

Correspondence

Impact of increased fishing on long-term sequestration of carbon by cephalopods

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Fish and other metazoans play a major role in long-term sequestration of carbon in the oceans through the biological carbon pump¹. Recent studies estimate that fish can release about 1,200 to 1,500 million metric tons of carbon per year (MtC year⁻¹) in the oceans through feces production, respiration, and deadfalls, with mesopelagic fish playing a major role^{1,2}. This carbon remains sequestered (stored) in the ocean for a period that largely depends on the depth at which it is released. Cephalopods (squid, octopus, and cuttlefish) have the potential to sequester carbon more effectively than fish because they grow on average five times faster than fish^{3,4} and they die after reproducing at an early age^{4,5} (usually 1–2 years), after which their carcasses sink rapidly to the sea floor⁶. Deadfall of carcasses is particularly important for long-term sequestration because it rapidly transports carbon to depths where residence times are longest^{1,6}. We estimate that cephalopod carcasses transfer 11–22 MtC to the seafloor globally. While cephalopods represent less than 5% of global fisheries catch⁷, fishing extirpates about 0.36 MtC year⁻¹ of cephalopod carbon that could otherwise have sunk to the seafloor, about half as much as that of fishing large fish⁸.

The global catch of cephalopods has increased eightfold since 1950 (Figure 1A), peaking at 5.5 Mt in 2015⁷. Since then, it has shrunk despite increasing fishing effort⁹, raising concerns of declining squid populations and increased fishing effort in the high seas (Figure 1B). Residence time of carbon in the oceans increases

exponentially with depth (Figure 1B). Thus, high-seas species hold the greatest potential for carbon sequestration by exporting carbon to the deep sea. Harvesting cephalopods that would otherwise sink to the continental slope or abyssal plain has therefore a stronger impact on long-term carbon sequestration than harvesting them on the continental shelf. Consequently, shifting fisheries efforts towards the high seas can severely reduce long-term carbon sequestration by cephalopods. Using

reconstructed catch data from the Sea Around Us⁷, we estimate that fisheries in 2019 extracted 0.36 MtC in cephalopod body mass that could otherwise have sunk to the seafloor (see Supplemental information, published with this article online).

Almost half of the reported cephalopod catch is taken from 17 major stocks for which estimates of stock biomass exist (Figure 1C). We use the biomass estimates of these major stocks to calculate the carbon flux by deadfall, fecal pellet flux,

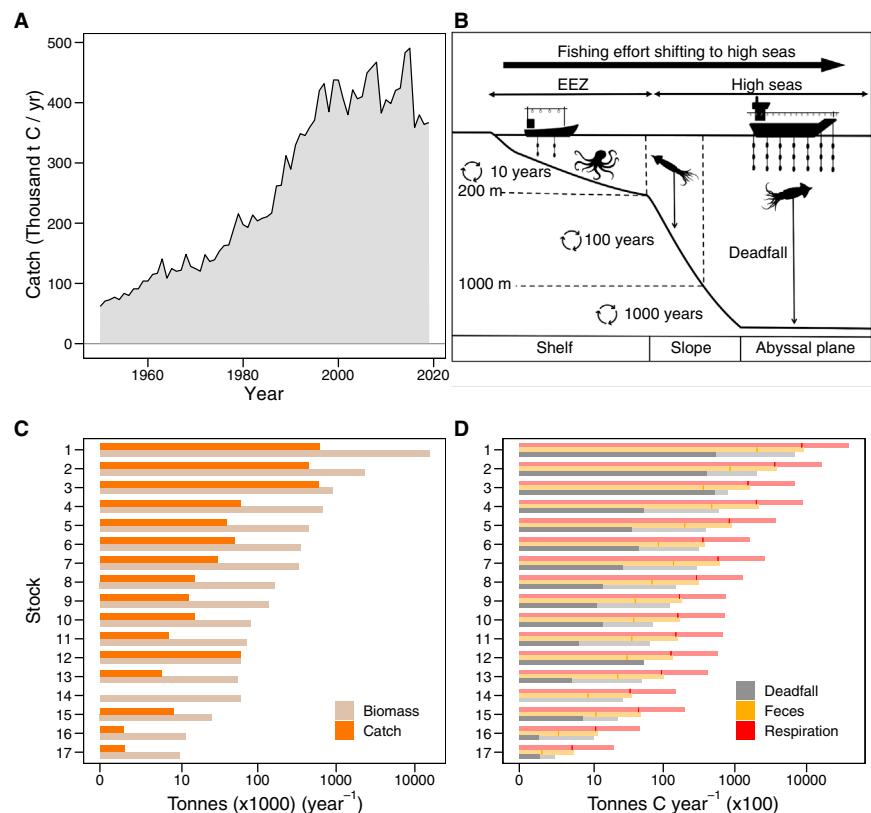


Figure 1. Carbon flux through cephalopods and the effect of fishing.

(A) Global catch of cephalopods in carbon equivalents; (B) graphic representation of carbon residence times as a function of depth, and current trend in cephalopod fisheries effort between economic exclusive zones (EEZ) and high seas; (C) estimates of stock biomass (thousand metric tons) and respective fisheries catch (thousand metric tons yr⁻¹) of 17 major cephalopod populations; (D) estimated flux of carbon in 17 major cephalopod populations via deadfall, respiration and fecal pellet flux (hundred metric tons yr⁻¹). Dark marks in red and yellow bars are sensitivity values calculated assuming cephalopods have a lower metabolism that is equivalent to fish (see Supplemental information). Dark bars on top of the grey bars indicate amount of carbon extracted by fisheries. 1 = *Dosidiscus gigas* in SE and equatorial Pacific; 2 = *Todarodes pacificus* in NW Pacific (Japan area); 3 = *Illex argentinus* in the SW Atlantic; 4 = *Doryteuthis opalescens* off North Carolina to Cape Cod; 5 = *Nototodarous gouldi (solarii)* off New Zealand; 6 = *Ommastrephes bartramii* in N Pacific; 7 = *Illex illecebrosus* off eastern USA; 8 = cuttlefishes from the International Council for the Exploration of the Sea (ICES) managed area; 9 = *Ocotpus vulgaris*, *Eledone* spp. from the ICES managed area; 10 = *Doryteuthis pealeii* off eastern USA; 11 = *Doryteuthis gahi* off Falkland (Malvinas) Islands; 12 = Ommastrephidae from the ICES managed area; 13 = *Onykia ingens* off Falkland (Malvinas) Islands; 14 = *Loligo reynaudii* off South Africa; 15 = *Octopus vulgaris* off NW Africa; 16 = *Heterololigo bleekeri* off Japan; 17 = *Enteroteuthis dofleini* in NE Pacific.

and respiration (see Supplemental information). We find that their combined deadfall flux is about 1.2 MtC yr⁻¹ (gray bars in Figure 1D), and fishing extirpates 0.15 MtC yr⁻¹ of it. Multiplying the deadfall flux by the residence time of the areas where cephalopod carcasses reach the seafloor, we estimate that they could be responsible for 693 MtC sequestered in the oceans. This value is small relative to the total carbon sequestered by the biological pump (0.05% of total)¹⁰, but it is relevant from a management perspective because fishing is one of the few ways humans can directly affect the biological pump. On top of this, the combined respiration and fecal pellet flux of cephalopods may add another 2.3–10.3 MtC yr⁻¹ to the carbon pool (red and yellow bars in Figure 1D), but the residence time of respired and fecal carbon is uncertain and depends on the position of cephalopods in the water column.

Global cephalopod biomass has been estimated to be 193–375 Mt wet weight⁴. While this value is highly uncertain, it would imply that 11–22 MtC of cephalopod carcasses sink to the seafloor every year (see Supplemental information). In comparison, carbon flux of fish deadfall is estimated to be about 65 MtC yr⁻¹⁽¹⁾. Furthermore, respiration and fecal pellet flux of cephalopods could potentially add another 169–326 MtC yr⁻¹ globally. While in absolute terms this is less than for fish (1,200–1,500 MtC yr⁻¹)^{1,2}, each ton of cephalopod releases more carbon than each ton of fish through respiration and fecal pellet flux because cephalopods' pace of life, growth and metabolism are faster^{3,4}. Residence time of this carbon in the water depends on the depth at which it is released, which is uncertain, and we therefore abstain from calculating the amount of carbon sequestered through respiration and fecal pellet flux.

The relative effect of fishing on deadfall flux is stronger on cephalopods than on fish. Fish usually continue living after reproducing and most of them will eventually be eaten by other predators. Thus, only a small fraction of them becomes deadfall⁸. Contrary to fish, most cephalopods that reach sexual maturity become

deadfall after reproducing. Therefore, although cephalopods represent less than 5% of fisheries catch⁷, the total amount of deadfall carbon extirpated by fishing of cephalopods (0.36 MtC yr⁻¹) is about half that of large fish (0.64 MtC year⁻¹)⁸. Regarding respiration and fecal pellet flux, fishing is expected to have a small effect on cephalopods because most cephalopods are caught close to the time of their post-reproductive death. The effect of fishing on fish respiration and fecal pellet flux is more complex, because captured fish could have lived longer before being caught, contributing to further respiration and fecal pellet flux. Beyond the direct effect of biomass extraction, fisheries can alter the ecosystem through complex trophic cascades. These may alter carbon fluxes in ways that could strengthen or weaken net sequestration of carbon by the system in ways that are difficult to predict.

Three species make up about half of global cephalopod catch⁷: jumbo flying squid *Dosidicus gigas*, Argentine shortfin squid *Illex argentinus*, and Japanese flying squid *Todarodes pacificus* (Figure 1C). Because these species reproduce and die on continental slopes or above abyssal plains, they are particularly relevant for long-term sequestration of carbon through deadfall. Increasing fishing pressure on these species is therefore concerning in relation to deadfall carbon, particularly for the jumbo flying squid and the Argentine shortfin squid, which have recently experienced a steep increase of fishing pressure by international fleets in unregulated high seas^{5,9}.

Our estimates of carbon flux by cephalopods and carbon sequestration are first-order approximations that are subject to uncertainties of biomass estimates, their precise deadfall location and metabolic variability. They serve as a starting point in assessing the carbon stocks of cephalopods within the framework of 'blue carbon', while also motivating better management of fisheries resources in the high seas. The life cycle and life history of cephalopods are such that they sequester carbon more effectively than fish, underscoring the need for prioritizing their inclusion in marine carbon stock assessments.

SUPPLEMENTAL INFORMATION

Supplemental information contains one figure, one table, experimental procedures, acknowledgements, and author contributions, and can be found with this article online at <https://doi.org/10.1016/j.cub.2024.04.023>.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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