

ECOLOGY

Let more big fish sink: Fisheries prevent blue carbon sequestration—half in unprofitable areas

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Contrary to most terrestrial organisms, which release their carbon into the atmosphere after death, carcasses of large marine fish sink and sequester carbon in the deep ocean. Yet, fisheries have extracted a massive amount of this “blue carbon,” contributing to additional atmospheric CO₂ emissions. Here, we used historical catches and fuel consumption to show that ocean fisheries have released a minimum of 0.73 billion metric tons of CO₂ (GtCO₂) in the atmosphere since 1950. Globally, 43.5% of the blue carbon extracted by fisheries in the high seas comes from areas that would be economically unprofitable without subsidies. Limiting blue carbon extraction by fisheries, particularly on unprofitable areas, would reduce CO₂ emissions by burning less fuel and reactivating a natural carbon pump through the rebuilding of fish stocks and the increase of carcasses deadfall.

INTRODUCTION

The continuous increase in CO₂ emissions from fossil fuel burning and other human activities is rising atmospheric CO₂ concentration [270 parts per million (ppm) before the preindustrial period versus 410 ppm now] and altering global climate with deleterious consequences on ecosystems, human health, and the economies (1, 2). In response, the Paris Agreement, adopted in 2015 at the 21st Conference of Parties under the United Nations’ Framework Convention on Climate Change, has the objective to limit global warming below 2°C relative to preindustrial levels by keeping atmospheric CO₂ concentration below 490 ppm by 2100 (3). Meeting this target will require multiple and urgent efforts to reduce CO₂ emissions, promote carbon sequestration, and develop negative-emission technologies.

In 2019, 66% of the signatories to the Paris Agreement have committed to include nature-based solutions (NBSs) in their climate change programs (4). These NBSs to climate change are the set of actions that protect or restore ecosystems to counter or mitigate negative effects of global changes, including the reduction in CO₂ atmospheric concentrations (4, 5). To date, most of these NBSs to climate change focus on carbon sequestration by primary producers in terrestrial or coastal ecosystems; these include, for instance, restoring forests or protecting mangroves (5, 6). The opportunities of NBSs to climate change in the ocean, with the exception of coastal ecosystems, have rarely been explored despite the fact that the ocean is a major carbon sink that sequester 2.5 billion metric tons of carbon (GtC) per year, or 22% of the global anthropogenic CO₂ emission (1). In particular, the potential role of marine vertebrates, representing an oceanic blue carbon stock of 0.7 Gt (7), has received little attention, even though these large animals can store carbon through different ways. For example, fish modify nutrient limitation and

promote the sequestration of carbon in coastal vegetated habitats, while coastal predators protect this blue carbon stock by limiting grazing (8, 9). The role of fish as direct carbon sink via carcasses deadfall has only been speculated previously (10). In contrast, contributions of whales to carbon sequestration have been quantified (11).

Yet, marine fisheries have depleted most fish stocks relative to preindustrial levels (12), thereby removing massive amounts of blue carbon from the ocean when fisheries catches were landed, processed, and consumed, therefore emitting atmospheric CO₂ (13). Furthermore, government subsidies have enabled fishing fleets to travel vast distances and burn large amounts of fossil fuel to reach remote fishing grounds in the high seas. In addition, these subsidies sustain fishing activities even when fish stocks and catch rates are low because of overexploitation (14). Currently, it has been estimated that more than half of the high-seas fishing grounds would be economically unprofitable for fishing fleets to operate in the absence of subsidies (14). Therefore, overexploiting fish stocks has likely reduced or even annihilated the contribution of marine vertebrates to blue carbon sequestration over vast ocean areas since decades.

Here, we focus on a previously underrecognized pathway of carbon sequestration by fish: their capacity to sequester carbon in the deep sea after their natural death. More precisely, we estimate how catching large fish from the ocean may have affected this carbon sequestration potential through the sinking of dead fish carcasses. On the basis of previous studies showing the deadfall of large pelagic fish into the deep sea (15, 16), we assume that, in the open ocean, carcasses of deceased fish sink to the bottom rather than being eaten in surface waters. We use global fisheries catches data since 1950 to estimate the spatial and temporal dynamics of the blue carbon extracted from the ocean and released into the atmosphere as a result of fishing, instead of being sequestered in the deep sea. We also estimate the extent to which fishing remote unprofitable areas in the high seas, with the support of subsidies, expands the blue carbon extirpation and contributes to CO₂ emissions into the atmosphere. To adopt a conservative strategy in our estimations, we only consider dense and large-bodied (>30 cm in total length) fusiform fish species, including most tunas, mackerels, sharks, and billfishes, since their carcasses are most likely to sink rapidly.

We use the Sea Around Us (SAU) database to assemble spatially explicit global fisheries catches since 1950 for 24 tuna, 20 mackerel,

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15 billfish, and 85 shark species (table S1), hereafter referred to as “large fish.” We assume that each individual fish contains, on average, 12.5% ($\pm 2.5\%$) of carbon relative to its whole-body wet weight (7, 17). We exclude areas shallower than 200 m and coastal upwelling regions, because these latter ecosystems can act both as a sink (upwelled nutrients stimulate phytoplankton productivity) and a source (upwelled waters are rich in dissolved inorganic carbon) of carbon (18). For each metric ton of carbon (tC) extirpated from the ocean by fisheries, we consider that 94% is emitted into the atmosphere as most of the body parts are either consumed or processed so the carbon is subsequently released through respiration, excretion, and waste treatment (13). The remaining 6% correspond to the carbon contained in fish bones, which is not reemitted into the atmosphere but rather sequestered in landfill (fig. S1) (19, 20). We estimate the average proportion of the extracted fish biomass that would have otherwise died from senescence and disease and sunk in the deep ocean if it had not been fished or predated (see the Methods and Supplementary Materials). Depending on the taxonomic group (i.e., tuna, mackerel, sharks, and billfish), we estimate that fishing prevents the sequestration of 28.8 to 94.6% of the extracted carbon (figs. S1 and S2).

RESULTS AND DISCUSSION

Blue carbon extraction since 1950

Between 1950 and 2014, the world’s fishing fleets have extracted 318.4 million metric tons (Mt) of large fish from the ocean, equivalent to 37.5 ± 7.4 Mt of carbon (MtC) released into the atmosphere. This means that fishing has prevented the sequestration of 21.8 ± 4.4 MtC through the sinking of fish bodies into the deep sea, after accounting for the consumption of biomass from predation (Fig. 1A). Most of this blue carbon extirpation (87.4%) is due to the fishing of Scombridae species (56.2% for tunas and 31.2% for mackerels), while shark and billfish catches represent 10.5 and 1.9% of the total, respectively (Fig. 1B). Industrial fisheries have extracted 84.8% of the total (33.6 ± 6.7 MtC), while artisanal, subsistence, and recreational fisheries have extracted 12.3% (4.9 ± 0.9 MtC), 1.97% (0.8 ± 0.1 MtC), and 0.9% (0.37 ± 0.07 MtC), respectively (Fig. 1C).

The spatial distribution of fished blue carbon since 1950 reveals a marked heterogeneity with a maximum of 533 kgC per hectare extracted in the Western Pacific Ocean, while 26.5% of the ocean surface shows no blue carbon extraction. The Pacific Ocean, where most tuna fisheries concentrate, accounts for 71.1% of the total blue carbon extirpated, and 49.1% takes place in the equatorial strip (i.e., between 10°S and 10°N latitude; Fig. 1D). The national fishing fleets with the largest overall blue carbon extraction are based in Japan, Indonesia, and Taiwan, with 22.2, 6, and 5.1% of the total, respectively (Fig. 1E). Combined with fishing fleets from the Philippines, Spain, USA, Ecuador, China, South Korea, and Thailand, these 10 countries account for 62% of total blue carbon extirpated since 1950.

Like any other food production sector, fishing also emits CO₂ by consuming and burning fuel. In the fishing sector, fuel consumption represents the majority of its carbon footprint (21). Using an emission intensity factor of 1.9 metric tons of CO₂ emitted per metric ton of fish landed (21), we estimate that 165.3 MtC were emitted between 1950 and 2014 due to the fuel consumption needed to extract blue carbon from the ocean. If we sum up large fish carbon exported (37.5 MtC) on land and the emissions due to fuel consumption (165.3 MtC; Fig. 1A), then we obtain a total of 0.2 GtC emitted in the atmosphere since 1950 by fisheries, equivalent to 0.73 GtCO₂.

Spatiotemporal dynamics of blue carbon extraction

Total blue carbon extraction from the ocean has increased steadily since 1950 (Fig. 2A). In 2014, fisheries extracted 1.09 MtC (± 0.2 MtC) of large fish, while only 0.13 MtC were removed from the ocean in 1950 (± 0.02 MtC), equivalent to an increase of almost one order of magnitude in 65 years. Among areas where blue carbon extraction occurs, 88.3% experienced an increase between 1950 and 2014 (Fig. 2A). Marine regions with the highest increase in blue carbon extraction from fishing are located in the Western Pacific and around the equatorial strip (Fig. 2B). In the early 1950s, blue carbon was mainly extracted in the Western Pacific and the Mediterranean Sea, while only 39% of ocean areas had reported extraction of large fish (Fig. 2C). Despite the high economic cost of fishing in the high seas (14), there has been a progressive expansion of exploited areas, reaching 72% of the ocean surface by the early 2010s (Fig. 2D and fig. S3). Recent hotspots of blue carbon extraction are located near the coasts of East and Southeast Asia (both in Indian and Pacific Oceans), as well as in the western equatorial strip of the Pacific Ocean due to the development of tuna fisheries (Fig. 2D). Considering that this blue carbon, except bones, exported to land from the ocean through fisheries catches and landings is emitted as CO₂ (3.75 MtCO₂), combined with CO₂ emissions due to fuel consumption by the fishing fleets (16.6 MtCO₂), a total of 20.4 MtCO₂ were estimated to have been emitted in 2014. This is equivalent to the annual emissions of 4.5 million cars, so 11.7% of the total number of cars registered in France or 0.05% of the global CO₂ emissions in 2014. This also represents almost 17% of the decrease in CO₂ emission in Europe between January and April 2020 due to the corona virus disease 2019 forced confinement (~ 123 MtCO₂ less compared to the same period in 2019) (22).

The profitability of blue carbon extraction

Reducing fisheries subsidies is being pursued as a policy to improve the ecological (23) and socioeconomic (14, 24) status of fisheries in the high seas (25). To evaluate whether subsidies reduction policies also contribute to carbon mitigation, we analyze catches of large-bodied fish from the high seas in 2014 and combine it with data on fisheries subsidies. Specifically, on the basis of published data on the profitability of high-seas fisheries (14), we separate areas that are either estimated to be profitable or unprofitable to fish without subsidies. We estimate the proportion of blue carbon extracted from each of these areas relative to the total catches from the high seas. Globally, 43.5% of the extracted blue carbon in the high seas comes from areas that would be unprofitable in the absence of subsidies (Fig. 3A). These unprofitable fishing grounds include some areas with the highest amounts of blue carbon extracted (in red in Fig. 3, C and D). These unprofitable and highly CO₂ emitter areas are mainly located between 20°S and 10°N latitude and along the Japanese coasts, in Central Pacific, South Atlantic, and North Indian Oceans. However, the proportion of unprofitable areas reduces to 23.1% if government subsidies are included (Fig. 3B). Almost half of the areas that are estimated to emit carbon from fishing activities while being economically unprofitable become profitable with subsidies. This profitability shift of the main blue carbon extraction areas mainly occurs in the central Pacific and Atlantic Oceans (from red to yellow in Fig. 3, C and D). Some areas would remain profitable to fish even without subsidies (blue cells in Fig. 3C) because of lower costs of fishing that are dependent on the characteristics of the fisheries, e.g., ship size, gear type, and engine (14). Our findings

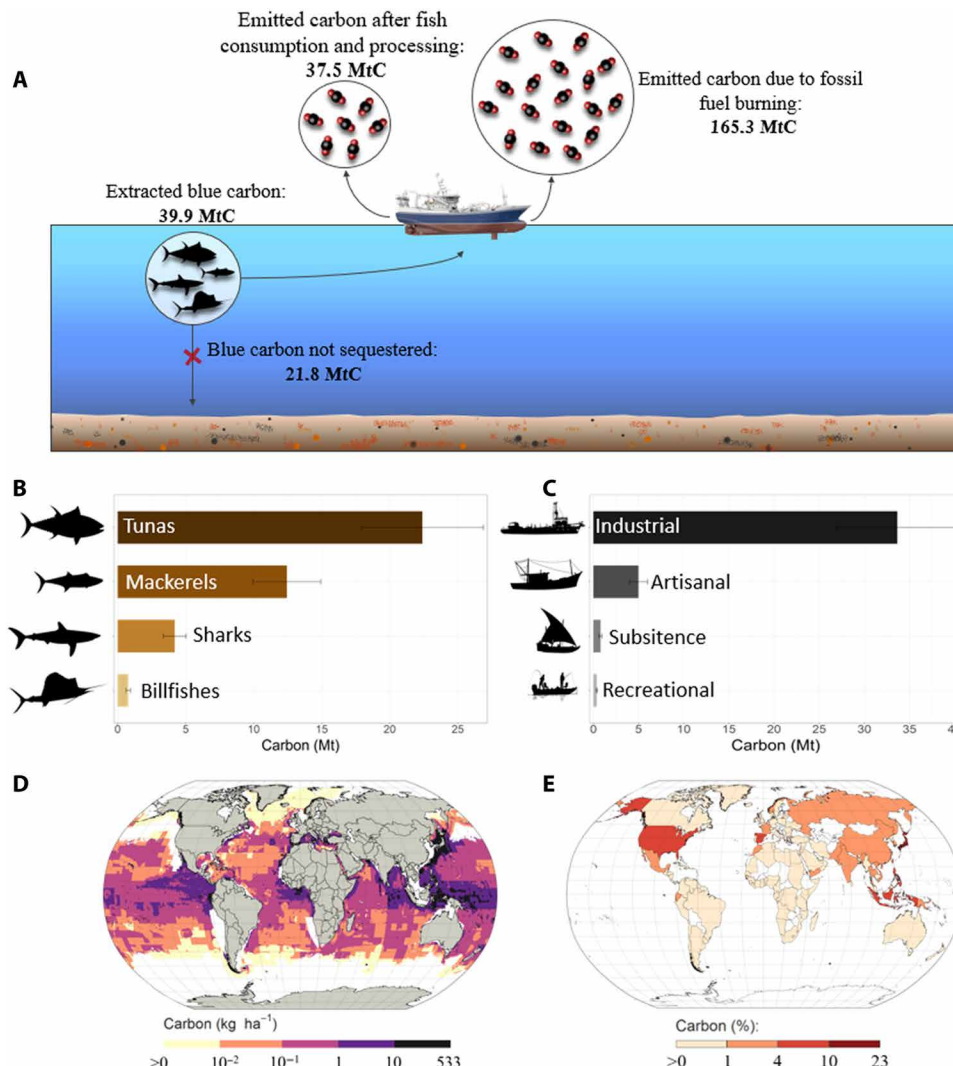


Fig. 1. Total blue carbon extraction of large fish since 1950. Fate of blue carbon and associated emissions (A). Blue carbon extracted by taxon (B) and by fishing sector (C). Error bars represent the lower and upper bounds of carbon content in fish bodies (10 and 15%, respectively). Spatial distribution of the blue carbon extracted since 1950 by fisheries (D). Percentage of countries' contribution to blue carbon extraction since 1950 (E). Countries in white have no reported catches.

thus show that government subsidies, through supporting large-scale exploitation of large-bodied fish that is economically unviable, exacerbate the depletion of a natural carbon sink.

Rebuilding fish stocks as a NBS to climate change?

Limiting or preventing blue carbon extraction at least on the unprofitable areas of the high seas while managing all fisheries to maintain the long-term viability and productivity of fish stocks would rebuild fish biomass and benefit carbon storage in three ways. First, reducing overall fishing effort would lower CO₂ emissions by burning less fuel. Second, rebuilding fish stocks would increase living biomass of large-bodied fish and thus promote the short-term carbon sequestration in the living compartment. Third, more abundant large-bodied fish would induce higher natural long-term carbon sequestration by increasing carcasses deadfall.

Previous studies evaluating the effectiveness, cobenefits, disbenefits, and governability of ocean solution to address climate change suggest that eliminating overfishing and setting up marine-protected

areas can support climate adaptation (26). Our findings further highlight the potential contributions of these interventions to climate mitigation through restoring blue carbon from eliminating overfishing in the high seas. This is in addition to a wide range of other ecological and socioeconomic benefits of effective fisheries management and spatial planning in the high seas, such as conserving biodiversity, reducing modern slavery in fisheries and inequalities between countries (14, 24, 27), improving the viability of small-scales fisheries (28), and, in general, achieving several sustainable development goals (29–31).

Our analyses provide solid, yet conservative, estimates on how fisheries, mainly industrial, have affected blue carbon sequestration since 1950. However, further studies are needed to provide comprehensive estimations of blue carbon potential from marine vertebrates and impacts of human activities on this sequestration pathway. Particularly, we have only included fisheries targeting large-bodied fish in areas with a mean depth of more than 200 m and excluded upwelling areas; thus, only 9.5% of the total catches in 2014 are considered

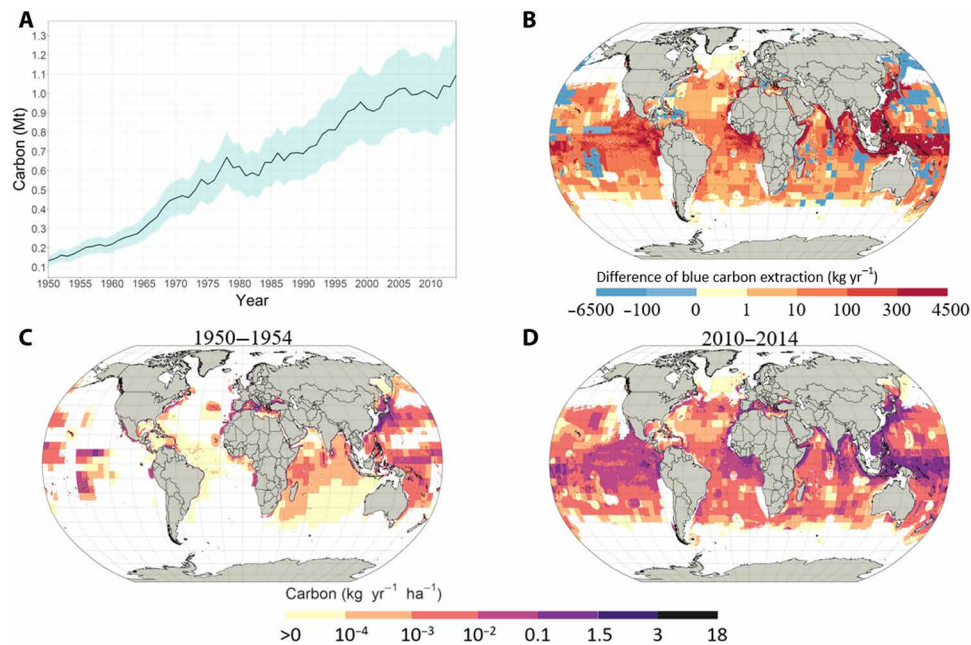


Fig. 2. Temporal and spatial changes in blue carbon extraction of large fish by fisheries. Temporal trends in the amount of blue carbon extracted from the oceans since 1950 by year (A). Annual difference of blue carbon (kilogram per year) extraction between the periods 1950 to 1954 and 2010 to 2014 in $0.5^\circ \times 0.5^\circ$ cells (B). Average annual carbon extraction (per year and hectare) between 1950 and 1954 (C) and 2010 to 2014 (D).

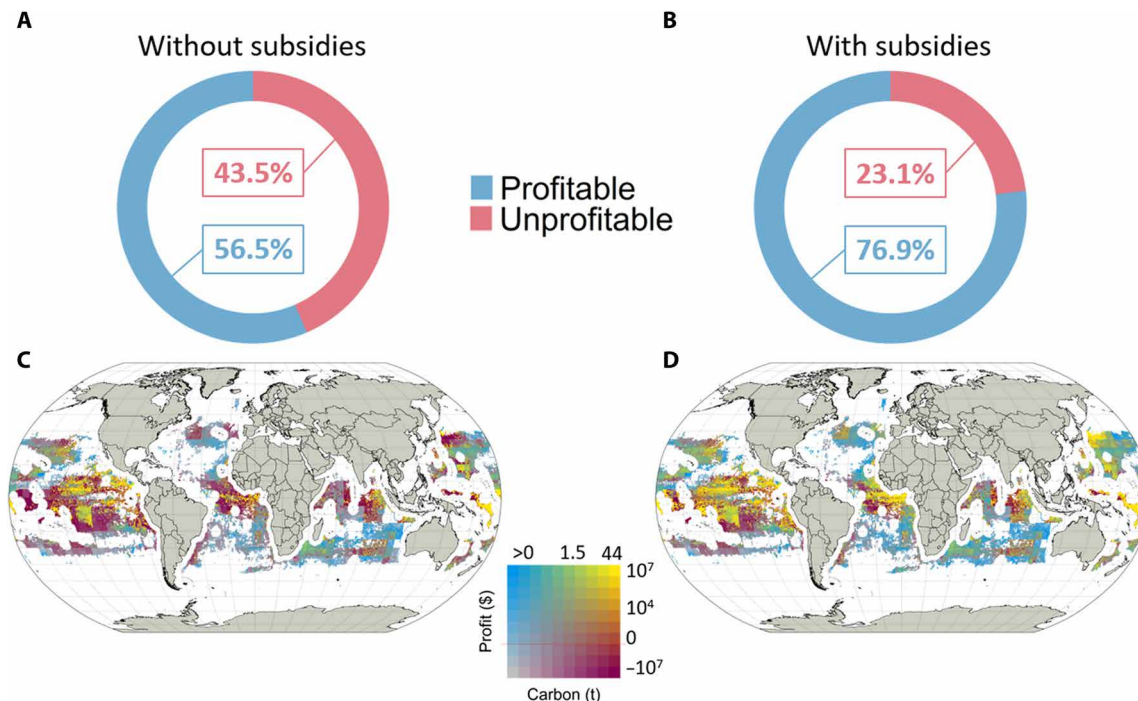


Fig. 3. Impact of government subsidies on blue carbon extraction in the high seas. Percentage of blue carbon extracted in profitable areas and unprofitable areas without subsidies (A) and with subsidies (B). Spatial variability of carbon extraction and economic viability without subsidies (C) and with subsidies (D).

in our study. To fully assess the effectiveness of measures promoting blue carbon sequestration by all marine vertebrates including mammals and small pelagic and mesopelagic species, it would be necessary to estimate the amount of carbon sequestered after natural death by more species. For example, if skipjack tuna (*Katsuwonus*

pelamis) stocks could recover to their preexploitation level only in the Western Pacific Ocean (32), then 1.63 MtC would be sequestered annually. This is only 6.8% of the annual amount of carbon sequestered by mangroves (24 MtC per year) (33); but if we include a recovery, even partial, of marine mammals and all other pelagic,

benthopelagic, and mesopelagic fish species, then we may expect far more (34–36). This means that we have likely underestimated not only the true role that marine vertebrates can have on carbon sequestration but also the impact of fisheries on this carbon sequestration. We suggest that measures to rebuild fish stocks to sustainable level, e.g., biomass above maximum sustainable yield (MSY ; $>B_{MSY}$) (37), could induce a much higher amount of carbon sequestered by large marine vertebrates, comparable to other coastal NBSs to climate change such as carbon mitigation potential of coastal wetland restoration (54 to 233 MtC per year) (38). A broader range of NBS, including different scenarios of ocean management, can be explored to understand how blue carbon from marine vertebrates can be restored and/or enhanced most effectively.

It is also important to consider the broader trade-offs of fish blue carbon-related NBSs with other society changes that aim to promote sustainable development. For example, limiting catches of large pelagic species on the high seas might lead to substitution of seafood by other sources of proteins and nutrients with bigger environmental and social footprints. Particularly, the carbon footprint of products derived from marine fisheries and destined to human consumption is much lower compared to other sources of animal protein (e.g., beef, lamb, and pork) (21). A replacement of fish protein by livestock protein would promote carbon sequestration by unfished large pelagic species but would simultaneously increase CO_2 emissions from the agricultural sector. However, given that many fish stocks are currently below their production potential because of overfishing (12), rebuilding overexploited fish stocks can ensure more sustainable seafood production, limiting the shift toward livestock protein while enhancing blue carbon sequestration with more large-bodied fish and sinking carcasses.

Conclusions and perspectives

Our findings provide a foundation to include other physiological and ecological processes influencing the carbon budget of a fish during all its life stages. Fish contributes to the inorganic carbon cycle through respiration (source of CO_2) (39) and the production of carbonate ($CaCO_3$), a by-product of osmoregulation process (40, 41). The sinking of the carbonate crystals could increase carbon sequestration, while the chemical reaction also produces some CO_2 and modifies ocean chemistry (40). The large-scale removal of ocean apex predators can shift the structure and functioning of ecosystems (42). In some cases, overfishing predators can induce trophic cascades that induce an increase in abundance of forage fish that are smaller bodied and lower in trophic level, a decrease in zooplankton biomass because of increased grazing by forage fish, resulting in an increase in phytoplankton biomass (43). Consequently, catching large fish could decrease carbon sequestration by zooplankton but increase that of phytoplankton. However, these cascading effects are not consistent across the ocean, and the effects of depleting large fish populations do not always spread toward the lowest trophic levels (44). If the loss of apex predators negatively affects the sequestration of carbon in coastal ecosystems (8), there is, to our knowledge, no evidence of this indirect impact in pelagic systems. Moreover, there is growing evidence that these apex predators provide nutrients via processes like excretion and defecation (9). Some species, such as sperm whales, play a key role in the creation of biogeochemical hotspots, promoting phytoplankton inflorescences and increasing the export of carbon in the deep ocean (45). Thus, species like tunas, billfishes, and sharks would certainly boost nutrient provision in some

oligotrophic zones of the high seas, which, by extension, would increase carbon sequestration in the deep ocean through marine snow sedimentation.

This study provides a first global and conservative estimate on how fisheries have contributed to reduce the carbon sequestration potential of large fish by removing them from the ocean. Since 1950, fisheries have emitted 0.2 GtC into the atmosphere and prevented the sequestration of 21.8 ± 4.4 MtC through blue carbon extraction. This direct impact of fisheries on blue carbon sequestration is much less than the annual sequestration capacity of ecosystems like mangroves (24 MtC per year) (33) or seagrasses (104 MtC per year) (46). However, we raise the issue of rapidly assessing the effect of measures promoting the recovery of fish stocks, on the reactivation of the natural capacity of large fish to sequester carbon through the sinking of their carcasses or through their potential indirect effect on the sequestration of carbon by other living compartments (i.e., phytoplankton). This would improve estimates to assess whether rebuilding fish stocks can be considered an additional NBS to climate change that has been ignored so far.

MATERIALS AND METHODS

Species and areas selection

We assume that a fish, when it is not fished or eaten by a predator, dies naturally and sinks in the deep ocean at such a rate that it does not have time to be degraded in the water column before it settles on the substrate. Then, the carbon contained in its body will be sequestered in the deep ocean over several decades or even millions of years (47, 48). Conversely, when an individual is fished, the carbon contained in its body is exported on land instead of being sequestered in the deep ocean. We chose to include in this study large (>30 cm) pelagic fishes (dense and/or fusiform) and large demersal sharks (already close to the substrate), which include pelagic and demersal sharks, Scombridae (tuna and mackerel), and billfishes. Only landings were included because discards are considered as sequestered in the deep ocean, at a rate that would be higher than if they were not fished. Other species (small pelagic, marine mammals, etc.) could have been included, but we adopted a conservative approach in estimating the impacts of fisheries on blue carbon sequestration, since these species are more likely to die from predation (little pelagic) or float after death (right whales and dolphins). Also, we excluded areas of the ocean with shallow depths (cells with average bathymetry of less than 200-m depth), where stored carbon could be remobilized in the water column. In addition, coastal upwelling systems can be a sink or a source of carbon (18). They act as a carbon sink when upwelled water, rich in nutrients, stimulates phytoplankton productivity, which promotes export of organic carbon. At the same time, upwelled waters are rich in dissolved inorganic carbon (DIC), which can lead to an outgassing of CO_2 (18). However, we ignore which part of the exported carbon can be sequestered and which part can be remineralized as DIC and outgassed. Therefore, we have chosen to remove catches in the four major eastern boundary upwelling systems (i.e., California, Peru-Chile/Humboldt, Canary, and Benguela upwelling systems). This very conservative approach in estimating impacts of fisheries on blue carbon sequestration undoubtedly provides underestimated values.

Catch data since 1950

Catch data from 1950 to 2014 were extracted from the SAU database. These data are reconstructed catch data. The SAU uses the

United Nations' Food and Agriculture Organization's reported catch data as baseline, combined with a catch reconstruction methodology, to provide a better estimate of world catches (49, 50). This methodology provides catch data from all fishing sectors (industrial, artisanal, subsistence, and recreational) not only by year, flag state (country), and catch type (landings versus discards) but also by functional and commercial group (50). Catch data are spatialized onto a grid of $0.5^\circ \times 0.5^\circ$ latitude and longitude cells.

Catch data from the SAU database are in metric tons of fresh biomass. To estimate the amount of blue carbon extracted because of large fish fisheries, data were converted to metric tons of carbon. We assumed that all fish have the same fraction of carbon in their biomass. On the basis of a study by Czamanski *et al.* (17), the average percentage of carbon in an individual belonging to the species *Scomber scombrus* (Atlantic mackerel, Scombridae) is 12.3 and 11% for *S. japonicus* (Spanish mackerel, Scombridae). Another study used a percentage of 15% for mesopelagic fishes (7). To take into account the potential variability in carbon content between species, we took three percentages of carbon: 10% (low estimation), 12.5% (17), and 15% (7). By summing all catches (C) in each cell, we estimated the amount of carbon extracted (E_{carbon}) within each 0.5° latitude \times 0.5° longitude grid cell

$$E_{\text{carbon}} = C \times 0.125 (\pm 0.025)$$

We estimated the contribution to blue carbon extraction for each taxon (tuna and tuna-like species, mackerel, sharks, and billfishes), fishing sector (industrial, artisanal, recreational, and subsistence), and fishing fleet (country) since 1950.

Estimation of carbon emitted and carbon not sequestered

Carbon reemitted into the atmosphere and the carbon that has not been sequestered in the deep ocean were estimated from the extracted carbon. The former corresponds to the carbon reemitted into the atmosphere after being consumed on land. Carbon contained in fish body is reemitted into the atmosphere, except carbon contained in fish bones, which is mainly buried and sequestered in landfills (19). Bones in tuna and mackerels species (87.4% of the total catch considered in this study) account for 6% of the total body weight (20, 51). Therefore, we removed 6% of the total catches so that bones are not included in our conservative estimates of CO_2 emitted. All the carbon contained in the 94% remaining fish biomass is released into the atmosphere as CO_2 through respiration, excretion, and waste treatment (13). Therefore, we assumed that the amount of carbon reemitted into the atmosphere is equal to 94% of the amount of carbon extracted by fisheries (fig. S1). Conversely, the amount of carbon that is not sequestered in the deep ocean is lower than the amount of carbon extracted by fisheries because only the portion of individuals that died from senescence or disease would have sequestered carbon. The other portion (the ones that would have died of predation if not fished) would not have sequestered carbon in the deep ocean. Therefore, we accounted for the loss of biomass production potential from the exploitation of standing fish stocks that would have contributed to the export of the blue carbon into the deep ocean. Using the Thompson and Bell's catch equation (52) and assuming that each population is at equilibrium, i.e., recruitment of young fishes = loss from predation, fishing, and other causes (largely senescence and disease), we estimated the annual average proportion of the extracted biomass that would have

died from senescence and disease if it had not been fished between 2005 and 2014. Because of the differences in exploitation status (from under- to overfished) across fish stocks, regions, and time period, we conservatively estimated the rate of carbon production by assuming that the stocks are fished at levels approximately required for MSY. We obtained a mortality rate from senescence and disease for each major taxonomic group (tuna, mackerel, sharks, and billfish) by following the method below (fig. S1).

At each time t , the biomass (B) decreases because of mortality such that

$$\frac{dB}{dt} = -ZB \quad (1)$$

where Z = total mortality rate (predation, fishing, senescence...).

The integration of the Eq. 1 gives the biomass that survived between t_0 and t_1 (B_t)

$$B_t = B_0 \cdot e^{-Zr(t_1-t_0)} \quad (2)$$

where B_0 is the initial biomass at t_0 .

To estimate the proportion of the biomass that died from senescence and disease between t_1 and t_2 , we had to estimate the biomass that died from fishing (C), defined by the Thompson and Bell's catch equation

$$C_{t_1,t_2} = \left(\frac{F}{Z}\right) \cdot (B_{t_1} - B_{t_2}) \quad (3)$$

where F is the fishing mortality rate and $\frac{F}{Z}$ is the proportion of biomass died from fishing.

Putting B_{t_2} in the form of Eq. 2 gives the following catch equation

$$B_{t_2} = B_{t_1} \cdot e^{-Zr(t_2-t_1)} \text{ and } B_{t_2} = B_{t_1} - \left(\frac{F}{Z} \cdot C_{t_1,t_2}\right) \\ C_{t_1,t_2} = \left(\frac{F}{Z}\right) \cdot B_{t_1}(1 - e^{-Zr(t_2-t_1)}) \quad (4)$$

With the same approach, the fished biomass that would have died from senescence and disease (noted as SB for sinking biomass) between t_1 and t_2 is

$$SB_{t_1,t_2} = \left(\frac{N}{Z}\right) \cdot B_{t_1}(1 - e^{-Zr(t_2-t_1)}) \quad (5)$$

where N is the mortality rate from other mortalities (senescence, disease, and other causes).

Using Eqs. 4 and 5, we obtain the fished biomass that would have sunk in the deep ocean if not fished with fishing at MSY, for each species i for which the required data for the calculations are available

$$\frac{C_{\text{MSY}}}{F} = \frac{B_{t_1}(1 - e^{-Zr(t_2-t_1)})}{Z} \text{ and } \frac{SB_{\text{MSY}}}{N_i} = \frac{B_{t_1}(1 - e^{-Zr(t_2-t_1)})}{Z} \\ SB_{\text{MSY},i} = \frac{C_{\text{MSY},i} \cdot N_i}{M_i} \text{ where } M = F \text{ at MSY} \quad (6)$$

In our study, C_{MSY} corresponds to the average annual blue carbon extracted between 2005 and 2014 (from the SAU database). N

is the mortality rate from senescence and disease, and M is the natural mortality rate (equal to the fishing mortality rate, F , with fishing at MSY). Several values of N and M at the species level were obtained from outputs of Ecopath with Ecosim models (<http://ecobase.ecopath.org/#docs>) and FishBase, respectively. As we do not have a value of N and M for each species, we grouped the estimates of SB by major taxonomic group (i.e., tuna, sharks, mackerel, and billfish). By dividing the biomass that would have sunk (SB_{MSY}) by the biomass extracted from ocean (C_{MSY}), we lastly obtained several sequestration factor when fishing at MSY ($S_{MSY,i}$) for each species i

$$S_{MSY,i} = \frac{SB_{MSY,i}}{C_{MSY,i}} \quad (7)$$

We applied to catches of each species considered in this study the median value of the S_{MSY} of the major taxonomic group to which it belongs to obtain the total extracted biomass that would have sunk in the deep ocean if not fished with fishing at MSY (SB_{Tot} ; figs. S1 and S2)

$$SB_{Tot} = \sum_{j=1}^n C_j \cdot \text{med}(S_{MSY,ij}) \text{ with } n = 4 \quad (8)$$

where $\text{med}(S_{MSY,ij})$ is the median value of S_{MSY} of all species i belonging to taxonomic group j , and C_j is the total catch of taxonomic group j from 1950 to 2014.

Two scenarios are possible once the carcass arrives on the substrate. The flesh of the carcass can be consumed by deep-sea scavengers at rates up to 32 kg per day (15) to be used for its metabolism. In this case, the carbon contained in the carcass is going to be remineralized in the deep sea and sequestered for decades to hundreds of years (47, 48). Otherwise, the carcass (mainly bones) is buried in the sediment, and the carbon is sequestered over several million years (47, 48). To our knowledge, no carcass burial rate exists, so we cannot distinguish between these two scenarios.

We mapped the spatial evolution of areas where carbon was removed. We estimated the average annual variation in the amount of carbon extracted in each cell between 1950 and 2014 by computing the variation in amount of blue carbon extracted annually on average between 1950 to 1954 and 2010 to 2014 and dividing this delta by 65 (number of years). We also mapped the average amount of blue carbon extracted by hectare each year in each for all decades since 1950.

Impact of government subsidies on blue carbon extraction

Using data from the study of Sala *et al.* (14), we assessed the extent to which fishing unprofitable areas, with the support of government subsidies, contribute to the blue carbon extirpation in the high seas. By computing the cost of fishing in the high seas (that takes into account fuel, labor, repair/maintenance transshipment, and fuel replenishment costs) and the incomes of high-seas fisheries (based on global catch and their landed value), they estimated the global profits of high-seas fisheries with and without government subsidies. We combined these data with the catch data of large fish from the SAU database in 2014 that occurred only in the high seas. We estimated the amount of blue carbon extracted in profitable and unprofitable areas with and without subsidies by mapping the profitability of fishing each $0.5^\circ \times 0.5^\circ$ cells and coupling these estimates to the amount of blue carbon extracted in each cell.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/6/44/eabb4848/DC1>

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