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Deep-sea hydrothermal vent ecosystem principles: Identification of ecosystem processes, services and communication of value

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ABSTRACT

Difficulties in quantifying the value of an ecosystem have prompted efforts to emphasize how human well-being depends on the physical, chemical and biological properties of an ecosystem (i.e., ecosystem structure) as well as ecosystem functioning. Incorporating ecosystem structure and function into discussions of value is important for deep-sea ecosystems because many deep-sea ecosystem services indirectly benefit humans and are more difficult to quantify. This study uses an ecosystem principles approach to illustrate a broader definition of value for deep-sea hydrothermal vents. Expert opinion, solicited using an iterative survey approach, was used to develop principles that describe hydrothermal vent processes and their links to human well-being. Survey participants established 28 principles relating to ecosystem structure (n = 12), function (n = 6), cultural services (n = 8) and provisioning services (n = 2), namely the provision of mineral deposits and genetic resources. Principles relating to cultural services emphasized the inspirational value of hydrothermal vents for the arts and ocean education, as well as their importance as a frontier in scientific research. The prevalence of principles relating to ecosystem structure and function (n = 18) highlights the need to understand subsequent links to ecosystem services. For example, principles relating to regulating services were not established by the expert group but links between ecosystem function and regulating services can be made. The ecosystem principles presented here emphasize a more holistic concept of value that will be important to consider as regulations are developed for the exploitation of minerals associated with deep-sea hydrothermal vents.

1. Introduction

The impact of humans on the natural world has led to alterations in the structure and function of ecosystems, resulting in a reduced capacity for many ecosystems to deliver the services from which humans derive benefit [1–3].

To improve environmental stewardship there has been a strong movement to summarize such services into an overall value [4]. The utilitarian valuation of marine environments is best illustrated by work within estuarine and coastal systems where, for example, the loss of 12,700 ha of seagrass in Australia (16% of the seagrass on the eastern bank of Northern Spencer Gulf) was estimated to result in a loss of AU$ 235,000 in fishery production each year [3,5]. Difficulties in valuation estimates however, even in accessible environments such as seagrass meadows, result in unreliable or unavailable estimates for the majority of ecosystem services (e.g., the role of seagrass meadows in: coastal protection, carbon sequestration, water purification, tourism, recreation, education and research; [3]).

The economic valuation of ecosystem services is often difficult because many services indirectly benefit humans. Referred to as supporting services within the Millennium Ecosystem Assessment [6], the indirect services (e.g., habitat provision and nutrient cycling) provide the functional basis for all services that directly contribute to human well-being [7]. The economic valuation of ecosystems can also carry ethical concerns due to the inappropriateness of expressing the intrinsic value of nature in monetary terms [8], and the limiting-effect that removing nature from its spatial and social context has on assessing value [9].

The contrasting ideologies of intrinsic and utilitarian focused conservation are often viewed as conflicting but there are efforts to incorporate different ways of valuing nature into conservation decision-making [10]. Efforts have been made to promote a broader sense of

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value that includes social, ecological and economic viewpoints [7]. To better integrate indirect services into discussions on value, emphasis has been placed on communicating ecological knowledge and demonstrating how human well-being depends on ecosystem structure and function [3,7,11].

The schematic presented by Le et al. [12] illustrates how all ecosystem services are supported by ecological functions (e.g., primary and secondary productivity, nutrient and element cycling, breeding grounds and nursery habitat), which are in turn supported by the physical, chemical and biological properties of a system (i.e., ecosystem structures). Ecosystem services are separated into three categories: provisioning services (i.e., the outputs and products generated by an ecosystem such as fish and pharmaceuticals; [6]), regulating services (i.e., benefits from the regulation of environmental processes such as carbon sequestration; [6]) and cultural services (i.e., non-material benefits such as educational opportunities and inspiration for the arts).

In the deep sea, previously remote environments are under increasing pressure for products such as fish, hydrocarbons and minerals [e.g., 11–14]. For example, hydrothermal vents are of interest to an emergent deep-sea mining industry, targeting polymetallic (particularly copper and zinc) sulphides [15]. On the international seabed, seven licenses are approved to explore minerals at hydrothermal vent systems within the Atlantic and Indian Oceans [16]. Within national waters, the first test of commercial-mining machinery took place off the island of Okinawa, Japan from August to September 2017, carried out by the Japan Oil, Gas and Metals National Corporation (JOGMEC; [17]).

Deep-sea industrialization has sparked interest in understanding the value and range of benefits gained from deep-sea ecosystems. Many deep-sea ecosystem services have been identified, with previous reviews highlighting the dominance of services that provide indirect benefits to humans [4,18]. The challenge of quantifying and assessing the value of deep-sea ecosystem services is exacerbated when you consider a general lack of public knowledge concerning deep-sea environments and the high level of scientific uncertainty, which makes it difficult to describe changes in ecosystem services [7,12,19].

In this paper, we use an ecosystem principles approach [7,20] to better communicate the benefits derived from deep-sea hydrothermal vents. Ecosystem principles define elements of how an ecological system is thought to operate [20], providing information that links ecosystem function to ecosystem services. The principles developed in this study illustrate a broader definition of value for deep-sea hydrothermal vent systems and present the ecological viewpoint, which is often removed from non-scientific discussions of value.

2. Material and methods

The Ecosystem Principles Approach (EPA) was developed as a method of incorporating ecological knowledge into 'units' of information (i.e., ecosystem principles; [7,20]). By condensing broadly-accepted scientific information into principles that describe ecosystem processes and their links to ecosystem services, the approach helps to communicate the ecological value scientists associate with an ecosystem to non-specialists [7]. The EPA summarizes ecological complexity in ways that are clear and easily understood, allowing different structural and functional elements of an ecosystem to be accounted for in decision-making [7,20]. The EPA highlights the interlinked nature of ecosystem processes and services, increasing consideration for ecological value alongside social and economic definitions of value [7]. This is particularly important within the deep sea because links between the ecological and socio-economic aspects of ecosystems are poorly understood, contributing to the under-valuation of deep-sea ecosystems [7]. By simplifying ecological knowledge, the EPA can also be used to increase knowledge about deep-sea ecosystem services amongst the public [7,12], increasing ocean literacy and recognition for deep-sea ecosystem value [21]. For more information on the EPA, please refer to Townsend et al. [20] and Jobstvogt et al. [7].

This study used the Delphi method (i.e., an iterative survey technique that aims to generate a consensus among participants; [22]) to solicit expert opinion and to generate ecosystem principles for deep-sea hydrothermal vents. It is important to note that this approach does not necessarily produce a correct answer or a singular truth but, by generating reliable group opinion, highlights important points for discussion [23].

A two-stage online survey was conducted using Qualtrics (Provo, Utah) software; a copy of each survey is included in the Supplementary material (S1, S2). Participants who self-identified as experts in deep-sea hydrothermal vent research were invited to participate in the survey through deep-sea email lists (i.e., the International Network for Scientific Investigations of Deep-Sea Ecosystems [INDEEP] and the Deep-Sea Biology Society), with a total audience of ~1100 individuals. Personal invitations were also sent to 71 leading experts in the field, identified using the INDEEP List of Experts and selecting profiles that specified expertise in hydrothermal vent habitats.

In Survey 1, participants were provided with an introduction to the Ecosystem Principles Approach and the iterative survey design. Participants were asked to rank the plausibility, level of supporting evidence, and the generality of 19 pre-established ecosystem principles. Each participant ranked the principles using a five-point Likert scale: plausibility (1 – 'not at all plausible' to 5 – 'entirely plausible'), level of supporting evidence (1- 'not supported at all' to 5 – 'entirely supported') and generality (1 – 'specific vent system', 2 – 'all vent systems', 3 – 'entire deep sea', 4 – 'all marine systems', 5 – 'global phenomenon'). If participants felt that a principle related to a specific vent system, they were asked to state the system in mind.

Survey 1 participants were also invited to provide up to three additional principles and to edit or comment on any of the existing principles. Additional principles were coded using NVivo 10 (QSR International), grouped by similarity and translated into additional principles to be included in Survey 2. Comments on existing principles were reviewed by the authors and edits were made where appropriate. Survey 1 was open from 31 October to 8 December 2016, with reminders sent during the penultimate and final weeks.

In Survey 2, participants who completed Survey 1 were asked to re-rank the agreed upon principles (i.e., principles that received a plausibility score of 4 or 5 from at least 60% of participants) as well as 15 additional principles suggested by Survey 1 participants. In total 32 principles were included in Survey 2. For principles carried forward from Survey 1, participants were provided with the percentage of participants who ranked the principle as 'highly plausible' (i.e., a score of 4) or 'entirely plausible' (i.e., a score of 5), the average score for the level of supporting evidence (i.e., 1.0 to 2.5 - 'Poor', 2.5 to 3.5 - 'Intermediate', 3.5 to 5.0 - 'Good) and the most common answer for generality.

Participants re-ranked the principles using the same five-point Likert scales as Survey 1. Following feedback from Survey 1 participants, the generality scale was changed to accommodate a 'most vent systems' option (i.e., 1 – 'species vent system', 2 – 'most vent systems', 3 – 'all vent systems', 4 – 'entire deep sea', 5 – 'all marine systems'). The change in scale does not impact the analysis as the 'global phenomenon' option included in Survey 1 was never the most popular response. Survey 2 was open from 23 April to 7 July 2017, with reminders sent to those who had yet to complete Survey 2, two, four and eight weeks after the initial invitation.

This research did not require Institutional Review Board approval. Participants were selected through an opt-in strategy and surveys did not include sensitive personal questions. Any demographic information was analyzed in aggregate to maintain participant anonymity. Participants were identifiable via email-addresses to the lead author only, with opinions and personal information kept confidential.

Table 1
Hydrothermal vent ecosystem principles that relate to ecological structures (e.g., physical structure, habitat dynamics, biodiversity, environmental conditions), with expert ratings on their plausibility, generality and evidence base.

	Principle	Plausibility	Generality	Evidence
1.1	Hydrothermal vent fluid creates high temperature gradients (i.e., from hydrothermal fluid to surrounding seawater) across small distances.	98%	All Vents	Good
1.2	Regionally, hydrothermal vents have high levels of endemic fauna relative to the surrounding deep-sea environment. This fauna is uniquely adapted to this environment.	95%	All Vents	Good
1.3	Hydrothermal vents are an example of an extreme environment in comparison to the non-vent deep seafloor, with spatial and temporal variation in fluid flow and a high abundance of compounds typically considered toxic (e.g., hydrogen sulphide) to the majority of marine organisms.	95%	All Vents	Good
1.4	Biodiversity at active, established hydrothermal vents is characterized by high density, high biomass and low diversity relative to the surrounding deep-sea environment.	92%	All Vents	Good
1.5	Locally, hydrothermal vents provide an abundance of hard substrata. The complex 3D structure of active and inactive vents increases habitat heterogeneity, the diversity of ecosystem niches and expands the habitable area for non-vent endemic taxa to colonize (e.g., deep-sea sponges, corals).	85%	All Vents	Good
1.6	Hydrothermal vents can harbor cryptic species.	83%	All Vents	Good
1.7	Hydrothermal vents occur in many biogeographic provinces, influenced by varying environmental factors (e.g., hydrography, depth) and therefore, harboring different species.	80%	All Vents	Good
1.8	Hydrothermal vents on fast-spreading areas experience frequent (decades to centuries) disturbance. The extirpation and recovery cycle leads to fauna that can grow quickly, reproduce quickly and recolonize new sites.	79%	All Vents	Good
1.9	Each hydrothermal vent field is a unique habitat due to their high spatial and temporal variability and their site-specific metabolic pathways, as determined by underlying geological and tectonic factors.	77%	All Vents	Intermediate
1.10	Hydrothermal vents on slow and ultra-slow spreading ridges are more stable than fast-spreading areas, experiencing disturbance on millennial, to tens of thousands of years.	72%	All Vents	Intermediate
1.11	Faunal community structure is supported through site-specific metabolic pathways, as determined by underlying geological and tectonic factors.	68%	All Vents	Intermediate
1.12	Extinct hydrothermal vents support unique microbial lineages and functional groups not found at active hydrothermal vents.	65%	All Vents	Intermediate

3. Results

Fifty-nine individuals completed Survey 1, 42 individuals completed both Survey 1 and 2. The results presented here represent views of the 42 participants who completed both surveys. This 71% response rate across both surveys is adequate, with 70% considered the threshold to providing reliable results through the Delphi method [22]. Most participants were from academia (36 of 42), including 6 graduate students, 8 post-doc or early-career scientists (i.e., < 7 years post-Ph.D.) and 22 established scientists (i.e., > 7 years post-Ph.D.); three participants did not specify their current role and three participants represented management and/or industry. Of the 71 experts personally invited to participate in the project, 42 completed Survey 1 and 23 completed both Survey 1 and 2, a response rate of 32%.

3.1. Ecosystem principles

Over the course of the Delphi survey 28 ecosystem principles were agreed upon by the expert group (see Tables 1–4). Six of the 19 principles included in Survey 1, and 3 of the 16 principles added by Survey 1 participants were removed due to a plausibility rating below 60% (Supplementary material, S3). As documented by Jobstvogt et al. [7], the plausibility of ecosystem principles was lower when there were only intermediate levels of supporting evidence. The only exception to this observation is the potential for proteomic and genetic research owing to the high levels of genetic novelty at hydrothermal vents (Principle 4.2), a principle that was thought to be plausible by 90% of participants despite an intermediate level of supporting evidence (Table 4).

Twenty-six of the agreed upon ecosystem principles were considered to be applicable to *all deep-sea hydrothermal vents*. The two remaining principles are thought to apply to *most vent systems* and relate to iron export (Principle 2.4) and the formation of sulphide minerals at hydrothermal vents (Principle 4.1).

3.2. Ecosystem principles relating to ecosystem structure

Principles relating to ecosystem structure fall into three main categories: geological setting, physical structure and biodiversity. Variation in the geological setting of hydrothermal vents results in site-specific metabolic pathways (Principe 1.9) that influences faunal community structure (Principle 1.11). Similarly, differences between fast-spreading areas and ultra-slow spreading ridges causes differences in the extirpation and recovery cycles of vents and the adaptations of organisms to natural disturbance (Principles 1.8 and 1.10). In terms of physical structure, high temperature gradients (Principle 1.1), toxic compounds (Principle 1.3) and the complex 3D structure associated with hydrothermal vents (Principle 1.5) influence the distribution and composition of hydrothermal vent fauna, which is characterized by high-density and low diversity relative to the surrounding deep sea (Principle 1.4). Site-to-site variation in community structure, due to site-specific metabolic pathways, is accompanied by high levels of endemism at a regional scale (Principle 1.2) and the occurrence of cryptic species (Principle 1.6) even within biogeographical provinces (Principle 1.7).

3.3. Ecosystem principles relating to ecosystem functions

Principles relating to ecosystem functions fall into two main categories: biochemical processes and connectivity. Hydrothermal vents host unique microbial communities that support diverse biochemical processes (Principle 2.2), including chemoautotrophic primary productivity (Principle 2.1) that supports secondary production at vent sites and within deep and mid-water communities (Principle 2.6). In terms of connectivity, most hydrothermal vent fauna relies on larval dispersal, with colonization influenced by oceanography, larval duration and behavior, as well as venting activity (Principle 2.3); the fragmented nature of hydrothermal vents leads them to be described as stepping stones within the deep sea (Principle 2.5).

Table 2
Hydrothermal vent ecosystem principles that relate to ecological functions (e.g., element cycling, productivity, dispersal and connectivity), with expert ratings on their plausibility, generality and evidence base.

	Principle	Plausibility	Generality	Evidence
2.1	Hydrothermal vents support high levels of chemoautotrophic primary productivity, increasing local energy availability and providing a source of labile organic material that supports high levels of secondary production and biomass.	100%	All Vents	Good
2.2	Hydrothermal vents host unique microbial communities that support diverse biochemical processes (e.g., synthesis of complex organic molecules), which in turn support other vent fauna.	95%	All Vents	Good
2.3	Most hydrothermal vent fauna have dispersal larval stages, allowing colonization of fragmented and ephemeral habitats. Connectivity depends on physical oceanographic processes, larval duration and behavior, as well as the occurrence and distribution of diffuse and intense venting.	93%	All Vents	Good
2.4	Hydrothermal vents export iron, an essential element in biogeochemical cycles	92%	Most Vents	Good
2.5	Hydrothermal vents can act as stepping-stones for dispersal, maintaining connectivity in the deep-sea.	83%	All Vents	Good
2.6	Organic matter generated at hydrothermal vents and supplied to deep and mid-water communities enable heightened biomass at depth (e.g., fish and plankton).	63%	All Vents	Intermediate

Table 3
Hydrothermal vent ecosystem principles that relate to cultural ecosystem services (e.g., aesthetics, education, scientific research/knowledge), with expert ratings on their plausibility, generality and evidence base.

Principle		Plausibility	Generality	Evidence
3.1	Many unknowns concerning hydrothermal vent connectivity, community succession and temporal variability maintain hydrothermal vent environments as a frontier in scientific research	100%	All Vents	Good
3.2	The aggregations of organisms at hydrothermal vents make them an inspirational environment (e.g. for art, books and exhibits).	98%	All Vents	Good
3.3	The iconic organisms and unique geological processes that characterize hydrothermal vents make them an important component of ocean education and outreach.	98%	All Vents	Good
3.4	Many unknowns concerning hydrothermal vent biodiversity and their continued discovery maintain hydrothermal vent environments as a frontier in exploration	95%	All Vents	Good
3.5	Hydrothermal vents are key sites for science and exploration	88%	All Vents	Good
3.6	Hydrothermal vent microbial communities are important in understanding the evolution of sulphide deposits.	71%	All Vents	Intermediate
3.7	Hydrothermal vent microbial communities are important in understanding the origins of life.	63%	All Vents	Intermediate
3.8	Hydrothermal vent fauna (non-microbes) represents evolutionary lineages of < 100 million years and can provide useful information on evolutionary and ecological processes	60%	All Vents	Intermediate

Table 4
Hydrothermal vent ecosystem principles that relate to provisioning ecosystem services (e.g., mineral deposits, bio-technology), with expert ratings on their plausibility, generality and evidence base.

	Principle	Plausibility	Generality	Evidence
4.1	The fluid from magmatically fed hydrothermal vent systems contain dissolved metal ions that form sulphide minerals as they precipitate upon contact with seawater.	95%	Most Vents	Good
4.2	Hydrothermal vents are hotspots for genetic novelty, containing large amounts of potential for genetic and proteomic research.	90%	All Vents	Intermediate

3.4. Ecosystem principles relating to ecosystem services

In terms of ecosystem services, the expert group identified nine principles relating directly to cultural services (Table 3) and two principles relating to provisioning services (Table 4). Individual principles relating directly to regulating services were not established by the expert group.

Ecosystem principles relating to cultural services fall into three main categories: scientific research, education and inspiration (Table 3). Hydrothermal vents continue to offer novel areas of scientific research with many unanswered questions concerning connectivity between sites, succession and temporal variation within hydrothermal vent communities (e.g., Principle 3.1). The uniquely adapted fauna that aggregate at certain hydrothermal vents were noted for inspiring art, books and exhibits (Principle 3.2), with the organisms and geological processes that characterize hydrothermal vents making them an important component of ocean education and outreach (Principle 3.3).

The ecosystem principles relating to provisioning services are associated with mineral deposits and genetic resources (Table 4). Firstly, the precipitation of sulphide minerals at most hydrothermal vents (Principle 4.1) results in some sites being an attractive frontier for deep-sea mining. Secondly, the novel genetic potential of hydrothermal vent fauna (Principle 4.2) is an attractive resource to biotechnology research and development, with potential production of bioinspired materials, industrial agents and pharmaceuticals.

4. Discussion

Eighteen of the 28 ecosystem principles relate to ecosystem structure (n = 12; Table 1) or ecosystem functions (n = 6; Table 2), highlighting the need to understand links between structure, function and ecosystem services. Fig. 1 depicts the importance of some ecosystem structures and functions in supporting a variety of ecosystem services. For example, the geological setting of each vent site varies, leading to site-specific metabolic pathways (Principle 1.9) that influence faunal community structure (Principle 1.11) and the dominant, high-density fauna found at vent sites (Principle 1.4). Similarly, the high-density faunal communities are supported by chemoautotrophic primary productivity (Principle 2.1) and the complex 3D structure that characterizes hydrothermal vents (Principle 1.5). The faunal communities, shaped by ecosystem structures (e.g., underlying geology) and ecosystem functions (e.g., chemoautotrophic primary productivity) provide inspiration for art, books and exhibits (Principle 3.2) and form an important component of ocean education and outreach (Principle 3.3).

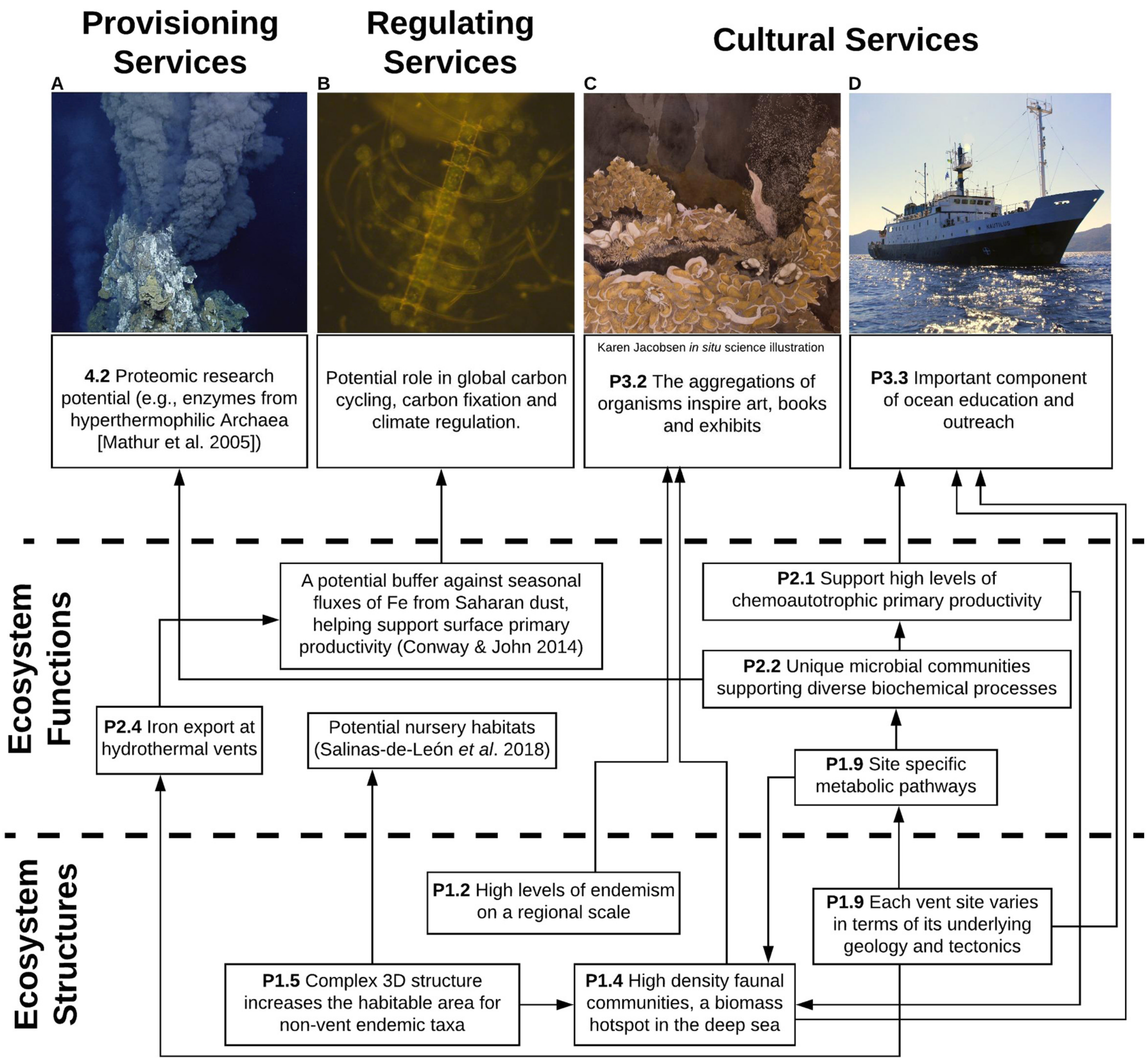

Fig. 1. Schematic illustrating the indirect and sometimes complex links between ecosystem structures, functions and services. The schematic is not exhaustive but illustrates how ecosystem services are dependent on underlying ecological factors. The services depicted here relate to (A) biotechnology research and development (black smoker image courtesy of Ocean Exploration Trust/Nautilus Live), (B) carbon cycling and climate regulation (chain forming diatom image courtesy of Z. Johnson [Duke University Marine Lab]), (C) marine wonderment and inspiration, depicted by a watercolor of a Pacific mussel bed community by Karen Jacobsen and (D) ocean education and outreach, depicted by EV Nautilus and the Ocean Exploration Trust that stream deep-sea expeditions online (image courtesy of Ocean Exploration Trust/Nautilus Live).

Individual principles relating to regulating services were not established by the expert group but links can be made between established principles and regulating services. For example, the unique microbial communities found at hydrothermal vents support a range of biochemical processes (Principle 2.2), which play a role in regulating services such as the global cycling of carbon, nitrogen, sulfur, arsenic and potentially heavy metals [12,24–26]. Hydrothermal vents can also act as a source of iron that, in the North Atlantic, is hypothesized to act as a buffer against seasonal variation in the supply of iron from Saharan dust [27]. Hydrothermal vent iron was found up to 1000 km west of the TAG hydrothermal vent field on the Mid-Atlantic Ridge, with additional supplies suspected from Rainbow and Lucky Strike vent fields south of the Azores [27]. The contribution of iron may influence surface productivity within the region and subsequently contribute to global cycling of carbon and carbon sequestration.

Hydrothermal vents have been described as an important component of a 'marine wonderment' industry, inspiring curiosity about the natural world [15]. Within this study, survey participants highlight the value of hydrothermal vents as a frontier in scientific research and exploration (Principles 3.1, 3.4, 3.5), as an inspirational environment (Principle 3.2) and an important component of ocean education (Principle 3.3). The cultural values people ascribe to hydrothermal vents, including their intrinsic value, will be particularly important to consider within areas beyond national jurisdiction where the seabed is considered the common heritage of humankind, and requires the conservation and preservation of resources (both natural and biological) for present and future generations [28].

Five survey participants questioned the generality of the principle relating to inspiration for the arts (Principle 3.2). Sites where fluid flow is waning were considered less charismatic than sites with intense fluid flow, and the Pacific hydrothermal vents hosting the giant tube worm (*Riftia pachyptila*) were thought to be particularly inspirational by one participant. Five participants also questioned the inspirational value of hydrothermal vents relative to other environments (e.g., coral reefs, kelp forests and polar oceans) and species (e.g., giant squid and angler fish). Such comparisons raise ethical concerns that make us question the appropriateness of assessing generality for principles relating to cultural services. In our view, comparing the scales of 'marine wonderment' should not be the goal; it is more important to highlight its existence. Four survey participants specifically mentioned evidence relating to the inspirational value of hydrothermal vents, including feedback from public events at museums and universities, as well as efforts by the Census of Marine Life to include writers, artists and photographers to document marine species and inspire the public (e.g., *Citizens of the Sea: Wondrous Creatures from the Census of Marine Life* [29]). One participant mentioned the Daytime Emmy nominated children's television program *Octonauts*, which has aired in over 100 countries [30]. Within three separate episodes the animated characters visit hydrothermal vents, introducing children to hydrothermal vent tubeworms, limpets, zoarcid fish, shrimp and yeti crabs. Partnered with BBC television series such as *Blue Planet II* (2017), for which "The Deep" episode reached a UK audience of ~14 million people the first week it aired [31], such programs highlight the inter-generational value of hydrothermal vents in terms of 'marine wonderment'.

4.1. Broader context

Since their discovery over 40 years ago, deep-sea hydrothermal vents have been a focal point for both cultural leaders and marine researchers. Relative to coastal marine ecosystems, much of the anthropogenic disturbances at hydrothermal vents has been non-catastrophic and non-extractive. To date, the greatest anthropogenic impact on vent community integrity has been overzealous scientific sampling to understand the fundamental ecology of these chemosynthetic ecosystems, low impact bioprospecting [e.g., 32] and the accidental transfer of organisms from one site to another (e.g. transfer of the limpet *Lepetodrilus gordensis* from an active to inactive site on the Gorda Ridge; [33]). The potential harm caused by extensive scientific sampling prompted the deep-sea research community to adopt a code of conduct for responsible science at hydrothermal vents [34].

Despite their remoteness, deep-sea ecosystems do not exist in isolation and there is a growing list of insidious threats that impact coastal as well as deep-sea ecosystems, including microplastics and plastic debris (e.g., [35–38]), ocean acidification and climate change (e.g., [39–42]). The highest profile threat to hydrothermal vent ecological integrity in the short to medium term is the commercial exploitation of seafloor massive sulphides [43]. Though deep-sea mining proposals have been floated for several decades, it is only in the past ten years that serious exploration for minerals has become financially and technologically viable [44].

Barring a few well-studied sites (e.g. Menez Gwen, Solwara 1, Lucky Strike, East Pacific Rise), our knowledge of the fundamental aspects of vent biology is limited, largely due to the inaccessible nature of the habitat and the high cost associated with sampling [45]. Although hydrothermal vents are globally widespread, they are biogeographically diverse with distinct endemic species, community structures, successional patterns and underlying geology (e.g., [46–49]). Knowledge gaps persist, including questions regarding taxonomic identification, species distribution patterns, community dynamics, population connectivity and physiological tolerances [45].

Due to the lack of quantitative, and even qualitative information, a precautionary approach to minimize risk to the ecosystem is recommended. The precautionary approach is emphasized within the mandate of the International Seabed Authority (ISA), which oversees exploration and exploitation of seabed minerals within areas beyond national jurisdiction [50,51]. Exploitation regulations are currently under development within the ISA [52], providing the opportunity to emphasize the ecological value scientists associate with hydrothermal vent ecosystems and promote environmental stewardship within the regulations [53]. The principles developed here communicate different aspects of value and should encourage structural and functional elements of hydrothermal vent ecosystems, as well as ecosystem services other than mineral resources, to be accounted for in decision making. For example, hydrothermal vents are characterized by site-to-site variation in community structure, which is driven by site-specific metabolic pathways (Principle 1.11). Site-to-site differences mean developing a representative network of protected areas for hydrothermal vents is extremely challenging, if not impossible [15]. To adequately implement the precautionary approach, the heterogeneity of hydrothermal vent community structure supports the protection of all active hydrothermal vents from mining activity. A management recommendation proposed by Van Dover et al. [15], which has yet to be considered within ISA regulations.

Although much has been learnt about hydrothermal vent ecology, as well as the cultural and provisioning value of deep-sea hydrothermal vents, all respondents agreed that there are still many unknowns concerning connectivity, variability and succession. Notably, while research has primarily focused on connectivity and ecosystem services among vent systems, or between vent and other chemosynthetic ecosystems such as methane seeps and whale falls, relatively little research has been done to establish the role active vents play more broadly. For example, the potential for iron supplied by hydrothermal vents to influence surface productivity [27] and the recent discovery that suggests the Pacific white skate (*Bathyraja spinosissima*) uses active hydrothermal vents as a nursery ground to incubate their eggs [54], emphasizes the broader values that may yet be discovered. In this study, we assessed expert opinion on ecosystem principles regarding within-vent structure, functions and services. There remains a largely unexplored field surrounding the broader role of active vents; a role that would only add to the number of ecosystem services that need to be considered in decision making, and increase the more holistic concept of value emphasized by these ecosystem principles.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.marpol.2019.01.003.

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