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A global assessment of seamount ecosystems knowledge using an ecosystem evaluation framework

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ABSTRACT

Seamounts are ubiquitous habitats of the deep-sea, collectively forming an area as large as Europe. Their characteristics have led marine scientists to hypothesize a series of 'seamount effects' enhancing numbers of endemic species, rates of production and bentho-pelagic trophic transfers. These effects have profound implications for deep-sea management; collating the existing body of seamount knowledge to describe potential effects on individual seamounts is therefore of paramount importance. In the course of this study, relevant literature was searched for key geological, oceanographic and ecological seamount attributes, and assembled in a 'Google Earth' map and in an online database (the Seamount Ecosystem Evaluation Framework, SEEF, www.seamounteef.org), comprising 597 seamounts located in the Atlantic, Pacific, Southern and Mediterranean basins. Data collated were described both in terms of quality and quantity, and the status of past and present global seamount knowledge was assessed. In addition, we investigated to what extent the available information supports seamount functioning hypotheses. The analysis confirms that seamounts remain largely unexplored, with only 0.4–4% of the total seamount population directly sampled for scientific purposes. Some of the seamount hypotheses tested are better supported than others, for example, some seamounts may represent 'oases' of the abyssal plains and some may play a role in connecting benthic and pelagic communities. However, seamounts present heterogeneous geophysical settings, suggesting that not all seamounts affect the food webs and biogeochemical fluxes in the surrounding ocean in the same way. Therefore, SEEF constitutes a tool to identify features playing a key role in deep-sea ecosystems.

1. Introduction

Seamounts are common habitats in all the world's oceans, occurring in higher abundances around mid-ocean ridges, island-arc convergent areas and above upwelling mantle plumes (Etnoyer et al., 2010; Staudigel and Clague, 2010; Wessel et al., 2010). Traditionally, they were defined as distinct topographical features greater than 1000 m in relief above the seafloor that do not break the sea surface (Menard, 1964). However, as no geological (Wessel, 2007) or ecological rationale seems to validate this height threshold, and smaller features can similarly host important deep-sea ecosystems (e.g., Koslow et al., 2001), recent reviews have abandoned the traditional size limit (e.g., Clark et al., 2010; Staudigel et al., 2010). We have followed this practice and considered isolated features down to 100 m in relief as seamounts.

The abundance and distribution of submarine features have been predicted many times, mostly based on satellite altimetry and ship-based sounding extrapolations (Costello et al., 2010; Hillier and Watts, 2007; Kim and Wessel, 2011; Kitchingman and Lai, 2004; Wessel, 2001; Wessel et al., 2010; Yesson et al., 2011). As none of these estimates can accurately count the number of small (<1 km) and deep features, they vary greatly depending on the assumptions made. Remarkably, even the most conservative models suggest that the total seamount population consists of at least tens of thousands of features (Kim and Wessel, 2011). Therefore, seamounts likely represent a major habitat of the deep-sea (*sensu* Costello, 2009), estimated to comprise an area as large as Europe (termed the 'seamount biome' by Etnoyer et al., 2010).

Besides abundance, there are other reasons that have triggered marine scientists' interest in seamounts for decades (Brewin et al., 2007). The typically volcanic origin of underwater mountains makes them valuable windows for geologists into submarine volcanism and plate tectonic dynamics (Koppers and Watts, 2010; Staudigel and Clague, 2010; Wessel, 2007). Their abrupt topography can interact with adjacent water masses and lead to a range of effects, including increase of turbulence mixing, alteration of global ocean circulation, generation of retention mechanisms (e.g., Taylor

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columns) and amplification and rectification of tidal currents – all processes that entrain the curiosity of oceanographers (Lavelle and Mohn, 2010; Roden, 1987; White et al., 2007). Their distinctness as three dimensional rocky habitats in flat and soft-sedimented deep-sea plains, the potential suitability for the application of island biogeography (MacArthur and Wilson, 1967) and the connections of seamounts with aggregating deep-sea organisms and large pelagic animals draw marine ecologists and biologists into seamount research (e.g., Hubbs, 1959; Morato et al., 2010a; Rowden et al., 2010a; Wilson and Kaufmann, 1987; Worm et al., 2003). Finally, the unsustainable use of some seamount resources challenges conservation scientists and governments to find policy instruments that encourage more sustainable fishing and mining activities (e.g., CBD, 2008; Pitcher et al., 2010a; Probert et al., 2007; Van Dover, 2011; Norse et al., 2012).

Lately, scientific attention focussed on seamount ecosystems has increased considerably, especially through international projects such as the Global Census of Marine Life on Seamounts (CenSeam) (Stocks et al., 2012). This accompanies the recognition that biological communities on seamounts can be highly vulnerable to human activities (Clark and Koslow, 2007; Clark, 2009; Pitcher et al., 2010a). Essentially, two main concerns are associated with seamount ecosystems. First, trawling causes physical disruption of reef building organisms and sediment re-suspension, which may severely affect the emergent filter feeders that tend to dominate seamount benthic communities (e.g., Althaus et al., 2009; Clark and Rowden, 2009; Williams et al., 2010). Second, target species on seamounts are typically long-lived and slow-growing, hence, extremely vulnerable to fishing (e.g., orange roughy and alfonsino) (Morato et al., 2006a; Pitcher et al., 2010a). As stocks are easily depleted, seamount fisheries move from one seamount to another in order to maintain high catches (Clark et al., 2010; Morato et al., 2006b; Pitcher et al., 2010a). Due to these concerns, the FAO refers to seamounts as examples of vulnerable marine ecosystems (VMEs) of the deep-sea in their international guidelines for the management of fisheries in the high- and deep seas (FAO, 2009).

Two ideas frequently encountered in seamount publications are the 'island' and 'oasis' hypotheses (McClain, 2007). According to the former, seamounts function as solitary islands on the abyssal plain, where speciation by isolation can result in high levels of endemism (Hubbs, 1959; Rogers, 1994; Wilson and Kaufmann, 1987). Results from recent studies have questioned this hypothesis (e.g., Cho and Shank, 2010; McClain et al., 2009; Miller et al., 2010; O'Hara, 2007; Samadi et al., 2006). As the degree of endemism will depend on genetic isolating mechanisms that differ between organisms, and studies of endemism are inherently biased by sampling effort and current knowledge of species diversity, the generalization that seamounts are hotspots of endemic species is today largely disavowed (reviewed in McClain (2007), Rowden et al. (2010a), Stocks and Hart (2007)).

Marine scientists have also described seamounts as areas where productivity, biomass and biodiversity of marine life thrive due to enhanced organic inputs: 'oases' in an otherwise scarce deep sea environment (Genin et al., 1986; Rogers, 1994; Samadi et al., 2006). Support for this idea came from studies showing higher biomass of benthic organisms on seamounts compared to adjacent continental slopes and abyssal plains (e.g., Rowden et al., 2010b; Samadi et al., 2006; Sautya et al., 2011) and from subsequent speculations suggesting that this high benthic biomass might attract aggregating deep sea fish (sensu Koslow, 1996) and pelagic visitors (tunas, billfishes, pelagic sharks, marine mammals, sea-turtles and sea-birds) (e.g., Amorim et al., 2009; Holland and Grubbs, 2007; Kaschner, 2007; Litvinov, 2007; Maxwell et al., 2012; Morato et al., 2010a; Santos et al., 2007). Several theories have been proposed to what may determine higher food availability on seamounts: trapping of vertical migrating zooplankton and micronekton on shallow seamount summits ('topographic blockage'); acceleration of horizontal currents that increases fluxes of imported planktonic organisms and suspended organic matter; or seamount-induced upwelling leading to an increase in primary production (Genin, 2004; Lavelle and Mohn, 2010; Morato et al., 2009; White et al., 2007) – all mechanisms that may endow seamounts with a characteristic trophic signature (Pitcher and Bulman, 2007). Recent reviews have pointed to allochtonous energy inflow rather that increased primary production above seamounts as the more likely mechanism behind the potentially increased biological activity in seamount ecosystems (Genin and Dower, 2007; Morato et al., 2009; Clark et al., 2010).

Recently, the lack of scientific evidence supporting many of these 'seamount paradigms' has been highlighted (McClain, 2007; Rowden et al., 2010a). In order for seamount science to advance, there is a need to revise traditional seamount knowledge (McClain, 2007; Rowden et al., 2010a) and to fill the existing knowledge gaps with new research (Clark et al., 2012). Clark et al. (2012) emphasized how compilation of seamount information in global databases has improved seamount research and that these efforts should be maintained and expanded. Two existing online databases store global seamount information that can be used for meta-analysis. SeamountsOnline (Stocks, 2009) is a collection of faunal records for around 300 seamounts, and includes an extensive reference database. The Seamount Catalog (Koppers et al., 2010) contains information on the geology and bathymetry for over 1800 seamounts. Large quantities of information are thus publicly available in global databases, but only covering specific fields such as species diversity or bathymetry. The Seamount Ecosystem Evaluation Framework (SEEF) was developed as a tool to synthetize interdisciplinary information on seamounts and to describe the ecological features found on seamounts that might determine their trophic functioning (e.g., productivity regimes leading to increased local biomass). SEEF was also intended to enable a quantification of present knowledge on seamount ecosystems, and to indentify research gaps. Pitcher and Bulman (2007) and Pitcher et al. (2007a, 2010b) described the framework, but they only tested it on a few seamounts.

We have developed SEEF into a database that combines and standardizes ecological and geological information from present databases, peer reviewed articles, books and 'gray literature'. The present work describes the development of the database, and shows how SEEF can be used to: (i) produce a global overview of present and past seamount knowledge, evaluating how many and how detailed individual seamounts have been explored; (ii) assess to what extent the information available in the literature supports the existence of 'seamount effects'. In particular, we used the information collected in the database to test: the island hypothesis, the oasis hypothesis and the role seamounts have for pelagic and benthopelagic organisms. Finally, we show how SEEF offers an intuitive form of systematizing and displaying seamount information. This system can allow scientists, managers, and general public to explore the current level of seamount knowledge across geographical areas and scientific fields and assess all the information available for the features of their interest.

2. Methods

The present study represents recent developments of the Seamount Ecosystem Evaluation Framework (SEEF), a framework initially developed by Pitcher and Bulman (2007) and Pitcher et al. (2007a, 2010b) with the aim of assessing both the extent of our knowledge about individual seamounts and the trophic functioning of seamount ecosystems. In these papers, a set of