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New framework reveals gaps in US ocean biodiversity protection

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SUMMARY

Human activities threaten Earth's biodiversity and its contributions to human well-being. In the ocean, our poor understanding of how biodiversity is distributed limits its management and protection, necessitating reliance on weak abiotic proxies. Here, we propose a scientific framework for assessing marine biodiversity at multiple spatial scales, which exposes gaps in biodiversity knowledge and protection. The framework prioritizes ecologically and societally important taxa, characteristics of effective networks, and existing data. Applying the framework to assess biodiversity inside and outside US marine protected areas, we reveal that these areas contain a fraction of the biodiversity found in US waters. We show that none of the nation's 24 marine ecoregions meet all criteria for an effective protection network and that biodiversity coverage in protected areas varies among regions and taxa. This marine biodiversity assessment highlights concrete recommendations for more strategic protection and validates a scientific framework generalizable to other spatial management uses.

INTRODUCTION

Earth's biodiversity includes roughly 1.9 million described species, of which about 226,000, or ~12%, live in the ocean. Up to 20,000 marine species are being described every decade, and most remain undiscovered.[1] The activities of and interactions among these organisms fundamentally influence how marine ecosystems function and the services they provide to

humanity.[2–4] In the ocean and along coasts, services provided by marine life include the primary protein source for 3 billion people, support for livelihoods, shoreline protection, and carbon sequestration that are collectively valued at US$50 trillion annually.[5,6]

Marine species and habitats are increasingly at risk from anthropogenic pressures, including climate change, globalized commerce, overfishing, land- and sea-use change, extractive industries, and other stressors.[7,8] The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) recently concluded that 1 million species are threatened with extinction worldwide.[9] In the ocean specifically, warming, acidification, and oxygen depletion threaten a major extinction event without aggressive efforts to curtail and reverse greenhouse gas emissions.[10] The urgency of the intertwined biodiversity and climate crises has produced calls for substantially expanding climate-smart biodiversity protection across both terrestrial and marine realms.[11–15]

The data challenge in marine biodiversity conservation

A fundamental challenge to marine biodiversity protection is the relatively poor and patchy understanding of the diversity and distribution of marine life (Figure S1), making it more difficult to strategically designate protective measures and assess their success. The marine environment presents unique challenges: the world ocean is vast, much of it is distant from human populations, its life is often hidden from view, and sampling presents formidable logistical difficulties. As a result, observations of ocean life are a fraction of those on land and are especially sparse in the water column and deep sea.[16–24]

Many parties have recommended investment in documenting patterns and processes of marine biodiversity to support global and national protection goals.[25,26] Major initiatives have expanded observations and developed standards for collection, taxonomy, data sharing, and reporting of marine biodiversity, spearheaded by the Organization for Economic Cooperation and Development,[27] the Census of Marine Life,[28] and later by the Global Ocean Observing System, Marine Biodiversity Observation Network, and related projects.[20,21,29–31] Those initiatives were successful in producing the Ocean Biodiversity Information System (OBIS), the Global Biodiversity Information Facility (GBIF), and the World Register of Marine Species (WoRMS), all of which have revolutionized marine biodiversity data collection, organization, and rigor.

Despite these advances in marine biodiversity data collection and collation, the continued relative scarcity of biological data (Figure S1) has led marine managers and conservation planners to rely on coarse abiotic proxies (e.g., temperature or depth) assumed to correlate with biodiversity. However, environmental proxies can over-predict the distribution of species while failing to identify the areas of greatest abundance, complicating the identification of effective conservation strategies.[32] The utility of such environmental surrogates is highly scale dependent, their predictive power varies among regions and taxa, and they rarely capture the typically patchy distributions of the species and habitats important for ecosystem management.[33–36] For example, analyses of benthic diversity from three ocean regions showed that sophisticated multivariate proxies based on 30 environmental variables predicted, on average, only 13%–35%

of variation in species abundances, with key predictors differing among regions such that environmental proxies could not be extrapolated elsewhere.[37] Environmental surrogates alone perform especially poorly in coral reefs, some of the ocean's most diverse ecosystems.[34] However, when biological observations are lacking, multivariate environmental proxies based on high-resolution data can still be valuable when limited to specific well-studied taxa of interest.[38]

Integrating biodiversity data for better area-based protection

The need for marine biodiversity data is especially acute in efforts to implement area-based protection, such as the Kunming-Montreal Global Biodiversity Framework target to conserve at least 30% of the world's land and sea area by 2030 through representative and well-connected protected areas.[39] Area-based protection is among the most effective measures for conserving marine species and ecosystems as it captures the full spectrum of taxa in a location and reduces their exposure to human impacts.[40,41] The most commonly recognized area-based protections are locally or federally designated marine protected areas (MPAs), but conservation benefits can also accrue in areas managed for other goals, collectively known as other effective area-based conservation measures or OECMs.[42–45] These can include, for example, fishery closures and areas managed by indigenous peoples or local communities under territorial-use rights. The most effective area-based measures are fully protected areas (FPAs), where extractive and destructive activities are prohibited and all abatable impacts are minimized.[41,46–49]

Frameworks for evaluating the implementation and conservation value of MPAs and MPA networks[46] are a crucial step forward in assessing existing and future marine protection. However, we urgently need a complementary framework that integrates empirical data about the species and habitats that MPAs are meant to protect. Protection decisions based solely on area or abiotic factors are likely to miss the important components of biodiversity that motivated protection in the first place.[32,50] Therefore, when evaluating the effectiveness of biodiversity protection, a crucial question must be answered: What species and habitats reside within the network of existing or planned protected areas?

A scientific framework to assess biodiversity protection now

Identifying priority areas to conserve (and the accompanying legislative tools) is only a first step in effective conservation. Our increasing knowledge of life's diversity—over 20,000 marine species were described between 1999 and 2008[1]—makes it imperative that we continue to monitor the effectiveness of conservation actions against both what they were designed to achieve and new conservation goals that arise from new information. For this reason, we develop an approach to support both conservation planning and biodiversity monitoring. We build on recent advances to address these data challenges[20,21,23,27–31] by outlining a general, operational framework for assessing marine biodiversity. Our approach prioritizes ecologically and societally important species and habitats, works at regional and national scales, is adaptable for a range
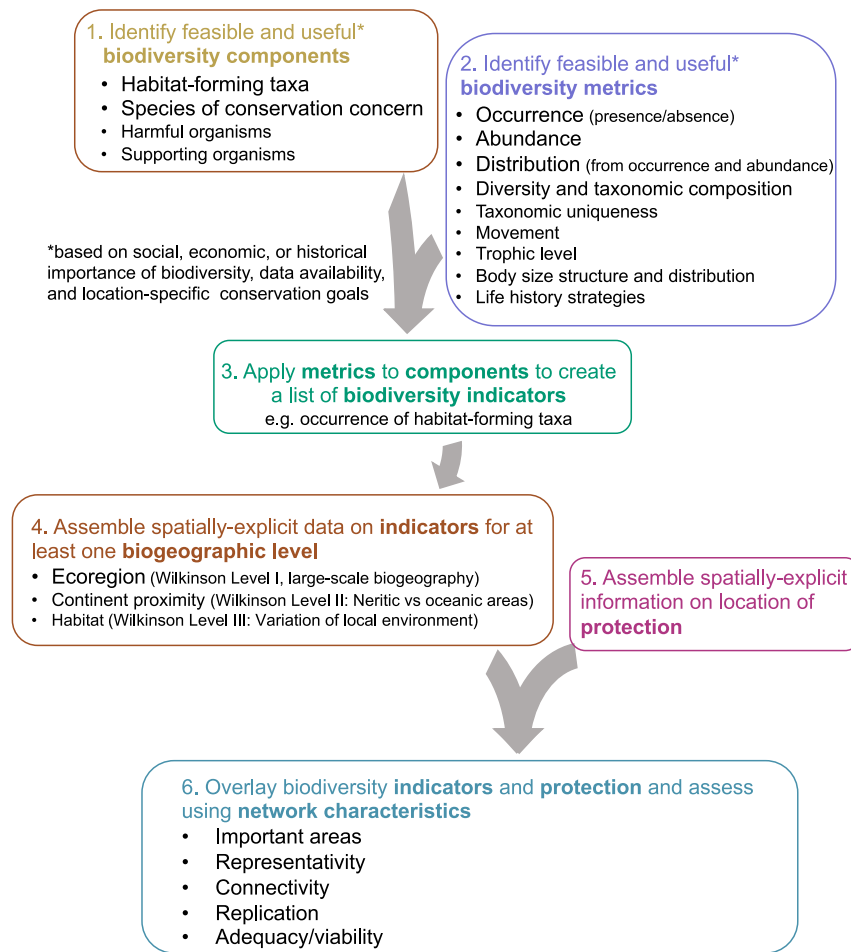
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Figure 1. Expert-derived general framework for time-bound, quantitative assessment of marine biodiversity
We outline the six steps needed to assess biodiversity in protected and unprotected areas. In steps 1, 2, and 4, font size indicates prioritization, with highest priority categories in largest font. See Figure S2 for application of this framework to US waters and Table S2 for details on each step.

ture underpinning ecosystems, (2) species of *conservation concern*, including threatened, charismatic, and/or culturally important species, (3) *harmful organisms* including invasive species and pathogens, and (4) *supporting organisms*, including keystones and important connector species in food webs (components are described in detail in Table S2).

Once target taxa from these categories have been identified as candidates for assessment or monitoring in the system of interest, the question becomes how to quantify them. We propose a set of *metrics,* arranged hierarchically from most essential (occurrence, distribution, abundance, diversity) to aspirational (e.g., trophic level), that best leverage available data, and are applicable at multiple scales (Figure 1; Table S2). Spatially explicit data for the chosen metrics and components are collated and aggregated into a set of biodiversity *indicators*, such as species diversity, distribution of a habitat-forming taxon, etc. (Figure 1). Application of the framework for specific goals and places will require developing targets in a context-specific process of community engagement.

of area-based applications, and can be implemented using existing data. It integrates heterogeneous data to define empirical baselines and exposes gaps in biodiversity knowledge and protection (Figures 1 and S2). The framework emerged from an expert working group and represents a consensus of international experts, including scientists, government decision-makers, and conservation practitioners (Table S1). It builds on and aligns with prior initiatives to characterize marine biodiversity, including the Global Ocean Observing System's Essential Ocean Variables schema,[31] and widely adopted criteria for protected area network effectiveness.[51]

What biodiversity to measure?
One participant early in the expert working group crystallized a central challenge: "I just want to know what to measure." With over 200,000 known marine species, it is obviously impractical to observe more than a fraction of marine biodiversity. Our proposed framework prioritizes biodiversity *components* (key species and functional groups) that are both ecologically and societally important, relatively feasible to measure, and for which data can be assembled at regional to national scales (Figure 1). These criteria align well with the Essential Ocean Variables and Essential Biodiversity Variables.[20,31] We prioritize focusing on four groups: (1) *habitat-forming* taxa that create the physical struc-

Assessing biodiversity protection at the national scale
Broad distributions and dispersal areas are common for taxa residing in a contiguous ocean environment. For this reason, marine conservation networks that distribute protection over a large spatial scale are most effective when relationships among areas are built into their design.[52,53] To assure effective networks, the Convention on Biological Diversity has adopted five "required network properties or components" for effective MPA networks (Convention on Biological Diversity (CBD) (Decision IX/20 Annex 2, Table S1).[51] By overlaying spatial information on biodiversity indicators with the location of protected areas, we can evaluate protection using these five network criteria: (1) *Important areas* (here we use a generic term) for areas which, under the CBD, are referred to as Ecologically or Biologically Significant Areas (see Secretariat of the CBD [2021] Special places in the ocean: A decade of identifying Ecologically or Biologically Significant Marine Areas. Montreal: Convention on Biological Diversity, page 68, for further information). These are locations critical for spawning, feeding, and/or other key life processes of specific valued taxa, often those of conservation concern that are commonly prioritized for inclusion in protected area networks.

(2) *Representativity* is the extent to which a network includes the full range of biodiversity within the region of interest. (3) *Connectivity* is the degree to which organisms can move among MPAs, facilitating dispersal-recruitment processes, metapopulation dynamics, and climate-induced range shifts. Connected networks of sites can also provide insurance against extinction or extirpation of species or populations residing in MPAs. (4) *Replication* is the number of redundant sites in a network that meet a particular management target, intended to insure against loss or degradation of ecological features within the network when individual MPAs are compromised. (5) *Viability and Adequacy* describe a network with size and protection sufficient to sustain key ecosystem features into the future.

At large spatial (e.g., national) scales, species and habitats can differ considerably among biogeographic regions with distinct physical, biological, and ecological characteristics,[54–57] which often also have distinct responses to management actions.[58] Depending on the size of the area being evaluated, it may be uninformative to treat the protected areas as belonging to a single network. For large nations, assessing and protecting biodiversity at the national scale thus must incorporate variation among biogeographic divisions within an exclusive economic zone (EEZ). We therefore recommend stratifying the assessment of biodiversity and protection at the smaller biogeographic scales at which dispersal among MPAs is more relevant to population processes. This stratification ideally should be defined by nature (e.g., ecoregions) rather than political boundaries, in addition to summaries at a national scale.

A NATIONAL ASSESSMENT OF MARINE BIODIVERSITY IN US MPAs

In the three decades since President Clinton's Executive Order calling for a concerted effort to protect marine life in United States waters, the US has greatly expanded the coverage of its marine waters in MPAs with 26% of the US EEZ now within an MPA of some kind.[59] The effectiveness of protection varies widely among nominal MPAs,[46] and the focus on area targets such as 30 × 30 (protecting 30% of area by 2030) has accordingly been criticized as prioritizing quantity over quality.[60–62] MPAs span a wide range of management regimes and effectiveness of protection. FPAs are most effective at increasing biomass, diversity, and body size of marine life.[47,48] Yet, only 3% of US waters are currently within FPAs, with almost all of that 3% contained in two large FPAs in the tropical Pacific. Outside of the tropical Pacific, only about 0.1% of US waters are fully protected. As a coarse but feasible estimate of protection of US marine biodiversity, we quantified biodiversity in (1) all MPAs and (2) all FPAs. The lack of formal designation of OECMs by the US precluded their inclusion in this analysis.

CASE STUDY: US PROTECTED AND UNPROTECTED WATERS

Methods summary
Quantifying how well MPA networks protect biodiversity begins with knowing what species and habitats occur within them. We applied the framework described above (Figure 1) in a national-scale assessment of US marine biodiversity, specifically

comparing inside and outside of protected waters (MPAs and FPAs). We adapted to the limited data availability and time-bounded requirements by using readily available open-access datasets (Table S3) to estimate coverage by protected areas for a subset of our proposed biodiversity indicators and network criteria. These data span multiple types, from georeferenced species records (OBIS), which we aggregated across all taxa and also subset to focus on species of conservation concern and non-native species, as well as remote sensing data (global distribution of mangroves), expert designation (biologically important areas [BIAs], important bird areas [IBAs]), taxon-specific habitat modeling (cold water corals), and a combination of observation, modeling, and expert interpolation (global distribution of coral reefs and seagrasses; Table S3). To address issues of variable quality of the input data, we used the most basic metric that was available (species presence/absence data). We assessed the protection of available indicators using the network criteria at a national scale (US EEZ), and for each of the 24 US marine ecoregions[15] used by the NOAA MPA Center (Figure S3). We emphasize that our purpose was to characterize the magnitude, composition, and geographic variation in biodiversity (species and habitats) in US waters generally, and more specifically comparing within and outside of MPAs. Analysis of the effectiveness of protection (see Edgar and co-workers[41,46]) was beyond the scope of the current study. An important remaining need is to assess biodiversity conservation in MPAs as a function of effectiveness, including features such as stage of establishment, presence of key social and ecological conditions, and level of protection.

Minding the gaps in the US MPA network
Our assessment found that existing MPAs capture only a portion of US marine species in OBIS and that neither the US as a whole, nor any of its 24 marine ecoregions, scored well (100% for important areas and >30% for all other criteria) on all five network criteria (Figures 2, 3, and S4–S11). We also identified substantial gaps in representation of both taxa and geographic regions: Our comparison among US ecoregions reveals that the summary figure of 26% of US waters within MPAs obscures large spatial variation and substantial gaps among regions in the area and types of species and habitats protected (Figures 3 and S4–S11).

The most basic network criterion is *representativity*, that the biodiversity within MPAs is representative of the full range of a region's biodiversity. At the national level, we found that MPAs did not cover a representative range of biodiversity, either when limited to our priority biodiversity components (Figure 2A) or when applied to total species richness (Figures 2B and S13). Of the 29,322 species found in the US EEZ, only 13,877 of them have been observed in MPAs, and 5,231 in FPAs. The lack of consistent abundance data in OBIS has the potential to bias these findings as we were unable to standardize richness by effort beyond number of records (see further discussion below). On an ecoregional scale, species representativity based on OBIS records varies widely, with the highest representativity found in the Pacific Islands, and the lowest in the Alaskan ecoregions, although we again should note that this analysis did not standardize for differences in effort among ecoregions (Figures 3A and S4). This pattern of strong regional variation also held when OBIS records were filtered to the subset of
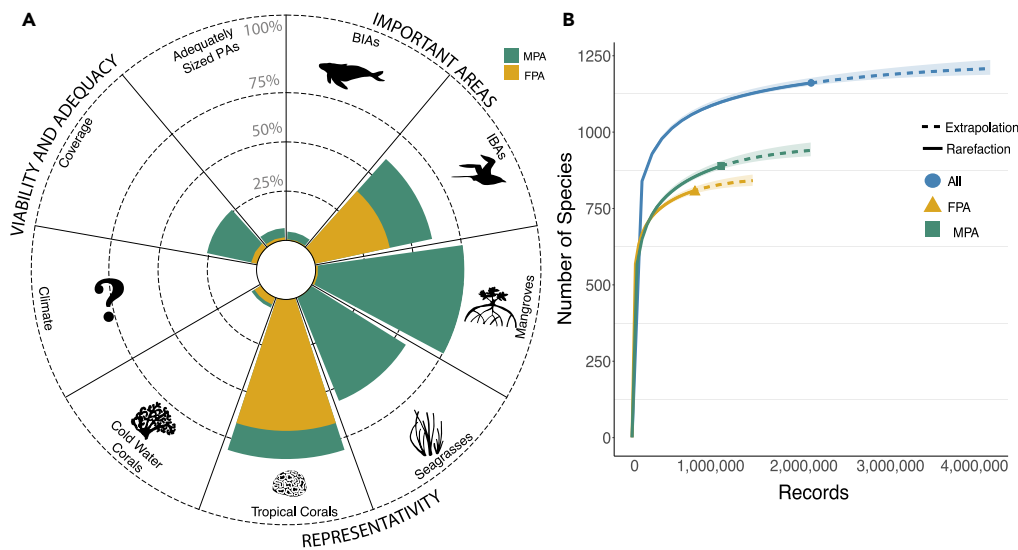
Figure 2. Summary indicators of US marine biodiversity coverage in protected areas summed across all regions in the EEZ

(A) Match of the US MPA network, aggregated at national level, to three of the Convention on Biological Diversity's five criteria for effective protected area networks. Wedges show percent of *important areas* for two taxa of conservation concern (seabirds and marine mammals) in MPAs and FPAs (goal is 100%), indicators of *representativity* of MPAs and FPAs for habitat-forming taxa (goal is 30%), and indicators of *viability and adequacy* (size adequacy, areal coverage, and unknown climate viability).

(B) *Representativity* of US species in the nationwide MPA network as estimated accumulation of species from a subset of OBIS records collected using systematic visual surveys, the most commonly reported group of methods for collecting species records submitted to OBIS (Figure S12). Records (here, surveys) were used as the unit of sampling effort and data were divided into fully protected areas, all marine protected areas, and the US EEZ as a whole.

species of conservation concern (IUCN red-listed species), a key biodiversity indicator (Figures 3A and S4B). These regional gaps in representativity are also well illustrated by tropical coral reefs, some of the most biodiverse habitats. Despite seemingly high representativity of tropical coral reefs in MPAs at the national scale (Figure 2A), most of the nation's protected reefs are in the two large MPAs in the Pacific Islands (Figures 3A and S6), whereas percent coverage of tropical reefs is low in the Caribbean Sea ecoregion (23% in MPAs, 2% in FPAs; Figure S6), where reefs are generally more vulnerable.[63] Similarly, cold-water corals harbor rich biodiversity in the deep sea[64] but cold-water coral habitat is poorly protected in most US waters (Figures 2A, 3A, and S6), mainly because most MPAs are in shallow water (Figure S8). Representativity of habitat-forming seagrasses and mangroves is greater than 30% in MPAs in most US ecoregions where they occur (according to the Global Distribution of Mangroves and Seagrasses), but they are nearly absent from FPAs (Figure S5), highlighting the vulnerability of these groups valued for blue carbon sequestration and other ecosystem services. Importantly, representativity is not determined solely by the geographic scale of protection. Instead, several regions with high MPA coverage, including Guam and Marianas and American Samoa, fare poorly in several representativity criteria, whereas other regions with low MPA coverage (Figure S7B) nevertheless achieve high representativity for certain groups (Figures S4–S6). For example, MPAs cover only 1% of the Carolinian Atlantic ecoregion (Figure S7B), yet those MPAs contain >50% of the region's mangrove and seagrass habitat (Figure S5), although <1% is in an FPA. Such regions can serve as models for strategic siting where available area for protection is small. Interestingly, we also found that represen-

tativity of depth in an ecoregion did not necessarily predict representativity of biodiversity, as MPAs in the Pacific Island ecoregions had the least similarity with the depth of the entire ecoregion (Figure S8) and yet had high representativity of multiple biodiversity indicators (Figures S4–S6).

Data on *important areas* are available on a national or ecoregional scale for marine mammals and seabirds.[65,66] Because of their critical role in species persistence (breeding locations) and ecosystem function (feeding locations), MPAs should aim to cover 100% of important areas, yet we found less than 60% of identified IBAs for marine species fall within MPAs, and for marine mammals <10% of identified BIAs are in protected waters (Figure 2A). Important areas for both seabirds and marine mammals are best covered by MPAs (nearly 100%) in the South Florida and Bahamian Atlantic ecoregion, but still have low coverage by FPAs in those regions (Figure S9). In contrast, <10% of important areas are in MPAs in any of the five Alaskan ecoregions, a major conservation gap given the region's importance to migrating whales and birds and its vulnerability to climate change (Figures 3A and S9).[67]

High network *connectivity* (number of MPAs <50 km apart, see experimental procedures) among US MPAs appears to be achieved in some regions, but FPAs are more widely separated (Figures 3B and S8). Averaged across US waters, the mean distance among five nearest neighbor MPAs is 34 km, but the mean distance among FPAs is 169 km, suggesting inadequate connectivity for this class of protection (see experimental procedures). This analysis is based on nearest linear distance and thus did not account for differences in depth, land barriers, and habitat type or oceanographic connectivity that could alter dispersal between MPAs, so our calculations probably
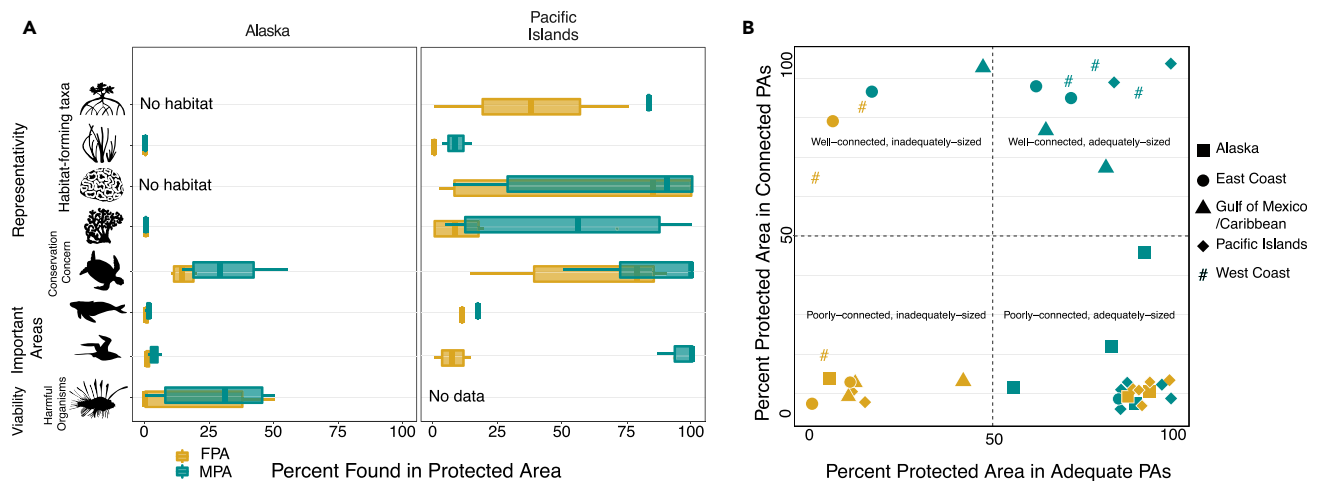
Figure 3. Summary indicators of US marine biodiversity coverage in protected areas for two marine regions representing the extremes of coverage
(A) Data on three network criteria (representativity, important areas, and viability) as percent of taxa, habitat, or important area found in MPAs and FPAs averaged across each ecoregion. Boxplots show median, 25% quartile, 75% quartile and 1.5*interquartile range (whiskers) for the Alaska and the Pacific Island ecoregions. (B) Adequacy and connectivity of MPAs and FPAs for each ecoregion as percent protected areas in adequate (>400 km^2) or connected (<50 km spacing) PAs.

overestimate connectivity. The Alaskan MPAs are the least well connected, reinforcing the vulnerability of MPAs in this area (Figures 3B and S10).

The criteria of network *Viability and Adequacy* are difficult to evaluate because they require data on population size and demographics of the protected species, which are most often unavailable. We used a threshold for area size roughly judged to be able to sustain populations of most species (>400 km^2, see experimental procedures) and found only about 6% of US MPAs and 7% of FPAs are of adequate size (Figures 2, 3B, and S7). This finding highlights that many existing MPAs could be undersized and may be made more effective if expanded. An exception to the general pattern was the set of Alaskan MPAs, which covers a small percentage of Alaskan ecoregions but mostly meet this provisional criterion of adequate MPA size (median = 9,531 km^2; Figure 3B). The contrast between size adequacy of Alaska's MPAs and their poor performance for other network criteria highlights the importance of assessing multiple network characteristics to inform strategic biodiversity protection. We further used existing biodiversity data on non-native species as another (limited) proxy for viability and adequacy, given that these species often disrupt native populations and ecosystems, which may impact the relative conservation value and viability of MPAs.[68] Of the 10 US regions covered by the non-native species (NEMESIS) database,[69] half have a large proportion (more than 50%) of known non-native species recorded within MPAs (Figure S10). By contrast, relatively few non-native species have been observed in FPAs, suggesting that they might be relatively more viable than MPAs in the near term, although this is likely driven by their smaller footprint.

Finally, *replication* or redundancy of MPAs provides insurance that species and habitats within a network are more likely to be sustained over the long term, even when the quality of some individual MPAs is compromised. We illustrate application of this criterion with the example of seagrasses because these habitat-formers occur in most US regions and provide a range of ecosystem services, including carbon sequestration. All US marine ecoregions with known seagrass populations except one contained seagrass in two or more MPAs (median 10; Figure S11), indicating reasonably good replication in coverage for this habitat type. However, many regions contained only a single FPA with seagrass (median = 2).

Filling the gaps in US marine biodiversity protection
Our assessment of marine biodiversity in US protected areas complements analyses of MPA coverage based on area under protection[46] and highlights several strategies for increasing biodiversity protection (Box 1). Our data on biodiversity distribution and network characteristics confirm that nationally summarized protection statistics mask strong variation in biodiversity coverage among regions and that marine life in much of US waters is inadequately protected. We found that MPAs within the Pacific Islands are closest to meeting goals of representing regional biodiversity from a range of habitats and taxa, including habitat-formers and species of conservation concern, in MPAs of adequate size. The five Alaskan regions, where MPAs cover a small percentage of marine area, lag farthest behind in most metrics and could therefore be prioritized for establishment of new conservation measures and increasing the protection level (from MPA to FPA) of existing MPAs (Figures 3A and S4–S11). Interestingly, the MPAs in both the Pacific Islands and Alaska are adequately sized, but connectivity is low in most Pacific Islands ecoregions and all Alaskan ecoregions. In these locations, connectivity could be increased by designating new intermediate MPAs, thereby decreasing the relative degree of geographic isolation of protected spaces. A clear priority for Alaska in particular, and the US more broadly, is protecting known important areas for marine birds, mammals, and other migratory species. Doing so would strengthen both protection for species of conservation concern and potentially increase connectivity, as many large vertebrates can migrate across entire ocean basins among breeding and feeding areas. Where

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Box 1. Recommendations for increasing area-based marine biodiversity protection

(1) Target new OECMS and MPAs in geographic areas and habitats with identified protection gaps.
(2) Increase protection level (from MPA to FPA) of existing MPAs in geographic areas and habitats with identified protection gaps.
(3) Enlarge small existing MPAs, particularly in regions with few to no large MPAs.
(4) Where MPAs are widely spaced, designate new MPAs to create stepping stones among them.
(5) Create new or expand existing MPAs in deeper waters.
(6) Formalize an official definition and delineation criteria for OECMs by the US

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existing MPAs are small but well connected, such as on the East Coast and Gulf of Mexico/Caribbean, enlarging them could help increase coverage of key taxa and habitats, especially highly mobile species and those with dispersing larvae. To cover a larger proportion of the biodiversity in the US, new protected areas should prioritize coverage of deeper waters, since existing MPAs in shallow water leave deep-sea and pelagic species and habitats unprotected.[70] These findings are meant to provide a starting point for more detailed future analyses of US marine biodiversity protection, which should be ongoing and iterative. Another tool for improving area-based biodiversity protection in the US would be the official definition and delineation of OECMs. Publication of FAO guidelines for OECMs in marine fisheries may encourage and support such a move by the US.[71]

Minding the gaps in US marine biodiversity data

Substantial data gaps compromised our ability to quantify US marine biodiversity on a national scale. Most saliently, our investigation of the data in OBIS yielded many interacting patterns of sampling bias. Documentation and monitoring of biodiversity in oceanic waters, including deeper depths, is much sparser than along the coasts, with OBIS records concentrated in shallow waters.[17] Our observation that the Pacific island ecoregions had high representativity for most biodiversity indicators but low representativity of depth classes (Figure S8A) further highlights this need—since the organisms living in deeper waters remain less characterized, they are not included in biodiversity representativity calculations. OBIS records also exhibit strong taxonomic biases—more than 65% of US marine species records in OBIS are vertebrates even though invertebrates constitute the vast majority of animal species. Algae and microbes are also poorly represented in OBIS. In addition, there are no public databases of marine pathogen distribution, hindering assessment of the growing threat of diseases to marine species and ecosystems.[72] Lack of data on these organisms limits the comprehensive assessment of MPA representativity and viability.

Lack of information on sampling protocols and sampling effort (i.e., number of individuals sampled at a given time point) hindered our ability to compare species richness across protected and unprotected waters. Only 48% of OBIS records contain information about sampling method and 57% contain information about abundance, making comparisons difficult (Figure S12). To account for this issue, we considered richness at the level of species records and created rarefaction curves for broad protocol categories (Figure S12). Given that we found high variability of sampling protocols used inside versus outside MPAs, we expect our reported richness estimates are influenced by variation in sampling methods and therefore the collected data (e.g., survey length can affect recorded richness). Specifically, we found that the majority of biodiversity data gathered inside MPAs and FPAs used generally defined "survey" methods (see experimental procedures), whereas surveys made up a much smaller proportion of sampling methods used outside of MPAs (Figure S12). Some of these biases are due to restrictions on sampling methods (e.g., trawls, grabs, and nets were not used in FPAs), while others are likely due to biases in the locations of studies (e.g., pots were only used in MPAs).

Even when considering effort at the coarse level of OBIS records, we found high geographic variability. Records of marine life in OBIS[73] were nearly twice as dense inside MPAs (1.0 obs km^{-2}) as outside (0.6 obs km^{-2}; Figure S4), suggesting that biodiversity studies are preferentially conducted within protected areas. This may be due to a number of factors including locations of field stations, investigator selection of sites where biodiversity is expected to be higher, dedicated funding programs for MPA monitoring, or difficulties of working in areas with relatively higher traffic and human impacts. Other geographic biases are found on the ecoregional level, where the number of records per area varies widely (Figure S14), with the highest sampling effort in the South Florida/Bahamian Atlantic region and very low effort in the Alaskan ecoregions. This data gap is likely greatly influencing the observed ecoregional variation in biodiversity, highlighting the need to use multiple data sources for a more complete picture that is less likely to be biased by uncertainty in any particular source of data (i.e., the high-quality species distribution models used here).

An increasingly important data gap relates to climate change, which will profoundly impact MPA effectiveness as organisms move and species distributions change in response to the shifting climate.[14,74–76] Ongoing environmental degradation and variability due to climate change is likely the largest threat to viability next to fishing, and will intensify impacts of harmful organisms, including pathogens and non-native species invasions, suggesting that protection that appears sufficient now may not be so in the future. Assessing viability of MPA networks under climate change requires more reliable projections and understanding of species' future distributions,[77] including in three dimensions[78] and for species immigrating from outside US waters. Changing climate is also affecting the distribution and condition of biogenic habitats essential to many species, altering the rates and extents of migration and larval dispersal, and will likely change which species are considered conservation priorities.[79] Our analyses provide an important baseline that can be used to help prioritize conservation decisions that address these issues, but assessment of long-term network viability under climate change will require improved models of species range shifts and interactions with both sufficient

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Box 2. Recommendations for increasing usability of biodiversity data

(1) Establish a systematic, regular re-assessment of key species and habitats across protected and unprotected US waters.
(2) Continue to develop and implement methods to synthesize and standardize existing data from multiple sources, including OBIS, GBIF, WoRMS, and GIS-based habitat maps.
(3) Increase collaboration with Indigenous and local communities to include traditional knowledge in biodiversity assessments.
(4) Increase deposition of biodiversity data in publicly accessible databases and connect them to OBIS and GBIF.
(5) Incorporate genetic data (e.g., from metabarcoding) into biodiversity assessments, and adapt public databases and clearing-houses to better accommodate such data.
(6) Improve knowledge of biodiversity in areas outside existing protected areas using the same sampling protocols used inside protected areas.
(7) Identify and formally designate important areas, particularly for migratory species of conservation concern and habitat-forming species.
(8) Improve models of species movement (migration and dispersal) to better characterize connectivity and size adequacy of MPAs.
(9) Improve and increase the breadth of species distribution models based on future climate scenarios.

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geographic scale and resolution to describe dynamics within smaller regions.

Several data gaps relate to large migratory vertebrates. First, important areas for marine mammals have not yet been formally designated in 7 of the 24 US ecoregions (Figure S9), highlighting a key knowledge gap and potential opportunity for biodiversity protection. Second, a biologically relevant evaluation of connectivity among MPAs is needed, particularly for migratory large vertebrates. However, the lack of standardized models of their movement patterns hinders our ability to estimate connectivity among MPAs and to assess and design biodiversity protection given legislation that mandates protection of many such migratory species.[52]

We emphasize that most of these caveats render our estimates of under-protection in the US MPA network conservative. Since records of marine life in OBIS[73] were denser inside MPAs than outside, we have likely overestimated the proportion of US marine species that occur within MPAs. In addition, due to lack of abundance data, we counted a species as present given even a single observation, a low bar that surely overestimates the number of species with viable populations in a given area. This is likely especially true for the non-native species as detection, especially early in invasions, is often difficult. Future analyses should produce more accurate estimates of representativity by moving away from richness as the only metric of diversity and incorporating other metrics such as evenness and dominance. Usable abundance data will advance the reliability and extent of the analyses that can be conducted; however, it will require more systematization and quality control of input data.

Filling the gaps in US marine biodiversity data
We offer this analysis as a template for a systematic, regular re-assessment of key species and habitats across protected and unprotected US waters. Going forward, we suggest that an initiative akin to the USGS terrestrial Gap Analysis Program[80] is needed to identify alignment between species distributions and seascape conservation. Our results also demonstrate both the promise and limitations of existing biodiversity databases and reveal several priorities for improving data collection and curation (Box 2). Continuing efforts to synthesize and standardize

data from multiple sources, including via OBIS, GBIF, and WoRMS, will improve large-scale assessments of biodiversity like this study. Deposition of existing data into these publicly accessible databases can be improved by strengthening requirements and incentives for deposition by agencies, funders, and journals. Standardization of abundance data in existing databases can expand the types of analyses possible and make them more biologically meaningful. However, the majority of records in these databases only contain one type of data: species occurrences collected through visual identification. Incorporation of genetic data (chiefly metabarcode data) can rapidly expand the quantity and taxonomic breadth of biodiversity data in databases, particularly for microscopic and cryptogenic organisms.[81] Working with Indigenous knowledge holders can capture time scales, interactions, and socio-ecological contexts missed by dominant scientific approaches,[82,83] although use of these different kinds of knowledge together remains a challenge. We advocate for increased collaboration between government and academic scientists and Indigenous scientists, knowledge holders, and communities to enhance biodiversity assessments while maintaining Indigenous data sovereignty.

Beyond integration of existing datasets, our analysis identified several priorities for future data collection. First, the bias in OBIS toward data collected within protected areas (Figure S4) highlights the importance of pairing data collection within protected areas with similarly designed surveys in unprotected waters and especially deeper waters, which are largely uncharacterized.[17] To fill these data gaps, additional data collection should prioritize non-vertebrates, including invertebrates, algae, and microbes, which make up most marine life and play critical roles in ecosystem functioning. Pathogens and parasites in particular often have large effects on ecosystem structure and functioning, and yet are largely lacking in assessments of protected areas. As diseases increase with climate change,[84] more information about these taxa will be crucial to ensuring network viability. Information about important areas can expand our ability to protect species of conservation concern and supporting organisms. Given the lack of designation of important areas in 7 of the 24 ecoregions, information about the location of important areas in these regions should be prioritized within biodiversity monitoring

programs. Furthermore, information is needed in all ecoregions about important areas for migratory species of conservation concern. Localized models of organismal dispersal and migration will help better characterize connectivity and size adequacy of MPAs. Finally, more complete species distribution models are needed that integrate current and future climate data, and species/trophic interactions.[85] Climate-induced changes in key species distributions should be documented and incorporated into biodiversity conservation priorities in an iterative process as new information becomes available.

Conclusions

Effectively sustaining biodiversity and living marine resources over the long term requires systematic and strategic characterization of (1) species and habitats of ecological and societal importance, (2) data and measurable targets to evaluate the presence and condition of living resources, and (3) management performance to guide ongoing strategic management. Our analysis of marine biodiversity in protected and unprotected US waters builds on previous efforts to observe, collate, and quantify marine biodiversity at large scales, but also serves as a launching point for more systematic future efforts. Periodic updates will be required and will be most successful when applied across scales and guided by the identification of region-specific priority species and habitats in cooperation with a range of stakeholders, including Indigenous stewards, industry, and conservation practitioners. The framework developed here (Figures 1 and S2) can help advance these goals by guiding practical decisions about assessment and monitoring of marine life to support management, as well as other operational frameworks such as the Natural Capital Protocol and Climate Disclosure Standards Board Framework. To strengthen decision-making for spatial management of US marine resources, we recommend establishing a systematic, regular re-assessment of key species and habitats across protected and unprotected waters, similar to the USGS terrestrial Gap Analysis Program, which overlays species distribution models with land stewardship information.[82] The actions recommended here would help advance national and global efforts to increase the area of the ocean under effective protection, including the 30 × 30 target agreed under the Kunming-Montreal Global Biodiversity Framework[39] as well as nature-based climate solutions such as those outlined in the US Ocean Climate Action Plan. Moving the US closer to this goal of 30% protection will require aggressive and strategic growth of the nation's MPAs, OECMSs, and other actions that improve the network's effectiveness, along with regularly updated and focused assessments to track changes in marine biodiversity and its drivers. The framework proposed here can help guide progress toward these goals while ensuring that protection decisions are rooted in data about biodiversity.

EXPERIMENTAL PROCEDURES

Resource availability
Lead contact
Requests for further information and resources and code can be directed to and will be fulfilled by the lead contact, Sarah Gignoux-Wolfsohn (sarah_gignouxwolfsohn@uml.edu).

Materials availability
This study did not generate new unique materials.

Data and code availability
All data are publicly available (Table S3). The code is available at https://github.com/jessecleary/MBD_Analysis, https://github.com/sagw/MBD

Development of recommendations
We virtually convened an international expert group of scientists, managers, and conservation practitioners from academic, government, and non-profit sectors in a series of 13 sessions between May and August 2020. The group's charge was to conduct a time-bound review of existing marine biodiversity observing programs and conservation planning schemes and develop recommendations for their application to a rapid assessment of available US data on marine biodiversity inside and outside protected areas.

Spatial data on US biogeography and protection
To demonstrate the marine biodiversity assessment framework in action, we assessed US marine biodiversity inside MPAs and FPAs as defined by the NOAA MPA Center.[59] Because OECMs have not been defined, designated, or mapped within the US, we did not consider them in our analysis. To mimic the conditions under which this framework would be applied by a government agency on an operational semi-annual basis, this analysis was time-bound and prioritized existing, easily accessible consolidated datasets (Tables S2 and S3). To capture variation in biodiversity across the US EEZ, we calculated our biodiversity indicators and network criteria within each of the 24 marine ecoregions of the US[86] (Figure S2).
US ecoregions
GIS data on North American ecoregions from Wilkinson et al.[86] were obtained from the Commission on Environmental Cooperation (CEC) Website. The level 1 polygons in these data were processed to further refine the Pacific Island ecoregions as suggested.[86] The "Pacific Remote" ecoregion was reapportioned so that "Johnston Atoll" was combined with the "Hawaii Archipelago" ecoregion and all of the other Pacific Island EEZs were treated as separate ecoregions. This new dataset of US Ecoregions contains 24 Ecoregions and formed the geographic unit of analysis for the gap assessment. NOAA defines marine waters as including the Great Lakes for purposes of MPA coverage, but this paper excludes the Great Lakes from analysis. US marine waters, as defined here, include all US territorial marine waters, federal and state, from the shoreline to the outer extent of the EEZ, including bays and estuaries.
NOAA MPA Inventory
Locations of protected areas were taken from the NOAA MPA Inventory database (December 2020 version) provided by the NOAA MPA Center. This dataset was spatially intersected with the US Ecoregions datasets to limit the MPAs to just those falling inside the Ecoregion polygons described above. This excluded MPAs in the Great Lakes and any portions of MPAs outside of the US Ecoregions polygons. A dataset of only the "Fully Protected" MPAs was created using the "Protection Level" attribute to only include MPAs with values of "No Take," "No Impact," or "No Access." MPA Areal coverage in each ecoregion was calculated using the MPA dataset and the Fully Protected MPA dataset with the ArcGIS Pro "Tabulate Intersection" tool and the US Ecoregions data. Tabular results were then analyzed with Python GeoPandas to calculate coverage percentages for each ecoregion.

Biodiversity indicators
Total richness
To estimate species occurrence across the entire US EEZ, data from the OBIS were obtained.[73] A US EEZ extraction of the November 2020 OBIS database was used. The approach and coverage of each individual dataset varies, so the aggregated US OBIS dataset is quite variable in terms of survey methods and geographic and taxonomic coverage. Because not all data in OBIS includes information on abundance (individual counts), we considered the presence of a species at a location at a time point an observation. Our dataset contained 8.6M records identified at the species level, representing 23,931 distinct species, from 906 distinct datasets across the US EEZ.

These 8.6M OBIS records were then subset into spatial datasets for each ecoregion, ecoregional MPA network, and ecoregional Fully Protected MPA network.
Species accumulation curves
For data with recorded sampling protocols in OBIS, we further categorized the 350 protocols into 10 broader categories: net (any protocol mentioning the use of a net excluding plankton nets or trawls), grab (destructive benthic sampling e.g., scoop, dredge), hook (use of fishing gear such as longline, hook and line, handline), visual (any visual observation-based protocol that does not mention the use of a systematic survey method), survey (any visual observation-based

protocol that mentions the use of a systematic survey method), pot (use of pots or traps to catch organisms), trawl (any protocol that collects organisms with any sort of trawl net), stranding, suction (any suction sampling technique), or other (Table S4). We then created species accumulation curves for each sampling category (except for hook, stranding, and suction which had too few data points) using the R package iNEXT[87] with each record treated as a sample. Curves were created for all records and records in MPAs and FPAs.

Occurrence of species of conservation concern

Species of conservation concern were identified in the full OBIS species list by selecting species on the March 2020 IUCN Red List,[88] and these records were tallied by ecoregion.

Occurrence of harmful organisms

We focused on non-native species as examples of organisms that pose threats to biodiversity because data on non-natives are readily available for several ecoregions. Non-native species were identified in the full OBIS species list by selecting species on the National Exotic Marine and Estuarine Species Information System species lists.[69]

Distribution of habitat-forming organisms

Seagrass distribution was assessed using the Global Distribution of Seagrasses dataset, version 7.0 from October 2020.[89] Mangrove distribution was assessed using the Global Distribution of Mangroves USGS dataset, version 1.3 from June 2015.[90] Coral Reef distribution was assessed using the WCMC Global Coral Reef dataset, version 4.0 from June 2018.[91] Distribution of cold-water octocorals was assessed using the habitat suitability model output from Yesson et al.[92] The "Consensus" layer from this octocoral modeling was used and then subset to only include cells with suitable habitat for all seven modeled octocoral taxa.

Distribution of important areas for species of conservation concern and supporting organisms

NOAA BIAs. Coverage of Cetacean BIAs was assessed using version 1 of the BIA dataset.[65] All individual BIAs were spatially dissolved before analysis to avoid double counting any overlapping BIAs. Coverage of IBAs was assessed using the March 2021 version of the IBA dataset,[66] which contained two datasets, Continental US and Overseas Territories. These datasets were first merged and then subset to US Ecoregions. Individual IBAs were spatially dissolved before analysis to avoid double counting any overlapping IBAs.

Depth

Bathymetry data for the US EEZ were extracted from the GEBCO 2019 global dataset (~400 m resolution[93]).

Evaluation of network characteristics

Spatial analyses were performed with ArcGIS Pro, R (dplyr,[94] vegan,[95] sf), and Python (GeoPandas, RasterIO, NumPy,[96] SciPy, ArcPy). The figures were produced with Python (Seaborn, Matplotlib) and R (ggplot2[97]). All area calculations were performed using the Eckert IV projection with the Central Meridian set to 140°W.

Representativity. We calculated species representativity using Python GeoPandas as the percentage of total species found in protected and unprotected waters within an ecoregion (or the entire EEZ) that were observed at least one time in MPAs or FPAs. These calculations were conducted using spatial datasets of OBIS records, with taxonomic description at the species level for each ecoregion, ecoregional MPA network, and ecoregional FPA network. For species of conservation concern, the OBIS data filtered to IUCN red list species was used.

Representativity of habitat-forming taxa was calculated as the percent of ecoregional habitat occupied by that taxon that was covered by an MPA or FPA, using ArcGIS Pro "Tabulate Intersection" on the US Ecoregions data. Tabular results were then analyzed with Python GeoPandas to calculate coverage percentages for each ecoregion.

Representativity of depth in MPAs and FPAs was calculated by first extracting bathymetry data for each ecoregion, ecoregional MPA network, and ecoregional Fully Protected MPA network with ArcGIS Pro. Summary statistics and histograms were created with Python NumPy. The Bray-Curtis Dissimilarity Index was run with Python SciPy to calculate differences in the bathymetry distribution histograms of MPAs and Fully Protected MPAs versus each ecoregion's depth distribution.

Adequacy/viability. To estimate size adequacy of MPAs we found no broadly accepted quantitative criteria, so as a first step we focused on locally recruiting species, with a modal larval dispersal range <15 km,[98] and assumed that, all else being equal, a protected area dimension of 20 × 20 km, or 400 km^2, would retain most recruitment within a reserve.[99] As a rough metric of adequacy, we measured the area of each PA and calculated the percentage of MPAs or FPAs in an ecoregion or EEZ that are >400 km^2 (adequately sized).

We used the number of non-native species present within a protected area as one measure of its viability (lower numbers of threats indicate more viable protected areas). We therefore calculated viability (with respect to harmful or-

ganisms) using Python GeoPandas as the percentage of NEMESIS species in OBIS found in protected and unprotected waters within an ecoregion (or EEZ) that were observed at least one time in MPAs or FPAs.

Connectivity. In the absence of an accepted general criterion, we estimated relative connectivity roughly as the mean linear distance to an MPA's five nearest-neighbor MPAs, judged against the rule of thumb that MPAs should be separated by <50 km (modal larval dispersal distance estimated for marine organisms along the Pacific coast of North America[98]; MPA proximity to neighboring MPAs was used as a proxy for connectivity. Proximity was assessed using the "Generate Near Table" tool in ArcGIS Pro run against the MPA dataset and the Fully Protected MPA dataset separately. Tabular results were then analyzed with Python GeoPandas to calculate the average proximity of the five nearest MPAs for each individual MPA. Any MPAs with a spatial overlap were excluded from the Nearest 5 calculation for an individual MPA. We defined "well connected" MPAs as those ≤ 50 km apart.

Important areas. The coverage of important areas by MPAs and FPAs in each ecoregion was calculated as the percent area of designated BIAs (marine mammals) or IBAs in an ecoregion that was covered by protected areas. These calculations used the MPA and FPA datasets with the ArcGIS Pro "Tabulate Intersection" tool on the US Ecoregions data. Tabular results were then analyzed with Python GeoPandas to calculate coverage percentages for each ecoregion.

Replication. To examine replication, we counted the number of MPAs or FPAs within an ecoregion or EEZ that contained seagrass.

AUTHOR CONTRIBUTIONS

Conceptualization, D.C.D. and J.E.D.; methodology, S.A.G.-W., D.C.D., J.C., P.N.H., C.R.A., N.J.B., G.C., P.C., S.D., S.D.G., L.A.L., C.J.L., E.M., A.M., P.J.M., D.N., B.P., E.P.P., M.L.P., M.M.R., R.R.E.S., T.T.S., D.P.T., L.V.W., and J.E.D.; investigation, S.A.G.-W., D.C.D., J.C., P.N.H., C.R.A., N.J.B., G.C., P.C., S.D., S.D.G., L.A.L., C.J.L., E.M., A.M., P.J.M., D.N., B.P., E.P.P., M.L.P., M.M.R., R.R.E.S., T.T.S., D.P.T., L.V.W., J.E.D., M.D., K.G.-C., D.E.J., L.M., J.S.-S., and L.W.; formal analysis, S.A.G.-W., J.C., P.N.H., S.D., and B.P.; resources, L.M., M.E.M., L.W., M.D., and D.E.J.; writing – original draft, S.A.G.-W., D.C.D., and J.E.D.; writing – review & editing, S.A.G.-W., D.C.D., J.C., P.N.H., C.R.A., N.J.B., G.C., P.C., S.D., S.D.G., L.A.L., C.J.L., E.M., A.M., P.J.M., D.N., B.P., E.P.P., M.L.P., M.M.R., R.R.E.S., T.T.S., D.P.T., L.V.W., J.E.D., M.D., K.G.-C., D.E.J., L.M., J.S.-S., and L.W.; visualization, S.A.G.-W., J.C., P.N.H., S.D., and B.P.

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