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

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Abstract :

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

Keywords : blue carbon, modelling, whaling, climate change scenarios, whales fall, deadfall carbon

Introduction

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

The ocean is a primarily regulator of the climate system, absorbing about 23% of anthropogenic CO_2 emissions (1) and maintaining a primary production equivalent to that of terrestrial ecosystems (4). In that context, particular attention has been given to understand the drivers of the biological carbon pump and its sequestration potential. Indeed, the open ocean's capacity to sequester carbon mainly relies on the export of organic carbon particles (dead organic matter, faeces) at depth where they can be sequestered for decades, centuries or even longer before returning to surface waters (5).

While the contribution of lower trophic levels (essentially phytoplankton and zooplankton) to the biological pump has been well explored for decades (6), the role of large vertebrates (fish and mammals) on ocean biogeochemistry and their ability to sequester carbon has been garnering increasing research attention (7–9). Indeed, some of these species, such as whales, are the largest of all time, thus storing vast amounts of carbon throughout their lifetime which can be exported in the deep ocean after their natural death (10). When reaching the seafloor, whales' carcasses can be consumed by the abyssal fauna and sustain local food web or be buried in the sediments, being trapped for centuries to millennia (11,12) (Figure 1). Therefore, whales generate carbon sequestration i.e., long-term (≥ 100 years) carbon removal from the atmosphere.

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

Materials and Methods

Modelling of whale population dynamics

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

The age-structure of the population

As carbon sequestration depends on whales' body mass, we derived the age structure of each species population from the outputs of the MICE model. The age structure of the population in a given year, i.e., the number of individuals in a given age class, was constructed using demographic parameters for each species derived from the MICE models (Supplementary Table 1). Whale population abundances provided by the MICE models correspond to mature females only. To obtain the total number, the number of males (E_{male}) was estimated from the number of females (E_{female}) and the sex ratio (q):

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

For each sex, the number of individuals (N) in each age class (a) between birth and maximum age (z) was then calculated from the number (E) of adult individuals between the age of maturity (T) and maximum age (z) and the survival rate (S or S_{juv}). A distinction was made between the survival rate of individuals under one year old (S_{juv}) and that of individuals over one-year old (S). These rates were species-specific (Supplementary Table 1)*,* considered constant and identical for males and females. 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:

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

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

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

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

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

The whale mortality and biomass

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

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

Secondly, to obtain the biomass of an age class, the number of individuals in this class was multiplied by the corresponding individual body mass. The biomass of individuals at each age follows the Von Bertalanffy equation, whose parameters, depend on both species and sex (10) (Supplementary Table 1). Let a the age, m_{inf} the maximum size of individuals, k the growth rate and a_0 the theoretical age at which the mass is zero, the mass m of an individual aged a is:

$$(5)$$

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

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

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

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

Carbon sequestration

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

Results

Carbon sequestration prior to commercial whaling

We first investigated the ability of the five baleen whale species to sequester carbon when they were at their pre-exploitation abundance. Dead whales represented each year a biomass of almost 4 million tonnes. The sinking of their carcasses generated a flux of 4.0×10^5 (range: $3.0 \times 10^5 - 5.0 \times 10^5$) tonnes of carbon per year ($tC.yr^{-1}$) towards the deep sea (Figure 2). However, all species did not contribute equally to this total carbon flux. Fin and blue whales contributed to 48% and 34%, respectively (Figure 2). The other three species had a marginal contribution, particularly the southern right whales, which accounted for only 0.7% of the total carbon flux.

Carbon sequestration dynamics from 1890 to 2100

We then predicted carbon sequestration dynamics from 1890 to 2100 under two climate change scenarios, both accounting for historical whaling. A stable phase from 1890 to 1912 was followed by a sharp drop in the amount of carbon sequestered over the exploitation period (Figure 3a and 3b). All species experienced a severe population decline, particularly the main sequestration contributors, fin and blue whales, which were reduced to approximately 3% and 0.5% of their pre-exploitation abundance, respectively (Figure 3c and 3d). As a result, carbon sequestration dropped to a minimum of 0.6×10^5 $tC.yr^{-1}$ (range: 0.4×10^5 and 0.7×10^5 $tC.yr^{-1}$) in 1972, so only 15% of the pre-exploitation level. In the model without climate change, carbon sequestration would reach 3.2×10^5 $tC.yr^{-1}$ (range: 2.4×10^5 and 4.0×10^5 $tC.yr^{-1}$) in 2100, so 80% of the sequestration potential before the whaling period. This recovery is mainly due to the predicted increase of Antarctic minke whales and the recovery, albeit slower, of all other species (Figure S3). In the model including the effects of climate change, only the

Antarctic minke whale would reach their pre-exploitation population size and their sequestration potential before the end of the 21st century (Figure S3). Under this scenario, the whale mediated carbon sequestration via carcasses sinking would reach 1.7×10^5 tC.yr^{-1} (range: $1.3 \times 10^5 - 2.1 \times 10^5$ tC.yr^{-1}) in 2100, so less than half of the pre-exploitation level, with Antarctic minke whales accounting for 47% of the total flux, against 5.6% before whaling. In both climate scenarios, fin whales were the major contributors until 1961. While large whales (mainly fin whales and blue whales) recover in the scenario without climate change and overcome the contribution of minke whales, the latter remain the main contributor until the end of the century in the scenario with climate change.

Finally, we showed that harmful consequences of whaling persist for many years after its end. By dramatically reducing population levels of the largest species, over-exploitation has created a carbon sequestration deficit. It represents the amount of carbon that has not been sequestered because of whaling compared to what would have been sequestered with whales' populations at their pre-exploitation levels. We calculated that from 1890 to 2100, the carbon sequestration deficit caused by whaling is on average 41.9×10^6 tC and 45.2×10^6 tC without and with climate change respectively (Figure 4a and 4b).

Discussion

The role of whales in the carbon cycle and carbon sequestration

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

Nevertheless, whales could play other important roles in the carbon cycle that are less explored. First, thanks to their longevity and high weight, they store large amounts of organic carbon in their body-mass throughout their lifetime, that can be up to one century for some species like blue whales (Figure S1). Secondly, whales have been shown to be efficiently recycle nutrients and boost primary production (29–32),. Indeed, the Southern Ocean is largely considered to be a Hight Nutrient Low Chlorophyll (HNLC) zone, i.e. a zone where macronutrients (nitrogen and phosphorus) concentrations are high but primary productivity is low (33). Phytoplankton growth is limited by the availability of trace elements (Fe, Cu, Zn, Co, Cd), especially iron (33) as confirmed by many short-term iron-addition experiments (34,35). In that context, southern whales play a critical functional role since they feed mostly on krill which is an iron accumulator (31,36). Thus, they can alleviate the growth limitation of

phytoplankton through the supply of iron-rich faeces. Indeed, whales' faeces are highly concentrated in iron (whales' faeces iron concentration was estimated by 145.9 ± 133.7 mg.kg^{-1}, being approximately ten million times that Antarctic seawater (31)). Plus, they are likely highly bioavailable as they are liquid and buoyant, remaining in the euphotic zone where whales defecate, and iron is also excreted with other nutrients, preventing phytoplankton growth from co-limitations and successive limitations. On the other hand, although krill can also recycle iron, the pool of iron in krill is probably poorly available for phytoplankton, as krill release most of its iron in dense and fast-sinking pellets (36). Therefore, whales play this unique role of fertilizer in the Southern Ocean. But even though they help maintain high levels of primary productivity, whales do not enrich i.e., bring new iron in the system themselves. Thus, they mainly generate 'regenerated' primary production, as opposed to 'new' primary production generated by the addition of new nutrients in the system.

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

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

Climate change and whaling footprint on whale mediated carbon sequestration

Although we showed that whales have the ability to sequester non negligeable quantities of carbon, their sequestration capacities have been largely impaired by commercial whaling, with consequences extending well beyond the exploitation period. Indeed, due to their long-life cycles, the recovery of whale populations after over-exploitation is a very slow process. Because of over-exploitation, their carbon sequestration capacity is currently limited in 2022 to 1.2×10^5 tC.yr^{-1} ($0.9 \times 10^5 - 1.4 \times 10^5$ tC.yr^{-1}), i.e. 30% of the pre-exploitation level. This has created a sequestration deficit reaching between 41.9

x10^6 tC and 45.2x10^6 tC on average in 2100, depending on the climate scenario. In addition to past whaling, the sequestration capacity of whales is now reduced by climate change. Indeed, the recovery of whale populations and of the carbon pump may be delayed and weakened by climate change since carbon sequestration barely reaches half of its historical value in the model with climate change. This is primarily explained by changes in the abundance and distribution of krill due to changing primary productivity patterns in the Southern Ocean (14). Furthermore, the distribution of krill is expected to contract southward due to increasing temperature and reduced sea-ice extent (43). This is particularly deleterious for whale species predominantly feeding in mid-latitudes areas (humpback whales, fin whales and southern right whales). Minke whales and blue whales could benefit from the ice-extent reduction in the Southern Ocean because of their ice-dependency, assuming they can shift their distribution southwards to follow the krill. However, the higher abundance of minke whales, which have been less exploited, may reduce the prey availability for other species. Consequently, the MICE model predicts slower recovery for blue whales, decline for humpback, fin and southern right whales, but rapid population increase for Antarctic minke whales during the 21st century in the scenario with climate change (14). As a result, despite an "explosion" of 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 change and whale populations could therefore occur in the southern hemisphere.

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

Restoration of whales and the associated carbon pump

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

whales, in particular under the legislation of the CCAMLR, would help maintain whales' population and associated carbon sequestration.

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

Limits and uncertainties

While our estimations are subject to several uncertainties, we adopted a conservative approach. First, our study is restricted to five baleen species in the southern hemisphere, whereas there are fifteen species of baleen whales globally. We considered here only baleen whales that were included in the MICE models (14,17), i.e. species commercially exploited in Antarctic waters, in most cases feeding predominantly on Antarctic krill and for which enough survey data were available. Therefore, our study may significantly underestimate the importance of carbon sequestration mediated by whales 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.

We used the most updated population dynamics and converted the number of individuals of each species accounting for sex and age variability in the body-mass. However, we ignored seasonal variations in body mass. Indeed, these migratory species experience significant weight variations during the year (46): 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.

Additionally, a main limitation in our study is the lack of empirical data on several processes. Indeed, carbon content in whale's tissues and the proportion of biomass reaching the deep ocean have not been experimentally measured on large whales. First, we used the same carbon content in whale's tissues for each species, ignoring the inter-specific variability. Secondly, it was assumed that the biomass-carbon conversion does not change with carcass degradation. However, not all tissues have the same carbon concentration (47) and some (fat tissue, muscle) may be consumed primarily by scavengers (48). 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. Finally, 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). The estimates we used are conservative, thus we provide a lower-bound of the potential whale-mediated carbon sequestration. Data collection on these crucial processes is therefore needed to refine our estimates.

Conclusion

We showed that despite efficient carbon sequestration capacities at their pre-exploitation levels, whale mediated carbon sequestration has dramatically dropped because of commercial whaling and will be far from complete recovery by the end of the century as a result of climate change. Therefore, our results call for protection and restoration of whale populations as a potential Blue Carbon Ecosystem (BCE) providing opportunities for climate change mitigation (49–51). Indeed, further research should refine the quantification of their carbon sequestration potential and explore other sequestration pathways, especially those mediated by bottom-up processes like nutrient cycling. Further identifying and quantifying the carbon sequestration capacities of marine vertebrates in general would provide additional evidence to support the protection of 30% of the oceans by 2030, a new target proposed to the United Nations (52). In the case of whales, protection should be designed as a meaningful assemblage including feeding and breeding grounds and migratory routes (45). In this way, restoring marine vertebrates could contribute to achieve our climate objectives while generating other services beneficial to the functioning of the biosphere and the well-being of human societies (53,54).

References

1.   Friedlingstein P, Jones MW, O'Sullivan M, Andrew RM, Bakker DCE, Hauck J, et al. Global Carbon Budget 2021. Earth System Science Data Discussions. 2021 Nov 4;1–191.

2.   Magnan AK, Pörtner HO, Duvat VKE, Garschagen M, Guinder VA, Zommers Z, et al. Estimating the global risk of anthropogenic climate change. Nat Clim Chang. 2021 Oct;11(10):879–85.

3.   UNFCCC. United Nations Framework Convention on Climate Change, COP 21 Climate Agreement (UNFCCC, Paris). 2015.

4.   Bar-On YM, Milo R. The Biomass Composition of the Oceans: A Blueprint of Our Blue Planet. Cell. 2019 Dec;179(7):1451–4.

5.   Siegel DA, DeVries T, Doney S, Bell T. Assessing the sequestration time scales of some ocean-based carbon dioxide reduction strategies. Environ Res Lett [Internet]. 2021 Jun 16 [cited 2021 Jun 17]; Available from: https://iopscience.iop.org/article/10.1088/1748-9326/ac0be0

6.	Boyd PW, Claustre H, Levy M, Siegel DA, Weber T. Multi-faceted particle pumps drive carbon sequestration in the ocean. Nature. 2019 Apr;568(7752):327–35.

7.	Bianchi D, Carozza DA, Galbraith ED, Guiet J, DeVries T. Estimating global biomass and biogeochemical cycling of marine fish with and without fishing. Science Advances. 2021 Oct;7(41):eabd7554.

8.	Saba GK, Burd AB, Dunne JP, Hernández-León S, Martin AH, Rose KA, et al. Toward a better understanding of fish-based contribution to ocean carbon flux. Limnology and Oceanography. 2021;66(5):1639–64.

9.	Mariani G, Cheung WWL, Lyet A, Sala E, Mayorga J, Velez L, et al. Let more big fish sink: Fisheries prevent blue carbon sequestration—half in unprofitable areas. Science Advances. 2020 Oct 1;6(44):eabb4848.

10.	Pershing AJ, Christensen LB, Record NR, Sherwood GD, Stetson PB. The Impact of Whaling on the Ocean Carbon Cycle: Why Bigger Was Better. Humphries S, editor. PLoS ONE. 2010 Aug 26;5(8):e12444.

11.	Jiao N, Herndl GJ, Hansell DA, Benner R, Kattner G, Wilhelm SW, et al. Microbial production of recalcitrant dissolved organic matter: Long-term carbon storage in the global ocean. Nature reviews Microbiology. 2010 Aug;8(8):593–9.

12.	Bax N, Sands CJ, Gogarty B, Downey RV, Moreau CVE, Moreno B, et al. Perspective: Increasing blue carbon around Antarctica is an ecosystem service of considerable societal and economic value worth protecting. Global Change Biology. 2021;27(1):5–12.

13.	Christensen LB. Marine mammal populations: Reconstructing historical abundances at the global scale. Fisheries Centre. University of British Columbia. Vol. 14. Vancouver; 2006. 161 p.

14.	Tulloch VJD, Plagányi ÉE, Brown C, Richardson AJ, Matear R. Future recovery of baleen whales is imperiled by climate change. Glob Change Biol. 2019 Apr;25(4):1263–81.

15.	Albouy C, Delattre V, Donati G, Frölicher TL, Albouy-Boyer S, Rufino M, et al. Global vulnerability of marine mammals to global warming. Sci Rep. 2020 Dec;10(1):548–60.

16.	Sanderson CE, Alexander KA. Unchartered waters: Climate change likely to intensify infectious disease outbreaks causing mass mortality events in marine mammals. Glob Change Biol. 2020 Jun 18;00(15163):1–18.

17.	Tulloch VJD, Plagányi ÉE, Matear R, Brown CJ, Richardson AJ. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. Fish Fish. 2018 Jan;19(1):117–37.

18.	Allison C. IWC individual and summary catch databases. 135 Station Road, Histon, Cambridge CB30QQ UK: International Whaling Commission; 2013. Report No.: 5.5.

19.	Martin SL, Ballance LT, Groves T. An Ecosystem Services Perspective for the Oceanic Eastern Tropical Pacific: Commercial Fisheries, Carbon Storage, Recreational Fishing,

and Biodiversity. Front Mar Sci [Internet]. 2016 Apr 27 [cited 2020 Jun 26];3. Available from: http://journal.frontiersin.org/Article/10.3389/fmars.2016.00050/abstract

20. Wang Z, Pierson RN. Total body carbon and oxygen masses: evaluation of dual-energy x-ray absorptiometry estimation byin vivoneutron activation analysis. Phys Med Biol. 2010 Sep;55(19):5953–63.

21. Bar-On YM, Phillips R, Milo R. The biomass distribution on Earth. Proc Natl Acad Sci USA. 2018 Jun 19;115(25):6506–11.

22. Jefferson TA, Stacey PJ, Baird RW. A review of Killer Whale interactions with other marine mammals: predation to co-existence. Mamm Rev. 1991 Dec;21(4):151–80.

23. Ford JKB, Reeves RR. Fight or flight: antipredator strategies of baleen whales. Mammal Review. 2008 Jan;38(1):50–86.

24. Lea JSE, Daly R, Leon C, Daly CAK. Life after death: behaviour of multiple shark species scavenging a whale carcass. Mar Freshw Res. 2018;70:302–6.

25. Whitehead H, Reeves R. Killer whales and whaling: the scavenging hypothesis. Biol Lett. 2005 Dec 22;1(4):415–8.

26. Treude T, Smith CR, Wenzhöfer F, Carney E, Bernardino AF, Hannides AK, et al. Biogeochemistry of a deep-sea whale fall: sulfate reduction, sulfide efflux and methanogenesis. Marine Ecology Progress Series. 2009 Apr 30;382:1–21.

27. Smith CR, Baco AR. Ecology of whale falls at the deep-sea floor. Oceanogr Mar Biol. 2003;44:311–54.

28. Howard J, Sutton-Grier A, Herr D, Kleypas J, Landis E, Mcleod E, et al. Clarifying the role of coastal and marine systems in climate mitigation. Front Ecol Environ. 2017 Feb;15(1):42–50.

29. Lavery TJ, Roudnew B, Gill P, Seymour J, Seuront L, Johnson G, et al. Iron defecation by sperm whales stimulates carbon export in the Southern Ocean. Proc R Soc B. 2010 Nov 22;277(1699):3527–31.

30. Maldonado MT, Surma S, Pakhomov EA. Southern Ocean biological iron cycling in the pre-whaling and present ecosystems. Phil Trans R Soc A. 2016 Nov 28;374(2081):20150292.

31. Nicol S, Bowie A, Jarman S, Lannuzel D, Meiners KM, Van Der Merwe P. Southern Ocean iron fertilization by baleen whales and Antarctic krill: Whales, Antarctic krill and iron fertilization. Fish Fish. 2010 Mar 30;11(2):203–9.

32. Ratnarajah L, Bowie AR, Lannuzel D, Meiners KM, Nicol S. The Biogeochemical Role of Baleen Whales and Krill in Southern Ocean Nutrient Cycling. Ban S, editor. PLoS ONE. 2014 Dec 3;9(12):e114067.

33. Moore CM, Mills MM, Arrigo KR, Berman-Frank I, Bopp L, Boyd PW, et al. Processes and patterns of oceanic nutrient limitation. Nature Geosci. 2013 Sep;6(9):701–10.

34. De Baar HJW, Boyd PW, Coale KH, Landry MR, Tsuda A, Assmy P, et al. Synthesis of iron fertilization experiments: From the Iron Age in the Age of Enlightenment. Journal of Geophysical Research: Oceans [Internet]. 2005 [cited 2020 Dec 3];110(C9). Available from: https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2004JC002601

35. Boyd PW, Watson AJ, Law CS, Abraham ER, Trull T, Murdoch R, et al. A mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. Nature. 2000 Oct;407(6805):695–702.

36. Cavan EL, Belcher A, Atkinson A, Hill SL, Kawaguchi S, McCormack S, et al. The importance of Antarctic krill in biogeochemical cycles. Nat Commun. 2019 Dec;10(1):4742.

37. Schmidt K, Atkinson A, Steigenberger S, Fielding S, Lindsay MCM, Pond DW, et al. Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. Limnology and Oceanography. 2011;56(4):1411–28.

38. Clarke A, Tyler PA. Adult Antarctic Krill Feeding at Abyssal Depths. Current Biology. 2008 Feb 26;18(4):282–5.

39. Atkinson A, Siegel V, Pakhomov E, Rothery P. Long-term decline in krill stock and increase in salps within the Southern Ocean. Nature. 2004 Nov;432(7013):100–3.

40. Pauli NC, Flintrop CM, Konrad C, Pakhomov EA, Swoboda S, Koch F, et al. Krill and salp faecal pellets contribute equally to the carbon flux at the Antarctic Peninsula. Nat Commun. 2021 Dec 9;12(1):7168.

41. Manno C, Fielding S, Stowasser G, Murphy EJ, Thorpe SE, Tarling GA. Continuous moulting by Antarctic krill drives major pulses of carbon export in the north Scotia Sea, Southern Ocean. Nature Communications. 2020 Nov 27;11(1):6051.

42. Belcher A, Henson SA, Manno C, Hill SL, Atkinson A, Thorpe SE, et al. Krill faecal pellets drive hidden pulses of particulate organic carbon in the marginal ice zone. Nat Commun. 2019 Feb 21;10(1):889.

43. Atkinson A, Hill SL, Pakhomov EA, Siegel V, Reiss CS, Loeb VJ, et al. Krill (Euphausia superba) distribution contracts southward during rapid regional warming. Nature Clim Change. 2019 Feb;9(2):142–7.

44. Craven D, Eisenhauer N, Pearse WD, Hautier Y, Isbell F, Roscher C, et al. Multiple facets of biodiversity drive the diversity–stability relationship. Nature Ecology & Evolution. 2018 Oct;2(10):1579–87.

45. Hindell MA, Reisinger RR, Ropert-Coudert Y, Hückstädt LA, Trathan PN, Bornemann H, et al. Tracking of marine predators to protect Southern Ocean ecosystems. Nature. 2020 Apr;580(7801):87–92.

46. Víkingsson GA. Body condition of fin whales during summer off Iceland. In: Blix AS, Walløe L, Ulltang Ø, editors. Whales, seals, fish and man [Internet]. Developments in Marine Biology. Amsterdam: Elsevier Science; 1995 [cited 2020 Jun 27]. p. 361–9. Available from: http://www.sciencedirect.com/science/article/pii/S0163699506800375

47. Jelmert A, Oppen-Berntsen DO. Whaling and Deep-Sea Biodiversity. Conserv Biol. 1996 Apr;10(2):653–4.

48. Curtis TH, Kelly J, Menard K, Laroche R, Jones R, Klimley A. Observations on the behavior of white sharks scavenging from a whale carcass at Point Reyes, California. Calif Fish Game. 2006;92:113–24.

49. Macreadie PI, Costa MDP, Atwood TB, Friess DA, Kelleway JJ, Kennedy H, et al. Blue carbon as a natural climate solution. Nat Rev Earth Environ. 2021 Nov 1;1–14.

50. Griscom BW, Adams J, Ellis PW, Houghton RA, Lomax G, Miteva DA, et al. Natural climate solutions. Proc Natl Acad Sci USA. 2017 Oct 31;114(44):11645–50.

51. Martin AH, Pearson HC, Saba GK, Olsen EM. Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation. One Earth. 2021 May 21;4(5):680–93.

52. Visconti P, Butchart SHM, Brooks TM, Langhammer PF, Marnewick D, Vergara S, et al. Protected area targets post-2020. Science. 2019 Apr 11;364:239–41.

53. Tavares DC, Moura JF, Acevedo-Trejos E, Merico A. Traits Shared by Marine Megafauna and Their Relationships With Ecosystem Functions and Services. Front Mar Sci. 2019 May 24;6:262–74.

54. Riisager-Simonsen C, Rendon O, Galatius A, Olsen MT, Beaumont N. Using ecosystem-services assessments to determine trade-offs in ecosystem-based management of marine mammals. Conserv Biol [Internet]. 2020 Apr 14 [cited 2020 Jun 26]; Available from: http://doi.wiley.com/10.1111/cobi.13512

Figure legends

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

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

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.
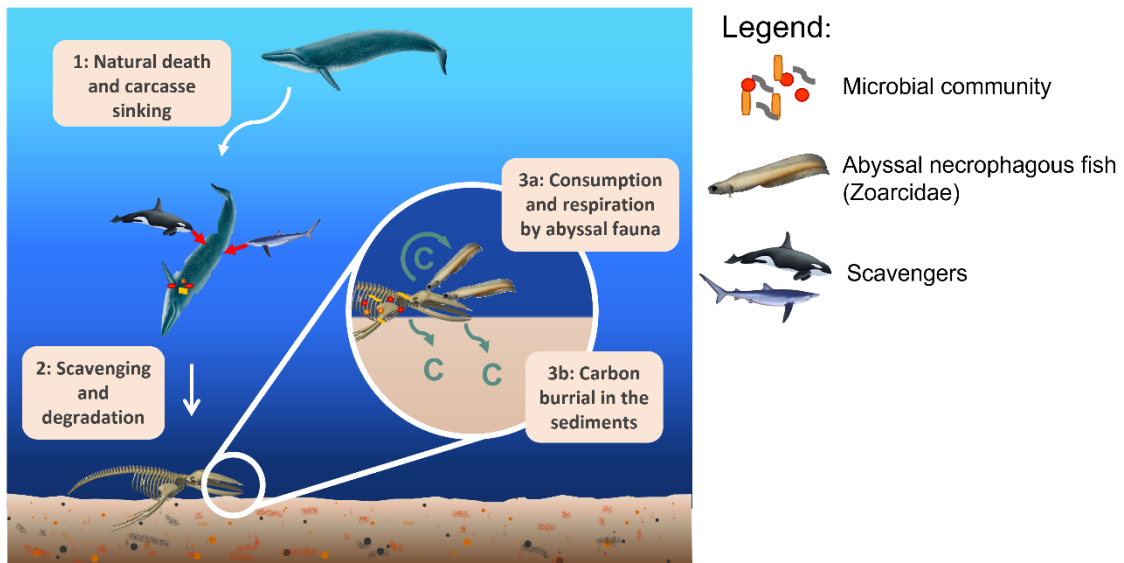
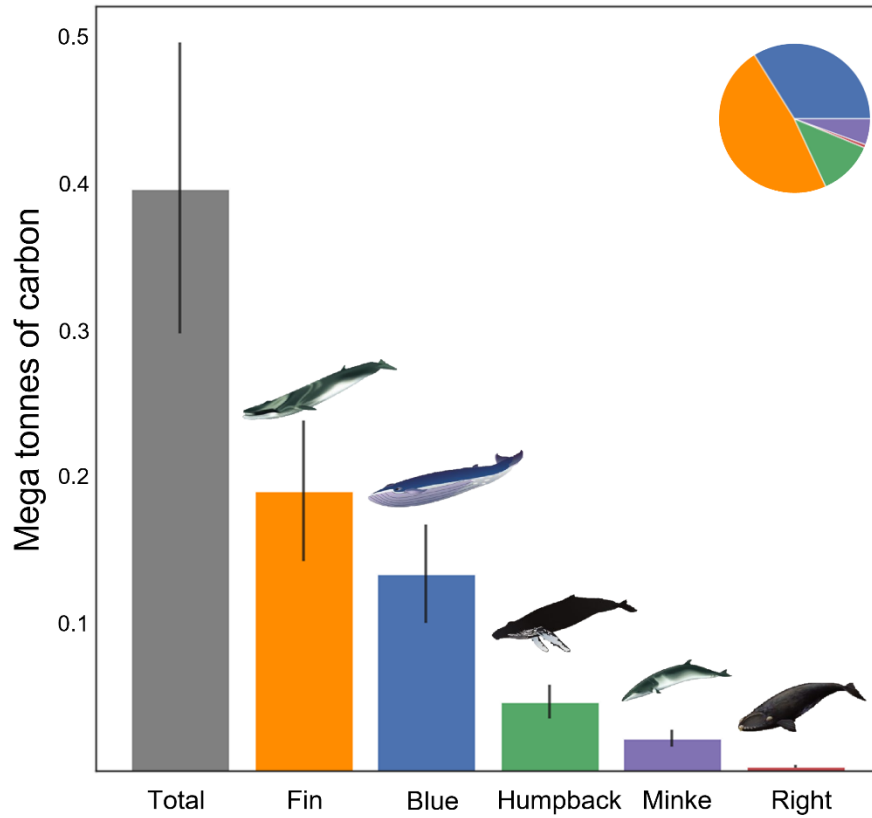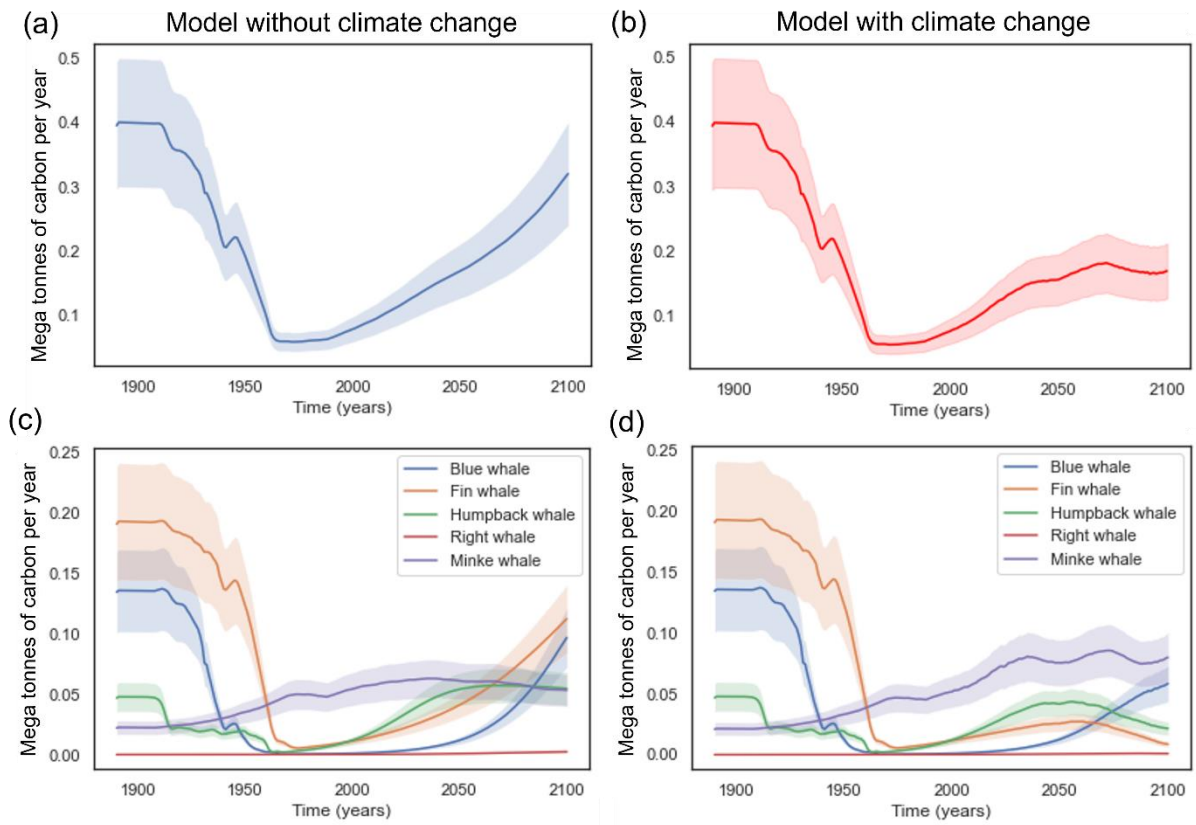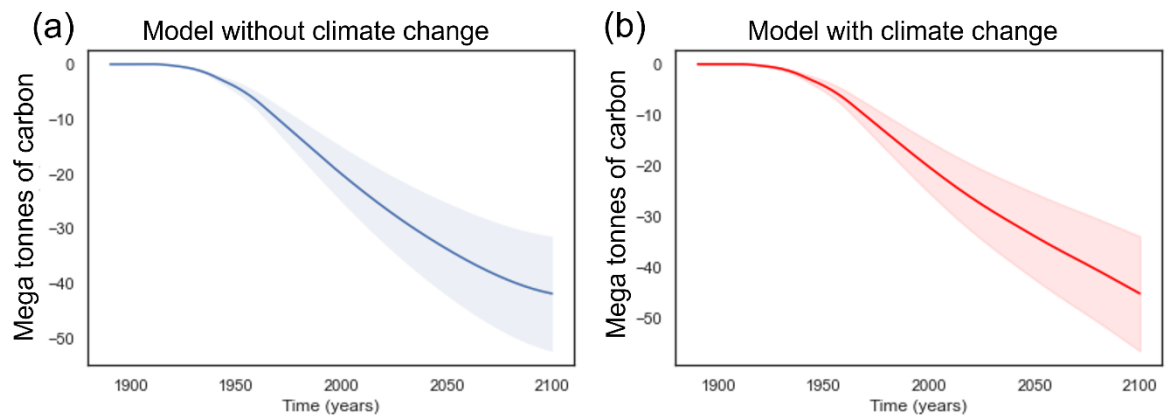**Figures**
Figure 1

Figure 2

Figure 3

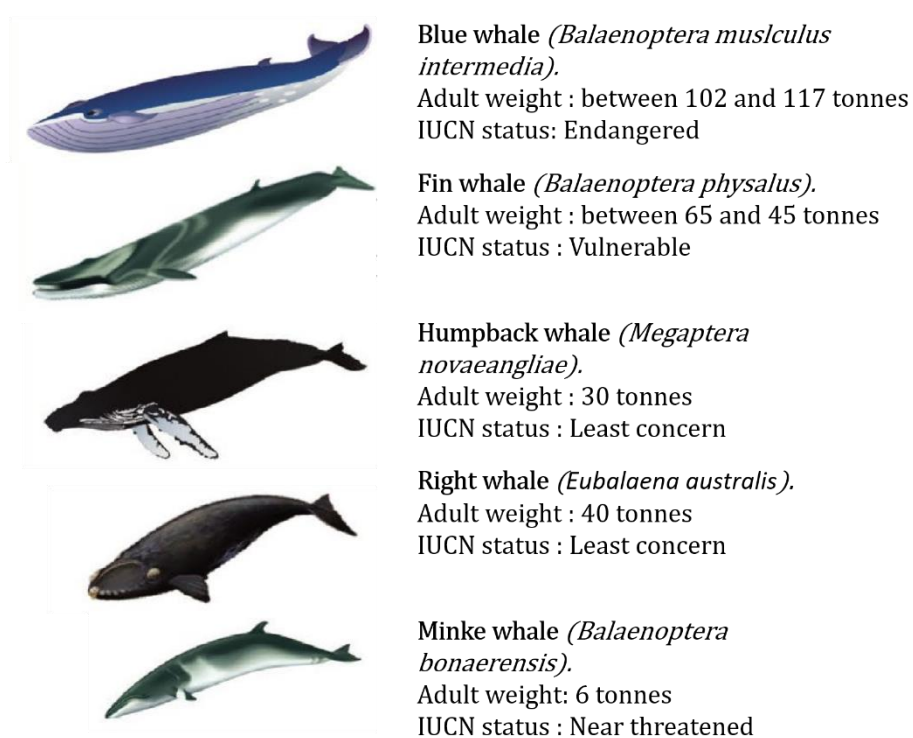Figure 4

Supplementary Materials

1. Whale species integrated in the model

This study focuses on the Southern Hemisphere populations of five baleen whale species that have been heavily exploited during the first half of 20th century: the blue whale (*Balaenoptera musculus intermedia*), the fin whale (*Balaenoptera physalus*), humpback whale (*Megaptera novaeangliae*), the southern right whale (*Eubalaena australis*) and the Antarctic minke whale (*Balaenoptera bonaerensis*). A comprehensive ecosystem models predicting past and future abundances for these species was developed by (1,2). These species are very diverse in terms of body size (from 6 tonnes for the Antarctic minke whale to 120 tonnes for the blue whale) and IUCN Red List of Threatened Species status (from "Endangered" to "Least Concern") (Supplementary Figure 1).

Blue whale *(Balaenoptera muslculus intermedia).*
Adult weight : between 102 and 117 tonnes
IUCN status: Endangered

Fin whale *(Balaenoptera physalus).*
Adult weight : between 65 and 45 tonnes
IUCN status : Vulnerable

Humpback whale *(Megaptera novaeangliae).*
Adult weight : 30 tonnes
IUCN status : Least concern

Right whale *(Eubalaena australis).*
Adult weight : 40 tonnes
IUCN status : Least concern

Minke whale *(Balaenoptera bonaerensis).*
Adult weight: 6 tonnes
IUCN status : Near threatened

Supplementary Figure 1. Weight and IUCN status of the five baleen whale species included in the study.

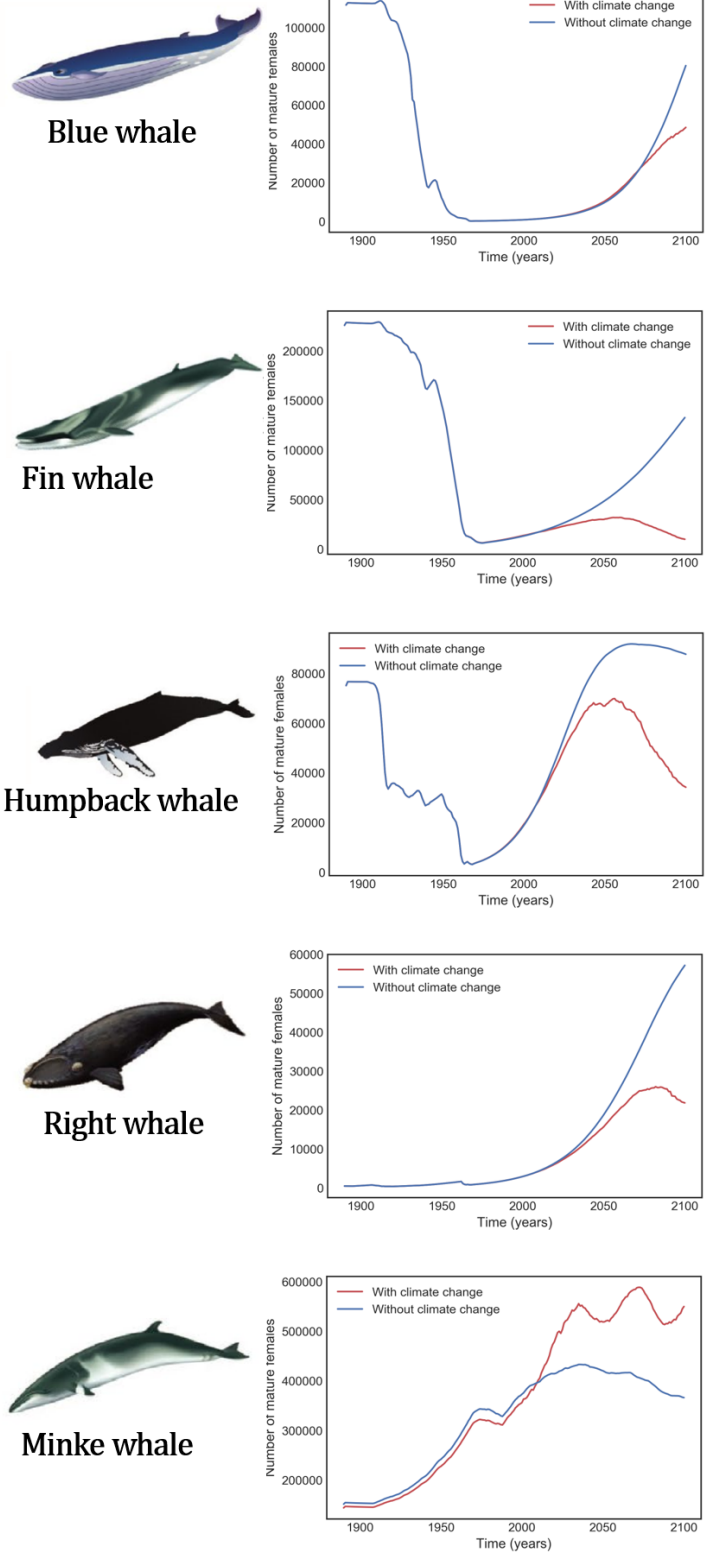### 2. Modelling of whale population dynamics

We based our carbon sequestration estimation on population dynamics for five southern baleen whales recently modelled by (1,2).

This is a Southern Hemisphere spatial 'Model of Intermediate Complexity for Ecosystem Assessments' (MICE) that estimates whale population sizes from 1890 to 2100. Whale abundances were estimated based on both the dynamics of their prey (Antarctic krill *Euphausia superba* and copepods; bottom-up process) and catches (whaling; top-down pressure). This model assumes that the studied whales are mainly localized in the Southern Ocean (between 40° and 80° S) during summer where they prey on krill and in the tropics (between 0 and 40° S) during winter where they migrate during the breeding season. It uses delay-difference equations to describe whale population dynamics at annual seasonal time-steps, linked to an age-structured population model for krill. The MICE model was coupled with a NPZD (Nutrient-Phytoplankton-Zooplankton-Detritus) model that considers the influence of climatic conditions on primary productivity to hindcast historical carrying capacity and predict future population trajectories.

To take into account the effects of climate change, we used two versions of the MICE models. In the first version, whale population dynamics were not coupled to changing climate conditions which were assumed to remain constant from 1890 to 2100. The second model integrates the impacts of climate change according to the RCP 8.5 ("business as usual") scenario, on krill and copepod prey availability through the NPZD outputs (1,2) (Supplementary Figure 3). Indeed, whales are expected to be affected by climate mainly through changes of abundance and spatial repartition of their prey (2). Catch data used in this model were the most up-to-date catch records from the International Whaling Commission (IWC) at the time of the study and they account for data falsifications and errors. Whale abundance trajectories were validated with survey data and a sensitivity analysis was performed to account for uncertainties. See (1,2)) for detailed description of equations and parameter settings.
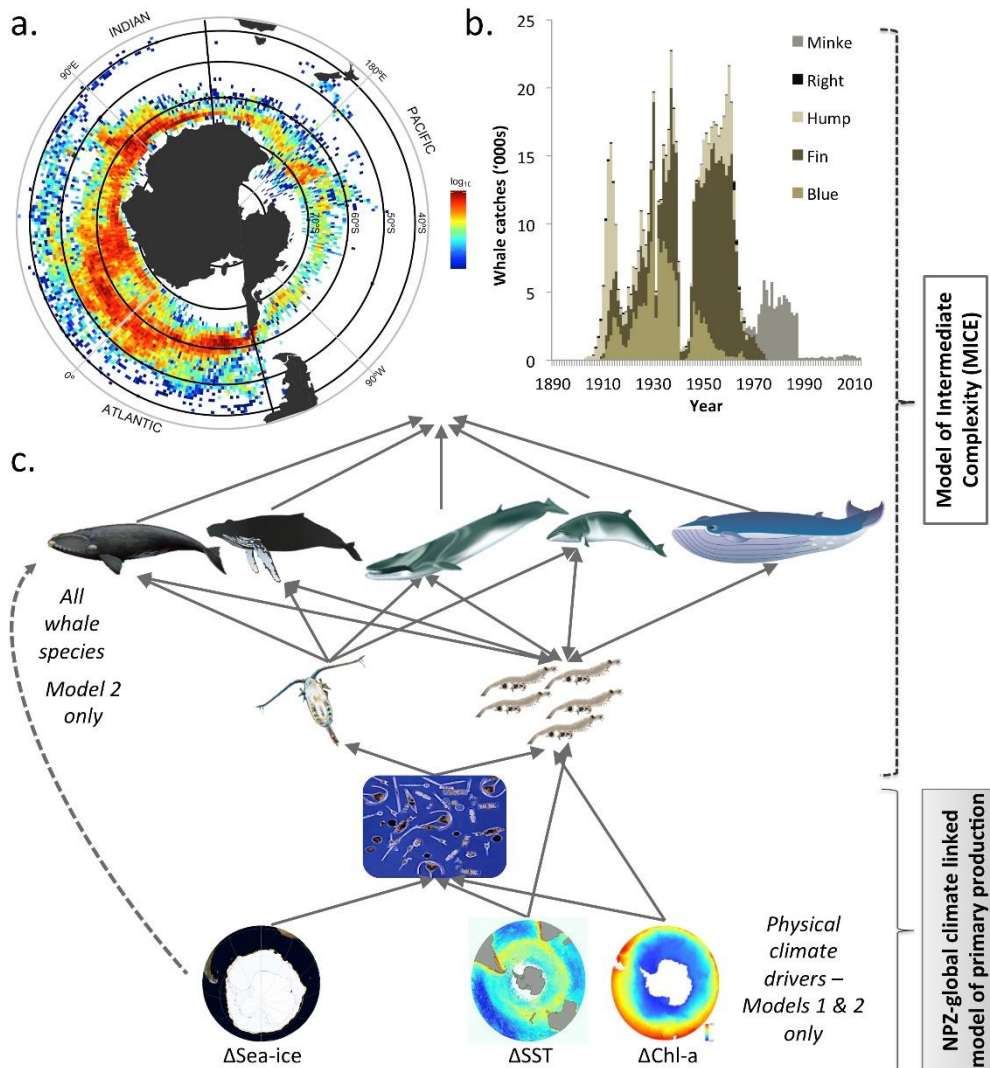
Supplementary Figure 2. Historical whale harvests shown by a) heat map, where black circumpolar bands identify the four latitude bands used in the model, and thick black lines at 60°W and 130°E identify breaks between the two oceanic regions modeled, and b) stacked column graph of total harvest over time between 1890 and 2015; c) schematic of direct interactions between physical climate drivers (bottom from left – changes in sea-ice, chlorophyll, sea-surface temperature) and biological features of models (phytoplankton, copepods, krill, and whales) detailing the relationships in the best-fit model that had environmental forcing from temperature and phytoplankton (Model 1) and alternative scenarios where sea-ice was also linked to future whale distribution (Model 2), or all climate drivers are excluded (Model 3). Arrows identify the direction of the driver and/or interaction, whales depicted from left to right are southern right, humpback, fin, antarctic minke, and blue (2). In this paper we used outputs from Model 2 and Model 3 as inputs for our carbon sequestration calculation.

Supplementary Figure 3. Predicted whale population dynamics (number of mature females) from 1890 to 2100 (2).

Supplementary Tables

1. Parameters used for carbon sequestration calculation

Supplementary Table 1. Whale population parameters for the five species from (1) and (3) for maximum age.

	Annual survival rate >1 year	Annual survival rate <1 year	Age at maturity (year)	Maximum age (year)	Sex ratio (female)
Blue whale	0.960	0.819	6	130	0.475
Fin whale	0.951	0.806	6	118	0.49
Humpback whale	0.922	0.760	5	74	0.54
Right whale	0.980	0.822	6	96	0.47
Minke whale	0.922	0.806	10	86	0.56

Supplementary Table 2. Female and male growth parameters for the five species corresponding to the Von Bertalanffy equation for each species: $m(a) = m_{inf} \cdot (1 - e^{-k(a-a_0)})$ (3).

	a_0 (year)		m_{inf} (tonne)		k (year^{-1})
	Female	Male	Female	Male	
Blue whale	4.5	4.9	117	102	0.2
Fin whale	4.8	5.3	64.5	55	0.2
Humpback whale	9.4	9.4	30	30	0.1
Right whale	9.4	9.4	40	40	0.1
Minke whale	1	1	6	6	0.2

References

1. Tulloch VJD, Plagányi ÉE, Matear R, Brown CJ, Richardson AJ. Ecosystem modelling to quantify the impact of historical whaling on Southern Hemisphere baleen whales. Fish Fish. 2018 Jan;19(1):117–37.

2. Tulloch VJD, Plagányi ÉE, Brown C, Richardson AJ, Matear R. Future recovery of baleen whales is imperiled by climate change. Glob Change Biol. 2019 Apr;25(4):1263–81.

3. Pershing AJ, Christensen LB, Record NR, Sherwood GD, Stetson PB. The Impact of Whaling on the Ocean Carbon Cycle: Why Bigger Was Better. Humphries S, editor. PLoS ONE. 2010 Aug 26;5(8):e12444.