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# Ecosystem function and services provided by the deep sea

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## Abstract

The deep sea is often viewed as a vast, dark, remote, and inhospitable environment, yet the deep ocean and seafloor are crucial to our lives through the services and provisions that they provide. Our understanding of how the deep sea functions remains limited, but when treated synoptically, a diversity of provisioning, regulating and cultural services become apparent. The biological pump transports carbon from the atmosphere into deep-ocean water masses which are separated over prolonged periods, reducing the impact of anthropogenic carbon release. Microbial oxidation of methane keeps another potent greenhouse gas out of the atmosphere while trapping carbon in authigenic carbonates. Nutrient regeneration by all faunal size classes provides the elements necessary to fuel surface productivity and fisheries, and microbial processes detoxify a diversity of compounds. Each of these processes occur on a very small scale, yet considering the vast area over which they occur they become important for the global functioning of the ocean. The deep sea also provides a diversity of resources, including fish stocks, enormous bioprospecting potential, and elements and energy reserves that are currently being extracted and will be increasingly important in the near future. Society benefits from the intrigue and mystery, the strange life forms, and the great unknown which has acted as a muse for inspiration and imagination since near the beginning of civilization. While many functions occur on the scale of microns to meters and time scales up to years, the derived services that result are only useful after centuries of integrated activity. This vast dark habitat, that covers the majority of the globe, harbors processes that directly impact humans in a diversity of ways, however the same traits that differentiate it from terrestrial or shallow marine systems also result in a greater need for integrated spatial and temporal understanding as it experiences increased use by society.





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## 1 Introduction

To meet the needs of humans it is vitally important to improve the management of Earth's ecosystems to ensure their conservation and sustainable use (Millennium Assessment, 2005). To improve this stewardship of the natural environment, it has become common practice to attempt to value ecosystems by assessing their functions and the services they provide to humans (Mace et al., 2009). This approach differentiates ecosystem functions, or the processes operating in an ecosystem (Loreau, 2008), from ecosystem services, which are the benefits that people obtain from ecosystems (Armstrong et al., 2010, 2012). To guide these discussions, theoretical frameworks have been developed that appear to be converging towards those differentiating provisioning, regulating, supporting, and cultural services (Millennium Assessment, 2005; Mace et al., 2009). Supporting services are those necessary for the production of all other ecosystem services, provisioning services are those products that are obtained from ecosystems, regulating services are the benefits obtained from the regulation of ecosystem processes, and cultural services are the non-material benefits obtained from ecosystems (Armstrong et al., 2010, 2012). Although this process has been criticized as reducing the focus on mechanisms underpinning the system (e.g. O'Neill, 2001), the ecosystem function and services assessment framework (Millennium Assessment, 2005) gives decision makers a mechanism to identify options that can improve the achievement of human-development and sustainability goals, better the understanding of the trade-offs involved – across sectors and stakeholders – in decisions concerning the environment, and align response options with the level of governance where they can be most effective. Moreover, the separation inherent to this framework does allow the clear identification of deep-sea functions and services needed to establish the mechanistic links that will increase our understanding of how deep-sea functions and services contribute to human welfare.

The deep sea, here defined as waters and seafloor deeper than the 200 m bathycline (Gage and Tyler, 1991), is the largest environment on earth – the seafloor represents





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63 % of the area of and the water column represents ∼ 98.5 % of the volume of the planet that can be permanently inhabited by animals. Its role in driving nutrient regeneration and in global biogeochemical cycles is essential to sustain primary and secondary production in the oceans (Danovaro et al., 2008b). In addition, it supports a high diversity of habitats and species (Hessler and Sanders, 1967; Grassle and Maciolek, 1992; Sogin et al., 2006; Ramirez-Llodra et al., 2010; Mora et al., 2011) as well as huge mineral resources (Herzig and Hannington, 1995; Kato et al., 2011). However, as the deep sea is inhospitable to humans, often remote, and the physical properties of water prevent easy observation and challenge directed study, deep-sea habitats receive much less attention than environments closer to home. This has delayed the acknowledgement of the vitally important ecosystem functions and services the deep sea provides (but see Armstrong et al., 2012). Unfortunately, this comes at a time when services from the deep sea are in increasing demand and under great pressure for its products, such as those from fishing, hydrocarbon extraction, and mining, all of which are rapidly expanding (e.g. Morato et al., 2006; Benn et al., 2010). Furthermore, the buffering capacity of the deep ocean is vital for mitigating the climatic changes caused by anthropogenic emissions. Here we review current knowledge on the functions and services provided by the deep sea, providing a foundation of knowledge for effective management, while identifying the traits that differentiate deep-sea habitats from other global biomes.

### 1.1 Major deep-sea habitats

The pelagic deep sea below 200 m comprises ∼ 95 % of the volume of the ocean and harbors on the order of $10^{28}$ prokaryotes (Whitman et al., 1998), a great diversity of fisheries and yet-to-be harvested fish stocks, and large pelagics such as the infamous "giant squid" (*Architeuthis* spp.). In addition, this habitat provides a foraging ground for surface predators including fish, pinnipeds, and cetaceans. In general, this high-pressure, dark environment is primarily cold and well oxygenated. Wide environmental variations do occur throughout the deep ocean, however, including the hypoxic to anoxic waters of oxygen minimum zones (OMZs); these relatively small areas (∼ 0.1 % of the ocean's volume; Codispoti et al., 2001) harbor significant biogeochemical processes including denitrification and anaerobic ammonium oxidation (anammox; Paulmier and Ruiz-Pino, 2009; Lam and Kuypers, 2011). Other chemically and thermally diverse deep-sea pelagic habitats include hydrothermal vent plumes (Dick et al., 2013) and the water column above cold seeps (Tavormina et al., 2008) that are hotspots of microbial diversity and serve as a link between the pelagic and benthic deep-sea environments. While this may be the largest habitat on the globe, it also remains the least known and understood.

The deep-sea floor is generally made up of soft-sediment habitats that are treated as different environments based on their depth. The continental margins extend from a water depth of ∼ 200–∼ 4000 m, whilst the abyssal plains occur from ∼ 4000 to 6000 m (Smith et al., 2008; Levin and Dayton, 2009; Ramirez-Llodra et al., 2010). Combined, these two habitats account for ∼ 85 % of the total deep seafloor. Separating the ocean basins are large underwater volcanic mountain ranges, which are termed Mid-Ocean Ridges. These chains extend up to 60 000 km in length and cover ∼ 10 % of the ocean floor. In contrast to the topographic highs of mid-ocean ridges, deep valleys, or trenches, are formed along subduction zones where they punctuate the bathyal and abyssal habitats and range in depth from 6000–11 000 m.

In addition to broad-scale deep-sea habitats, there are many smaller habitats that add to the heterogeneity and diversity of the deep sea. Some of the more pervasive, important regional habitats include seamounts, canyons and channels, fjords, hydrothermal vents, and methane seeps (Ramirez-Llodra et al., 2010; Fig. 1). Seamounts, large under-water mountains, occur either singularly or as a chain and rise up in stark contrast to the surrounding "featureless" seafloor (Rowden et al., 2005; Narayanaswamy et al., 2013). These undersea mountains comprise a mixture of soft and hard substrata and often harbor numerous fragile, vulnerable and long-lived epifauna that create areas of high biodiversity and rich fishing grounds (Clark et al., 2008, 2010; Chivers et al., 2013; Fig. 1f). Canyons form deep incisions on the margin where they act as conduits





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for shelf-slope exchange and create essential habitats for the local fauna (Sardá et al., 2009; de Leo et al., 2013; Fig. 1a). They are also regions of increased biomass and productivity (de Leo et al., 2010, 2013; Vetter et al., 2010) and are subject to disturbances such as when dense water from the shelf descends down the continental slope (Canals et al., 2006) or via mass wasting events (de Stigter et al., 2007). Chemosynthetic habitats, including vents and seeps, have a very distinct high density faunal community associated with them (Fig. 1e). Although they do not necessarily have a high level of diversity, they exhibit a high level of endemism, an endemism that appears to increase with increasing depth (Levin et al., 2000). Estimates vary for how many of each of these individual habitats exist, for example the total number of known seamounts increases with satellite and sub-sea surface exploration (Morato et al., 2013 and references therein) and other habitats are constantly being created (Biastoch et al., 2011), both of which increase the number of known deep-sea features.

Biogenic habitats, areas of extensive three-dimensional structure created by organisms themselves, can create habitats covering tens of square kilometers of deep seafloor (Fig. 1a and f). The structure of these habitats and the actions of their denizens can change to the surrounding environment through shifting near-bed hydrodynamic regimes, aggregating organic matter and changing sediment characteristics (Roberts et al., 2006). Biogenic habitats often harbor high diversities of associated species as a result of increasing habitat diversity (for example providing hard and stable substratum for benthic organisms), access to enhanced dietary resources and providing a refuge from predators or physical disturbance. Owing to several of these characteristics, biogenic habitats provide a nursery for several deep-sea species (Miller et al., 2012).

Probably the best known example of biogenic habitat in the deep sea is created by cold water corals. Scleractinian (e.g. *Lophelia pertusa, Madrepora oculata*; Fig. 1f), gorgonian and antipatharian corals can form complex hard structures with their skeletons (Roberts et al., 2006). These reefs occur globally in deep waters (> 2000 m depth) and are colonized by a huge range of benthic and demersal organisms (Serpetti et al.,





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2013). In addition, many other examples of biogenic habitat occur in the deep sea. Habitats formed of large sponges and their spicules occur in many high-latitude areas (Rice et al., 1990; Gutt and Starmans, 1998; Klitgaard and Tendal, 2004; Hasemann and Soltwedel, 2011). Seabed fluid flow can often support large complex habitats comprised of clams, mussels and tubeworms (Van Dover, 2000; Cordes et al., 2010a, 2010b). Deep-sea deposit feeders, such as thalassinid shrimps, polychaetes, echiurans and sipunculans, create extensive burrow systems which irrigate and transport organic material into subsurface sediments (Levin et al., 1997; Hughes et al., 2005; Shields and Kedra, 2009), creating a complex three-dimensional sedimentary matrix providing particular niches for other benthic fauna (e.g. Braeckman et al., 2011). Mobile epifaunal megabenthic organisms can create and modify seabed habitats in high densities, especially urchins (Vardaro et al., 2009) and holothurians (Billett et al., 2010), and large beds of echinoderms (Bowden et al., 2011). Even large-sized protists can form extensive habitats and alter local biodiversity, such as xenophyophore grounds in many deep-water areas (Levin, 1991) and beds of the tube-forming protist *Bathysiphon filiformis* in submarine canyons (De Leo et al., 2010; Fig. 1a).

### 1.2 Diversity and ecosystem function

It is now well acknowledged that the deep sea has a relatively high diversity (Hessler and Sanders, 1967; Grassle and Maciolek, 1992; Rex and Etter, 2010), although this can vary dramatically depending on the habitat being investigated (Levin et al., 2001). A general positive relationship has been established between diversity and ecosystem functioning and efficiency in a wide range of deep-sea ecosystems. However, the strength of this diversity–function relationship may differ substantially among habitats (Danovaro et al., 2012). For instance, in deep-sea sediments, species richness and diversity of functional traits are positively related, with changes in species numbers affecting functional diversity and related ecological processes (Danovaro et al., 2008b). However, this relationship is stronger on continental slopes, where reduced diversity may lead to a greater loss of function in comparison to deep basins (Danovaro et al., 2012).





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It is often assumed that the positive relationship between biodiversity and ecosystem function can reach saturation (Loreau, 2008), at which point diversity has increased to the extent that there is the potential for species with particular ecological traits that enhance the overall functioning of the ecosystem (including ecosystem engineers e.g. cold-water corals) or for species that may deteriorate ecosystem processes to become established. In addition, it is thought that these more diverse systems induce a complementarity between species with facilitation and resource partitioning leading to overall higher function (Loreau et al., 2001). Facilitative, or positive, interactions between species may contribute positively to ecosystem function, whilst other, more negative, interactions such as selective predation and niche displacement may counteract an increase in function. Whatever the causal processes underlying deep sea diversity and ecosystem function, the richness and variety of organisms in the deep-sea is important as they underpin the many facets of ecosystem function and the goods and services we ultimately receive. In addition, biodiversity contributes to ecosystem resilience, with increased morphological, genetic and functional diversity leading to greater stability in terms of being able to respond rapidly to changes in the environment. A variety of recent papers have discussed this topic in detail (e.g. Loreau, 2008; Levin and Dayton, 2009).

## 2 Supporting functions and regulating services

### 2.1 Water circulation and $CO_2$ exchange

Many of the functions and services of the deep sea result from a combination of its vast size and the long duration of time that it is separated from the earth's atmosphere (Table 1). The water masses that bathe the deep-sea environment are formed largely in the North Atlantic and the Southern Ocean with additional input from the Sea of Okhotsk and the Mediterranean Sea. As soon as these cold (mean temperature 4 °C) dense water masses sink below the photic zone they are cut off from the atmosphere





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for approximately 1000 yr, supplying all the world's deep ocean areas in the "global conveyor belt" also known as the "thermohaline circulation" that eventually resurfaces in areas of upwelling and the North Pacific. This creates more than one billion square kilometers of water separated from direct contact with the atmosphere allowing an incredible buffering capacity for nutrient and carbon cycles.

Since the industrial revolution ~ 300 Gt of the greenhouse gas $CO_2$ have been released by anthropogenic activities into the atmosphere (Canadell et al., 2007; Fig. 2). The impact of this $CO_2$ on the temperature of the globe is largely mediated by dissolution of this gas in the surface ocean and its transport through the thermohaline circulation into the deep sea. The deep sea currently stores approximately 37 000 Gt carbon and has already absorbed a quarter of the carbon released from human activities (Canadell et al., 2007; Sabine and Feely, 2007).

### 2.2 Nutrient cycling and the biological pump

As particles sink through the water column they are stripped of their easy-to-digest (labile) compounds, releasing nutrients and energy into the deep sea, a process that both sequesters atmospheric carbon and releases nutrients that eventually fuel production (Fig. 2). The vast majority of the deep sea relies on primary production that occurs in the surface water (i.e., photosynthesis by phytoplankton). As these particles sink through the deep pelagic they are degraded by microbes and higher trophic levels, such as zooplankton and especially large gelatinous fauna (Robison, 2004). This biological activity dictates the duration that the exported carbon is separated from the atmosphere. If biomass is respired in the water column or on the seafloor, this carbon will be kept out of the atmosphere until the water rises to the surface again and releases the carbon back (1000 yr time scales). However, if this carbon is buried in sediments, the $CO_2$ is removed from the atmosphere for geologic time scales (thousands to millions of years). Around 55 % of the carbon that sinks below 1000 m is respired in the water column prior to its deposition on the seafloor (Jahnke, 1996) leaving only ~ 1 % of the carbon fixed at the surface to be deposited on the seafloor (Lutz et al.,



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2007). This quantity of carbon exponentially declines with increasing water depth (Martin et al., 1987) although the rate of decline is location specific (Buesseler et al., 2007) and asymptotic for much of the deep sea. While most of the carbon that is deposited is difficult-to-digest (refractory) (Kiriakoulakis et al., 2001), areas of high deposition, including oxygen minimum zones and areas of river discharge (Berner, 1989 and see discussion in Cowie et al., 1999) can result in labile carbon being buried within the seafloor. This flux of particles out of the surface waters provide a second way in which carbon is naturally captured from the atmosphere and transferred to the deep sea, further mitigating the climate impacts of $CO_2$ emission but over different time scales.

Although we focus on carbon here, the deep-sea environment plays a key role in the cycling of other nutrients such as nitrogen, silica, phosphorus, hydrogen and sulfur (Fig. 2). Specifically with regards to nitrogen cycling, microbially-mediated processes such as nitrification, nitrogen fixation, and anammox occur in both the pelagic and benthic deep ocean providing sources, sinks, and transformation of N among N pools (Gruber and Sarmiento, 1997; Wuchter et al., 2006; Francis et al., 2007; Ward et al., 2009; Ulloa et al., 2012; Fig. 2). Nitrogen is selectively removed from dissolved organic material throughout the water column and sediments (Bronk, 2002; Hunter et al., 2012), and nitrogen cycling in the benthos releases nutrients such as nitrate, nitrite, and ammonium back into the water column (Laverock et al., 2011). Nutrients regenerated at the seafloor are ultimately recycled and returned back to the surface through thermohaline circulation (often in areas of upwelling) for the process to start again in addition to, as we discuss below, its role in deep fixation (Fig. 2).

Methane provides another key greenhouse gas whose potency is mitigated through deep-sea biological activity; a molecule of methane is 21 times more efficient at warming our atmosphere than a molecule of $CO_2$. Vast reservoirs of methane exist in the deep sea (500–10 000 Gt C methane; Kvenvolden, 1993) and while most of this potential fuel source is kept trapped in the form of hydrates by the temperature and pressure pervasive there, one of the key services provided by deep-sea communities is the rapid consumption of the small proportion that is released (Reeburg, 2007; Knittel and Boetius, 2009). As a result, while methane itself provides 17 % of greenhouse gas forcing, oceanic sources currently only contribute approximately 2–4 % of the methane emitted to the atmosphere (Judd et al., 2002; IPCC, 2007; Reeburg, 2007). The majority of methane that is released from marine reservoirs is consumed within the sediment, leaving pelagic communities to oxidize methane only in areas where there is sufficient methane release to surpass this benthic filter (sensu Sommer et al., 2006), often this is caused by geological activity (such as explosive mud volcanoes (Niemann et al., 2006; Reeburg, 2007), hydrothermal vents and cold seeps (e.g. Sommer et al., 2010), or inadvertent hydrocarbon releases (Valentine et al., 2010; Rivers et al., 2013)). As an added benefit, the anaerobic oxidation of methane leads to the precipitation of carbonates creating an additional trap of carbon (Aloisi et al., 2002), sequestering it for an indefinite time period. While this service of consuming methane may largely be keeping methane sources in check, at times throughout earth's history perturbations have released these methane reservoirs causing massive extinction events, including a loss of > 70 % of marine invertebrate species 183 mya (Kemp et al., 2005). Thus the marine oxidation of methane is a key ecosystem service that occurs within the deep ocean realm.

### 2.3 In situ primary and secondary production

One of the greatest paradigm shifts in the past decade is the role of chemosynthetic production in non-"extreme" deep-sea environments (Middelburg, 2011). Organisms attached to sinking particles produce hydrolytic enzymes that transform organic material from the particulate to the dissolved phase at a rate faster than which it is consumed (Fig. 2). This imbalance in enzyme efficiency and consumption results in a "plume" of fresh dissolved organic carbon (DOC) that trails these particles as they sink, providing substrates for planktonic microbes in the deep ocean (Smith et al., 1992; Vetter et al., 1998). Although the DOC pool in the deep ocean is approximately equal to that of $CO_2$ in the atmosphere at around 700 GtC, it is largely refractory and inaccessible, even to microbes (Hansell et al., 2012). However, the significantly larger dissolved in-





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organic carbon (DIC) pool (∼ 38 100 Gt C) is also utilized by microbes in the deep sea through chemoautotrophic primary production (Ingalls et al., 2006; Hansman et al., 2009; Herndl and Stepanauskas, 2011). This dark $CO_2$ fixation is on the order of heterotrophic production (Alonso-Sáez et al., 2010; Reinthaler et al., 2010; Herndl and Reinthaler, 2013), and can be performed by both bacteria and archaea (Herndl et al., 2005). Chemoautotrophs require reduced inorganic compounds as energy sources to fuel DIC fixation, and evidence is mounting that these may include ammonia, urea, sulfide, and hydrogen (Wuchter et al., 2006; Swan et al., 2011; Alonso-Sáez et al., 2012; Anatharaman et al., 2013) compounds that are often provided by the degradation of sinking organic matter.

Ultimately, secondary production, the formation of heterotrophically fueled biomass, is arguably the primary supporting service resulting in the provision of biomass for human consumption, most notably finfish, shellfish and cetaceans. Additionally, this production is the result of respiration – where $CO_2$ is released and oxygen consumed – and thus is involved in the regulation of gas cycling and carbon sequestration in the deep sea. Secondary production is driven by the quality and quantity of the food resources available (Ruhl et al., 2008; Smith et al., 2008). Depth is often cited as the driving factor of secondary production as a result of reduced POC flux at greater depths; however, interannual variability and total surface production also impact the distribution of biomass (Ruhl et al., 2008; Wei et al., 2010). Despite this clear benthic-pelagic link, deep ocean communities' carbon demand can exceed the vertical supply, with this imbalance being potentially met by lateral advection or by food resources not accounted for in current assessments (Burd et al., 2010). A similar situation is observed in submarine canyons and trenches, which act as depocenters by topographically channeling organic matter, allowing biomass to exceed that of other deep sea habitats by orders of magnitude (de Leo et al., 2010).

While secondary production is difficult to measure directly, it can be estimated as a function of benthic biomass, trophic transfer efficiency, and metabolic rate. Compared to the rest of the marine environment, the deep-sea floor is estimated to contain





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78.9 % of the total benthic biomass; 50 % of total marine benthic biomass is found below 3000 m (Wei et al., 2010). Deep-sea floor biomass is also high at high latitudes with over a quarter of global biomass contained within the 13.4 % of the seafloor found at > 60° N or S (Wei et al., 2010). Whilst the nuances of how depth and organic matter input influence secondary production remain debated, total biomass of all benthic size classes generally declines with increasing water depth from the continental margins to the abyssal plains. The exception to this is bacteria, which dominate the biomass of the abyssal plain and below (Wei et al., 2010). Thus the activity of microbes including their respiration and biochemical processes (e.g. nitrification/denitrification, amino acid oxidation) are a key component as to the type and abundance of nutrients released back into the pelagic realm. These microbes also experience top down forcing from viral populations (Suttle, 2005; Danovaro et al., 2008a) and grazing by many size classes of animals (e.g. Howell et al., 2003; Ingels et al., 2010). In addition, the transfer efficiencies associated with the benthic food web also appear to be influenced by faunal-bacterial interactions that in turn regulate preferential uptake of C and N (Hunter et al., 2012). The overall production by animals is further influenced by predatory and competitive interactions, facilitation and complementarity among species, and environmental drivers such as temperature and oxygen availability. The suite of interactions form regulating services that affect the magnitude and complexity of secondary biomass production in the deep sea.

A variety of habitats are created by large deposits of organic matter, including fish, whale, jellyfish, wood, and kelp "falls", creating areas of enhanced secondary and primary production. Among the best studied of these are whale falls where large cetacean biomass can support communities that are divergent from background communities for up to a century (Smith and Baco, 2003). Wood and leaf deposits create an additional type of similar habitat on shelf, fjord, slope, and abyssal habitats near wooded continental margins (Wolff, 1979; Pailleret et al., 2007). These terrigenous deposits create both an additional type of carbon sequestration, while providing high levels of primary and secondary production to the deep-sea floor (Turner, 1977; Bernardino et al., 2010).





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Somewhat surprisingly, many falls also result in in situ primary production. Degrading wood material can stimulate chemosynthetic production with trophic transfer up to fishes and lobsters (McLeod and Wing, 2007, 2009) and whale falls have worms whose symbionts harness the energy stored in the whales to fix carbon while free-living bacteria perform a diverse suite of chemical magic to fix carbon (Treude et al., 2009).

Methane seep and hydrothermal vent communities provide an outlier of intense secondary production in the deep sea. Biomass of methane-consuming bacteria and archaea are directly consumed by a diversity of metazoans (Levin and Michener, 2002; Van Gaever et al., 2009; Levin et al., 2010; Thurber et al., 2012, 2013) and the flux of energy out of the benthos, largely in dissolved form (Valentine et al., 2005), may be an important source of support for deep-sea populations. This results in vent and seep biomass that far exceed that of the background community; vents can be found with > 70 kg animal $m^{-2}$ (Gebruk et al., 2000) and seeps can exceed 30–51 kg animal $m^{-2}$ (Olu et al., 1996). Even just considering the microbial community in this context, these habitats are an important sink for oxygen (Boetius and Wenzhofer, 2013) and thus both primary and secondary production. Furthermore, the hard substrate habitat created by the microbial processes at seeps provides a habitat for corals and other ecosystem engineers that create additional hotspots of secondary production (Cordes et al., 2008; Lessard-Pilon et al., 2010) and fish (Sellanes et al., 2012; Fig. 1)

### 2.4 Waste absorption and detoxification

The deep sea provides an area where waste products are stored as well as detoxified through biotic and abiotic processes. Contaminant absorption onto sinking particles (reviewed in Dachs et al., 2002), dense shelf water cascades (Canals et al., 2006), and deliberate human activity (Thiel, 2003), transport pollutants from surface waters and continental shelf sediments to the deep ocean basin. These pollutants include persistent organic pollutants, microplastics, sewage, and oil, and can be buried or removed through processes such as bioturbation and bioremediation. Of special note are the organic pollutants, since they accumulate in the tissue of higher predators that are often





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harvested, and thus their removal from the surface ocean has a direct benefit to the toxicity of global food stuffs. However, since deep-sea fish live much longer when they are harvested they can provide an even more concentrated source of the pollutants to its human consumers through bioaccumulation (Froescheis et al., 2000; Looser et al., 2000). Deposition into the sediment provides the greatest benefit to society. In addition to being a sink for pollutants, a variety of biotic processes can detoxify "waste" or potential pollutants. A recent example of this occurred during the 2010 Macondo oil spill where members of the deep-sea microbial community in the Gulf of Mexico were capable of degrading hydrocarbons and gases released from the well (Valentine et al., 2010; Lu et al., 2012) and recently more bacteria with the potential to oxidize hydrocarbons have been recognized (Kube et al., 2013; Naether et al., 2013).

## 3 Provisioning services

### 3.1 Fisheries

One of the most tangible ecosystem services from the deep sea are fish stocks and other biological products (such as coral jewelry), which are increasingly finding their way into human diets and lives. Overexploitation of shallow water and shelf-depth fish stocks has led to an increase in the harvesting of deeper fish stocks over the past 40 yr (Morato et al., 2006). These fish are one mechanism by which species from below 200 m, and in certain cases below 1000 m (Bailey et al., 2009), transfer energy back to the surface water. Currently at least 27 species of fish are harvested in the deep-sea (Norse et al., 2012). However, in many cases, these fisheries are not deemed sustainable owing to the incredibly slow growth of the species of interest, the large bycatch of non-target species produced by certain fishing gears (Norse et al., 2012) and populations showing major declines (Bailey et al., 2009). In addition, the fishing methodology can greatly impact the services provided by the deep sea owing to damage of three dimensional seafloor structures (Roberts, 2002; Puig et al., 2012) and illegal, unreg-





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ulated and unreported fishing practices undermine sustainable fisheries management at a substantial social and economic cost (Flothmann et al., 2010). Precious materials such as cold water corals are also harvested for jewelry (Foley and Armstrong, 2010).

However, one of the main links between global fisheries and the deep sea result from nutrient regeneration. The most productive fisheries in the world occur in areas of strong upwelling, where deep-sea nutrients are brought back to the surface where they fuel photosynthetic production and harvested food stocks (Fig. 2). In addition, many cetacean, pinniped, and fish species, including Sperm whales (*Physeter macrocephalus*) and Elephant Seals (*Mirounga* spp.), forage in the deep-sea even though they are caught in surface waters.

### 3.2 Oil and gas

Once oil and gas reserves on land had been proved profitable, industrial exploitation of this resource quickly moved into shallow marine areas and, in the 1960s, into offshore areas. As easily accessible resources declined, technology for offshore drilling improved, and large reserves of hydrocarbons were found, the oil and gas industry moved into deeper and deeper waters. In the Gulf of Mexico, major reserves are being accessed in waters as deep as 3000 m. Currently drilling for oil and gas is routine in the deep sea (UK > 9000 wells > 30 m depth and 328 > 200 m depth – data from the UK Department of Energy and Climate Change; Norway 1390 > 30 m and 546 > 200 m depth – data from the Norwegian Petroleum Directorate; Gulf of Mexico 3800 offshore wells – data from National Ocean and Atmospheric Association), with major deep-water production in areas such as the Arctic, northern north Atlantic (UK and Norwegian waters), east and west Africa, Gulf of Mexico, South America, India, Indonesia and Australia. Oil and gas revenues from offshore areas are enormous, the industry is a major employer, and technological developments here have many ramifications for other deep-water industries. Clearly, although this service is important, exploitation of these resources needs to proceed with caution to avoid major broad-scale disturbance to the deep-sea environment as dramatically shown by the destruction of the Deepwa-





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ter Horizon and subsequent oil spill from the Macondo well affecting a large area of the Gulf of Mexico (White et al., 2012; Montagna et al., 2013).

While oil represents a utilized service, vast deposits of methane in the seafloor may be a fuel that can bridge the gap of dwindling oil supplies prior to more sustainable solutions being implemented. As a result of anaerobic respiration in the deep sea floor by archaea, the reservoirs of methane discussed above are produced and trapped in the deep subsurface or, under certain circumstances, form methane hydrates on the seafloor. These reserves are extremely extensive in some areas, including the Arctic, and are globally estimated to hold twice the combustible carbon known from all other fossil fuels (Glover and Smith, 2003). Commercial exploitation of methane hydrates is a proven technology, adopting similar methods to traditional oil and gas drilling activities, and several industrial concerns are considering commercial exploitation of this resource at a large scale. While the exploitation of methane reservoirs is being developed further, the potential of hydrogen generation, subsequent mixing of the produced hydrogen with natural gas, its transport via the existing pipeline network and the introduction of it into existing subsurface storage facilities as an energy reserve to be called upon in the future is also being considered (Schmitz, 2011; Pichler, 2013).

### 3.3 Mining

A variety of processes in the deep sea lead to large areas of concentrated metals reserves on the abyssal floor, at hydrothermal vents, and in certain areas covered by rich crusts of minerals. Many of these metals are integral to current electronics and since terrestrial supplies are dwindling, the deep-sea supplies are highly likely to be mined within the decade. Precipitation of manganese and other metals around seed particles under deep-sea conditions over timescales of millions of years has produced extensive deposits of fist-sized polymetallic nodules (reaching densities of hundreds per $m^2$) and crusts (thin (< 20 cm) surficial deposits). Although these deposits occur across a lot of the world's deep water areas (Fig. 3), the ore quality and nodule density varies and the most likely commercial deposits occur in the Clarion Clipperton Fracture Zone (CCFZ)





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in the Pacific Ocean (Glover and Smith, 2003). Seabed fluid flow and precipitation of geological minerals at the seafloor (for example at hydrothermal vents) has led to the creation of massive seafloor sulfides (SMS deposits), which contain high-grade metal ores in significant and commercially attractive quantities. The deep sea also contains areas of sediment rich in metals (Atlantis II Deep, Red Sea; Thiel, 2003), significant phosphorus deposits (Thiel, 2003) and sediments elevated in rare earth elements (Kato et al., 2011), which may all also be profitable to exploit. Commercial scale mining of deep-sea mineral deposits has been considered and trialed since the 1970s. There are current exploration claims and active investigation throughout the CCFZ for manganese nodules, on the mid-Atlantic ridge (for SMS deposits) and production activities beginning imminently in Papua New Guinea (SMS; Nautilus Minerals).

### 3.4 Disposal

The vast depth of the deep sea makes it an area that has been used as a dumping ground for many types of waste, including radioactive substances, munitions, animal carcasses (Morton, 2003), sewage sludge, plastics and mine waste (reviewed in Thiel, 2003 and Ramirez-Llodra et al., 2011, 2013). The slow turnover time of the deep sea (1000 yr) and low oxygen concentration (relative to air) means that many substances disposed of in the deep sea will be sequestered in relatively stable states for long periods of time, during which many are likely to be broken down (through decomposition, rusting and the aforementioned detoxification) into non-harmful substances. The deep sea has also been considered a potential dumping ground for gas, because at the high pressures and temperatures found there cause gases, including $CO_2$, to form a supercritical fluid easing its sequestration. However, depositing $CO_2$ in this maner leads to the acidification of surrounding waters with detrimental impacts on marine life (Thistle et al., 2006, 2007; Bernhard et al., 2009). These impacts may limit the expansion of $CO_2$ depositon from an experimental to realized service. A more plausible solution is using carbon capture and storage whereby $CO_2$ is captured and then stored under the seafloor in depleted oil and gas reservoirs or deep saline aquifers. Recently, however,





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concerns for potential leakage of $CO_2$ and escape of formation water for the benthic environment have been investigated in numerous scientific projects.

### 3.5 Bioprospecting and other provisioning services

Resources in the deep sea are increasingly being exploited by bioprospecting. The deep ocean is the source of a number of novel natural products isolated from the highly diverse and species-rich deep-sea faunal communities (Skropeta, 2008), in particular from those found at hydrothermal vents (Thornburg et al., 2010). Many of these chemicals may have pharmaceutical properties and applications including antibiotics, anti-inflammatories, and anti-cancer compounds. Additionally, deep-sea natural products have commercial uses in cosmetics, nutritional supplements, and industrial and manufacturing processes.

The deep sea has long been an environment hosting military activities, allowing for covert transportation, weaponry, and surveillance. Military munitions disposal to the deep ocean has also been documented (HUMMA final report, 2010). Technological advances from deep-sea military operations have led to numerous commercial marine applications in underwater communications, navigation, and propulsion.

In addition to oil and gas there are other ways in which energy can be extracted from the deep sea. One example is the collection of power from the hydrothermal vent fields using thermoelectric generators, either by tapping a temperature gradient directly from the plumes of a hydrothermal vent, or using high-pressure thermosyphons installed in a well on the hydrothermal mounds (Parada et al., 2012). Since the 1980s, Ocean Thermal Energy Conversion (OTEC) technology has provided the opportunity to harness the temperature differences between cool surface water and colder deep-sea water to create electricity. The technology is currently mainly still evaluated for economic feasibility, but interest in the implementation of such technology on industrial scales is rising with increasing energy demand globally (Yeh et al., 2005). However, in Okinawa, Japan, OTEC has been tested since April 2013 whereby deep water (600 m) is pumped up to be used in convection turbines. Aside energy, there are multiple uses for the pathogen-free and nutrient-rich cold seawater pumped up from the deep sea such as mariculture, refrigeration, air-conditioning, and production of potable water (Dylan, 1995; Yeh et al., 2005). Despite the perception of OTEC technology as being sustainable exploitation of renewable energy, the construction of the needed large-scale deep-water infrastructure and potential alteration of oceanic thermohaline circulation because of necessary massive OTEC seawater flow rates (Nihous, 2007) means that it is a potential threat to other functions and services the deep ocean provides.

## 4 Cultural services

Cultural services provided by the deep sea are the non-material benefits humans enjoy. These services can range from the valuable scientific knowledge that can be obtained from deep-sea environments, the educational value and the economic benefits generated by exploration and discovery (and the technological development that accompanies these), to the more purely aesthetic and inspirational services, including literature, entertainment, ethical considerations, tourism, and spiritual wealth and wellbeing. Despite the obvious distance and inaccessibility of the deep sea, these environments have pervaded ancient and modern culture to a surprising degree.

Some of the main cultural services provided by the deep sea can be described as educational and scientific, two services that receive significant investment despite today's economic climate. The apparent lack of general public and scientific knowledge on the deep sea stands in contrast to the size of the deep sea and its importance in the Earth's biological and climatic systems. As a result, education management organizations are currently promoting the ocean literacy concept, which includes the understanding of the essential principles and fundamental concepts of the ocean, communication about the ocean in a meaningful way and the stewardship involved (Strang and Tran, 2010). One of the roles provided by the deep sea to human culture is in providing a repository for information on past conditions of the planet, stored in the fossil remains of planktonic organisms (e.g. foraminifera, coccolithophores) preserved in deep-marine sediments.

This deep-sea paleo-climatological service is of immediate benefit to assessing and predicting current and future climatic effects on our environment and human wellbeing. In a similar way, the deep sea has conditions suitable for exceptional preservation of historical cultural artefacts, including ancient Black Sea shipwrecks (Ballard et al., 2001) and potentially much more recent artefacts from polar expeditions (Shackleton's Endurance, Glover et al., 2013).

Although the anthropocentric view of Earth has mostly revolved around terrestrial environments, references to the deep sea and its importance for humanity can be found throughout history and literature. While the history of the study of deep-sea fauna spans a mere 130 yr, references to exploring the deep ocean go much further back. The importance of deep sea cartography in Hellenic civilizations, for instance Oleson (2000) illustrates the fascination and exploration potential of the deep ocean dating from several millennia ago. Exploration of the deep ocean has grown vastly since technological advances have allowed easier access to the deep sea. Modern high-resolution deep-water biological investigations are far removed in scope and technology from the first glimpses of deep-sea life recovered in the early 1800s on sounding casts or from the hand-hauled nets deployed in the 1870s from the sailing vessel *HMS Challenger*. Scientific advances and the linked exploitation of deep-sea marine resources today elicit significant investment, which drives increasing marine technological development, involving industries that generate substantial economic wealth and extraction of deep-sea resources beneficial for human welfare and development.

With historical exploration and the ensuing fascination with deep-sea life also came inspiration for literature, arts and entertainment, which can all be seen as more pure aesthetic services (Fig. 1). The deep sea has inspired literature since early human civilization. Plato first mentions the myth of the engulfing of Atlantis by the ocean around 360 BC. This tradition has continued with novels like *20 000 Leagues Under the Sea* and *Moby Dick*. The entertainment value provided by the deep sea is still very much present today as exemplified by numerous recent documentaries, films and even cartoons (e.g. BBC's documentary *Blue Planet – The Deep*, children's program *Octonauts*, and Disney/Pixar's film *Finding Nemo*). Another service with aesthetic and entertainment value that benefits from deep-sea functions is the growing whale watching tourist industry, which can provide substantial economic benefits to coastal communities. Growth and aggregation of whales and dolphins depend to a large extent on deep-sea supporting services, such as seamount habitats or water circulation in upwelling areas (Johnston et al., 2008). A newly emerging industry is that of in-situ deep-sea tourism, whereby human-occupied underwater vehicles are offered to explore deep-water environments in person; an example of a cultural service with exploration and entertainment value that is – for now – only accessible to wealthy individuals. The inspiration and awe that the deep ocean brings us at many different levels of human culture is also present spiritually, with mention in scripture (e.g. Bible: Genesis 1:1–3, Proverbs 8:26–28; Quran: 24:40) as well as various indigenous cultures and classical religions displaying important elements of worship and ceremony related to marine mammals (e.g. New Zealand Maoris) and gods representing oceans and seas (Greek Poseidon). Related to spiritual values are the ethical values that are often assigned to marine life and increasingly to deep-sea animals and environments. Public pressure for conservation of deep-sea habitats, such as coral reefs and vents, can be seen as an important contributor to or result of the increasing non-use or existential value of the deep sea.

## 5 Discussion

It is difficult to discuss the deep sea without being waylaid by a severe lack of data, the conceptual challenge of its size, and the unexplored habitats that likely add heterogeneity and diversity in unknown ways. However, when the current state of knowledge is viewed synoptically, these intellectual shortcomings can be dwarfed through integrating our perception of the diverse chemical, micro- and macro-biological, and environmental reactions that have been discovered over the more than a century of its study. What results is an understanding of how the temporal and spatial diversity in the





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deep sea creates a system with far reaching linkages both within its realm as well as society as a whole.

### 5.1 Temporal and spatial relationships

Many of the functions provided by the deep sea, even though they occur on small scales in time and space, have direct implications to global services owing to the large size of the environment (Fig. 4). Even regional-scale activities, such as harvesting of deep-sea fish, may have broad temporal and spatial implications for ecosystem services – as these are usually species that are very long-lived (Cailliet et al., 2001) and the species have either little spatial pattern potentially leading to broad ranges (Haedrich and Merrett, 1990) or ranges that reflect a similar distribution to water masses (Koslow, 1993). Even processes thought to proceed at low rates, such as chemoautotrophy in the pelagic and abyssal seafloor (Nauhaus et al., 2007; Reinthaler et al., 2010; Middelburg, 2011), can have major implications when scaled up to the huge areas and volumes of the deep sea, playing an important role in processes such as energy flow, carbon cycling and sequestration at the global scale.

In addition to the vast nature of the habitat, there can also be long separation of function and service within the deep sea (Fig. 4). An example of this is that nutrient regeneration, often dominated by microbial activity (Azam et al., 1983), is a feature that occurs so pervasively that their provisioning of surface production for both the generation of oxygen as well as food stuffs means it has global application. This is even more provocative since in certain instances there are great spatial and temporal distances between function and service, for example nutrients regenerated in the North Atlantic may not reach surface waters in the North Pacific for millennia. There is even greater separation of service and function for the creation of oil and gas reservoirs. Oil reserves are the result of geological transformation of organic matter buried in deep ocean sediments. Methane hydrates reserves are largely formed through microbial mediated methanogenesis and although the formation occurs on relatively "rapid" time scales it takes centuries to build up to potentially harvestable concentrations. The same is true for manganese nodules and polymetallic crusts, whose formation is slow yet even now have yet to provide a service although they likely will in the near future.

### 5.2 Interrelatedness and threats to ecosystem services and functions

The biological, physical, and chemical properties of the ecosystem combine to form complex processes that result in globally important services. These regulating and provisional services are connected both to their functions and to each other in a variety of ways (Fig. 5). In many instances, one function provides a diversity of services, for example circulation, or more specifically the separation of the deep sea from the atmosphere over long periods of time, provides at least three regulating and four provisioning services.

The services provided by the deep sea are not impervious to human impacts. The concern as to the susceptibility of overfishing the slow growing and long lived species of fish and coral in the deep sea is a topic of debate and concern (Bett, 2001; Morato et al., 2006; Althaus et al., 2009). Climate change itself will impact the functions discussed in the deep sea through ocean acidification, declining oxygen and productivity and increasing temperature (Mora et al., 2013). These impacts are likely to affect diversity of the supporting functions discussed here including biodiversity, nutrient cycling, biomass, and primary and secondary productivity (Jones et al., in review). While the scale and magnitude of these impacts are difficult to predict, the interrelated nature of the impacts indicate that they will be pervasive in the overall function. In addition, some of these impacts are as widespread as the function providing habitats themselves, further confounding predictive capability.

### 5.3 Current challenges in function and service evaluation

While numerous studies have sought to quantify various ecosystem functions in the deep sea (for a review see Smith et al., 2008) and described the various services provided by the different functions, we know of no studies that have yet put a monetary





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value on the extent of ecosystem functions and services in the deep sea although multiple frameworks have been constructed to facilitate this sort of key analysis (van den Hove and Moreau, 2007; Armstrong et al., 2010, 2012). This lack of knowledge makes ocean management extremely difficult, especially with regards to managing the exploitation of marine resources as it is presently impossible to know the full "cost" that we will have to pay for exploiting a specific resource. By evaluating ecosystem functions and services provided by the deep sea we will be able to understand the cost vs. benefit of exploitation, which will assist us in making better management decisions as it pertains to exploitation of the deep-sea services.

To fully understand the ecosystem functions provided by the deep sea as a whole, it is important to be able to compare specific functions across a variety of spatial and temporal scales. However, comparisons amongst studies are often plagued by the fact that different techniques are used. A good example of this is in studies that use different mesh sizes to separate animals by body size, with some separating macrofauna on a 300 micron mesh while others use a 500 micron mesh. The use of two techniques automatically imposes differences in various properties that relate to ecosystem functioning and services (e.g. biodiversity, productivity), hampering comparisons across ecosystems.

By the very nature of the mechanisms that lead to ecosystem services, a holistic and multidisciplinary approach is necessary to study it. Collaborations between biogeochemists, physiologists, empirical and observational ecologists who deal with microbes to megafauna in both pelagic and benthic environments, and climate scientists, but also socio-economists are required to understand and further quantify the services provided by the deep sea. However, owing to the pervasive nature of the function of the deep sea, and the threats to it, an important additional link is needed between each of these scientists and the stakeholders of the deep sea, which is the global population.





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## 6 Conclusions

- The deep sea is the world's largest environment and comprises a multitude of different habitats and a major proportion of the world's species
- Although over a century of research has been undertaken in the deep sea, our understanding of this environment is limited. However, with the advances we have already made we can begin to understand its role in global energy, nutrient, and biological cycles.
- Services provided by the deep sea are vital to support the current way of life for many humans, providing energy, metal and mineral resources, food and other goods.
- Vast area and long residence times typify deep-sea environments meaning that even fast processes on small spatial scales create massive services, although in many cases the processes are far removed from their resultant services.
- Many of the functions of the deep sea result in interrelated regulating and provisioning services.
- The stakeholders of the deep sea are not limited to one country or area, but instead consist of the entire global population.
- The deep sea plays an important cultural role, providing inspiration for the arts and having far-reaching influence even for those that never leave the land
- Further research should aim to build upon existing frameworks to quantify the monetary value of the deep sea while creating a more uniform approach to its study.

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**Table 1.** The ecosystem functions, services and goods provided by the deep sea.

| Ecosystem Functions | | Ecosystem Services | | Examples of Goods |
|---|---|---|---|---|
| Supporting Functions | Nutrient Cycling | Provisioning Services | Minerals | Oil and Gas, Mining |
| | Water Circulation | | Species Diversity | Bioprospecting, Medicines |
| | Chemosynthetic Primary Production | | Fishing | Food |
| | Secondary Production | | Large Area | Disposal, Military Uses |
| | Climate Regulation | | High Pressure, Cold Remote Environment | Storage Sites for CO2 |
| | Species Diversity and Evolution | | Waves And Currents | Electricity Generation |
| | | | Temperature Gradient in Water and Sediments | Geothermal Energy |
| | | | Biomaterials and Metals | Jewellery |
| | | Regulating Services | Gas Cycling and Climate Regulation | Equitable Climate |
| | | | Waste Detoxification and Purification | Pollution Control |
| | | | Biological Regulation | Degradation/Storage of Waste<br>Top Down Control |
| | | | Nutrient Regeneration | Food Stocks<br>Oxygen Production |
| | | Cultural Services | Preserving Conditions | Preserved Archaeological Remains |
| | | | Long-Term Sedimentation of Biological Material | Paleoclimate Archive |
| | | | Environmental Setting/ Charismatic Fauna | Indirect Uses –<br>Inspiration for Literature/Arts<br>Documentaries<br>Exploration<br>Educational – Ocean Literacy<br>Heritage<br>Tourism |





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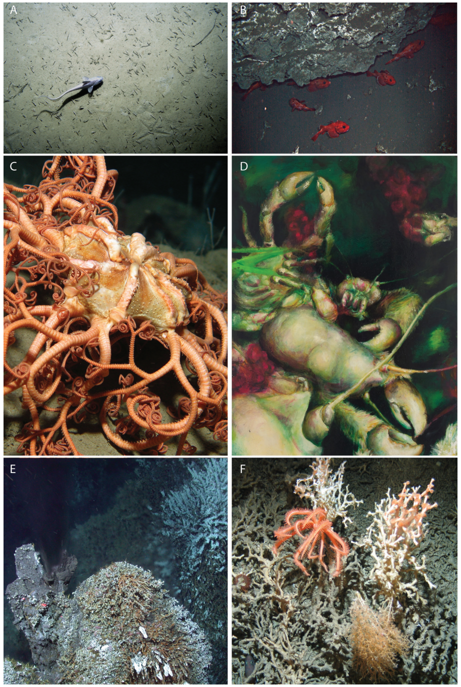


**Fig. 1. (A)** *Bathysiphon filiformis* in Kaikora Canyon, NZ (Credit: D. Bowden, NIWA); **(B)** a large authigenic carbonate at Hydrate Ridge, CA, USA being used as a refuge by *Sebastes* sp. (Courtesy of L. Levin); **(C)** this was the first species ever recovered from the deep sea, *Gorgonocephalus caputmedusae*; **(D)** art has been inspired by the strange fauna of the deep sea for many years. This is an example by Lily Simonson (http://oldgenres.com/) who uses deep-sea fauna as a muse for her paintings. **(E)** Hydrothermal vents provide areas of intense secondary production and potential resources for mining (Courtesy of B. Grupe/R. Lee). **(F)** Ecosystem engineers, such as these deep-sea corals provide both jewelry as well as areas of increased secondary production and demineralization (Credit: Department BIS, UK).





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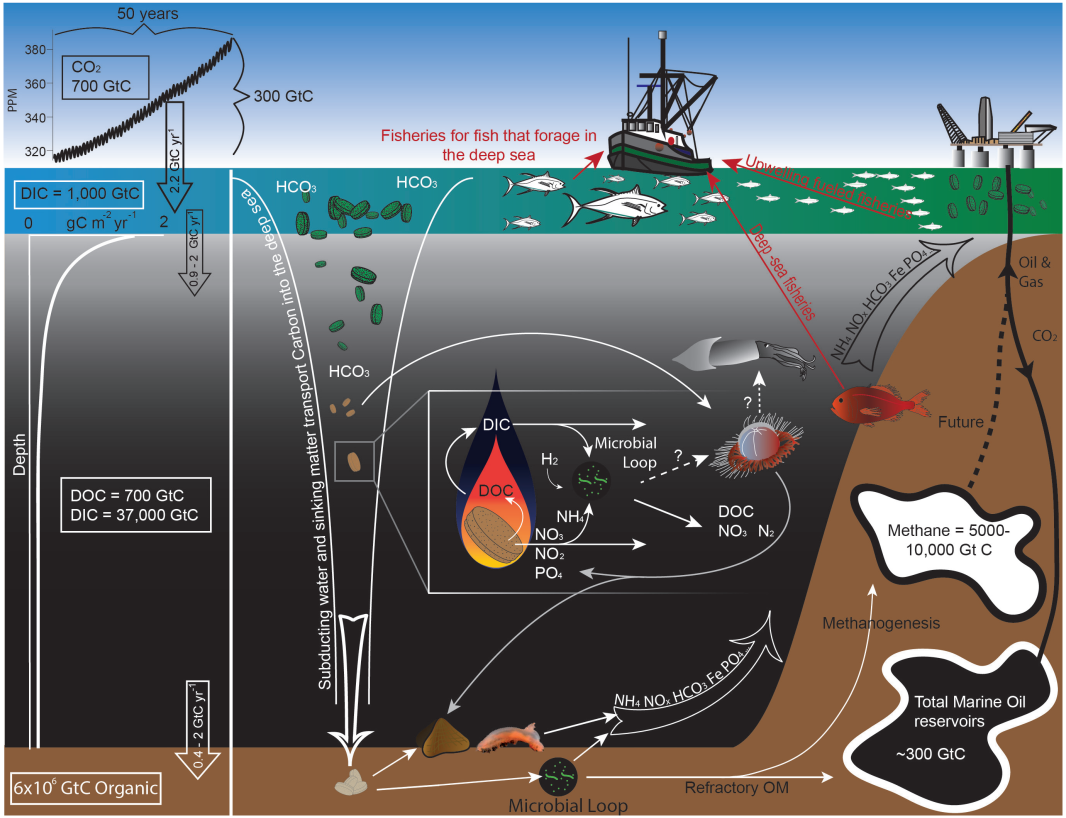


**Fig. 2.** Schematic of carbon flow and a subset of the resources and functions of the deep sea. Data include the Keeling and Martin Curves (Martin et al., 1987) and values from Longhurst (1991), Sabine and Feely (2007), Canadell et al. (2007); US EPA. Arrows represent flow of matter or carbon and the upwelling of nutrients. Dotted lines are potential or unquantified flows. $NO_x = NO_2$ and $NO_3$. Not to scale.





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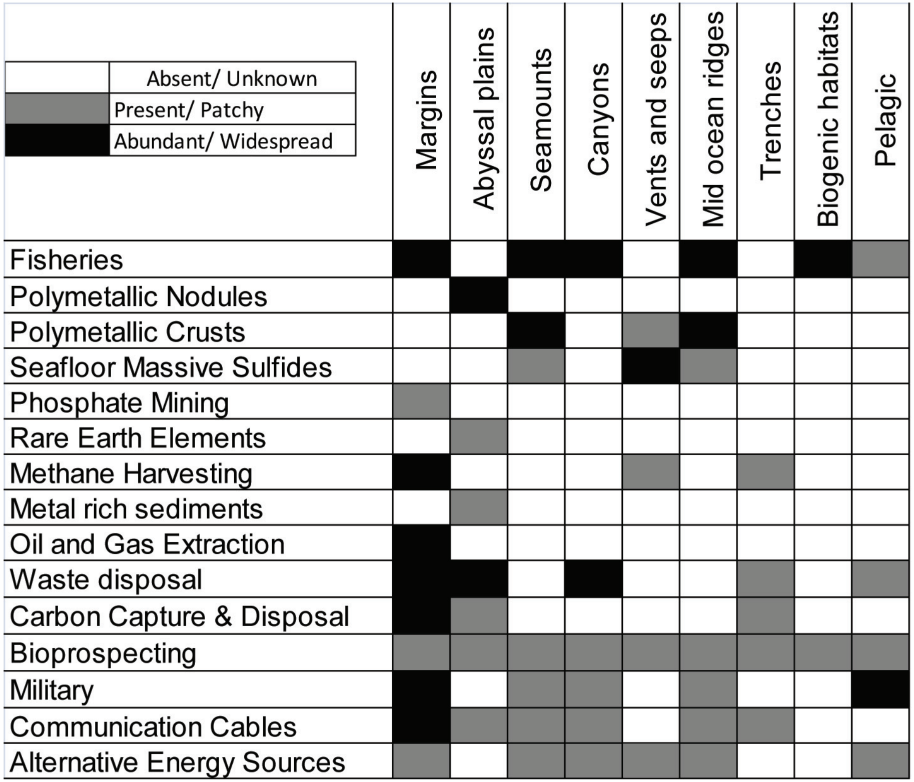


**Fig. 3.** The distribution of regulating and provisioning services among the habitats present in the deep sea.





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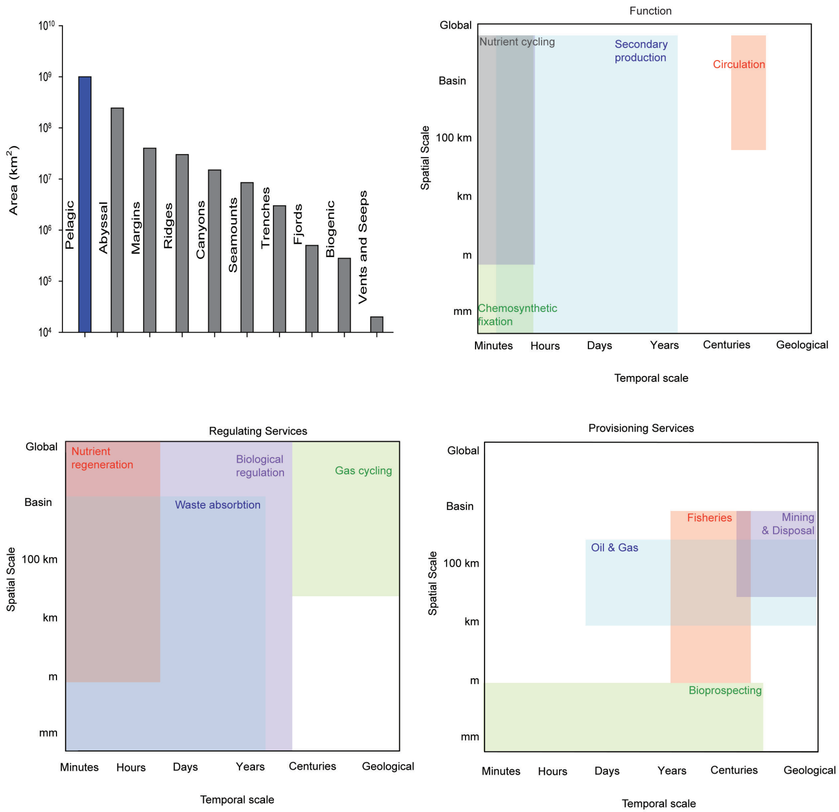


**Fig. 4.** The **(A)** spatial extent of each of the main deep-sea habitats (pelagic is in km$^3$ while all other habitats are in km$^2$). Note that many of these habitats can be any range of size from small to those depicted. The relationship between spatial and temporal scale for: **(B)** supporting, **(C)** regulating and **(D)** provisioning services of the deep sea. Note log scale in A and approximate scales in **(B–D)**.





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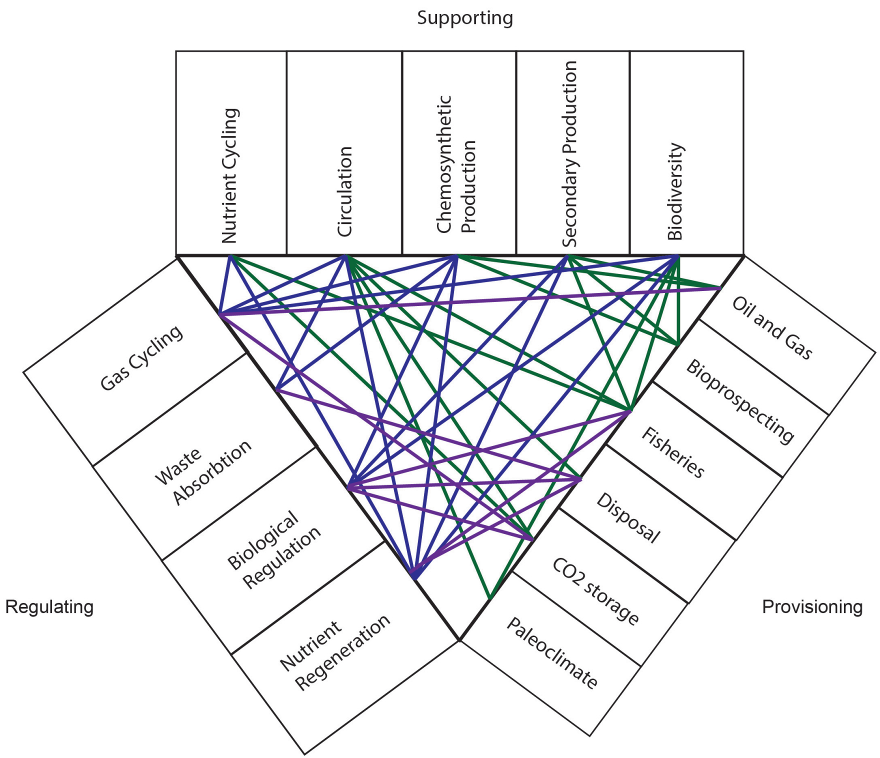


**Fig. 5.** The links among the supporting, provisioning, and regulating services within the deep sea. Color is used to indicate the linkages among each of the different overarching service classes.





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