On Modeling the Macroecology of Baleen Whale Migration

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Abstract

Long distance migrations are well known to occur in many baleen whale species. Yet, a global synthesis of this information is lacking. Here, we study baleen whales as a group and at a global scale, first analyzing the grey and peer-reviewed literature for information on the location of baleen whale calving and feeding grounds around the world. This information was then combined with modeled-data produced from an Earth System Model to estimate the global distribution of baleen whale calving and feeding habitats. A simple network theoretic heuristic was then used to identify the shortest over-water path connecting habitats. These shortest paths map well to known major migration routes for a number of species, suggesting that migration has evolved primarily to minimize travel distances. Identifying distance minimizing routes globally, that have demonstrable consistency to known migration routes for certain baleen whale species, offers a useful baseline perspective on large-scale migration patterns, from which many perturbations can by judged. As an example, we used our modeled migration routes to identify regions of the ocean that are likely hotspots of whale ship-strikes. Such information is useful for developing global conservation and management priorities for baleen whales.

Introduction

That baleen whales migrate is well known [1, 2]. One can observe them doing so from the numerous whale watching tours that are available around the world, and scientists have photographed and tagged individual whales, and tracked their travels [3–8]. From such data, and other sources of information, such as historical whaling charts [9], persistent long distance migration routes have been identified around the world, from the Gulf of California, the Hawaiian islands and the China Sea, to the Bering and Chuckchi Seas; from South Africa, Australia, New Zealand, Chile and Argentina, to the Southern Ocean and the Antarctic peninsula; from the Caribbean and the west coast of Africa, to the north Atlantic and Arctic. The list goes on. However, this information is rarely synthesized, with most studies focusing on migration patterns in specific regions and on specific species. Here, we make a global analysis of migration for baleen whales as a group, identifying the factors that likely determine migration patterns throughout the world's oceans.

Annual migrations are commonly seen in baleen whales of different species, for example in humpback [10] and gray whales [1], where individuals travel between warm low-latitude breeding grounds, and productive high-latitude feeding grounds [2]. Other baleen species are known to have more diffuse migration patterns, such as blue [5], sei [11] and fin [2] whales, but of those that make latitudinal migrations, they are thought to do so to secure better chances of survival for their calves in warmer low-latitude waters [2, 12], and feed on the abundance of copepods, euphausiids (krill) and small fishes at high latitudes in summer months [13, 14].

Low-to-high-to-low latitudinal migrations have been observed directly for many areas of the world's oceans (see our Supplementary Information for a bibliography). Yet comparisons between regions are lacking, and a global synthesis of migration routes would develop our understanding of why certain baleen whale species, behave in such a (bioenergetically) expensive manner. Here, we develop a macroecological study, using network theoretic algorithms and output from an Earth System Model (ESM) to infer the location of migration pathways in the global ocean. ESMs have been developed primarily to explain the

major biogeochemical cycles of the earth, ultimately giving us a predictive capacity for future climate states [15]. To make these calculations, earth-system scientists include descriptions of phytoplankton and (in some cases) zooplankton dynamics [16]. Here, we use a recent iteration of an ESM [17] that includes "large zooplankton", which approximates the dynamics of copepods and euphausiids, as well as providing information useful for estimating the abundance of small fishes. This ESM data is interpolated to calving and feeding locations found from a literature review, and then a machine learning algorithm is used to define potential calving and feeding habitats globally. Major migration pathways between modeled calving and feeding habitats are then identified using a modified Dijkstra's algorithm, which finds the shortest ocean-path between a given calving and feeding location.

Estimating the distribution of baleen whale calving and feeding habitats, and migration routes is not without uncertainty, for it is well known that baleen whale species differ in their use of the ocean. However, the global scale of our analysis offers a course grained view of species-specific information, and allows us to look at how baleen whales as a group, might occupy broad, basin-scale, regions of the global ocean. Furthermore, this large-scale perspective allows us to estimate the impact of humans on baleen whales, and we do so in the context of whale ship-strikes, thought to be a large source of mortality for migrating whales [18, 19]: using our modeled migration routes with cargo ship-track data, we infer hot-spots of potential ship-strikes globally.

Methods

The Earth System Model

The Carbon, Ocean Biogeochemistry and Lower Trophics (COBALT) marine ecosystem model provides the biogeochemical and planktonic food web information that we used to estimate potential whale migration routes [17]. COBALT is run as part of the Modular Ocean Model (MOM) version 4.1 [20], with 60 year simulations (1948-2008) forced by the Common Ocean-Ice Reference Experiment (CORE-II) data

71 set [21]. The horizontal resolution of the simulation is 1° Latitude/Longitude, except along the equator

72 where the resolution is refined to $1/3^o$, and the model uses 50 vertical layers, with a resolution of 10m

73 over the top 200m.

74   The representation of planktonic food web dynamics within COBALT is based on body-size, and

75 provides information relevant to our study of baleen whale migration. In particular, medium-sized zoo-

76 plankton are parameterized to represent small and medium copepods ($0.2 - 2mm$ in equivalent spherical

77 diameter or ESD), and large-sized zooplankton are parameterized to represent large copepods and small

78 euphasiids ($2 - 20mm$ ESD). Furthermore, COBALT employs a density dependent mortality term for

79 medium and large zooplankton. This represents the mortality of these zooplankton to higher-predators,

80 namely small fishes. Although COBALT does not model fish explicitly [17], this implicit representation

81 of small-fish feeding rates, has been used to model upper trophic levels explicitly [22] and for this appli-

82 cation, provides information on the spatial distribution of a major source of food for certain baleen whale

83 species.

Baleen whale habitats

85 Data from the COBALT retrospective ocean-ice ecosystem simulation was used in a classification algo-

86 rithm to identify likely baleen whale calving and feeding habitats globally. These data were chosen for

87 their relevance to baleen whale habitats, and include: monthly COBALT temperature data averaged

88 over the top 200m (^oC), medium and large zooplankton (copepods and small euphausiids) biomass in-

89 tegrated over the top 200m (g carbon m^{-2}; our analysis is based on relative difference in zooplankton

90 abundances, so the exact units are unimportant), medium and large zooplankton mortality rates to small

91 fishes integrated over the top 200m (g carbon $m^{-2}\ day^{-1}$), depth (km). All data were taken for the

92 period 1988-2008. Baleen whales generally calve during the winter, and feed during the summer, and

93 hence these data were filtered for these times, producing time average austral winters and boreal sum-

94 mers (june, july, august), and boreal winters and austral summers (november, december, january). For

95 illustrative purposes we show COBALT's annual average sea-surface temperature (Fig. 1a) and average

96 total abundance of medium and large zooplankton (Fig. 1b).

97 These time-averaged COBALT data fields were then linearly interpolated in space (the modeled data

98 are on a 1° grid) to feeding and calving locations identified from a literature search: 33 and 36 feeding

99 and calving sites respectively (Fig. 1). See the Supplementary Information for the bibliography of

100 compiled literature, and the precise locations. Using this point-data, a machine learning algorithm - a

101 bagged classification tree - was used to estimate the distribution of feeding and calving habitat at all

102 other locations globally [23]. The algorithm was used on feeding and calving habitats separately. Taking

103 feeding habitat as an example: the bagged classification tree required as input, a categorical response

104 variable - a vector of 1s and 0s relating to those ocean locations where we identified the presence and

105 absence of feeding respectively, from the literature. The other input is a matrix of predictor variables:

106 the interpolated COBALT data at the feeding presence and absence locations. The output of the bagged

107 classification tree, is another vector of 1s and 0s, relating to the classification of all ocean locations as

108 either feeding habitat or not.

109 Absence locations were created by inspecting the distribution of zooplankton abundances, temper-

110 ature, depth and irradiance across feeding and calving locations, and then using logical arguments to

111 select ocean locations beyond the tails of these joint distributions. This essentially identifies areas of

112 the ocean where calving and/or feeding does not happen. These are more accurately *pseudo-absence*

113 locations because they are chosen, rather than identified [24], and for each run of any classification tree,

114 100 pseudo-absence points were selected randomly in this manner. With this information, the bagged

115 classification tree then predicted the most likely habitat type (calving or feeding, or pseudo-absence) at

116 every COBALT grid-cell, producing global maps of feeding and calving habitat.

117 Because the pseudo-absence points were chosen randomly, we repeated the classification process two

118 hundred times, building a distribution of likely feeding, calving and pseudo-absence locations. Finally,

119 because our concern is with the major migration routes, we isolated the most likely calving and feeding

120 locations by choosing those areas with a 50% or greater probability of feeding or calving classification.

121 Implicit to the bagged classification process is a k-fold cross-validation test of precision [25]. Here, part of

122 the training data is left out and validated against, with the classification tree made using the remaining

123 data. This process is repeated k times, producing an estimate of the expected classification error.

124 To assess the accuracy of the feeding and calving habitat classification trees, we compared its results

125 with another set of information gained from the literature - we collected as much information as we could

126 from peer and non-peer reviewed articles and numerous websites (representing the grey literature; see

127 supplementary information) on the global distribution of calving and feeding habitats for a number of

128 baleen whale species. The majority of this information was not geo-referenced in any detail, and as a result

129 we had to visually overlay their maps, and estimate by-hand the distribution of baleen whale habitats and

130 migration routes. This information was then compare qualitatively with the habitat distribution maps

131 produced from the bagged-classficiation tree. This information was also used to divide the global feeding

132 and calving habitat distributions, produced from the classification trees, into geographically consistent

133 regions.

Baleen whale migration pathways

135 Once global distributions of baleen whale calving and feeding habitats were made using the bagged-

136 classificiation tree, we identified potential migration pathways using a modified Dijkstra's algorithm [26].

137 This algorithm calculates the shortest-path between two nodes in a network. Here, we considered each

138 COBALT grid-cell centroid a node in an ocean network. Then the great-circle distance (km) between each

139 grid cell centroid and the centroid of every neighboring cardinal grid cell was calculated. These defined

140 the edges in the ocean network. The result was a highly sparse matrix (or network): each row representing

141 a grid-cell, with eight real-valued distances associated with its cardinal neighbors. Connections to land

142 grid-cells were assigned an infinite distance. Dijkstra's algorithm was then applied to this ocean network,

143 identifying the shortest over-water or "ocean distance" between two given locations in the sea. However,

144 because the network is constructed over a grid, unrealistic city-block paths were typical solutions. To

145 solve this problem we added small amounts of white noise to the network edges, and applied Dijkstra's

146 algorithm a number of times (typically 1000), creating a set of candidate shortest paths. From the set

147 of candidate shortest paths we calculated the most likely (or expected) shortest path between a given

148 calving-feeding grid cell pair. Using this information, we identified the shortest path between calving

149 and feeding regions. This approach is still a heuristic, and as a result the shortest paths are not exact

150 solutions. An example shortest path is shown in Fig. 2. Here, numerous candidate paths are identified

151 by the black dots, and the expected shortest path in red. The starting location is off Costa Rica, and the

152 destination location is off Vancouver Island. The shortest path hugs the coast, and resembles the path

153 taken by baleen whale species that migrate in this region (for example, blue whales [5]).

Results

155 When compared qualitatively to the information gained from the literature (Fig. 3), the habitat clas-

156 sification algorithm identified realistic calving and feeding regions (Fig. 4; green and orange regions

157 respectively; habitat regions are the same across all panels), and average cross-validation error for both

158 calving and feeding trees was satisfyingly low (0.07 and 0.05 respectively after 50 trees; see Supplementary

159 Information Fig. S1). Feeding habitats were identified mostly at high latitude: the Sea of Okhotsk, the

160 Bering sea, the northwest Atlantic, the northeast Atlantic, Greenland, the North Sea, the Barents sea, the

161 Crozet Islands, the south coast of Australia, southern New Zealand, the Patagonia Shelf and the whole of

162 Antarctica. Calving habitats were found predominantly at in shallow, warm, low latitudes regions: Baja

163 California, the off Costa Rica and Ecuador, off northwest Africa below the Cape Verde islands, the Gulf

164 of Guinea, off the west-coast of Madagasca in the Mozambique channel, in the Arabian Sea, the Bay of

165 Bengal, areas off the northwest and northeast coasts of Australia, and Fiji. These feeding and calving

166 distributions map well to areas identified qualitatively from the peer-reviewed and grey literature (Fig.

167 3).

168   The partitioning of global habitat into geographically consistent regions, based on qualitative infor-

169 mation gained from the literature, is shown in Fig. 4 (regions in different shades of green and orange).

170 For example, the Hawaiian Islands, the Gulf of California, and the eastern tropical Pacific were all divided

171 into separate calving regions. Similarly for the distribution of feeding habitat, areas such as Antarctica,

172 the Bering Sea, and the North Sea are separated into distinct feeding regions. While agreement on a

173 regional scale is good, there are a few noticeable calving regions not seen in the literature (Fig. 3). For

174 example northern New Zealand and the Gulf of Mexico are classified as calving habitat, but there is little

175 evidence for this [27]. Similarly for feeding grounds, the classification tree identified the southern half of

176 New Zealand, but there was little evidence in the literature that this is a major feeding area for baleen

177 whales. However, that is to say there is little evidence that *contemporary* whale distributions cover these

178 areas [27]. Both are interesting as they constitute potential feeding and calving regions for right whales,

179 species which have been essentially exterminated and may show significant range contraction. There is

180 evidence that Southern New Zealand was a feeding ground and Northern New Zealand was a calving

181 area for Southern Right Whales before they were almost wiped out [28]. Similarly, the Gulf of Mexico

182 may have been an extension of the Florida East Coast calving area for Northern Right Whales, with a

183 few individuals spotted in the GOM in the past several decades. Considering there are only about 400

184 Northern Right Whales currently, it seem highly plausible that the GOM/Caribbean was an important

185 calving area for them when they numbered in the 10's of thousands [29].

186   Globally, the first, second and third shortest paths that minimize over-water distance are shown in

187 Fig. 4a, b & c respectively. The maximum, minimum and mean path lengths (km), for these three sets

188 are: first - 7291, 696, 3037; second - 9469, 2091, 5014; third - 10828, 2414, 6948. Beyond these simple

189 statistics, what is evident are the realistic migration routes. These shortest paths between every calving

190 region and their three nearest feeding regions describe all migration routes identified in the grey literature

191 (Fig. 3). For example, from Hawaii, the three nearest feeding regions are the Sea of Okhotsk, the Bering

192   Sea, and the waters off the northwest US and Canada. From the southeast Caribbean, shortest migration

193   routes connect to the waters of the northeast US and Canada, to Greenland, and to the North Sea. In the

194   southern hemisphere, many calving locations connect to the Southern Ocean and Antarctica, traversing

195   many degrees of latitude, for little change in longitude. There are however shortest paths that traverse

196   several degrees on longitude. These are most commonly the third shortest paths, for example connecting

197   Madagascar and northwest Australia, with the Crozet Islands (Fig. 4c).

198   Discussion

199   Baleen whale feeding and calving regions were identified, using peer-reviewed and grey literature infor-

200   mation on calving and feeding locations, within a bagged-classification tree. Then, using a modified

201   Dijkstra's algorithm, we identified paths that minimized the ocean distance between feeding and calving

202   regions. Both the global distribution of feeding and calving habitats and the shortest paths connecting

203   them, map well to the known distributions of these habitats and migration routes for certain species. Our

204   results suggest that baleen whale migration has evolved to minimize ocean-distances between calving and

205   feeding habitats. Other factors, such as predator avoidance (e.g. from killer whales) are likely to play a

206   role too in shaping where baleen whales go, but at smaller spatial scales [12].

207   This analysis is global in scale, and baleen whales were analyzed as a group. This latter step places

208   constraints on our analysis, as it is known that migration patterns, and behavior in general, can differ

209   greatly between whale-species. This is reflected in the specificity of most whale-movement data, which

210   is typically collected for particular individuals and groups of certain whale species, in specific regions,

211   where focused observational and tagging efforts can give fine-scale knowledge of movements [5, 8]. The

212   global-scale analysis presented herein lacks the detail of regional, species specific studies, however, it

213   provides a coarser global perspective on large-scale movements of baleen whales and the mechanisms

214   underlying them. Indeed, the large scale of our analysis does not preclude species-specific use: different

215 baleen whale species show common reliance on broad ocean areas (at scales: $> 1000s\ km$) citeGregr2001,

216 and hence our modeled baleen whale habitat maps and migration routes may capture patterns that are

217 general across species. Furthermore, simply having a global atlas of possible migration routes allows us

218 to gauge how humans may have impacted whale migrations around the world.

219 As an example, we use our global atlas of baleen whale migration to identify hot-spots of potential

220 ship strikes. Ship strikes are thought to be a large source of mortality for some whale groups [18, 19].

221 But like assessments of migration, most analyses of ship strikes are at regional scales. In contrast,

222 our work here can help identify global patterns of ship strike potential. Using information from the

223 PASTA MARE project [30], we interpolated normalized shipping density (a score between [0,1]; see Fig.

224 S2 for a detailed description) to locations along the major whale migration pathways, resulting in the

225 identification of potential ship-strike hot-spots (Fig. 5). Japanese waters emerge as having the highest

226 strike risk for a given whale migrating in this area. Secondary hot-spots occur in Indonesian waters,

227 off South Africa, off Puerto Rico and off New Foundland, Canada. Although this brief analysis looks

228 only at ship strike potential along migration routes, ignoring strikes in calving and feeding regions, this

229 information can be useful for developing global conservation and management priorities. Two important

230 caveats to this analysis is that first, these strike risk estimates ignore any regional-scale measures to

231 reduce risk, for example as has been successfully done for the North Atlantic Right Whale [31]. Second,

232 we assume a *pristine* ocean, for we do not account for the effect of historic whaling on contemporary whale

233 densities. Thus, inferring ship-strike potential in this way is likely inaccurate due to the loss of migration

234 routes/populations from whaling [9]. Indeed, a worthwhile effort is the comparison of contemporary

235 migration routes with our estimates of migration in a pristine ocean. Through this, one can identify (or

236 at least hypothesize for) the loss of particular migration routes.

237 Looking to the past is important, but equally so is to understand how humans may continue to impact

238 whale migration in the future. Our feeding and calving habitat maps, and migration routes were trained

239 on Earth System Model data, averaged over the period 1988-2008. As a result our modeled distributions

240 of feeding and calving habitats are specific to this period. It is possible too, to use our techniques to

241 project how habitat distributions and migration routes might change in the future. The Earth System

242 Model data used in this analysis, as well as looking back in time in hindcast simulations, also look forward

243 in time and project the distribution of oceanographic variables such as temperature and the abundance

244 of zooplankton [15,17]. Thus, with this information it is possible, in future work, to estimate how baleen

245 whale migration feeding and calving habitats might move under different future climate scenarios.

246 To improve the accuracy of these future projections, especially the estimates of migration routes, there

247 are several modifications that could be made to our *basic* approach. We say basic because our migration

248 route-finding algorithm does not include any biological information. Hence, we cannot answer the question

249 of what condition whale individuals might be in, for example, if calving and feeding habitats move further

250 apart in the future, or if their quality (e.g. the abundance of large zooplankton or krill) might diminish.

251 It is critical to do so because individual condition can have a highly non-linear relationship with travel-

252 distance/time [32], and slight increases in the shortest migration path distance, could be detrimental to

253 whale health, rendering certain migration routes impossible. The experience along a migration route is

254 important too. For example, it is expected that areas of the surface ocean are likely to warm in the

255 coming decades. This may incur a significant bioenergetic cost on migrating whales, as biomass specific

256 respiration rates are positively related to temperature [33]. In other words, baleen whales are likely to

257 expend more energy on their annual migrations in the future, and the consequences of this change are

258 unknown.

259 In addition, there are several algorithmic modifications to our approach that can be made. First, we

260 have only identified paths that minimize ocean distance. It is possible too, to find paths between two

261 locations is the sea that minimize travel-time. We have done so in our context (Fig. S3), assuming that

262 baleen whales swim with a constant speed of 80 $km\ day^{-1}$ [5], and instead of distances as network edges

263 (see methods) we assign travel times, accounting for ocean currents. Applying Dijkstra's algorithm to

264 this network creates solutions to what is known as the *Zermelo navigation problem*, that is, finding the

265 path that minimizes travel time between two locations in the sea [34]. The resulting migration routes

266 are shown in Fig. S3, and we find little difference between these and the distance minimizing routes.

267 This is due to the fast swimming speeds of baleen whales. However, solutions to Zermelo's problem for

268 other species that swim more slowly, for example for marine turtles [34], have identified multiple possible

269 migration routes, depending on the movement rule employed. This brief analysis reveals the numerous

270 ways in which potential migration routes can be identified, and how this information can be used to

271 develop hypotheses about the optimal movement strategies that marine species have evolved.

272 In summary, we estimated the distribution of baleen whale feeding and calving habitats globally, and

273 the migration routes connecting them. We have shown evidence that baleen whales, as a group, have

274 migration routes that minimize distance (and/or travel time), and we have also discussed that the main

275 utility of our macroecological analyses is in the generation of hypotheses and questions. For example, do

276 baleen whales minimize travel distance or time? Answers to these questions may come from evolutionary

277 agent-based simulations that have been employed in idealized settings to answer similar questions [35].

278 Indeed, combining these tools with Earth System Model data, will better position us to understand where

279 baleen whales migrate to and from, how they do it, and why.

Acknowledgments

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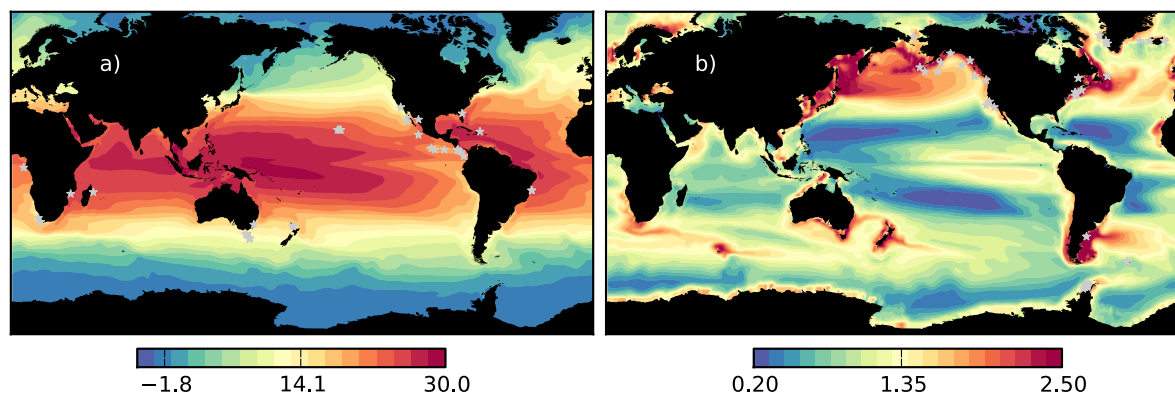
Figures

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Figure 1. (a) Annual average sea surface temperature (^oC) and (b) the annual average total abundance of medium and large zooplankton (g carbon m^{-2}) from COBALT. Data are integrated over the top 200m, and baleen whale calving and feeding locations overlaid on Fig. 1a and b respectively (grey stars)
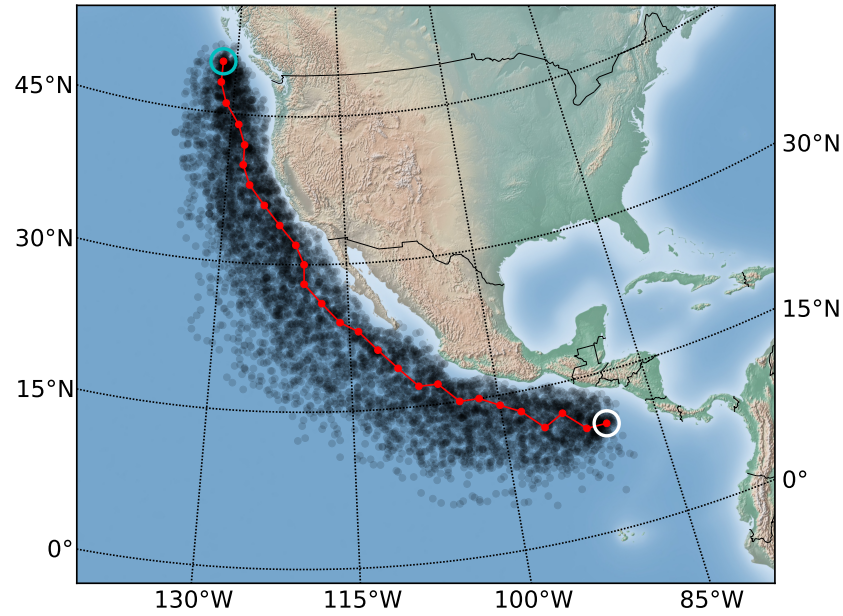
Figure 2. An outline of our route-finding algorithm. Black dots comprise locations along multiple candidate shortest paths, found using our modified Dijkstra's algorithm, connecting the starting location (white circle) and terminus (blue circle). The red line is the expected shortest route, over all candidate shortest paths.
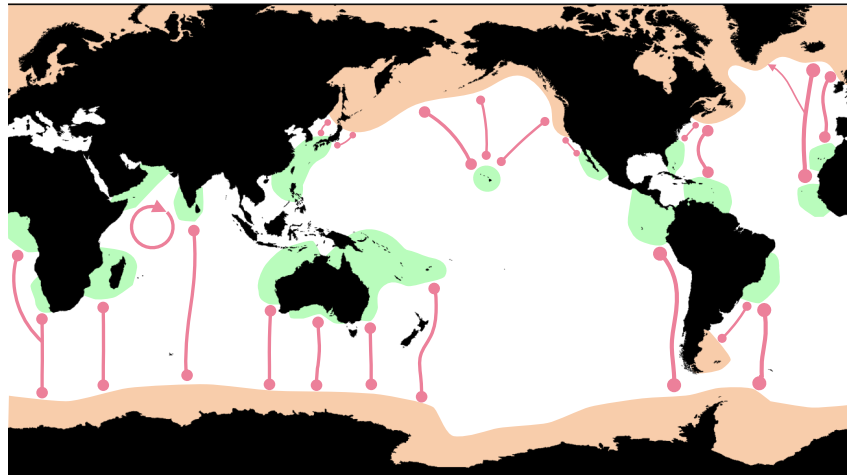
Figure 3. The distribution of baleen whale calving (green) and feeding (orange) habitats, and major migration routes, estimated qualitatively from the literature (peer and grey literature, as well as numerous website; see supplementary information). The major migration routes are generalizations of many specific regional examples, and are only meant to describe the major patterns of baleen whale migration at a global scale. Further, these routes are used to connect the feeding and calving regions, we do not attempt to describe whale movement within these habitats. The circular arrow in the Indian ocean identifies a resident group found there [36].
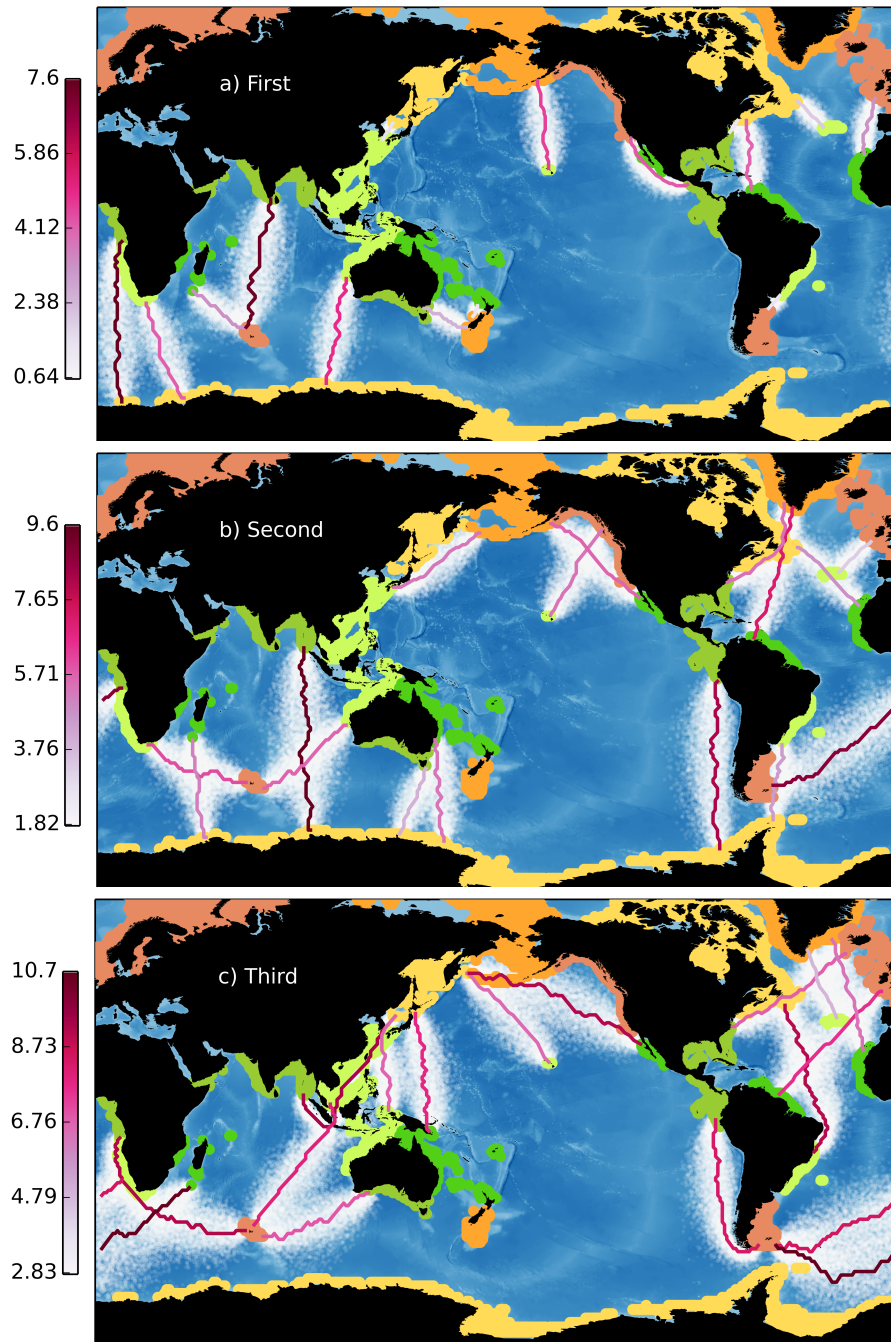
Figure 4. First (a), second (b) and third (c) shortest migration paths between all calving and feeding regions, identified using our modified Dijkstra's algorithm. Calving regions are identified in green, the feeding regions in orange. The different shades of green and orange are used to simply differentiate the regions. Shortest paths are those that minimize ocean distance (colorbar: $1000's\ km$). These paths are not exact solutions to the shortest-path problem, hence there are curves and bends to them. However, these do not impact the comparison of migration routes and distances between regions of the world's oceans.
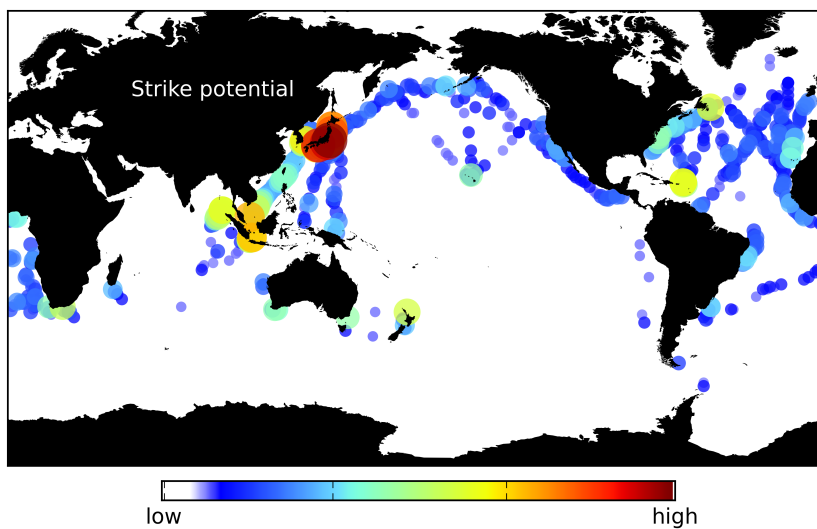
Baleen whale strike potential. Along with color, the size of the dots denotes whale strike potential: the larger the higher potential. See Fig. S2 for a description of the shipping data.

Supplementary Information 1

Literature Review

We collected information on the distribution of baleen whale calving and feeding habitats, and their migration routes. Quantitative - geo-referenced - information was obtained from peer-reviewed literature and is listed in Table A1, with corresponding articles in the subsequent bibliography. Qualitative information - non geo-referenced - from the grey-literature: websites and non-peer reviewed publications are listed at the end.

Habitat type	Latitude	Longitude	Species	Reference
Calving	5	-80	Humpback	1
Calving	18	-108	Humpback	2
Calving	20	-150	Humpback	2
Calving	20	-160	Humpback	2
Calving	20	-156	Humpback	11
Calving	-16	-38	Humpback	13
Calving	-32	17	Right	14
Calving	-18	37	Humpback	15
Calving	-2	8	Humpback	16
Calving	-17	51	Humpback	16
Calving	9	-83	Humpback	17
Calving	9	-84	Humpback	17
Calving	9	-84	Humpback	17
Calving	8	-82	Humpback	17
Calving	9	-84	Humpback	17
Calving	-41	145	Right	18
Calving	-36	175	Right	18
Calving	-36	150	Right	18
Calving	-34	18	Right	18
Calving	-43	147	Right	18
Calving	-37	174	Right	18
Calving	-41	145	Right	18
Calving	-43	148	Right	18
Calving	9	-92	Blue	19
Calving	9	-98	Blue	19
Calving	28	-115	Blue	20
Calving	26	-115	Blue	20
Calving	34	-119	Blue	20
Calving	10	-100	Blue	20
Calving	31	-81	Right	20

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Calving	-42	-63	Right	23
Calving	-16	-38	Humpback	24
Feeding	35	-125	Humpback	1
Feeding	60	-147	Humpback	2
Feeding	55	-140	Humpback	2
Feeding	40	-70	Humpback	3
Feeding	50	-50	Humpback	3
Feeding	65	-15	Humpback	3
Feeding	67	-55	Humpback	4
Feeding	64	-51	Humpback	5
Feeding	65	-30	mix (fin,blue, sei, humpback)	6
Feeding	65	-51	mix (fin,blue, sei, humpback)	7
Feeding	64	-50	mix (fin,blue, sei, humpback)	8
Feeding	50	-50	mix (humpback, fin, minke)	9
Feeding	-64	-63	Humpback	10
Feeding	-64	-62	Humpback	12
Feeding	-64	-63	Humpback	17
Feeding	-65	-65	Humpback	17
Feeding	-65	-63	Humpback	17
Feeding	-65	-64	Humpback	17
Feeding	-65	-62	Humpback	17
Feeding	41	-69	Right	21
Feeding	65	-24	Minke	22
Feeding	-54	-38	Right	23
Feeding	-63	-62	Humpback	12
Feeding	50	-132	Gray	25
Feeding	67	-170	Gray	26
Feeding	49	-68	mix(fin, minke)	27
Feeding	42	-70	Humpback	28
Feeding	43	-66	Humpback	28
Feeding	34	-120	Humpback	28
Feeding	37	-123	Humpback	28
Feeding	48	-125	Humpback	28
Feeding	57	-135	Humpback	28
Feeding	56	-153	Humpback	28
Feeding	52	-155	Humpback	28
Feeding	52	-163	Humpback	28
Feeding	54	-166	Humpback	28

Table 1: Habitat type, location, species and reference number for literature identifying baleen whale calving and/or feeding locations. References are listed in the bibliography below.

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Whale Migration Websites

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www.whales.org.au

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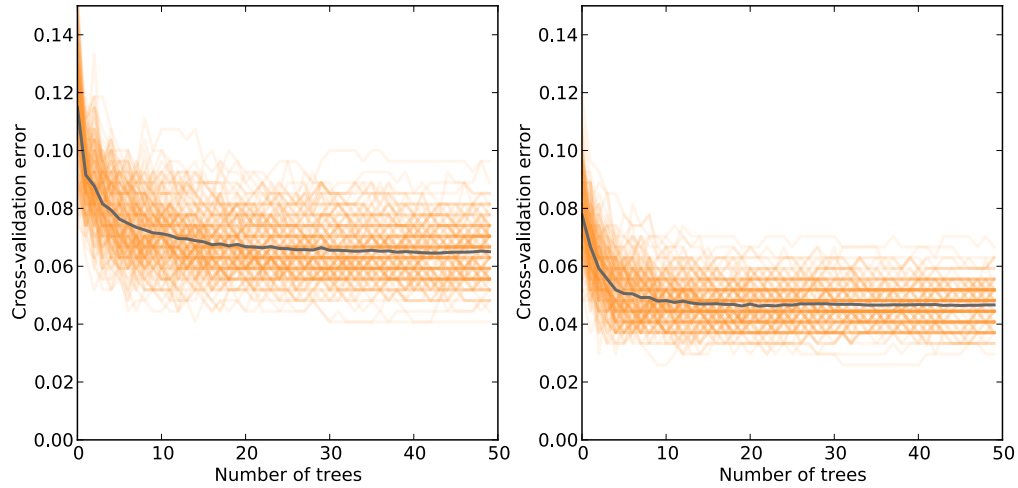
Supplementary Figures

Figure S1: (a). Habitat modeling cross-validation error for calving (left) and feeding (right) habitats. The classification tree algorithm is applied multiple times (orange lines), as pseudo-absence locations are chosen at random. This results in an expected cross-validation error (grey line).
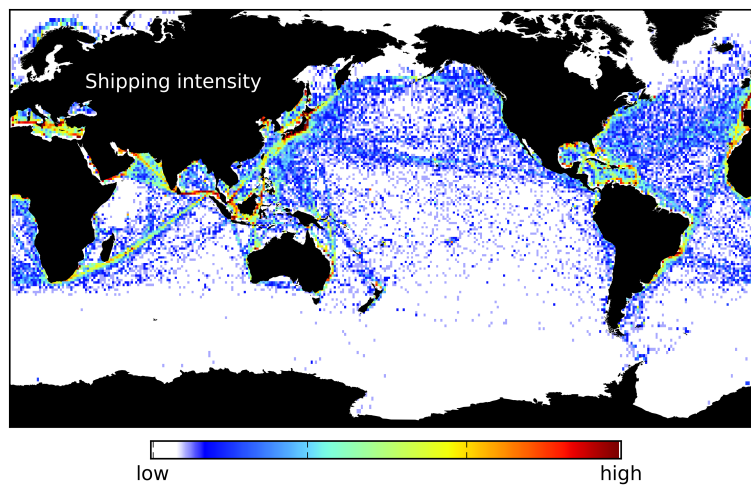
Figure S2: Ship density from the PASTA MARE project. This is defined as the average number of vessels within a grid cell, based on 10 global Satellite-Automatic Identification System (S-AIS) scenes. Each global S-AIS scene retains one position report per vessel within a time frame of 8 days. The data used covers the period from 1 January 2010 – 31 March 2010. We log-transformed this data then normalized it to [0,1], before interpolating to locations along the major migration pathways, inferred from our ocean-distance minimizing algorithm. For more information on this data see https://webgate.ec.europa.eu/maritimeforum/content/1603
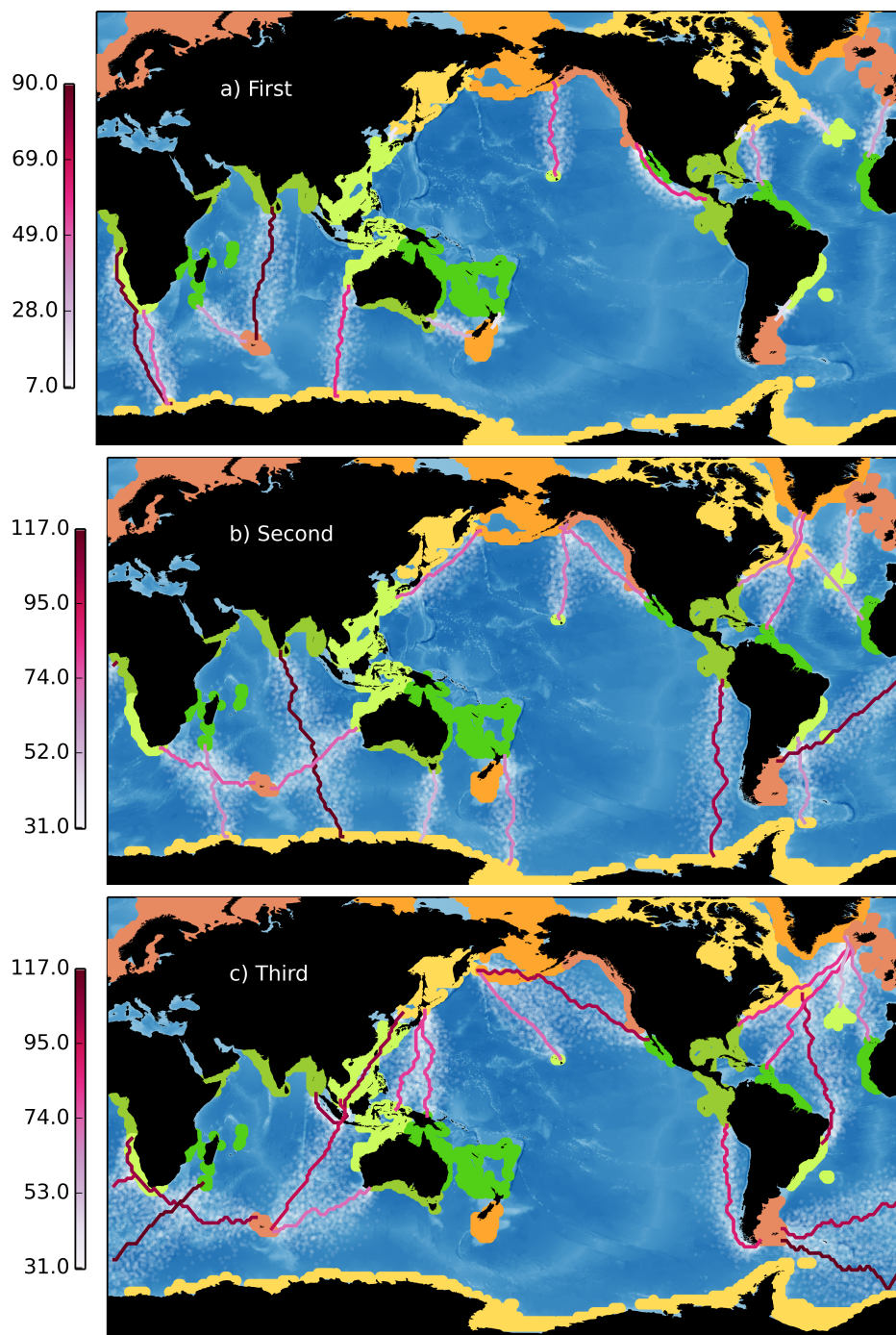
Figure S3: First (a), second (b) and third (c) shortest migration paths between all calving and feeding regions. Calving regions are identified in green, the feeding regions in orange. The different shades of green and orange are used to simply differentiate the regions. Shortest paths are those that minimize travel time (colorbar: *days*); assuming a constant swimming speed of $80\ km\ day^{-1}$