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The contribution of whales in supporting marine ecosystem services

Produced by Conservation Strategy Fund for the International Whaling Commission

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Prepared for the International Whaling Commission
by Conservation Strategy Fund

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MARCELLO
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PHOTOGRAPHY

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Executive summary

This study presents a novel and integrated framework to assess the role of cetaceans in supporting ecosystem services and generating economic value. It responds to a long-standing gap in both ecological and economic literature regarding the absence of a structured approach linking whale mediated ecological functions to measurable contributions to human wellbeing. The analysis combines ecological theory, natural capital principles, and economic valuation methods, and applies them to a case study of the Southeast Alaska (SEAK) humpback whale population.

The Keystone Species Contribution Pathway

At the core of this study is the development of the Keystone Species Contribution Pathway (KSCP), a novel conceptual and analytical framework that traces how cetaceans contribute to ecosystem services through a sequence of ecological processes. Unlike earlier approaches that assume a direct relationship between whales and ecosystem service benefits, this framework explicitly models the causal chain from ecosystem structure to ecological function to service provision and ultimately to economic value .

The KSCP is grounded in the natural capital approach and aligns with ecosystem service cascade logic. It identifies how whales influence key ecological processes such as nutrient cycling and carbon transfer, which in turn affect ecosystem functions (e.g., primary productivity, trophic dynamics), leading to ecosystem services such as fisheries productivity and climate regulation. This structured pathway allows for a more scientifically robust and transparent valuation process, while also making explicit the assumptions and uncertainties embedded in each step.

Case study: Contributions to fisheries productivity and climate regulation

The framework was applied to the North Pacific humpback whale population in Southeast Alaska, focusing on two key ecosystem services: fisheries productivity and climate regulation. Preliminary results show that humpback whales contribute an estimated total annual economic value of approximately $6 million through these pathways. The vast majority of this value (approximately 98%) is derived from the KSCP-fisheries pathway, reflecting the role of whales in enhancing primary productivity through nutrient cycling (i.e., the “whale pump”) and subsequent trophic transfer to fish biomass.

The contribution to climate regulation, estimated through whale-fall carbon sequestration, is comparatively smaller but potentially significant, with a preliminary annual value of approximately $127,000, corresponding to around 600 tCO_2 per year sequestered .

Scenario analysis further demonstrates that these values are sensitive to changes in whale abundance, reinforcing the importance of conservation and population recovery. However, the study also highlights that these relationships may not be strictly linear, and future modeling should incorporate ecological thresholds, density dependence, and other nonlinear dynamics.

We caution that these estimates are preliminary only, using a preliminary set of assumptions based on the current state of scientific knowledge. These estimates and assumptions must continue to be updated and refined as scientific knowledge advances and as recommended in this report’s research agenda. As such, these values should be treated as examples of the

possible outputs generated by the KSCP but they should not be cited or used for policy or management purposes.

Financial mechanisms for cetacean conservation

Building on the valuation results, the study identifies a portfolio of financial mechanisms that could potentially support cetacean conservation and scaling investment. Market-based instruments such as whale-watching fees, tourism levies, and ecotourism concessions emerge as particularly promising, with the global whale-watching industry already valued in the billions and demonstrating strong potential for reinvestment into conservation. Examples such as conservation fees per visitor and marine park “nature fees” illustrate how revenue can be directly linked to ecosystem protection.

Public and international finance remains essential, including Official Development Assistance (ODA), multilateral funding (e.g., GEF, World Bank), and conservation trust funds, which provide large-scale and long-term funding streams. Regional cooperation mechanisms, such as marine corridor agreements, also play a key role in managing migratory species across jurisdictions.
Emerging financial innovations, such as blended finance, performance-based bonds, and impact-linked loans, offer new opportunities to mobilize private capital by linking financial returns to ecological outcomes. However, our analysis emphasizes that no single mechanism is sufficient. Instead, a strategic mix of instruments, supported by strong governance and transparency, is required to close the marine conservation finance gap.

Institutional arrangement

To operationalize these financial mechanisms, a multi-level institutional arrangement is proposed, anchored in the IWC and supported by national, regional, and private actors. The IWC would play a coordinating role, guiding methodological development and facilitating collaboration, supported by a dedicated economic analysis working group to strengthen the integration of science and policy .

A central innovation is the proposed Common Asset Trust (CAT) for whales, which treats whale populations as blue global commons. The CAT would function as an independent mechanism to pool and allocate funds from multiple sources providing stable, long-term financing while aligning incentives with conservation outcomes.

At regional and national levels, existing governance structures (e.g., MPAs and fisheries regulations) would implement actions supported by CAT financing. The effectiveness of this arrangement will depend on transparent governance, strong institutions, and inclusive participation of local communities and stakeholders.

Research agenda

The study outlines a strategic research agenda to strengthen both ecological and economic components of the framework. Key priorities include improving empirical estimates of whale-mediated nutrient dynamics, validating primary productivity responses, refining trophic transfer processes, and obtaining updated whale population abundance estimates. Additional

work is needed to better quantify carbon sequestration pathways and to strengthen the linkage between ecological processes and economic outcomes.

Future research should also incorporate market dynamics, expand valuation to additional ecosystem services, and develop spatially explicit and integrated ecological–economic models. Advancing toward models that capture feedbacks and nonlinear dynamics is identified as a critical long-term objective.

Recommendations to the IWC

It is recommended that the IWC adopt a proactive role in advancing this framework and its applications. Key actions include convening an interdisciplinary expert workshop to refine assumptions and expand the research agenda, establishing a formal economic analysis working group, and promoting pilot applications across different regions to test and refine the framework.

Additional priorities include strengthening data collection, fostering international collaboration, enhancing communication of results, and supporting the integration of valuation outputs into conservation finance strategies.

Main conclusions

This analysis represents the first systematic effort to quantify the contribution of cetaceans to ecosystem service provision using a structured ecological–economic framework. The introduction of the KSCP constitutes a significant conceptual advancement, enabling a more rigorous and transparent understanding of how whales contribute to human wellbeing. The preliminary results of the case study demonstrate that these contributions may be economically significant, even when considering a limited set of ecosystem services. At the same time, important knowledge gaps remain, requiring continued research and interdisciplinary collaboration. We reinforce that the model estimates provided should be used as examples of how the KSCP might be operationalized but not used as absolute values.

Ultimately, the findings reinforce a central conclusion: cetaceans are not only conservation priorities but may also provide key functional assets within marine natural capital systems. Recognizing and operationalizing this role through appropriate institutional arrangements and financial mechanisms can unlock new pathways for sustainable ocean governance and long-term conservation impact.

1. Introduction

Among the many reasons why our planetary development has allowed the global loss of nature, the undervaluation of ecosystems in cost-benefit analysis is a core one, hiding from the decision-making process our dependency on a healthy environment for our well-being and survival. We inherited from centuries ago (e.g., during the industrial revolution) a development paradigm based on the perspective of an “empty world” (Costanza, Cumberland, et al., 2014), meaning a planet empty of people and their built capital, and abundant in nature, and consequently the wrong assumption that global environmental impacts are close to being impossible because of this abundance of natural resources. Today we live in a “full world”, where human population and consumption have sky-rocked, growing the economy to the extent of pushing planetary boundaries (Rockström et al., 2009), where the limiting factor for development is not built or human capital, but natural capital (i.e., stock of ecosystems) (Hernández-Blanco & Costanza, 2019).

This same paradigm led to the near extinction of many species of whales around the world during the peak of the industrial whaling era (Baker & Clapham, 2004), valuing whales only as a commodity instead of having a systemic and cross-cultural valuation framework for these marine mammals and their habitats (Pascual et al., 2023). Moreover, the undervaluation of the nature and the benefits we derived from her (i.e., ecosystem services) is related with market failures at all levels in managing public goods in a sustainable way. A public good exists when goods (or services) are non-rival (one individual may benefit from the existence of an environmental attribute and this does not reduce the benefit another individual can receive for that same attribute) and non-excludable (it is difficult or impossible to exclude individuals from benefiting). This contrasts with private goods, which are both rival and excludable.

In the case of whales, we can argue that they occupy multiple categories of resources depending on perspective. When considered as harvestable biomass or subject to disturbance, they resemble common-pool resources (rivalrous and difficult to exclude, vulnerable to overuse) (Table 1). As contributors to ecosystem regulation, as well as having cultural or existence values, they function as public goods, since these benefits are non-rival and non-excludable. In special contexts, whales can also be treated as private goods (commodities in regulated trade) or club goods (exclusive tourism or conservation initiatives). Thus, whales straddle all four quadrants from Table 1, but their most critical framing is as common pool resources and public goods, requiring governance that recognizes both dimensions.

Table 1. Types of goods

	Excludable	**Non-Excludable**
Rivalrous	Private Goods: Whale meat in regulated markets (if harvested legally under quotas)	Common-Pool Resources: Wild whale populations subject to hunting, ship

		strikes, or disturbance; whale-watching congestion.
Non-Rivalrous	Club Goods: Exclusive whale-watching tours or private conservation experiences (benefits limited to paying members)	Public Goods: Supporting ecosystem services (nutrient cycling, carbon sequestration), existence and cultural values.

Markets work best with private (rival and excludable) goods and services. Because of the nature of many ecosystem services (especially regulating and cultural services) being a public good, including those supported by keystone species such as whales, markets for them do not exist and therefore there is limited potential to manage them with conventional markets. And because of the difficulties in estimating the value of these non-marketed services, ecosystems (and species) are often undervalued in benefit-cost analysis of conservation versus commercial uses, causing their degradation and loss globally.

Another key market failure affecting the health of ecosystems and their extent is the lack of the internalization of externalities (i.e., a positive or negative outcome of a given economic activity that affects a third party that is not directly related to that activity) by economic activities. This means that markets often do not reflect the full costs or benefits of a change in the provision of benefits to society from nature. Whales are subject to a range of externalities that are insufficiently captured by market mechanisms, leading to their under-protection and continued vulnerability. Negative externalities arise primarily from human activities such as industrial shipping, which generates noise pollution that disrupts whale communication and migration (Reeve, 2012), or from fisheries, where bycatch and prey depletion reduce whale populations and their ecological functions (Dolman & Brakes, 2018). Similarly, vessel strikes, chemical pollutants, and climate-induced habitat changes impose social and ecological costs that are borne collectively but not reflected in the price signals governing maritime transport, fishing, or energy sectors. At the same time, positive externalities associated with whales, such as their role in nutrient cycling, carbon sequestration, and the enhancement of marine biodiversity, are also excluded from market valuation, resulting in systematic underinvestment in their conservation. The coexistence of these unpriced costs and benefits underscores the market failure inherent in managing whale populations and highlights the need for policy instruments and financial mechanisms that internalize these externalities to align private incentives with social and ecological welfare.

To overcome these market failures, the economic valuation of ecosystem services has been conducted at multiple geographical scales all over the planet for more than two decades (Costanza et al., 2017). The value of ecosystem services is the relative contribution of ecosystems to well-being. These values will depend on current and future human preferences (based on culture) and needs, on how people perceive the impact of protecting or losing ecosystems for their well-being. In this way, ecosystems’ values can be considered not only in monetary terms, but also in terms of aesthetic, spiritual or totemic values, and can therefore be expressed quantitatively (e.g., fish catch, water use) or qualitatively, as a principle or core belief

(e.g., the right of species or ecosystem to exist), importance (e.g., coastal protection provided by a mangrove) or a preference (maintaining forest ecological characteristics to support tourism), making key to address in an integral way the multiple values that ecosystems provide to people and the rest of nature.

In the case of whales, the concept of granting legal personhood to whales has gained traction within the broader "Rights of Nature" movement, which challenges anthropocentric legal frameworks by recognizing non-human entities as rights-bearing subjects. A landmark example emerged in April 2024, when Indigenous leaders from Aotearoa (New Zealand), the Cook Islands, Tahiti, and Tonga signed *He Whakaputanga Moana*, a treaty declaring whales and dolphins to be legal persons. The treaty asserts that cetaceans have inherent rights to freedom of movement, a healthy environment, and the ability to thrive alongside humanity. While not yet binding in national legal systems, this Indigenous-led initiative reframes whales as beings with legal standing rather than resources to be managed and creates opportunities for guardianship arrangements that could hold states and corporations accountable for harms inflicted on whale populations. Legal personhood not only complements economic framings of whales as public goods or common-pool resources, but also underscores their intrinsic value, offering a normative framework for conservation that extends beyond conventional market mechanisms.

It is key to highlight that the main goal of estimating the value of ecosystem services is to demonstrate how protecting, restoring and using sustainably natural resources not only have positive outcomes in securing the health of ecosystems, but also the high return of investment that this will produce and therefore stabilize the social and economic dimensions of development.

With this context in mind, in 2016, the International Whaling Commission (IWC) adopted the resolution on Cetaceans and their Contribution to Ecosystem Functioning (Resolution 2016-3), instructing the Conservation Committee to undertake the review of ecological, management, environmental, social and economic aspects related to the contributions of cetaceans to ecosystem functioning as a matter of importance. To implement this goal, the IWC has held three workshops on this subject, two jointly led by the IWC Scientific Committee and the Convention on Migratory Species (CMS) during 2021 and 2023 on cetaceans and ecosystem functioning (SC/68C/REP/03; SC/69B/REP/04) that reviewed concepts on nutrient circulation, ocean fertilization, whale falls and cetaceans as predators, as well as modelling approaches; and another workshop led by the IWC Conservation Committee during 2022 to review the socio-economic values of the contribution of cetaceans to the ecosystem functioning (CC/68/REP/SEVCEF/01). Furthermore, at IWC's 68th meeting, a short-term workplan was agreed to advance the development of a pilot project to assess the socio-economic values of a single (or set of) species or populations of cetaceans to the well-being of people and the rest of nature.

Objectives of this study

As a first step to better understand the contribution of cetaceans to the provision of ecosystem services, this project has three interrelated objectives:

1. Create a research framework to assess the economic role of cetaceans in supporting marine ecosystem services
2. Apply some of these models (with available ecological and economic data) to a specific population/area as a general case study
3. Provide general guidelines on how these economic valuations can be used to influence whale conservation and management, either through market or policy developments.

It is key to highlight that this study is not intended to assess the full value of any target species/populations, or assemblage of species, rather it is intended to provide a representation of which ecosystem functions may provide specific ecosystem services and how any specific ecosystem service value can be determined.

2. Need for a new framework on cetaceans and ecosystem services

In the past decade, there has been a significant misinterpretation on the concept and mechanisms of ecosystem services, where some scholars have stated that species such as whales directly provide these benefits to society (e.g., Berzaghi et al., 2022; Cook et al., 2020; Melo et al., 2024; Sheehy et al., 2022). Nevertheless, this is fundamentally incorrect. First, and the most obvious reason, is that species are not ecosystems, and therefore species cannot be compared with ecosystems at the level of provision of benefits to humans. Second, a lack of understanding of the ecological dynamics behind the provision of ecosystem services forms the basis of this argument, and therefore this leads to the assumption that species can be entirely responsible for providing services (e.g., climate regulation). Finally, provisioning services (e.g., food, raw materials) are commonly the focus of economic valuations of species.

For example, Cook et al. (2020) assess the benefits from whales such as meat and materials from the whale's bones and baleen. In addition to the false interpretation previously mentioned, these uses derive from the extraction of one element (i.e., the animal or a part of it) from the ecosystem, which is often done in an unsustainable way. Seeing food as an ecosystem service from these marine mammals directly is similar to arguing that salmon provides a direct ecosystem service when it is fished, when in reality food provisioning is a service from the entire marine or freshwater ecosystem that sustain the populations of these fishes of commercial interest.

Furthermore, there is a consistent misinterpretation of the concepts of ecosystem functions and ecosystem services, which tend to be used interchangeably in the academic literature (see Box 1 for clarification). For example Melo et al., provide a similar list as Cook et al. 2020 on the ecosystem services "provided" by several species of baleen whales, including food products, tourism, enhanced biodiversity and climate regulation, among others. Animal Welfare Institute et al., (2017) reflecting on the concept of Total Economy Value, reported that whales have use values through enhanced productivity, and nonuse values through enhanced biodiversity and evolutionary potential, where in reality these two are ecosystem functions that do not have a value unless there is a benefit to humans, which is not always the case.

This has led to the application of misguided methodologies looking to estimate the economic value of these services. For example, Animal Welfare Institute et al., (2017) recommended as part of a workshop in 2017 to conduct a "complete evaluation of the economic value of ecosystem services provided by cetaceans for each focus area…". Chami et al. (2022), in addition to referring as well as the provision of ecosystem services by whales, make a series of assumptions that support the current state of confusion. First, the authors refer to the carbon stored in whale biomass as a service, this is problematic because most whales (except for the bowhead whale) live less than 100 years, which is the minimum time required for carbon to be considered effectively sequestered (Pearson et al., 2024). Second, by avoiding conducting an

in-depth analysis of the pathway involved in the contribution from whales to primary productivity, the authors assumed that this contribution can be estimated in one percent of current phytoplankton production, without considering the ecological and oceanographic variables involved in this complex system. A third very general assumption is also made in terms of fisheries enhancement, considering also a contribution of one percent of all commercial fishing.

Even at the International Whaling Commission (IWC) there has been some level of internal confusion which has been inherited from a scientific literature that is still evolving and that as mentioned have not agreed on a common language aligned with the natural capital approach (Bateman & Mace, 2020; Turner & Daily, 2008; Hernández-Blanco & Costanza, 2019; Costanza et al., 2014). For example, Roman et al. (2021), following Tavares et al. (2019), proposed a list of traits of cetaceans related to ecosystem functions and services. Nevertheless, many of the functions proposed are actually ecosystem processes, and the proposed services are all ecosystem functions, and therefore not mentioning ecosystem services completely. These authors seem to consider ecosystem services in terms of how the species contribute with the ecosystem, but without then considering a demand of these functions from humans, which is essential for an ecosystem service to exist.

This list was also used in a workshop on cetacean ecosystem functioning organized by the IWC and CMS in April 2021, where one of the authors of this report (Hernández-Blanco) provided a modified version of this table in order to reflect the ecosystem services that were being in reality considered (Appendix 4). The review of the table on cetacean traits showed that four (mortality rates, macronutrients in whale feces, excretion rates, and body mass) of the 26 traits identified in the 2021 IWC-CMS workshop report could be used potentially for a valuation of ecosystem services as they could be potentially related to benefit to humans, specifically to climate regulation (through carbon sequestration). Seventeen could be associated with ecosystems functions that could potentially support ecosystem services that significantly contribute to the productivity of economic activities (i.e., fisheries). The remaining five traits could not be related to ecosystem services from a socio-economic perspective.

Moreover, during the second IWC-CMS Workshop on Cetacean Ecosystem Functioning held in November 2023 in Bonn, Germany, it was evident that there were methodological and conceptual differences between ecologists and economists on how to assess the contribution of cetaceans to the provision of ecosystem services. Product of the group discussions during the workshop, it was considered of greatest importance to conduct a **pilot project focused on creating a research framework to assess the role of cetaceans in supporting marine ecosystem services**. This framework would explore all potential ecosystem services supported by cetaceans and identify what data gaps can be addressed in the future to allow economic valuation of these ecosystem services.

The following key questions were agreed the pilot project should consider to the extent possible:

- What are the ecosystem services to which cetaceans contribute?
- What are the linkages between the ecosystem services to which cetaceans contribute (e.g., climate regulation, nutrient cycling contributing to primary productivity and habitat provisioning)?
- Which ecosystem services can be valued with existing data and current economic valuation tools?
- How do these values change as cetacean populations increase or decline due to natural and anthropogenic drivers of change?
- Which ecosystem services to which cetaceans contribute should be prioritized for analysis (considering the availability of data and models, together with the likely [relative] magnitude of the associated values)?
- How can economic valuations of the ecosystem services to which cetaceans contribute be used to inform whale conservation and management?

Considering this, here we attempt to provide this framework for the first time in the literature, acknowledging the novelty of the topic and the many questions that remain unanswered to be able to make the links between cetaceans and ecosystem services. Thus, the main objective is to create a general framework and set of models that will spark discussions on how to further develop these models through in-depth research with a much longer timeline. Therefore, we do not intend our results to be final, rather to be the guidance.

3. Framework to assess the role of cetaceans in supporting the provision of ecosystem services

To address the first objective of this study, this section presents a proposal of the research framework to assess the role of cetaceans in supporting the provision of ecosystem services. This is composed of:

- A theoretical framework, providing the overarching concepts and theories that explain why the study is relevant and how it is situated within broader academic understanding of the topic. Here, we assess the natural capital approach and specifically the relationship between ecosystem health and the provision of ecosystem services. This is a first distinction from some of the current literature on species and ecosystem services, in which our approach considers the species or group of species (in this case cetaceans) as part of the biotic components of ecosystem health.
- A conceptual framework, which maps the expected relationships between key elements of the study, translating abstract theory into a practical model for analysis. The central point of analysis here is the species role in maintaining the structure and function of the ecosystem (i.e., ecosystem health)
- A methodological framework, that specifies the tools and procedures for data collection and analysis, ensuring that theory and concepts are operationalized in practice. Based on a series of ecological and economic methods, the role of cetaceans in supporting the provision of ecosystem services can be assessed, highlighting (as it will be done in detailed later) that due to the novelty of the topic, this will be a first qualitative attempt to do so.

In the following subsections we describe each of the three types of frameworks that together makes the research framework (Figure 1).

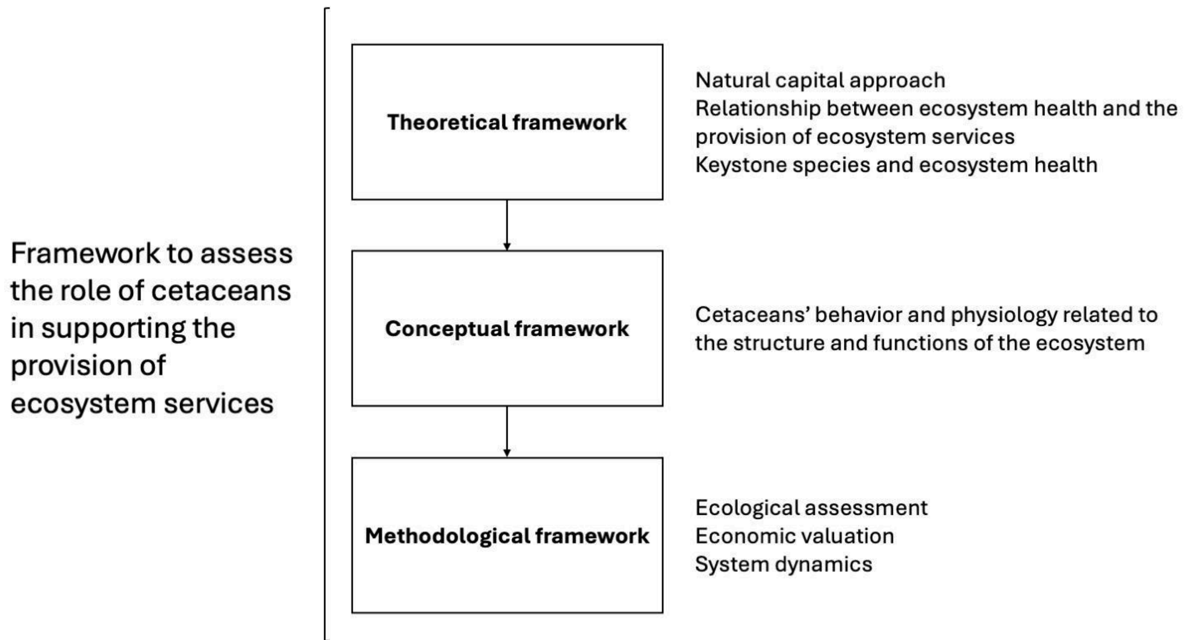

Figure 1. Schematic representation of the general framework, composed by the three types of frameworks.

3.1 Theoretical framework: Natural capital, ecosystem health and ecosystem services

Human well-being depends on natural capital (i.e. the planet's stock of natural ecosystems and resources) for the provision of **ecosystem services**, such as oxygen, food, water, climate regulation, protection from natural phenomena, recreation and inspiration, among many others (Hernández-Blanco & Costanza, 2019; Daily, 1997; Millennium Ecosystem Assessment, 2005). To better understand the "pathway" the ecosystem services follow from natural capital to human well-being, Haines-Young & Potschin (2010) described a "cascade" that describes this production line (Figure 2). The cascade starts with the **ecosystem structures, process**, which produce **ecosystem functions**. If these functions benefit people, then they are considered ecosystem services (See Box 1).

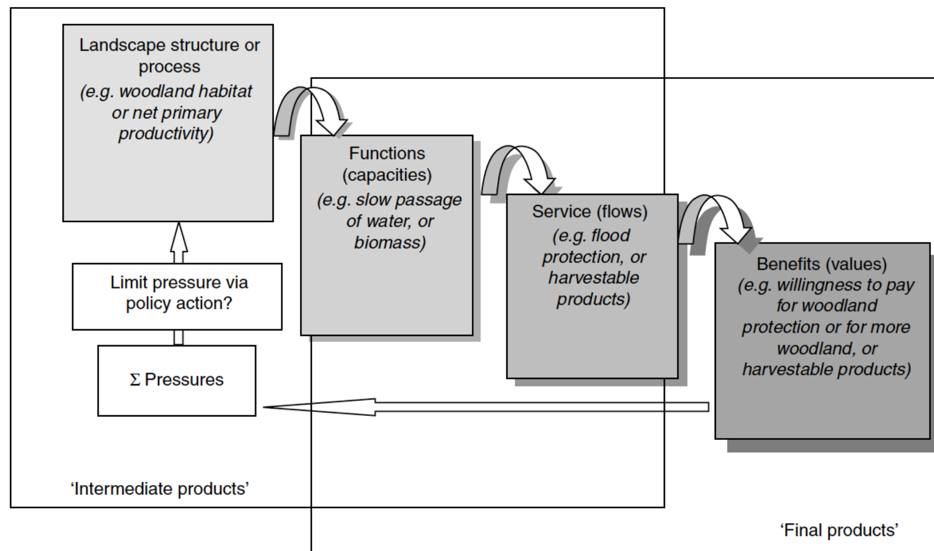

Figure 2. Ecosystem services cascade. Haines-Young & Potschin (2010).

For example, in seagrass meadows, the structural components include dense stands of seagrass plants, sediment substrates, and associated fauna. These structures underpin processes such as photosynthesis and sediment stabilization, which in turn generate functions like primary production and nutrient retention. Some of the services derived from these functions include enhanced fish nursery habitats that support fisheries and improved water quality that benefits coastal communities (Orth et al., 2006). Similarly, in coral reefs, the structural complexity provided by living corals and reef morphology sustains processes of habitat provision, competition, and calcification. These processes result in functions such as biodiversity maintenance and coastal protection, which translate into services such as tourism opportunities, shoreline stabilization, and a source of protein for millions of people (Moberg & Folke, 1999).

A third example is found in mangrove forests, whose structure consists of woody vegetation, root systems, and associated sediments. This structure supports processes including organic matter deposition, detritus breakdown, and nutrient cycling. The resulting functions include carbon sequestration and nursery provision for juvenile fish, mollusks and crustaceans, among others. At the service level, these functions translate into climate regulation through carbon storage, storm protection for coastal settlements and other associated ecosystems, and the maintenance of productive fisheries that sustain local economies (Hernández-Blanco et al., 2021).

Box 1. Key concepts

Functional traits: morphological, biochemical, physiological, structural, phenological, or behavioral characteristics that are expressed in phenotypes of individual organisms and are considered relevant to the response of such organisms to the environment and/or their effects on ecosystem properties (Violle et al., 2007).

Effect traits of a species underlie its impacts on ecosystem properties (Diaz et al., 2013)

Ecosystem structure: The physical and biological components of an ecosystem, including species composition, abundance, diversity, and spatial arrangement, together with abiotic features such as soil, water, and climate ("*What is there*").

There are currently several typologies of ecosystem services (Millennium Ecosystem Assessment, 2005b; TEEB, 2010; Costanza et al., 2017; Haines-Young & Potschin, 2017), including specific ones of those from coastal and marine ecosystems (Barbier, 2017; Hattam et al., 2015; Böhnke-Henrichs et al., 2013) (Table 2).

Table 2. Coastal and marine ecosystem services. Based on Böhnke-Henrichs et al., 2013.

Provisioning services	**Regulating services**	**Cultural services**
Fisheries	Air purification	Recreation and tourism
Seawater	Climate regulation	Aesthetic information
Raw materials	Disturbance prevention or moderation	Inspiration for culture, art and design
Genetic resources	Regulation of water flows	Spiritual experience
Medicinal resources	Waste treatment	Information for cognitive development
Ornamental resources	Coastal erosion prevention	Cultural heritage and identity
	Biological control	

It is important to highlight that natural capital and its services do not generate human well-being in isolation, it needs to interact with the human capital (i.e. individual human beings and their attributes, including physical and mental health, knowledge, and other capacities that enable people to be productive members of society), the social capital, (i.e. the web of interpersonal connections, social networks, cultural heritage, traditional knowledge, and trust, and the institutional arrangements, rules, norms, and values that facilitate human interactions and cooperation between people), and the built capital (i.e. the buildings, machinery, transportation infrastructure, and all other human artifacts and services) (Costanza et al. 2014).

For example, the ocean (i.e., natural capital) provides food in the form of fish (i.e., ecosystem service), and in order to receive this benefits through fisheries, it is needed the knowledge on fishing techniques (i.e., human capital), the fishing gear (i.e., built capital), and comply with local and national regulations on where fisheries are allowed (i.e., social capital) and where its future maintenance relies on. Hence, without any of these four capitals, it is impossible for the ecosystem services to flow independently or in an isolated way to human well-being from the natural capital. Coastal protection from mangroves is another example on how the interaction of the four types of capitals is needed. In order for mangroves (i.e., natural capital) to provide this ecosystem service, they need to be in areas where they protect people (i.e., human capital) and their social networks such as families and friends (i.e., social capital), infrastructure such as roads and housing developments (i.e., built capital). Therefore, as it will be discussed later, it is incorrect to suggest that species or a group of species such as cetaceans provide ecosystem services directly.

Moreover, the provision of ecosystem services depends on the condition of the ecosystem, which is often referred to as ecosystem health (Costanza 1992; Rapport, 1995; Rapport et al. 1998). Costanza (1992) states that 'an ecosystem is healthy if it is stable and sustainable, that is,

if it is active and maintains its organization and autonomy over time and is resilient to stress'. Costanza (1992) proposes vigor, organization, and resilience as the main features of ecosystem health. The vigor of a system is a measure of its activity or metabolism and can be measured through indicators such as gross primary production and net primary production. The organization of an ecosystem refers to the number and diversity of interactions among the components of the system, which can be measured through its biodiversity and by the number and strength of pathways of exchange among components of the system. Finally, resilience refers to the ecosystem's ability to maintain its structure (i.e. organization) and function (i.e. vigor) in the presence of stress (Costanza & Mageau, 1999; Mageau et al., 1995).

Furthermore, the organization of the ecosystem then can be considered as its structure, which is composed by its biotic and abiotic elements. And the vigor then can be considered as the ecosystem process and functions that is produced by the interaction of the elements of the structure of the ecosystem (Figure 3).

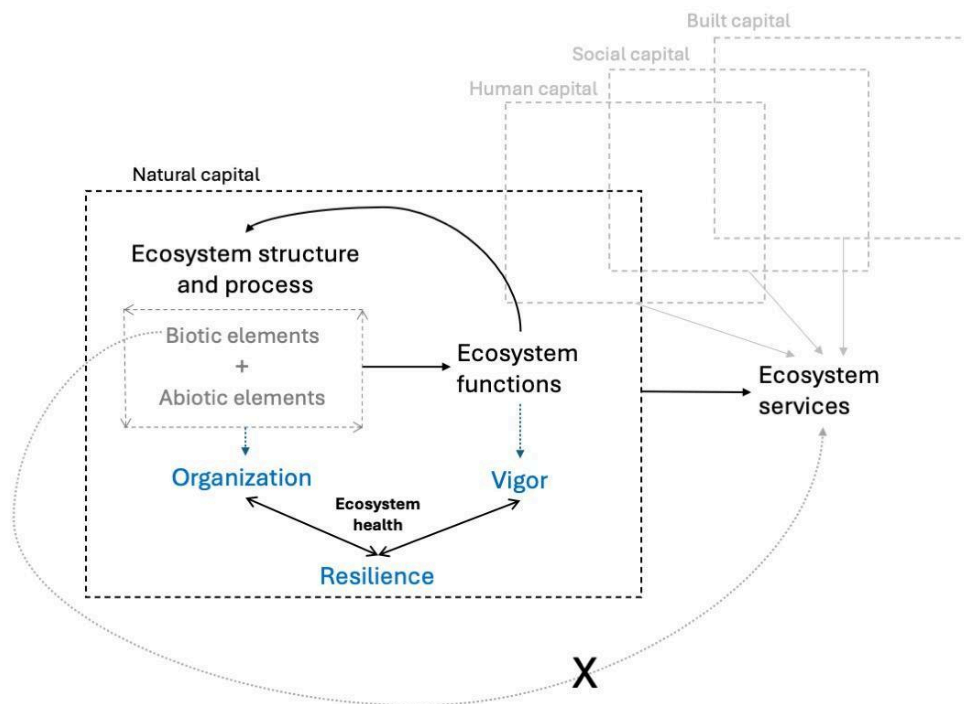

Figure 3. The four types of capitals interacting to provide ecosystem services, and the relationship with the components of ecosystem health with ecosystem structure and functions.

Breaking the resilience boundary of ecosystem's health will turn the system towards another stable state, making a significant change in the metabolism and structure of the ecosystem. These changes in stable states with different ecosystem health often represent a reduction in the benefits people obtain from the previous stable states (Hernández-Blanco et al., 2020; Rapport et al., 1998). Moreover, it is worth highlighting that ecosystem health is often assessed in a disaggregated way, analyzing individual ecosystems. In reality, nature is a web of ecosystems which are interlinked across land and seascapes. For example, the catchment

system of forests, agricultural fields, mangroves and coral reefs in the Great Barrier Reef in Australia (Thorburn et al., 2013; Packett et al., 2009; Kroon et al., 2016; Schaffelke et al., 2005).

Role of keystone species in supporting ecosystem services

The provision of ecosystem services requires the whole ecosystem, which is not only defined by its components (i.e., structure), but mainly by the interaction webs built within which species can potentially influence other species (i.e., ecosystem processes); these interactions can include both biological processes (e.g., competition, predation, and mutualism) and physicochemical processes (e.g., nutrients, impact on water limitation, and temperature) (Estes et al., 2011). Therefore, species that play a role in supporting ecosystem functions and services at the same time depend on other species and abiotic elements in the ecosystem (Mace et al., 2012). For example, kelp forests provide primary production, carbon sequestration, and complex habitat that generate services such as fisheries, coastal protection, and tourism, and sea otters are key to maintaining these functions by preying on sea urchins, whose grazing can otherwise devastate kelp stands. Yet sea otters themselves rely on the kelp forest for shelter from predators and as a hunting ground rich in prey like sea urchins, crabs, and fish (Estes & Duggins, 1995).

As stated before, the theoretical framework presented here considers the network dynamics of nature, and therefore the value of species based on maintaining the balance and function of the system in order to keep providing benefits, rather on the disruption of this network through the consumption of the species based on the consideration that it is the final benefit (as Cook et al., 2020 consider all provisioning services). Haines-Young and Potschin (2010) briefly consider this approach, which calls for the incorporation of functional traits from species (especially keystone species) on ecosystem services assessments, since these traits determine the effect of species on ecosystem processes or services and their response to stressors (i.e., resilience) (De Bello et al., 2008).

Each species (individual organisms, from a species, strictly speaking) plays a different role in supporting different ecosystem services (e.g., Daniels et al., 2018; Balvanera et al., 2006; Costanza et al., 2007; Kremen, 2005; Díaz et al., 2013). Luck et al. (2003) address the connection between population diversity and ecosystem services, considering changes in the size, number, distribution and genetic composition of populations and its impact on the function of ecosystems and the consequent provision of services. Therefore, in their framework, the supply of ecosystem services is determined by the diversity of the populations. Considering this, they introduced a new population categorization called “service-providing-unit” (SPU), which provide, or might provide in the future, a recognized ecosystem service at some temporal or spatial scale. Moreover, Luck et al. (2003) point out that it is likely that multiple species contribute to a particular service, which is related to ecological redundancy.

Luck et al. (2009) expanded their earlier application of SPUs to the population, functional group and community levels. Also, they point out the need to quantify the organism's characteristics that provide ecosystem services, namely functional traits, which can be classified as response trait (i.e., attribute of an organism to respond to environmental changes) and effect traits (i.e., attribute of an organism that has an effect on ecosystem processes). Furthermore, based on the concept of "ecosystem service providers" (ESP) from Kremen (2005), which can be populations, species, functional groups (guilds), food webs or habitat types that produce ecosystem services (again, clarifying that our vision is that species or individuals don't provide ecosystem services directly), Luck et al. (2009) propose that the SPU and ESP concepts represent a continuum that they call simply the "service provider" (SP) concept. This concept is based on the quantification of the characteristics from the organism that are needed to deliver (or to contribute as is our vision) ecosystem services.

Nevertheless, our theoretical framework differs from the SPU concept since we argue that it is not appropriate to consider a species or population as a direct provider of ecosystem services. Our framework considers species and populations as contributors to the provision of ecosystem services.

This theoretical framework described here focuses on animals, recognizing that other organisms (e.g., plants, bacteria, fungi, and protists) also have a key role. Animals, regardless of the type of ecosystem, species, or functional types, influence ecosystems mainly through (1) predation, (2) foraging, (3) frugivory and seed dispersal, (4) grazing effects, (5) nutrient deposition (e.g., defecation, urination), and (6) ecosystem engineering (Estes et al., 2011; Roman, 2023; Schmitz & Sylvén, 2023). Each one of these ecological processes that influence ecosystems have different impacts in one or more ecosystem functions, mainly (1) biological control, (2) pollination, (3) carbon sequestration, (4) fire regulation, (5) water regulation, and (6) nutrient cycling. Finally, these ecosystem functions determine the provision of (1) food productivity, (2) water provision and regulation for different purposes, (3) climate regulation, and (4) disease control (Figure 4).

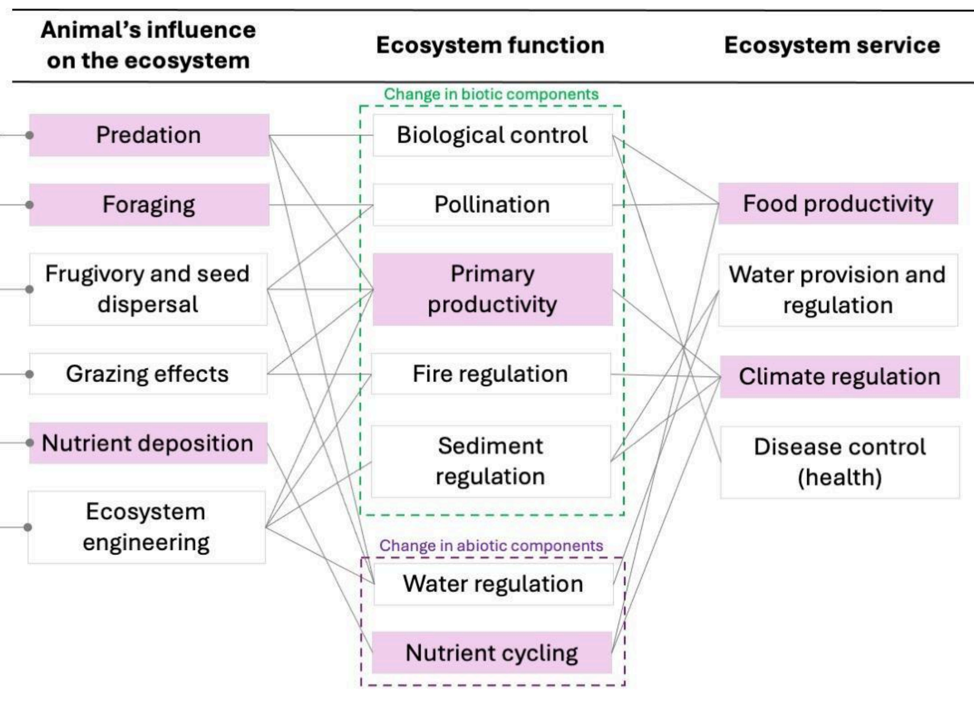

Figure 4. Relational ways in which animals can influence ecosystems as well as the production of ecosystem functions and services. In purple are highlighted those that apply for cetaceans under this study.

It is worth saying that these interactions do not happen linearly or in isolation. Many of these interactions will produce a mix of ecosystem functions that depend on them (e.g., predation on herbivores to maintain plant biomass). Also, it is important to take into consideration the timeframe and the main supplier of the ecosystem service. For example, Berzaghi et al. (2022) consider the carbon stored in the elephant populations, which is arguably more a flow than a stock, since this carbon will only be kept in the animals while they are alive (~60–70 years), and will end up in different stocks or flows depending on the pathway it follows after the animal dies. For example, carbon could accumulate in the ground, which I would then account as the contribution of elephants through nutrient deposition to nutrient cycling or primary productivity. On the other hand, part of the carbon could also transfer to other animals through consumption. Therefore, we need to model the potential pathways and quantities of stocks and flows of carbon so we can take this type of role into consideration.

Another key point to address in assessing the role of species in supporting the provision of ecosystem services is the role that keystone species play. Through their activities and abundance, keystone species have a disproportionately high impact on the stability of the ecosystem structure (Paine, 1969), and therefore on the production of ecosystem functions. Keystone species therefore maintain the health of an ecosystem by maintaining its structure and vigor, which in turn determine ecosystem's resilience. One of the most assessed roles of

keystone species is their dynamic influence on the trophic level, often producing a cascade of effects (i.e., trophic cascades), which can be direct (e.g., predation) or indirect (e.g., behavioral changes) (Paine, 1995).

Finally, it is worth noting that the contribution of species to the ecosystem health and ecosystem services is multispatial, since one species can play a role in different types of ecosystems through different biological functions, which can have an economic impact, especially for local communities. For example, the parrot fish spends the majority of its time grazing on algae and other calcified surfaces in coral reefs, keeping the health of the ecosystem and therefore its resilience (Bellwood & Choat, 1990; Bonaldo et al., 2014). In their absence, the system would shift to another stable state (i.e., dominated by algae), and hence there would be a significant change in some ecosystem functions, such as the provision of habitats for these and many other species, as well as in high valuable ecosystem services as tourism and recreation and as the provision of food (UN Environment et al., 2018). Aside from the role of grazers on coral reefs, parrotfish are also ecosystem engineers, playing a key role as bioerosion agents and therefore producing large quantities of carbonate sediment as a by-product of their grazing (Morgan & Kench, 2016). For example, in the Maldives, parrotfish generate more than 85% of the 5.7 kg/m^2 of new sand-grade sediment produced on the outer reef flat each year (Perry et al., 2015). This way, parrotfish contribute to the building of these islands that many people visit every year, and therefore their role on beaches also has a significant value.

3.2 Conceptual framework: Cetaceans behavior and physiology related to the structure and function of the ecosystem

Based on the theoretical framework presented in the previous section, the conceptual framework is a zoom in analysis on the ecosystem structure and process portions of the ecosystem services cascade with a focus on the ecological role of cetaceans. The goal is to better understand the ecosystem functions derived from the interaction (ecosystem processes) between cetaceans and other biotic and abiotic elements (structure), which can potentially lead to the production of ecosystem services. In other words, our premise is based on the role that cetaceans have in maintaining or enhancing the health of coastal and marine ecosystems so they can provide ecosystem services (those from Table 2). Therefore, the provider of the ecosystem service is always the ecosystem, in this case coastal and marine ecosystems, instead of wrongly assuming a direct link between cetaceans and ecosystem services.

Our concept framework, based on the seminal paper of Roman et al. (2014) and complemented with other analysis (e.g., Katona & Whitehead, 1988; Paine, 2006; Roman et al., 2021), considers eight mechanisms or ecological pathways by which whales influence marine ecosystems that can potentially lead to the provision of ecosystem services. Each of these ecological pathways can be categorized according to three tiers of potential impact on ecosystem functions (Figure 5). Each of these pathways occur in one ecosystem (e.g., euphotic

zone), or between several ecosystems (e.g., euphotic zone and deep sea, pelagic zone and kelp forests). Therefore, the direction of the pathways is multidimensional in its impact on the provision of ecosystem services.

Tier 1 pathways: Influence on ecosystem functions without the influence of other species.

1. Physical ecosystem engineering. Cetaceans act as large-scale physical ecosystem engineers by altering the structure and dynamics of marine habitats through their movement, feeding behavior, and interactions with prey. Their repetitive diving and surfacing cycles generate vertical mixing that can influence the distribution of nutrients, oxygen, and heat in the water column. Feeding behaviors such as lunge feeding, benthic suction feeding, and bubble-net feeding physically reorganize prey fields, disturb sediments, and modify turbulence regimes, creating localized changes in habitat conditions for plankton and fish (Goldbogen et al., 2008). The sheer displacement of water by their large bodies also contributes to microscale mixing and can enhance encounter rates between predators and prey.
2. Carbon sequestration through whale falls. When whales die and their carcasses sink to the seafloor, they transport large quantities of organic carbon from the surface to the deep sea, often below 1,000 meters where carbon can be sequestered over century-to-millennial timescales. This flow of carbon bypasses recycling in the upper ocean and contributes directly to long-term storage in sediments and deep benthic systems (Smith & Baco, 2003). This contribution depends on the probability of a whale fall sinking below 1000m.
3. Carbon sequestration in biomass. Living whales store substantial amounts of carbon in their tissues, but long-term sequestration (≥100 years) applies meaningfully only to species with exceptionally long lifespans. Bowhead whales, which can live well over a century, and in some documented cases close to 200 years (George et al., 2011), are the only cetaceans whose biomass carbon remains locked away for a period consistent with climate-mitigation thresholds for sequestration.

Tier 2 pathways: Influence other species that conduct ecosystem functions.

4. Enhancing primary productivity for fisheries. Cetaceans stimulate marine primary productivity by redistributing limiting nutrients across ocean layers and large spatial gradients. Through the “whale pump,” deep-feeding species release nutrient-rich fecal plumes and urine at the surface, replenishing iron, nitrogen, and phosphorus in the euphotic zone where phytoplankton require them for growth. Through the “whale conveyor belt,” migrating whales transport nutrients from high-latitude feeding areas to

low-latitude breeding grounds via excretion, placental materials, and carcasses, creating cross-basin nutrient subsidies that enhance localized productivity and food-web support (Roman et al., 2014). This contribution is especially relevant in nutrient-limited oceans, as well as in whale "hotspots" and during "hot moments", such as in the case of feeding areas.

5. Carbon sequestration through carbon stored in additional phytoplankton. By increasing nutrient availability, cetaceans can stimulate additional (i.e., new) phytoplankton growth, which fixes atmospheric CO_2 through photosynthesis. A portion of this new production eventually dies, aggregates, and sinks below 1,000 meters, where its carbon becomes sequestered from the atmosphere over long timescales (Boyd & Trull, 2007). This pathway represents an indirect but potentially significant contribution to carbon sequestration, as whale-enhanced primary productivity amplifies the effectiveness of the ocean's biological carbon pump.
6. Habitat through whale falls for potential species of commercial interest. Sunken whale carcasses create complex, high-value deep-sea habitats that support diverse and specialized biological communities, including species of potential scientific or commercial interest (Smith & Baco, 2003). Whale falls provide a rare, concentrated source of organic matter in food-limited deep-sea environments and sustain sequential ecological stages—from mobile scavengers to chemoautotrophic communities—that can persist for decades. Therefore, whale falls function as ecological "islands" that enrich deep-sea ecosystems and may harbor species with future biotechnological or pharmaceutical relevance.

Tier 3 pathways: Influence other species that influence one or more additional species that conduct ecosystem functions.

7. Whales as consumers, influencing food web dynamics. Whales function as top or mesopredators in marine food webs, exerting biological control over prey populations and shaping trophic interactions. Their consumption of organisms such as krill, squid, and small pelagic fish, influence the abundance, behavior, and spatial distribution of species that, in turn, interact with commercially important taxa. For instance, sperm whales prey heavily on large squid, which are themselves major consumers of fish species of economic value (Coll et al., 2013). Nevertheless, this potential type of biological control service hasn't been analyzed in detail in the literature.
8. Whales as prey. Many whale species are also prey for apex predators such as killer whales, and changes in whale populations can trigger large ecological cascades with consequences for ecosystem services. When great whale abundance declines, predators like orcas may shift to alternative prey—sometimes to species with key ecological

roles—potentially destabilizing food webs. A well-documented example involves orcas switching from great whales to sea otters in the North Pacific, which reduced otter populations, allowed sea urchins to proliferate, and led to widespread kelp forest loss (Estes et al., 1998). These kelp declines diminished blue carbon storage, reduced habitat for commercially important species, and altered coastal ecosystem functioning.

Trophic downgrading (i.e. the removal of large apex consumers) (Estes et al., 2011), caused by industrial whaling prior to the international moratorium, produce a wide spectrum of changes in ecological dynamics that we are still starting to understand its impact on ecosystem health, especially in terms of generating ecosystem functions. This can produce the emergence of new stable states, which can be beneficial or not to human well-being. Therefore, in the case of this tier, the contribution of cetaceans to the provision of ecosystem services is assessed as a ripple effect, a cascade of changes that not only produce changes to other species, but to entire ecosystems.

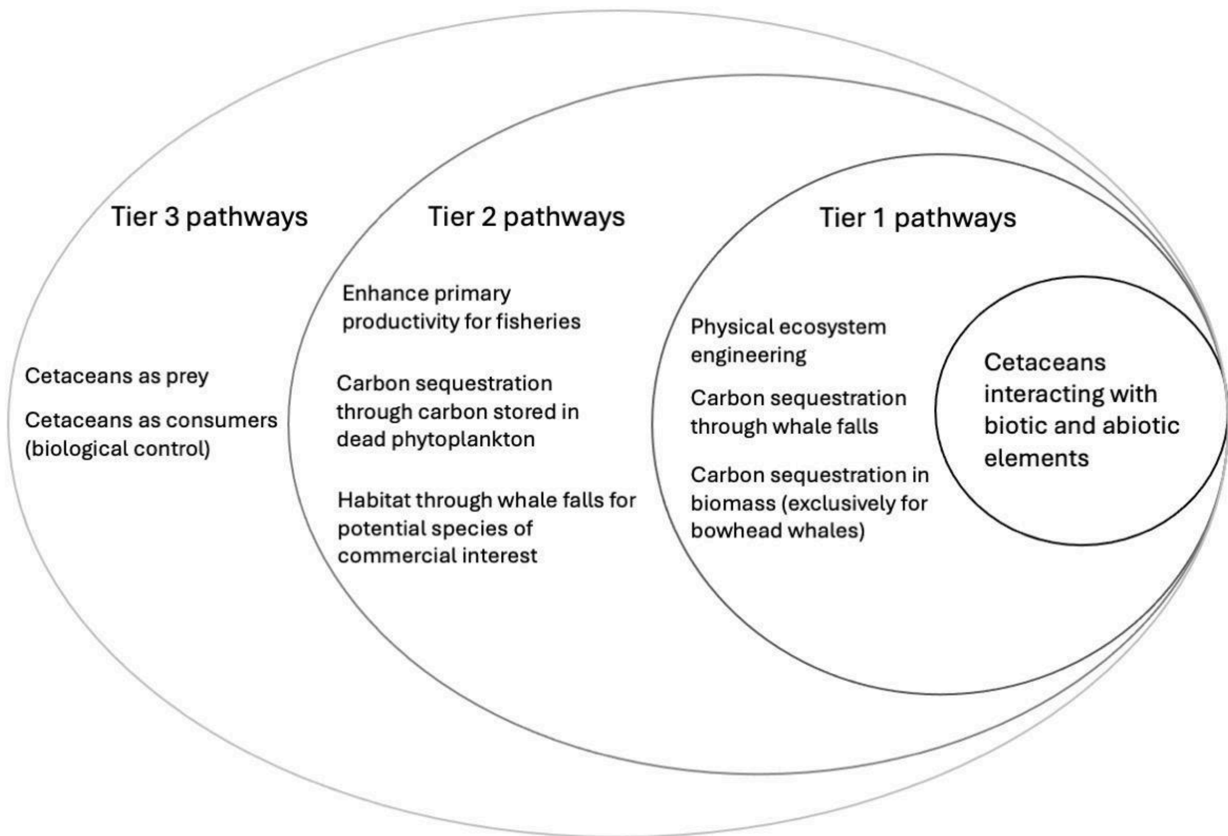

Figure 5. Cetaceans' contributions to the provision of ecosystem services.

Considering these eight contribution pathways, cetaceans can support the following five coastal and marine ecosystem services from Table 2.

1. **Fisheries**. Fisheries are a provisioning ecosystem service that supply wild aquatic organisms, mainly fish and invertebrates, that are essential for global food security, cultural identity, livelihoods, and national economies. They depend on functioning food webs, nutrient availability, stable population dynamics, and habitat integrity, all of which determine the productivity and reliability of marine harvests. Ecological processes shaping primary production, trophic transfer, and predator–prey balance strongly influence the sustainability of fisheries and their capacity to support coastal communities. Cetaceans contribute to these foundations by recycling nutrients that stimulate phytoplankton growth, physically structuring prey distributions, and modulating mesopredators, thereby supporting ecosystem productivity and stability (Roman & McCarthy, 2010; Lavery et al., 2014).
2. **Climate regulation**. Climate regulation is a critical regulating service involving the biophysical processes that govern greenhouse-gas concentrations, carbon cycling, energy balance, and climate stability. It encompasses carbon sequestration, carbon storage, albedo effects, and the functioning of ocean–atmosphere feedbacks that shape global climate. Oceans play a central role in this service through the biological carbon pump, phytoplankton production, and long-term carbon burial in deep-sea sediments. Cetaceans may strengthen these processes by stimulating new phytoplankton productivity through nutrient release, storing carbon in their biomass (in the case of cetaceans that live >100 years, like the bowhead whale), and transferring organic carbon to the deep sea when they die and sink (Pershing et al., 2010; Roman & McCarthy, 2010; Smith & Baco, 2003).
3. **Genetic resources**. Genetic resources refer to the hereditary material contained in organisms (i.e., genes, alleles, and entire genomes) that supports adaptation, evolutionary potential, and innovation in fields such as biotechnology, bioengineering, and medicine. These resources are fundamental for maintaining the resilience of ecosystems under environmental change and for enabling future discoveries based on traits evolved in diverse and extreme habitats. In the marine realm, deep-sea ecosystems are especially important sources of unique genetic material because they host organisms with metabolic pathways and physiological adaptations not found elsewhere. Cetaceans contribute to this service most distinctively through whale falls, which create rare, nutrient-rich islands on the deep-sea floor that host highly specialized assemblages of bacteria, invertebrates, and chemosynthetic organisms. These communities exhibit genetic traits adapted to anoxic conditions, sulfide-rich environments, and extreme pressure, expanding the global pool of genetic novelty (Smith & Baco, 2003). The evolutionary experimentation that occurs at whale falls

produces unique lineages and metabolic pathways, particularly among chemosynthetic bacteria, that represent potential valuable and largely unexplored genetic resources with potential relevance for biotechnology and future bio-discovery (Goffredi et al., 2004).

4. **Medicinal resources**. Medicinal resources encompass biochemical compounds, metabolic pathways, enzymes, and microbial products derived from organisms that have actual or potential applications in drug discovery, disease treatment, and biomedical research. These resources often arise in environments where organisms evolve unique chemical strategies for survival, generating bioactive molecules with properties not present in more common habitats. Whale falls could play a role in sustaining such biochemical diversity by creating deep-sea oases dominated by chemosynthetic bacteria, *Osedax* worms, and other specialized fauna whose metabolic systems produce a wide range of novel compounds. These organisms employ enzymatic and biochemical pathways adapted to anoxic, sulfide-rich conditions, including bone-degrading enzymes, sulfur-oxidizing metabolic cycles, and molecular mechanisms for coping with extreme chemical stress (Goffredi et al., 2004). Such biochemical innovations represent promising sources of new antimicrobial, anti-inflammatory, and enzymatic agents (Smith & Baco, 2003).
5. **Biological control**. Biological control is a regulating service involving the natural suppression or regulation of species populations through predation, competition, parasitism, and behavioral interactions. It maintains ecological balance by preventing outbreaks of dominant species, supporting trophic stability, and reducing risks of ecosystem collapse. Effective biological control underpins the resilience of food webs, protects habitat-forming species, and limits overgrazing or over predation that could destabilize ecosystems such as coral reefs and kelp forests. Cetaceans contribute to this service through their roles as apex predators and ecological engineers, influencing the abundance and behavior of prey and mesopredators and promoting balanced trophic dynamics (Estes et al., 2011).

We are deliberatively excluding other ecosystem services, mainly cultural, such as recreation and tourism (i.e., whale watching) and spiritual experience, among others, since they our outside the mandate from the IWC (Resolution 2016-3) to undertake the review of ecological, management, environmental, social and economic aspects related to the contributions of cetaceans to ecosystem functioning. Ecosystem services such as disturbance prevention or moderation, such as the one provided by kelp forests, could also be incorporated in the future through an extensive analysis of mainly tier 3 pathways.

For this study, we will assess two ecosystem services: (1) climate regulation and (2) fisheries productivity (Figure 6). These services were recommended by Animal Welfare Institute et al.,

(2017) as the ones that should be prioritized in future research, and they provide a good starting point in terms of balancing complexity and available data.

Figure 6. Cetaceans as part of the structure and processes of marine ecosystems. The interaction with the other three capitals was not included for simplicity reasons.

Using a modified version of the ecosystem service cascade from Haines-Young & Potschin (2010), the contribution of cetaceans to the provision of ecosystem services can be described in five main stages of ecosystem services production (Figure 7). The cascade starts with a clear understanding of the food web of the species under analysis, in this case humpback whales (*Megaptera novaeangliae*) in the North Pacific. We created a food web diagram (Figure 8) with the help of experts in a 1-day workshop held at the University of Alaska Southeast on August 18th, 2025 (See Supplementary Materials). The diagram depicts the trophic interactions of humpback whales within a pelagic marine food web. At its base, the web is sustained by primary producers, specifically phytoplankton (diatoms and dinoflagellates), which convert inorganic matter and sunlight into organic matter through photosynthesis. These producers are consumed by primary consumers, including small copepods (<2 mm) and large copepods (≥2 mm), as well as herbivorous euphausiids (krill).

Moving upward, secondary consumers are represented by omnivorous euphausiids, which exploit both phytoplankton and smaller zooplankton prey, thus bridging primary producers and higher trophic levels. Forage fish species—herring, sand lance, capelin, sardines, and anchovies—form a critical intermediate trophic level by feeding on euphausiids and copepods. Other forage fishes (salmon, pollock, myctophids, and eulachon) diversify this level, providing redundancy and trophic stability.

Humpback whales occupy a top consumer niche in this system. They feed directly on euphausiids, copepods, and forage fishes, integrating energy from both zooplankton- and fish-based pathways. Their mortality also contributes to detrital and scavenger pathways, supporting pelagic, deep-sea, and even terrestrial scavengers through whale falls and strandings. Orcas (*Orcinus orca*) are identified as natural predators of humpback whales, thus connecting the whales themselves into higher predatory dynamics.

To better understand the social-ecological system, human extraction is represented through fisheries, which directly exploit forage fish such as herring, sardines, and anchovies. This anthropogenic interaction highlights the competition between humans and humpback whales for shared prey resources, with potential implications for both whale populations and broader ecosystem stability.

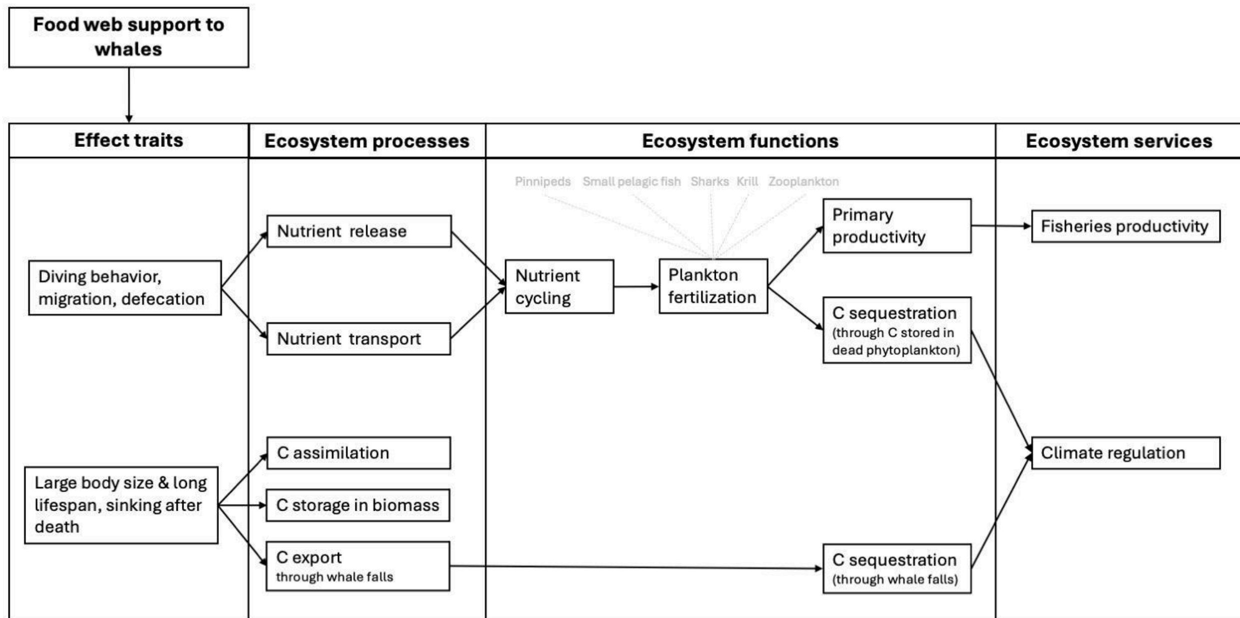

Figure 7. Cascade of the contribution of whales to the provision of ecosystem services.

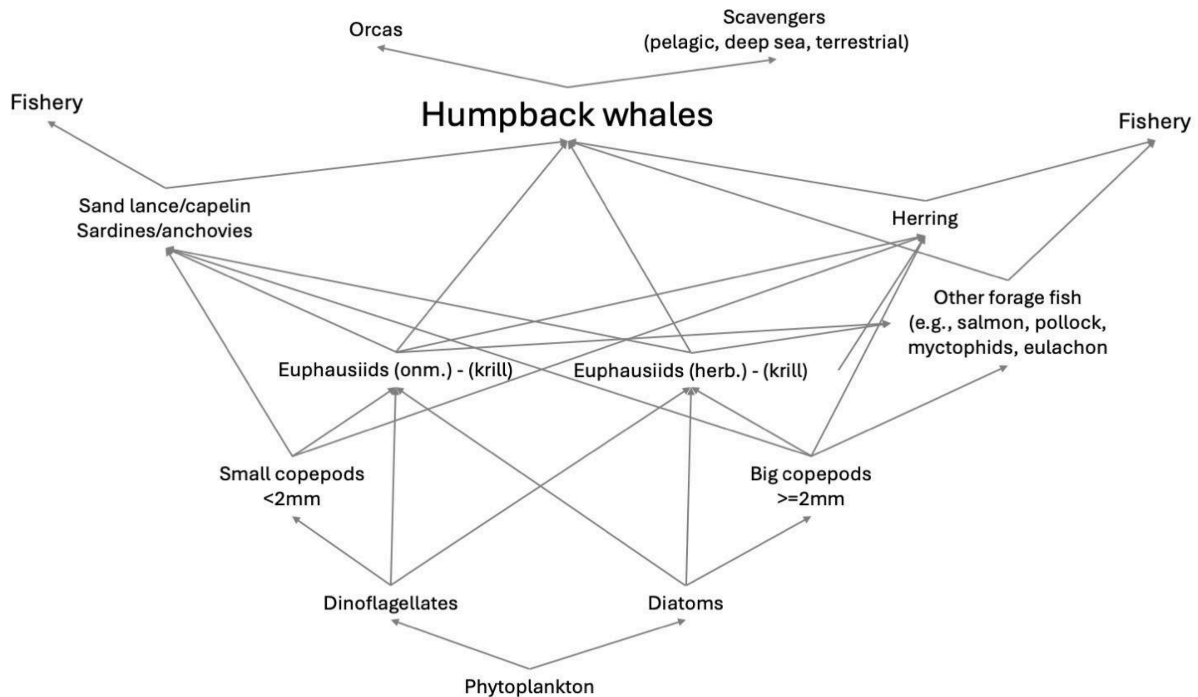

Figure 8. North Pacific humpback whales' food web diagram.

At the foundation, whale effect traits are divided into two main groups. First, traits related to behavior—such as diving, feeding strategy, long-distance migration, and defecation—mediate the redistribution of nutrients within and across ecosystems. Second, traits associated with large body size and mass, long lifespan, and post-mortem sinking govern the storage and export of carbon over ecological and geological timescales (Castro-Tavares et al., 2019). These traits initiate a set of ecosystem processes. Behavioral traits underpin nutrient release and transport, while morphological and life-history traits enable carbon assimilation, storage in biomass, and eventual carbon export through whale falls.

These processes feed into ecosystem functions. Nutrient release and transport collectively contribute to nutrient cycling, which in turn fertilizes phytoplankton communities. This many enhance additional primary productivity and facilitate carbon sequestration through the sinking of phytoplankton-derived organic matter. In parallel with phytoplankton fertilization through their feces, carbon assimilation and storage in whale biomass, together with the export of organic matter through whale falls, provide additional long-term pathways for carbon sequestration. The diagram thus captures the dual role of whales in supporting both bottom-up productivity and long-term biogeochemical regulation.

Finally, these functions underpin ecosystem services of direct relevance to human societies. Enhanced primary productivity sustains fisheries productivity, providing food and economic benefits. Carbon sequestration, whether mediated by phytoplankton or whale falls, contributes to climate regulation, a critical regulating service with global implications. The cascade therefore

demonstrates how whales act as ecological engineers, linking their biological traits and ecological roles to services that sustain both local economies and global climate stability.

In the case of phytoplankton fertilization, it is important to note that a wide range of marine animals besides whales play a critical role in this ecosystem function by recycling and redistributing nutrients within the euphotic zone, and that is precisely why our concept framework is based on the **contribution** of whales, which is the **relative contribution to the provision of ecosystem services**. For example, pinnipeds such as seals and sea lions excrete nutrient-rich waste products at the surface after foraging dives, thereby contributing to localized nitrogen recycling that stimulates primary production in coastal ecosystems (Rhodes-Reese et al., 2021). Similarly, dense schools of small pelagic marine fish such as anchovies, sardines, or herring excrete ammonia and/or urea into the water column, supplying regenerated nitrogen that supports phytoplankton growth, particularly in oligotrophic and coastal upwelling systems (Le Mézo et al., 2022). Another example are sharks, through their wide-ranging feeding and migratory movements, which redistribute nutrient subsidies across habitats, with excretion and carcass deposition increasing nutrient availability and indirectly supporting phytoplankton productivity (Hussey et al., 2014). At a broader scale, Antarctic krill serve as a key vector of nutrient regeneration, releasing substantial amounts of iron and nitrogen during feeding and through fecal pellet production, a process especially significant in the iron-limited Southern Ocean (Tovar-Sanchez et al., 2007). A final example are zooplankton that contribute to nutrient recycling via excretion, sloppy feeding, and diel vertical migrations, effectively regenerating nutrients in the euphotic layer and sustaining primary production (Steinberg & Landry, 2017).

Considering this proposed whale contribution ecosystem services cascade, and based on the concepts on species provider based on effect traits from Luke et al., (2003, 2009), Kremen (2005) and Díaz et al., (2013), we introduce a new concept called "**Keystone Species Contribution Pathway" (KSCP)**, a trait-based indicator on the contribution of keystone species to ecosystem functions and services. The KSCP is composed by both the direction of the contribution as well as by its magnitude, working in a way like a physics-style vector. In other words, the KSCP is the species **quantified pathway of contribution from traits to services**.

Considering the cascade from Figure 7, the KSCP includes the following ten elements (variables):

(1) Number of individuals (population size)
(2) Mass
(3) Trophic impact
(4) Longevity (for multi-year analysis)
(5) Physical impact
(6) Range of the population (including migrations)
(7) Community assemblage (including other species that can also contribute).
(8) Nutrients in feces/urine
(9) Nutrient availability at time x and location y

10) Effect traits (e.g., food intake rate, dietary preference, feeding strategy, dive depth, excretion rate)

In step 3 from the methodological framework, we introduce a series of functions to estimate three KSCP's for humpback whales considering these variables.

3.3 Methodological framework: Process to assess the contribution of cetaceans in supporting the provision of ecosystem services

The methodological framework is based on Hernández-Blanco (2025), consisting of 5 steps to estimate the contribution of cetaceans to the provision of ecosystem services, and potentially the economic value of this contribution.

Step 1. Select the species/population of interest

The first step will be choosing the species/population whose contribution to ecosystem functions will be valued economically. This can be done in different ways, and can also depend on the context and policy objectives of which the study is embedded in, but the following selection criteria can provide some guidance: (1) Status of the population (especially if it is vulnerable or endangered), (2) potential changes in population in the future, (3) whether the species is a keystone species and/or umbrella species, (4) if there are already ecological and economic data that can be used in the analysis, and (5) the level of dependency from human beneficiaries on the functions that these species support.

In the case of this study, it will be the North Pacific humpback whale population.

Step 2. Set the spatial scope

This involves setting the physical and ecological limits within the ecosystem(s) of interest. The range of the selected species/population needs to be mapped, considering all the possible biotic and abiotic components of the structure of the system (1) in which the species depend on, and (2) have an impact on (recognizing that on many occasions these two would be the same). Furthermore, it is important to recognize that the limits of the study will be arbitrary to some degree since such limits do not really exist in nature.

Step 3. Identify the role the species/population play in supporting ecosystem functions

From an economic perspective, this means estimating the supply. The goal is to identify the roles of the species in supporting ecosystem functions in the spatial scope of the study, or to

determine if the species has an impact on a partial or complete bundle of functions. The role or contribution was described in the conceptual framework. Here we formalize the KSCP of humpback whales by means of a function that estimates their contribution to the ecosystem service cascade. The function operationalizes the KSCP by linking effect traits (e.g., nutrient release, population size, spatial range) to incremental nutrient supply, primary production, and potential fisheries yield. Therefore, the function provides a quantitative measure of both the direction and magnitude of the whales' contribution along the cascade of ecosystem services.

3.1 Fisheries productivity

To estimate the contribution of North Pacific humpback whales to fisheries productivity via plankton fertilization, **KSCP-fisheries**, we developed a novel function based on variables related to each of the phases of the cascade presented before. The estimate of the **KSCP-fisheries** can be done in four stages:

Stage 1: Whale-driven supply

We model population-level nutrient input as

$$T_N = p \times q_n \times D_{feeding} \quad \text{Eq. 1}$$

$$T_{NA} = \frac{T_N}{A} \quad \text{Eq. 2}$$

T_N = Total nitrogen added by the population per unit time (e.g., mol N day^{-1}).

p = number of whales considered in the area in the season

q_n = per-whale daily nutrient release rate.

$D_{feeding}$ = number of feeding days

T_{NA} = Per-area nutrient flux

A = Area of study area

It is important to clarify that there might be an overlap of what is considered new nutrients versus recycled nutrients due to the difficulty for this first simple model to assess the exact depth at which whales are feeding.

Stage 2: Nutrient limitation adjustment

In this stage we adjust the whale-derived nutrient input from T_{NA} to account whether phytoplankton actually need those nutrients. This means that if the water is already nutrient-rich, additional inputs don't help much, and conversely if the water is nutrient-poor (limiting), additional inputs from whales are highly valuable. In other words, we introduce a "nutrient demand factor" reducing or keeping the effect proportional to the real ecological context.

Therefore:

$$T_{NN} = T_{NA} \times g(n) \qquad \text{Eq. 3}$$

T_{NN} = Per-area nutrient flux needed, or the additional usable nitrogen from whales

This demand factor can be expressed in the following way:

$$g(n) = \frac{N^*}{N^* + n} \qquad \text{Eq. 4}$$

g(n) = growth demand factor

n = the ambient nutrient concentration in the surface/mixed layer (µM of the limiting nutrient)

N^* = the half-saturation constant (µM) (the concentration at which phytoplankton growth reaches half of its maximum rate)

Some clarification points:

(1) g(n) ranges between 0 and 1
(2) T_N should always be multiplied by g(n)
(3) g(n) is not calculated for each whale. The estimate of nutrients *n* (e.g., average nitrate µM) in the study area and season, and apply one g(n) value to the whole T_N. This is because phytoplankton experience the ambient nutrient field, not individual whales.
(4) To estimate *n*, we recommend following these steps:
    a. Decide exactly what *n* should represent (i.e., nutrient that limits phytoplankton in the system).
    b. Use across the study the same depth layer (euphotic or mixed layer depth (MLD)).
    c. If MLD is used, the less time-consuming way to estimate it is to consider a fixed "surface layer" (e.g., top 15 or 20m in summer)

d. If field data are not possible (normally expensive and time consuming), data on *n* can be extracted from global datasets (e.g., World Ocean Atlas). The extracted values need to be for the study area (polygon), season (months) and the surface/MLD levels.
e. Convert units from mg NL^{-1} to µM if needed.

Stage 3: Primary production boost

The goal of this stage is to determine how many units of plankton are produced per unit of effective nutrient. This change in primary productivity (i.e., additional plankton growth) can be expressed as:

$$\Delta PP = \sigma \times T_{NN} \quad \text{Eq. 5}$$

ΔPP = Additional primary production (annualized boost of PP) (mg C m^{-2} d^{-1})

σ = conversion from limiting nutrient input to new primary production (i.e., how much additional carbon (plankton growth) is produced per unit of additional nitrogen)

Some clarifications:

(1) In the absence of enrichment data[1], σ can be considered in the case of nitrogen as the Redfield ratio to convert N to C using fixed elemental ratios: 106 C : 16 N. 6.625 (mol C per mol N), which is ~79,500 mg C per mol N. In real ocean conditions, the effective σ can be lower and variable.
(2) The units of σ are mg C m^{-2} day^{-1} per mmol N m^{-2} day^{-1}.

Stage 4: Induced changes in fisheries productivity

Following the cascade from Figure 7, the fourth and final stage of the **KSCP-fisheries** function, addresses the question of how much of the additional plankton that was produced through the contribution of whales actually becomes additional fish that people catch? This is the core idea of the KSCP, to define these pathways since not all additional plankton ends up in commercial fisheries. Some gets eaten by other species or goes to parts of the food web that are not fished.

This pathway and impact can be estimated by the following equation:

Eq. 6

[1] empirical data extracted from bioassays where phytoplankton cultures or natural seawater samples are given extra nitrate and then the increase of PP is measured.

$$\Delta Y = NC_{AC} \times M(t, c) \times \Delta PP$$

ΔY = <u>Additional fisheries yield</u> attributable to whale-drive fertilization (tons yr^{-1} of catch) in the study area and season

ΔPP = Additional primary production (annualized boost of PP) (mg C m^{-2} d^{-1})

NC_{AC} = net conversion from additional primary production to additional catch (0-1)

M(t,c) = adjustment multiplier to capture food-web routing and community context

Some clarifications:

(1) NC_{AC} and M(t,c) work in the equation to convert/rout the carbon into catch. It is a conversion <u>fraction</u> between 0 and 1, so it is dimensionless. It considers:
    a. Trophic transfer (only part of ΔPP reaches fish biomass through the food web).
    b. Biomass -> catch (only part of fish biomass is harvested).
    c. Carbon -> wet weight (if ΔPP is in tons of C, this needs to be converted to wet-mass).

(2) The goal of using M(t,c), which is also a dimensionless adjustment, is to capture the food-web routing and community context.
    a. t (trophic routing): This term of the equation answers the following question: Does additional plankton actually flow to the target of commercial interest? It considers things like diet pathways, transfer efficiencies along the relevant chain, and the share of flow that reaches the fish group(s). It can be estimated through several methods, such as Ecopath/Ecosim models, Mixed Trophic Impact (taking the sign/magnitude of PP towards target groups to derive a routing fraction), and empirical elasticity. Because these methods can be time consuming, to start we recommend setting t = 1 and keep NC_{AC} conservative.
    b. c (community assemblage): This term of the equation answers the following question: Does the current species mix amplify or dampen routing to the target fish? (e.g., strong forage-fish link vs. a community dominated by competitors or non-harvested pathways). It considers relative abundance/biomass of key mediators (forage fish, copepods), competitors, and predators that alter how marginal PP is partitioned. This can be estimated using multispecies survey indices (relating years with high mediator biomass (e.g., euphausiids) to stronger PP -> fish coupling; and using a scale c between 0.9–1.1) or expert elicitations.

Again, because these methods can take a significant number of resources, to start we recommend c = 1.

3.2 Climate regulation

Following the ecosystem service cascade from Figure 7, whales contribute to the ecosystem service of climate regulation through two different KSCPs: (1) Carbon sequestration from new primary productivity boost, and (2) carbon sequestration through whale falls.

3.2.1. Carbon sequestration from new primary productivity boost

To estimate the contribution of North Pacific humpback whales to carbon sequestration from additional/induced primary productivity, **KSCP-CsPP** (carbon sequestration primary productivity), we build on the equations from Stages 1-3 from the KSCP-fisheries, which determines the additional primary productivity (ΔPP) generated from the additional n Eq. 7 provided by whales in a specific area. This can be done by estimating (1) the extra carbon that sinks and (2) stays in the deep sea.

$$\Delta C_{deep} = \Delta PP \times f_{export} \times f_{sequestered}$$

Where:

ΔC_{deep} = Carbon sequestered from PP boost (g C m^{-2} $year^{-1}$)

f_{export} = fraction of primary production that sinks below the surface

$f_{sequestered}$ = fraction of the exported carbon that is sequestered.

Some clarifications:

(1) f_{export} is the fraction of the organic carbon produced by phytoplankton (ΔPP) that sinks out of the surface layer, which is approximately the upper 100m of the ocean, (i.e., euphotic or mixed layer). Most of the carbon fixed by phytoplankton is quickly recycled near the surface through respiration or grazing, but a small share forms particles or aggregates that begin to sink. This is the part that “leaves” the surface system and represents potential for long-term storage.

(2) For $f_{sequestered}$, two alternative sequestration routes can be considered, depending on oceanographic context and data availability:

   a. Depth-based sequestration (≥1000 m). In open-ocean systems, sequestration is approximated as the fraction of exported organic carbon that sinks below 1000m, where return to the surface occurs on centennial timescales or longer.

   b. Time-based sequestration (≥100 years). In coastal and fjord systems where depths do not exceed 1000m, sequestration can be defined as the fraction of exported carbon that is isolated for at least 100 years, primarily through sediment burial and long-residence deep basin retention.

(3) As a starting point, Table 3 presents ranges for both f_{export} and $f_{sequestered}$, which can be used to test this methodological approach for the North Pacific.

(4) Additional PP ((ΔPP) is only created when new nutrients are introduced into the system, and the definition of additional depends on the depth and location of the nutrients. Otherwise, whales recycle nutrients that are there already and do not necessarily stimulate additional or extra PP. Therefore, the vertical and horizontal spatial scales of where those nutrients come from it is an important variable to consider.

Table 3. Percentage ranges of organic carbon that sinks in the euphotic layer (f_{exp}) and organic carbon that seeks deeper than 1000m (f_{seq}).

Parameter	Reported Range	Context (Depth or Process)	Primary Sources
f_{exp}	0.02–0.50	Fraction of NPP exported below euphotic zone	Boyd & Trull, 2007
	0.05–0.30	Temperature-dependent e-ratio	Laws et al., 2000
	0.01–0.45	Empirical Ez-ratios (1–100 m below euphotic zone)	Buesseler & Boyd, 2009
f_{seq}	0.06–0.25	Fraction of export reaching >1000 m (deep-sea sequestration)	Boyd & Trull, 2007

3.2.1. Carbon sequestration from whale falls

The final contribution that we considered in our cascade from whales to the provision of ecosystem services, is the climate regulation mediated by carbon sequestration from whale falls, **KSCP-CsWF**. This contribution pathway is based on the logic that a portion of the carbon of dead whales is sequestered in the deep sea. This can be estimated, at least as a first approximation, through the following equation:

Eq. 8

$$C_{wf} = p \times \mu \times \overline{m} \times \alpha c \times f_{deep} \times f_{perm}\left(1 - f_{removed}\right)$$

Where:

C_{wf} = carbon in whale falls

p = population size

μ = annual mortality rate

$\overline{m}$ = mean mass at death

αc = carbon per unit mass

f_{deep} = fraction of carcasses that end up at/under a sequestration depth *z*

f_{perm} = fraction of deep carbon that remains isolated over horizon *H*

$f_{removed}$ = managed removals

Some clarifications:

(1) αc represents the proportion of a whale's body that is made of carbon. It's used to convert the animal's total wet weight into an amount of carbon that can potentially be stored when the whale dies.
(2) f_{deep} is the fraction of dead whales whose carcasses end up sinking to a depth deep enough for long-term carbon storage (usually deeper than 1000m). It accounts for losses that occur when whales are eaten at the surface, refloat, or wash ashore, and therefore never reach the deep sea.
(3) Once a carcass reaches the deep ocean, only part of its carbon will remain isolated for centuries. f_{perm} represents that portion, combining processes such as burial in sediments and retention of dissolved carbon in deep, slowly mixing waters. The rest may eventually return to the surface through ocean circulation.
(4) $f_{removed}$ captures any human or natural processes that take the carcass out of the deep-sea pathway before carbon can be sequestered (e.g., towing carcasses to shore, removing them for research, or disturbance from trawling that resuspends buried material).

(5) H is the time period over which carbon must remain isolated from the atmosphere to count as sequestered. Many carbon accounting frameworks use 100 years, but longer horizons such as 1000 years can also be applied depending on the study or policy context.
(6) z is the depth beyond which carbon is considered effectively locked away from the atmosphere. It usually corresponds to the base of the permanent thermocline around 1000m but can vary depending on regional oceanography or chosen accounting standards.

While our functional approach quantifies the contribution pathway of whales in the ecosystem services cascade, a complementary systems ecology network analysis could situate this pathway within the broader ecosystem web. Such an analysis would allow comparison of whales' relative contribution against other nodes (e.g., seabirds, small pelagics, physical inputs) and quantify indirect feedbacks.

Step 4. Identify the main beneficiaries of the supported functions

The beneficiaries of the functions supported by cetaceans represent the demand, which will lead to the identification and prioritization of the ecosystem services. The role of the species will be then a portion of the value of these ecosystem services. Table 4 provides a list of the main beneficiaries from each ecosystem service that were described previously that can be potentially influenced by cetaceans.

Table 4. Beneficiaries of ecosystem services supported by cetaceans.

Ecosystem service	Main beneficiaries	
Fisheries	Commercial fishers and fishing enterprises	Benefit from increased fish biomass, improved recruitment, and higher long-term yields resulting from nutrient enhancement or trophic regulation by cetaceans.
	Processing, distribution, and export sectors	Gain from increased and more stable supply, allowing expanded processing volumes, market access, and export revenues.
	Coastal communities dependent on fisheries	Small-scale fishers, cooperatives, and fishing households benefit through income stability, food security, and reduced vulnerability to stock declines.

Ecosystem service	Main beneficiaries	
	National and regional economies	Fisheries contribute to GDP, employment, foreign exchange earnings, and national food systems; enhanced productivity strengthens these macroeconomic outcomes.
	Consumers	Experience improved availability, diversity, and potentially lower prices of fish products derived from healthier stocks.
Climate regulation	Global society	Reduced global climate damages benefit all individuals through lower risks of extreme weather, sea-level rise, heat-related mortality, agricultural losses, and biodiversity decline.
	Climate-vulnerable countries and communities	Low-lying coastal nations, small island developing states (SIDS), and climate-sensitive economies gain disproportionately from avoided climate impacts.
	Future generations	Long-term carbon storage (e.g., durable deep-sea whale-fall carbon) protects intergenerational welfare by reducing cumulative atmospheric CO_2.
	National governments and climate-policy institutions	Benefit through lower mitigation costs, improved national carbon balances, and support for achieving NDCs, net-zero targets, and blue carbon commitments.
	Private sector actors with climate-exposure risks	Agriculture, insurance, infrastructure, coastal tourism, and energy sectors benefit from reduced climate variability and lower climate-related financial risks.
Genetic resources	Biotechnology and industrial enzyme industries	Benefit from novel genetic material that may enhance enzyme efficiency, metabolic pathways, bioengineering processes, or industrial biocatalysis.
	Pharmaceutical and biomedical R&D	Gain from unique genetic sequences and biochemical mechanisms with potential therapeutic or diagnostic applications.
	Academic and scientific research institutions	Benefit from access to rare genetic diversity that supports evolutionary studies, microbial ecology, genomics, and environmental biotechnology.
	Future generations (option value)	Benefit from preserved opportunities to apply genetic resources in biotechnology, adaptation, synthetic biology, or conservation innovation.

Ecosystem service	Main beneficiaries	
	Governments and multilateral institutions	Benefit from enhanced national capacity to participate in genetic-resource governance regimes (e.g., Nagoya Protocol, BBNJ Agreement).
Medicinal resources	Pharmaceutical companies and drug developers	Directly benefit from novel bioactive compounds that may lead to antibiotics, anticancer drugs, antivirals, or anti-inflammatory agents.
	Healthcare systems and patients	Benefit from improved therapeutics, reduced disease burden, better treatment effectiveness, and potentially lower long-term healthcare costs.
	Biomedical researchers and research institutions	Gain access to unique biochemical structures that inform drug discovery, natural-product chemistry, metabolic engineering, and molecular biology.
	Global public health	Novel compounds—especially from rare ecosystems like whale falls—can help address antibiotic resistance, emerging diseases, and unmet medical needs.
	Future generations	Benefit from the preserved potential for breakthrough medical innovations.
Biological control	Commercial and artisanal fishers	Benefit from improved fish recruitment, higher biomass, and more stable populations resulting from reduced predation pressure by mesopredators.
	Seafood processing, retail, and export sectors	Benefit from more reliable supply and improved quality of fish stocks.
	Coastal communities and livelihoods	Experience greater food security, income stability, and resilience in marine-dependent communities.
	Marine ecosystem managers and conservation agencies	Benefit from lower ecosystem-restoration costs and reduced need for artificial population control measures.
	Consumers and national economies	Indirectly benefit through stable seafood availability, reduced price volatility, and stronger marine-based economic activity.

Step 5. Conduct the economic analysis

In simple terms, the value of ecosystem services is the relative contribution of ecosystems to

well-being (Turner et al. 2016). Valuation is a tool for evaluating the trade-offs required to achieve a shared goal, where in the past and in the present these trade-offs have been addressed mainly through marketed goods and services (e.g., fuel or food) using commodity prices, leaving outside the equation other goods and services that currently do not have a price but that contribute equally or even more greatly to well-being (Turner et al. 2016).

Valuing ecosystem services has been criticized as unwise or even impossible because we supposedly cannot put a value on “intangibles” like human life and nature. In reality we implicitly value these things on a daily basis through, for example, measures to protect human life, such as construction standards for housing and public infrastructure that will require spending more money in order to preserve human lives (Costanza et al. 1997). Therefore, the overall goal is not to put a price tag on nature for exchange purposes, but to visualize the effect of a change in ecosystem services provision to human wellbeing in terms of a rate of trade off against other things people value (Turner et al. 2003).

After the identification, quantification, and mapping of ecosystem services for a particular area or scale, there are different types of methods used to conduct a Total Economic Valuation (TEV). These can be divided into revealed preference, stated preference, and non-preference based methods. Revealed preference methods estimate the benefits from ecosystems based on market prices, which limits the use of these methods to only a few ecosystem services that are traded in markets (mostly provisioning services) (Turner et al. 2016). Revealed preference methods analyze the choices of people in real world settings and infer the value from those observed choices (Costanza et al. 2011). Non-preference methods recognize the limits of an individual’s information about ecosystem services’ connection to their wellbeing and use modelling and other techniques to estimate these connections.

Stated preference methods try to construct pseudo markets through the use of surveys in which people are asked to state their willingness-to-pay for ecosystem services that are not traded in current markets. These methods therefore rely on the response of people to hypothetical scenarios (Costanza et al. 2011). Stated preference approaches have limitations because people surveyed often do not completely understand or are not aware of the relation between healthy ecosystems and human well-being, also because they do not feel comfortable in stating trade-offs for ecosystems in monetary units, and finally because the willingness-to-pay can be significantly different to the real payment when it comes to that point (Turner et al. 2016).

Table 5 summarizes the different methods for ecosystem services valuation using conventional economic valuation and non-monetizing valuation.

Table 5. List of methods for ecosystem services valuation.

Conventional economic	Revealed-preference	*Travel cost*: valuations of site-based amenities are implied by the

valuation	approaches	costs people incur to enjoy them (e.g., cleaner recreational lakes).
		Market methods: valuations are directly obtained from what people must be willing to pay for the service or good (e.g., timber harvest)
		Hedonic methods: the value of a service is implied by what people will be willing to pay for the service through purchases in related markets, such as housing markets (e.g., open-space amenities)
		Production approaches: service values are assigned from the impacts of those services on economic outputs (e.g., increased shrimp yields from increased area of wetlands)
	Stated-prefe rence approaches	*Contingent valuation*: people are directly asked their willingness to pay or accept compensation for some change in ecological service (e.g., willingness to pay for cleaner air)
		Conjoint analysis: people are asked to choose or rank different service scenarios or ecological conditions that differ in the mix of those conditions (e.g., choosing between wetlands scenarios with differing levels of flood protection and fishery yields)
	Cost-based approaches	*Replacement cost*: the loss of a natural system service is evaluated in terms of what it would cost to replace that service (e.g., tertiary treatment values of wetlands if the cost of replacement is less than the value society places on tertiary treatment)
		Avoidance cost: a service is valued on the basis of costs avoided, or of the extent to which it allows the avoidance of costly averting behaviors, including mitigation (e.g., clean water reduces costly incidents of diarrhea)
Non-monetizi ng valuation	---	*Individual index-based methods*, including rating or ranking choice models, expert opinion
		Group-based methods, including voting mechanisms, focus groups, citizen juries, stakeholder analysis

Due to the nature of the service, each ecosystem service can be valuated through one or more particular methods. For each service, the amenability to economic valuation and the transferability across sites will vary from low to high. Table 6 summarizes the set of methods that are appropriate to value each ecosystem service (Turner et al. 2016).

Table 6. Valuation methods for each ecosystem service (Farber et al., 2006).

Ecosystem services		Amenability to economic valuation	Most appropriate method for valuation	Transferability across sites
Provisioning service	Water supply	High	AC, RC, M, TC	Medium
	Food	High	M, P	High
	Raw material	High	M, P	High
	Genetic resources	Low	M, AC	Low
	Medicinal resources	High	AC, RC, P	High
	Ornamental resources	High	AC, RC, H	Medium
Regulating services	Gas regulation	Medium	CV, AC, RC	High
	Climate regulation	Low	CV	High
	Disturbance regulation	High	AC	Medium
	Biological regulation	Medium	AC, P	High
	Water regulation	High	M, AC, RC, H, P, CV	Medium
	Soil retention	Medium	AC, RC, H	Medium
	Waste regulation	High	RC, AC, CV	Medium High
	Nutrient regulation	Medium	AC, CV	Medium
Cultural services	Recreation	High	TC, CV, ranking	Low
	Aesthetics	High	H, CV, TC, ranking	Low
	Science and education	Low	Ranking	High
	Spiritual and historic	Low	CV, ranking	Low

AC=avoided cost, CV=contingent valuation, H=hedonic pricing, M=market pricing, P=production approach, RC=replacement cost, TC=travel cost.

Due to constraints in time and budget, it is often not possible to conduct original/primary studies to value ecosystem services (Wilson & Hoehn 2006; Plummer 2009), which has led to a wider use of secondary data (Richardson, Loomis, Kroeger, & Casey 2015) for this purpose through valuation techniques such as value/benefit transfer. Although this technique has limitations, it is sometimes the only option to inform policy decisions that require a first approximation to natural capital valuation (Richardson et al. 2015).

In simple terms, value transfer consists in "applying economic value estimates from one location to a similar site in another location" (Plummer 2009). The site where primary data was collected and processed is called the study site, and the site to which this data (i.e., ecosystem services values) is going to be applied is called the policy site (because the values are commonly used for policy decisions such as land use change or the establishment of financial mechanisms) (Plummer 2009). The transfer can be spatial (across different sites, national, or international) or temporal (where the study site and the policy sites are different moments in time) (Navrud & Bergland 2004). The aggregation of economic methods through a value transfer make the technique useful in academic and policy settings in which ecosystem services values are not

required with a high level of accuracy but need to be accurate enough to support a project or policy, but are not suitable when more accurate values are required, in cases such as the calculation of compensation payments for environmental damages (polluter pays principle) (Navrud & Ready 2007).

In the case of the two ecosystem services supported by cetaceans in which this report focuses on (i.e., climate regulation and fisheries productivity), as a starting point, the following methods can be applied to estimate their economic value. For fisheries productivity, the objective is to identify valuation methods that can translate the ecological contributions of cetaceans into measurable economic outcomes associated with commercial or subsistence fisheries. The valuation approaches most commonly applied in this context include production function methods, which link whale-mediated ecological processes to changes in fish biomass or yield, and market price–based approaches, which monetize these changes using observed prices or surplus measures.

Production function

The production function approach is probably one of the most conceptually rigorous methods for valuing the contribution of cetaceans to fisheries productivity because it establishes an explicit biophysical–economic link between ecological processes and market outputs (Barbier, 2007). In this method, ecosystem services are understood as inputs into a production function that generates goods valued in markets, which in this case are commercial fish species. Cetaceans contribute to this production function through several mechanisms as mentioned before. These mechanisms alter primary productivity, nutrient availability, and food web pathways, effectively shifting the ecological production frontier by increasing the biomass of fish populations or enhancing their growth rates.

Technically, the production function approach requires specifying how changes in whale abundance or behavior generate measurable changes in a biophysical variable (ΔX), which then translates into changes in the stock or flow of fish biomass (ΔB). For example, an increase in nutrient supply (ΔN) induced by whales may raise phytoplankton productivity (ΔPP), which then affects zooplankton and ultimately forage fish biomass according to trophic transfer efficiencies or ecological coefficients. This biophysical change becomes an input into a fisheries production function, such as:

$$Y = f(B, E) \qquad \text{Eq. 9}$$

where Y is fishery yield, B is biomass influenced by whale-driven processes, and E is fishing effort. The change attributable to cetaceans is then:

$$\Delta Y = f(B + \Delta B) - f(B) \qquad \text{Eq. 10}$$

This change can be monetized through prices or welfare-based measures. The main limitation of this method is data intensity, requiring ecological parameters (e.g., nutrient recycling rates, trophic efficiencies) that are still being refined for cetaceans.

Market prices

The market price method is typically used in combination with the production function approach because it supplies the monetary valuation step once biophysical changes have been estimated. Unlike stated preference methods, it does not infer hypothetical willingness to pay; instead, it uses observed market prices (e.g., ex-vessel prices of target species) to value the marginal changes in fish catch or biomass (Hernández-Blanco & Costanza, 2019).

The market price method assumes competitive markets with prices that reflect the marginal value of output. When applied to whale-mediated fisheries enhancement, the value of the service is generally computed as:

$$V_{fisheries} = P \times \Delta Y \quad \text{Eq. 11}$$

where P is the observed market price of the harvested fish and ΔY is the change in harvest attributable to cetaceans (Costanza et al. 1997; Hernández-Blanco, et al., 2021).

The main limitations of this method are (1) the inclusion (not always) of distortions (e.g., subsidies), (2) prices value only the use component of the service, and (3) prices reflect average rather than marginal values unless carefully adjusted. Nevertheless, when used in conjunction with a well-specified production function, market prices can offer a robust and transparent way to estimate the economic value of the marginal productivity contributions of cetaceans to fisheries.

In terms of climate regulation, the goal is to value the carbon sequestration and storage services supported by cetaceans (e.g., whale falls, enhanced primary production and export). It is important to note that different methods are used to estimate the economic value of climate regulation depending on if carbon sequestration rates (which is a flow) or carbon stocks (a stock) are considered.

Social Cost of Carbon (valuing annual carbon sequestration)

The Social Cost of Carbon (SCC) provides a welfare-based valuation of the annual carbon sequestration supported by cetaceans by estimating the global economic damages avoided when one tonne of CO_2 is removed from the atmosphere–ocean system. Defined as the discounted present value of the incremental harm caused by an additional tonne of CO_2

emissions, the SCC is derived from integrated assessment models (IAMs) that couple simplified atmospheric physics, carbon-cycle dynamics, socioeconomic pathways, and climate–damage functions (Hope, 2006). When applied to ecosystem services, the SCC is used in reverse: the removal and long-term sequestration of CO_2, whether through enhanced biological production or organic carbon export, represents a negative marginal emission, which, multiplied by the SCC, yields the monetary value of the avoided climate damages.

In the case of the contribution from cetaceans to climate regulation, this approach values the flow component of the ecosystem service, meaning the annual net amount of carbon (in CO_2-equivalent terms) that is sequestered through ecological processes such as nutrient fertilization that increases primary production and deep-ocean export. The valuation follows two steps. First, biophysical quantification determines the annual rate of carbon sequestration, either from a boost on phytoplankton or from whale falls (both ending up in the deep ocean), which we can denote as ΔC annual. Second, this quantity is multiplied by an SCC value, which is often expressed in USD per tCO_2. Therefore, to obtain the annual monetary value of cetacean-mediated carbon sequestration, the following equation can be used:

$$V_{seq} = \Delta C_{annual} \times SCC \qquad \text{Eq. 12}$$

The SCC is particularly appropriate for valuing cetacean contributions to climate regulation because it incorporates the full global externality of carbon removal, including impacts on agriculture, health, sea-level rise, infrastructure, and biodiversity (Tol, 2011). Its main limitations stem from model uncertainty and ethical considerations surrounding discounting, but it is often the most widely used and scientifically endorsed metric for evaluating the global welfare benefits of carbon sequestration.

Marginal Abatement Cost (valuing long-term carbon stocks)

The Marginal Abatement Cost (MAC) method provides a cost-based valuation of long-lived carbon stocks, such as the carbon sequestered in deep-sea sediments following whale falls or other cetacean-mediated pathways that result in multi-century storage. Unlike the SCC, which measures avoided damages, the MAC approach estimates the minimum cost society would incur to replicate the same amount of carbon storage using alternative mitigation or removal technologies (Hanley & Barbier, 2009). In practice, MAC values are obtained from marginal abatement cost curves, which rank mitigation options, such as reforestation and coastal wetland restoration to direct air capture (DAC) and bioenergy with carbon capture and storage (BECCS), by the cost of reducing or removing one tonne of CO_2 (IPCC, 2022).

Applying MAC to climate regulation influenced by cetaceans involves quantifying the amount of carbon stored in long-lasting pools, ΔC_{stock}, such as the fraction of a whale carcass that reaches bathyal or abyssal depths and becomes incorporated into sediments where remineralization rates are extremely slow (Smith & Baco 2003). Because these carbon pools satisfy the criterion of durability emphasized in climate mitigation science (i.e., storage on centennial to millennial

timescales), their economic value can be proxied by the market or modelled cost of achieving equivalent sequestration through engineered means. The valuation formula is:

$$V_{stock} = MAC \times \Delta C_{stock} \qquad \text{Eq. 13}$$

This method requires to know how much carbon is stored in a spatial unit (e.g., meter or hectare) of the deep sea, as well as the quantity of the carbon that can be related to whales, as well as the MAC of that meter or ha.

In addition to reflecting the cost of creating an equivalent amount of long-term carbon storage through engineered mitigation options, the MAC can also be used to quantify the opportunity cost of preserving existing carbon stocks. Under this interpretation, the value of a carbon pool, such as the long-lived organic carbon stored in deep-sea whale-fall deposits, corresponds to the economic benefits forgone by not undertaking activities that would release or disturb that carbon, such as deep-sea mining, trawling, or seabed infrastructure development. This aligns with MAC applications in terrestrial ecosystems, where the protection of forests, peatlands, or mangroves is valued in terms of the avoided emissions that would occur under land-use change (Hernández-Blanco et al., 2021). Applied to cetacean-mediated carbon storage, the opportunity-cost perspective treats the maintenance of deep-sea carbon pools as an abatement action since foregoing destructive seabed activities society avoids the need to compensate for the resulting emissions through alternative, often more expensive, mitigation measures.

MAC-based valuation is also highly relevant for conservation finance, as it expresses the economic significance of cetacean mediated carbon stocks in the same units used by climate mitigation planning, carbon pricing schemes, and technological investment decisions. However, it requires careful interpretation, especially considering that it does not measure social damages avoided but instead reflects the opportunity cost of achieving equivalent storage through alternative mitigation pathways.

In the case of the other three ecosystem services (i.e., genetic resources, medicinal resources and biological control) that are potentially supported by cetaceans, different methods can be applied to estimate their economic value. For genetic resources, valuation methods address benefits that are predominantly option-based, since the potential uses of genetic material, especially from ecosystems like whale-fall communities, are uncertain and may only become apparent in the future. Because most genetic benefits are non-market, uncertain, and highly irreversible once lost, the most appropriate economic frameworks are option value and R&D replacement costs.

Option Value (genetic resources)

The option value (OV) method captures the benefit of preserving genetic material today to maintain the possibility of future use, particularly important for whale-fall microbial genomes,

whose biochemical pathways remain largely unexplored. In environmental economics, OV arises when the benefits of future information outweigh the gains from irreversible exploitation (Smith, 1983).

A general expression for option value is:

$$OV = E\left[V_{future}\right] - V_{current} \quad \text{Eq. 14}$$

Where:

$E[V_{future}]$ = expected value of future use if the resource is conserved

$V_{current}$ = value under immediate use or irreversible loss

<u>R&D Replacement Cost (genetic resources)</u>

The replacement-cost method estimates the monetary value of genetic resources by determining how much it would cost to create equivalent genetic information through research and synthetic biology if natural sources were lost (Cabeza & Moilanen, 2006). Therefore, in simple terms, this can be expressed as:

$$V_{RC} = C_{synth} - C_{nat} \quad \text{Eq. 15}$$

Where:

C_{synth} = cost of reproducing the genetic information using lab-based methods (genome mapping, directed evolution, enzyme engineering)

C_{nat} = cost of accessing genetic material through natural collection or observation

In the case of medicinal resources, similar to genetic resources, valuation methods focus on capturing the uncertain but potentially high economic value associated with discovering new pharmaceuticals or biochemical compounds derived from nature. Therefore, the most appropriate approaches are those that explicitly incorporate probabilities of discovery, research pathways, and option value under uncertainty.

<u>Option value (medicinal resources)</u>

Medicinal discovery involves extreme uncertainty, making option value particularly relevant. The formulation mirrors that used for genetic resources but applies specifically to pharmaceutical potential:

$$OV_{med} = E\left[V_{drug}\right] - V_{loss} \quad \text{Eq. 16}$$

Where:

$E[V_{drug}]$ = expected future value of discovering medicinal compounds

V_{loss} = value if the species/ecosystem is lost before discovery

<u>R&D Replacement cost for pharmaceuticals</u>

Similar to genetic resources, this method compares the cost of synthesizing medicinal compounds in the lab with the cost of accessing natural biochemical diversity:

$$V_{RC} = C_{synthdrug} - C_{natprosp} \quad \text{Eq. 17}$$

Where:

$C_{synthdrug}$ = cost of producing equivalent molecules through chemical synthesis, AI-driven drug pipelines, or combinatorial chemistry, among other methods

$C_{natprosp}$ = cost of field sampling and natural compound isolation

For biological control, valuation methods aim to quantify the economic benefits of natural trophic interactions that suppress pests supporting ecological stability or enhancing the provisioning of services such as fisheries. Because these benefits occur through regulation of population dynamics, the most suitable methods are those that link ecological changes to economic outcomes. Production function methods provide the most robust framework, connecting whale-mediated biological control, such as the suppression of mesopredators, to changes in fish biomass or harvests. In parallel, damage-cost-avoided methods estimate the economic losses that would occur in the absence of natural regulation, such as reduced commercial fish stocks due to unchecked mesopredators.

<u>Production function approach (parallel to fisheries)</u>

Biological control can be valued using a production function that links whale-mediated suppression of mesopredators (e.g., squid) to changes in fish biomass and fishery yields (Barbier, 2007).

A general representation is:

$$Y = f(B(M, W), E) \quad \text{Eq. 18}$$

Where:

Y = fishery yield

B = fish biomass

M = mesopredator abundance

W = whale abundance or predation intensity (biological control factor)

E = fishing effort

The change in yield attributable to biological control:

$$\Delta Y = f\left(B_{withwhales}\right) - f\left(B_{withoutwhales}\right) \quad \text{Eq. 19}$$

Monetization uses ex-vessel prices or producer surplus:

$$V_{BC} = P \times \Delta Y \quad \text{Eq. 20}$$

Where:

P = price of harvested fish (or marginal value).

Damage Cost Avoided

The damage cost avoided (DCA) method estimates the value of biological control by measuring the economic losses prevented due to whale-mediated trophic regulation. For example, whales may suppress squid populations that would otherwise consume juvenile fish, reducing future yields. DCA quantifies the difference between damages under a counterfactual "no whales" scenario and damages under current conditions (Navrud et al., 2017). Damages may include reduced commercial fishery yields, lost producer surplus, higher management costs for artificial control, and increased ecological volatility, among others. This method can be applied through the following simple equation:

Eq. 21

$$V_{DCA} = D_{nowhales} - D_{withwhales}$$

Where:

$D_{nowhales}$ = damages without biological control (e.g., lost catch, reduced recruitment)

$D_{withwhales}$ = damages with observed control

The following table summarizes the methods that can be applied to estimate the economic value of the ecosystem services that were identified in this report that are influenced (at least partially) by cetaceans. These methods are the most used, but it is not an exhaustive list which can be expanded in the future.

Table 7. Methods to estimate the economic value of fisheries and climate regulation.

Ecosystem service supported by cetaceans	Economic method
Fisheries productivity	Production function
	Market prices
Climate regulation	Social Cost of Carbon (flow)
	Marginal Abatement Cost (stock)
Genetic resources	Option value
	R&D Replacement Cost
Medicinal resources	Option value
	R&D Replacement Cost
Biological control	Production function approach (parallel to fisheries)
	Damage Cost Avoided

An alternative to attempt to estimate the value of KSCP, but in a much more indirect way, is the application of stated preference methods. As explained previously, this family of methods create

pseudo markets by asking people their willingness to pay for non-marketed benefits they are aware they receive. There are two main methods that could potentially be used for marine ecosystem services supported by cetaceans, contingent valuation and choice experiments. Contingent Valuation (CV) is the most established stated-preference method and has been widely used to value ecosystem services, especially non-marketed ES. CV directly asks respondents their willingness to pay (WTP) or willingness to accept (WTA) compensation for a specific, clearly defined change in environmental quality or ecosystem-service provision. Surveys are designed around a hypothetical but plausible scenario, making explicit the ecological outcome being valued, the population affected, the payment vehicle (e.g., tax, fee, donation), and the institutional context for implementation.

The most defensible elicitation format is the dichotomous choice referendum, where respondents vote “yes” or “no” on a proposed environmental improvement at a randomly assigned cost. This format mimics real-world collective decision-making, reduces strategic bias, and aligns with NOAA Panel recommendations (Arrow et al., 1993). CV is particularly well suited for capturing non-use values such as existence, bequest, and altruistic values, which are uniquely important for biodiversity and conservation assessments but cannot be recovered from observed behavior.

The second method under this family is Choice Modelling (CM), also called Choice Experiments or Conjoint Analysis. This method extends stated-preference valuation by presenting respondents with a set of alternative scenarios, each described by multiple attributes, which can include different levels of provision of ecosystem services and associated costs, and asking them to choose their preferred option. In this way, choosing across alternatives reveals the marginal rate of substitution between attributes, allowing estimation of attribute-level marginal values (e.g., value per unit increase in water clarity, species abundance, or carbon sequestration). This makes CM particularly powerful in contexts involving multi-attribute environmental changes, trade-offs, or complex policy packages. Therefore, CM often produce more detailed valuation outputs than CV, because it offers both total values for bundled changes and marginal values for individual ecosystem services. This method is especially useful for valuing complex environmental programs, for distinguishing the value of multiple ecosystem-service components, and for informing policy design where trade-offs must be quantified.

In both cases, the contribution of cetaceans to the provision of benefits to people could be valued by eliciting people’s willingness to pay to protect or restore the population of whales under the understanding of the potential contributions they provide to maintain ecosystem health and ecosystem services. This would capture the aggregated value of those contributions and would be highly dependent on the respondent’s background (e.g., if they are fishers). Another way would be to ask people for their willingness to pay to protect or restore the habitats in which these whales that contribute to ecosystem health depend on. The boundaries of the analysis could be focused on feeding ground’s habitats, such as kelp, or breeding areas habitat such as mangroves, or their entire blue corridor. All of this in the case of migratory species.

One final alternative method that could be explored in the future is a type of benefit transfer function based on key variables such as the ones used in our equations for the KSCP, including traits. As previously explained, benefit transfer refers to the practice of estimating the economic value of an ecosystem service in a policy site (the site of interest) by using existing valuation estimates generated in a study site. The main underlying assumption is that ecosystem services with similar ecological, social, and economic characteristics will generate comparable economic values across contexts. This method often take two major forms: (1) value transfer, in which mean or median WTP estimates from a study site are directly applied to a policy site (adjusted for income or inflation), and (2) function transfer, in which the functional relationship between ecosystem attributes and willingness to pay is transferred instead of a single value. The latter is generally considered more robust, particularly when conditions differ between the study and policy sites or when the valuation must respond to changes in ecological variables.

In simple terms, a function transfer involves transferring an empirically estimated valuation function, which was typically derived from primary stated or revealed preference studies, from one context to another. Therefore, instead of directly applying a point estimate, as in the value transfer, the benefit function is imported, which can be a function similar to the following one:

$$V_{ES} = f(X,\ S,\ C) \qquad \text{Eq. 22}$$

where X represents ecosystem characteristics (e.g., species abundance, habitat quality), S represents socio-demographic variables (e.g., income, education, cultural preferences), and C represents contextual or policy-specific factors.

For example, the value of increased fisheries productivity from phytoplankton fertilization by the whale pump in one site (i.e., study site) could be transferred by adjusting this value through the creation of a function (if not was created in the primary study) based on some of the ten variables listed in the conceptual framework (e.g., mass, nutrients in feces/urine, effect traits, etc.).

Furthermore, if the level of accuracy wants to be improved, provided there's enough data, the next and final option of transfer is the meta-analytic benefit transfer. This type of transfer is an advanced valuation method that uses econometric meta-analysis to estimate a generalized, cross-study function that predicts economic values for ecosystem services based on variation in ecological, socio-economic, and methodological attributes across multiple primary valuation studies. Instead of relying on a single WTP estimate or a single valuation function, meta-analysis compiles a dataset of valuation results (often dozens or hundreds of estimates) and regresses these values on predictors that explain why WTP varies across studies. The resulting meta-regression equation serves as a transferable valuation function:

$$V_{ES} = \beta_0 + \beta_1 X + \beta_2 S + \beta_3 Q + \beta_4 M + \varepsilon \qquad \text{Eq. 23}$$

Where:

X = ecological/ecosystem attributes (e.g., traits, population size, etc.)

S = socio-economic variables (e.g., income, education)

Q = characteristics of the environmental change (e.g., magnitude, duration)

M = methodological variables (survey mode, payment vehicle, elicitation format)

β = estimated coefficients reflecting cross-study pattern

ε = random error

Therefore, if policy-site values of these variables can be substituted into the meta-regression model, it is possible to generate a context-adjusted WTP estimate. Meta-analysis accounts for heterogeneity across studies, which allows to statistically correct for differences in study design, valuation method, ecological context, and sample characteristics, reducing in this way the "study-site idiosyncrasy" that limits the external validity of single-study transfers.

A final key aspect of the economic valuation methods that is worth noting is that one of the main goals is to measure the change of benefits under different scenarios. Both natural and anthropogenic drivers of change can modify the stocks and flows of this model, which will impact the species population and consequently the value of species contribution to the provision of ecosystem services. Examples of scenarios that can be modeled include Business-as-Usual (baseline scenario that assumes current trends and practices continue without significant changes), rewilding efforts, conserving current population, population decrease (at different levels), and local extinction, among others.

Ideally, participatory approaches to scenario planning with a wide set of actors will complement the modeling of the selected scenarios, including especially the beneficiaries of the services dependent on the selected species for the assessment, and those who might bear the costs of the changes in the species population.

It is also important to mention that there are other similar methodological approaches in the literature, most notably the one from Daniels et al. (2018). Nevertheless, the approach we present here differs in two main points. The first one is that Daniels et al. (2018) focus on functional groups rather than species, which can represent both benefits and limitations. The second difference is that their approach considers only marketed services, while the approach presented here considers both marketed and non-marketed services.

4. Case study: The North Pacific humpback whale population

Considering the farmwork developed in Section 2 and the findings from the systematic literature review (Appendix 2 and 3), in this section we describe how the framework can be applied to the Norh Pacific humpback whale population. We applied the fisheries and whale falls models, but decided not to apply the model on carbon sequestration from additional primary productivity since (1) SEAK waters do not reach a 1000m depth (one of our key parameters) and we didn't have robust local data on the percentage of carbon exported that is buried in sediments for >100 years (the alternative key parameter). It is important to highlight that our results represent a first attempt to implement the framework, based on simple modeling and limited data extracted from studies from a very nascent filed, and therefore our estimates should be considered a first approximation to the value of the contribution of whales to the provision of ecosystem services in SEAK.

4. 1. Study area

To better capture the spatial scale over which humpback-mediated nutrient inputs affect primary production, we restricted our analysis to the Southeast Alaska feeding Biologically Important Area (BIA) for humpback whales. The BIA polygons are defined by NOAA's Biologically Important Areas program for cetaceans (Harrison et al., 2023) (Figure 9). The Southeast Alaska feeding BIA for humpback whales varies in area depending on the season (Table 8). We selected the summer season as our study area because it provides a larger representativeness of the feeding area, but our analysis can be conducted with any of the three seasons of the BIAS as

part of a sensitivity or scenario analysis. We then restricted the summer feeding area to the study region defined in Hendrix et al., 2012 in order to assess exclusively the area for what we have data on population size.

Table 8. BIAs extensions in Southeast Alaska. Harrison et al., 2023

Season	Months	BIA size (km^2)	Hendrix et al. 2012 study area (km^2)
Fall	September - November	22,092.17	8,334.47
Spring	March - May	10,393.30	6,214.11
Summer	June - August	26,629.86	11,316.66

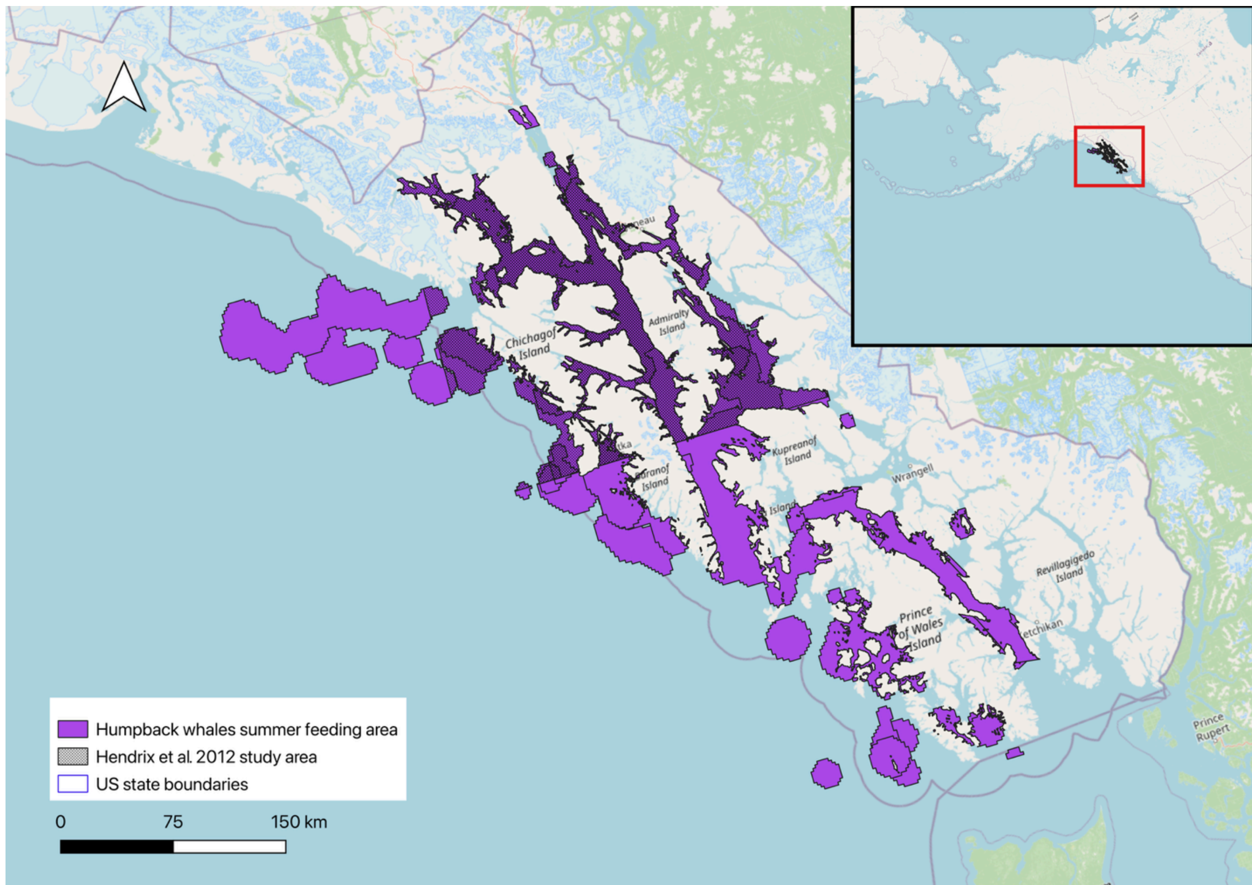

Figure 9. Study area, Southeast Alaska feeding grounds restricted by the study region from Hendrix et al., 2012

4.2. Fisheries productivity – Enhancing primary productivity for fisheries (KSCP-fisheries)

Stage 1. Whale-mediated nitrogen release in the Southeast Alaska

To estimate the nitrogen release in Southeast Alaska (SEAK) from North Pacific humpback whales, we used the BIA summer feeding area previously described, a total population of 1,585 as estimated by Hendrix et al. (2012), an a daily per-capita nitrogen release (*qn*) of 9.42 kg N whale^{-1} d^{-1} from the whole-animal nitrogen budget in (Roman & McCarthy (2010) (Table 9. We multiplied *qn* by the Southeast Alaska humpback whale feeding season (May – September; 150 days) (Schuler et al., 2019). We estimated that the nitrogen contribution from humpback whales in SEAK (T_N) as **2.2 million kg N whale^{-1} yr^{-1}**.

Table 9. Total nitrogen added by the population

Variable	Data	Units	Source
qn / day	9.42	kg N whale^{-1} day^{-1}	Roman & McCarthy (2010)
qn / $D_{feeding}$	1,413.00	kg N whale^{-1} yr^{-1}	
P	1,585.00	individuals	Hendrix et al (2012)
T_N - Total N release by all humpbacks in SEAK during feeding season	**2,239,605.00**	**kg N whale^{-1} yr^{-1}**	
T_N (ton)	**2,239.61**	**ton N whale^{-1} yr^{-1}**	

Stage 2. Nutrient limitation adjustment

The whale-derived nitrogen input per unit area in the Southeast Alaska (SEAK) (T_{NA}) summer feeding grounds was calculated by distributing the total annual nitrogen provided by humpback whales in the feeding area (Stage 1) over the spatial extent of the study area described above, resulting in 197.9 kg N km^{-2}yr^{-1}, equivalent to **0.094 mmol N m^{-2} d^{-1}** using a molar mass of nitrogen of 14 g mol^{-1} (Table 10).

Table 10. Per-area nutrient flux mediated by whales

T_{NA}	197.90	kg N km^{-2}yr^{-1}
T_{NA} (g)	197,903.35	g N km^{-2}yr^{-1}
Molar mass of N	14	g mol^{-1}
T_{NA} (mol)	14,135.95	mol N km^{-2}yr^{-1}

Km^2 to m^2	1,000,000	m^2
T_{NA} (mol, m^2)	0.014	mol N m^{-2} yr^{-1}
T_{NA} daily*	9.42×10^{-5}	mol N m^{-2} yr^{-1}
T_{NA} mmol	**0.094**	**mmol N m^{-2} yr^{-1}**

*Considering 150 days

We then computed the nutrient-limitation adjustment using the agreed functional form g(n) (equation 4), where *n* is the nitrogen supply rate relevant to phytoplankton limitation, *n* is taken as the sum of background nitrogen supply and whale-derived supply, $n = n_{base} + T_{NA}$. We adopt a background shelf nitrogen supply n_{base} = 4.0 mmol N $m^{-2}d^{-1}$ (Hermann et al., 2009) and set $N = n_{base}$ as a normalization choice (so limitation is centered around background conditions). This results in a g(n) = 0.494. Finally, the usable whale-derived nitrogen is obtained by applying equation 3, resulting in 0.047 mmol N $m^{-2}d^{-1}$ (Table 11), which is equivalent to 97. 8 kg N $km^{-2}yr^{-1}$(Table 12)

Table 11. Additional usable nitrogen from whales

N	4
n	4.094
g(n)	**0.494**
T_{NN}	**0.047 mmol N $m^{-2}d^{-1}$**

Table 12. Additional usable nitrogen from whales converted to km per year

mmol - mol	4.66×10^{-5}	Mol
mol - g N	0.00065	g N $m^{-2}d^{-1}$
g -kg, day - yr. M^2 - km^2	**97.8**	**kg N $km^{-2}yr^{-1}$**

yr = considering 150 days (i.e., feeding season year)

Stage 3. Primary production boost

This stage translates the usable whale-derived nitrogen flux estimated in Stage 2 into an incremental primary production response using elemental stoichiometry. The output of Stage 2 provides the areal rate of whale-mediated nitrogen that is effectively available to alleviate nutrient limitation in surface waters (T_{NN}). To estimate the corresponding carbon fixation potentially supported by this nitrogen input, we apply Redfield stoichiometry, assuming a canonical phytoplankton molar C:N ratio of 106:16 (Redfield, 1934), equivalent to 6.625 mol C mol^{-1}N. Under this assumption, incremental primary production attributable to whale-recycled

nitrogen (ΔPP) is estimated multiplying T_{NN} by the Redfield ratio, resulting in **0.3085 mmol C $m^{-2}d^{-1}$**, which is equivalent to 0.0037 g C $m^{-2}d^{-1}$.

This estimate represents a nutrient-supported production potential, rather than realized net primary production. It assumes that nitrogen remains the limiting nutrient, that Redfield stoichiometry provides a reasonable first-order approximation for phytoplankton elemental composition, and that the usable nitrogen estimated in Stage 2 is taken up efficiently by primary producers within the relevant spatial and temporal domain.

Stage 4. Translation of incremental primary production into fisheries production

This stage links whale-mediated increases in primary production to fisheries-relevant outcomes by translating incremental primary production (ΔPP) into an "additional yield" proxy (ΔY) using a simplified trophic-transfer representation. Considering equation 6, where NC_{AC} is the net conversion from incremental primary production to incremental yield and M(t,c) is a dimensionless multiplier capturing food-web routing and community context. For the baseline implementation presented here, M(t, c) is set to 1 to provide a transparent reference case, and the conversion factor NC_{AC} is parameterized as the compounded effect of biomass transfer across trophic steps linking primary producers to the harvested group.

To operationalize NC_{AC}, we represent the transfer of carbon through the pelagic food web using a standard trophic efficiency formulation, where $NC_{AC} = TE^n$, and TE is the average trophic transfer efficiency per trophic step and *n* is the effective number of trophic transfers between phytoplankton and the target species or group, approximated from published trophic levels as $n = TL - 1$. A baseline value of TE = 0.10 per transfer is consistent with widely used fisheries–primary production frameworks and synthesis results (Pauly & Christensen, 1995). Values of *n* were selected to reflect dominant trophic pathways inferred from published Gulf of Alaska ecosystem syntheses and species diet/food-web characterizations, distinguishing lower-trophic forage pathways (e.g., herring and Dungeness crab, n=2) from higher-trophic predators (e.g., salmon, cod, halibut, n=3) (Aydin et al., 2005; Witherell et al., 2000).

Given the Stage 3 estimate of incremental primary production supported by usable whale-derived nitrogen (ΔPP = 0.3085 mmol C $m^{-2}d^{-1}$) the baseline Stage 4 implementation yields pathway-specific ΔY values of 0.003085 mmol C $m^{-2}d^{-1}$ for n=2 groups and 0.0003085 mmol C $m^{-2}d^{-1}$ for n=3 groups (Table 13). Aggregated over the study area and 150 days for interpretive scaling, these correspond to 62.85 t C yr^{-1} (for n=2 pathways) and 6.28 t C yr^{-1} (for n=3 pathways). These results are presented as non-additive pathway estimates, which means that summing across species would require an explicit allocation of incremental production across pathways, which is the intended role of M(t,c) in more detailed applications.

Table 13. Whale-mediated increases in fisheries productivity

Species / group	Explicit trophic pathway	Approx. trophic position	Derived (n)	$NC_{AC} = TE^n$	ΔY (mmol C m^{-2} d^{-1})	Aggregated over SEAK BIA (t C yr^{-1})*	References
Pacific herring(*Clupea pallasii*)	Phytoplankton (1) → Zooplankton (2) → Herring (≈2.5)	≈2.5	2	0.01	**0.003085**	62.85	Aydin et al. 2007
Walleye pollock (*Gadus chalcogrammus*)	Phytoplankton (1) → Zooplankton (2) → Forage fish (3) → Pollock (≈3.5)	≈3.5	2	0.01	**0.003085**	62.85	Witherell et al. 2000; Aydin et al. 2007
Dungeness crab (*Metacarcinus magister*)	Phytoplankton (1) → Detritus/Benthos (2) → Crab (≈2.5–3)	≈2.5–3.0	2	0.01	**0.003085**	62.85	Stevens et al., 1984
Pacific salmon (Sockeye, Coho, Chinook)	Phytoplankton (1) → Zooplankton (2) → Forage fish (3) → Salmon (≈4–4.5)	≈4.0–4.5	3	0.001	**0.0003085**	6.28	Aydin et al. 2007
Pacific cod (*Gadus macrocephalus*)	Phytoplankton (1) → Zooplankton (2) → Forage fish (3) → Cod (≈4.0)	≈4.0	3	0.001	**0.0003085**	6.28	Witherell et al. 2000; Aydin et al. 2007
Pacific halibut (*Hippoglossus stenolepis*)	Phytoplankton (1) → Zooplankton (2) → Forage fish (3) → Piscivores (4) → Halibut (≈4.5)	≈4.5	3	0.001	**0.0003085**	6.28	Clark et al., 1999; Aydin et al. 2007

*Aggregation uses study area and 150 days. These are non-additive pathway estimates. Summing across species would require an explicit allocation of ΔPP across pathways via M(t,c).

Economic valuation

The economic value of whale-supported fisheries production was estimated using a dockside (i.e., ex-vessel) valuation approach, which is standard in fisheries economics and ecosystem service assessments. This approach **values additional biological production at observed first-sale prices** and avoids assumptions about fishing effort, fleet behavior, management responses, or market feedbacks. The economic analysis uses as inputs the species-specific production proxies derived in Stage 4, expressed as annual increments in carbon biomass (ΔY_i, t C yr^{-1}). These production proxies represent alternative food-web pathways through which whale-mediated primary production could support commercially important species and are treated as non-additive.

To convert carbon production to landed biomass, using Stage 4 outputs which are expressed in tonnes of carbon per year were converted to wet biomass using a constant carbon content assumption. Following commonly used values in marine ecosystem and fisheries studies, carbon content was assumed to represent 12% of wet biomass, such that 1 tC is equivalent to 8.33 t of wet biomass (1/0.12) (Pauly & Christensen, 1995). This single conversion factor was applied uniformly across species to maintain transparency and comparability. The resulting values represent potential additional biomass production, not realized landings.

In terms of the ex-vessel prices, species-specific economic values were calculated using observed ex-vessel (i.e., dockside) prices, defined as the price received by fishers at first sale. Prices were obtained from official US government sources:

- NOAA Fisheries standard ex-vessel price tables for Alaska groundfish and Pacific halibut, as published in the annual Observer Fee rule.
- Alaska Commercial Fisheries Entry Commission (CFEC) fish ticket–based statistics, accessed via Alaska Department of Fish & Game commercial fisheries reports, for Pacific salmon, Pacific herring, and Dungeness crab.

Where prices were reported in U.S. dollars per pound, they were converted to U.S. dollars per metric tonne using a fixed conversion factor (1 t = 2,204.62 lb).

Finally, to estimate the economic value of the contribution of whales to the productivity of fisheries, for each species or species group *i*, the annual economic value of whale-supported production (ΔV_i)) was calculated as:

$$\Delta V_i = \Delta Y_i \times \theta \times P_i \qquad \text{Eq. 24}$$

where ΔY_i is the Stage-4 production proxy (t C yr^{-1}), θ is the carbon-to-biomass conversion factor (8.33 t biomass per t C), and P_i is the species-specific ex-vessel price (USD per t biomass). Results are reported by species and pathway and are not summed across species, as each represents an alternative routing of incremental production through the food web.

Results

When valued at observed ex-vessel prices, whale-supported production generates species-specific annual dockside values (Table 14). We estimated the total value of the contribution of the North Pacific humpback whales to the increase of fisheries productivity as $5.9 million per year. Differences in economic value across species reflect both biological factors (trophic pathway length) and market conditions (ex-vessel prices). High-value species such as Pacific halibut and Dungeness crab account for a disproportionate share of the estimated fisheries economic value attributable to whale-mediated productivity effects, reflecting market prices rather than modeled changes in biomass or harvest quantities.

It is important to highlight that these results represent the potential dockside value of additional biological production supported by whale-mediated nutrient recycling, rather than realized fishery revenues. To clarify, the *potential dockside value of additional biological production* refers to the economic value of the extra fish biomass that the ecosystem is capable of producing due to whale-mediated nutrient recycling, valued at observed ex-vessel prices, reflecting an ecosystem service to productive capacity, independent of whether that biomass is actually harvested. On the other hand, *realized fishery revenues* refer to the actual income earned by fishers, which depends on fishing effort, quotas, management rules, market conditions, and fleet behavior, and therefore these revenues may be lower (or zero) even if biological production increases.

Table 14. Species-specific annual dockside values from increase in fisheries productivity

Species / group	Δ_{Yi} (t C yr^{-1})	Conversion: t biomass yr^{-1} (= t C x 8.33)	Ex-vessel price ($ / lb)	Price ($ / t biomass)	Final value ΔV_i ($ yr^{-1})	Price source
Pacific herring	62.85	523.53	0.3	661.39	**346,254**	ADFG, 2025
Walleye pollock	62.85	523.53	0.14	308.65	**161,585**	NMFS & NOAA, 2024
Dungeness crab	62.85	523.53	4	8,818.48	**4,616,716**	ADFG, 2025
Pacific salmon (avg.)	6.28	52.35	1.05	2,314.85	**121,189**	ADFG, 2025
Pacific cod	6.28	52.35	0.36	793.66	**41,550**	NMFS & NOAA, 2024
Pacific halibut	6.28	52.35	5.05	11,133.33	**582,860**	NMFS & NOAA, 2024
Total economic value of the contribution of whales to fisheries productivity					**5,870,155**	

4.3. Climate regulation – Carbon sequestration from whale falls (KSCP-CsWF)

We estimated carbon sequestration mediated by whale falls using a population-based carbon-flux approach consistent with the whale-fall model presented in equation 8. However, because individual whale-fall ecology papers typically do not report all required quantitative parameters (e.g., mortality, biomass at death, carbon content, deep-sinking fraction, and long-term isolation fraction) in a directly parameterizable form, we employed a collapsed literature parameter that integrates these biological and fate components into a single annual per-capita flux term. Specifically, Pershing et al. (2010) report a species-specific "Gross Flux" of carbon from whale carcasses in units of tons C per individual per year (t C whale^{-1} yr^{-1}), derived from age-structured population modeling and species-specific mass assumptions. We interpreted this "Gross Flux" for humpback whales (C_{wh}) as an integrated estimate of μ x m x α_c x f_{deep} x f_{perm} for the species, enabling estimation of total whale-fall carbon export as

$$C_{wf} = p \times C_{wh} \times \left(1 - f_{removed}\right) \quad \text{Eq. 26}$$

For the SEAK humpback whale case study, we used the study population size applied in the previous models and assumed that $f_{removed}$ = 0 in the baseline (i.e., no systematic removal preventing carcasses from contributing to whale falls). Carbon quantities (t C) were converted to carbon dioxide equivalents (tCO_2) using the molecular-weight ratio 44/12. The economic value of whale-fall carbon sequestration was estimated using the U.S. Environmental Protection Agency's SCC for the 2025 emissions year ($212 per ton of CO_2), consistent with the valuation approach applied in the phytoplankton-boost carbon model.

<u>Results</u>

Using the humpback whale per-capita carcass carbon "Gross Flux" reported by Pershing et al. (2010) (C_{wh} = 0.103 t C whale^{-1} yr^{-1}) and a Southeast Alaska humpback whale abundance of p = 1,585, total whale-fall mediated carbon export was estimated at 163.26 t C yr^{-1} (assuming no removals, $f_{removed}$ = 0) (Table 15). Converting to carbon dioxide equivalents yields 598.60 tCO_2 yr^{-1}. Finally, we estimated the economic value of carbon sequestration mediated by whale falls as $126,900 per year (Table 16). It is key to highlight that we are assuming that all whales die and sink in areas with depths of at least 1000 meters outside SEAK (since maximum depths in SEAK are 600m approximately).

Table 15. Whale-mediated carbon sequestration from whale falls.

Variable	Value	Units
p	1585	individuals
C_{wh}	0.103	t C whale^{-1} yr^{-1}
$f_{removed}$	0	dimensionless

Annual whale -fall carbon	163.26	t C yr-1
Annual whale -fall carbon (CO2e)	598.60	t CO2e yr-1
SCC	212	$ yr-1
Economic value of C_{wf}	**126,903.55**	**$ yr-1**

4.4. Final results and scenario analysis

Considering the economic value of each of the two contributions from humpback whales in SEAK to the provision of the two targeted ecosystem services, the total annual value of this contribution was estimated as $6 million (Table 16). 98% of this value comes from the KSCP-fisheries.

Table 16. Summary of the economic value of the contribution of North pacific humpback whales to the provision of 2 ecosystem services.

Ecosystem service	Contribution from cetaceans	Annual economic value of the contribution for SEAK population
Fisheries productivity	Enhancing primary productivity for fisheries	5,870,155
Climate regulation	Carbon sequestration through whale falls	126,903.55
Total annual economic value of the contributions to ES from the SEAK humpback population		5,997,058

To assess how changes in whale abundance influence the estimated contribution of whales to ecosystem service provision, a set of population-based scenarios was developed relative to current abundance levels. The current population estimate was treated as the baseline condition, against which all scenario results were compared, rather than as a scenario itself. Two scenarios were defined to represent plausible deviations from current population size: (1) a decline scenario, representing a 25% reduction in abundance (75% of the current population), and (2) a recovery scenario, representing a 25% increase in abundance (125% of the current population). The magnitude of these changes was selected to reflect realistic short- to medium-term variation in whale populations, consistent with empirically observed recovery dynamics (Hendrix et al. 2012). Estimates from SEAK indicate population growth rates of approximately 5% per year following the cessation of commercial whaling, suggesting that changes of this magnitude could occur over decadal timeframes (Hendrix et al. 2012). However, we caution that while this rate of growth is possible and has been previously documented, escalating threats such as climate change may hinder continued growth at this level. Namely, the North Pacific Marine Heatwave of 2014-2016 caused an overall 20% decline in the

abundance of North Pacific humpback whale population, which includes SEAK (Cheeseman et al., 2023). Still, we consider this recovery scenario for illustrative purposes.

In addition to these two scenarios, a historical depleted state was included as a benchmark to provide context on ecosystem service contributions under substantially reduced whale populations. This benchmark was based on abundance estimates from the mid-1980s (approximately 393 individuals) compared to more recent estimates (approximately 1,585 individuals) (Hendrix et al. 2012), corresponding to roughly 25% of the current population. This historical reference point is not interpreted as a plausible future scenario, but rather as an illustrative counterfactual representing a previously depleted system state.
For each scenario, changes in ecosystem service values were estimated by scaling the contribution of whales proportionally to changes in population size relative to the baseline. This approach assumes that the contribution of whales to ecosystem services varies approximately linearly with abundance. Therefore, although this provides a transparent and tractable basis for scenario analysis, it does not account for potential nonlinear ecological dynamics, including threshold effects, density dependence, or saturation processes in trophic interactions. As such, the resulting estimates should be interpreted as first-order approximations of how ecosystem service provision may respond to changes in whale populations.

The results of this scenario analysis shows that changes in whale population size produce significant and proportional variations in the estimated value of the whale-mediated ecosystem services. Under the decline scenario (−25%), the value of ecosystem services decreased markedly. Fisheries-related contributions declined to $4.42 million per year, while climate regulation values decreased to $95,178 per year. Conversely, under the recovery scenario (+25%), ecosystem service values increased reaching $7.32 million per year for fisheries productivity and $158,629 per year for climate regulation (Table 17).

The relative magnitude of ecosystem service contributions differed substantially between services. Across all scenarios, the fisheries-related pathway accounted for the vast majority of total value, exceeding climate regulation values by more than an order of magnitude. This indicates that whale-mediated nutrient cycling and its effects on primary productivity constitute the dominant pathway through which whales contribute to economically valued ecosystem services in the study area (at least for the contributions considered in this case study).

The historical depleted state highlights the extent to which ecosystem service provision has been reduced under past low-abundance conditions. At approximately 25% of current population levels, the contribution of whales to fisheries productivity was estimated at $1.48 million per year, while climate regulation contributions were reduced to $31,726 per year. Overall, the results indicate a near-proportional relationship between whale abundance and the value of ecosystem services, with both decline and recovery scenarios producing symmetric changes around the baseline. While this proportionality reflects the underlying assumptions of the model, it provides a transparent first-order approximation of how ecosystem service provision may respond to changes in whale populations.

Table 17. Results from scenario analysis for the economic value of the whale-mediated ecosystem services

	Population	PP boost - Fisheries productivity ($/year)	Whale falls - Climate regulation ($/year)
Baseline	1,585	5,870,155	126,903.55
S1. Plausible decline (-25%)	1,189	4,415,468	95,177.67
S2. Plausible recovery (+25%)	1,981	7,316,398	158,629.44
Historical depletion (-75%)	396	1,480,466	31,725.89

4.5. Data gaps

It is important to note that important data gaps exists and that should be acknowledged in order to interpret our results properly. First, there are still significant uncertainties on the biophysical measurement of whale-mediated ecological processes, which is the starting point of the methodological framework we developed and applied. For our case study, we tried to draw on the best available empirical literature for nutrient excretion rates, prey consumption, trophic transfer efficiencies, and phytoplankton responses, but many of these parameters are derived from sparse observations, small sample sizes, or studies conducted in different oceanographic contexts. In particular, uncertainty remains high around the magnitude and variability of nutrient recycling through the whale pump, the fate of released nutrients across dissolved and particulate pools, and the subsequent propagation of these nutrients through primary production and higher trophic levels.

A second important gap relates to spatial and temporal attribution. Our case study in SEAK relies on simplifying assumptions to link whale presence and feeding activity to ecosystem service production within a defined study area and time horizon. However, fine-scale data on whale residency time, feeding intensity, prey field dynamics, and nutrient dispersion are limited. As a result, the models cannot fully estimate where and when ecosystem service benefits are realized, as well as the extent to which benefits generated in feeding areas may be received outside the study area. This creates uncertainty in attributing observed or modeled ecosystem service flows (e.g., enhanced fisheries productivity) to specific locations, management units, or accounting periods.

A final substantial uncertainty arises at the interface between biophysical estimates and economic valuation. Market and non-market valuation of the contribution of cetaceans to the provision of ecosystem services relies on benefit transfer, price proxies, and scaling assumptions that are unavoidable given the absence of primary valuation studies for these specific pathways.

For example, in the case of carbon sequestration, there is ongoing debate regarding appropriate definitions (e.g., depth-based versus time-horizon-based sequestration), permanence thresholds, and attribution of additionality, all of which can affect the interpretation of results. Therefore, our estimates should be interpreted as first-order approximations that establish plausible magnitudes rather than precise values.

Nonetheless, in a nascent field where empirical data are still emerging, such estimates play a critical role in bounding uncertainty, identifying research priorities, and informing policy discussions that would otherwise proceed in the absence of any quantitative signal. Once these data gaps are filled, we can then plug the values from new and targeted research into our models for more robust approximations.

5. Financing whale conservation under a novel governance approach

The protection of the North Pacific humpback whale population requires localized and transboundary and multi ecosystem protection. In the case of the first approach, it means implementing conservation and restoration strategies that address immediate local threats, such as unsustainable fishing, vessel strikes, and plastic pollution. On the other hand, their protection also requires the conservation and restoration of their entire blue corridors, including the multiple ecosystems that are adjacent to them (e.g., kelp forests that provide habitat for forage fish in feeding grounds, or mangrove forests that provide sediment retention for clearer waters in breeding grounds).

In this section, we provide a first analysis of the potential financial mechanisms that can be used to internalize both positive and negative externalities with the goal to significantly strengthen the current funding flow that goes to the protection of whale and their habitats. In the case of positive externalities, we propose financial solutions that could potentially incorporate the value of the contribution of whales to the provision of ecosystem services. In terms of negative externalities, we provide examples of financial solutions that look to internalize the cost of the impact to whales and their habitats from key economic activities, with the goal of providing attractive incentives to these activities to transform their business.

Furthermore, we provide a proposal of novel institutional arrangement that can manage these funds in the most efficient way to secure the sustainable stewardship of whales at local and internal levels. Nevertheless, this by no means is an exhaustive analysis of the multiple governance schemes that can be put in place at any geographical scale, rather an example to illustrate how current efforts can be organized under proven governance principles that especially apply for non-excludable and non-rivalrous goods and services such as the ones whales contribute to provide to people’s well-being.

5.1. Financial mechanism proposal

We conducted literature review using a tiered, question-driven approach to identify and evaluate the most relevant and effective financial mechanisms for cetacean conservation. The review was structured around three central research questions, each targeting a different objective and level of specificity. Financial mechanisms were then extracted and assessed for their applicability to cetacean conservation and cetacean habitat restoration, with attention to real-world examples, enabling conditions, benefits, and implementation challenges.

Return-based investments

Most effective financial mechanisms identified:

1. Blue bonds and debt-for-nature swaps
2. Microfinance facilities and loans
3. Impact investment & impact-oriented equity
4. Peer-to-Peer investing and crowdfunding

Debt-related instruments, like blue bonds and debt-for-nature conversions, are being increasingly applied to marine environments, and growing in both credibility and scale. These instruments are especially useful for nature-based solutions since they offer a favorable risk-return profile and enable returns for investors without requiring an “exit” event. Blue bonds, which are a subset of green bonds, are defined as “debt instruments where proceeds are used exclusively to finance or refinance projects with marine environmental benefits” (Stewart et al., 2022). They are typically issued by local and national governments, corporations, and multilateral development agencies looking to borrow money for investors (Barbier & Burgess, 2021). Despite their critical importance, biodiversity conservation and sustainable land use, including ecosystem conservation and restoration, still account for only about 3% of global green bond issuance, although investment in these areas is growing rapidly (Chahine & Liagre, 2020). Examples such as Seychelles' pioneering blue bond issuance in 2018, which catalyzed $15 million for sustainable fishing, protected areas and others, shows the effectiveness of this mechanism in relation to marine and cetacean habitat conservation.

Debt-for-nature conversions, on the other hand, restructure national debt into lower-cost private bonds, often with financial guarantees, and redirect savings to marine protected areas and blue-economy projects, including those that support cetacean habitats. Recent debt conversion initiatives in Barbados, Gabon, and Ecuador show that high-quality sovereign deals can deliver ocean protection outcomes and reliable conservation finance (see TNC’s Nature Bonds Toolkit). Although few studies directly evaluate these conversions in terms of species’ conservation outcomes (including cetaceans), examples such as Gabon's $500 million issuance, which unlocked $163 million for marine managements, protecting sharks, rays, dolphins, and whales, show that debt conversions can clearly benefit cetacean habitats (Winters, 2023).

Microfinance is also a valuable funding mechanism for small-scale businesses and individuals to support cetacean conservation, including government programs, for-profit, non-profit microfinance institutions (MFIs), and village savings and loan (VSL) groups. Among these, government entities, nonprofits, and VSL groups align most closely with sustainable ocean economy goals, with several projects successfully implemented in key marine ecosystems worldwide to promote conservation and sustainable local livelihoods. One specific example is the BNP Paribas's Blue Finance Facility, which provides long-term loans (typically 7-10 years) to community businesses in marine protected areas (e.g., Indonesia, Philippines, Tanzania). Despite defaulting risks amid climate threats to coral reefs, this mechanism supports sustainable fishing and ecotourism that protect marine ecosystems that cetaceans depend on, while benefitting over 110,000 people, (BNP Paribas, 2025).

Impact investment and impact-oriented equity are other interesting instruments to deploy private capital, often alongside concessional or de-risking instruments, to support enterprises that generate measurable ecological benefits and financially viable ocean-positive business models. Aggregators and impact funds are of particular importance because they pool multiple small ocean-positive ventures into single investment vehicles, reducing risk and transaction costs while channeling capital toward sustainable fisheries, aquaculture, ecotourism, and restoration (Studer, 2021). For instance, Mirova's Sustainable Ocean Fund (SOF) invests in the company SafetyNet Technologies, which develops precision fishing tools to improve sustainability and reduce bycatch of dolphins, in addition to monitoring cetacean populations (Mirova International Sustainable Equity Fund, 2023).

Lastly, Peer-to-Peer (P2P) investing and crowdfunding are also debt instruments that enable direct, often cross-border financial transfers for cetacean conservation, bypassing traditional institutions. The Pacific Whale Fund (PWF), launched under the Moananui Sanctuary's Moananui Blueprint in 2025, stands out as one of the most successful P2P investing initiatives for cetacean conservation, aiming to mobilize €100 million through innovative financial instruments to fund nature-based solutions, indigenous-led projects, and legal personhood advocacy for whales in the Pacific (Moananui Sanctuary, 2025). This hybrid model attracts diverse investors while generating sustainable revenue for ocean regeneration and community stewardship. Other smaller traditional crowdfunding or community grant efforts also exist, such as regional whale heritage areas (typically smaller grants of around $15,000), which operate on a much smaller financial scale and are more community- and project-specific, but are still relevant (Adventure Travel Conservation Fund, 2025).

Economic instruments

Most effective financial mechanisms identified:

1. Taxes, fees, quotas and direct payments in the fishery sector
2. Whale-watching / ecotourism fees, tourism concessions and land easements
3. Green taxes and levies

Taxing the fishery sector or introducing fishing fees and quotas can generate dedicated funding for cetacean conservation while guiding market behavior toward biologically and economically sustainable fish stocks and harvests. Fishing quotas—especially through catch-share systems—generally stabilize fisheries, reducing harmful gear use and decreasing bycatch pressure in areas where dolphins, whales, and porpoises are incidentally captured (Birkenbach et al., 2023). Some studies indicate that these systems could promote the conservation of threatened populations while at the same time enhancing the well-being of resource harvesters, but they would only be effective under strict conditions with robust monitoring, and, even then, associated costs must be carefully valued and equitably shared among stakeholders (Gerber et al., 2014; Onofri & Nunes, 2015).

Direct market payments, such as buyouts or compensation, can significantly enhance cetacean conservation. For example, the PACE-Vaquita program in Mexico compensates fishermen to reduce or stop gillnet fishing in order to protect the endangered vaquita porpoise, using a voluntary buyout and gear-switching model, launched in 2008, as a pioneering incentive for cetacean conservation (Niesten & Gjertsen, 2010).

Other incentive-based conservation strategies are playing a growing role in protecting cetacean habitats, especially in regions threatened by land development and resource extraction. Mechanisms such as ecotourism agreements, land easements, whale-watching fees, and tourism concessions shift economic value from extractive to non-consumptive uses (Murphy, 2013). With the global whale-watching industry valued at USD 3.1 billion in 2024 and projected to reach USD 5.6 billion by 2033, this sector represents a powerful opportunity for sustainable financing while generating local jobs (Market Intelo, 2025). Since 2015, the Prince of Whales Whale Watching in British Columbia has raised over $300,000 through a mandatory $5 Salish Sea Conservation Fee per passenger—up from $2 in 2018—to fund whale conservation, salmon restoration and education, with a pledged $1 million donation by 2023 and encouragement for industry-wide adoption (Prince of Whales, 2023). Governments can also harness and reinvest revenues through tools like visa fees, airport taxes, and green levies, as illustrated by Palau's Green Fee, which raised over $13 million for marine conservation, showing the effectiveness of well-structured environmental taxation backed by public support and strong leadership (Reef Resilience Network, 2024).

It is important to highlight that the success of these approaches hinges on transparent governance and public trust. Research indicates that willingness to pay entrance or conservation fees increases when visitors understand how their funds contribute to marine biodiversity and whale protection, demonstrating the importance of citizen engagement and environmental education (Barbaccia et al., 2025). In Hawaii, surveys showed that 80% of ecotourists were willing to pay a fee, but only 30% trusted public entities to manage collected funds. Responding to that concern, places like Cancun have established a public-private advisory council to ensure transparency in fee allocation (Saltza & Kittinger, 2022). Bonaire National Marine Park's "Nature Fee" system, which charges up to US$25 per person for scuba diving and US$10 for other water-based activities, stands out as a best-practice example of how to directly reinvest tourism revenue into marine park management. Taking proper environmental precautions, this is a model that can also work for whale-watching.

Grants and other transfers

Most effective financial mechanisms identified:

1. Official Development Assistance (ODA) and bi-/multi-lateral agreements
2. Voluntary Regional Cooperation
3. Conservation Trust Funds (CTFs)

Coordination through bilateral and multilateral aid (e.g., GEF, the World Bank, and the GCF), remains a critical source of large-scale finance for marine biodiversity and, by extension, cetacean conservation. Several countries direct ODA specifically toward marine and fisheries sectors. The Republic of Korea, for example, supports technology transfer, capacity building, and improved sanitary management of fishery products in developing nations (Korean Ministry of Oceans and Fisheries, 2024). In 2022 alone, targeted ODA mobilized approximately US$25.8 billion for global biodiversity initiatives (OECD, 2024).

Specific multilateral treaties have also garnered crucial resources to protect cetaceans. The best example of course is IWC. The IWC's 2025/2026 budget proposes approximately $2.8 million for 2025 and $3.1 million for 2026, including funding for cetacean research such as Atlantic humpback whales, databases, and Southern Right Whale monitoring (IWC Budgetary Sub-Committee, 2024), as well as smaller funds targeting grants for priority projects, strandings response, and developing country participation (IWC, 2022). Although convention-specific funds remain limited relative to the global financing needs for cetacean conservation and marine biodiversity, they still represent critical funding streams that support these efforts and help engage diverse sectors in scaling up essential investments.

Voluntary (Regional) Marine Conservation Agreements (MCAs) are another major source of funding for cetacean conservation, the most important of which is the Eastern Tropical Pacific Marine Corridor (CMAR). This is a major voluntary regional cooperation program among Colombia, Costa Rica, Ecuador and Panama to voluntarily coordinate 20+ million hectares of marine protected areas, reducing threats like bycatch and ship strikes to migratory whales through shared governance and funding (Conservation International, 2023, 2025). It is financed by GEF (initial $16 million and a follow-on $15.6 million), the Connect to Protect Coalition ($118.5 million) and the Broad Philanthropic Coalition (over $150 million), seeking long-term financial sustainability through partnerships but operating via project-specific funding and national contributions (Bezos Earth Fund, 2025; Blue Nature Alliance, 2021; Murphy, 2023). Other important MCAs include the Pelagos Sanctuary Agreement in Europe (Triton, 2025) and the North-East Asia Marine Protected Area Network (NEAMPAN) (ESCAP, 2025). Studies suggest these arrangements support flexible cooperation and shared management across Exclusive Economic Zones for migratory species while reducing jurisdictional fragmentation and enabling coordinated threat reduction, making them more adaptive than binding treaties in high seas or straddling-stock contexts with complex property rights (Ellett et al., 2025).

The Agreement on Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic (ACCOBAMS) is a particularly interesting case because it is an MCA that evolved into a Conservation Trust Fund (CTF). CTFs are defined as "private, legally independent institutions that provide sustainable financing for biodiversity conservation", a model which is perfectly adaptable to specific goals such as cetacean conservation. They capture long-term, stable financing from multiple donors to support a wide range of environmental actions directed at protected areas, sustainable livelihoods, biodiversity protection and others. ACCOBAMS' primary Trust Fund is financed by mandatory contributions from its 24 contracting parties and

provides for monitoring cetaceans, vessel speed enforcement, noise pollution, local whale conservation groups, and the management of whale-watching impacts (ACCOBAMS, 2016), with a Supplementary Conservation Fund (SCF) established to accept voluntary donations from other sources (ACCOBAMS, 2023). CTFs also face key challenges such as securing sufficient initial endowments, establishing robust governance structures, and addressing funding gaps amid escalating climate and development pressures (Tolisano et al., 2013).

Business and markets

Most effective financial mechanisms identified:

1. Voluntary & blue carbon markets
2. Ecotourism as a financial mechanism
3. Corporate Social Responsibility & ESG investments

Although whales offer genuine ecological carbon benefits and local co-benefits, uncertainty in quantifying these services and concerns over market integrity make whale-specific carbon credits premature for large-scale financing. Carbon finance may support cetacean conservation if grounded in strong science, conservative market standards, and complementary funding, but until research and governance frameworks evolve, the literature suggests that focus should remain on established blue carbon habitats and other forms of conservation finance (Alves et al., 2022; Collins et al., 2025; Durfort et al., 2022; Mariani et al., 2020; Pearson et al., 2023).

For example, tourism, and whale-watching specifically, is a multi-billion-dollar global industry that not only sustains local livelihoods and amenities but also offers a promising foundation for conservation finance through fees or revenue-sharing mechanisms (Suárez-Rojas & León, 2025). Successful long-term ecotourism models, such as Norway's Whalesafari, illustrate how tourism revenue can be effectively integrated with scientific research and community development (Suárez-Rojas et al., 2023). In regions like Baja California, economic-rent analyses have quantified the significant producer-side benefits, highlighting the potential to redirect a portion of this value toward conservation through appropriate financial instruments (Raschke, 2017). Moreover, studies show that tourists are often willing to pay premiums for ecolabels or sustainability certifications, creating further opportunities for raising conservation funds via entrance fees or surcharges (Lissner & Mayer, 2020). However, without proper regulation, activities such as whale-watching can become harmful, underscoring the need for sustainability measures such as capacity limits, regulatory oversight, and equitable benefit-sharing with local communities (Malinauskaite, 2021).

There are as well good examples of Corporate Social Responsibility policies and ESG investments from the private sector aiming to conserve whale habitat and minimize disturbance, particularly when it is part of broader corporate governance structures including NGOs and industry associations. For instance, the adoption of the Baltic and International Maritime Council

(BIMCO)’s North Atlantic right whale protocols, including dynamic speed zones and rerouting, reflects growing corporate responsibility in reducing ship strikes on endangered whales (BIMCO, 2025). Similarly, the Mediterranean Shipping Company (MSC) supported endangered fin whale tagging in Chile’s Humboldt Archipelago and reduced vessel speeds on 94% of transits in the Puget Sound during the 2024–2025 Quiet Sound initiative, helping Southern Resident killer whales communicate and hunt more effectively (Mediterranean Shipping Company, 2025).

Plastic waste and pollution are also being targeted by initiatives such as the Ocean Cleanup, backed by private donors and partners, which aims to eliminate 90% of floating ocean plastic by 2040, tackling in this way a major threat to cetaceans with marine co-benefits (Slat, 2025). However, while ESG frameworks increasingly incorporate biodiversity into their action frameworks, they still retain anthropocentric biases and lack standardized, consistent biodiversity impact metrics. “Raising awareness” is not enough when innovative metrics such as Equivalent Biodiversity Area and ROI analyses offer potential for quantifying conservation benefits (Boyd et al., 2012). Overall, challenges remain in capturing indirect ecosystem services and ensuring compliance regarding voluntary adherence to good corporate practices.

Financial efficiency & risk management

Most effective financial mechanisms identified:

1. Public-private partnerships
2. Blended finance
3. Performance-linked loans and pay-for-performance bonds

Agreements between governments and private entities to support ocean conservation have existed for decades, but they remain more common in coastal than offshore or high-seas contexts, largely due to challenges around unclear or non-tradable marine property rights (Agardy et al., 2014). Nonetheless, there are cases of successfully implemented public-private partnership (PPP) agreements even in this context, given the right policy framework. A traditional pathway is public-finance-led partnerships, exemplified here by the Clean Oceans Initiative 2.0, through which public development banks provide grants and concessional loans to finance ocean cleanup and pollution-prevention infrastructure, with private actors engaged mainly as implementers and technology providers rather than capital sources. The initiative surpassed its €4 billion commitment ahead of schedule and has expanded from remediation to prevention, setting a €3 billion financing target for 2026–2030 (European Investment Bank, 2025).

However, markets have seen a strong surge in blended finance in recent years, defined as the use of catalytic capital from public or philanthropic sources to increase private sector investment in sustainability projects (Convergence Blended Finance Inc., n.d.). Due to its unique combination of various funding sources, such as grants, concessional loans, guarantees, and

private capital, this innovative financial architecture offers a powerful way to unlock investment for high-risk, underfunded marine priorities. Recent UN-led approaches in this sphere include the Ocean Action 2030, which deploys concessional capital, guarantees, and structured advisory services to reduce risk and build bankable pipelines (United Nations Capital Development Fund, 2025), and One Ocean Finance, which advances a system-level platform to mobilize investment from ocean-dependent industries and other sources, addressing chronic underfunding of SDG 14 and prioritizing equitable access for Small Island Developing States and Least Developed Countries (Sustainability Online, 2025). These types of investments are also increasingly included in global convention-specific funds, such as the $8.25 million GEF grant provided to the Coalition on Private Investment in Conservation (Blarel et al., 2023).

Many of the challenges that blended structures are designed to overcome (e.g., geographic remoteness, high monitoring costs and risks, uncertain revenue streams, and the need for sustained ecosystem management) can serve cetacean conservation purposes. Lowering risk for commercial lenders and impact investors through grant-funded technical assistance and loan guarantees, blended finance can make conservation-aligned enterprises bankable. Tailored loans for small-scale fishers, paired with guarantees that reduce investor exposure, demonstrate how similar approaches could support whale-safe fisheries, vessel-monitoring systems, or responsible whale-watching operators that would otherwise struggle to access credit. These vehicles can also aggregate multiple small or early-stage projects into a single investment portfolio, reducing transaction costs and creating opportunities for scale (Convergence Blended Finance Inc., n.d.). For example, the Blue Alliance blended finance vehicle, backed by a US$5.2 million investment from the Global Fund for Coral Reefs (UNDP), aims to unlock an additional US$20 million in private impact capital to support reef-positive businesses and marine protected area (MPA) co-management through a mix of grants, impact loans, and guarantees, targeting sectors like ecotourism, sustainable fisheries, and blue carbon, which also benefit cetacean conservation by reducing habitat degradation, supporting sustainable livelihoods, and improving MPA enforcement in areas where whales and dolphins are present (Blue Alliance, 2025; Global Fund for Coral Reefs, 2025). In general, however, overly complex deal structures and small project size can erode the cost-of-capital advantages of blended finance by driving up transaction costs, indicating that its effectiveness for marine and cetacean conservation depends on scale, standardization, and streamlined implementation (Müller, 2023).

From climate-driven habitat changes to vessel strikes and entanglement, threats to cetacean populations are diverse in scale. Conditional lending is a recently growing solution to manage those risks. In Mexico, outcome-based payments are being made to landowners that successfully protect the Laguna San Ignacio—a vital gray whale breeding site—from coastal development, with significant compliance rates. Impact (or pay-for-performance) bonds also significantly reduce risk by tying investor repayments to successful restoration—as verified by independent bodies—transferring project risks from the state to private investors (EDF & Ventures, 2018). The World Bank has recently issued a $150 million Wildlife Conservation Bond ("Rhino Bond") to support black rhino population recovery in South Africa; with similar financing models proposed for endangered whale species (World Bank, 2025). However, applicability remains challenging due to the complexity of monitoring highly migratory

populations. These examples of outcome-based financing show promise for conservation, but their success depends on well-defined, measurable outcomes, long-term funding commitments, and robust contract design to manage risks and ensure ecological integrity (Seneca Impact Advisors, 2024).

This review demonstrates that a diverse and rapidly evolving suite of financial mechanisms is now available to support cetacean conservation (summarized in Tables 18 and 19) each offering different strengths depending on context, scale, and financing needs. Return-based investments such as blue bonds, debt-for-nature swaps, microfinance, impact investment, and emerging P2P platforms are helping redirect global capital toward marine protection, with several instruments already delivering measurable benefits for whales and dolphins through improved fisheries management, expanded protected areas, and strengthened community enterprises. Economic instruments, including fishery sector quotas, ecotourism fees, green levies, and easement-based incentives, show considerable potential to align market behavior with ecological sustainability, particularly when supported by strong governance and transparent revenue allocation. Grants, ODAs, regional cooperation agreements, Conservation Trust Funds and public-private partnerships remain essential backbones of financing, securing long-term support for transboundary conservation efforts such as CMAR, ACCOBAMS, and global whale research programs.

Across all mechanisms reviewed, the effectiveness of financial tools ultimately rests on the enabling environment in which they operate: robust institutions, clear regulatory frameworks, reliable monitoring systems, and meaningful participation of Indigenous peoples and coastal communities. Innovative approaches, including blended finance, performance-linked lending, and outcome-based conservation bonds, are expanding the frontier of marine conservation finance by transferring risk, creating stronger incentives for environmental results, and mobilizing private capital at a scale not previously possible in cetacean conservation. Among these, performance-based bonds and impact-linked loans stand out as especially promising due to their ability to tie investor returns directly to ecological outcomes, while hybrid models such as P2P investing and crowdfunding are democratizing access to marine conservation finance and engaging a far broader community of supporters.

Ultimately, no single financial mechanism is sufficient to address the multiple, interconnected threats faced by cetaceans. Instead, a strategic mix of return-based investments, regulatory tools, grant funding, market mechanisms, and risk-sharing instruments will be necessary to close the marine conservation finance gap. Scaling these approaches will also demand innovative partnerships across governments, NGOs, private investors, communities, and multilateral institutions. As global interest in sustainable ocean economies continues to rise, there is a significant opportunity to harness this momentum to ensure long-term, equitable, and ecologically grounded financing for the world’s cetacean populations and the habitats on which they depend.

Table 18. Species-based financial mechanisms.

Financial mechanism	Examples	Species targeted	Source
Peer-to-Peer (P2P) investing and crowdfunding	Pacific Whale Fund (Moananui 2025 Blueprint), aiming to mobilize €100 million to fund nature-based solutions, Indigenous-led projects, and legal personhood advocacy for whales	Several whale species	Moananui Sanctuary, 2025
Quotas in the fishery sector	Catch-share systems have reduced harmful gear use and decreased bycatch pressure in 39 US fisheries	Dolphins, whales, and porpoises are incidentally captured	Birkenbach et al., 2023
Direct payments	PACE-Vaquita program in Mexico, compensates fishermen to reduce or stop gillnet fishing, using a voluntary buyout and gear-switching model	Vaquita porpoise	Niesten & Gjertsen, 2010
Green taxes and levies	Prince of Whales Whale Watching in British Columbia has raised over $300,000 through a mandatory $5 Salish Sea Conservation Fee per passenger, and pledged $1 million donation by 2023	Whale species (primarily orcas)	Prince of Whales, 2023
Bi-/multi-lateral agreements	International Convention for the Regulation of Whaling (IWC) has implemented a global whaling moratorium, manages vulnerable populations, coordinates wide-reaching efforts in bycatch reduction and habitat protection, and funds cetacean research directly	Atlantic humpback whales, Southern Right Whale	IWC Budgetary Sub-Committee, 2024

Financial mechanism	Examples	Species targeted	Source
Grants	$15,000 grant to support the World Cetacean Alliance in establishing a new Whale Heritage Area, creating a global online platform to connect and empower community-led whale conservation efforts worldwide	Southern Right Whales (Santa Catarina Nursery Area, Brazil) and other cetaceans, such as dolphins	Adventure Travel Conservation Fund, 2025
Conservation Trust Funds (CTFs)	ACCOBAMS' primary Trust Fund provides cetacean monitoring, vessel speed enforcement, noise pollution, local whale conservation groups, and the management of whale-watching impacts	Prioritizes habitats essential for cetacean migration, reproduction, and foraging, including coastal and pelagic zones	ACCOBAMS, 2016
Ecotourism as a financial mechanism	Norway's Whalesafari Andenes collaborates with marine biologists, incorporates research into its tours, and emphasizes public outreach, making it a model for science-based tourism that supports whale conservation through ecotourism practices	Sperm whales, orcas (killer whales), and humpback whales	Suárez-Rojas et al., 2023
Corporate Social Responsibility & ESG investments	The Mediterranean Shipping Company (MSC) supported endangered fin whale tagging in Chile's Humboldt Archipelago and reduced vessel speeds on 94% of transits in the Puget Sound during the 2024–2025 Quiet Sound initiative	Southern Resident killer whales	Mediterranean Shipping Company, 2025

Financial mechanism	Examples	Species targeted	Source
Pay-for-performance bonds	In 2022, the World Bank issued a $150 million Wildlife Conservation Bond ("Rhino Bond") to support the recovery of black rhino populations in South Africa. This type of instrument could be applied to whales, but monitoring difficulties are a significant challenge	Black rhinoceros	World Bank, 2025

Table 19. Habitat-based financial mechanisms.

Financial mechanism	Examples	Whale-related ecosystems	Source
Blue bonds	$15 million blue bond issuance in the Republic of Seychelles	Marine and coastal ecosystems, coral reefs	Yoshioka, 2020
Debt-for-nature swaps	$500 million debt conversion for ocean conservation in Gabon	Diverse coastal and marine ecosystems, including those with global importance for humpback whales' annual migration to their mating and calving areas	Winters, 2023
Microfinance facilities	BNP Paribas's Blue Finance Facility	Marine Protected Areas in Indonesia, Philippines, Tanzania	BNP Paribas, 2025
Impact Investment & Impact-Oriented Equity	Mirova's Sustainable Ocean Fund (SOF) investment in the company SafetyNet Technologies	Species monitored during the trials included dolphins, Skipjack Tuna, Brown crab, European lobster, cod, nephrops (scampi/ langoustine) and turtles	Mirova International Sustainable Equity Fund, 2023
Green taxes and levies	Palau's Green Fee, which raised over $13 million for marine conservation	39 Protected Areas in Palau, including 29 marine sites, such as coral reefs, coastal and marine habitats	Reef Resilience Network, 2024

Financial mechanism	Examples	Whale-related ecosystems	Source
Official Development Assistance (ODA)	The Republic of Korea supports technology transfer, capacity building and improved sanitary management of fishery products in developing nations	Mangrove planting, coastal resource improvement	Korean Ministry of Oceans and Fisheries, 2024
Voluntary Marine Conservation Agreements (MCAs)	The Eastern Tropical Pacific Marine Corridor (CMAR) is a cooperation program among Colombia, Costa Rica, Ecuador and Panama to voluntarily coordinate 20+ million hectares of MPAs, reducing threats like bycatch and ship strikes to migratory whales through shared governance and funding	Migration corridors for whales in Central and South America, core areas include coral reefs, pelagic waters, and coastal zones like Cocos Island, Galapagos, Malpelo, Gorgona, and Coiba	Conservation International, 2023, 2025
Blended finance	$8.25 million GEF grant provided to the Coalition on Private Investment in Conservation	Mangroves, coastal wetlands, coral reefs	Blarel et al., 2023
Blended finance	The Global Fund for Coral Reefs (GFCR) is a blended finance fund that combines concessional public and philanthropic capital with private investment to de-risk and scale revenue-generating marine enterprises and projects	Coral reefs and associated ecosystems	Global Fund for Coral Reefs, 2025
Blended finance	Blue Alliance blended finance vehicle, backed by a US$5.2 million investment from the GFCR, designed to support reef-positive businesses and marine protected area (MPA) co-management	Interconnected marine ecosystems across the Eastern Tropical Pacific, including open-ocean habitats, coastal and island-associated waters, coral reef environments, and migratory corridors	Blue Alliance, 2025
Pay-for-performance bonds	Outcome-based payments to landowners in Mexico linked with the successful protection of Laguna San Ignacio	Vital gray whale breeding site	Seneca Impact Advisors, 2024

Financial mechanism	Examples	Whale-related ecosystems	Source
Public-private partnerships	Through the Clean Oceans Initiative 2.0, public development banks set a €3 billion financing target for plastic-pollution financing	Marine ecosystems	European Investment Bank, 2025
Public-private partnerships / blended finance	UN Ocean Action 2030, launched in 2025 by the Ocean Panel and World Resources Institute	Coastal ecosystems	United Nations Capital Development Fund, 2025
Public-private partnerships / blended finance	One Ocean Finance, launched by a collective of UN agencies and global partners, aiming to unlock billions in new financing from ocean-dependent industries and blue economy sectors	Marine and coastal ecosystems, particularly mangroves and seaweed	Müller, 2023

5.2 Institutional arrangement proposal

Resources owned in common can be effectively managed through collective institutions that assure cooperative compliance with co-designed rules and agreements. Here we propose the creation of Common Asset Trusts (CATs) to protect the North Pacific humpback whales population and their habitat. In essence a CAT is a collection of agreements and poly-centrically governed institutions in support of a shared purpose, sustainable management of public goods. To achieve this purpose, the design of these agreements and institutions can be guided by Ostrom's principles for sustainable commons management (Ostrom, 2008; Costanza et al., 2020), which are functionally identical to core design principles for successful cooperation in the face of social dilemmas identified by evolutionary biologists (Atkins et al., 2019; Wilson et al., 2013). These eight core design principles for effective and sustainable commons management are: (P1) clearly defined boundaries, (P2) proportional equivalence between benefits and costs, (P3) collective choice arrangements, (P4) monitoring, (P5) graduated sanctions, (P6) conflict resolution mechanisms, (P7) minimal recognition of rights to organize, and (P8) polycentric governance.

To design a CAT for the protection of humpback whales and their habitat, following Hernández-Blanco (2019) we propose a 7-step process (Figure 10), which is in close relation with Ostrom's principles for managing the commons. The first step is to identify the marine and coastal ecosystems that are going to be the subject of the CAT, taking into consideration properties such as location, extension and health of the ecosystem. The second step is to agree on the benefits (i.e., ecosystem services), and their value, that the CAT will focus on to ensure its sustainable use by the beneficiaries. Next, stakeholders of the CAT should have a clear understanding of the main threats the ecosystem faces, in order to address them efficiently. The institutional arrangement is the fourth step of this process, and it's the heart of the CAT, in which the rules of stewardship will be agreed among the stakeholders under a polycentric governance system.

The stewardship rules of the trust will produce the agreed management strategies to protect and restore the ecosystem and the benefits it provides to the trustees. These management strategies will consist of a wide arrangement of management actions, the exact identity of which will depend on the ecosystem (due to system specificity of function), the level of threats it faces, and the agreed division of benefits among the trustees. The sixth step is the creation of the financial mechanism of the CAT (i.e., how funds are going to be collected and used to finance the management strategies). We propose that these funds should come from the main externalities to the trust, both positive (i.e., benefits to specific beneficiaries, which can translate into instruments such as fees, ecosystem services markets), and negative (i.e., those who degrade the natural capital should be charged a fee or sanctioned). Finally, the process needs to be iterative, through monitoring and evaluation, allowing the CAT to adapt and evolve to new social and environmental conditions.

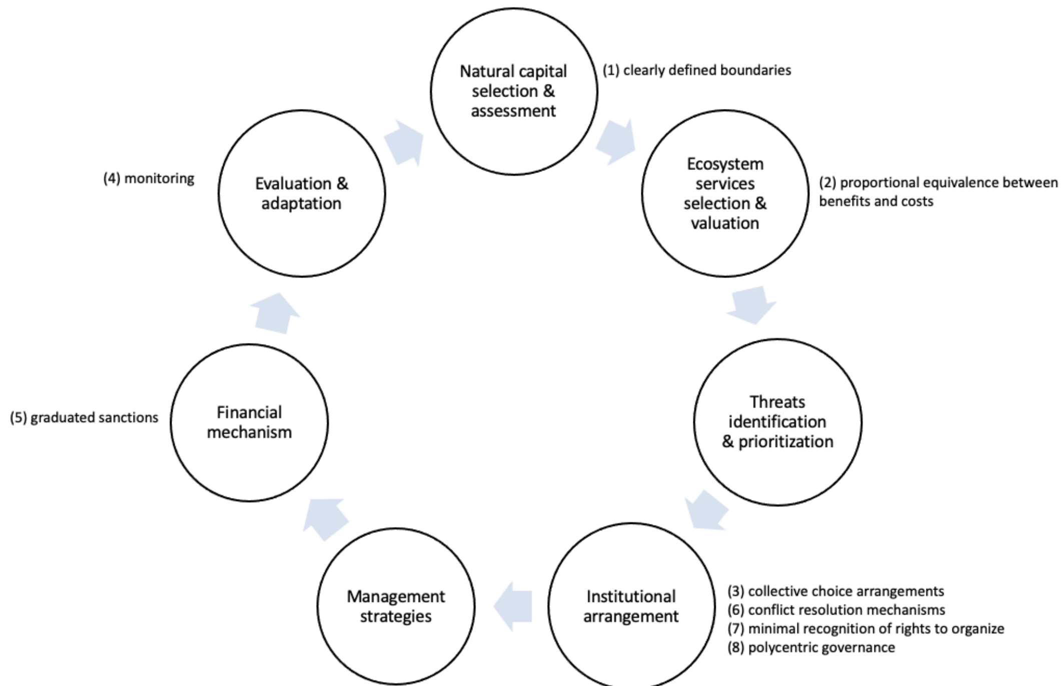

Figure 10. Process to design a CAT for the conservation and restoration of North pacific humpback whales population, indicating how each step is related to Ostrom's principles.

In the case of humpback whales, through their migrations in different parts of the world, they move constantly between national jurisdictions, as well as between the EEZ and ABNJ, making them a transboundary common-pool resource with significant challenges to protect since the responsibility for their stewardship is divided between countries with different world views, political contexts, cultures, environmental awareness, and funding capabilities. To address this complex conservation need, governance systems must be designed with an authoritative reach equal to the geographical scale of the life history dynamics of these animals, which would require as well a cross-scale networks of resource management (Markelova & Mwangi, 2012).

Therefore, in order to select the ecosystem to protect and restore (Step 1) for the well-being of humpback whales, as well as ours from the benefits we derive from their existence, it is important to have a good understanding of the connectivity these animals display, in terms on how and when they use different parts of the ocean, as well as the importance of specific sites (e.g. for breeding and feeding) and routs (UNEP-WCMC, 2019). In this sense, a CAT should focus on these priority areas, which has been identified through complementary frameworks such as the blue corridors (Johnson et al., 2022) and the Important Marine Mammal Areas (IMMAs) (Tetley et al., 2022).

In terms of ecosystem services (Step 2), the CAT can start with those described earlier in this report, plus additional ones (e.g., tourism). We could also include those services provided by

the ecosystems that conform the whale's blue corridor (e.g., kelp forests, mangroves), being careful in avoiding double counting in case the benefits from these services are also considered as part of another governance or financial framework. Valuing the role of humpback whales in the provision of ecosystem services has several implications for the design of new management strategies for their conservation and restoration. First, by acknowledging the multiple beneficiaries of these services at different geographical scales, cost-benefit analysis can incorporate this value by giving these animals "a voice" in decision making, proving that their existence (beyond moral reasons), is economically desirable. Second, whales have decreased dramatically because they have been exterminated from the ocean at no cost for those who have an impact on their populations and a great cost for society as a whole, and valuing their contributions to our well-being them will allow to internalize these externalities either from fines (for negative externalities) to other financial mechanisms that reward those who protect them (for positive externalities).

Regarding threats (Step 3), humpback whales face multiple ones such as climate change (affecting prey availability and changes in phenology and demography), pollution (including chemical, plastic and noise), ship strikes and unsustainable fishing (including bycatch, entanglement in fishing gear such as by ghost nets and reduction of prey availability), among others (Johnson et al., 2022). Furthermore, these threats do not act in insolation, they rather put at risk to the survival of this species in a complementary and accumulative way. For example, the reduction of krill due to an unsustainable fishing of this species (Schiermeier, 2010; Trebilco et al., 2020) (an open access resource) has a direct impact on whales in their feeding areas in the Southern Ocean (Santora et al., 2010; Weinstein et al., 2017).

We can argue that these threats are the product of assigning a value of zero to whales, and therefore the industries behind these drivers of change do not have any incentive (beyond the moral imperative, which should be enough) to internalize these negative externalities on whales. Having a transboundary common pool resource therefore means that the mechanism to internalize externalities will need to happen in different countries for the benefit of the same countries, or most probably, for other countries. And here it is where the institutional arrangement (Step 4) is completely different from others managing common pool resources.

We propose the creation of a CAT called the Humpback Whale Transboundary Trust (HWTT), a multisectoral and transboundary trust catalyzed by public-private partnerships. The trust will be polycentric (Ostrom et al., 1961; Carlisle & Gruby, 2019; Gjerde & Yadav, 2021); Mahon & Fanning, 2019), compromised by all governments (national and local) that benefit from whales in the target area, as well as by those industries who pose a threat on this species, such as fisheries, shipping and tourism. The CAT will also consider industries which also benefit/depend on whales, such as fisheries and tourism. Finally, international organizations such as the International Whaling Commission, the International Maritime Organization and the World Bank, among others, can play a role in hosting the trust as an impartial international actor, as well as by helping mobilize the funding needed (Step 6, more on this later).

The CAT will define its rules and governance in relation with the common goal of providing the multigovernmental and multisectoral protection this species needs to survive and to thrive. The HWTT will also decide the management strategies (Step 5) needed to achieve this goal. These strategies will be focused on (1) key areas such as feeding and reproduction areas, and on (2) reducing the negative impact from the industries mentioned before. In term of key areas, recent efforts such as the identification of blue corridors and Important Marine Mammal Areas (IMMAs) (Tetley et al., 2022) can be used as part of the prioritization criteria.

In terms of impacts, the HWTT can start for example by focusing on shipping, enforcing practices such as shifting lanes and speed regulations (Guzman et al., 2020). These practices can have a direct impact on the industry in terms of reducing operational costs (e.g., California-based Blue Whales Blue Skies). Sustainable practices can also be complemented by high penalties to shipping boats if they collide with a whale (currently it is free to kill a whale under these circumstances) and therefore a cost-benefit analysis of implementing the strategies mentioned before can make it evident that they make both economic and business sense. Sustainable fishing can also be part of the conservation strategies that the CAT can support, both through the blue corridors by eliminating bycatch and the disposal of fishing nets, ropes and plastics.

To fund these strategies (Step 6), funding sources will be related to externalities. Financial instruments to internalize negative externalities can include high penalties for whale strikes, taxes on plastic, shipping, carbon and unsustainable shipping, among others. For positive externalities, the HWTT can develop instruments such as user fees (e.g. for whale watching), biodiversity markets related to the role of whales in providing ecosystem services, and Payment for Ecosystem Services (PES) schemes in which some of the actors involved in the trust, such as fishermen and tourist operators, can play a role in the conservation of these animals through citizen science for example.

A key task of the HWTT will be designing a procedure on how to best distribute the funds collected by these financial instruments, since some of the funds might be collected in one country but invested in another one. We propose to start focusing in directing the funds to key areas such as feeding and breeding areas as it was mentioned before. This does not mean that a portion of the funds cannot stay in the country where they were collected, which could be the case for example to allocate a portion to cover operational and administrative costs.

Finally, evaluation and monitoring activities of the CAT (Step 7) will need to be across countries, acknowledging the impacts (both positive and negative) through the connectivity nature of the blue corridors. To address this, and to make these activities cost-effective, initiatives such as citizen science can be implemented. For example, recent developments in Artificial Intelligence for conservation through tools such as Flukebook or Happywhale (Cheeseman et al., 2023), where users upload photos to the web interface of the tool and the platform automatically detects specific cetacean features in those photos using algorithms for cetacean photographic ID. Therefore, tools like these ones could be fed by thousands of photos taken by fishermen,

tourism operators and tourists in order to monitor the humpback whales' population through their migratory corridors.

Figure 11 provides a schematic summary of the HWTT.

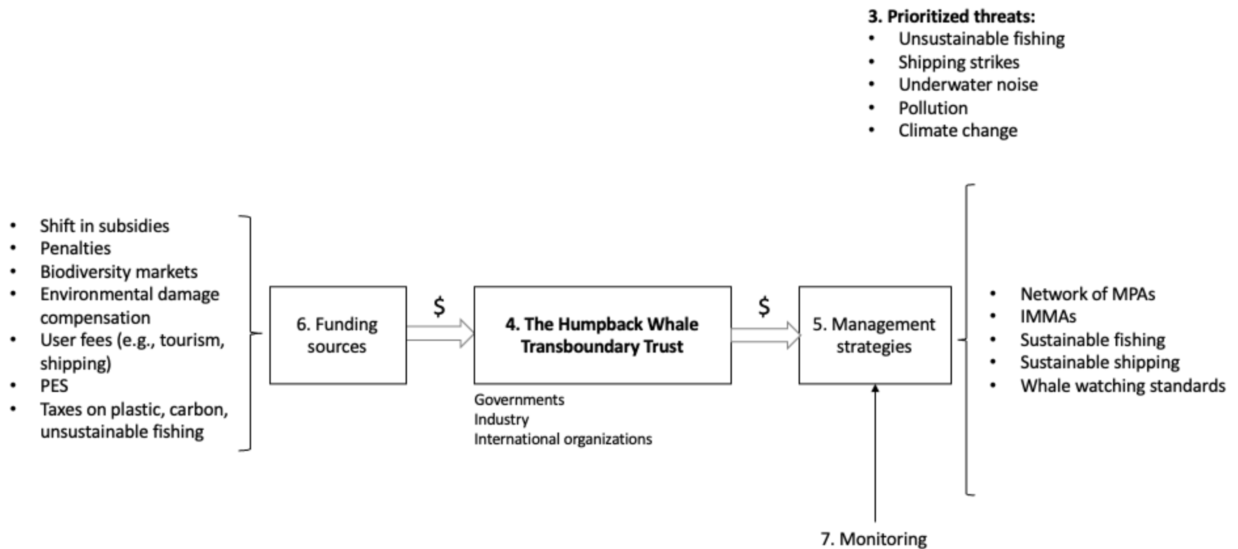

Figure 11. General structure of the Humpback Whale Transboundary Trust.

This general proposal of a CAT to protect the North Pacific humpback population, including its blue corridor and adjacent ecosystems, is a first attempt provide innovative institutional arrangements that can enhance the governance of the species and its habitats. One key opportunity that a scheme like this one might find political traction is through the recent ratification of the High Seas Treaty, where whale sanctuaries could be established in the high seas as novel Marine Protected Areas, as in the case of the blue corridor between Alaska and Hawaii (but other could be consider as well), with the advantage that this corridor connects two states of the US and therefore the design and implementation of legislation could potentially find less barriers.

6. Research agenda

Although the results of the pilot project demonstrate clear and measurable contributions from whales to the provision of ecosystem services, they still rely on important assumptions and limited empirical data due to the novelty of the topic. The following research priorities focus on improving both the ecological and economic assessment portions of the KSCP, with the aim of producing more accurate and policy-relevant estimates.

a) Updated whale population abundance estimates. This is a fundamental parameter in the calculations yet recent estimates are missing for many populations.

b) Whale-mediated nutrient dynamics: Current estimates of nutrient release rely on limited observations and extrapolation across species and regions. Improved empirical measurements are needed on excretion rates, nutrient forms, and their persistence in the euphotic zone to better quantify their effect on primary productivity.

c) Primary productivity responses: The model assumes proportional increases in primary productivity (ΔPP) from whale-derived nutrients. Responses may be nonlinear and context dependent. Empirical validation is needed to determine how nutrient inputs translate into productivity across different ecosystems.

d) Trophic transfer processes: The conversion of primary productivity into fish biomass is simplified in current models. More accurate estimates of trophic transfer efficiency and food web responses are needed, including potential nonlinearities and ecological feedbacks.

e) Carbon pathways and sequestration: Uncertainty remains in how whale-mediated processes contribute to long-term carbon storage. Key priorities include refining estimates of export efficiency, sequestration fractions, and whale-fall contributions.

f) Biophysical–economic linkages: The production function approach provides a strong conceptual basis but depends on current limited empirical validation. Strengthening the linkage between ecological changes (e.g., ΔPP) and economic outcomes (e.g., fisheries production) is a key priority.

g) Expansion of valuation pathways: The current framework focuses on fisheries and climate regulation. Future work could incorporate additional contributions (Figure 5) to additional ecosystem service (Table 2).

h) Market dynamics and economic responses: Current estimates assume that changes in biomass translate directly into economic value using fixed prices. Incorporating market responses, price elasticity, and management constraints would improve the realism of valuation results.

i) Reducing reliance on ecological and economic data transfers: Valuation currently relies on transferred parameters and generalized assumptions. Expanding primary data collection and region-specific valuation studies would improve accuracy and credibility.

j) Integrated ecological–economic modeling: Future work should move toward coupled models that capture feedbacks, nonlinear dynamics, and system interactions. This would allow for a more realistic representation of how whale populations influence ecosystem services over time.

k) Strategic research pathway: In the short term, efforts should focus on parameter refinement and sensitivity analysis. Medium-term priorities could include spatially explicit models and expanded valuation

l) Scenario planning: More sophisticated scenario planning analysis could include some of research needs mentioned before, such as nonlinear ecological dynamics, including threshold effects, density dependence, or saturation processes in trophic interactions.

m) Economic valuation of blue corridors: Estimating the value of the habitats that whales depend on throughout their migration (e.g., kelp forests, mangroves, coral reefs) can provide an additional important investment justification to protect whale's populations by protecting these ecosystems, especially for all the other co-benefits these ecosystems provide.

n) Relational values: Although it was not the objective of this pilot project, non-monetary analysis such as identifying relational values can be important to include non-market

values with market ones, therefore providing a more pluralistic valuation of the contributions of whales to the provision of benefits to the wellbeing of society.

o) Natural capital accounting: As policy interest increases on building ocean accounts under the System of Environmental Economic Accounting (SEEA) from the UN, the KSCP concept could contribute significantly to the creation of condition accounts.

7. Recommendations to the IWC

a) Interdisciplinary expert workshop: The IWC should convene a workshop bringing together ecologists, economists, and modelers to review assumptions, validate parameters, and identify priority areas for improvement. This would help align methodologies and strengthen scientific credibility. This workshop should be 100% practical rather focused on presentations. The main idea is to expand the research agenda with more questions, and provide answers when possible or at least a potential roadmap.

b) A formal working group on economic analysis should be created within the IWC, which could work as a bridge between the Scientific and Conservation Committees. This group would guide methodological development, coordinate research, and provide technical advice to member states to guide future research on applying the KSCP concept in other case studies, as well as to provide key insights for other relevant economic topics of the IWC (e.g., shipping, whale watching, sustainable fishing), where assessments of cost-benefit analysis, economic impact analysis, and economic valuation of ecosystem services will provide key policy insights. One of the authors of this report (MHB) is willing to lead the efforts for setting this group.

c) Pilot applications and case studies: The framework we developed should be applied to additional regions to test its robustness and adapt it as needed. Comparative case studies would help refine methods and demonstrate broader applicability.

d) Link to conservation finance: The framework can support the development of conservation finance mechanisms by demonstrating the economic value of the ecosystem services supported by whale populations. The IWC can help translate these insights into practical tools for investment and policy design.

e) Data collection and collaboration: The IWC should promote coordinated data collection on key ecological processes, including nutrient cycling, carbon dynamics, whale population dynamics, and whale distribution, among others. Partnerships with research institutions and international organizations will be essential.

f) Communication and outreach: Clear communication of results is critical for policy uptake. The IWC should develop concise and accessible outputs that translate these technical findings into actionable insights for decision-makers.

8. Conclusion

We developed a framework for the first time in the academic literature to assess the contributions of cetaceans to the provision of ecosystem services, following a systematic analysis of ecological and economic theory, based on the natural capital approach, resulting in the creation of the novel concept of the Keystone Species Contribution Pathway. Our framework takes a different approach to some of the prevailing ones who wrongly assumed a direct link between cetaceans and ecosystem services.

Based on the three levels of our framework, we were able to create simple yet robust models that represent a first attempt to quantitatively measure cetaceans' contributions to the provision of ecosystem services. These models were able to estimate for the first time the economic value of the contribution of North Pacific humpback whales to fisheries productivity and climate regulation. These values are a first attempt and represent a first-order of magnitude approximations. Furthermore, these models can be applied to other species of cetaceans around the world to start better envisioning the role these animals play in supporting human well-being. These key outcomes represent a milestone in the process that started a decade ago when the IWC adopted the resolution on Cetaceans and their Contribution to Ecosystem Functioning (Resolution 2016-3) and the participatory process that followed afterwards.

Moreover, as umbrella species, whales help benefit the health of multiple ecosystems and their species beyond what our models estimated. In this way, their blue corridors and the adjacent ecosystems produce a sort of "ecosystem services spillover effect". Therefore, in terms of valuing the economic benefits of the protection of whales, the value goes beyond the contribution of these animals to the provision of ecosystem services and should include the value of the benefits provided by the multiple ecosystems across multiple spatial boundaries that sustain their population.

It is key to understand that the economic valuation of natural capital, including the contribution of species to this value, should not be the only tool or criteria to make a decision about nature conservation, and therefore our assessment need to be complemented by other key criteria

such as the intrinsic value of the ecosystem in terms of culture and spiritual benefits, especially for indigenous populations and local communities. For example, our results can be combined with novel legislations such as the one led in 2024 by indigenous leaders from Polynesia, including New Zealand, Tonga, Tahiti, Hawai'i, and the Cook Islands, that resulted in the signature of the *He Whakaputanga Moana* (Declaration for the Ocean), which recognizes whales as legal persons with inherent rights.

Finally, it is key to highlight again that the main objective of this report was to provide a general framework to start a line of research on the contribution of whales to the provision of ecosystem services that is extremely nascent, and therefore our work focused on providing common ground and the seeds for much longer and much in-depth ecological and economic analysis.

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Appendix 1. Systematic literature review

We conducted a systematic literature review with three objectives:

1. Understand the current prevailing approaches and frameworks that consider the contribution of whales to the provision of ecosystem services in order to identify key improvement opportunities.
2. Have the scientific basis to construct our framework to assess the role of cetaceans in supporting the provision of ecosystem services.
3. Collect data that could potentially be applied to a case study on the North Pacific humpback whales to illustrate our framework.

Please refer to the Supplementary Material for a detailed description of the method applied to conduct this systematic literature review.

The systematic literature review followed the PRISMA approach (Page et al., 2021). The review aimed to identify peer-reviewed and grey literature examining the role of whales in supporting the provision of ecosystem services, with a particular emphasis on nutrient cycling, productivity enhancement, and climate regulation.

First, a structured search was conducted using Google Scholar in June 2025, guided by predefined keywords and Boolean combinations grouped into four thematic clusters:

- Nutrient cycling and productivity: “whale pump”, “whale conveyor”, “whale fall”, “whale feces” productivity, “nutrient cycling”, “nutrient transport”, “nitrogen cycling”, “biogeochemical cycling”, “primary production”, “phytoplankton bloom”, “phytoplankton growth”, and “fisheries productivity”.
- Carbon and climate regulation: “carbon sequestration”, “carbon sink”, “carbon storage”, “carbon export”, and “climate regulation”.
- Ecosystem engineering and services: “ecosystem engineer(s)”, “ecosystem function(s)”, “ecosystem service(s)”.
- Taxonomic terms: combinations of “whale(s)” or “cetacean(s)” with the above themes.

We selected these keywords based on the contribution pathways identified by the seminal paper of Roman et al. (2014) in order to have a clear search scope. This search returned 214 records. An additional 72 documents were identified from earlier literature reviews and expert-curated sources. All records were imported into Zotero, merged into a single collection, and de-duplicated using Zotero’s built-in duplicate detection tool. After removing duplicates, 233 unique records remained and were exported to Covidence for screening (Figure 12).

To identify and select relevant studies for the systematic literature review, a two-stage screening process using Covidence was employed. In the first stage, titles and abstracts of all retrieved studies were screened to exclude irrelevant studies. In the second stage, full-text articles were assessed against a predefined set of eligibility criteria. Reasons for exclusion were recorded within Covidence using the following customized list designed to reflect the ecological focus of this review:

- Data in paper comes from other paper that was already included
- Data are not provided on the direct link to ecosystem functions
- No full text available
- Language barrier (non-English articles without reliable translations)
- Wrong study type (e.g., opinion pieces, news articles, or non-scientific sources)
- Irrelevant ecological process (e.g., no link to nutrient cycling, productivity, or climate regulation)
- Wrong species (e.g., terrestrial species)
- Unrelated topic
- Not linked to any ecosystem function/service

Inclusion criteria were applied conceptually, without requiring their explicit entry into Covidence. Studies were included if they (1) focused on cetaceans (with a focus on humpback whales) or included them in multi-species assessments and (2) addressed ecological processes with relevance to ecosystem service provision (e.g., nutrient cycling, carbon sequestration, fishery enhancement), and (3) provided conceptual frameworks applicable for the scope of work of this study.

The screening process resulted in the selection of 71 papers for data extraction. Information about the author, year, geographic focus, type of ecological function or service, methodological approach, and key findings was extracted. Where available, quantitative estimates of ecological effects or ecosystem service values were recorded. This data is provided in Appendix 2 as a supplemental spreadsheet.

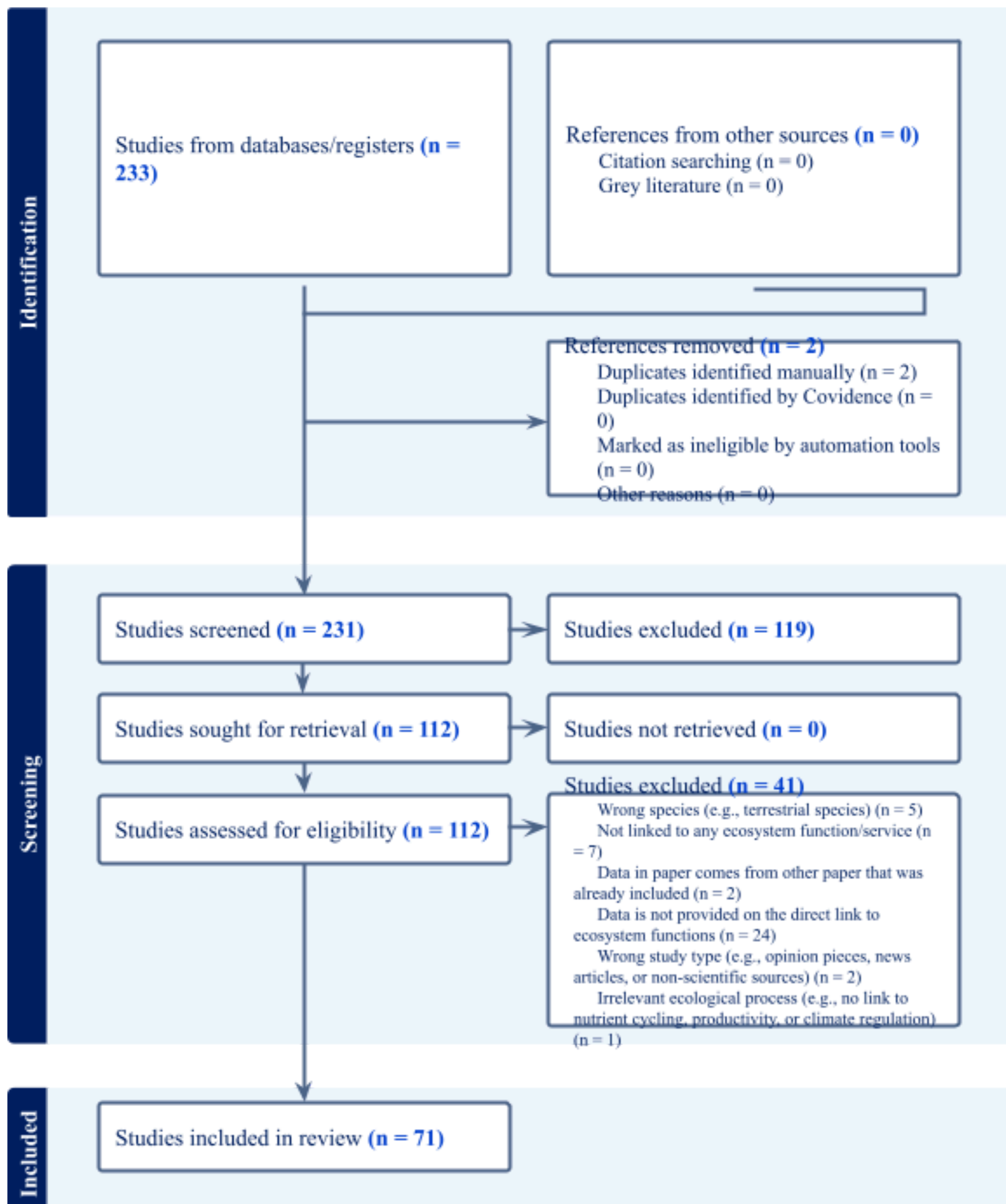


Figure 12. Screening process results.

Appendix 2. Data extraction spreadsheet

Attached to this report as an Excel file.

Appendix 3. Co-design and validation workshop

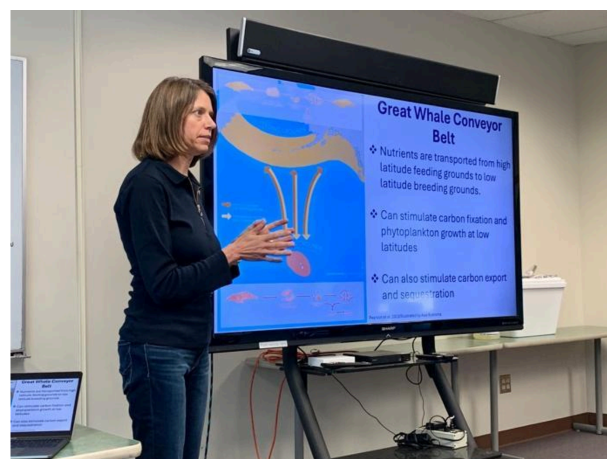
To better understand the potential role of humpback whales in the provision of ecosystem services, a 1-day workshop was held in Juneau, Alaska, on August 18th, 2025, with experts from

multiple scientific disciplines, including marine mammals, oceanography, fisheries and ecological economics, among others (see participants list later in this section).
The workshop had three main objectives:

- Map and understand the current food web of humpback whales and other cetaceans in the North Pacific.
- Build the links and pathways of the role of humpback whales in the North Pacific in supporting nutrient cycling, fisheries productivity and carbon sequestration.
- Identify drivers of change and its impact on humpback whales in the North Pacific.

To avoid replicating information, the systematized results of the workshop (e.g., food web, contribution pathways) are incorporated in section 3.2 as part of the design and implementation of the framework.
A summary of each session for each objective is provided below.

1. Introduction to natural capital valuation: With the goal of providing a common language to all participants, Marcello Hernández-Blanco provided an overview of the concepts of natural capital and ecosystem services, as well as the methodological approaches to value them. A core topic discussed was the concept of ecosystem health, since the approach of this project focuses on the role of cetaceans in maintaining an ecosystem healthy so it can provide benefits to people. Following this idea, an ecosystem service cascade framework was introduced to the participants, to better visualize how whales fit in the structure of the ecosystem and how this helps provide ecosystem functions, and if there are a group of people that benefit from these functions, then an ecosystem service with a potential economic value exists.



2. Mapping humpback whale's food web: As explained in step 3 of the general framework, the first step to identify the role that a species plays in supporting ecosystem services is to understand its interactions with the other biotic and abiotic elements of the system, where a trophic dynamic analysis can be fundamental. Therefore, the second presentation of the workshop was from Heidi Pearson, where she provided an overview of

the North Pacific humpback whale ecology, including migrations, abundance, nutrient cycling supported by this species, feeding habits and finally a simplified food web for Southeast Alaska that included other animal groups such as seabirds and pinnipeds.
After Pearsons's presentation, the first group exercise of the workshop was done, where participants were asked to map collectively the food web of North Pacific humpback whales. Due to the expertise of the participants, it was decided that the exercise was going to be focused on Alaska, and therefore it is important to note that the food web mapped will change in other feeding areas of the North Pacific population (e.g., Japan). The web was kept at a medium resolution to have a clearer perspective of the interactions of the groups (Figure 13). For example, it was highlighted that phytoplankton can be divided in different species, as well as copepods as the main grazers of the system. In terms of fish species, the group highlighted those of commercial interest (e.g., herring) since one of the ecosystem services that are part of this research is the provision of food through fisheries.

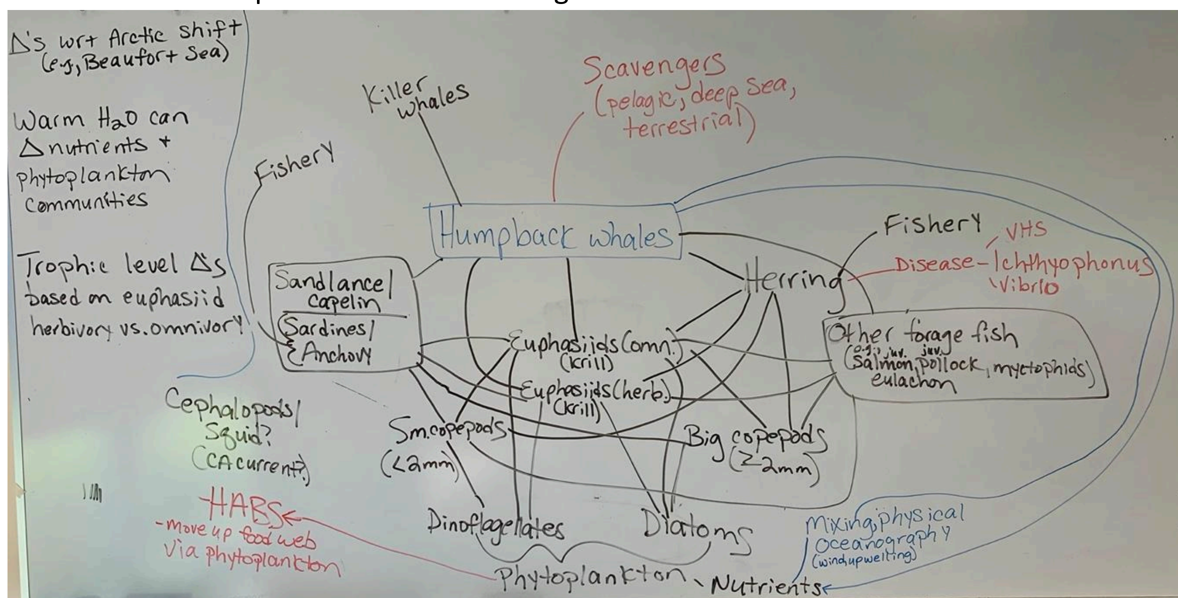


Figure 13. Result of the food web mapping exercise.

A key aspect to consider for future research is how this food web is actually multidimensional, where adding the dimensions of space and time can make an important contribution to understand the complexity of the system. For example, changes in water temperature (e.g., induced by climate change) can change prey preferences, as well as the composition of diatoms and dinoflagellates. An obvious time-space consideration that needs to be incorporated is the feeding-breeding times and places of North Pacific humpback whales.

3. Links and pathways of the role of humpback whales in the North Pacific in supporting ecosystem services: Also as part of step 3 of the proposed framework, the participants started an exploratory discussion on the *potential* links and pathways of the role that humpback whales *might* have in supporting the two ecosystem services in which focuses this project: (1) climate regulation and (2) food provision (i.e., fisheries). In terms of climate regulation, the group highlighted that, contrary to what other scholars have pointed out (e.g., Chami et al., 2019), for

humpback whales it is not possible to account the carbon in their bodies as a contribution to climate regulation since they live around 75 years, and therefore that carbon is stored for a period of that that is insufficient to be considered sequestered under standards such as the ones from the IPCC. Moreover, we cannot consider all phytoplankton stimulated by whales to lead to carbon sequestration. Therefore, only the carbon through whale falls was considered to be an appropriate, quantifiable contribution pathway (Figure 14).

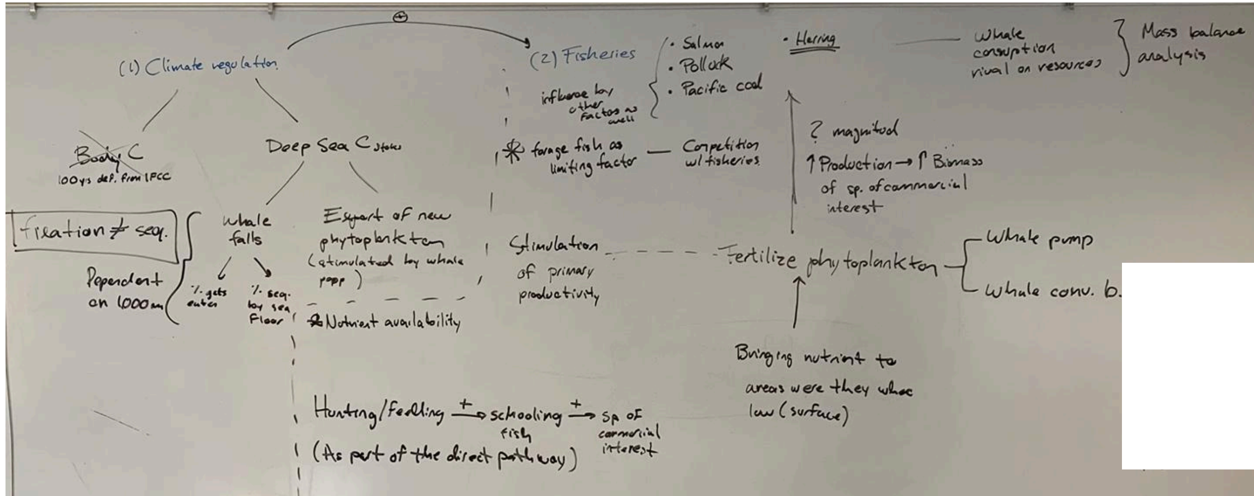


Figure 14.Result of the contribution pathways exercise.

Regarding fisheries, the discussion centered around the whale pump and the whale conveyor belt. Nevertheless, the participants are still unsure if a direct pathway can be established between North Pacific humpback whales and fisheries productivity, since the latter depends on multiple factors that could potentially have a disproportionate effect. Moreover, the participants pointed out that forage fish is a limiting factor.

4. Drivers of change and its impact on humpback whales in the North Pacific. The last group exercise produced the following list of threats to North Pacific humpback whales what could potentially cascade in the change of ecosystem health and ecosystem services:

- Vessel strikes
- Entanglement
- Pollution (e.g., plastic, noise)
- Sea surface temperature
- Prey availability
- Competition (other species and industrial fisheries)
- Harmful algal blooms (HABs)
- Predation (e.g., from orcas)

Main conclusions of the workshop

The workshop produced all the outcomes set in the objectives. It also helped building capacities on the natural capital approach and valuation for the participants, who hopefully will bring this vision to their lines of work. The expertise of the participants was at the highest level, and their willingness to cooperate with this project were key determinants for the successful results.
Aside from the outcomes that will be directly incorporated in the main framework and analysis, two main conclusions can be drawn from the discussions among the participants. First, because the topic of this project is very novel, there are still many significant knowledge gaps in all the scientific fields involved (e.g., ecology, oceanography, ecological economics), and therefore establishing connections between cetaceans and ecosystem services are still almost impossible with at least a moderate confidence level. Related to the previous point, the experts and the project team members consider that the main outcome of the project should be to develop a research agenda based on the framework that will be proposed, paving the way for a wide variety of research avenues that will be needed to close the current knowledge gap in many aspects of the ecosystem service cascade involving humpback whales. Therefore, the collaboration and coordination among research initiatives is a key leverage point to move in the right direction.

Workshop agenda
Location: University of Alaska Southeast, Glacier View Room.
Date: August 18th, 2025
Duration: 9:00 AM – 4:00 AM

8:30 – 9:00 AM | Registration and coffee

9:00 – 9:30 AM | Welcome and opening remarks
- Brief round of introductions
- Project overview and workshop goals
- Overview of agenda and expected outcomes

9:30 – 10:30 AM | Session 1: Food web of North Pacific humpback whales
- Objective 1 – Map and understand the current food web of humpback whales and other cetaceans
- Presentation: Ecology and trophic role of North Pacific Humpbacks – Heidi Pearson
- Interactive mapping activity: Co-create a food web diagram with expert inputs
- Discussion: Knowledge completeness and gaps

10:30 – 10:45 AM | Coffee Break

10:45 AM – 12:15 PM | Session 2: Whale-driven ecosystem functions
- Objective 2 – Trace links between whales and ecosystem functions

- Presentation: The role of keystone species in supporting the provision of ecosystem services – the case of cetaceans – Marcello Hernández-Blanco
- Group Discussion:
    - Breakout groups to identify and map functional pathways
    - Groups rotate to cross-fertilize insights
    - Group presentations and discussion

12:15 – 1:15 PM | Lunch Break

1:15 – 2:30 PM | Session 3: Drivers of change of ecosystem health and whale impacts
- Objective 3 – Develop scenarios of change
- Divers of change Workshop:
    - Break into groups to build scenarios
    - Group presentations and discussion

2:30 – 2:45 PM | Coffee Break

2:45 – 4:00 PM | Session 4: Synthesis and crosscutting themes
- Interactive plenary discussion:
    - Identify clear pathways and uncertainties
    - Prioritize links and gaps using (e.g., dot-voting)
    - Next steps

<u>List of participants (from left to right)</u>
1. Marcello Hernández-Blanco, Conservation Strategy Fund
2. Mike Navarro, University of Alaska Southeast
3. Yumi Arimitsu, Ocean Bight, LLC
4. John Moran, NOAA/NMFS
5. Rob Suryan, NOAA/NMFS
6. Gabrielle Lopez, University of Alaska Southeast
7. Linnea Pearson, Alaska Department of Fish and Game
8. Carley Lowe, NOAA/NMFS
9. Heidi Pearson, University of Alaska Southeast

Appendix 4. List of traits from the 2021 IWC-CMS workshop

Trait	Description	Functions	Services	Ecosystem Service Category1 (as determined by Socio-Economic workshop participants)	Ecosystem Service subdivision1 (as determined by Socio-Economic workshop participants)
Nutrient transfer and circulation					
Body size and latitude	Cetaceans in tropical systems are dominated odontocetes (mostly smaller species: beaked whales, blackfish, delphinids), which largely replace mysticetes	Energy conversion by feeding on individual prey in a more oligotrophic environment vs engulfing swarms.	Vertical transport of nutrients - either by relatively shallow divers that feed nocturnally on diel migrating prey or deep divers. Smaller but more numerous whale falls	Supporting	*Nutrient cycling*
Capital breeding	Stored energy used for reproduction and survival	Long-distance migration, winter calving and fasting	Transport of nutrients from highly productive foraging grounds to nutrient poor, low latitude feeding grounds, in the form of carcasses, placentas, skin sloughing, feces, and urine	Supporting	*Nutrient cycling*

Epidermal molt	Killer whales and other migratory species travel thousands of kilometers each year for skin molt migration. Also some behaviors such as breaching (e.g. humpback whales) remove skin but also ectoparasites and epibionts.	Routine skin maintenance, feeding/molting hypothesis	Nutrient transport, microbial connectivity, food for scavengers and detritivores	Supporting	*Nutrient cycling*
Life span	Time in years	Nutrient storage	Nutrient cycling and maintenance of trophic interactions and ecosystem resilience and stability	Supporting	*Nutrient cycling*
Migration	Distance traveled per day, month, or year. Populations show range of movements from resident species (Gulf of California fin whale) to highly migratory (North Pacific gray whales, many humpback whale populations) For migratory species, length of stay in breeding or feeding areas	Nutrient transport, dispersal of microbes and other organisms, deep-sea whale-fall communities	Resource subsidies from high nutrient foraging areas to more oligotrophic winter or calving areas, provision of whale-fall communities along migratory pathways	Supporting	*Nutrient cycling*

Mortality rate	Number of deaths per unit of time in a particular area	Nutrient transport, carcass succession and decomposition in deep sea, coast lines, and breeding areas	Biodiversity promotion in the deep sea, maintenance of gene flow and genetic diversity,	Provisioning	*Genetic resources*
Prey for predators	Cetaceans as prey to killer whales and sharks, including 50 cm cookiecutter sharks	Providing prey for a range of predators	Killer whales and large sharks are a source of carcasses for scavengers and detritivores. For small sharks: a source of nutrient movement from surface layers to mid-water communities	Supporting	*Nutrient cycling*
Whale pump	Nutrients moved from aphotic zone to the surface	Similar to that of the biological pump, nutrient transfer from depth to surface and across migration routes	Nutrient cycling and promotion of biological diversity, particularly nitrogen, phosphorus and iron	Supporting	*Nutrient cycling*
Body size and soft-tissue lipid content	Mass, percent weight	Organic and inorganic nutrient storage and transport through growth, migration, mortality, and sinking	Transport of organic matter and inorganic nutrients from productive upper ocean to food-poor deep sea, provision of food to deep- sea, shallow-water and terrestrial scavengers, formation of reducing habitats at seafloor, nutrient cycling, carbon sequestration	Supporting	*Nutrient cycling*

Bone lipid content	Percent and total mass of lipids in skeleton	Provision of persistent organic and sulfide- rich habitat at seafloor	Promotion of habitat heterogeneity (including organic-rich and chemoautotrophic habitats) and biodiversity at the deep- sea floor, evolution of novel whale-fall species, ecological and evolutionary stepping stones for hydrothermal vent and methane seep faunas	Supporting	*Habitat provisioning*
Iron content in feces	Percent of iron content in whale feces, stimulation of primary and secondary productivity (krill) in feeding grounds	Provision of iron-rich sources to support and enhance phytoplankton and zooplankton growth	Nutrient enrichment of feeding grounds, stimulation of productivity throughout the wider marine ecosystem	Supporting	*Nutrient cycling*
Macronutrients in whale feces	Amount of nitrogen (NH4+) and phosphorous (PO43-) in whale feces	Stimulation of phytoplankton growth	The growth rate of phytoplankton from areas of whale populations	Regulating	*Carbon sequestration and climate regulation*
Social and reproductive behavior	Group size	Nutrient provision	Concentration of nutrients via hot spots and hot moments	Supporting	*Nutrient cycling*
Feeding-related traits					
Consumption rate	Amount of prey or milk ingested per unit of time	Trophic dynamics and cascades, nutrient storage and transfer	Ecosystem resilience and stability	Not ecosystem service	

Diel feeding patterns	Most feeding occurs at night and tracks deep scattering layer - mostly in the tropics	Allows animals to feed on vertically migrating midwater prey.	Vertical transport of nutrients from midwater to the surface	Supporting	*Nutrient cycling*
Excretion rate	Amount of excreted material per unit of time (g/day)	Nutrient storage, vertical nutrient subsidies, and community shaping by altering primary productivity	Nutrient cycling, enhanced primary productivity, carbon storage and sequestration	Regulating	*Carbon sequestration and climate regulation*
Feeding distance	Distance between the breeding location and foraging area	Nutrient storage, movement of nutrients from areas of high productivity to areas that are typically in lower latitudes and often lower productivity	Nutrient cycling and promotion of biological diversity	Provisioning	*Genetic resources*
Diving behavior	(Maximum) dive depths	Diving for foraging	Displacements more deeply, more movement of nutrients in the water column	Supporting	*Nutrient cycling*
Trophic Level	Trophic level of species in relation to prey consumption	Diet composition and trophic level ranges	Some nutrients are bio-accumulated in the food web. Cetaceans also exert top down controls on food webs	Not ecosystem service	
Surplus killing	Killing either more or much larger prey than can be consumed	Food source for deep and shallow water organisms and terrestrial scavengers	Can provide large amounts food (tons) for benthic scavengers and detritivores	Not ecosystem service	

Cetaceans as 'beaters' of live prey for seabirds	Feeding/traveling whales and dolphins opportunistically providing live prey for seabirds	Seabirds catch prey that would not normally be available to them	The prey is dispersed as guano at sea and at colonies	Not ecosystem service	
Cetaceans providing carrion for scavenging seabirds	Large, predatory odontocetes break up large prey and scraps are scavenged by seabirds	Seabirds feeding on prey normally too large for them	The prey is dispersed as guano at sea and at colonies	Not ecosystem service	
Provision of habitat, contribution to biodiversity & "blue carbon"					
Skeleton size and calcification	Mass and surface area/volume ratio of largest vertebrae, skull, and long bones	Provision of persistent organic or sulfide-rich habitat at seafloor, provision of hard substrate in soft-sediment habitats	Promotion of habitat heterogeneity (including organic-rich and chemoautotrophic habitats) and biodiversity at the deep- sea floor, evolution of novel whale-fall species, ecological and evolutionary stepping stones for vent and seep faunas	Supporting	*Habitat provisioning*
Carcass sinking to deep-sea floor	Nutrient food source for deep ocean fauna	Food source for many specialized deep-sea species, not found elsewhere. Many different stages, and last for decades on the sea-floor.	Physically modify and create new habitats. A number of stages supporting different species including 102 species 'whale fall specialists' that are not found elsewhere and need a whale fall to complete life cycles.	Supporting	*Habitat provisioning*

Body Mass	"Size matters", with high metabolic efficiency, larger animals store more carbon compared to smaller ones	Storing carbon, preventing it from being released into the atmosphere	Contribution to blue carbon as a "nature-based solution" (NBS)	Regulating	*Carbon sequestration and climate regulation*
Reproduction rate	Number of calves per year	Reproduction	More offspring more biomass for the ecosystem	Not ecosystem service	

The contribution of whales in supporting marine ecosystem services

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Photo: Marcello Hernández-Blanco

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