



The Role of Predator Removal by Fishing on Ocean Carbon Dynamics

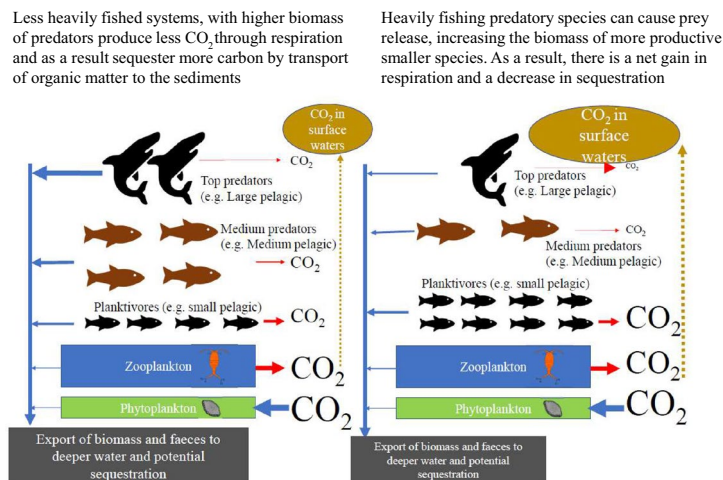
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Abstract

Total ocean carbon exceeds 40,000 GT either dissolved in the water column or buried in ocean sediments, and the ocean continues to sequester carbon from the atmosphere. Selective removal of predatory fish through extractive fishing alters the community structure of the ocean. This altered community results in increased biomass of more productive, low trophic level fish, higher overall fish respiration rates and lower carbon sequestration rates from fish, despite possible decreases in total fish biomass. High-pressure fishing on high trophic level fish, a globally occurring phenomenon, may result in as much as a 19% increase in respiration from fish communities overall. This increase in respiration will reduce sequestration rates and could prove highly significant in global carbon budgets. Preliminary estimates suggest a loss of sequestration equating to around 90Mt C.year⁻¹ (~ 10% of total ocean sequestration or ~ 1% of anthropogenic fossil fuel emissions per year). Ultimately, to reduce these carbon emissions, fishing needs to be carbon optimised, alongside other fisheries management outcomes, which may mean that fewer higher trophic level fish are removed. This study highlights the potential magnitude of fishing on ocean carbon dynamics and presents the key uncertainties (including understanding the effects of fishing on zoo- and phytoplankton communities) we need to urgently research to accurately quantify the effects and model future fishing practices.

Graphical Abstract



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1 Introduction

The climate crisis and biodiversity loss are human-driven changes to our environment (Steffen et al. 2015), with major implications for ocean ecosystems (Stafford and Jones 2019). Nature-based solutions (NbS) are part of the solution to both the biodiversity and climate crises we currently face (Seddon et al. 2020; Stafford et al. 2021). Marine NbS are a priority focus of policy makers as part of a net-zero drive in many countries, however, only coastal habitats such as seagrass, mangroves and saltmarsh are routinely considered, despite the bulk of carbon sequestration occurring in ocean sediments (Herr and Landis 2016; Parker et al. 2020; Stafford et al. 2021). Within the ocean carbon cycle, photosynthesis and respiration, which sequester and produce carbon respectively, are not fully balanced. Photosynthesis captures more carbon than is ultimately respired, with estimates between 0.1 and 2% of primary productivity (the production or fixation of organic carbon from carbon dioxide) eventually reaching ocean sediments (Herndl and Reinthaler 2013; Howard et al. 2017), and around 1% being a typically reported figure (reviewed by Basu and Mackey 2018). However, respiration is by far the most important carbon source on the planet, with the decomposition of organic material also being an important terrestrial source of carbon (Broadmeadow and Mathews 2003; Steffen et al. 1998). A smaller, but highly significant amount of carbon entering the atmosphere and oceans ($\sim 9\text{Gt C}\cdot\text{year}^{-1}$ or 10% of carbon from all sources including decomposition and respiration), comes from the burning of fossil fuels (Friedlingstein et al. 2020).

Within marine systems, animals have much higher biomass compared to primary producers (a 5:1 ratio), where phytoplankton, the main component of primary production, has only 0.2% of the biomass of terrestrial plants (Bar-On et al. 2018). As such, changes to animal biomass may play an important role in the carbon cycle, and changes in levels of respiration and carbon sequestration. Ultimately, in marine environments, primary productivity must be balanced by the sum of respiration and sequestration, hence increases in respiration must lead to decreases in sequestration rates.

Spiers et al. (2016) suggested that fishing predators from ocean ecosystems would create an increase in biomass of lower trophic levels, and an overall increase in ocean respiration, therefore reducing the ability of the ocean to absorb or sequester atmospheric CO_2 . The study was based on a probabilistic model and did not attempt to quantify the magnitude of the change. However, subsequently, new data have come to light that support ‘prey release’ through predator removal by fishing (sensu Soulé et al. 1988). Here we review and revise the hypothesis in the light of these new studies and

provide the first approximation of the magnitude of current fishing practices on ocean carbon sequestration.

2 Fishing Predators Creates ‘Prey Release’

Several studies have been published, mainly within the last 10 years, which examine increases in fisheries catch through ‘prey release’ where predator removal has resulted in higher catches and biomass of fish at lower trophic levels (e.g. Andersen et al. 2015; Pauly et al. 1998; Ruppert et al. 2013; Szuwalski et al. 2017). With greater removal of predatory fish from the sea, studies have predicted that catches could in theory double due to increased biomass of lower trophic level fish (Andersen et al. 2015). Data-driven studies demonstrate that in many cases, increased catches and biomass of lower trophic level species have occurred (Ruppert et al. 2013; Szuwalski et al. 2017). A recent study from the East China Sea combined models and data, showing clear increases in catches and biomass at lower trophic levels (Szuwalski et al. 2017). However, this study clearly demonstrated overall biomass of the ocean fell, due to an inverted pyramid of biomass, counter to the hypothesis in Spiers et al. (2016).

3 Lower Trophic Levels are More Productive

Ocean primary producers are dwarfed in terms of biomass compared to consumers (primary producers weighing only 1 GtC in total support 5GtC of consumer biomass, Bar-On and Milo 2019). This is due to their high productivity levels or high rates of organic matter production, but short life spans. Equally, consumer biomass is much lower in the ocean than on land (5 GtC compared to 20 GtC, Bar-On et al. 2018). Since at least half the global carbon budget occurs in the ocean (Broadmeadow and Mathews 2003; Friedlingstein et al. 2020), this lower overall biomass of consumers compared to terrestrial habitats indicates secondary productivity of consumers must also be high.

Empirical data used to parameterise Ecopath models commonly used in fisheries studies clearly demonstrate that productivity decreases with increased trophic level (Christensen et al. 2009). Furthermore, in data primarily derived from ectothermic fish, the link between productivity and respiration is largely linear (Clarke 2019). Therefore, it follows that a given biomass of lower trophic level fish will respire more than the same biomass of predatory fish (see ‘Estimating Productivity and Respiration Changes due to Selective Fishing of Predatory Fish’ section below).

4 The Role of Plankton

The productivity of zooplankton is around 80 times higher than for a typical fish (Christensen et al. 2009), and clearly, given its role at the base of the food web, phytoplankton is higher still (Bar-On and Milo 2019). Hence, any effect on plankton biomass or productivity may greatly affect net ocean respiration levels. However, combined modelling and data studies in the North Sea have demonstrated that phyto- and zooplankton are more heavily influenced by bottom-up processes, while fish are more affected by top-down predation processes, with the planktivorous, lower trophic level fish forming an important role between top-down and bottom-up effects (Lynam et al. 2017). The evidence for top-down control of forage fish (Andersen et al. 2015; Pauly et al. 1998; Ruppert et al. 2013; Szuwalski et al. 2017), contrasts with recent studies showing a lack of evidence for bottom-up processes of forage fish on higher trophic levels (from multiple study locations globally) (Free et al. 2021; Ruppert et al. 2013), indicating that the removal of predators may result in large changes to fish communities, but little change to zooplankton biomass. Such a lack of change in zooplankton biomass may arise from internal predator–prey dynamics within zooplankton communities (Hill Cruz et al. 2021). However, multiple predictions (e.g. Spiers et al. (2016) for open ocean systems, figure S4 in Lynam et al. (2017), for the North Sea, and Frank et al. (2005) for Eastern Canada) show typical fishing practices which reduce predatory fish may increase slightly smaller, more productive zooplankton density. Potentially, given the high levels of plankton productivity, this could result in considerably more ocean respiration than the figures provided below.

Equally, while many studies suggest phytoplankton density is driven by nutrient and sunlight availability (Boyd et al. 2010; Brun et al. 2015), studies do show grazing effects from zooplankton (Hill Cruz et al. 2021; Spiers et al. 2016), although Shurin et al. (2002) suggest marine planktonic trophic cascades are some of the weakest across all ecosystems. While in some cases, grazing can increase phytoplankton productivity, lower biomass of phytoplankton could also mean decreases in primary productivity. In Black Sea ecosystems, where ecosystem functioning effects of trophic cascades initiated by predator removal have been evaluated, they appear to show reduced oxygen concentration in the water, through increased respiration and decomposition (Daskalov et al. 2007).

5 Estimating Productivity and Respiration Changes due to Selective Fishing of Predatory Fish

The role of plankton in overall productivity and net respiration is potentially important. However, due to the lack of certainty, and the best fisheries data sets available not including plankton data, we have left plankton dynamics out of the following calculations. However, the balance of evidence discussed above indicates that the inclusion of plankton may increase the magnitude of increase in net respiration.

For the East China Sea, data in Szuwalski et al. (2017) show that: in the 1980s, there was 4Mt of biomass in named commercial species (for examples of species, see Fig. 1); current fishing practices reduced this to 2.8Mt; and careful single species management scenarios could reduce biomass to 2.6Mt. However, when the species are multiplied by standard productivity estimates of Christensen et al. (2009), the current fishing process, which heavily removes predators, resulted in the overall productivity of the named fish stocks increased by 19%. Under single species management scenarios, productivity fell by 33% (Table 1). Despite the confusion around the taxonomic and functional status of ‘other species’ in the East China Sea which may make up considerable amounts of the total biomass (Liang and Pauly 2017), these data on prey release detailed in Szuwalski et al. (2017) are important in providing biomass information of many different species from multiple trophic levels, over a time period where fishing pressure increased greatly in this area (Chen et al. 1997; Liang and Pauly 2017). Therefore, we have used these data in our analysis rather than other data, from other locations, where fishing pressure has been more regulated and constant in recent decades.

6 Estimating the Effect of Fishing on Global Carbon Budgets

To remove uncertainty, we have again excluded any role of plankton from our estimates, however, even without potential changes in zooplankton biomass and productivity, we can calculate that changes in productivity of fish, through trophic level changes to community structure caused by fishing, could equate to decreases in sequestration of around 90Mt C.year⁻¹ through increased respiration. In context, this is 10% of the estimated carbon sequestration of the ocean, or ~1% of global emissions from the burning of fossil fuels (Table 2).

Fig. 1 Examples of different categories of fish of different trophic levels used in the East China Sea calculations. Data is obtained from www.fishbase.se. Images are all taken from Wikimedia Commons under Creative Commons Licences (a) CC by 2.5 (b) CC0 1.0 (c) CC BY-SA 2.0



Trichiurus lepturus L.
Large pelagic
Size: ~1 m
Trophic level: 4.4



Scomber japonicus (Houttuyn, 1782)
Medium pelagic
Size: ~30 cm
Trophic level: 3.4



Sardinops sagax (Jenyns, 1842)
Small pelagic
Size: 10-20 cm
Trophic level: 2.8

7 Conclusions

Any estimates provided in this study must not be treated as an exact indication of the decrease in carbon sequestration of the oceans due to fishing, but rather as a first approximation. The argument above is presented to highlight the potential magnitude of the effect of many current fishing practices on ocean carbon budgets and to serve as a call for more urgent research in this area. Our results are compromised by a lack of knowledge of biomass changes in ‘other’ species in the East China Sea system we have used to produce our data (Liang and Pauly 2017; Szuwalski et al. 2017), lack of such detailed knowledge of the trophic effects of fishing in other parts of the world, the effect of grazing on productivity and most of all, limited understanding of the effects of changing fish trophic structure on plankton.

Equally, understanding how these changes to carbon sequestration occur needs more research. Different species and functional groups can aid or hinder the export of carbon from the surface to the deep sea. For example, larger marine animals may store carbon in their bodies, and have been shown to be a significant sequestration source when they die (Mariani et al. 2020). Fish and large gelatinous zooplankton can also play a considerable role in carbon flux from surface waters when alive (Luo et al. 2020; Saba et al. 2021), whereas copepod dense zooplankton may result in decreases in sequestration by breaking up larger organic particles (Mayor et al. 2020).

Finally, fishing per se should not be seen as negatively affecting carbon sequestration. While we have focussed on typical fishing practices that disproportionately affect high trophic levels, the data we present also suggest that different fisheries management policies may be beneficial to ocean

Table 1 Calculation of changes in productivity in named species as a result of different fishing management scenarios. Biomass figures presented in grams. Productivity estimates are in arbitrary units

	Biomass 1980 (1)	Diet (2)	Description (3)	Current fisheries practice predicted biomass (4)	Single species management predicted biomass (5)	Productivity estimate (6)	1980 productivity level (7)	Predicted productivity—current fisheries practice (8)	Predicted Productivity single species management (9)
<i>Trichurus lepturus</i> L	2.2E+12	Fish	Large Pelagic	4.4E+11	1.3E+12	0.3	6.6E+11	1.3E+11	4.0E+11
<i>Muraenesox cinereus</i> (Forskål 1775)	4.7E+11	Fish	Large Demersal	9.4E+10	3.3E+11	0.3	1.4E+11	2.8E+10	9.9E+10
<i>Scomber japonicus</i> (Houttuyn 1782)	3.3E+11	Fish	Medium Pelagic	3.3E+11	2.6E+11	0.5	1.7E+11	1.7E+11	1.3E+11
<i>Decapterus maris-adsii</i> (Temminck and Schlegel 1843)	2.8E+11	Copepod	Small Pelagic	4.2E+11	2.0E+11	0.9	2.5E+11	3.8E+11	1.8E+11
<i>Pampus argenteus</i> (Euphrasen 1788)	2.7E+11	Plankton	Large Pelagic	8.1E+10	1.4E+11	0.3	8.1E+10	2.4E+10	4.1E+10
<i>Engraulis japonicus</i> (Temminck and Schlegel 1846)	1.9E+11	Copepod	Small Pelagic	9.3E+11	1.3E+11	0.9	1.7E+11	8.4E+11	1.2E+11
<i>Larimichthys polyactis</i> (Bleeker 1877)	1.1E+11	Fish	Medium Pelagic	7.7E+10	7.7E+10	0.5	5.5E+10	3.9E+10	3.9E+10
<i>Nemipterus virgatus</i> (Houttuyn 1782)	1.0E+10	Fish and crustacean	Medium Pelagic	7.0E+09	9.0E+09	0.5	5.0E+09	3.5E+09	4.5E+09
<i>Sardinops sagax</i> (Jenyns 1842)	6.0E+10	Copepod	Small Pelagic	2.1E+11	4.8E+10	0.9	5.4E+10	1.9E+11	4.3E+10
<i>Larimichthys crocea</i> (Richardson 1846)	3.0E+10	Fish	Medium Pelagic	3.0E+09	1.2E+10	0.5	1.5E+10	1.5E+09	6.0E+09
<i>Thamnaconus modestus</i> (Günther 1877)	5.0E+10	Plankton	Small Pelagic	1.8E+11	6.0E+10	0.9	4.5E+10	1.6E+11	5.4E+10
Total	4.0E+12			2.8E+12	2.6E+12		1.64E+12	1.96E+12	1.11E+12

Calculations and Data Sources: (1) Data taken from Szuwalski et al. (2017, Figure S4). (2) Diet obtained from Fishbase.org (3) Classification based on weight Szuwalski et al. (2017, Fig. 4)—> =5 kg = large, >0.5 kg = medium < =0.5 kg = small and behaviour data from fishbase.org, set into productivity categories used in Table 2 in Christensen et al. (2009). (4 & 5) Biomass 1980 * proportion change data for different fishing management strategies from Szuwalski et al. (2017, Fig. 4). (6) Productivity values per unit biomass for categories in 'Description' column, taken from Christensen et al. (2009). (7) Biomass 1980 * Productivity estimate. (8) Current fisheries practice predicted biomass * Productivity estimate. (9) Single Species management predicted biomass * productivity estimate. Biomass is given in grams. Note – 'other' species shown in Szuwalski et al. (2017) are excluded from these calculations as they constitute multiple species across multiple trophic levels and are based on combined limited catch data per species and are therefore not suitable for this analysis

Table 2 Calculation and assumptions of loss of carbon sequestration through fishing of predominately predatory fish

Description of calculation or assumption	Details
Productivity of fish compared to zooplankton in the ocean	Zooplankton have ~50× productivity of typical fish (Christensen et al. 2009) Zooplankton biomass ~1.6 times that of fish (Bar-On et al. 2018) Total zooplankton productivity = 1.6 * 50 = 80 times that of fish
Respiration by fish in ocean as a percentage of total respiration	Bulk of ocean biomass is animal and protist (Bar-On et al. 2018), decomposers will play less of a role. As ~80:1 zooplankton to fish productivity, assume fish equate to 1% of ocean respiration
Typical change in fish productivity due to fishing	Predatory fish are reduced throughout oceans, but pressure in China may be greater (see main text). Assume 10% productivity change across globe, rather than 19% from East China Sea
Change in respiration due to fish productivity change	90 Gt C.year ⁻¹ respiration by ocean * 0.01 (1% percentage contribution of fish) * 0.1 (10% change due to changes in productivity) = 90Mt C.year ⁻¹
Percentage of total ocean carbon sequestration	~1% of 90 Gt C.year ⁻¹ as primary production (Basu and Mackey 2018). (90Mt / (90Gt * 0.01)) * 100 = 10%
Fishing related changes in sequestration as a percentage of global emissions	Current estimates of 9Gt C.year ⁻¹ from fossil fuel emissions (Friedlingstein et al. 2020) (90Mt / 9 Gt) * 100 = 1%

carbon budgets. For example, if the assumptions on plankton dynamics presented in this study are correct, then reducing the catch of larger, higher trophic level fish, and increasing catches of smaller pelagic fish, using low carbon fishing practices (e.g. Hilborn et al. 2018), may provide significant carbon benefits, both in terms of ocean sequestration and in terms of emissions reductions in catching fish. Allowing a more natural offshore ecosystem, and focussing on smaller-scale, lower impact inshore fishing where bycatch is also actively mitigated (e.g. Stafford 2019), may also be beneficial. However, more research of prey release on lower trophic levels, including plankton, is urgently needed to fully develop carbon metrics for fishing, which can be used alongside other fisheries management objectives.

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Availability of data and material All data and calculations are detailed in the tables of this article, and data is initially derived from fully cited sources.

Code availability Not Applicable.

Declarations

Conflicts of interest The author(s) declare no competing interests.

Ethical approval No ethics approval was deemed necessary by Bournemouth University Ethics Committee, as no original data were collected.

Consent to participate Not applicable.

Consent for publication Approved by all authors and institutions.

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