Natural Climate Solutions in the Open Ocean:

Scientific Knowledge and Opportunities Surrounding Four Potential Pathways for Carbon Dioxide Removal or Avoided Emissions

Environmental Defense Fund
Natural Climate Solutions

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About this report

This is one of three reports produced by the Environmental Defense Fund (EDF) ocean science team as part of a two-year EDF project on natural climate solutions (NCS). With financial support from the Bezos Earth Fund, EDF seeks to build consensus around the scientific readiness, market suitability, socioeconomic dimensions and pathways to large-scale uptake of NCS within four major parts of the earth system – tropical forests, temperate forests, working (agricultural) lands and the oceans. The ultimate objective of EDF's work is to identify scalable interventions that could preserve or magnify NCS pathways and that are ready to implement – i.e., interventions that are likely to result in durable carbon sequestration via a NCS pathway, are likely to generate co-benefits and that present low risk of adverse social, economic or ecological adverse impacts. We also identify where further scientific and policy research is needed to result in NCS that meet these criteria.

Within the ocean system specifically, EDF is examining three sets of potential NCS interventions:

- Interventions in the open ocean, including carbon sequestration via the rebuilding of biomass in large marine mammals and epipelagic fishes, and the potential for avoided emissions by restricting or limiting new fishing in the mesopelagic ocean and/ or benthic trawling,

- various interventions to conserve, restore and increase the productivity of macroalgal (seaweed) systems (natural beds and farms) to avoid GHG emissions and sequester more carbon (C) and

- interventions to conserve, restore and manage vegetated, coastal blue carbon ecosystems such as mangroves, marshes and seagrasses to avoid GHG emissions and increase C sequestration.

The present report attempts to describe the state of the science, including key uncertainties, surrounding the first set of pathways - those based on open ocean ecosystems. EDF has prepared companion reports on the state of the science surrounding the surrounding the coastal and macroalgae pathways. Together, these ocean system reports served as inputs for a series of complex systems mapping workshops in which EDF engaged more than 60 outside experts to critically evaluate our initial findings; to identify co-benefits, risks, tradeoffs and equity concerns associated with the various pathways; and identify any promising additional pathways for carbon sequestration or avoided emissions. As such, the present report is just a starting point for discussion and exploration of the scientific and socioeconomic dimensions surrounding open ocean blue carbon pathways, and does not necessarily reflect the consensus of EDF's open ocean blue carbon workshop participants. EDF is separately investigating the market readiness of pathways associated with forest and agricultural systems.

Executive Summary

Natural Climate Solutions (NCS) aim to avoid greenhouse gas (GHG) emissions or sequester carbon from the Earth's atmosphere by protecting, managing, restoring or enhancing ecosystems. While there are now formal standards for carbon credits based on NCS in nearly every major terrestrial or coastal biome except the world's deserts, the open ocean continues to lag behind other biomes in both the scientific knowledge and market readiness needed to support high-quality, NCS-based carbon credits and reliable pathways for carbon dioxide removal (CDR) or negative emissions technologies more generally.

In this report, we review the role of the ocean in absorbing and sequestering carbon from the atmosphere and examine the state of the science surrounding four proposed ocean NCS pathways that aim to enhance or preserve one or more biogeochemical processes that make up the ocean's biological pump:[1] Carbon sequestration via the rebuilding of large marine animal biomass, particularly baleen whales; enhancing carbon sequestration via the rebuilding of epipelagic fish populations; avoided emissions and protection of an existing, natural carbon sequestration pathway via limitation/prohibition on targeting of mesopelagic fishes, which are increasingly believed to play a large, critical role in mediating carbon sequestration within the ocean; and avoided emissions via limitation/prohibition of anthropogenic activities such as deep-sea mining and

benthic trawling that disturb organic carbon currently stored in seafloor sediments.[2] Not contained in this preliminary report on the science surrounding open-ocean blue carbon are the consensus findings from a workshop of scientific and policy experts convened by EDF in late 2021. Consensus findings from this workshop concerning the market readiness, scientific uncertainties and potential policy interventions surrounding each of the pathways described here will be published in a separate venue in 2022 or early 2023.

EDF believes it unlikely that dramatic increases in whale populations, large increases in fish biomass and average size, and reduced anthropogenic remineralization of carbon stored in ocean sediments would not help to at least partially reinforce the many biogeochemical processes that help sequester carbon in the oceans. It also seems clear that interventions designed to achieve these outcomes – as well as those aimed at conservation of mesopelagic populations and ecosystems – would produce many co-benefits that would further justify such action. However, we find there is significant scientific uncertainty surrounding the magnitude of carbon that could be sequestered, or new emissions avoided, via these four pathways. The uncertainties surrounding some of these pathways are greater than others and some approaches – such as the protection of as-yet-unexploited mesopelagic ecosystems – would

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[1] The ocean's "biological pump" is one of the two primary systems through which the ocean sequesters carbon. In its simplest form, this pump is a three-part system: First, one or more limiting nutrient(s) are delivered to the surface ocean. These nutrients fuel new primary production by phytoplankton, drawing down atmospheric CO_2. A fraction of the carbon incorporated in this new phytoplankton biomass is then "exported" to deeper ocean waters where it can be sequestered

from the atmosphere. This export occurs through a variety of processes, including gravitational sinking of particles containing dead biomass and "active transport" of the carbon to depth by higher trophic level organisms, including zooplankton and mesopelagic fishes.

[2] The state of the science surrounding a fifth ocean-based NCS pathway, open ocean farming of macroalgae (seaweeds), is reviewed in a separate report.

conserve biogeochemical pathways that sequester many petagrams of carbon each decade, with few, if any, apparent downsides. This range of uncertainties and trade-offs thus provides us with an opportunity to prioritize investment in some clear, win-win solutions in the near term, while pursuing targeted research to reduce key uncertainties surrounding the others.

Estimating carbon fluxes with the accuracy and precision necessary to support high-quality carbon credits remains a particular challenge for ocean scientists due to the vast scales and spatial and temporal heterogeneity of ocean biogeochemical processes, high research costs, the inability of most remote sensing technologies to "see" below the first few centimeters of the ocean's surface and the many logistical and physical impediments associated with the study of biological and chemical processes that take place a fluid medium, often at extremes of temperature and pressure. Critically, we find there has been little or no direct consideration in the ocean NCS literature of how climate change will affect the efficiencies or timescales of C sequestration via these pathways; this is due in part to the failure of some ocean circulation models to capture to the effects of climate-related changes on various ocean processes (Siegel, DeVries, et al. 2021). While there is substantial evidence that many components of the biological pump have been and will likely continue to be affected by climate-related changes, such as increased ocean stratification (Li et al., 2020; Fu, Randerson and Moore 2016), ocean acidification (Bopp et al., 2013), deoxygenation of the ocean interior (Keeling, Körtzinger and Gruber 2010) and massive shifts in the relative abundances and geographies of phytoplankton populations (Henson et al., 2021; Benedetti et al., 2021), claims of decadal- to centennial-scale carbon sequestration via NCS pathways in the ocean should be viewed with skepticism until questions of permanence, leakage and additionality are addressed in a more holistic manner.

In the case of large marine mammals specifically, we find there are many reasons to rebuild great baleen whale populations that are not directly related to carbon sequestration. In addition, there is some evidence that whales can mediate the flow of carbon to the deep ocean at various points in their life cycles either directly (through natural sinking of whale carcasses) or indirectly (via the fertilization of surface ocean primary production by buoyant whale feces). Moreover, an increase in whale populations could sequester additional carbon within living biomass. However, we find that large uncertainties remain around many aspects of this proposed pathway: For example, we do not know with certainty whether whales act as net sources or sinks of carbon with respect to the atmosphere when all aspects of their life histories are considered, let alone how much carbon the restoration of a single additional whale might sequester, or how we might track and attribute such sequestration.

The potential magnitude of direct carbon storage and sequestration via incorporation into living biomass and whale falls, respectively, can be estimated with reasonable precision due to the consistency of whale migration routes, relatively robust data on whale populations and the organisms' large size (e.g., Pershing et al., 2010). Standing biomass, particularly for great baleen whales, has considerable scope to increase, even if climate effects shift the margins of carrying capacity. Due to the substantial degree to which whales' demand for krill has been previously underestimated and the tight, iron-mediated food web coupling between whales, krill and diatoms in the Southern Ocean (Savoca et al., 2021), active interventions to increase krill abundances may be required to support the rebuilding of whale populations, in addition to other proposed interventions, such as reductions in ship strikes (Smetacek 2021).

However, estimates of the fraction of carbon export from the surface ocean that can be attributed to fertilization by whale feces are poorly constrained. Critical biogeochemical uncertainties continue to surround questions of carbon export efficiency and the bioavailability of iron excreted by whales, perhaps in part because of insufficient communication between marine mammal specialists, oceanographers, ecologists and biogeochemists. For example, there are sparingly few direct measurements in the scientific literature of the bioavailability of the iron in whale feces (Ratnarajah et al. 2017). Previous studies have typically assumed that a large fraction of this iron was available to phytoplankton (e.g., Lavery et al., 2010; 2014), even though iron bioavailability to phytoplankton is a highly variable product of interactions between multiple biogeochemical parameters (Hassler et al., 2012). Savoca et al. (2021) used novel and rigorous methodology to persuasively demonstrate, based on a combination of models and observational methods, that we have likely dramatically underestimated the amount of krill consumed by whales. However, due to the lack of available data on iron bioavailability, the authors relied upon assumed values from Ratnarajah et al. (2016) to estimate rates of primary production stimulated by whale fecal fertilization.

In addition, scientists have not demonstrated a reliable connection between stimulation of surface

productivity and carbon export (Boyd et al., 2007; Buesseler et al., 2008). The addition of iron to surface waters has been shown to stimulate phytoplankton growth in natural systems (Duprat, Bigg and Wilton 2016; Blain et al., 2007) and in both laboratory and large-scale field experiments (Buesseler et al., 2004; Watson et al., 2008); however, depending on the circumstances, much of the newly fixed carbon can be quickly respired back to CO_2 (Charette and Buesseler 2000; Buesseler et al., 2008). Thus, even a very large phytoplankton bloom, fertilized through whale feces or some other means, will not necessarily sequester carbon from the atmosphere.

While none of the open-ocean NCS pathways we reviewed are scientifically mature enough to support high-quality carbon credit schemes, multiple lines of evidence suggest a relatively large source of emissions (ca. 2.25 Pg C yr^{-1}, commensurate with the scale of current anthropogenic emissions; Boyd et al., 2019) could be avoided by limiting or prohibiting the harvest of mesopelagic fish communities. While the biomass of these fishes and the absolute quantity of carbon they move during their diel vertical migrations both remain uncertain, even the minimum estimates of carbon flux associated with these organisms – around 1 Pg yr^{-1} – indicate that they mediate a massive transfer of carbon within the ocean, and that large-scale biomass removal though commercial fishing would therefore almost certainly disrupt one of the largest zoogeochemical transfers of carbon on the planet. We thus find that limiting harvest of these species is a conservative policy intervention that could be taken today to prevent further deterioration of the ocean's capacity to sequester atmospheric carbon and to avoid GHG emissions, buying scientists more time to develop and deploy the necessary models and observing technologies.

Epipelagic fisheries present another ready target for policy intervention based not on the potential for new sequestration – the science surrounding carbon export by these fishes remains far too uncertain – but focused instead on a reduction in current emissions. Nearly 82% of the emissions associated with targeting large pelagic species came directly from fuel use, and only 57% of the global offshore catch would be profitable without current fuel subsidies. (Mariani et al., 2020). Emissions could also be reduced by reducing fish catches, improving nearshore fishery production to disincentivize transit further offshore in response to stock depletion, improving catch efficiency, reducing the amount of bottom trawling and ending overcapitalization and fuel subsidies. However, intriguing issues remain about whether and how goal setting for fisheries based mainly on

target species suitability to support yield adequately supports future system performance for other outcomes, including carbon processing. Setting and achieving new management goals for fisheries that include the protection of the roles that fish play in carbon sequestration is an urgent priority for fisheries that target species clearly involved in nutrient regeneration, such as Southern Ocean krill.

We identify several significant research needs that could accelerate the development of sufficiently precise estimates of sequestration or avoided emissions from all four of these ocean NCS pathways to support high-quality carbon credits and justify other investments to protect or accelerate them. These needs include:

- Greater scientific dialogue and increased collaboration between ocean scientists and those working on terrestrial systems, and among scientists from traditionally siloed subdisciplines within ocean science, particularly marine mammal physiologists, marine microbial ecologists, marine invertebrate biologists and marine biogeochemists/chemical oceanographers, including both observational practitioners and theoreticians/modelers,

- the incorporation into any future estimates of carbon sequestration by fishes or marine mammals of more robust statistical methods for evaluating uncertainties in both various model parameters and overall results,

- the production of new models, observing technologies and data to constrain over broad spatial scales the total biomass of fish in the mesopelagic ocean and the fluxes mediated by these communities, including a robust set of empirical conversion factors for scaling measurements of fish biomass to units of carbon,

- development of biogeochemical models that account for the full life-cycle carbon emissions of marine mammals,

- additional field and laboratory studies to ascertain the bioavailability of krill-derived iron in whale feces and the fractions of both surface ocean primary production and carbon export that can be directly attributed to whale fertilization,

- and development of more robust estimates of carbon emissions from disturbed seafloor sediments, including models that account for the exact manner of disturbance, previous disturbance history, and accurately estimate the quantity and timescale over which remineralized CO_2 will return to the atmosphere.

Finally, we identify a particular problem of attribution and specificity that would serve as a severe practical impediment to the development of high-quality carbon credits based on conservation of large marine animals. Marine species move within three dimensions in a fluid medium, sometimes across very long distances, making it very difficult to track the carbon within them in a manner comparable to the chain of custody auditing performed within traditional carbon markets based on terrestrial plants and trees. Even when we have achieved sufficient scientific knowledge of the complex biogeochemical and physical processes that govern carbon cycling by marine animals, innovative market design, particularly around monitoring and verification, will be required to ensure the integrity of any credits sold in this area. In particular, there is an urgent need for development of innovative methods that can apportion to marine reserves or marine protected areas (MPAs) an appropriate fraction of the carbon sequestration associated with migratory animals that do not spend their entire lives within those reserves' boundaries.

Recent discussion about the carbon market value associated with the rebuilding of whale populations makes the need for scientific guidance in this area particularly urgent. Importantly, each of these NCS pathways is unto itself a no- or minimal-regrets conservation strategy, replete with potential co-benefits for people and society. The ecosystem restoration and/or enhancement necessary in each case – protecting mesopelagic fishes on the one hand, or rebuilding whale populations on the other – will almost certainly make the oceans more resilient in the face of climate change, stabilize global fisheries populations and support human livelihoods, regardless of how much carbon is sequestered.

Definitions:

Carbon market: A market in which units — allowances or credits — are traded between entities. When units are used for voluntary purposes or where carbon credits are certified solely by voluntary programs or standards, the market is often referred to as a "voluntary" carbon market. Where units are used to satisfy legal compliance obligations, this is often referred to as a "compliance" market.

Nature-based solutions (NBS): The full range of values humans derive from natural systems, defined by IUCN (2020) as "actions to protect, sustainably manage, and restore natural or modified ecosystems, that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits".

Natural climate solutions (NCS): A subset of NBS that directly addresses the GHG reduction benefits (i.e., increase carbon storage and/or avoid greenhouse gas emissions) that humans derive from natural systems via conservation, restoration, and/or improved management actions.

Carbon Dioxide Removal: process in which carbon dioxide gas (CO_2) is removed from the atmosphere and sequestered for long periods of time.

Monitoring, Reporting and Verification: A system or protocol for tracking specific methods and outcomes, transparently communicating specific information, and validating that the information is accurate and complete. Often abbreviated as MRV.

Carbon capture and storage: the process of trapping carbon dioxide produced by burning fossil fuels or any other chemical or biological process and storing it in such a way that it is unable to affect the atmosphere.

Blue Carbon: carbon sequestered mangrove forests, seagrass beds and tidal marshes (Mcleod et al., 2011). More recently, some have broadened the definition to include all carbon "captured by the world's ocean and coastal ecosystems" (NOAA NOS, 2021).

Mesopelagic fishes: Fishes that live in the ocean's "Twilight Zone" — depths between approximately 660 feet (200 m) to 3,300 feet (1,000 m) beneath the ocean's surface. These tiny fishes, numbering in the hundreds of millions, perform diel vertical migrations, swimming upward every night to feed on prey at the ocean's surface, then retreating back downward at daybreak. As they retreat, these fish bring many gigatons of carbon back down with them to the ocean interior.

Epipelagic fishes: Fishes that live primarily within the surface ocean, down to an approximate depth of 660 feet (200 m). This category of fishes can include highly migratory predatory species such as tunas and swordfish. While these fishes are often considered epipelagic species, emerging scientific evidence shows they can and do make very deep dives beneath the ocean's surface.

Introduction

Emerging pathways for natural climate solutions (NCS) in the open ocean

Global pathways for natural climate solutions and carbon dioxide removal (CDR)

Natural climate solutions (NCS) aim to avoid greenhouse gas (GHG) emissions or sequester carbon from the Earth's atmosphere by protecting, managing or restoring ecosystems (Griscom et al., 2017). These natural solutions lie along a broad spectrum of CDR pathways that includes other extreme "engineered" solutions, such as the various forms of carbon capture and storage (CCS) and artificial fertilization of the oceans with iron or other nutrients. While there is a strong argument that no climate solution requiring human intervention can truly be considered "natural" (e.g., Osaka, Bellamy and Castree 2021), some CDR pathways require substantially more modification of ecosystems through human engineering than others; as is the case for nearly all strategies aimed at capturing and storing carbon dioxide, the timescale over which the approach sequesters carbon will depend heavily on the location and methods employed (Siegel, DeVries, et al., 2021). In contrast, natural climate solutions typically offer one or more co-benefits for people and nature, in addition to their central function as mechanisms for carbon sequestration emissions avoidance: Through the preservation or enhancement of biogeochemical processes, these NCS can make ecosystems more resilient in the face of climate change, provide food for growing populations and support human livelihoods in industries as diverse as outdoor recreation, agriculture and marine operations (Leavitt et al., 2021).

Interest in NCS, which can form the basis for carbon credits or offsets, has focused primarily on pathways in terrestrial or coastal biomes, including agroforestry practices (E. K. Anderson and Zerriffi 2012), management of temperate forests (Ontl et al., 2020), revegetation or avoided conversion of tropical forests and tropical wetlands such as mangrove swamps (Griscom et al., 2020), and modification of agricultural practices to preserve or increase stocks of carbon in terrestrial cropland soils (Oldfield et al., 2021; Bossio et al., 2020). NCS pathways have also been characterized and quantified in vegetated, coastal marine blue carbon ecosystems such as salt marshes, mangrove swamps, kelp forests and seagrass beds, which provide a host of co-benefits, in addition to high rates of carbon sequestration (Lovelock and Duarte 2019; Duarte et al., 2013). These blue carbon ecosystems support high areal rates of primary productivity compared with other biomes but face significant threats from coastal human development (Duarte 2017). Rapid growth in our knowledge of the complex biogeochemical cycles that define these ecosystems (Lovelock and Duarte 2019) has stimulated interest in new market-based mechanisms to finance their restoration and conservation (Vanderklift et al., 2019; Stuchtey et al., 2020), and at least one independent carbon offset standard based on the REDD+ framework now includes avoided conversion or revegetation of coastal blue carbon ecosystems (Verified Carbon Standard 2020).

Diving deep: NCS and CDR pathways in the oceans

While there are now formal standards for carbon credits based on natural climate solutions in nearly

every major terrestrial or coastal biome except the world's deserts, the open ocean continues to lag behind other biomes in both the scientific knowledge and market readiness needed to support high-quality, NCS-based carbon credits and reliable pathways for CDR or negative emissions technologies more generally (Gattuso et al., 2018; National Academies of Sciences, Engineering, and Medicine 2019; Gattuso et al., 2021). Covering 71% of the Earth's surface and storing more carbon than all soils and forests combined, the ocean system (water, marine biota and ocean sediments) is unique in its massive scale, remoteness and biogeochemical and physical complexity. Our knowledge of the oceans has trailed that of most terrestrial biomes due to a number of challenges that follow from these unique characteristics. These include the spatiotemporal variability of ocean processes, high research costs, the inability of most remote sensing technologies to "see" below the first few centimeters of the ocean's surface and the many logistical and physical impediments associated with the study of biological and chemical processes that take place in a fluid medium, often at extremes of temperature and pressure (Mann and Lazier 2005). Indeed, even the determination of boundaries between various biomes within the ocean has proven a considerable challenge (Fay and McKinley 2014) and we still do not know what forms of life or how many organisms inhabit vast swaths of the ocean interior such as the mesopelagic, or "ocean twilight zone," which encompasses the area from 100 to 1000 m below the sea surface (St. John et al., 2016; Irigoien et al., 2014). That two discoveries now fundamental to our understanding of biogeochemical cycles in the ocean emerged only within the 50 years indicates just how young our study of the oceans truly is, and how much more we have to learn.[3]

Ocean-based CDR pathways, including NCS, have nevertheless gained widespread interest among scientists, corporations, government entities and environmental organizations (Bindoff et al., 2019; Canadell et al., 2021; Gagern and Kapsenberg 2021), leading at least one group of authors to assert an urgent need for evaluation of both "potential hype and opportunity" within this growing sector (Boettcher et al. 2021).[4] The open ocean's very large carbon stores, distance from human populations, natural chemical buffering capacity (with regard to the carbonate

system) and physical scale make the biogeochemical processes that define ocean biomes an attractive potential basis for exploitation as CDR and NCS approaches. In addition, the many anthropogenic threats facing the world's oceans (e.g., overfishing, declines in large marine animal populations, ocean acidification, eutrophication, loss of coastal habitats that provide critical ecosystem services and possible deoxygenation of the ocean interior) have driven specific interest in ocean-based NCS as a means of financing conservation or restoration initiatives in marine systems though the sale of "blue bonds" or carbon credits (Hoegh-Guldberg et al., 2019; Rahim 2020). Proposed CDR pathways based on the enhancement of natural ocean biogeochemical processes or, in some cases, storage of terrestrial or atmospheric carbon in the ocean, include:

- Chemical manipulation to enhance the ocean's natural carbon solubility sink and reverse the effects of ocean acidification (i.e., "artificial alkalinization," by means of electrochemistry or addition of minerals such as olivine),

- bioenergy with carbon capture and storage (BECCS) based on the use of marine (rather than terrestrial) biomass,

- artificial fertilization of the ocean with iron or other nutrients,

- artificial upwelling or downwelling of nutrient- or carbon-rich waters, respectively,

- injection of captured, liquid-phase CO_2 into or onto the seafloor, and

- sinking of either terrestrial or marine biomass into the deep ocean.

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[3] The fact that much of the primary production in the surface ocean is limited not by nitrogen or phosphorus, but by the availability of iron, was not empirically demonstrated until the mid-1990s; and scientists did not confirm the existence of hydrothermal vents on the seafloor until 1977 (Martin et al., 1994; Ballard 1977).

[4] In response to this interest, a study panel convened by U.S. National Academies of Sciences, Engineering, and Medicine (NASEM) with funding from the ClimateWorks Foundation completed an extensive survey of the scientific, economic and social aspects of various marine CDR approaches (the National Academies of Sciences, Engineering, and Medicine, 2022).

Several of these approaches (specifically, upwelling/ downwelling and nutrient fertilization) rely on the premise that nutrient delivery to the surface ocean will catalyze the fixation of CO_2 from the atmosphere by phytoplankton, with a fraction of the newly fixed biomass then sinking into deeper waters where the carbon within it necessarily becomes sequestered.[5] This report does not focus on the scientific or social merits of these CDR pathways since they have been extensively evaluated elsewhere.[6]

In addition to these ocean or marine CDR approaches, sometimes collectively referred to as "mCDR" (e.g., Boettcher et al., 2021), a number of ocean-based natural climate solutions have been proposed with the aim of either avoiding new emissions from the ocean system or capturing and storing carbon within it. NCS that perform the latter function are considered "natural" approaches to CDR. NCS pathways proposed for the open ocean include:

- Carbon sequestration via the rebuilding of large marine animal biomass, particularly baleen whales, with the assumption that some carbon will be stored within these animals' biomass while most is sequestered via the natural sinking of carcasses to the seafloor and/or fertilization of primary production in the surface ocean,

- enhancement of carbon sequestration via the rebuilding of epipelagic fish populations (i.e., those that live primarily within the surface ocean, down to an approximate depth of 200 m),

- avoided emissions and preservation of an existing sequestration capacity via limitation/prohibition on targeting of mesopelagic fishes, which are increasingly believed to play a large, critical role in mediating carbon sequestration within the ocean,

- avoided emissions via limitation/prohibition of anthropogenic activities that disturb organic carbon currently stored in seafloor sediments (e.g., deep-sea mining, benthic trawling), which can convert stored carbon to CO_2 and "short circuit" the major mechanism for storage of carbon in the ocean over geological timescales, and

- farming of macroalgae (seaweeds) in the open ocean, sometimes called ocean afforestation, with different proposals for allocation of biomass to human uses versus sinking in the deep ocean via either natural or artificial means.

Report overview

Within this context of increasing interest in ocean-based natural climate solutions, this report reviews the current scientific knowledge surrounding the first four of these proposed "open ocean" NCS pathways.[7] We first present a primer on ocean biogeochemistry, including current estimates of ocean sequestration rates and carbon storage. We describe the roles played by important biological components of the ocean carbon storage system, including phytoplankton and zooplankton, and assess briefly how the biogeochemical fluxes mediated by each of these are expected to change under future climate scenarios. We then review and synthesize the current scientific knowledge surrounding each of the open ocean NCS pathways, followed by a summary in each instance of key uncertainties and questions that require further research. Finally, we conclude by highlighting some common themes, potential interventions to implement each of the pathways and critical directions for further study that were identified during the consensus workshop convened by EDF in late 2021.

An important caveat: No substitute for reduced emissions

This report is furnished with an important caveat: No strategy for removal of existing CO_2 from the Earth's atmosphere is a substitute for avoided or reduced emissions, even when removal is accomplished through some form of NCS or via a hybrid approach such as bioenergy with carbon capture or storage (BECCS). For two primary reasons, there is no way to fully reverse the warming effect of new GHG emissions when one fully evaluates their impact over the decadal to centennial timescales most immediately relevant for climate change. First, certain impacts of new GHG emissions are committed nearly as soon as the contribution of these emissions to

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[5] The dependence of many ocean CDR and NCS pathways on this premise is discussed in greater detail later in the report. The first subordinate implicit assumption – that delivery of sufficient quantities of limiting nutrient(s) to marine phytoplankton will stimulate a bloom in primary production – is backed by nearly 150 years of scientific evidence and has been repeatedly validated in both laboratory and field experiments (Watson et al., 2008; Martin et al., 1994). However, the extent to which this newly fixed phytoplankton biomass will then sink into the deep ocean and become sequestered is highly uncertain

and remains the subject of intensive, current-day research within oceanography and marine biogeochemistry (Bishop and Wood 2009).

[6] See, e.g., NASEM (2022).

[7] Current scientific knowledge surrounding pathways for carbon sequestration via the open-ocean farming of macroalgae and preservation/restoration of traditional coastal blue carbon systems are reviewed in separate companion reports available on the EDF web site.

warming is realized; for example, the effect of new emissions on heating and acidification of the ocean interior and, due to the presence of multiple positive feedbacks, new melting of polar ice leading to global sea level rise, cannot be fully reversed by removal of an equivalent quantity of CO_2 in the future (Gruber 2011; Golledge et al., 2015; Levermann et al., 2013). Second, experiments in global climate models show that CO_2 removal from the atmosphere will become less and less effective over time as much of the anthropogenic carbon that has already been "pushed" into the ocean and land carbon reservoirs over the past 150 years moves back into the atmosphere

through a massive process of chemical reequilibration between the main components of the surface Earth system (Canadell et al., 2021). For example, for a 100 Pg C removal of CO_2 from the atmosphere today, only about a quarter of the removed CO_2 will appear to remain out of the atmosphere after 80 –100 years (Keller et al., 2018).[8] Thus, while solutions that remove carbon from the atmosphere can assist us in our critical effort to limit global warming, a method or policy intervention that reduces or avoids new emissions should take priority if there is a choice between the two.

Storage, uptake and sequestration of carbon in the ocean

Carbon is absorbed, cycled and sequestered within the ocean by both physical (abiotic) and biogeochemical processes. As a gross simplification, the sequestration of carbon within the ocean can be divided into two component subsystems that depend on combinations of these processes: First, CO_2 is absorbed from the atmosphere by the surface ocean; then, some fraction of the carbon in the absorbed CO_2 is exported to deeper ocean waters where it can be locked away from the atmosphere in various forms for periods ranging from months to millennia. The relative importance of abiotic and biogeochemical processes within each of these subsystems helps to determine the timescales over which this carbon is sequestered.

The various proposed ocean CDR approaches described in the previous section are generally designed to enhance or manipulate specific process(es) within one of these two subsystems. Because the NCS pathways specifically considered in this report rely largely on the enhancement or preservation of biogeochemical mechanisms as opposed to those controlled by ocean physics, we briefly examine the specific functions of phytoplankton, zooplankton, fishes and marine animals within the ocean carbon cycle and discuss the known and projected impacts of climate change on the roles played by each of these groups.
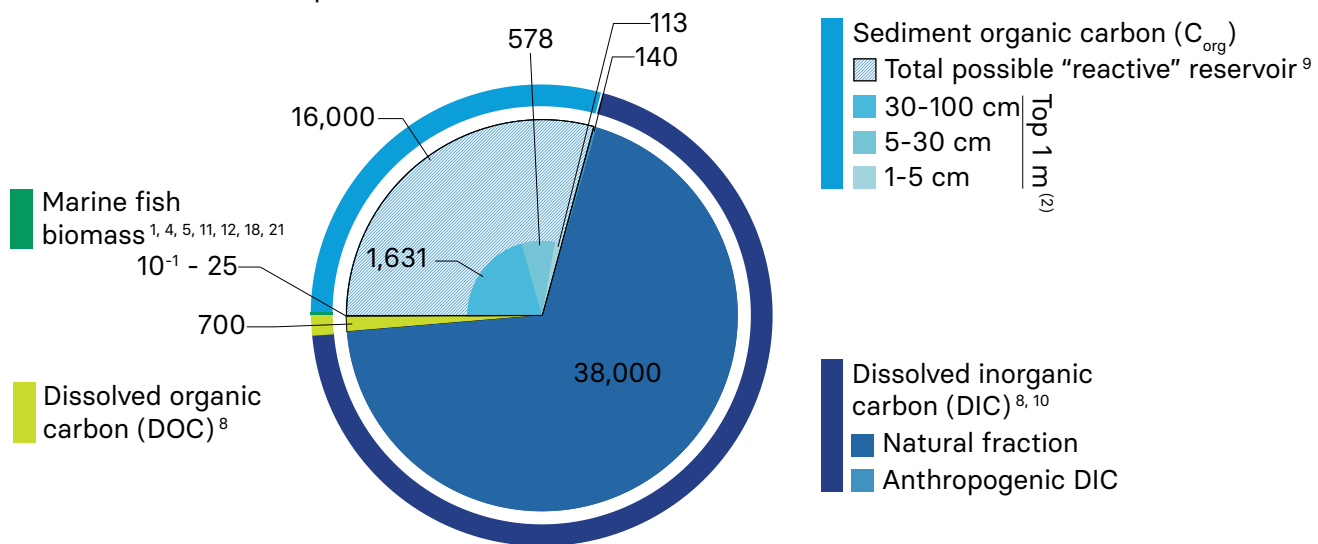
FIGURE 1.
Overview of the carbon stored within the major reservoirs of the ocean system; all quantities are in Pg C. For some reservoirs (e.g., marine fishes and ocean sediments) the amount of storage is not well constrained.
[1] T. R. Anderson et al., 2019 [2] Atwood et al., 2020 [4] Bar-On, Phillips,and Milo 2018 [5] Bianchi et al. 2021 [8] Emerson and Hedges 2008 [9] Estes et al., 2019 [10] Gruber et al., 2019 [11] Irigoien et al., 2014 [12] Lam and Pauly 2005 [18] Proud et al., 2019 [21] Wilson et al., 2009

[8] The authors of the 2021 Intergovernmental Panel on Climate Change (IPCC) summarize this quite simply: "An emission of CO_2 into the atmosphere is more effective at raising atmospheric CO_2 than an equivalent CO_2 removal is at lowering it." (Canadell et al., 2021)

Deep blue storage: Carbon reservoirs in the ocean

The global ocean system – water, biota and sediments – stores between 41,000 and 55,000 Pg C, more carbon than in all terrestrial forests and soils combined (Mackenzie and Lerman 2006; Estes et al., 2019; Atwood et al., 2020).[9] Approximately 38,000 Pg of this larger pool is stored within ocean waters as dissolved inorganic carbon (DIC; i.e., carbonate species), with a smaller 700 Pg C pool stored in various dissolved organic molecules known as dissolved organic carbon (DOC) (Emerson and Hedges 2008; Fig. 1). The ocean DIC reservoir includes approximately 140 Pg of anthropogenic carbon absorbed from the atmosphere since 1800, amounting to approximately 0.4 % of the total current ocean inventory (Gruber et al., 2019). The top meter of marine sediments stores an estimated 2,300 Pg of organic C, with recent work suggesting the total amount of organic carbon below the ocean floor may be as much as 16,000 Pg (Estes et al., 2019; Atwood et al,. 2020; Fig. 1).

The amount of carbon stored in living marine biota (phytoplankton, zooplankton, fishes and marine animals, including marine mammals; Fig. 2) is highly uncertain, but there is no doubt it is orders of magnitude lower than the amount of carbon in ocean water or marine sediments. Traditional mass balance approaches have suggested living marine biota could contain no more than 1 – 3 Pg C (Mackenzie and Lerman 2006; Emerson and Hedges 2008), although more recent work focused on "twilight zone" mesopelagic communities (i.e., those fishes found between 200 and 1000 m deep) suggests the amount of carbon in ocean biota could be substantially greater. For example, Irigoien et al. (2014) estimated that fishes inhabiting the mesopelagic between 40° N and 40° S likely themselves contain between 1.4 and 1.9 Pg C, but could contain as much as 25 Pg C.[10] A very recent estimate by Bianchi et al. (2021) places the modern-day total biomass of marine fishes at 4.7 Pg (containing roughly 0.6 Pg C, based on a C : biomass ratio of 1:8). Previous quantification efforts (Wilson et al., 2009; Lam and Pauly 2005, based on reanalysis of data in Gjøsaeter and Kawaguchi 1980)
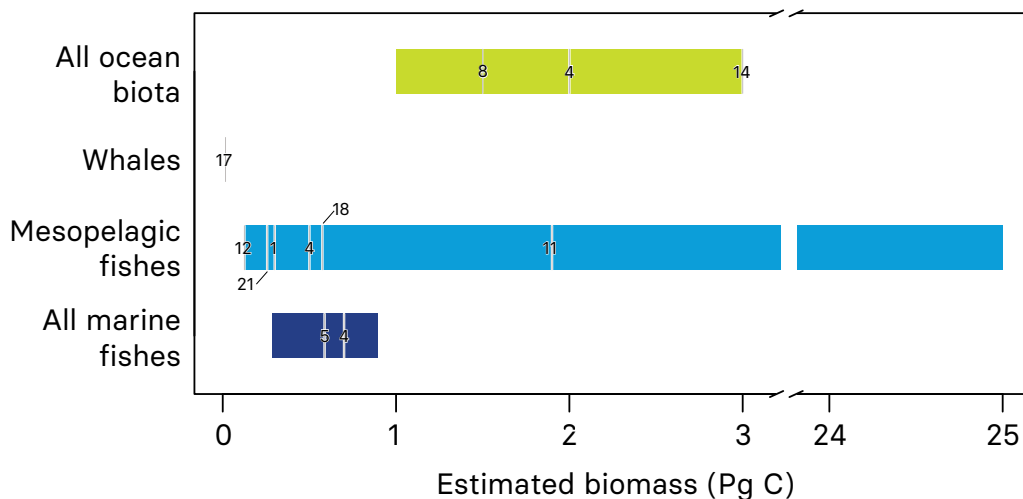
FIGURE 2.
Range plot showing the wide variation in estimates of biomass among different reservoirs within the ocean. Shaded bars indicate the overall range of estimates within each category, including the associated uncertainties (if given). Vertical lines indicate individual estimates assembled from the scientific literature; numbers correspond to the references given below.
[1] T. R. Anderson et al., 2019 [4] Bar-On, Phillips and Milo 2018 [5] Bianchi et al., 2021 [9] Emerson and Hedges 2008 [11] Irigoien et al., 2014 [12] Lam and Pauly 2005 [14] Mackenzie and Lerman 2006 [17] Pershing et al.,2010 [18] Proud et al., 2019 [21] Wilson et al., 2009

[9] This range of values reflects differences among authors in the quantity of sediment organic carbon assumed to be part of the "fast" carbon cycle relevant for decadal- to millennial-scale changes in climate.

[10] Irigoien et al. (2014) used acoustic observations from a circumnavigation of the oceans to estimate the biomass of mesopelagic fishes at between 11 Pg. and 15 Pg. To obtain

the values we report here, we applied to these estimates the assumption by Mariani et al. (2020) that mesopelagic fish biomass contains 12.5% C by mass. Importantly, we note that this conversion itself represents a substantial source of uncertainty in quantifying the role of fishes within the carbon cycle. Other recent studies have applied a C : biomass conversion of 10% (Bianchi et al., 2021; Saba et al., 2021) and, alternatively, as much as 15% (Bar-On, Phillips and Milo 2018).

had estimated the biomass of mesopelagic fishes to be an order of magnitude lower at approximately 1 Pg (containing 0.12 Pg C, based on a C : biomass ratio of 1:8, or 12.5%). Irigoien et al. suggested their greater 2014 values were in fact likely to be underestimates of the true biomass in mesopelagic fishes because they did not include productive higher latitude areas or mesopelagic invertebrates. In contrast, the biomass of epipelagic fishes, which include foraging species such as herrings, anchovies and sardines, in addition to salmon, tunas and billfishes, is reliably believed to be approximately 1 Pg (0.12 Pg C; Wilson et al., 2009); the estimate for this group of fishes is more certain since these species constitute the basis for most of the world's major commercial fisheries.

Uptake of atmospheric CO_2 by the ocean

Physical forces drive most of the ocean's absorption of CO_2 from the atmosphere. At a given location, the net flux of CO_2 into or out of the ocean (i.e., absorption or "off-gassing"/evasion) is determined by the relative concentration of dissolved CO_2 in the water compared to the concentration in the overlying atmosphere. The difference between these two concentrations determines the gradient across the air-sea interface and thus the direction and magnitude of the flux. The concentration of CO_2 in the atmosphere (412 ppm at Mauna Loa, Hawaii, as of October 2021) rises and falls seasonally by hemisphere due to natural annual cycles in primary production, but has been increasingly approximately exponentially since the onset of the Industrial Revolution.[11] The concentration of CO_2 in the ocean (usually described in terms of partial pressure, or pCO_2) is largely determined by water temperature (colder waters can hold more CO_2), salinity and biological processes (chiefly, the drawdown of DIC during photosynthesis). Thus, while physical processes dominate absorption of CO_2 by the ocean, biogeochemical processes do play an indirect role by helping set the surface layer concentration; water temperature tends to be relatively more important in determining variation in pCO_2 in the subtropics, while biogeochemical processes tend to dominate at high latitudes, in waters near the equator and in regions where strong upwelling is present (Takahashi et al., 2002).

The balance of these processes currently serves to make the ocean a strong sink for atmospheric CO_2. The surface ocean currently absorbs approximately 2.5 Pg C yr^{-1} from the atmosphere, but models and reconstructions of past ocean chemistry indicate that the ocean in fact served as a source of CO_2 to the atmosphere prior to the onset of the Industrial Revolution (Hauck et al., 2020; Sabine and Feely 2007). Thus, nearly all of the CO_2 absorbed by the ocean today is anthropogenic; fully 23% of all anthropogenic CO_2 emissions from 2010 –2019 have ended up in the ocean, with the rest remaining in the atmosphere or being stored by terrestrial ecosystems (Canadell et al., 2021). The continued rise in atmospheric CO_2 concentrations continues to "push" more and more carbon into the ocean, though there is increasing evidence that the ocean's natural ability to absorb CO_2 may be weakening (Canadell et al., 2021).

Carbon cycling and export from the surface ocean: The solubility and biological pumps

Overall rates of export and the solubility pump

Once in the ocean, the vast majority of absorbed CO_2 dissolves into various carbonate species, collectively referred to as dissolved inorganic carbon (DIC). A portion of this carbon can then be exported to deeper waters, beginning the process by which it can be sequestered from the atmosphere over the decadal to centennial timescales relevant for climate change. In total, the surface ocean exports 8 – 15 Pg C yr^{-1} in a variety of particulate and dissolved forms which are discussed in the following paragraphs (Sabine and Feely 2007; Hauck et al., 2020; Fig. 3). A collection of physical processes, known as the ocean solubility pump, are responsible for some of this carbon export (Sarmiento and Gruber 2006a). Much of this physical export of dissolved carbon happens at high latitudes near the Earth's poles, where parcels of colder, saltier water sink toward the ocean floor because they are more dense than warmer, fresher waters.

Carbon export via the biological pump

In contrast to the solubility pump, which exports carbon in dissolved forms, the majority of carbon export from the surface ocean occurs via a set of biogeochemical processes collectively known as the ocean biological pump[12] that send carbon to the deep ocean in various particulate (or larger) forms (Ducklow, Steinberg and Buesseler 2001). The majority of proposed ocean CDR approaches – and all of the natural climate solutions considered in this report – are designed to enhance or sustain various processes that directly support this particulate carbon export system. Carbon export through the biological

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[11] keelingcurve.ucsd.edu; accessed October 2, 2021.

[12] Sometimes referred to in plural form, i.e., "biological pumps," when there is a desire to distinguish among the many component biogeochemical processes.

pump begins with delivery of limiting nutrient(s) to the ocean's surface; this can occur via injection of nutrient-rich water from depth, lateral input from rivers or other coastal sources, or deposition from above of nutrient-rich atmospheric dust, which can be carried many hundreds of kilometers across the globe from desert source regions such as the Sahara (Emerson and Hedges 2008). These nutrients – typically nitrate, an oxidized, bioavailable form of nitrogen, or, in the case of certain high-latitude regions, iron – fuel primary production by marine phytoplankton (net primary production in the oceans is approximately 50 Pg C yr^{-1}; Field et al., 1998). Some of this phytoplankton biomass fuels secondary production at higher trophic levels, which can redistribute the constituent carbon and nutrients throughout the ocean, both horizontally and vertically.

The final component of the biological pump consists of carbon export: About one-fifth of this newly fixed organic matter (containing approximately 10 Pg C yr^{-1} globally; Emerson and Hedges 2008) is chemically reshaped, repackaged and remineralized by bacteria, zooplankton and abiotic processes, and then exported from the surface layer as particulate organic carbon, or POC (Buesseler and Boyd 2009; Buesseler et al., 2007). In the classic representation, the pump consists of a gravitationally controlled, downward rain of carbon-containing particles – often referred to as "marine snow" due to its appearance – that includes zooplankton fecal pellets and mucus, tiny parts of dead of animals and phytodetritus (the biomass of dead phytoplankton) (Alldredge and Silver 1988). This rain of particles also contains significant quantities of the minerals that many algae use to build their cell walls, chiefly amorphous biogenic silica (opal) from the frustules formed by diatoms, and calcium carbonate from shield-like coccoliths produced by coccolithophores (Iversen and Ploug 2010). These minerals can help to "ballast" sinking particles, adding density that makes the particles sink more rapidly out of the surface layer into the deep ocean (Klaas and Archer 2002), and provide some level of "armoring" that hinders metabolism of the associated organic matter by heterotrophic bacteria (Katz et al., 2004). To emphasize the particular contribution of this particulate inorganic carbonate (PIC) export by coccolithophores, scientists sometimes divide the biological pump into a "soft tissue pump," which refers to the export of POC, and a "carbonate pump," which refers to the export of coccoliths (e.g., Sarmiento and

Gruber 2006a).[13] Calcium carbonate exported via the carbonate pump accounts for approximately 6% of total annual export via the biological pump (Sarmiento et al., 2002).

As these particles containing POC and PIC sink within the water column, various physical and biogeochemical processes remineralize the carbon within them, reducing what is often a heavy blizzard of marine snow at the base of the surface layer to mere flurries by the time the storm reaches the seafloor. On average, between just 0.2 – 0.4 Pg C yr^{-1} of the 10 Pg C yr^{-1} exported from the surface ocean (2 – 4%) ends up in seafloor sediments (Middelburg 2019). This pattern of flux attenuation can be roughly approximated by a power-law function, with processes such as aerobic respiration by particle-attached bacteria, physical fragmentation and repackaging of particles by zooplankton acting in concert to turn the sinking carbon back into DOC and CO_2 (Martin et al., 1987; Collins et al., 2015). In addition, much of the PIC from coccolithophores dissolves back into its ionic components (chiefly calcium and carbonate) as the particles enter deeper waters that are more acidic.

Wide variation in the efficiency of the biological pump: A continuing focus of scientific inquiry

While we know generally how much carbon the ocean sequesters each year, the biological pump is not uniformly efficient. Global mean annual export and sedimentation rates conceal massive variation across both space and time in the fraction of surface ocean POC that is exported and eventually sequestered in the deep ocean (Buesseler et al., 2007). The wide spatiotemporal variation in this ratio, often termed the export efficiency of the biological pump, is a primary reason it is so difficult to predict whether a given ocean NCS will successfully sequester carbon. In general, high-latitude ocean biomes such as the subpolar North Atlantic and Southern Ocean, where primary production is highly seasonal and dominated by algae including diatoms and coccolithophores, support the highest export efficiencies. The ocean's lowest export efficiencies are found in oligotrophic, or nutrient poor, regions of the tropical and subtropical surface oceans, including the subtropical ocean gyres that account for the majority of Earth's total ocean area (Henson, Le Moigne and Giering 2019). However, while these generalities hold true at annual timescales, high rates of surface productivity do not necessarily lead to high-carbon export efficiencies; in some cases,

[13] This carbonate pump is a pathway distinct from the physical solubility pump, even though both involve the export of carbonates.

the two may even be inversely correlated (Henson, Le Moigne and Giering 2019). The many factors that drive these variations in export efficiency include:

- Differences in the kind and number of phytoplankton responsible for primary production at a given time and location within the surface ocean,

- the form and quantity of nutrients delivered to those phytoplankton and

- variations in time and across all three dimensions of space in the activities of heterotrophic bacteria and zooplankton, which metabolize, repackage and shuttle POC within the water column at rates that depend on variables as diverse as water temperature, oxygen concentration, the presence of marine viruses and the lipid or mineral content of the input biomass.

The causes of these variations constitute a central and enduring focus of research in oceanography and climate science and remain one of the fields' greatest scientific uncertainties; indeed, a wide-ranging, current National Aeronautics and Space Administration (NASA) study effort is still examining many of the same questions concerning rates of ocean carbon export that were posed more than 40 years ago by the earliest scientists working in the field (Siegel, Cetinić, et al., 2021; Deuser and Ross 1980). Of critical relevance to nearly all ocean-based CDR and NCS approaches, one observation about the biological pump has remained remarkably consistent despite the evolution of science in this area: The depth at which particulate carbon is turned back into CO_2 determines how long carbon is sequestered from the atmosphere (Saba et al., 2021; Siegel, DeVries, et al., 2021). In general, the deeper carbon gets in the water column, the longer the timescale of sequestration.[14]

Mediators of carbon export via the biological pump: Phytoplankton, zooplankton, fishes and whales

Given the many uncertainties and sources of variation in export efficiency, some scientists have further deconstructed the biological pump into as many as five different subordinate processes to query or highlight the contributions of individual groups of marine organisms to overall export. This approach has proven useful for estimating how much of the downward carbon flux and observed attenuation can

be attributed to the vertical migrations of mesopelagic fishes and zooplankton compared with export via simple gravitational sinking (e.g., Boyd et al., 2019). Others have sought to emphasize the roles of more specific groups of marine animals in mediating carbon fluxes within the ocean by advancing new concepts, such as a distinct "whale pump" (Roman and McCarthy 2010; Lavery et al., 2010). Despite a lack of scientific consensus, whale conservation has received subsequent interest as a possible carbon sequestration strategy from carbon market advocates at the International Monetary Fund (Chami et al., 2019) and in the popular media (Yeo 2021; Carrere 2021). In a series of infographics, one conservation group affiliated with the United Nations Environment Program (UNEP) has even proposed nine separate, distinct ocean carbon pumps and sequestration pathways mediated by whales and fishes (Lutz et al., 2018); the graphics have been widely circulated on the Internet.

Phytoplankton and primary production

Primary production in the oceans

Phytoplankton, a functional classification that includes both small marine algae and cyanobacteria, are the cornerstone of productivity in the world's oceans. When supplied with adequate quantities of nutrients and sunlight – the biosphere's primary energy source – these organisms act as the biological engines of the surface ocean, fixing CO_2 into biomass at a rate of 50 Pg C yr^{-1} (Field et al., 1998). Global variations in both phytoplankton abundances and species assemblages help set the stage for carbon export: The quantity and quality (i.e., biochemical composition) of the phytoplankton biomass that is produced determine in part how much carbon is exported from the surface ocean, and the rate at which exported POC is remineralized once it sinks or is transported below the surface layer. Some parts of the ocean support higher rates of primary production than others, some ocean biomes are characterized by a high degree of seasonality while others sustain more even rates of production throughout the year, and some biomes support a diversity of species while others are dominated by just a few major taxa.

Nutrient-limited ocean biomes, including the subtropical gyres

Low- and mid-latitude oligotrophic regions, including the subtropical gyres, support lower areal rates of net

[14] Saba et al. (2021) estimated that the average residence time of a carbon atom in the ocean – an indicator of sequestration time – increases from 14 years at a depth of 100 m to 104 years at a depth of 400 m. At 1000 m, carbon is effectively sequestered for over 350 years.

primary productivity than those that receive regular inputs of nutrients from coastal sources or from upwelling (Falkowski 2014). Primary production in these regions is generally dominated by phytoplankton of very small cell size, including the cyanobacteria *Prochlorococcus* and *Synechococcus*; the former is the smallest and most abundant photosynthetic organism on Earth, and the two species together account for over 50% of all primary production in the oceans (Partensky, Blanchot and Vaulot 1999; Biller et al., 2015). Primary production in oligotrophic systems is generally thought to be limited by the supply of nitrogen, or co-limited by both nitrogen and phosphorus, at least over the relatively short timescales of biomass turnover in the surface ocean (Moore et al., 2008).[15] As stated in the previous section, export efficiency tends to be very low in low- to mid-latitude oligotrophic systems; in part, this is because the majority of new biomass is quickly recycled by heterotrophic bacteria, with the remainder assimilated by higher trophic level organisms (Henson, Sanders and Madsen 2012; Fenchel 2008). The sinking speed of smaller plankton cells is also slower than that of larger-celled organisms, which allows for more bacterial degradation, with concomitant production of carbon dioxide, before the organisms can sink out of the photic zone.

High-latitude ocean biomes, including iron-limited HNLC regions

In contrast, primary production in high-latitude ecosystems tends to be dominated by massive, seasonal blooms of diatoms, coccolithophores and other species of microalgae. These systems can support high export efficiencies when a comparatively weaker microbial loop and active downward transport of carbon by zooplankton combine to send large seasonal pulses of POC rich in opal and/or calcium carbonate into the ocean interior (Henson, Le Moigne and Giering 2019). Despite their similar patterns of carbon export, these systems are characterized by divergent regimes of nutrient limitation. Phytoplankton growth in the subpolar North Atlantic Ocean is generally limited by nitrogen availability, while primary production in the Southern Ocean and subpolar North Pacific Ocean is limited instead by the supply of bioavailable iron. Along with the Equatorial Pacific Ocean, the Southern and North Pacific oceans are termed "high-nutrient, low-chlorophyll," or HNLC, regions: The surface waters in these biomes are replete in concentrations of both

major plant macronutrients, nitrogen and phosphorus – yet phytoplankton there do not exhibit continuous exponential growth.

Although the limitation of growth by iron was hypothesized in some phytoplankton species as early as the 1930s, widespread iron growth limitation in HNLC biomes was not demonstrated empirically until much later in the century (Martin et al., 1994). Unlike the macronutrients nitrogen and phosphorus, iron is an essential micronutrient in photoautotrophic organisms: While it severely limits primary production – the element is a critical component of several proteins used for energy transfer during photosynthesis (Schoffman et al., 2016) – very little iron is required to release the organism from limitation if it is supplied in an amenable form. This peculiarity is what makes artificial iron fertilization potentially attractive as an ocean-based CDR strategy: Comparatively little mass of the element can theoretically stimulate large amounts of phytoplankton growth (Watson et al., 2008). However, as discussed in the previous section, surface phytoplankton growth does not always result in increased export of fixed carbon to depth. In addition, not all iron is equal: Only iron that is bioavailable, i.e., in a form that can be accessed and used by the cell, can release phytoplankton in these biomes from limitation. Because iron is so essential for photosynthesis and several other metabolic functions in both phytoplankton and heterotrophic organisms, there is very little "free" iron in the ocean; most of it is complexed to organic ligands, any free iron in the ocean is rapidly scavenged and quickly assimilated by biota (Sutak, Camadro and Lesuisse 2020). Marine microorganisms as different as *Synechococcus* and the diatom *Phaeodactylum tricornutum* deploy a complex array of extracellular siderophores – molecules designed to chelate, or bind to, iron – to quickly lock up any available supplies of the element (Rudolf et al., 2015; Coale et al., 2019). While diatom species are often the first and most dominant primary producers in HNLC waters to respond following fertilization with iron (Boyd et al., 2007), other phytoplankton taxa can account for large fractions of primary production when waters are less replete in silicate (Buesseler et al., 2005). The causes of iron limitation in the ocean – in particular, the biogeochemical mechanisms through which iron is interconverted between bioavailable forms and inaccessible organic complexes – remain a key focus

[15] Many geochemists and chemical oceanographers take the seemingly contrary view that phosphorus is ultimately limiting in nearly all systems over millennial and longer timescales, due to the fact that nitrogen can be fixed biologically from

a practically unlimited supply in the atmosphere, while no analogous pathway exists for phosphorus. However, the two views are not incompatible if one considers ocean processes at the two very different timescales (S. V. Smith 1984).

of current research in marine ecology and the earth sciences. Among the recent discoveries in this area is the importance of sunlight in reducing Fe^{3+} to the more bioavailable Fe^{2+} state in offshore waters and transitional systems such as the southern California Current (Hogle et al., 2018).

Zooplankton

Zooplankton, along with heterotrophic bacteria, are the ocean's secondary producers: They consume, repackage and process the carbon fixed by the billions of phytoplankton that drive the biological pump. Grazing by zooplankton is a key top-down trophic control on primary production by phytoplankton, and zooplankton in turn serve as prey for high-trophic level organisms such as whales and fish. In addition, zooplankton, including copepods such as *Calanus finmarchicus* and the Antarctic krill *Euphausia superba*, mediate a critical downward flux of fixed carbon that can amount to as much as 55% of overall export of POC from the ocean's surface (Boyd et al., 2019). After rising into surface waters at night to feed on phytoplankton, zooplankton retreat to depth during the day where they digest the consumed biomass and excrete it in fecal pellets, thus "repackaging" slow sinking phytoplankton cells into a faster-sinking form that can accelerate particle export (Stamieszkin, Steinberg and Maas 2021). Zooplankton also contribute to POC flux via the shedding of mucus, the sinking of whole or partial individuals, mortality during deep hibernation, and the release of organic and inorganic compounds through various biological and physical mechanisms such as "sloppy feeding" (Collins et al., 2015; Steinberg et al., 2008). These diel vertical migrations are particularly important in sustaining the biological pump in high latitude ecosystems, where zooplankton can comprise a significant fraction of overall planktonic biomass and sustain migrating populations of great baleen whales. The degree of temporal and spatial coupling between the phytoplankton and zooplankton communities in these highly seasonal systems is a key determinant of carbon export and ecosystem function.

Observed and predicted effects of climate change on ocean plankton

The effects of climate change and anthropogenic mobilization of CO_2, particularly those associated with ocean acidification and increases in sea surface temperatures, have already been observed in both phytoplankton and zooplankton communities. In addition, a recent series of increasingly sophisticated modeling studies indicate that the populations of marine microorganisms are likely to experience profound shifts in the coming decades under nearly all anthropogenic emissions scenarios. Due to the critical role of plankton in driving the biological pump, these predicted shifts make it even more difficult to predict how much carbon could be sequestered in future decades by any CDR or NCS pathway that depends on particulate carbon export.

Phytoplankton

Anthropogenic increases in sea surface temperature have been hypothesized as a main driver of community change in phytoplankton (Mousing, Ellegaard and Richardson 2014). More recently, secondary effects of ocean warming, such as increased stratification and decreased nutrient availability, have emerged as direct mechanisms of observed changes (Angus Atkinson et al., 2021). In the North Atlantic, for example, pico- and nanophytoplankton such as *Synechococcus* have increased in abundance over the past 60 years at the expense of larger-celled diatoms (Schmidt et al., 2020). This increase in smaller organisms, whose cells contain lower concentrations of essential biomolecules, reduces both nutrient availability and trophic transfer efficiency in pelagic systems (Angus Atkinson et al., 2021). These trends are not just confined to the North Atlantic. Flombaum et al. (2013) estimate that global abundances of Synechococcus will increase 14% by 2100, with a 50% increase possible at mid-high latitudes. The increasing domination of marine primary production by smaller-celled cyanobacteria at the expense of larger-celled algae such as diatoms and coccolithophores may herald a future ocean in which the global biological pump functions at the low efficiencies observed in the current-day subtropical gyres, exporting less overall particulate carbon (Fu, Randerson and Moore 2016). One recent modeling study predicted that the distributions of a broad range of representative phytoplankton species are moving poleward at a median speed of 35 km per decade in response to warming ocean temperatures (Benedetti et al., 2021)

Phytoplankton communities have also been dramatically affected by ocean acidification, with the most acute impacts in systems such as the Southern Ocean, where a large percent of primary production and export can be attributed to coccolithophores (Bopp et al., 2013; Dutkiewicz et al., 2015). Increasing acidification shifts the distribution of carbonate species within seawater, making it more difficult for coccolithophores and other calcifying marine organisms such as pteropods to precipitate the calcium carbonate necessary for their cell structures (Seibel, Maas and Dierssen 2012). In addition, ocean acidification increasingly threatens to short circuit the carbonate pump within these systems due

to the shoaling (i.e., upward movement within the water column) of the lysocline, or depth at which the rate of dissolution of calcite begins to increase dramatically. As particles containing PIC sink within the water column, this lysocline shoaling causes them to dissolve earlier during their downward transit, resulting in less carbon being sequestered in the deep ocean (Gruber 2011). Work now also suggests that the ability of phytoplankton to acquire iron is linked to carbonate ion availability; because ocean acidification shifts carbonate speciation away from the carbonate ion toward bicarbonate and aqueous CO_2, the phytoplankton protein with the highest affinity for iron uptake – phytotransferrin – may be replaced with lower affinity mechanisms (McQuaid et al., 2018). The stakes of such a change are high considering the importance of diatoms for both primary production and carbon export.

Zooplankton

The effects of climate change within the oceans are expected to cause parallel shifts in zooplankton populations, particularly among species such as Antarctic krill that depend for part or all of their life histories on the presence of sea ice (Flores et al. 2012). Studies have also documented the effects on various zooplankton species of ocean acidification (Seibel, Maas and Dierssen 2012) and changes in fishing patterns (A. Atkinson et al., 2009). Any shifts in zooplankton populations that occur out of step with shifts in traditionally associated phytoplankton assemblages will have significant consequences for ecological structure and function, including carbon export and ecosystem function.

Multiple studies suggest that between now and 2100, the net primary productivity of the Southern Ocean will increase (e.g., Pinkerton et al., 2021), but there is significant uncertainty about how this will affect krill productivity. Theoretically, increased primary production could enhance the growth of Antarctic krill. Evidence to support this idea includes the fact that krill primarily feed on marine algae, meaning there are few to no trophic intermediaries (dependents)

for them to be successful if they are presented with sufficient food supply. But climate change is expected, in the next 80 years, to decrease Antarctic ice area by approximately 25%. Krill depend on ice for both refuge and because it is supports a critical part of their life history – they feed on algae growing on the undersides of icebergs (Flores et al. 2012). Though ice extent is expected to decrease, new research suggests that reduced thickness and expanded ice ridges will facilitate more primary production and better krill refuge (Veytia et al., 2020). Thus, in the higher latitudes, krill populations may increase in coming decades, while decreasing in areas with no sea ice, even as other free-living zooplankton species shift to fill the new niche. Veytia et al. (2020) argue that such a shift will favor highly mobile predators and disadvantage mid-high latitude, less mobile species. The biggest uncertainty around such an increase is the temporal match between the krill life cycle and possible changes in plankton bloom timing. If the two are not coupled, krill recruitment may decline, and result in a lower energy input into the system.

In the North Atlantic, a long-time series of zooplankton survey data documented clear phase shifts in community composition. The copepod *C. finmarchicus* – a staple, high-energy food source for higher trophic level organisms – is being replaced by smaller, less energy rich copepods, such as *Pseudocalanus spp.* (Johnson et al., 2011). This shift is believed to be caused primarily by ocean warming (Grieve, Hare and Saba 2017), lack of top-down control following near extirpation of great baleen whales in the region (Berge et al., 2012) and competition with smaller nano- and picophytoplankton (Angus Atkinson et al., 2021). Down-scaled climate models predict the density of *C. finmarchicus* will decline by as much as 50% by 2081 under a high greenhouse gas scenario (Grieve, Hare and Saba 2017). The significance of this shift has been particularly severe in the Norwegian Sea, where *C. finmarchicus* has traditionally accounted for 43% of all zooplankton biomass (0.082 Pg yr^{-1}) consumed by pelagic fish stocks.
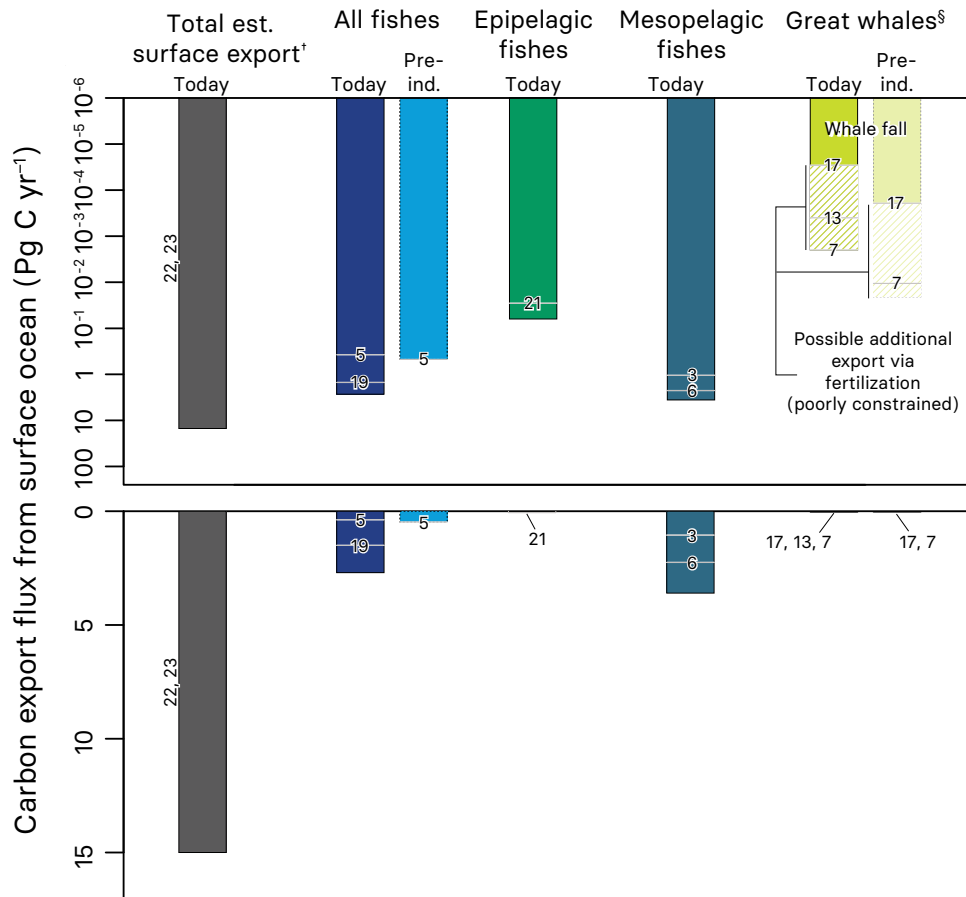
FIGURE 3.

Magnitudes of various downward carbon export fluxes from the surface ocean to the ocean interior. The same data are shown on both logarithmic (top) and linear (bottom) scales. Shaded bars encompass the overall range of export estimates within each category or subcategory, including the associated uncertainties (if given). Where the magnitudes of the attributed fluxes have been estimated separately for the current ("Today") and pre-Industrial Revolution ocean ("Pre-ind.," i.e., before the onset of commercial fishing and whaling), the estimates are presented side by side. Horizontal lines indicate individual values assembled from the scientific literature; numbers correspond to the references given below. The estimates from Durfort et al. (7) appeared in a preprint and have not been peer reviewed. † Includes the export attributed to both the biological carbon pump and solubility pump. § The hypothesized contributions of whales to carbon export via whale fall and, indirectly, via fertilization of iron-limited phytoplankton, are plotted separately.

[3] Aumont et al., 2018 [5] Bianchi et al., 2021 [6] Boyd et al., 2019 [7] Durfort et al., 2021 [13] Lavery et al., 2010 [17] Pershing et al., 2010 [19] Saba et al., 2021 [21] Wilson et al., 2009 [22] Sabine and Feely 2007 [23] Hauck et al., 2020

Role of fishes and marine mammals in the ocean carbon cycle

Fishes have not been traditionally evaluated alongside phytoplankton, zooplankton and bacteria as integral components of the biological pump. Seldom-crossed disciplinary boundaries between fisheries, biologists and oceanographers, a historical view of fishes as an extractable commodity apart from other ocean biota, and empirical geochemical evidence that fishes and other large marine organisms do not constitute or mediate ocean carbon fluxes of the same magnitudes as other ocean system components, have led to the exclusion of fish from most geochemical models of the ocean carbon cycle.[16] However, several recent studies have sought to shift this view by focusing on various aspects of fish populations and commercial fisheries for their geochemical significance as components of the global carbon cycle or, alternatively, as targets for policy interventions that could avert significant new GHG emissions (Wilson et al., 2009; Boyd et al., 2019; Mariani et al., 2020; Bianchi et al,. 2021; Saba

[16] Consider the following statement contained in one of the primary texts on the ocean carbon cycle: "Higher levels of the food chain such as fish are generally thought not to be of importance in controlling the chemical composition of most of the surface ocean." (Sarmiento and Gruber 2006b)

et al., 2021). This literature has emerged alongside another set of recent studies that have made similar arguments for various roles of whales in the carbon cycle (Pershing et al., 2010; Roman and McCarthy 2010; Lavery et al., 2010; Durfort et al., 2021). Fishes and whales are hypothesized to contribute to the global carbon cycle via five primary pathways:

- As short-lived reservoirs for carbon through storage in their living biomass,

- by redistributing carbon and nutrients throughout the sea via vertical (i.e., within the water column) or horizontal migrations, including the "whale pump" fertilization mechanism through which iron-rich, largely buoyant whale feces are hypothesized to stimulate surface ocean primary productivity, followed by export of some of the newly fixed carbon,

- through mixing of waters or resuspension of sediments (i.e., bioturbation), which may be important in redistributing nutrients within systems characterized by a high degree of stratification (Roman et al., 2014),

- by directly exporting carbon from the surface ocean to depth during whale fall or fish fall (i.e., the natural sinking of dead whales or fish to the bottom of the ocean), and

- in the case of fishes, via intestinal precipitation of calcium carbonates, followed by export to depth of significant quantities of PIC in fish feces.

Fishes

The previous discussion of ocean carbon reservoirs reviewed estimates of carbon in the biomass of marine fishes that ranged from 0.12 - 1.9 Pg C (Wilson et al., 2009; T. R. Anderson et al., 2019; Bar-On, Phillips and Milo 2018; Proud et al., 2019; Mackenzie and Lerman 2006; Bianchi et al., 2021; Irigoien et al., 2014), with the uncertainty analysis employed in one study suggesting the true biomass of mesopelagic fishes alone could contain as much as 25 Pg C (Irigoien et al., 2014). These disparate estimates were produced from methods as varied as simple geochemical mass balance, data-constrained ecosystem models with uncertainty analyses of various robustness, interpretation of acoustic data collected during a scientific circumnavigation of the Earth and extrapolations from FAO data tables. While there remains significant uncertainty about the total quantity of carbon in the biomass of extant fishes, there is little doubt that commercial fishing

has reduced standing fish stocks over multiple generations, but especially during the post-World War II era. Yet even two of the most recent estimates of total reduction in fish biomass differ by an order of magnitude. Bianchi et al. (2021) estimated that human activities have reduced the biomass of all fish and commercially targeted species by 32% and 67%, respectively, relative to the preindustrial era; using the assumption of Mariani et al. (2020) that mesopelagic fish biomass contains 12.5% carbon by mass, this 32% reduction in biomass corresponds to a decline in reservoir size of 0.3 Pg C. Using different methods, Mariani et al. (2020) estimated that the loss of carbon in fish biomass due to offshore commercial fishing since 1950 was 0.038 Pg C, an order of magnitude less.[17]

Adding further to this uncertainty, estimates of the total contribution of fish to carbon export also vary by an order of magnitude. Taking into account the various possible direct and indirect pathways through which fish may contribute to the biological pump, Saba et al. (2021) estimated that fish are in some way responsible for an average of 16.1% (± 13%) of total biological carbon flux out of the euphotic zone, equating to 1.5 ± 1.2 Pg C yr^{-1}. Using different methods, Bianchi et al. (2021) estimated that fish are responsible for 3.0 Pg of "particle production" per year, a reduction of 0.8 Pg from the preindustrial era; applying the same C : biomass ratio of 1:8, these equate to a current flux and reduction from preindustrial times of 0.4 Pg C yr^{-1} and 0.1 Pg C yr^{-1}, respectively. Mariani et al. (2020) estimated that between 1950 and 2014 the contribution of fish to export flux from deadfall alone was reduced by a total of 21.8 ± 4.4 × 10-3 Pg due to commercial fishing. Finally, using a very different approach based largely on a geochemical mass balance using values assembled during a literature review, Boyd et al. (2019) estimated that mesopelagic fishes may be responsible for mediating the export of as much as 3.6 Pg C yr^{-1} from the ocean's surface through diel vertical migrations similar to those of zooplankton (median estimate, 2.25 Pg C yr^{-1}; range, 0.9 – 3.6 Pg C yr^{-1}, equivalent to 13 – 25% of the total annual ocean C export flux). Aumont et al. (2018) used a coupled model approach to place the global magnitude of the fish-mediated C export flux at 1.05 Pg C yr^{-1} (about 18% of total surface carbon export), while Davison et al. (2013) estimated that fish-mediated export in the northeast Pacific Ocean accounted for 15 – 17% of total carbon export.

[17] One possible explanation for this discrepancy may be methodological: Mariani et al. (2020) considered only those fish with adult length > 30 cm, which would have caused them to exclude major fisheries such as herring, anchovy, etc.

The continuous intestinal precipitation and excretion of carbonates is the fourth major mechanism through which fish are hypothesized to contribute to the ocean carbon cycle (Wilson et al., 2009).[18] Fish use bicarbonate and intestinal proteins to precipitate calcite ($CaCO_3$) in their intestinal lumen then, to compensate, release acid in their gills (Wilson, Wilson and Grosell 2002). Much of the $CaCO_3$ precipitated in fish intestines sinks into the deep ocean as part of the larger flux of PIC; once in the deep ocean, these particles dissolve, adding alkalinity at depth. Thus, unlike in the case of corals and pteropods, which can subsidize alkalinity into the deep ocean only once, when their skeletons dissolve after death, fish provide an input of dissolvable $CaCO_3$ to the deep sea continuously throughout their lifetimes. This injection of alkalinity into deeper waters is facilitated by the unique form of calcite precipitated in fish intestines; elevated concentrations of magnesium, compared, e.g., to the calcite precipitated by coccolithophores, makes the $CaCO_3$ in fish feces soluble even above the calcite and aragonite lysoclines (Woosley, Millero and Grosell 2012). Collectively, precipitation of these carbonates may take up 0.04 – 0.11 Pg C yr^{-1} from surface seawater, representing 3% – 15% of the total global biological production of carbonates in the surface ocean (Wilson et al., 2009). Importantly, while scientists have observed steep decreases in calcification rates when organisms such as coccolithophores and pteropods were exposed to conditions representative of future ocean pH, calcification rates in fish tend to increase in proportion to the concentration of dissolved CO_2 (Heuer et al., 2016). For this reason, there is some speculation that as the oceans become more acidic, fish will become more important players in the global ocean inorganic carbonate cycle (Wilson et al., 2009).

Marine mammals

The 1.6×10^{-2} Pg C currently contained in the biomass of eight of the largest whale species is an order of magnitude smaller than the 10.3×10^{-2} Pg C these species were estimated to contain prior to the start of commercial whaling (Pershing et al., 2010). While there are no estimates of the total biomass of all marine mammals, we find the estimates for these large whales likely to be much more reliable than any large-scale estimates of fish biomass, since marine mammals follow predictable migration routes, the number of individuals in each population is generally

well known and allometric methods for determining biomass are increasingly robust.

The potential contribution of whales to carbon export via whale fall is the most scientifically comprehensible of the various pathways through which marine mammals are hypothesized to contribute to carbon flux. Based on an exhaustive review of the relevant literature, Smith and Baco (2003) concluded that roughly 50% of whale falls result in export of carbon to the seafloor, though they did not provide quantitative estimates of direct carbon sequestration. Pershing et al. (2010) estimated that whale falls of the eight large species in their previously cited 2010 study may account for 2.9 ×10^{-5} Pg C yr^{-1} in direct carbon export.

By making several additional assumptions – the uncertainties inherent in which are discussed in the following section of this report – a handful of scientists have ascribed primary production and, in some cases, additional carbon sequestration to whales by invoking the "whale pump" fertilization hypothesis. According to this hypothesis, whale feces either rich in iron or other nutrients can fertilize the growth of phytoplankton in HNLC regions such as the Southern Ocean, leading to some amount of sequestration after a fraction of the new biomass is exported to depth. Durfort et al. (2021) have concluded in a recent preprint –not yet peer reviewed – that five large species of whales may sequester as much as 2×10^{-3} Pg C yr^{-1} if one considers both whale falls and the export of phytoplankton biomass that can be attributed to fertilization of Southern Ocean surface waters by their iron-rich whale feces. Others have suggested that Southern Ocean sperm whales may stimulate the sequestration of 4×10^{-4} Pg C yr^{-1} via this mechanism, while Southern Ocean blue whale populations could stimulate up to 0.13 Pg C yr^{-1} in new primary production if populations were fully restored to pre-whaling abundances (Lavery et al., 2010; 2014). In very recent work, Savoca et al. (2021) concluded that pre-whaling populations of four species could have stimulated 11% (range, 1.4 - 74.9%) of current-day total net primary productivity across a vast swath of the Southern Ocean. Working in the Gulf of Maine, Roman and McCarthy (2010) quantified the delivery by whale feces of nitrogen to stratified surface waters, where they hypothesized the subsidy would similarly stimulate primary production. However, neither Savoca et al. (2021) nor Roman and McCarthy (2010) quantified an accompanying carbon export flux.

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[18] In tropical regions, herbivorous and coral-eating fishes associated with reef ecosystems can also excrete large amounts of coral and coralline algae remnants that are incorporated into underlying sediments or sediments below deeper surrounding ocean waters (Grupstra et al., 2021).

Evaluation of four natural climate solutions in the open ocean based on current science

Potential for enhancing carbon sequestration through rebuilding of epipelagic fish populations

There are many reasons to rebuild depleted populations of epipelagic fishes to the kinds of target levels most frequently used in fisheries management, including single-species or single-fishery maximum sustainable yield (MSY). However, MSY typically correlates to abundances and spawning biomasses significantly reduced from so-called "virgin" (unfished) biomasses, often on the order of 30% – 50% of original biomass. Even the generally higher-biomass target of maximum economic yield (MEY) still correlates to biomasses much lower than in unfished populations. Taken together, these fisheries yields and profit-based targets (with global removals in the 80+ million metric ton per year range) impose poorly understood, system-scale alterations in marine ecosystem structure and function, including for carbon processing and sequestration. These shifts surely include both direct effects on carbon processing by fishes themselves, including sinking of dead fish akin to "whale falls," but also the indirect effects of fish foraging activities that could have implications for overall carbon sinking dynamics. In addition, significantly reduced total target species abundance likely induces ecological cascades, typically poorly understood.

While we agree emphatically that the consequences of goal setting for widespread fisheries removals ought to be understood in terms of such system alterations, we find the idea intriguing but premature that higher biomass targets for fished populations and higher aggregate abundances of targeted marine species could be set specially to assist in more rapid carbon drawdown. The current science surrounding this set of pathways is too uncertain to justify shifting targets for exploited populations on the basis of potentially enhanced carbon export alone. There are, at present, fundamental uncertainties in biomass estimates of marine fish stocks, larger uncertainties in the direct and indirect carbon export consequences of those estimates, and even larger unknowns in how those affect overall system performance, and thus, implications for overall carbon export fluxes. These uncertainties make it difficult to establish reliable baselines against which any gains in epipelagic fish populations could be precisely measured, and make the attribution of export to any individual or group of fishes equally difficult.

There are several additional considerations that make it difficult to validate models of the sort presented by Mariani et al. (2020). First, unlike in the case of whales, there have been very few actual observations of natural senescence or resulting deadfalls of epipelagic fishes. Recent papers make uniform assumptions across fish size spectra (>30 cm) that fish dying of senescence or disease rapidly sink and are sequestered at depth. More likely, smaller fish in particular will be subjected to higher predator/scavenger fields as they approach death and eventually sink. There is little empirical basis for suggesting small (~30 cm) mackerel in the open ocean are exported to the deep sea as efficiently as large (100 kg) tuna. Second, we do not understand the life cycle emissions of most fish species: Even if the natural deadfall of a restored fish population could be validated as part of the ocean carbon export flux at a given location within the ocean, we do not know the degree to which fish themselves serve as net sinks of carbon when their entire life cycles are taken into account, much less how that affects overall carbon dynamics in the ocean.

Notwithstanding these significant uncertainties, there are existing systems and frameworks in which fisheries goal-setting processes could be adapted to test the effects of management for objectives other than those used in traditional fisheries management. Examples include institutions already obliged to consider non-fisheries (ecosystem) outcomes, including the program areas of the U.S. and the European Union, as well as the Arctic Council. Perhaps the most interesting is the Southern Ocean, where krill are already managed as a fisheries target, but serve a potentially important role in iron and other nutrient regeneration. A krill fisheries management plan that sets in motion scientific processes to adequately manage for system outcomes would be especially important, as the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR) already requires those considerations. Because most models of future marine productivity suggest that high-production areas will shift poleward (Benedetti et al., 2021), the necessity of these approaches will take on added significance.

The contribution of fishes to inorganic carbon export via carbonate excretion is also uncertain, yet we find it is significantly better constrained than the potential deadfall flux. Given the likely increase in the strength of this flux with continuing ocean acidification, we

believe this path to sequestration warrants further study. We noted in particular that most research on piscine carbonates has focused on waters in the tropics (Salter, Perry and Smith 2019); studies must be expanded to additional species and biomes. In addition, the export efficiencies of particles containing piscine PIC need to be validated with empirical observations to narrow the broad possible contribution to overall calcium carbonate production proposed by Wilson et al. (2009).

The most promising immediate climate action involving epipelagic fishes may be various interventions aimed at reducing fuel use by the fishing fleet that targets these species. For example, Mariani et al. (2020) found that 82% of the emissions associated with targeting large pelagic species came directly from fuel use, and that only 57% of the global offshore catch would be profitable without fuel subsidies. Emissions could be reduced by reducing fish catches, improving nearshore fishery production to disincentivize transit further offshore in response to stock depletion, improving catch efficiency and ending overcapitalization and fuel subsidies.

Potential for avoided emissions by limiting or prohibiting new harvest of mesopelagic fishes

The science surrounding the carbon export mediated by mesopelagic fish populations is also uncertain, yet we find these species' present contribution to global sequestration likely massive enough to warrant immediate pursuit of limitations or prohibitions on their harvest. Even though we know very little about these species or the extent to which they mediate carbon export to depth, there is evidence they are nevertheless already being targeted for exploitation (Scoulding et al., 2015; Caiger, Lefebve and Llopiz 2021), necessitating the urgent need for intervention. Boyd et al. (2019) synthesize previous work in two different Pacific Ocean ecosystems to present a convincing global estimate of the flux mediated by these species – approximately 2.25 Pg C yr^{-1} – which is of the same order of magnitude as another recent estimate obtained by different methods of the total contribution of fish to carbon export (Saba et al., 2021). As many as 20% – 90% of mesopelagic species migrate diurnally over significant depth ranges, accelerating the transport of a very substantial amount of carbon to deeper waters; this export may be nearly as critical for carbon export as gravitational sinking alone (Boyd et al., 2019). Yet because these species have traditionally not been targeted by commercial fisheries, it is unclear how mesopelagic systems will respond to fishing or environmental

change, either in form (e.g., changes in biomass or community composition) or function (e.g., their role in exporting carbon) (Caiger, Lefebve and Llopiz 2021). Conservation strategies spanning pelagic to mesopelagic zones may help identify cost-effective CO_2 mitigation wedges (*sensu* Pacala and Socolow 2004).

Key research needs

We find that there are several specific areas of science central to this pathway where additional research is needed to reduce uncertainties:

- Due to the variation across multiple orders of magnitude in current estimates of marine fish biomass, new models, observing technologies and data, are needed to better constrain the total biomass of fish in the mesopelagic ocean and the fluxes mediated by these communities, including a robust set of empirical conversion factors for scaling measurements of fish biomass to units of carbon.

- Empirical, geographically bounded estimates of mesopelagic fish biomass and the export flux they mediate will be needed before any avoided emissions could be claimed by particular nations, organizations or industries; such estimates will require robust and creative accounting of uncertainties due to the fact that migratory fish do not remain in one location. Estimates could be broken out by ocean basin, exclusive economic zone (EEZ), biogeographic province (e.g., as in Longhurst 2010) or somehow associated with existing or proposed marine protected areas (MPAs) to support current conservation initiatives such as that described in Sala et al. (2021).

- Due to the very similar functional roles played by mesopelagic fish and zooplankton, which also shuttle carbon to depth during diel vertical migrations on an equally large oceanic scale (Steinberg et al., 2008), new observational methods and models are both needed to better partition the active transport of carbon attributed to these two groups of organisms. Current methods and models may overestimate the contributions of one or both groups due to their inability to discriminate among them.

- Further research on the composition of mesopelagic communities is needed to identify the different roles played in the carbon cycle by small fishes, believed to make up a substantial fraction, if not the majority, of mesopelagic biomass and larger species, such as cephalopods.

Potential for new carbon sequestration through rebuilding of large marine mammal communities, including whales

Despite heightened public interest in this pathway and the other many imperatives for continued rebuilding and conservation of marine mammal populations,[19] we find that while there is very good reason to enhance great whale population recovery using all possible speed, the current science is too uncertain to yet support the emplacement of a reliable scheme for carbon credits based on carbon sequestration by whales. There are overall too few scientific studies in this area – less than 10 in total – from which to draw any broad conclusions. However, we find the state of knowledge differs substantially between the two primary pathways through which whales are hypothesized to contribute to carbon flux. We believe current estimates of the potential export flux due to whale falls are scientifically sound, but likely relatively small in magnitude compared with the scale of anthropogenic emissions or other potential NCS sequestration pathways. In contrast, the few existing estimates in the scientific literature of additional carbon sequestration by whales via fecal fertilization of surface water (sometimes termed "indirect sequestration") share several common sources of uncertainty that cast doubt on the total magnitude of the potential flux and reduce the pathway's potential to serve in the near term as a source of carbon credits.

Sequestration via whale fall

Global whale populations remain at fractions of their pre-whaling abundances, leaving substantial room for the growth of any potential co-benefits, such as additional carbon sequestration, that would come with population recovery. For example, the current population of Southern Ocean blue whales is estimated to be between to be 1% – 2% of historical carrying capacity (Attard, Beheregaray and Möller 2016; Branch et al., 2007) yet there is substantial evidence that populations continue to expand steadily in the absence of large-scale whaling (Branch, Matsuoka and Miyashita 2004). Within this context, Pershing et al. (2010) calculated that the restoration of large baleen whale populations to estimated pre-whaling abundances could sequester 1.6×10^{-4} Pg of additional carbon each year through increased whale

falls. Whale falls do not occur randomly in space and are concentrated along key migration routes; because these routes involve travel through some of the deepest parts of the ocean, and because whale carcasses are heavy and sink rapidly,[20] the carbon in whale carcasses that sink to the ocean bottom (roughly 50% are assumed to do so; C. R. Smith and Baco 2003) is likely to be sequestered over timescales of decades to centuries (Saba et al., 2021). This is true even when bacteria and detritivores remineralize the carcass back into CO_2; as long as this remineralization occurs at the seafloor, the evolved dissolved inorganic carbon will remain locked away in the deep ocean for a length of time determined solely by thermohaline circulation and the ca. 1500 year timescale of interior ocean ventilation. (Sarmiento and Gruber 2006c).

A key finding of Pershing et al. – that the scaling of metabolic efficiency with organismal mass makes larger organisms comparatively more efficient at assimilating and sequestering carbon – implies that a focus on rebuilding populations of larger animals may be the best return on investment from a carbon sequestration standpoint. When generalized to other taxa, this finding also has significant implications for the targeted conservation of fishes based on size fraction. We explore this relationship between organismal mass and metabolic efficiency in a short appendix to this report.

Sequestration via fecal fertilization: The "whale pump"

The "whale pump" hypothesis is predicated on two sets of critical assumptions that have not been sufficiently verified through empirical observations. The first of these centers around the form and bioavailability of the nutrients delivered to the surface ocean in whale feces, while the latter concerns the relationship between primary production and export efficiency. While two of the studies we reviewed (Lavery et al., 2014; Savoca et al., 2021) sought to test the sensitivity of primary production or export calculations to variation in the mathematical parameters and scaling factors associated with these assumptions – a standard practice in biogeochemical modeling – a simple inspection of the calculations in other studies indicates the degree to which their authors' findings rest almost uniformly on just one or two values chosen from an extraordinarily thin literature.

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[19] For example, healthy whale populations increase fishery productivity and ecosystem stability and are the basis for industries such as ecotourism.

[20] The rapid sinking of a large, dense mass such as a carcass provides less opportunity for heterotrophic bacteria to turn the constituent carbon back into CO_2 near the sea surface, compared with bacterial remineralization of slower sinking marine particles composed of phytodetritus.

In the first case, calculation of primary production stimulated by nutrients in whale feces requires knowledge of both the concentration and bioavailability of the specific nutrient(s) assumed to be limiting to phytoplankton growth. When the whale pump hypothesis is applied to the Southern Ocean, an HNLC region in which iron is generally the limiting nutrient, this calculation requires assumptions about the concentration of iron in whale feces, and its bioavailability.[21] The existing literature contains only a handful of empirical observations of the former – most provided without uncertainties due to the absence of replication during sample collection (Nicol et al., 2010; Wing et al., 2014; Durfort et al., 2021) – and we know of only one set of indirect empirical measurements of the latter (Ratnarajah et al., 2017). Even this lone assessment of bioavailability was incomplete in that it focused on just two of the many chemical and physical properties known to affect iron bioavailability in the ocean; importantly, it did not include nutrient amendment experiments with phytoplankton cultures or any evaluation of the effect of chelation of iron from whale feces by ligands, which bind 99.9% of the dissolved iron in nearly all natural ocean waters (Gledhill and Buck 2012).

Two whale pump modeling studies have invoked the assumption that all the iron in whale feces becomes available for assimilation by phytoplankton, despite a very large body of scientific work in bioinorganic chemistry, chemical oceanography and biogeochemistry that suggests there is almost never a case in which large quantities of dissolved iron remain bioavailable over the timescales needed to sustain phytoplankton growth that leads to measurable carbon export. For this reason alone, these studies (Lavery et al., 2010; 2014) likely represent substantial overestimates of the amount of primary production one can fairly attribute to whale fertilization. Due to the sparsity of direct measurements of whale fecal Fe bioavailability, even Savoca et al. (2021), whose work represents a massive advance in the field, extrapolated their results to obtain rates of net primary productivity (though not carbon export) based on assumed model parameters from Ratnarajah et al. (2016). Durfort et al. (2021) incorporated into their model the whale fecal iron speciation and

size fractionation data of Ratnarajah et al. (2017), assuming that 12.2% of the fecal iron was bioavailable to phytoplankton while acknowledging this assumption was the single greatest source of uncertainty in their study. That study, currently in preprint, estimates that the restoration of baleen whales to pre-whaling abundances could result in a total additional sequestration of 8.7×10^{-3} Pg C yr^{-1} if fertilization is considered in addition to whale fall (Durfort et al., 2021).

The use in any of these models of a single value for bioavailability (whether 100% or 12.2%) is even more puzzling given the known heterogeneity in both the speciation and origin of iron Antarctic krill, these whales' primary food source and the source of nearly all the iron excreted in whale feces (Nicol et al., 2010).[22] Isotope analysis of iron in krill suggests the majority is lithogenic – establishing that the largest source of iron in the Southern Ocean comes from the sediments, from both nearshore and offshore regions (Schmidt et al., 2011; Schlosser et al., 2018). Yet Schmidt et al. (2016) found that the proportion of lithogenic iron in krill and apparent follow-on phytoplankton growth vary widely in both space and time, and are dependent on depth and proximity to shelf sediments or glacial flour.[23] In some cases, they found 90% of labile iron was sourced from the benthos.

The second major set of assumptions in the whale pump model concerns the fraction of primary production attributed to fertilization by whale feces that is then exported to a sufficient depth where it can be considered sequestered from the atmosphere. There is ample evidence from the Southern Ocean and elsewhere that export efficiency is not necessarily correlated with the rate of surface ocean productivity (Henson, Sanders and Madsen 2012; Buesseler et al., 2007). Perhaps most relevant, a very broad range of export efficiencies have been observed during iron fertilization experiments in the Southern Ocean, including cases in which almost no carbon was exported (Buesseler et al., 2004; Charette and Buesseler 2000; Boyd et al., 2007). It is clear then that one cannot assume that all, or even a majority, of the biomass from a phytoplankton bloom catalyzed by nitrogen- or iron-rich whale feces will end up sinking into the ocean interior. Several studies

[21] The work of Roman and McCarthy (2010) is not discussed in this section as it was centered on fertilization of phytoplankton in the Gulf of Maine by the nitrogen in whale feces; fecal nitrogen concentrations were measured directly in that study and incorporated into a simple model.

[22] Krill are known to mediate significant fluxes of iron within the Southern Ocean; an excellent review is contained in Cavan et al. (2019).

[23] Glacial flour is the fine powder of silt- and clay-sized particles that a glacier creates as it slides over bedrock; this flour becomes suspended in meltwater and is discharged into receiving waters at the glacier's terminus.

within the whale pump literature make unreasonable assumptions in this area, with one study (Lavery et al., 2010) assuming an export efficiency of nearly 100%. We believe this is an even further basis for our conclusion that most existing estimates of carbon sequestration associated with the whale pump represent substantial overestimates of actual or potential sequestration.

Additional uncertainties surrounding sequestration by whales: Lifetime emissions, resource competition with fishers and attribution of export flux

Even if one accepted these estimates of sequestration without correcting for the uncertainties we have described – and one developed some verifiable means of attributing carbon export to a whale or group of whales – we still would not be able to say whether a given whale is a net sink for carbon over the course of its lifetime. Consider, for example, the case of toothed whales, which do not feed directly on krill but instead forage deep within the ocean for higher trophic level prey such as cephalopods. Replenishment of higher trophic level consumers takes exponentially more primary production. Assuming a standard trophic transfer efficiency of 10%, it would take 10 kg of primary production to produce 1 kg of krill. Similarly, a 1 kg squid at trophic level 4 requires approximately 10^3 kg of primary production. Consuming high trophic-level organisms which already reside at depths where they serve as a reservoir of sequestered carbon could result in net carbon release rather than sequestration. Indeed, predators within Southern Ocean ecosystems have been hypothesized as a major source of carbon to the atmosphere within a system that otherwise serves as a net sink for carbon (Huntley M. E., Lopez M. D. and Karl D. M. 1991). Most recently, Savoca et al. (2021) found that previous studies have substantially underestimated (by two to three times) the quantity of krill consumed by whales, with important implications for carbon accounting and iron-mediated food web linkages between diatoms, whales and krill in the Southern Ocean.

Whether a species is a net carbon source or sink may not be the only pertinent question related to blue carbon. Nutrient fertilization might end up making toothed whales net carbon sources, but at the same time might stabilize or indirectly support processes that contribute to making a system a net carbon sink. Understanding the prey (cephalopod) community ecology through studies like that of Visser et al. (2021) is a needed step toward better development of carbon budgets for the mesopelagic and deep sea. Unfortunately, mesopelagic ecosystem dynamics are insufficiently characterized at present to evaluate consequences of this type of top-down control.

Another largely unexplored facet of resource competition is between fishermen and whales. In certain cases, learned behavior from sperm whales or orcas (taking fish out of nets or plucking fish from longlines) exacerbates these technical interactions. Only one study to date has sought to evaluate such tradeoffs in great baleen whales, finding that primary production stimulation from blue whales in the Southern Ocean largely offsets fishing competition (Lavery et al., 2014).

Finally, as for fishes, calculating the precise contribution of individual marine mammals to ocean carbon sequestration is extremely difficult due to the number of different, interconnected biogeochemical processes that must be considered. In addition, nearly all the parameters required for these calculations (e.g., nutrient concentrations, or the strength of advective mixing between ocean water masses) vary significantly over time and across the expansive spatial scales of the oceans, demanding the attachment in nearly all cases of significant uncertainties. However, using even the most generous scientific assumptions such as those we have challenged here, it is extremely doubtful that rebuilding of large marine animal populations could sequester additional carbon in quantities commensurate with the petagram scales of anthropogenic emissions.

Key research needs

We find several aspects of this potential sequestration pathway need further scientific attention. These include:

- Development of biogeochemical models that account for the full life cycle carbon emissions of marine mammals,

- spatial characterization of great baleen whale mortality due to falls, ship strikes, predation and natural senescence,

- modeling of ecosystem stability both with and without top-down control by whales, to determine whether their presence in the ecosystem stabilizes or enhances carbon sequestration, even if whales themselves do not serve as carbon sinks,

- modeling of the effects of top-down control by toothed whales on net carbon export,

- development of innovative methods that can apportion to marine reserves or MPAs an appropriate fraction of the carbon sequestration associated with highly migratory whales that do not spend their entire lives within those reserves' boundaries,

- additional field and laboratory studies on the bioavailability of krill-derived iron in whale feces and the fractions of both surface ocean primary production and carbon export that can be directly attributed to whale fertilization, and

- the incorporation into any future estimates of carbon sequestration by marine mammals of more robust methods for evaluating uncertainties in both various model parameters and overall results (e.g., a bootstrap Monte Carlo approach).

Avoided emissions through reductions in seafloor trawling

The final NCS pathway we evaluate in this report is the potential for reduced or avoided emissions through limitation or reduction in seafloor trawling (Fig. 4). Sala et al. (2021) present an expansive strategy for ocean conservation based on the creation of marine protected areas (MPAs) that includes an estimate of the carbon footprint resulting from mechanical turbation of sediments from trawl fisheries. The authors estimated that trawling results in remineralization of organic matter in surface sediments equivalent to a substantial 1.47 Pg CO_2 yr^{-1}, though it is somewhat misleading to imply these emissions will have an immediate or even decadal-scale impact on the Earth's climate since any newly evolved dissolved inorganic carbon will almost certainly remain trapped in bottom waters for decades to centuries according to the ca. 1500 year timescale of ocean ventilation (Sarmiento and Gruber 2006c). Importantly, the authors' estimate of carbon emissions from trawling assumes that (1) organic carbon in the resuspended sediment is fully transformed to "aqueous CO_2," i.e., dissolved inorganic carbon and (2) the turbation due to trawling penetrates to a uniform 1 m depth across all of the ocean's trawled sediments. We find that emissions from trawling may be overestimated in the study due to the simplifications inherent in the underlying assumptions, but conclude ocean bottom trawling may represent a target for policy intervention that could reduce anthropogenic emissions.

For example, De Borger et al. (2021) performed a similar, but more detailed analysis of the biogeochemical effects of trawling on a variety of different sediment types. Drawing heavily on empirical observations, the authors considered aerobic and anaerobic changes in the carbon and nitrogen cycles after successive trawling events. Consistent with the mechanism proposed by Sala et al., De Borger et al. found there is enhanced mineralization of organic carbon stored in marine sediments after successive
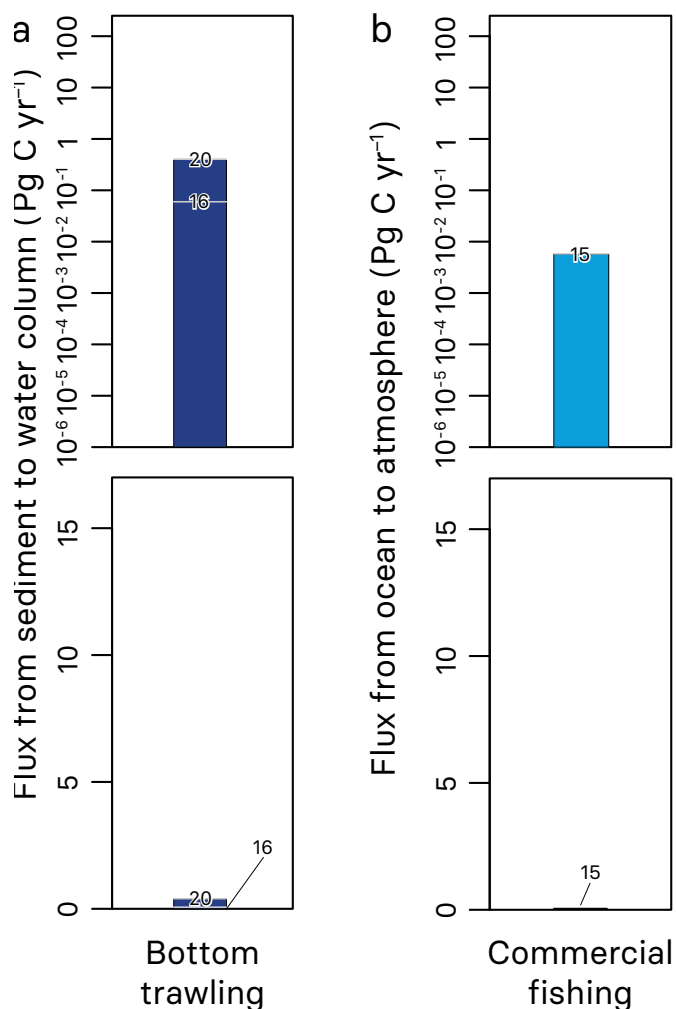
FIGURE 4.
Magnitudes of estimated anthropogenic carbon fluxes associated with fishing: (a) remineralization of carbon from ocean sediments due to bottom trawling and (b) combined atmospheric emissions from fuel combustion and fish biomass conversion to CO_2 during human use or consumption. The same data are shown on both logarithmic (top) and linear (bottom) scales. Shaded bars encompass the overall range of export estimates within each category or subcategory, including the associated uncertainties (if given). Horizontal lines indicate individual values assembled from the scientific literature; numbers correspond to the references given below.
[15] Mariani et al., 2020 [16] Paradis et al., 2021
[20] Sala et al., 2021

trawling. However, unlike Sala et al. Borger et al. found biogeochemical effects did not penetrate deeply into most sediments (disturbance typically extended to no more than 5 cm), suggesting that the simple extrapolation by Sala et al. was not appropriate. Further, Borger et al. noted that resettlement of organic carbon and other sediment post-disturbance

–not included in either model – would likely vary widely depending on the sediment size and local oceanographic processes. The shallower average penetration depth proposed by De Borger et al. can be applied to the same generous estimate of sediment organic carbon storage used in the Sala et al. analysis (Atwood et al., 2020) to arrive at a substantially smaller estimate of overall remineralization. More importantly, the Sala et al. analysis did not consider the wider ramifications on sediment biogeochemistry from trawling, specifically on rates of nitrification and denitrification. The latter accounts for a third of all marine surface nitrogen loss (Middelburg et al., 1996) and can be a powerful counter to eutrophication (Borger et al., 2021). Because the ocean nitrogen cycle is intimately coupled to the carbon cycle, the approach and execution of the Sala et al. paper does not capture the total scope of the problem.

Notwithstanding methodological critiques of the Sala paper, sediment resuspension and the fate of resuspended organic carbon are important missing pieces in the global accounting of direct, mitigatable anthropogenic carbon emissions. Drawing on detailed data obtained from the study of a single canyon in the NW Mediterranean, Paradis et al. (2021) likened the trawling of shelf systems to agricultural tilling given the scale of disturbance. The authors of that study found that roughly 30% of organic carbon was removed in the top 1 cm of sediment after one pass of a bottom trawl, and collectively, as much as 0.06 Pg of organic carbon could be mineralized from the current global extent of trawling grounds – one order of magnitude smaller than the flux claimed by Sala et al. For comparison, agricultural tillage releases ~ 66 – 90 Pg C yr^{-1} (Lal 2004). Of course, understanding the ultimate carbon footprint of all this aqueous inorganic carbon remains a serious limitation on understanding potential carbon benefits.

In situ and model studies support the notion of increased oxidation and decreased nitrification resulting from most bottom trawling. In Borger et al. (2021), at all experimental sites, trawling instantly reduced rates of denitrification due to injection of oxygen and loss of electron acceptors such as NO_{3-}.

Overall they demonstrated that coarse sediments, which are typically characterized by higher oxygen concentrations, are less affected than finer grain sediments undergoing higher rates of denitrification. Unexpectedly, they found management of trawling depth alone is not likely to effectively mitigate loss of denitrification and organic carbon. Perhaps most striking, the authors found that the greatest difference in sediment organic carbon content was between untrawled substrates and those trawled once; as a result, they argued that spatial quotas and closed areas may be effective carbon mitigation approaches.

Areas for further research

We conclude that restrictions or prohibitions on bottom trawling or other sediment-disturbing activities such as deep-sea mining, which is not discussed here, may represent effective interventions to reduce or avoid carbon emissions. However, work is needed to better constrain the global flux of carbon from sediments as a result of these activities, and to better understand the longer-term fate of resuspended organic matter. We do not yet know what portion may resettle, what proportion will be remineralized and what proportion will eventually reach the atmosphere over a given timescale. These rates appear to vary as a function of the depth of water in which the trawling occurs, how deeply the trawl method penetrates into bottom sediments and the preexisting sediment and nutrient loads in various environments. Studies are needed to understand if trawling changes local ocean chemistry to the extent that it may affect vertebrate and invertebrate respiration and feeding. Finally, future estimates of the remineralization of sediment organic matter due to trawling must include a robust appraisal of the likely timescale of ventilation from bottom waters of the associated carbon dioxide. Because bottom fishing does not randomly target the ocean bottom, concentrations of this form of anthropogenic CO_2 are likely to be higher in some locations than others; the superposition of high-intensity fishing areas over the path of the ocean's thermohaline circulation will determine when different quantities of this CO_2 reach the atmosphere.

Conclusions

While none of the open ocean NCS pathways we reviewed are scientifically mature enough to support high-quality carbon credit schemes, multiple lines of evidence suggest a relatively large source of emissions could be avoided by limiting or prohibiting harvest of mesopelagic fish communities. There are currently too few direct observations of the mediation of ocean carbon cycling by these species to fully substantiate this, but biogeochemical models indicate mesopelagic fishes and invertebrates must play a very large role in moving carbon from the surface ocean to depth through their diel vertical migrations. Limiting harvest of these species is a conservative policy intervention that could be taken today to prevent further deterioration of the ocean's capacity to sequester atmospheric carbon and to avoid GHG emissions, buying scientists more time to develop and deploy the necessary models and observing technologies.

Epipelagic fisheries present another ready target for policy intervention based not on the potential for new sequestration – the science surrounding carbon export by these fishes remains far too uncertain – but focused instead on a reduction in current emissions. The vast majority of emissions associated with targeting large pelagic species came directly from fuel use. These emissions could be reduced by reducing fish catches, improving nearshore fishery production to disincentivize transit further offshore in response to stock depletion, improving catch efficiency, reducing the amount of bottom trawling and ending overcapitalization and fuel subsidies. However, intriguing issues remain about whether and how goal setting for fisheries based mainly on target species suitability to support yield adequately supports future system performance for other outcomes, including carbon processing. Setting and achieving new management goals for fisheries that include the protection of the roles that fish play in carbon sequestration is an urgent priority for fisheries that target species clearly involved in nutrient regeneration, such as Southern Ocean krill.

In the case of large marine mammals specifically, we find there are many reasons to rebuild great baleen whale populations that are not directly related to carbon sequestration. In addition, there is some evidence that whales can mediate the flow of carbon to the deep ocean at various points in their life cycles either directly (through natural sinking of whale carcasses) or indirectly (via the fertilization of surface ocean primary production by buoyant whale feces). Moreover, an increase in whale populations could sequester additional carbon within living biomass. However, we find that large uncertainties remain around many aspects of this proposed pathway: We lack the knowledge, for example, to determine whether these organisms serve as net sources or sinks of carbon with respect to the atmosphere when their entire life histories are considered. Thus, while there is very good reason to enhance great whale population recovery using all possible speed, the current science is too uncertain to yet support the emplacement of a reliable scheme for carbon credits based on carbon sequestration by whales.

We identify several significant research needs that could accelerate the development of sufficiently precise estimates of sequestration or avoided emissions from all four of these ocean NCS pathways to support high-quality carbon credits and justify other investments to protect or accelerate them. These needs include:

- Greater scientific dialog and increased collaboration between ocean scientists and those working on terrestrial systems, and among scientists from traditionally siloed subdisciplines within ocean science, particularly marine mammal physiologists,

marine microbial ecologists, marine invertebrate biologists and marine biogeochemists/chemical oceanographers, including both observational practitioners and theoreticians/modelers,

- the incorporation into any future estimates of carbon sequestration by fishes or marine mammals of more robust statistical methods for evaluating uncertainties in both various model parameters and overall results,

- the production of new models, observing technologies and data to constrain over broad spatial scales the total biomass of fish in the mesopelagic ocean and the fluxes mediated by these communities, including a robust set of empirical conversion factors for scaling measurements of fish biomass to units of carbon,

- development of biogeochemical models that account for the full life-cycle carbon emissions of marine mammals,

- additional field and laboratory studies to ascertain the bioavailability of krill-derived iron in whale feces and the fractions of both surface ocean primary production and carbon export that can be directly attributed to whale fertilization, and

- development of more robust estimates of carbon emissions from disturbed seafloor sediments, including models that account for the exact manner of disturbance and previous disturbance history, and that accurately estimate the quantity and timescale over which remineralized CO_2 will return to the atmosphere.

Finally, we identify a particular problem of attribution and specificity that would serve as a severe practical impediment to the development of high-quality carbon credits based on conservation of large marine animals. Marine species move within three dimensions in a fluid medium, sometimes across very long distances, making it very difficult to track the carbon within them in a manner comparable to the chain of custody auditing performed within traditional carbon markets based on terrestrial plants and trees. Even when we have achieved sufficient scientific knowledge of the complex biogeochemical and physical processes that govern carbon cycling by marine animals, innovative market design, particularly around monitoring and verification, will be required to ensure the integrity of any credits sold in this area. In particular, there is an urgent need for development of innovative methods that can apportion to marine reserves or MPAs an appropriate fraction of the carbon sequestration associated with migratory animals that do not spend their entire lives within those reserves' boundaries.

Recent discussion about a possible carbon market value of whale restoration makes the need for scientific guidance in this area particularly urgent. Importantly, each of these NCS pathways is unto itself a no- or minimal-regrets conservation strategy replete with potential co-benefits for people and society. The ecosystem restoration and/or enhancement necessary in each case – protecting mesopelagic fishes on the one hand, or rebuilding whale populations on the other – will almost certainly make the oceans more resilient in the face of climate change, stabilize global fisheries populations and support human livelihoods, regardless of how much carbon is sequestered.

Appendix

## The scaling of metabolic efficiency with organismal size

Central to the findings of Pershing et al. (2010) is an argument concerning the scaling of relative metabolic efficiency with organismal mass. Going back to physiological first principles, it is a well conserved trait that large organisms are more efficient, on a per-mass basis. Relevant to biological carbon stores and respiration, the authors argue that large whales are more efficient (less respiration) than small whales, seals, birds, etc. They argue that the historic large whale-dominated ecosystem in the Southern Ocean supported much more overall biomass than the current state. Pershing et al. state that:

> The amount of krill that supported the 3.36×10^5 blue whales lost from the Southern Ocean (from whaling) could support 2.26×10^6 minke whales (7 tons each) or 5.26×10^8 penguins (5 kg each). However, the biomass in these populations would be only 50% or 8%, respectively, of the biomass of the missing blue whales.

Given the suggestion that the restoration of various fish populations might also provide a pathway for carbon sequestration, it is worth positing how fish might fit into this narrative. There exists literature that models standard metabolic rates across fish, birds and mammals. For each group, standard metabolic rates are well conserved on the log scale ($r^2 \sim 0.95$; White, Phillips and Seymour 2006).

Pershing et al. implicitly assume that blue whales were largely replaced by penguins and smaller whales after depletion from industrial whaling. To evaluate metabolic tradeoffs in comparison to a blue whale as the gold standard, we calculated the standard metabolic rates of fishes, birds and mammals over a wide range of sizes and calculated the relative metabolic cost compared to a 150 ton (adult) blue whale (Fig. 5). Our results support the assertions in Pershing et al. – that any bird or small mammal is at a minimum one order of magnitude less efficient than great baleen whales. Even the difference between relatively large whales and blue whales is considerable.

So, all else being equal, the system can hold more biomass if it is allocated to large whales as opposed to birds or smaller mammals. However, we found that all fish have much lower metabolic costs, regardless of size. For example, a system could support 10 times more biomass of small fish (100 g), and over 260 times more biomass of relatively large fish (3.5 kg). Illustratively, a small poikilotherm-dominated system theoretically could hold at least 10 times more biomass over a blue whale system, but much less if dominated by smaller marine mammals and birds.
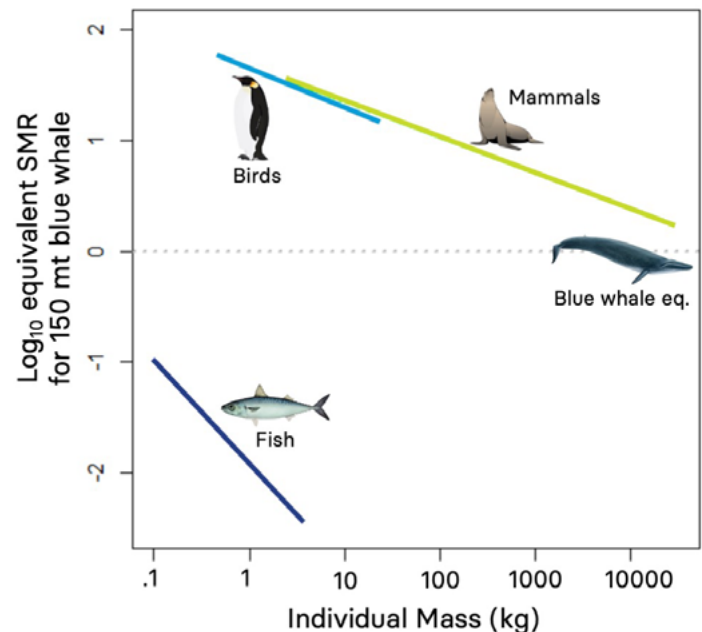
FIGURE 5.

Standard metabolic rates of fishes, birds and mammals over a wide range of sizes relative to a 150 ton (adult) blue whale. The y-axis represents the relative metabolic efficiency (log scale) for 150 mt equivalent mass of an organism. Y=0 suggests metabolic efficiencies match that of a blue whale, while a 1 means they are 0.1 as efficient, and -1 means 10 times as efficient, etc.

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