

RESEARCH ARTICLE

Industrial fisheries have reversed the carbon sequestration by tuna carcasses into emissions

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Abstract

To limit climate warming to 2°C above preindustrial levels, most economic sectors will need a rapid transformation toward a net zero emission of CO₂. Tuna fisheries is a key food production sector that burns fossil fuel to operate but also reduces the deadfall of large-bodied fish so the capacity of this natural carbon pump to deep sea. Yet, the carbon balance of tuna populations, so the net difference between CO₂ emission due to industrial exploitation and CO₂ sequestration by fish deadfall after natural mortality, is still unknown. Here, by considering the dynamics of two main contrasting tuna species (*Katsuwonus pelamis* and *Thunnus obesus*) across the Pacific since the 1980s, we show that most tuna populations became CO₂ sources instead of remaining natural sinks. Without considering the supply chain, the main factors associated with this shift are exploitation rate, transshipment intensity, fuel consumption, and climate change. Our study urges for a better global ocean stewardship, by curbing subsidies and limiting transshipment in remote international waters, to quickly rebuild most pelagic fish stocks above their target management reference points and reactivate a neglected carbon pump toward the deep sea as an additional Nature Climate Solution in our portfolio. Even if this potential carbon sequestration by surface unit may appear low compared to that of coastal ecosystems or tropical forests, the ocean covers a vast area and the sinking biomass of dead vertebrates can sequester carbon for around 1000 years in the deep sea. We also highlight the multiple co-benefits and trade-offs from engaging the industrial fisheries sector with carbon neutrality.

KEYWORDS

blue carbon, climate change, modeling, Natural Climate Solutions, population dynamics

1 | INTRODUCTION

To avoid damageable and irreversible climate change impacts (Armstrong McKay et al., 2022; Boyce et al., 2022; Calel et al., 2020; Cinner et al., 2022; Hoegh-Guldberg et al., 2019; Mora et al., 2018; Rode et al., 2021), the world needs to rapidly reduce emissions of

greenhouse gases by human activities according to Paris Agreement pledges (Meinshausen et al., 2022). Yet, human population growth, economic development, and climate warming itself are boosting the global demand for food and energy which generates most of emissions (Clark et al., 2020; Ivanovich et al., 2023; Sarkodie et al., 2020; van Ruijven et al., 2019; Zheng et al., 2020). The challenge for all

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sectors of the economy is thus to target a net zero emission of greenhouse gases in the short term and not to turn natural resources acting as CO₂ sinks into new sources.

Tuna fisheries represent a key food production sector that sustains economy and employment worldwide with reported landings of more than 7 million tons a year, with Pacific Ocean tuna fisheries accounting for around 74% of total global catches in 2016 (Coulter et al., 2020; FAO, 2020). Under the increasing demand for tunas, technological advances, and support of subsidies, industrial fishing fleets have rapidly expanded over the oceans and reached even the most remote fishing grounds in the high seas (Sala et al., 2018; Tickler et al., 2018). The modern tuna fishing industry relies heavily on fossil fuel for vessel propulsion over vast distances and a range of ancillary activities (e.g., onboard freezing) adding up 2 kg of emitted CO₂ per kg of landed fish (Parker et al., 2018). This industry can thus annihilate or even reverse the natural carbon sequestration potential of tuna populations.

Indeed, tunas can be considered as sinks of CO₂ through the deadfall of blue carbon, so the carbon stored in their body that reaches the deep-sea floor after their natural death (senescence or disease) where it remains sequestered for a long time (1000 years) (Mariani et al., 2020; Pinti et al., 2022). Yet, industrial fisheries have drastically reduced the size of tuna populations (Juan-Jordá et al., 2011; Pons et al., 2018) and consequently the unevaluated sequestration capacity of this natural carbon pump toward the deep sea. The carbon balance of tropical tuna populations is thus totally unknown between a fisheries sector burning more fossil fuel to operate from where fish are consumed (Watson et al., 2015), suggesting an overall increasing source of CO₂ emissions, and the deadfall of such large-bodied fish indicating a potential carbon sequestration that has never been estimated (Mariani et al., 2020). Moreover, the rising of sea surface temperature, which modifies thermal structure and oxygen concentration affecting tuna populations (Taboada et al., 2022), and the increasing rate of tuna exploitation, largely sustained by harmful capacity-enhancing subsidies (Machado et al., 2021), may have shifted this balance over the last decades but unequally across the ocean.

Here, we used tuna catches and simulations from a spatial ecosystem and population dynamics model (SEAPODYM) to assess the spatial distribution of this carbon balance across the Pacific for two species since the development of the tuna purse seine fishery in the 1980s. Finally, we explained the spatiotemporal distribution of carbon balance using several key environmental but also human factors.

2 | MATERIALS AND METHODS

2.1 | The SEAPODYM model

We used observed tuna catches and simulations from a spatial ecosystem and population dynamics model (SEAPODYM) that has been parameterized to mimic the spatiotemporal patterns of tuna catches per unit of effort and size frequency of catches across

the Pacific since the 1980s taking into account age-structured predation rates, dispersal capacity, climate, and primary production (Lehodey et al., 2008; Senina et al., 2019). More precisely, SEAPODYM includes two different dynamical models: (i) an ecosystem model of spatiotemporal dynamics of functional groups of lower- and mid-tropic level organisms, simulating the abundance of food for tunas, and (ii) a model describing full spatiotemporal dynamics of a single species population with the parameter estimation methods allowing integration of fisheries and tagging data. The underlying continuous equations of SEAPODYM are classical advection–diffusion–reaction equations with aging term, describing the dynamics of a biomass density in time, age, and two-dimensional space. SEAPODYM predicts the biomass of modeled species at a given age, time and spatial location, as well as the catch and size frequency of catch.

We considered two tropical tuna species with contrasted life-history traits (Horswill et al., 2019) which sustain some of the largest and most valuable fisheries in the world (Coulter et al., 2020; McKinney et al., 2020): the skipjack tuna (*Katsuwonus pelamis*) which is a small and fast-growing species (Von Bertalanffy growth rate of 0.47, 30 cm long, and 3 kg weight on average) with relatively stable populations accounting for 57.83% of tuna catches so 2.9 million tons in 2018 (McKinney et al., 2020), and the bigeye tuna (*Thunnus obesus*) which is a large and slow-growing species (Von Bertalanffy growth rate of 0.12, 140 cm long, and 90 kg weight on average) with decreasing and vulnerable populations (Juan-Jordá et al., 2011), but still accounting for 7.84% of tuna catches so 406,257 tons in 2018 (McKinney et al., 2020). The parameters to be estimated control the dynamic processes that are linked to the environment: reproduction, natural mortality, and movement. The parameters for the model of a highly migratory skipjack tuna were estimated by integrating historical fisheries data and tagging data (Senina et al., 2019). The reference model of bigeye tuna population was obtained based on fisheries data, although the tagging data were also used to condition the estimation of movement parameters (Senina et al., 2020). The originality of SEAPODYM is to integrate both fisheries (longline, purse seine, and pole-and-line catches and efforts) and individual tagging data to inform model parameters. SEAPODYM models were run between 1983 and 2009 for the two species across the Pacific.

2.2 | From tuna population dynamics to carcass deadfall

Mortality rate for each year and each size class of modeled tuna populations was calculated from the simulations under non-fishing and fishing scenarios. The model includes two theoretical mortality functions: one accounts for mortality due to predation (including cannibalism) rapidly decreasing with age, while the other represents other types of death such as senescence, starvation, and disease. To calculate the biomass sinking to the ocean floor we focused only on the second function. However, this theoretical function implemented in SEAPODYM is highly dependent on the environment

(food availability, temperature) and cannot be used directly outside the model. To overcome this limitation, we decided to calculate a mortality rate inferred from a simulation without fishing mortality, and then to remove the part due to the mortality by predation expressed by the model's theoretical function that, unlike the other one, depends little on environmental parameters. There is certainly some predation mortality at larger sizes that is implicitly included in the mean mortality coefficient. Therefore, this approach provides a conservative estimation of the biomass proportion sinking to the bottom.

From month to the next, we calculated the number of disappearances in each cohort to determine the proportion of "naturally" dead individuals over this period. Overall, the abundance of fish by cohort decreases with age, while their individual weight increases. The decrease in abundance through age can be modeled by a decreasing exponential curve that represents the mortality rate of older individuals. The parameters of this function were estimated on the basis of maximum life expectancy for each species (15 years for bigeye tuna and 5 years for skipjack tuna) but also considering the number of individuals joining this age class each month and the total number of individuals in this elder age class. To avoid overestimating the sinking biomass and carbon sequestration, we only considered age classes corresponding to individuals weighing more than 1 kg, assuming that below this weight, dead individuals would not sink and die from predation. Thus, for all the considered age classes, we subtracted the theoretical predation mortality rate (M_{preda}) from the inferred total mortality rate (M_{inferred}) to obtain the senescence (and related) mortality rate ($M_{\text{senescence}}$), which applied to the population allows us to calculate the carcass deadfall for each month and each age class as follows:

$$M_{\text{senescence}}(\text{age}) = M_{\text{inferred}}(\text{age}) - M_{\text{preda}}(\text{age})$$

$$M_{\text{preda}}(\text{age}) = \alpha \times e^{-\beta \times \text{age}}$$

with M representing the mortality rate of each size class each month. For this, we considered that each individual tuna contains, on average, $12.5 \pm 2.5\%$ of carbon in its fresh biomass (Bar-On et al., 2018; Czamanski et al., 2011).

2.3 | Carbon emissions and deficit of sequestration due to fisheries

Industrial fisheries impacted carbon sequestration at two levels. First, the tuna biomass landed did not sink but was instead extracted from the water and then mostly consumed as human food. We thus considered that the carbon of fished tuna carcasses was reemitted to the atmosphere in a relatively short time, except for the bones which represent 6% of the biomass (Garrido Gamarro et al., 2013; Nicholson, 1998). Second, fishing activities require the combustion of fuel, which represents another source of carbon in the atmosphere. The CO_2 emission rate emitted per unit of fish landed was estimated according to the fishing methods used

(Parker et al., 2018; Tyedmers & Parker, 2012). The three major fishing techniques are purse seine (23% of bigeye tuna catches and 65% of skipjack tuna catches) with a fuel rate of 398 Lt^{-1} of fish caught, longline (70% of bigeye tuna catches and less than 1% of skipjack tuna catches) with 1027 Lt^{-1} of fish caught and pole and line (3% of bigeye tuna catches and 24% of skipjack tuna catches) with 1485 Lt^{-1} of fish caught. These values were estimated for 2011 but we considered them constant across the entire period (Parker et al., 2018; Tyedmers & Parker, 2012). Given the diversity of tuna products and the complexity of supply chains, we could not account for postharvest emissions due to food processing, retail, and packaging, nor from transportation so our estimations are conservative.

We define the carbon balance as the net difference between CO_2 emission due to industrial exploitation and CO_2 sequestration by fish deadfall after natural mortality for a given tuna population and a given period. We then assessed the spatial distribution of this carbon balance across the Pacific within $6^\circ \times 6^\circ$ grid cells for the two species in the early period of development of the tuna purse seine fishery in the 1980s and once this fishery was fully deployed in the 2000s (Lehodey et al., 2008; Senina et al., 2019). The sequestration deficit corresponds to the difference in sequestration by the two populations modeled with and without fishing scenarios.

2.4 | Uncertainty

We considered two levels of uncertainty to estimate the carbon source-sink dynamics of tuna populations. The first uncertainty is related to the carbon content in fish body fixed at $12.5 \pm 2.5\%$. This confidence interval was calculated based on different values available in the literature (Bar-On et al., 2018; Czamanski et al., 2011) from which we estimated the 95% confidence interval. The second uncertainty lies in the CO_2 emission rate per unit of fish landed (E_{fuel}) which differs among species and fishing techniques (Parker et al., 2018; Tyedmers & Parker, 2012). Given the limited data available for each fishing technique, we calculated uncertainty on purse seine data (noted $E_{\text{fuel_PS}}$, $n=11$) and assumed that uncertainty for all other fishing methods (i.e., longline, pole, and line) was the same. Given the lack of knowledge of probability law on the 11 measures, we used an estimator (u_{fuel}) of the standard deviation:

$$u_{\text{fuel}} = \frac{1}{\sqrt{n}} \cdot \sqrt{\frac{1}{n-1} \sum_{i=1}^n (E_{\text{fuel_PS}_i} - \overline{E_{\text{fuel_PS}}})^2}$$

To obtain an uncertainty at 95%, we multiplied u_{fuel} by the Student coefficient at 10 degrees of freedom and divided it by the mean ($\overline{E_{\text{fuel_PS}}}$) to obtain a relative uncertainty ($u_{\text{fuel_rel}}$). To take into account all types of fishing methods, we applied this relative uncertainty to the mean CO_2 emission rates from all fishing methods, weighted by their contribution to total catches of each species. For the skipjack tuna, we obtained $2.04 \pm 0.22 \text{ kg}$ of CO_2 emitted for each kg of fish landed, versus 2.78 ± 0.29 for the bigeye tuna.

Finally, we combined the two levels of uncertainty (body carbon content and CO₂ emission rate) on the carbon source–sink value by applying a quadratic propagation of each uncertainty effect. The global two-level uncertainty u_{TOT} on the carbon source–sink balance equals:

$$u_{\text{TOT}}(\text{CO}_2) = \sqrt{\sum_{u=1}^2 \left(\left(\frac{\partial \text{CO}_2}{\partial u_i} \right) \cdot u_{\text{reli}} \right)^2}$$

2.5 | Estimation of explanatory factors

To better understand the context within which tuna populations can be CO₂ sinks or sources we estimated five potential explanatory factors for each grid cell and each period: (i) marine primary productivity, which is the basis of the food chain toward predators, (ii) exploitation rate, which is the fraction of the population fished over a given period of time, (iii) sea surface temperature, which determines individual metabolism and growth rate, (iv) distance to the nearest harbor, which is a proxy of human impacts, and (v) transshipment intensity, which has a positive effect in term of CO₂ release by reducing fuel consumption but can also increase fishing pressure by reducing operating costs and favoring illicit activities and subverting regulations.

Marine primary production was quantified as monthly temporal mean in chlorophyll *a* concentration from 2002 to 2009 (Tyberghein et al., 2012). Exploitation rate was expressed as the monthly average proportion of fish stock removed by fishing, calculated on the two time periods, from 1983 to 1988 and from 2005 to 2010. SST is extracted from two Earth System Models, Institut Pierre Simon Laplace climate model 5A-MR (IPSL-CM5A-MR) and the NOAA Geophysical Fluid Dynamic Laboratory Earth System Model 2G (GFDL-ESM2G), and quantified as the annual mean for the two historical time periods, under the Representative Concentration Pathways 8.5 (RCP 8.5) (Schwalm et al., 2020). Finally, we used two proxies of fisheries geographical expansion. First, we estimated the distance of each grid cell to the nearest large or medium harbor, with port locations obtained from the World Port Index database. Then, transshipment intensity from

2012 to 2018 (i.e., cumulated events of transfer of fresh catch from a fishing vessel to a larger refrigerated cargo ship, far from a home port) was obtained from Global Fishing Watch database (Miller et al., 2018). We also calculated the delta in exploitation rate (ΔER), in sea surface temperature (ΔSST), and in CO₂ balance (ΔCO_2) for each grid cell as the difference between average annual values for the period 2005–2010 and average annual values for the period 1983–1988.

2.6 | Modeling the CO₂ balance

We analyzed linear relationships between the CO₂ balance within 6°×6° grid cells and marine primary productivity (logPP), exploitation rate (ER), sea surface temperature (SST), distance to the nearest harbor (logNH), and transshipment intensity (logTI) while accounting for any spatial dependence in the residuals. For this we applied generalized least squares (GLS) models, implemented in the R package *nlme*, which are known to provide unbiased estimates of regression coefficients when spatial data violate standard regression assumptions (Beale et al., 2010; Beguería & Pueyo, 2009). We also included a quadratic term for sea surface temperature in the models to account for potential nonlinear relationship with CO₂ balance given that each species has an optimal thermal niche (Boyce et al., 2008).

Since we had no a priori expectation about the form of the spatial autocorrelation among grid cells, we used AIC to compare four commonly used models of spatial autocorrelation: Spherical, Exponential, Gaussian, and Rational Quadratic. For each analysis, we report statistics from the fit that included the spatial autocorrelation function yielding the lowest AIC value (Table 1). Then we used the best fit model out of eight (four spatial autocorrelation forms with or without the quadratic SST term) to produce partial regression plots showing the effect of each factor while controlling for others and space. These plots were built with the *visreg* R package. We finally used GLS to explore how changes in the two main factors (sea surface temperature and exploitation rate) are associated with the changes in CO₂ balance of tuna populations between the late 2000s and the 1980s while controlling for spatial autocorrelation among grid cells.

TABLE 1 Results from generalized least squares (GLS) models predicting the CO₂ balance of tuna populations across the Pacific as a function of five factors (see Section 2).

| | df | Skipjack tuna | | Bigeye tuna | |
|---|----|---------------|-------------------|-------------|-------------------|
| | | t-Value | p-Value | t-Value | p-Value |
| Mean sea surface temperature (SST) | 1 | -2.17 | .03* | -1.20 | .23 ^{NS} |
| SST ² | 1 | — | — | 1.99 | .046* |
| Primary production (Chla) | 1 | -0.18 | .85 ^{NS} | 2.20 | .027* |
| Exploitation rate (ER) | 1 | 8.35 | <.001*** | 11.3 | <.001*** |
| Distance to the nearest fishing harbor (Dist) | 1 | 1.23 | .22 ^{NS} | 2.70 | .007** |
| Transshipment (Trans) | 1 | 0.22 | .82 ^{NS} | 3.96 | .001*** |

Note: df is the degree of freedom for each factor (^{NS}, not significant, **p* < .05, ***p* < .01, ****p* < .001). SST² is for the squared term of the mean Sea Surface Temperature.

3 | RESULTS

3.1 | The long-term dynamics of the carbon balance

The SEAPODYM model reveals a decrease in the Pacific fish stocks from 10.9 Megatonnes (Mt) for the skipjack tuna in 1983 to 9.5 Mt in 2009 (Figure 1a) and from 4.2 Mt for the bigeye tuna in the 1983 to 2.8 Mt in 2009 (Figure 1b). This decrease is mainly associated with the increase in exploitation rate (% of the total biomass removed by month) from 0.5% for the skipjack tuna in the 1980s to 1.5% in 2009 (Figure 1c) and from 0.33% for the bigeye tuna in the 1980s to 0.62% in 2009 (Figure 1d). By contrast, a scenario without fishing over the same period shows a fluctuating but stable skipjack tuna stock (Figure 1a) and a slight increase in the bigeye tuna stock (Figure 1b).

When applying a natural mortality rate per age class and considering only the deficit of sequestration due to fishing, the carbon sequestration capacity has decreased for both species since the 1980s decreasing from 8.8 (± 1.8) to 7.03 (± 1.4) Mt CO₂ year⁻¹ in 2009 for the skipjack tuna (Figure 1e) and from 0.58 (± 0.12) to 0.34 (± 0.07) Mt CO₂ year⁻¹ for the bigeye tuna (Figure 1f). In 2009, the deficit of

sequestration compared to a scenario without fishing reaches 2.5 Mt CO₂ year⁻¹ for the skipjack tuna, so -26%, and 0.59 Mt CO₂ year⁻¹, so -62%, for the bigeye tuna.

The skipjack tuna stock was still a sink of CO₂ in 2009 but its sequestration capacity dropped by 6 Mt CO₂ year⁻¹, or 62% since 1980s relative to a scenario without fishing, with <3.5 (± 1.4) Mt CO₂ year⁻¹ since 2007 (Figure 1e). The bigeye tuna stock became a source of CO₂ in the early 1990s under fishing pressure and its exploitation induced a net emission of around 0.23 (± 0.09) Mt CO₂ year⁻¹ in the late 2000s (Figure 1f). Compared to a scenario without fishing, the net balance of CO₂ sequestration was reduced by 1.2 Mt CO₂ year⁻¹ for the bigeye tuna in 2009.

3.2 | Heterogeneity of the carbon balance across the Pacific

In the 1980s, skipjack tuna populations act as a net sink of CO₂ in 95.7% of the cells (Figure 2a), sequestering on average 21.6 (± 4.9) kt of CO₂ per grid cell and per year so 0.5 (± 0.11) kg CO₂ · ha⁻¹ annually with a marked peak (230.2 \pm 51.7 kt of CO₂ or 5.2 \pm 1.2 kg CO₂ · ha⁻¹

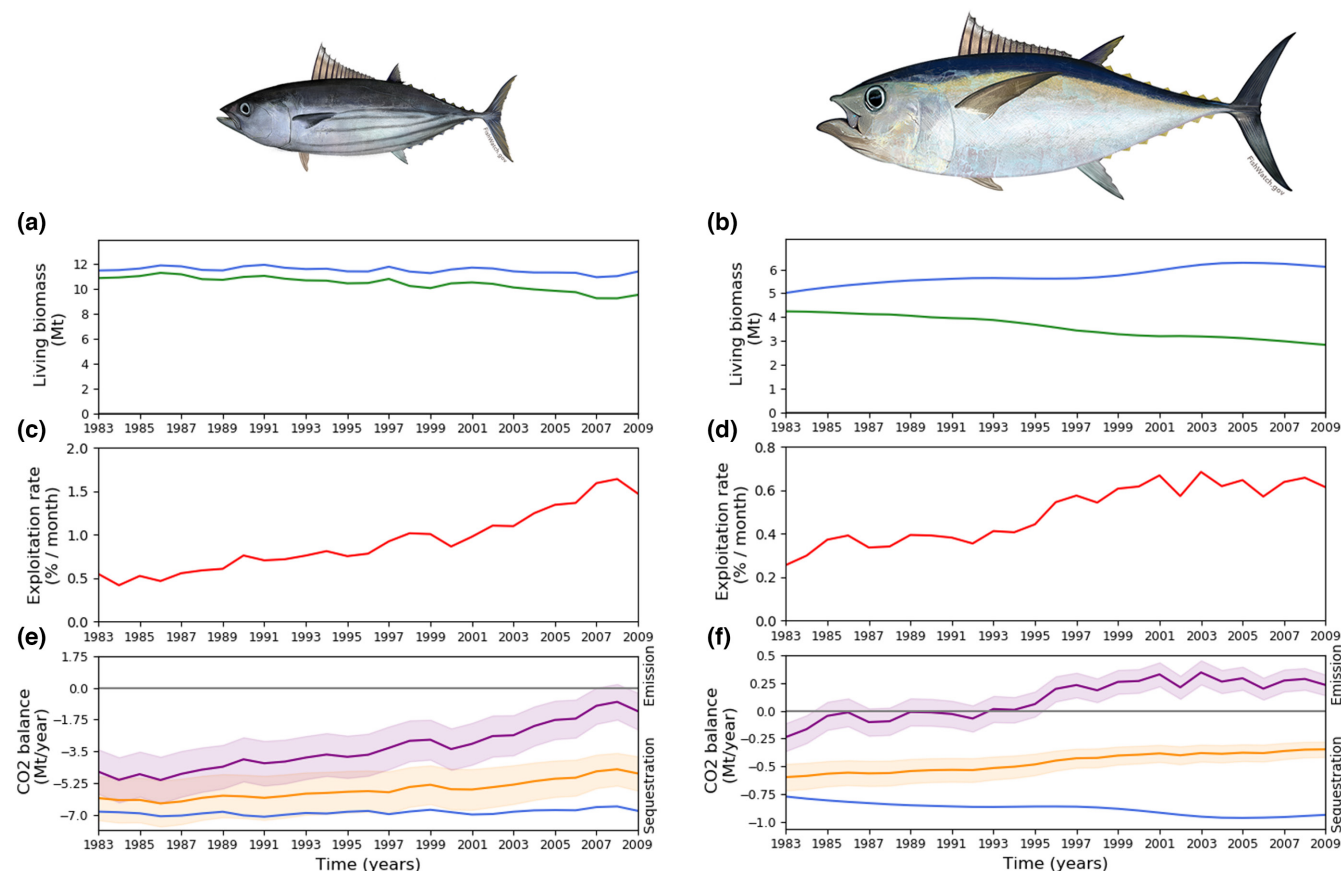


FIGURE 1 Temporal trends in fish stock (a, b), exploitation rate (c, d), and CO₂ balance between sequestrations and emissions (e, f) since 1980 in the Pacific for the skipjack tuna (*Katsuwonus pelamis*, left panels) and the bigeye tuna (*Thunnus obesus*, right panels). The blue lines (a, b, e, f) represent the stocks and CO₂ balances without fishing. The green lines (a, b) represent the stocks under exploitation. The orange lines (e, f) represent the CO₂ balances considering only the deficit of sequestration due to fishing while the purple lines also include fuel emissions including uncertainty.

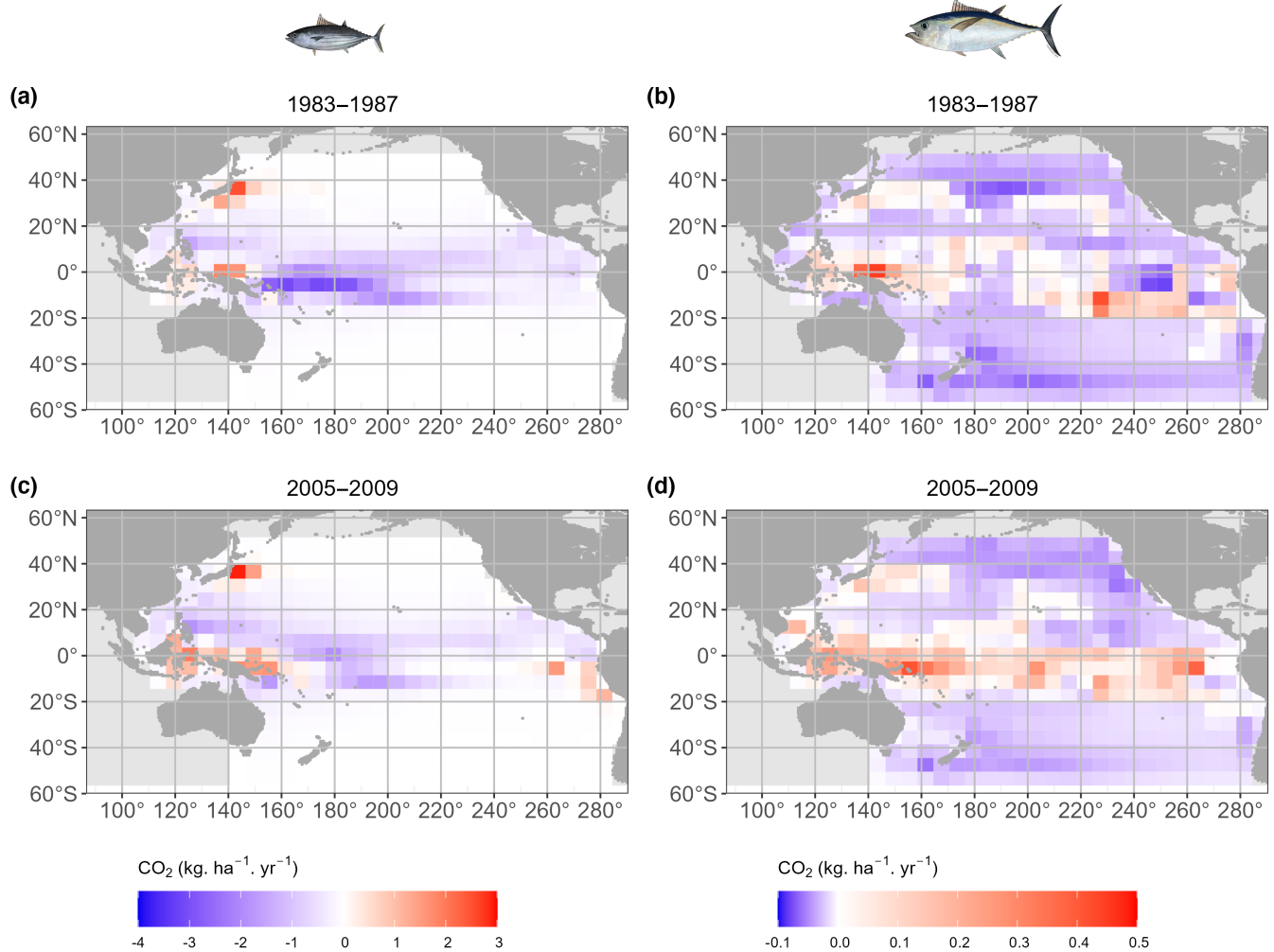


FIGURE 2 Temporal and spatial changes in CO_2 balance between sequestration and emission across the Pacific for the skipjack tuna (*Katsuwonus pelamis*) on left panels (a, c) and the bigeye tuna (*Thunnus obesus*) on right panels (b, d) populations. CO_2 sink tuna populations are in blue while source populations are in red.

annually) in the West Pacific (170° longitude) and close to equator (-5° latitude). Skipjack tuna populations act as a net source of CO_2 in the remaining cells (4.3%) with emissions reaching on average $16.1 (\pm 5.13)$ kt of CO_2 per grid cell and per year, so $0.41 (\pm 0.12)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually. These source populations are mainly located in the West Pacific, close to Japan and Indonesia (Figure 2a).

By contrast, bigeye tuna populations in the 1980s were already net sources of CO_2 in 21.8% of the cells, emitting on average $2.8 (\pm 0.57)$ kt of CO_2 per grid cell and per year, so $0.065 (\pm 0.01)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually. Those CO_2 sources were mainly located in the tropical East and West Pacific (Figure 2b). In most temperate areas, except close to Japan, bigeye tuna populations were sinks of CO_2 but with an average of only $1.18 (\pm 0.32)$ kt of CO_2 removed from the atmosphere per grid cell so $0.032 (\pm 0.008)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually (Figure 2b).

In the late 2000s, skipjack tuna populations turned from sinks to net sources of atmospheric CO_2 in 5.5% of the cells, mainly in the East and West Pacific close to the mainland (Figure 2c). Other areas, mainly located in the Central Pacific, remained a net sink of CO_2 with

up to $12.6 (\pm 3.2)$ kt of CO_2 removed from the atmosphere per grid cell, or $0.29 (\pm 0.07)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually, so 40% less than the mean sink value estimated in the 1980s. Pacific bigeye tuna populations were net CO_2 sources in the tropics (between 20°S and 20°N latitude) in the late 2000's with a peak in the equatorial West Pacific at $18.2 (\pm 1.8)$ kt of CO_2 added to the atmosphere, or $0.41 (\pm 0.04)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually, so more than six times the mean source value estimated in the 1980s (Figure 2d). Most temperate and sub-tropical populations remained net CO_2 sinks but of lower magnitude than in the 1980s with a peak at only $2.2 (\pm 0.44)$ kt of CO_2 removed from the atmosphere per grid cell so $0.06 (\pm 0.01)$ $\text{kg CO}_2 \cdot \text{ha}^{-1}$ annually.

3.3 | Drivers of the carbon balance

The CO_2 balance of skipjack tuna populations in the late 2000s is weakly explained ($R^2 = .25$) by a model selected on AIC criteria with a Gaussian spatial autocorrelation but without the sea surface temperature quadratic term (Table 1). Exploitation rate ($t = 8.35$,

$p < .001$) and SST ($t = -2.61$, $p = .03$) have by far the main and only significant effects on carbon balance followed by distance to the nearest port ($t = 1.22$, $p = .22$) while the other factors have no effect. Partial plots show that skipjack tuna populations become CO₂ sources when exploitation rate increases above $\log_{10}(\text{ER}+1) = 0.1$ so 0.25 or 25% (Figure 3a). When all other factors have an average value, skipjack tuna populations are stronger CO₂ sinks when SST increases (Figure 3c) but become weaker CO₂ sinks further from the nearest seaport (Figure 3g), although the impact of this factor is not significant ($p > .05$).

For bigeye tuna populations, the CO₂ balance in the late 2000s is well explained ($R^2 = .59$) by a model retaining the SST quadratic term and a Gaussian spatial autocorrelation (Table 1). Areas with SST between 10 and 15°C are the strongest CO₂ sinks while areas with SST higher than 25°C become CO₂ sources when all other factors are fixed at the mean (Figure 3d). Like for the skipjack tuna, the main effect is exploitation rate ($t = 11.30$; $p < .001$) but all other factors significantly explain CO₂ balance with transshipment ($t = 3.96$; $p < .001$), distance to the nearest harbor ($t = 2.70$; $p = .007$), and primary production ($t = 2.20$; $p = .027$) having positive effects, so favorizing

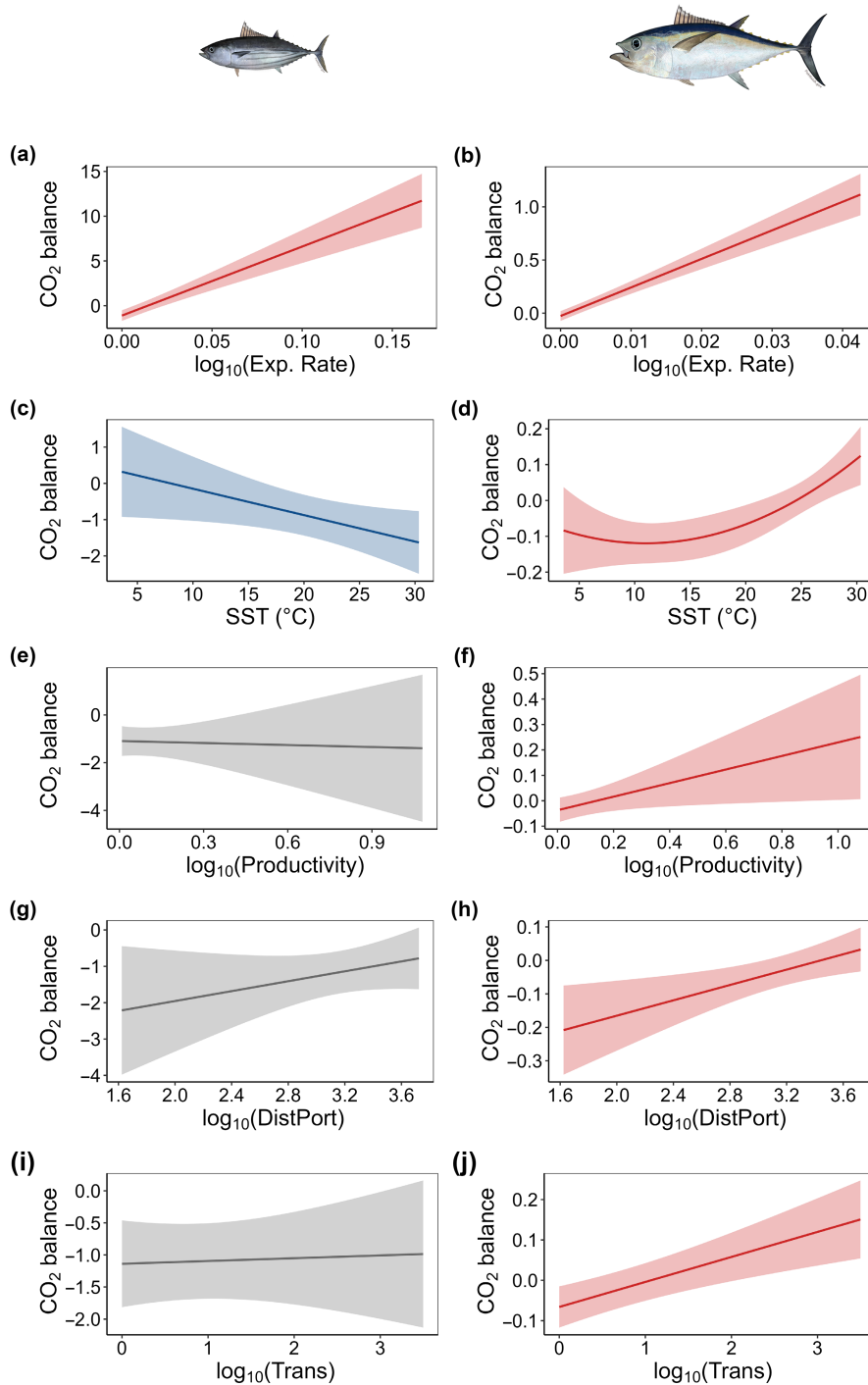


FIGURE 3 Relationships between the CO₂ balance of tuna populations and the explanatory factors. (a, b) Exploitation rate (Exp. Rate, log₁₀-transformed); (c, d) sea surface temperature (SST), (e, f) marine primary production (productivity, log₁₀-transformed), (g, h) distance to nearest fishing harbor (DistPort, log₁₀-transformed) and (i, j) transshipment activity (Trans, log₁₀-transformed) for the skipjack tuna (*Katsuwonus pelamis*, left panels) and the bigeye tuna (*Thunnus obesus*, right panels). These partial plots are obtained from generalized least squares models fitted with data in the 2000s. In red, the factor positively impacts the CO₂ balance (i.e., increases emissions), in blue, the factor negatively impacts the CO₂ balance (i.e., increases sequestration), in gray, the factor has no significant impact on the CO₂ balance.

emissions (Table 1). Partial plots reveal that only unexploited areas can be CO₂ sinks (Figure 3b). Areas with high primary production (Figure 3f), far from fishing harbors (Figure 3j) and under important transshipment activities are the main CO₂ sources (Figure 3j).

For the skipjack tuna, the selected model without the SST quadratic term and a rational quadratic spatial autocorrelation weakly explains changes in CO₂ balance between the two periods ($R^2 = .12$). This change is only and significantly explained by change in exploitation rate ($t = 4.57$, $p < .001$) while change in SST has no influence ($t = 0.63$, $p = .52$) (Table 2). The partial plot shows that the increase in exploitation rate induced a major increase in CO₂ balance toward emissions between 1980s and 2000s (Figure 4a) while increasing SST could not significantly reverse this trend (Figure 4c). The change in CO₂ balance for bigeye tuna populations is also weakly explained by a model retaining the SST quadratic term and a Gaussian spatial autocorrelation ($R^2 = .19$). As for the skipjack tuna, exploitation rate increase between 1980s and 2000s induced a highly significant

increase in CO₂ emissions ($t = 6.20$, $p < .001$, Figure 4b) while the change in SST had a marginal influence (Figure 4d) for both linear and quadratic terms (Table 2).

4 | DISCUSSION

The Agriculture, Forestry, and Other Land Use (AFOLU) sector has the potential to provide about a third of the climate mitigation needed by 2030 to meet the goals of the Paris Agreement (Griscom et al., 2019). For instance, forestland in the United States can sequester up to 2.13 tCO₂·ha⁻¹ annually (Domke et al., 2020) while regrowing natural forests has the potential to accumulate the equivalent of between 0.21 and 22 tCO₂·ha⁻¹ annually over the next 30 years depending of the ecozone (Cook-Patton et al., 2020). These numbers are several orders of magnitude higher than those for tunas (maximum of 5.2 kg CO₂·ha⁻¹ annually for the skipjack). However,

TABLE 2 Results from generalized least squares (GLS) models predicting the change in CO₂ balance of tuna populations across the Pacific as a function of changes in two factors (see Methods).

| | Skipjack tuna | | Bigeye tuna | | |
|------------------------------------|---------------|---------|----------------------|---------|----------------------|
| | Df | t-value | p-value | t-value | p-value |
| Mean sea surface temperature (SST) | 1 | 0.63 | .52 ^{NS} | 1.05 | .29 ^{NS} |
| SST ² | 1 | — | — | -1.12 | .26 ^{NS} |
| Exploitation rate (ER) | 1 | 4.57 | <.001 ^{***} | 6.20 | <.001 ^{***} |

Note: SST² is for the squared term of the mean Sea Surface Temperature.

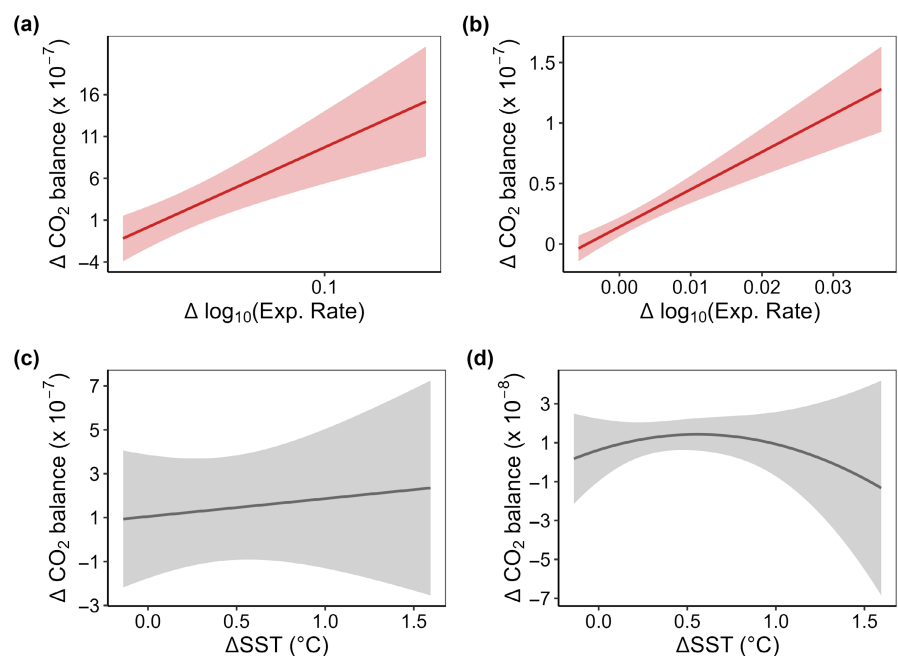


FIGURE 4 Relationships between the change in CO₂ balance (difference in the data between the 1980s and the 2000s) of tuna populations and the explanatory factors, so exploitation rate or Exp. Rate (a, b) and sea surface temperature or SST (c, d) for the skipjack tuna (*Katsuwonus pelamis*, left panels) and the bigeye tuna (*Thunnus obesus*, right panels). In red, the factor positively impacts the CO₂ balance (i.e., increases emissions), in gray, the factor has no significant impact on the CO₂ balance.

the time during which carbon is sequestered also differs, with higher values for fish compared to forests, even if fish carcasses are not buried in the deep-sea sediment. Indeed, burial rates of carbon in the ocean, so carbon trapped in the sediment for millennia, is very low, around 0.1% of the primary production, a process that tends to weaken with climate change (Li et al., 2023). This low burial rate, associated with the presence of scavengers in the deep sea consuming the most edible parts of fish carcasses, leads to the remineralization of carbon into CO₂. Even in this case, the sequestration time of fish carcasses is estimated around 800 and 1000 years in the deep sea (Pinti et al., 2022), making them a more efficient carbon sink in terms of sequestration time compared to terrestrial organisms having a median carbon turnover time of 43 years.

This taxonomic and spatial extension would need subsequent research to perform a full life cycle analysis of the fishing industry. For this, we need to assess the contributions of fish to the oceanic carbon cycle including fecal pellet carbon export (Bianchi et al., 2021), respiration (Saba et al., 2021), and fertilization (Dupont et al., 2023), as well as emissions throughout the entire supply chain (Poore & Nemecek, 2018). For instance, it is roughly estimated that supply chain emissions account for 10–40% of the total CO₂ emissions (Tyedmers & Parker, 2012). So, tunas and other marine vertebrates certainly represent an underestimated carbon sink toward climate change mitigation and an additional option in the portfolio of NCS. However, it would also be necessary to study whether the deficit of predation due to the extraction of predators is not inducing an increase in the biomass of prey, in particular the mesopelagic micronekton (Pinti et al., 2023), which would then compensate a part of the loss in carbon sequestration due to top predator exploitation.

Yet, we show that exploitation by fisheries and to a lesser extent SST, can profoundly shape the CO₂ balance of tuna populations which were mainly acting as CO₂ sinks in the 1980s and have partly become CO₂ sources in the 2000s due to both fuel consumption to reach remote areas (Watson et al., 2015) and decreasing stocks (Pons et al., 2017) under higher exploration rate which reduces the sinking of dead carcasses. For both species, exploitation rate is indeed the main factor explaining the CO₂ balance of tuna populations across the Indo-Pacific Ocean (Table 1) and through time (Table 2). Our quantitative assessment suggests that only unexploited or marginally exploited bigeye tuna populations can remain CO₂ sinks (Figure 3b) while an upper limit of 25% exploitation rate would be needed to maintain skipjack tuna populations as CO₂ sinks in the Pacific (Figure 3a). Yet, skipjack tuna catches continue to rise reaching up to 3 million metric tons in 2018 globally (McKinney et al., 2020). This increase could be associated with better recruitment conditions due to ocean warming as suggested by stock assessment studies (Castillo Jordán et al., 2022). For bigeye tuna, the situation is more contrasted from just above the maximum level of exploitation rate in the western central Pacific Ocean, and just below in the eastern Pacific Ocean, to strong overfishing in the Indian Ocean (Ducharme-Barth et al., 2020; ISSF, 2023). So, even if tuna populations are recovering since the 1990s owing to proactive fisheries management approaches (Pons et al., 2018), more radical

interventions may be necessary to reverse the CO₂ balance of these populations, to quickly rebuild all these fish stocks above their target management reference points. This could be even revised to higher values, to increase carbon sequestration and potentially monetize this ecosystem service, like for whales, owing to a rigorous valuation of carbon dioxide removal (Pearson et al., 2023).

Trends in sea surface temperature have an opposite impact on the CO₂ balance of both species in line with their optimal thermal niche (Boyce et al., 2008). The tropical skipjack tuna increases its carbon sinking capacity under higher temperature (Figure 3c), at least till 30°C but the more temperate bigeye tuna is becoming more a source of CO₂ above 20°C, as one moves away of the optimal thermal niche of adults, roughly between 10 and 17°C outside the breeding period (Fuller et al., 2015; Hampton et al., 2023). So, we highlight a positive feedback loop between climate change and blue carbon export for the bigeye tuna, so climate change leads to lower population sizes and lower sequestration potential through the sinking of dead carcasses (Taboada et al., 2022), or fecal pellets which is not included in our assessment (Bianchi et al., 2021). This negative effect could be reinforced by the ocean deoxygenation associated with climate change and ocean warming, since tuna species are known to be sensitive to low oxygen concentrations (Findlay, 2023; Mislan et al., 2017).

The CO₂ balance for the largest species (bigeye tuna), only targeted by industrial fisheries, is also positively related to transshipment. Transshipment allows fishing boats to remain on the high seas away from the coast for long periods of time to minimize fuel costs and maximize catches, hence economic profits (Boerder et al., 2018). If that practice may reduce the fuel cost per catch, it increases fishing pressure and facilitates illegal, unreported and unregulated (IUU) fishing, as well as instances of forced labor (McDonald et al., 2021), particularly in remote and poorly monitored international waters. Thus, a better ocean stewardship is needed, particularly to reinforce control and protection efforts in the high sea (areas beyond national jurisdictions) (Sala et al., 2021), to reduce capacity-enhancing subsidies which sustain overexploitation (Sala et al., 2018) and to regulate and monitor transshipment (Seto et al., 2020). Rebuilding most pelagic fish stocks through effective management can be achieved within a few decades (Costello et al., 2016; Duarte et al., 2020) while measures to reduce CO₂ emissions due to fishing operations can be immediate by curbing harmful and unfair subsidies (Sala et al., 2018; Sumaila et al., 2014). However, leading the industrial fisheries sector toward carbon neutrality by promoting fish blue carbon sequestration requires to tackle two major challenges. First, seafood may not be substituted by other sources of proteins with higher environmental impacts such as land degradation, water use, biodiversity loss, energy consumption, and pollution (Herrero et al., 2013; MacLeod et al., 2020; Zhang et al., 2017). For instance, beef is the least efficient source of calories and protein, generating much more greenhouse gas emissions per unit of protein than pork, chicken, egg production, and wild fish (de Vries & de Boer, 2010; Hilborn et al., 2018). Second, reducing catches should not jeopardize food security and tuna-dependent economies in developing countries like some

island states of the Indian and Pacific oceans where fish are a major source of protein and micronutrients essential for human health (Bell et al., 2021; Hicks et al., 2019; McClanahan et al., 2015). The cumulative benefit of management actions has been demonstrated (Melnychuk et al., 2021) and could be an effective strategy to address these two challenges, especially in the high seas where catches benefits mainly to food-secured countries (Schiller et al., 2018). For instance, agreements within regional tuna fisheries management organizations to implement measures for faster rebuilding of overfished stocks to above their target management reference points. In the meantime, additional spatial management measures to limit fishing effort and eliminate IUU on the high seas would maintain catches in the EEZs of developing countries and their associated economic revenues (Popova et al., 2019), without jeopardizing the food security of wealthy countries (Schiller et al., 2018), the main actors in high seas fishing (McCauley et al., 2018). We thus highlight the potential multiple co-benefits from engaging the industrial fisheries sector with carbon neutrality. Yet, even if large animals have the greatest potential to facilitate climate change mitigation at a global scale, they only hold two petagrams (Pg; 10^9 tonnes) carbon (fish: 0.7Pg carbon) so the total amount of carbon stored in all wild animals is small compared to emissions of the total agriculture, forestry, and land use sector (10Pg carbon per year) (Malhi et al., 2022), and the global net anthropogenic annual GHG emissions (~59Pg in 2019; IPCC). Even with the most radical interventions to restore nature and promote its solutions for climate, Natural Climate Solutions will only be effective if combined with a drastic reduction of emissions toward the achievement of Paris agreements (Dooley et al., 2022).

AUTHOR CONTRIBUTIONS

All authors conceived the ideas and designed the methodology; Suzie Derminon, Gaël Mariani, and Inna Senina collected the data; David Mouillot, Suzie Derminon, and Gaël Mariani analyzed the data and participated in script development; David Mouillot, Suzie Derminon, Gaël Mariani, and Marc Troussellier led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for submission.

ACKNOWLEDGMENTS

PL's contribution was partially funded from the European Union's Horizon 2020 research and innovation programme OCEAN-ICU, under grant agreement no. 101083922. Views expressed in the paper do not necessarily represent the views of these agencies or organizations.

CONFLICT OF INTEREST STATEMENT

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

The modelled data provided by the SEAPODYM model and used in this presented analyses are available publicly in the repository "Outputs of the SEAPODYM reference models of Pacific skipjack and bigeye tuna populations" (<https://doi.org/10.17605/OSF.IO/PXNFK>).

The 3D ocean data used to inform the SEAPODYM model are also available (<https://data.umr-lops.fr/pub/AFCM85/>). The executable files for SEAPODYM, together with the input and output files, are those used in a previous study (Bell et al., 2021, Nature Sustainability). They are available on a repository (<https://osf.io/qa8w4/>). Historical data are provided through the following links for the Skipjack (<https://osf.io/turh8>) and the Bigeye tuna (<https://osf.io/cbgn6>). There is also a SEAPODYM project GitHub (<https://github.com/PacificCommunity/seapodym-codebase>).

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How to cite this article: Mouillot, D., Derminon, S., Mariani, G., Senina, I., Fromentin, J.-M., Lehodey, P., & Troussellier, M. (2023). Industrial fisheries have reversed the carbon sequestration by tuna carcasses into emissions. *Global Change Biology*, 29, 5062–5074. <https://doi.org/10.1111/gcb.16823>