Pelagic protected areas: the missing dimension in ocean conservation

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Fewer protected areas exist in the pelagic ocean than any other ecosystem on Earth. Although there is increasing support for marine protected areas (MPAs) as a tool for pelagic conservation, there have also been numerous criticisms of the ecological, logistical and economic feasibility of place-based management in the dynamic pelagic environment. Here we argue that recent advances across conservation, oceanography and fisheries science provide the evidence, tools and information to address these criticisms and confirm MPAs as defensible and feasible instruments for pelagic conservation. Debate over the efficacy of protected areas relative to other conservation measures cannot be resolved without further implementation of MPAs in the pelagic ocean.

Introduction

The marine pelagic environment is the largest realm on Earth, constituting 99% of the biosphere volume [1]. In addition to supplying >80% of the fish consumed by humans [2], pelagic ecosystems account for nearly half of the photosynthesis on Earth [3], directly or indirectly support almost all marine life and even play a major role in the pace and extent of climate change [4]. Pelagic ecosystems (see Glossary), defined here as the physical, chemical and biological features of the marine water column, now face a multitude of threats including overfishing, pollution, climate change, eutrophication, mining and species introductions (Box 1). These threats can act synergistically [5–7] and can fundamentally alter pelagic ecosystems; important ecosystem components have been supplanted by opportunistic species [5,8], and some pelagic ecosystems have undergone dramatic shifts to undesirable states [9,10]. Although the extent of human impact in the pelagic ocean is a source of substantial debate [11–13], it is clear from declines in many species (e.g. [14-16]) that there

is inadequate protection for pelagic biodiversity and ecosystems [17]. Protected areas are being used to safeguard all other major ecosystems on Earth [18,19], but a combination of concerns over their feasibility and utility in pelagic environments has limited the establishment of pelagic protected areas (Box 2).

Compared to other environments, the pelagic ocean has relatively few regulations specifically targeting the conservation of biodiversity [20]. The governance of pelagic environments is, moreover, complicated by the pelagic ocean including waters both within national jurisdiction (near shore and exclusive economic zones; EEZs) and outside (the 'high seas'). Of those conservation regulations that exist, the vast majority are associated with the management of pelagic fisheries. This is partly because fisheries represent the largest anthropogenic threat, but also because in many regions, fisheries might be the sole

Glossary

Benthic ecosystem: physical marine substrate, its ecological processes and those organisms living in close relationship with it.

Biodiversity surrogate: data used as a proxy for the distribution of biodiversity. **Eddies**: ocean current moving vertically in a semiclosed, circular motion.

Exclusive economic zone (EEZ): area of the sea over which a state has special rights to the use of marine resources.

Fish aggregation device (FAD): a drifting or tethered buoy used by pelagic fisheries to attract and detect pelagic fish schools.

Frontal system: boundary separating two masses of water of different densities, typically warm water (less dense) and cold water (more dense). High seas: oceanic waters beyond the limits of territorial and/or economic jurisdiction of a state.

Regional Fisheries Management Organization (RFMO): multinational body responsible for the management of fish stocks on the high seas and fish stocks which migrate through the waters of more than just a single state.

Upwelling: wind-driven and/or topographic-induced motion of dense, cooler and usually nutrient-rich water toward the ocean surface.

Vessel-monitoring system (VMS): satellite-based, positional tracking system used to monitor the activity of fishing vessels.

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Pelagic ecosystem: physical, chemical and biological features of the marine water column of the open oceans or seas rather than waters adjacent to land or inland waters.

Remote sensing: acquisition of *in situ* information by remote devices such as satellites, planes or buoys floating at sea.

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Box 1. What is a pelagic protected area?

A marine protected area (MPA) is an area of sea explicitly dedicated to the protection and maintenance of marine biodiversity, ecosystems and cultural resources, and is managed for this purpose. The use of MPAs to limit the distribution of extractive, destructive and polluting activities has been widely embraced as a powerful tool for the conservation of marine environments [60]. Although individual species can be important factors in the creation of protected areas, one of their principal utilities is that they can provide broader protection to local habitats and ecosystems than many other management controls. Pelagic protected areas should be seen simply as a subset of MPAs, whose explicit goal is protection of the threedimensional marine water column and the biodiversity it contains.

MPAs contrast with other forms of management, such as total allowable catch, that emphasize controls on the mode or overall extent of activities, rather than where the activity occurs. Although our focus is principally on the use of protected areas for the conservation of biodiversity and ecosystem functioning, protected areas have been implemented to maximize or sustain the commercial harvest of pelagic species [21].

Pelagic MPAs and threat mitigation

As a conservation action, MPAs are a response to either current or future environmental threats, and must therefore be defensible as a method of mitigating these threats. Because pelagic systems are not static on the same scale as most benthic marine habitats, the use of protected areas to help mitigate threats to pelagic biodiversity represents a departure from conventional thinking regarding their utility.

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Whereas there is no question that protected areas will be neither the best nor only required response to some threat, it is our opinion that well-selected pelagic MPAs can directly or indirectly help address the eight major threats to pelagic ecosystems identified in Figure I. Of course, some threats are more easily obviated through MPAs than others. For entirely anthropogenic threats such as harvesting, mining or non-extractive use, MPAs can result in direct localized abatement. Through a reduction in cumulative impact, MPAs can also help mitigate the severity of threats where direct abatement is not possible [39]. For example, if pelagic systems of the Black Sea had not suffered severe pollution and overfishing, they would have been less vulnerable to invasive species [10]. Similarly, most climate change adaptation science for biodiversity is predicated on the notion that reducing multiple stressors will make ecosystems more resilient and therefore better able to withstand climate change [74]. Although this idea might still be somewhat speculative in pelagic oceans, the cosmopolitan nature of many species makes other management responses such as assisted migration less useful. The existence of a protected area can also create power to leverage restrictions on harmful activities outside its boundaries, for example the establishment of the Pelagos Marine Sanctuary in the Mediterranean led to reforms in catchment pollution controls on mainland Italy [63].





industry exploiting pelagic resources. Although there has been an increase in the use of spatial closures for fisheries management [21], conventional fisheries approaches to conservation typically emphasize restrictions on total catch or allowable gears, rather than specifying where fishing can occur.

Recent years have seen a rapid increase in the implementation of marine protected areas (MPAs) for conservation in both national waters [19] and the high seas [22]. Although many of these MPAs include pelagic environments, we believe these are largely inadequate for pelagic conservation for two reasons. First, many of these protected areas are designed to restrict threats to benthic environments such as mining or bottom trawling, and often fail to arrest exploitation of the associated pelagic environment (e.g. Huon Marine Reserve off southern Australia; http://www.environment.gov.au/coasts/mpa/southeast/ huon/management.html). Second, even in cases where pelagic waters are protected, this is often coincidental and not explicitly based on the occurrence of pelagic features. Such coincidental protection is inadequate, as benthic habitats are unlikely to be good surrogates for

Box 2. The missing protected area

Of all of Earth's major habitats, the pelagic ocean is almost certainly the least covered by protected areas. Depending on what is considered a protected area, the total percentage of the world's oceans in MPAs is between 0.08% and 0.65% [19]. Although pelagic ecosystems represent one of, if not the, largest marine habitat types, the proportion of their distribution in protected areas does not even register in a recent review of the global MPA network [19]. Although there is no doubt that such analyses are difficult because of the paucity of information on the distribution of marine habitats, given the vast majority of MPAs, both in territorial waters and the high seas, are biased toward benthic features [19,22], it is likely that <0.1% of pelagic habitat is currently protected. Compare this to the least protected terrestrial habitat (temperate grasslands), with 4.6% of its area under protection [18].

Existing pelagic protected areas

Spatial closures are, however, used to protect a variety of pelagic species. Area-specific, seasonal fisheries closures are used to limit incidental capture of non-target species in pelagic longline fisheries. For instance, closures limit pelagic fishing around several fixed areas in the Gulf of California [69], and around the dynamic distribution of southern bluefin tuna habitat off the east coast of Australia [50]. None of these areas, however, prevent all pelagic fishing from occurring. Similarly, MPAs for the specific protection of marine mammals exist in both territorial and high seas waters. These MPAs focus on areas of key habitat for marine mammals such as frontal systems (e.g. the Pelagos Marine Sanctuary [63]) or calving areas (e.g. the Great Australian Bight Marine Park). Although these MPAs aim to limit threats to marine mammals, they remain essentially multiple-use zones. Whereas the implementation of these protected areas largely remains too recent and limited to determine their effectiveness for pelagic conservation (see discussion on establishing effectiveness in main text), they do, however, clearly demonstrate that MPAs can be designed to protect a variety of pelagic features and are logistically and economically feasible.

pelagic habitats. Although it is widely recognized that commitments for the establishment of protected areas under agreements, such as the Convention on Biological Diversity, extend to pelagic zones [19,23], few pelagic protected areas exist (Boxes 1,2).

The current lack of pelagic protected areas, nevertheless, does not in itself represent a justification for their creation. The pelagic ocean is a uniquely dynamic environment, such that the lessons learned and evidence provided through the implementation of MPAs in near-shore benthic systems cannot, necessarily, be transferred to pelagic systems. Many pelagic species are exceptionally mobile [24], discrete pelagic habitats are difficult to identify and are likely to be transient in space and time [25] and the majority of pelagic environments (64%) occur outside national jurisdictions [26]. As a result of these fundamental differences, numerous criticisms have been leveled against the use of MPAs for the conservation of pelagic environments (summarized in Table 1). These criticisms reflect real challenges that have restricted the implementation of pelagic MPAs up to this point.

If the increasing calls for protected areas to play a role in pelagic conservation [26–29] (including a 2008 resolution by the CBD Conference of Parties [23]) are to be heeded, two important questions must be addressed. (i) Are MPAs defensible and feasible tools for the conservation of pelagic biodiversity and ecosystems? (ii) Should we pursue their implementation over other conservation mechanisms? Given a growing concern over the governance and conservation of pelagic resources, especially those in the high seas [22,23,29], it is timely to offer some perspectives on both progress and challenges with regard to these two questions. Here we detail several significant challenges and address each by drawing on evidence from recent research, methodological advances in pelagic science, as well as actual examples of implementation. Together, these allow us to answer question (i) in the affirmative. Further, we contend that the answer to question (ii) is unlikely to be resolved without further implementation of protected areas in the pelagic zone.

Biological challenges

Many pelagic species are highly mobile, with some species covering thousands of kilometers annually [24]. Short of protecting entire ocean basins, it is clearly impossible to encompass the full distribution of individuals of such species within an MPA. It could be reasonably argued that establishing an MPA over just a small portion of a species's annual distribution is of limited value, given individuals will remain exposed to threats outside the protected area. This represents a significant criticism of pelagic MPAs, because among the most mobile of all organisms are charismatic or commercially valuable species such as tunas, cetaceans, sea turtles and seabirds, all of which would be considered important targets for conservation action.

Although the protection of far-ranging species presents a major challenge for spatial management, there are good reasons to believe MPAs can be effective tools for the conservation of many pelagic species. Species are not equally vulnerable over their entire range. Often they exhibit increased vulnerability in a small number of demographically critical areas, such as breeding or foraging areas [30] or migration routes [31]. In other cases, there is only limited overlap between the range of a species and that of serious threatening processes [32,33]. In just the same way as small protected areas help conserve migratory bird species [34], MPAs encompassing critical habitat, or in places that will minimize area-specific threats, have the potential to dramatically reduce overall mortality even though they might protect only a tiny proportion of a species's range. For example, Hyrenbach et al. [35] report that relatively small MPAs off the coast of California could effectively protect the foraging grounds, and substantially reduce overall mortality, of the blackfooted albatross, a species that breeds 4500 km away. Rapid advances in satellite tagging technology have improved our ability to determine the location of these critical areas [24,31,33,36]. There have also been similarly large improvements in our ability to model and map the distribution of threats in the open ocean [37,38].

Mobile pelagic species can also suffer from the cumulative impact of sublethal stressors. Chronic exposure to chemical and acoustic pollution from shipping, military activities or oil and gas exploration and exploitation can lead to immunosuppression and reproductive failure in marine mammals [39]. Similarly, acoustic pollution and resource competition due to human exploitation of prey species can cause both nutritional stress and negative behavioral changes in pelagic predators [40–42]. Examples

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Table 1.	Common	criticisms	of MPAs for	[,] pelagic con	servation an	d management,	, along with	potential	solutions and	counter-
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Issue		Challenges	Solutions and counter-arguments		
Biological	Many pelagic species are highly mobile , often covering thousands of kilometers annually.	Spatial protection is either impossible across whole ranges or for all life-history stages, or the area required for conservation management would be unreasonably large.	Many threats to pelagic organisms are either site specific or cumulative, and can be reduced through spatial protection [39]. In addition, many organisms either show site fidelity or have relatively small and defined areas of critical habitat within their range or life histories [30,35].		
		Regulations or moratoria on gears or catch are more appropriate for limiting incidental capture of threatened pelagic fauna.	Although catch and gear regulations are an important component of pelagic conservation, they have so far proved inadequate in protecting many target and bycatch [2,14].		
Physical	The pelagic ocean is characterized by physical processes that are dynamic in space and time .	The environment is too dynamic to be represented in static reserves. Mobile reserves would be too difficult to enforce.	Many important pelagic features are either spatially or temporally predictable [28,48,49], and so static or dynamic MPAs need to be designed accordingly [45,53]. For features with less predictability, mobile fisheries closures have been effectively implemented off eastern Australia based on near real-time predictions of pelagic habitat [50]. Governance issues are also addressed below.		
Design	The pelagic ocean is generally data poor compared with terrestrial or coastal systems.	Lack of data on the complexities of pelagic ecosystems limits the selection and design of MPAs.	Widespread data sets, especially time-series data on remotely sensed physical and biological features (e.g. chlorophyll), are more abundant than commonly perceived and are useful for MPA selection [25,46,57,58]. In contrast to fisheries catch limits, the selection of pelagic MPAs does not have to rely on full understanding of ecosystem functions.		
	There is a lack of well-established design principles to inform the selection of pelagic MPAs.	Design principles for pelagic MPAs will need to be developed <i>de novo</i> .	Some existing conservation planning tools and methods can be used in the pelagic ocean (e.g. Marxan [45]), and good case studies are starting to appear [53]. New challenges will lead to novel solutions with broad impact.		
Governance	MPAs might need to extend outside a country's EEZ.	Beyond national jurisdictions there is no legal basis for MPAs.	Numerous existing international and regional agreements can be exercised to regulate MPAs in the high seas [62].		
	Exploitation of the pelagic ocean is generally difficult and expensive to observe, and it is therefore challenging to enforce regulations.	MPAs will be more difficult and expensive to enforce, especially in developing nations, than traditional catch or gear restrictions.	Widespread adoption of satellite VMSs, and financial support for this in developing nations, will improve remote surveillance.		

include: human competition for sardine or anchovy, forcing Cape gannets off South Africa to feed primarily on less nutritious discards from the hake fishery, severely reducing breeding success [41]; and drifting fish aggregation devices (FADs) attracting tropical tuna schools to waters with scarce food supplies [42]. Even if individuals only inhabit protected areas (or areas where fishing on drifting FADs is prohibited) for part of the year, they will still benefit from diminished exposure to these stressors and therefore an increase in fitness. This is especially true where protection coincides with energetically demanding periods such as breeding.

Even where pelagic MPAs are recognized as a potentially useful tool, the high mobility of pelagic species leads to the common perception that the area required for adequate protection is so large that socioeconomic costs of closure would be prohibitive [1,43]. Although a politically important criticism, as it highlights the potential impact of closed areas on fisheries and other extractive industries such as oil and gas, there is substantial evidence to the contrary. As discussed above, protection can be directed to a few critical areas, such that the area required to protect many pelagic species and processes represents only a small proportion of the total seascape and is comparable to the proportion of area required in near-shore or terrestrial systems [29,44,45]. For example, Alpine and Hobday [45] show that it would require just 13% of the pelagic area off eastern Australia to protect 20% of the annual distribution of 40 important pelagic species and major physical processes such frontal systems and upwelling areas. Additionally, extractive industries in the pelagic ocean tend to target small areas of high productivity, such that total area protected and financial impact are not likely to be well correlated. It is, however, possible to explicitly minimize the impact that pelagic MPAs have on industries such as fishing, by considering the spatial and temporal distribution of their effort and income during the design process [45].

Physical challenges

The pelagic environment is characterized by physical processes that are highly dynamic in space and time. These include ocean currents, thermal fronts, upwelling and downwelling regions and eddies and wind-driven mixing. More than simply transient features on the pelagic seascape, these processes largely control the abundance, distribution and composition of biological life in the pelagic realm [46] and, as such, serve as an important surrogate

for much pelagic biodiversity. Acknowledging this fundamental reality could be seen as directly contradicting the role of discrete spatial management in protecting pelagic biodiversity and ecosystem processes; increasing dynamism reduces the efficacy of fixed closed areas [47]. The use of protected areas to conserve dynamic pelagic systems can, however, be reconciled by considering two key points. First, nearly all important physical processes in the pelagic environment exhibit some level of spatial or temporal predictability, with corresponding biological and physical responses that can be exploited in the design of MPAs [28,48,49]. Second, unlike in terrestrial or coastal environments, pelagic protected areas need not be fixed, but rather can track the dynamics of pelagic features that serve as important surrogates for pelagic biodiversity [50].

Pelagic MPAs will require different design responses depending on the physical features they are targeting for protection. Some physical processes are related to fixed bathymetric features: elevated productivity resulting from localized upwelling at seamounts [51], and thermal fronts aggregate prey species at continental shelves [52], thereby concentrating top predators [28]. These features could reliably be represented in permanent and spatially fixed MPAs. For other events that are spatially predictable but temporally variable such as wind-driven upwelling or migration of species to particular areas, static MPAs could be applied seasonally [53]. Features that are temporally predictable but spatially dynamic, such as major currents and fronts that move through known trajectories, can be represented either within a series of fixed reserves designed to capture the feature at different times through the year [45], or within a larger single reserve aligned along the likely axis of movement [31,53].

A more sophisticated approach to the dynamism of the pelagic ocean is to implement spatial management that mirrors this property, with closures that are truly mobile and change with time. This logical solution has typically not been considered feasible because of enforcement difficulties and costs. However, just as the pelagic environment is more dynamic than terrestrial or coastal areas, so are those users who exploit this environment. As most of the pelagic ocean lacks static property rights, resource users are highly mobile and accurate navigators. Advances in satellite positioning and communications mean that information can be conveyed to remote vessels in near real time. Because of these factors, there is little doubt that dynamic protected areas will be easier to implement in pelagic ecosystems than elsewhere. In addition, the total area required for effective protection using dynamic MPAs is likely to be far less than under static MPAs. As an example of the exciting real potential for dynamic pelagic MPAs, mobile fisheries closures for southern bluefin tuna have been effectively implemented off eastern Australia since 2003 based on near real-time predictions of the species's preferred pelagic habitat [50]. Such solutions invariably require strong support and participation from fishing industries.

Design challenges

Even with broad agreement that well-designed and -located MPAs would be a valuable tool for pelagic management, there are still concerns over a lack of data, methods and tools to enable defensible selection of the best areas for protection.

Data

The pelagic ocean is generally data poor compared with terrestrial or coastal systems. Additionally, the selection of terrestrial and coastal protected areas has typically been based on broad, static biodiversity surrogates such as habitats, which have traditionally been difficult to identify in the pelagic ocean. From these realities has come the criticism that the complexities of pelagic systems are not well characterized and that it is therefore difficult to make informed decisions on the placement of MPAs [54]. However, in our opinion, these perceived limitations actually favor the use of MPAs. The selection of protected areas on land or in the sea does not rely on a full understanding of ecosystem dynamics and functioning to have broad benefits. This is in contrast to other forms of marine management such as conventional fisheries regulations which, to be effective as conservation tools, require detailed species-level information. For example, high seas longline fisheries catch as many as 100 species as bycatch, and the expectation that appropriate catch limits, or gear modifications, can be applied and monitored for all of these species and their complex interaction with abiotic changes is unrealistic. In this regard, MPAs represent a more precautionary approach to pelagic conservation than relying on management controls over a few species to provide protection for entire ecosystems.

Far from being devoid of data, the pelagic ocean is covered by extensive data sets useful for designing protected areas. Rapid advances in remote data collection mean that broad surrogates for biodiversity and its dynamics are now arguably easier to obtain for the pelagic ocean than for coastal benthos. The elevated primary and secondary productivity that is closely linked to the occurrence of many pelagic species [49,55,56] can be inferred from remotely sensed surrogates such as sea-surface chlorophyll, sea-surface temperature or sea-surface height. Remotely sensed data can also be usefully applied in combination with fisheries data to differentiate distinct and temporally variable pelagic 'habitats' [25,31,46,57,58]. As a basis for identifying potential MPA sites, remotely sensed data have two strong advantages: they are relatively cheap (or free) to acquire and generally have extensive and consistent spatial coverage. The necessary reliance on remotely sensed surrogates for biodiversity actually eliminates many of the challenges of incorporating spatially biased ecological data that are routinely faced during the design of coastal MPAs.

MPA selection

MPAs will be most effective at achieving multiple objectives if their selection is the outcome of a formal spatial prioritization that addresses quantitative conservation objectives (e.g. percentage representation), qualitative design criteria (e.g. size or orientation), patterns of threat and competing demands for resource use [59]. Although there is a well-developed theory to support the selection of coastal and benthic-based MPAs [60], the absence of

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Box 3. Selecting pelagic MPAs: eastern Australia case study

Conservation planning software is routinely used in the design of terrestrial and coastal conservation area networks and can help provide efficient economic, social and ecological solutions to the representation of biodiversity [59]. Inputs into such software are generally static representations of biodiversity distribution, so their



Figure I. Examples of remotely sensed data for the east coast of Australia that are useful for describing oceanographic properties. (a) Sea-surface height (SSH) for the 7 day period centered on August 1, 2002, from which upwelling (low SSH) and downwelling (high SSH) eddies can be identified. (b) Frontal index map for the same period showing the number of times that a pixel contained a front.

structured planning approaches in the pelagic ocean means that conservation management competes weakly with more extensively developed methods such as those for fisheries management. Exacerbating this problem is the fact that systematic conservation planning approaches, now the standard for identifying both terrestrial and coastal protected areas [59], have generally failed to adequately deal with dynamic systems [61].

Despite the relative dearth of literature on selecting pelagic MPAs, large steps have been taken toward developing a systematic framework. Hyrenbach *et al.* [28] identified important features of the pelagic ocean that are application to dynamic pelagic ecosystems has been limited. One simple way to address this dynamism is to consider the distribution of pelagic features at different times throughout the year.

Alpine and Hobday [45] describe the use of the conservation planning software Marxan (http://www.uq.edu.au/marxan) to assist in developing a pelagic MPA network along Australia's east coast. The primary goal of the MPA network was to protect five pelagic species targeted by the eastern Australian tuna and billfish longline fishery, as well as providing ecosystem-wide protection from negative fishery impacts. The identification of candidate MPAs was based upon the distribution of 35 pelagic species, collected through fisheries and tagging data, and the distribution of physical habitat features, obtained primarily from remote sensing. The process targeted both static features such as seamounts and shelf breaks, as well as dynamic hydrographic features (thermal fronts, and upwelling and downwelling eddies; Figure I). The distribution of species and dynamic habitat features were divided into four seasons, each considered as a separate conservation feature. Marxan was then used to select MPA networks that captured 20% of the extent of each feature, while trying to minimize the impact of the MPA network on fisheries' revenue (Figure II). By basing such an MPA network on dynamic environmental data, it better reflects the nature of this pelagic system and the distribution of key features at any point in time. Such an approach provides a useful template for the implementation of MPAs in other dynamic open ocean environments elsewhere in the world.



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Figure II. Priority areas for pelagic MPAs off the east coast of Australia, as identified by the conservation planning software Marxan. The color of each cell indicates the frequency with which that site was selected as part of the 'best' MPA network across 100 runs of Marxan. Red cells were nearly always included as part of the optimal reserve network and can therefore be considered highly important areas for efficient pelagic conservation. Each potential MPA network aimed to capture at least 20% of the extent of 40 different physical and biological pelagic features, across all four seasons of the year, while at the same time minimizing the impact of prospective MPAs on fisheries revenue. Reproduced from Ref. [45] with permission.

suitable targets for spatial protection, categorizing them as static bathymetric, persistent hydrographic or ephemeral hydrographic, and suggested a series of MPA design considerations for each category. Alpine and Hobday [45] extended these ideas by showing how quantitative targets can be applied to pelagic features, as well as to selected individual species (Box 3). Their study also demonstrated how freely available reserve selection software can be used to design an efficient network of pelagic MPAs that minimized the impact on existing fisheries. Similarly, Lombard *et al.* [53] provided an example of how the boundaries of MPAs can be defined to adequately capture important

pelagic processes around islands in the Southern Ocean and are likely to aid compliance.

Governance challenges

The vast majority of the pelagic ocean is both beyond the sight of land and distant from ports. Restricting access to such areas presents a substantial governance challenge owing to the fragmented and sectoral management framework common for most offshore regions, particularly in countries with limited resources and on the high seas. Within the 200 nautical mile (nm) EEZ, coastal states have the legal ability to establish and enforce laws to protect their marine resources. States can thus establish pelagic protected areas out to 200 nm and develop management regimes, assuming the appropriate national legislation exists and the applicable international rules are complied with. On the high seas, there is no single body with the authority to establish protected areas or to regulate access to and use of an area for more than one purpose. This has been seen as a major obstacle to the establishment of MPAs to protect valuable pelagic resources.

With respect to fishing activities, progress can nevertheless be made through Regional Fisheries Management Organizations (RFMOs). The 1995 United Nations Fish Stocks Agreement specifically calls on its state parties to 'protect biodiversity in the marine environment.' Although many regional fisheries management organizations have not yet used their authority to protect biodiversity, increased international scrutiny is prompting action at least with respect to deep sea biodiversity: the UN General Assembly adopted a resolution in 2006 specifically calling for RFMOs to manage deep sea bottom fisheries on the high seas to protect biodiversity. As a result, several largescale areas have been closed to benthic fishing [62]. These powers could equally be used to protect pelagic biodiversity.

High seas shipping activities could also be regulated through measures adopted by the International Maritime Organization. However, this would still not address other high seas activities such as scientific research, ocean dumping, potential CO_2 sequestration activities such as ocean fertilization, or of course military activities subject to sovereign immunity. What is lacking is a functional coordinating mechanism to ensure comprehensive management of the activities that could occur in or impact a specific area. Whereas some suggest that a new international agreement is an essential next step to enable coordinated management of high seas MPAs, ad hoc agreements between states, such as was done in the Pelagos Sanctuary [63], could also be utilized, at least as an interim step.

Enforcement challenges

Regardless of the legal support for protected areas, the pernicious influence of illegal, unreported and unregulated (IUU) fishing in the high seas and national waters of both developing and developed countries remains a major challenge for pelagic MPAs. In national waters, the problem hinges on a lack of technical capacity to monitor remote vessel activities and enforce MPA violations. Trends in Ecology and Evolution Vol.xxx No.x

New information-sharing networks such as the voluntary International Monitoring, Surveillance and Control Network of enforcement professionals (http://www.imcsnet.org) and improved technical tools (e.g. remote sensing, synthetic-aperture radar and vessel-monitoring systems [VMS]) provide hope that these challenges will soon be overcome. As well as assisting enforcement, VMS can aid compliance by including boundaries of pelagic MPAs and issuing automatic warnings to vessels when these boundaries are approached. VMS technology is currently used successfully in many fisheries, such as in the Southern Ocean to monitor exploitation of distant stocks of Patagonian toothfish. Because of the real potential to detect violations remotely, ensuring widespread compliance with spatial restrictions might be easier than catch or gear restrictions [29].

A new international agreement under negotiation on port state measures could enhance the ability of all states to enforce fisheries regulations by building up a global cooperative system whereby states would be able to arrest foreign vessels for violations when these vessels call on domestic ports. This agreement could help build enforcement capacity in developing countries while negating the need for expensive at-sea operations [62].

MPAs versus other conservation strategies

Protected areas are not a panacea for the conservation of pelagic biodiversity. MPAs are just one component of the pelagic conservation landscape, and should be complemented by other forms of management. Just as with all other ecosystems, there are likely to be cases in the pelagic ocean where protected areas will not be the best conservation action. It is therefore important to try and identify areas or situations where pelagic protected areas offer benefits that other regulatory mechanisms cannot.

In our opinion, a good place to start would be to encourage the protection of representative examples of all pelagic habitats, in line with international conventions for biodiversity conservation [23]. Representation could be based on recently available biogeographic classifications of the pelagic realm into distinct ecological provinces [25,57]. In addition, the CBD provides seven detailed criteria for identifying ecologically significant areas in the open ocean in need of protection [23]. Used in conjunction with the data and MPA selection methods described above, these classifications and criteria provide a rational basis for identifying the first tier of sites for pelagic MPAs.

Another important role for pelagic MPAs will be in protecting pelagic environments that are considered particularly vulnerable to rapid ecosystem shifts in response to climate change [64,65]. In such cases, protection might help buffer rapid changes in productivity that can dramatically affect species' abundance [6,64,65] but are not immediately reflected in harvest or activity restrictions. As discussed above, pelagic MPAs are potentially easier to enforce than catch or gear restrictions for fisheries, or operational restrictions for other extractive industries, and so might be a preferable form of management in international waters (the high seas) and in the national waters of countries with limited regulatory capacity, such as those off the southwest coast of Africa [66]. Once in

place, legislated MPAs are less prone to political manipulation than harvest quotas [21] or temporal moratoria.

Alternate mechanisms for biodiversity protection exist in many industries that operate in the pelagic ocean, for example seismic surveys for oil and gas [67]. Most pelagic fisheries have a well-developed management science and numerous regulatory measures aimed specifically at biodiversity conservation, particularly through the reduction of bycatch. It is likely that this overlap in objectives partly explains the unfortunate view of MPAs as a threat to conventional fisheries management [68], something that has, without question, hindered their implementation. We believe instead that MPAs (for conservation) should largely be viewed as a complementary management strategy, employed in conjunction with less spatially restrictive measures [69]. Of course, this should not stop fisheries concerns influencing the location of pelagic MPAs, or stop conservation considerations influencing fisheries regulations; measures such as streamers and circle hooks on long lines are, and should continue to be, important conservation measures for some pelagic species [70]. Such speciestargeted gear restrictions might be preferable to MPAs for pelagic megafauna where vulnerability is not highly clustered in space or time, or are only threatened by a single fishery. Similarly, we see little reason why the conservation of species targeted by pelagic fisheries, especially those fisheries with minimal bycatch, should not be principally managed through catch restrictions. By contrast, in regions where several different pelagic fisheries operate (e.g. the North Sea), or in fisheries with a large number of bycatch species, pelagic protected areas will be an important conservation tool. It is vital that conservation biologists and fisheries scientists work together when developing pelagic MPAs, both because the effectiveness of MPAs depends also on what happens outside protected areas and because the impact of protected areas will need to be considered when determining fisheries restrictions such as catch quotas [47,68].

Establishing effectiveness

The limited implementation of pelagic MPAs (Box 2) currently means that their effectiveness as tools for the conservation of pelagic biodiversity remains largely unproven. Similarly, the complex and dynamic nature of ocean ecosystems is such that even thorough modeling studies are unable to draw robust conclusions about the efficacy of pelagic protected areas [47]. It is our opinion that unequivocal proof is too great a benchmark to set before implementation; consider the challenge of demonstrating the impact of near-shore MPAs despite large-scale implementation [71], and that debate over the efficacy of conventional fisheries management measures still rages after many decades of use [12,72]. Indeed, failing to implement pelagic protected areas for want of more evidence will make it substantially more difficult to ever acquire this evidence.

The creation of pelagic MPAs should be treated as largescale adaptive management experiments. With low investment in immovable infrastructure and the high adaptive capacity of most stakeholders, pelagic protected areas lend themselves to adaptive adjustment of designations. The experimental establishment of pelagic protected areas,

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however, needs to be accompanied by a clear framework for monitoring and learning about the response of the system. At present, few fisheries-independent measures of pelagic ecosystem and biodiversity health exist, with a key exception being the condition and fecundity of shorebreeding fauna such as birds and seals. Not only will new metrics, other than commercial catch records, need to be developed, but additional ways to obtain the necessary data are also required.

Future directions

We are much closer to providing transparent and useful advice on the location of pelagic MPAs than is commonly thought. Extensive data on physical, biological and socioeconomic factors can be used in concert with new conservation planning techniques to guide the defensible selection and design of pelagic MPAs. Advances in satellite technology can facilitate compliance and open the way for pelagic MPAs that are dynamic in space and time. However, it is important not to understate remaining challenges.

Effective collection and interpretation of the data discussed above require continued and improved engagement between marine conservation planners, fisheries managers and the oceanographic community. Although new and tractable approaches to reserve selection in dynamic environments are emerging [61,73], their use in pelagic systems will require extending classical conservation planning from two to four dimensions, with the inclusion of both depth and time components. There remains an urgent need for a more integrated approach to management of nonfisheries threats (e.g. pollution) and IUU activities (e.g. ship discharges, dumping) on the high seas [62]. Similarly, the cost of remote monitoring and surveillance technologies is a significant obstacle to its use in developing nations. Universal mandate of such technologies, combined with expansion of the existing program of subsidies which operate in many developing nations, is an important governance step for pelagic MPAs.

Despite the challenges highlighted here, there are also enormous opportunities for implementing MPAs in the pelagic ocean: weak private property rights, limited habitat transformation and potentially lower costs of protected area management. As a result, it appears likely that solutions to the broad challenge of conservation planning and management for dynamic systems will be primarily advanced in the pelagic ocean. Indeed, given the new challenges presented by a rapidly changing climate, the future of MPAs more generally might lie in creative solutions developed in the pelagic ocean. We believe that pelagic MPAs have now come of age as an important tool in the planet's last frontier of conservation management.

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References

1 Angel, M.V. (1993) Biodiversity of the pelagic ocean. Conserv. Biol. 7, 760–772

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- 2 Pauly, D. et al. (2002) Towards sustainability in world fisheries. Nature 418, 689–695
- 3 Field, C.B. et al. (1998) Primary production of the biosphere: integrating terrestrial and economic components. Science 281, 237–240
- 4 Hays, G.C. et al. (2005) Climate change and marine plankton. Trends Ecol. Evol. 20, 337–344
- 5 Oguz, T. and Gilbert, D. (2007) Abrupt transitions of the top-down controlled Black Sea pelagic ecosystem during 1960-2000: evidence for regime-shifts under strong fishery exploitation and nutrient enrichment modulated by climate-induced variations. *Deep Sea Res. Part I Oceanogr. Res. Pap.* 54, 220–242
- 6 Miller, K.A. (2007) Climate variability and tropical tuna: management challenges for highly migratory fish stocks. *Mar. Policy* 31, 56–70
- 7 Frederiksen, M. *et al.* (2004) The role of industrial fisheries and oceanographic change in the decline of the North Sea black-legged kittiwakes. J. Appl. Ecol. 41, 1129–1139
- 8 Lynam, C.P. et al. (2006) Jellyfish overtake fish in a heavily fished ecosystem. Curr. Biol. 16, R492-R493
- 9 Bakun, A. and Weeks, S.J. (2004) Greenhouse gas buildup, sardines, submarine eruptions and the possibility of abrupt degradation of intense marine upwelling ecosystems. *Ecol. Lett.* 7, 1015–1023
- 10 Daskalov, G.M. et al. (2007) Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. Proc. Natl. Acad. Sci. U. S. A. 104, 10518–10523
- 11 Sibert, J. et al. (2006) Biomass, size, and trophic status of top predators in the Pacific Ocean. Science 314, 1773–1776
- 12 Polacheck, T. (2006) Tuna longline catch rates in the Indian Ocean: did industrial fishing result in a 90% rapid decline in the abundance of large predatory species? *Mar. Policy* 30, 470–482
- 13 de Mutsert, K. et al. (2008) Reanalyses of Gulf of Mexico fisheries data: landings can be misleading in assessments of fisheries and fisheries ecosystems. Proc. Natl. Acad. Sci. U. S. A. 105, 2740–2744
- 14 Lewison, R.L. *et al.* (2004) Quantifying the effects of fisheries on threatened species: the impact of pelagic longline on loggerhead and leatherback turtles. *Ecol. Lett.* 7, 221–231
- 15 Baum, J.K. and Myers, R.A. (2004) Shifting baseline and the decline of pelagic sharks in the Gulf of Mexico. *Ecol. Lett.* 7, 135–145
- 16 Crawford, R.J.M. et al. (2007) Trends in numbers of Cape gannets (Morus capensis), 1956/57-2005/2006, with a consideration of the influence of food and other factors. ICES J. Mar. Sci. 64, 169–177
- 17 Verity, P.G. et al. (2002) Status, trends and the future of the marine pelagic ecosystem. Environ. Conserv. 29, 207–237
- 18 Hoekstra, J.M. et al. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecol. Lett. 8, 23–29
- 19 Wood, L.J. et al. (2008) Assessing progress towards global marine protection targets: shortfalls in information and action. Oryx 42, 340-351
- 20 Vallega, A. (2000) Sustainable Ocean Governance: A Geographical Perspective. Routledge
- 21 Roberts, C.M. et al. (2005) The role of marine reserves in achieving sustainable fisheries. Philos. Trans. R. Soc. B Biol. Sci. 360, 123–132
- 22 Corrigan, C. and Kershaw, F. (2008) Working toward High Seas Marine Protected Areas: An Assessment of Progress Made and Recommendation for Collaboration. UNEP-WCMC
- 23 CBD. (2008) Decisions Adopted by the Conference of the Parties to the Convention on Biological Diversity at Its Ninth Meeting (Decision IX/ 20, Annexes I–III), Convention on Biological Diversity
- 24 Block, B.A. et al. (2005) Electronic tagging and population structure of Atlantic blue-fin tuna. Nature 434, 1121–1127
- 25 Hardman-Mountford, N.J. *et al.* (2008) An objective methodology for the classification of ecological pattern into biomes and provinces for the pelagic ocean. *Remote Sens. Environ.* 112, 3341–3352
- 26 Norse, E. (2006) Pelagic protected areas: the greatest park challenge of the 21st century. Parks 15, 33–40
- 27 Pelagic Working Group. (2002) Pelagic Predators, Prey and Processes: Exploring the Scientific Basis for Offshore Marine Reserves, Proceedings of the First Pelagic Working Group Workshop, January 17, 2002, Santa Cruz, CA
- 28 Hyrenbach, K.D. et al. (2000) Marine protected areas and ocean basin management. Aquat. Conserv.: Mar. Freshwat. Ecosyst. 10, 437–458
- 29 Sumaila, U.R. et al. (2007) Potential costs and benefits of marine reserves in the high seas. Mar. Ecol. Prog. Ser. 345, 305–310

- 30 Louzao, M. et al. (2006) Oceanographic habitat of an endangered Mediterranean procellariiform: implications for marine protected areas. Ecol. Appl. 16, 1683-1695
- 31 Schillinger, G.L. *et al.* (2008) Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* 6, e171
- 32 Weimerskirch, H. et al. (2006) Postnatal dispersal of wandering albatrosses Diomedea exulans: implications for the conservation of the species. J. Avian Biol. 37, 23–28
- 33 Ferraroli, S. et al. (2004) Where leatherback turtles meet fisheries. Nature 429, 521–522
- 34 Martin, T.G. et al. (2007) Optimal conservation of migratory species. PLoS ONE 2, e751
- 35 Hyrenbach, K.D. et al. (2006) Use of marine sanctuaries by far-ranging predators: commuting flights to the California current system by breeding Hawaiian albatrosses. Fish. Oceanogr. 15, 95–103
- 36 Piatt, J.F. et al. (2006) Predictable hotspots and foraging habitat of the endangered short-tailed albatross (*Phoebastria albatrus*) in the North Pacific: implications for conservation. Deep Sea Res. Part II Top. Stud. Oceanogr. 53, 387–398
- 37 Zacharias, M.A. and Gregr, E.J. (2005) Sensitivity and vulnerability in marine environments: an approach to identifying vulnerable marine areas. *Conserv. Biol.* 19, 86–97
- 38 Halpern, B.S. et al. (2008) A global map of human impact on marine ecosystems. Science 319, 948–952
- 39 Hooker, S.K. and Gerber, L.R. (2004) Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. *Bioscience* 54, 27–39
- 40 Sara, G. et al. (2007) Effect of boat noise on the behaviour of bluefin tuna Thunnus thynnus in the Mediterranean Sea. Mar. Ecol. Prog. Ser. 331, 243–253
- 41 Gremillet, D. et al. (2008) A junk food hypothesis for gannets feeding on fishery waste. Proc. R. Soc. Lond. B Biol. Sci. 18, 1–9
- 42 Hallier, J. and Gaertner, D. (2008) Drifting fish aggregation devices could act as an ecological trap for tropical tuna species. *Mar. Ecol. Prog. Ser.* 353, 255–264
- 43 Boersma, P.D. and Parrish, J.K. (1999) Limiting abuse: marine protected areas, a limited solution. *Ecol. Econ.* 31, 287–304
- 44 Roberts, C.M. et al. (2006) Roadmap to Recovery: A Global Network of Marine Reserves. Greenpeace International
- 45 Alpine, J.E. and Hobday, A.J. (2007) Area requirements and pelagic protected areas: is size an impediment to implementation? *Mar. Freshw. Res.* 58, 558-569
- 46 Palacios, D.M. et al. (2006) Oceanographic characteristics of biological hot spots in the North Pacific: a remote sensing perspective. Deep Sea Res. Part II Top. Stud. Oceanogr. 53, 250–269
- 47 Martell, S.J.D. et al. (2005) Interactions of productivity, predation risk, and fishing effort in the efficacy of marine protected areas for the central Pacific. Can. J. Fish. Aquat. Sci. 62, 1320–1336
- 48 Wiemerskirch, H. (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res. Part II Top. Stud. Oceanogr. 54, 211–223
- 49 Etnoyer, P. et al. (2004) Persistent pelagic habitats in the Baja California to Bearing Sea (B2B) ecoregion. Oceanography (Wash. D.C.) 17, 90-99
- 50 Hobday, A.J. and Hartmann, K. (2006) Near real-time spatial management based on habitat predictions for a longline bycatch species. Fish. Manag. Ecol. 13, 365–380
- 51 Boehlert, G. (1987) A review of the effects of seamounts on biological processes. *Geophys. Monogr.* 43, 319–334
- 52 Young, J.W. et al. (2001) Yellowfin tuna (Thunnus albacares) aggregations along the shelf break off south-eastern Australia: links between inshore and offshore processes. Mar. Freshw. Res. 52, 463–474
- 53 Lombard, A.T. *et al.* (2007) Conserving pattern and process in the Southern Ocean: designing a marine protected area for the Prince Edward Islands. *Antarct. Sci.* 19, 39–54
- 54 Sale, P.F. et al. (2005) Critical science gaps impede use of no-take fishery reserves. Trends Ecol. Evol. 20, 74–80
- 55 Pinaud, D. and Weimerskirch, H. (2007) At-sea distribution and scaledependent foraging behaviour of petrels and albatrosses: a comparative study. J. Anim. Ecol. 76, 9–19
- 56 Gremillet, D. et al. (2008) Spatial match-mismatch in the Benguela upwelling zone: should we expect chlorophyll and SST to predict marine predator distributions? J. Appl. Ecol. 45, 610–621

- 57 Devred, E. et al. (2007) Delineation of ecological provinces using colour radiometry. Mar. Ecol. Prog. Ser. 346, 1–13
- 58 Zainuddin, M. et al. (2006) Using multi-sensor satellite remote sensing and catch data to detect ocean hot spots for albacore (*Thunnus* alalunga) in the northwestern North Pacific. Deep Sea Res. Part II Top. Stud. Oceanogr. 53, 419–431
- 59 Possingham, H.P. *et al.* (2006) Protected areas: goals, limitation and design. In *Principles of Conservation Biology* (3rd edn) (Groom, M.J., ed.), pp. 509–533, Sinauer Associates
- 60 Lubchenco, J. et al. (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecol. Appl. 13, S3–S7
- 61 Pressey, R.L. et al. (2007) Conservation planning in a changing world. Trends Ecol. Evol. 22, 583–592
- 62 Gjerde, K.M. et al. (2008) Options for Addressing Regulatory and Governance Gaps in the International Regime for the Conservation and Sustainable Use of Marine Biodiversity in Areas beyond National Jurisdiction. IUCN
- 63 Notarbatolo di Sciara, G. et al. (2008) The Pelagos Sanctuary for Mediterranean marine mammals. Aquat. Conserv. Mar. Freshwat. Ecosyst. 18, 367–391
- 64 Beaugrand, G. et al. (2008) Causes and projections of abrupt climatedriven ecosystem shifts in the North Atlantic. Ecol. Lett. 11, 1157–1168
- 65 Soto, C.G. (2002) The potential impacts of global climate change on marine protected areas. *Rev. Fish Biol. Fish.* 11, 181–195
- 66 SEAFO. (2006) Conservation Measures 06/06: On the Management of Vulnerable Deep Water Habitats and Ecosystems in the SEAFO Convention Area, SEAF Organisation. (http://www.seafo.org/Cons%

Trends in Ecology and Evolution Vol.xxx No.x

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- 67 Compton, R. et al. (2008) A critical examination of worldwide guidelines for minimising the disturbance to marine mammals during seismic surveys. Mar. Policy 32, 255–262
- 68 Field, J.C. et al. (2006) Does MPA mean 'major problem for assessments'? Considering the consequences of place-based management systems. Fish Fish. 7, 284–302
- 69 NOAA. (2000) Regulatory Amendment 1 to the Atlantic Tunas, Swordfish, and Sharks Fishery Management Plan: Reduction of Bycatch, Bycatch Mortality, and Incidental Catch in the Atlantic Pelagic Longline Fishery, Highly Migratory Species Division, National Marine Fisheries Service, National Oceanic and Atmospheric Administration
- 70 Gilman, E. et al. (2006) Reducing sea turtle by-catch in pelagic longline fisheries. Fish Fish. 7, 2–23
- 71 Willis, T.J. et al. (2003) Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? Environ. Conserv. 30, 97– 103
- 72 Schrank, W.E. (2007) Is there any hope for fisheries management? Mar. Policy 31, 299–307
- 73 Game, E.T. et al. (2008) Planning for persistence in marine reserves: a question of catastrophic importance. Ecol. Appl. 18, 670–680
- 74 Hughes, T.P. et al. (2005) New paradigms for supporting the resilience of marine ecosystems. Trends Ecol. Evol. 20, 380–386
- 75 Kappel, C.V. (2005) Losing pieces of the puzzle: threats to marine, estuarine, and diadromous species. Front. Ecol. Environ. 3, 275–282