Supporting Information

A spatially explicit estimate of the pre-whaling abundance of the endangered North Atlantic right whale

Conservation Biology 2016, DOI: 10.1111/cobi.12664

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Contents

Appendix S1. Detailed maps............................................................................................................................................. 2

Appendix S2. Historical context of right whaling .............................................................................................................. 5

Appendix S3. Abundance modeling .................................................................................................................................... 9

Appendix S4. Summarized comparison between the North Atlantic and North Pacific right whales .. 13
Appendix S1. Detailed maps

Figure S1. Number of right whales struck by whalers June to September, based on 1840-1849 American whaling records, within the envelope of their predicted distribution (gray cells with less than 3 days of effort were not included in the abundance model) (this figure corresponds to Fig. 1a of the main text).

Figure S2. Predicted right whale abundance from a Generalized Additive Model (GAM) fitted to the historical catch data within the envelope of the species’ predicted distribution (white, cells outside this envelope; rel., relative abundance from the sample of whaling data analyzed; low and high, values of absolute abundance per cell after calibration with total mortality data across the North Pacific) (this figure corresponds to Fig. 1b of the main text).
Figure S3. Predicted abundance from a GAM fitted to historical catches of North Pacific right whales and extrapolated to the North Atlantic within the envelope of predicted distribution (see legend in Fig. S2) (this figure corresponds to Fig. 1c of the main text).
Figure S4. Absolute values of SE for the model estimates of right whale abundance (higher values represent higher uncertainty) (this figure corresponds to Fig. 1d of the main text).
Appendix S2. Historical context of right whaling

Right whaling in the North Atlantic

The earliest known records of exploitation of the North Atlantic right whale (*Eubalaena glacialis*) come from the Gulf of Biscay, ca. 1000 AD (Aguilar 1986). Today, this species has a small population of c. 500 individuals found only in the western North Atlantic (Reilly et al. 2012; Pettis 2013) but it previously occupied a much broader range, spending the summer in feeding grounds across the North Atlantic (Monsarrat et al. 2015) and calving during the winter in lower latitude coastal areas that included the Gulf of Biscay. Pregnant females give birth to a single calf around early January, and then mothers and calves remain together in these calving grounds until early spring, when they migrate northwards to the feeding grounds (Curry & Brownell Jr 2014). Both while in the calving grounds and during the spring migration, cows and calves remain close to the coast, a behavior that likely evolved at least partly as a defense against killer whales (Ford & Reeves 2008) but which brought them within dangerous reach of human predators. The traditional Basque whaling relied on this coastal behavior, targeting particularly cows and calves. As described by Rondelet (1558; p.353):

“The whalers keep watch in high places to see the approaching whales, and when they see them they play the drum as a sign, and then everybody rushes equipped with what is necessary. They have several sloops, each with ten strong rowers, as well as other men with harpoons [...] that they throw at the whale with all their strength, leaving ropes connected to said harpoons, until [the whales] lost their blood and their life. Then they tow the whale to shore, and share it according to the number of harpoons that each one has thrown, that they recognize from their marks. One takes males with more difficulty, females more easily particularly if they are followed by their little ones, because while they try to save them they miss the possibility to escape.”

Further north, in Iceland and Norway, right whales were also taken (among other species) by Norse fishermen, who threw spears to wound whales in the expectation that they would subsequently die and beach (Lindquist 1994, 1997; Reeves et al. 2007). This method was much less efficient than Basque shore whaling, and the targeted whales approached land less predictably than those in the Gulf of Biscay, possibly explaining why Norse whaling remained a small scale activity whereas Basque whaling developed into a fully fledged industry. Medieval Basque whaling was driven by demand for salted meat and oil. Whale meat was reportedly not very tasty, except for the tongue (“very delicious and tender”; Rondelet 1558, p.351), but it had the great advantage of being an acceptable food during the many Catholic holidays when meat was forbidden (Pichon 1846), as the aquatic nature of whales meant they were considered a type of fish (Rondelet 1558). Whale oil was also a main
resource as lamp fuel, and bones were used as construction materials such as garden fences (Rondelet 1558).

By the early 16th century, Basque whalers had extended their whaling grounds considerably, both through the progressive expansion into the neighboring coasts of today’s Spanish Cantabria, Asturias and Galicia (Aguilar 1986; Azpiazu 2000), and through longer voyages across the North Atlantic to Ireland (Edvardsson & Rafnsson 2006), Norway (Smith et al. 2006), and Newfoundland and Labrador (Aguilar 1986; Huxley 1987; but see McLeod et al. 2008). Whereas the former still targeted whales in their winter coastal calving grounds, the latter involved months-long expeditions into the right whales’ summer feeding grounds, with large whaling boats operating as the mother ship to a flotilla of rowing sloops that approached and killed the whales. New methods for processing the floating whale carcasses in the high seas (Duhamel du Monceau 1782) allowed whaling to expand from coastal areas and into the open seas. Whaling efforts also extended to other target species, particularly the bowhead whale (*Balaena mysticetus*), an Arctic relative of right whales, even more productive in terms of oil and baleen (Muscovy Company 1905). Other nations entered the whaling business, particularly the English and the Dutch, mainly targeting bowheads but also capturing right whales (Reeves et al. 2007).

European colonization of what would become the United States of America opened another front of exploitation of the North Atlantic right whale. From the 17th century onwards (peaking in the early 18th century) shore whaling from Massachusetts to Delaware Bay targeted the western population along the spring migration route from the winter calving grounds off Florida, Georgia, and the Carolinas to the summer feeding grounds further north (Reeves & Mitchell 1986a; Reeves et al. 1999). As coastal whales became scarcer, American whalers ventured further away from the shore in progressively longer trips, their focus turning to sperm whales (*Physeter macrocephalus*) with their highly valuable spermaceti and sperm oil (Dudley 1725). With the entire North Atlantic as a whaling arena, the small remaining concentrations of right whales were quickly exhausted as soon as they were discovered. These included small pockets of whales in winter calving areas off Mauritania (Cintra Bay; 1850s-1860s) and off northern Florida, Georgia, and South Carolina (1870s-1880s), as well as summer feeding concentrations south of Greenland (Cape Farewell; 1860s-1890s) and off the Hebrides islands (by Norwegian shore whalers; 1900s-1920s) (Collett 1909; Reeves & Mitchell 1986b; Reeves et al. 2007).

North Atlantic right whales finally gained legal protection in 1935, ending “one of the most extensive, prolonged and thorough campaigns of wildlife exploitation in all of human history” (Reeves et al. 2007; p. 41).
Right whaling in the North Pacific

North Pacific right whales (*Eubalaena japonica*) were taken by aboriginal people on both sides of the Pacific Ocean, but presumably in small numbers (Tomilin 1967; Omura 1986; Huelsbeck 1988; Lee & Robineau 2004; Reeves & Smith 2006). A coastal whaling fishery began in Japan in the 17th century, targeting migratory whales, and taking up to 50 right whales annually (Omura 1986). It applied a “net whaling” method, whereby dozens of boats cooperated to entangle the whales in nets before harpooning them. Net whaling also occurred off southern Sakhalin Island prior to 1904 (Tomilin, 1957). It is not known whether this method had significant effects on the population (Brownell Jr. et al. 2001).

The history of large-scale commercial exploitation of the North Pacific right whale is very different from that of its North Atlantic congener. By the late 1700s, right whales had become scarce in the North Atlantic prompting the expansion of the whaling fisheries into other ocean basins. Led by American offshore whalers, operating mainly from New England ports (e.g., New Bedford, Nantucket), this would soon become the first global-scale industry. By the 1770s whalers were exploring the Brazil banks off eastern South America where southern right whales (*Eubalaena australis*) were taken (Smith et al. 2012). In 1789, a whale-ship ventured around Cape Horn and captured the first sperm whale in the South Pacific (Scammon 1874), opening the way for the expansion of the whaling industry westwards and northwards into the Pacific right and sperm whaling grounds (Scammon 1874).

The first North Pacific right whales were reportedly taken off the Kodiak Islands in 1835 (Scammon 1874; Scarff 2001). They were at that time a common species, their summer feeding grounds spanning the temperate and sub-arctic North Pacific, particularly in the Gulf of Alaska, off Kamchatka, in the Sea of Okhotsk, and in the Sea of Japan (Gregr 2011a; Smith et al. 2012; Monsarrat et al. 2015). By 1850 they had become rare and by 1860 they were nearly extirpated (Scarff 2001; Josephson et al. 2008), as the result of an extraordinary concentration of whaling effort across their entire summer range (Smith et al. 2012). Whalers then moved further north to the newly discovered grounds of even more desirable bowhead whales (Bockstoce 1995). But the right whale fishery persisted at lower levels, even after right whales had become legally protected in 1931, with > 650 taken in illegal Soviet catches during the 1960s (Rocha et al. 2014; Brownell Jr. et al. 2001; Reilly et al. 2008).

North Pacific right whales are now very rare, with a total population estimated at possibly around 500 individuals, the vast majority of them summering in the Okhotsk Sea or off the Kuril Islands and
Kamchatka (Reilly et al. 2008). The species clearly undertakes some migration northward in summer and southward in winter, but their current wintering grounds are unknown. Historical records indicate that they were taken from December to March along the south and west coasts of Japan, in February and March in Formosa Strait and the East China Sea, and around the Bonin Islands in February (Reeves & Mitchell 1986b) but the precise location of their breeding grounds has never been established.

Whereas the ecology of the North Pacific right whale is more poorly known than that of its North Pacific congener, the history of its commercial exploitation is much better documented. Indeed, 19th century American whalers kept detailed logbooks where they noted for each day the vessel location and information on whether whales were encountered (and, if so, number of whales seen, struck, or secured and processed on board). Substantial work has gone into compiling these records into a common database: first by Lt. Commander Matthew Fontaine Maury (in the 1840s), then by Charles Haskins Townsend and his assistant Arthur C. Watson (in the 1920s), and more recently by the Census of Marine Life (CoML) World Whaling History project (2001 to 2010; Smith et al. 2012). Because these data cover the entire summer distribution of the North Pacific right whale, and include the beginning of its commercial exploitation, they provide a detailed picture of the spatial distribution of the pre-whaling population of this species.
Appendix S3. Abundance modeling

Model development

We focused on records from the summer (June to September) feeding period of North Pacific right whales (Clapham et al. 2004) because the North Pacific was well explored by American whalers in this season (Smith et al. 2012), and hence summer catches provide a good overview of the spatial distribution of the entire North Pacific right whale (NPRW) population. We focused on strikes during the 1840-1849 period because this corresponds to the bulk of NPRW exploitation (80% of the whales strikes; Scarff, 2001), and is short enough in relation to the life cycle of right whales (NARWs reach sexual maturity at about nine years; Kraus et al. 2001) that the population growth rate can be assumed to have had a negligible impact on relative abundance as estimated from the number of whales struck. We mapped on a 1°x1° grid the number of struck whales per cell within the envelope of predicted distribution of right whales in summer (Monsarrat et al. 2015), keeping only those cells that had a sampling effort of at least three days (in order to reduce the risk of false absences – visited cells where whales were present but not recorded). We did not correct for sampling effort (number of visits per cell) because whaling effort was clearly driven by abundance, with whalers focusing on those areas known to be suitable to the target species (“preferential sampling”; Diggle et al. 2010). We assumed that whales did not change their distribution substantially during the analyzed period (e.g., by moving away from the exploited areas, or because of environmental variation), which we believe to be reasonable given the short duration of the period.

We selected as predictors environmental variables known to be correlated with the distribution of right whales and/or their main prey in summer. These included: three climatic variables (averaged over June to September) – sea surface temperature (Norberg & DeAngelis 1997; Gregr & Coyle 2009), mixed layer depth (Baumgartner & Mate 2003) and net primary productivity (Norberg & DeAngelis 1997); and three bathymetric features – depth, slope and distance to land (Hamazaki 2002; Kaschner et al. 2006; Gregr 2011b; Torres et al. 2013) (Table S1). We focused on environmental datasets that cover both the North Pacific and the North Atlantic basins, and have a spatial resolution of at least 1 degree of latitude/longitude.

We used a Generalized Additive Model (GAM; Hastie & Tibshirani 1986) to model relative abundance. Species abundance is generally modeled with a Poisson distribution, which is appropriate to the nonnegative, discrete nature of count data (Cameron et al. 2013). However, standard Poisson often fails to fit overdispersed data commonly associated with ecological counting datasets (Barry & Welsh 2002). Negative Binomial regression has the ability to deal with extra-Poisson variation (Lawless 1987; Ver Hoef & Boveng 2007). We tested residual overdispersion for both Poisson and
Negative Binomial distributions, by comparing the value of the dispersion parameter $\phi$ described by (Zuur et al. 2009). The predictive power of the Poisson model was slightly higher but only the Negative Binomial accounted efficiently for overdispersion in the residuals (Table S2) so we have fitted our model with the latter. We allowed for four degrees of freedom for each spline to avoid overfitting and selected the default thin plate regression splines as the smoothing function (Wood 2003). GAM was implemented using the mgcv package (Wood 2011) in R (R Development Core Team 2013) where the dispersion parameter $\theta$ of the Negative Binomial is determined internally in model fitting.

**Model Validation**

We quantified the model accuracy with a comparison between the predicted and observed values per cell using the full dataset and a 50-fold cross validation using a random half of the dataset to build the model and the remaining data to test the predictions (Fielding & Bell 1997).

For both of these approaches, we calculated Pearson’s correlation coefficient $r$, measuring the linear dependence between predicted and observed values (varies from -1 for a perfect negative correlation to 1 for a perfect positive correlation); Root Mean Square Error RMSE, representing the standard error of the differences between predicted values and observed values; and the average error $\text{AVE}_{\text{error}}$, the mean error between observed and predicted values. The closer RMSE and $\text{AVE}_{\text{error}}$ are to zero, the better the prediction (see Potts & Elith 2006).

We obtained reasonably high values for Pearson’s correlation coefficient ($r = 0.56$ in the validation with the full dataset; $r = 0.46$ in the 50-fold cross validation with half of the dataset), and low values of RMSE and $\text{AVE}_{\text{error}}$ (RMSE = 2.25 and $\text{AVE}_{\text{error}} = 0.033$ in the validation with the full dataset; RMSE= 2.55 and $\text{AVE}_{\text{error}} = 0.014$ in the cross validation with half of the dataset), indicating good performance of the model in the North Pacific (Table S2).
**Table S1.** Environmental predictors used in the analysis.

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Variable</th>
<th>Derived from</th>
<th>Period averaged</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>SST</td>
<td>Sea Surface Temperature (°C)</td>
<td>NODC WOA94</td>
<td>1900-1992</td>
<td>Levitus &amp; Boyer, 1994</td>
</tr>
<tr>
<td>MLD</td>
<td>Mixed Layer Depth (m)</td>
<td>NODC WOA94</td>
<td>1900-1992</td>
<td>Monterey &amp; Levitus, 1997</td>
</tr>
<tr>
<td>DEPTH</td>
<td>Depth (m)</td>
<td>NOAA-NGDC ETOPO1</td>
<td>-</td>
<td>Amante &amp; Eakins, 2009</td>
</tr>
<tr>
<td>LANDDIST</td>
<td>Distance to Land (km)</td>
<td>AquaMaps</td>
<td>-</td>
<td>Kaschner et al., 2008</td>
</tr>
</tbody>
</table>

**Table S2.** Comparison between the explicative and predictive performances of Negative Binomial and Poisson GAMs.

<table>
<thead>
<tr>
<th></th>
<th>Negative Binomial (θ = 0.91)</th>
<th>Poisson</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2$</td>
<td>0.30</td>
<td>0.37</td>
</tr>
<tr>
<td>Deviance explained (%)</td>
<td>31.9</td>
<td>37.8</td>
</tr>
<tr>
<td>Validation with the full dataset</td>
<td>$r = 0.56$</td>
<td>$r = 0.63$</td>
</tr>
<tr>
<td></td>
<td>RMSE = 2.25</td>
<td>RMSE = 2.11</td>
</tr>
<tr>
<td></td>
<td>AVE$_{\text{error}}$ = 0.033</td>
<td>AVE$_{\text{error}}$ &lt; 1e$^{-10}$</td>
</tr>
<tr>
<td>50-fold cross validation with $\frac{1}{2}$ of the data</td>
<td>$r = 0.46$</td>
<td>$r = 0.52$</td>
</tr>
<tr>
<td></td>
<td>RMSE = 2.55</td>
<td>RMSE = 3.41</td>
</tr>
<tr>
<td></td>
<td>AVE$_{\text{error}}$ = -0.014</td>
<td>AVE$_{\text{error}}$ = -0.12</td>
</tr>
<tr>
<td>Residuals overdispersion</td>
<td>NO (φ = 1.13)</td>
<td>YES (φ = 2.92)</td>
</tr>
</tbody>
</table>

$\theta$, dispersion parameter for the negative binomial; $r$, Pearson correlation coefficient; RMSE, Root Mean Square Error; AVE$_{\text{error}}$, Average error; $\phi$, residuals dispersion parameter.
Figure S5. Smooth functions for the four selected predictors. SST, sea surface temperature; LANDDIST, distance to land; DEPTH, mean depth; MLD, mixed layer depth. Solid lines represent the smooth functions and grey intervals are one standard-error above and below the estimate. The rug plot along the x-axis corresponds to the distribution of the response variable along the environmental gradient. The y-axis represents the effect of each covariate, with zero meaning no effect.
Appendix S4. Summarized comparison between the North Atlantic and North Pacific right whales

Table S3. Comparison between the North Atlantic and the North Pacific right whales.

<table>
<thead>
<tr>
<th></th>
<th>North Atlantic right whale</th>
<th>North Pacific right whale</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Timing of commercial exploitation</strong></td>
<td>11th to the early 20th centuries</td>
<td>1835 to the 1960s (ca. 80% of catches 1840-1849)</td>
</tr>
<tr>
<td><strong>Type of whaling</strong></td>
<td>Mostly shore-based, also offshore</td>
<td>Offshore</td>
</tr>
<tr>
<td><strong>Main whaling nations</strong></td>
<td>French and Spanish Basques, Americans</td>
<td>Americans</td>
</tr>
<tr>
<td><strong>Whaling data</strong></td>
<td>Scarce, biased towards recent dates,</td>
<td>High-quality catch records and distribution</td>
</tr>
<tr>
<td></td>
<td>biased towards coastal areas</td>
<td>information from whaling logbooks</td>
</tr>
<tr>
<td><strong>Previous estimates of pre-exploitation abundance</strong></td>
<td>14,100 individuals (95% CI 10,100 – 27,800; Christensen 2006); “At least a few thousand wales present in the mid-1600’s” (Reeves et al. 2007)</td>
<td>9,720 individuals (95% CI 8,540-12,600; Christensen 2006)</td>
</tr>
<tr>
<td><strong>Estimates of pre-exploitation abundance (this study)</strong></td>
<td>9,075-21,328 individuals (estimated carrying capacity)</td>
<td>14,611-34,342 individuals (estimated total mortality between 1840-1849)</td>
</tr>
<tr>
<td><strong>Current population</strong></td>
<td>ca. 500</td>
<td>ca. 500</td>
</tr>
<tr>
<td><strong>Estimated depletion rate (this study)</strong></td>
<td>94-98%</td>
<td>97-99%</td>
</tr>
<tr>
<td><strong>IUCN Red List status</strong></td>
<td>Endangered</td>
<td>Endangered</td>
</tr>
</tbody>
</table>
Literature Cited


Lindquist, O. 1994. Whales, dolphins and porpoises in the economy and culture of peasant fishermen in Norway, Shetland, Faeroe Islands and Iceland, ca. 900-1900 AD, and Norse Greenland, ca 1000-1500 AD. Faculty of Arts, University of St Andrews, Scotland. Available from http://www.fishernet.is/is/hvalveidar/19/35.


