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DSCC Seamounts, VMEs and Spatial management

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Seamounts, VMEs And Spatial Management

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Introduction

In this paper we will:

- 1) describe the VME indicator species as best as they are known from seamounts in the Pacific;
- 2) examine the ecosystem concept and how it is applied in the context of VME indicator species and the distribution of VMEcosystems on seamounts and similar features and the factors that might influence their local placement;
- 3) assess what we know, or can know, about VME indicator species distribution and abundance on seamounts as recorded from trawl bycatch;
- 4) determine whether it is possible to model accurately for spatial management purposes the distribution of these species when trawl bycatch is the only information source; and
- 5) examine the issue of potential recovery of VMEcosystems following trawling based on what we know so far but also from the perspective of likely sources of larvae.

Seamount habitats harbor unique and novel communities. The further from the continental land masses that they occur, the more distinct is their fauna. Seamounts, for the most part, are extinct volcanos that never extended far enough from the seafloor to break the sea surface and function as

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islands (Wessel et al., 2010). Others were volcanic islands that eroded and subsided so their peaks now reside below sea level. And still others, fitting the definition of a seamount by rising more than 1000 m above the surrounding seafloor, are raised blocks of volcanic material formed along the earth's spreading ridges. Hills and knolls are smaller structures (<1000 m) that are common in some areas, such as the Tasman Sea, and may be very abundant globally (Yesson et al., 2011). Because of their volcanic origin, these features are mostly composed of basalt. "Sand" can be a conspicuous part of the substrate, but for the most part the sand-sized particles are the calcareous tests (shells) of dead planktonic organisms that have settled from the overlying water column. It takes many thousands to millions of years for this biogenic sand to accumulate, so sandy substrates are usually found on older seamounts in depressions conducive to deposition.

Seamounts at any depth are large objects that intersect ocean currents. The water has no choice but to go around or over the seamount, depending on where on the seamount the flow occurs. Due to the law of conservation of volume, and the fact that water cannot be compressed, what must change is the velocity of the flow (von Arx, 1962). As a result, there are places on seamounts where the water flows much faster than it does in the surrounding water mass, or at other sites on the seamount surface. As well, due to friction and drag, at many places on the seamount the flow decreases to very low velocities close to the seamount surface.

Seamounts of sufficient height and size intersect the flow of currents and generate upwelling of deeper nutrient rich water and produce areas in the surface water of enhanced primary production, especially at low latitudes (Leitner et al., 2020). Sometimes these areas foster pelagic ecosystems that are enriched relative to the surrounding water and often become the focus of pelagic fisheries.

These various features of seamount habitats are the properties that contribute to their harboring diverse assemblages of suspension-feeding organisms, attached to the hard substrate, and often extending a meter or more into the overlying water. Many, if not most, of these organisms have life styles and life history features that serve as indicators of vulnerable marine ecosystems (VMEs, but we will use VMEcosystems, to distinguish between the ecosystem and the indicator species usage of the acronym VME). In general, the VME indicator species are long-lived, with ages extending from many decades to several centuries and longer; they are fragile, having become adapted to places where water flow, even when enhanced, generally does not exceed a few centimeters per second; their reproductive habits, when known, suggest infrequent or aperiodic spawning, often on scales of years between spawning events, the exception perhaps being in areas with seasonal phytoplankton blooms; and their larvae are mostly unknown, as is the distance they are capable of travelling (FAO, 2009).

The problem with the issue of VMEcosystems and deciding how to manage them is that they are so far not well defined. Noteworthy is that the original UNGA resolution 61/105 included the phrase "vulnerable marine ecosystem" as critical terminology (paragraphs 76-95) so the Expert Consultation tasked to develop the initial draft of the guidelines needed to start with this as the foundation for the guidelines (FAO, 2009). The panel initially considered how to address the ecosystem-scale scope of the term but found that a broad definition would in all likelihood fail in the required Technical Consultation part of the process (the draft guidelines needed to be adopted by member states and it took two meetings to negotiate the language in the draft guidelines before it

was approved). Indeed, paragraphs 14-16 in the guidelines that describe and define VMEcosystems acknowledge that RFMOs (and member states) would want some flexibility in implementation.

The concept of vulnerability is a critical element for implementing the guidelines. Paragraph 14 states (*italics ours for emphasis*): “[v]ulnerability is related to the likelihood that a population, community, or habitat will experience substantial alteration from short-term or chronic disturbance, and the likelihood that it would recover and in what time frame. *These are, in turn, related to the characteristics of the ecosystems themselves, especially biological and structural aspects.* VME features may be physically or functionally fragile. The most vulnerable ecosystems are those that are both easily disturbed and very slow to recover, or may never recover.” Therefore, the concept of a VME is linked to the **ecosystem** in which populations, communities and habitats are nested and interact at a functional level.

In much of the literature and discussion on the issue, the concept of indicator species has been conflated with the ecosystem itself so that when some authors speak of VMEs they are simultaneously speaking of the presence of indicator species but also, by inference, the presence of the ecosystem. The problem, of course, is that the ecosystem then comes to be defined by the presence of the abundant indicator species (Morato et al., 2018). We see many examples where the occasional presence of indicator species is interpreted to mean that we are not in a VMEcosystem. However, it is important to remember that these are *indicator species*, they are meant to represent all the other species not considered or sampled in the ecosystem.

1. Seamount corals and sponges as VME indicators species

The determination of whether a vulnerable marine ecosystem is present is predicated on finding pre-determined indicator species (UNGA Resolution 64/72)³. The characteristics of indicator species, and example taxa, were determined by a conference of scientists convened by the FAO to have a certain set of attributes that make them especially vulnerable to the impacts of bottom contact fishing gear. By now, these attributes are well recognized (FAO, 2009): 1, uniqueness or rarity of the species; 2, functionally significant to the habitat; 3, fragility of the species; 4, life-history characteristics that make probability of recolonization after impact low or unpredictable; and 5, species that create through their structural complexity habitat for other species. These characteristics have been used by RFMOs to develop region-specific lists of indicator species.

On seamounts much attention has been given to species of corals and sponges since many of the species examined so far fit at least one, and often several, of the criteria to be considered as a VME indicator species (Ardron et al., 2014). Unfortunately, the taxonomic work has not yet been done to establish exactly all the species present and how broadly those species are distributed. What we have seen, however, from expeditions across the central Pacific (Kennedy et al., 2019) and along the New England and Corner Rise seamount chains (Lapointe et al., in press) as well as the Emperor

³ Paragraph 119 (c): Establish and implement appropriate protocols for the implementation of paragraph 83 (d) of its resolution 61/105, including definitions of what constitutes evidence of an encounter with a vulnerable marine ecosystem, in particular threshold levels **and indicator species**, based on the best available scientific information and consistent with the Guidelines, and taking into account any other conservation and management measures to prevent significant adverse impacts on vulnerable marine ecosystems, including those based on the results of assessments carried out pursuant to paragraph 83 (a) of its resolution 61/105 and paragraph 119 (a) of the present resolution;

seamount chain (Watling et al., unpublished), is that some species are very broadly distributed while others are found only rarely, paralleling what is known from terrestrial communities. Ecologically rare species have unusual life-history characteristics that allow them to reproduce and colonize some habitats, but also have higher extinction risk (Harnik et al., 2012). In our efforts to protect biodiversity, those rare species should be especially protected.

Incomplete taxonomy is a significant problem for policy makers and managers. There is the implicit assumption that gorgonians are gorgonians, sponges are sponges, etc. But we know from recent ROV work that has been done in the Pacific and elsewhere, that each species occupies its preferred areas or sub-habitats of the seamounts (Kennedy et al., 2019; Victorero et al., 2018). So, to just combine all gorgonians into one VME indicator species category creates severe problems when linking biodiversity conservation to fishery management decisions. For example, bamboo corals that grow as unbranched colonies, sometimes called “whips,” have generally been assumed to belong to the genus *Lepidisis*. However, Heestand Saucier, Watling, and France (in prep.), utilizing both molecular genetic and morphological data from approximately 400 bamboo coral specimens, show that whip bamboos are found in 6 different molecular clades on the bamboo evolutionary tree. It is likely that at least 6 different genera and an untold number of species are involved. In the end, researchers do not yet have a good idea of “uniqueness and rarity” of octocoral species (Thoma et al., 2009). Sponge taxonomy in the Pacific is in even worse shape as there has been very little work on the molecular genetics of that evolutionary group and the morphological studies are just beginning.

Sponges and octocorals are significant members of the ecosystem because they can enhance local biodiversity by providing habitat for other, smaller, species, often with discrete commensal relationships. There are several good examples, and more are being discovered as diving by ROVs on seamounts becomes more widespread. One example is the relationship of brittle stars with octocorals. This relationship can be one-to-one, as with the brittle star *Ophiocreas oedipus* and its host coral, *Metallogorgia melanotrichos* (Mosher and Watling, 2009), or it can be several-to-one as in the case of some species of *Asteroschema* which can live on several species of octocorals in the genera *Paramuricea* or *Paragorgia* (Watling et al., 2011). Interestingly, while there are many species in both of those coral genera, not all of them host brittle stars. Another example is the perhaps parasitic relationship of zoanthid anemones which colonize one to a few octocoral species. On the sponge side, there is a new sea anemone that has recently been described living on and in the tissue of sponges (Sanamyan et al., 2012). It is not known yet how many species of sponges this anemone can colonize, but so far it is at least two. Also, but yet unpublished, is the discovery of a new genus and species of hydroid living in the open spaces of the sponge *Walteria flemmingi*. Undoubtedly, as more taxonomic work is done, other very tight associations of species to particular hosts will be found. Because the deep sea has been stable for so very long (at least 23 million years) (Kennett, 1977; von der Heydt and Dijkstra, 2006) the evolutionary process has produced more commensal to parasitic relationships than one might have expected.

Seamounts generally occur in areas where currents are not strong. Even in areas where the flow is accelerated by an intervening ridge, the flow is generally less than 5-10 cm s⁻¹. These relatively low flow velocities have allowed corals and sponges to grow significant distances into the overlying water. The largest gorgonian seen so far is from Twin Banks, Hawaii, and was 6.7 m tall (Watling et

al., 2013c); a sponge in the same area was measured at 5 m diameter (Wagner and Kelley, 2017). Many octocoral “bushes” can grow to heights of about 1 m (Watling and France, 2011), and hard coral thickets can be 0.5 m or more off the seafloor (Thresher et al., 2011). Most of the large corals collected from the Tasmanian seamounts by a ROV were not massive (personal observation). For example, the largest of the coral bushes, which filled a 15 L bucket, weighed only 1.2 kg. Other tall corals were less than 1 kg. The two others that were weighed were 150 g or less. In other words, size does not equate to robustness or massiveness, so when impacted by trawl gear moving at up to 4 knots, ca. 200 cm s⁻¹), the corals will exhibit their fragility and be broken into multiple pieces.

Recolonization of impacted areas depends on successful reproduction of the potential colonizers elsewhere. Only for a few species do we know the mode of reproduction of deep-sea octocorals (Watling et al., 2011). What seems to be clear, however, is that octocoral colonies are either male or female, for the most part, although we have discovered one species that is hermaphroditic (A. Simpson, in prep.). It is not known when or how frequently octocorals spawn; does the whole colony spawn or just part of it? It is not known how long the larvae live in the plankton. A very few species are known to be brooders (Mercier and Hamel, 2011), allowing the larvae to develop while still in contact with the female parent colony. On the other hand, it seems likely that many species also must release larvae with the capability of dispersing over long distances. The evidence for this is indirect, but seamounts that are more than 100 km from the nearest seamount have corals on them. So, it is likely that larvae can traverse large distances of water too deep for them to survive in were they to settle to the bottom (studies have shown depth preferences of deep-sea octocorals, with most being present between 800 and 2500 m). On the other hand, we don’t know how often larvae are able to make that jump or the viability (fitness) of larvae of different sizes. Colony size is positively correlated to oocyte size for both *Primnoa resedaeformis* and *Paramuricea placomus* (Fountain et al., 2019) so it is reasonable to suspect larvae produced from larger colonies have greater dispersal potential. On Twin Banks, as noted above, we discovered giant corals and sponges, but nowhere at that site were there any small colonies of any of the species. In fact, it is quite variable from seamount to seamount whether there is what looks to be, based on size, a stable-age distribution of corals, or whether the corals are all of one size, suggesting a widespread settlement event at some time in the past. The corals at Twin Banks were probably 200 years or more old, judging by their extremely large size (Watling et al., 2011), so it is probable that there had been no recruitment event there in the past couple of centuries, or if there had, it was not successful.

Some seamounts, especially at high latitudes (but see Baco et al., 2017 for an example of a low latitude example) harbor extensive thickets or reefs created by colonies of hard corals. In the Southwest Pacific, the coral *Solenosmilia variabilis*, is the primary species in the coral thickets (Thresher et al., 2011). Elsewhere, *Madrepora* or *Desmophyllum* can fill the same role. The importance of these thickets is that they form habitat for an unknown number of other species, most of which have not been documented. On the Tasmanian seamounts we found that most of the octocorals were growing on the dead skeletons of the *Solenosmilia* colonies. In addition, from the images you can see large sea urchins and other invertebrates also taking advantage of this habitat. Smaller species such as bryozoans and hydroids are also present (Thresher et al., 2011). When most people think of VMEcosystem habitats, reefs and thickets are what come to mind. But seamounts, especially along ridges created by the erosion and slumping of the seamount flanks, can have high densities bush-like octocorals with an understory of smaller species, including sponges. Diversity in

these “coral gardens” or “forests” is probably quite high, but they have not been sampled in order to find out.

2. Distribution of VMEcosystems on and among seamounts

Many studies, from ROV dives to towed camera transects, have shown that VME indicator species are not homogeneously distributed across seamount substrates (Victorero et al., 2018). The major reason, of course, is that seamounts are complex geomorphological structures. They consist largely of basalt rock in the form of ridges and flat plains, but also as vertical cliffs and all manner of slopes in between. Depending on the geological history of the seamount, there may also be areas of compressed ash, or breccias consisting of stones and boulders of various sizes and biogenic sand. All these factors contribute to seamounts possessing a variety of possible habitats in which vulnerable species can live (Auster et al., 2005).

Most of the focus on seamount habitats has been on the rocky outcrops and their charismatic megafaunal species, the corals and sponges. But the few studies conducted on seamount sandy habitats shows they harbor unique small species, some of which have so far been found nowhere else. A good example is the finding of 54 new species of the sediment-dwelling harpacticoid copepods on the flat summit of Great Meteor Seamount in the Northeastern Atlantic (George and Schminke, 2002). Dredging the summits of the Meteor and Lusitanian seamount groups, which are separated by about 1000 km, produced 30 new species of small snails in the family Rissoidae (Gofas, 2007). Most of the snails were endemic to one or a few of the seamounts and there was almost no similarity between the two groups of seamounts even though they are loosely connected by the Azores Current. Unfortunately, the sand-dwelling fauna, with the exception of xenophyophores, has not been studied so we have no data to inform managers about the uniqueness or rarity of that fauna, nor has that fauna been given any attention as to whether they should be classified as VME indicator species. Based on what is known to date, it seems that disruption of the seamount summit habitats on a regular basis could push some of these unknown species into an Allee effect from which they would never recover (Courchamp et al., 1999).

The ICES WGDEC (Working Group on Deep-Sea Ecology) has been asked, over the past several years, to help with a definition of VMEcosystem. This effort so far has lead to a series of discussions about VME indicator species and their distributions, and to one paper where the characteristics of the indicator species are mapped and rated in importance in an effort to delimit the VMEcosystems in the areas of the NE Atlantic where bottom trawl fishing is occurring (Morato et al., 2018).

But, are these just numbers games that have forgotten or ignore the foundational concepts of the ecological sciences? Scientists learn in school about the progression from species populations to communities to ecosystem to biomes. But this “levels of organization” approach allows us only to see the biotic components (O’Neill et al., 1986). But the understanding and delimitation of the ecosystem also requires a “process-functional” approach which accounts for energy flow. Thus, “in one dimension it (the ecosystem) is structured according to constraints involving organism interaction and natural selection. In another dimension it is structured according to constraints that involve mass balance and thermodynamics” (p. 209). In the sea, which is a relatively open system, ecosystems are typically large (Sherman and Duda, 1999), boundaries are created by water masses and fronts, thus encompassing several hundred thousand square kilometers of ocean surface. At

depth, we do not yet know the extent of the ecosystem, although there are proposals for province boundaries (Watling et al., 2013a).

In our opinion, most people, when referring to VMEcosystems are in fact really talking about VMCommunities. For example, Rowden et al. (2017) effectively mapped the distribution of the hard coral, *Solenosmilia variabilis*, over several seamounts. They found the distributions of brisingid starfish and crinoids to closely parallel that of the hard coral. They refer to this as the *Solenosmilia* VME, but in fact, it is the *Solenosmilia* **community**. There are other communities on those seamounts that are generally not discussed in detail (Clark et al., 2015), made up of gorgonians, black corals, sponges, and small organisms living in the sand. It is possible that, with the exception of the sand, one could think of the coral groups and sponges as forming a suspension-feeder community, partly separate from, but perhaps also overlapping with the *Solenosmilia* community. The sand community comprises worms, nematodes, harpacticoid copepods, etc., but are poorly studied. These communities are connected through water flow, larval distribution, fish feeding, etc., thus justifying the concept of the seamount as a series of functionally interrelated communities making up part of an ecosystem which potentially comprises many seamounts.

Ecosystems are composed of many habitat types that support communities of several kinds (see the classic text by Allee et al., 1949, for example). Valentine (1973) applied this concept to palaeontological data to show how groups of communities and their ecosystems then made up provinces and that changes in ecosystems through time would change the make-up of the provinces. As an example, we know that seamount communities undoubtedly have changed during the course of glacial advances and retreats. During glacial advances, as the intermediate depth water became colder and saltier, the hard coral, *Desmophyllum dianthus*, undergoes population explosions, dramatically increasing in numbers, but in the present interglacial period, *D. dianthus* is present but not highly abundant (Robinson et al., 2007; Thiagarajan et al., 2013)

Does the VMEcosystem cover only a single seamount or are there multiple seamounts in a VMEcosystem? The communities that make up an ecosystem can range over very large distances. Common examples are the communities of sandy beaches or rocky shores along continental coastlines both of which are commonly thought of as ecosystems. Each contains their own common set of species, and each might not be contiguous throughout the range, but each also might have in common the dispersal of individuals from one part of the ecosystem to another either through the movements of the larval or adult stages of the populations. The same can be said for seamounts within a biological province. A community dominated by several species of bamboo corals or the scleractinian *Solenosmilia* might extend along the whole or part of a seamount chain, or range over seamounts located in large sections of the ocean basin. Those distributions and estimates of the genetic connectivity or how much genetic variation exists over the whole of the range of a species is just becoming known (e.g., Radice et al., 2016). Some information is available for species, such as brittle stars and chirostylid galatheid crabs associated with the corals, rather than the corals themselves (Cho and Shank, 2010; Samadi et al., 2006).

Part of this answer rests in mapping the distribution of biogeographic provinces in the ocean, which is based on mapping the distributions of species that make up the communities that have so far been investigated. While deep-sea biogeography has been an area of study since the time of Ekman (Watling et al., 2013a), the mapping of organisms associated with seamounts has lagged due to

difficulties of sampling in such harsh environments. The possibility of losing dredges was very real, but samples were occasionally obtained adventitiously by manned submersibles, however it was only the recent funding for deep-diving ROVs and provision of exploratory ship time that has allowed scientists to begin to map the bathyal benthos of the ocean (Kennedy et al., 2019). Much of the data thus procured has been archived in OBIS (Ocean Biogeographic Information System) and is available to anyone who wants to use it (e.g., Costello et al., 2017).

Various methods have been used to try to delimit the boundaries of bathyal biogeographic provinces. Watling et al. (2013a) used water mass data as a proxy to hypothesize the boundaries of the provinces at bathyal and abyssal depths. Some limited testing of those ideas has shown them to not be too far off the mark, although some changes need to be made (Watling, 2009; Watling et al. in prep.). Others have gathered large amounts of hydrographic data and used clustering algorithms to try to find patterns in the water characteristics, at large (Sayre et al., 2017) and small (Beger et al., 2020) scales. Others have taken data from OBIS and applied clustering algorithms, sometimes not discriminating between the water column and benthos species (Costello et al., 2017), or have divided the ocean into grids of 1° or 5°, etc. (Edler et al., 2017).

The result of these peregrinations has been a diversity of biogeographic classifications, many of which do not comport with any historical biogeographical perspective. That is, merely representing which squares in the ocean are most similar to each other (e.g., Beger et al., 2020; Sayre et al., 2017) does not provide any information about the history and continuity of the biogeographical units, which of course, must exist. This continuity is manifested through larval dispersal by currents, as well as by larger organisms dispersing by swimming, all the while staying within some geographic boundaries, which can be defined by water masses .

Another reason biogeographical papers should be treated with caution is that they oversimplify for the purpose of classification: for example, Beger et al. (2020) cluster physical and chemical data, such as temperature, oxygen concentration, as well as nutrients and light, and those clusters are assumed to represent what the bathyal species are responding to. But if the divisions are too fine, as they seem to be, they are not likely to predict differences in species composition. For instance, the most important physical parameter is likely to be temperature since it regulates metabolic rate (Somero et al., 2017). Variations in other parameters are less consequential, including oxygen until the values begin to get below 1 ml/l. pH has the potential to matter, but so far there is no demonstration that it does for gorgonian corals, but at some point, will matter for hard corals due to aragonite saturation. Variations in nitrate and other nutrients of interest to phytoplankton, as well as photosynthetic radiation, will not make a significant difference to the deep water species, except to the extent that surface production will impact the deep communities. Knowing the depth of the mixed layer helps (Yool et al., 2007), but it is important to know how much of the surface production goes through the bottom of the mixed layer to gain some understanding of the extent to which the deep is being fed (Lutz et al., 2007).

More useful, perhaps, for differentiating seamounts as VMEcosystems, is to try to determine which of the many seamounts in the ocean are similar to each other in some characteristic way. Clark et al., (2011) developed a classification system using several physical and biological features including summit depth, organic matter flux, distance to nearest seamount, and dissolved oxygen in the surrounding water. This method divided the global 10,604 large seamounts with summit depths in

the bathyal (<3500 m) into 194 classes distributed over the 14 bathyal provinces of Watling et al. (2013). In the biogeographic province in which the Louisville seamounts are located (BY6), there were 517 seamounts divided into 17 classes, of which four occurred at various points along the chain.

3. Can VME indicator species distributions be determined by trawl bycatch?

Surveying of seamount communities by research submersible, ROV, or even towed camera systems is expensive. As a result, most of the information about VME indicator species is provided in the form of trawl bycatch by observers on fishing vessels. And, indeed, the indication that a VMEcosystem might be present is predicated on the amount of indicator species found in the trawl net when the net is hauled aboard a fishing vessel. The question, though, is, to what extent does the content of the trawl net reflect the impact of the trawl on the VME indicator species growing on the seafloor? That is, are all the pieces of broken corals and sponges, for example, retained in the trawl net, or is there some fraction that is left on the seafloor or falls from the net during the ascent to the fishing vessel? Does the trawl routinely impact, through breakage or disruption, everything that is in its path when in contact with the seafloor?

Geange et al. (2020) acknowledge that trawls are inefficient at catching things other than fish. Unfortunately, there are not many studies directly indicating what the catch efficiency of non-fish by bottom trawls is likely to be. Freese et al. (1999) working in shallow cold waters of Alaska were able to dive on a trawl track made by a bottom trawl in a previously untrawled area. They showed that the catch efficiency for the organisms disturbed by the trawl was 10% or less. Auster et al. (2011) noted that catch efficiency is not well known but that several groups of corals overrun by trawls do not show up in the net at all.

This conclusion is borne out circumstantially by examining with cameras areas where trawling has occurred and comparing those with equivalent areas where trawling has not occurred. For example, Clark and Driscoll (2000) towed cameras over several seamounts off Chatham Rise and found that there were essentially no corals present on the seamounts that were heavily trawled whereas corals were moderately abundant on the non-trawled seamounts (Clark and Rowden, 2009). Similarly, bare, or nearly bare, substrate has been seen on other seamounts subject to bottom trawling (Baco et al., 2019; Waller et al., 2007; Williams et al., 2010).

However, when proposing catch thresholds that might trigger a “move-on” rule in the SPRFMO area, Geange et al. (2020) suggested using trawl bycatch amounts that, by weight, represented the highest levels. For example, the 98th percentile of bycatch for Gorgonacea is roughly 35 kg. Williams et al. (2010) estimated the catch efficiency for a deep-sea trawl net to be 0 to <0.01 for Gorgonacea. Therefore, one can presume that if 5 kg of corals are found in the net, it would have gone over 500 kg of corals. One can seriously doubt that 450 kg of corals was not impacted. Using the maximum estimated catch efficiency, a bycatch of 35 kg of gorgonians would mean that the tow went through as much as 3500 kg of corals. We know that these corals do not weigh very much on an individual basis, perhaps about 1-1.5 kg each for the largest ones. That would mean that more than 3500 corals were impacted during that single tow. Those kinds of numbers are indicative of very dense coral gardens, atypical for most seamount ecosystems which have patches of gorgonians, sponges, etc., separated by areas of bare basalt. The precautionary approach would be to use a value far less than

the 98th percentile of trawl catches when setting limits for the move-on rule. Or, rather than using a “move-on” rule, do not allow trawl gear to touch the seamount surface at all.

4. Can spatial management tools be useful for delimiting VMEcosystems?

For spatial management one needs to know the rough distribution of VME indicator species over all parts of the seamount. A typical ROV dive of 10-12 hours might cover a transect of 1-2 km, usually less than 1 km. It is very rare that more than 2 or 3 ROV dives are conducted on any one seamount. In the NW Atlantic, Kelvin seamount was visited 7 times, each dive on a different part of the seamount, and Manning Seamount was the subject of 6 Alvin dives, 3 ROV dives, 1 autonomous vehicle (AUV) dive and 2 towcam dives (Lapointe et al. in press). Unfortunately, four of the Alvin dives were on the summit, covering the same part of the ecosystem and the AUV and towcam dives have not been analyzed. On Kelvin, the dives occurred at a variety of depths as well as on different parts of the seamount. In the Pacific, Davidson Seamount has been visited multiple times with 33 video transects conducted over most of the depth range of the seamount (McClain et al., 2010). However, those transects were arranged to go over the summit along the long axis of the seamount and do not sample much of the sides. Other ROV programs, such as those of the *Okeanos Explorer* or *Nautilus*, are exploratory and rarely do more than two dives on any seamount (Kennedy et al., 2019). As a result we have a more or less detailed look at the distribution of organisms on only three seamounts and so cannot say much about the distribution of communities on any one seamount. In the SW Pacific, a towcam system was used to cover at least the summit area of a number of seamounts. In most cases those seamounts had relatively small summit areas so the towcam transects were arranged to produce coverage of a significant proportion of the summit and approaching flanks. In other cases, such as the Louisville Seamounts, most of the transect coverage was on the summits (Clark et al., 2015).

In order to determine the boundary of an ecosystem it is important to know the limits of the component communities, both horizontally, which as we have seen are difficult to know, and vertically. Efforts to plot or model the distribution of the most abundant indicator species may not account for the whole ecosystem (Rowden et al., 2017). As well, we know that fishing at a selective depth can have impacts far deeper than the target fishing depth due to the vertical movements of many fish species (Priede et al., 2011). For several seamounts in the Louisville Seamount chain, various models were applied to towed camera image data to determine or predict that three VME indicator species, *Solenosmilia variabilis* coral heads and matrix, brisingid starfish, and crinoids, were located near the summit edges, and that other parts could be trawled due to the absence or low abundance of those species. Rowden et al. (2017) refer to the *S. variabilis* matrix as if it is a VMEcosystem on its own, and so, by presumption, the remainder of the summit of the seamount does not belong to that ecosystem and is therefore not vulnerable. We have already suggested that Rowden et al. (2017) were actually determining the extent of the *Solenosmilia* community, which is only a part of the larger ecosystem. Whole seamounts need to be treated as VMEcosystems (Watling and Auster, 2017), or as part of a larger ecosystem.

Since so little is known about reproduction and recruitment of VME indicator species, predictions about the fate of the entire VMEcosystem would seem to be difficult to make. Further, since the ecosystem contains species that are both known as indicators as well as myriad numbers of others not so designated, it is possible that the VMEcosystem could be impacted by the loss of those

unknown species. A good example might be the species that are commensals on the colonies of the octocorals. In many cases the symbiont numbers are much lower than the numbers of coral colonies, which we know since we do not see commensals on all the host colonies. How much loss of host colonies would it then take to cause the commensal species to collapse due to their own Allee effect? If those commensals are food for some of the fish species present, what do those fish species turn to for a food source? Another example might be the small species, copepods and snails, living in the biogenic sands of the seamount summits. Their habitat is likely to be seriously disturbed by the passage of trawl gear. Thus, while the VME indicator species are important for helping to delimit the VMEcosystem, they are not the only species that might be impacted due to the fishery operating on a seamount. In the absence of more detailed data, it seems prudent to consider the whole of a seamount as a VMEcosystem (Watling and Auster 2017).

5. What is the likelihood of a seamount VMEcosystem recovering after trawling?

Recovery of communities on seamounts will rely on local larval production or delivery of larvae from afar. In the former case, the production of larvae will depend on the state of surviving colonies, whether the ecosystem can support the production of sufficient energy to allow the colony to generate viable reproductive products, and whether the surviving colonies are within reach of each other such that spawning and fertilization will be able to occur. At some point, it is possible that production of larvae will not occur due to various factors contributing to the Allee effect for the species. The possibility of recolonization will then depend on arrival of propagules from other seamounts or ridges where the species occurs. Whether larvae can reach the impacted seamount or not will depend not only on distance and larval viability, but also on the vagaries of currents. Is the impacted seamount downstream of seamounts that could send propagules or is it located such that only the occasional current eddy delivers larvae on an aperiodic basis, often at intervals of decades or centuries?

We know that most seamount-dwelling octocorals live for many decades to several centuries, and that at depths greater than 1000 m growth is very slow. Nevertheless, it seems likely that some colonies can begin to produce gonadal products when quite young, so it is possible for some larvae to be produced early in the life of the colony. However, the interval from gonadal development to spawning is not known so it is not possible to determine how often larvae might be produced. In any case, studies examining previously trawled seamounts suggest that timelines of recovery are likely to be very long, perhaps from 40 years or so at 300-600 m depth, to many more decades in deeper water.

Conclusions

“An ‘ecosystem plan’ that fails to protect all of the species associated with a particular natural community can only be characterized as deficient” (Wilcove, 1994: 327). This statement was written as part of the legal argument for saving the whole of the old growth forest of the northwestern U.S. as habitat for the northern spotted owl. Wilcove showed that a management plan targeted at a single species was unlikely to protect the full diversity of species in the ecosystem.

Identifying the presence, distribution, and abundance of an indicator species defines the state of that species at a moment (or period) in time. It does not define the composition of an associated

community, the suite of species interactions that define and sustain the community, or the flows of materials and energy that define the bounds of the ecosystem. Most important, it is those details about species interactions (including population connectivity, energy flow that mediates growth and reproduction, and interactions mediated by the local oceanographic regime) that will be needed to understand and predict the extent to which fishing and other human activities produce significant adverse impacts. Significant adverse impacts to indicator species alone simply defines a set of minimum bounds on the effects of human actions on VMEcosystems. Survey data on density and distribution of indicator species, while necessary, produces a static snapshot in time. Habitat suitability models and related geo-spatial analyses give an impression of precision and quantitative certainty while implicitly ignoring critical but poorly known elements of the ecology of communities and ecosystem dynamics. Management decisions, especially given the known characteristics of VMEcosystems, should be made with explicit admission of the limits to understanding and the consequences of errors in decision-making.

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