Aligning marine species range data to better serve science and conservation

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Species distribution data provide the foundation for a wide range of ecological research studies and conservation management decisions, yet most species ranges remain unknown, and existing range maps often suffer from data limitations and inconsistencies. AguaMaps and the International Union for Conservation of Nature (IUCN) are two distinct efforts to map marine species distributions at a global scale. Together these databases represent 24,637 species (92.9% within AquaMaps, 16.3% within IUCN), with only 2,279 shared species. Here we examine differences in predicted species ranges between the two datasets and find that these misalignments mainly result from divergent methodologies that introduce differing frequencies of commission and omission errors. We illustrate the scientific and management implications of these differences by repeating two recent applications - an assessment of global biodiversity within the Ocean Health Index and a global analysis of gaps in coverage of marine protected areas - and find significantly different results depending on how the two datasets are used. Until a single, highly accurate dataset of global marine species ranges becomes available, understanding the implications of dataset differences for conservation planning and decisionmaking remains essential.

marine spatial planning | species distribution model | extent of occurrence | spatial ecology | limits of distribution

Introduction

Knowing where species exist and thrive is fundamental to the sciences of ecology, biogeography, and conservation, among many others. This knowledge provides foundational information for understanding species ranges and diversity, predicting species responses to human impacts and climate change, and managing and protecting species effectively. A rich literature tackles the many dimensions of these questions.

One major outcome of this body of science is the various compiled databases of species distribution maps. Two global-scale repositories predict marine species ranges throughout the world's oceans – AquaMaps (1) and International Union for Conservation of Nature (IUCN) (2). These two spatial datasets have been used in hundreds of studies and applications for a wide range of purposes, including assessing marine species status (3, 4, 5), evaluating global biodiversity patterns (6, 7, 8, 9), predicting species range shifts (10), and setting conservation priorities (11).

The two datasets ostensibly describe the same information, but significant differences in methodology and intent could lead to dramatically different understandings of our marine ecosystems, with significant implications for policy and conservation recommendations. Importantly, biases in taxonomic or spatial coverage within a dataset could shift management and conservation actions away from places or species that are most in need. Inaccurate indications of presence or absence could lead to ineffective marine reserve systems and management plans (12, 13).

To understand the implications of differences between the AquaMaps and IUCN datasets, we compare how each data source represents the global spatial and taxonomic distribution of

marine species. Most notably, AquaMaps includes range maps for many more species (currently 22,889 species; 92.9% of total), such that most global analyses related to marine biodiversity to date have used AquaMaps (IUCN range map data exist for only 4,027 unique marine species). For the 2,279 species (9.3% of total) mapped in both datasets, we examine how well the maps align, determine several issues that lead to misalignment between predicted species distributions, and outline possible improvements.

We then reexamine two recent marine biodiversity studies - an assessment of the status of global biodiversity within the Ocean Health Index (3, 4) and a global analysis of gaps in protection afforded by marine protected areas (MPAs) (11) - as case studies to explore the implications of prioritizing one data set over the other. The results highlight possible consequences of different data use decisions on our understanding of marine biodiversity status and protection.

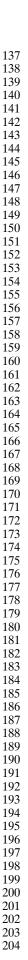
Results and Discussion

The IUCN publishes species range maps based on expert input of spatial boundaries of a given species' "limits of distribution" (2) essentially a refined extent of occurrence, based on observation records and informed by expert understanding of species' range and habitat preferences. In contrast, AquaMaps models species distribution based on environmental preferences (e.g., temperature, depth, salinity) deduced from occurrence records, published species databases such as FishBase, and expert knowledge. The AquaMaps model overlays these environmental preferences atop a map of environmental attributes on a 0.5 degree grid, creating a global map of "probability of occurrence" for each species (14, 15). Studies using AquaMaps data frequently define "presence" by applying a probability threshold, e.g., the Ocean Health Index

Significance

Successful conservation of marine species critically depends on detailed and accurate understanding of where species exist and where they do not. By systematically comparing two widely used global datasets of marine species range maps, we find substantial differences that highlight inconsistencies in our understanding and communication of species ranges. Knowing where and why these inconsistencies occur will substantially improve our ability to develop effective and efficient conservation strategies that support resilient ocean ecosystems.

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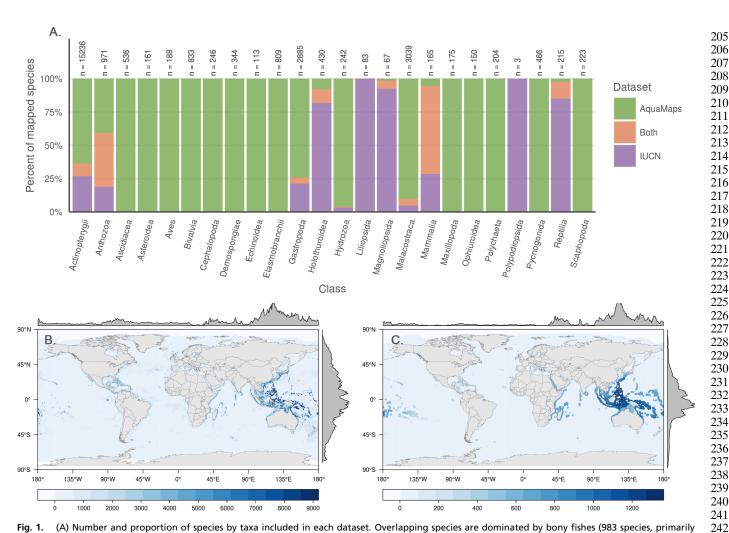


Fig. 1. (A) Number and proportion of species by taxa included in each dataset. Overlapping species are dominated by bony fishes (983 species, primarily tropical taxa) and corals (396 species). (B, C) Global marine species count per cell according to (B) AquaMaps and (C) IUCN. The margin frequency plots show relative species count per cell at each latitude and longitude.

defines presence as 40% or greater probability of occurrence (3, 4).

The methodologies behind the creation of these datasets imply differences in prediction of species distribution due to errors of commission (falsely indicating species presence) and omission (falsely indicating species absence). Geographic range data such as IUCN range maps frequently introduce commission errors, while species distribution models such as AquaMaps will likely introduce fewer commission errors but more omission errors. Each type of error bears different implications for conservation goals: commission errors can result in prioritizing areas not relevant to conservation goals, while omission errors may result in protected area networks that fail to include important habitat and range (12). By comparing maps resulting from IUCN and AquaMaps methodologies, we can identify and possibly address mechanistic causes for each type of error.

The two datasets have notably different taxonomic (Fig. 1A) and regional (Figs. 1B, 1C) coverage. AquaMaps encompasses a broader range of taxa than IUCN, as IUCN spatial data files are only available for select taxonomic groups that have been comprehensively assessed. While species numbers in both datasets peak in tropical latitudes near the equator, species counts for IUCN maps drop quickly beyond 30°N and 30°S, while species counts for AquaMaps remain robust well into temperate latitudes. The longitude frequency plots show a slight shift in the IUCN dataset away from the Atlantic and eastern Pacific com-

pared to AquaMaps. To achieve more comprehensive global coverage of species ranges these two datasets can be used together, but the underlying methodological differences complicate such direct comparisons.

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To explore differences in species distribution and range between the two datasets, we plotted the distribution alignment (how much of the smaller range falls within the larger range, i.e., where on the map) against the area alignment (ratio of smaller range area to larger range area, i.e., how much of the map) for each shared species (Fig. 2A). This analysis revealed a general negative linear pattern, suggesting that increasing similarity in range area correlates with decreasing distribution alignment. AquaMaps tends to extrapolate species ranges into suitable areas beyond known occurrences, such that each additional unit of range predicted by AquaMaps will fall in different locations than an additional unit of range predicted using IUCN methodology. For species with dissimilar range areas, predicted distribution for the smaller range can more easily fall within the generous bounds of the larger range. For species with increasingly similar range areas, differences in methodology become more difficult to "hide," and the distribution alignment generally becomes poorer.

The mean distribution alignment for species included in both datasets was 63%; the mean area alignment was 54.5%. By dividing the map-paired species into quadrants based on these means, we highlight categories of relationships that help further explain

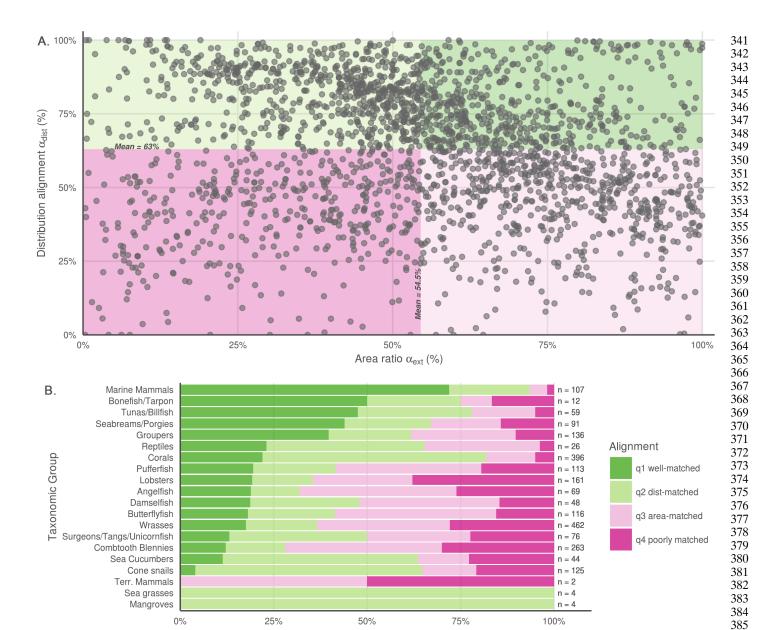


Fig. 2. (A) Distribution alignment (overlap of smaller range within larger) versus area ratio (the ratio of smaller range area to the larger range area) for 2,279 species included in both IUCN and AquaMaps datasets. The upper right quadrant (quadrant 1) comprises species whose maps largely agree (better than median value) in both spatial distribution and the extent of described ranges (n = 466; 20.1 %). The upper left quadrant (quadrant 2) comprises species whose maps agree well in distribution, but disagree in area (n = 687; 29.7 %). The lower right quadrant (quadrant 3) includes species for which the paired maps generally agree in range area, but disagree on where those ranges occur (n = 691; 29.9 %). The lower left quadrant (quadrant 4) indicates species for which the map pairs agree poorly in both area and distribution (n = 470; 20.3 %). (B) Alignment quadrant breakdown of species by taxonomic group.

Percent of species by quadrant

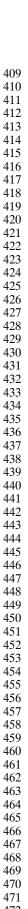
this general pattern. Representative maps from each category are provided in the supplemental materials (Fig. S1).

The upper right quadrant includes species (n=527) whose described ranges are above average in alignment of both spatial distribution and area. These species tend to be well-studied and include wide-ranging pelagic organisms such as marine mammals, tunas, and billfishes (Fig. 2B). This result is not surprising, as species with very large ranges are likely to be more aligned regardless of methodology simply because their ranges span nearly the entire map.

The area-mismatched ranges contained in the upper left quadrant (n = 709) include many species whose spatial distribution is similar, but where the IUCN range is notably larger, often extending into deeper water. For example, corals dominate this

quadrant (n = 237; 33.4% of all species in this quadrant), and IUCN range maps tend to extend corals into waters beyond their preferred depths, likely introducing errors of commission (Fig. S3). Ocean depth preference is explicitly included in AquaMaps models, while depth is frequently overlooked as a factor in IUCN range maps. Simply clipping IUCN range maps to known depth preferences would resolve many of these mismatches.

Species found in the lower right quadrant (n = 635) often represent cases of "two wrongs make a right." For these species, IUCN ranges frequently overextend into unsuitable depths, as in the case of many upper left quadrant species, while at the same time AquaMaps ranges often aggressively extrapolate presence into locations where IUCN predicts absence, introducing additional commission errors. Consequently, area ratios are close to



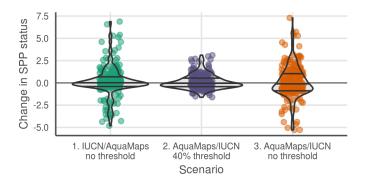


Fig. 3. Change in status score for the Species Subgoal within the global Ocean Health Index under three different scenarios. Scenario 1 shows the effect of reducing the probability threshold to 0% for AquaMaps presence to more accurately track the definition of IUCN "limits of distribution." Scenario 2 shows the effect of prioritizing AquaMaps data over IUCN, while maintaining the 40% presence threshold. In general, AquaMaps ranges are smaller than IUCN ranges, so most overlapping species will see a decrease in represented range. Scenario 3 shows the effect of prioritizing AquaMaps data over IUCN, and simultaneously eliminating the presence threshold. The zero threshold in scenario 3 drives a decrease in scores relative to scenario 2.

100%, though similar areas are unhelpful when the distributions are poorly aligned.

The most vexing cases are in the lower left quadrant (n = 443), where neither distribution nor area match well. Data-poor species are more common in this quadrant; indeed, the median number of species occurrence records (averaging occurrences from the Ocean Biogeographic Information System (OBIS) (16) and the Global Biodiversity Information Facility (GBIF) (17)) for this quadrant is 24 records, compared to a median of 97 records for species across the other three quadrants. When extrapolating from limited observations, the AquaMaps model often predicts species presence well beyond known occurrences, introducing commission errors; at the same time, IUCN range maps generally target known occurrences, possibly introducing omission errors for data-limited species.

Implications

Method-driven differences in commission and omission errors produce clear and significant disagreement in species range descriptions between AquaMaps and IUCN datasets. To examine the implications of these differences, we repeated two recent studies, varying only the prioritization of one data set over the other.

Case Study: The Ocean Health Index

The global Ocean Health Index (OHI) (3, 4), a composite index comprising ten sustainable benefits provided by a healthy ocean, uses species spatial distribution data and IUCN Red List conservation status to calculate biodiversity status (scored from zero to 100) for each of the world's 221 exclusive economic zones. To maximize the number of represented species, OHI gleans spatial distribution data from Red List-assessed species in both IUCN and AquaMaps datasets (n = 7,963), prioritizing IUCN data for the 2,026 species included in both sources. OHI currently uses a probability of occurrence threshold of 40% to determine species presence for AquaMaps data.

We calculated the OHI species status score under several scenarios to observe the impact of toggling the prioritized data set from IUCN to AquaMaps, and toggling the AquaMaps presence threshold from 40% to 0% (Fig. 3). Reducing the threshold increases the apparent range of a species, so a decrease in a region's score under scenario 1 would indicate increased spatial representation of threatened species for that region. Shifting priority from IUCN to AquaMaps may increase or decrease a species' apparent range, so a decrease in region score for scenario 2 may indicate a decrease in spatial representation of low-risk

species, an increase in spatial representation of high-risk species, or a combination of both. Scenario three combines effects of scenarios 1 and 2.

Given that only 25.4% of species are included in both datasets, it is surprising that changing the priority for overlapping species from IUCN maps to AquaMaps would result in substantial country-level score shifts as seen in scenarios 2 and 3. While the mean global score did not vary significantly from scenario to scenario, select countries gained up to 7.5 points while others dropped as many as 5 points. This result indicates that especially on a national or regional scale, an arbitrary change in how the two datasets are combined can result in a different assessment of species conservation status.

Case Study: MPA Gap Analysis

Klein et al. (11) compare the global distribution of species to the global distribution of marine protected areas to assess how well current MPAs overlap with species ranges and identify which species fall through gaps in protection. The study relied on the AquaMaps database, using a probability of occurrence threshold of 50% or greater, to determine species presence, and the World Database of Protected Areas to define zones of marine protection. They found that the global MPA network leaves 90.5% of marine species with less than 5% of their overall range represented within MPAs, and 1.4% of species have no protection at all (i.e., "gap" species).

We recalculated the amount of under-protected and gap species using either IUCN or AquaMaps data (using the most recent AquaMaps data and a 0% threshold to allow the most meaningful comparison to IUCN's "limits of distribution", Fig. 4). We found a five-fold increase in the proportion of gap species (6.4% of species vs. 1.2%) and dramatically larger proportion of species with less than 2% of their range protected (73.2% of species vs. 47.7%). However, this comparison also indicates a larger proportion of well-protected species with greater than 10% of range protected (2.9% of species vs. 1.5%). Conclusions drawn from each of these datasets would paint dramatically different pictures of the protection afforded by our current global MPA network.

Conclusions

AquaMaps and IUCN range maps show reasonable agreement for many well-studied species, but substantial differences illustrate uncertainty in our understanding of spatial distribution for many others. Although many other approaches exist for species distribution modeling, these two are the only ones applied globally across different marine taxa. Identifying and addressing differences in these datasets will increase their utility for research and conservation actions. Several likely drivers of commission and omission errors between these datasets point to a few important ways to improve range alignment.

For IUCN range data, clipping ranges to known depth limits improves output for many species, most notably corals and reefassociated fishes. If species' depth limits are not known, simple rules of thumb will likely reduce commission errors without introducing substantial omission errors. For example, for most corals, researchers could clip range maps to the photosynthetic limit of 200 meters. For AquaMaps range data, dependent primarily on environmental and physical preferences and conditions, implementing area restrictions based on biogeographical criteria such as Marine Ecoregions of the World (18) would likely decrease commission errors and improve predictive power, especially for data-poor species. For either data set, maps based on few occurrences are more likely to include errors of commission and omission. Occurrence counts from external sources such as OBIS or GBIF can help identify relatively data-poor species; additionally, the "occurcells" attribute in the AquaMaps data set, which counts the number of half-degree cells used to generate the

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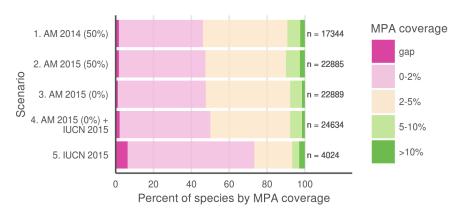


Fig. 4. Percent of species range covered by MPAs based upon methods in Klein et al. (2015). Scenario 1 replicates the original results, measuring protected range of species in AquaMaps 2014 dataset, with a 50% presence threshold, against the 2014 World Database of Protected Areas, filtered for IUCN categories I-IV that overlap marine areas. Scenario 2 updates the results using AquaMaps 2015, showing very small changes despite the inclusion of an additional 5,545 species. Scenario 3, using 2015 AquaMaps data, drops the presence threshold to zero, showing an expected decrease in gap species, but also a decrease in species with 5% or greater protected range. Scenario 4 adds an additional 1745 species unique to IUCN, resulting in increases in gap species and species with less than 2% coverage. Scenario 5 examines species MPA coverage using only the IUCN dataset.

environmental envelope for each species, can be used in a similar manner.

Many studies using AquaMaps data test the sensitivity of results by varying the probability of occurrence threshold to determine presence. This decision ultimately represents a trade-off between errors of commission (low threshold) and omission (high threshold). Using AquaMaps in conjunction with IUCN can mitigate potential errors, while also increasing the taxonomic and spatial breadth of coverage, as long as the differences between the datasets can be reasonably minimized. In this case, we recommend a presence threshold of 0% as it most closely approximates the "limits of distribution" criterion defined by IUCN data providers.

Effective management and protection of marine species depends on a robust understanding of where species exist and where they do not; without this knowledge we risk wasting resources protecting low-value regions while missing opportunities to protect critical ones. By identifying the differences between these two fundamental marine species range datasets and understanding the likely mechanisms causing these discrepancies, we improve our ability to develop strategic and effective conservation policy that supports a resilient ocean ecosystem.

Methods

Comparison of taxonomic and regional distribution: To examine the overall taxonomic distribution across the spatial datasets (Fig. 1A), we grouped species by taxonomic class and data source (IUCN, AquaMaps, or both), and examined the proportion of each class represented in each data source category.

To compare the spatial representation of the two datasets directly, we rasterized the IUCN species polygons to the same 0.5° grid as the AquaMaps species maps; species presence within a grid cell was determined by any non-zero overlap of a species polygon with the cell, and number of species per cell was simply the count of the species present. For the AquaMaps dataset, we determined per-cell species count by including all species with non-zero probability of occurrence, to best approximate the "extent of occurrence" generally indicated by IUCN maps. We represented relative distribution of species count for each dataset by plotting average species count against latitude and longitude (Fig. 1B, 1C).

Comparison of paired maps: Using genus and species binomials as a matching key, we selected the subset of marine species that have range maps in both IUCN and AquaMaps current native distribution. To avoid double-counting, we removed subpopulations and species aliases. We determined species presence within each spatial cell using the same criteria outlined above.

Overlaying paired distribution maps for a given species, we defined and calculated *distribution alignment* and *area ratio* and plotted these in Fig. 2A:

 Kaschner K et al. (2015) AquaMaps: Predicted range maps for aquatic species. World wide web electronic publication, www.aquamaps.org, Version 08/2015.

$$lpha_{dist} = rac{A_{small \, Olarge}}{A_{large}} * 100\%$$
 $lpha_{area} = rac{A_{small}}{A} * 100\%$

For each species with ranges described in both IUCN and AquaMaps, A_{small} and A_{largs} indicate the smaller and larger range representation (regardless of which dataset). A_{small} neargs represents the amount of overlapping area between the two datasets. We visually inspected a random selection of paired distribution maps from each quadrant to identify possible mechanistic causes of misalignment. To verify that IUCN predicted unsuitable habitat for depth limited species, we used QGIS (19) to overlay a selection of IUCN and AquaMaps maps with a 200-meter bathymetry contour.

Methods for OHI case study: Using methods and supplemental materials from OHI (3, 4), we modified the original code for OHI 2015 Species status (SPP), allowing for flexibility in prioritized data source and AquaMaps presence threshold. We ran the SPP code three times, prioritizing IUCN over AquaMaps for a 0% threshold, and prioritizing AquaMaps over IUCN for both a 40% and 0% threshold. We compared each of these to the output of the published OHI 2015 SPP model (which prioritizes IUCN over AquaMaps at a 40% threshold).

Methods for MPA Gap Analysis case study: Based upon the methods described in Klein et al. (11), we reconstructed the analysis using the subset of protected areas from the World Database on Protected Areas (WDPA) (20) spatially covering a marine area and classified as IUCN I-IV. The WDPA polygons and marine polygons were rasterized to 0.01° and then aggregated to AquaMaps native 0.5° cells, to calculate proportion of protected area and marine within each cell. After verifying our results using the 2014 AquaMaps dataset, we updated the analysis using the 2015 AquaMaps dataset at a presence threshold of 50% (to compare to Klein et al. directly) and 0% (to better compare with IUCN spatial data). To analyze MPA coverage against IUCN spatial data, we extracted IUCN polygon weights per 0.5° cell for each species and compared against the protected area raster. Finally, we combined AquaMaps data (at 0% threshold) and IUCN data, using AquaMaps for the 2,279 overlapping species and again compared against the protected area raster.

All processing was completed using R statistical software (21), and all code and intermediate data are available on GitHub at https://github.com/O-HI-Science/IUCN-AquaMaps.

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