Prioritizing global marine mammal habitats using density maps in place of range maps

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Despite lessons from terrestrial systems, conservation efforts in marine systems continue to focus on identifying priority sites for protection based on high species richness inferred from range maps. Range maps oversimplify spatial variability in animal distributions by assuming uniform distribution within range and de facto giving equal weight to critical and marginal habitats. We used Marxan ver. 2.43 to compare species richness-based systematic reserve network solutions using information about marine mammal range and relative abundance. At a global scale, reserve network solutions were strongly sensitive to model inputs and assumptions. Solutions based on different input data overlapped by a third at most, with agreement as low as 10% in some cases. At a regional scale, species richness was inversely related to density, such that species richness hotspots excluded highest-density areas for all species. Based on these findings, we caution that species-richness estimates derived from range maps and used as input in conservation planning exercises may inadvertently lead to protection of largely marginal habitat.

Marine ecosystems are increasingly dominated by human activities, causing widespread loss of populations and species (Worm et al. 2006, Halpern et al. 2008). Parties to the Convention on Biological Diversity have pledged to reduce the current rate of species loss in both the terrestrial and marine environments in order to preserve wild species and allow for their sustainable use. The October 2012 United Nations Biodiversity Conference in Hyderabad, India reached an agreement to double resources for biodiversity protection by 2015, with a special focus on 'biodiversity-rich' marine areas. One way to pursue this goal is by engaging in systematic conservation planning (Margules and Pressey 2000), including the use of no-take marine protected areas (MPAs) to slow biodiversity loss and promote recovery of depleted species and populations (Lubchenco et al. 2003). Important questions remain about the value of MPAs for highly mobile or migratory species (Boersma and Parrish 1999, Hyrenbach et al. 2000, Hooker et al. 2011), and where to locate and how to design MPAs so that they will do the most good while minimizing societal cost (Brown et al. 2001). Much

theoretical work has been devoted over the past decade to addressing such questions in terrestrial systems (Myers et al. 2000, Rodrigues et al. 2004).

In recent years, a number of initiatives have sought to ensure that marine mammals are represented in spatial and MPA network planning (e.g. International Conference on Marine Mammal Protected Areas (Hoyt 2012); US National Marine Fisheries Service Cetacean and Sound Field Mapping Projects (<http://cetsound.noaa.gov/index.html>)). Many species of marine mammals are in a stage of recovery from overexploitation by commercial hunting, or continue to be subject to unsustainable levels of bycatch in commercial or artisanal fisheries (Hooker and Gerber 2004, Read et al. 2006). Further, increasing levels of chemicals and noise in addition to climate change represent serious threats for many species (Erbe et al. 2012). In the context of marine conservation planning to identify areas to protect these species, data gaps are a significant problem (Schipper et al. 2008). Density estimates for cetaceans (whales, dolphins and porpoises) are available for only ~25% of the world's oceans, with a strong geographic bias toward waters under the jurisdiction of affluent countries, and only ~6% has been surveyed often enough to detect trends (Kaschner et al. 2012). Rare species, which may be most in need of

protection, may not even be detected until an area has been surveyed multiple times (Kaschner et al. 2011).

A defining challenge in conservation is decision-making under extreme uncertainty (Ludwig et al. 1993). In the absence of good global estimates of abundance and distribution of many marine mammal species, a paucity of data has been used to justify reliance on coarse-resolution range maps (which often represent broad polygons that join a small number of known locations) as a proxy for distribution (Schipper et al. 2008), and these have been used to prioritize areas for protection (Tittensor et al. 2010, Pompa et al. 2011). Range maps are readily available and therefore represent an attractive source of information for use in planning and modelling (Ceballos and Ehrlich 2002). However, they can misrepresent distribution boundaries, include areas of non-habitat, and imply homogeneous density within range (Schipper et al. 2008). They therefore seem an incongruous input for modeling exercises focusing on 'spatial conservation prioritization' (Moilanen and Wilson 2009).

In terrestrial ecology, it is well established that range maps have some utility for answering large-scale questions of basic ecology (Hurlbert and White 2005), but that they are generally uninformative for conservation planning and implementation (Gaston and Rodrigues 2003, Hurlbert and Jetz 2007, Hooker et al. 2011). Two key assumptions of using range maps for spatial planning are untenable: 1) all parts of a species' range are equally valuable for conservation, and 2) protecting some fraction of the range, without associated information on what proportion of the population would thus be protected, is sufficient to ensure population viability (Rodrigues et al. 2004). Range maps that over- or underestimate species occurrence can misguide conservation action (Elith et al. 2006), therefore it is essential to assess the sensitivity of model outputs to the inputs used. Any approach that seeks to optimize reserve networks based on range maps implicitly sets the protection of species richness as a conservation target, because an area used by multiple species will provide a more efficient solution than multiple areas used by single species.

In the marine realm, despite these known issues, a perceived lack of alternatives to range maps (caused by the paucity of data and very heterogeneously distributed sampling effort) has resulted in their continued use as inputs in spatial planning exercises. For instance, a recent effort identified 9 key conservation sites for 123 marine mammal species and suggested that these sites covering only about 2.5% of the oceans could provide meaningful protection for 84% of all marine mammal species (Pompa et al. 2011). Here, we investigate the theoretical effectiveness of range maps for identifying priority sites for biodiversity conservation efforts, at both global and regional scales. Employing widely used conservation planning algorithms, we compared the effect of different types of global species distribution data inputs on protected area network solution outputs. In a data-rich region (British Columbia (BC), Canada), where spatially explicit abundance estimates were available for 11 species, we also compared locations of species-specific core habitats, defined as areas containing the highest animal densities and hypothesized to have excellent habitat quality, with locations of species richness hotspots, defined as areas with the highest number of species, to investigate the relationship between animal density and species richness. And finally, we examined the effect

of expansive and restrictive definitions of individual species ranges (corresponding roughly to the commonly applied IUCN extent of occurrence (EOO) and area of occupancy (AOO) concepts) on estimates of species richness.

Material and methods

In our analyses, we differentiate among three kinds of spatially explicit data inputs: 'range maps' (polygons defining extent of a species occurrence and assuming presence within and absence without); 'distribution maps' (in this case, relative environmental suitability (RES, Kaschner et al. 2006) estimates used as a proxy for relative abundance); and 'density maps' (based on measured or modeled abundance per unit area).

Global analyses

We used Marxan ver. 2.43 (Ball et al. 2009) to explore the sensitivity of global marine mammal protected area (MMPA) network solutions to different types of input data, varying in coarseness and assumptions about the actual distribution of species within the known maximum extent of occurrence. We derived five input data sets and conducted all analyses at a 0.5 degree latitude by 0.5 degree longitude grid cell resolution (Table 1). We used global predictions of RES produced by niche envelope models, which range from 0 (unsuitable) to 1 (suitable), to predict the range and distribution of 115 marine mammal species (Kaschner et al. 2006). We used both an expansive ($RES > 0$; referred to as $Range_{full}$) and a restrictive ($RES > 0.6$; referred to as $Range_{core}$) threshold to convert continuous RES values for each cell to presence (1) or absence (0). The $Range_{full}$ maps closely resembled existing IUCN range maps for most species. The $Range_{core}$ maps limit the analysis to predicted high-quality habitat for multiple species. Although $Range_{core}$ maps represent a subset of $Range_{full}$ for each species alone, cumulative species richness patterns based on these core maps vary substantially from $Range_{full}$ (compare with Kaschner et al. 2011, Supporting information Fig. S1). The selected threshold of $RES > 0.6$ for our restrictive range was supported by previously published validation analyses, during which biodiversity patterns generated based on this presence threshold showed the best model fit with observed line transect survey-derived estimates of marine mammal species richness (Kaschner et al. 2011). We also used the continuous RES values (referred to as RES), as a proxy for the relative species-specific abundance within

Table 1. Description of input data sets used in global Marxan analyses.

Dataset	Data type	Transformation	Threshold	Grid cells included
$Range_{full}$	presence–absence	none	0.0	all
$Range_{core}$	presence–absence	none	0.6	all
RES	index of abundance	none	0.0	all
RES_{sq}	index of abundance	squared	0.0	all
RES_{survey}	index of abundance	none	0.0	surveyed

the full range, under the assumption that cells with high RES values correspond to areas with high relative abundance and therefore function as core habitat. This assumption is supported by previous validation analyses (Kaschner et al. 2006), which indicated that there is a strong positive relationship between predicted RES values and observed sightings per unit effort using data collected during dedicated large scale marine mammal surveys across a range of different species, geographic areas and time periods. Similarly, to emphasize potential differences in habitat quality, we also calculated the squared multiplier of RES (RES_{sq}), which upweighted high RES cells, therefore steepening the putative distribution gradients, in an attempt to focus reserve selection on high-use cells within the range without selecting a threshold. Finally, we derived a fifth input data set that reflected data gaps in global cetacean visual line transect survey coverage (referred to as RES_{survey}). This data set included continuous RES values for cells that had been surveyed (Kaschner et al. 2012) and excluded all other cells.

We ran 100 replicates of each input data scenario using the richness heuristic algorithm, which adds cells to the reserve network that has the most unrepresented species

(Game and Grantham 2008). We parameterized Marxan to spatially aggregate solutions to produce more functional reserve networks, and used planning unit area as a surrogate for cost. For visual comparison, we mapped the 'best' protected area solution for each input data scenario, defined as the most efficient solution that represented at least 10% of every species' total 'abundance' (i.e. the sum of RES values) in the smallest area (Fig. 1a–e). Note that although validations suggest that for many species RES is correlated with relative abundance, RES does not provide an actual abundance estimate; it is treated as an index of abundance that provides biologically plausible estimates of heterogeneous distribution (i.e. uneven density across the range).

We produced kernel density plots (Fig. 2) of the distributions of all pairwise comparisons of 100 solutions to calculate proportional area overlap both within (intra-scenario) and among (inter-scenario) reserve network solutions for each input data scenario. Intra-scenario comparisons were conducted to quantify the variability due to random process variance across 100 solutions using the same input data. Inter-scenario comparisons quantified the similarity across 100 solutions using different input data sets.
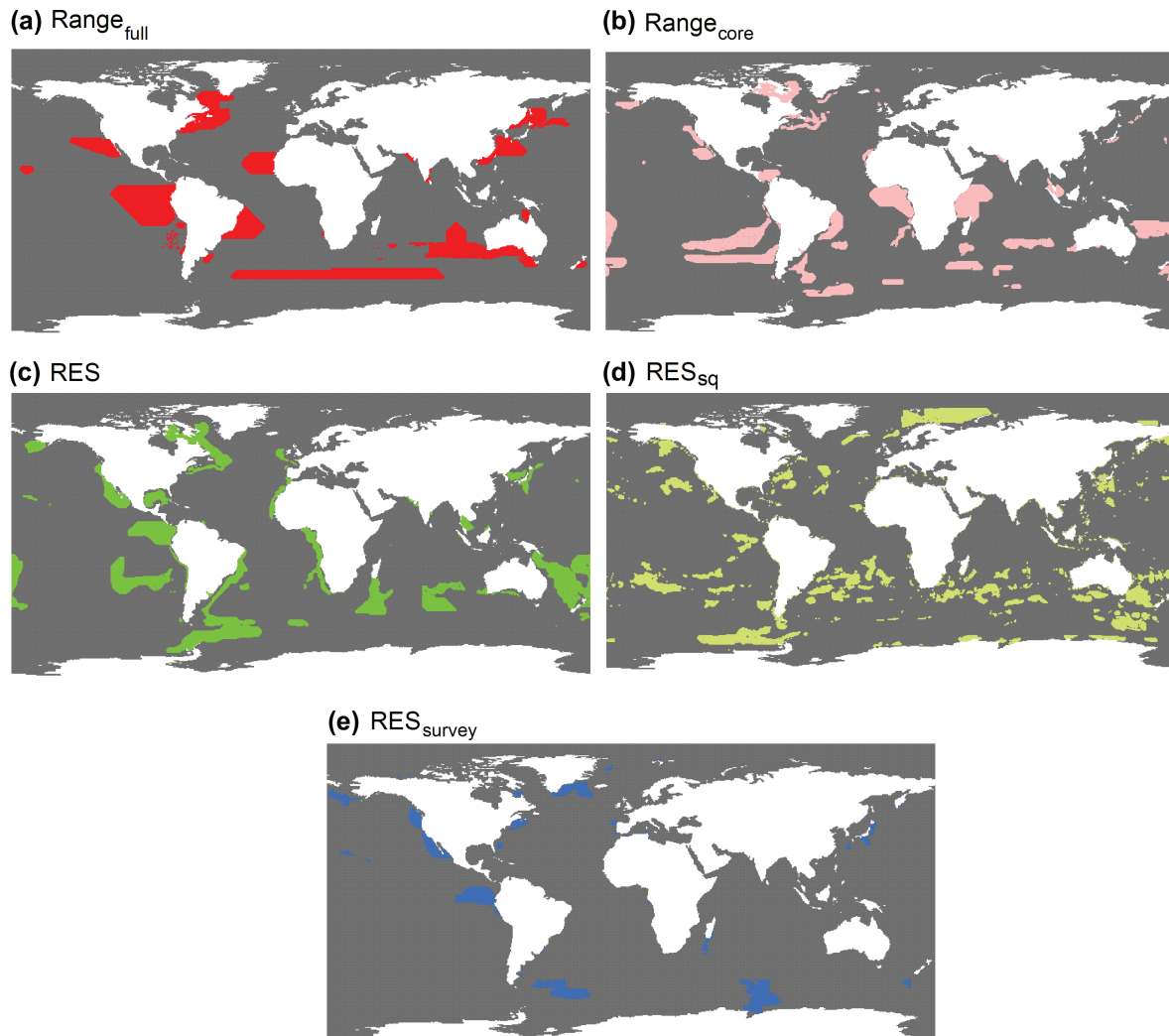

Figure 1. Global analysis: the respectively 'best' Marxan solution (i.e. the most efficient one, or smallest total area that represents at least 10% of every species' total 'abundance') from 5 input data scenarios ((a) $Range_{full}$, (b) $Range_{core}$, (c) RES, (d) RES_{sq} and (e) RES_{survey}; see Table 1 for definitions).
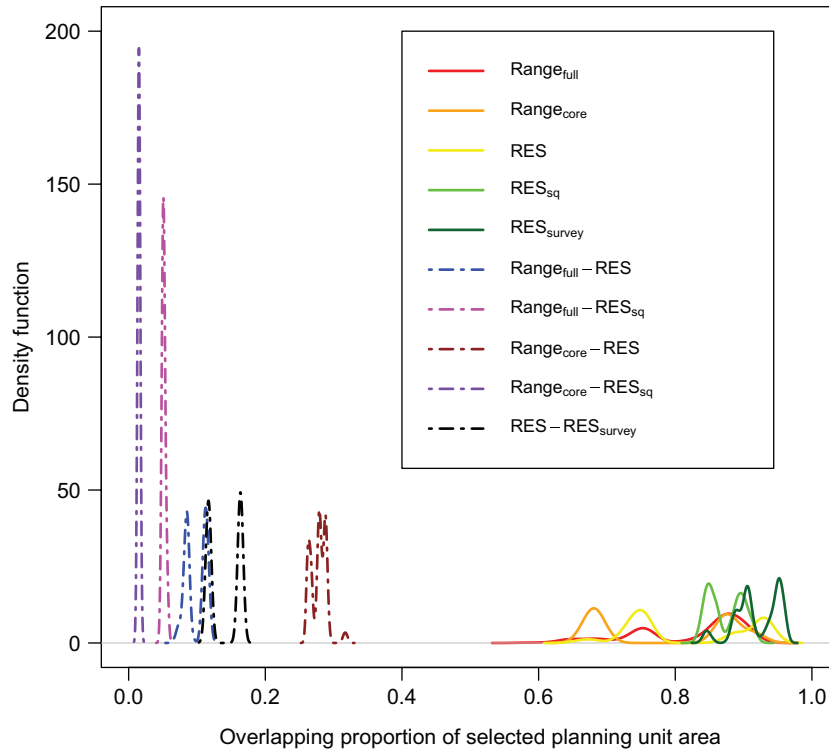
Figure 2. Global analysis: overlap showing similarity in Marxan solutions (Fig. 1), given the 5 inputs (Range$_{full}$, Range$_{core}$, RES, RES$_{sq}$ and RES$_{survey}$). Kernel density plots show distributions of all pairwise comparisons of selected planning units for 100 solutions. Proportional area overlap was calculated for both intra-scenario (among 100 solutions using the same input data) and inter-scenario (across 100 solutions using different input data) solutions.

Regional analyses

We chose a data-rich region (BC, Canada), where effort and sightings data from four replicates of systematic sightings surveys have generated density surfaces (i.e. spatially explicit abundance estimates) for 11 marine mammal species, at a spatial resolution of 2×2 nautical mile grid cells (Williams and Thomas 2007, Williams et al. 2011a). These surfaces represent estimates of mean animal density in each grid cell, based on data collected during surveys conducted between late spring to early summer, 2004–2008. To illustrate spatial patterns of core habitat and overlap of such habitat between different species, we categorized cells for each species based on kernels of that species-specific density (i.e. cells containing the top 25, 50, 75, 97.5 and 100% species population, normalized to the population size of each species). These core-to-peripheral, two-dimensional kernel density maps result from adding different extents of peripheral range successively. The outermost two rings correspond to what is usually referred to as range maps. In this study, the 100% density map represents the full range extent containing all cells with density > 0, corresponding to the IUCN definition of 'extent of occurrence'. The 97.5% density map excludes all near-zero density cells that cumulatively contain the last 2.5% of the total population, corresponding roughly to the IUCN definition of 'area of occupancy' (Gaston 1991).

In order to investigate the likelihood that areas where species richness is high (i.e. the number of species per cell is high) correspond to areas of low species-specific density, we used the expansive 'extent of occurrence' definition of range

and calculated species richness as the number of species for which the estimated density in the respective cell was > 0 for each cell across the map (this is equivalent to species richness patterns based on the Range$_{full}$ data set in the global analysis). We then compared species richness for each cell to the average density of all species for each cell by plotting identified core habitats and species richness hotspots on a map.

To assess the effect of range definition on species richness calculations, we then proceeded to calculate species richness using the 'area of occupancy' range definition (i.e. excluding all cells containing only very low densities). Based on both types of range definitions (extent of occurrence and area of occupancy) we then grouped cells containing different normalized densities for each species into different classes, defined in 6.5% increments up to 97.5% (of the total population) but only adding 2.5% in the final bin. The 6.5% threshold was based on the only quantitative target currently available for protecting critical habitat of an endangered marine mammal in Canada's Pacific region (Williams et al. 2009). As a result, any given cell might be in different density classes for different species and may thus be counted more than once in the subsequent analysis. For each density class (combined for all species) we then calculated the mean species richness across all cells.

Results

At a global scale, resulting patterns of species-rich areas varied dramatically among the five inputs we considered

(Fig. 1a–e). Marxan solutions from these five inputs had very little overlap (Fig. 1, 2). We found some intra-scenario variability (Fig. 2, solid lines), but much greater inter-scenario variability (Fig. 2, dashed lines), which suggests that the proposed protected area networks are strongly dependent on the type of input data used. We found large disparities between Marxan solutions using range and RES inputs: mean overlap between solutions based on $Range_{core}$ vs RES was 28%; mean overlap between solutions based on $Range_{full}$ vs RES was 10%. Areas that were prioritized for protection using range input data had even less area overlap with RES_{sq} input data, suggesting that heterogeneity of species distribution affects sensitivity of protected area network solutions to data inputs (i.e. range, distribution, or density maps). Analyses that incorporated known data gaps by using only RES values from cells where line transect surveys have taken place (Kaschner et al. 2012) resulted in solutions that were as divergent as those derived from binary range maps, with a mean of 14% area overlap between the RES and RES_{survey} scenarios (Fig. 2).

In our regional scale case study, we considered spatially explicit density maps for marine mammals in western Canada generated from observed abundances (Williams and Thomas 2007, Williams et al. 2011a). We found no spatial overlap in core habitats (i.e. areas of highest density) for any of the 11 marine mammal species. When we considered range maps incorporating increasing kernel density classes, we found almost no species overlap for areas that contained the highest proportion of each species' population (i.e. the top 6.5–25% of the population) across all species (Fig. 3). Range maps that included up to 75% of the population of each species still had very few cells that contained more than 2 or 3 species. Substantial overlap (i.e. values of species richness approaching the maximum possible value of 11) was not seen until we included 97.5% of the population of each species. A near doubling of mean species richness (from ~5 to ~9) was observed when 100% density ranges (sensu extent of occurrence; very low density cells included) were used for each species rather than 97.5% density (sensu area of occupancy) (Fig. 3). We observed an inverse relationship between species richness and mean density among all species, indicating that cells with higher species richness tended to correspond to cells where individual species occurred in relatively low densities (Fig. 4). When plotted on a map, this corresponded to a complete lack of overlap between areas of highest density (red cells correspond to the 11 core habitat areas – i.e. the fewest high density cells needed to protect 6.5% of the population of each species) and those of highest species richness (blue cells where species richness > 8, Fig. 4). Results averaged across all species again showed an increase in species richness towards the periphery of species' ranges (Fig. 5).

Discussion

Our analyses provide novel quantitative evidence of the inadequacies of range maps for marine mammal conservation planning that have been well established in the terrestrial realm (Hurlbert and Jetz 2007), but are often ignored in the marine environment. Conservation planning exercises that rely solely on range maps as input implicitly assume uniform habitat use, treating areas of high and low density as equivalent, and disregarding important differences between core and marginal habitats. Identification of high-quality, core, or high-density habitat is an essential component of endangered species conservation, management and recovery planning, and range maps are clearly inadequate for the task. In practice, systematic reserve selection algorithms are so sensitive to data inputs that range and distribution maps might give solutions that do not agree at even the largest spatial scales – broad regions within ocean basins. It has been noted previously that marine biodiversity hotspots do not coincide with productivity (i.e. density) in terms of fish catches (Worm et al. 2003), but this has not halted efforts to use species richness hotspots for conservation planning. In immediately practical terms, our results highlight the importance of including information on relative marine mammal occurrence or density, whether obtained empirically from surveys, predicted from models, or derived from expert opinion, in exercises attempting to identify priority sites for marine mammal protection.

It is important to distinguish between two kinds of diversity: mean species diversity at a given location, often measured at a somewhat local scale (α diversity), and the variability in species diversity due to differences among locations (β-diversity) (Whittaker 1972, Buckland et al. 2005). Our global and regional analyses suggest that the steeper the density gradient of the species in question, the less accurately a range map will approximate its distribution and the more unreliable the inferences about patterns in species richness will be (Fig. 1, 2). Prioritizing the most species-rich grid cells conflates α- and β-diversity, resulting in an approach that searches for shortcuts by prioritizing cells with the highest number of species, however rarely individuals from some or all of those species may visit those cells. We show in our regional analyses that targeting the cells with the greatest species richness protects only marginal habitat of multiple species while neglecting the core (critical) habitat of individual species. This finding opens up exciting research opportunities to explore mechanisms to explain the phenomenon we observe. There is evidence that niche partitioning, likely due to inter-specific variation in prey species and foraging strategies, drives the habitat preferences and distributions of many marine mammal species (Gibbs et al. 2011). Species richness is the least informative biodiversity metric, and abundance-based biodiversity indices appear better suited to measure spatial or temporal patterns to guide protected-area planning (Gotelli and Colwell 2001, Buckland et al. 2005) and ensure that reserve networks protect viable populations of all species of concern (Manel et al. 2002). As the quantity and quality of information available for decision-making increases, managers can consider increasingly sophisticated tools to protect specific habitat needs (Hooker et al. 2011, Rogers et al. 2013), such as foraging hotspots (Ashe et al. 2010). One lesson to emerge from the protected-area literature is that MPAs can shift human activities, and placing MPAs unknowingly in marginal habitats could actually shift human activities into critical habitats (Rojas-Bracho et al. 2006).

On the basis of our results, we caution against the use of maps containing known data gaps, which performed as poorly as range maps (i.e. $Range_{full}$) in comparison to our distribution map (i.e. RES) (Fig. 2). There are emerging
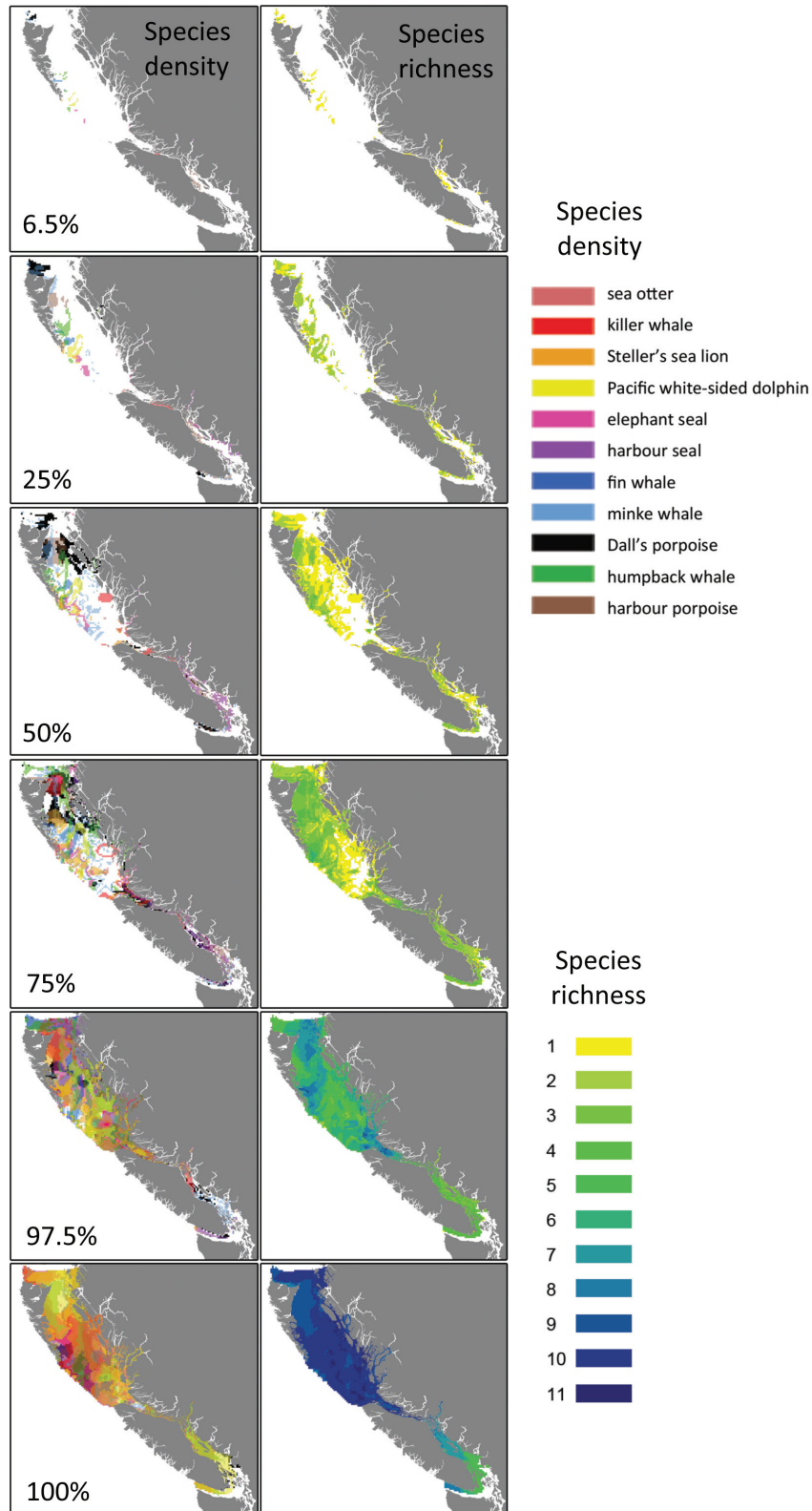
Figure 3. Regional analysis: Increasing two dimensional percentage kernel distribution for all species (left) and the resulting species richness calculations based on overlaps between these (right).

statistical methods to predict density from sparse or spatially biased data (Williams et al. 2011b), however, at larger scales, even extensive collections of available occurrence data sets such as those provided by OBIS-SEAMAP (<http://seamap.

env.duke.edu/>) are currently insufficient to generate global density layers for most marine mammal species. As an alternative, a number of international collaborations are already underway to produce density surface maps for cetacean
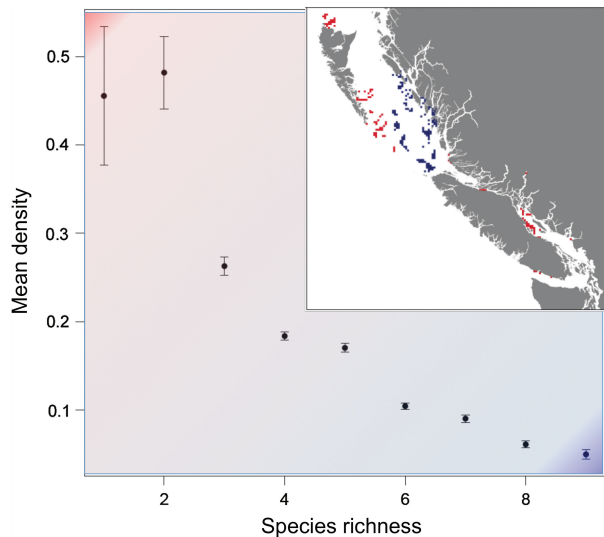
Figure 4. Regional analysis: mean density (number of individuals per grid cell) of all species present in cells of given species richness (calculated for extent of occurrence, i.e. the range polygon needed to contain 100% population size of each species). Lack of spatial correspondence between areas of highest density (red cells; corresponding to the top 6.5% density kernel) and areas of highest species richness (blue cells) is shown in inset panel. The shading illustrates the gradient from highest density/lowest richness (red) to lowest density/highest richness (blue) that is also shown in a spatially explicit context in the inset map.

species worldwide by combining abundance data from different monitoring techniques with spatial modeling approaches to infer marine mammal density in currently unsurveyed areas (e.g. CESAB project PELAGIC < http://cesab.org/images/projects/finches2011/PelagicEN.pdf >). Ongoing efforts to design marine mammal protected areas and networks would benefit greatly from the availability of global density layers. Although range maps offer a tempting shortcut,
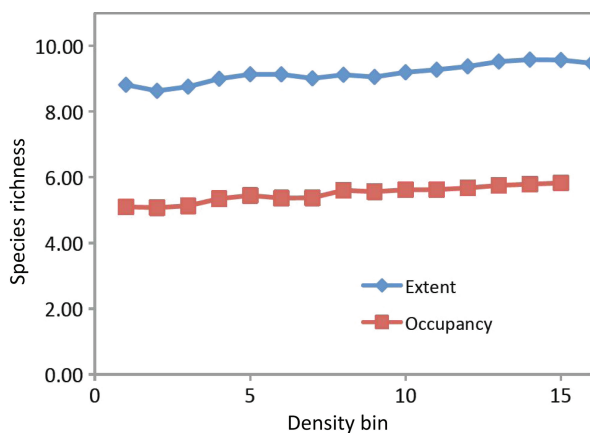

Figure 5. Regional analysis: effect of range definition on estimated species richness. Comparison of mean species richness calculated based on extent of occurrence (i.e. 100% of population size), and area of occupancy (i.e. 97.5% of population size, excluding the lowest density cells) definitions of range, and cells allocated to discrete kernel density bins for each species based on normalized population size contained within the cells. Bins ranked from 1–16, containing cumulative increments of 6.5% of population size up to 97.5%, but only adding 2.5% in the final bin.

particularly in the marine environment, it is important to avoid ending up with protected areas that look efficient on paper but in fact might confer protection to only a small number of individuals of each species.

Defining networks of protected areas that benefit multiple species involves tradeoffs and value judgments, and ultimately reflects management objectives rather than mathematical solutions alone. More expansive definitions of critical habitat for highly mobile predators require the inclusion of information on life history functions (e.g. breeding or feeding), residency, site fidelity or other behavioral aspects of habitat use throughout the year in predictive habitat models (Hooker et al. 2011). If conservation practitioners aim to protect critical habitat in MPAs, threats may also need to be treated explicitly in the design and monitoring processes. The question of how to protect habitat for ecologically and behaviorally diverse species that vary widely in their conservation status, vulnerability to different stressors, and use of habitat is a complex one.

We agree that it is important to situate protected areas where they can benefit multiple species, but our analyses illustrate that a given habitat is rarely of equal value to different species. Protecting species-rich cells implies that a) species are prioritized equally regardless of how abundant or how endangered they are and b) area-based 'protection' is adequate even though protected areas may not fully protect the animals from threats that originate elsewhere and can not be stopped at an MPA border (Hatch and Fristrup 2009).

To be clear, we are strongly supportive of the Hyderabad targets to protect 'biodiversity-rich' marine areas. Limited resources require that conservation efforts focus on the species that need it most. Our analyses show that the protection of core habitats represents a more meaningful starting point than protecting an arbitrary subset of their range. Given the global disparity in the quality and quantity of information available on marine mammal distribution and abundance (Kaschner et al. 2012) this necessitates analytical methods that account for spatially biased data, as the rush to protect species-rich regions identified with inadequate data may result in reserve networks that do little to protect biodiversity over the long term (Grand et al. 2007). Effective species-based conservation planning, at minimum, starts with unbiased data on species occurrence within their range. Given the high cost of filling in data gaps with real density data at a global scale (Kaschner et al. 2012), more realistic alternatives to simple polygons defining range could include expert opinion-based distribution maps, statistical models of effort and sightings, or ecological niche models like RES (Guisan and Thuiller 2005, Kearney and Porter 2009).

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