1   # The collapse and recovery potential of carbon sequestration by baleen whales in the Southern Ocean

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Abstract

Limiting climate warming below 2°C requires both reducing anthropic greenhouse gas emissions and sequestering more atmospheric carbon. Natural Climate Solutions (NCS) rely on the ability of ecosystems to capture and store carbon. Despite the important role of marine megafauna on the ocean carbon cycle, its potential as a NCS has not yet been explored. Here, we quantify the amount of carbon potentially sequestered by five baleen whale species across the Southern Hemisphere between 1890 and 2100 through both the sinking of carcasses after natural death and the fertilisation of phytoplankton by nutrients in faeces. At their pre-exploitation abundances, the five whales could sequester 10.6 10^6 tonnes of carbon per year (tC.yr^{-1}) but this natural carbon sink was reduced at 2 10^6 tC.yr^{-1} in 1965 due to commercial whaling. However, the restoration of whale populations could sequester 8.7 10^6 tC.yr^{-1} at the end of the 21st century suggesting an efficient but neglected NCS that remains to be estimated globally including all marine vertebrates.

Keywords: Natural Climate Solutions, climate change, population dynamics, modelling, krill

Introduction

The concentration of atmospheric carbon dioxide (CO_2) has dramatically increased since the beginning of the industrial era, from about 277 parts per million (ppm) in 1750 to over 410 ppm today [1]. The rise of this greenhouse gas (GHG) in the atmosphere is changing the climate with a range of damaging consequences for ecosystems and human societies [2,3]. Thus, at the Paris Agreements in 2015, the international community set the objective of containing the global warming below +2C° compared to pre-industrial levels [4]. The signatory states made the commitment not only to reduce their GHG emissions, but also to implement negative emission actions to remove CO_2 from the atmosphere. These actions can be based on emerging technologies like geoengineering [5,6] but can also rely on the natural capacity of ecosystems to sequester and store carbon [7,8]. These Natural Climate Solutions (NCSs) represent the set of actions for the protection, restoration or sustainable management of ecosystems with the aim of increasing long-term carbon sequestration and limiting the emissions of GHG.

Surprisingly, the open ocean is not subject to any NCS though it absorbs about 22% of anthropogenic CO_2 emissions [1] and maintains a primary productivity equivalent to that of terrestrial ecosystems [9]. No NCS is based on marine megafauna either although some of these species are the biggest in the animal kingdom, thus accumulating a large amount of carbon over several decades. Marine mammals, especially whales, could therefore have a disproportionate influence on the functioning of ecosystems but also on the global carbon cycle. Here, we focus on baleen whales since they have been identified as ecosystem engineers having an important role in biogeochemical cycling and carbon sequestration[10] [11]. However, the carbon pump mediated by whales remains poorly understood and quantified. Indeed, carbon sequestration has only been assessed at a given time [12] or for a limited number of species[13]. One step further, some studies highlighted the importance of megafauna, especially whales, for carbon sequestration through the impact of whaling[14] but we still lack a long-term dynamic of this sequestration potential under scenarios mixing climate change and whaling.

Whaling has indeed reduced the size of populations by an average of 70% [15] and by up to 99.5% for some species such as the blue and southern right whale [16]. Since 1986, an international moratorium of the International Whaling Commission (IWC) allows populations to recover, but other pressures threaten their recovery, including climate change [17–19]. Therefore, it is essential to evaluate the whale potential for carbon sequestration under different future climatic scenarios. Here we provide the first quantification of both historical and forecasted whale-mediated carbon sequestration trajectories in the southern hemisphere. For this purpose, we used whale abundances modelled from harvesting and survey data from 1890 to the present day and abundances predicted up to 2100 under two climatic

92   scenarios [16,17], one excluding effects of climate change and the other including effects of climate

93   change predicted under the most pessimistic but also the most realistic RCP8.5 scenario[20] .

94   Whales can sequester carbon via different mechanisms. Here, we considered two sequestration

95   pathways. First, these massive animals can sequester the carbon contained in their biomass via the

96   sinking of their carcasses into the deep ocean after natural death [14] (Fig. 1a). Secondly, whales can

97   contribute to carbon sequestration indirectly via the fertilisation of surface waters. Indeed, the

98   development of phytoplankton can be limited by the low concentration of nutrients such as nitrogen,

99   phosphorus or iron [21]. Nutrients egested by whales, via their faeces, can thus stimulate phytoplankton

100   productivity and increase carbon sequestration via dead phytoplankton cells that sink into the deep

101   ocean [22] (Fig. 1b). On top of that, southern whales feed mostly on krill which is an iron accumulator[23,24]

102   so they can recycle this limiting nutrient in the Southern Ocean. Although the recycling of iron and the

103   subsequent fertilization process mediated by whales were already evaluated[13,25], the two

104   sequestration pathways (carcasses and fertilization) have never been estimated simultaneously for a

105   community of baleen whales during a long-time period.

106   In this study, we focused on Southern Hemisphere populations of five species that have been heavily

107   exploited during the first half of 20th century: the blue whale (*Balaenoptera musculus*), the fin whale

108   (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), the southern right whale

109   (*Eubalaena australis*) and the Antarctic antarctic minke whale (*Balaenoptera bonaerensis*), for which

110   comprehensive ecosystem models predicting future abundances were developed[16,17]. These species

111   are very diverse in terms of body size (from 6 tonnes for the antarctic minke whale to 120 tonnes for

112   the blue whale) and IUCN Red List of Threatened Species status (from Endangered to "Minor Concern")

113   (Supplementary Fig. 1). This model is mainly localized in the Southern Ocean (between 40° and 80° S)

114   during summer when these whales prey on krill; and in the tropics (between 0 and 40° S) during winter

115   when they migrate for the breeding season [26].

116   The population dynamics of these five species were estimated from 1890 to 2100 for the Southern

117   Hemisphere using a MICE (Model of Intermediate Complexity for Ecosystem Assessments) model [16,17].

118   Whale abundances were explained by both the dynamics of their prey (Antarctic krill *Euphausia*

119   *superba* and copepods) and the catches (whaling) that were progressively banned between 1960 and

120   1980. The MICE model was coupled with a NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus)

121   model that considers the influence of climatic conditions on primary productivity to hindcast historical

122   carrying capacity and predict future population trajectories. To take into account the effects of climate

123   change, two versions of the MICE model were used. In the first version, whale dynamics were not

124   coupled to changing climate conditions which were assumed to remain constant from 1890 to 2100.

125   In the second model, the effects of climate change according to the RCP 8.5 "business as usual"

126   scenario impacted krill and copepod prey availability for whales through the NPZD outputs [16,17]. The

127   outputs of this MICE model were used as inputs for our new carbon sequestration assessments. To

128   calculate the carbon sequestrated via carcasses, we estimated the carbon concentration of carcasses

129   and the biomass of carcasses reaching the deep ocean (see method). For the fertilization sequestration

130   pathway, we estimated the amount of iron supplied to the euphotic zone by whales, and the

131   supplementary amount of carbon sequestrated by phytoplankton owing to this additional nutrient

132   supply (see methods). By coupling these two processes to the whale abundance trajectories we

133   estimated the trend of the whale-mediated carbon pump from 1890 to 2100 including uncertainties.

134   We show that, by the end of the century, southern whales could sequester between $5.2 \ 10^6$ tC.yr^{-1} and

135    $8.9 \ 10^6$ tC.yr^{-1}, depending on the climate change trajectory. It represents between 50% and 84% of the

136   pre-exploitation level after a drop at $2 \ 10^6$ tC.yr^{-1} in 1965 due to whaling. We also show that whale-

137   mediated carbon sequestration is predominantly due to the fertilization pathway. Our study suggests

138   that this often-neglected carbon sequestration performed by all marine mammals [27] but also seabirds

139   [27–29] and fish [30–32] could be considered as a NCS where populations are restored.

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Results

142   **Carbon sequestration prior to commercial whaling**

143   We first present estimates of the amount of carbon sequestered by the five baleen whale species

144   across the Southern Hemisphere when they were at their biotic capacity, i.e. at their pre-exploitation

145   levels. Using whale parameters and outputs from the MICE model [16,17] (see Methods), the annual

146   amount of sequestered carbon was estimated by considering the natural mortality of whale

147   populations as well as the biomass and carbon content of the carcasses (Supplementary Fig. 1). The

148   total pre-exploitation number of mature individuals is about 1.2 million for the five species across the

149   Southern Hemisphere [16]. Dead whales represent each year a biomass of almost 4 million tonnes in this

150   region. The sinking of their carcasses generates a flux of $2.5 \ 10^5 \pm 0.5 \ 10^5$ tonnes of carbon per year

151   (tC.yr^{-1}) towards the deep ocean (Fig. 2a). However, not all species contribute equally to this total

152   carbon flux. Fin and blue whales contribute at 48% and 34% respectively (Fig. 2a). The other three

153   species have a marginal contribution, particularly southern right whales, which account for only 0.7%

154   of the total carbon flux.

155   Living individuals also promote carbon sequestration by stimulating phytoplankton growth via

156   fertilization by egestion. The Southern Ocean is a 'High Nutrient Low chlorophyll' zone because

concentrations of macronutrients (nitrates and phosphates) are high but primary productivity is low [21]. Primary productivity, through phytoplankton growth, is thus limited by the availability of trace elements (Fe, Cu, Zn, Co, Cd), especially iron [21]. Iron-rich whale faeces thus stimulate phytoplankton growth and, by extension, carbon sinking [33]. To quantify this sequestration pathway, we estimated the amount of iron supplied in the euphotic zone by whales based on the egestion rate and the bioavailable iron concentration in faeces. At their biotic capacity, the five species defecate about 9.3×10^3 tonnes (range: 3.2×10^3 - 18.4×10^3 tonnes) of iron. About 11×10^2 tonnes of this iron (12.2%) can be used by phytoplankton (see Methods). The phytoplankton carbon flux at 200 metres depth is then 10.4×10^6 tC.yr^{-1} (range: 3.6×10^6 - 20.5×10^6 tC.yr^{-1}). This is about 40 times more than sequestration via carcasses (Fig. 2b). The main contributing species are fin whales (47%), followed by blue and southern right whales with 24% and 16% respectively. Finally, antarctic minke and humpback whales contribute at only 8% and 5%, respectively (Fig. 2b).

Overall the five whales at their pre-exploitation abundances across the Southern Hemisphere can sequester up to 10.6×10^6 tC.yr^{-1} (range: 3.8×10^6 - 20.8×10^6 tC.yr^{-1}). The indirect sequestration pathway, via the stimulation of phytoplankton growth, represents about 98% of the total carbon flux towards the deep sea.

Carbon sequestration dynamics from 1890 to 2100

We predicted carbon sequestration dynamics from 1890 to 2100 under various exploitation levels and climate change scenarios. A stable phase from 1890 to 1912 was followed by a sharp drop in the amount of carbon sequestered over the exploitation period (Fig. 3). Indeed, all species experienced population declines, particularly the main contributors (fin and blue whales), which were reduced to approximately 3% and 0.5% of their pre-exploitation stock, respectively (Supplementary Fig. 2). As a result, carbon sequestration from these Southern Hemisphere whales decreased to a minimum of 2×10^6 tC.yr^{-1} (range: 0.9×10^6 and 3.7×10^6 tC.yr^{-1}) in 1965, i.e. 19% of the pre-exploitation level. In the model without climate change, carbon sequestration would reach 8.9×10^6 tC.yr^{-1} (range: 3.4×10^6 and 17×10^6 tC.yr^{-1}) in 2100 under the predicted increase of antarctic minke whale populations and the recovery of all other species. However, in the model including the effects of climate change, no species, other than the antarctic minke whale, would be able to recover to their pre-exploitation level before the end of the 21st century. The antarctic minke whale would increase rapidly and reach a population size greater than that predicted in the model without climate change (Supplementary Fig. 2). However, this population increase alone would not be sufficient to recover pre-exploitation level for carbon sequestration until 2100. By the end of the century, the whale-mediated carbon pump would reach

190 5.2 10^6 tC.yr^{-1} (range: 2.2 10^6 - 9.6 10^6 tC.yr^{-1}), i.e. only half of the pre-exploitation level, under the

191 major influence of antarctic minke whales.

192 For both models, fin whales were the major contributors until 1959 then antarctic minke whales

193 became the main contributors (Fig. 3) even though they are smaller (sequestering individually less

194 carbon). Owing to their high abundance and low exploitation rate, antarctic minke whales are

195 responsible for roughly 51% of the total carbon sequestration between 1959 and 2100 in the model

196 without climate change and 66% in the model with climate change, whereas they account only for 8%

197 of pre-exploitation sequestration. By comparison, southern right, humpback and blue whales have a

198 minor contribution throughout this period with, on average, 10%, 9% and 8% respectively between

199 1959 and 2100.

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201 **Deficit of carbon sequestration due to whaling**

202 Finally, we present the cumulated deficit in carbon sequestration over the whole period (1890 to 2100)

203 due to whaling and under two scenarios of climate change. This deficit was estimated as the difference

204 between the total sequestration (direct and indirect ways) estimated through time under population

205 fluctuations (Fig. 3) and the total sequestration at the carrying capacity (pre-exploitation level). It thus

206 expresses the amount of carbon that has not been sequestered since 1890 and will not be till 2100 due

207 to the combined effects of whaling and climate change. This deficit would reach more than 1Gt.C in

208 2100 without climate change (Fig. 4a) but 1.2 Gt.C under the more realistic "business as usual" scenario

209 with climate change (Fig. 4b). This deficit is unequally distributed among species with the collapse of

210 the carbon sequestration driven largely by the blue, fin and southern right whales. Conversely,

211 antarctic minke whales provide a surplus of sequestration since 1930, this surplus increasing even

212 further under the climate change scenario to reach 250 Mt.C.

213

214 # Discussion

215 **Contribution of whales to the carbon cycle in the Southern Ocean**

216 To date, some studies have examined the two mechanisms of carbon sequestration by marine

217 megafauna but separately, for a single species or for a small area [13,14,34]. No studies have predicted

218 future carbon sequestration and deficit given changing whale abundances across the Southern

219 Hemisphere under various scenarios. Here, we estimate the amount of carbon sequestered by five

220 southern baleen whale populations from 1890 to 2100 under the joint pressure of whaling (top-down

221 effect) and climate change that will affect the amount of prey available (bottom-up effect).

222   The five whale populations at their carrying capacity (pre-exploitation level), represent an annual

223   sequestration potential of 2.5 10^5 ± 0.5 10^5 tC.yr^{-1} via carcasses sinking toward the deep ocean. This

224   estimate is 30% higher than that of Pershing et al. [14] who estimate this sequestration at 1.6 10^5 tC.yr^{-1}

225   with four additional species (grey whale, sei whale, Bryde's whale, bowhead whale) taken into

226   account. This difference is explained by their lower estimates of carrying capacities. Our estimates

227   were based on hindcasting population dynamics given historical whaling and fitted to current surveys,

228   so are likely more robust estimates of historical carrying capacities.

229   For the five whale species, the fertilization-induced sequestration reaches up to 10.4 10^6 tC.yr^{-1} with a

230   range of 3.6 10^6 – 20.5 10^6 tC.yr^{-1} at carrying capacity or pre-exploitation level. Previous estimate of

231   the indirect sequestration by sperm whales in the Southern Ocean was 0.4 10^6 tC.yr^{-1}, which is

232   consistent with our results given the population size of sperm whales compared to those of the five

233   species of baleen whales [13]. Given the difference of population size between sperm whales and our

234   five baleen whale species, our results are of the same order of magnitude as this previous assessment.

235   Indeed, these baleen whales represent a biomass about 100 times larger than that of sperm whales

236   and they consume prey (krill) richer in iron (1.7.10-4 Kg iron/Kg dry weight [23]) than sperm whales which

237   mainly consume cephalopods (0.75.10-5 Kg iron/Kg dry weight [13]).

238   We show that the role of whales in carbon sequestration resides more in their capacity to boost other

239   biological carbon pumps (like marine snow) through fertilization than in exporting their own biomass

240   (carcasses) in the deep sea (98% against 2% of the total flux). Thanks to these two sequestration

241   pathways, the annual carbon flux induced by whales prior to their exploitation (10.6 10^6 tC.yr^{-1} on

242   average) was comparable to the carbon fluxes observed in other ecosystems, especially coastal ones,

243   such as mangroves (31.2 10^6 - 34.4 10^6 tC.yr^{-1}) or salt marshes (4.8 10^6 - 87.2 10^6 tC.yr^{-1}) (Supplementary

244   Table 1).

245   Due to their long-life cycles, the recovery of many baleen whale populations after over-exploitation

246   has been a very slow process. Therefore, the consequences of whaling extend well beyond the

247   exploitation period and currently limit sequestration of these five baleen whales to 3.4 10^6 tC.yr^{-1} (1.4

248   10^6 – 6.1 10^6 tC.yr^{-1}), i.e. 32% of the pre-exploitation level. In the model without climate change, the

249   carbon sink could be restored at 84% of its pre-exploitation level by 2100, then reaching 8.9 10^6 tC.yr^{-1}

250   . However, the recovery of whale populations and of the carbon pump may be delayed and weakened

251   by climate change [17,18]. This can be explained by changes in the abundance and distribution of krill due

252   to changing primary productivity patterns in the Southern Ocean[17]. Furthermore, the distribution of

253   krill is expected to contract southward due to increasing temperature and reduced sea-ice extent [35].

254   This could exacerbate even more our results by affecting whale populations predominantly feeding in

mid-latitudes areas (humpback whales, fin whales and southern right whales) although copepods also make up a large proportion of the diet of southern right whales. Antarctic minke whales and blue whales could benefit most, especially in the Pacific area, of the ice-extent reduction in the Southern Ocean because of their ice-dependency, assuming they can shift their distribution southwards to follow the krill[17]. However, since antarctic minke whales would increase under marked climate change scenario (due to increasing biomass of krill at high latitudes where they are distributed), prey availability for other species may be reduced. Our MICE model includes interspecific competition between the five whale species, and thus accounts for associated effects of changing prey availability on whale recovery given changing whale densities. As a consequence, the recovery of some species is predicted to slow down, with estimated declines again during the 21st century for humpback, fin and southern right whales[17]. As a result, despite a predicted increase of antarctic minke whale populations, the total carbon flux would not return to its pre-exploitation level due to the negative impact of climate change on other species. A negative feedback loop between climate and whale populations could therefore occur in the southern hemisphere. However, these results should be taken with caution as they present several uncertainties.

Limits and uncertainties

This first estimate of the carbon flux generated by whales is restricted to five baleen species in the southern hemisphere, whereas there are fifteen species of baleen whales globally. Indeed, the number of species considered here was restricted to those included in the whale populations models [16,17] (i.e. species commercially exploited in Antarctic waters, in most cases feeding predominantly on Antarctic krill, for which enough survey data were available). Therefore, our model may significantly underestimate the importance of carbon sequestration mediated by whales in the Southern Ocean and at global scale by excluding other southern species (Bryde's whale, Pygmy right whale and Dwarf antarctic minke whale), northern species (bowhead whale, gray whale, omuras whale, northern right whale) and toothed whales. Moreover, the indirect carbon sequestration mechanism was only considered during the summer period, when the whales are located in the Southern Ocean. During winter, they migrate towards tropical regions to breed. However, other nutrients (nitrogen, phosphorus) also excreted by whales [34] limit phytoplankton productivity in these areas [21]. Thus, they could indirectly promote carbon sequestration during the breeding season and migration. The carbon sequestration induced by whales is therefore likely to be much larger and extends towards the tropics.

Estimates of carbon sequestered via carcasses are subject to several uncertainties. First, we assume that the biomass-carbon conversion does not change with carcass degradation. However, not all

tissues have the same carbon concentration [36] and some (fat tissue, muscle) may be consumed primarily by scavengers [37]. In order to gain precision, it seems essential to determine the carbon level in the different types of tissue (bone, muscle, blubber, viscera) for each species. On the other hand, the proportion of biomass reaching the deep ocean before being consumed or remineralised is uncertain and probably highly variable, depending on the presence of scavengers or currents for example. Finally, these migratory species experience significant weight variations during the year [38]: they may gain several tonnes during the summer and be considerably thinner at the end of the breeding season. The amount of carbon sequestered therefore depends on the seasonality of natural mortality, which is not taken into account in our study.

The main uncertainty in our estimated indirect sequestration is the amount of bioavailable iron provided by whales at sea surface. First, iron concentration values in whale faeces were obtained with few replicates, and those of antarctic minke whales were estimated from available data for other species. Surprisingly, the iron concentration in southern right whale faeces [27] is higher than that of other species, whereas it would be expected to be lower. Indeed, the proportion of krill, an iron accumulator, in their diet is lower compared to other species [23]. This may be indicative of high intraspecies, temporal or spatial variability in faecal iron concentration. On the other hand, individual variability within species has also been ignored. Iron retention in the body varies with age and reproductive status [39]. To address this issue, the population could be divided into different categories (juveniles, adults, pregnant or lactating females) and the iron concentration in the faeces could be estimated for each category.

Secondly, to estimate the response of phytoplankton to the iron supply, the fraction of iron contained in faeces, which is finally incorporated by phytoplankton, needs to be estimated. This is influenced by both bioavailability of the iron supply and the fate of this iron. On the one hand, iron bioavailability in the ocean is influenced by many processes (dissolved or particulate form, degree of oxidation, complexation with organic ligands, etc.) [40]. No studies have estimated the bioavailable fraction of iron released by whales. We considered the dissolved iron or the iron dissolving in the first 12 hours to be bioavailable but our values are probably underestimated. Indeed, iron particles are small (a few micrometres) and their density is close to water density so they sink slowly and could remain for several days in the euphotic zone where dissolution may continue [41]. In addition, the dissolution experiment of Ratnarajah et al. [41] was conducted in the dark. Light can increase dissolution (photo-dissolution) [42,43]. On the other hand, both heterotrophic bacteria and autotrophic phytoplankton depend on the available iron pool for growth. So, auto- and heterotrophs could compete for iron when dissolved organic carbon limitation of bacterial growth is alleviated[44]. However, heterotrophic bacteria can also recycle iron, increasing iron solubility and availability by recycling particulate iron into

322 dissolved iron, producing organic ligands binding to the iron and increasing iron suspension and

323 bioavailability [45].

324 These various processes can either increase or decrease the availability of iron for phytoplankton

325 making difficult to assess the bioavailability and fate of iron supplied by whales in the euphotic zone.

326 Therefore, a better estimation of the amount of iron released by the different whale species and its

327 availability for phytoplankton seems essential to precisely quantify the indirect sequestration pathway.

328 Finally, to quantify the additional carbon sequestered owing to iron inputs by whales, experimental

329 measurements of carbon exported at 200 meters in response to iron addition were used[33]. These data

330 may be a source of overestimation since we assume that all carbon exported at 200 metres will

331 sediment and be sequestered. However, organic matter may be remineralised before reaching the

332 deep ocean [46] or be broken down into smaller particles that sink more slowly [47].

333

334 **Importance of whale diversity for carbon sequestration**

335 We studied five species of baleen whales, diverse in size, longevity and life cycles, each contributing

336 differently to the two carbon sequestration pathways. Sequestration via carcasses sinking is mainly

337 supported by the most massive species such as blue and fin whales, which can reach approximately

338 117 and 65 tonnes per individual, respectively. In contrast, the indirect sequestration pathway

339 depends mainly on the smaller but more abundant antarctic minke whale. This is explained by the fact

340 that prey consumption (determining the amount of faeces) is a hypo-allometric function of body mass

341 [48], whereas in the case of carcasses, the carbon sequestration is a linear function of body mass.

342 Considering that biomass and abundance are the two components that determine the relative

343 contribution of a species to carbon sequestration, the direct pathway is more dependent on individual

344 body mass while the indirect pathway is more dependent on the number of individuals. Southern right

345 whales are also weaker contributors to the direct sequestration pathway because of their tendency to

346 float after death. Conversely, their strong iron concentration in faeces make them very efficient in

347 sequestering carbon via the fertilization pathway.

348 This complementarity between species, resulting from the diversity of their traits, helps to maintain

349 the different sequestration pathways. More generally, this functional complementarity is key to

350 support ecosystem multifunctionality[49,50] and increases the associated ecosystem services [51].

351 Moreover, it is generally considered that the stability of a system increases with the diversity of its

352 components; this is the portfolio effect. In ecology, this results into a positive diversity-stability

353 relationship: the specific diversity of a community stabilises its functioning through time and under

354 disturbances[52]. Thus, ecological processes performed by a diverse community are more stable over

time and less subject to fluctuations than individual species [53,54]. The two main factors in this relationship: the asynchrony between populations, and the average stability of each population [54]. In our case, the important increase in antarctic minke whales, which have a higher breeding rate and have been less exploited, along with the over-exploitation of other species, is stabilizing the overall abundance of Southern Ocean whales. Thus, antarctic minke whales maintain, at least partially, the carbon sink and limit the loss of sequestration under over-exploitation. Their increase throughout the 21st century is also a key resilience factor since they allow a faster recovery of carbon flux towards its historical value. However, even if the carbon flux partially recovers at the end of the century, the relative species contributions to the carbon flux are very different from those of the pre-exploitation period, especially in the model including climate change. Thus, we have a functional recovery but from an ecological and conservation point of view the southern whale community is not returning to its former state.

Restoring whale populations: a Natural Climate Solution?

To consider whale population restoration as a Natural Climate Solution (NCS), several criteria must be met: effectiveness, the presence of co-benefits and the limitation of associated disadvantages, and the governability, i.e. the ability to implement this solution, while managing the conflicts and benefits generated by its implementation [55].

To maintain the global warming at a maximum of +2°C, total emissions must be less than 810 10^9 tCO$_2$-eq between 2016 and 2100 [6] and achieve zero net emissions by 2075 [56]. This implies not only reducing GHG emissions but also offsetting unavoidable emissions. For example, in the field of road transport, our annual emissions are expected to decrease from 5.75 10^9 tCO$_2$-eq.yr^{-1} in 2015 to 2.6 10^9 tCO$_2$-eq.yr^{-1} in 2050 thanks to energy efficiency gains and cleaner fuels [57]. By 2050, southern baleen whales should be able to offset 0.7% of these persistent road transport emissions by sequestering an average of 17 10^6 tCO$_2$-eq.yr^{-1}. In addition, by 2100, GHG emissions from all transports should not exceed 1.8 10^9 tCO$_2$-eq.yr^{-1} [57]. According to the model predictions without climate change, these remaining emissions could be compensated up to 1.8% by southern baleen whales, which would sequester about 32.6 10^6 tCO$_2$.yr^{-1} in 2100. On the other hand, if climate change continues to follow a RCP 8.5 scenario [20], southern whales would be able to sequester only 19 10^6 tCO$_2$.yr^{-1}, offsetting 1.1% of global transport emissions in 2100. Moreover, if they are managed to be restored to their pre-exploitation levels by the end of the 21st century, they could compensate up to 2.1% of these emissions. Thus, although many whale populations have been severely depleted by whaling, restoring their populations could contribute, even marginally, to achieving our carbon neutrality objectives.

388 In addition, the presence of whales is associated with many other benefits, promoting the good health
389 of ecosystems and some services to human societies. Indeed, whale carcasses are an essential source
390 of food for abyssal ecosystems [10,58]. Thanks to their enriching action on their planktonic environment,
391 they can be described as ecosystem engineers, favouring lower trophic levels [59]. Whales enhance krill
392 growth through increased phytoplankton production [39], which also participates very efficiently in
393 carbon sequestration through the production of fast-sinking particulate faeces [24]. In addition, whales
394 have a strong cultural and aesthetic value: tourism associated with whale watching generates more
395 than US$2.5 billion per year and 19,000 jobs worldwide [60]. The recovery of their populations could
396 therefore enable the development of a sustainable tourism economy. Thus, restoring whale
397 populations would promote some socio-economic co-benefits in the Southern Ocean, whether in
398 terms of mitigating climate change, maintaining biodiversity, or tourism activities.

399 In addition to the moratorium established in 1986 by the International Whaling Commission (IWC),
400 some further measures can be taken to promote the recovery of whale populations. Indeed, several
401 anthropogenic activities continue to threaten whales. Ship strikes are now among the main causes of
402 mortality [61]. Noise generated by boats also alters whale mortality and reproduction rates by modifying
403 key behaviours related to feeding, reproduction or communication [62]. In 2016, the IWC created a
404 strategic plan to monitor collisions between cetaceans and vessels in order to develop approaches and
405 solutions to achieve a permanent reduction in ship strikes by 2020. Although effective in terms of
406 mortality reduction, the restriction of maritime routes and fishing zones as well as the reduction of
407 authorised speed can create conflicts of interest with fishing and maritime transport [63]. However, the
408 main threat to the recovery of whale populations in the coming years may likely be climate change
409 [17,18], including the increased spread of disease [19] and the decrease in krill prey density and southward
410 contraction of geographic distributions [35]. Although krill is not currently overexploited [64], the demand
411 has been increasing since the 2000s and is expected to increase in the coming years [35]. Continuing to
412 promote sustainable exploitation of krill in the Southern Ocean could therefore be a main lever for
413 actions to preserve whale populations and their associated services. The restoration of whale
414 populations in the Southern Ocean must therefore be accompanied by various concrete measures to
415 manage this ecosystem. We can conclude that the restoration of baleen whale populations meet all
416 criteria in terms of carbon sequestration effectiveness, co-benefits and governability to be considered
417 as a NCS.

418 More generally, other species including marine mammals, birds and fish could generate a substantial
419 carbon pump through similar mechanisms. A more ambitious NCS could therefore emerge, based on
420 various vertebrate species. However, populations should be at their maximum size in order to benefit
421 from the full potential of these NCSs. Identifying and quantifying these NCSs could motivate the

422   protection of the oceans to reach 30% coverage by 2030, the new target proposed by the United

423   Nations [65]. In this way, restoring marine vertebrate populations could contribute to achieving our

424   climate objectives while generating other services beneficial to the functioning of the biosphere and

425   the well-being of human societies [66,67].

426

Materials and Methods

Model of intermediate complexity for ecosystem assessment

429   We used outputs from a Southern Hemisphere spatial 'Model of Intermediate Complexity for

430   Ecosystem Assessments' (MICE) for phytoplankton, krill (*Euphausia superba*) and five baleen whale

431   species, which estimates whale population trajectories from 1890 to 2100. The model uses the most

432   up-to-date catch records from the International Whaling Commision (IWC) that account for data

433   falsification and errors. These data thus represent the most updated catch series, and our model

434   estimates represent the most up to date population trajectories for the main baleen whales in the

435   Southern Hemisphere. MICE are well-suited for developing predictions of large-scale system dynamics

436   requiring an understanding of ecological interactions between species and processes, by restricting

437   focus to key ecosystem components, and through parameter estimation fitted to data and sensitivity

438   analyses, can account for key uncertainties. The model uses delay-difference equations to describe

439   whale dynamics at annual seasonal time-steps, linked to an age-structured population model for krill

440   (see Tulloch et al. [16,17] for detailed description of equations and parameter settings for the base model).

441   Prey dynamics (krill and copepods) are linked to primary productivity outputs from a coupled Nutrient-

442   Phytoplankton-Zooplankton-Detritus model (NPZD). The model thus includes two-way interactions

443   between whales and prey, with bottom-up environmental forcing and top-down consumption of

444   changing prey base by whales. As the model is restricted to southern whale populations, we considered

445   that whales feed exclusively on krill and in smaller proportion on copepods.

446   Two versions of the model were used, a climate-forced version linking prey dynamics to future

447   changing temperature and Chl-a outputs from the NPZD model driven by Representative

448   Concentration Pathways (RCP) 8.5 adopted by the Intergovernmental Panel on Climate Change (IPCC)

449   Fifth Assessment Report (AR5)[56], and another where these links to changing environmental conditions

450   were excluded. Both models were fitted to an index of abundance from available surveys for the five

451   whale species and first simulate historical whale trajectories from 1890-2013 for two regions (Pacific,

452   and Atlantic/Indian), and two seasons (feeding and breeding), driven largely by the historical

453   commercial whaling records from the IWC.

454 We obtained the following outputs from the two MICE models to input into our model: (i) Time series

455 of population abundance estimates from 1890-2100, for females only, for each species and Area of the

456 model (P = Southern Hemisphere Pacific, and A= Southern Hemisphere Atlantic/Indian) and (ii)

457 Biological parameters and carrying capacity estimates for each species in the model (Supplementary

458 Table 2).

459

460 **Carbon sequestration by whale carcasses**

461 The weight of whales, and by extension the amount of carbon they contain, depends on their age. The

462 age structure of the population in a given year, i.e. the number of individuals in an age class, was

463 constructed using demographic parameters for each species derived from the MICE model

464 (Supplementary Table 2). The population abundance numbers provided by the MICE model correspond

465 to mature females. To obtain the total number, the number of males (E_{male}) is estimated from the

466 number of females (E_{female}) and the sex ratio (q):

467 $$E_{tot} = E_{female} + E_{male} \quad ; \quad E_{female} = q.E_{tot} \quad ; \quad E_{male} = (1-q).E_{tot} \quad \Rightarrow \quad E_{male} = \frac{(1-q)}{q}.E_{female} \quad (1)$$

468 For each gender, the number of individuals (N) in each age class (a) between birth and maximum age

469 (z) is then calculated from the number (E) of adult individuals between the age of maturity (T) and

470 maximum age (z) and the survival rate (S or S_{juv}). A distinction is made between the survival rate of

471 individuals under one year old (S_{juv}) and that of individuals over one-year old (S). These rates are

472 species-specific (Supplementary Table 2), considered constant and identical for males and females.

473 The number of individuals of a given year class (individuals aged a) is written as a function (2)

474 of the number of individuals aged T:

475 $$\forall a \in \,]0,z] \quad N_{a+1} = S.N_a \Rightarrow N_a = S^{a-T}.N_T \quad ; \quad For \quad a = 0, \quad N_0 = S_{juv}^{-1}.S^{1-T}.N_T$$

476 The number of individuals in T years can be found with the parameters of the model:

477 $$\sum_{a=T}^{z} N_a = E \quad \Rightarrow \quad N_T.\sum_{a=T}^{z} S^{a-T} = E \quad \Rightarrow \quad N_T = \frac{E}{\sum_{a=T}^{z} S^{A-T}} \quad (3)$$

478 Thus, the age structure of the population can be written as a function of N_T:

479 $$N_0 = S_{juv}^{-1}.S^{1-T}.N_T \ ; \ N_1 = S^{1-T}.N_T \ \cdots \ N_{T-1} = S^{-1}.N_T \ ; \ N_T \ ; \ N_{T+1} = S.N_T \cdots \ N_z = S^{z-T}.N_T \quad (4)$$

480 This age structure calculation is applied every year from 1890 to 2100. We assume that age structure

481 does not vary over time. Indeed, the mass of individuals is almost constant in adulthood. It is therefore

482 assumed that no adult year class is more impacted by whaling than another. Among juveniles, very

483 few catches have been reported for the whale species in this study [68].

484 In order to calculate the number of individuals dying naturally each year, the natural mortality rate (1-

485 S or 1-S_{juv}) was applied to the numbers in each age class (Supplementary Table 2). This gives the

486 number of individuals dying per age class in a given year.

487 To obtain the biomass of an age class, the number of individuals in this class was multiplied by the

488 corresponding individual body mass. The mass of individuals at each age follows the Von Bertalanffy

489 equation, whose parameters, depend on both species and sex [14] (Supplementary Table 3). Let a the

490 age, m_{inf} the maximum size of individuals, k the growth rate and a_0 the theoretical age at which the

491 mass is zero, the mass m of an individual aged a is:

492
$$m(a) = m_{inf}(1 - e^{-k(a-a_0)}) \tag{5}$$

493 The total population biomass (B_{tot}) was calculated from the biomass of each age class (B_a) as follows:

494
$$B_{tot} = \sum_{a=0}^{z} B_a \quad with \ B_a = m_{female}(a).N_{female,a} + m_{male}(a).N_{male,a} \tag{6}$$

495 To assess the amount of carbon sequestered by the sinking of whale carcasses, the biomass was

496 converted into carbon mass. Several estimates of carbon content in whale tissues are available: 10.5%

497 [36] and 15% [9]. A carbon rate of 12.5% ± 2.5% was thus used, assuming that this rate is identical for all

498 individuals without distinction of species, sex or age. To calculate the amount of carbon, the biomass

499 was multiplied by this carbon rate.

500 The fate of the carcasses depends on several factors. Attacks by predators such as killer whales (*Orcinus*

501 *orca*) are rare and very rarely lethal [69,70]. Most dead individuals should therefore sink and sequester

502 carbon in the deep sea. However, carcasses do not sink in their entirety to the ocean floor because

503 they are partly consumed by scavengers like sharks [71] or killer whales [72] or degraded by

504 microorganisms. It was estimated that between 50% and 90% of a carcass reaches the ocean floor [73].

505 The conservative estimate of 50% has been used for all species except southern right whales, which

506 tend to float after death due to a higher proportion of blubber [74]. For southern right whales we

507 considered that only 10% of carcass biomass is sequestered in the deep sea [14].

508

509 **Indirect carbon sequestration via fertilization**

510 Whales play also a role in the carbon cycle through their ability to fertilize the ocean with nutrients

511 contained in their faeces (Fig. 1b). Migratory baleen whales spend the summer in the Southern Ocean

512 where food is abundant. During their migration and the breeding season in the tropics they feed only

513 in small quantities [75]. Thus, we considered carbon sequestration via fertilization only in the

(7)

514 Southern Ocean, the main feeding ground for migratory baleen whales that eat krill. Several estimates
515 of daily prey consumption (noted R in Kg) exist [48]. Owen et al. [76] recommend using the allometric
516 expression of consumption as a function of whale body mass with the parameters provided by Innes
517 et al. [77] to obtain an upper bound, and using the formula based on metabolic rate to obtain a lower
518 bound, with the expression of the ADMR (Average Daily Metabolic Requirement) given by Boyd [76].
519 Thus, the estimates of minimum (equation 7), maximum (equation 8) and average (equation 9) daily
520 consumption were defined as follows:

521
$$Rj_{min} = \frac{ADMR}{0.8 \cdot 3900} \quad ; \quad ADMR = 2529.1\, m^{0.524}$$

522 with m the body mass (Kg), the energy intake from the crustaceans (3900 (KJ/Kg)) and 0.8 the
523 assimilated proportion in relation to the ingested mass.

$$(8)$$
524
$$Rj_{max} = A \cdot m^{B} \quad ; \quad A = 0.42 \; et \; B = 0.67$$
525
$$Rj_{mean} = \frac{Rj_{min} + Rj_{max}}{2} \qquad (9)$$

526 Consumption of prey during the summer season accounts for 83% of the annual consumption [48,75].
527 Thus, the quantity of prey consumed yearly in the Southern Ocean is written as:

528
$$R_{SO} = 0.83 \cdot 365 \cdot Rj \qquad (10)$$

529 One part of the prey ingested (25%) is directly used by the whale for its metabolism. Only 75% of the
530 wet weight of ingested prey is therefore defecated [13,39]. Furthermore, since prey consumption depends
531 on the mass of individuals, the age structure was reused to obtain the number and biomass of
532 individuals in each age class. Finally, the annual amount of faeces defecated by all individuals aged a
533 (D_a) is calculated as follows:

534
$$D_a = 0.75 \cdot R_{SO}(a) \cdot N_a \qquad (11)$$

535 These faecal masses were then summed for all age classes to obtain the total amount of faeces
536 produced by each whale species in the Southern Ocean (D_{tot}).

537
$$D_{tot} = \sum_{a=0}^{z} D_a \qquad (12)$$

538 To assess the amount of iron released by whales, experimental measurements of iron concentration
539 in the faeces of blue, humpback and fin whales conducted by Nicol et al. [23] were used (Supplementary
540 Table 4). For humpback and fin whales, only a mean value was given. We applied the Taylor's law [78] to
541 estimate the associated variance (V) of a biological measure from its mean (μ) using the power

542 relationship $V = a\,\mu^b$. The numerical values of parameters a and b were estimated from the means and

543 variances of measurements made on blue and pygmy whales (*Balaenoptera musculus brevicauda*).

544 Antarctic minke whales are phylogenetically related to blue and fin whales [79], they belong to the same

545 genus (Balaenoptera) and have similar diets [16]. The iron concentration in antarctic minke whale faeces

546 was therefore estimated as the average concentration of blue and fin whales. For southern right

547 whales, the measurements of Wing et al. [27] were used (Supplementary Table 4). Finally, the mass of

548 iron (m_{iron} in mg) defecated by each whale species is obtained by converting the wet mass of faeces

549 (D_{tot}) to dry mass, considering that the faeces are 75% water, and multiplying this quantity by the iron

550 concentration ($[Fe]$ in mg/Kg, dry mass):

551
$$m_{iron} = 0,25.\,D_{tot}.\,[Fe] \tag{13}$$

552 The need for whales to return to the surface to breathe and the limited duration of their dives suggest

553 that all faeces are released into the euphotic zone [80]. However, only one part of the iron defecated can

554 benefit to phytoplankton productivity. Indeed, iron can take different chemical forms and many factors

555 influence its bioavailability (dissolved or particulate form, degree of oxidation, complexation with

556 organic ligands). Iron in dissolved form (< 0.2 μm) is generally considered to be the most bioavailable

557 fraction [81]. More than 87% of the iron in whale faeces is in particulate form (> 0.2 μm) [41]. However,

558 particulate iron can dissolve over time and become more bioavailable. The proportion of bioavailable

559 iron in whale faeces was estimated to be 12.2% after 12 hours based on the results of a dissolution

560 experiment of particulate iron from whale faeces [41]. This rate was used to obtain the amount of

561 bioavailable iron released by whales in the euphotic zone.

562 The iron provided to the sea surface by the whales stimulates phytoplankton growth. However, not all

563 of the fixed carbon is sequestered in the deep sea because a part is rapidly remineralised. Several

564 studies have measured the amount of carbon sequestered in response to natural iron input in the

565 euphotic zone [33,82]. Lavery et al. [13] use the average molar ratio between the additional carbon

566 sequestered at 200 metres and the additional dissolved iron from two natural enrichment studies [33,82]:

567
$$\frac{C_{exported}}{DFe_{additional}} = 5.10^4 \; mol.\,mol^{-1} \tag{14}$$

568 Knowing the molar mass of iron (55.8 in g/mol), carbon (12 in g/mol) and the mass of iron (m_{iron} in g),

569 the additional amount of sequestered carbon (m_{carbon} in g) is written as:

570
$$m_{carbon} = \frac{12.\,m_{iron}}{55,8}\frac{C_{exported}}{DFe_{additional}} \tag{15}$$

571

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Figure legends

Figure 1. The two main ways of carbon sequestration in the deep ocean by baleen whales. Directly through the sinking of their carcasses (a) and indirectly through the fertilization of the ocean by nutrients in faeces and the sinking of resulting surplus of phytoplankton (b).

Figure 2: Amount of carbon sequestered annually in the deep Southern Ocean by baleen whales. Via the pathway of whale carcasses (a) and the pathway of phytoplankton fertilization (b) for each whale species and all together at the pre-exploitation level with associated uncertainty. On the top right, the relative contribution of each species. Errors bars represent high and low estimations for carbon sequestration.

Figure 3: Dynamics of carbon sequestration generated by the five baleen whale species. Via the two pathways (carcasses and fertilization) between 1890 and 2100 without climate change (a) and with climate change (b). Above the curves the species with the highest contribution to the total sequestration is represented. Vertical bars represent the switch between two major contributing species. Shaded areas represent the high and low estimations for carbon sequestration.


Figure 4: Cumulative carbon sequestration deficit from 1890 to 2100 in the deep Southern Ocean by baleen whales. The total amount of non-sequestered carbon is compared to the pre-exploitation levels of whale populations, without climate change (a) and with climate change (b). Cumulative carbon sequestration deficit for each species without climate change (C) and with climate change (D). Shaded areas represent the high and low estimations for carbon deficit.
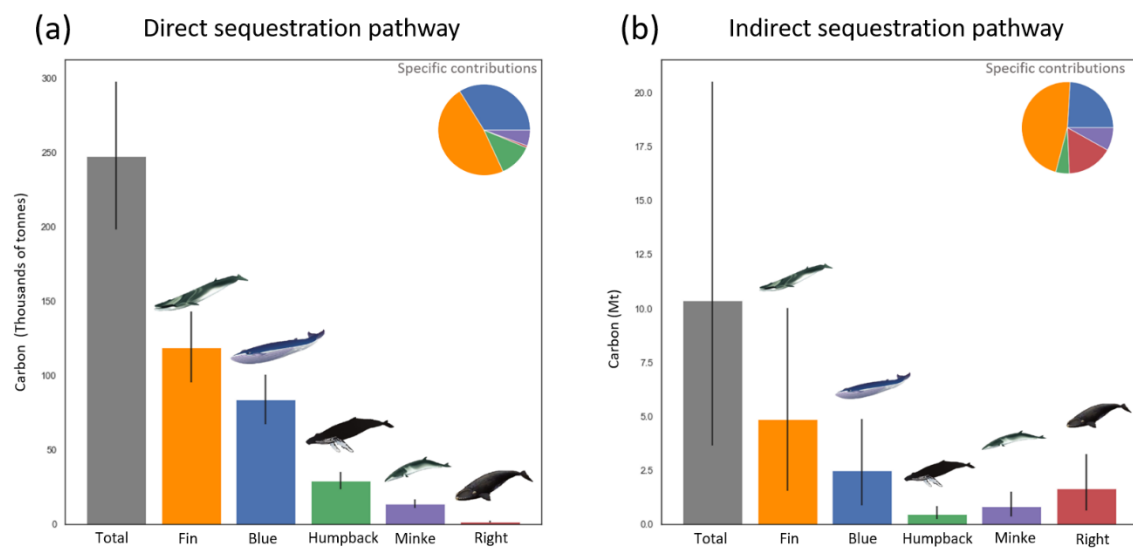
766 **Figures**

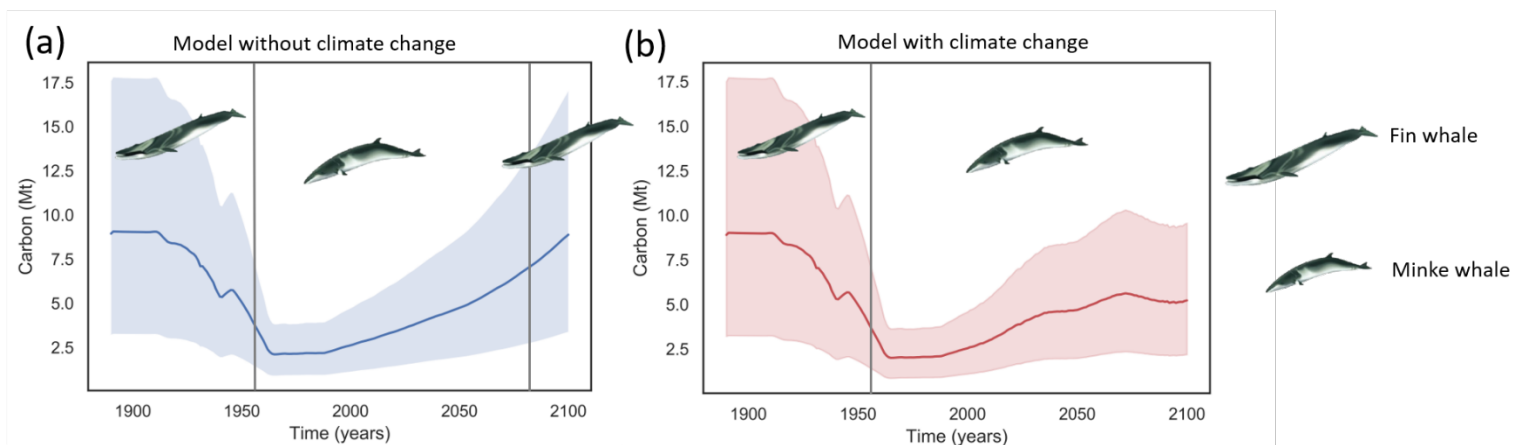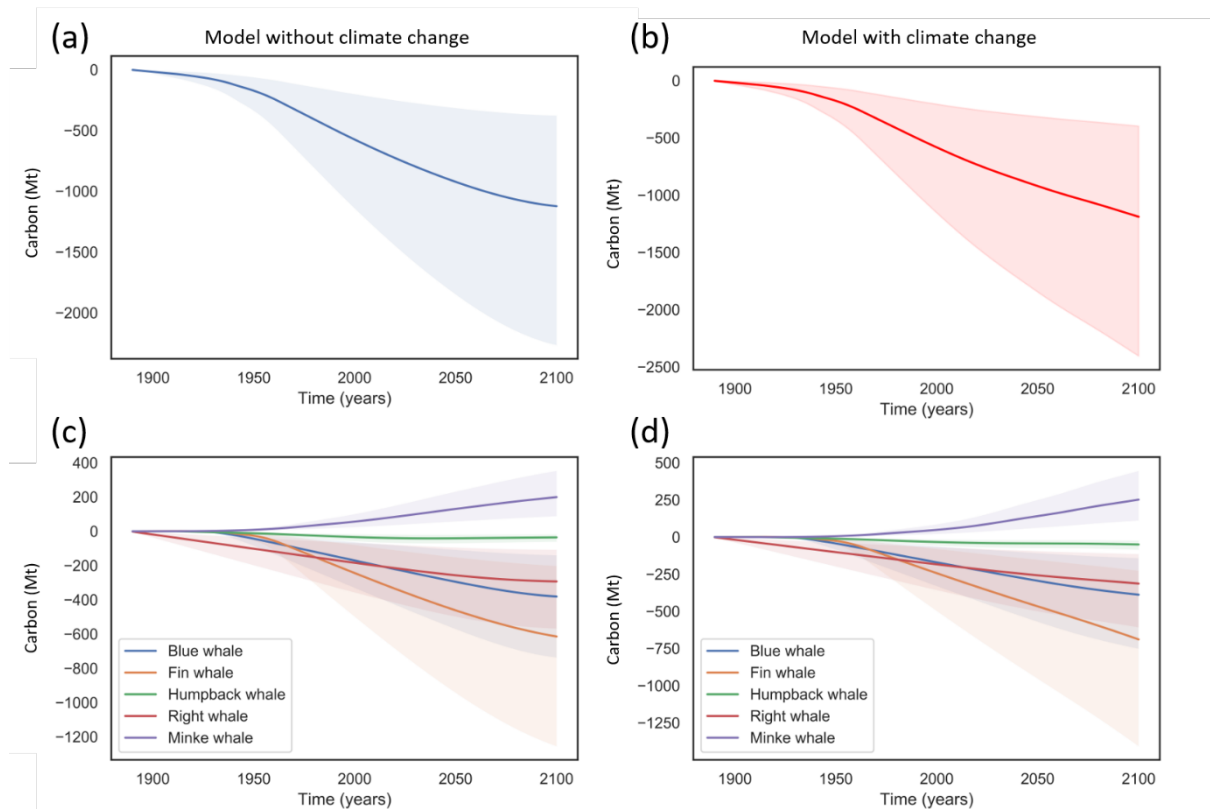767

768 Figure 1
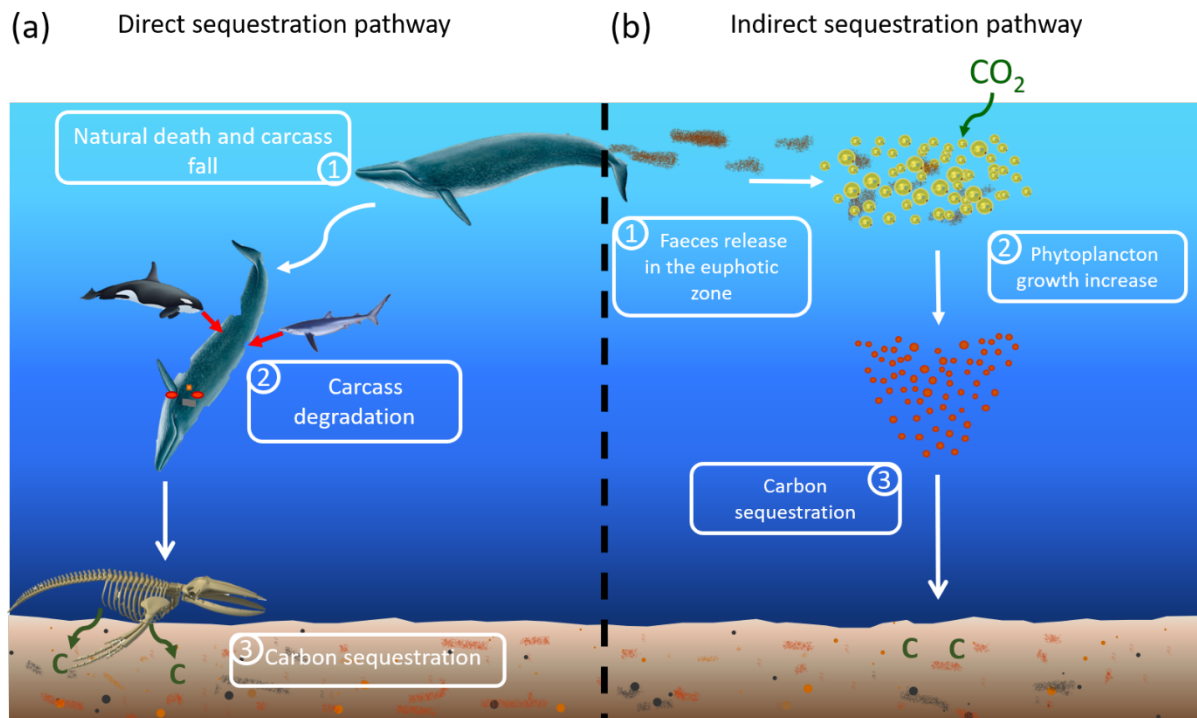
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