

Review

Integral functions of marine vertebrates in the ocean carbon cycle and climate change mitigation

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SUMMARY

In the last decade, the ocean has absorbed a quarter of the Earth's greenhouse gas emissions through the carbon (C) cycle, a naturally occurring process. Aspects of the ocean C cycle are now being incorporated into climate change mitigation and adaptation plans. Currently, too little is known about marine vertebrate C functions for their inclusion in policies. Fortunately, marine vertebrate biology, behavior, and ecology through the lens of C and nutrient cycling and flux is an emerging area of research that is rich in existing data. This review uses literature and trusted data sources to describe marine vertebrate C interactions, provides quantification where possible, and highlights knowledge gaps. Implications of better understanding the integral functions of marine vertebrates in the ocean C cycle include the need for consideration of these functions both in policies on nature-based climate change mitigation and adaptation, and in management of marine vertebrate populations.

INTRODUCTION

Marine vertebrates range in size from millimeters to the 30 m long blue whale (*Balaenoptera musculus*),^{1,2} have lifespans from weeks to centuries,^{3–6} and occupy all but the lowest trophic levels. Some undertake vast migrations across oceans, while others have a home range of just meters.^{7,8} Some feed in shallow waters but live at depth, others feed at depth but return to shallow waters.^{9–12} Some marine vertebrates release sperm and eggs to the water column, others produce fertilized eggs which may be abandoned, and mammals can nurse their live-born young for several years.^{13–15} These diverse ecologies have multiple interactions with the carbon (C) cycle, many unexplored.

The C cycle describes the movement of C through various forms and environments, on all timescales, from rapid recycling of CO₂ between the atmosphere and ocean surface, to fossilized C stored for millions of years in rock and oil deposits. Global anthropogenic C emissions over the last 10 years have been estimated at 9.6 ± 0.5 Gt C year⁻¹ from fossil fuels and 1.6 ± 0.7 Gt C year⁻¹ due to land-use change, with atmospheric CO₂ increasing at 5.1 ± 0.02 Gt C year⁻¹.¹⁶ C sinks (processes that remove C from the atmosphere) are therefore important for climate change mitigation and adaptation. The ocean is a significant active carbon sink, estimated to have absorbed 2.5 Gt C of anthropogenic emissions between 2010 and 2019, while terrestrial uptake was 3.4 Gt C.¹⁶ C absorbed from the atmosphere into the ocean has the potential to be released, fixed (converted to organic C), stored (held for up to 100 years), or sequestered

(held for more than 100 years).¹⁷ Atmospheric CO₂ is passively dissolved in ocean surface waters, driven by the solubility and biological pumps.¹⁸ Dissolved CO₂ in surface waters is readily exchanged back into the atmosphere, and in the water column it can contribute to ocean acidification. Phytoplankton and other marine plants remove dissolved CO₂ from well-lit surface waters, converting it to organic C. For organic or inorganic C (DIC) to be stored on a timescale of multiple decades, it must be transferred through food webs, enter sediments, or sink below the surface layer (i.e., the photic zone or mixed layer depth, whichever is deeper).¹⁷ Thus, processes that transfer C and provide the nutrients that enable C fixation are critical to the ocean's function as a C sink.^{19,20} For 2010–2019, the ocean stock of dissolved DIC was 38,000 Gt C, while the combination of organic C in the water column, marine biota, coasts, and surface sediments represented approximately 2,500 Gt C.¹⁶ If C sinks below the sequestration depth (usually estimated as 1,000 m in open oceans, shallower in coastal ecosystems), or becomes buried in sediments it can be sequestered, effectively retired from the C cycle, potentially for millions of years.^{17,21}

Marine vertebrates influence C outcomes in the ocean, including the capacity of ecosystems to release, fix, store, or sequester C.^{22–25} Marine vertebrates themselves also function as C stores^{26–28} and contribute to C flux (downward movement of C to deeper waters and sediment)²⁹; the more quickly particles sink, the less likely they are to be remineralized in the microbial loop.^{30,31} Marine vertebrates cycle C directly and indirectly through at least 14 discrete interactions, which can be grouped



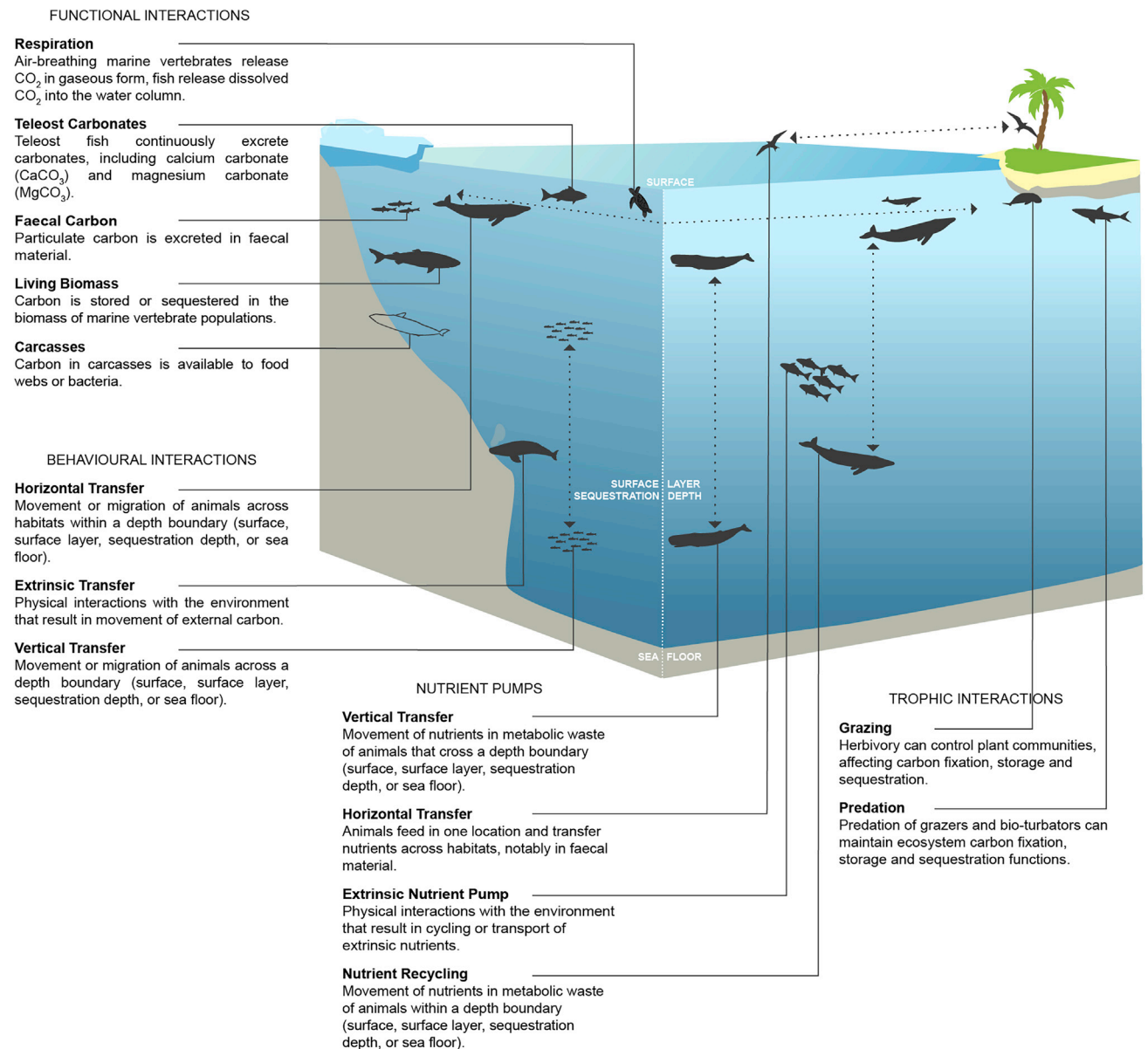


Figure 1. Marine vertebrate C interactions

Conceptual diagram of the life processes and behavior through which marine vertebrates interact with C. Interactions may be performed by many different vertebrate species, not only those depicted.

into four categories: (1) functional C interactions, including accumulation of C in biomass and metabolic excretion of C; (2) behavioural C interactions: transfer of C within and between ecosystems as a result of movement and behavior; (3) trophic interactions: physical modification of habitats and control over prey populations in ways that can affect C fixation, storage, and sequestration; and (4) nutrient pumps: provision of nutrients that enable C fixation or maintain storage and sequestration in biomass (Figure 1). Differences in biology and ecology result in different functional roles by species and populations, spatially and temporally.

Understanding the functional role of marine vertebrates is essential to avoid unintentional adverse changes to this aspect

of the ocean C sink. Narratives regarding oceans as infinite have evolved with the realization that changes to ocean functions have already occurred and are not simple to undo.³² For effective policies and actions to maintain or enhance the ocean C sink for climate change mitigation and adaptation, for example by protecting coastal ecosystems, it is therefore important that functional roles of marine vertebrates in the C cycle, and impacts of their disruption, are also explored.^{33–35} The combination of increased scientific and political focus on marine ecosystems as C sinks in the context of climate change action, advances in empirical research on marine vertebrates' ecological roles and influencing factors, and a growing awareness of the role of animals in nutrient cycling (zoogeochimical effects),³⁴ represents

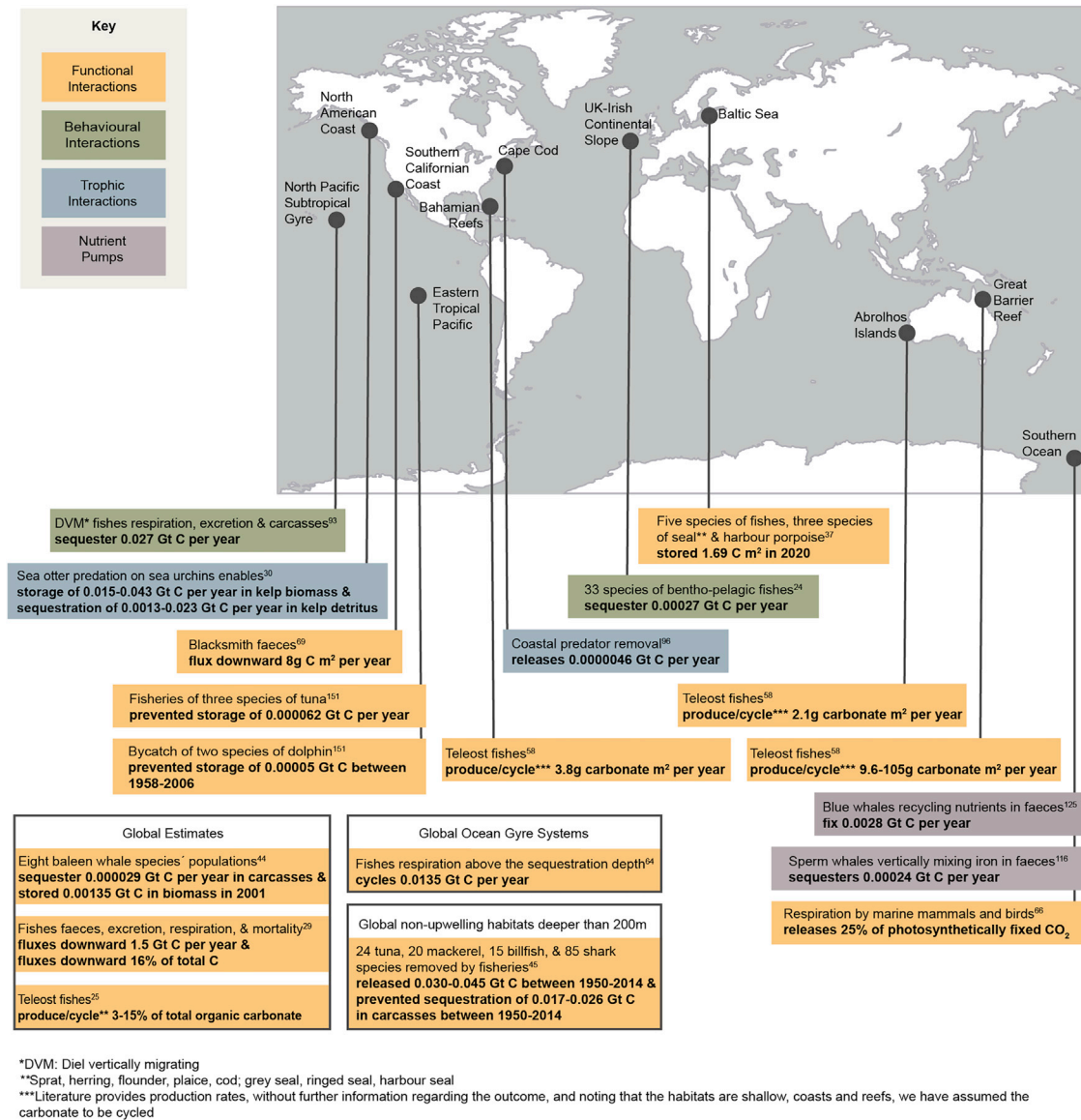


Figure 2. Map of estimated C interactions and outcomes

Locations with quantified C interactions and outcomes associated with marine vertebrates. Potential C outcomes: released, C is released directly to the atmosphere; fixed, inorganic C is transformed to organic C; cycled, organic or inorganic C is released to the water column above the sequestration depth; upward flux, organic or inorganic C is released to the water column above its source or removed to other biospheres (freshwater, terrestrial biomes); downward flux, C is released to the water column below the sequestration depth or in a form that sinks below its source; stored, C is held or released in a form that does not re-enter the water column above the sequestration depth or the atmosphere for up to 100 years; sequestered, C is held or released in a form that does not re-enter either the water column above the sequestration depth or the atmosphere, for over 100 years.

a wealth of data and opportunity for application. To know how a marine vertebrate contributes to the C function of the ecosystem, and whether it results in a net source or sink, C interactions must be identified, estimated, and mapped within the complex, intertwined flows of C and other nutrients through their food webs and the ecosystem.

This review defines different ways in which marine vertebrates influence C cycling, both directly and by facilitating other C vectors. Many aspects of marine vertebrate biology and ecology are well documented, yet rarely considered in the context of C cycling. The biggest knowledge gaps are quantification of C

interactions and probable C outcomes. Our recommendations for future research include synthesis studies, whole-system approaches, and development of new methodologies to bring together information from various disciplines at a scale that can be used to inform management decisions and policies.

MARINE VERTEBRATE CARBON INTERACTIONS

The following are known and hypothesized interactions between marine vertebrates and C, including quantification (Gt C) and outcomes for C where possible. Figure 2 provides a definition

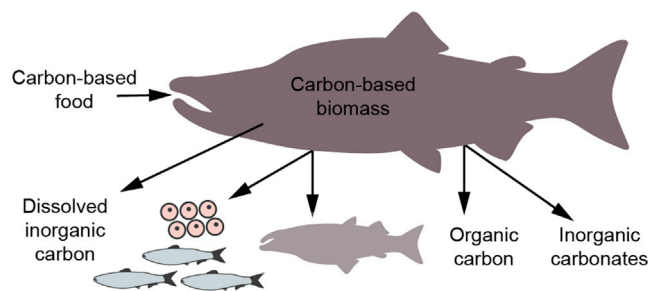


Figure 3. Functional carbon interactions of a fish

Sockeye salmon (*Oncorhynchus nerka*) consume organic C, respire dissolved inorganic CO₂, accumulate organic C in biomass, release organic C-based biomass during reproduction and in carcasses, and deposit organic and inorganic C in excreted material.

of the potential outcomes of marine vertebrate interactions with C, and maps all interactions or outcomes that have been estimated or measured in terms of C. This section is split into two themes: direct C interactions, in which animals release, deposit, store, transfer, or otherwise cycle C through their own metabolic processes and behaviors; and indirect C interactions, in which the metabolic processes or behaviors of marine vertebrates affect C that is at least one step removed from the animal. Overlaps occur between the functional and behavioral interactions, for example, respiration by fish releases dissolved DIC into the water column, thus the outcome is cycled C. However, if the fish undertake vertical migration, they may release C through respiration below the sequestration depth, thus the outcome of respiration with vertical transfer can be sequestered C. As this is an emerging area of research, the information and figures related to the role of marine vertebrates in the C cycle presented here are exploratory and have a high degree of uncertainty.

Direct C interactions

Direct C interactions include both functional and behavioral interactions. These are ways in which marine vertebrates have a direct impact on C cycling.

Functional C interactions

C fuels the life processes of marine vertebrates, including growth, reproduction, movement, excretion, and respiration (Figure 3), which have various C outcomes (Figure 4). C accumulated in marine vertebrate biomass (living biomass) through food web transfer can be stored or sequestered for the lifespan of the individual and scaled up to the population level.^{36,37} Global population figures are scarce, but fisheries stock assessments estimate the number of reproductive fish (spawning stocks) in populations of commercially targeted species. Given that approximately 11% of the wet weight of fish is C,^{38,39} the International Council for the Exploration of the Sea Spawning stock biomass figures for 2019⁴⁰ indicate that the population of reproductive anchovy (*Engraulis encrasicolus*) in the Bay of Biscay represents a C store of 1.33×10^{-5} Gt C year⁻¹, and that herring (*Clupea harengus*) in the nine fishing areas reported by ICES⁴¹ store 6.97×10^{-4} Gt C year⁻¹. Reported catch of marine and diadromous fishes from global capture fisheries was 84.4 million tonnes in 2018,⁴² which is likely to be an underestimate.⁴³ These fisheries may therefore have removed an estimated 9.3×10^{-3} Gt C from the ocean in 2018; for context, carbon in the living

biomass of eight baleen whale species (*Balaenoptera musculus*, *B. physalus*, *Megaptera novaeangliae*, *B. borealis*/*B. brydei*, *B. acutorostrata* and *B. bonaerensis*, *Eschrichtius robustus*, *Eubalaena* spp., and *Balaena mysticetus*) in 2001 was estimated to be less than one-sixth of this mass⁴⁴ (Figure 2). Globally, since 1950, marine fisheries are estimated to have prevented sequestration of $1.74\text{--}2.62 \times 10^{-2}$ Gt C through removal of tuna, mackerel, billfish, and shark species from non-upwelling habitats deeper than 200 m.⁴⁵

All marine vertebrate populations self-perpetuate through reproduction. Successful fertilization generates new vertebrate biomass, thus C stored in the biomass of stable populations represents a carbon pool that can be considered sequestered, potentially infinitely. During reproduction, and sometimes when not mating, marine vertebrates may release C into the ocean via gamete biomass. The fate of gametes that are not fertilized, and the C therein, has not been explored. Many vertebrate species produce offspring that have a planktonic or other larval stage, or a vulnerable juvenile stage. The recruitment of larvae or juveniles to adult life stages may be relatively low in some species, representing a flow of C through carcasses. When marine vertebrate carcasses of all life stages sink to the ocean floor, the C formerly stored in their biomass can enter benthic food webs and sediments,⁴⁶ with potential to be sequestered for millions of years, depending on the depth and sediment dynamics.²¹ Carcasses are an important source of energy transfer, but C outcomes have not been widely explored.⁴⁷ In areas of high productivity, carcasses of adult marine vertebrate megafauna, such as whale sharks (*Rhincodon typus*) and large rays (genus *Mobula*), can represent a significant source of C transfer from surface to deep sea ecosystems.⁴⁸ However high regionally, C in vertebrate carcasses may be negligible when considered in the context of the global C sink, as is seen with relatively low estimates of C sequestered globally by the sinking carcasses of eight baleen whale species⁴⁴ (Figure 2). However, Pershing et al.⁴⁴ estimated that whale falls would remove 1.6×10^{-4} Gt C year⁻¹ if baleen whale stocks were restored to pre-whaling densities.

C is released by marine vertebrates in metabolic waste, including fecal material, carbonates, and respired CO₂. Marine vertebrates can provide a vector for C flux within the water column, and between ecosystems, by releasing C in rapidly sinking feces.^{19,31} The C-rich fecal pellets associated with northern anchovy (*E. mordax*) of the Santa Barbara Channel, US, can transport C from surface waters to depth at an average sinking rate of 787 m/day.³¹ Similarly, fecal pellets produced by Peruvian anchoveta (*E. ringens*) had an average sinking rate of 1,100 m/day.⁴⁹ These rates are comparable with those measured for phytodetritus and some zooplankton, which form the basis of C flux models. For instance, marine snow as well as small fecal pellets produced by some zooplankton, such as copepods and euphausiids, exhibited sinking rates from <10 to hundreds of meters per day,^{50–52} while faster sinking rates (up to thousands of meters per day) were observed in larger, high-mass fecal pellets produced by other zooplankton, such as salps, pteropods, and chaetognaths.^{53–55} Fish contribute $16\% \pm 13\%$ to total downward C flux globally, equivalent to 1.5 ± 1.2 Gt C year⁻¹.²⁹ The higher potential for storage or sequestration of C associated with rapidly sinking pellets⁵⁶ suggests that deposition of C by

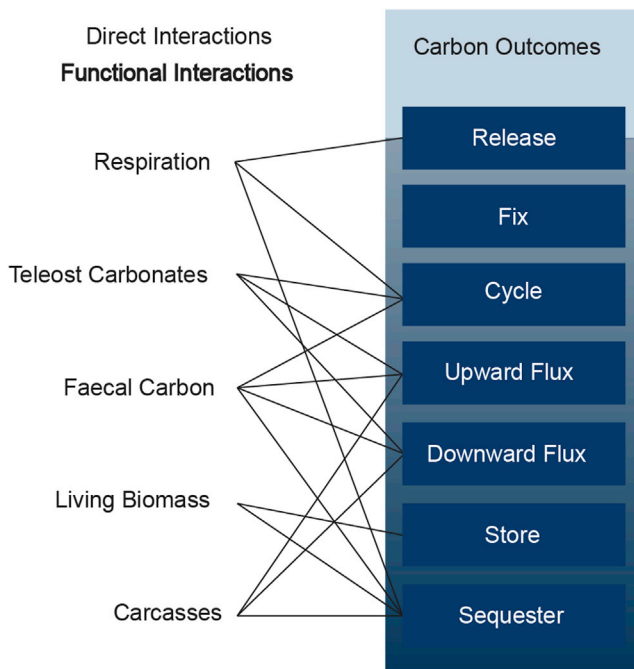


Figure 4. Potential C outcomes of functional interactions
Direct, functional interactions through which marine vertebrates engage with the C cycle: known and hypothesized carbon outcomes of each interaction are indicated.

marine vertebrates should be incorporated into biogeochemical and C flux models. To date, studies on fish fecal pellets have measured size, production rate, C content, and sinking rate, but this information is not available for many species, and the fate of C released in vertebrate feces in different habitats and conditions is unexplored. While most of the work on C flux in marine vertebrate fecal matter has focused on fish, organic C is also found in digested wax esters (lipids) released in whale feces. Whales release buoyant fecal plumes in the mixed layer. Thus, in contrast to rapidly sinking fish fecal pellets, C excreted through this pathway is likely to stimulate C cycling in the upper water column.⁵⁷ In addition to C, waste transports other nutrients, such as nitrogen and iron, which are also important for the biological C cycle (see nutrient pumps).

Teleosts (i.e., modern bony fish), of which there are >25,000 species, excrete dissolved DIC in the form of calcium carbonate (CaCO_3) or magnesium (MgCO_3) carbonate, which is metabolized as an outlet for waste products in the seawater they drink.^{58–60} Teleost carbonate production rates vary as a function of biomass and temperature (Table 1).⁵⁸ The structure of carbonate produced by teleosts varies by family assemblage and includes both highly soluble forms and forms stable enough to accumulate in marine sediment.⁵⁸ Teleost carbonate could represent an important source of mud grade (<63 μm) and fine sand grade (typically <30 μm) carbonate to sediments (Figure 2) and, by enhancing oceanic alkalinity through dissolution, provide a natural buffer against ocean acidification.^{25,58,61} Globally, teleosts may contribute 3%–15% of total oceanic carbonate production.²⁵ The production of teleost carbonates is expected to increase with warmer sea temperatures and dissolved CO_2

concentration, both predicted effects of climate change. Thus, the role of teleost carbonate may be even more important in the future.⁶⁰

Fish respire dissolved CO_2 , which, when released within the surface layer, can be taken up by phytoplankton to support photosynthesis, released back to the atmosphere, or remain in the water column, where it may contribute to ocean acidification. When released below the surface layer, the CO_2 can be stored or sequestered in the water column.^{30,62,63} Del Giorgio and Duarte⁶⁴ estimated that fish respiration in the ocean gyre systems is $1.35 \times 10^{-2} \text{ Gt C year}^{-1}$, based on the total reported fisheries catches for 1988–1991, assuming that catch represents 20% of the total fish production and that fish respiration is nine times greater than total fish production. In this same study, total respiration in the open ocean (including vertebrates) was estimated to be $66 \text{ Gt C year}^{-1}$. Note, however, that abundance of higher trophic levels in ocean gyres is relatively low compared with coastal and shelf habitats.⁶⁵ In 2018, global reported catch for marine and diadromous fishes in capture fisheries was 84.4 Mt.⁴² Using Del Giorgio and Duarte's aforementioned formula, total global fish respiration can be estimated at $3.8 \times 10^{-1} \text{ Gt C year}^{-1}$. Air-breathing marine vertebrates release CO_2 in gaseous form, which is assumed to return directly to the atmosphere⁶⁶ (Figure 2).

Behavioral C interactions

The following are interactions whereby marine vertebrates affect C outcomes through their behavior, i.e., foraging behavior, swimming, and migration (Figure 5). Because of the huge variability in behaviors within and between species and populations, there are likely to be many variations on the following themes.

When marine vertebrates use more than one habitat, they provide a vector for C movement, exporting C from donor to recipient habitats.^{19,67,68} For example, Bray et al.⁶⁹ quantified C flow for a planktivorous fish, the blacksmith (*Chromis punctipinnis*), that release fecal carbon in shelters adjacent to feeding sites (Figure 2). The C in marine vertebrate biomass and metabolic excretions becomes available for food webs and bacterial communities in recipient ecosystems. Local movement can transfer C within one habitat or across adjacent habitats, while migratory animals and currents that disperse gametes and larvae can transfer C across vast distances.¹⁹ These movements may occur across a horizontal or vertical gradient within the water column; for example, across habitats at similar depths (horizontal transfer), from terrestrial or shallow ecosystems to deep seas and sediments, or vice versa (vertical transfer). Marine vertebrates with freshwater or terrestrial spawning, nesting, or nursing grounds are an important C flow out of marine ecosystems, including salmon, sea turtle hatchlings, and seal carrion during pupping season.^{67,68,70,71} Unfertilized gametes, larvae, and juvenile stages that are vulnerable to predation are likely to be a significant vector for C in the ocean.

Outcomes for C depend on the form of C (including size and buoyancy) and dynamics of the recipient ecosystem.¹⁹ Marine vertebrates that use vertically distinct habitats provide a vector for upward or downward C flux. For example, animals that feed in shallow, coastal, or near-surface ecosystems and move toward pelagic, benthic, open ocean ecosystems, or below the surface layer, have the potential to increase downward C flux, storage, and sequestration.¹⁹ Animals that move in the opposite

Table 1. Variability of teleost carbonate production rates relative to concentration of fish biomass

Teleost carbonate production rate (g m ² year ⁻¹)	Location	Relative concentration of fish biomass
20–105	12.5% of tropical outer parts of the Great Barrier Reef	high
9.6	tropical southern section of the outer Great Barrier Reef	high
2.1	subtropical offshore Abrolhos Islands	relatively low

As reported by Salter et al.⁵⁸

direction could reduce the sequestration potential for the C that they transfer, although may enable C fixation through transfer of nutrients (see nutrient pumps). Through diel vertical migration (DVM), fish residing in the mesopelagic zone (200–1,000 m) feed in epipelagic waters at night and return to depths during the day where C is either stored in biomass, deposited in feces, excreted as dissolved waste products (DIC and/or dissolved organic carbon), or released as CO₂ through respiration. When this C is released below the surface layer, it may be stored or sequestered. Although relatively few studies have estimated active transport in DVM fish, they have demonstrated significant contributions to total downward C flux. When compared with the total sinking flux measured by sediment traps, the average estimates of active flux of POC by fish range between 0.3% and 40%²⁹ (Figure 2). Conversely, through their vertical migration, mesopelagic fish are theorized to provide an upward alkalinity pump that buffers ocean acidification in surface waters by releasing carbonates in waters above sequestration depth.⁷² Marine mammals and other animals that dive to feed then return to the surface may provide an upward flux for C; however, this is yet to be estimated. Current research into the roles of air-breathing vertebrates in the C cycle focuses on the movement of nutrients, from depth to the surface layer, or from oligotrophic to productive ocean regions, that can enhance C fixation (see nutrient pumps).

As well as moving C that passes through their bodies, marine vertebrates interact with extrinsic forms of C in their habitats. Transfer of C between marine ecosystems depends on both the strength and direction of water movement, and the processes that lead to the creation of C that can be transported, such as detritus.¹⁹ Nest building by wrasses (e.g., *Crenilabrus melops*), which collect and assemble algal material into a dense structure,⁷³ moves C in the algal material and creates detritus when the nests are eventually abandoned. Benthic feeding mammals, such as gray whales (*Eschrichtius robustus*)^{74,75} and walrus (*Odobenus rosmarus*),⁷⁶ may re-suspend C from the sediments they disturb. There are many other marine vertebrate behaviors that could be viewed in this context, with as yet unexplored and unquantified links to C outcomes.

Indirect C interactions

Marine vertebrate interactions with nutrients and other life forms, including plants and invertebrates, can be complex and ambiguous, but are important for determining C outcomes in any ecosystem^{77–79} (Figure 6). We term these indirect C interactions, which include trophic interactions and nutrient pumps.

Trophic interactions

Marine vertebrates generate both direct and indirect effects on primary producers and other consumers through grazing and

predation, as well as behaviors that engage with C fixing, cycling, and storage components of their habitats.⁸⁰ Plant-eating marine vertebrates not only convert plant biomass into different forms of C, as described in the functional interactions above, but also modify plant communities with consequences for C outcomes in the ecosystem. By eating and removing plants, grazers can alter the potential for C fixation; however, the net outcomes for C may be unclear. For example, fish that eat phytoplankton can decrease C fixation by removing photosynthesizing cells; however, phytoplankton reproduce rapidly, so the disruption to C fixation may be minimal. Furthermore, the C consumed by planktivorous fish can cycle through any of the interactions described in the sections above, including conversion into longer-lived biomass and rapidly sinking fecal pellets. Thus, the net outcome could increase C storage and sequestration. In addition, by grazing preferred locations, or selecting preferred species and depositing their seeds in feces, grazers can modify and maintain community structure, influencing rates of C fixation, storage, and sequestration in sediments. For example, grazing by dugongs (*Dugong dugon*) can maintain an early successional state in seagrass communities^{81,82} and the grazing activity of green turtles (*Chelonia mydas*) and dugongs can increase light availability⁷⁷ and regulate growth and competition between species of seagrass (*Zostera capricorni*, *Halophila ovalis*, *Halodule uninervis*, *Cymodocea* spp.).^{83,84} Dugongs and green turtles are observed to increase productivity in grazed species (*H. ovalis*),⁸³ and disperse seeds of at least three seagrass species (*Z. muelleri*, *Halodule uninervis*, and *Halophila decipiens*), aiding connectivity, resilience, and recovery of these species.⁸⁵ However, grazing by megaherbivores such as turtles and sirenians can also reduce seagrass meadow structure and reduce the amount of productivity fated to the detrital pool, thereby reducing the ability for these habitats to act as a carbon sink and mitigate climate change.⁸⁶

Grazing intensity varies according to number and type of grazers, plant species composition, carrying capacity of the ecosystem, and predation pressure. The evolution of marine vertebrate herbivores and evolutionary responses to grazing pressure by plants have shaped shallow coastal ecosystems.⁸⁷ Kelp forests, seagrass meadows, and salt marshes are broadly highlighted as significant C sinks.⁸⁸ Seagrasses can maintain growth and photosynthesis under high grazing pressure by fish.⁸⁹ However, in ecosystems where predators are removed, overgrazing by turtles and dugongs can reduce active C sequestration and release C from sediments.^{26,90,91} Thus, vertebrates can indirectly influence C in an ecosystem through predation. In kelp forests, sea otters (*Enhydra lutris*) exert control over food webs by preying on sea urchins (*Strongylocentrotus*

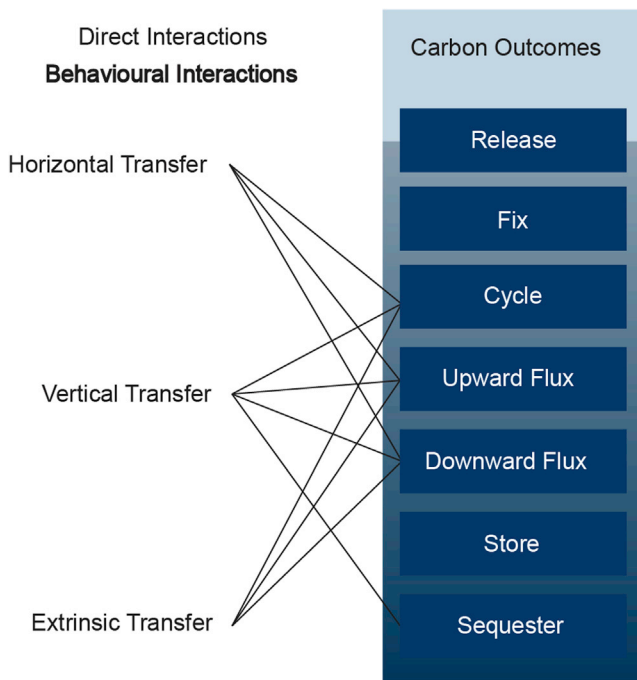


Figure 5. Potential C outcomes of behavioral interactions
Direct behavioral interactions through which marine vertebrates engage with the C cycle: known and hypothesized C outcomes of each interaction are indicated.

spp.), which reduces grazing pressure and allows kelp forests to flourish^{78,92,93} (Figure 2). Similarly, Atlantic cod (*Gadus morhua*) maintain kelp forest cover through predation on sea urchins.⁹⁴ In temperate coastal marshes, predatory fish (e.g., striped bass, *Morone saxatilis*) and crabs (e.g., blue crab, *Callinectes sapidus*) can exert top-down control of populations of burrowing and herbivorous crabs (*Sesarma reticulat*) that graze on cordgrass (e.g., *Spartina alterniflora*).^{95,96} In coral reef ecosystems, herbivorous fish graze in the proximity of patch reefs, which offer refuge from predators, resulting in increasing algal biomass, canopy height, and sedimentary carbon stocks with distance from refuges²² (Figure 2). In seagrass ecosystems in Elkhorn Slough, California, sea otter predation restricts *Cancer* crab populations, which in turn reduces crab predation on epiphyte grazers (isopod, *Idotea ressecata*; sea slug, *Phyllaplysia taylori*). Epiphyte grazers subsequently maintain grazing of eelgrass epiphytes (diatoms; red alga, *Smithora naiadum*), and thus healthy eelgrass (*Zostera marina*) cover is maintained.^{97,98} In tropical and subtropical seagrass meadows (including Bermuda [Northwest Atlantic Ocean], Shark Bay [Western Australia, Eastern Indian Ocean], Derawan [Indonesia], and Lakshadweep [India, Central Indian Ocean]), healthy populations of tiger sharks (*Galeocerdo cuvier*) control green turtle populations and behavior. As a result, turtle grazing has minimal impact on seagrass cover (*Amphibolis antarctica*, *H. uninervis*, *Cymodocea angustata*, and *Halophila ovalis*).²⁶ Similar controls have been observed between tiger sharks and dugong feeding behavior on seagrass (*C. angustata*, *H. uninervis*, and *H. ovalis*) in Shark Bay.^{99,100} The impacts of predators on grazer behavior in seagrass ecosystems have not been estimated in terms of C; however, the high C

sequestration rates in healthy seagrass ecosystems is well documented.¹⁰¹

Top-down relationships between predators and communities are also observed in pelagic ecosystems but have not been linked to C outcomes. For example, the disruption of Atlantic cod populations in most North Atlantic fisheries led to increased abundance of northern shrimp (*Pandalus borealis*), which forage in sediments between 100 and 500 m depth.¹⁰² In sediment communities, increased abundance of bioturbators (organisms that physically disturb sediment, e.g., by burrowing or digging) can result in enhanced oxygen provision,¹⁰³ used as a proxy for organic matter processing (i.e., OC). However, the impact of sediment disturbance by shrimp on C longevity at these depths is unknown. In the Baltic sea, Eriksson et al.¹⁰⁴ found that ephemeral and bloom-forming algae cover increased when predatory fish were absent, which reduced the water quality and light for perennial marine plants. Similar results were found when predatory fish were absent from shallow coastal seagrass and macroalgal habitats in the northern Atlantic Ocean.¹⁰⁵ These conditions, which are also seen when nutrients are over-enriched, disrupt community interactions, and can affect C outcomes.¹⁰⁶ For example, bloom-forming algae are remineralized by bacteria in coastal habitats, as opposed to the debris of macroalgae, which can reach marine canyons.^{107,108} The overall C outcomes may depend on the length and complexity of the food web.¹⁰⁵

Nutrient pumps

Marine vertebrates provide a vector for nutrient transport via excretion, egesta, and movement within and between habitats.^{109,110} These processes can result in horizontal nutrient transfer across ecosystems, vertical mixing across the surface layer, or nutrient recycling.^{111,112} Nutrients provided by marine vertebrates can be a source of nutrition for other animals, enabling maintenance of healthy populations that store C in biomass. For example, sinking or suspended iron-rich fecal material from fish may support communities in pelagic and mesopelagic habitats.¹¹³ Import or recycling of limiting nutrients in surface waters (e.g., Fe, N, P) can enhance phytoplankton growth, contribute toward C fixation, and therefore drive the biological C cycle. As described above, the biotic, chemical, and physical features of the environment are important in determining the fate of organic C. It is widely accepted that input of nutrients from outside a system (allochthonous nutrients) enables new primary production (as defined by Dugdale and Goering¹¹⁴), which equates to C sequestration through flux.^{17,21,115} In contrast, autochthonous nutrients (those recycled within a system) support total primary production without stimulating new production.¹¹⁶ Thus, the below section has some commentary on whether the interactions described could enable new versus total production, which relates to the potential for C sequestration. However, the proportion and fate of nutrients excreted or transported by marine vertebrates are unknown, and not all of the nutrients are taken up by phytoplankton or marine plants; some nutrients can be consumed by bacteria and viruses.¹¹⁷ The estimates below do not necessarily consider microbial uptake.

New primary production can be stimulated by marine vertebrates that import nutrients to nutrient-poor habitats. The “great whale conveyor belt” describes how nutrients in whale by-products (e.g., urine, placenta, skin cells, carcasses) can be

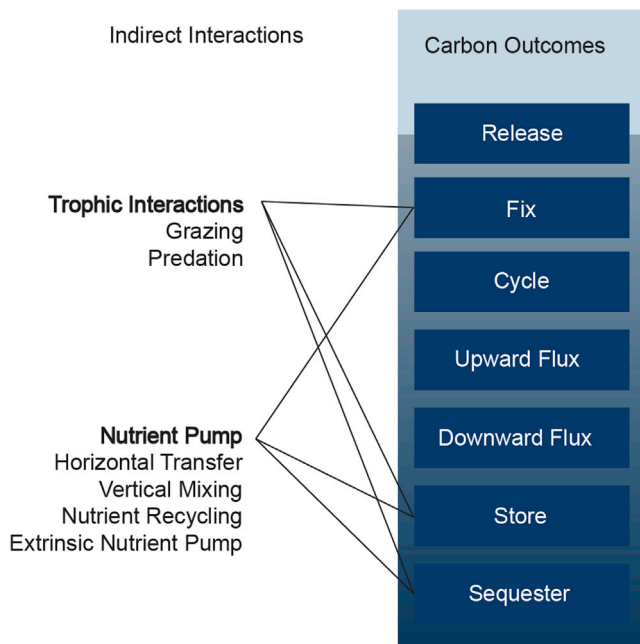


Figure 6. Potential C outcomes of indirect interactions
Indirect trophic interactions and nutrient pumps through which marine vertebrates engage with the carbon cycle: known and hypothesized C outcomes of each interaction are indicated.

transported by baleen whales migrating between typically nutrient-rich, high-latitude feeding grounds to typically nutrient-poor, low-latitude breeding grounds. Roman et al.²⁷ estimated that the 2001 Southern Ocean population of blue whales transported 8.8×10^{-8} Gt N year⁻¹ from Antarctic feeding grounds to tropical breeding grounds via N-rich urea released through catabolism of lipids and proteins during fasting. Using the calculations given in Roman et al.,²⁷ an additional 5.1×10^{-7} Gt C year⁻¹ would be stored or sequestered by phytoplankton. In comparison, the pre-whaling population was estimated to have stimulated the storage and sequestration of an additional 1.4×10^{-4} Gt C year⁻¹. There is some uncertainty in these calculations, as recent research shows that blue whales can feed in breeding areas¹¹⁸ and, while they do lose body mass, it may not be as much as previously thought (J. Roman, 2019, personal communication, April 19).

There are multiple examples of horizontal nutrient transfer that are likely to contribute to C storage and sequestration that are yet to be quantified. Grunts (family Haemulidae) in the Florida Keys feed away from reefs at night and release nutrients (N and P) while sheltering on reefs during the day, where coral growth is 1.5 times faster than at sites where grunts are rare.¹¹⁹ Gray reef sharks (*Carcharhinus amblyrhynchos*) egest nutrients on near-shore reefs from prey consumed offshore¹¹⁰ and seabirds (tropicbirds, *Phaethon lepturus*; terns, *Thalasseus bergii*, *Sterna* spp., *Onychoprion* spp., *Gygis alba*; shearwaters, *Puffinus bailloni*, *Ardenna pacifica*; noddies, *Anous* spp.; frigatebirds, *Fregata* spp.; and boobies, *Sula* spp.) stimulate new primary production on island, coastal, and coral reef ecosystems by excreting guano rich in nutrients from pelagic waters.¹²⁰ At Palmyra Atoll, seabird guano fertilizes plankton, which conse-

quently provides a food source for giant manta rays (*Manta birostris*).²⁰ In the Sargasso Sea, juvenile fish (*Caranx* spp., *Canthirhines pullus*, *Stephanolepis hispidus*) contribute to new primary production by excreting nitrogen in a form available for uptake by *Sargassum*,¹²¹ which is a globally significant vector for C sequestration in coastal sediments and the deep sea.^{122,123} In the sub-polar Auckland Islands, pelagic-feeding marine vertebrates, including southern royal albatross (*Diomedea epomophora*), Hooker's sea lions (*Phocarctos hookeri*), and southern right whales (*Eubalaena australis*), enrich coastal ecosystems with iron-rich guano and fecal material.¹²⁴ Salmon (*Oncorhynchus* spp.) returning to spawning streams in North America transfer nutrients to freshwater and terrestrial plants.^{67,68}

Marine vertebrates that feed at depth and return to the surface to breathe, recover from diving, rest, or warm up provide an opportunity for movement of nutrients from depth to surface waters, which can stimulate primary production. This has been documented for whales, where the term “whale pump” describes vertical transport of nutrients from depth to the surface layer, where whales release nutrient-rich fecal plumes, which can stimulate new phytoplankton growth^{111,125–130} (Figure 2). Movement patterns of various vertebrates suggests that they may transfer nutrients in this manner. For example, Emperor penguins (*Aptenodytes forsteri*), some pinniped species, young white sharks (*Carcharodon carcharias*), and blue sharks (*Prionace glauca*) are known to hunt beneath the surface layer and return to the surface.^{9,131–133} However, marine vertebrates that feed and release egesta within the surface layer support total, rather than new, primary production.^{20,117,126} Blue whales in the Southern Ocean typically both feed and defecate within the surface layer¹²⁵ (Figure 2). Other species that may support C fixation in this manner include Auckland Island shags (*Phalacrocorax colensoi*), black-backed gulls (*Larus dominicanus*), brown skuas (*Catharacta skua*), and northern giant petrels (*Macronectes halli*) in the sub-Antarctic Auckland Islands,¹²⁴ and North Atlantic right whales (*E. balaena*) in the Bay of Fundy.¹¹² More information on the nutrient content of excreted materials and excretion patterns are needed to estimate import to the surface layer, recycling of nutrients and C fixation through these behaviors.

Marine vertebrates may enhance nutrient availability from sources external to the animal (extrinsic transfer). For example, resuspension of sediment by gray whales and humpback whales (*Megaptera novaeangliae*) may release nutrients from the sediment back to the water column, where they can be used in C fixation²⁷ and schooling animals can create turbulence and drag in the water column as a by-product of their movement, mixing layers of stratified water.¹³⁴ As discussed above, where extrinsic mixing brings nutrients into the surface layer from other sources, it could drive new primary production and thus sequestration, while recycling nutrients within the surface layer may contribute to total primary production. Marine vertebrate movement may not be an important contributor to global ocean circulation,¹³⁵ but could be important for local C fixation and sequestration, which has global relevance in the context of climate change. Huntley and Zhou¹³⁴ found that an average school of 100 Atlantic bluefin tuna (*Thunnus thynnus*) can create vertical eddies daily that span up to 20 km², which can contribute to mixing of the coastal and continental shelf waters that these fish inhabit during maximal stratification. Herring schools in the Norwegian Sea

may affect regional-scale ocean turbulence, and anchovy (*E. ringens*) schools may have been an important vertical mixing mechanism in stratified coastal habitats before the collapse of these fisheries in the 1970s.¹³⁴ However, no estimates of C fixation enabled by the extrinsic movement of nutrients have been published.

HUMAN ACTIVITIES

Globally, ocean ecosystems are undergoing or expected to undergo a suite of changes, for example, due to climate change, coastal and seabed development, fisheries, aquaculture, and pollution.^{136,137} The C interactions of marine vertebrates are dependent on linkages between species, food webs, and ecosystems, while C outcomes are dependent on the form of C and the physical, chemical, and biological parameters at the site where C is released. Thus, the consequences for C flows due to population, behavioral, or ecosystem disruptions may be incongruent.¹³⁸ A few examples of human activities and the complexity of potential impacts on the C functions of marine vertebrates are outlined below.

Fisheries

Fisheries can affect the functional, behavioral, and indirect marine vertebrate interactions with C, but the altered outcomes for C are not well understood. Capture fisheries directly removed at least 9.3×10^{-3} Gt C in fish biomass from the ocean in 2018. However, additional changes occur in the biomass of the population that remains in the ocean, and their associated ecological roles. For example, mean size of adults may be reduced in the fished population, leading to reduced capacity for C storage in individual biomass. Fish size is also often linked to fecundity and recruitment success of juveniles.^{139,140} The trophic role of the fished population may be disrupted, with consequences for other links in the food web. Removal of predators causes downstream effects on the abundance and behavior of other organisms throughout the food web.¹⁰⁴ Where marine vertebrate predators control the population growth and behavior of grazers and bioturbators, they are critical to the ecosystems C function.⁸⁰ Disrupting predator communities can therefore affect C in sediments, the capacity of plants to draw down CO₂,^{22,26,93} and transport of C by movement and behavior of prey,¹³⁸ in addition to the functional C interactions of the predator itself.

Climate change

Transfer of C through vertebrate movement has historically represented a predictable and reliable input of C to recipient ecosystems, but these flows are being reduced, removed, or otherwise modified due to climate change.^{141,142} Some of the better-known impacts of climate change on marine vertebrates are the changes to timing of migrations and reproductive behavior,¹⁴³ and alterations to species ranges due to temperature change, which are visible in fisheries catch records.¹⁴⁴ Flows of carbon will consequently change in both the former and newly adopted habitats.¹⁴⁵

Work to identify the level of resilience and responses of marine vertebrate populations to climate change is ongoing, but increasingly suggests that better management of fisheries and habitat protection may be integral to reducing the effects of

climate change on marine vertebrates, assuming the root causes of climate change are also addressed.^{146–148} Thus, fisheries and climate change impacts and management are connected. However, management regimes will also affect the flow of C through ecosystems by implicit selection, with implications for C interactions and outcomes in the managed area.³⁵ For example, high-mobility species or individuals may receive less protection from area-based management than those with more sedentary behavior; potential for transfer of C between habitats may therefore be affected.^{149,150}

DISCUSSION

The existence of marine vertebrates in any ecosystem inevitably influences C outcomes in that ecosystem. Although few published studies are available, these suggest that marine vertebrates may be an important contributor to C flux,^{25,30,31} regulate C flows within and between ecosystems,^{19,20} and affect overall ecosystem health.^{22,80,99} Every marine vertebrate will deliver most of the functional interactions, while behavioral and indirect interactions will be driven by the ecology, behavior, and life history of the species. Of the literature included in this review, **Figure 2** maps the 16 publications that have measured or estimated marine vertebrate C interactions. These estimates cover varying time and spatial scales and represent patchy species and ecosystem coverage; it is therefore likely that marine vertebrates affect C outcomes to a larger extent than current estimates imply. For example, four of the publications in **Figure 2** have been based on a single species^{69,93,116,125}; only whales and DVM fishes are included in studies that quantify more than one interaction. Furthermore, only four publications have quantified human impacts on C outcomes.^{44,45,96,151} Given the limited scope of this literature, the combined estimates of C sequestered through these relatively few examples total 0.028–0.05 Gt C year⁻¹. In comparison, DVM zooplankton between 60°N and 60°S were recently estimated to sequester 6.5 Gt C year⁻¹.¹⁵² While global estimates of the functional roles of marine vertebrates in C cycling will be on a different scale to the vastly more abundant lower trophic levels, the transfer of extrinsic C, trophic interactions, and nutrient pumps provided by marine vertebrates may have disproportionate implications for C storage in reservoirs through multiplier effects.³³ It is also likely that forage fish play a dominant role in passive C flux through fecal pellets, while mesopelagic fish likely play a dominant role in active flux through DVM.^{24,29,31} The importance of DVM fish for climate change mitigation has already been identified as a reason to protect myctophids (which are not yet a target for fisheries) from exploitation until their role in C transfer is better understood,¹⁵³ and for establishment of protected areas in the high seas to protect the water column (i.e., not only seafloor habitats).¹⁵⁴

The interactions in this review are presented in isolation for simplicity, yet all are intrinsically linked. For example, C fixation facilitated by marine vertebrate nutrient pumps can interact with marine vertebrates through top-down control and, upon entering the food web, C can follow a number of pathways in succession, with potential to be transported to another ecosystem. Marine vertebrate biology, behavior, and ecology through the lens of C and nutrient cycling and flux is an emerging area of research with the benefit of extensive back catalogs of

data. Filling in the gaps with regard to interactions and their interlinkages could be relatively quick, especially where literature on bioenergetics, behavior, populations, food webs, and habitats exists, and if existing researchers consider their subjects from this new perspective. As a wider diversity of marine vertebrates are explored in the context of their C functions, additional interactions will likely emerge.

Disruption of marine vertebrate populations affects the capacity of marine ecosystems to fix, store, and sequester C, depending on behaviors and trophic levels affected.^{35,45,155} Discerning the impacts of changes to C flows is complex, as the altered outcomes for C are dependent on multiple dynamic factors: not only changes to the population biology and behaviors, but also the food webs, bacterial communities, and physical and chemical properties of the ecosystems involved. Linking documented changes in marine vertebrate populations and behaviors to their C functions, and estimating these impacts in terms of C cycling, is a first step toward understanding the changing dynamics of the biological C cycle in the Anthropocene. While outside the scope of this review, invertebrates and zooplankton, implicit features in marine vertebrate interactions with C through food webs, also have significant roles in oceanic C function. For example, krill (*Euphausia superba*) contribute to downward C flux through fecal material and provide nutrients for C fixation through schooling behavior^{137,156} and salps (*Thalia democratica*, *Salpa* spp., *Wheelia cylindrica*, and *Iasis zonari*) contribute to downward C flux through fecal material and sinking carcasses.^{51–53,55,157} Interdisciplinary approaches will be required to integrate biogeochemistry with the ecology of vertebrates, their food sources, and the bacteria, plants, and other organisms that use their metabolic products.

With sustainable development of oceans and “blue growth” on international political agendas, and growing interest in the protection of ocean habitats for climate change mitigation and adaptation through ecosystem services, increased knowledge of the functional roles of marine life is essential to inform scientific advice, policy decisions, and effective climate action.^{153,158,159} Leveraging naturally occurring C fixation, storage, and sequestration interactions for climate change mitigation and adaptation can be a strategy with lower risk and lower cost than many geo-engineering solutions.^{160,161} However, due to the escalating severity of the climate crisis, this strategy should be viewed as an addition to, not a replacement for, strategies to directly reduce greenhouse gas emissions. Holistic management approaches are necessary to enhance or protect marine vertebrate populations and their functional roles in the ocean as a C sink.¹⁶²

Research needs

Carbon interactions and outcomes of very few marine vertebrate populations, species, and ecosystems have been estimated. There are a number of research needs to establish a clearer understanding of the overall significance of marine vertebrates in C cycling in certain ecosystems or regions, their importance for climate change mitigation and adaptation, and the best management strategies to secure these functions. Here, we suggest some directions for future research.

Whole-system approaches

Estimates of animal effects and biogeochemical processes at a system level are needed to identify the strength of marine verte-

brate C interactions and outcomes, and overall ecosystem C function. For example, including marine vertebrates in research to establish a net C outcome for an ecosystem or region, or estimating all functional, behavioral, and indirect interactions in a given area for a particular species. Animals are likely to influence C outcomes at ecosystem or regional levels, thus research at this scale would be most useful.³³ Furthermore, many animals are managed at these ecological scales by national governments or regional governing bodies, thus policies to secure marine vertebrate C interactions and outcomes could be readily developed at this scale.³³

Synthesis studies

Very few global and regional assessments of C cycling and flux include vertebrates, arguably because the scale of vertebrate contribution to C flux is thought to be of little consequence. Synthesis studies are required to identify the potential volumetric significance of marine vertebrates regionally, or in different ecosystems, despite their relatively small biomass (i.e., in comparison to plankton) and compare these with other C fluxes and C cycle components. Synthesis studies that identify inherent biases in current marine vertebrate C flux studies would also be useful to help prioritize species that are likely to have a greater or keystone role in C cycling or flux for future research using whole-system approaches.

Methodologies

New thinking regarding methodologies to estimate C interactions and C outcomes is required. Challenges include the constraints of measuring changes in the ocean and accounting for environmental controls on C outcomes that may obscure the relationships between marine vertebrates and C cycling.¹³⁸ Given the range of movement, behavior, size, depth, distribution, and other ecological differences within and between marine vertebrate species and life stages, as well as the dynamic nature of marine ecosystems, a combination of methods from different fields will likely be necessary. For example, combining behavioral observations with bioenergetics, chemical analyses, oceanographic modeling, and nutrient modeling could be fruitful.

CONCLUSION

This review highlights the current state of knowledge of the roles of marine vertebrates in C cycling. It shows that the life processes, behaviors, and trophic interactions of marine vertebrates are an inextricable component of the ocean C cycle. Publications are currently too few to reflect the true complexity and magnitude of all of the functional roles of marine vertebrates in C cycling; however, current research conveys important contributions, particularly to C flux and ecosystem health. The scope for future research spans from simply identifying functional roles, to addressing logistics (e.g., methods to quantify the relative contributions of the different processes by which marine vertebrates move C), to understanding and managing impacts of human activity on the C function of marine vertebrates. Understanding of marine vertebrate C interactions and C outcomes can initially be developed rapidly, as existing biological, physical, and chemical research can be used and supplemented with quantification of C associated with the functional roles of marine vertebrates. Mapping C outcomes associated with moving animals in ocean systems undergoing changes will require systems

approaches and new thinking. The challenge is understanding this complexity well enough to inform effective policies and management actions, especially considering that these functions are absent in current management strategies that aim to address climate change or secure sustainable development.

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AUTHOR CONTRIBUTIONS

A.H.M. and E.M.O. conceptualized the review. A.H.M. was lead author of the manuscript and produced the figures. H.C.P. and G.K.S. provided substantial edits on the manuscript. H.C.P., G.K.S., and E.M.O. provided guidance on writing and figures, as well as useful comments on the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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