



NOTE

Are we missing important areas in pelagic marine conservation? Redefining conservation hotspots in the ocean

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ABSTRACT: The protection of biodiversity is one of the most important goals in terrestrial and marine conservation. Marine conservation approaches have traditionally followed the example of terrestrial initiatives. However, patterns, processes, habitats, and threats differ greatly between the 2 systems—and even within the marine environment. As a result, there is still a lack of congruence as to how to best identify and prioritize conservation approaches moving from the static terrestrial and nearshore realm into a more fluid, 3-dimensional pelagic realm. To address this problem, we investigate how the conservation science literature has been used to inform and guide management strategies in the marine system from coastal to pelagic environments. As cumulative impacts on the health of the oceans continue to increase, conservation priorities have shifted to include highly dynamic areas of the pelagic marine system. By evaluating whether priorities match science with current place-based management approaches (i.e. marine protected areas, MPAs), we identify important gaps that must be considered in current conservation schemes. Effective pelagic MPA design requires monitoring and evaluation across multiple physical, biological, and human dimensions. Because many threatened and exploited marine species move through an ephemeral and ever-changing environment, our results highlight the need to move beyond traditional, 2-dimensional approaches to marine conservation, and into dynamic management approaches that incorporate metrics of biodiversity as well as oceanographic features known to promote multilevel, trophic productivity.

KEY WORDS: Hotspot biodiversity · Conservation planning · Dynamic ocean management · Large marine protected areas · Pelagic · Productivity · Terrestrial conservation

INTRODUCTION

There is widespread consensus that we are facing a global conservation crisis (Pimm et al. 1995, MEA 2005, Brooks et al. 2006, CBD 2010). There has been a

substantial decline in both the diversity and abundance of species worldwide, owing to increasing human pressures (Jackson et al. 2001, Myers & Worm 2003, Sala & Knowlton 2006, Halpern et al. 2008, Baum & Worm 2009, Cardinale et al. 2012, Merrie et

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al. 2014, McCauley et al. 2015). Conservation efforts have been underway to prioritize and preserve the parts of the land and sea that are most under threat. Historically, action plans have been aimed at preservation of at-risk biodiversity (Myers et al. 2000, Roberts et al. 2002). As such, spatially explicit, systematic management of threatened areas, the species that inhabit these areas, and the ecosystem resources these areas provide, has typically been adopted as a conservation strategy.

Threats in the ocean, however, are less visible than those on land and, as a result, we know far more about terrestrial ecosystems and the extent of human impacts on land than we do in the ocean (Hoekstra et al. 2005, Game et al. 2009). While it was once thought that the oceans' resources were inexhaustible (Huxley 1883, Orbach 2003), escalating threats to the marine environment and the cumulative impacts have called attention to the need for marine conservation strategies (Pew Oceans Commission 2003, Lourie & Vincent 2004, Crain et al. 2008, Halpern et al. 2008). Despite increasing focus, marine conservation has historically lagged behind terrestrial approaches (MacArthur 1964, Sloan 2002, Kaplan et al. 2013, Maxwell et al. 2015). Whereas habitat loss is the dominant threat to terrestrial species, overexploitation by humans is the dominant threat in marine systems (Carr et al. 2003, Halpern et al. 2006, 2008, Jackson 2008, Norse 2010, FAO 2014). In response, international efforts have called for the protection of 10% of all coastal and marine areas from exploitation by 2020 (CBD 2010), with most marine protected areas (MPAs) managed using static reserve techniques, similar to the management approaches applied in terrestrial resources (e.g. MacArthur 1964, Myers 1988, Norse & Crowder 2005).

Marine conservation approaches increasingly involve place-based management strategies such as marine spatial planning and marine protected areas, which are based on terrestrial conservation objectives to conserve the target resources within a spatial boundary (Hyrenbach et al. 2000, Carr et al. 2003, Maxwell et al. 2015). An increasing number of internationally recognized organizations now include spatial protection of marine ecosystems in their conservation portfolios, such as Conservation International's 'Hotspots and high biodiversity wilderness areas', WWF-US's 'Global 2000: priority ecoregions', and BirdLife International's 'Important bird and biodiversity areas' (Mittermeier et al. 1998, Myers et al. 2000, Olson & Dinerstein 2002, Myers 2003, BirdLife International 2013). All of these schemes are managed within traditional place-based prescriptions,

targeting the areas of greatest species diversity, or biodiversity 'hotspots' (Halpern et al. 2006, Holmes et al. 2012). Yet the ocean is more dynamic and complex in processes, scales, and threats than most terrestrial systems (Maxwell et al. 2015). As a result, it is uncertain whether current spatial approaches to mitigating anthropogenic threats are likely to be effective in the marine environment, with the potential that current marine conservation schemes may be missing important areas of the ocean. To explore this question, we investigate how well conservation prioritization has overlapped with the dominant threats identified in the terrestrial and marine environments. Specifically, we (1) summarize how well the scientific empirical literature has been used to inform and guide conservation management strategies in marine and terrestrial systems. (2) We then discuss the challenges of applying terrestrial schemes to marine conservation and the conceptual frameworks needed to successfully implement marine conservation. (3) Finally, we recommend 3 additional conservation strategies to help us to more effectively mitigate anthropogenic threats to marine resources.

'HOTSPOTS' AS A CONSERVATION TOOL

'Hotspot' is one of the most fundamental terms used in both terrestrial and marine systems to identify regions in need of conservation focus. The term was first coined by Myers (1988) to identify geographic regions of 'exceptional concentrations' of endemic species undergoing exceptional loss of habitat, and a 'hotspot' originally highlighted where the greatest number of terrestrial species could be protected per conservation dollar invested (Myers 1988, 1990, 2003, Myers et al. 2000). Since its inception more than 20 years ago, the original hotspot definition has evolved as researchers have expanded upon and revised the criteria. In practice, hotspots now describe a geographical area (terrestrial or marine) ranking highly in one or more of the following biological criteria: species richness, species endemism, number of rare, threatened, or endangered species, complementarity, taxonomic distinctiveness, and degree of habitat loss (Reid 1998, Roberts et al. 2002, Brummitt & Lughadha 2003, Possingham & Wilson 2005). While the term has evolved from its original definition, in its most general sense, conservation biologists use 'hotspots' as a value-laden term to call attention to important areas of biodiversity under imminent threat (Myers 1988, Prendergast et al. 1993, Mittermeier et al. 1998, Reid 1998, Myers et

al. 2000, 2003, Roberts et al. 2002, Kareiva & Marvier 2003). The term 'hotspot' has become prevalent within academia, with nearly 1500 articles published in conservation literature using the term since Myers first coined it in 1988 (Fig. 1). While there have been criticisms of the hotspots approach (Harcourt 2000, Kareiva & Marvier 2003, Orme et al. 2005, Possingham & Wilson 2005), after over 20 years of use, it has become a fixture within conservation biology as a guide to global conservation efforts. For this reason, its consistent use throughout the field serves as a marker for how scientists and practitioners assign critical importance to a species, habitat, or threat in each system.

HOTSPOTS IN THE SCIENTIFIC LITERATURE

We evaluated all academic peer-reviewed research publications from 1988 to 2010 that define hotspots for conservation and compare how the term is used to prioritize important areas within each system. The review included all publications from *Biosis Previews* and *Web of Science*, 2 highly used and widely accessible academic search engines. All articles containing the keywords: 'hotspot' and/or 'hot spot' and 'conservation', were downloaded and entered in a database describing content, context, and detailed use of the term 'hotspot'. For consistency, book chapters, conference proceedings, non-English journal articles, and any grey literature were omitted from our database. From this comprehensive database, we placed the results of the literature review into 2 dom-

inant conservation objectives: species diversity (i.e. species richness, endemism, or rarity) and trophic-wide productivity (i.e. high concentrations of primary producers, secondary, tertiary consumers, and top predators). These 2 conservation objectives are hereafter known as 'biodiversity hotspots' and 'productivity hotspots', respectively. We then used these empirically defined 'hotspot' objectives to highlight disparity and overlap between conservation approaches, moving from the terrestrial to coastal to pelagic marine environment.

We found that in the past 20-plus years, the use of the term 'hotspot' has increased steadily. Despite the overall increase, over 80% of the 1471 studies were applied to the terrestrial systems, and less than 20% of all published hotspot literature focused on marine 'hotspots' (Fig. 1). Across both systems, results showed that 'hotspots' were most commonly referred to as areas of high biodiversity, followed by areas of high productivity. Biodiversity hotspots were most frequently used to describe a geographical area (terrestrial or marine) ranking highly in one or more of the following biological criteria: species richness, species endemism, or number of rare or threatened species. Approximately 89% of terrestrial articles used 'hotspot' to identify biodiversity under threat, with 66% using the original Myers definition (Myers 1988, 1990, 2003, Myers et al. 2000) (Fig. 2). Of the 287 marine articles, 54% defined hotspots of marine biodiversity, while 49% used the term to define areas of high productivity (i.e. primary production or nutrient concentrations) and/or species abundance (for foraging, reproduction, or recruitment purposes)

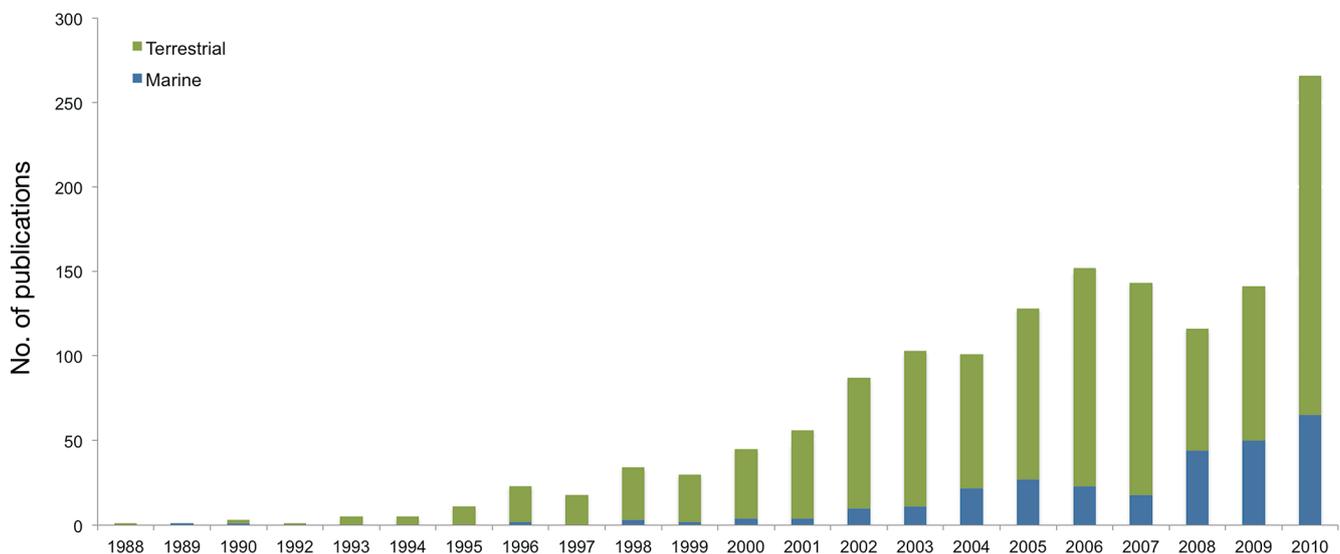


Fig. 1. Number of marine and terrestrial conservation hotspot publications from 1988 to 2010 (n = 1471)

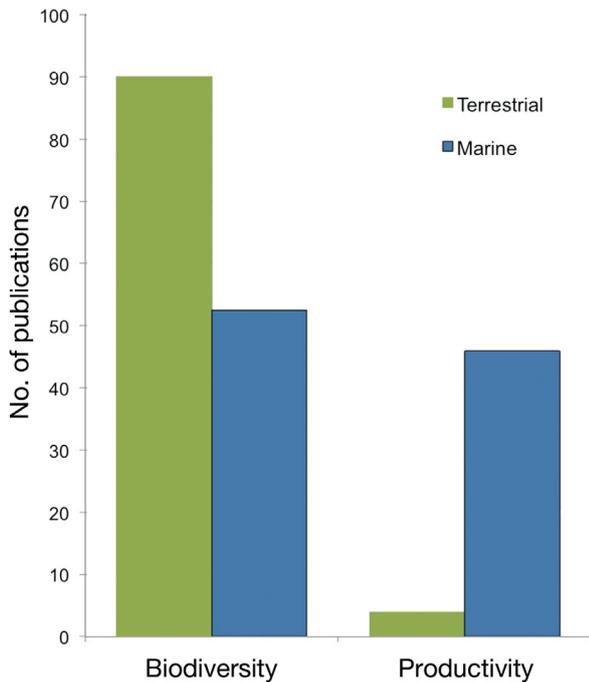


Fig. 2. Number of marine and terrestrial conservation hotspot publications focused primarily on biodiversity vs. productivity

(Fig. 2). Of these, only 3% of marine articles defined hotspots as important areas of marine biodiversity and productivity. The original Myers definition was used by 7% of marine articles.

CHALLENGES TO MARINE CONSERVATION

Results of our literature review showed that an overwhelming number of terrestrial and marine scientists identify and define 'hotspots' in the traditional, original sense: as areas of high species diversity under threat (Fig. 2). The focus on biodiversity in the terrestrial system is not surprising; reducing extinction risk and habitat loss has been identified as an effective way of protecting many species at once (Worm et al. 2005, Baillie et al. 2008, Bode et al. 2008). In the marine environment, such an approach may be suitable for shallow and/or coastal habitat (i.e. seagrass beds, kelp forests, and rocky intertidal zones), which are more static in nature, contain diverse levels of sessile endemic organisms, and thus fit well into terrestrial hotspot characterizations (see Roberts et al. 2002). The open ocean, however, is a far more complex, multidimensional system than its terrestrial counterpart. For this reason, terrestrial approaches may not be transferable to the pelagic marine environment.

Complexity of the pelagic marine environment

Unlike coastal and terrestrial regions, pelagic habitats are largely based on properties of water masses, surface currents, and wind-driven mixing (Bograd et al. 2009, Game et al. 2009, Ban et al. 2014). Away from shore, dynamic coupling between physical and biological processes spreads interactions away from geomorphic features, and over much larger spatial and shorter temporal scales (Hyrenbach et al. 2000). While there are geographically predictable locations of high productivity and diversity in the ocean (e.g. seamounts, reefs, shelf breaks), the horizontal and vertical transport of resources and organisms leads to a more dynamic and patchy environment, organisms with complex life histories and migratory behaviors, and less clearly biogeographically defined habitats (Levin & Whitfield 1994, Carr et al. 2003, Lourie & Vincent 2004). Biophysical processes such as upwelling, frontal gradients, and eddies entrain high levels of primary production that promote complex trophic linkages, and the predictable formation of these features causes species to repeatedly exploit these areas during predictable times of the year (Hyrenbach et al. 2000, Croll et al. 2005, Sydeman et al. 2006, Foley et al. 2010, Scales et al. 2015, Pikesley et al. 2013). In addition, individual movement, larval dispersion, and nutrient transport can occur across permeable habitat boundaries (Foley et al. 2010), which means that greater horizontal and vertical transport of energy and producer turnover can lead to greater patchiness of resources. As such, the community of species utilizing these areas is not always static, but rather dynamic in composition, distribution, and abundance, presenting unique challenges for determining hotspots in the marine environment.

Highly productive and highly exploited

Terrestrial productivity and biodiversity are often highly coupled in space and time (Steele 1985, Steele et al. 1994, Gaston 2000, Richmond et al. 2007). In contrast, while oceanic areas of high productivity may have high biodiversity (e.g. the global distribution of species richness in marine mammals, see Pompa et al. 2011), the two are not necessarily, nor inherently, congruent (Angel 1993). In fact, some of the most productive marine regions (e.g. the North Atlantic, Polar Seas, eastern boundary upwelling zones) are relatively low in species diversity (Botsford et al. 1997, Leslie 2005, Schipper et al. 2008) compared to the high levels of diversity found in

coral reef systems or seamounts (Morato et al. 2008, 2010, Maxwell et al. 2012). This becomes increasingly important when prioritizing marine areas with the goal of preserving valuable economic and ecological resources as they relate to areas most under threat. In effect, some important areas of marine productivity can be spatially or temporally decoupled from regions of high biodiversity, yet both are important for the overall maintenance of ecosystem function and services (Leslie & McLeod 2007).

In fact, the majority of overexploitation does not necessarily occur in the most diverse, or species-rich areas of the oceans (i.e. coral reefs), but in the highly productive marine areas that may extend from the shelf and further offshore. For example, productive areas such as upwelling regions account for only 0.1% of the ocean surface (Ryther 1969), yet they support up to 50% of the world's fisheries production (Valavanis et al. 2004). Exploitation of these highly productive marine regions has resulted in significant declines in populations of target species (e.g. tuna, billfish, and sharks), as well as the decline of non-target species incidentally taken in fisheries operations (e.g. sea turtles, seabirds, and marine mammals) (Lewison et al. 2004, Myers et al. 2007, Schipper et al. 2008). While habitat destruction remains a primary threat to terrestrial and coastal ecosystems, the greatest threat in the open ocean is the overexploitation of top predators, keystone species, and other structure-forming species (Pauly et al. 1998, Carr et al. 2003, Norse & Crowder 2005, Worm et al. 2006, Myers et al. 2007, Halpern et al. 2008, Heithaus et al. 2008, Jackson 2008, Schipper et al. 2008, Baum & Worm 2009, Hazen et al. 2013). Therefore, a focus on biodiversity alone may leave critical gaps in the way in which we manage the open ocean and fail to protect some of the most important areas of the ocean.

Indeed, marine conservation scientists recognize this. The presence of productivity hotspots within marine literature shows that the original definition of a 'hotspot' has evolved to match the different conservation needs associated with marine systems (Figs. 2 & 3). This suggests that while scientists also refer to productivity as a means to drive conservation of important ecosystem resources in the marine system, they recognize that threatened species and habitats are not limited to areas of heightened biodiversity, like in the terrestrial system. Specifically, research biologists ascribe an additional focus on areas of high productivity, which may require a suite of priority setting criteria that go beyond those used for terrestrial or even coastal conservation (Lewison et al. 2015, Maxwell et al. 2014)

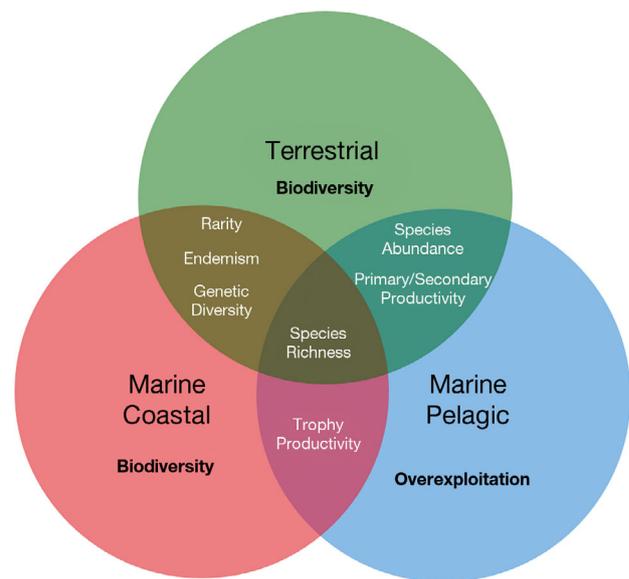


Fig. 3. Literature review results, comparing and contrasting primary threats (dark font) and conservation focus of the term 'hotspot' (white) by scientists in the terrestrial, marine coastal and pelagic systems

Putting marine conservation into practice

Over the past few decades, as marine conservation research has grown, conservation organizations have shifted their focus. An increasing number of international organizations have expanded their conservation programs to incorporate productive marine ecosystems into their portfolios and prioritization schemes. However, it is not clear if this has translated into effective conservation action.

To examine this, we compared how well results from our academic literature review are reflected in the strategic planning of marine conservation organizations over the past 10 years. Specifically, we compared the overlap of academically defined 'hotspots' with published examples of global conservation planning or action (Gilman et al. 2011). Only a decade ago, a synthesis of marine conservation planning approaches by Leslie (2005) found that few organizations were prioritizing important marine areas by objectives other than biodiversity. More recently, Gilman et al. (2011) reviewed 20 terrestrial and marine conservation organizations for design criteria. Fifteen of the 20 organizations now have marine prioritization schemes, all of which focus on marine biodiversity (e.g. species richness, endemism, rarity/threatened status). The Gilman et al. (2011) review showed that an overwhelming majority of conservation organizations still use biodiversity as the main

criteria in marine conservation planning and design. Of these, only 7 include productivity (biomass, abundance, or biophysical processes) in their design criteria for marine conservation planning (Table S1 in the Supplement at www.int-res.com/articles/suppl/n029p229_supp.pdf). As such, while some organizations are shifting focus to include biological productivity, such priority-setting criteria still largely fail to include important metrics beyond species diversity. A primary focus on biodiversity may exclude important marine regions of high productivity and biomass; these areas may be particularly important for large marine predators, which are in many cases imperiled species. Marine conservation organizations may benefit by incorporating additional criteria that include biophysical features in their priority-setting process (e.g. environmental and ecological factors, stock recovery, and endangered species) (see Table S1).

MOVING FORWARD IN PELAGIC CONSERVATION STRATEGIES

With this conceptual framework in mind, how do we best identify and quantify marine important biodiversity and productivity regions in the open ocean and assure that these are aligned with anthropogenic threats and focus for conservation action? Three non-exclusive strategies can help with achieving such alignment: (1) inclusion of productivity in priority-setting exercises; (2) large-scale protected areas and (3) incorporation of dynamic marine features.

Inclusion of productivity

A strategy that focuses on protecting processes, patterns, and features that promote enhanced biological productivity in addition to biodiversity will have a greater probability of including important conservation features. As noted by Angel (1993, p. 769), 'any conservation protocol that focuses purely on regions of high species richness runs the serious danger of overlooking those regions where processes are occurring that support the maintenance of that richness'.

Large-scale protected areas

Large-scale pelagic MPAs are likely more effective in including and thus protecting both wide-ranging habitats and oceanographic features such as fronts or eddies that are responsible for increasing or concen-

trating productivity in pelagic environments (Game et al. 2009, Toonen et al. 2013, Maxwell et al. 2014, Young et al. 2015). For example, the Pelagos Marine Sanctuary was designed to incorporate persistent frontal features in the Mediterranean Sea that facilitate the congregation of productivity, prey and a number of marine mammal species (Notarbartolo-Di-Sciara et al. 2008). While criticisms of large-scale MPAs exist regarding the feasibility of enforcing such large areas, they offer the potential to gain ecosystem levels of protection that will allow conservation practitioners to meet multiple conservation objectives in the complex marine environment (Leenhardt et al. 2013, Wilhelm et al. 2014).

Incorporation of dynamic features

More dynamic management approaches across physical, biological, and human dimensions are often more likely to include important conservation targets than traditional, 2-dimensional approaches. Dynamic ocean management, while in its infancy, is emerging as a means of protecting dynamic features and species in the ocean by allowing for protected or managed areas to move in time (Maxwell et al. 2015). The use of MPAs that are dynamic in time and space would allow for the inclusion of many of the key features such as eddies and fronts responsible for primary productivity over large-scale areas, while also protecting the mobile marine species that rely on these features. Implementation of such dynamic areas has occurred in many parts of the world (Maxwell et al. 2015, Lewison et al. 2015) and the technology necessary to implement dynamic management already exists (Hobday & Pecl 2014). While implementation may still be challenging for many organizations, dynamic management allows for ecosystem-based management that reflects the dynamic nature of marine environments (Maxwell et al. 2015).

CONCLUSIONS

We have shown that the marine conservation research literature is shifting away from a terrestrial-based biodiversity perspective to one more appropriate to the processes, scales, and spatio-temporal dynamics of marine systems. Nonetheless, the focus of conservation strategies in relation to species, processes, and threats, has lagged behind this changing perspective. Whereas the maintenance of biodiversity and habitat has been the primary conservation

objective in terrestrial and coastal marine systems (Baillie et al. 2008, Bode et al. 2008, Halpern et al. 2008), protection of species from overexploitation should be the primary focus in pelagic marine systems. Therefore, a focus on marine biodiversity alone may fail to protect some of the most important areas of the ocean from overexploitation, specifically the open ocean. Moving forward, the incorporation of dynamic and highly productive features, distributions, and processes in addition to biodiversity in management strategies, represents a great opportunity to advance our ability to support, prioritize, and manage the pelagic environment.

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