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Review of deep-water ecosystems, biodiversity, VMEs, Ecosystems Approach studies, and identification of best practice

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Glossary of Terms

Abyssal Plain — A large area of extremely flat or gently sloping ocean floor just offshore from a continent and usually at depths >2000m. The abyssal plain begins where the continental margin and slope end.

Bathymetry — Water depth relative to sea level.

Benthic — Of, or relating to, or living on or in the bottom of a body of water or the seafloor.

Biodiversity — The variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems.

Biogeographic — Relating to the geographic occurrence of lifeforms (fauna and flora) at the scale of large regions with distinct landscapes/seascapes, flora and fauna.

Bioregion — Assemblages of flora, fauna and the supporting geophysical environment contained within distinct but dynamic spatial boundaries. Biogeographic regions vary in size, with larger regions often found where areas have more subdued environmental gradients. These are defined and delineated at the meso-scale.

Biome — A major regional ecological community of plants and animals extending over large natural areas. In the sea, these equate to geological units or hydrographic features such as coastal, demersal, shelf and slope, abyssal, neritic, epipelagic, mesopelagic and bathypelagic.

Biotone — Zones of transition between core provinces.

Circulation regime — Areas within water masses that have differing circulations and resulting in differing retention, mixing and transport of water properties and biological processes and organisms.

Continental margin — The submerged prolongation of a land mass from the coastline, which consists of seabed and subsoil of the continental shelf, slope and rise, but not the deep ocean floor.

Continental rise — The sloping part of the ocean floor at depths of about 2000-4000m, between the continental slope and the abyssal plain.

Continental shelf — The shelf-like part of the ocean floor beside continents and extending from the coast to a depth of about 200m. The shelf is divided into inner-shelf (the area closes to the coastline), outer-shelf (the area adjacent to the shelf break) and mid-shelf (the region between the inner and outer shelf).

Continental slope — The sloping, often steep, part of the ocean floor bordering the continental shelf; divided into the upper slope (200-700m) which is adjacent to the shelf break, mid-slope (700-1400m) and lower slope (1400-3000m).

Demersal — Occurring or living on or near the bottom of an aquatic environment. Generally used in reference to mobile fish and crustaceans whose life history is related to seafloor processes.

Ecosystem — A dynamic complex of plant, animal and micro-organism communities and their non-living environment interacting as a functional unit. In practice, ecosystems are mapped and described using biophysical data.

Ecosystem approach — A strategy for the integrated management of land, water and living resources that promotes conservation and sustainable use in an equitable way (CBD decision V/6).

Ecosystem-based management (EBM) — Management that recognises that maintaining the structure and function of ecosystems is vital, and that human uses and ecosystem health are interdependent. EBM considers ecological, social and cultural objectives for an ecosystem, but makes ecological sustainability the primary goal of management.

Endemic — Native to, or confined to a certain region.

Endemism — A situation in which a species or other taxonomic group is restricted to a particular geographic region, owing to factors such as isolation or in response to soil or climatic conditions.

Exclusive Economic Zone (EEZ) — Ocean areas from the coast to usually 200 nautical miles offshore, where the adjacent nation has exclusive economic rights and the rights and freedoms of other states are governed by the relevant positions of the United Nations Convention on the Law of the Sea.

Geomorphological feature — Major element of the seabed such as a seamount, canyon, basin, reef or plateau distinguished by its shape.

Geomorphology — The study of the shape of the earth’s surface and how it changes through time.

Habitat — A geographic area that can provide for the key activities of life - the place or type of site in which an organism naturally occurs.

Meso-scale — Large spatial unit (in terms of 100s or 100s of kilometres in length).

Mixed layer — The layer of water between the ocean surface and a depth usually ranging between 25 and 200m, where the density is about the same as at the surface. The water conditions in the mixed layer remain similar due to wind mixing.

Offshore — The area of the Exclusive Economic Zone extending seaward from 3 nautical miles.

Pelagic — Of, relating to, or living in the water column of the open oceans or seas.

Province — A large-scale biogeographic unit derived from evolutionary processes in which suites of endemic species co-exist.

Provincial bioregion — A large biogeographic region based on broad-scale distribution of fauna.

Shelf break — The abrupt change in seabed gradient that occurs at the boundary between the outer continental shelf and the upper continental slope, usually at about 200 metres water depth.

Transition — A zone of overlap between provinces. The transitions are not simply 'fuzzy' boundaries but are areas that represent unique communities and ecological processes that tend to be richer than the provinces.

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The ecology of deep-sea ecosystems

1. Introduction

The marine environment is a diverse and complex habitat for the growth of organisms, including animals, plants, algae, fungi, protozoa, archaea, bacteria and viruses. Organisms have evolved to survive in all marine habitats, ranging from the poles to the equator, and from shallow regions, where sunlight is the principal source of energy, to the dark deep abyss, where chemosynthesis can supplement what little solar-derived energy arrives from the surface far above. About 90% of all marine life lives in the sunlit region.

The rate of solar energy capture in near-surface habitats is critically dependent upon the presence of phototrophic organisms. Their population size, and hence productivity, is in turn determined by the supply rate of growth-limiting nutrients, which are present mostly in the deep sea, well below the depth of penetration of sunlight. Physical processes bring nutrients to the surface to fuel photosynthesis and to sustain life in the ocean. Unlike photosynthetic environments, chemosynthetic environments depend on organisms capable of deriving energy not from sunlight, but from the oxidation of inorganic chemicals, such as sulphates or ammonia. These chemicals are most plentiful around the geologically active boundaries of tectonic plates and whale carcass falls (see Section 4.3), therefore, such environments tend to be very localized and ephemeral.

Many marine macro-habitats can be identified, studied and compared; however, due to their relatively small size (Rex & Etter, 1998) most marine organisms live in microhabitats where the physical, chemical and biological properties may be different from those in the surrounding area. The enormous habitat diversity of the global ocean leads to niche and resource partitioning, contributing to high microbial biodiversity in the sea.

2. 'Key' abiotic characteristics of the deep sea environment

The 'deep-sea floor' is defined as that portion of the ocean bottom beyond the continental shelf. The continental shelf differs in depth in different parts of the world; it can be fairly shallow, between 100 and 200m water depth in the NE Atlantic (Gage and Tyler, 1991) or deeper (400-800m) off Antarctica (the global mean is 133m – Pinet, 1998). The ecosystems of the deep-sea are broadly divided into those which relate either to the pelagic or to the benthic zones, which can be further subdivided according to depth and other physical characteristics as shown in Figure 1. In this review the focus is on the biology and habitats of the deep benthic and bentho-pelagic zones. These zones are broadly defined by the bathyal, abyssal and hadal depths (see Figure 1). The bathyal zone generally corresponds to the limits of the continental slope, which represents the sloping sea bottom of the continental margin that begins at the shelf edge and ends at the top of the continental rise or in a deep-sea trench (Pinet, 1998). The transition zone between the lower part of the continental slope and the relatively flat abyssal plain is known as the continental rise and tends to be located anywhere between 3,000 and 4,000m in depth, which marks the start of the abyssal zone and the abyssal plain. The abyssal plain ranges in depth between 3,000 and 6,000m, but tends to be found on average at a depth of 4,000m. It is a relatively flat and featureless landscape covering a vast area of the Earth's surface, perhaps as much as 50% of the total surface area. Beyond the abyssal plain lies the haldal zone, characterised by deep sea trenches which are the deepest places on Earth. These trenches are created by geological plate tectonic subduction processes and are therefore generally associated with increased geological activity, giving rise to submarine volcanoes and earthquakes. Increased geological activity is also observed around mid oceanic ridges such at the Mid Atlantic Ridge. In both cases, such geological activities are responsible for creating large seamounts, which are abrupt 'eruptions' of the seabed (often extinct volcanoes) rising several hundred metres from the seafloor (see Section 4.2). The deep sea trenches are most commonly found around the margins of the Pacific and Indian oceans occurring between 6,000 and 11,000m.

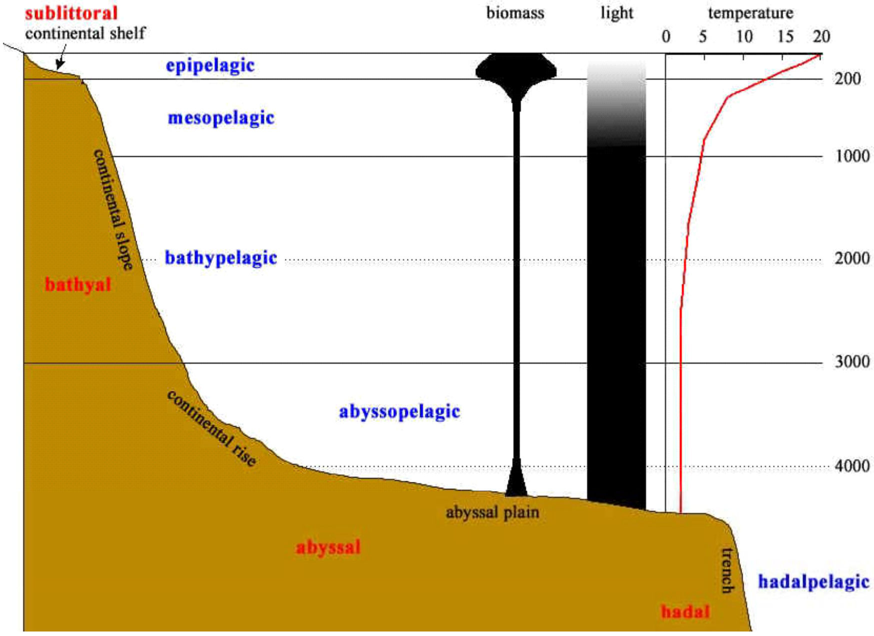

Figure 1. The principal pelagic and benthic 'provinces' of deep sea ecosystems. Showing also the gradients in the 'key' environmental variables of light and temperature and gradients in overall levels of biomass.

The nature of the seabed and its associated habitats are set within this geological and environmental context. Recent studies have revealed that the deep sea is not the tranquil, homogeneous environment it was once considered to be and that within each of the zones described above, there are distinct and dynamic habitats and biological communities (Gage and Tyler, 1991). Through the use of modern acoustic deep-sea mapping technologies it is now possible to identify and describe the complexity of seabed features and habitats (e.g., Figure 2).

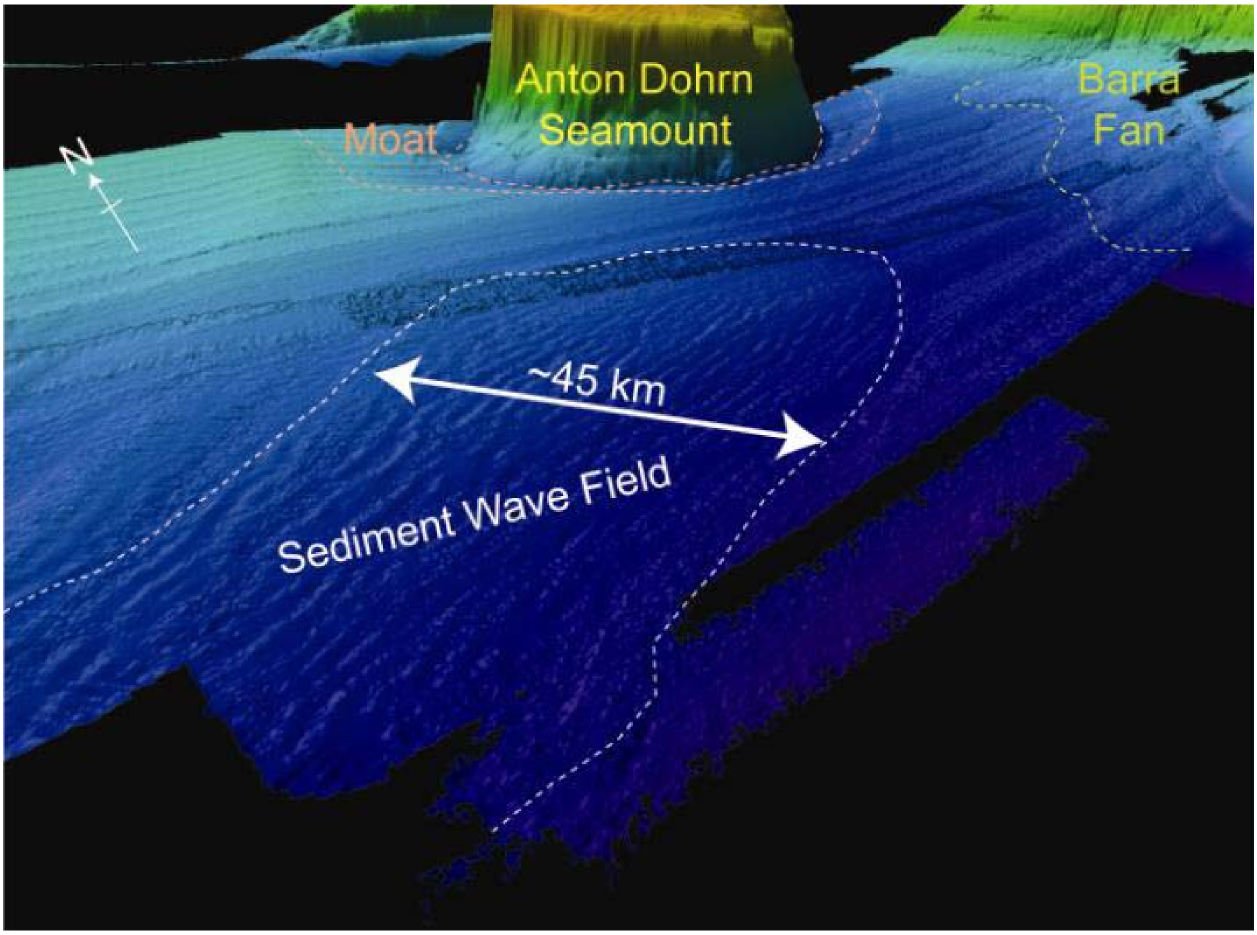

Figure 2. Sediment waves and Anton Dohrn Seamount (Image: NOCS).

The combination of physical characteristics – or abiotic factors – of the deep-sea environment is what deep-sea life-forms must contend with to survive. These are light, pressure, temperature, oxygen and food. The geological setting that defines the landscape of the deep-sea environment, the substrate type and prevailing deep sea currents all have an important role in determining the status of such factors, and their different combinations have led to the fascinating adaptations of deep-sea life-forms that have become adapted to see, feel, feed, reproduce, move, and avoid being eaten by predators in those settings.

Variations in the dominant gradients associated with these principal environmental characteristics which determine the habitats for important deep sea communities are further described below:

2.1. Light

The layer of water that is exposed to sufficient sunlight for photosynthesis to occur is known as the photic zone. The depth of the photic zone (or euphotic depth) can be greatly affected by seasonal turbidity. Typical euphotic depths vary from only a few centimetres in highly turbid eutrophic estuaries, to around 200m in the clear open ocean. This lower depth limit coincides approximately with the point of the continental shelf break and is called 'daytime depth of the deep scattering layer'. The scattering layer is thought to have a strong influence on the depth distribution patterns of biodiversity and biomass observed in the oceans (see Section 2.5). Below the photic zone is the dis-photic zone, where levels of light are insufficient for photosynthesis, or at least insufficient for photosynthesis at a rate greater than respiration. The bottom most zone, below the photic and dis-photic zones, is called the aphotic zone. Most deep sea ocean waters belong to this zone.

Cleary, light attenuation is a function of water depth, water clarity, surface light intensity and quality (wavelength). The light attenuation relationship between these variables has been well studied and is shown in Figure 3.

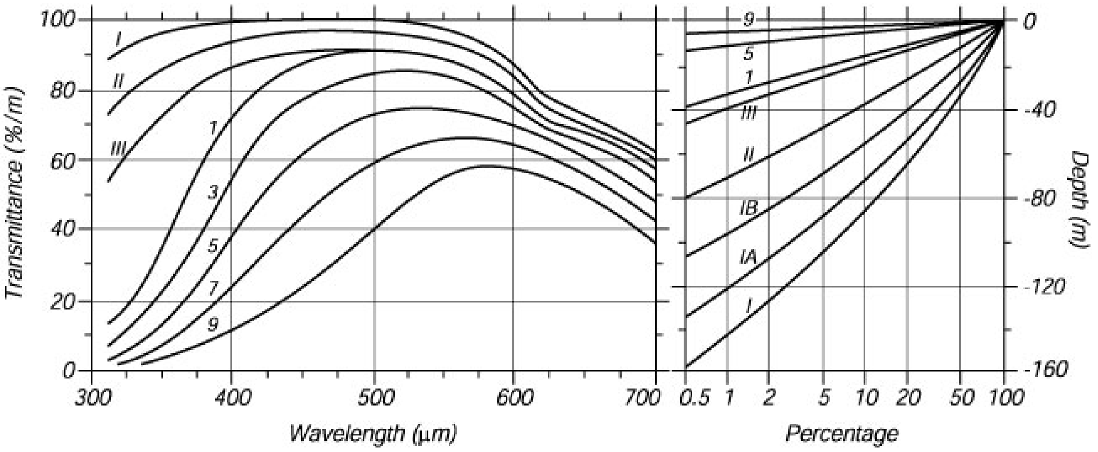

Figure 3. The attenuation of daylight in the ocean (transmittance) as a function of wavelength, where I: extremely clear ocean water, II: turbid tropical-subtropical water, III: mid-latitude water and 1-9: coastal waters of increasing turbidity. The diagram on the right represents the percentage of 465nm light reaching the indicated depths from the same types of water (Jerlov, 1976).

Below the depth where no surface light can penetrate, the only natural light source is bioluminescence, a biologically driven chemical reaction that is produced by some organisms. Whilst this source of biological light is important for attracting prey or in communication using specific light patterns, it does not contribute to primary production. All oceanic primary production which relies on photosynthesis therefore occurs in depths shallower than about 200m and often at depths much less than 100m.

2.2. Pressure

Considering the volume of water above the deepest parts of the ocean, it is not surprising that vertical pressure is one of the most important environmental factors affecting deep-sea life. Vertical pressure increases by 1 atmosphere for each 10m in depth. On average, the pressure in the deep sea ranges between 200 and 600atm. Horizontal pressure gradients are also important, although much less in absolute terms than the vertical pressure gradients, they nevertheless drive the horizontal flows in the ocean. The horizontal variation in pressure in the ocean is entirely due to variations in the water mass caused by differences in temperature salinity and turbidity. Such variations in water mass drive the deep ocean currents which have a profound influence on the deep-sea biology. Advances in deep-sea technology have enabled scientists to collect species samples under pressure so that they reach the surface for study in good condition. Without this technology, the animals would die shortly after being collected as the absence of pressure would cause their organs to expand and possibly explode. With good samples, it has been observed that the flesh and bones of deep sea marine creatures are relatively soft and flaccid, which is an adaptation to withstand the pressure.

2.3. *Temperature*

The difference in temperature between the photic, or sunlit, zones near the surface and the deep-sea are dramatic. Temperatures vary more in the waters above the euphotic depth where thermoclines, or the separation of water layers of differing temperatures, are more common. Below the photic zone the temperature of the ocean drops gradually with depth. With the exception of hydrothermal vents (see Section 4.3) where hot water is emitted into the cold surrounding waters, the deep sea temperature remains between 0 and 4°C (see Figure 1).

2.4. *Oxygen*

The dark, cold waters of the deep are also oxygen-poor environments. Consequently, deep-sea life requires little oxygen. Dissolved oxygen is transported to the deep sea from the surface when the temperature of surface waters decreases, becoming denser and causing the water to sink. Most of this oxygen-rich water comes from Arctic regions. Surprisingly, the deep sea is not the most oxygen-poor zone in the ocean. The oxygen minimum zone lies between 500 and 1,000m, where there are more organisms that consume oxygen, thus depleting the oxygen during respiration. In addition, the bacteria that feed on decaying food particles descending through the water column also require oxygen.

2.5. *Energy (food)*

There are two principal sources of energy which fuel biological communities in deep sea ecosystems, namely; i. fixed carbon from photosynthesis, all of which is imported from the much shallower photic zone (indirect sources of energy), and ii. primary production directly derived from chemosynthetic processes not involving photosynthesis (direct deep sea primary production). Estimates which account for the overall balance between these two sources of energy in the deep sea environment are not clear, but recent studies suggest that chemosynthetic sources could be the most dominant source of primary production overall in the deep sea environment (Vanreusel *et al* 2009), particularly in the abyssal areas which are most distant from the original photosynthetic sources of primary production.

The only ***Photosynthetic source of carbon*** in the deep sea is from the production of phytoplankton in the photic zone, which in turn is largely consumed by the herbivores, which are then preyed on by the carnivores. A certain amount of the energy from this food chain reaches the deep sea as a continuous rain of dead organisms or their products. The quantities of these materials reaching the seabed declines with increasing depth and the resulting production of benthic invertebrates, which are very largely dependent on such energy input, could never support the observed demersal fish populations. The rapid sinking of large, dead organisms to the sea bed can provide a valuable food source for some scavenging fish species. However, there is little doubt that the success of the benthopelagic fishes of the slopes results from the transfer of the energy of surface production downwards, via the mesopelagic fauna of both fishes and invertebrates. One pathway is via the overlapping food chains of organisms that occupy specific depth ranges. Many mesopelagic organisms also carry out daily vertical migrations feeding near the surface at night and returning to depths of about 1,000m during the day where they form a deep-scattering layer. Where this downward vertical migration impinges onto the slope or the sides of seamounts it provides a source of food for demersal fish. The horizontal impingement of the scattering layer onto the slope or the horizontal movements of the demersal fish into the scattering layer will also increase feeding opportunities. It is proposed that the abundance, diversity and peak biomass at mid-slope depths is a consequence of the efficient transfer of surface production into deep water via overlapping mesopelagic food chains and the daily or seasonal transfer by vertical migration (Gordon, JDM in JNCC web report[1]).

The lack of any photosynthetic primary production in the deep sea is the main reason the deep sea has relatively low levels of organic carbon and animal biomass compared to the relatively shallow photic waters of the continental shelf. In the deep sea, low temperatures and a limited supply of food typically result in relatively low rates of growth, respiration, reproduction, recruitment and bioturbation in comparison to shallow-water ecosystems (Gage and Tyler, 1991; Smith and Demopoulos, 2003). The biomass of deep-sea benthic assemblages is less than that of shallow-water or terrestrial assemblages because of the low flux of photosynthetic sources of energy (Smith and Demopoulos, 2003).

Although they lack photosynthetic primary production, deep-sea ecosystems can be highly dynamic. In the Northeast Atlantic (at the Porcupine Abyssal Plain) large fluxes of highly labile organic matter arrive at the seafloor following the spring phytoplankton bloom (Billett et al., 1983). Deep-sea ecosystems react rapidly and vigorously to this freshly deposited phytodetritus, and it has been linked to the seasonal variability in reproduction and recruitment in certain species, relatively rapid growth rates, and seasonal growth-banding in skeletal parts of deep-sea deposit-feeding invertebrates (Gage and Tyler, 1991; Tyler et al., 1992).

Deep-sea creatures have also developed specialised feeding mechanisms because of the lack of light and because food is scarce in these zones. Some food comes from the detritus of decaying plants and animals from the upper zones of the ocean. The corpses of large animals that sink to the bottom provide infrequent feasts for deep-sea organisms and are consumed rapidly by a variety of scavenging species. The deep sea is home to jawless fish such as the lamprey and hagfish, which can burrow into carcasses, quickly consuming them from the inside out. Some deep-sea fish have large and expandable jaws and stomachs to hold large quantities of scarce food. These fish don't expend energy swimming in search of food, instead they remain in one place and ambush their prey.

There are many types of ***Chemosynthetic source of carbon*** in the deep sea.Chemosynthetic ecosystems form where chemical energy from subsurface geological or microbiological processes becomes available at the seafloor. “Chemosynthesis” means that organisms can utilize chemical energy — in the

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[1] Website address: http://www.jncc.gov.uk/page-2525

form of hydrogen, methane, hydrogen sulphide and iron — to fix CO2 just as plants do, but without sunlight. The discovery of hydrothermal vents, cold seeps and gas hydrates in subsurface sediments and rocks showed that significant ecosystems are fuelled by reduced chemical substances (H_2S, H_2, Fe) and hydrocarbons (e.g. CH_4). These ecosystems show the highest biomasses and productivity of all those found in the deep sea. Observation of the European continental margins using in situ video and photography with deep submersibles (Vanreusel *et al* 2009) provides evidence of a wide range of active cold-seep ecosystems associated with fluid, gas, and mud escape structures. Such structures often emit methane and other hydrocarbons and are colonized by specific anaerobic subsurface microbiota which use hydrocarbons as an energy source and seawater sulfate to respire, thus producing high fluxes of hydrogen sulfide. Most cold seeps also appear to support highly productive communities consisting of specialized animals that can cope with elevated concentrations of chemical compounds and low oxygen levels at and below the sediment-water interface. Among the most remarkable of the fauna exploiting the abundant chemical energy of seeps are large worms and mussels storing bacterial symbionts in their tissues, which provide energy to their hosts. These special chemosynthetic habitats are further discussed in Section 4.3 below.

3. Deep-sea habitat classification schemes

As the pressure on deep-sea ecosystem continues to increase through increased human activity, so does the need to identify effective management strategies and tools to sustain its resources. Classification systems are one such tool which have an important role in management of the marine environment. They were first developed and applied to manage shallow shelf sea ecosystems (Allee et al., 2000 and Connor et al., 2004 – see also EUNIS). They divide the marine environment into understandable distinct units that can be quantified and mapped for planning purposes and provide a framework for describing function and sensitivity of habitats. Without such classifications it is very difficult to know which areas and parts of a marine ecosystem require protection. The uses of the habitat classification system are broad and can include spatial planning, predictive modelling of habitats, habitat management, use in monitoring and conservation strategies, reserve network design, scientific study and education. These varying uses all have different needs from a classification system, but specifically in the context of the deep sea, attempts have been made to extend the classification criteria (see below) into a system for the deep sea (Greene et al., 1999 Valentine et al., 2005 Auster et al., 2005). Common features or requirements of any classification system must:

- be scientifically sound, adopting a logical structure in which the types are clearly defined on ecological grounds, avoiding overlap in their definition and duplication of types in different parts of the system, and ensuring that ecologically-similar types are placed near to each other and at an appropriate level (within a hierarchical classification);
- provide a common and easily understood language for the description of marine habitats;

- be comprehensive, accounting for all the marine habitats within its geographic scope;
- be practical in format and clear in its presentation;
- focus on the natural community and its physical environment;
- include sufficient detail to be of practical use for conservation managers and field surveyors allowing mapping of ecological units, but be sufficiently broad (through hierarchical structuring) to enable summary habitat information to be presented at national and international levels or its use by non-specialists;
- be sufficiently flexible to enable modification resulting from the addition of new information, but stable enough to support ongoing uses. Changes should be clearly documented to enable reference back to previous versions (where possible, newly defined types need to be related back to types in earlier versions of the classification);
- accommodate limited data and available technology
- provide the basis for developing functional links between underlying mechanisms structuring the ecosystem and the described biological community.

However, given the unique environmental conditions and vast spatial scales occupied by deep-sea ecosystems, it is not surprising that the emphasis to date has been on defining largely physical classification schemes. In a study of the benthic environment of the deep sea off south eastern Australia, Williams et al. (in review) applied the hierarchical scheme of Greene et al., 1999 to define 7 levels of habitat type, each described in relation to mapping by scientific survey, use by its fauna and commercial fishing, and for the implications of these attributes for marine resource managers (see Table 1).

Table 1. Classification scheme modified after Green et al 1999, and Williams et al (in review) based upon deep-sea habitats off south east Australia.

Classification level	Habitat description	Spatial scale	Relevance to ecology, mapping, use and management
1. Province	Eastern province of south-eastern Australia large marine domain. Biogeographic Region	Provincial	Regional ecosystems delimited by biogeographic and physiographic features
2a. Biome	Continental slope (200-1,500m depth range)	Provincial	Primary division of regional ecosystems by physiography (especially depth) to broadly define distinct community types and physical environments
2b. Sub-biome	Upper continental slope (200-700m depth range)	Provincial	Secondary division providing depth boundaries for community structure, and composition of species and life history stages. Suites of species targeted by particular fishing methods/fleets
3. Major bio-geomorphological features	Canyons, Terraces, Seamounts, etc.	Large mega-habitat (10-100km)	Boundaries for local ecosystem structures and processes, e.g. topographic features, enhanced productivity, biological aggregations. Mapping of entire units using swath acoutics may be cost-effective. Large individual fishing grounds with multi-sector activity. Areas amenable to spatial management based on broadly defined goals
4. Primary habitat (biotope) facies	Elongate rocky banks interspersed with sediment patches (sloping flank of canyon). Patchy mosaic of mixed substrata: 'hard' and 'soft' seabed types (terrace). Sediment in large clear patches (terrace)	mega-habitat. (1-10km)	Habitat values defined by coarsely resolved physical attributes and associations with communities and individual species. Spatial extent (approximate boundaries) of general bottom types (textures) resolved by swath acoustics (acoustic facies). Differentiation of fishing grounds used by specific fishing sectors. Areas amenable to specific management goals, e.g. for fishery habitat
5. Secondary habitat (biotope) facies	Outcropping sedimentary claystones. Subcropping sedimentary claystones. Debris/rubble of cobble/boulder clasts. Debris/rubble of gravel/pebble clasts. Highly irregular calcareous muddy sands. Unrippled calcareous muddy sands.	meso-habitat (10m-1km)	Fine scale resolution of habitat boundaries/patch structure by 'ground-truth' targeted physical sampling of acoustic facies. Associations define essential fish habitat, e.g. for spawning, nursery, feeding, etc. Features known and targeted by individual fishers from particular sectors. Specific management goals set, and performance criteria evaluated based on monitoring at this level or lower
6. Primary biological facies	Based on video observations	macro-habitat (1m-10m)	Community dominants identified by targeted biological sampling. Fine scale resolution of community boundaries/habitat associations. Biodiversity distributions mapped. Impacts of fishing recognised in photographic images. Monitoring of fauna for management performance assessment
7. Secondary biological facies	Based on video observations	micro-habitat (<1m)	Precise role of habitat detailed. Impacts of fishing quantified. Monitoring of individual animal attributes such as density, size and growth rate

Indeed, the above classification has many similarities with that proposed by Global Opens Oceans and Deep Sea habitats bioregional classification group (GOODS) which recently prepared a report for the Convention on Biological Diversity Conference of the Parties in Bonn (May, 2008).

4. Major bio-morphological features (large mega-habitats)

4.1. Continental slope

Although the continental slope occupies only about 15% of the ocean floor it is nevertheless biologically the most productive habitat below the shelf (see Section 2.5) and is a major repository of organic carbon. Research carried out under the Hotspot Ecosystem Research on the Margins of European Seas (HERMES) project has revealed that open slopes are hotspots of biodiversity in which species richness is higher than that reported for bathyal and abyssal plain ecosystems. However, a unique, general driver capable of explaining the small or local-scale spatial patterns of biodiversity was not identified. This result is not surprising, considering the multiplicity of interactions among local ecological characteristics, environmental factors, and sedimentological conditions (i.e., mud, sand, gravel, rock, or a combination of either) in each specific slope environment. This complexity probably has considerable influence on the conditions, allowing settlement of a high number of species. The patterns of deep-sea biodiversity along the slope are different from those hypothesized so far, drawing a mosaic of life more complex and varied than previously imagined (Danovaro et al., 2009).

4.2. Seamounts

There are up to 100,000 seamounts in the world’s oceans with an elevation greater than 1,000m (Wessel, 2001). However, smaller features are significant in terms of their influence on species distribution and abundance. As a result, a new definition of seamounts has been accepted recently by biologists: “protruding irregularities or bottom features that rise greater than 100m from the sea floor” (Rowden et al., 2005). Studies have suggested that the biodiversity of seamounts can be high and that there is a high level of endemism associated with them (De Forges et al., 2000). In the southwestern Pacific ocean, for example, up to a third of species sampled from seamounts have been new to science and even adjacent seamounts appear to have quite different communities of species. In some cases, the high diversity of species is associated with fragile cold-water corals reefs. To date, the most diverse group of organisms found on seamounts are corals belonging to the Scleractinia (stony corals), Octocorallia (gorgonians), Antipatharia (black corals), Stylasterida (hydrocorals) and Zoantharia (zoanthids) (Rogers, A. Deep-sea biodiversity: a quick guide). Analysis of the distribution of corals on seamounts has shown that the distribution of the main groups is significantly affected by depth. It has also revealed that several areas in the world have a high diversity of corals on seamounts, including the southwestern Pacific, the northeastern Pacific and the North Atlantic. However, sampling strongly influences this dataset and high diversity in the North Atlantic is probably a result of comparatively large study effort in this area. It is notable that the distribution of corals on seamounts does not reflect the overall global distribution of many coral species. Corals frequently are not sampled on seamounts in parts of the world where they occur in other habitats. This reflects the low overall sampling effort, especially in some localities, but also suggests that the distribution of organisms on seamounts is strongly influenced by the physical characteristics at a particular locality and that seamounts may operate like submarine islands.

The high diversity and abundance of organisms on and around seamounts is thought to result from increased primary productivity resulting from localised upwelling of nutrients into the photic zone, combined with processes such as trapping of plankton by the seamount itself (i.e., trophic focusing) (Rogers, 1994; Genin, 2004). Some species of fish spawn over seamounts, including orange roughy and the Japanese eel. As a result of increased food abundance, seamounts are a focus of activity for large ocean predators like sharks and tuna fish. Due to the larger populations of fish in these areas relative to their surroundings, overexploitation by the fishing industry has caused some seamount populations o fish and of other coral-associated species to decrease considerably.

The Global Census of Marine Life on Seamounts website[2] has information and links to resources on seamount biology. Seamounts Online[3], a web-based information system for seamount biology, holds data on species that have been recorded from seamounts.

4.3. Hydrothermal vents, hydrocarbon seeps & other reducing habitats

Hydrothermal vents and hydrocarbon seeps have very specialised faunas, characterised by low biodiversity but very high endemism. The animal communities in these habitats are driven by chemosynthesis, the bacterial oxidation of hydrogen sulphide or methane. These habitats cover very small areas of the seabed and are located along mid-ocean ridges or back-arc basins (hydrothermal vents) or along continental margins (seeps). Specialised animal communities occur in the deep sea around these habitats and are not typical of shallow-water vents and seeps. These habitats have now been found all over the world and it is likely that many more will be discovered. Some similarities exist between the fauna of seeps and that associated with the breakdown of whale carcasses.

The primary production at hydrothermal vents is generated by bacteria through chemosynthesis. The bacteria are chemoautotrophic and tend to be members of the most ancient group, the Archaea. At hydrocarbon seeps, the source of energy is methane-rich fluids of thermogenic and/or biogenic origin. Production of sulfide by sulfate reduction also plays an important role.

Since the first discovery of hydrothermal vents, more than 500 species have been identified around hydrothermal vents and seeps (Perry, 2009). Of these, about 95% have been new to science, among them the red tube-worm *Riftia* sp. (Vestimentifera) and the Archaea. Hydrothermal vent faunal assemblages tend to be dominated by molluscs, annelids, and crustaceans. Most other hard bottom habitats

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[2] Website: http://censeam.niwa.co.nz
[3] Website: http://seamounts.sdsc.edu

are mostly comprised of cnidarians, sponges, and echinoderms. A recent study by Zeppilli and Danovaro (2009) revealed that metazoan species found in proximity to a shallow-water hydrothermal vent were a subset of those inhabiting the surrounding sediments, but were characterised by lower abundances. The authors go on to hypothesise that the assemblages close to a vent are the result of colonization from adjacent areas.

Invertebrate diversity is significantly higher at seeps than at vents (Turnipseed et al., 2003). Lower diversity at vents may be a consequence of a greater physiological barrier to invasion at vents than at seeps. Diversity is lowest where spacing between vents is greatest, suggesting that risks of extinction as a result of dispersal-related processes may contribute to the pattern of diversity observed at vents.

Other reducing habitats such as cold seeps, whale falls or oxygen minimum zones also develop chemically-driven communities with similar species and physiology to the vent animals. Seafloor oxygen minimum zones typically occur between 200 and 1,000m depth and are found in the eastern Pacific, NW Pacific margin, Philippines area, Bay of Bengal, Arabian Sea and SW Africa beneath the Benguela current (Rogers 2000; Levin 2003). Despite very low oxygen concentrations, protozoan and metazoan life thrive in these ecosystems. The high concentrations of organic matter sustain dense populations of sulphide-oxidising bacteria (i.e., Begiattoa, Thioploca, Thiomargarita) and a low biodiversity but high density of protozoan and metazoan life. The main groups are foraminiferans, nematodes, ciliates, flagellates, polychaetes, gastropods and bivalves with specific adaptations, such us high concentrations of haemoglobins, large respiratory surfaces, small thin bodies, high concentrations of pyruvate oxydoreductases and presence of sulphide-oxidising symbionts (Levin, 2003).

Global species richness on whale carcass falls (407 species) is high compared with cold seeps and rivals that of hydrothermal vents, even though whale-fall habitats are very poorly sampled. Population-level calculations suggest that whale falls are relatively common on the deep-sea floor, potentially allowing macrofaunal species to specialise on these habitat islands; to date, 21 macrofaunal species are known only from whale falls and may be whale-fall specialists. Nonetheless, whale falls also share 11 species with hydrothermal vents and 20 species with cold seeps, and thus may provide dispersal stepping stones for a subset of the vent and seep faunas (Smith & Baco, 2003).

4.4. Canyons

Canyons are hotspot ecosystems on continental margins, characterised by a high biodiversity (Ramirez Llodra & Billet, 2006). These geological features are subject to vigorous currents and act as major pathways for organic carbon transportation, and fast down flux of organic matter from the land to the deep sea. Canyons contain a variety of substrata, such as hard rock walls and mobile sediments on the canyon floor that sustain complex ecosystems with a high degree of endemic species. Canyons are often the site of increased biological activity and are important hotspots for commercial species. This manifests as very abundant populations of a limited number of species and the occurrence of large marine predators such as whales.

The seabed within canyons is very heterogenous and different groups of animals live either on the exposed rock at the rim or in the sediment on the slopes and base. Typical rock-dwelling species are gorgonians, sponges and other filter-feeding organisms. On the sediment are found echinoderms, crabs and other mobile organisms. There are even giant single-celled organisms called xenophyophores living on the sediment at great depths. In certain parts of the canyons the rock exposure forms overhangs, underneath which are found communities of filter-feeding bivalves, such as oysters and an ancient invertebrate group called the brachiopods. Such spots are exceptionally biodiverse and contrast with other parts of the canyon where biodiversity can be very low (HERMES, 2007).

4.5. Ocean trenches

Hadal trenches remain one of the least understood habitats on Earth. Hadal trenches account for the deepest 45% of the oceanic depth range and host active and diverse biological communities. Species tend to be endemic to a single trench or group of trenches (Vinogradova, 1997). Species composition, density, biomass and diversity of hadal zones often contrast to that of the surrounding abyssal area. There is a general decrease in the abundance and biomass of organisms with increasing depth. Nonetheless, sampling campaigns in hadal trenches have revealed a diverse array of metazoan organisms consisting primarily of benthic fauna, such as fish, holothurians, polychaetes, bivalves, isopods, actinians, amphipods and gastropods. The richness of trench communities, thought to originate from the abyssal plains, also declines with depth, although the relative role of increased pressure versus other environmental correlates remains unresolved (Jamieson et al., in press).

The assemblages of benthic nematodes, harpacticoid copepods, kinorhynchs, polychaetes and gastrotrichs in the Atacama Trench are approximately one third smaller than their bathyal relatives, although the selective pressure(s) driving this response remain unclear. Meiofaunal dwarfism contrasts starkly with the gigantism noted for some trench-dwelling crustaceans, including amphipods, tanaids, mysids and almost all isopods. These species are larger than any other representative of the genus, and their unusually large size might be a response to ephemeral food resources, competition or predation.

The ‘carbonate compensation depth’ (CCD), the depth at which calcium carbonate (calcite and aragonite) supply equals the rate of solvation and below which no calcium carbonate is preserved, has been proposed as a physiological barrier to deep ocean colonisation. Calcium carbonate is widely used as a structural component by foraminiferans, corals, crustaceans and molluscs. The CCD range is 4,000-5,000m in the Pacific Ocean, but tends to occur at shallower depths towards higher latitudes. As carbonate solubility increases with increasing hydrostatic pressure, ossification becomes more difficult, explaining why ossified groups (e.g. ophiuroids and echinoids) tend to be replaced by softbodied organisms (e.g. holothurians, and soft and organic walled foraminifera) with increasing depth (Jamieson et al., in press).

5. Primary habitat (biotope) facies

5.1. Mud

By far the most common seabed sediment in the deep sea is mud, perhaps representing as much as 80% of the total sediment in the marine environment. Despite its apparently featureless nature, recent research has shown that deep-sea mud supports a previously unexpected wealth of biological diversity. It is quite possible that the majority of animal species on this planet live in deep-sea mud. Of the tens of millions of animal species that probably live on Earth today, it is likely that over 75% of them will be found on the deep-sea floor – although to date only aware of a tiny fraction of this diversity has been described.

Deep-sea sediments are primarily composed of clays or materials produced by living organisms, depending upon the numbers of animals in the overlying waters. Abyssal clay covers most of the deep-ocean floor. It accumulates very slowly (1mm per 1,000 years), and it is mostly made up of clay-sized particles from the continents, carried to the sea by wind and rivers and spread by currents. Materials derived from the remains of living organisms accumulate in different thicknesses and distributions. In very deep waters the sediment blanket may be thousands of metres thick. The study of these thick layers of deep-sea mud is often used to answer questions about climate change, as these sedimentary layers preserve a unique record of past change.

5.2. Sand

The sandier sediments are home to more abundant populations of megabenthos, such as the white stalked sponges. Other seabed habitats are also indicative of significant bottom water flows that result in the transport of fine sediments giving rise to sandy contourite deposits and barchan sand-dune fields (see Figure 2).

5.3. Rock

In areas subjected to significant bottom currents such as the foot of the Faroe Plateau, coarse sediments such as gravels, boulders and bedrock tend to dominate the seabed, which allows the attachment and development of larger sessile megabenthos communities predominantly made up of sponges and corals. The often-complex three-dimensional structure of these attached communities offers additional habitat for epibenthic and demersal organisms seeking shelter, food or aggregation landmarks (see Section 6).

5.4. Iceburg ploughmarks

In certain mid-latitutude locations of the NE and NW Atlantic there are areas on the upper part of the continental slope (at about 300-500m) that form bands known as the “iceberg ploughmark zone”. During glacial periods, grounding icebergs gouged furrows in the seabed turning coarser sediments (cobbles and boulders) aside in an action similar to that of a plough harrow. The action of bottom currents has subsequently, at least partially, infilled the furrows with finer sediments. These processes have acted to produce a complex, spatially heterogeneous, mosaic habitat that can repeatedly alternate from “piles of boulders” to open fine sediment areas. The coarse sediment (cobble and boulder) area can support diverse biological communities that exhibit significant local variation in their composition and abundance.

6. Biological Facies

6.1. Cold-water coral reefs

Cold-water coral reefs develop in areas where there is a combination of specific physical and biological characteristics, including the presence of hard substrates, the occurrence of specific water masses, and strong currents, bringing a rich food supply (Rogers, 1999; Freiwald et al., 2004). With such requirements, cold-water coral reefs tend to occur on the shelf break and continental slope around the world but are also found in fjords and on seamounts and banks (Rogers, 1999). Their distribution in the NE Atlantic, which appears to be a global hotspot for cold water corals, is shown in Figure 4 and Figure 5. As with tropical, shallow water reefs, a rich fauna of animals is associated with coldwater corals reefs. These animals are found on the living coral, on and in the dead coral framework and in the sediments associated with the coral reef. Over 1,300 species have been found associated with reefs formed by the coral *Lophelia pertusa* off the coasts of Europe (Roberts & Gage, 2003). On the seamounts south of Tasmania, reefs formed by the coral *Solenosmilia variabilis* are also associated with a rich fauna up to one third of which are new species (De Forges et al., 2000).

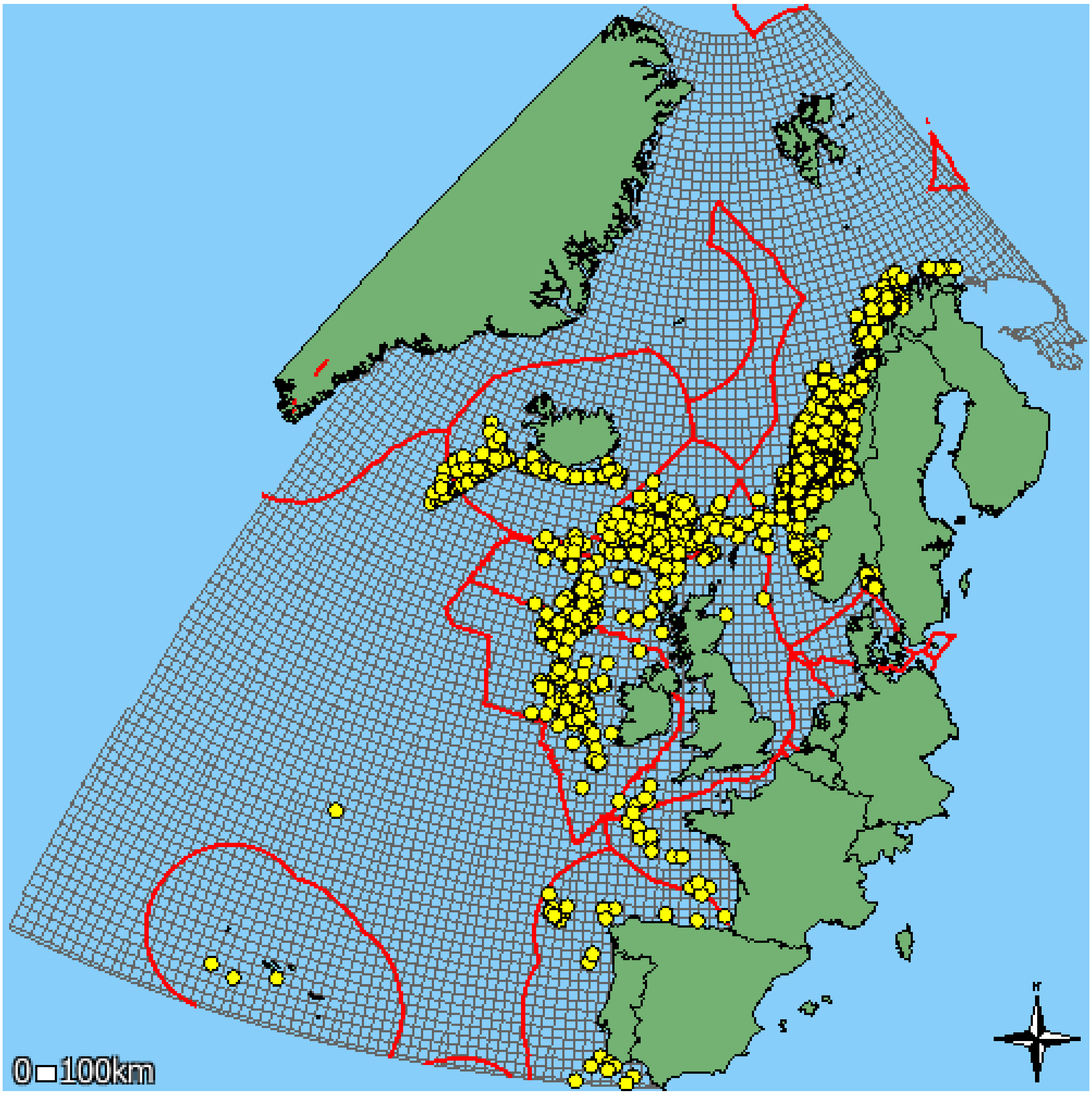

Figure 4. The distribution of cold water coral reefs (*Lophelia pertusa*) in the NE Atlatic.

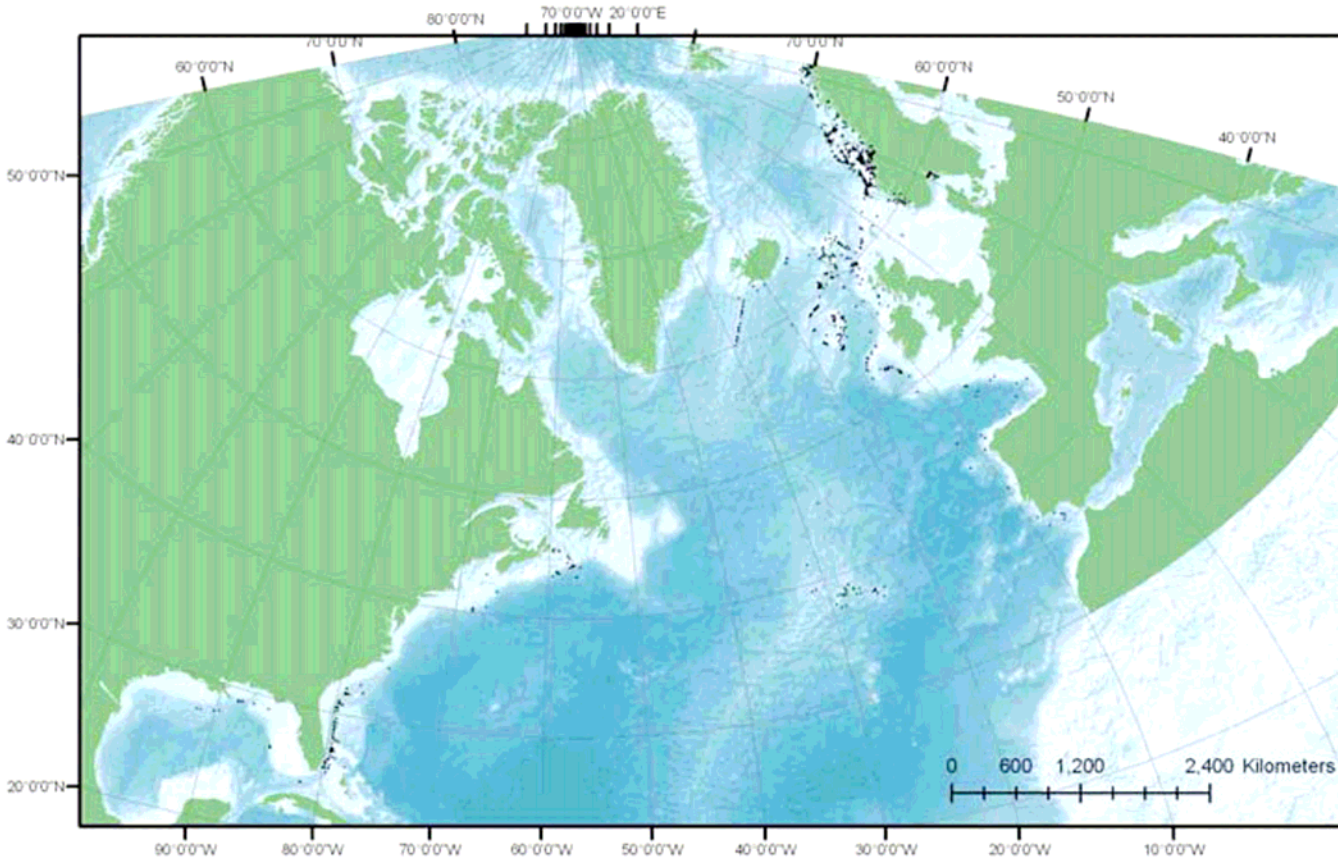

Figure 5. Occurrences of the reef forming scleractinian coral *Lophelia pertusa*.

Some groups of animals have a much lower diversity on *Lophelia* reefs than in tropical shallow water reefs including the reef-building corals themselves, molluscs and fishes. The majority of associated organisms are found in deep-sea habitats outside of the reef and only a few species appear to only live amongst *Lophelia* frameworks and not anywhere else. Deep-water coral reefs show other similarities with shallow-water tropical reefs. Many of the processes of reef growth (accretion) and destruction (erosion) are very similar between shallow and deep reefs. Many of the same groups of organisms, such as sponges and worms are involved in bioerosion of both shallow and deep-water reefs (Rogers, 2004).

Evidence for commensal relationships is sparse for deep-water reefs but these habitats are difficult to observe and have only been studied for a short time. One example of such an interspecies relationship has been identified between the reef-building coral *Lophelia pertusa* and a large, predatory, tube-dwelling polychaete worm called *Eunice norvegicus*. These worms build paper-like tubes amongst the branches of the reef and the corals secrete calcium carbonate that solidifies around the tubes providing protection for the worms (Kaszemeik & Freiwald, 2002; Roberts, 2005). The worms in turn are extremely aggressive and will attack predators such as sea urchins that approach the living parts of the corals. The worms may also steal food from the coral polyps (kleptoparasitism). There is even evidence that the worm tubes may act as a substrate for the settlement of coral larvae. These worms are found associated with *Lophelia pertusa* wherever it forms reefs in the NE Atlantic.

Lophelia pertusa also acts as a nursery area for many juvenile animals. This includes the juvenile stages of commercially valuable fish species such as redfish (*Sebastes* spp). Damage to deep-water corals reefs can effectively destroy these nursery grounds potentially having marked knock-on effects on the surrounding ecosystem.

Lophelia has also been reported growing on active oil platforms and on the decommissioned Brent Spar platform (Bell and Smith, 1999). An inshore reef complex has recently been mapped in the entrance to the Sea of Hebrides and there are many records of *Lophelia* on the Rockall Bank. Recently, the North East Atlantic Fisheries Commission prohibited bottom trawling and fishing with static gear from a number of large areas in the Rockall and Hatton banks (www.neafc.org), with the aim to protect deep-water corals.

The other deep-water area to receive protection (trawling ban) is the *Darwin Mounds* region, inhabited by deep-water corals as well as very delicate giant protists (xenophyophores), which can grow to sizes of 20cm or more (Hughes et al., 2003; Masson et al., 2003).

6.2. 'Coral garden'

The main characteristic of a coral garden is a relatively dense aggregation of colonies or individuals of one or more coral species. Coral gardens can occur on a wide range of soft and hard seabed substrata. For example, soft-bottom coral gardens may be dominated by solitary scleractinians, sea pens or certain types of bamboo corals, whereas hard-bottom coral gardens are often found to be dominated by gorgonians, stylasterids, and/or black corals (ICES 2007).

The biological diversity of coral garden communities is typically high and often contains several species of coral belonging to different taxonomic groups, such as leather corals (Alcyonacea), gorgonians (Gorgonacea), sea pens (Pennatulacea), black corals (Antipatharia), hard corals (Scleractinia) and, in some places, stony hydroids (lace or hydrocorals: Stylasteridae). However, reef-forming hard corals (e.g., *Lophelia*, *Madrepora* and *Solenosmilia*), if present, occur only as small or scattered colonies and not as a dominating habitat component. The habitat can also include relatively large numbers of sponge species, although they are not a dominant component of the community. Other commonly associated fauna include basket stars (Gorgonocephalus), brittle stars, crinoids, molluscs, crustaceans and deep-water fish (Krieger and Wing 2002). Krieger and Wing (2002) conclude that the gorgonian coral *Primnoa* is both habitat and prey for fish and invertebrates and that its removal or damage may affect the populations of associated species.

Densities of coral species in the habitat vary depending on taxa and abiotic conditions (e.g., depth, current exposure, substrate). The few scientific investigations available indicate that smaller species (e.g., the gorgonians *Acanthogorgia* and *Primnoa*, and stylasterids) can occur in higher densities, e.g. 50-200 colonies per 100m^2, compared with larger species, such as *Paragorgia*, which may not reach densities of 1 or 2 per 100 m^2. Depending on biogeographic area and depth, coral gardens containing several coral species may in some places reach densities between 100 and 700 colonies per 100m^2. These densities merely indicate the biodiversity richness potential of coral gardens. In areas where the habitat has been disturbed, by for example, fishing activities, densities may be significantly reduced.

It is not currently possible to determine threshold values for the presence of a coral garden as knowledge of the *in situ* growth forms and densities of coral gardens (or abundance of coral by-catch in fishing gear) is very limited, due to technical or operational restrictions. Visual survey techniques will hopefully add to our knowledge in the coming years.

Non-reef-forming cold-water corals occur in most regions of the North Atlantic, most commonly in water with temperatures between 3 and 8°C in the north, but also in much warmer water in the south (e.g., around the Azores). Their bathymetric distribution varies between regions according to different hydrographic conditions, but also locally as an effect of topographic features and substrate composition. They can be found as shallow as 30m depth in Norwegian fjords and down to several thousand meters on open ocean seamounts. The habitat is often subject to strong or moderate currents, which prevents silt deposition on the hard substrate that most coral species need for attachment. The hard substrate may be composed of bedrock or gravel/boulders, the latter often derived from glacial moraine deposition, whilst soft sandy/clay sediments can also support cold-water corals (mostly seapens and some gorgonians within the Isididae).

6.3. Gorgonian fields

Coral gardens are a heterogeneous type of deep-seabed habitat that could be divided into two or more habitats. Bamboo coral fields are one candidate, with stands of *Keratoisis ornata* or other Isidae corals on soft/sandy deep bottoms. Off Canada *Acanella arbuscula* seems to be a key habitat structuring species (Mortensen et al., 2006). In the Norwegian fjords Andfjorden and Hardangerfjorden, *Isidella lofotensis* have been observed in restricted areas in relatively high densities and with several associated species between the braches. Coral gardens also partly overlap with another threatened habitat, sea pens and burrowing megafauna, which should be kept separate from this habitat to avoid confusing comparisons.

6.4. Sponge aggregations

Demosponge aggregations, or '*osterbund*' as they are more commonly known, have been observed at mid-slope depths (c. 500m) north and west of Shetland, coinciding with iceberg ploughmark terrain (Bett, 2001) in regions where the currents are elevated and resuspension and transport of particles are enhanced (Klitgaard et al., 1995). The morphology of the sponges influences the occurrence and composition of the associated fauna, the majority of which use them as a substrate (Klitgaard, 1995; Figure 6). Unlike Demosponges, hexactinellid sponges form aggregations in areas of open sediment. The HMS '*Lightning*' and '*Porcupine*' research cruises in the late 1800s first observed hexactinellid sponge aggregations in the northern Rockall Trough (Thompson, 1873). More recent surveys have found hexactinellids to be a principal component of the megafaunal community at 1,000-1,400m in the SEA7 survey area NW Scotland (Hughes and Gage, 2004; Davies et al., 2006). They also occur in the Porcupine Seabight (southwest of Ireland) (Rice et al., 1990). Hexactinellid sponge aggregations create a very distinct habitat. Analysis of the abundance and taxonomic composition of the macrobenthos suggests the presence of sponge spicule mats at the sediment surface substantially modifies the fauna by increasing the numerical abundance of macrobenthos with increasing spicule abundance (Bett and Rice, 1992).

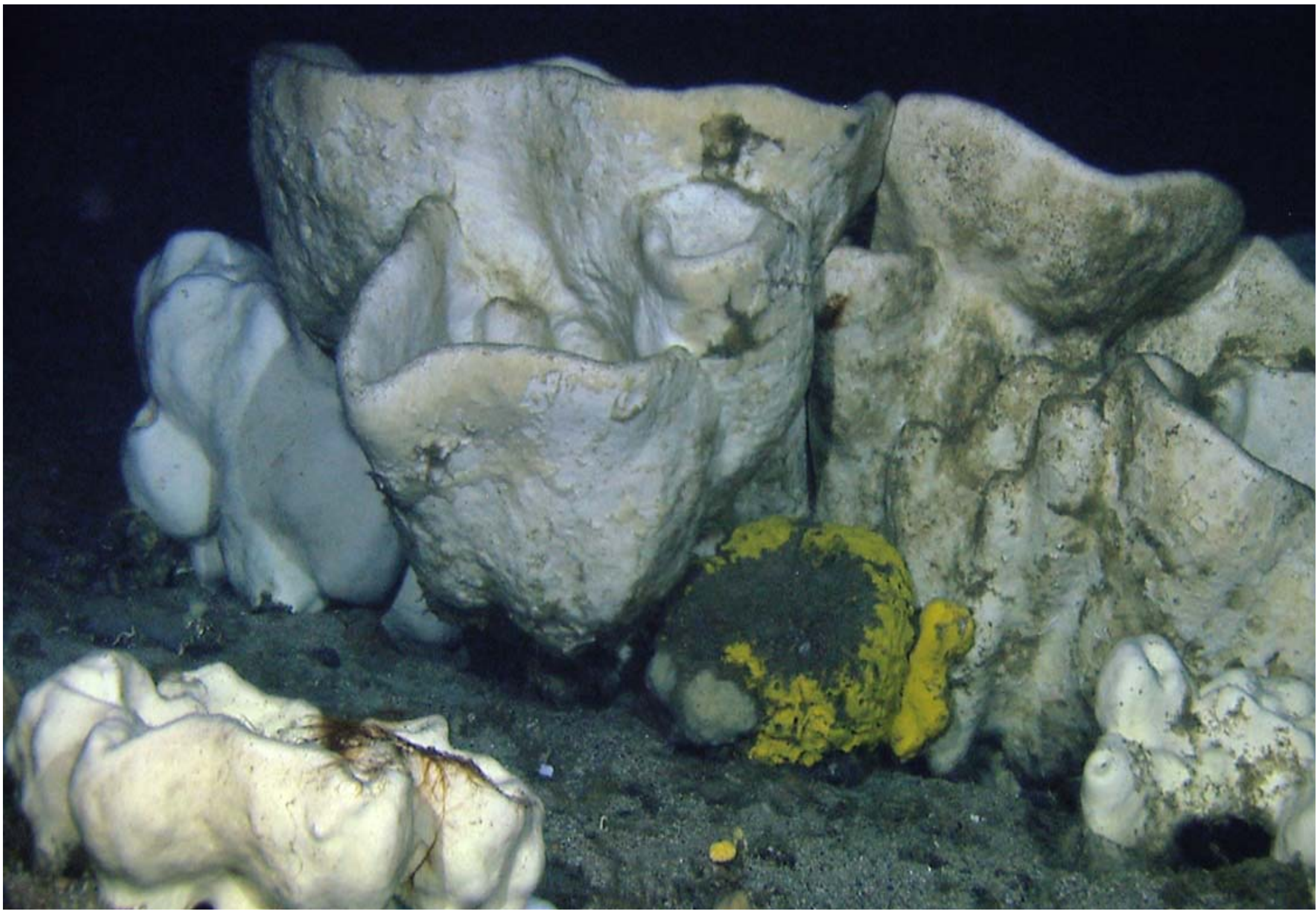

Figure 6. Geodia sp. dominating sponge grounds off the coast of Sørøysund, Finnmark, Northern Norway (photo courtesy of MAREANO/Institute of Marine Research). The yellow sponge in the foreground (*Aplysella sulphurea*) is growing over another species, *Stryphnus* sp.

The fauna associated with the sponge grounds is rich and has a higher diversity compared with surrounding sediments. The associated fauna are dominated by epifaunal groups such as encrusting sponges, hydroids, zoanthrians, bryozoans, and ascidians (Klitgaard, 1995; Klitgaard and Ten-dal, 2004). Rockfish, especially *Sebastes* species, live in openings and in between sponges. Young redfish (*Sebastes* spp.) are regularly observed on sponge grounds sometimes seeking shelter inside the cavities of large sponges. In samples taken using fishing gear there are often several species of groundfish represented, such as cod and ling, along with the sponges in the catch (Figure 7). The general co-occurrence of structure-forming invertebrates with groundfish has been described by Hixon et al. (1991) for three deep rocky banks off the coast of Oregon. In their study, species distribution and abundance varied by location based on differences in habitat availability between locations; for ex-ample, juvenile rockfish (*Sebastes* spp.) were most abundant in rock ridge and boulder habitat where sponges and the basket stars (*Gorgonocephalus eucnemis*) were the most common megafaunal invertebrates.

Figure 7. A large catch of *Geodia* sponges "ostur" from the continental slope off Norway at about 350 m depth. Photo courtesy of H.T. Rapp.

6.5. *Xenophyophora fields*

Xenophyophores are marine protozoans, giant single-celled organisms found throughout the world's oceans, but in their greatest numbers on the abyssal plains of the deep ocean. Xenophyophores are delicate organisms with a variable appearance. Most xenophyophora are epifaunal and bury themselves up to 6cm deep into the sediment. Xenophyophores may be an important part of the benthic ecosystem by their bioturbation of the sediments and by providing a habitat for other organisms.

6.6. *Actiniaria fields*

Late juvenile redfish *Sebastes fasciatus* (11–20 cm total length), have been reported being associated with dense patches of cerianthid anemones *Cerianthus borealis* in the Gulf of Maine (Fuller et al., 2008). The small fish may use the cerianthid habitats on an encounter basis or they may serve as a protective corridor for moving between boulder sites (Auster et al., 2003). Similar associations have been observed at greater depths during the MAREANO habitat mapping programme in 2008.

7. Biodiversity

For a detailed review of diversity metrics and the definition of biodiversity see ICES (2009), but the Convention on Biological Diversity[4] defines biodiversity as the variability among living organisms (e.g. number of different species). In simple terms, *biodiversity* is the number of species measured in a given area. The number of species is also referred to as *species richness*. Biodiversity can be much more comprehensive than just the number of species however; it can include genetic variation within species, the variety of species in an area, and the number of habitats within an area. *Species evenness*, or how well distributed abundance or biomass proportion are among species within a community, is also an important factor in assessing biodiversity. For example, when evenness is close to zero, it indicates that most of the individuals belong to one or a few species/categories which is less diverse than when the evenness is close to one, indicating that each species/categories consists of the same number of individuals.

However, it is evident based upon the limited review above, that species richness and productivity in the deep-sea exhibit very different spatial and temporal characteristics compared with the relatively shallow shelf sea systems. What is noteworthy is that within the deep sea, hotspots of higher biodiversity occur which also support higher rates of ecosystem processes such as productivity (Danovaro et al., 2008). For example, higher benthic diversity may increase bioturbation, (with a consequent increase of benthic fluxes and redistribution of food) and promote higher rates of detritus processing, digestion and reworking (therefore increasing organic matter remineralisation). This diversity may be related in part to the need for some deep-sea organisms to maximize what little organic carbon resources are available to them. Therefore, over time a functionally efficient and diverse benthic community evolves which actually enhances productivity. This is generally not the case in shallow shelf systems which by comparison are not energy limited and tend to be highly productive, usually dominated by relatively few species in terms of both biomass and numerical abundance. There is therefore an interesting relationship in the deep sea between productivity and diversity which should be further explored. Given this, it is clear that any anthropogenic effects which may negatively impact biodiversity in the deep sea are likely to have a negative impact on ecosystem function, possibly much more so than for shelf sea ecosystems. With this in mind, some further consideration of deep-sea ecosystem function and structure is provided below.

The most species-rich environments of the deep sea are associated with the surface and upper layers of the sediments that cover most of the deep-sea bed of the abyssal plain. The sediments are inhabited by species of animals belonging to a range of phyla, varying in size from single-celled protists to large sea cucumbers and urchins. The most diverse groups are the small animals including the tiny nematode worms, the segmented polychaete worms, molluscs, including bivalves and gastropods and peracarid crustaceans (Gage & Tyler, 1991). However, this does not take into account the density, frequency and spatial distribution of individual species

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[4] Website address: www.cbd.int

found in a given area. When such factors are taken into account (see ICES, 2009) a widely observed gradient in deep sea diversity is revealed. This is best highlighted by using data from ten years of standardized fish community surveys carried out by Fisheries Research Services (FRS) using the FRV Scotia. Diversity of the bentho-pelagic and demersal fish assemblage recovered using the Shannon Diversity Index (*H'*), as well as a descriptor of community relatedness, taxonomic diversity (Δ*) are shown in Figure 8 and Figure 9.

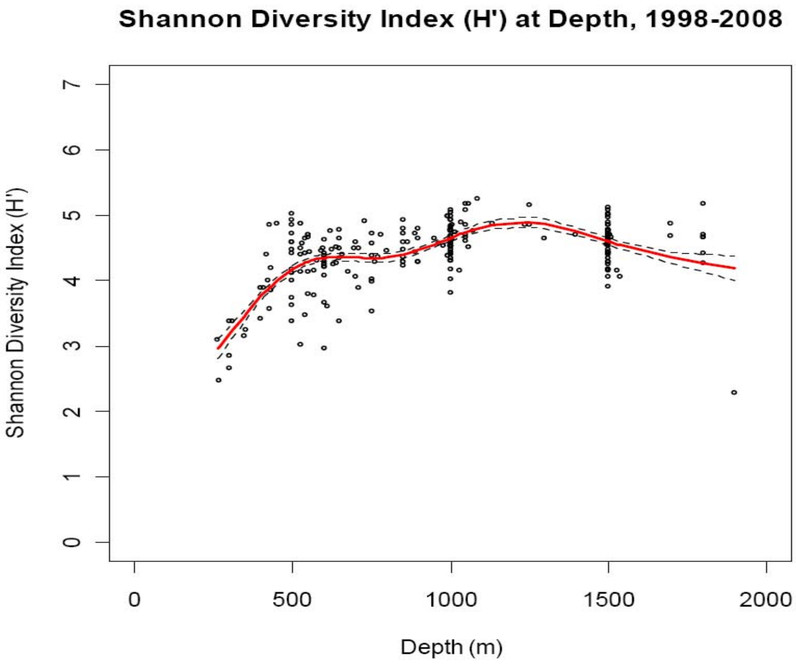

Figure 8. Fish community Shannon diversity with depth off NW Scotland (NE Atlantic, from ICES, 2009).

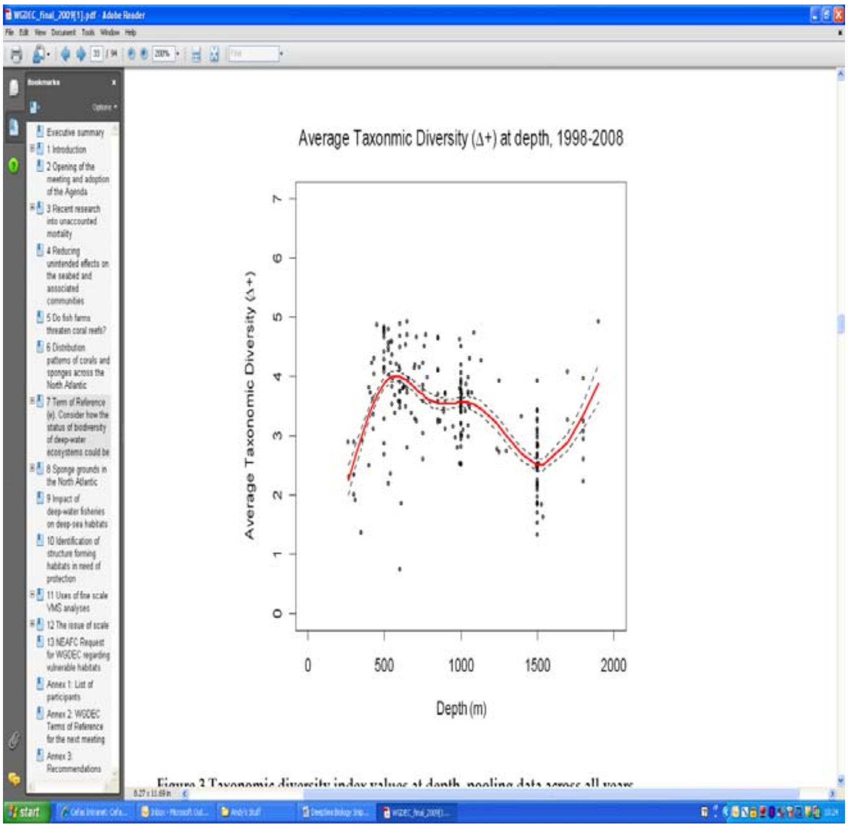

Figure 9. Fish community average taxonomic diversity with depth off NW Scotland (NE Atlantic, from ICES, 2009).

It has been suggested that the peak in the depth-related trend in taxonomic diversity around 500m relates to the overlap between shelf and slope ichthyofauna communities. Taxonomic diversity then decreases with depth until the abyssal species begins to appear in catches around 1,800m. Shannon diversity index values vary without any real trend with depth.

7.1. Ecosystem functioning

As already mentioned, ecosystem function involves the study and quantification of biological processes, which can be summarised as production, consumption and transfer of organic matter to higher trophic levels, decomposition of organic matter and nutrient regeneration (Naeem et al., 1994; Danovaro et al., 2008). Terrestrial and shallow-water ecologists have recognised that altering the composition of biological communities has a strong potential to alter ecosystem functioning; biodiversity loss may impair the functioning and sustainability of ecosystems (Solan et al., 2004; Hooper et al., 2005). A recent study of the relationship between ecosystem functioning and biodiversity in the deep sea has shown that a higher biodiversity supports increased efficiency and higher rates of ecosystem processes (Danovaro et al., 2008). It is argued that because the deep sea plays a key role in ecological and biogeochemical processes at a global scale, conservation of deep-sea biodiversity is necessary for the sustainable functioning of the World’s oceans.

7.2. Ecosystem structure

Ecosystem structure largely relates to the physical and spatial aspects of an ecosystem, for example, species population density, species diversity, physical structure and biomass, and by abiotic factors, for example, sediment structure and processes such as currents and the thickness of the benthic boundary layer. If a human activity has an impact on the structure of an ecosystem (for example, demersal trawling impacting deep-water coral reef habitats), this in turn may affect the functioning of that ecosystem, especially if there are no other species present in the community or ecosystem that are able to provide the same function.

8. Relationship between biodiversity, environmental conditions and fish

Deep-sea organisms experience far more stability in terms of water temperature, salinity and currents than do their shallow-water counterparts and may not tolerate even small changes in these environmental parameters. Individuals, populations and communities will be affected by local and regional changes in upper ocean primary productivity, organic-carbon flux and thermohaline circulation driven by climate change (Glover and Smith, 2003).

It has been shown that accumulations of large suspension feeders show a tendency to aggregate near the shelf break in regions with a critical slope where the bottom slope matches the slope of propagation of internal tidal waves (Klitgaard et al. 1997). Klitgaard et al. (1997) extended the theories of Frederiksen et al. (1992) for the distribution of *Lophelia pertusa* to explain the distribution of ostur. The causal link is thought to be an increase in the supply of food related to the incidence of internal waves which results in re-suspension and transport of organic material. However, Rice et al. (1990) noted that *P. carpenteri* is not found within the areas of enhanced current produced by the critical slope angle but is associated with them, the sponge being particularly abundant along their lower boundaries and downstream of these enhanced current regions. Again the increased food supply was cited as a possible reason, but clearly the mechanisms operating in this case are possibly different.

Furthermore, hydrographic conditions with elevated current speeds and high food supply, together with availability of hard bottom substrates are favourable for sessile suspension feeders, including cold-water corals. Corals (Antipatharia, Gorgonacea, Pennatulacea, Scleractinia, Stylasteriidae and Zooantharia) may occur in great abundance, especially along the edges and summits of topographic seabed structures such as banks or seamounts. It is therefore not surprising that deep-sea fisheries concentrate on such productive areas, such as seamounts and canyon walls, where levels of biodiversity and endemism in the benthic fauna can be high (De Forges et al., 2000) although the degree of endemism can be low on north Atlantic seamounts (Hall-Spencer et al., 2007).

In a study in the Bay of Biscay by Mendes (2003), significant associations were described between different deep sea fish species and the environmental conditions. Specifically, four different dive transects were analysed with respect to environmental characteristics from which a total of 19 fish groups were ordered by means of canonical correspondence analysis (see Figure 10). Their results revealed that macrofauna were dominated by a diversity of suspension feeders, indicating different gradients of bottom hydrology, particularly vertical and horizontal current flow conditions. Physical, geological and biological factors revealed different strategies of habitat selection in fish. The most represented species, the orange roughy (*Hoplostethus atlanticus*) showed a clear association with complex substrates, including coral reefs. Others, such as *Coryphaenoides rupestris* and *Synaphobranchus kaupi*, showed higher flexibility of adjustment to changing environments.

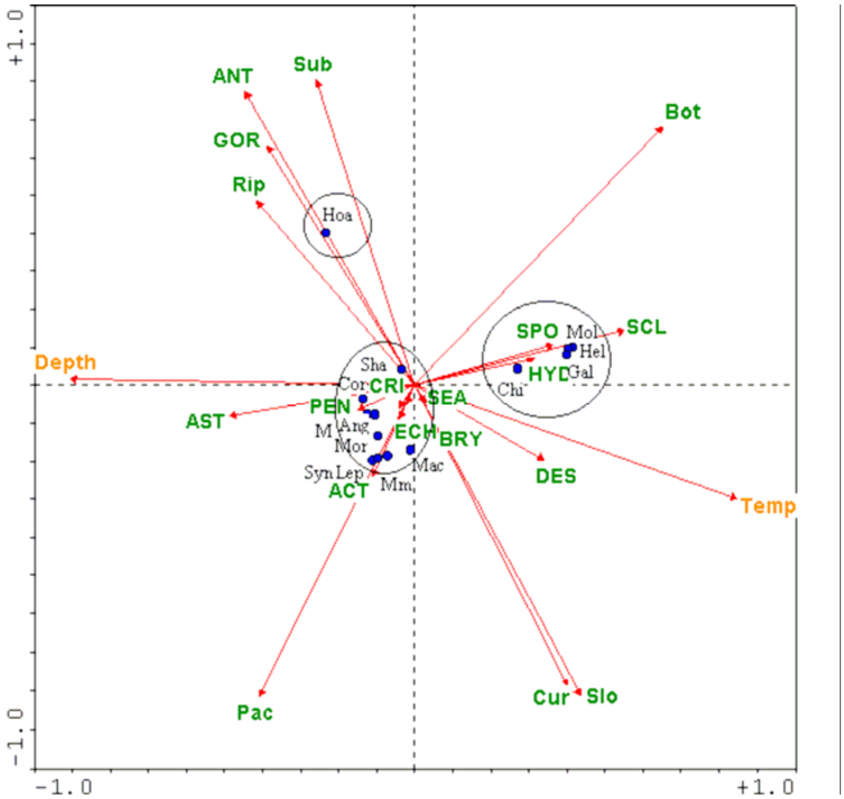

Figure 10. Canonical correspondence analysis (CCA) ordination diagram of all the dives with fish species (blue circles) and environment variables (arrows); first axis is horizontal, second axis vertical. The fish species are: Cor=Coryphaenoides rupestris, Ang=Anguilliformes, Lep=Lepidion eques, yn=Synaphobranchus kaupi, Chi=Chimaerids, Mac=Macrouridae, Sha=Sharks, Hoa=Hoplostethus atlanticus, Mor=Moridae, M=Mesopelagic fishes, Mm=Mora moro, Gal=Galeus melastomus, Mol=Molva molva, Hel=Helicolenus dactylopterus. The environmental variables are: ACT=Actinians, Temp=Temperature, PEN=Pennatularians, Depth=Depth, AST=Asteroidea, SPO=Sponges, Cur=Current, Rip=Ripple marks, Slo=Slope, Pac=Packing, HYD=Hydrozoans, CRI=Crinoids, Bot=Bottom texture, Sub=Substrate, DES=Desert, ANT=Antipatharians, GOR=Gorgonians, Cur=Current, ECH= Echinoids, BRY=Bryozoans, SEA=Sea cucumber, SCL= Scleractinians.

9. Indicators for ecosystem management

The abundance of ecosystem indicators under consideration has increased substantially over the last decade (see contributions in Cury and Christensen 2005) and, along with habitat classification schemes, the development of indicators of environmental status are an integral part in delivering an ecosystem approach to management (Rogers and Greenaway, 2005).

In general, an indicator can be defined as a parameter or value derived from a measure which provides information about the state of an environment (OECD, 1993), in this case, specifically identified habitat and biological facies. Indicators have two major functions:

1. They reduce the number of measurements and parameters normally required to give a precise characterisation of the environment – because something is already known about the properties of the habitat being monitored and assessed. However, too few or even a single indicator may be insufficient to provide all the necessary relevant information.
2. They simplify the communication process by which survey results are provided by the user.

Therefore, the selection of indicators has to be undertaken with a great deal of care and attention, particularly in understanding the functional/structural dependencies, since there is a risk that a vital piece of information may be missing from the indicator. To overcome this risk, in part, a more integrated habitat-based approach is being now favoured, that is a shift away from the specific conservation of a particular species to one of protecting the habitat which the species depends. Accordingly, the OSPAR Commission in 2005 has followed this approach through the recognition of "sponge aggregations" as habitats on their list of threatened and declining species.

Table 2. Possible indicators of deep sea habitat status based upon determination of overall habitat and biological facies extent and density – such as would apply to "sponge aggregations" as recognised by OSPAR.

Pressure (Impact)	Possible Indicators
Fishing - demersal trawling (habitat structure changes - abrasion; removal of target species)	– Biological facies extent and density (e.g., sponge aggregations, cold water coral reefs, coral gardens, etc.) – Mega (primary) habitat extent and biology (e.g., seamounts, reefs, slopes, etc.) – Evidence of trawl scars and impacts (extent and density)

Whilst these indicators provide an estimate of the status and trends in important & vulnerable benthic habitats, there is also a need to consider the status and trends of many other components of the ecosystem, including the human activities themselves.

From a fisheries perspective, a group was set up in 2005 called 'IndiSeas' under the auspices of the EUR-OCEANS European Network of Excellence (www.eur-oceans.eu). It aims were to evaluate the effects of fisheries on marine ecosystems by using a panel of ecological indicators of states and trends, and to facilitate effective communication of these effects, largely by using work already achieved by the SCOR/IOC Working Group 119 on "Quantitative Ecosystem Indicators", and specifically on the results of Rice and Rochet (2005) who outline some specific practical criteria for the selection of ecosystem indicators which were adopted by the SCOR-IOC Working Group, namely:

- ecological significance (i.e. are the underlying processes essential to the understanding of the functioning and the structure of marine and aquatic ecosystems?)
- measurability: availability of the data required for calculating the indicators
- sensitivity to fishing pressure
- awareness of the general public

The last of these criteria was of particular importance to the aims of the 'IndiSeas' WG, that is the awareness of the general public concerning the meaning (what information is communicated) of each indicator. For example, among potential size-based indicators, preference was given mean length rather than the slope of the size spectrum since this would be more difficult to communicate to the general public. In addition to these practical selection criteria, the indicators were selected to address four specific management objectives: Conservation of Biodiversity (CB), ecosystem Stability and Resistance to perturbations (SR), Ecosystem structure and Functioning (EF) and Resource Potential (RP).

Several categories of ***ecological indicators*** were distinguished (Cury and Christensen 2005): namely; **i**. size-based, **ii**. species-based, and **iii**. trophodynamic indicators. The eight indicators outlined in Table 3 (described below) were selected based on the above criteria, and are proposed as a minimum set of indicators for diagnosing the status of an ecosystem in relation to fisheries pressure. Six of the indicators were used to measure the state (S) of the ecosystem and six were used to measure trends (T) over time. Data for the indicators are derived primarily from fisheries independent surveys and commercial fisheries data, with auxiliary information where indicated. In addition to the full indicator name, a shorter "headline label" was attributed to each of the indicators (Table 3) to make them more readily comprehensible. Furthermore, the indicators are all formulated positively so that a low value of an indicator means a high impact of fishing and a high value a low impact of fishing

Total biomass of surveyed species is a conservative property of an ecosystem; as species are fished and their biomass reduced, other species increase in abundance and "replace" these species in the foodweb. With the removal of top predators lower trophic levels can be expected to increase. Thus changes in total biomass can reflect changes in ecosystem productivity. ***1/(landings /biomass)*** measures the inverse level of exploitation or total fishing pressure on the ecosystem. This indicator varies in the same direction as the other indicators in the selected suite, as it decreases when fishing pressure increases. A decrease is considered negative and is a measure of "resource potential". ***Mean length of fish in the community*** is an indicator of the impact of fishing on an ecosystem, that is, the reduction of mean length of fish in the community (Shin et al. 2005). From a single species perspective, the removal of larger fish, which are more fecund and produce more viable eggs than smaller fish (Longhurst 1999), compromises productivity. From an ecosystem perspective, the removal of larger species changes the size structure of the community and potentially ecosystem functioning. “Fish size” is thus a measure of ecosystem structure and functioning and is used to measure state and trend. ***Trophic level of landings*** measures the average trophic level of species exploited by the fishery, and is expected to decrease in response to fishing, since fisheries tend to target higher trophic level species (Pauly et al. 1998). A decrease in trophic level of landings and total catch indicates “fishing down the food web” (Pauly et al. 1998), and a change in the structure of the community and potentially ecosystem functioning. “Trophic level” is a measure of ecosystem structure and functioning and is used to measure state and trend. Trophic level of individual species is either estimated through modelling, or taken from global database such as Fishbase. ***Proportion of predatory fish*** is a measure of the diversity of fish in the community. Predatory fish are all surveyed fish species that are piscivorous, or feeds on invertebrates that are larger than 2 cm. “% predators” is a measure of conservation of biodiversity and is used to measure state and trend. ***Proportion of under and moderately exploited stocks*** represents the success (or not) of fisheries management. Ideally, in a precautionary world, all stocks should be moderately exploited to ensure sustained biodiversity and sustainable ecosystems. “% of sustainable stocks” is a measure of conservation of biodiversity. The FAO classification of stocks as underexploited, moderately exploited, fully exploited etc (*http://www.fao.org/docrep/009/y5852e/Y5852E10.htm#tbl*) was used to define these categories for the stocks in each ecosystem under consideration in the current time period. Thus this indicator is used to compare the state of ecosystems. ***Mean life span*** is a proxy for mean turnover rate of species and communities, and is meant to reflect the buffering capacity of a system. The life span or longevity is a fixed parameter per species, and therefore the mean life span of a community will reflect the relative abundances of species with differential turnover rates. Fishing affects the longevity of a given species (direct effect of fishing and genotype selection), but the purpose here is to track changes in species composition (same principle as for mean TL of catch). “Life span” is thus a measure of ecosystem stability and resistance to perturbations and is used to measure state and trend. ***1/Coefficient of variation of total biomass*** measures the stability of the ecosystem, and is measured as the coefficient of variation (CV) over the last 10 years. As with “fishing pressure”, it is expressed as an inverse to make it conform with the directionality of the other indicators. Thus a low 1/CV indicates low “biomass stability”, low ecosystem Stability and Resistance to perturbations. Since this indicator is measured over a 10 year time period, it is only used to measure state.

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Table 3. List of indicators from the ‘IndiSeas’ WG for assessing the status of marine ecosystems in relation to fisheries pressure.

Indicators	**Headline label**	**Calculation, Notations, Units**	**(S)tate, (T)rend**	**Expected Trend**	**Management Objectives**	**Management Direction**
Total biomass of surveyed species	biomass	B (tons)	T	D	RP	Reduction of overall fishing effort and quotas
1/(landings /biomass)	inverse fishing pressure	B/Y retained species	T	D	RP	Reduction of overall fishing effort and quotas
Mean length of fish in the community	fish size	$\overline{L} = \frac{\sum_i L_i}{N}$	S,T	D	EF	Reduction of overall fishing effort and fishing effort on large fish species
TL landings	trophic level	$\overline{TL}_{land} = \frac{\sum_i TL_i Y_i}{Y}$	S,T	D	EF	Decrease fishing effort on predator fish species
Proportion of under and moderately exploited stocks	% sustainable stocks	number (under+moderately exploited species)/total no. of stocks considered	S	D	CB	Decrease fishing effort on overexploited species. Diversify resource composition
Proportion of predatory fish	% predators	prop predatory fish= B predatory fish/B surveyed	S,T	D	CB	Decrease fishing effort on predator fish species
Mean life span	life span	$\frac{\sum_s (age_{max} B_s)}{\sum_s B_s}$	S,T	D	SR	Decrease fishing effort on long-living species
1/Coefficient of variation of total biomass	biomass stability	mean(total B for the last 10 years) /sd(total B for the last 10 years)	S	D	SR	

10. Ecosystem Approach to Fisheries Management

In 2000, the ICES Advisory Committee on Fishery Management (ACFM) expressed the view that most deep-water species in the ICES area are, at present, harvested outside safe biological limits as embodied in the precautionary approach (Anon., 2000). They indicate that the level of exploitable biomass in 1998 of orange roughy*,* black scabbardfish*,* roundnose grenadier, deep-water sharks (principally the leafscale gulper shark *(Centrophorus squamosus)* and the Portuguese dogfish *(Centroscymnus coelolepis)* and blue ling *(Molva dypterygia)* were below the precautionary reference level and, for some species, they were close to or possibly below the precautionary limit point, an observation also supported by Basson et al (2001). This advice came at the same time as increasing global political commitments to adopt ecosystem-based fisheries management (EBFM) , to ensure that the planning, development, and management of fisheries will meet social and economic needs, without jeopardizing the options for future generations to benefit from the full range of goods and services provided by marine ecosystems (FAO, 2003).

Specifically, the U.N. Convention on Biological Diversity defined Ecosystem-Based Management (EBM) as: *"…an approach based upon the application of appropriate methodologies focused on levels of biological organization which encompass the essential processes and interactions among organisms including humans and their environment*". Similarly, the U.S. Commission on Ocean Policy noted that *"U.S. ocean and coastal resources should be managed to reflect the relationships among all ecosystem components, including human and nonhuman species and the environments in which they live. Applying this principle will require defining relevant geographic management areas based on ecosystem, rather than political, boundaries."* Other definitions of EBM embody the recurring themes of the need to understand and account for interactions among the parts of the system, the recognition that humans are an integral part of the ecosystem, and that EBM is fundamentally a place-based management framework.

In 2008 the Northwest Atlantic Fisheries Organisation established an expert scientific working group with the explicit aim of identifying the methods and practices to best implement the Ecosystem Approach to Fisheries Management (EAFM). It was recognised by WGEAFM that the implementation of the ecosystem approach to fisheries management requires ecosystem assessments that are essentially the counterparts of stock assessments currently used in support of conventional single-species stock assessments, but with the 'key' difference that they consider all relevant components including multiple fish stocks. The EAFM is also included as a concept in the Common Fisheries Policy as set out in Article 2(1) of the CFP reform in 2002.[5]. In this case it is clear that the CFP is not, itself, based on the EAFM, but rather that it is aiming at its progressive implementation. A clear problem for the CFP in this regard is that its decisions (e.g. on MSY etc.) tend to be based on

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[5] Regulation (EC) No 2371/2002 of 20 December 2002 on the conservation and sustainable exploitation of fisheries resources under the Common Fisheries Policy.

individual stocks rather than multiple species harvesting which would be necessary if the ecosystem as a whole were to be considered.

For this purpose, Integrated Ecosystem Assessments (IEA) have been defined as: *'a synthesis and quantitative analysis of information on relevant physical, chemical, ecological, and human processes in relation to specified ecosystem management objectives'* (Levin *et. al*. 2009). Integrated Ecosystem Assessments are designed to meet multiple objectives and they can be considered as a tool, a product, and a process. They are a tool that uses integrated analysis and ecosystem modeling for synthesis. IEAs are product for managers and stakeholders who rely on scientific support for policy and decision making. Finally, IEAs are a process including the identification of management objectives by managers and stakeholders, the development of quantitative assessments, and the evaluation of alternative management strategies.

The steps involved in the development of an IEA are depicted in Figure 11*,* which begins by scoping and identifying the goals and objectives, but EBFM requires managers to take account of how fisheries impact a wide range of marine ecosystem components when setting their ecosystem objectives (Heslenfeld and Enserink, 2008). To achieve such objectives, the mechanistic relationships between the state of these components or attributes and one or more manageable anthropogenic activities needs to be understood (Jennings, 2005). Therefore, for scientists charged with the provision of advice in support of EAFM, determining the theoretical, mechanistic links between state and so-called pressure indicators often poses the greatest challenge (Greenstreet, 2008). To implement an EAFM successfully, therefore, it is not only necessary to have a suite of indicators that accurately portray the "state" of various ecosystem components (see section 9), but it is also critical to have indicators that describe changes in the level of different manageable human activities. Only by adequately covering both aspects will the mechanistic links between "cause" and "effect" be well enough understood to provide the advice required (Daan, 2005).

In order to provide some transparency in quantifying the many potential and actual interactions between ecosystem components interaction tables which define the relationships between human activities (pressures) and ecosystem state (state changes) have been developed (see *indicators* special edition of ICES Journal of Marine Science 2008). The distinction between using such tables to identify significant interactions between human activities (pressures) and ecosystem components is important and valuable particularly in relation to identifying appropriate levels of monitoring, but this is not widely appreciated. Although the approach is useful and significant, it is only one piece of the framework. Indeed, the approach has some limitations in that not all relevant and significant interactions between components are described. A more realistic, and arguably ecosystem relevant, approach would be to consider and examine all the interactions between relevant components in the form of a triangular matrix (Figure 12). Such a matrix allows the components which contribute to both thematic and sectoral assessments to visualised at the same time.

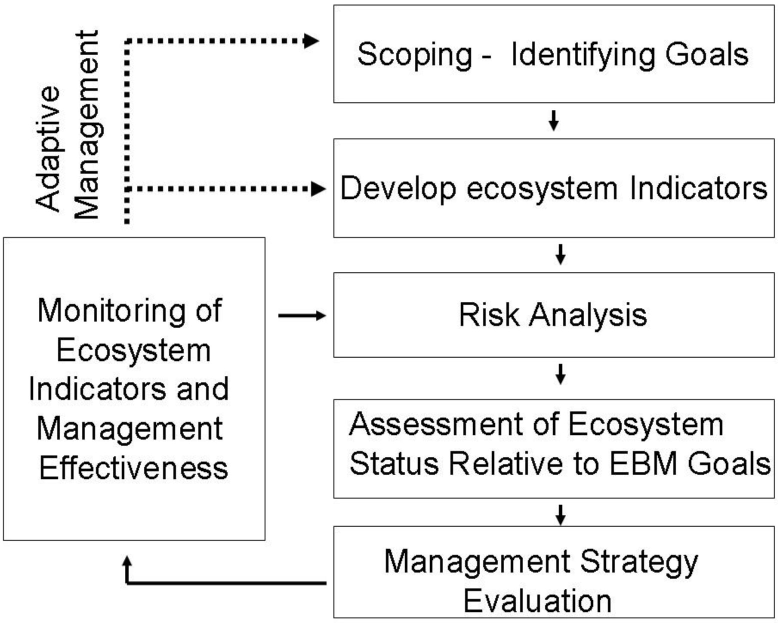

Figure 11. (from Levin *et al*. 2009). A Five-Step Process of Integrated Ecosystem Assessment. An IEA begins with a scoping process to identify key management objectives and constraints, identifies appropriate indicators and management thresholds, determines the risk that indicators will fall below management targets, and combines risk assessments of individual indicators into a determination of overall ecosystem status. The potential of different management strategies to alter ecosystem status is evaluated, and then management actions are implemented and their effectiveness monitored. The cycle is repeated in an adaptive manner.

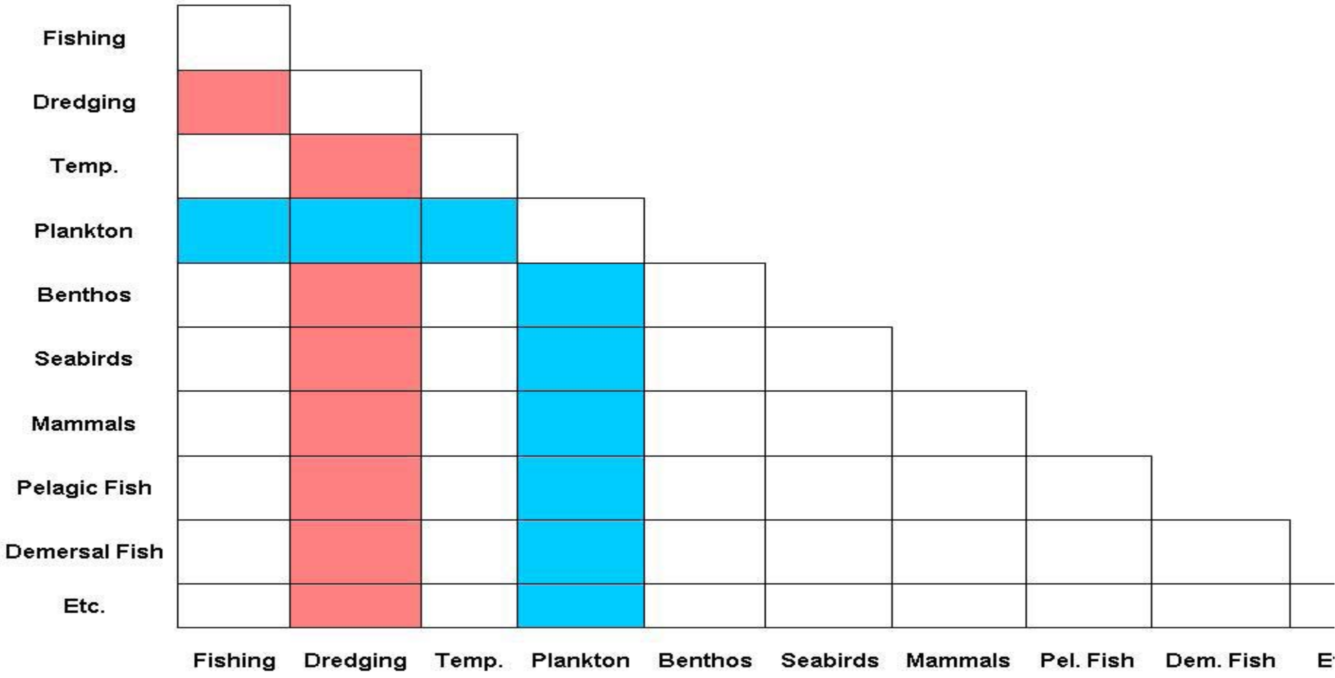

Figure 12. Example of a matrix approach used to describe the relationship or degree of interconnection between human pressures (sectoral activities such as fishing) and ecosystem components (such as benthos). The specific interactions between all sectors and ecosystem components can be readily observed. For example, the specific interactions (as impacts) between dredging and all other components of the system can be documented (highlighted in red), this would be an example of a sectoral or sector specific assessment. In addition the interactions between plankton and all other ecosystem components, including sectoral pressures, can be evaluated and this would be described as a thematic assessment.

In considering the development of an EAFM in the NAFO region WGEAFM highlighted the following pragmatic approach being developed in the Northeast United States as showing some promise , namely: (1) the identification and definition of ecological subunits on the shelf, based on an analysis of physiographic, oceanographic and ecological variables, (2) the implementation of a spectrum of different multispecies and full ecosystem models which can be used to assess ecosystem temporal state and function, particularly of higher order variables such as primary productivity and total biomass, and (3) an evaluation of the management options using existing management tools for specifying ecosystem exploitation rates.

Furthermore, there is an explicit and pragmatic relationship between the application of an IEA and the steps for implementing EAFM for any given spatially defined marine ecosystems subject to fisheries management (Figure 13).

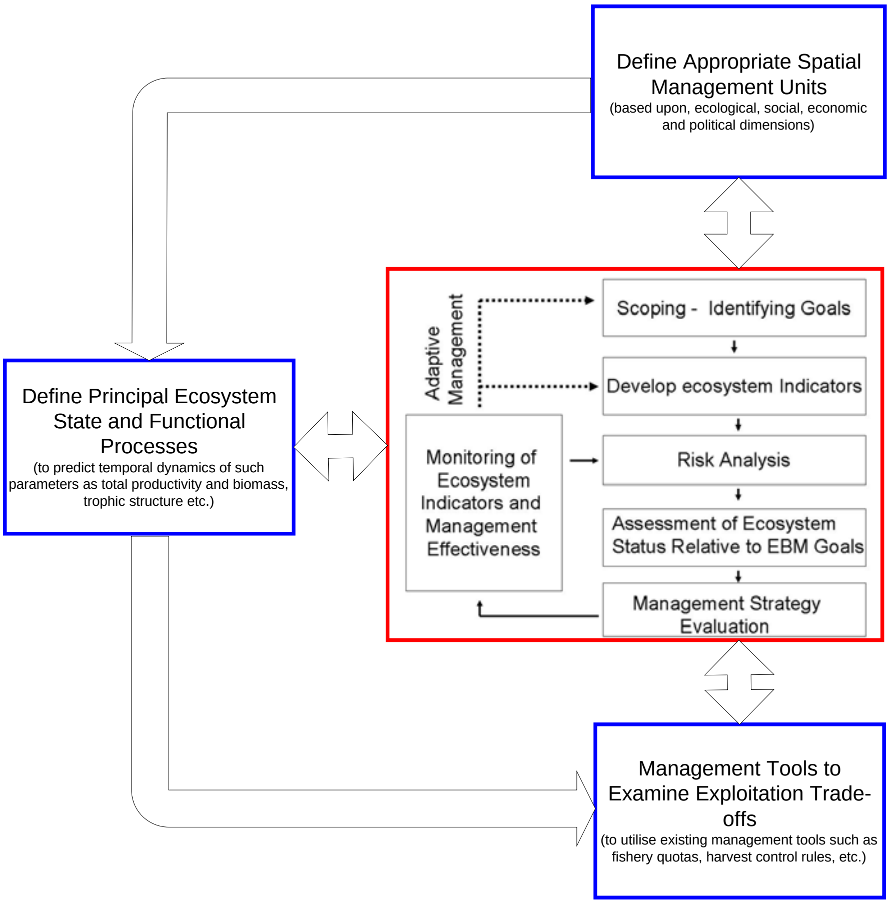

Figure 13 The relationship between the 3 practical steps in moving towards the implementation of an ecosystem approach to fisheries management (blue boxes) and the steps required to deliver effective holistic integrated ecosystem assessments (IEA) shown in the red box.

10.1. Defining Appropriate Spatial Management Units

The specification of spatial management units is a critical pre-requisite to the development of effective ecosystem approaches to management in both the shelf and deep sea ecosystems. In general defining spatial management units requires mapping areas of the seabed in order to define the most biologically productive, diverse and human exploitable (resourceful) habitats. The spatial mapping and assessment of seabed is well established for the relatively shallow and well mixed shelf marine ecosystems, but the approaches and assessment methods deployed in the relatively shallow (<100m) photic seas are not likely to be the most appropriate methods for application in the deep sea environment. In addition, by developing effective predictive and observational methods to identify the most biologically sensitive (diverse) and productive habitats of the deep sea, it is likely that the most potentially productive fisheries will be identified. In this respect it is likely that the geology, sedimentology, hydrography and the presence of chemosynthetic sources of primary production are likely to be the most important factors in mapping out such areas in the deep sea environment. Furthermore, there is a need to identify such Vulnerable Marine Ecosystems (VMEs) and to protect them (in part) from the adverse effects of human activities. The type, area, and number of areas which should be protected in the deep sea is a complicated task influenced by many factors, but in general the degree of protection a reserve can offer to a species can be assessed by its dispersal capability and how restricted the species is to a particular site (Kenchington, 1990). Species with low dispersal that are restricted to small areas are likely to be well protected by small reserves. However, highly mobile species may require extremely large reserves to provide adequate protection. Some estimates suggest that 50–90% of the total utilised habitat is needed (Clark, 1996; Lauck et al., 1998). The initial theory behind designing marine protected areas was developed for terrestrial systems and adapted for the coastal realm (Soule´ and Terborgh, 1999; Carr et al., 2003).

In addition, it has been suggested that the impacts of fishing on the lower parts of many shelf ecosystems could be having an indirect, but significant, impact on deep sea ecosystems by virtue of many deep sea fish species having large vertical (depth) distributions (Bailey et al., 2009). As many of the fishes whose abundances have declined in deep water shelf areas also include the apex predators in deep sea habitats, ecosystem-level changes are possible, but the relative importance of predator pressure in structuring deep-water communities remains unclear (Bailey et al. 2006). The possible vulnerability of deep-water communities to impacts, which are occurring in shallower waters, implies that proposals for future deep-water marine protected areas are likely to be of limited effectiveness unless fleet fishing effort is controlled in the surrounding (including shallower) areas.

10.2. Defining Ecosystem State and Functional Processes

A wide range of analytical methods should be employed (including a range of model types) to define and understand the principal dynamic properties of the spatially defined ecosystem. In terms of the models available these can be classified in increasing order of complexity as:

- Fishery Production Potential Models
- Aggregate-Species Surplus Production Models
- Multispecies Production Models (e.g. Lotka-Volterra models)
- Size Spectrum Models
- Ecosystem Network Models (e.g. EcoPath)
- Age/Size Structured Multispecies Models (e.g. Multispecies Virtual Population Analysis)
- Dynamic Ecosystem Models (e.g ATLANTIS)

The models differ not only in complexity but along a continuum from holism to reductionism (with the models classified as embodying higher levels of complexity also incorporating higher levels of structural detail. The choice of appropriate models depends on the specific objectives of the analysis and factors such as the interplay between model complexity and parameter uncertainty. In the NAFO region attention is being focused in the use of the first two of these approaches to estimate the productive capacity (or carrying capacity) of the system for a given set of environmental/climate conditions. The fishery production potential models trace the flow of energy from primary producers through to the harvested components of the system.

The aggregate-species surplus production approach was actually first used in NAFO's predecessor institution, ICNAF, to generate estimates of system-wide maximum sustainable yield for the Northeast U.S. Continental Shelf. This early analysis showed that the estimate of system-wide MSY was approximately 30% lower than the result obtained if estimates from individual species stock assessments were simply summed. It was inferred that interactions among species meant that all species could not simultaneously be at biomass levels resulting in MSY (B_{msy}). These models also provide estimates of the level of fishing mortality that results in MSY (F_{msy}) and these estimates are also lower for the aggregate species model than for most of the individual species F_{msy} levels.

The basic conclusion emerging from initial results suggests that there are important constraints on available energy must be considered in setting harvest policies at an ecosystem level and in the deep seas estimating this accurately over space and time will be a challenge. Further consideration of food requirements for threatened species and apex predators under rebuilding strategies highlights the potential constraints on available energy to meet overall ecosystem management objectives. This perspective necessarily involves direct consideration of possible trade-offs among harvested species if all cannot simultaneously be at B_{msy} levels. Furthemore, the transfer and recycling of energy and nutrients between the relatively shallow shelf sea areas and the deep sea is likely to play an important role in determining the overall levels of deep sea productivity in any given region. It is likely that the mixing of predominantly shelf living fish species with deep sea species will be at its greatest where the flux of energy from the shelf to the deep sea is also high. In addition, mixing may be high in areas where the production of deep sea chemosynthetic sources of energy is also high. These assertions require further investigation, but determination of such processes is likely to be of fundamental importance in establishing meaningful definitions of what constitutes a deep sea fishery from a management perspective.

11. Recommendations

11.1. Further evaluate the relationships between deep sea habitats, species diversity and production

It is apparent through this brief review of the ecology of deep-sea ecosystems and management approaches that sufficient worldwide literature and open access data sources now exist (ICES, 2007 – see Figure 14 and the Seamounts website[3]) on the status of several of the important (diverse and productive) deep-sea biological facies. It is our opinion that a more focused assessment of the status of these facies in association with fish, other fauna and environmental conditions could be further developed to a point where we can quantify and explain (and therefore predict) gradients in biodiversity and productivity in deep sea ecosystems. Especially to better understand and therefore to predict the location and extent of biodiverse and productive so called 'hot spot' habitats in relation to larger physio-graphic features.

It has already been suggested by ICES (2009) that using the information on the location of sponge and coral grounds it should be possible to evaluate the association of fish within these areas through analyses of the trawl survey data. Specifically, in order to validate the generality of the high biodiversity associated with sponge & coral grounds, detailed data on the associated fauna from the Atlantic is required. Clearly this type of research would lend itself very well to the development of predictive biological facies models of the deep sea.

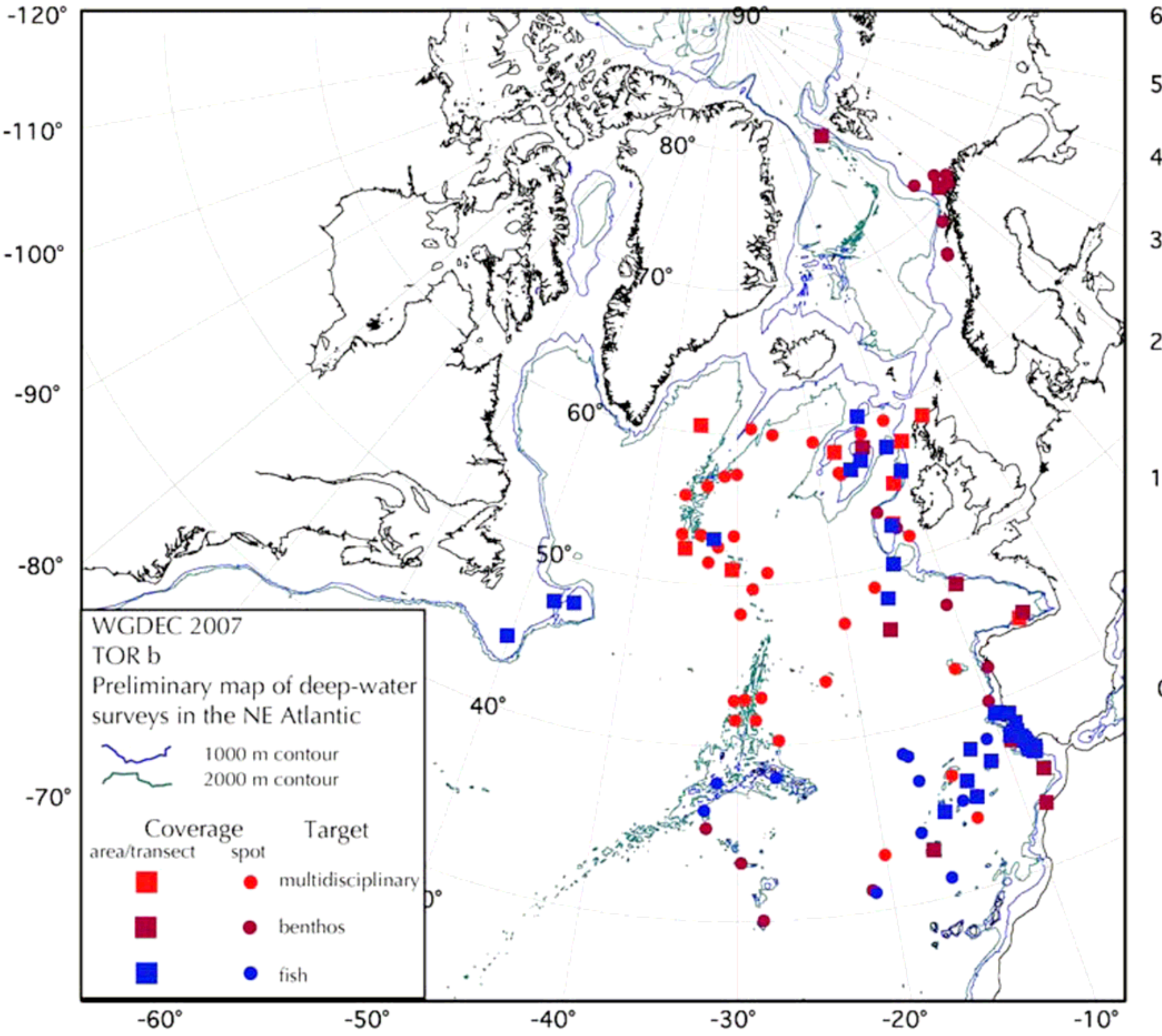

Figure 14. Surveys with deep sea biological and habitat data held in WGDEC data base (ICES, 2007).

11.2. *Investigate the development of methods to map, estimate and predict the occurrence of chemosynthetic sources of primary production in the deep sea.*

Chemosynthetic ecosystems including hot vents, cold seeps, mud volcanoes and sulphidic brine pools are highly diverse deep-water habitats determined by dynamic, small- and large-scale geological processes, which vary substantially in time and space. Organisms in chemosynthetic habitats require specific conditions, such as temperature, presence of sulphide and methane, hard ground or particle flux, to maintain their populations. Life histories and dispersal of organisms restricted to these isolated ecosystems remains a major question for understanding the interconnectivity and resilience of these dynamic ecosystems, but identifying potential areas of the deep sea environment based upon an understanding of the controlling factors would represent a large step forward in better estimating the potential for deep sea productivity – links with the FP7 research project on Hotspot Ecosystem Research and Man's Impact On European Seas (HERMIONE) will be important.

11.3. *Better understand the spatial distribution and dispersal capabilities of deep-sea organisms*

Successful management, protection and restoration of deep-sea habitats require a sound scientific basis, which is currently lacking. Increased mapping and basic ecological research is needed to understand the distribution and dispersal capabilities of deep-sea organisms which will assist in the design of marine reserves. Research should be directed towards answering (1) How large must the reserve be? (2) How many must there be? And (3) Where should they be located? (Carr et al., 2003).

11.4. *Develop and prepare a deep sea 'hot-spot' habitat classification*

By examining the nature and controlling factors which determine hot-spot biological productivity and diversity it should be possible to map potential hot-spot areas within the broader scale physiographic features in which they occur, e.g. slope, sea mounts, abyssal plain, canyons, ocean ridges. Such maps would greatly assist in identifying the most effective spatial management units in the deep sea based upon optimised area, ecosystem diversity and production analysis.

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