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ECONOMIC VALUATION OF ECOSYSTEM SERVICES PROVIDED BY DEEP-SEA SPONGES
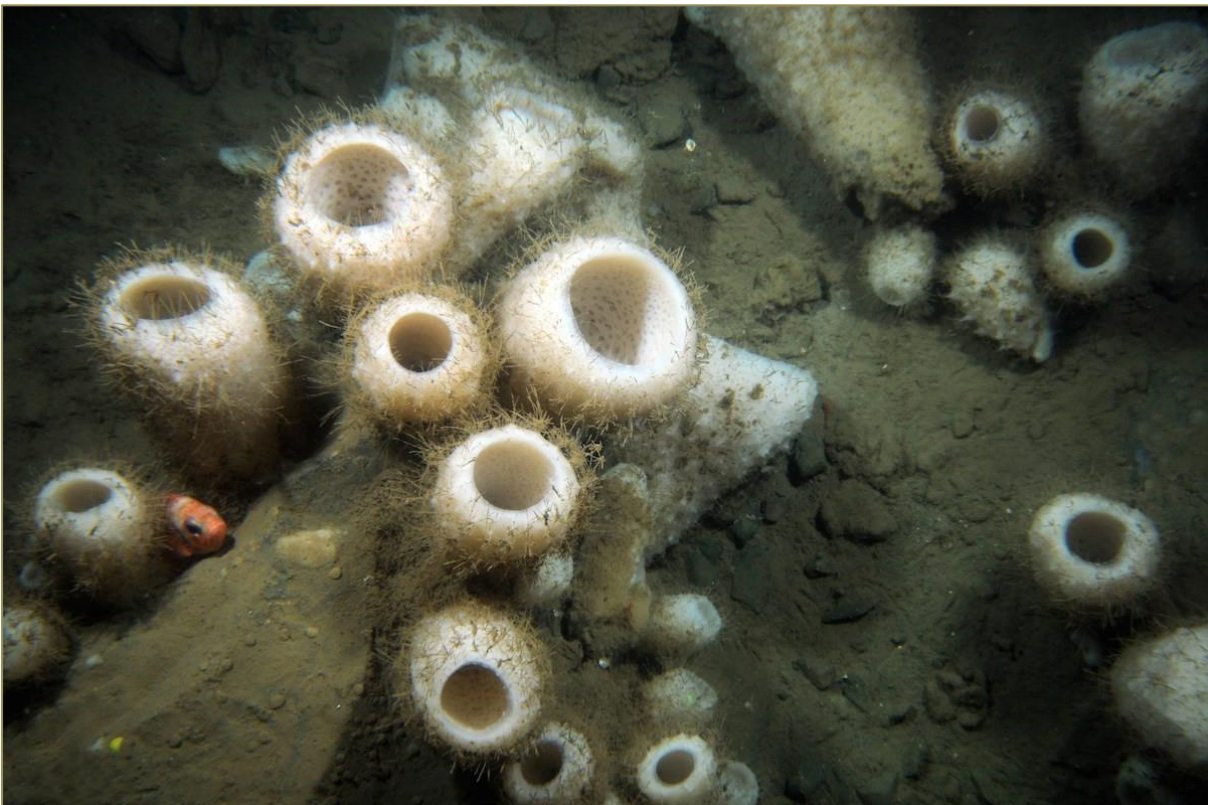
ECONOMIC VALUATION OF ECOSYSTEM SERVICES PROVIDED BY DEEP-SEA SPONGES

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PREPARATION OF THIS DOCUMENT

This circular was prepared under the auspices of the SponGES project investigating "Deep-sea sponge grounds ecosystems of the North Atlantic: an integrated Approach towards their Preservation and Sustainable Exploitation" and supported by the European Union's Horizon 2020 research and innovation programme (Grant agreement No. 679849).

The content of this circular addresses the SponGES project Deliverable D8.1 –report on the baseline data for economic valuation of deep-sea sponge ecosystem services – serving as a control point for Task 8.1 of SponGES Work Package 8 (WP8) focusing on "Resource Management and Conservation".

The economic valuation framework of ecosystem services from deep-sea sponges has been presented at two side events that were held at FAO headquarters in Rome, Italy during the General Fisheries Commission for the Mediterranean (GFCM) Fish Forum on 10-14 December 2018, and during the "ABNJ Deep-sea Meeting" on 7-9 May 2019, respectively.

The author has received valuable specific inputs in the form of preliminary data analysis and discussions which took place at the Department of Fisheries and Oceans, Bedford Institute of Oceanography, Dartmouth, Nova Scotia, Canada, as well as by participating in the NAFO Joint Commission-Scientific Council Working Group on the Ecosystem Approach Framework to Fisheries Management (WG-EAFFM) on 16-18 July 2018 at NAFO's Headquarters in Halifax, Nova Scotia.

The report has been largely shared and discussed with participants of the SponGES project as well as with the EU project reviewers Dr. Evangelos Papathanassiou and Prof. Alan Deidun. At different stages of its development, the approaches employed and achievements attained have been presented and discussed during Annual General Assembly Meetings which were held in Porto, Portugal on 16-20 April 2018, in Wageningen, Netherlands on 20-24 May 2019, and during an online SponGES Final Project Meeting on 10-12 November 2020.

ABSTRACT

This report was commissioned under the SponGES project as a pivotal information item (Deliverable 8.1) with a direct impact on resource management and conservation of deep-sea sponges in the North Atlantic. It is based on information available in the scientific literature at the time of writing, but also indicates the research areas where discoveries and research advances are shortly expected. The report is aimed at a generic public with no specialized knowledge on sponges or on economic valuation. It is outlined in a way to provide essential background information but makes reference to a comprehensive list of scientific publications for further insights.

The initial part provides basic information on the definition of ecosystem services, on an ecosystem service classification framework, and on common approaches undertaken for ecosystem service valuation. In this introductory overview, the economic valuation of deep-sea sponges is placed in the wider context of ecosystem services provided by the deep sea. Common challenges encountered in the economic valuation of deep-sea sponges as well as deep-sea ecosystems are discussed, and a summary is provided of approaches found in the literature for the economic valuation of deep-sea ecosystem services.

The ecosystem services provided by sponges were categorized under The Economics of Ecosystems and Biodiversity ecosystem service classification. This classification distinguishes four main categories of ecosystem services: provisioning services; regulating services; habitat services; and cultural services. Four ecosystem services associated to deep-sea sponges, one for each category, were selected and used to exemplify the level of information needed for an economic valuation as well as common challenges and data gaps encountered.

In particular, deep-sea sponges were analysed as a potential source for pharmaceuticals and biotechnology applications (provisioning services), as natural filtering systems of the deep sea (regulating services), as habitat for commercial fish species (habitat services), and as promising candidates for scientific research and education (cultural services). The overall description of baseline ecological and economic data required for a monetary valuation of these four ecosystem services was further complemented by detailed examples on how economic valuation approaches could be applied to existing baseline data. These examples, described in stand-alone text boxes, show the complexity of the economic valuation of deep-sea sponges. At the same time, they also provide some insight on what the economic relevance of deep-sea sponge ecosystem services could be in future, when, with advances in scientific research, the full ecological and consequently economic importance of deep-sea sponges will become more evident.

The final part of the report outlines the way forward, pointing out the research priorities for making advances in the economic valuation of ecosystem services provided by sponges. It presents an overview of current drivers on research on deep-sea sponges, existing and required investments, and challenges posed to policymakers in considering present and future trade-offs in the management of the deep sea. It wraps up by summarizing the economic benefits, ecological reasons and cultural value of sponges as a possible UNESCO site of outstanding universal value, recommending the precautionary principle in the conservation and management of deep-sea sponge grounds.

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ACKNOWLEDGEMENTS

ABBREVIATIONS AND ACRONYMS

AAAS	American Association for the Advancement of Science
AML	acute myeloid leukaemia
CV	contingent valuation
CICES	Common International Classification of Ecosystem Services
DCE	discrete choice experiment
DOM	dissolved organic matter
EEA	European Environment Agency
EFH	essential fish habitat
EMA	European Medicines Agency
EMB	European Marine Board
FDA	Food and Drug Administration (the United States of America)
MEA	Millennium Ecosystem Assessment
MPA	marine protected area
MSC	Marine Stewardship Council
NAFO	Northwest Atlantic Fisheries Organization
OSPAR Convention	Convention for the Protection of the Marine Environment of the North-East Atlantic
PPP	purchasing power parity
R&D	research and development
SEEA	System of Environmental-Economic Accounting
SEEA-EEA	System of Environmental-Economic Accounting Experimental Ecosystem Accounting
TAC	total allowable catch
TEEB	The Economics of Ecosystem and Biodiversity
TEV	total economic value
UNESCO	United Nations Educational, Scientific and Cultural Organization
VME	vulnerable marine ecosystem
WHO	World Health Organization

To Hans Tore Rapp
who inspired this study
through his dedication to research on
deep-sea sponges

1. INTRODUCTION

1.1. Sponges: simplicity at odds with complexity

The economic valuation of ecosystem services from deep-sea sponges poses several challenges. Many of these challenges are inherent to sponges' biological and ecological traits as well as to the location of sponge grounds in very remote marine areas.

The study and understanding of these marine organisms is advancing rapidly thanks to specific research funding, advances in molecular approaches, and increased capabilities in deep ocean technology. However, the investigation of sponges requires a multifaceted approach. Sponges represent a very interesting and unique group of organisms, which can be considered a conundrum of simplicity and complexity.

Sponges are considered the most primitive multicellular animals (Simion *et al.*, 2017). Their body structure is essentially an aquifer system[1] where water is actively pumped inside the sponge body through the movement of specialized cells. Water enters from the pores placed on the sponge body surface and exits through one or more efferent channels. This constant water flow enables food collection, oxygen supply and waste excretion.

A skeleton made of calcareous or siliceous spicules, fibres of spongin or both supports and protects the soft inner body of the sponge. The skeleton, along with other traits, allows for the separation of sponges into four classes: **Calcarea**, **Hexactinellida**, **Demospongiae**, and **Homoscleromorpha**. Therefore, species identification often requires collection and microscopic examination of sponge skeletons (van Soest, 1990).

Sponge species are difficult to classify, and phylogenetic relationships among major groups and subgroups of sponges are still largely unresolved (Cárdenas, Perez and Boury-Esnault, 2012). The taxonomic identification of sponges is complicated by their unique morphological traits and intraspecific variability in shape and colour. In the last 30 years, the development of molecular biology has allowed for a range of new technique to investigate phylogenetic relationships among sponges, so that genetic characterization is becoming increasingly important in sponge classification (Borchiellini *et al.*, 2000).

Sponges have a peculiar cellular organization, combining nearly undifferentiated cells (e.g. amoebocytes) with highly specialized ones (e.g. choanocytes). Sponge cells do not organize in proper tissues and organs. Many physiological functions are carried out through their aquifer system, as sponges do not have, for instance, digestive and circulatory systems. Sponges can be considered as primitive multicellular animals. In fact, in the evolutionary tree, sponges are the first and most simple members of Metazoa to depart and differentiate themselves from all other multicellular animals (Porifera sister hypothesis) (Simion *et al.*, 2017).

Besides their simple body structure, sponges have proved to be a very successful taxonomic group able to adapt and survive in time. This evolutionary success is ascribed to unspecialized cells able to transform themselves into other cell types when in need, and to the large array of symbiotic micro-organisms that can be found inside cells, between cells, and/or in the other sponge gelatinous matrix (mesohyl) (Thomas *et al.*, 2016). In so-called high microbial abundance sponges, associated bacteria

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[1] The only exception is constituted by carnivorous sponges, in which the aquifer system is absent.

can represent up to the 38 percent of sponge wet weight (Vacelet and Donaday, 1977). Sponges have complex symbiotic microbial communities, which can differ among sponge species but also differ among individuals belonging to the same species even when spatially close (Busch *et al.*, 2020; Hardoim *et al.*, 2012). This strict association has led to their being considered single ecological units (holobionts).

Sponge holobionts produce a diverse array of compounds that are not directly involved in the sponge normal growth, development or reproduction. For this reason, they are collectively referred to as secondary metabolites. These secondary metabolites often show marked bioactivity, and their production is often believed to be induced as a response to predation, wounding, antifouling strategy, and stress in general (Koopmans, Martens and Wijffels, 2009).

Secondary metabolites enable great chemical versatility and thus provide sponges with a greater capacity to face biotic and abiotic stressors, and to adapt and survive (Thomas et *al.*, 2016). This ecological adaptability is likely to have supported the current worldwide distribution of sponges, which occur in many of the world's oceans from the polar regions to the tropics, and in shallow waters as well as in deep-sea waters.

In the deep sea, considered as those marine areas below 200 m depth (Gage and Tyler, 1991), sponges may form extensive aggregations (i.e. deep-sea sponge grounds), typically occurring on continental shelves, slopes, deep ridges, seamounts and canyons (Tabachnik and Collins, 2008; Maldonado *et al.*, 2017). Deep-sea sponge grounds constitute complex structural habitats in otherwise homogeneous seafloor environments, creating important hotspots for biodiversity (Hogg *et al*., 2010) with relevant associated micro and macro fauna (Hawkes *et al.*, 2019). The geographical distribution of deep-sea sponge grounds seems to be determined by specific environmental parameters, such as hydrography and temperature (Rice, Thurston and New, 1990; Murillo *et al*., 2012), salinity and silicate (Beazley *et al*., 2015; Howell *et al.*, 2016), as well as concentration of organic carbon (Barthel, Tendal and Thiel, 1996; Howell *et al*., 2016).

In the deep sea, there is no primary production from photosynthesis. The deep-sea oligotrophic conditions are partly mitigated by chemosynthetic primary production supplied by specialized bacteria living in hydrothermal vents, cold-water methane seeps, and partly by transport of nutrients.

Most deep-sea organisms rely at some level on food inputs from the photic zone, which sinks and/or is transported to deeper layers by a variety of mechanisms. Bentho-pelagic coupling is a fundamental process through which inorganic and organic nutrients, mass and energy are exchanged between the pelagic and benthic zones. Processes occurring in the deep sea may also contribute at different levels to climate regulation, as for instance, by preventing carbon dioxide and methane in the deep sea from reaching the atmosphere and reducing greenhouse gas emissions through the ocean-atmosphere interface.

Sponges are filter feeders, feeding both on bacteria (bacterioplankton, picoplankon) and dissolved organic matter (DOM) with variable effectiveness depending on the sponge species and the relative abundance of these prevailing food types. Deep-sea sponges are directly involved in the carbon cycle as they consume large quantities of organic carbon to meet their high energy requirements. Scaling up this process, the occurrence of remarkably large sponge aggregations on the seafloor can influence the rate of food intake, respiration, absorption and recycling of several nutrients. Thus, sponge metabolism can affect bentho-pelagic coupling and cycling rates of nutrients such as carbon, nitrogen, phosphorus and silicon in the deep sea (Maldonado, Ribes and van Duyl, 2012). Thus, deep-sea sponge grounds can play an important ecological role within the deep-sea ecosystem.

This overview shows that despite sponges having a primitive cellular-level organization, a relative high level of functional complexity hides beyond the sponge's apparently basic life form. In particular, investigation of sponges implies: the characterization of sponge-associated micro and macrofauna; the

classification of sponge-symbiotic organisms; research on the bioactivity of secondary metabolites produced by sponges; and the identification of sponge metabolic requirements and sources of nutrients consumed. The geographical distribution of sponges, the actual area covered by deep-sea sponge grounds, and the estimated density of individuals are necessary information to model the role played by sponges in nutrient availability and cycling in the deep sea.

Therefore, research on deep-sea sponges is complex and deeply weaved into microbiology, ecology, evolution, taxonomy, genetics, molecular biology and biotechnology. Owing to this complexity, the identification and full accounting on the importance of deep-sea sponges and the ecosystem services they provide will advance in parallel with progress in scientific research.

1.2. Economic valuation

Economic valuation is the process of assigning monetary/or other values to the benefits conveyed by ecosystem services. Based on The Economics of Ecosystem and Biodiversity (TEEB) (TEEB, 2010), Figure 1 illustrates how economic valuation can be considered a tiered approach.

Tier 1 deals with the identification of ecosystem services and acknowledging their value. Even a qualitative assessment describing the provision of ecosystem services concurs to recognize their value. Recognition of a value does not necessarily require value quantification. A philosophical position that attributes to ecosystems and ecosystem services an "intrinsic value" is often opposed to the idea of quantifying its value as such intrinsic value cannot be captured by any instrumental or utilitarian approach (Sagoff, 1997).

Tier 2 deals with the measurement of the change in the provision of benefits delivered by ecosystem services. The process of quantifying the provision of ecosystem services and demonstrating their value is meant to help in incorporating this value in decision-making (TEEB, 2010).

Figure 1
A tiered approach to the economic valuation of ecosystem services

Tier 1 Qualitative assessment of ES → Understand what ES are provided

Tier 2 Quantitative assessment of ES flow in physical terms → Measure changes in the provision of benefits from ES

Tier 3 Quantitative assessment of ES economic value → Measure changes in the provision of benefits from ES in monetary terms
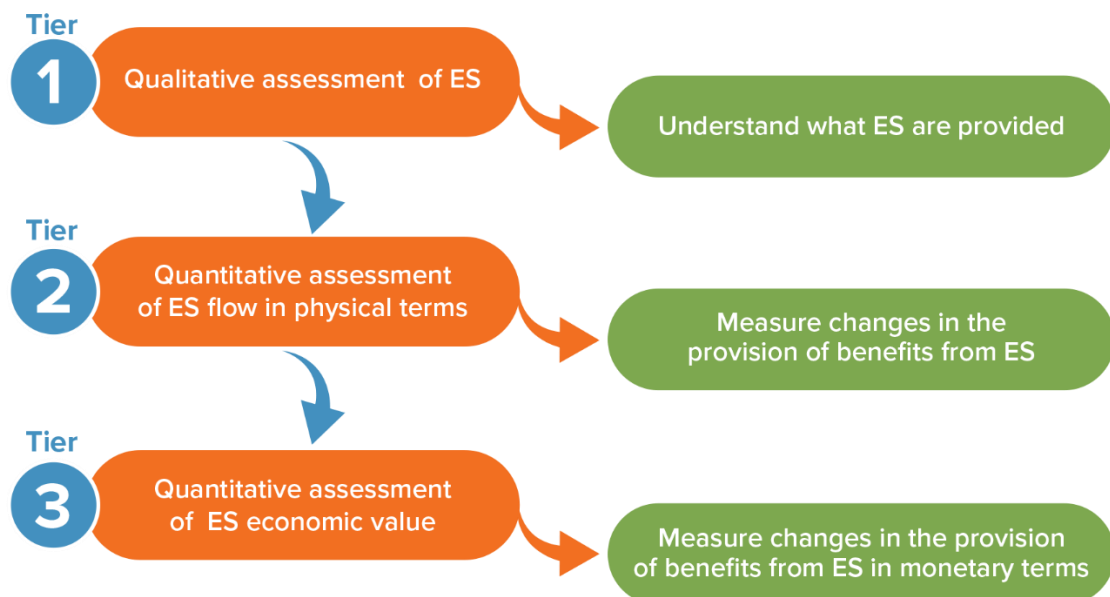
Note: ES = ecosystem services.

Tier 3 deals specifically with an economic assessment of ecosystem service values. Assessed values can include both use and non-use values, and different valuation methods are available to be applied according to the appropriate context.

Basic information encompassing all levels from a qualitative assessment (Tier 1) to a quantitative assessment of ecosystem service value (Tier 3) is provided in the following paragraphs.

1.2.1. Definition of ecosystem service

Natural capital, the world's stocks of natural assets (which include geology, soil, air, water and all living things) underpins economies, societies and individual well-being. In order to make natural capital relevant to society and decision makers, the ecosystem service framework was first proposed by the Millennium Ecosystem Assessment (MEA) (MEA, 2005).

In the MEA ecosystem service framework, the benefits that humans receive from ecosystems are grouped into four types of categories:

- **Provisioning services:** the goods or products people obtain from ecosystems (e.g. food, water, timber and fibre).
- **Regulating services:** the benefits obtained from the regulation of ecosystem processes (e.g. climate regulation, erosion control, and waste-water treatment).
- **Cultural services:** the non-material benefits obtained from ecosystems (e.g. aesthetic, spiritual, educational, recreational).
- **Supporting services:** natural processes that help maintain other ecosystem services (e.g. primary production, and nutrient cycling).

Further research work clarified the pathway that links the natural capital of ecosystems to the value they have for human society. This pathway is represented by the "ecosystem service cascade" model (Figure 2), initially proposed in Haines-Young and Potschin (2010) and further refined by De Groot et al. (2010). The cascade comprises different layers: biophysical structures; ecological functions; ecosystem services; societal benefits; and ecosystem service values. Each layer feeds the subsequent one in a sort of cascade, or similar to a production chain.

Figure 2

Illustration of the ecosystem service cascade model
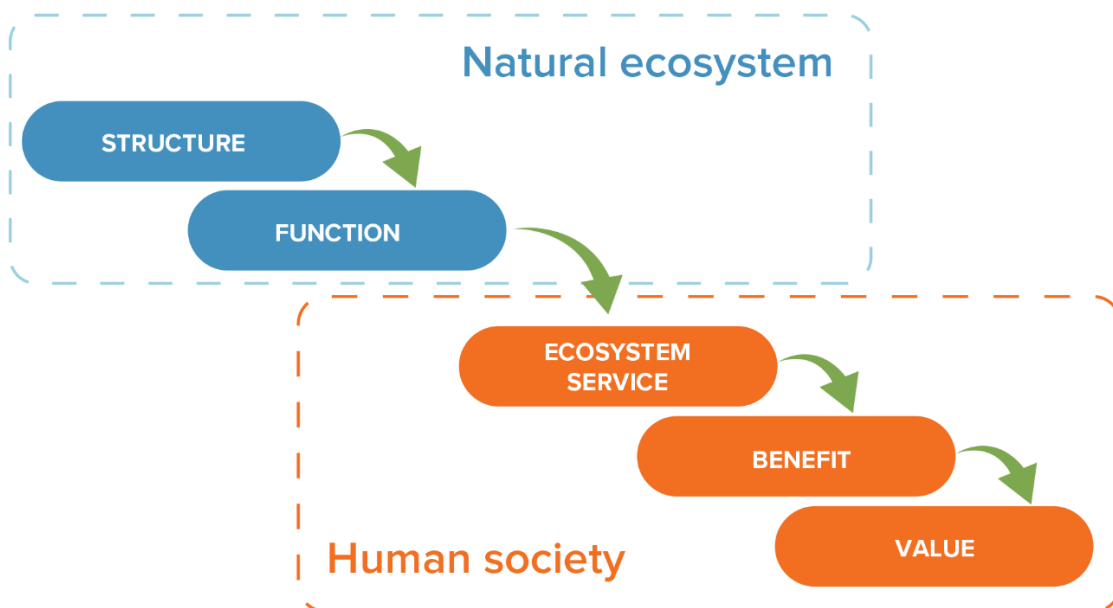
Source: Adapted from Haines-Young and Potschin, 2010.

At the top of the ecosystem service cascade are ecosystems, characterized by specific biophysical structures and functions, which together contribute to ecosystem functioning and maintenance. Ecosystem functions exist independently of any human enjoyment, use or valuation. It is only when one or more ecosystem functions combined together provide, directly or indirectly, a contribution to human well-being that ecosystem services are generated. Ecosystem services provide contributions (often in combination with other inputs) to human well-being through the benefits that they sustain. The value of these benefits can be expressed in many different ways by means of quantitative or qualitative criteria.

This ecosystem service cascade helps to distinguish different concepts. Thus, ecosystem services are not properly the benefits, as initially defined by the MEA (MEA, 2005), but they are considered as direct and indirect contributions of ecosystems to human well-being (TEEB, 2010). The concept of contribution to human well-being addresses the fact that some ecosystem services might require other capital inputs for their provision (see examples in Böhnke-Henrichs *et al.*, 2013). When ecosystem services are delivered to some beneficiaries, then benefits can be identified and measured, and consequently their value can be assessed.

The ecosystem service cascade is a highly simplified representation of reality. Ecosystem services often result not only from one single ecosystem function but from a bundle of ecosystem functions. In the same way, an ecosystem service might convey not only one type of benefit but a bundle of benefits (Austen *et al.*, 2019).

This ecosystem service cascade is often read from the top down, but the conceptual model should not be considered as linear. There are several feedback loops created by its interlinked nature, and by the management and use of the ecosystems by humans, which ultimately affect ecosystem service provision (Balvanera *et al.*, 2014).

As pointed out by Haines-Young and Potschin (2010, the linkages among the different elements of the ecosystem service cascade should also be considered, and questions should be raised such as:

- What are the major drivers of change impacting the flow of ecosystem services?
- What are the critical elements and thresholds in the ecosystem structure/function necessary to maintain ecosystem functioning?
- To what extent can an ecosystem be restored once damaged? What would be the timeline for its natural regeneration?
- Can all contributions made by ecosystem services to human well-being be translated into values?
- How are ecosystem services values, once made explicit, reflected into current management and use of ecosystems?

Commonly, this complexity is not fully translated in the valuation process. Assessing and quantifying every element of the ecosystem service cascade remains challenging, especially when ecosystem functioning is still poorly understood. In this case, indicators are used to capture the most emergent features of ecosystem complexity.

Indicators can measure ecosystem services as well as ecological functions contributing to the delivery of ecosystem services (Hattam *et al.*, 2015). In a similar way, indicators can measure benefits of human use or enjoyment of ecosystem services, and indicators of value can be used to assess these benefits.

1.2.2. Ecosystem service classification frameworks

The first step in an ecosystem valuation is selecting an ecosystem service classification framework. Besides the MEA (2005) classification of ecosystem services, there are other two major classification

frameworks: the Common International Classification of Ecosystem Services (CICES), and TEEB. The correspondence among the three classification systems is shown in Appendix 1.

As pointed out by Fisher *et al.* (2007), there is no single classification system for ecosystem services that is appropriate for use in all cases. The following paragraphs provide an overview on the different classification frameworks with their pros and cons. Reasons for selecting the TEEB classification for this study are also discussed.

MEA ecosystem service classification

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CICES ecosystem service classification

The first draft of the CICES was developed in 2008 during an international expert meeting organized by the European Environment Agency (EEA), together with the United Nations Environment Programme and the German Federal Ministry of Environment (EEA, 2011). Subsequentially, this initial draft has been revised several times and refined by Haines-Young and Potschin (Haines-Young and Potschin, 2012, 2018). The CICES was developed as part of the System of Environmental-Economic Accounting (SEEA),[2] which also includes a module on SEEA Experimental Ecosystem Accounting (SEEA-EEA) for assessing ecosystems and ecosystem services (United Nations, Organisation for Economic Co-operation and Development and World Bank, 2013; United Nations, undated).

Although the CICES was originally developed for terrestrial ecosystems, it can be adapted to marine ecosystem services (Culhane *et al.*, 2018). However, the use of the CICES for the accounting of marine ecosystems is still in a testing phase (Dvarskas, 2019).

The CICES is based on the ecosystem service cascade model (Figure 2). In the CICES, there are only three groups of ecosystem services (provisioning, regulating and cultural), as supporting services fall into ecosystem "functions" rather than "services" (Haines-Young and Potschin, 2012). The main reason for eliminating the supporting services category is to avoid the issue of double counting ecosystem services in valuations (Haines-Young and Potschin, 2012). Those features that in the MEA would be considered supporting services, in the CICES are considered as preconditions – underpinning elements within an ecosystem, required for the provision of a service (Potschin-Young *et al.*, 2017).

The SEEA-EEA, in its first release (United Nations, Organisation for Economic Co-operation and Development and World Bank, 2013), complied completely with the CICES approach and did not consider supporting services as a category of ecosystem services. However, in its second revision, the SEEA-EEA is currently making a proposal for a distinction between intermediate and final ecosystem services (Hein *et al.*, 2019). The concept of intermediate service (i.e. a service from one ecosystem asset to the next) was introduced to represent some important supporting services. The choice was motivated

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[2] The SEEA initiative, led by the United Nations, is a framework to collect and integrate within the same framework environmental and economic data (United Nations, 2014).

by the consideration that "if there were no place for intermediate services in the accounts, the accounts would be of less value in terms of providing the knowledge base for managing the ecosystem" (Hein *et al.*, 2019).

The CICES classes of ecosystem services are further split into divisions, groups and classes (Haines-Young and Potschin, 2018). This hierarchy was created for the purpose of economic accounting. However, the large number of categories and classes of the CICES make it difficult to have an overview at a more aggregated level (Hasler, 2016).

TEEB ecosystem service classification

The TEEB classification (TEEB, 2010) used the conventional categories of provisioning, regulating and cultural services and added habitat services as a new category. This latter only partially overlaps with the MEA's supporting services category. Habitat services include habitat and genetic diversity as fundamental services to maintain species life cycles and overall species biodiversity.

The TEEB classification has been specifically adapted for marine ecosystems by Böhnke-Henrichs *et al.* (2013) and further refined in Hattam *et al.* (2014). These classifications, as the CICES, clearly distinguish among ecosystem functions, ecosystem services and benefits. Moreover, Böhnke-Henrichs *et al.* (2013) and Hattam *et al.* (2014) provide a list of indicators related to marine ecosystem services that can help to frame the economic valuation assessment.

Another advantage of the TEEB classification is that it highlights the importance of habitat services and genetic diversity, which are two main characteristics of deep-sea sponges. The TEEB classification adapted to marine ecosystem included 21 ecosystem services provided by coastal and marine environments (Böhnke-Henrichs *et al.*, 2013). The refinement carried out by Hattam *et al.* (2014) in association with suggested indicators is reported in Appendix 2, but coastal related ecosystem services were omitted.

This classification can be considered as the basis to identify ecosystem services delivered by deep-sea sponges.

1.2.3 Plurality of values associated to ecosystem services

An economic valuation offers the possibility to compare the diverse benefits received by ecosystems by measuring and expressing them in a common denominator, typically a monetary unit. Although monetary units are used, the valuation process is not restricted to ecosystem services that are traded in the market and directly generate monetary benefits. On the contrary, the valuation process aims to also include those "less tangible" benefits that have no directly observable monetary benefits (Pagiola, von Ritter and Bishop, 2005).

A classification of the plurality of values that can be associated to ecosystem and ecosystem services is provided by the total economic value (TEV) framework (Figure 3) – a widely used framework that considers the utilitarian value of ecosystems (MEA, 2005). It was developed within the neoclassical economic paradigm to reflect the concept that individuals can hold multiple values towards ecosystem services (TEEB, 2010). It is a taxonomy commonly used in empirical analysis to provide recognition

Figure 3
Total economic value of ecosystem services and related benefits
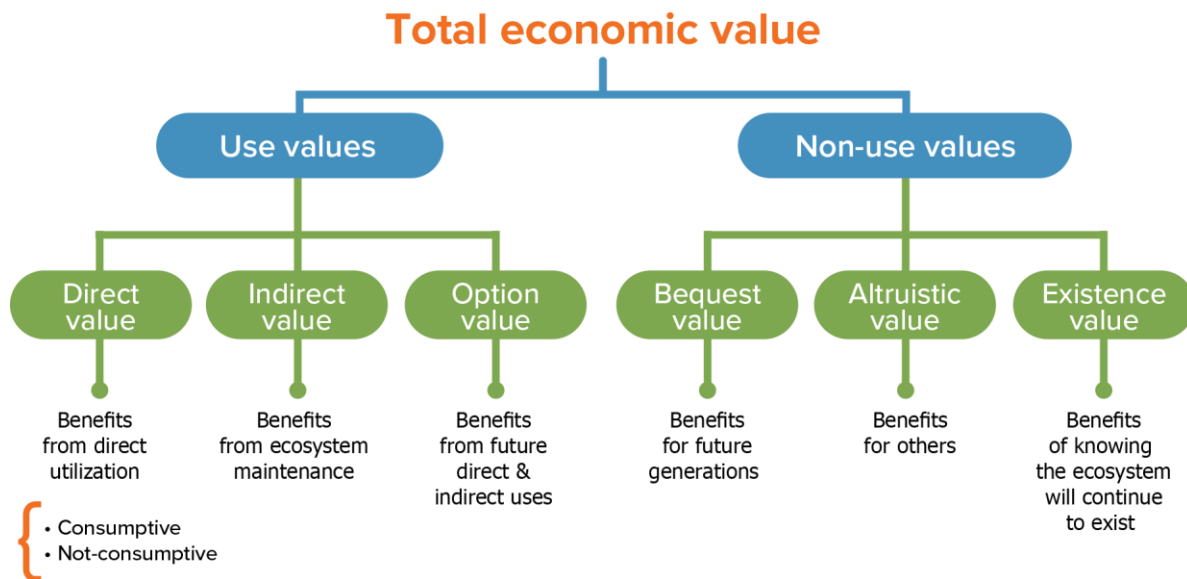
Source: Adapted from TEEB, 2010.

of the existing different types of values (National Research Council, 2005). The TEV framework can also apply to the deep-sea ecosystem as well as to deep-sea sponges ecosystem services.

In the TEV framework, the first distinction is between use and non-use values. Use values are associated with current or future (potential) use of a resource or ecosystem service, while non-use values arise simply from the continued existence of the resource and are unrelated to its use.

Use values can be further distinguished in three classes according to whether they provide direct or indirect benefits at the present time or whether benefits are likely to be available in future (option value). Direct use values can be consumptive when, for example, they are related to resources extracted from an ecosystem (e.g. seafood), or non-consumptive (e.g. recreation or education) when a direct use does not involve a decrease in the quantity of the resources available (but in some cases there can be a decrease in quality). Thus, direct use values are associated to provisioning services and several cultural services,

Indirect values are related to those ecosystem services that provide intermediate inputs for the production of final goods and services to humans (MEA, 2005). Regulating services, by controlling air quality, climate, hydrological cycles and water circulation, pest and diseases, and waste, ultimately determine suitable conditions for ecosystem use or enjoyment with direct uses (MEA, 2005).

Option values are related to the benefits that could be received in the future, despite the current lack of uses of the ecosystem and/or its resources. These values are often associated to benefits deriving from bioprospecting activities, which deal with the exploration of biological material for its genetic and biochemical properties that are considered potentially commercially valuable (Reid *et al.*, 1993). Option values can also be attributed to biodiversity (at the species, population and gene level), which can be considered as a form of insurance for the future (Baumgärtner, 2007). In fact, biodiversity confers resilience to ecosystem functioning and buffers abrupt regime shifts in the ecosystem with potential irreversible negative consequences for human well-being.

While use values involve some form of interactions with ecosystems, non-use values do not. Non-use values pose greater challenges in their valuation as they involve the sense of satisfaction or production of experiences that occur in the valuer's mind (Pascual *et al.*, 2010).

Altruistic value is related to benefits received by human society but not on a personal level. This value derives from the satisfaction of knowing that other individuals (excluding oneself) can currently enjoy goods and services. One example showing this altruistic value is making donations to promote marine-oriented recreational opportunities specifically tailored for people with disabilities.

While altruistic value looks at benefits received by contemporaries, bequest value is related to the desire to pass benefits from ecosystem services to future generations. Bequest value is highly intertwined with the idea of sustainable development, which aims at a use that does not deplete resources and them from becoming unavailable for future generations (Hallwood, 2014). For example, two studies assessed that different indigenous fishing communities in Madagascar (Oleson *et al.*, 2015) as well as in Fiji (O'Garra, 2009) were willing to pay a substantial portion of their income to protect marine ecosystems traditionally used as fishing grounds for future generations.

Existence value is related to the satisfaction of knowing that the deep sea and/or some particular species and/or features in it exist and will continue to exist. For example, an individual might place existence value on the existence of deep-sea sites recognized by the United Nations Educational, Scientific and Cultural Organization (UNESCO) as being of outstanding universal value (Freestone *et al.*, 2016) even if the remote location of these sites prevents any direct fruition.

1.2.4. Valuation methods

This section provides an overview of the available methods through which different types of values, described in Section 1.2.3, can be measured. The most widely used valuation methods can be grouped into five broad families:

- market-based;
- cost-based;
- revealed preferences;
- stated preferences;
- non-monetary.

Table 1 provides examples found in the literature on how these methods have been applied in the valuation of deep-sea ecosystem services. More details on these economic valuation studies are provided in the following sections illustrating the different valuation methods.

Table 1

Valuation methods used for different deep-sea ecosystem services

Category	Ecosystem service	Valuation method	Application to the deep-sea context
Provisioning services	Seafood	Market value	Bensch *et al.* (2009); Gianni (2004); FAO (2020); Sumaila *et al.* (2010)
	Medicinal resources	Market value	FAO (2020)
	Ornamental resources	Market value	FAO (2020)
	Raw materials	Market value	FAO (2020)
Regulating services	Carbon sequestration	Market value	Armstrong *et al.* (2010), FAO (2020); Martin *et al.* (2016); Trueman *et al.* (2014)
Habitat services	Habitat	Production function	Foley *et al.* (2010);
	Gene-pool protection[1]	Stated preferences	Aanesen *et al.* (2015); Glenn *et al.*, (2010); Jobstvogt *et al.* (2013); Wattage *et al.* (2011)
		Replacement cost	Barbier *et al.* (2014); Van Dover *et al.* (2014)
		Non-monetary techniques	Falk-Andersson *et al.* (2015); Jobstvogt *et al.* (2014a)
Cultural services	Scientific research and education	Market value	FAO (2020)
	Recreation and leisure	Market value	FAO (2020)

[1]Considered here as the conservation of deep-sea sponge ecosystems.

Market-based valuation methods

Market-based valuation methods consider the value at which environmental goods and services are traded in markets or in trading systems for specific resources (e.g. sequestered carbon). Market price is not equal to value. First, market price includes the resource cost (UNEP-WCMC, 2011). For example, in the case of fish, fish prices at landing also include the cost of the vessel, fuel, nets and labour, which do not form part of value of the fish commodity. Second, market price does not reveal the "consumer surplus"[3] (UNEP-WCMC, 2011).

In its simplest form, market prices and quantities are used to estimate the total expenditure by the purchaser (equivalent to the gross revenue received by the producer). This gross value should be considered as the lower bound of the real value (Pascual *et al*., 2010).

Market-based valuation is one of the most common techniques easily applied to traded fish species. This valuation technique can also be used in surrogate markets to estimate the value of reduced carbon

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[3] True economic value is revealed by consumer surplus, which is the difference between what consumers are willing to pay for a good and what actually is paid (market price) (Schuhmann, 2012).

emissions. The major advantage of market-based methods is that they are relatively easy to calculate and rely on information of quantity and prices that can be retrieved from economic statistics.

In the deep-sea context, a recent FAO desktop study has carried out a big data-mining effort to provide an economic valuation of deep-sea ecosystem services on a global scale (FAO, 2020). The study used a market-based approach to value the provision of deep-water fish, the harvest of precious corals, the use of substances of marine origin as pharmaceuticals, the extraction of deep and ultradeep oil, the potential mining of mineral resources from the seafloor, and the carbon sequestration carried out by the deep sea.

The major limitation of market-based valuation methods is that markets exist only for a minority of ecosystem services and, where markets do exist, they are often distorted (e.g. owing to subsidies, non-accounted externalities, or non-fully competitive markets) (Pascual *et al*., 2010). In this case, market price should be considered as a proxy of the value rather than the value itself.

Production functions represent another market-based valuation method. In this approach, the economic valuation considers the economic loss related to a decrease in the service provision. More specifically, this method estimates how much a given ecosystem service (regulating, supporting service, etc.) contributes to the delivery of another service or commodity that is traded on an existing market (Pascual *et al*., 2010). One case found in the literature estimated the role played by benthic habitats as essential fish habitats (EFHs) and showed how a decrease in habitat can be associated to a decrease in fish catch (Foley *et al.*, 2010).

Production functions are not easily applied to ecosystem service valuation owing to the lack of a full understanding of ecosystem complexity. Ecosystems typically respond non-linearly to perturbations. Production functions need to address interdependences among ecosystem services, critical points (thresholds) and the timescale at which ecosystem services are amenable to repair (Daily *et al.*, 2000).

Cost-based valuation methods

Cost-based valuation methods are a particular group of methods that do not assess the economic value associated to benefits but rather proxies related to costs. There are three main methods: avoided costs, replacement/restoration costs, and substitute costs.

Avoided costs refer to the delivery of ecosystem services that have positive impacts on human well-being, which can be measured, for example, in avoided medical care and saved sick days (i.e. avoided cost of illness).

Replacement/restoration costs are the estimated costs that could be incurred by society to replace or restore a destroyed/damaged ecosystem service. For example, a cost-based valuation was used to assess the restoration costs of aggregations of *Lophelia pertusa* destroyed by fishing trawlers (Barbier *et al.*, 2014; Van Dover *et al.*, 2014).

Substitute costs estimate the value of a non-marketed product based on the market value of an alternative product providing the same or similar benefits.

The main advantage of these methods is that estimated values are easily understood by policymakers and by the public at large. These estimates can be effective in communicating the opportunity costs associated with failure to protect natural ecosystems (Schuhmann, 2012).

However, their main disadvantage is that they assess costs rather than benefits. The benefits derived from the preservation of ecosystem services *in situ* can be very different from avoided costs or costs of replacing ecosystem services with artificial technology. It is also unlikely that human-made alternatives will provide the full range of benefits provided by natural ecosystems (Schuhmann, 2012).

These cost-based estimates are not suitable for cost–benefit analysis, as estimated benefits would be identical to the costs, thus leading to circularity of appraisal (Provins *et al.*, 2015). This also implies that a cost-based valuation method leaves a potential information gap on the (unaccounted for) true gains derived from preventing ecosystem service disruption. Despite these limitations, cost-based estimates are quite commonly used in the absence of other evidences, as often an imperfect estimate is better than no value at all (Provins *et al.*, 2015). When applied, cost-based estimates should be considered to provide only partial, lower-bound indications of the true value (Daily *et al.*, 2000).

Revealed preferences

The revealed preferences approach measures the benefits received from ecosystem services by interpreting behaviour, consumer choices, and purchases in markets associated with benefits conveyed by ecosystem services. It includes different valuation techniques such as hedonic pricing, avertive behaviour, and travel costs. However, this group of methods is difficult to apply to the deep-sea ecosystem context owing to the remoteness of the deep sea and the lack of a direct impact of the deep seas on human livelihoods.

Hedonic pricing is not applicable to the deep sea as it infers the benefits conveyed by ecosystem services through variations in property prices of houses. For example, housing prices along the coastline, close to beaches and/or with a view of the sea tend to exceed those of inland houses, owing to the additional recreational and aesthetic values of coastal and waterfront properties.

Avertive behaviour is a revealed preference method that measures consumer behaviour of individuals taking costly actions to avoid exposure to environmental hazards/nuisances. In general, this method is not easily applied owing to the difficulty in linking a given consumer choice to an environmental nuisance, as consumers might not be aware of the environmental issues and/or there could be multiple benefits behind such purchasing choices.

The consumer choice of buying more expensive fish, certified by the Marine Stewardship Council (MSC) as "sustainably" caught, can be considered a particular case of avertive behaviour. There are more than 170 fisheries certified by the MSC, including several deep-sea fisheries (Christian *et al.*, 2013). For example, consumers may be willing to pay extra money for purchasing halibut from the MSC West Greenland halibut fishery, which implements innovative technology for bycatch reduction (MSC, 2019).

The travel-cost method is often used to measure recreational values, as it looks at consumption behaviour of people travelling to a recreational site. The price paid for whale watching or scuba diving with sharks can reveal the value associated with the conservation of charismatic marine megafauna (Rogers *et al.*, 2015).

One of the major limitations of the travel-cost method for the deep sea is its remote location and its limited accessibility. In the FAO (2020) study, the recreational value of the deep sea was estimated based on the price paid for deep-sea dives with submersibles to visit sites such as the wreck of the RMS *Titanic*, seascapes and boulder formations, cold-water coral gardens, glass sponges, sharks and other deep-sea creatures. However, information was not extensively available as this is a very exclusive type of tourism in which operators are reluctant to share financial data on their business activities.

Stated preferences

This group of methods includes: contingent valuation (CV); and discrete choice experiment (DCE). Both methods acquire information by means of direct surveys. Individual preferences are assessed through questionnaires administered in person, by mail or by telephone. The great relevance of stated preferences is that they are the only methods capable of attributing a monetary value to non-use values.

In a CV study, one option for change is presented to respondents. The respondent are asked to choose whether they would support this option and consequently what price they would be willing to pay for it (i.e. willingness to pay); alternatively, the respondents can choose the current status (with no change) and no extra price paid.

In a DCE, multiple options are presented to respondents in the form of scenarios. Each scenario is made of different attributes, and one of these attributes is the associated cost to be paid. Respondents are asked to select the preferred scenarios or to rank them.

One important advantage of stated preferences is that they assess hypothetical situations in which the consequences of changes in provision of ecosystem services can be valued, even if the changes have not yet occurred. This *ex ante* valuation can provide useful advice for policymaking and decision-making (Nunes and Nijkamp, 2006). However, the hypothetical nature of these surveys raises the question of whether respondents' answers would in a hypothetical setting correspond to their behaviour if they were faced with costs in real life (i.e. hypothetical bias) (Pascual *et al.*, 2010).

There are a few studies that have used stated preferences techniques to assess the value of the deep sea. In Scotland, the United Kingdom of Great Britain and Northern Ireland, a DCE asked local households for their willingness to pay for a fourfold increase in additional marine protected areas (MPAs) in the Scottish deep sea. Under different scenarios, these additional MPAs would impact: (i) both the oil and gas, and the fisheries sectors; or (ii) the fisheries sector only (Jobstvogt *et al.*, 2013). In Ireland, a one-choice modelling survey investigated the preferences of the population regarding the protection of cold-water corals in relation to different extents of management of MPAs (Glenn *et al.*, 2010; Wattage *et al.*, 2011).

The major disadvantage of stated preferences techniques is that they need to be skilfully designed in order to avoid potential numerous biases and to make the survey representative of societal preference. Moreover, their implementation on a large scale can be very expensive (Armstrong *et al.*, 2010).

There is considerable literature dealing with the proper design of direct surveys. Many factors need to be taken into account, particularly when considering the deep sea, such as: the occurrence of charismatic species; familiarity with the topic and the degree of background information provided prior to the questionnaire (Armstrong *et al.*, 2010; Jobstvogt *et al.*, 2013); cultural diversity; income; education; and environmental awareness (Ressurreição *et al.*, 2012).

Non-monetary techniques for the valuation of ecosystem services

Non-monetary techniques for the valuation of ecosystem services include a large family of research techniques that try to capture preferences, needs or demands expressed by people towards ecosystem services in terms of individual preferences as well as collective preferences.

These techniques that can be divided in two main groups:

- individual index-based methods (including rating or ranking choice models, and expert opinion);
- group-based methods (including voting mechanisms, focus groups, citizen juries, stakeholder analysis, and discourse-based analysis).

In the deep-sea context, focus groups and questionnaires have been used to investigate attitudes and preferences of fishers, sailors and other citizens with no direct activity at sea on the protection and management of cold-water coral (Falk-Andersson *et al.*, 2015).

The Delphi[4] technique involves a specific focus group in which experts on a particular topic are brought together to determine consensus on a particular issue. It has been used among a group of deep-sea scientists to help delineate the ecological value of deep-sea submarine canyons. The scope was to distil the complex ecological knowledge of deep-sea experts into readily understandable units of information (i.e. "ecosystem principles") that could be used by policymakers and managers in decision-making (Jobstvogt *et al.*, 2014b).

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[4] The name comes from the ancient Greek city of Delphi, where people used to consult the oracle housed in the Temple of Apollo temple to receive answers and have their futures foretold.

2. ECOSYSTEM SERVICES FROM DEEP-SEA SPONGES

2.1. Deep-sea sponges: linking ecological functions and ecosystem services

The number and type of ecosystem services delivered by deep-sea sponge grounds is highly dependent on the structural characteristic of the sponge aggregation in terms of: (i) sponge species composition; (ii) sponge species abundance; and (iii) overall associated biodiversity comprising species diversity (including vertebrates, invertebrates[5] and symbiotic micro-organisms) and gene diversity. Sponge grounds can be considered a community of diverse species, and the interactions among these species are what determine sponges' ecological functions. Figure 4 provides an overview of the main ecological functions associated to deep-sea sponge ecosystem services.

Figure 4

Linkages between structure, functions and services provided by deep-sea sponge grounds
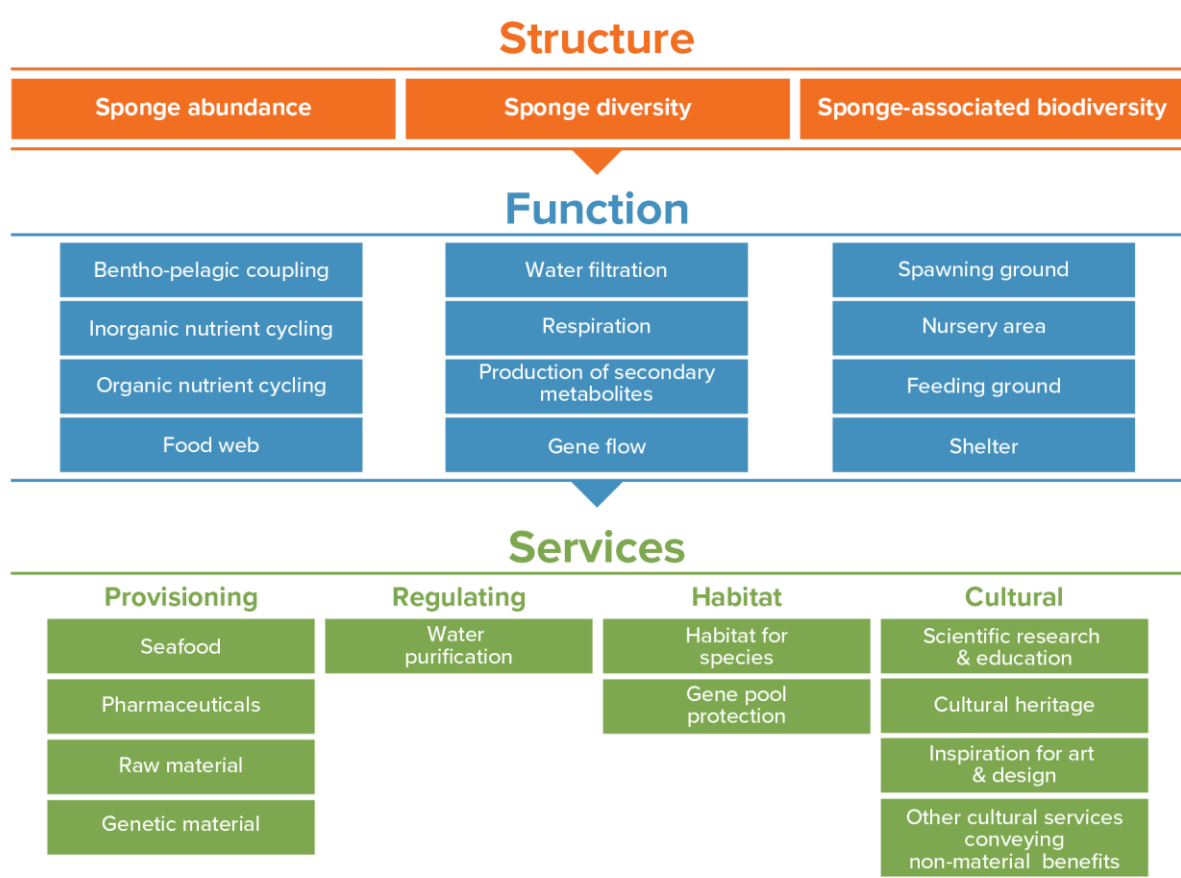
Source: Modified from Le, Levin and Carson (2017) to be applied to deep-sea sponge ecosystem services.

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[5] Invertebrates associated to deep-sea sponge grounds and seafloor sediment can be of different sizes including microfauna (size < 0.1 mm), meiofauna (size 0.1 – 1 mm) macrofauna (size > 1 mm) and megafauna (size > 10 mm) (Lalli and Partson, 1997; Hawkes *et al.,* 2019).

Deep-sea sponge aggregations constitute a unique feature on the deep-sea seabed. The three-dimensional structure created by deep-sea sponges can be used as shelter and provision of camouflage for enhanced protection against predators (Freese and Wing, 2003). Deep-sea sponge grounds can be selected by specific organisms as spawning sites, nursery grounds or feeding areas. If any of these functions are in place, sponge aggregations can be considered to have a role as habitat providers.

Sponges can also function as nutrient cyclers. The water circulation created by the pumping activity of sponges occurring in sponge grounds and associated fauna results in the filtration and removal of organic matter and other nutrients such as oxygen, silicon and nitrogen from the water column, thus influencing the exchange of energy, mass and nutrients between the pelagic and benthic zones (i.e. bentho-pelagic coupling) (Pile and Young, 2006).

Sponges can support food webs both directly and indirectly. They do so directly by constituting food for other organisms, although predation is better known in shallow-water sponges (Bell, 2008; Wulff, 2006); and they do so indirectly by enhancing the survival and reproduction of other organisms and thus supporting the overall biodiversity of deep-sea food webs.

The production of secondary metabolites by sponges, which is directly related to their associated symbiotic bacteria, can make sponges an important provider of bioactive metabolites for pharmaceutical applications.

Based on the ecosystem service cascade model (Figure 1), the composite of the above-described ecological functions can be translated into ecosystem services upon a few conditions:

- ecological function (functions), sustaining the delivery of the ecosystem services, are ascertained;
- forms of capitals (such as intellectual capital, labour and equipment) are in place, when necessary for contributing to ecosystem services provision;
- beneficiaries of the analysed ecosystem services are identified.

Below, an overview of potential ecosystem services derived by deep-sea sponges is provided. Some of the listed ecosystem services are still only potential, as one or more of these three conditions might be still lacking.

2.1.1. Provisioning services

Seafood

Deep-sea sponges may play a key role in seafood provision. This ecosystem service is mainly based on ecological functions related to habitat use and/or food webs. A direct proof of the ecological importance of deep-sea sponge grounds for some commercial fish stocks needs to be established. Seafood is a vital source of human nutrition. Thus, beneficiaries can be easily identified on the basis of the geographical area where the commercial fisheries operate as well as on the geographical area in which seafood is traded.

Pharmaceuticals and genetic material

Deep-sea sponges can also be important in producing new pharmaceuticals through the discovery of new bioactive molecules (i.e. leads). This ecosystem service is mainly based on the production of secondary metabolites by deep-sea sponges and gene diversity found in deep-sea sponges and their associated microbiomes. Prospecting activities on deep-sea sponges is still ongoing. Direct beneficiaries would be the people affected by specific diseases, but also society as a whole through the reduced/avoided costs for medical care in the event of disease remission.

Raw material

Deep-sea sponges are currently used as a model of bio-architecture to produce novel biomaterials. Mimics of sponge-derived biosilica are under investigation as potential biomaterials for bone replacement and regeneration (Dudik *et al.*, 2018; Wang *et al.*, 2014). Future ecosystem services could be provided by sponges in improved human healthcare. In prospect, patients in need of bone replacement or bone regeneration will represent direct beneficiaries.

2.1.2. Regulating services

Regulating services provided by deep-sea sponges are strictly related to sponges' rate of food intake, respiration, and absorption and release of nutrients. In particular, the contribution of sponges to the bentho-pelagic coupling and to the overall biogeochemical cycling of carbon, nitrogen, phosphorous and silicon in the deep sea, is also related to functions enhancing biodiversity of deep-sea sponge communities such as habitat or food webs.

The maintenance of proper functioning of the deep sea benefits human society as a whole. The major challenge concerns the identification of direct beneficiaries of deep-sea regulating services owing to the remoteness of the deep sea. The quantification of deep-sea sponge regulating services could be valuable, particularly to managers and policymakers by providing increased decision capacity.

Water purification

Deep-sea sponge grounds may play a key role in water purification. This ecosystem service is linked to the functions of water pumping and filtering activity carried out by deep-sea sponges.

However, to quantify the water purification services, the effect of bacteria and dissolved organic matter (DOM) removal from the water column needs to be modelled, and impacts at the ecosystem level assessed. Without this broader picture, it is difficult to identify specific stakeholders that might receive benefits from this service.

2.1.3. Habitat services

Habitat for species

Deep-sea sponge grounds can constitute habitat for a large variety of species. In particular, marine benthic and pelagic species, including commercially important vertebrates and invertebrates, could use deep-sea sponges as: feeding grounds, shelter, spawning grounds or nursery areas (see example in Meyer *et al.*, 2019). Overall deep-sea sponge grounds could thus be playing a role in fish stock recruitment. Fish could be caught at great distances from sponges' essential fish habitats (EFHs) and, therefore, direct beneficiaries, such as fishers, might be not proximal to deep-sea sponge grounds.

Gene-pool protection

Deep-sea sponge grounds are characterized by high genetic diversity, comprising both genetic diversity of sponges and their microbial community as well as genetic diversity of their associated invertebrate and vertebrate fauna. However, metrics that can quantify gene pool protection are still poorly developed (Böhnke-Henrichs *et al.*, 2013).

2.1.4. Cultural services

Scientific research and education

Deep-sea sponges and sponge grounds represent a unique feature of the deep-sea ecosystem. Human society as a whole can be considered as benefiting from increased knowledge related to scientific research and education.

Cultural heritage

Deep-sea sponges are part of the world's natural heritage. This value has already been recognized as they have been listed by the Oslo–Paris Convention for the Protection of the Marine Environment of the North-East Atlantic (the OSPAR Convention).The OSPAR List of Threatened and/or Declining Species and Habitats include deep-sea sponge aggregations as threatened and/or endangered (OSPAR, 2008).

Inspiration for art and design

Deep-sea sponges have a characteristic skeleton that creates interesting geometric patterns that can inspire art and design. For example, the deep-sea sponge (*Euplectella aspergillum*) known as the Venus' flower basket, is characterized by having a skeleton made of an elaborate cylindrical lattice-like structure. This geometric pattern has inspired both an art installation in Washington (Aferros studios, 2017), and the design of a building in London (Davidson, 2009).

Other cultural services conveying non-material benefits

Deep-sea sponge aggregations can also convey benefits related to non-material or non-use values. Ecosystem services related to leisure, aesthetic appreciation spiritual experience, sense of place, awareness of the diversity of life forms, are examples of these kinds of cultural services. People might receive the benefits of these ecosystem services through fruition of books, documentaries or deep-sea footage (filmed using remotely operated vehicles), which are mostly available on the Internet free of charge.

In the world's pluralistic human society, diverse stakeholders might perceive and value differently the importance of deep-sea sponge conservation. Motivation for deep-sea sponge conservation can include option value, altruistic value, bequest value, existence value or a mix of them. No generalization can be made, as the attitude of different stakeholders will vary according to: needs and involvement in activities with a direct use/impact on these resources; education and awareness; income and wealth; and expectations about the future (Barbier *et al*., 2009). Therefore, the valuation of these cultural services requires a specific assessment such as that conveyed by state preferences valuation techniques or by non-monetary valuation techniques such as deliberative processes.

2.2. Challenges in the economic valuation of deep-sea sponges

Ecosystem services delivered by the deep sea differ substantially from terrestrial and marine coastal ecosystem services as they are:

- not yet comprehensively identified (Le, Levin and Carson, 2017);
- large-scale, transboundary (Le, Levin and Carson, 2017);
- not proximal to human beneficiaries (Costanza, 2008);
- running on extremely long times scales (Devine, Baker and Haedrich, 2006);

- difficult to monitor, so that knowledge about their baseline, variability and irreversible thresholds[6] are unknown (Le, Levin and Carson, 2017);
- largely non-restorable, owing to high incurred costs and doubtful success (Van Dover *et al.*, 2014);
- supported by a significant share of unexplored and undiscovered biodiversity (Ramirez-Llodra et *al.*, 2010).

These characteristics also apply to many ecosystem services provided by deep-sea sponges. However, in the case of deep-sea sponges, there are additional challenges for their economic valuation. As scientific research on deep-sea sponges is still advancing, knowledge on ecosystem function is still progressing and does not seem to have reached the phase at which ecosystem services can be valued. Among provisioning services, the value of new pharmaceuticals obtained from, or biomaterials inspired by, deep-sea sponges depends greatly on the final outcome of ongoing bioprospecting[7] activities. This value might not be fully accountable at the present time, while leads are still to be discovered or going through the testing phase.

The importance of deep-sea sponges to seafood provision depends on the extent to which commercial fish stocks use sponge habitats. Adult individuals of commercial fish stocks could use sponge grounds as a preferred habitat, resulting in a significantly higher catch rate on sponge grounds rather than outside. In this case, sponge grounds could be accounted for in terms of the benefits related to the supply of fish (provisioning services). Sponge grounds providing spawning and nursery areas could be accounted for in terms of the benefits of habitat provision and recruitment of fish stock (habitat services). The ecological linkage between deep-sea sponge grounds and commercial fish stocks requires: an in-depth knowledge of the biology of the different fish species; data for tracking fish movements and migrations; the identification of the spawning areas; and the estimation of fish catch and fishing effort inside and outside sponge grounds.

The assessment of the role played by sponges in the turnover of energy, organic matter and inorganic nutrients in the deep sea (regulating services) is probably one of the most challenging to accomplish. This assessment requires not only measuring different metabolic parameters at the individual level but also at the population level. This implies moving from laboratory-controlled conditions to *in situ* measurements through incubation chambers placed on sponge grounds to track overall fluxes of organic matter and inorganic nutrients of deep-sea sponge communities. Challenges include: the technical difficulties of operating sophisticated equipment at great depths; the quantification of these fluxes; the modelling of observed patterns into mathematical functions; and the capacity to make some generalizations among patterns observed on deep-sea sponge grounds located in different geographical areas and subject to different environmental conditions.

Deep-sea sponge grounds also provide cultural services. However, the remoteness of locations where deep-sea sponges live, the scarce familiarity of the general public with deep-sea ecology and features, and the fact that little educational material (e.g. books, documentaries and videos) is available on the market make this assessment not an easy one.

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[6] An ecological threshold is a "tipping point" at which ecosystem conditions undergo a rapid and possibly irreversible change exceeding normal ranges (Groffman *et al.*, 2006).

[7] Seeking leads for new drugs from natural products. Bioprospecting is the exploration of biological material for commercially valuable genetic and biochemical properties (Reid *et al.*, 1993).

For the reasons outlined above, revealed preference methods cannot be applied, while the stated preference methods require specifically designed surveys. Thus, the contribution of deep-sea sponges to increased knowledge and understanding of the deep sea through scientific research and education is the only cultural service that can be assessed through a desktop study.

2.3. Selected deep-sea sponge ecosystem services

Four ecosystem services (and related ecosystem functions), one for each category among provisioning, regulating, habitat and cultural services, were selected for the current study (Table 2). This choice was aimed at showing the diversity of ecosystem services potentially delivered by deep-sea sponges and as well as illustrating the diversity of economic valuation approaches that can be applied to deep-sea sponges.

Table 2

Selected ecosystem services and related ecological functions

Category	Ecosystem service	Ecological function
Provisioning	Pharmaceuticals	Secondary metabolite production
Regulating	Water purification	Water pumping and filtration
Habitat	Habitat for commercial fish species	Food webs and habitat
Cultural	Scientific research and education	n.a.

n.a. = not applicable.

The assessment of the potential of new drugs developed from deep-sea sponges fits into one of the five research priorities identified by the European Marine Board (EMB) to address key societal challenges (Børresen *et al.*, 2014). The EMB recommends following the signs of success on new potential pharmaceuticals from sponges (EMB and Marine Biotechnology ERA-NET, 2017). In fact, the EMB recommends targeting marine species living in unusual and extreme environments to increase the chances of success in finding new bioactive leads for the development of novel drugs, treatments, and health and personal care products (Børresen *et al.*, 2014). One of the long-term challenges (2020–2030) identified by the EMB deals with the exploration of the deep sea and its biodiversity hotspots. There is already a strong policy demand for sponge-derived pharmaceuticals as provisioning services. In the road map for European research in marine biotechnology, a key action is to increase policy and public awareness on the source of bioactive leads and biotechnology applications from marine organisms (EMB and Marine Biotechnology ERA-NET, 2017).

The assessment of ecological linkages between deep-sea sponges and commercial fish stocks is also high on the international policy agenda as it represents key information to respond to international regulations for the protection of vulnerable marine ecosystems (VMEs) from destructive fishing practices.

In particular, in 2006 the United Nations General Assembly committed nations that engage in bottom fisheries activities on the high seas to take a series of actions to protect VMEs (i.e. United Nations General Assembly Resolution 61/105) (UNGA, 2007). As a follow-up process, in 2009, a set of international guidelines for the management of deep-sea fisheries in the high seas were negotiated and issued by FAO (FAO, 2009) and subsequently included United Nations General Assembly Resolution 64/72 (UNGA, 2009) aimed at strengthening the implementation of the previous resolutions. The direct or indirect role of deep-sea sponge grounds in the provision or recruitment of fish stocks is highly relevant in better understanding potential trade-offs occurring between sponge conservation and bottom fisheries.

Among cultural services, deep-sea sponges also provide opportunities for scientific research, new discovery and knowledge. The assessment of the scientific and educational value of deep-sea sponges can provide a broad indication of the value of this ecosystem to society globally, without accounting for individual preferences. Recognizing this value is also relevant, and advancing scientific knowledge is also a prerequisite for the delivery of several deep-sea sponge-related services with direct value (e.g. provision of seafood and pharmaceuticals) as well as indirect value (e.g. regulating services).

For each of the four selected ecosystem services, the following themes were developed according to data availability:

- methodological approach;
- baseline data for economic valuation;
- economic valuation – case study examples.

The methodological approach section describes the valuation method that fits better to the analysed ecosystem services. It includes references to financial as well as scientific aspects that need to be considered in the economic valuation. The baseline data section describes information about the current knowledge of ecological functions involved in the delivery of the ecosystem service, and points out any existing data gaps. On the basis of existing data availability for the analysed ecosystem services, examples of economic valuation referred to specific case studies are provided.

3. DEEP-SEA SPONGES FOR PHARMACEUTICAL AND BIOTECHNOLOGY APPLICATIONS

3.1. Methodological approach

The economic valuation of pharmaceuticals derived from deep-sea sponges is possible when the isolated lead with some detected bioactivity has completed the different phases of research and development (R&D), preclinical testing, and clinical testing trials (Figure 5).

During the R&D, a collected sample from a deep-sea sponge specimen is screened to detect signs of biochemical activity. **Advanced molecular essays and techniques** are often used for this purpose by using a collection of small molecules (inhibitors, antagonists and agonists) that represent targets for cell signal transduction and biomolecular pathways. There are libraries of compounds specifically assembled to test different types of bioactivity such as anticancer, anti-inflammation, antiviral, DNA repairing, neuronal signalling, and metabolism related pathways (APExBio technology, 2013).

Once bioactivity has been detected, the active compound needs to be isolated and sufficient quantities of the compound need to be produced for further testing. The preferred method is total chemical synthesis, but this can be a complex process. As an example, **discodermolide,** an anticancer pharmaceutical extracted from a deep-sea marine sponge, required a 39-step synthesis (Freemantle, 2004), while the synthesis of **eribulin mesylate** (Box 2) required a 60-step synthesis (Pilla, 2019).

Preclinical tests are conducted on animals, while the clinical trials are conducted on humans. Preclinical development is aimed at discovering drug adverse effects and at managing potential toxic, pharmacokinetic and metabolic issues of the new compound (Sereno, 2010).

Figure 5
Development phases and pipeline for a new pharmaceutical product
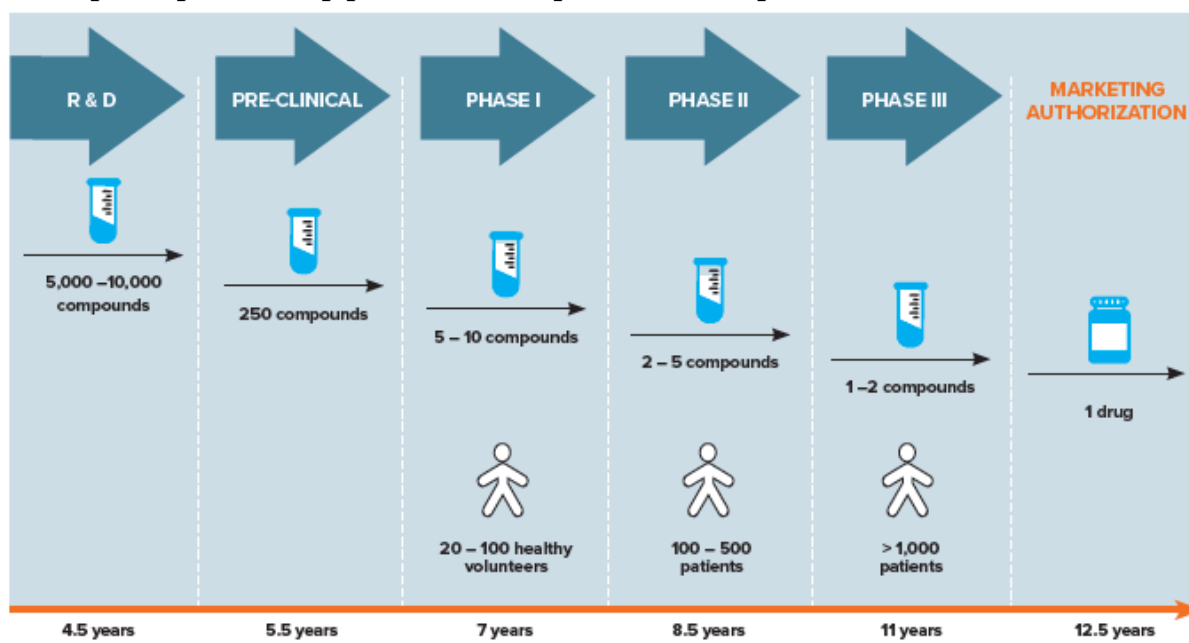
Sources: modified from APBI, undated; AGCS, undated; Innovation.org, 2007

During the preclinical phase, a patent process is usually initiated, which can last several years. A utility patent is a legal device that grants an inventor market exclusivity, that is a monopoly over the invention. In the United States of America, a utility patent usually expires 20 years after the initial date on which the patent application submission was filed (Gupta *et al.*, 2010). Therefore, the period for which the patent is in force depends on how long it takes the United States Patent and Trademark Office to examine the patent request. If the period goes beyond 14 months from the date of filing, an extension can be requested (Stim, 2018).

In Phase I of the clinical trials, tests are conducted on healthy volunteers to check the safety of the drug by administering subtherapeutic doses in ascending order. In Phase II of the clinical trials, tests are conducted on patients affected by the disease that the drug aims to treat. During this phase, tests are conducted to ascertain a therapeutic effect as well as possible side effects of the tested drug. Results obtained from Phase II are still limited to providing sufficient evidence on the efficacy of the drug. In Phase III of the clinical trials, tests are conducted on a larger sample of patients affected by the disease to test the efficacy, effectiveness and safety of the drug.

Only if the drug successfully passes through all the clinical phases is it approved by the appropriate regulatory authority such as the Food and Drug Administration (FDA) in the United States of America and/or the European Medicines Agency (EMA) in the European Union, and commercial drug production and distribution can begin.

The majority of drugs do not reach the market (Mayer *et al.*, 2010). Therefore, the economic valuation of new drugs developed from deep-sea sponges can be estimated, through a market-based valuation technique, for the few drugs that have currently completed the entire drug development pipeline (Figure 4).

Drug pricing changes along the supply chain, which is articulated in three major steps: (i) from the manufacturer to the wholesaler; (ii) from the wholesaler/distributor to the pharmacy; and (iii) from the pharmacy to the patient/consumer (Matthingly, 2012). The economic valuation will be affected by the choice of which segments along the supply chain are considered.

The prices of pharmaceuticals are influenced by negotiations and interactions among the key players in the pharmaceutical market: consumers, pharmaceutical industry, healthcare providers, and government (Grund, 1996). Governments generally try to control drug prices through cost-containment policies. They can also directly support pharmaceutical R&D for treating diseases that are so rare (orphan disease) that produce drugs without government assistance would not be profitable.

For widespread diseases the global potential demand for drug supply and the average price at the consumer level can show the societal impact of the development of new drugs. However, identifying a representative unit price on a global market spanning across countries can be challenging, and prices in different countries need to be adjusted by means of a purchasing power parity (PPP) conversion.

A market-based valuation cannot be easily used for orphan diseases (Table 3). A review of the economic value of orphan drugs concluded that a standard economic valuation is not suitable for orphan diseases owing to the low number of patients, and the lack of information on the life quality, long-term outcomes, and impact on disease-related dimensions such as financial, emotional and social aspects (Cote *et al.*, 2015).

Table 3

Proposed methodology for the valuation of deep-sea sponges as sources of new pharmaceuticals

Ecosystem services	Disease characteristics	Benefits	Valuation method	Economic value
Medicinal resources	Common disease	New pharmaceuticals derived from deep-sea sponges	Market-based	Market value of pharmaceuticals estimated at the manufacturer level
				Market value of pharmaceuticals estimated at the consumer level
	Rare (orphan) disease	New pharmaceuticals derived from deep-sea sponges	Not available	Not available

Another challenge in the economic valuation of pharmaceuticals concerns the estimation of the option value of potential future drug development. However, the major obstacle in using these techniques is the difficulty of gaining access to confidential information from pharmaceutical companies.

Pharmaceutical companies themselves use economic valuation assessments of the potential revenues (option value) when they make corporate finance plans, and set early-stage investments for R&D. A specific market-based valuation technique, known as real options valuation, is used to model situations where investments are carried out at multiple stages, so that investment in one option provides the opportunity to invest in the next stage (Brous, 2011; Sereno, 2010; Hartmann and Hassan, 2006).

Pharmaceutical companies need to take several investment decisions while facing a high level of uncertainty. This series of investments are needed to move forward in the drug development pipeline in order to cover: initial research costs to discover a new bioactive lead; costs of patent filing procedures; preclinical phase testing; fees for maintaining patent rights; clinical phase testing; fees for FDA/EMA approvals; and market launch costs of the new drug (Sereno, 2010; Gupta *et al.*, 2010). At any stage of the drug development process, the pharmaceutical company can decide whether to continue in the series of required investments or to abandon the project (Sereno, 2010). These decisions are taken on the basis of the option value of new drug development, which factors in both technology risks and product market risks (Brous, 2011).

As the economic and financial information needed to assess the option value of R&D of new pharmaceuticals or biotechnology is not publicly disclosed, a very rough idea of the possible option value can be conveyed by estimating the market share that these could occupy in the future. However, these forecasts can be considered only speculations affected by large uncertainty, also considering the existing gap between ongoing research and future markets (Box 3).

3.2. Baseline data for economic valuation

3.2.1. Occurrence of bioactive compounds from deep-sea sponges

A wide variety of marine-derived compounds and biotechnological materials are used in cosmetics, pharmaceuticals, textiles, manufacturing and other industrial sectors. In particular, sponges are considered a phylum that is extremely important for pharmaceutical applications given that in 2010, 30 percent of 15 000 natural isolated compounds were derived from sponges (Murti and Agrawa, 2010).

Marine sponges produce a wide range of unique metabolites that enable them to survive in challenging environments, which makes them attractive sources of candidate pharmaceuticals. In particular, sponges, which are often associated with bacteria, are considered a kind of underwater "pharmacy" as they can be used to extract substances called polyketides,[8] with anti-inflammatory, hypocholesteromeric, anticancer, immunosuppressive, neurosuppressive, muscle-relaxant, antiviral, antimalarial, antibiotic and antifouling properties (Anjum *et al.*, 2016; Perdicaris, Vlachogianni and Valavanidis, 2013; Ravich, Kathiresan and Balaram, 2007). In some cases, it is uncertain whether these polyketides are produced by the sponge itself, by the micro-organisms inhabiting the sponge, or by the interaction between the micro-organisms and the sponge, although sponges represent the source material for isolating these metabolites.

In particular, triterpenoids are the most abundant secondary metabolites present in marine sponges, and a large number of these compounds have shown anticancer properties in preclinical phases (Li and Kim, 2015). Some bioactive compounds have also been identified in deep-sea sponges (Table 4). However, none of these compounds has currently reached the end of the drug development pipeline.

Table 4
Examples of bioactive compounds extracted from deep-sea Demospongiae

Order	Genus/species	Compound	Property	Sample depth (m)	Geographical area	Reference
Haplosclerida	*Xestospongia* sp.	Alisiaquinones	Antimalaria	250–400	Australia	Desoubzdanne *et al.*, 2008
Haplosclerida	*Petrosia* sp.	Duryne	Anticancer	415	Japan	Hitora, *et al.*, 2011
Lithistida	*Discodermia* sp.	Discodermolide	Anticancer	185–220	Bahamas	Paterson and Florence, 2009
Lithistida	*Leiodermatium* sp.	Leiodermatolide	Antibacterial and anticancer	618	Bahamas	Skropeta and Wei, 2014
Lithistida	n.d.[1]	Neopeltolide	Anticancer antifungal	442–433	Jamaica	Wright *et al.*, 2007
Lithistida	*Corallistes* spp.	Corallistins	Anticancer	350	New Caledonia	Motuhi *et al.*, 2016
Lithistida	*Macandrewia azorica*	Azoricasterol	Anti-HIV	600	Portugal	Gross, Reitner and Koenig, 2004
Poecilosclerida	*Lissodendoryx* sp.	Isohomohalichondrin B	Anticancer	> 100	New Zealand	Hickford, Blunt and Munro, 2009
Poecilosclerida	*Spongosorites* sp.	Dragmacidin G	Antibacterial and anticancer	630	United States of America	Wright *et al.*, 2017
Poecilosclerida	*Latrunculia* sp.	Dihydrodiscorhabdin B	Anti-HCV, antimicrobial and antimalarial	230	Alaska	Na *et al.*, 2010

n.d. = no data.
[1]Species belonging to the family Neopeltidae.

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[8] Polyketides are a large class of structurally diverse natural products exhibiting a vast array of biological and pharmacological activities such as antibacterial, antifungal, anticholesterol, antiparasitic, anticancer, and immunosuppressive properties (Chan *et al*., 2009).

For example, **discodermolide,** a natural polykeptide isolated from the deep-sea sponge *Discodermia dissoluta* in the Caribbean Sea by Harbor Branch Oceanographic Institution, Inc., Fort Pierce, Florida was licensed to the Swiss pharmaceutical company Novartis, which initiated research for a large-scale *in vitro* synthesis of discodermolide as a pancreatic anticancer drug (AAAS, 1998; Freemantle, 2004). Originally, discodermolide was extracted from a *Discodermia dissoluta* specimen collected at a depth of 33 m off the Bahamas (Freemantle, 2004). However, several other species belonging to the genus *Discodermia,* and containing discodermolide, were later found in species retrieved at depths of between 185 m and 220 m (Paterson and Florence, 2009). Research and development on discodermolide carried out by Novartis was interrupted during combined Phase I/II of the clinical trials owing to encountered problems in terms of efficacy and toxicity (Molinski *et al.*, 2009).

The collection of another deep-sea sponge belonging to the genus *Leiodermatium* in the Bahamas, off Wemyss Bight at a depth of 618 m, led to the discovery and isolation of **leiodermatolide**, which showed a potent antimitotic activity in human lung carcinoma, pancreatic carcinoma and colorectal carcinoma (Paterson *et al.*, 2011).

The sponge was subsequently collected off the coast of Fort Lauderdale, Florida, USA at a depth of 401 m; these specimens contained approximately ten-fold more leiodermatolide that the Bahamian specimens (Wright *et al.*, 2017a). Currently, the discovery of leiodermatolide is protected by innovation patent, and there is ongoing research for its molecular synthesis (Skropeta and Wei, 2014).

New Caledonia has been the focus of several pharmacological bioprospecting studies. In the 1980s, an antitumor metabolite called **girolline** was extracted from the deep-sea sponge *Cymbastela cantharella*, originally collected at a depth between 10 m and 40 m, and tested by the pharmaceutical company Rhône-Poulenc for its antiproliferative and antiplasmodial activities (Ahond *et al.*, 1988).

In 1992, the purchase of a research vessel, the RV *Alis*, which was able to dredge at depths of 600 m, allowed access to new biological resources (Motuhi *et al.*, 2016). In particular, it was discovered that sponges of the genus *Corallistes* contained substances called **corallistins** with strong anticancer properties (Motuhi *et al.*, 2016). Molecules isolated from *Xestospongia* spp. collected by trawling on a seamount at a depth between 250 m and 400 m depth off the south of New Caledonia (Norfolk Rise) showed antimalaria properties (Desoubzdanne *et al.*, 2008).

Another deep-sea sponge, collected at a depth of 630 m off the coast of Long Island, Bahamas and belonging to the genus *Spongosorites,* was found to contain a natural product called **dragmacidin G**, with potent antibacterial activity against the drug-resistant bacteria "methicillin-resistant *Staphylococcus aureus*" as well as antitumoral properties against pancreatic cancer (Wright *et al.*, 2017b).

3.2.2 Economic valuation of new pharmaceuticals from deep-sea sponges

Despite the large numbers of novel isolated compounds from marine sponges with tested bioactivity (Anjum *et al.*, 2016; Perdicaris, Vlachogianni and Valavanidis, 2013; Ravich, Kathiresan and Balaram, 2007), including several from deep-sea sponges (Table 4), only very few have been marketed as pharmaceutical products. It is estimated that only 1–2 percent of preclinical candidates of marine-derived pharmaceuticals become commercially produced (FAO, 2003a).

Three specific challenges are encountered in drug development from deep-sea sponges. The first deals with the collection of specimens in the deep sea. The collection of deep-sea organisms is very expensive as it requires navigation and exploration time, and costly equipment such as submersibles and remotely operated vehicles. Although these figures are not updated, to give an idea of transfer costs, it should be considered that the Harbor Branch Oceanographic Institute used to charge USD 12 000 a day for ship time, plus about USD 4 500 a day for diving with the submersible (Newman and Cragg, 2005).

The second challenge is that secondary metabolites, which often show bioactivity properties, are often produced by sponges in trace amounts (Molinski *et al.*, 2009; Newman and Gragg, 2005). Thus, one of the major challenges is the availability of appropriate amounts of these compounds that are required in order to detect bioactivity as well as to run preclinical and clinical trials.

The initial collection of specimens is relatively small, usually not exceeding 1 kg. If bioactivity is discovered, then the collected quantity increases to 1–5 kg (Koyama, 2009). If the bioactive compound reaches the clinical trial stage, thousands of kilograms may be required to support further analyses, depending on the organism (Koyama, 2009).

At this point, being able to reproduce the active lead synthetically becomes mandatory as the retrieval of biological material from the wild poses serious concerns regarding the conservation of existing deep-sea sponge grounds. Historically, there has been only one case of a large amount of sponges collected to advance in R&D (Box 2). In general, pharmaceutical companies develop protocols to produce the metabolites of interest using chemical synthesis.

The aquaculture of deep-sea sponges is not always easy. Deep-sea sponges can be sensitive to the season in which transplants are made and to changes in culture parameters (Munro *et al.*, 1999), and the incurred production costs of aquaculture can be significant (Fajarningsih, 2013). More often, pharmaceutical companies attempt to produce metabolites of interest *in vitro* by means of cell cultivation or synthetic production of these substances based on molecular modelling of metabolites extracted from marine organisms (Hogg *et al.*, 2010). Molecular modelling creates a synthetic molecule, which is often similar but not identical to the original bioactive natural compound found in the marine organism. These synthetic molecules are called analogues and, more precisely, are considered "direct analogues" showing both chemical similarities and displaying the same related pharmacological properties (Wermuth, 2006).

The fact that new pharmaceuticals of marine origin are similar but not identical to the original natural compound raises the methodological problem of which pharmaceuticals are to be considered as being derived from marine organisms (FAO, 2020). After the initial drug has been developed, pharmaceutical companies usually continue R&D, which can lead to new formulations clinically superior to the previous drug formulation. This is carried out to improve drug design, to diminish side effects, and to lower drug dosage, but also to be able to file a new patent for the improved formulation in order to retain the market monopoly (Gupta *et al.*, 2010). Therefore, the same pharmaceutically active principle can lead to different marketed products. For this reason, when assessing the economic value of pharmaceuticals of marine origin, it is critical to decide which generation to consider. For example, the FAO (2020) study considered only the "first generation" of drugs containing as an active ingredient the direct analogue of the natural compound discovered in the marine organism.

To date, few compounds of sponge-derived origin have reached the end of the drug development pipeline and have been marketed as pharmaceutical products. One example, further described in Box 1, is represented by cytarabine, whose bioactive lead **cytosine arabinoside** (ara-C) was initially discovered in the shallow-water sponge *Tectitethya crypta* (Malve, 2016). This was a milestone in pharmaceutical research, which occurred in the 1950s, and from that moment, scientific interest in marine organisms as a source for pharmaceutical products was sparked (Munro *et al.*, 1999).

Based on accessible information, the market value of cytarabine at the manufacturer level is conservatively estimated at USD 175 million/year for the year 2017, while the market value at the consumer level is tentatively estimated at USD 2.8 billion/year for 2012 (Box 1).

Estimating the market value of cytarabine presents several challenges linked to: a wide global market for cytarabine; the price variation found across countries; the association of cytarabine to other pharmaceuticals in different treatment protocols; the large number of pharmaceutical companies producing and marketing different products containing cytarabine; the large number of countries in

which cytarabine is marketed; and the lack of detailed statistics on the global incidence of acute myeloid leukaemia (AML) for which cytarabine is considered the key pharmaceutical to be used in chemotherapy. All these gaps in data availability determine some uncertainty in the economic valuation of cytarabine.

A second example, further described in Box 2, is represented by Halaven®, whose bioactive principle is **eribulin mesylate.** This is a completely synthetic compound analogue of the natural **Halichondrin B,** which was first isolated from the Japanese marine sponge *Halichondria okadai* and subsequently found in other shallow-water sponges belonging to the genera *Axinella*, *Phakellia* as well as in the deep-sea sponge *Lissodendoryx* (Swami, Shah and Goel, 2015).

Halaven® is produced and marketed only by the pharmaceutical company Eisai as the drug is still under patent protection. This determines that the estimate of the market value at the manufacturer level (USD 373 million) is assessed with greater confidence than in the case of cytarabine, for which various pharmaceutical companies are in play.

Since 2016, Halaven® has also been approved by the FDA for the treatment of unresectable or metastatic liposarcoma in patients who have received prior chemotherapy containing an anthracycline drug (FDA, 2020). The time series (2010–17) in sales of **eribulin** reported by Tay-Teo, Ilbawi and Hill (2019) does not show a relevant increase in 2016–17 compared with the previous years. Therefore, despite not all 2019 eribulin sales being directed to the treatment of metastatic breast cancer, the bias introduced in the estimate of USD 373 million is expected to be marginal.

As in the case of cytarabine, the market value at the consumer level is several orders of magnitude higher (USD 1.1 billion) than the market value estimated at the manufacturer level. This reflects the price increase in the drug supply chain as well as the large distribution of Halaven® in more than 70 countries. However, the future introduction of generic forms of eribulin mesylate is likely to soon change the global current existing market for Halaven®.

In 2019, Emcure Pharmaceuticals Ltd, one among the top ten pharmaceutical companies in India, has announced the launch of the world's first generic version of Halaven® which will be called Eribilin. In its first phase, Emcure's Eribilin will be marketed only in India, as it has been approved by the Drug Controller General of India. However, when Eisai's Halaven® patent expires in July 2023 (FDA, 2020), Emcure's plan is to register and sell Eribilin also on the international market (Biospectrum, 2019).

Emcure Pharmaceuticals Ltd announced that, while in India the cost of a vial of Halaven® is about USD 420 (INR 31 880), Eribilin will be sold at a price that is 40 percent lower (USD 252, corresponding to INR 19 000). This reduced price will overcome problems related to the limited access and affordability of Halaven® for lower-income people. Through the marketing of Eribilin, Emcure Pharmaceuticals plans to capture 25 percent of the current market for Halaven® (Pilla, 2019).

In conclusion, the economic valuation of cytarabine and Halaven® provide opportunities to apply market-based valuation techniques, and to highlight potential challenges encountered in retrieving data and estimating market values at the global level. Despite possible limitations in data coverage and bias introduced by large-scale extrapolations, these two case studies show the large potential and economic value of sponges for pharmaceutical applications.

3.2.3. Economic valuation of new biotechnology inspired by deep-sea sponges

The high bioprospecting potential of deep-sea sponges is not restricted to pharmaceuticals, but includes also other possible innovative biotechnology applications. One area of research is the potential use of deep-sea sponges as bio-architectural models. As the result of evolution, living organisms often present structures showing effective structural performance, material composition and functional organization (Zhang *et al.*, 2017). The geometries created by the deposition of biosilica spicules create mesh or

honeycomb structures, which constitute open and ductile structural systems – strong and permeable, and resilient against deformation under external loading (Aluma, Ilan and Sherman, 2011; Weinstock, 2006).

The design process of creating new architectural forms inspired by sponges can be articulated in five steps: (i) study of a prototype; (ii) imitation based on the prototype pattern; (iii) creation of a new form, which is usually computer-assisted and carried out by adjusting design parameters or adding interferences; (iv) application, which consists in the selection and optimization of only a few design variations; and (v) fabrication of the new form (Zhang *et al.*, 2017). However, when a sponge's bio-architecture is used in the context of bone-tissue bioengineering (Box 3), the process is further complicated by the need to test the efficacy and safety of natural or synthetic bone grafts.

Research on bone-tissue engineering is carried out within the medical branches of orthopaedics and dentistry. When fractured, bone tissue is usually able to regenerate itself by repairing the damage. However, in traumas or diseases leading to bone loss or fractures wider than 0.1 mm, with inadequate vascularization, bone tissue may not be properly replaced (Wang and Yeung, 2017; Granito, Custodio and Rennó, 2017).

In these situations, the transplanting of bone tissue is often necessary. Worldwide, bone transplants are is the second most frequent tissue transplantation, after blood transfusion (Campana *et al.*, 2014). There are three possible approaches for bone transplants. The first, which is considered the gold standard, is the transplant of bone tissue from one body area to another in the same patient. However, this approach often requires the patient to undergo two surgeries, with possible complications such as pain, infection, scarring, blood loss, and donor-site morbidity (Polo-Corrales, Latorre-Esteves and Ramirez-Vick, 2014). The second is the retrieval from a donor of bone tissue to be transplanted, but often availability is limited, and complications include infections or immune rejection. The third approach is to create bone-graft substitutes by bone-tissue engineering. In bone-graft substitutes, some progenitor cells or growth factors that can stimulate bone-tissue growth are incorporated into a scaffold (natural or synthetic) mimicking the bone microenvironment. The ideal material for replacing bone tissue should be proved to be biocompatible, bioresorbable, osteo-conductive, osteo-inductive, structurally similar to bone, porous, mechanically resistant, easy to use, safe, and cost-effective (de Grado *et al.*, 2018).

Sponges, and in particular sponges with silica skeletons, are potentially good candidates as bone-graft substitutes, as their bio-architecture closely resembles that of bone tissue, and biosilica, in initial experiments of transplants on animals, seems to show many of the above-mentioned properties (Crovace *et al.*, 2016).

Future prospects show global demand for bone grafts and bone-graft substitutes rising to USD 2.7 billion in 2026 (ZionMarket Research, 2019). However, at the present stage, the relevance of deep-sea sponges for bone-graft substitute can only be considered as a possible, but not certain, future use. The likelihood of using biosilica and/or developing synthetic implants mimicking natural biosilica structure as bone-graft substitute depends much on the outcomes of current scientific investigation including *in vivo* studies, *in vitro* studies, and clinical tests aimed at testing this biomaterial in different surgical procedures.

BOX 1 - CYTARABINE, A SPONGE-DERIVED DRUG FOR ACUTE MYELOID LEUKAEMIA

Acute myeloid leukaemia (AML) is an uncommon, aggressive, fast-growing cancer beginning inside bone marrow and spreading into the blood system, making up about 1 percent of cancers that require intensive treatment (Leunis *et al.*, 2013; Gursoy, 2014; Cancer.net, 2020). The incidence of the disease is higher among people over 65 years of age (17.6 affected people out of 100 000 people) compared with people under 65 (1.8 affected people out of 100 000 people) (Gursoy, 2014).

World Health Organization (WHO) statistics do not subclassify leukaemias into acute and chronic, and myeloid or lymphoid, but in 2018 the overall leukaemia cases were 437 033 (The Global Cancer Observatory, 2019). Nevertheless, WHO leukaemia statistics provide a baseline considering that in 2012 the global number of people affected by AML and acute promyelocytic leukaemia was 351 965, while the number of recorded deaths was 265 461 (Union for International Cancer Control, 2014).

Since receiving its first approval in 1969 from the United States Food and Drug Administration (FDA), cytarabine has been considered the key pharmaceutical in chemotherapy for AML (Martins *et al.*, 2014). However, the use of cytarabine has been also extended to the treatment of other types of leukaemias, such as acute lymphocytic leukaemia, acute promyelocytic leukaemia, and meningeal leukaemia, as well as non-Hodgkin's lymphoma (Martins *et al.*, 2014).

The bioactive compound of cytarabine is constituted by **cytosine arabinoside (ara-C),** which was isolated for the first time in the 1950s from the shallow-water sponge *Tectitethya crypta* (Martins *et al.*, 2014). The discovery of ara-C sparked great scientific interest in marine organisms as a source for pharmaceutical products (Munro *et al.*, 1999).

Cytarabine has the capacity to diffuse across membranes and thus is able to enter into cells. This property has been further enhanced by a liposomal formulation of cytarabine called DepoCyt®, which is able to enter brain cells for treating meningeal leukaemia (Martins *et al.*, 2014).

Since cytarabine has been available over the counter for more than 50 years, its market is very articulated and involves several pharmaceutical companies. Cytarabine was originally launched by Upjohn Company in the 1970s under the brand name Cytostar (Fajarningsih, 2013). In 1969, the original patent expired, and several other companies entered the market including: West-Ward Pharmaceuticals (in 1989), Hospira (in 1990), Fresenius Kabi USA (in 1994), Mylan Labs (in 2011), Meitheal Pharmaceuticals (in 2017), and Grand Pharma (in 2019) (FDA, 2020).

Starting in 1999, DepoCyt® was produced and marketed by Pacira Pharmaceuticals (Elvidge, 2017). While the production of DepoCyt® by Pacira was discontinued in 2017 owing to undisclosed manufacturing problems, in the same year a new product for the treatment of AML entered the market. It is sold under the name of VYXEOS® and is composed of a liposome-encapsulated combination of cytarabine and daunorubicin produced by Jazz Pharmaceuticals (Stenger, 2017). In 2017, sales of VYXEOS® by Jazz Pharmaceuticals totalled USD 75 million (Dearment, 2018), and in 2020 its use was approved in more than 30 countries (Pharmiweb.com, 2020).

Information on annual sales of cytarabine from the above pharmaceutical companies could not be retrieved as publicly available information. The overall cytarabine market was estimated by Mayer *et al.* (2010) at about USD 100 million/year. Following this indication, its market value at the manufacturer level was estimated at USD 108 million/year for 2014 (in which DepoCyt® was still on the market) and at USD 175 million/year for 2017 (when VYXEOS® entered the market) (FAO, 2020).

The estimates by FAO (2020) should be considered as minimum figures based on limited data availability. The global market for cytarabine is currently spread across all continents, with key countries and territories being: the United States of America, Canada, Germany, France, the United Kingdom of Great Britain and Northern Ireland, Italy, the Russian Federation, China, Japan, the Republic of Korea, India, Australia, Taiwan Province of China, Indonesia, Thailand, Malaysia, the Philippines, Viet Nam, Mexico, Brazil, Turkey, Saudi Arabia, and the United Arab Emirates (Qyresearch, 2020).

The global market value for AML, comprehensive of several types of therapeutic drugs, was reported to be USD 701.6 million/year. However, a large share of this value can be attributed to cytarabine as it is the most effective drug in AML treatment (Research and Market, 2019).

Chemotherapy for AML treatment usually consists of two phases, both of which make use of cytarabine. The first phase, called induction, is aimed at killing the largest possible number of leukaemia cells. Generally, during induction, cytarabine is administered continuously for 7 days, followed by intravenous administration of daunorubicin for 3 days. This standard induction treatment generally achieves complete remission in about 70 percent of patients in the 18–60 age group (Tallman, Gilliland and Rowe et al, 2005).

The second phase, called consolidation, is aimed at destroying any remaining leukaemia cells in order to prevent a relapse over the following few months. During consolidation, high doses of cytarabine are administered to patients under 60 years of age for a cycle of 5 days. Generally, the patient receives a total of 3–4 cycles (American Cancer Society, 2018).

Besides this general protocol, there is a multiplicity of AML treatments involving the use of cytarabine. The dosage, as well as association with other pharmaceuticals, varies according to the type of AML, and the age and health conditions of the patient (Bccancer, 2014; Leunis *et al.*, 2013).

A study in the Netherlands on 202 AML cases assessed the cost of different chemotherapy protocols (Leunis *et al.*, 2013). In 2010, the average cost of the induction and consolidation phases were USD 3 499 and USD 4 493, respectively. In the induction phase, cytarabine was used in association with other pharmaceuticals, whereas high doses of cytarabine were administrated in the consolidation phase. The above costs are comprehensive of all pharmaceuticals used, not just cytarabine.

Altogether, the cost of AML chemotherapy was almost USD 8 000/patient for a complete induction and consolidation cycle. These costs multiplied by the reported number of AML cases in 2012 (n = 351 965) give an estimated global market value for cytarabine-based chemotherapy of USD 2.8 billion/year.

This figure should be considered as indicative of an undeniably large global cytarabine market. Some uncertainty is associated with this estimate owing to the fact that cytarabine-based chemotherapy costs were extrapolated at the global level, without taking into account the diversity of countries within the global cytarabine market and the multitude of existing chemotherapeutic protocols.

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BOX 2 - HALAVEN®, A SPONGE-DERIVED DRUG FOR ADVANCED BREAST CANCER TREATMENT

The World Health Organization (WHO) considers breast cancer the most frequent form of cancer, and the one causing the greatest number of cancer-related deaths among women, with 2.1 million cases each year and 627 000 deaths in 2018 (WHO, 2020).

Halaven® is an anticancer drug developed from deep-sea sponges, currently approved for treatment of metastatic breast cancer in more than 65 countries worldwide (Eisai, 2019a). It represents the ultimate single-agent therapy for women with metastatic breast cancer, particularly for those patients affected by a human epidermal growth factor receptor (HER2)-negative type of breast cancer.

The discovery of Halaven® is significant considering that women with locally advanced or metastatic breast cancer have a poor prognosis, with only about 25 percent surviving beyond 5 years (Tremblay *et al.*, 2016; Eisai, 2019a).

The bioactive substance in Halaven® (**eribulin mesylate**) is a synthetic analogue of the natural compound Halichondrin B, first isolated in 1986 from the Japanese marine sponge *Halichondria okadai*. Halichondrin B naturally occurs in sponges in the very low concentration of about 8.8 parts per billion (Molinski *et al.*, 2009).

In the 1990s, Halichondrin B was also discovered in the deep-sea sponge *Lissodendoryx* sp., found exclusively off the Kaikoura Peninsula off the east coast of New Zealand's South Island. A considerable amount of *Lissodendoryx* biomass (1 tonne out of a total estimated biomass of the sponge ground of 300 tonnes) was dredged to advance preclinical trials (Munro *et al.*, 1999).

In 1998, the United States National Cancer Institute in partnership with Eisai Company in Japan and its United States subsidiary Eisai Corporation of North America succeeded in the chemical synthesis of an analogue of **eribulin mesylate**, which was filed for patent in 1999 (Lens.org, 2020) and subsequentially marketed as Halaven® (Molinski *et al.*, 2009: Shetty and Gupta, 2014).

After 25 years of laboratory research, in 2010 the use of Halaven® was approved by the Food and Drug Administration (FDA) in the United States of America, and in 2011 by the European Medicines Agency (EMA) (FDA, 2010; Eisai, 2011). Halaven® is currently produced by Eisai Corporation, and in 2017 sales at the manufacturer level were recorded at USD 356 million (Tay-Teo, Ilbawi and Hill, 2019), while in 2019 sales increased to about USD 373 million (Eisai, 2020a). The economic relevance of Halaven® in the global cancer drug market is much higher than estimated sales at the manufacturing level.

Halaven®-treated patients receive a median of five cycles of therapy. Each Halaven® cycle lasts 21 days, with a 1 mg/2 ml Halaven® vial administered on days one and eight of the cycle (Eisai, 2010). The wholesale price of Halaven® in the United States of America is USD 1 241/vial (Drugs.com, 2020); thus, the medical costs of a single Halaven® cycle is USD 2 482, while the cost of a 5-cycle therapy is estimated at about USD 12 410.

This is to be considered a reasonable estimate of incurred drug costs by patient by year taking into account that, in the United States of America, Eisai offers a programme insurance, reimbursing up to USD 18 000 per year per patient, which will cover not only drug costs but also hospital care costs (Eisai, 2019b).

As it is estimated that between 6 and 10 percent of women with breast cancer will have metastatic disease at the time of breast cancer diagnosis (Metastatic Breast Cancer Network, 2019c), the global number of women using Halaven® therapy could be estimated at 126 000 people/year, 6 percent of 2.1 million cases reported by WHO (2020).

The main challenge of calculating the global market flow associated to Halaven® therapy is the price variation of Halaven® among countries. Halaven® is currently approved in more than 70 countries worldwide, including the United States of America, Japan and countries in Europe and Asia (Eisai, 2020b, 2019d).

An average unit price, adjusted to the different purchasing power parity (WBG, 2020), among 10 countries across 4 continents revealed an average cost of USD 818 for a 1 mg/2 ml vial (see Appendix 3). Therefore, the calculated cost of a 5-cycle therapy is estimated to be about USD 8 810, and the calculated overall market flow associated to Halaven® therapy about USD 1.1 billion/year.

The social impact of Halaven® therapy is an increase of the survival of women diagnosed with metastatic breast cancer. During Phase III of clinical trials, patients treated with Halaven® (n = 508) survived 2.5 median months longer than patients in the control experimental group (n = 254) treated with other existing protocols (Eisai, 2014).

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BOX 3 - OPTION VALUE DEEP SPONGE-DERIVED BIOSILICA IMPLANTS FOR BONE-DEFECT REPAIR

Current and future challenges for global health include the increasing number of road traffic accidents with orthopaedic injuries, as well as the growing worldwide geriatric population and its vulnerability to various health issues including osteoporosis, bone fractures, and degenerative bone and joint diseases.

Sponges can be an important source of biomaterial for bone-graft substitutes. Among marine organisms, they have a porous skeleton system, where inorganic siliceous or calcareous spicules are interspersed into an organic matrix made of spongin. This architecture resembles very closely that of bone tissue, making sponge skeleton an ideal prototype for bone scaffolds. In addition, sponge spicules contain a central axial filament, made of silica proteins (silicateins). These proteins function as enzymes catalysing silica formation and deposition (Cha *et al.*, 1999; Müller *et al.*, 2009).

Research has succeeded in reproducing in the laboratory biosilica and biosilica-based materials using recombinant silica proteins assembled in proper conditions of temperature and pH (da Silva Raminhos Natálio, 2010). Several experiments with biosilica have been conducted in rabbits and rats to study its osteogenic properties to support cell growth and to stimulate bone formation and mineralization (da Silva Raminhos Natálio, 2010; Crovace *et al.*, 2016).

The potential of deep-sea sponges in bone-tissue engineering is currently under investigation. Deep-sea sponges, belonging to the class **Hexactinellidae** (or "glass sponges"), have a skeleton with high silicon content, representing more than 75 percent of the sponge dry biomass (Barthel, 1995). The skeleton of **Hexactinellidae** sponges creates complex structures, representing possible new models for bone scaffolds (Dudik *et al.*, 2018). The complex process through which inorganic silicon is incorporated into **Hexactinellidae** skeleton (i.e. biosilicification) to date is not fully understood, being regulated by different proteins and biochemical pathways (Otzen, 2012).

The economic value of future use (option value) of deep sponge-derived silica for bone-defect repair could be very promising. Currently, the global market demand for bone grafts and bone-graft substitutes is very high. The increasing tendency towards minimally invasive surgeries is further increasing the demand for bone grafts and substitutes (ZionMarket Research, 2019). In 2018, the global market demand for bone grafts and bone-graft substitute was estimated to be about USD 2.7 billion but this is expected to rise to USD 4.2 billion by 2026, considering a compound annual growth rate of 5.6 percent (ZionMarket Research, 2019).

The social impacts of future development of bone-tissue bioengineering can be very high, considering that it can be used for bone-defect repair in spinal fusion, dental repair, joint reconstruction, hip fractures, and for craniomaxillofacial, foot and ankle, and long bones.

In addition, in the future, biosilica and biosilica-based materials could also be used to alleviate the effect of osteoporosis, which in 2018 was estimated to affect about 200 million people worldwide, only accounting for the incidence in women (ZionMarket Research, 2019).

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4. DEEP-SEA SPONGES AS SYSTEM FILTERS OF THE DEEP SEA

4.1. Methodological approach

Sponge water-pumping activity is the key physiological parameter that determines the metabolic rate and influences fluxes of nutrients processed by sponges in the water column. The water is pumped inside the body of the sponge as a result of the slightly negative pressure generated by flagellated cells in choanocyte chambers, which constitute the basic pumping units. The water then exits from exhalant channels that further merge in external openings (oscula) (Morganti *et al.*, 2019). Sponges gain their nutrition through filtration, which is mediated by the flow of water created by the pumping activity. Moreover, sponges are able to take up and release a variety of compounds, and in particular, they play an important role in the cycles of carbon (C), nitrogen (N), phosphorous (P), and silicon (Si) (Maldonado, Ribes and van Duyl, 2012).

The quantification of these nutrient fluxes in the deep sea requires high technology approaches and expensive tools. First, the physiology of each sponge species needs to be investigated in relation to the variations of the biotic and abiotic parameters. Nutrient fluxes in sponges are generally assessed by estimating the uptake and efflux rates in isolated individuals. Initial *in vitro* measurements take place in laboratory tanks. Individuals can be kept in closed vessels where the water is stagnant, and the variation of given parameters or food concentration is assessed over time.

In vitro measurements are also useful for monitoring the response of the sponge to experimental treatments mimicking environmental conditions and stressors (Bart *et al.*, 2020; Stevenson *et al.*, 2020). However, *in vitro* experiments can often lead to altered physiological parameters, as deep-sea sponges are not easily acclimatized to laboratory conditions, and sponges often show a decrease in their water-pumping rate and overall metabolic processes (Morganti *et al.*, 2019).

Owing to the fact that closed systems do not represent the natural marine environment well, an advanced approach of investigation is to carry out *in situ* measurements to assess feeding, respiration rate, inorganic nutrient uptake and release as well as sponge-ground mediated energy and nutrient fluxes at community level (Maldonado, Ribes and van Duyl, 2012; Leys *et al.*, 2011).

In situ benthic measurements of net sponge fluxes include a) sampling the water inhaled and exhaled by the sponges in either deep-sea habitats using manned submersibles and ROVs (Pile and Young, 2006) or in shallow water using scuba diving (Morganti *et al.*, 2017), or b) sampling through incubation chambers that may target either sponge individuals that are isolated from the external environment (Maldonado *et al.* 2020a, Maldonado *et al.*, 2020b; López-Acosta *et al.*, 2019) or small portions of the bottom and its benthic community (Roth et al., 2019; Yates and Halley, 2003).

Carbon and nitrogen budgets are usually assessed using enriched stable isotope tracers with pulse and chase experiments. Enriched stable isotope tracers are dissolved in seawater in the proximity of the sponge, and the transfer of these compounds and/or of its symbionts in the sponge is tracked over a given time interval, called the chase period.

Scientific research is advancing in the measurement of nutrient fluxes in several species of sponges. However, sometimes, even if a given flux is measured, the pathway of the uptake and release of a given compound and the involvement of the sponge cells versus its symbiotic organisms can be difficult to discriminate (Rix *et al.*, 2020).

The second level of complexity in the estimation of nutrient fluxes is to move from individual to community. For this purpose, larger and more sophisticated chambers, directly placed on the seafloor can be used to incubate the whole benthic community. This type of chamber can measure net fluxes, considering the possible interactions of different trophic levels within the community (de Goeij, personal communication).

A further level of complexity concerns the scaling up of nutrient fluxes recorded at a local scale (deep-sea sponge ground) to mathematically model the balance of major biogeochemical cycles at a regional scale. The greater the spatial scale, the greater will be the approximation introduced by this type of extrapolation. In fact, the spatial variation of regulating ecosystem services provided by sponges is highly influenced by the density of sponges and by the variability in local environmental parameters (nutrients and water conditions).

Owing to logistical difficulties and modeling challenges, the quantification of nutrient fluxes across extensive sponge-ground areas and the understanding of sponge impacts on the deep-sea ecosystem are still largely unknown. However, new advances in the understanding of the silicon fluxes in the deep sea and the role played by deep-sea sponges have been made (Maldonado *et al.*, 2020b). How to translate the importance of sponge-related ecosystem functions into sponge-related ecosystem services is still to be unraveled.

The ecosystem service cascade model (Haines-Young and Potschin, 2010) implies that an ecosystem service can be quantified when it is delivered to the beneficiaries. The benefits can then be identified and measured, and consequently the ecosystem service value estimated (see Section 1.2.1).

A methodology for the economic valuation of regulating services conveyed by sponges is not readily available in the literature. The main obstacle is determined by the fact that a consolidated knowledge necessary to build a large-scale model of the role played by sponges in the regulation of the deep-sea ecosystems is still missing. Thus, it is difficult to determine the benefits related to the maintenance of nutrient fluxes mediated by sponges in the deep sea, and to identify the repercussions of these nutrient cycles on human society.

Usually, the ecosystem service of waste-water treatment, which deals with the removal from the marine environment of contaminants and organic nutrients of anthropogenic sources, is considered for coastal marine areas or for ships' ballast waters (Armstrong *et al.*, 2012).

A new experimental approach, published by Pham *et al.* (2019), and fully described in Box 4, was used to consider water-pumping activity and filtration from an economic perspective. This approach was not meant to replace an economic valuation of sponge-related regulating services, which might be possible in the future with an increased understanding and modelling of nutrient fluxes mediated by sponges. However, the approach undertaken helped, considering, in economic terms, the massive water-pumping activity and efficient filtration carried out by sponges in the deep sea.

4.2. Baseline data for economic valuation

4.2.1. Evidence on the effects of water-pumping activity of deep-sea sponges on nutrient availability

Water-pumping capacity is key in sponge physiology as all main physiological functions of feeding, respiration, excretion and reproduction are mediated by the water flow through the sponge's body. Sponge pumping activity is highly variable among species. Sponges with low microbial abundance are believed to show a higher pumping rate than sponges with high microbial abundance (Weisz, Lindquist and Martens, 2008). In some species of sponges, the water-pumping rate greatly varies among individuals belonging to the same sponge ground. Sponge individuals are also known to periodically interrupt water-pumping activity following a random pattern (Morganti *et al.*, 2019; Pham *et al.*, 2019). The density of sponges per unit area and, more specifically, the density of oscula (each representing a pumping unit) per unit area are important factors determining the structural water-pumping capacity of sponges and sponge grounds. Sponges density can be different among locations and within the same location in different sponge patches. For example, on the Norwegian continental shelf, in the Traena MPA, *Geodia* sponge grounds (dominated by *Geodia barretti*, *G. atlantica*, *G. macandrewii*, *G.phlegraei*, and *Stryphnus fortis)* recorded an average sponge density of 1 individual/m^2, while in some

areas the density was to up to 6 individuals/m^2 (Kutti, Bannister and Fosså, 2013; Cathalot *et al.*, 2015). By comparison, the estimated average density of *Geodia* sponges in the Flemish Cap area, in the Western Atlantic is three orders of magnitude lower than in *Geodia* sponge grounds in the Traena MPA (Pham *et al.*, 2019). In the Northeast Pacific, in British Columbia, Canada, *Aphrocallistes vastus* forms a reef covering kilometres of seafloor in the Strait of Georgia. On the reef, formations of sponges occur at extremely high densities, with an average number of 33 oscula/m^2 but in some areas recording up to 46 large oscula/m^2 (Kahn *et al.*, 2015).

Sponges are well known as being able to filter large volumes of water. For example, a specimen of *Geodia* with a wet weight of 1 kg can filter almost 350 litres of water in a day (Leys *et al.*, 2018). The water-pumping rate is directly linked to sponge metabolism (Morganti *et al.*, 2019). The energy requirements of water-pumping activity for different sponge species is still under investigation. Preliminary results suggest that water pumping is an expensive process that concurs to sponge high metabolism and oxygen consumption (Leys *et al*., 2011; Ludeman, Reidenbach and Leys, 2017). At the same time, the volume of water that is pumped daily by sponges directly affects the magnitude of nutrient fluxes and transport of organic carbon and inorganic nutrients (e.g. silicate, nitrate, nitrite, ammonium and phosphate) from pelagic areas to benthic areas.

Differently from cold-water corals, sponges do not store carbon in their skeleton, but they concur to transport organic carbon from the water column to the sediment. Sponges remove DOM and bacteria from the water column and make them available in the form of detritus to other organisms of the benthic community (Maldonado, Ribes and van Duyl, 2012). This transport and exchange of nutrients, known as bentho-pelagic coupling, is a fundamental process that concurs to lessen the oligotrophic (food-limiting) conditions of the deep sea.

Sponges are filter feeders and, through water pumping, are able to efficiently remove particulate organic carbon (constituted by bacteria and detritus) from the water column. In a day, a dense sponge ground can efficiently clear all bacteria found in a water column up to 170 m deep (Leys *et al.*, 2018). Sponges also consume large quantities of DOM, constituting up to 97 percent of sponge diet (Rix *et al.*, 2020). A recent study has demonstrated that DOM is taken up both by symbiontic bacteria and sponge cells (Rix *et al.*, 2020).

In the literature, it is reported that sponge grounds can ingest between 29 mg C/m^2 and 1 970 mg C/m^2 per day, depending on sponge density, their metabolic rates, and local availability of bacteria and DOC as carbon sources (Beazley *et al.*, 2015). The capacity of sponges to rely on different sources of organic carbon has been suggested as a key factor in the formation of sponge grounds with a high density of individuals (Perea-Blázquez, Davy, and Bell, 2012). The relative amount of particulate organic carbon and DOM available for deep-sea sponges varies geographically and with depth (Leys *et al.*, 2018).

To date, carbon budgets have been measured in a limited number of deep-sea sponges. Owing to the cost and challenging logistics, few studies have ventured to attempt *in situ* measurement of carbon budget at the community level. Table 5 gives some examples of *in vitro* and *in situ* studies.

Table 5

Examples of *in vitro* and *in situ* studies related to water pumping capacity of different deep-sea sponge species

Geographical area	Sponge ground (dominant species)	Sponge Biomass (kg ww/m^2)	Water-pumping capacity – daily (l/m^2)	Water-pumping capacity – daily (l/kgww)	Mean C uptake – daily (mg C/m^2)	Efficiency of bacteria removal (%)	Source
Northeast Pacific (Strait of Georgia)	*Aphrocallistes vastus*	n.a.	210 000	n.a.	3 400	90	Kahn *et al.*, 2015
Norwegian Sea Trænadypet MPA	*Geodia barretti*	1.8	2 000	260	200	n.a.	Kutti, Bannister and Fosså, 2013
Træna MPA Norwegian continental shelf	*Geodia barretti, G. atlantica, G. macandrewii*	6.3	n.a.	n.a.	183 100	n.a.	Cathalot *et al.*, 2015
Laboratory	*Geodia barretti*	n.a.	n.a.	347		99	Leys *et al.*, 2018
Laboratory	*Geodia barretti*	n.a.	n.a.	600		n.a.	Kutti, Bannister and Fosså, 2013

n.a. = not available; ww = wet weight.

In the northern Norwegian shelf, *in situ* assessments of daily carbon consumption by *Geodia barretti* estimated a range of 30–400 mg C/m^2 with an average value of 200 mg C/m^2 (Kutti, Bannister and Fosså, 2013). By scaling up *Geodia barretti* water-pumping activity and consequent carbon uptake to the whole Trænadypet MPA (of 300 km^2), Kutti, Bannister and Fosså (2013) estimated that the population of *G. barretti* alone could filter every day about 250 million m^3 of water and consume 60 tonnes of carbon, having a significant impact on the nutrient cycling of the benthic boundary layer. The whole benthic community of Trænadypet MPA constituted by cold-water corals and sponge grounds, covering only 2 percent of the MPA's seafloor, was jointly responsible for 36 percent of the benthic carbon processing and used about 5 percent of the total estimated primary production in the area (Cathalot *et al.*, 2015; Schluter *et al.*, 2000).

In which way can sponges' water-pumping activity potentially affect nutrient fluxes in the deep sea? The scientific community suspects that owing to the high water-pumping rates, in areas with high sponge abundance, sponges may play an important role in the regulation of the carbon, nitrogen and silicon cycles (Maldonado, Ribes and van Duyl, 2012; Leys *et al.*, 2018; Cathalot *et al.*, 2015).

Dissolved organic matter constitutes the largest reservoir of carbon of the ocean, but it can be exploited only by few organisms. It is primarily used by heterotrophic microbes (i.e. viruses, bacteria, archaea, and microeukaryotes), which are estimated to recycle up to 50 percent of total marine productivity (Azam, 1998). This recycling activity is often referred to as the microbial loop. Sponges influence the microbial loop directly, as, being the oldest animal phylum, they are also able to exploit DOM from the water column. As DOM represents the largest reservoir of organic carbon in the ocean, sponges' capacity to use this resource is likely to have given them an evolutionary advantage (Pawlik *et al.*, 2020; Rix *et al.*, 2020). In particular, as sponges trap suspended particles and process them, they facilitate their decomposition by the benthic community in the sediment, preventing the establishment of anoxic (low-oxygen) conditions (Pham *et al.*, 2019).

Another potentially relevant effect of sponge metabolism on nutrient cycling is related to the release of nitrogen as nitrate (NO_3). Laboratory measurement of the nitrogen budget of *Geodia barretti* has shown that the sponge is able to take up bacterial nitrogen and ammonium (NH^+_4) and process these compounds to release nitrate (Leys *et al.*, 2018). Nitrate, if brought to the photic zone by upwelling water movements, is critical to supporting the oceans' primary productivity (Pham *et al.*, 2019).

Silicate constitutes another key nutrient playing an important role in modulating ocean primary productivity and the capacity of the ocean to sequester CO_2. Siliceous sponges, found in the classes of **Hexactinellidae** and **Demospongiae**, show an active uptake of dissolved silicon from the water column (Maldonado *et al.*, 1999; Maldonado *et al.*, 2011; Reincke and Barthel, 1997). Sponges use biosilica to build their skeleton. The bioaccumulation of silicon is substantial, as the siliceous skeleton can represent up to the 95 percent of the sponge's body dry weight (Maldonado, Ribes and van Duyl, 2012).

Only recently, the molecular transporters for silicon across the cell membrane of sponges have been identified, leading to a deeper understanding of the ecological and evolutionary significance of the Si uptake kinetics in sponges (Maldonado *et al.*, 2020a).

Moreover, *in situ* measurements have been carried out and quantitative models of silicon utilization have been built for dense aggregations of *Vazella pourtalesi* on the Scotian Shelf, Nova Scotia, Canada (Maldonado *et al.*, 2020b). Deep-sea sponges consume massive quantity of dissolved silicon from the water column (silicic acid), which they use to produce their siliceous skeletons. Therefore, silicon is first accumulated in the biomass of living sponges and then accumulated in the sediment through burial of siliceous spicules from dead sponges. As these sponge aggregations are known to have occupied the same places for several millennia, the silicon reservoir in the sediments rises to enormous amounts. About half of the spicules' silica in the sediment is readily dissolved back into silicic acid before being permanently buried (Maldonado *et al.*, 2019). In the aggregations of *Vazella pourtalesii* it has been demonstrated that the silicate released from the spicule-rich sediments enriches the bottom water associated to *Vazella* sponge grounds. Such a local turnover from biogenic silica to silicic acid favors the persistence and growth of deep-sea grounds. The overall ecological and biogeochemical process shows a clear role of *Vazella* sponge grounds in the bentho-pelagic coupling of the marine silicon cycle (Maldonado et al. 2020a, Maldonado *et al.*, 2020b).

The consequences of a decrease in or interruption of deep-sea sponge water-pumping activity – owing to habitat destruction, significant change in environmental parameters related to siltation, and/ or climate changes – are likely to be felt in term of carbon, nitrogen and silicon as well as a possible onset on anoxic conditions in the detritivore community (Maldonado, Ribes and van Duyl, 2012; Maldonado *et al.*, 2012).

Owing to the fact that sponge-mediated nutrient fluxes are not yet completely understood and quantified, benefits cannot be fully accounted and, consequently, sponge-mediated regulating services cannot be valued in economic terms.

4.2.2 Economic valuation of regulating services of deep-sea sponges

The benefits conveyed by deep-sea sponges in concurring in the regulation of deep-sea ecosystems include filtering suspended particles, transporting nutrients, and processing dissolved compounds. However, an economic valuation of these regulating services cannot be currently carried out. In fact, scientific research is still advancing in the collection of evidence and measurement of sponges' metabolic patterns in different species, locations and under different environmental conditions. In particular, the assessment of the carbon budget of a sponge ground would ideally need replicated measures *in situ* to account for the likely seasonality pattern and consequent variability of food availability (Leys *et al.*, 2018).

In order to assess the benefits associated to sponges' regulating services, the effects of sponge physiology needs to be scaled up to the ecosystem level. This implies being able to model the nutrient fluxes across existing different trophic levels.

However, sponges, being such efficient filter filtering organisms, can be considered a filtering ecological system living in the deep sea. In Box 4, the ecological function of water-pumping activity carried out by sponges and associated removal of bacteria and other dissolved organic nutrients in seawater (i.e. water filtration) is assimilated and compared with the functioning of a waste-water plant. This comparison provides a preliminary quantitative economic assessment from which start to consider the relevance of the massive water-pumping activity and filtration carried out by deep-sea sponges.

BOX 4 - WATER-PUMPING CAPACITY AND FILTRATION OF *GEODIA* IN THE FLEMISH CAP AREA

Deep-sea sponge grounds are constituted by sponge aggregations of demosponges and/or glass sponges, and are often dominated by few species. Sponge aggregations develop in suitable environmental conditions, and their spatial arrangement often follows depth contours and topographical features such as shelf plateaux near the shelf breaks, slopes and ridges, which create particular underwater local currents (Hogg *et al.*, 2010; Klitgaard and Tendall, 2004; Maldonado *et al.*, 2017; Murillo *et al.*, 2012) .

Sponge grounds, comprising more than 30 species but dominated by *Geodia* species (*Geodia barretti*, *Geodia macandrewii*, *Geodia phlegraei*, *Stryphnus ponderosus* and *Stelletta normani*) occur in the Flemish Cap area, where a particular water circulation is created by the mixing of cold water of the Labrador Current with warmer water influenced by the Gulf Stream (Murillo *et al.*, 2012). The Flemish Cap lies offshore, east of St. John's, Newfoundland and Labrador, beyond the 200 nautical miles delimitating Canada's exclusive economic zone; therefore, it is in international fishing waters and within the 3LMNO management divisions of the Northwest Atlantic Fisheries Organization (NAFO). It is a wide plateau with a radius of about 200 km (estimated at the 500 m isobaths). The shallower areas (less than 150 m) are found at its centre, while the deepest areas (below 1 200 m) are found at the border with the Flemish Pass (Murillo *et al.*, 2012).

A recent study modelling the geographical distribution and extent of *Geodia* sponge grounds on the Flemish Cap estimated a total sponge biomass of about 231 000 tonnes (wet weight) over an area of about 135 000 km^2. The largest biomass (between 60 percent and 66 percent) is found in the Flemish Cap within NAFO division 3M (Pham *et al.*, 2019). The Flemish Cap area is also an area targeted by ground fishery, where five main fish – Greenland halibut (*Reinhardtius hippoglossoides*), Atlantic halibut (*Hippoglossus hippoglossus*), winter flounder (*Pseudopleuronectes americanus*), Atlantic cod (*Gadus morhua*), redfish (*Sebastes* spp.) – are fished with different gear and at different depths, together with other minor fishery of other groundfish species (NAFO, 2019).

The impact of trawling on *Geodia* sponge grounds varies according to location and depth, but can be substantial in sites with high sponge density. For example, 5 tonnes of sponges were removed by a single trawl of a research vessel (Murillo *et al.*, 2012). Comprehensively, it was estimated that between 2010 and 2012 about 2 500 tonnes of sponges were removed by trawling activities in the Flemish Cap area, before NAFO (in 2012) closed 14 areas to bottom fisheries to protect vulnerable marine ecosystems (VMEs) (NAFO, 2012; Pham *et al.*, 2019). A study by Pham *et al.* (2019) assessed that the removal of 2 500 tonnes of live sponges by trawling activities resulted in a decrease in the pumping capacity of the sponge ground of 627 million litres of water per day.

Through water pumping, sponges are capable of filtering vast volumes of water to feed on bacteria (bacterioplankton, picoplankon) and dissolved organic matter. The efficiency of sponges in removing bacteria from the water column is extremely high, being less efficient at larger particle size (Reiswig, 1971. Laboratory tank measurement on *Geodia* detected a 99 percent efficiency in bacteria removal (Leys *et al.*, 2018). For this reason, the ecological function of sponge grounds can be likened to a waste-water treatment plant and, in particular, to the initial primary and secondary treatments in which a first separation/coarse filtration occurs, and suspended bacteria are first used to process the sludge, and break down the organic matter, and then the bacteria are removed by chlorination, ultraviolet irradiation or ozonation.

The water-pumping capacity (627 million litres/day) of removed sponge biomass in Flemish Cap (2 500 tonnes) is similar to that of the Ashbridges Bay Treatment Plant (ABTP), operating in the city of Toronto and serving a population of 1.5 million people, and characterized by an average treatment capacity of 598 million litres/day (Toronto Water, 2016, 2017, 2018).

The capital and operating costs of the ABTP of primary and secondary waste-water treatments were estimated comprehensively at USD 187 million over a 3-year period, the same time length in which sponge removal occurred (Pham *et al.*, 2019).

This comparison with a human-engineered system shows the costs associated to a system capable of clearing bacteria from seawater at a rate similar to that of *Geodia* sponge biomass removed by trawling activity. The economic valuation in this case is referred to the ecological function rather than the ecological service. In fact, owing to the complexity of the deep sea and its remote location, it is hard to model the ecological consequences of such decreased ecological function in the deep sea and to identify potential affected beneficiaries.

At the same time, the comparison helps to put ecological considerations under an economic perspective. The whole sponge ground mapped in the Flemish Cap area is estimated to filter more than 56 000 million litres of seawater daily, which is two orders of magnitude greater than the loss of water-pumping capacity of removed sponge biomass (Pham *et al.*, 2019). This indicates the potential prohibitive replacement cost associated to such filtering activity, but also highlights the fact that humans have no means to replicate with artificial infrastructures the water-pumping capacity and filtering activity of the *Geodia* sponge grounds in the Flemish Cap area.

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5. DEEP-SEA SPONGES AS HABITAT FOR COMMERCIAL FISH SPECIES

5.1. Methodological approach

5.1.1. Identification of fish-habitat association

In order to assess the ecosystem services provided by deep-sea sponges as habitat for commercial fish species, evidence should be collected on fish-habitat association and its effect on the demography of fish populations. A positive effect of deep-sea sponge grounds on fish populations can occur in the entire fish life cycle or just at one specific life stage. Fish adults could use deep-sea sponge grounds as feeding grounds, refuge areas, breeding sites and spawning grounds, whereas larvae and juveniles can use them as refuge areas or feeding sites. The nature of the fish-habitat association could be obligate, such that the deep-sea sponge grounds could represent an EFH or could be part of a facultative/opportunistic relationship.

The investigation of the fish-habitat relationship can advance by means of an increasing level of understanding by:

- observing/inferring the species-habitat association;
- identifying the functional role played by the habitat on a given fish species.

The fish-habitat association can be spurious owing to the confounding effect of several environmental factors (biotic and abiotic) operating over multiple spatial scales (Gulland, 1966; Johnson *et al.*, 2013; Milligan *et al.*, 2016;). The distinction between a spurious versus a causal species-habitat relationship requires repeated, statistically significant, species-habitat co-occurrence associated to behavioural observations or other elements further revealing habitat selection and its functional role.

Sampling design needs to consider fish mobility and potentially broad spatial ranges of deep-sea fish as well as stratification according to other potential confounding variables. The most important variable is water depth (Gulland, 1966; Knudby, Brenning and LeDrew, 2010), which is often, but not always, associated to lower temperature, owing to the effect of submarine currents. Another confounding variable that has been found in the study of fish association with deep-sea sponges as well as cold-water corals is the effect of isolated boulders and seamounts, as some fish species, such as *Sebastes* spp., also show some association towards these vertical reliefs (Miller *et al.*, 2012; Mortensen and Buhl-Mortensen, 2005; Du Preez and Tunnicliffe, 2011).

A robust sampling design factoring in different multiple drivers, as well as carried over appropriate temporal and spatial scales, is not easily achievable in the deep-sea environment (Milligan *et al.*, 2016). The overall survey of deep-sea benthic fishes is considered a very difficult, time-consuming and expensive task (Cailliet *et al.*, 1999).

Different challenges are faced according to the investigation technique used. Marine benthic surveys include two large groups of sampling methods: (i) benthic sleds or trawls; and (ii) visual fish surveys carried out with underwater imagery systems including: drop-down video, towed video, baited remote underwater video systems, and autonomous underwater vehicles or ROVs (Flannery and Przeslawski, 2015).

Several commercial deep-sea fish species inhabit the continental slopes at depths between 200 m and 4 000 m (Milligan *et al.*, 2016). Therefore, even just deploying or retrieving fishing gear or imaging equipment at particular locations of the deep-sea seafloor can be difficult owing to the time needed to reach the seafloor, currents and/or harsh weather and oceanographic conditions (Cailliet *et al.*, 1999; Eerkes-Medrano *et al.* 2020).

In both groups of techniques, fish surveys can be biased by induced fish avoidance or attraction. In fact, different fish species can escape from the fishing gear or be attracted or repelled by the light produced by the underwater imagery system (Stoner *et al.*, 2008). In imagery underwater surveys, data analysis protocols need to be implemented in order to minimize the probability of double counting swimming individuals (Meyer *et al.*, 2019; Devine *et al.*, 2020).

Species identification is usually easier in sampling through fishing gear because of the possibility to handle and examine the specimen on board. However, bringing deep-sea fish to the surface can lead to trauma in the fish body owing to change in temperature and pressure, with possible alteration of key features in taxonomic identification (Cailliet *et al.*, 1999). Differently, species identification in imaging sampling surveys can be hampered by light conditions, distance, and length of the observation, and complete taxonomic identification for some species can be limited or impossible.

Sampling through fishing gear also enables sex identification and direct body measurements, which constitute important data to build age-structured population models. Individuals belonging to different age classes can potentially have distinct habitat use. This is particularly relevant for oceanic pelagic deep-sea fish, which undertake offshore–coastal migration at different stages of their life cycle (see an example described in Box 5). However, as many fish species show age-related schooling behaviour, sampling through fishing gear, if not properly repeated in time and space, can lead to an age composition of the catch very different from that of the overall fish stock (Gulland, 1966).

Underwater imagery sampling is a non-destructive type of fish survey, but it is expensive, and difficult to use in extensive (in space and time) monitoring. If it does not cause attractive or adverse behaviour, it is unique in the possibility to provide behavioural clues on fish-habitat use.

For the above-mentioned reasons, fishing gear and underwater imagery are often used in conjunction as considered complementary tools in deep-sea fish surveys (e.g. Hawkes *et al.*, 2019).

5.1.2. Fish-habitat models

The integration of quantitative habitat effects of fishing in population is one of the major new frontiers currently faced by fisheries managers. Traditionally, fish stock assessment has been based on surplus production models and particularly described by the Gordon–Schaefer model (Gordon, 1954) and its variations, which take into consideration the logistical growth of a fish population targeted by the fisheries sector.

Surplus production models are single-fish species models. They assume that the variation in fish population biomass is linked to increases, owing to growth and reproduction, and decreases, owing to natural and fishing mortality. The objective of these models is to determine the optimum level of fishing effort producing the maximum yield that can be sustained without affecting the long-term productivity of the stock (i.e. maximum sustainable yield) (FAO, 2003b).

Although surplus production models are a key tool in fisheries management, the importance of incorporating a habitat effect in this modelling has been recognized as a fundamental missing component (Armstrong and Falk-Petersen, 2008; Brown *et al.*, 2019). Challenges are inherent to the need for a robust dataset providing evidence of habitat effect in fish population dynamics and to the analytical complexity of developing fish-habitat models (Brown *et al.*, 2019).

There are a multitude of possible approaches to describe fish-habitat relationships. The choice of a particular model depends on specific research goals as well as the fish and habitat characteristics under investigation (De Kerckhove, Smokorowski and Randall, 2008).

Models are useful for representing the complexity of species-habitat interactions in quantifiable terms and to be able to make simulations of the consequence of habitat change. In this context, the ultimate goal of studying fish-habitat association is to model the effect of the deep-sea sponge ground on the recruitment and/or increased growth rate of the commercial harvested fish stock.[9]

The required model should be able to describe an enhanced effect of a deep-sea sponge ground on fish demography. Habitat may affect fish population growth rate in different ways: by influencing individual growth; by affecting the spawning production per individual and/or by influencing the survival of individuals at any life stage (Brown *et al.*, 2019).

This type of modelling may require very fine-grained data. In fact, an essential nursery habitat for demersal marine species can be associated to specific characteristics and unique conditions identified at the scale of microhabitat rather than generically associated to habitat types (Stoner, 2003).

The key outcome of the required fish-habitat modelling is the amount of fish biomass of a given commercial fish stock that can be attributed to the effect of habitat. Once this can be quantified, the economic valuation can be carried out by considering the average fish price that fishers receive directly for their catch (ex-vessel fish price) and/or considering the increased economic flow from fish landed as well as fish frozen or processed fish products (Table 6).

Table 6
Proposed methodology for the valuation of deep-sea sponges as habitat for commercial fish species

Ecosystem services	Benefits	Valuation method	Economic value
Habitat for commercial fish species	Increased recruitment/survival of fish population	Production function approach	Landed value of the amount of fish biomass attributable to the effect of habitat
			Landed value of the amount of fish biomass and related fish processed products attributable to the effect of habitat

5.2. Baseline data for economic valuation

5.2.1. Occurrence of association between fish species and deep-sea sponge grounds

In the deep seas, the availability of a firm substrate tends to decrease along the continental slope with increasing depths (Buhl-Mortensen *et al.*, 2010). The occurrence of deep-sea sponge grounds is

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[9] A fish stock is defined as a population of fish that maintains itself over time in a particular area (Booke, 1981).

particularly relevant in creating additional habitat complexity on the seafloor of the deep sea. Owing to the high habitat complexity provided, sponge grounds can host an increased diversity and abundance of organisms linked to increased niche availability (Beazley *et al.*, 2013).

From an ecological point of view, deep-sea sponge species can play the same ecological role as colonial stony coral forms ("reef-like") and arborescent gorgonian octocorals ("tree-like"), providing additional three-dimensional structural habitat that can be used as shelter for predator avoidance, nursery grounds and foraging sites (ICES, 2015). This convergence is also enhanced by the fact that, in some locations, deep-sea sponge aggregations are found in association with cold-water corals (Lancaster *et al.*, 2014; Cathalot *et al.*, 2015).

There is a consensus in the scientific community on the likelihood that deep-sea sponge grounds could support rich fish assemblages by providing additional habitat with high structural complexity (Armstrong, Foley and Kahui, 2016; Baillon *et al.*, 2012; D'Onghia *et al.*, 2012; Kenchington, Power and Koen-Alonso, 2013; Chu and Leys, 2010; Lancaster *et al.*, 2014). Nevertheless, the scientific community is still cautious about making any type of generalization and drawing firm conclusions (ICES, 2015) owing to the lack of a robust set of evidence caused by the many methodological difficulties associated with deep-sea fish surveys (Buhl-Mortensen *et al.*, 2010; ICES, 2015).

The collection of repeated evidence in time and space requires dedicated research effort. Even when carrying out a dive transect, the fish encounter rate in the deep sea is generally quite low, and, therefore, observations of fish-habitat co-occurrence often result into a small sample size (Cailliet *et al.*, 1999). The low fish density in the deep sea is well known, and it is also the reason why deep-sea fisheries strategically target oceanic topographical structures such as seamounts, ridge systems and banks where some deep-sea fish species tend to be found in aggregations (FAO, 2010–2020).

The fish species that are more likely to be directly associated to deep-sea sponge grounds are demersal fish species, living on or near the bottom of the seafloor and feeding on benthic organisms, followed by pelagic fish (including mesopelagic and bathypelagic fish), which could use deep-sea sponge grounds more opportunistically (Kenchington *et al.*, 2013). The role played by deep-sea sponge grounds is likely to differ among distinct commercial fish species. Some demersal and oceanic pelagic fish species could use sponge grounds as feeding grounds, taking advantage of the increased food availability related to the diverse and abundant occurrence of macro invertebrates associated to these habitats (Buhl-Mortensen *et al.*, 2010; Hawkes *et al.*, 2019).

Some fish species could use deep-sea sponge grounds as a refuge against predators, especially at early development stages. For example, redfish belonging to the genus *Sebastes* are frequent in deep-sea sponge grounds, and field observations reported individuals living both inside and between sponges (Richards, 1986; Freese and Wing 2003; Marliave *et al.* 2009). In particular, the finger-like shape of sponges in the genus *Aphrocallistes* can offer a mimetic refuge for juvenile red rockfish (Freese and Wing, 2003).

Some other demersal fish species could use deep-sea sponge grounds as protected sites for reproduction. On the summit of the Schulz Bank, a seamount located on the Arctic Mid-Ocean Ridge, the artic skate (*Amblyraja hyperborea*) was observed on deep-sea sponge grounds with a relatively high occurrence of juveniles, 27 percent of the total sample (n = 46). In addition, a large number of skate eggs (about 902 eggs/ha) suggested the possible use of reproduction sites and nursery grounds (Meyer *et al.*, 2019).

However, for the majority of recorded fish-habitat observations available in the literature, the functional role played by deep-sea sponge grounds still needs to be unravelled. Table 7 reports observations of commercial demersal and deep-sea pelagic fish species on different types of deep-sea sponge grounds.

Table 7

Reported associations between deep-sea sponge grounds and commercial demersal and deep-sea pelagic fish species

Location	Sponge grounds	Common name	Fish species	Source
Northwest Atlantic, Grand Banks and Flemish Cap	*Geodia* sponge grounds dominated by *Geodia barretti*, *G. phlegraei*, *G. macandrewii*, *Stryphnus ponderosus* and *Stelletta normani*	Roughhead grenadier	*Macrourus berglax*	Kenchington, Power and Koen-Alonso (2013)
		Roundnose grenadier	*Coryphaenoides rupestris*	
		Blue antimora	*Antimora rostrata*	
		Greenland halibut	*Reinhardtius hippoglossoides*	
		Kaup's arrowtooth eel	*Synaphobranchus kaupii*	
		Black dogfish	*Centroscyllium fabricii*	
		Deepwater catshark	*Apristurus profundorum*	
Northwest Atlantic, Emerald Basin Nova Scotia, Canada	Hexactinellidae monospecific sponge ground formed by the glass sponge *Vazella pourtalesi*	Pollock	*Pollachius virens*	Fuller (2011); Fuller (2008) vs Hawkes *et al.* (2019)
		Pink shrimp	*Pandalus montagui*	Hawkes *et al.* (2019)
		Northern shortfin squid	*Illex illecebrosus*	
		Atlantic herring	*Clupea harengus*	
		Haddock	*Melanogrammus aeglefinus*	
Northwest Atlantic Strait of Georgia, northeastern Gulf of Alaska	Hexactinellidae sponge grounds dominated by *Aphrocallistes vastus*	Redfish	*Sebastes* spp.	Marliave *et al.* (2009); Freese and Wing (2003)
		Squat lobster	*Munida quadrispina*	Chu and Leys (2010)
		Spot prawn	*Pandalus platyceros*	
		Redfish	*Sebastes* spp.	
		Alaska pollock	*Theragra chalcogramma*	
		Ratfish	*Hydrolagus colliei*	
Schultz Bank	*Geodia* sponge grounds dominated by *Geodia parva* and *Stelletta rhaphidiophora*	Roughhead grenadier	*Macrourus berglax*	Meyer *et al.* (2019)
		Greenland halibut	*Reinhardtius hippoglossoides*	
		Arctic skate	*Amblyraja hyperborea*	
Northeast Atlantic, Rosemary Bank seamount MPA	*Geodia* sponge grounds dominated by *G. atlantica*, *G. barretti*, *G. macandrewii*, *G. pachydermata* and *G. phlegrae*	Baird's smoothhead	*Alepocephalus bairdii*	Eerkes-Medrano *et al.* (2020)
		Roundnose grenadier	*Coryphaenoides rupestris*	
		Orange roughy	*Hoplostethus atlanticus*	

5.2.2. Economic valuation of deep-sea sponge grounds as habitat for commercial fish species

Deep-sea sponge grounds are benthic biotic formations that create three-dimensional structures representing unique habitats on the seafloor of the deep sea that can be used by a large number of invertebrates as well as fish species (Hogg *et al.*, 2010; Pham *et al.*, 2015; Van de Hove and Moreau, 2007). Although, the biodiversity of invertebrate species and micro-organisms associated to deep-sea sponge grounds is disproportionally greater than the biodiversity of associated commercial fish species (see Buhl-Mortensen *et al.*, 2010), the latter are considered in the economic valuation because they can be more directly linked to an economic dimension.

Important information showing the positive effect of deep-sea sponge grounds on some commercial fish stocks can be derived by comparing populations inhabiting areas with deep-sea sponge grounds and areas without such benthic formations. However, this comparison will only be able to reveal significant differences if:

- deep-sea sponge grounds constitute an EFH;[10]
- deep-sea sponge grounds constitute a facultative fish habitat but one conveying substantial added benefits to the recruitment or growth of fish populations.

Demonstrating fish-habitat associations requires a sampling design that takes into consideration multiple factors. As a result of the complexity of these type of investigation, no study has yet been able to demonstrate a direct role of deep-sea sponge grounds in an increased recruitment/survival of fish population of some commercial fish species. However, owing to the fact that sponge grounds have already been characterized as biodiversity hotspots for invertebrates (Hawkes *et al.*, 2019), collecting greater evidence on the supporting role of benthic habitats on commercial fish species is likely to be just a matter of time.

A practical example showing the complexity of this type of investigation and the multitude of variables potentially at play is described in Box 5, where the working hypothesis on the potential role played by *Vazella* sponge grounds in Emerald Basin, Nova Scotia, Canada, on the juveniles and small adults of pollock (*Pollachius virens*) is outlined. Sampling needs to compare areas inside and outside *Vazella* sponge grounds. It needs to be stratified in order to consider potential confounding variables related to water temperature and depth. On a temporal scale, it needs to consider the seasonality of fish movements as well as potential seasonal fluctuations in food availability on the *Vazella* sponge ground. Other factors influencing sampling outcomes are: pollock's strong schooling behaviour (among individuals of the same size); the area of an individual daily home range and movements carried out within the home range; and the frequent vertical movement in the water columns, as pollock spends less time on the bottom than do other gadoid fish (Neilson *et al.*, 2002). Biometric measurement of length and weight, sex identification, sexual maturity and age determined by means of otolith analysis are important in reconstructing population age classes in order to distinguish between effects on size of age from the possible effect on size of higher food availability in *Vazella* sponge grounds.

Average body-size parameters, possibly associated to stomach content analysis, can be useful in corroborating the hypothesis of sponge grounds as "fattening stop-overs", promoting the growth of juveniles and small adults and favouring future larger spawnings. Once the species-habitat association

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[10] In the United States Magnuson-Stevens Fishery Conservation and Management Act (16 U.S.C. § 1802), essential fish habitats are defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, or growth to maturity." According to this definition necessary means "the habitat required to support a sustainable fishery and the managed species' contribution to a healthy ecosystem."

is verified, an effect on the demography of pollock's fish stock needs to be modelled and tested in order to quantify a potential positive impact of *Vazella* sponge grounds on the Canadian pollock fishery.

The pollock fishery in Canadian waters is regulated by a management plan, which establishes maximum fishing limits (total allowable catches [TACs]) implemented through a system of fishing licences (Fisheries and Oceans Canada, 2018). The current limited economic value of USD 2.5 million/year estimated for the pollock landings occurring in the NAFO division 4VWX +5 management unit is mainly related to the limited average landed quantity (3 237 tonnes/year), which does not even reach the amount allowed by the TAC system (Fisheries and Oceans Canada, 2019).

The current limited economic value is not representative of the potential option value it could have in future when the fish stock is fully recovered. On this respect, gaining a better understanding of ecology and habitat use of the pollock fish stock in its Eastern Component, where the fish stock shows a rather slow growth rate, could benefit the pollock fishery management plan, and provide future increased economic benefits related to larger fish catches.

BOX 5 - WORKING HYPOTHESIS: *VAZELLA* SPONGE GROUNDS PLAYING A ROLE ON THE RECRUITMENT OF CANADIAN POLLOCK FISH STOCKS?

Pollock (*Pollachius virens*) is a commercial demersal/pelagic fish species that occurs off the eastern coast of North America. In particular, along the Canadian Atlantic coast, three fish stocks are found on the Scotian Shelf, the Bay of Fundy, and the Canadian portion of Georges Bank, respectively (Neilson, Stobo and Perley, 2006).

The life cycle of pollock includes some offshore and in-shore movements (Armannsson *et al.*, 2007; Clay *et al.*, 1989). Adults spawn offshore over hard, stony or rocky bottoms (Neeson, 2006). Spawning requires low water temperatures, and spawning activity is triggered at a temperature of about 8 °C, but peaks at 4.5–6 °C (Neeson, 2006). On the Scotian Shelf, spawning is thought to occur between November and March (O'Boyle *et al.*, 1984; Fortier and Quiñonez-Velazquez, 1998).

Traditionally, pollocks' spawning locations are known to occur off the Canadian coast on the Scotian Shelf. In particular, pollock spawning areas have been recorded in the Emerald Bank, in Sable Island as well as in the Gully on the eastern Scotian Shelf (Mayo, McGlade and Clark, 1989).

Vazella pourtalesi sponge grounds are found in the Emerald Basin, Nova Scotia, at a distance of 50–60 nm from the coast, at depths of 150–210 m (Beazley *et al.*, 2018), and occupy an area of about 8 000 km2 (Kenchington *et al.*, 2010). *Vazella* sponge grounds are associated to relatively warm waters characterized by a minimum temperature, recorded on the seafloor, often above 5 °C (Beazley *et al.*, 2018), which do not make *Vazella* sponge grounds ideal as spawning grounds for pollock.

Nevertheless, *Vazella* sponge grounds on the Scotian Shelf are located in a traditional fishing area for groundfish, including pollock (Fuller and Cameron, 1998; Fuller, 2011), although photo-transects carried out in 2011 did not record such species-habitat associations (Hawkes *et al.*, 2019), likely due to the downward view of the camera.

Eggs and larvae, respectively, are transported and swim towards coastal areas. In fact, pollock juveniles belonging to the 0-year and 1-year age groups are predominantly caught in coastal sheltered areas (Clay, *et al.*, 1989). Two-year old juveniles start migrating back offshore and, usually, in the Canadian population, individuals reach maturity at 3–4 years old (Trippel *et al.*, 1997; Clay *et al.*, 1989; Fisheries and Oceans Canada, 2007).

Pollock is considered an opportunistic predator, and its diet preference changes with fish growth and age. Crustaceans are the most important food item among smaller adults (41–65 cm), while fish becomes increasingly important among medium-sized adults (66–95 cm), and molluscs (the *Loligo* squid) are also prey for the largest adults (larger than 95 cm) (Tyrrell *et al.*, 2007). The high abundance of crustaceans belonging to the genus *Pandalus* in *Vazella* sponge grounds, together with northern shortfin squid (*Illex illecebrosus*) and other clupeid fish species (Hawkes *et al.*, 2019) could suggest that these areas represent potential favourable feeding grounds for pollock juveniles migrating from the coast offshore as well as for adults.

Although this hypothesis has not been verified, this case study exemplifies the difficulties encountered in assessing the role played by benthic habitats on fish stocks. In fact, the complexity of the fish life cycle intersects with the multivariate nature of fish-habitat surveys and, ultimately, with fishery management regulations.

Canada's Department of Fisheries and Oceans (DFO) is responsible for managing pollock stocks in Canadian waters through the implementation of integrated fisheries management plans and definition total allowable catches of pollock (Fisheries and Oceans Canada, 2019; Wildling and Bradt, 2015). The pollock fishery occurs in the North Atlantic Fisheries Organization (NAFO) division 4VWX +5 management unit, and is split into the Eastern Component (4VW) and the Western Component (4X +5) (Fisheries and Oceans Canada, 2007). The TAC varies slightly from year to year. In 2018–2019, the TAC for the Western and the Eastern Components were 5 137 tonnes and 900 tonnes, respectively (Fisheries and Oceans Canada, 2019). The difference in the TACs is due to the fact that in the Eastern and Western Components there are two discrete pollock populations, and the population the Eastern Component is growing at a slower rate than in the Western Component (Fisheries and Oceans Canada, 2007). Pollock is generally harvested by different fishing fleet segments. It is caught mainly with bottom trawls and gillnets, but also by longline gear (Wildling and Bradt, 2015; Fisheries and Oceans Canada, 2018). The pollock fisheries are open all year-round. However, the high catch rates on the Scotian Shelf usually occur in the late-autumn and winter period when pollock is found in large aggregations associated to spawning (Neilson and Perley, 1996; Neilson *et al.*, 2002). In the Nova Scotia region, Canadian fisheries statistics on pollock, between 2014 and 2018, report average annual catches of 3 237 tonnes and a reported average value of pollock landings (2014–18) of CAD 3.7 million, corresponding to USD 2.5 million/year (Fisheries and Oceans Canada, 2017). In Nova Scotia, the average pollock unit price (2014–18) fluctuated between CAD 1.32 and CAD 0.87, which is within the average landed price for groundfish species (CAD 0.70 – CAD 1.50) (Fisheries and Oceans Canada, 2018).

In 2018, the world demand for pollock fillet (raw and frozen) was reported to exceed USD 67 million. The global pollock market involves trades among 48 countries; China and Lithuania accounting for 39 percent and 19 percent of total world imports, respectively (TrendEconomy, 2019). Canada is currently only a minor pollock producer and exporter. In 2018, Canada exports amounted to USD 427 706, representing only 0.61 percent of the world export value, and were dwarfed compared with those of Norway, which were two orders of magnitude higher (USD 46 476 853) (TrendEconomy, 2019). The major importer of Canadian fish products is the United States of America. In 2011, the United States of America imported 54 percent of Canada's fish products exports, among which 56 tonnes of Canadian pollock were imported at USD 74 273, with an average unit price of USD 1.3/kg (Wildling and Bradt, 2015).

The current limited relevance of the Canadian pollock fishery at the international and national level sharply contrasts with the importance it had before the collapse of the Atlantic northwest cod fishery in 1992 and consequent fishery moratorium, which indirectly also affected the pollock catch (Fisheries and Oceans Canada, 2007). In 1987, pollock landings peaked at 46 000 tonnes (Fisheries and Oceans Canada, 2007). Although this historical large catch rate was not sustainable, it indicates the possibility of a large-scale pollock fishery in Canadian waters, far greater than the average amount currently caught (3 237 tonnes). However, a large-scale pollock fisheries will not be allowed until the Eastern Component properly rebuilds (Fisheries and Oceans Canada, 2007).

In this context, a deeper understanding of the potential role played by *Vazella* sponge grounds in conjunction with other factors could help understand the reasons for the slow growth of the pollock population in its Eastern Component. This information could support a pollock fishery management plan aimed at rebuilding pollock fish stocks, paving the way for a larger, sustainable pollock fishery in the future.

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6. DEEP-SEA SPONGES AS PROMISING CANDIDATES FOR SCIENTIFIC RESEARCH AND EDUCATION

6.1. Methodological approach

The economic value that can be associated to the interest raised by deep-sea sponges for scientific research and education was estimated using a cost-based approach (Table 8). In fact, the investments made in scientific research and education can be considered a signal of societal interest in the study and understanding of these organisms. Concern, curiosity, and a sense of belonging to nature are important drivers in scientific research and education. Scientific research inevitably has a component in education as the majority of projects, especially those with extensive field research or large amounts of data to process, usually engage students at different academic levels (bachelors, masters and doctorate). Part of the costs related to education, such as use of equipment, and time of staff in supervisory roles, is usually absorbed by the overall project funding, whereas other costs can be covered by additional grants and scholarships supporting students aiming at developing a career in ocean science. For these reasons, in the economic valuation, scientific research and education are inevitably interconnected.

Table 8

Proposed methodology for the valuation of deep-sea sponges as relevant ecosystem for scientific research

Ecosystem services	Benefits	Valuation method	Economic value
Scientific research and education	Increased knowledge on deep-sea sponge	Cost-based approach	Investments made to increase knowledge on deep-sea sponges

Investments in the field component of research on deep-sea sponge grounds are usually substantial owing to the costs related to the transfer to distant offshore areas, equipment needed to sample these remote sites, and use of large research vessels. Consequently, field sampling (ship time) is usually restricted in time and space, while the largest amount of time of a research project is dedicated to the investigation phases such as laboratory research, data analysis, and dissemination of results.

For this reason, a consideration of the overall project investments is a more robust indicator than just focusing on investments allocated towards deep-sea field data collection. In fact, it turns out that investments in deep-sea expeditions (including fuel, crew's salary, researchers' salaries, supplies, and transfer to vessel departure location) capture, overall, a small fraction of the total research investments of a multi-year research project.

Funding aimed at increasing knowledge on deep-sea sponges includes both public and private investments. Private investments are often more strictly linked to biotechnological applications and

bioprospecting activities, thus focusing more on use values (direct present value or a future option value).

Public investments often comprise benefits derived by both use and non-use values. Increased knowledge can support a better management of areas where deep-sea sponge grounds are found and, consequently, support their conservation as areas of high biodiversity (indirect value), conservation for future uses (option value), for future generations (bequest value), or just to allow these life forms to be on the planet (existence value). Owing to the plurality of values behind public investment in deep-sea sponge research, these investments can better represent the interest towards deep-sea sponges of a multitude of stakeholders and, ultimately, of society at large.

Public funding for scientific research and education can be raised at both the national and international level. However, retrieving information on funding disbursed at the national level can be challenging. Not only national projects might be mentioned without reference to their budget, but more often, every project, especially those targeting the deep sea, rely on multiple budget sources. In particular, the use of a research vessel or specific equipment for the deep sea is often part of specific grants released by national institutes (e.g. the National Science Foundation in the United States of America). There are institutions, such as the University National Oceanographic Laboratory System in the United States of America, and the Marine Science Co-ordination Committee in the United Kingdom of Great Britain and Northern Ireland, that coordinate the use of research vessels for nationally funded ocean research, and projects such as the European Union-funded Eurofleets, which supports transnational access of research vessels in Europe, and international efforts that support free-of-charge access to research vessel fleets (Nieuwejaar et al., 2019).

Several deep-sea projects might not be completely dedicated to studying deep-sea sponge grounds, but might have specific components dealing with them (such as the ATLAS project). Therefore, the identification of investments made in deep-sea sponge research requires detailed knowledge of projects goals and related allocated budgets.

Owing to limitations in data availability, the data presented in this report include only investments made at the international level by the European Union, where funded projects and budgets are available through a publicly accessible database (CORDIS, 2020). Data were retrieved by using a query with the keyword phrase "deep-sea sponge", and projects were selected for the period 2010–2020. The whole budget was considered for the sponge-dedicated projects and, in the absence of detailed budget information, arbitrarily 50 percent of the budget was considered for those deep-sea projects with less restricted focus on sponges (e.g. ATLAS and PharmaSea).

6.2. Baseline data for economic valuation

6.2.1. International funding for scientific research on deep-sea sponges

Deep-sea sponges are high in the scientific research agenda owing to the interest raised by their unique features in several fields, such as microbiology, molecular biology, and ecology as well as for the high potential in biotechnological applications. Deep-sea science is a young field compared with many other science disciplines. Investigation and characterization of deep-sea sponge grounds is also quite recent, as the first full characterization of a sponge ground was carried out in 1987 during the inter-Nordic BIOFAR 1 programme around the Faroe Islands (Klitgaard, Tendal and Westerberg, 1997).

Therefore, it is not surprising that scientific research is still ongoing and that, just in the last few years, new sponge species have been described (Kersken, Janussen and Arbizu, 2018; Carvalho et al., 2020), new bioactive compounds have been isolated (Li, Janussen and Tasdemir, 2020; Ragini, Piggott and Karuso, 2019), sponge cell lines have been reproduced in the laboratory (Conkling et al., 2019), the community of symbiotic bacteria living of sponges has been better characterized (Bayer et al., 2020; Steinert et al., 2020), and a better understanding has been gained of biosilicification and reconstruction

of silica cycling (Maldonado *et al.*, 2020; Maldonado *et al.*, 2019; Hendry *et al.*, 2019) as well as of deep-sea metabolism and physiology (Rooks *et al.*, 2020; Rubin-Blum *et al.*, 2019). Moreover, the influence of environmental factors on the distribution of deep-sea sponges in different locations as well as the impact of commercial bottom trawl fishing (Vieira *et al.*, 2020; Murillo *et al.*, 2020) have recently been investigated (Davison *et al.*, 2019; Ramiro-Sánchez *et al.*, 2019; Hanz *et al.*, 2019; Vad *et al.*, 2020), just to mention a few discoveries and research contributions.

Many of these findings were possible thanks to dedicated investments made by the European Union in the scientific research of deep-sea sponges, deep-sea sponge grounds, and deep-sea sponge biotechnological applications. Table 9 reports the projects on deep-sea sponge research funded by the European Union between 2010 and 2020 (CORDIS, 2020).

Table 9

European Union-funded projects related to deep-sea sponges, active 2010–2020

European Union project	Project length	Project grant (EUR million)	Conversion rate (USD/EUR)	Project grant (USD million)
PharmaSea[1]	2012–2017	6 597 350	0.778	8 479 884
SponGES	2016–2020	10 275 365	0.903	11 379 142
ATLAS[1]	2016–2020	4 583 908	0.903	5 076 311
BluePharmTrain	2013–2017	3 896 333	0.754	5 167 550
BioSilica	2011–2017	2 183 600	0.719	3 036 996
Fibrogelnet	2013–2017	910 726	0.754	1 207 860
DeepSym	2018–2020	195 455	0.847	230 761
Adaptomics	2017–2019	195 455	0.885	220 853
Total	2010–2020	28 838 192	n.a.	34 799 357

n.a. = not applicable.
[1]Only half of the whole allocated budget is shown in the table.
Source: CORDIS, 2020.

The overall disbursement was about EUR 29 million, corresponding to about USD 35 million, with an average investment over the last decade of less than USD 4 million/year. By comparison, it should be noted that the total disbursement of the European Maritime and Fisheries Fund in the period (2014–2020) amounted to EUR 6.4 billion (European Union, no date).

To put these investment figures in prospective, it should be considered that research on deep-sea sponges can be associated to high field costs. Van Dover *et al.* (2014) reported that the daily cost of field sampling in the deep sea is about USD 80 000, including the research vessel R/V *Knorr* (USD 43 000/day) equipped with ROV *Jason* (USD 22 000/day) and the autonomous underwater vehicle *Sentry* (USD 15 000/day) from the Woods Hole Oceanographic Institution.

The daily cost related to expedition cruises carried out within the SponGES project was about USD 46 000 including rental of a research vessel (USD 26 000), scientific team and other personnel on board (USD 15 000), and ROV and other equipment (USD 5 000) (Tore Rapp, personal communication).

By comparison, it should be considered that a simple seafloor survey to run a 100-mile pipeline costs about USD 50 million (Carlyle, 2013), and that to repair a submarine cable costs on average between USD 1 million and USD 3 million (Veverka, undated).

Comprehensively, public investments made in deep-sea sponge-related projects indicate the awareness of the importance of advancing in scientific research at an international level. Scientific investigation is needed for developing future pharmaceuticals and biotechnological solutions, as well as to increase current knowledge of deep-sea sponge grounds for better-informed management decisions concerning their present and future protection as VMEs.

However, the recent country survey carried out by UNESCO (2017) showed that investment in ocean science accounts for between 0.1 percent and 21 percent of natural science expenditure among the 24 countries surveyed and represents only a very small fraction (between < 0.04 percent and 4 percent) of total R&D expenditure. Moreover, the average yearly funding and the average length of European Union-funded projects can represent limiting factors for long-term data collection in the deep-sea (Rogers *et al.*, 2015; FAO, 2020). Therefore, adequate funding for research remains the key driver able to advance the understanding of deep-sea sponges and, consequently, assess the ecosystem services provided by deep-sea sponges in both ecological and economic terms.

7. THE WAY FORWARD

This report presents an overview of the benefits potentially conveyed by deep-sea sponge grounds. It offers available baseline data for an economic valuation, providing ground-based reasons for long-term conservation of deep-sea sponge grounds.

Research on deep-sea sponges is still progressing, and current knowledge in some areas is more advanced than in others. This is directly reflected in the economic valuation of different categories of ecosystem services. The potential of deep-sea sponges in the development of new pharmaceuticals and biotechnological applications is more advanced than in regulating, habitat or cultural services.

What are the current drivers of research on deep-sea sponges? What type of financial investments are needed to advance understanding of deep-sea sponges? How should research priorities be identified?

Bioprospecting activities for the collection of deep-sea sponges are ongoing. Every day, researchers are at work to screen new compounds extracted from marine organisms, including deep-sea sponges, in order to find that particular molecule that will be able to make it to the end of the R&D pipeline.

The chemical variety of compounds found in sponges is astounding. Sponges can be considered as a marine pharmacy, based on a review of marine sponge-derived natural products, which identified more than 4 850 different compounds (Mehbub *et al*., 2014).

Given that on average it takes longer than 12 years for a molecule to go through all laboratory testing, from preclinical to clinical trials, the current low number of marketed pharmaceuticals derived from sponges is due to the time-lag effect of R&D investments in the pharmaceutical industry. However, having more sponge-derived drugs is just a matter of time. Private pharmaceutical companies have high economic interests in the biotechnological potential of sponges, although not all costs associated with the discovery and development of new drugs are borne by the private sector alone.

A study conducted by the Tufts Center for the Study of Drug Development in the United States randomly sampled 106 new drugs from 10 different pharmaceutical companies, and estimated that the cost of developing a new drug is almost USD 2.6 billion (DiMasi, Grabowski and Hansen, 2016). The pharmaceutical industry has already put in place mechanisms to ensure the economic viability of the large investments required by R&D. Pharmaceutical companies dynamically assess the financial risks of R&D through real option valuations. Moreover, when a new compound is discovered, pharmaceutical companies protect the intellectual property of this discovery with patent filing. A patent for a new drug provides the pharmaceutical company with a monopoly on drug production and commercialization, which typically lasts for 20 years. This patent protection mechanism enables pharmaceutical companies to earn high revenues, and in turn be able to further invest in R&D. When the drug patent reaches its expiration date, pharmaceutical companies start to fall down their "patent cliff", because at that point they have to face a large number of competitors in the pharmaceutical market, including the commercialization of generic drugs.

Usually, a large share of investments in the development of new drugs comes from the private sector. However, in several cases, public–private partnerships and engagement of not-for-profit funding for research can leverage R&D, particularly in the case of orphan diseases in situations where there is little or no economic incentive to develop pharmaceutical products.

The R&D on pharmaceuticals on marine-derived products, and in particular on sponges, is a bioprospecting activity that has been ongoing for more than 50 years. Two successful examples of this bioprospecting have led, to date, to a worldwide market for two sponge-derived anticancer drugs: cytarabine and Halaven®. Based on the economic valuation assessed in this report both drugs can be considered as "blockbusters", as they can be considered successful drugs with annual revenues exceeding USD 1 billion.

Research and development on new pharmaceuticals derived from sponges operates in its own niche with little interaction with other economic sectors. Theoretically, the impact of bioprospecting activity on sponge conservation is expected to be rather limited, as the biological material collected in initial R&D phases is usually quite small, between 1 kg and 5 kg (Koyama, 2009). However, as the bioactive compound can occur in the sponge tissue in extremely low concentration, historically, there has been one isolated case of massive collection (1 tonne) of sponge biomass for pharmaceutical purposes (Munro *et al.*, 1999). The investment cost for this field collection was reported to exceed USD 500 000 (Newman and Cragg, 2005).

Pharmaceutical companies are becoming increasingly capable of carrying out a chemical synthesis of the bioactive compounds initially isolated in the marine organisms. In the literature of the sector, it is explicitly recognized that the capacity to synthesize the molecule of interest *in vitro* represents a major turning point in R&D, enabling future large-scale drug production. The current understanding is that R&D on deep-sea sponges as a source of pharmaceuticals will proceed in the future as already part of a well-equipped "train of pharmaceutical research", and it is likely to produce additional cases of sponge-derived drugs. In this R&D train, future production of biomaterial derived from sponge lags a bit behind. The development of new biomaterials or synthetic materials inspired by natural organisms is also subject to rigorous testing procedures and, currently, experiments have been conducted only on laboratory animals. Forecasting the outcomes of the current R&D on sponge-derived biosilica is hard at this stage. Given that this investigation is still in its early stage, the private sector has not fully engaged in testing bone-graft substitutes, and research advances are mainly supported by the public sector through projects run by academia.

However, while research on pharmaceutical and biotechnological opportunities provided by deep-sea sponges is advancing in its own specialized niche, a completely different scenario occurs for deep-sea regulating and habitat services associated to deep-sea sponges. The main distinction is that while pharmaceutical and biotechnological benefits can be investigated and developed "*in vitro*", benefits related to the ecological role played by deep-sea sponges can only be conveyed through the conservation of sponge grounds.

Sponge aggregations are recognized as singularly vulnerable habitats that deserve legal protection. They are classified as VMEs (FAO, 2009), meet the criteria of ecologically and biologically significant areas (Hogg *et al.*, 2010), and have also been included in the Oslo–Paris OSPAR Convention (OSPAR, 2008). As deep-sea sponge grounds are not only found within country's exclusive economic zones but also in areas beyond national jurisdiction, their conservation falls under Sustainable Development Goal 14 "Conserve and sustainably use the oceans, sea and marine resources for sustainable development" of the United Nations 2030 Agenda for Sustainable Development (United Nations, 2020). Their protection and management also fall under the new global agreement on the conservation and sustainable use of marine biological diversity of areas beyond national jurisdiction (BBNJ Agreement) established by the United Nations General Assembly and adopted with Resolution 72/249 (United Nations, 2018). The preservation of potential benefits associated to the regulating and habitat services provided by deep-sea sponges needs to be considered in the light of an integrated and inter-sectoral management of the deep sea.

Deep-sea sponges are subject to several potential anthropogenic stressors linked to bottom fisheries, and oil, gas and mineral extractive activities in the deep sea. Deep-sea sponge grounds can be physically destroyed by trawling activities or other dredging occurring on the seafloor. They can be damaged by fishing nets scraped across the seabed, but they can also be affected by suspended sediment that can clog their water-pumping system. Plumes of suspended sediments can be raised by trawling activities and, potentially, at a larger scale, by deep-sea mining operations. As researchers seek to gain more information on the tolerance and response of sponges to sediment smothering, and to spatially model the potential dispersion of sediment by potential mining operations, policymakers and government

bodies need to evaluate potential trade-offs among conflicting uses of the deep sea and to avoid irreversible impacts on VMEs.

First baseline information clearly includes detailed mapping showing the past and present distribution of sponge grounds in the deep sea. However, distribution maps alone will not suffice. The understanding of regulating and habitat services associated to deep-sea sponges is also fundamental for a strategic long-term vision.

Even if a full economic valuation could not be attained in this report, some food for thought has been provided. Deep-sea sponges can be considered as one of the major filtering systems of the deep sea, owing to their capacity to process large volume of waters and significantly affect the concentration of some nutrients in the water column. Scientists believe that sponge grounds are likely to significantly affect some biogeochemical cycles in the deep sea, including those of carbon, nitrogen and silicon.

The information currently available is not sufficient to create robust scenarios on what the cascade effects in the deep-sea ecosystem associated to a possible decrease in sponges' water-pumping capacity will be. However, preliminary estimates show that sponges' water-pumping capacity and filtering cannot be easily replaced by existing, engineered, advanced technologies, and that incurred costs would be prohibitive.

For this reason, precautionary measures should be taken regarding the protection of deep-sea sponge grounds by means of closures to trawling and other damaging activities in MPAs. Yet, regulatory measures should also consider that, as plumes of suspended sediments are capable of travelling large distances, sponges can also be impacted by activities occurring outside the boundaries of a given MPA.

Another reason for protecting sponges in the deep sea is that deep-sea sponge grounds are considered to be hotspots of biodiversity. In this regard, they can contribute to gene-pool protection by maintaining inter- and intra-specific genetic diversity of several deep-sea species. Sponges' three-dimensional structures are likely to benefit not only invertebrate species but particularly also species associated with the seafloor more consistently (demersal fish species) or opportunistically (pelagic fish species).

Recognizing a possible habitat role played by deep-sea sponges for some commercial fish stock would be pivotal for fisheries management and spatial planning. The association between some commercial fish species and deep-sea sponge grounds has been observed, but data are still insufficient to derive sponges' functional role on deep-sea fish stocks. Thus, the impact of destruction of deep-sea sponge grounds on deep-sea fisheries in ecological/economic terms cannot be explicitly assessed.

A precautionary approach should be endorsed as the economic value at stake is considerable. For example, the market value of landings of the six fish species: roughhead grenadier (*Macrourus berglax*), roundnose grenadier (*Coryphaenoides rupestris*), Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* spp.), pink shrimp (*Pandalus borealis*) and haddock (*Melanogrammus aeglefinus*) observed in association with *Geodia* sponge grounds is estimated, comprehensively for the Northeast and Northwest Atlantic, at about USD 1.3 billion/year (FAO, 2020).

Advancing the scientific understanding of regulating and habitat services provided by deep-sea sponges requires dedicated effort and a sufficient amount of time and resources allocated in order to be able to have repeated observations and measures in different sites and in different environmental/ecological conditions. Gaining further quantitative information and understanding on the ecological and economic consequences of the destruction of deep-sea sponges in several areas is certainly to be considered a research priority.

The investments made by the European Union in the period 2010–2020 have been reported as an indication of the relevance of deep-sea sponges being recognized by governance at the international level. However, the perception of the general public towards the conservation of deep-sea sponges is

currently a major data gap that needs to receive attention, and funding should be allocated for survey programmes. Previous investigations on cold-water corals have shown that the conservation of these benthic habitats has value to people even if they do not have any direct fruition of these habitats. They have also shown that people would select scenarios in which these habitats are protected, and interviewed respondents would be willing to pay for their conservation.

Currently, there is no survey on the people's willingness to pay towards deep-sea sponge ground protection, but a similar proactive attitude of the general public can be expected when sufficient information on deep-sea sponge grounds is provided.

Sponges living in the deep sea tend to be slow-growing organisms, which makes them particularly vulnerable to damage caused by seafloor disturbance. Some massive specimens or their reef formations can be considered part of our common cultural heritage. An isolated massive glass sponge, belonging to the subfamily *Lanuginellinae*, recently discovered at a depth of more than 2 000 m, measuring over 3.5 m in length, 2.0 m in width and 1.5 m inheight, exceeded the dimensions of the largest sponge previously known (Wagner and Kelley, 2017). Unique formations are also represented by *Vazella pourtalesi* sponge grounds found on the continental shelf off the Canadian coast, where individual sponges can reach one metre in height and occur in sufficient numbers to create dense aggregations (Hawkes *et al.*, 2019).

The World Heritage Convention, ratified in 1972, is an international environmental agreement for protecting sites of outstanding universal value. Some of the criteria used to select UNESCO sites of outstanding universal value can also be applied to marine ecosystems (Abdulla *et al.*, 2013). While several coral reefs are already included among World Heritage marine sites, there is the also potential for inclusion of deep-sea sponges characterized by exceptional natural beauty (criterion vii), but also features contributing to exceptional ecological or ocean processes (criterion ix), or supporting an exceptional level of biodiversity (criterion x).

The ecological importance of deep-sea sponge grounds and their economic relevance need to be further divulged. Raising public awareness, integrating knowledge on deep-sea sponges into education and learning programmes, and providing recreational opportunities for the general public are essential for mainstreaming deep-sea sponge conservation and for a sustainable and equitable use of this unique biodiversity.

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APPENDIX 1 - CLASSIFICATION OF ECOSYSTEM SERVICES

Table A1.1

Classification of ecosystem services according to different classification frameworks

Service	TEEB[1]	MEA[2]	CICES[3]
Provisioning	Food	Food	Terrestrial plant and animal for nutrition
			Freshwater plant and animal for nutrition
			Marine plant and animal for nutrition
	Medicinal resources	Genetic resources	Biotic material
		Biochemicals, natural medicine and pharmaceuticals	
	Raw material	Fibre	Fibre and other material
Regulating	Waste treatment	Water purification and waste treatment	Bioremediation
			Filtration, sequestration, storage of wastes
	n.a.	n.a.	Mediation of nuisances of anthropogenic origin (smell, noise and visual)
	Local climate and air quality	Air-quality regulation	Regulation of temperature and humidity
	Carbon sequestration and storage	Climate regulation	Regulation of chemical composition of atmosphere and oceans
	Moderation of extreme events	Water regulation	Hydrological-cycle and water-flow regulation
		Natural-hazard regulation	Buffering and attenuation of mass movements
			Fire protection
			Wind protection
	Erosion prevention	Erosion regulation	Erosion control
	Biological control	Pest regulation	Pest control
		Disease regulation	Disease control
	Maintenance of soil fertility	Soil formation	Regulation of soil quality (weathering, decomposition and fixing processes)
		Nutrient cycling	
	Pollination	Pollination	Pollination
Habitat	Habitat for species	Provision of habitat	Habitat
	Maintenance of genetic diversity	Biodiversity	Gene-pool protection
			Seed dispersal
	n.a.	Primary production	n.a.

Service	TEEB[1]	MEA[2]		CICES[3]
Cultural	Spiritual experience and sense of place	Spiritual and religious value		Sacred or religious meaning
		Sense of place		Symbolic meaning
		Cultural heritage value		Cultural heritage
		Cultural diversity		
	Tourism	Recreation and ecotourism		Ecotourism
	Recreation			Entertainment
				Leisure
	Aesthetic appreciation and inspiration for art, culture and design	Aesthetic values		Aesthetic experience
		Knowledge system		Scientific investigation
		Education		Education and training
		Existence value and other non-use value		Existence
				Bequest

[1] The Economics of Ecosystems and Biodiversity (2010).
[2] Millennium Ecosystem Assessment (2005).
[3] Common International Classification for Ecosystem Services (2018).
Notes:
n.a. = not available
CICES version 5.1 . Different ecosystem services categories are shown in the table with different degree of details. Provisioning services are pooled all together to match the single MEA category "food" without distinction if species are cultivated, reared or wild animal and plants.
Regulating services are shown with breakdown to the class level.
Cultural services are shown with breakdown to the class level.
CICES abiotic services are not represented, and the category freshwater is also not shown.

APPENDIX 2 - INDICATORS OF DEEP-SEA SERVICES AND ASSOCIATED BENEFITS

Table A2.1

Suggested indicators of provisioning services and associated benefits applied to the deep sea

Provisioning service	Indicator to measure ecosystem service flow	Indicator to measure benefits provided by ecosystem service
Seafood[1]	Biomass (tonnes/km^2) Abundance (no./km^2) of fish Quality of fish stock (e.g. species composition, age profile, length profile, percentage affected by disease, mortality rates)	Grams of protein/year/head or per household Landings data at particular times and places (tonnes) Monetary value of fish landings
Other raw biotic materials[2]	Biomass available in a fixed area (tonnes/km^2) Concentration (g/litre of seawater, or tonnes/km^2 of sediment) Purity	Tonnes of raw material Monetary value of raw material No. of jobs in industries using marine-specific biotic resources
Ornamental resources[3]	Biomass available in a fixed area (tonnes/km^2) Concentration (g /litre of seawater, or kg/m^2 of sediment); Purity	Tonnes Monetary value of ornamental resources No. of jobs in industries using marine ornamental resources
Genetic resources[4]	Occurrence (presence/absence of desirable species) Diversity (diversity of desirable species) Endemism and uniqueness of species	No. of known existing genes of potential use (relating to option value) Monetary value No. of jobs in industries using marine genetic resources
Medicinal resources[5]	Total quantity available in a fixed area (g_/raw material) Concentration of raw material (g/litre of seawater, g/m^3 of sediment)	No. of medicines, improvements in mortality rates and quality of life, etc. Monetary value of medicinal resources No. of jobs in pharmaceutical industries using marine-derived medical resources

Notes and abbreviations:
No. = number.
Ecosystem service definitions reported in Hattam *et al.* (2015).
[1] Seafood: All available marine flora and fauna extracted from unmanaged marine environments for consumption by humans.
[2] Other biotic raw material: Extraction of all other renewable biotic resources.
[3] Ornamental resources: Any material that is extracted for use in decoration, fashion, handicrafts, souvenirs, etc.
[4] Genetic resources: The provision/extraction of genetic material from marine flora and fauna for use in non-medicinal contexts.
[5] Medicinal resources: Any material that is extracted from or used in the marine environment for its ability to provide medicinal benefits.
Sources: Hattam *et al.*, 2015; FAO, 2020.

Table A2.2

Suggested indicators of regulating services and associated benefits applied to the deep sea

Regulating service	Indicator to measure ecosystem service flow	Indicator to measure benefits provided by ecosystem service
Climate regulation[1] and carbon sequestration	Modelled or empirically determined carbon levels of dissolved organic or inorganic carbon (mg C/m^3); buried particulate organic or inorganic carbon (mg C/m^2)	Shadow price of carbon Monetary value
Water circulation[2]	Changes in seabed morphology using side-scan sonar	n.a.
Gas regulation and methane absorption	n.a.	n.a.
Waste-water treatment[3]	Microbial reduction and cycling of excess nutrient facilitated through bioturbation	Costs of primary vs tertiary sewage treatment; replacement cost analysis; cost to change the system to comply with European Union directives vs paying infraction costs Monetary value

Notes and abbreviations:
n.a = not available
Ecosystem service definitions reported in Hattam *et al.* (2015).
Climate regulation: The contribution of a marine ecosystem to the maintenance of a favourable climate through impacts on the hydrological cycle, temperature regulation, and the contribution to climate-influencing substances in the atmosphere.
[2] Water circulation: The contribution of marine ecosystems to the maintenance of localized coastal current structures.
[3] Waste-water treatment: The removal of contaminant and organic nutrient inputs to marine environments from humans.
Sources: Hattam *et al.*, 2015; FAO, 2020.

Table A2.3

Suggested indicators of cultural services and associated benefits applied to the deep sea

Cultural service	Indicator to measure ecosystem service flow	Indicator to measure benefits provided by ecosystem service
Scientific research [c] and education	Deep-sea species, habitats and ecosystem features	No. of research articles and scientific findings Investment made in scientific research & education
Recreation and leisure[1]	Abundance and diversity of key species of recreational interest Area of biotopes of key interest to recreational users	No. of tourists engaging in dives with submersible in the deep sea; Price paid for touristic dives with submersible in the deep sea No of wildlife watchers engaging in observation of charismatic marine megafauna associated with deep sea Price paid for observation of charismatic marine megafauna associated with the deep sea
Aesthetic experience[2]	Uniqueness of a site 1 / (number of sites with similar features)	No. of visitors to installations reproducing through tridimensional, interactive, sensorial experience of being in the deep sea[6] Price paid to access such tridimensional installations

Cultural service	Indicator to measure ecosystem service flow	Indicator to measure benefits provided by ecosystem service
Inspiration for culture, art and design[3]	Marine themed media (e.g. films) Marine themes artwork and installations Use of marine themes in design (bionics, biomimetics) Employment	No. of documentaries/films/ deep-sea footages, books, paintings/music, performances, etc. dedicated to the deep sea Monetary value of revenue generated from films and other above listed products No. of jobs to promote culture, art and design inspired to the deep sea and associated monetary value
Spiritual experience[4]	n.a.	No. of people that attach spiritual and religious significance the deep sea Discourse analysis to identify features of spiritual experience and connection to the deep sea
Cultural heritage[5]	Cultural importance of a site	Discourse analysis to identify associations between relevant themes

Notes and abbreviations:
n.a. = not available
No = number
Ecosystem service definitions reported in Hattam *et al.* (2015).
[1] Recreation and leisure: The provision of opportunities for tourism, recreation and leisure that depend on a particular state of marine ecosystems.
[2] Aesthetic experience: The contribution that a marine ecosystem makes to the existence of a surface or subsurface landscape that generates a noticeable emotional response within the individual observer.
[3] Inspiration for culture, art and design: The contribution that a marine ecosystem makes to the existence of environmental features that inspire elements of culture, art and/or design.
[4] Spiritual experience: The contribution that a marine ecosystem makes to formal and informal collective religious experiences.
[5] Cultural heritage: The contribution that a marine ecosystem makes to education, research, and individual and collective cognitive development.
Example reported by Solly, 2019.
Sources: Hattam *et al.*, 2015; FAO, 2020.
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Table A2.4

Suggested indicators of habitat services and associated benefits applied to the deep sea

Habitat service	Indicator to measure ecosystem service flow	Indicator to measure benefits provided by ecosystem service
Biodiversity / gene-pool protection[1]	Provision of food resources for key species/communities of concern Maintenance of resilient and robust community structure	Potential for option value (meta-analysis, choice experiments, analysis of option value: monetary value)
Habitat for species[2]	Provision and maintenance of suitable habitat Provision and maintenance of complex structure providing suitable habitat	Dependence of off-site fisheries/catch percentage Maintenance of fishing activity No. of jobs and associated monetary value

Notes and abbreviations:
No = number.
Ecosystem service definitions reported in Hattam *et al.* (2015).
[1]Gene-pool protection: The contribution of marine habitats to the maintenance of viable gene pools through natural selection and/or evolutionary processes that enhances adaptability of species to environmental changes, and the resilience of the ecosystem.
[2] Habitat for species: The contribution of a particular marine habitat to migratory and resident species' populations through the provision of critical habitat for feeding, or reproduction and juvenile maturation.
Sources: Hattam *et al.*, 2015; FAO, 2020.

APPENDIX 3 - PRICE OF HALAVEN® IN SELECTED COUNTRIES

Table A3.1
Reported prices for a vial of 1 mg/2 ml of Halaven® sold in six countries worldwide

Country	Currency	Price in original currency	Year	PPP # (USD = 1.000)	Adjusted price (USD)	Reference
Australia	AUD	854	2018	1.47	583	https://www.pbs.gov.au/medicine/item/10140Q-10144X-11199K-11212D; https://www.pbs.gov.au/info/news/2018/12/advice-pricing-eribulin-halaven
Canada	CAS	498	2013	1.21	413	http://www.pmprb-cepmb.gc.ca/view.asp?ccid=764&lang=en
Japan	JPY	64 070	2011	105.38	608	https://www.eisai.com/news/news201155.html
India	INR	31 880	2019	18.96	1 682	https://www.moneycontrol.com/news/business/companies/emcure-launches-knock-off-of-eisais-cancer-drug-halaven-at-40-lower-price-in-india-3756941.html; https://dir.indiamart.com/impcat/halaven.html
Italy	EUR	800	2012	0.69	1 164	http://www.osservatorioinnovazione.net/schede/sch2643.pdf; http://www.informazionisuifarmaci.it/eribulina
United Kingdom of Great Britain and Northern Ireland	GBP	313	2011	0.68	459	https://www.nice.org.uk/guidance/ta250/documents/breast-cancer-advanced-eribulin-final-appraisal-determination-document2; https://www.keionline.org/21712
United States of America	USD	1 241	2020		1 241	https://www.drugs.com/price-guide/halaven#
World average value					818	

Source: World Bank. 2020.