by approximately 350.000 harbour porpoises (*Phocoena phocoena*)(Hammond et al. 2002, 2013, 2017). Through large-scale, international, decadal live-surveys (SCANS), no changes in harbour porpoise population size were detected over the past three decades, but a shift in the summer distribution from north (SCANS, 1994) to south (SCANSII, 2005) was observed. Strandings of harbour porpoises in especially the southern North Sea increased significantly since the 1990's (Camphuysen et al. 2008, Keijl et al. 2016, Haelters et al. 2018). Since 2004, there were periods with excessively high number of stranded porpoises (IJsseldijk & ten Doeschate et al. 2020), raising concerns whether these were solely a result of a higher abundance of porpoises in the southern North Sea, or may also reflect elevated mortality levels.

Elevated mortality could be a result of increased threats and pressures that negatively affect the population. The North Sea is a worldwide hotspot of anthropogenic activities, where nearly all known anthropogenic stressors occur and overlap (Halpern et al. 2008, 2015). Harbour porpoises in the North Sea are impacted by anthropogenic disturbance, including from fishery activities (bycatch and competition (Kirkwood et al. 1997, Leeney et al. 2008, IJsseldijk et al. 2018a), chemical pollution (Pierce et al. 2008, Weijs et al. 2009, Jepson et al. 2016) (van den Heuvel-Greve et al. *in prep*), noise pollution from shipping (Wisniewska et al. 2018), seismic surveys and underwater explosions (von Benda-Beckmann et al. 2015, Aarts et al. 2016), and more recently, the exponential growth of industrial offshore activities for the large-scale construction of wind farms (Madsen et al. 2006, Gilles et al. 2009). International legislation require to minimize disturbance and negative impacts from human activities on the marine mammal populations. It is therefore essential to quantify and qualify spatiotemporal mortality trends and threat-specific mortality (IJsseldijk & ten Doeschate et al. 2020). This highlights the need to assess whether excessive strandings are the result of changes in porpoise occurrence or whether excessive strandings reflect elevated mortality for example caused by increased anthropogenic activities.

The main goal of this study was to assess if stranding frequencies along the Dutch coast could be explained by local population density, which was measured by a large number of standardized observers along the coast. We try to assess in which month coastal sighting best explained the number of stranded porpoise found along the coast, using sighting and stranding data spanning 29 years (1990-2018). In addition, we estimate discrepancies between the observed strandings and predicted strandings based on sightings, which may signpost temporal excessive high or low mortalities. Such corrections should improve the credibility of stranding records as a population indicator that can be used for conservation purposes.

2 Methods

2.1 Strandings data

Harbour porpoise stranding records in the Netherlands are managed by Naturalis Biodiversity Centre, Leiden. Data records and photographs of stranded individuals are available online (www.walvisstrandigen.nl). The Dutch stranding network consists of a consortium of a large number of organizations and volunteers, with full coverages along the south-western coastline (expected to near 100%). Coverage in the northern areas (Wadden Sea and Frisian islands) is expected to be lower, since some of the islands are uninhabited. A total of 9229 harbour porpoise stranding records from 1990-2019 both dead and alive, were included in this study, with each record representing a stranding event of a single individual. Two records with no data for the month were excluded. For those records where comments were provided regarding the stranding event and/or status of decomposition of the stranded individual, a distinction could be made between alive (n=300), fresh (n=2223) and animals with advanced signs of decomposition (n=3622). This information was unknown for n=3084 recorded strandings.

2.2 Coastal sighting data

Harbour porpoise local abundance was analysed by extracting sightings from the Seawatch database of the Dutch Seabird Group (Nederlandse Zeevogelgroep NZG/CVZ database) and www.trektellen.nl (Camphuysen 2011). For the analysis, we used coastal sighting data from 1989 (one year before 1990) until June 2018. The counts are conducted year-round, with slightly increased intensity during periods of (waterbird) migration in spring (March-May) and autumn (August-October). Observations are from vantage points (dune-tops, piers, dikes), with observatories normally at a height of 5-15 m above sea level, to provide views over the near shore strip (up to 5-10 km distance) of coastal sea (Fig. 1). Harbour porpoises are detected predominantly within 2 km from the location of the observer. Observers recorded date, duration of the observation period (start and end time), and weather characteristics and logged their sightings usually per hour of observation. The weather characteristics scored per sighting were: wind force (weak, moderate or strong), wind direction (onshore, offshore or other), cloud cover (overcast, partly or no cloud cover) and visibility (good, moderate or bad). The observers are well-trained and sufficiently experienced in cetacean identification.

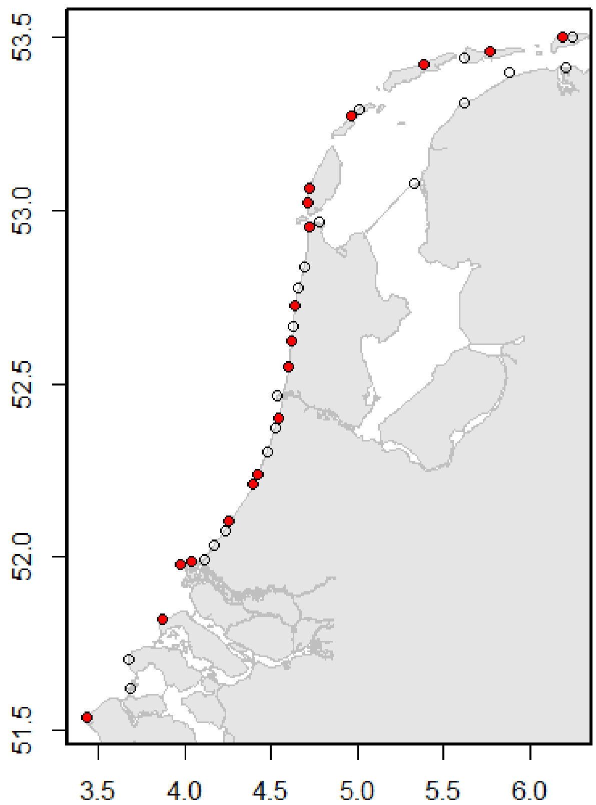

Figure 1. Location of coastal observation points (black open circles) and those with sufficient data (red circles) included in the analysis.

2.3 Correcting for wind effects on sightings

To correct for the effect of weather conditions on sighting probability, the number of porpoises observed N_t was modelled as a function of several weather-related covariates:

$$N_t \sim NB(\gamma_i, \theta) \quad \text{eq. 1}$$

$$\gamma_t = exp(year{:}month + observation\ site + part\ of\ day + wind\ force + wind\ direction + cloud\ cover + visibility + \log(observation\ duration))$$

Where NB represents a negative binomial distribution, γ_i the expected sighting rate and θ the dispersion parameter. All explanatory variables were included as factor variables. These explanatory variables were year (1989 - 2018), month (January – December), part of day (morning, mid-day or late afternoon), observation site (18 unique sites), wind force (weak, moderate and strong), wind direction (onshore, offshore or other), cloud cover (overcast, partly and no cloud cover) and visibility (good, moderate and bad). The log of the observation duration was included as the model offset. Next, the fitted model was used to predict the expected sighting rate (number of porpoises per hour) for each year and month combination using fixed values for the observation conditions. Predictions were made for one observation site, namely "Castricum aan Zee" (site id=527), which is centrally located along the Dutch shore and had a high observation effort. The fixed values for the other conditions were part of day = morning, wind force = weak, wind direction = onshore, cloud cover = overcast and visibility good. These model-based estimates of the sighting rate (O_t; number of porpoises per hour) were used in subsequent analysis.

2.4 Data exploration

Data exploration consisted of estimating and presenting total number of strandings by month and year. A distinction was made between all strandings and those classified as 'fresh' or 'alive'. The porpoise sighting rates in each month might predict the stranding rate in the following month. For example, sightings in summer might reflect local recruitment and influence the stranding rates in the following winter. Therefore, we investigated how well the number of porpoise stranded in a specific month *m* could be explained by the porpoise sighting rate in any of the *n* months in the preceding year, the same year and the following year.

$$S_t \sim NB(\lambda_t, \phi) \qquad \text{eq. 2}$$

$$\lambda_m = exp(\beta_0 + \beta X_n)$$

In total this resulted in 432 models (i.e. 12 strandings months x 12 sighting months x 3 years). For each model, the General Linear Model (GLM) equivalent of R^2 (i.e. 1-(deviance/null deviance)) was calculated and plotted as raster object (library: raster). Models were fitted using the R-function glm.nb (library: MASS).

2.5 Modelling strandings as function of coastal sightings

The temporal variation in stranded porpoises was modelled as a function of the coastal sightings to examine and quantify general trends and seasonal patterns. In addition, we assessed differences between the observed and predicted strandings based on coastal sightings, to determine periods of unusual higher or lower mortality numbers.

Estimating the optimal sighting window to predict the number of stranded porpoises

Prior inspection of the number of stranded porpoises and sighting rate on a month-by-month basis revealed an obvious temporal mismatch, with high number of stranded animals found in July and August, while sighting rates during those months were low. To capture a possible temporal delay in porpoise strandings, the monthly porpoise sighting rate O_t was replaced by a time decaying weighted average X_t of the sighting rate in preceding months:

$$X_t = \sum_{m=0}^{11} O_{t-m}\, w_m \qquad \text{eq. 3}$$

$$w_m = \frac{(m+1)^{-\alpha}}{\sum_{m=0}^{11}(m+1)^{-\alpha}}$$

Here, *m* represents the number of months prior to *t.* The parameter α controls the steepness of the decay. If α is large, X_t is very similar to O_t. If α is very small, X_t is approximately equal to the average porpoise sighting rate. α was varied between 0.01 and 1 at steps of 0.01, and the estimated weighted average sighting rate X_t was included as explanatory variable in the model as outlined below. The value of α that produced the model with the lowest Deviance Information Criterium (DIC) was used for subsequent analysis.

Do coastal sightings predict the number of stranded animals?

The first model formulation was designed to properly test if the monthly number of stranded porpoises S_t could be explained by delayed porpoise sighting rate X_t. The base-model was formulated as follows:

$$S_t \sim NB(\lambda_t, \phi) \quad \text{eq. 4}$$
$$\lambda_t = exp(\beta_0 + \alpha_m X_t + \upsilon_t)$$

Where S_t and λ_t are the observed and expected number of strandings per month, respectively. *NB* is a negative binomial distribution with mean and dispersion parameter ϕ. β_0 is the intercept and α_m represents the parameters of the month (*m*) specific effects. υ_i represents a autoregressive AR1 temporal correlation.

$$\upsilon_1 \sim N(0, \tau_\upsilon (1 - \rho^2)^{-1}) \quad \text{eq. 5}$$
$$\upsilon_t \sim \rho \upsilon_{t-1} + \varepsilon_t, t = 1, \ldots, T$$
$$\varepsilon_t \sim N(0, \tau_\varepsilon)$$

The performance of this model (based on DIC) was compared with a model without the inclusion of a dependence on the sighting rate, but with inclusion of the autoregressive temporal correlation structure, i.e.

$$\lambda_t = exp(\beta_0 + \upsilon_t) \quad \text{eq. 6}$$

What are the periods of unusual higher or lower mortality numbers?

Instead of modelling the number of stranded porpoises as a function of sighting rate, the ratio between the number of stranded animals per month S_i and monthly average sighting rate (O_i) was modelled, which was achieved by including $log(X_i)$ as the model offset.

$$S_t \sim NB(\lambda_t, \phi) \quad \text{eq. 7}$$
$$\lambda_t = exp\big(\beta + \alpha_m + \upsilon_t + \log(X_t)\big)$$

Here υ_t describes the seasonal trend in deviations in the number of stranded animals relative to the expected values based on coastal sightings.

3 Results

3.1 Corrected coastal porpoise sightings

A model was fitted to the coastal sightings of porpoises to correct for the effect of weather related environmental conditions (see Appendix A, Table S1). As expected, the highest porpoise sighting rates were recorded during low wind force conditions (i.e. highest parameter estimate for WINDKzwak, Table S1), while strong winds resulted in the lowest sighting rate. The observed sighting rates were also higher under good visibility, high cloud cover and offshore winds (see Appendix A, Table S1). Sighting rates were also slightly higher later during the day (day section 2 and 3). There were also differences in sighting rates between the observer sites. The sighting rate (corrected for sighting conditions) was highest at site Castricum (site no. 527), Maasvlakte II (no. 1272) and Camperduin (no. 429) and the average sighting rate was lowest at Ouddorp Light house (no. 410), Westkapelle (no. 3) and Maasmond (no. 147). The fitted model was subsequently used to estimate for one central observation site (Castricum, no. 527) and a fixed set observation conditions (weak on shore wind, good visibility and heavy cloud cover). Despite the potential effect of wind, there was still a large correspondence between the observed and corrected porpoise sighting rates (**Fig. 2**). Note that the absolute values of the corrected model-based sighting rates were on average higher because the model-based estimates were made for more favourable weather conditions.

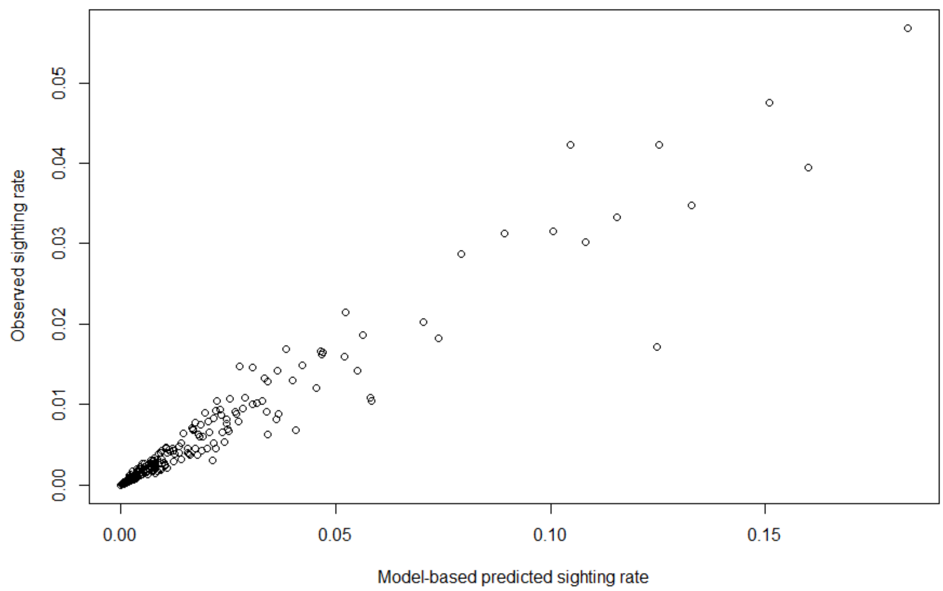

Figure 2. The observed sighting rate (not corrected for observation conditions) versus the model-based predicted sighting rate for each year-month combination.

3.2 Annual and seasonal patterns in sighting rate

The observed sighting rate increased up to around 2005, after which it fluctuated and remained high with around 0.08 porpoise per hour. The highest average sighting rate was in 2013, and the lowest sighting rate in the last decade was in 2015 (**Fig. 3**).

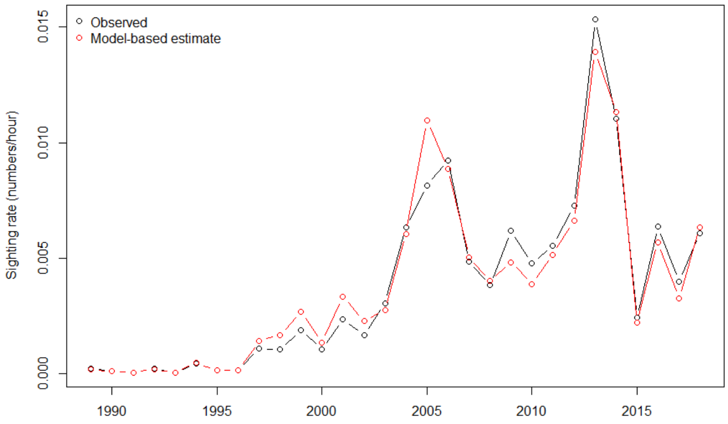

Figure 3. Annual variation in sighting rate. Note that for plotting purposes, the model-based estimates were corrected to ensure that the mean model-based estimated sighting rate was equal to the observed sighting rate.

The sighting rates were highest during the winter months, with a peak in February. The sighting rates were lowest in May and June (**Fig. 4**)

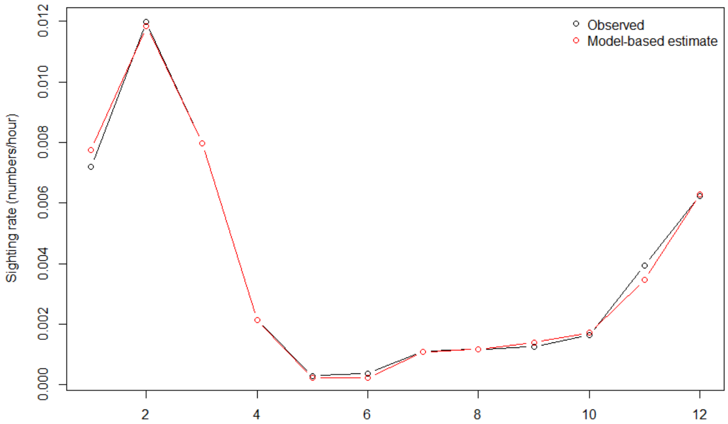

Figure 4. Monthly variation in sighting rate. See also Figure 3.

Although the monthly pattern in porpoise sighting rate was fairly consistent between years, there were some annual variations. For example, the highest average sighting rate observed was in January 2014 (**Fig. 5**).

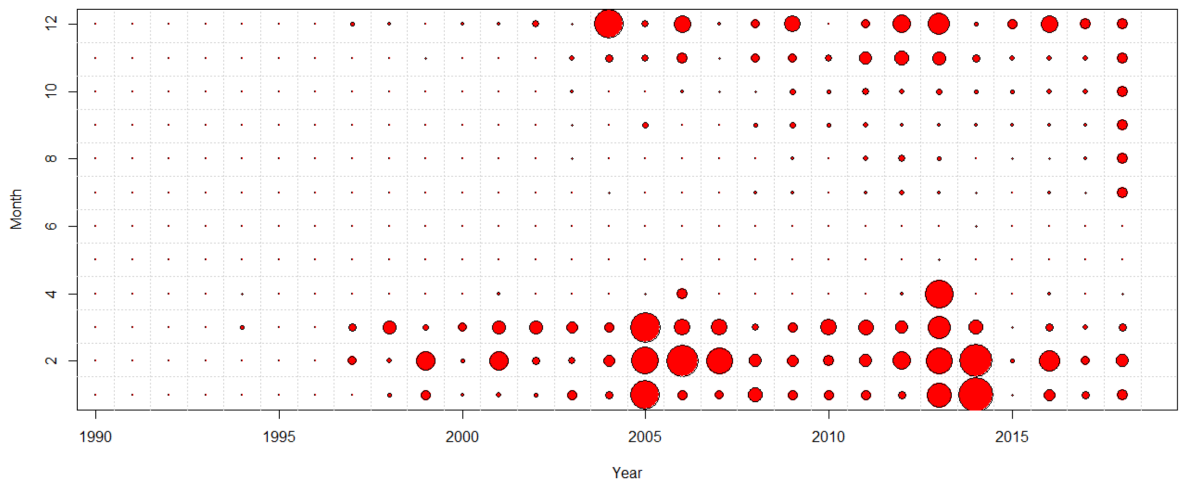

Figure 5. Seasonal and annual patterns in observed sighting rate (1990-2018).

3.3 Annual and seasonal patterns in strandings

The number of stranded animals rapidly increased up to 2006, after which the general trend seemed to be less consistent, with large inter-annual variability (**Fig. 6a**). Largest number of stranded animals were reported in 2011 and 2013. In the last decade, the lowest stranding number was recorded in 2015. In this year, porpoise sightings were also very low (**Fig. 3**). When the annual pattern in strandings and coastal sightings were normalized (i.e. subtracting the average value and dividing by its standard deviation), normalized strandings were lower from 1997 up to 2007 (**Fig. 6b**). From 2008 up to 2018 the normalized strandings exceeded the normalized sighting rate, except for 2013 and 2014. While both 2011 and 2013 were characterized by a high numbers of porpoises washing ashore, only 2011 was particularly high compared to the normalized stranding rate (**Fig. 6b**). The total number of stranded porpoises (between 1990 and 2018) revealed that most porpoise were found ashore in July and August, with a smaller peak in March (**Fig. 6c**). In March, a much larger proportion of fresh animals were found ashore and total number of porpoises recorded as fresh are highest in that month. The normalized monthly pattern in porpoise strandings and coastal sightings showed some similarity in early spring, although the peak in strandings (March) occurs a month after the peak in coastal sightings (February) (**Fig. 6d**). Both strandings and sightings were very low in May and June. However, while strandings were at their highest in July and August, the coastal sightings were very low. The monthly pattern of strandings of fresh porpoises appears to show more similarity with the monthly pattern in coastal sighting rate, although patterns in the summer months still differ (**Fig. 6d**).

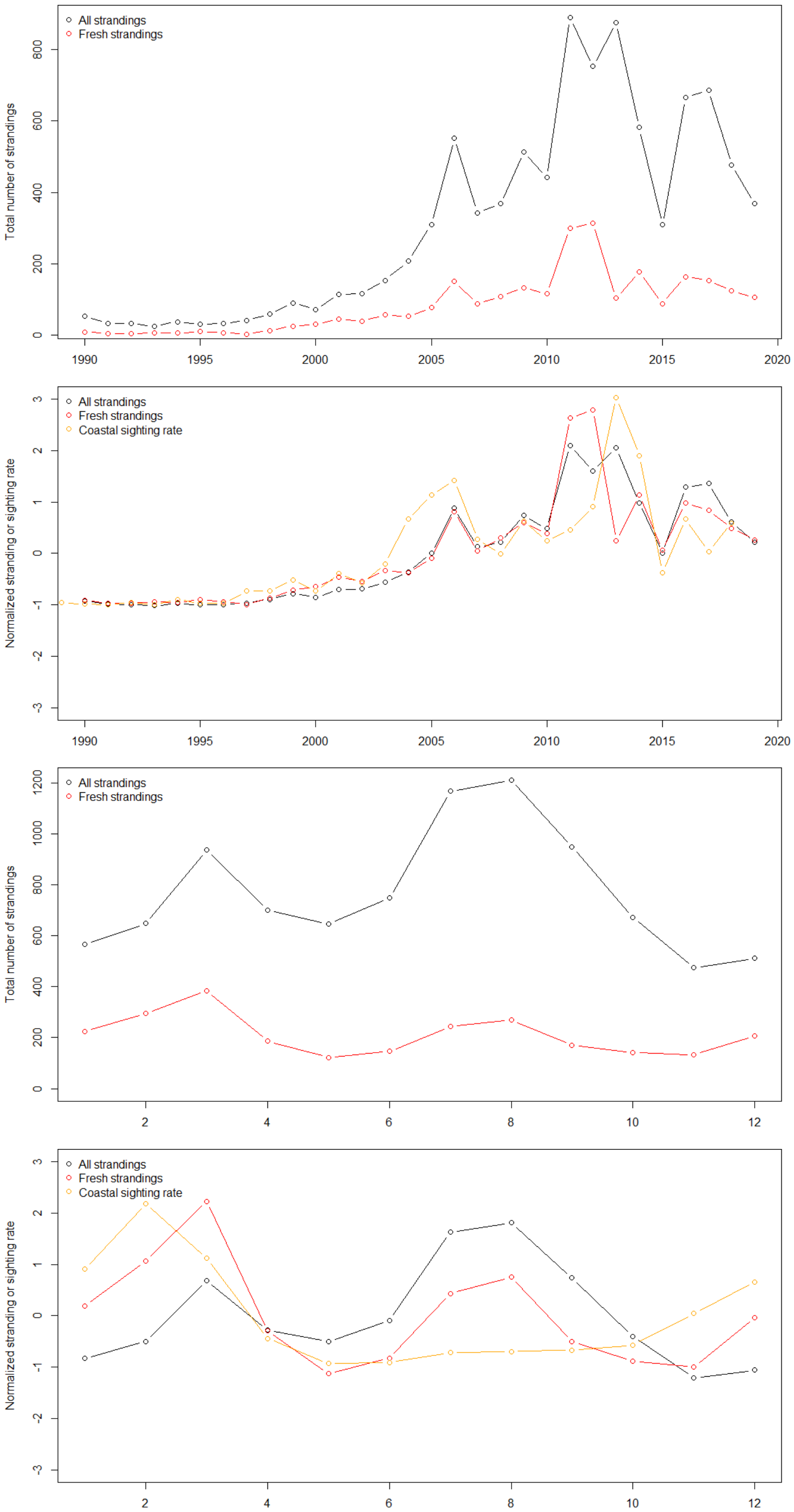

Figure 6. Annual and monthly patterns in strandings. **a**. Annual pattern in number of stranded animals (black = all, red = fresh and alive). **b.** Annual pattern in the normalized porpoise strandings and sightings. **c.** Monthly pattern in all (black) and fresh (red) porpoise strandings. **d.** Monthly pattern in the normalized porpoise strandings and sightings.

When we inspect the porpoise strandings for all year and month combinations, some inter-annual changes become apparent, with the summer peak in porpoise strandings becoming more prominent in the last decade, compared to the peak in March which was more prominent in the 2000's (**Fig. 7**).

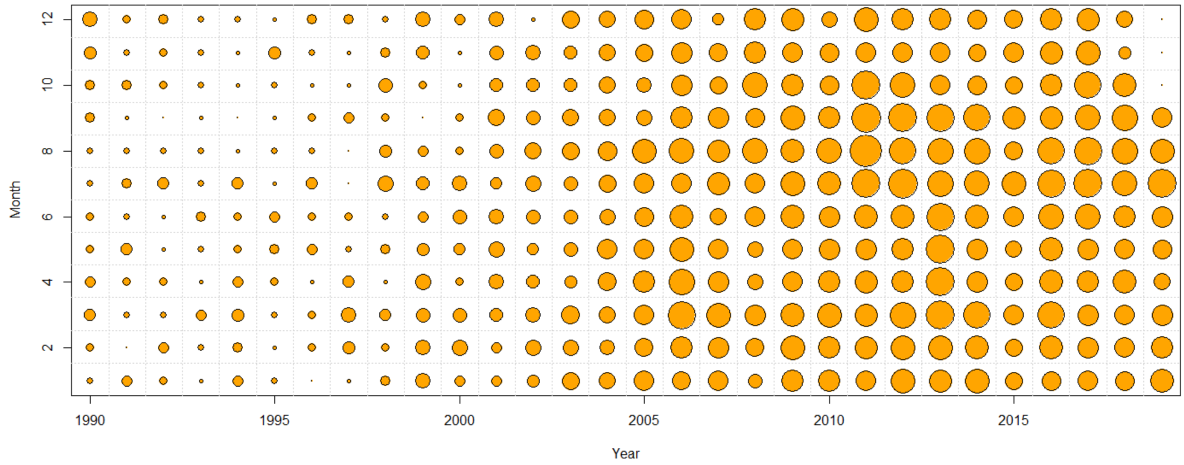

Figure 7. Seasonal and annual patterns in stranding rate (1990-2019).

3.4 The ability to predict strandings based on coastal sightings

Sightings in a specific month can be related to the number of stranded porpoises in a specific month, and this reveals large differences in the strength of the correlation. Sightings in July, August and September correlated well with the number of strandings observed in each month (**Fig. 8**). For example, the number of stranded porpoises in January in year *y* correlate strongly with the porpoise sighting rate in July and August the preceding year (i.e. *y*-1), despite the relatively low absolute sighting rate in those months. The stranding rates in summer were also strongly correlated with the summer sighting rates during the preceding and following year. This is caused by strong correlations between years. In contrast, February and March, characterised by the highest sighting rates, correlate less well with the number of stranded porpoises in late summer (July – September). Temporal variability in the sighting rates in June seem to show very little resemblance with the patterns in the strandings (i.e. very low R^2 values).

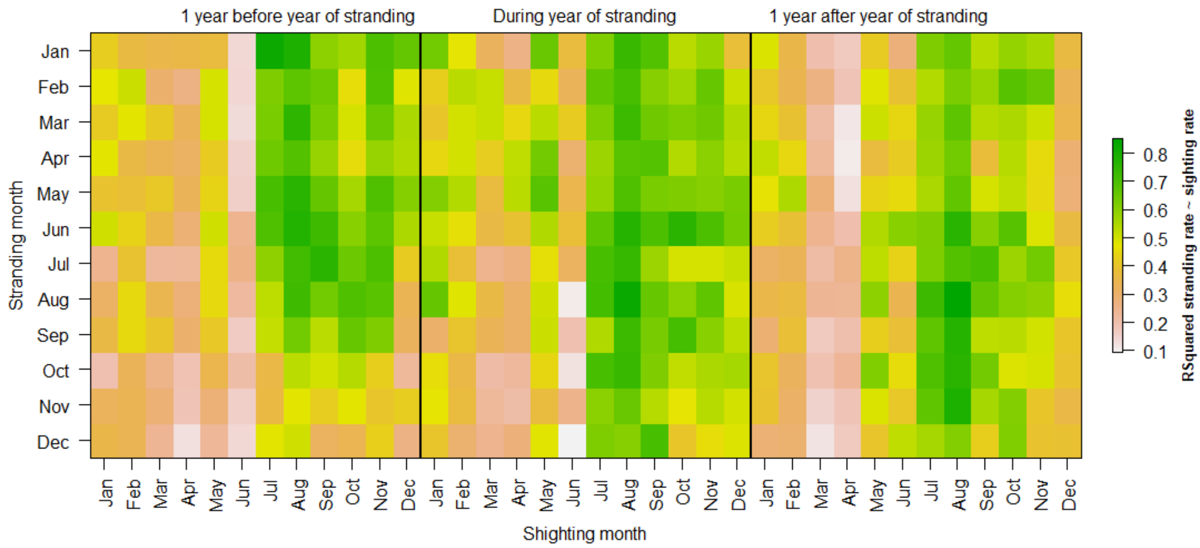

Figure 8. R^2 of model were a stranding in each month is explained by the sighting rate in another month. The middle column represents coastal sighting rates from the same year as a stranding. The left column relates the strandings in year y with the sightings in year y-1 and the right column relates

the strandings in year y with the sightings in year y+1. For example, the strandings in March (3rd top row) are best described by the sightings in August of the preceding year.

If there would be a close correspondence between the monthly stranding and sighting rate, the diagonal of the middle panel of Figure 8 would reveal overall high R^2 values, which is not apparent. This suggest that the sighting rate in a specific month is a poor predictor of the number of strandings in that same month. This is also supported by the parameter estimate α that governs steepness of the decay in the weights for the sighting rate (Supplement Figure S1). A value of $\alpha = 0.01$ resulted in the lowest DIC (2186.1 compared to 2193.0 for $\alpha = 1$). In other words, the number of strandings in a specific month can be best explained by the average sighting rate during the 12 months preceding that month (Supplement Figure S2). This weighting parameter $\alpha = 0.01$ was used for subsequent analysis.

The observed correlation between sightings and strandings as shown in Figure 8 might be the consequence of other confounding temporal processes. To test whether sighting rates significantly contribute to explaining the observed variation in porpoise strandings, a model with only an AR1 structure (eq. 6) was compared to a model with an AR1 structure and also the inclusion of a dependency on the sighting rate (eq. 4). The latter resulted in a slightly lower DIC (2186.1 versus 2188.5) and lower WAIC (2192.2 versus 2193.8). A model without an AR1 structure but with the inclusion of a dependency on the sighting rate resulted in a much lower DIC compared to a similar model (without an AR1 structure), but inclusion of month as a factor variable, i.e. 2639.8 versus 2898.8.

When this comparison is repeated for the fresh and alive stranded porpoises, the inclusion of a dependency on sighting rate leads to a much better model fit, compared to a model with only an AR1 correlation structure (DIC 1550.1 versus 1589.9). A model without an AR1 structure but with the inclusion of a dependency on the sighting rate resulted in a much lower DIC compared to a similar model where the dependency on the sighting rate was replaced by the inclusion of month as factor variable, i.e. 1814.2 versus 2022.9. So in summary, there is sufficient evidence that coastal sightings can explain patterns in strandings, particularly for the fresh and alive stranded porpoises, but a first order autoregressive correlation structure is able to absorb a large part of the temporal variability.

3.5 Residuals observed and predicted sightings

To constrain the dependency between sightings and strandings, the ratio between these two was modelled. This was achieved by including the log of the corrected sighting rate (x) as model offset (eq. 7). In the first eight years (1990-1997) the observed number of stranded animals was higher than the expected number of stranded animals, which was partly due to very low sighting rates in those years (**Fig. 9**). From around 1997, less porpoises stranded than expected based on the sightings. This, however, changed in more recent years, with the number of porpoise strandings exceeded the predicted number of strandings based on the coastal sightings (**Fig. 9-10**). Particularly the number of harbour porpoise strandings in 2011 was excessively high.

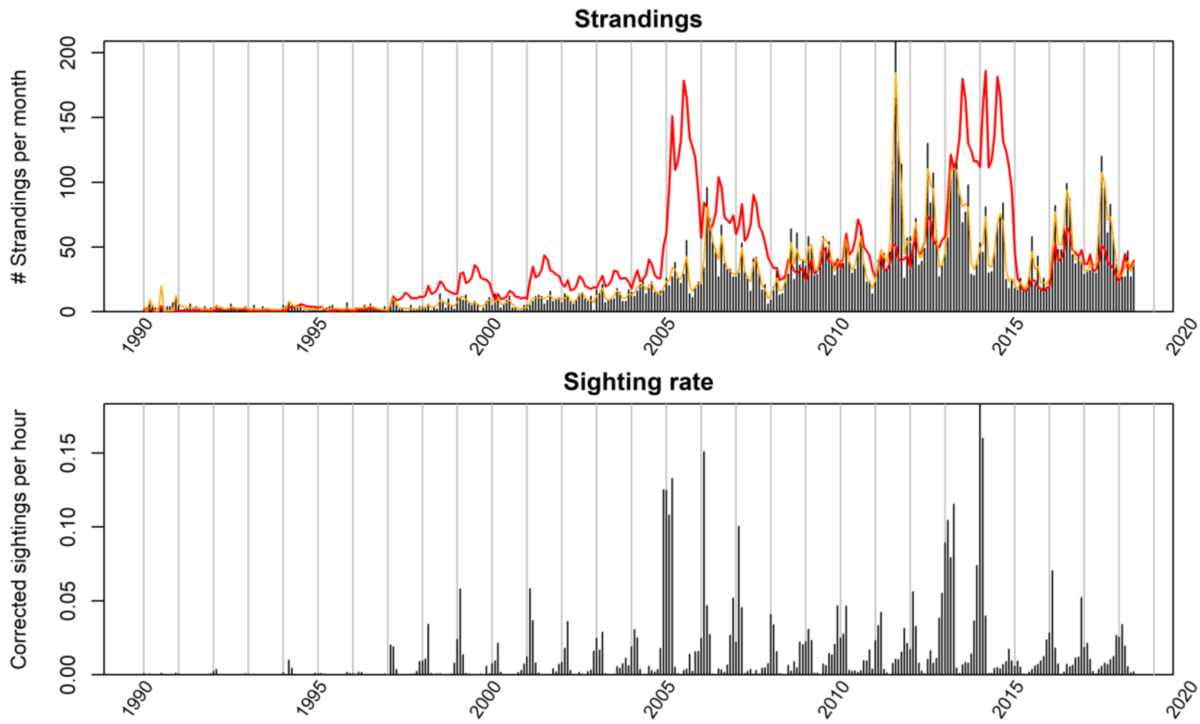

Figure 9. The top figure represents the observed (vertical bars) and expected number of all stranded porpoises based on a model relying solely on the weighted average sighting rate of the preceding 12 months (red line). The thin orange line represents the expected number of porpoise strandings when including an autoregressive temporal correlation structure in the model, which closely corresponds the observed number of strandings. The bottom figure represents the variability in sightings per hour (corrected for wind) on a monthly basis. This data defines the model-based expectations as included in the top-figure (the red line).

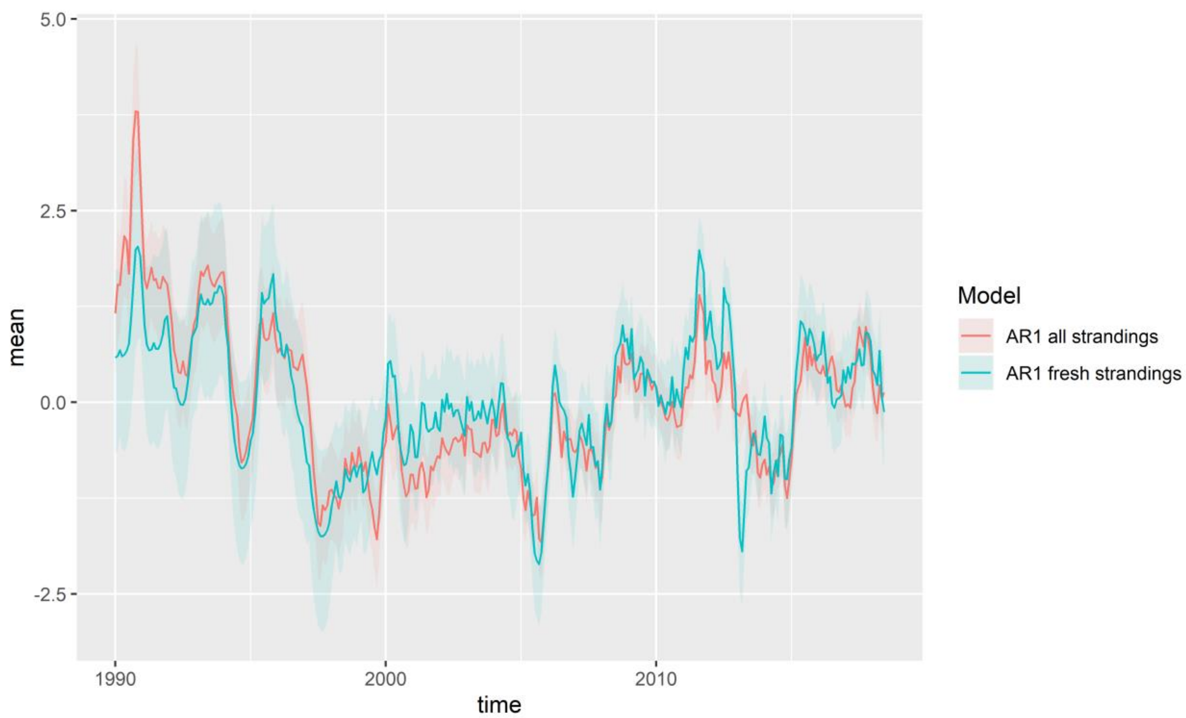

Figure 10. Residual pattern between the observed and expected (based on the sightings) porpoise strandings as captured by the temporal correlation structure. Values are on log-scale. Peak values (above the mean of 0) imply more than expected porpoise strandings and low values (below the mean of 0) imply less than expected strandings.

A fairly similar pattern was observed for the fresh strandings, although there was closer resemblance between the observed and expected strandings **(Fig. 11**).

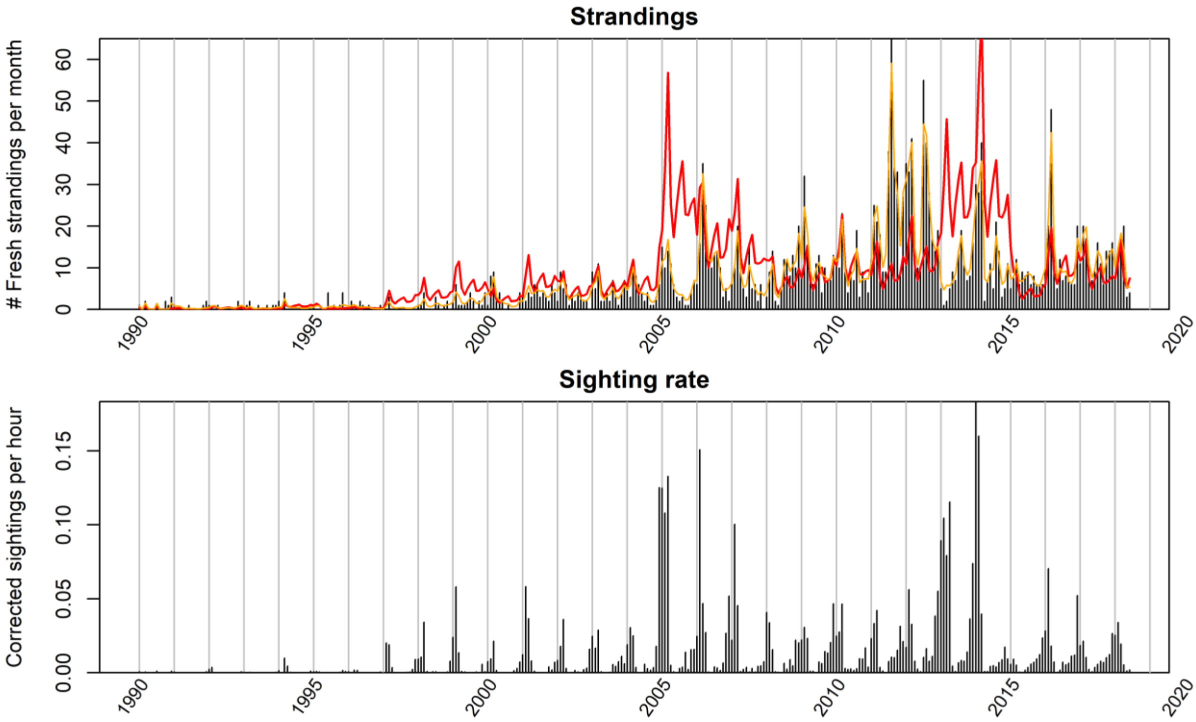

Figure 11. Observed (vertical bars) and expected number of fresh (i.e. alive and fresh) stranded porpoises. See Figure 9 for more details.

4 Discussion

Here, we demonstrated that coastal sightings of harbour porpoises strongly correlated with stranding rates of this species throughout the study period (1990-2018), but with large inter-annual fluctuations. An increase in local abundance largely explains the general increase in strandings of harbour porpoises on the Dutch coast. There was, however, a strong seasonal miss-match between stranding and sighting rates. Despite low absolute sighting rates in late summer, sighting rates in July - August were the best predictor for the monthly variability in the number of stranded porpoises, even for those found ashore in late winter and early spring. In addition, we found that the number of stranded porpoises classified as fresh were more closely related to the seasonal and annual variability in coastal sightings. Lastly, we demonstrated that the number of stranded porpoises exceeded the number expected based on the sightings in certain periods, indicating temporal elevated mortality levels.

The summer sighting rates as the best predicator for the number of strandings could be explained by reproduction and subsequent (post-weaning) mortality. Parturition in the North Sea occur between May-August (Sørensen and Kinze 1994, Addink et al. 1995, Lockyer 2003), with the highest number of stranded calves on particularly the northern Dutch coast in the late calving season (IJsseldijk & ten Doeschate et al. 2020). Harbour porpoises of up to ten months may be maternally dependent (Lockyer 2003). The pattern of mortality over a typical mammalian lifespan consists of an initial period of high juvenile mortality (Boveng and Barlow 1991), and high sighting rates in summer may therefore reflect calves and juvenile porpoises, hence the breeding population, with strandings in subsequent months proportionally to these summer sightings. We therefore hypothesize that a large proportion of porpoises sighted in February and March are "migrants". This is supported by aerial surveys that reveal much higher population size estimates for the Dutch North Sea in March, compared to summer (Geelhoed et al. 2013, Aarts et al. 2016, Gilles et al. 2016). In addition, there is some anecdotal evidence. For example, one albino porpoise observed in Den Helder on 25 February 2012 was re-sighted three days later near Juist (Germany), 187 km from its first sighting (C. Rebel & K. Camphuysen pers. comm.). During the summer months porpoise abundance in the Dutch part of the North Sea is lower, but a substantial number of mother-calve pair are sighted further offshore in Dutch waters (Geelhoed et al. 2013). The porpoises observed offshore in summer reflect a more resident and breeding population that eventually disperse into the shallow, coastal waters.

We were unable to account for spatial differences in sightings given the lack of continuous and long-term sighting records in the most northern part of the study area. In another study on porpoise strandings (IJsseldijk & ten Doeschate et al. 2020), the Dutch coast was subdivided in two regions, with the Dutch Delta as part of one region (together with the Belgian and southern English coasts), and the rest of the Netherlands represented in another region. Although seasonality in porpoise strandings in both of these two regions was characterised by a bimodal pattern, with a peak in March/April and a second peak in August, these peaks were not homogeneous between both regions. Especially the region containing the Dutch mainland and Wadden area showed a proportionally higher peak in the stranding pattern in August compared to the peak in March. This might suggest a seasonal difference in stranding frequency between the Delta and mid-northern parts of the Dutch coast, possibly reflecting spatiotemporal differences in distribution. However, in the previous study, the Dutch Delta was grouped with southern England and Belgium, so strandings in these areas could also account for the spatial difference observed. In this study, it was not possible to assess the coastal sightings on a similar spatial scale, due to the lack of observation sites with >5000 hours of observation effort in northern Netherlands, including the Wadden islands. We therefore assessed the Netherlands as one unit in this study, without further differentiation into specific regions.

When accounting the stranding for the sighting rate, the temporal patterns in the residuals showed that in the early 1990's (when porpoise sightings were still rare (Camphuysen 2004, 2011)) and after 2010, the number of stranded porpoises exceeded the expected number of porpoise strandings based on the sightings. Especially in the summer of 2011, the number of dead porpoises found ashore were excessively high. Possible reasons for the general perceived elevated mortality rate in the last decade might have either been a natural cause, like redistribution of porpoises relative to the coast or increased mortality due to increased density dependent competition near carrying capacity. Alternatively, elevated mortalities might have a human-related cause, like increased anthropogenic activities at sea. However, the elevated mortality in the summer of 2011 most likely reflects a period of unusual mortality and warrants further in-depth investigations into the causes. The declaration of an unusual mortality event (UME) for a common species in an area is often challenging and requires understanding of the 'normal' stranding patterns, for which the quantification of the multiple components that are involved in the stranding process are needed (Hart et al. 2006, Williams et al. 2011, Ten Doeschate et al. 2018). In the current study, we have done this for changes in local abundance, however, other processes involved in the stranding process are previously characterized. These include physical processes, like drift and carcass buoyancy, social processes, like changes in reporting effort, and biological processes, like changes in distribution or increases in mortality (Peltier et al. 2013).

The physical processes of strandings, including those in the North Sea, have been studied by others (Peltier et al. 2012, 2013). Through drift modelling, Peltier et al. (2013) showed that the probability of a carcass to strand (logically) increases with an animal dying closer to shore. For animals that died further from the coast, the probability of stranding was higher in winter than summer as a result of seasonal variation in wind force. Finally, authors reported the lowest expected stranding numbers in April-May for the south-eastern North Sea (Peltier et al. 2013). Although the latter corresponds to the low stranding rates in April-May on the Dutch coast as demonstrated here and (IJsseldijk & ten Doeschate et al. 2020), the lower probability of strandings in summer as a result of seasonal variation in wind force suggests that the already apparently high number of summer strandings reflect only a minority of all drifting carcasses in this period. In addition, in our study there was sufficient evidence that coastal sightings explain patterns in strandings in particularly the fresh and alive stranded porpoises. This suggests that the carcasses that wash up in advanced state of decomposition might have died further offshore, therefore out of sight, and needed more time to eventually strand. This was specifically apparent in summer, as we demonstrated increases in strandings that could not be explained by sightings in July - August. It was outside the scope of this study to incorporate the effect of wind and temperature on strandings. However, increases in temperature in the summer might be accounted for the increase in more decomposed cases in this period (Santos et al. 2018). Analysis in combination with the effect of wind and drift could prove the offshore origin of the majority of stranded porpoises in July - August. Incorporating our methods with those of Peltier et al. (2013) or other drift modelling approaches (Hart et al. 2006, Santos et al. 2018) that could be adapted for the North Sea, would be a worthwhile follow-up assessment towards the establishment of mortality hotspots.

The other potential bias is the social component which influences stranding reporting. This was demonstrated in a study on harbour porpoises stranded on the Pacific Northwest coast of the USA in 2006. A UME was declared following a marked increase in stranding numbers, but pathological assessment of animals stranded in this period, compared to animals stranded post-UME revealed no single cause to explain the increase. A combination of a growing population of porpoises in the area, together with a more well established stranding network likely resulted in the elevation in stranding records (Huggins et al. 2015). In the Netherlands, beaches are very populated and easy accessible. Coverage of the coast is expected to be near 100% for the Delta and mainland area, but lesser in the northern Netherlands (expected up to 80%, (Peltier et al. 2013)). It should however be noted that these are estimates, as methods to quantify the social biases are lacking. However, since the early 20th century, the Natural History Museum Leiden (Naturalis) has actively been collecting strandings data (van Deinse 1931, Camphuysen et al. 2008). Although a rise in the quality of the data collection is expected throughout the study period, especially since the introduction of the mobile phone and its ability to directly report strandings and accompany those with pictures, the quantity has likely not changed as a direct effect of these technologies.

After reducing potential physical and social biases that influence stranding records, and after correcting for the effect of increases in local abundance, other explanations for elevations in mortality levels can be explored. The biological aspect within the stranding process is of primary interest in the context of conservation management (Ten Doeschate et al. 2018). Marine mammal mortality events can be direct consequence of anthropogenic activities (Fernández et al. 2005, Schwacke et al. 2014, Sharp et al. 2019), as well as disease outbreaks (Rubio-Guerri et al. 2013, Kemper et al. 2016), and nutritional deficiency (Trites and Donnelly 2003). Sometimes, there is a combination of factors involved, and pinpointing one cause not possible (Mazzariol et al. 2011, IJsseldijk et al. 2018c). In the Netherlands, post-mortem examinations on stranded marine mammals have been conducted since 2006 (IJsseldijk et al. 2018b). Databases hold information on causes of death, individual health, disease burden and nutritional condition. Additionally, data and tissue samples to study life history, diet and contaminant levels of harbour porpoises can readily be available. The assessment of a combination of these data together with time-area information of anthropogenic activities can be analysed to determine trends, but also changes e.g. pre, during and post defined UMEs.

To minimise disturbance and negative impacts on wildlife populations when giving permission to proposed anthropogenic activities, managers need to consider the potential impact of such activities. Where trends in abundance are useful for the identification of population size and structure, information on finer-scale spatiotemporal variation in population distribution is a vital focus in conservation management, e.g. for determining area-time closures in relation to human activity or assigning Marine Protected Areas. When the statistical credibility of the stranding records are improved, such as by reducing potential biases like demonstrated in this study, these records could serve a valuable source of information in a monitoring perspective and a cost-effective method to assess fine-scale population changes. To be able to assess the consequences of anthropogenic noise and to prove or disproof its link to elevated mortalities, a model incorporating time-area-exposure data and mortality numbers, subsequently corrected for sightings to reduce the bias of changes in local abundance and for environmental conditions like wind direction and drift, should be developed. If elevated stranding rates are consequently following a noise-events, like after underwater clearance of unexploded ordnance (UXO) or pile-driving for the construction of windfarms, this could be identified (Ketten 2004, 2012, Danil and St. Leger 2011). Von Benda-Beckmann et al. (2015) and Aarts et al. (2016) previously investigated the cumulative number of porpoises acoustically exposed to detonation of UXO and the impact of this on the population in the southern North Sea. These authors used harbour porpoise distribution data gained from aerial surveys, and concluded that thousands of porpoises suffered of permanent hearing loss as a consequence of detonation of UXO in a one year period. With a full dependence on sounds for communication and predation in cetaceans, permanent hearing loss would results in sudden death. Assessment of strandings data, which are more continuously recorded that the aerial surveys and provide fine-scale resolutions, could therefore allow the identification of noise-related stranding peaks.

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7 Appendix

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Call:
glm.nb(formula = NR.WAARNEMINGEN ~ -1 + factor(JAAR):factor(MAAND) +
    factor(TELPOST) + factor(DAGDEEL) + WINDK + WINDR1 + WINDR2 +
    WOLKD + ZICHT + offset(log(DUURM)), data = zeetrek.s, init.theta = 0.2195934195,
    link = log)

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-1.3913  -0.4369  -0.1903   0.0000   6.4337

Coefficients: (7 not defined because of singularities)
                                   Estimate Std. Error z value Pr(>|z|)
factor(TELPOST)3                 -7.690e+00  2.125e-01 -36.182  < 2e-16 ***
factor(TELPOST)29                -6.059e+00  1.793e-01 -33.783  < 2e-16 ***
factor(TELPOST)71                -6.542e+00  1.788e-01 -36.582  < 2e-16 ***
factor(TELPOST)97                -6.725e+00  1.838e-01 -36.598  < 2e-16 ***
factor(TELPOST)110               -5.795e+00  1.904e-01 -30.437  < 2e-16 ***
factor(TELPOST)126               -5.990e+00  2.186e-01 -27.401  < 2e-16 ***
factor(TELPOST)147               -7.220e+00  3.075e-01 -23.482  < 2e-16 ***
factor(TELPOST)159               -5.254e+00  1.844e-01 -28.488  < 2e-16 ***
factor(TELPOST)235               -6.985e+00  2.720e-01 -25.677  < 2e-16 ***
factor(TELPOST)252               -6.208e+00  1.888e-01 -32.880  < 2e-16 ***
factor(TELPOST)402               -5.202e+00  2.499e-01 -20.817  < 2e-16 ***
factor(TELPOST)410               -7.915e+00  2.955e-01 -26.787  < 2e-16 ***
factor(TELPOST)429               -5.176e+00  1.786e-01 -28.982  < 2e-16 ***
factor(TELPOST)518               -5.561e+00  2.364e-01 -23.526  < 2e-16 ***
factor(TELPOST)527               -5.001e+00  1.874e-01 -26.680  < 2e-16 ***
factor(TELPOST)704               -6.522e+00  3.900e-01 -16.723  < 2e-16 ***
factor(TELPOST)1116              -6.219e+00  2.031e-01 -30.628  < 2e-16 ***
factor(TELPOST)1272              -5.087e+00  2.365e-01 -21.510  < 2e-16 ***
factor(DAGDEEL)2                  7.286e-02  3.367e-02   2.164 0.030456 *
factor(DAGDEEL)3                  8.471e-02  4.276e-02   1.981 0.047596 *
WINDKmatig                        5.271e-01  4.547e-02  11.593  < 2e-16 ***
WINDKzwak                         9.738e-01  4.714e-02  20.660  < 2e-16 ***
WINDR1afl                         4.294e-01  3.840e-02  11.181  < 2e-16 ***
WINDR1rest                        3.377e-01  3.960e-02   8.527  < 2e-16 ***
WINDR2tegen                       1.358e-02  3.765e-02   0.361 0.718327
WINDR2zij                         1.278e-02  4.067e-02   0.314 0.753262
WOLKDonbew                       -2.765e-02  4.367e-02  -0.633 0.526629
WOLKDzwaar                        3.832e-01  3.820e-02  10.034  < 2e-16 ***
ZICHTredel                       -3.914e-02  3.190e-02  -1.227 0.219847
ZICHTslecht                      -3.644e-01  6.129e-02  -5.945 2.76e-09 ***
factor(JAAR)1989:factor(MAAND)1  -2.248e+00  4.378e-01  -5.136 2.81e-07 ***
factor(JAAR)1990:factor(MAAND)1  -3.630e+00  7.578e-01  -4.790 1.67e-06 ***
factor(JAAR)1991:factor(MAAND)1  -3.922e+00  7.809e-01  -5.023 5.09e-07 ***
factor(JAAR)1992:factor(MAAND)1  -2.461e+00  4.725e-01  -5.209 1.90e-07 ***
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factor(JAAR)1993:factor(MAAND)1	-4.109e+00	7.588e-01	-5.415	6.13e-08	***
factor(JAAR)1994:factor(MAAND)1	-2.873e+00	4.491e-01	-6.397	1.58e-10	***
factor(JAAR)1995:factor(MAAND)1	-3.631e+00	6.255e-01	-5.806	6.42e-09	***
factor(JAAR)1996:factor(MAAND)1	-3.439e+00	5.641e-01	-6.096	1.09e-09	***
factor(JAAR)1997:factor(MAAND)1	-3.466e+01	1.908e+06	0.000	0.999986	
factor(JAAR)1998:factor(MAAND)1	-1.056e+00	3.846e-01	-2.745	0.006057	**
factor(JAAR)1999:factor(MAAND)1	-9.860e-02	3.207e-01	-0.307	0.758502	
factor(JAAR)2000:factor(MAAND)1	-1.254e+00	4.185e-01	-2.997	0.002731	**
factor(JAAR)2001:factor(MAAND)1	-7.791e-01	3.079e-01	-2.531	0.011382	*
factor(JAAR)2002:factor(MAAND)1	-1.152e+00	3.799e-01	-3.032	0.002428	**
factor(JAAR)2003:factor(MAAND)1	-7.301e-02	2.925e-01	-0.250	0.802878	
factor(JAAR)2004:factor(MAAND)1	-3.312e-01	3.088e-01	-1.072	0.283523	
factor(JAAR)2005:factor(MAAND)1	1.549e+00	2.244e-01	6.901	5.17e-12	***
factor(JAAR)2006:factor(MAAND)1	-7.493e-02	2.709e-01	-0.277	0.782051	
factor(JAAR)2007:factor(MAAND)1	-1.851e-01	3.057e-01	-0.605	0.544855	
factor(JAAR)2008:factor(MAAND)1	4.303e-01	2.898e-01	1.485	0.137660	
factor(JAAR)2009:factor(MAAND)1	-1.727e-01	2.354e-01	-0.733	0.463287	
factor(JAAR)2010:factor(MAAND)1	-6.351e-02	2.522e-01	-0.252	0.801203	
factor(JAAR)2011:factor(MAAND)1	-1.402e-01	2.616e-01	-0.536	0.591953	
factor(JAAR)2012:factor(MAAND)1	-4.347e-01	2.250e-01	-1.932	0.053378	.
factor(JAAR)2013:factor(MAAND)1	1.214e+00	2.082e-01	5.832	5.46e-09	***
factor(JAAR)2014:factor(MAAND)1	1.932e+00	2.120e-01	9.116	< 2e-16	***
factor(JAAR)2015:factor(MAAND)1	-1.513e+00	3.047e-01	-4.967	6.79e-07	***
factor(JAAR)2016:factor(MAAND)1	6.725e-02	2.298e-01	0.293	0.769759	
factor(JAAR)2017:factor(MAAND)1	-3.617e-01	2.372e-01	-1.525	0.127277	
factor(JAAR)2018:factor(MAAND)1	-4.396e-02	2.265e-01	-0.194	0.846074	
factor(JAAR)1989:factor(MAAND)2	-3.091e+00	6.260e-01	-4.937	7.94e-07	***
factor(JAAR)1990:factor(MAAND)2	-3.411e+01	1.836e+06	0.000	0.999985	
factor(JAAR)1991:factor(MAAND)2	-4.857e+00	1.022e+00	-4.751	2.02e-06	***
factor(JAAR)1992:factor(MAAND)2	-1.954e+00	4.211e-01	-4.640	3.49e-06	***
factor(JAAR)1993:factor(MAAND)2	-3.467e+01	1.865e+06	0.000	0.999985	
factor(JAAR)1994:factor(MAAND)2	-3.463e+01	1.625e+06	0.000	0.999983	
factor(JAAR)1995:factor(MAAND)2	-3.289e+00	5.624e-01	-5.848	4.96e-09	***
factor(JAAR)1996:factor(MAAND)2	-4.343e+00	7.425e-01	-5.849	4.96e-09	***
factor(JAAR)1997:factor(MAAND)2	-2.756e-01	3.175e-01	-0.868	0.385395	
factor(JAAR)1998:factor(MAAND)2	-9.148e-01	4.069e-01	-2.248	0.024566	*
factor(JAAR)1999:factor(MAAND)2	7.845e-01	2.825e-01	2.777	0.005489	**
factor(JAAR)2000:factor(MAAND)2	-1.034e+00	3.539e-01	-2.923	0.003467	**
factor(JAAR)2001:factor(MAAND)2	7.870e-01	2.550e-01	3.086	0.002026	**
factor(JAAR)2002:factor(MAAND)2	-3.957e-01	3.292e-01	-1.202	0.229391	
factor(JAAR)2003:factor(MAAND)2	-4.578e-01	2.886e-01	-1.586	0.112634	
factor(JAAR)2004:factor(MAAND)2	1.403e-01	2.996e-01	0.468	0.639577	
factor(JAAR)2005:factor(MAAND)2	1.405e+00	2.560e-01	5.486	4.10e-08	***
factor(JAAR)2006:factor(MAAND)2	1.738e+00	2.505e-01	6.938	3.97e-12	***
factor(JAAR)2007:factor(MAAND)2	1.332e+00	3.008e-01	4.428	9.51e-06	***
factor(JAAR)2008:factor(MAAND)2	2.452e-01	3.149e-01	0.779	0.436135	
factor(JAAR)2009:factor(MAAND)2	1.457e-01	2.365e-01	0.616	0.537903	
factor(JAAR)2010:factor(MAAND)2	4.423e-02	2.945e-01	0.150	0.880616	
factor(JAAR)2011:factor(MAAND)2	2.317e-01	2.629e-01	0.881	0.378229	
factor(JAAR)2012:factor(MAAND)2	7.521e-01	2.184e-01	3.443	0.000575	***
factor(JAAR)2013:factor(MAAND)2	1.372e+00	2.233e-01	6.143	8.10e-10	***

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factor(JAAR)2014:factor(MAAND)2   1.797e+00  2.271e-01   7.915 2.48e-15 ***
factor(JAAR)2015:factor(MAAND)2  -1.056e+00  2.726e-01  -3.875 0.000107 ***
factor(JAAR)2016:factor(MAAND)2   9.768e-01  2.245e-01   4.351 1.35e-05 ***
factor(JAAR)2017:factor(MAAND)2  -2.107e-01  2.551e-01  -0.826 0.408699
factor(JAAR)2018:factor(MAAND)2   2.504e-01  2.351e-01   1.065 0.286809
factor(JAAR)1989:factor(MAAND)3  -2.948e+00  4.565e-01  -6.458 1.06e-10 ***
factor(JAAR)1990:factor(MAAND)3  -3.763e+00  7.520e-01  -5.004 5.62e-07 ***
factor(JAAR)1991:factor(MAAND)3  -3.450e+01  1.418e+06   0.000 0.999981
factor(JAAR)1992:factor(MAAND)3  -4.799e+00  1.030e+00  -4.659 3.17e-06 ***
factor(JAAR)1993:factor(MAAND)3  -4.146e+00  6.069e-01  -6.831 8.42e-12 ***
factor(JAAR)1994:factor(MAAND)3  -9.755e-01  2.620e-01  -3.723 0.000197 ***
factor(JAAR)1995:factor(MAAND)3  -3.688e+00  6.186e-01  -5.962 2.50e-09 ***
factor(JAAR)1996:factor(MAAND)3  -2.641e+00  3.226e-01  -8.185 2.71e-16 ***
factor(JAAR)1997:factor(MAAND)3  -3.387e-01  2.496e-01  -1.357 0.174908
factor(JAAR)1998:factor(MAAND)3   2.553e-01  2.636e-01   0.968 0.332846
factor(JAAR)1999:factor(MAAND)3  -6.665e-01  3.016e-01  -2.210 0.027096 *
factor(JAAR)2000:factor(MAAND)3  -2.124e-01  2.630e-01  -0.808 0.419366
factor(JAAR)2001:factor(MAAND)3   3.231e-01  2.330e-01   1.387 0.165579
factor(JAAR)2002:factor(MAAND)3   3.081e-01  2.369e-01   1.301 0.193308
factor(JAAR)2003:factor(MAAND)3   8.683e-02  2.579e-01   0.337 0.736360
factor(JAAR)2004:factor(MAAND)3  -5.941e-02  2.582e-01  -0.230 0.817993
factor(JAAR)2005:factor(MAAND)3   1.611e+00  2.248e-01   7.167 7.65e-13 ***
factor(JAAR)2006:factor(MAAND)3   5.697e-01  2.420e-01   2.354 0.018561 *
factor(JAAR)2007:factor(MAAND)3   5.378e-01  2.606e-01   2.063 0.039078 *
factor(JAAR)2008:factor(MAAND)3  -5.302e-01  2.987e-01  -1.775 0.075877 .
factor(JAAR)2009:factor(MAAND)3  -1.277e-01  2.230e-01  -0.573 0.566856
factor(JAAR)2010:factor(MAAND)3   5.621e-01  2.120e-01   2.652 0.008002 **
factor(JAAR)2011:factor(MAAND)3   4.654e-01  2.035e-01   2.287 0.022192 *
factor(JAAR)2012:factor(MAAND)3   2.155e-01  1.976e-01   1.091 0.275243
factor(JAAR)2013:factor(MAAND)3   1.095e+00  1.997e-01   5.485 4.13e-08 ***
factor(JAAR)2014:factor(MAAND)3   4.062e-01  2.077e-01   1.956 0.050500 .
factor(JAAR)2015:factor(MAAND)3  -1.630e+00  2.692e-01  -6.053 1.42e-09 ***
factor(JAAR)2016:factor(MAAND)3  -3.785e-01  2.179e-01  -1.737 0.082388 .
factor(JAAR)2017:factor(MAAND)3  -9.360e-01  2.304e-01  -4.063 4.84e-05 ***
factor(JAAR)2018:factor(MAAND)3  -3.047e-01  2.209e-01  -1.379 0.167810
factor(JAAR)1989:factor(MAAND)4  -3.469e+01  1.529e+06   0.000 0.999982
factor(JAAR)1990:factor(MAAND)4  -4.418e+00  7.344e-01  -6.016 1.79e-09 ***
factor(JAAR)1991:factor(MAAND)4  -3.428e+01  1.140e+06   0.000 0.999976
factor(JAAR)1992:factor(MAAND)4  -3.463e+01  1.576e+06   0.000 0.999982
factor(JAAR)1993:factor(MAAND)4  -3.471e+01  1.378e+06   0.000 0.999980
factor(JAAR)1994:factor(MAAND)4  -1.766e+00  2.713e-01  -6.512 7.43e-11 ***
factor(JAAR)1995:factor(MAAND)4  -3.449e+01  1.237e+06   0.000 0.999978
factor(JAAR)1996:factor(MAAND)4  -2.785e+00  3.233e-01  -8.615  < 2e-16 ***
factor(JAAR)1997:factor(MAAND)4  -1.996e+00  3.266e-01  -6.112 9.87e-10 ***
factor(JAAR)1998:factor(MAAND)4  -3.399e+00  6.178e-01  -5.502 3.76e-08 ***
factor(JAAR)1999:factor(MAAND)4  -3.376e+00  5.443e-01  -6.203 5.53e-10 ***
factor(JAAR)2000:factor(MAAND)4  -2.819e+00  4.041e-01  -6.976 3.03e-12 ***
factor(JAAR)2001:factor(MAAND)4  -1.190e+00  2.972e-01  -4.005 6.20e-05 ***
factor(JAAR)2002:factor(MAAND)4  -2.170e+00  3.377e-01  -6.426 1.31e-10 ***
factor(JAAR)2003:factor(MAAND)4  -3.526e+00  5.522e-01  -6.386 1.70e-10 ***
factor(JAAR)2004:factor(MAAND)4  -1.976e+00  3.193e-01  -6.189 6.06e-10 ***
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factor(JAAR)2005:factor(MAAND)4  -1.632e+00  3.093e-01  -5.276 1.32e-07 ***
factor(JAAR)2006:factor(MAAND)4   3.032e-02  2.488e-01   0.122 0.903008
factor(JAAR)2007:factor(MAAND)4  -3.394e+00  4.728e-01  -7.179 7.03e-13 ***
factor(JAAR)2008:factor(MAAND)4  -3.524e+00  5.435e-01  -6.485 8.87e-11 ***
factor(JAAR)2009:factor(MAAND)4  -3.121e+00  3.936e-01  -7.928 2.22e-15 ***
factor(JAAR)2010:factor(MAAND)4  -2.194e+00  2.786e-01  -7.875 3.39e-15 ***
factor(JAAR)2011:factor(MAAND)4  -1.978e+00  2.586e-01  -7.649 2.02e-14 ***
factor(JAAR)2012:factor(MAAND)4  -1.203e+00  2.339e-01  -5.143 2.71e-07 ***
factor(JAAR)2013:factor(MAAND)4   1.471e+00  1.956e-01   7.520 5.46e-14 ***
factor(JAAR)2014:factor(MAAND)4  -3.362e+00  3.887e-01  -8.650  < 2e-16 ***
factor(JAAR)2015:factor(MAAND)4  -3.828e+00  4.553e-01  -8.407  < 2e-16 ***
factor(JAAR)2016:factor(MAAND)4  -1.281e+00  2.355e-01  -5.439 5.36e-08 ***
factor(JAAR)2017:factor(MAAND)4  -2.460e+00  2.887e-01  -8.519  < 2e-16 ***
factor(JAAR)2018:factor(MAAND)4  -1.591e+00  2.472e-01  -6.436 1.23e-10 ***
factor(JAAR)1989:factor(MAAND)5  -3.453e+01  1.637e+06   0.000 0.999983
factor(JAAR)1990:factor(MAAND)5  -3.434e+01  1.502e+06   0.000 0.999982
factor(JAAR)1991:factor(MAAND)5  -5.322e+00  1.028e+00  -5.176 2.27e-07 ***
factor(JAAR)1992:factor(MAAND)5  -3.468e+01  1.689e+06   0.000 0.999984
factor(JAAR)1993:factor(MAAND)5  -3.456e+01  1.392e+06   0.000 0.999980
factor(JAAR)1994:factor(MAAND)5  -4.286e+00  6.202e-01  -6.910 4.83e-12 ***
factor(JAAR)1995:factor(MAAND)5  -3.466e+01  1.452e+06   0.000 0.999981
factor(JAAR)1996:factor(MAAND)5  -4.783e+00  7.379e-01  -6.482 9.03e-11 ***
factor(JAAR)1997:factor(MAAND)5  -3.466e+01  1.747e+06   0.000 0.999984
factor(JAAR)1998:factor(MAAND)5  -3.441e+01  1.818e+06   0.000 0.999985
factor(JAAR)1999:factor(MAAND)5  -3.819e+00  7.397e-01  -5.164 2.42e-07 ***
factor(JAAR)2000:factor(MAAND)5  -3.458e+01  2.085e+06   0.000 0.999987
factor(JAAR)2001:factor(MAAND)5  -3.213e+00  5.000e-01  -6.427 1.30e-10 ***
factor(JAAR)2002:factor(MAAND)5  -3.453e+01  1.908e+06   0.000 0.999986
factor(JAAR)2003:factor(MAAND)5  -4.409e+00  1.050e+00  -4.199 2.68e-05 ***
factor(JAAR)2004:factor(MAAND)5  -4.795e+00  1.019e+00  -4.706 2.53e-06 ***
factor(JAAR)2005:factor(MAAND)5  -3.620e+00  6.072e-01  -5.962 2.50e-09 ***
factor(JAAR)2006:factor(MAAND)5  -3.713e+00  6.350e-01  -5.847 5.01e-09 ***
factor(JAAR)2007:factor(MAAND)5  -2.456e+00  3.989e-01  -6.157 7.43e-10 ***
factor(JAAR)2008:factor(MAAND)5  -4.279e+00  7.586e-01  -5.641 1.69e-08 ***
factor(JAAR)2009:factor(MAAND)5  -3.226e+00  3.872e-01  -8.332  < 2e-16 ***
factor(JAAR)2010:factor(MAAND)5  -2.465e+00  2.998e-01  -8.222  < 2e-16 ***
factor(JAAR)2011:factor(MAAND)5  -3.005e+00  4.001e-01  -7.512 5.84e-14 ***
factor(JAAR)2012:factor(MAAND)5  -2.329e+00  3.050e-01  -7.638 2.21e-14 ***
factor(JAAR)2013:factor(MAAND)5  -1.743e+00  2.670e-01  -6.530 6.58e-11 ***
factor(JAAR)2014:factor(MAAND)5  -3.378e+00  4.505e-01  -7.498 6.49e-14 ***
factor(JAAR)2015:factor(MAAND)5  -3.995e+00  5.449e-01  -7.332 2.26e-13 ***
factor(JAAR)2016:factor(MAAND)5  -4.329e+00  6.205e-01  -6.976 3.04e-12 ***
factor(JAAR)2017:factor(MAAND)5  -3.567e+00  4.123e-01  -8.650  < 2e-16 ***
factor(JAAR)2018:factor(MAAND)5  -3.007e+00  3.227e-01  -9.318  < 2e-16 ***
factor(JAAR)1989:factor(MAAND)6  -3.464e+01  2.494e+06   0.000 0.999989
factor(JAAR)1990:factor(MAAND)6  -3.400e+01  2.500e+06   0.000 0.999989
factor(JAAR)1991:factor(MAAND)6  -3.410e+01  1.541e+06   0.000 0.999982
factor(JAAR)1992:factor(MAAND)6  -3.474e+01  2.194e+06   0.000 0.999987
factor(JAAR)1993:factor(MAAND)6  -3.504e+01  2.290e+06   0.000 0.999988
factor(JAAR)1994:factor(MAAND)6  -3.464e+01  1.855e+06   0.000 0.999985
factor(JAAR)1995:factor(MAAND)6  -3.460e+01  1.907e+06   0.000 0.999986
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factor(JAAR)1996:factor(MAAND)6	-3.431e+01	1.311e+06	0.000	0.999979	
factor(JAAR)1997:factor(MAAND)6	-3.459e+01	1.896e+06	0.000	0.999985	
factor(JAAR)1998:factor(MAAND)6	-3.428e+00	1.051e+00	-3.263	0.001102	**
factor(JAAR)1999:factor(MAAND)6	-3.441e+01	3.398e+06	0.000	0.999992	
factor(JAAR)2000:factor(MAAND)6	-3.483e+01	3.415e+06	0.000	0.999992	
factor(JAAR)2001:factor(MAAND)6	-3.450e+01	2.598e+06	0.000	0.999989	
factor(JAAR)2002:factor(MAAND)6	-3.437e+01	2.004e+06	0.000	0.999986	
factor(JAAR)2003:factor(MAAND)6	-3.467e+01	2.154e+06	0.000	0.999987	
factor(JAAR)2004:factor(MAAND)6	-3.436e+01	2.425e+06	0.000	0.999989	
factor(JAAR)2005:factor(MAAND)6	-3.478e+01	2.676e+06	0.000	0.999990	
factor(JAAR)2006:factor(MAAND)6	-4.478e+00	1.031e+00	-4.343	1.41e-05	***
factor(JAAR)2007:factor(MAAND)6	-1.940e+00	4.143e-01	-4.682	2.84e-06	***
factor(JAAR)2008:factor(MAAND)6	-3.468e+01	2.396e+06	0.000	0.999988	
factor(JAAR)2009:factor(MAAND)6	-4.496e+00	1.020e+00	-4.407	1.05e-05	***
factor(JAAR)2010:factor(MAAND)6	-2.261e+00	4.155e-01	-5.442	5.26e-08	***
factor(JAAR)2011:factor(MAAND)6	-3.455e+01	2.048e+06	0.000	0.999987	
factor(JAAR)2012:factor(MAAND)6	-3.449e+00	6.314e-01	-5.462	4.71e-08	***
factor(JAAR)2013:factor(MAAND)6	-3.393e+00	5.716e-01	-5.935	2.95e-09	***
factor(JAAR)2014:factor(MAAND)6	-1.795e+00	3.361e-01	-5.340	9.31e-08	***
factor(JAAR)2015:factor(MAAND)6	-2.698e+00	3.940e-01	-6.847	7.54e-12	***
factor(JAAR)2016:factor(MAAND)6	-2.676e+00	4.253e-01	-6.292	3.14e-10	***
factor(JAAR)2017:factor(MAAND)6	-1.961e+00	3.366e-01	-5.826	5.67e-09	***
factor(JAAR)2018:factor(MAAND)6	-2.582e+00	3.757e-01	-6.873	6.27e-12	***
factor(JAAR)1989:factor(MAAND)7	-3.440e+01	1.549e+06	0.000	0.999982	
factor(JAAR)1990:factor(MAAND)7	-3.197e+00	5.491e-01	-5.822	5.80e-09	***
factor(JAAR)1991:factor(MAAND)7	-3.473e+01	2.021e+06	0.000	0.999986	
factor(JAAR)1992:factor(MAAND)7	-3.449e+01	1.563e+06	0.000	0.999982	
factor(JAAR)1993:factor(MAAND)7	-3.444e+01	1.445e+06	0.000	0.999981	
factor(JAAR)1994:factor(MAAND)7	-3.487e+01	1.984e+06	0.000	0.999986	
factor(JAAR)1995:factor(MAAND)7	-3.461e+01	1.481e+06	0.000	0.999981	
factor(JAAR)1996:factor(MAAND)7	-3.450e+01	1.292e+06	0.000	0.999979	
factor(JAAR)1997:factor(MAAND)7	-3.455e+01	1.531e+06	0.000	0.999982	
factor(JAAR)1998:factor(MAAND)7	-3.594e+00	7.364e-01	-4.881	1.06e-06	***
factor(JAAR)1999:factor(MAAND)7	-4.356e+00	1.050e+00	-4.148	3.35e-05	***
factor(JAAR)2000:factor(MAAND)7	-4.381e+00	1.053e+00	-4.162	3.16e-05	***
factor(JAAR)2001:factor(MAAND)7	-3.468e+01	2.308e+06	0.000	0.999988	
factor(JAAR)2002:factor(MAAND)7	-2.776e+00	4.284e-01	-6.480	9.17e-11	***
factor(JAAR)2003:factor(MAAND)7	-4.167e+00	7.406e-01	-5.626	1.85e-08	***
factor(JAAR)2004:factor(MAAND)7	-1.522e+00	3.545e-01	-4.295	1.75e-05	***
factor(JAAR)2005:factor(MAAND)7	-2.145e+00	3.824e-01	-5.610	2.02e-08	***
factor(JAAR)2006:factor(MAAND)7	-1.861e+00	3.465e-01	-5.372	7.80e-08	***
factor(JAAR)2007:factor(MAAND)7	-3.670e+00	7.691e-01	-4.772	1.82e-06	***
factor(JAAR)2008:factor(MAAND)7	-1.398e+00	3.560e-01	-3.928	8.57e-05	***
factor(JAAR)2009:factor(MAAND)7	-1.277e+00	2.597e-01	-4.918	8.75e-07	***
factor(JAAR)2010:factor(MAAND)7	-2.829e+00	4.359e-01	-6.490	8.61e-11	***
factor(JAAR)2011:factor(MAAND)7	-1.229e+00	3.008e-01	-4.086	4.39e-05	***
factor(JAAR)2012:factor(MAAND)7	-9.356e-01	2.722e-01	-3.438	0.000587	***
factor(JAAR)2013:factor(MAAND)7	-1.352e+00	2.855e-01	-4.737	2.17e-06	***
factor(JAAR)2014:factor(MAAND)7	-1.677e+00	3.038e-01	-5.520	3.39e-08	***
factor(JAAR)2015:factor(MAAND)7	-1.981e+00	3.098e-01	-6.392	1.64e-10	***
factor(JAAR)2016:factor(MAAND)7	-1.306e+00	2.589e-01	-5.045	4.53e-07	***

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factor(JAAR)2017:factor(MAAND)7  -1.507e+00  2.653e-01  -5.680 1.35e-08 ***
factor(JAAR)2018:factor(MAAND)7          NA         NA      NA       NA    
factor(JAAR)1989:factor(MAAND)8  -3.422e+01  1.164e+06   0.000 0.999977    
factor(JAAR)1990:factor(MAAND)8  -3.431e+01  1.383e+06   0.000 0.999980    
factor(JAAR)1991:factor(MAAND)8  -3.436e+01  1.373e+06   0.000 0.999980    
factor(JAAR)1992:factor(MAAND)8  -3.409e+01  1.041e+06   0.000 0.999974    
factor(JAAR)1993:factor(MAAND)8  -3.428e+01  1.254e+06   0.000 0.999978    
factor(JAAR)1994:factor(MAAND)8  -3.434e+01  1.093e+06   0.000 0.999975    
factor(JAAR)1995:factor(MAAND)8  -3.415e+01  1.176e+06   0.000 0.999977    
factor(JAAR)1996:factor(MAAND)8  -3.423e+01  1.189e+06   0.000 0.999977    
factor(JAAR)1997:factor(MAAND)8  -3.457e+01  1.410e+06   0.000 0.999980    
factor(JAAR)1998:factor(MAAND)8  -3.408e+01  1.431e+06   0.000 0.999981    
factor(JAAR)1999:factor(MAAND)8  -3.447e+01  1.892e+06   0.000 0.999985    
factor(JAAR)2000:factor(MAAND)8  -3.452e+01  1.868e+06   0.000 0.999985    
factor(JAAR)2001:factor(MAAND)8  -3.434e+01  1.639e+06   0.000 0.999983    
factor(JAAR)2002:factor(MAAND)8  -3.868e+00  7.349e-01  -5.263 1.41e-07 ***
factor(JAAR)2003:factor(MAAND)8  -1.541e+00  2.815e-01  -5.474 4.41e-08 ***
factor(JAAR)2004:factor(MAAND)8  -2.226e+00  3.745e-01  -5.942 2.81e-09 ***
factor(JAAR)2005:factor(MAAND)8  -1.928e+00  3.191e-01  -6.042 1.52e-09 ***
factor(JAAR)2006:factor(MAAND)8  -2.036e+00  3.591e-01  -5.671 1.42e-08 ***
factor(JAAR)2007:factor(MAAND)8  -2.191e+00  3.970e-01  -5.519 3.40e-08 ***
factor(JAAR)2008:factor(MAAND)8  -2.330e+00  3.954e-01  -5.893 3.80e-09 ***
factor(JAAR)2009:factor(MAAND)8  -1.429e+00  2.445e-01  -5.843 5.12e-09 ***
factor(JAAR)2010:factor(MAAND)8  -2.237e+00  3.390e-01  -6.598 4.17e-11 ***
factor(JAAR)2011:factor(MAAND)8  -9.140e-01  2.384e-01  -3.835 0.000126 ***
factor(JAAR)2012:factor(MAAND)8  -4.778e-01  2.190e-01  -2.181 0.029169 *  
factor(JAAR)2013:factor(MAAND)8  -1.148e+00  2.332e-01  -4.925 8.43e-07 ***
factor(JAAR)2014:factor(MAAND)8  -1.883e+00  2.966e-01  -6.349 2.16e-10 ***
factor(JAAR)2015:factor(MAAND)8  -1.501e+00  2.569e-01  -5.843 5.14e-09 ***
factor(JAAR)2016:factor(MAAND)8  -1.588e+00  2.696e-01  -5.890 3.87e-09 ***
factor(JAAR)2017:factor(MAAND)8  -1.223e+00  2.521e-01  -4.851 1.23e-06 ***
factor(JAAR)2018:factor(MAAND)8          NA         NA      NA       NA    
factor(JAAR)1989:factor(MAAND)9  -3.442e+01  1.274e+06   0.000 0.999978    
factor(JAAR)1990:factor(MAAND)9  -3.422e+01  1.033e+06   0.000 0.999974    
factor(JAAR)1991:factor(MAAND)9  -3.446e+01  1.279e+06   0.000 0.999979    
factor(JAAR)1992:factor(MAAND)9  -3.435e+01  1.127e+06   0.000 0.999976    
factor(JAAR)1993:factor(MAAND)9  -3.452e+01  1.229e+06   0.000 0.999978    
factor(JAAR)1994:factor(MAAND)9  -5.304e+00  1.017e+00  -5.217 1.81e-07 ***
factor(JAAR)1995:factor(MAAND)9  -3.405e+01  1.104e+06   0.000 0.999975    
factor(JAAR)1996:factor(MAAND)9  -3.438e+01  1.312e+06   0.000 0.999979    
factor(JAAR)1997:factor(MAAND)9  -4.178e+00  6.348e-01  -6.582 4.64e-11 ***
factor(JAAR)1998:factor(MAAND)9  -3.409e+01  1.593e+06   0.000 0.999983    
factor(JAAR)1999:factor(MAAND)9  -3.871e+00  7.716e-01  -5.017 5.24e-07 ***
factor(JAAR)2000:factor(MAAND)9  -3.442e+01  1.662e+06   0.000 0.999983    
factor(JAAR)2001:factor(MAAND)9  -4.839e+00  1.029e+00  -4.703 2.56e-06 ***
factor(JAAR)2002:factor(MAAND)9  -3.425e+01  1.604e+06   0.000 0.999983    
factor(JAAR)2003:factor(MAAND)9  -1.796e+00  3.141e-01  -5.719 1.07e-08 ***
factor(JAAR)2004:factor(MAAND)9  -2.707e+00  4.116e-01  -6.576 4.83e-11 ***
factor(JAAR)2005:factor(MAAND)9  -6.471e-01  2.591e-01  -2.497 0.012512 *  
factor(JAAR)2006:factor(MAAND)9  -2.761e+00  4.523e-01  -6.105 1.03e-09 ***
factor(JAAR)2007:factor(MAAND)9  -3.691e+00  6.299e-01  -5.860 4.62e-09 ***
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factor(JAAR)2008:factor(MAAND)9	-1.099e+00	3.127e-01	-3.514	0.000442	***
factor(JAAR)2009:factor(MAAND)9	-6.087e-01	2.264e-01	-2.689	0.007175	**
factor(JAAR)2010:factor(MAAND)9	-1.016e+00	2.316e-01	-4.385	1.16e-05	***
factor(JAAR)2011:factor(MAAND)9	-9.466e-01	2.204e-01	-4.295	1.75e-05	***
factor(JAAR)2012:factor(MAAND)9	-1.213e+00	2.169e-01	-5.590	2.26e-08	***
factor(JAAR)2013:factor(MAAND)9	-1.209e+00	2.245e-01	-5.387	7.17e-08	***
factor(JAAR)2014:factor(MAAND)9	-1.327e+00	2.377e-01	-5.581	2.40e-08	***
factor(JAAR)2015:factor(MAAND)9	-1.317e+00	2.378e-01	-5.536	3.09e-08	***
factor(JAAR)2016:factor(MAAND)9	-1.407e+00	2.386e-01	-5.896	3.71e-09	***
factor(JAAR)2017:factor(MAAND)9	-1.319e+00	2.351e-01	-5.610	2.03e-08	***
factor(JAAR)2018:factor(MAAND)9	NA	NA	NA	NA	
factor(JAAR)1989:factor(MAAND)10	-3.412e+01	1.067e+06	0.000	0.999974	
factor(JAAR)1990:factor(MAAND)10	-3.432e+01	1.233e+06	0.000	0.999978	
factor(JAAR)1991:factor(MAAND)10	-4.476e+00	7.295e-01	-6.137	8.43e-10	***
factor(JAAR)1992:factor(MAAND)10	-3.444e+01	1.226e+06	0.000	0.999978	
factor(JAAR)1993:factor(MAAND)10	-5.472e+00	1.021e+00	-5.360	8.33e-08	***
factor(JAAR)1994:factor(MAAND)10	-5.205e+00	1.026e+00	-5.073	3.91e-07	***
factor(JAAR)1995:factor(MAAND)10	-4.103e+00	6.286e-01	-6.528	6.69e-11	***
factor(JAAR)1996:factor(MAAND)10	-3.422e+01	1.197e+06	0.000	0.999977	
factor(JAAR)1997:factor(MAAND)10	-3.734e+00	5.369e-01	-6.953	3.57e-12	***
factor(JAAR)1998:factor(MAAND)10	-3.406e+01	1.388e+06	0.000	0.999980	
factor(JAAR)1999:factor(MAAND)10	-3.420e+01	1.977e+06	0.000	0.999986	
factor(JAAR)2000:factor(MAAND)10	-2.889e+00	5.198e-01	-5.557	2.74e-08	***
factor(JAAR)2001:factor(MAAND)10	-1.884e+00	3.625e-01	-5.198	2.01e-07	***
factor(JAAR)2002:factor(MAAND)10	-2.491e+00	4.002e-01	-6.225	4.83e-10	***
factor(JAAR)2003:factor(MAAND)10	-1.248e+00	2.761e-01	-4.521	6.16e-06	***
factor(JAAR)2004:factor(MAAND)10	-2.032e+00	3.960e-01	-5.130	2.89e-07	***
factor(JAAR)2005:factor(MAAND)10	-2.442e+00	3.437e-01	-7.105	1.20e-12	***
factor(JAAR)2006:factor(MAAND)10	-1.375e+00	3.044e-01	-4.516	6.31e-06	***
factor(JAAR)2007:factor(MAAND)10	-1.790e+00	3.289e-01	-5.442	5.27e-08	***
factor(JAAR)2008:factor(MAAND)10	-1.721e+00	3.203e-01	-5.371	7.81e-08	***
factor(JAAR)2009:factor(MAAND)10	-6.751e-01	2.167e-01	-3.115	0.001841	**
factor(JAAR)2010:factor(MAAND)10	-1.034e+00	2.324e-01	-4.450	8.60e-06	***
factor(JAAR)2011:factor(MAAND)10	-5.435e-01	2.031e-01	-2.675	0.007468	**
factor(JAAR)2012:factor(MAAND)10	-8.649e-01	2.229e-01	-3.880	0.000104	***
factor(JAAR)2013:factor(MAAND)10	-6.334e-01	2.177e-01	-2.909	0.003625	**
factor(JAAR)2014:factor(MAAND)10	-1.084e+00	2.297e-01	-4.718	2.38e-06	***
factor(JAAR)2015:factor(MAAND)10	-1.026e+00	2.402e-01	-4.272	1.94e-05	***
factor(JAAR)2016:factor(MAAND)10	-8.467e-01	2.233e-01	-3.792	0.000150	***
factor(JAAR)2017:factor(MAAND)10	-9.426e-01	2.191e-01	-4.302	1.69e-05	***
factor(JAAR)2018:factor(MAAND)10	NA	NA	NA	NA	
factor(JAAR)1989:factor(MAAND)11	-3.437e+01	1.540e+06	0.000	0.999982	
factor(JAAR)1990:factor(MAAND)11	-3.441e+01	1.359e+06	0.000	0.999980	
factor(JAAR)1991:factor(MAAND)11	-3.452e+01	1.670e+06	0.000	0.999984	
factor(JAAR)1992:factor(MAAND)11	-3.426e+01	1.365e+06	0.000	0.999980	
factor(JAAR)1993:factor(MAAND)11	-4.601e+00	7.457e-01	-6.169	6.86e-10	***
factor(JAAR)1994:factor(MAAND)11	-3.460e+01	1.613e+06	0.000	0.999983	
factor(JAAR)1995:factor(MAAND)11	-2.803e+00	3.723e-01	-7.529	5.13e-14	***
factor(JAAR)1996:factor(MAAND)11	-3.418e+01	1.259e+06	0.000	0.999978	
factor(JAAR)1997:factor(MAAND)11	-2.462e+00	4.090e-01	-6.020	1.74e-09	***
factor(JAAR)1998:factor(MAAND)11	-3.742e+00	1.026e+00	-3.649	0.000264	***

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factor(JAAR)1999:factor(MAAND)11 -1.506e+00  4.120e-01  -3.656 0.000256 ***
factor(JAAR)2000:factor(MAAND)11 -2.152e+00  4.977e-01  -4.325 1.53e-05 ***
factor(JAAR)2001:factor(MAAND)11 -2.589e+00  5.210e-01  -4.969 6.74e-07 ***
factor(JAAR)2002:factor(MAAND)11 -2.137e+00  4.093e-01  -5.220 1.79e-07 ***
factor(JAAR)2003:factor(MAAND)11 -8.617e-01  3.573e-01  -2.411 0.015894 *
factor(JAAR)2004:factor(MAAND)11 -3.901e-01  2.762e-01  -1.413 0.157746
factor(JAAR)2005:factor(MAAND)11 -5.273e-01  2.454e-01  -2.149 0.031651 *
factor(JAAR)2006:factor(MAAND)11  1.071e-02  2.720e-01   0.039 0.968593
factor(JAAR)2007:factor(MAAND)11 -1.701e+00  3.468e-01  -4.906 9.29e-07 ***
factor(JAAR)2008:factor(MAAND)11 -1.853e-01  2.863e-01  -0.647 0.517608
factor(JAAR)2009:factor(MAAND)11 -2.524e-01  2.531e-01  -0.997 0.318598
factor(JAAR)2010:factor(MAAND)11 -4.513e-01  2.359e-01  -1.913 0.055760 .
factor(JAAR)2011:factor(MAAND)11  1.729e-01  2.118e-01   0.817 0.414168
factor(JAAR)2012:factor(MAAND)11  3.694e-01  2.078e-01   1.778 0.075432 .
factor(JAAR)2013:factor(MAAND)11  3.193e-01  2.015e-01   1.585 0.113008
factor(JAAR)2014:factor(MAAND)11 -4.230e-01  2.231e-01  -1.896 0.057992 .
factor(JAAR)2015:factor(MAAND)11 -7.600e-01  2.193e-01  -3.465 0.000530 ***
factor(JAAR)2016:factor(MAAND)11 -7.892e-01  2.377e-01  -3.320 0.000899 ***
factor(JAAR)2017:factor(MAAND)11 -7.680e-01  2.394e-01  -3.208 0.001335 **
factor(JAAR)2018:factor(MAAND)11         NA         NA      NA       NA
factor(JAAR)1989:factor(MAAND)12 -2.989e+00  5.201e-01  -5.748 9.05e-09 ***
factor(JAAR)1990:factor(MAAND)12 -3.122e+00  4.441e-01  -7.032 2.04e-12 ***
factor(JAAR)1991:factor(MAAND)12 -3.478e+00  6.379e-01  -5.452 4.99e-08 ***
factor(JAAR)1992:factor(MAAND)12 -3.537e+00  5.461e-01  -6.477 9.37e-11 ***
factor(JAAR)1993:factor(MAAND)12 -4.180e+00  7.597e-01  -5.503 3.73e-08 ***
factor(JAAR)1994:factor(MAAND)12 -3.158e+00  5.479e-01  -5.765 8.19e-09 ***
factor(JAAR)1995:factor(MAAND)12 -3.382e+00  5.396e-01  -6.269 3.64e-10 ***
factor(JAAR)1996:factor(MAAND)12 -3.903e+00  6.284e-01  -6.210 5.30e-10 ***
factor(JAAR)1997:factor(MAAND)12 -1.073e+00  3.026e-01  -3.545 0.000393 ***
factor(JAAR)1998:factor(MAAND)12 -1.216e+00  4.276e-01  -2.844 0.004449 **
factor(JAAR)1999:factor(MAAND)12 -3.550e+00  1.036e+00  -3.427 0.000611 ***
factor(JAAR)2000:factor(MAAND)12 -1.272e+00  3.683e-01  -3.455 0.000551 ***
factor(JAAR)2001:factor(MAAND)12 -1.303e+00  3.412e-01  -3.821 0.000133 ***
factor(JAAR)2002:factor(MAAND)12 -5.089e-01  2.836e-01  -1.794 0.072759 .
factor(JAAR)2003:factor(MAAND)12 -1.454e+00  3.559e-01  -4.085 4.40e-05 ***
factor(JAAR)2004:factor(MAAND)12  1.552e+00  2.449e-01   6.339 2.31e-10 ***
factor(JAAR)2005:factor(MAAND)12 -5.119e-01  2.566e-01  -1.995 0.046072 *
factor(JAAR)2006:factor(MAAND)12  6.712e-01  2.762e-01   2.430 0.015098 *
factor(JAAR)2007:factor(MAAND)12 -1.265e+00  3.312e-01  -3.818 0.000135 ***
factor(JAAR)2008:factor(MAAND)12 -2.677e-01  2.534e-01  -1.056 0.290776
factor(JAAR)2009:factor(MAAND)12  5.670e-01  2.163e-01   2.621 0.008769 **
factor(JAAR)2010:factor(MAAND)12 -1.937e+00  3.108e-01  -6.231 4.64e-10 ***
factor(JAAR)2011:factor(MAAND)12 -2.189e-01  2.136e-01  -1.025 0.305280
factor(JAAR)2012:factor(MAAND)12  7.316e-01  2.057e-01   3.557 0.000375 ***
factor(JAAR)2013:factor(MAAND)12  1.026e+00  2.064e-01   4.970 6.69e-07 ***
factor(JAAR)2014:factor(MAAND)12 -1.032e+00  2.410e-01  -4.282 1.85e-05 ***
factor(JAAR)2015:factor(MAAND)12 -1.143e-01  2.298e-01  -0.497 0.618961
factor(JAAR)2016:factor(MAAND)12  6.784e-01  2.147e-01   3.159 0.001580 **
factor(JAAR)2017:factor(MAAND)12         NA         NA      NA       NA
factor(JAAR)2018:factor(MAAND)12         NA         NA      NA       NA
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Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for Negative Binomial(0.2196) family taken to be 1)

    Null deviance: 235494  on 100605  degrees of freedom
Residual deviance:  23500  on 100222  degrees of freedom
AIC: 67801

Number of Fisher Scoring iterations: 1


              Theta:  0.21959
          Std. Err.:  0.00429

 2 x log-likelihood:  -67033.44500
```

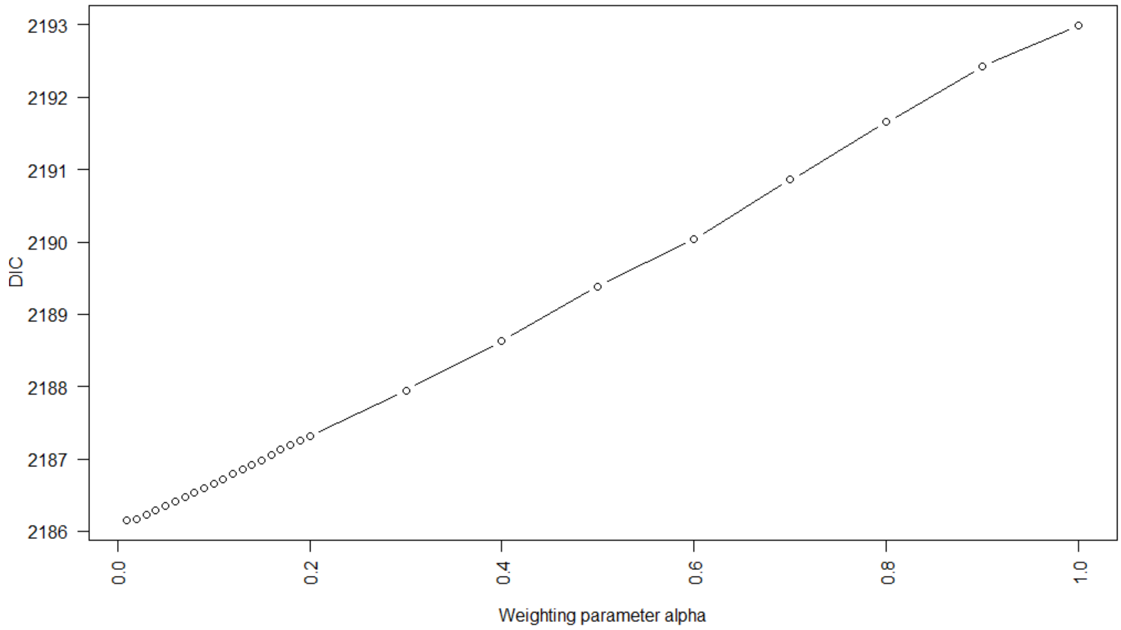

Figure S1. DIC as a function of the weighting parameter alpha (α). High values for α imply that stranding rate are mostly related to sighting rate in the preceding month, while low values for α imply that the stranding rate are related to the average sighting rate of all preceding 12 months.

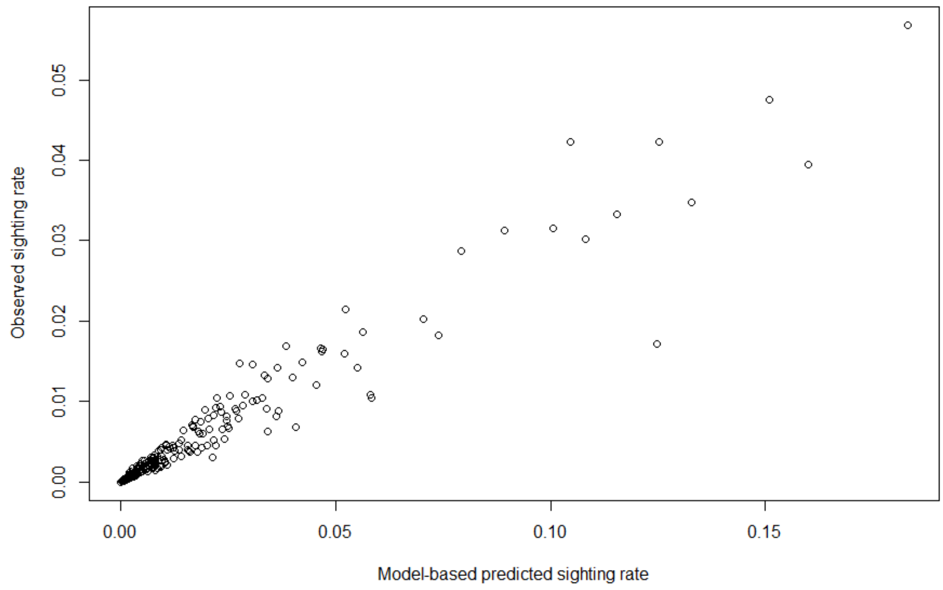

Figure S2. The observed sighting rate (not corrected for observation conditions) versus the model-based predicted sighting rate for each year-month combination.