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## Recovery of carbon benefits by overharvested baleen whale populations is threatened by climate change

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## 48 **Abstract**

49 Despite the importance of marine megafauna on ecosystem functioning, their contribution to the  
50 oceanic carbon cycle is still poorly known. Here, we explored the role of baleen whales in the  
51 biological carbon pump across the southern hemisphere based on the historical and forecasted  
52 abundance of five baleen whale species. We modelled whale-mediated carbon sequestration  
53 through the sinking of their carcasses after natural death. We provide the first temporal dynamics of  
54 this carbon pump from 1890 to 2100, considering both the effects of exploitation and climate change  
55 on whale populations. We reveal that at their pre-exploitation abundance, the five species of  
56 southern whales could sequester  $4.0 \times 10^5$  tonnes of carbon per year ( $\text{tC.yr}^{-1}$ ). This estimate dropped  
57 to  $0.6 \times 10^5$   $\text{tC.yr}^{-1}$  by 1972 following commercial whaling. However, with projected restoration of  
58 whale populations under a RCP8.5 climate scenario, the sequestration would reach  $1.7 \times 10^5$   $\text{tC.yr}^{-1}$  by  
59 2100, while without climate change, recovered whale populations could sequester nearly twice as  
60 much ( $3.2 \times 10^5$   $\text{tC.yr}^{-1}$ ) by 2100. This highlights the persistence of whaling damages on whale  
61 populations and associated services as well as the predicted harmful impacts of climate change on  
62 whale ecosystem services.

63

## 64 **Introduction**

65 The concentration of atmospheric carbon dioxide has dramatically increased since the beginning of  
66 the industrial era, from about 277 parts per million in 1750 to over 412 ppm today (1). The rise of this  
67 greenhouse gas in the atmosphere is changing the climate with a range of damaging consequences  
68 for ecosystems and human societies (2). Since the Paris agreement in 2015, the international  
69 community set the objective of containing the global warming below  $+2\text{C}^\circ$  compared to pre-industrial  
70 levels (3).

71 The ocean is a primarily regulator of the climate system, absorbing about 23% of anthropogenic  $\text{CO}_2$   
72 emissions (1) and maintaining a primary production equivalent to that of terrestrial ecosystems (4).  
73 In that context, particular attention has been given to understand the drivers of the biological carbon  
74 pump and its sequestration potential. Indeed, the open ocean's capacity to sequester carbon mainly  
75 relies on the export of organic carbon particles (dead organic matter, faeces) at depth where they  
76 can be sequestered for decades, centuries or even longer before returning to surface waters (5).

77 While the contribution of lower trophic levels (essentially phytoplankton and zooplankton) to the  
78 biological pump has been well explored for decades (6), the role of large vertebrates (fish and  
79 mammals) on ocean biogeochemistry and their ability to sequester carbon has been garnering  
80 increasing research attention (7–9). Indeed, some of these species, such as whales, are the largest of  
81 all time, thus storing vast amounts of carbon throughout their lifetime which can be exported in the  
82 deep ocean after their natural death (10). When reaching the seafloor, whales' carcasses can be

83 consumed by the abyssal fauna and sustain local food web or be buried in the sediments, being  
84 trapped for centuries to millennia (11,12) (Figure 1). Therefore, whales generate carbon  
85 sequestration i.e., long-term ( $\geq 100$  years) carbon removal from the atmosphere.

86 Yet, whale populations have been dramatically reduced by historical whaling. The majority of this  
87 defaunation occurred in the 20<sup>th</sup> century with some populations reduced by >99%, like the southern  
88 right (*Eubalaena australis*) and Antarctic blue whales (*Balaenoptera musculus intermedia*) (13). Since  
89 1986, they have been protected from commercial whaling by an international moratorium of the  
90 International Whaling Commission (IWC). However, their recovery is now imperilled by climate  
91 change via the reduction of prey abundance, increased extreme climate events (El Niños and  
92 heatwaves) and disease spread (14–16). While the dynamics of these populations have already been  
93 modelled (14,17), the influence of whaling and then of protection on the carbon sequestration  
94 mediated by these marine mammals remains poorly understood and unquantified. Thus, the long-  
95 term dynamics of whale mediated carbon sequestration in the southern hemisphere need to be  
96 assessed accounting for both past whaling and various future climate scenarios. Here, we quantified  
97 the role of whales in carbon sequestration through carcasses sinking using historical and forecasted  
98 whale abundance estimates under two climate scenarios.

99

## 100 **Materials and Methods**

### 101 **Modelling of whale population dynamics**

102 We used population dynamics for five southern baleen whales that have been recently modelled  
103 (14,17) as inputs for our carbon sequestration assessment. This is a Southern Hemisphere spatial  
104 ‘Model of Intermediate Complexity for Ecosystem Assessments’ (MICE) that estimates whale  
105 population sizes from 1890 to 2100. Whale abundances were estimated based on both the dynamics  
106 of their prey (Antarctic krill *Euphausia superba* and copepods; bottom-up process) and catches  
107 (whaling; top-down pressure). To account for the effects of climate change, we used two MICE model  
108 outputs. In the first version, whale population dynamics were not coupled to changing climate  
109 conditions which were assumed to remain constant from 1890 to 2100. The second model integrates  
110 the impacts of climate change according to the RCP 8.5 ("business as usual") scenario, on krill and  
111 copepod prey availability. See supplementary materials for more information on the population  
112 model assumptions and outputs.

113

### 114 **The age-structure of the population**

115 As carbon sequestration depends on whales’ body mass, we derived the age structure of each  
116 species population from the outputs of the MICE model. The age structure of the population in a  
117 given year, i.e., the number of individuals in a given age class, was constructed using demographic

118 parameters for each species derived from the MICE models (Supplementary Table 1). Whale  
 119 population abundances provided by the MICE models correspond to mature females only. To obtain  
 120 the total number, the number of males ( $E_{male}$ ) was estimated from the number of females ( $E_{female}$ ) and  
 121 the sex ratio ( $q$ ):

$$123 \quad E_{tot} = E_{female} + E_{male} \quad ; \quad E_{female} = q \cdot E_{tot} \quad ; \quad E_{male} = (1 - q) \cdot E_{tot} \quad \Rightarrow \quad E_{male} = \frac{(1-q)}{q} \cdot E_{female} \quad (1)$$

127 For each sex, the number of individuals ( $N$ ) in each age class ( $a$ ) between birth and maximum age ( $z$ )  
 128 was then calculated from the number ( $E$ ) of adult individuals between the age of maturity ( $T$ ) and  
 129 maximum age ( $z$ ) and the survival rate ( $S$  or  $S_{juv}$ ). A distinction was made between the survival rate of  
 130 individuals under one year old ( $S_{juv}$ ) and that of individuals over one-year old ( $S$ ). These rates were  
 131 species-specific (Supplementary Table 1), considered constant and identical for males and females.  
 132 The number of individuals of a given year class (individuals aged  $a$ ) is thus written as a function of the  
 number of individuals aged  $T$ :

$$133 \quad \forall a \in ]0, z] \quad N_{a+1} = S \cdot N_a \quad \Rightarrow \quad N_a = S^{a-T} \cdot N_T \quad ; \quad \text{For } a = 0, \quad N_0 = S_{juv}^{-1} \cdot S^{1-T} \cdot N_T \quad (2)$$

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

$$136 \quad \sum_{a=T}^z N_a = E \quad \Rightarrow \quad N_T \cdot \sum_{a=T}^z S^{a-T} = E \quad \Rightarrow \quad N_T = \frac{E}{\sum_{a=T}^z S^{a-T}} \quad (3)$$

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

$$139 \quad N_0 = S_{juv}^{-1} \cdot S^{1-T} \cdot N_T \quad ; \quad N_1 = S^{1-T} \cdot N_T \quad \dots \quad N_{T-1} = S^{-1} \cdot N_T \quad ; \quad N_T \quad ; \quad N_{T+1} = S \cdot N_T \quad \dots \quad N_z = S^{z-T} \cdot N_T \quad (4)$$

### 141 **The whale mortality and biomass**

142 We applied this age structure every year from 1890 to 2100 in order to calculate the number of dying  
 143 individuals and their biomass within each age class. We assumed that age structure did not vary over  
 144 time. Indeed, the body mass of individuals is almost constant in adulthood so we considered that no  
 145 adult year class is more impacted by whaling than another. Among juveniles, very few catches have  
 146 been reported for the whale species of this study (18).

147 First, in order to calculate the number of individuals dying naturally each year, the natural mortality  
 148 rate ( $1-S$  or  $1-S_{juv}$ ) was applied to each age class (Supplementary Table 1).

149 Secondly, to obtain the biomass of an age class, the number of individuals in this class was multiplied  
 150 by the corresponding individual body mass. The biomass of individuals at each age follows the Von

151 Bertalanffy equation, whose parameters, depend on both species and sex (10) (Supplementary Table  
152 1). Let  $a$  the age,  $m_{inf}$  the maximum size of individuals,  $k$  the growth rate and  $a_0$  the theoretical age at  
153 which the mass is zero, the mass  $m$  of an individual aged  $a$  is:

$$154 \quad m(a) = m_{inf}(1 - e^{-k(a-a_0)}) \quad (5)$$

155 Then, the total population biomass ( $B_{tot}$ ) was calculated from the biomass of each age class ( $B_a$ ) as  
156 follows:

$$157 \quad B_{tot} = \sum_{a=0}^z B_a \quad \text{with } B_a = m_{female}(a) \cdot N_{female,a} + m_{male}(a) \cdot N_{male,a} \quad (6)$$

158  
159 Finally, to assess the amount of carbon sequestered by sinking whales' carcasses, the biomass was  
160 converted into carbon mass. A previous study assumed a total body carbon content for dolphins of  
161 25% (wet weight) (19) based on estimates on humans (20). A lower estimation of 15% (wet weight)  
162 was found assuming 70% of water content and 50% of carbon in the dry weight (21). We used these  
163 15%, 25% and 20% as lower, upper and mean estimate of the carbon content in the whale biomass,  
164 respectively. We assumed that the carbon content is identical for all individuals without distinction of  
165 species, sex or age.

## 166 **Carbon sequestration**

167 To estimate the amount of carbon sequestered via whale carcasses sinking into the deep ocean (i.e.,  
168 deadfall carbon), we estimated the proportion of carcasses that reaches the deep sea. Indeed, the  
169 fate of the carcasses depends on several factors. We assume that most adult individuals dies of  
170 senescence or disease since attacks by predators such as killer whales (*Orcinus orca*) are thought to  
171 be rarely lethal, especially on adults (22,23). However, carcasses do not sink in their entirety to the  
172 ocean floor because they are partly consumed by scavengers like sharks (24) or killer whales (25) or  
173 degraded by microorganisms (26). We used a conservative estimate of 50% (27) for all species except  
174 for southern right whales, for which we considered that only 10% of carcass biomass reaches the  
175 deep sea because of their high proportion of blubber making them float after death (10). We  
176 considered that whales' dead tissues reaching the seafloor before degradation (remineralisation) are  
177 sequestered (5).

178

179

180

## 181 **Results**

### 182 **Carbon sequestration prior to commercial whaling**

183 We first investigated the ability of the five baleen whale species to sequester carbon when they were  
184 at their pre-exploitation abundance. Dead whales represented each year a biomass of almost 4

185 million tonnes. The sinking of their carcasses generated a flux of  $4.0 \times 10^5$  (range:  $3.0 \times 10^5 - 5.0 \times 10^5$ )  
186 tonnes of carbon per year ( $\text{tC.yr}^{-1}$ ) towards the deep sea (Figure 2). However, all species did not  
187 contribute equally to this total carbon flux. Fin and blue whales contributed to 48% and 34%,  
188 respectively (Figure 2). The other three species had a marginal contribution, particularly the southern  
189 right whales, which accounted for only 0.7% of the total carbon flux.

190

### 191 **Carbon sequestration dynamics from 1890 to 2100**

192 We then predicted carbon sequestration dynamics from 1890 to 2100 under two climate change  
193 scenarios, both accounting for historical whaling. A stable phase from 1890 to 1912 was followed by  
194 a sharp drop in the amount of carbon sequestered over the exploitation period (Figure 3a and 3b). All  
195 species experienced a severe population decline, particularly the main sequestration contributors, fin  
196 and blue whales, which were reduced to approximately 3% and 0.5% of their pre-exploitation  
197 abundance, respectively (Figure 3c and 3d). As a result, carbon sequestration dropped to a minimum  
198 of  $0.6 \times 10^5 \text{ tC.yr}^{-1}$  (range:  $0.4 \times 10^5$  and  $0.7 \times 10^5 \text{ tC.yr}^{-1}$ ) in 1972, so only 15% of the pre-exploitation  
199 level.

200 In the model without climate change, carbon sequestration would reach  $3.2 \times 10^5 \text{ tC.yr}^{-1}$  (range:  
201  $2.4 \times 10^5$  and  $4.0 \times 10^5 \text{ tC.yr}^{-1}$ ) in 2100, so 80% of the sequestration potential before the whaling period.

202 This recovery is mainly due to the predicted increase of Antarctic minke whales and the recovery,  
203 albeit slower, of all other species (Figure S3). In the model including the effects of climate change,  
204 only the Antarctic minke whale would reach their pre-exploitation population size and their  
205 sequestration potential before the end of the 21<sup>st</sup> century (Figure S3). Under this scenario, the whale  
206 mediated carbon sequestration via carcasses sinking would reach  $1.7 \times 10^5 \text{ tC.yr}^{-1}$  (range:  $1.3 \times 10^5 -$   
207  $2.1 \times 10^5 \text{ tC.yr}^{-1}$ ) in 2100, so less than half of the pre-exploitation level, with Antarctic minke whales  
208 accounting for 47% of the total flux, against 5.6% before whaling. In both climate scenarios, fin  
209 whales were the major contributors until 1961. While large whales (mainly fin whales and blue  
210 whales) recover in the scenario without climate change and overcome the contribution of minke  
211 whales, the latter remain the main contributor until the end of the century in the scenario with  
212 climate change.

213 Finally, we showed that harmful consequences of whaling persist for many years after its end. By  
214 dramatically reducing population levels of the largest species, over-exploitation has created a carbon  
215 sequestration deficit. It represents the amount of carbon that has not been sequestered because of  
216 whaling compared to what would have been sequestered with whales' populations at their pre-  
217 exploitation levels. We calculated that from 1890 to 2100, the carbon sequestration deficit caused by

218 whaling is on average  $41.9 \times 10^6$  tC and  $45.2 \times 10^6$  tC without and with climate change respectively  
219 (Figure 4a and 4b).

220

## 221 **Discussion**

### 222 **The role of whales in the carbon cycle and carbon sequestration**

223 Although our estimates are accompanied by a wide range of uncertainty, we showed that whales – as  
224 massive and fast-sinking organisms - efficiently sequester carbon after natural death. Through this  
225 process, they trap carbon away from the atmosphere for centuries to millennia, helping to mitigate  
226 climate change. However, the annual sequestration capacity of whales in the southern hemisphere is  
227 one or two orders of magnitude smaller than sequestration carbon flux estimated on Blue Carbon  
228 Ecosystems (BCE) like mangroves, tidal marshes or seagrasses, sequestering annually  $31.2 - 34.4 \times 10^6$   
229  $\text{tC.yr}^{-1}$ ,  $4.8 - 87.2 \times 10^6 \text{tC.yr}^{-1}$ , and  $41.4 - 82.8 \times 10^6 \text{tC.yr}^{-1}$  on a global scale respectively (28).

230 Nevertheless, whales could play other important roles in the carbon cycle that are less explored.  
231 First, thanks to their longevity and high weight, they store large amounts of organic carbon in their  
232 body-mass throughout their lifetime, that can be up to one century for some species like blue whales  
233 (Figure S1). Secondly, whales have been shown to be efficiently recycle nutrients and boost primary  
234 production (29–32),. Indeed, the Southern Ocean is largely considered to be a High Nutrient Low  
235 Chlorophyll (HNLC) zone, i.e. a zone where macronutrients (nitrogen and phosphorus) concentrations  
236 are high but primary productivity is low (33). Phytoplankton growth is limited by the availability of  
237 trace elements (Fe, Cu, Zn, Co, Cd), especially iron (33) as confirmed by many short-term iron-  
238 addition experiments (34,35). In that context, southern whales play a critical functional role since  
239 they feed mostly on krill which is an iron accumulator (31,36). Thus, they can alleviate the growth  
240 limitation of phytoplankton through the supply of iron-rich faeces. Indeed, whales' faeces are highly  
241 concentrated in iron (whales' faeces iron concentration was estimated by  $145.9 \pm 133.7 \text{ mg.kg}^{-1}$ ,  
242 being approximately ten million times that Antarctic seawater (31)). Plus, they are likely highly  
243 bioavailable as they are liquid and buoyant, remaining in the euphotic zone where whales defecate,  
244 and iron is also excreted with other nutrients, preventing phytoplankton growth from co-limitations  
245 and successive limitations. On the other hand, although krill can also recycle iron, the pool of iron in  
246 krill is probably poorly available for phytoplankton, as krill release most of its iron in dense and fast-  
247 sinking pellets (36). Therefore, whales play this unique role of fertilizer in the Southern Ocean. But  
248 even though they help maintain high levels of primary productivity, whales do not enrich i.e., bring  
249 new iron in the system themselves. Thus, they mainly generate 'regenerated' primary production, as  
250 opposed to 'new' primary production generated by the addition of new nutrients in the system.



251 On the other hand, krill is known to feed a lot in the benthos (37,38), bringing new iron in the system.  
252 Thus, whales and krill could maintain highly productive systems through these processes, potentially  
253 boosting the biological carbon pump and sequestering carbon.

254 As only the new primary production leads to additional carbon fixation by the phytoplankton and  
255 carbon sequestration in the deep ocean (through particles flux toward the depth), it remains difficult  
256 to quantify the fraction of new and regenerated primary production and subsequent carbon  
257 sequestration mediated by whales. Nevertheless, studies showed that krill was more abundant in the  
258 Southern Ocean before whales defaunation (39), indicating that whales and krill were highly  
259 mutualistic. Since krill can export carbon at depth very efficiently through various processes (fast  
260 sinking of faecal pellets, sinking of exuviae (40–42)), we suggest that the pre-whaling ocean  
261 sequestered much more carbon than a megafauna-depauperated ocean. The role of whales in the  
262 carbon cycle, mainly through their indirect role of nutrient cycling represents an avenue for future  
263 research, especially regarding climate change mitigation and potential identification of new Natural  
264 Climate Solutions (NCS). In order to have an exhaustive overview of the impact of whales on the  
265 carbon cycle and their potential as an NCS, we need comprehensive studies that compare the carbon  
266 cycling of the entire food web in the presence or absence of whales.

267

#### 268 **Climate change and whaling footprint on whale mediated carbon sequestration**

269 Although we showed that whales have the ability to sequester non negligible quantities of carbon,  
270 their sequestration capacities have been largely impaired by commercial whaling, with consequences  
271 extending well beyond the exploitation period. Indeed, due to their long-life cycles, the recovery of  
272 whale populations after over-exploitation is a very slow process. Because of over-exploitation, their  
273 carbon sequestration capacity is currently limited in 2022 to  $1.2 \times 10^5 \text{ tC.yr}^{-1}$  ( $0.9 \times 10^5 - 1.4 \times 10^5 \text{ tC.yr}^{-1}$ ),  
274 i.e. 30% of the pre-exploitation level. This has created a sequestration deficit reaching between  $41.9$   
275  $\times 10^6 \text{ tC}$  and  $45.2 \times 10^6 \text{ tC}$  on average in 2100, depending on the climate scenario. In addition to past  
276 whaling, the sequestration capacity of whales is now reduced by climate change. Indeed, the  
277 recovery of whale populations and of the carbon pump may be delayed and weakened by climate  
278 change since carbon sequestration barely reaches half of its historical value in the model with climate  
279 change. This is primarily explained by changes in the abundance and distribution of krill due to  
280 changing primary productivity patterns in the Southern Ocean (14). Furthermore, the distribution of  
281 krill is expected to contract southward due to increasing temperature and reduced sea-ice extent  
282 (43). This is particularly deleterious for whale species predominantly feeding in mid-latitudes areas  
283 (humpback whales, fin whales and southern right whales). Minke whales and blue whales could  
284 benefit from the ice-extent reduction in the Southern Ocean because of their ice-dependency,  
285 assuming they can shift their distribution southwards to follow the krill. However, the higher

286 abundance of minke whales, which have been less exploited, may reduce the prey availability for  
287 other species. Consequently, the MICE model predicts slower recovery for blue whales, decline for  
288 humpback, fin and southern right whales, but rapid population increase for Antarctic minke whales  
289 during the 21<sup>st</sup> century in the scenario with climate change (14). As a result, despite an "explosion" of  
290 minke whale populations, the total carbon flux would not return to its pre-exploitation level due to  
291 the negative impact of climate change on other species. A negative feedback loop between climate  
292 change and whale populations could therefore occur in the southern hemisphere.

293 On the other hand, thanks to their rapid increase, Antarctic minke whales can maintain, at least  
294 partially, the carbon sink and limit the carbon sequestration deficit due to over-exploitation. Their  
295 increase throughout the 21<sup>st</sup> century is a key resilience factor since they allow a faster recovery of  
296 carbon flux towards its historical value. The asynchrony between the different population dynamics  
297 enable the overall carbon sequestration of the whale community to be more resilient, thus exhibiting  
298 a positive relationship between diversity and stability under the portfolio effect (44).

299

### 300 **Restoration of whales and the associated carbon pump**

301 Even though whales are vulnerable to climate change, primarily through the decrease in krill prey  
302 density and southward contraction of geographic distributions (43), their restoration could be  
303 promoted by mitigating current threats. In addition to the moratorium established in 1986 by the  
304 International Whaling Commission (IWC) that protects whales from commercial exploitation,  
305 restriction on maritime routes, fishing zones and authorised speed of boats can reduce the mortality  
306 and low reproduction rates associated with ship strikes and noise generated by boats. Promoting  
307 sustainable exploitation of krill, the whales' primary prey in the Southern Ocean, would also preserve  
308 whale populations and their associated carbon sequestration. Thus, the protection of both krill and  
309 whales, in particular under the legislation of the CCAMLR, would help maintain whales' population  
310 and associated carbon sequestration.

311 Although our study does not account for the spatial distribution of whales, and thus, cannot map the  
312 associated carbon flux toward the depth, conservation strategies should be determined regarding  
313 their feeding, breeding grounds and migratory routes. Coupling tracking studies and assessment of  
314 the whales mediated services like carbon sequestration could help identify areas of ecological  
315 importance and inform policies in the design of protected areas (45). This would be especially  
316 relevant for fin whales and blue whales that were the main contributors to the carbon sequestration  
317 in the past, and that are currently categorised as 'vulnerable' and 'threatened' by the IUCN (see  
318 Figure S1).

319

### 320 **Limits and uncertainties**

321 While our estimations are subject to several uncertainties, we adopted a conservative approach.  
322 First, our study is restricted to five baleen species in the southern hemisphere, whereas there are  
323 fifteen species of baleen whales globally. We considered here only baleen whales that were included  
324 in the MICE models (14,17), i.e. species commercially exploited in Antarctic waters, in most cases  
325 feeding predominantly on Antarctic krill and for which enough survey data were available. Therefore,  
326 our study may significantly underestimate the importance of carbon sequestration mediated by  
327 whales at global scale by excluding other southern species (Bryde's whale, Pygmy right whale and  
328 Dwarf Antarctic minke whale), northern species (bowhead whale, gray whale, omuras whale,  
329 northern right whale) and toothed whales.

330 We used the most updated population dynamics and converted the number of individuals of each  
331 species accounting for sex and age variability in the body-mass. However, we ignored seasonal  
332 variations in body mass. Indeed, these migratory species experience significant weight variations  
333 during the year (46): they may gain several tonnes during the summer and be considerably thinner at  
334 the end of the breeding season. The amount of carbon sequestered therefore depends on the  
335 seasonality of natural mortality, which is not taken into account in our study.

336 Additionally, a main limitation in our study is the lack of empirical data on several processes. Indeed,  
337 carbon content in whale's tissues and the proportion of biomass reaching the deep ocean have not  
338 been experimentally measured on large whales. First, we used the same carbon content in whale's  
339 tissues for each species, ignoring the inter-specific variability. Secondly, it was assumed that the  
340 biomass-carbon conversion does not change with carcass degradation. However, not all tissues have  
341 the same carbon concentration (47) and some (fat tissue, muscle) may be consumed primarily by  
342 scavengers (48). In order to gain precision, it seems essential to determine the carbon level in the  
343 different types of tissue (bone, muscle, blubber, viscera) for each species. Finally, the proportion of  
344 biomass reaching the deep ocean before being consumed or remineralised is uncertain and probably  
345 highly variable (depending on the presence of scavengers or currents, for example). The estimates  
346 we used are conservative, thus we provide a lower-bound of the potential whale-mediated carbon  
347 sequestration. Data collection on these crucial processes is therefore needed to refine our estimates.

348

## 349 **Conclusion**

350 We showed that despite efficient carbon sequestration capacities at their pre-exploitation levels,  
351 whale mediated carbon sequestration has dramatically dropped because of commercial whaling and  
352 will be far from complete recovery by the end of the century as a result of climate change. Therefore,  
353 our results call for protection and restoration of whale populations as a potential Blue Carbon  
354 Ecosystem (BCE) providing opportunities for climate change mitigation (49–51). Indeed, further  
355 research should refine the quantification of their carbon sequestration potential and explore other

356 sequestration pathways, especially those mediated by bottom-up processes like nutrient cycling.  
357 Further identifying and quantifying the carbon sequestration capacities of marine vertebrates in  
358 general would provide additional evidence to support the protection of 30% of the oceans by 2030, a  
359 new target proposed to the United Nations (52). In the case of whales, protection should be designed  
360 as a meaningful assemblage including feeding and breeding grounds and migratory routes (45). In  
361 this way, restoring marine vertebrates could contribute to achieve our climate objectives while  
362 generating other services beneficial to the functioning of the biosphere and the well-being of human  
363 societies (53,54).

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528 **Figure legends**

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530 Figure 1. Conceptual diagram of the carbon sequestration mediated by baleen whales. (1) After  
531 natural death, the carcasses start sinking. (2) They can be partially consumed by scavengers like killer  
532 whales and sharks as well as degraded by microorganisms. Once a carcass has reached the seafloor,  
533 the organic carbon in tissues can be (3a) consumed and respired at depth by local abyssal fauna (like  
534 zoarcidae) and microorganisms. Once respired, the inorganic carbon can be brought back to the  
535 surface water and outgassed into the atmosphere on a time scale from centuries to thousands of  
536 years depending on the depth and the water circulation (5). Or (3b) it can be buried in the sediments  
537 where it can be trapped on longer time scales, up to millennia (12).

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540 Figure 2: Amount of carbon sequestered annually by each whale specie and for all the five species  
541 together (total) at their pre-exploitation levels through the sinking of the carcasses. On the top right,  
542 the relative contribution of each species. Errors bars represent high and low estimations for carbon  
543 sequestration given parameter uncertainties.

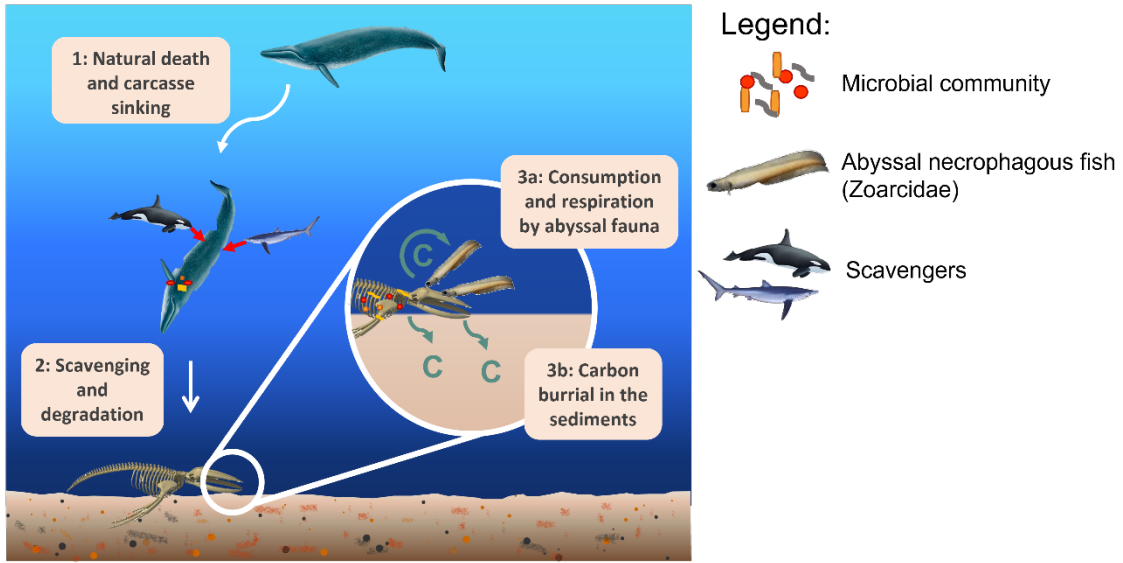


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Figure 3: Dynamics of carbon sequestration mediated by the five baleen whale species between 1890 and 2100 without climate change (a and c) and with climate change (b and d). Panels (a) and (b) represent the total sequestration by the five whale species. Panels (c) and (d) represent the sequestration dynamic for each species. Shaded areas represent the high and low estimations of carbon sequestration given parameter uncertainties.

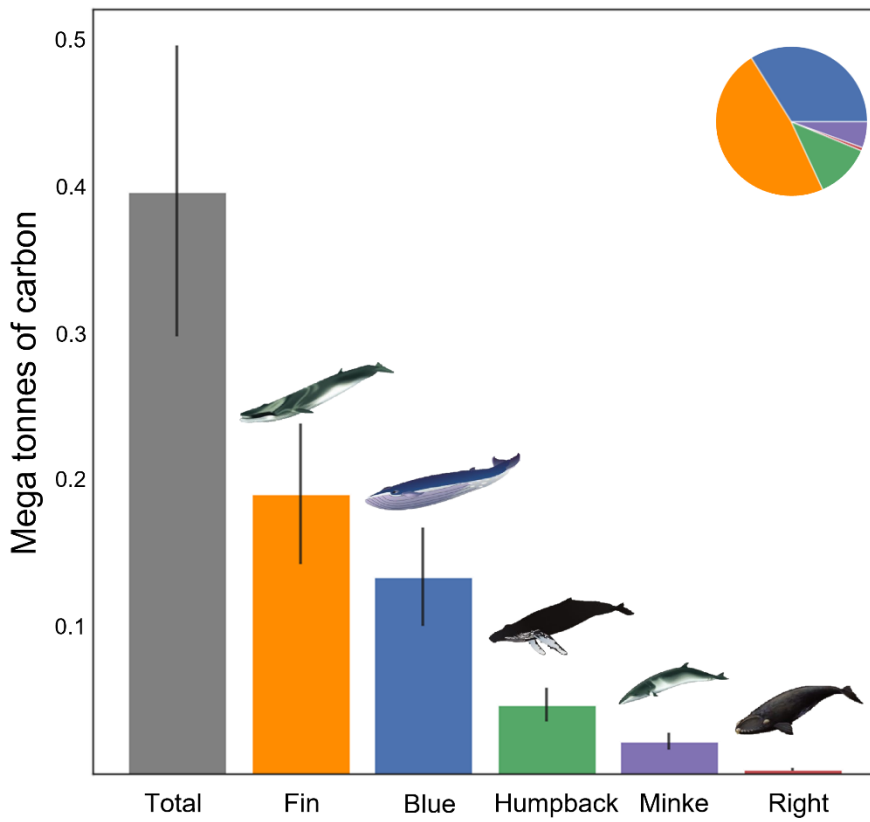
Figure 4: Cumulative carbon sequestration deficit from 1890 to 2100 without climate change (a) and with climate change (b). For each year, the total amount of non-sequestered carbon is compared to that corresponding to the pre-exploitation levels of whale populations. Shaded areas represent the high and low estimations for carbon deficit given parameter uncertainties.

**Figures**  
Figure 1



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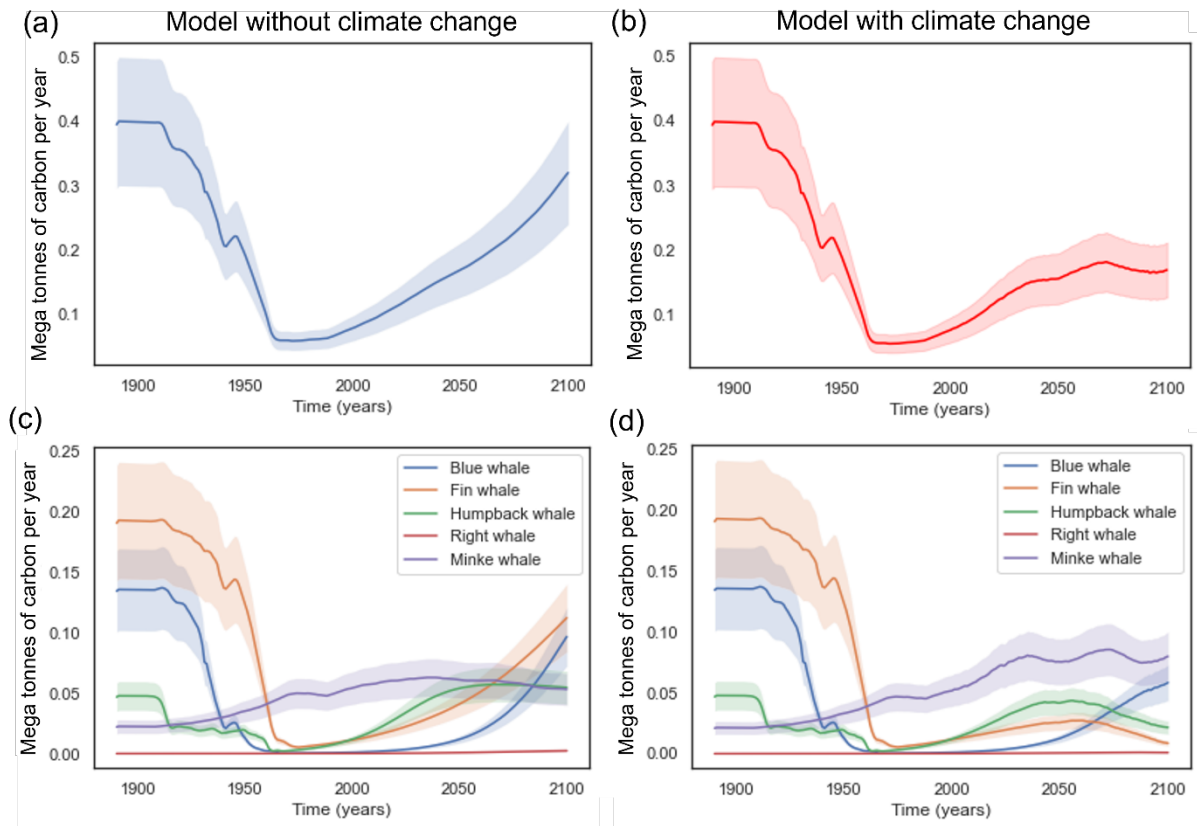
Figure 2



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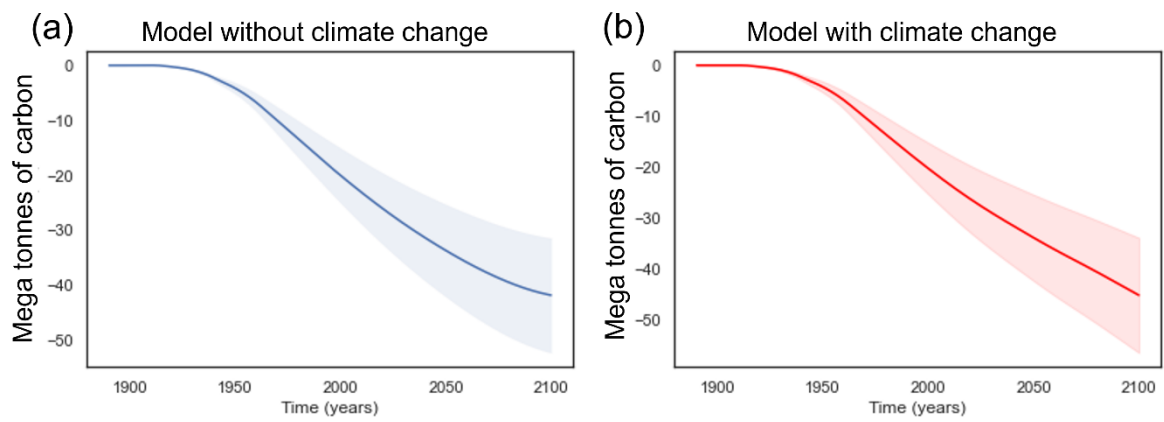
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Figure 3



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Figure 4



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