Evaluating the Use of Surrogates of Marine Mammal Species Representation in

Biodiversity Conservation Planning

by

Yaiyr Astudillo-Scalia

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Graduate Supervisory Committee:

Fábio Suzart de Albuquerque, Co-Chair
Pierre Deviche, Co-Chair
Beth Polidoro
Nicholas Kellar

ARIZONA STATE UNIVERSITY

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ABSTRACT

Biodiversity is required to guarantee proper ecosystem structure and function. However, increasing anthropogenic threats are causing biodiversity loss around the world at an unprecedented rate, in what has been deemed the sixth mass extinction. To counteract this crisis, conservationists seek to improve the methods used in the design and implementation of protected areas, which help mitigate the impacts of human activities on species. Marine mammals are ecosystem engineers and important indicator species of ocean and human wellbeing. They are also disproportionally less known and more threatened than terrestrial mammals. Therefore, surrogates of biodiversity must be used to maximize their representation in conservation planning. Some of the most effective surrogates of biodiversity known have only been tested in terrestrial systems. Here I test complementarity, rarity, and environmental diversity as potential surrogates of marine mammal representation at the global scale, and compare their performance against species richness, which is the most popular surrogate used to date. I also present the first map of marine mammal complementarity, and assess its relationship with environmental variables to determine if environmental factors could also be used as surrogates. Lastly, I determine the global complementarity-based hotspots of marine mammal biodiversity, and compare their distributions against current marine protected area coverage and exposure to global indices of human threats, to elucidate the effectiveness of current conservation efforts. Results show that complementarity, rarity, and environmental diversity are all efficient surrogates, as they outcompete species richness in maximizing marine mammal species representation when solving the minimum-set coverage problem. Results also show that sea surface temperature, density, and bathymetry are the top

environmental variables most associated with complementarity of marine mammals. Finally, gap analyses show that marine mammals are overall poorly protected, yet moderately exposed to hotspots of cumulative human impacts. The wide distribution of marine mammals justify global studies like the ones here presented, to determine the best strategy for their protection. Overall, my findings show that less popular surrogates of biodiversity are more effective for marine mammals and should be considered in their management, and that the expansion of protected areas in their most important habitats should be prioritized.

DEDICATION

It is said that it takes a village to raise a child. I argue that it also takes a village to produce a Doctor. I would like to dedicate this work to my son, Diego, for whom I continue to get up in the morning and one of the reasons I persevered through the process of reaching this milestone. To my mother, Mirtha, and sisters Anahí, Déborah, and Verushka, all of whom have contributed many hours of child care so that I could dedicate my time and attention to pursuing my degree; most especially my mother. Without all your support, this would have never happened like it did. For this, I wholeheartedly thank you. To my divine guidance, which never abandons me or lets me down. May it continue to guide me in the future. To those who have come before me and taught me and inspired me to keep going, and to those who will come after me: if I can do it, so can you.

To my parents, Mirtha and Gustavo, for instilling in me a thirst for knowledge and justice, and my older sisters Neddy and Ingrid for setting an example of how to successfully pursue higher degrees in "foreign" lands. To the future of our planet and its biodiversity. May we succeed in restoring our home Earth to its pristine balance.

And last, but not least, to the future of my home country Venezuela and my people. May all my efforts in achieving this degree turn me into someone who can help restore you to better days. Here is to a future of freedom, prosperity, and happiness. And so it is.

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CHAPTER 1

INTRODUCTION

1.1 Biogeography and Conservation Planning

Knowing the broad-scale patterns of species distributions is imperative in conservation science, since it allows us to identify the areas most suited for the design and implementation of conservation planning initiatives, such as the establishment of protected areas or reserves. These areas are built especially to halt biodiversity loss, protect ecosystem services, and protect recreational and scenic values (Margules and Pressey 2000). Since biodiversity is distributed unevenly, conservation planning allows the utilization of strategies for managing the whole landscape, such as the minimum and the maximum coverage problem. The former aims to select the least number of sites that will represent the most number of species, whereas the maximum coverage problem represents the largest number of species in a given number of sites (Moilanen et al. 2009, Albuquerque and Beier 2015a, 2015b, 2015c, Albuquerque and Gregory 2017).

The effectiveness of conservation planning is thus commensurate with the quantity and quality of data used in optimization analyses and modeling efforts. Comprehensive data also allow for studies that identify gaps between protection coverage and important biodiversity areas, both locally and globally. For terrestrial mammals, this is less of a challenge because the data available are less limited than those of marine systems (Tittensor et al. 2010). For mammals and other species there have been several global studies that investigate the effectiveness of conservation efforts in terrestrial systems (e.g., Brooks et al. 2004, 2006, Eken et al. 2004, Rodrigues et al. 2004, Cardillo et al. 2005, 2006, Wilson et al. 2011, Venter et al. 2014); in comparison, similar studies in

marine systems are fewer (e.g., Schipper et al. 2008, Wood et al. 2008, Pompa et al. 2011, Klein et al. 2015). Therefore, a major challenge in conservation planning is to identify conservation areas for marine species, in this case for marine mammals, and understand the factors and processes that explain the spatial distribution of those areas.

1.2 Surrogates of Biodiversity

In conservation planning, knowledge about the components and measures of biodiversity is insufficient; therefore, better known species are used as surrogates to represent those less known species that are presumably also present in the same area (Rodrigues and Brooks 2007). Rodrigues and Brooks (2007) found that this cross-taxon surrogacy can be an effective approach in conservation planning, especially when the different species all occur within the same system (e.g., marine). Other studies have found that environmental variables could also be used as surrogates of biodiversity (Albuquerque and Beier 2015b, 2015c, Beier et al. 2015). The use of surrogates is especially useful because the areas of the world that have the highest biodiversity (i.e., developing countries in the tropics; Albuquerque and Beier 2015b) are also areas with more limited access to resources for conservation planning and management.

1.3 Marine Mammals as Sentinel Species

Marine mammals are apex predators and therefore serve an important role in marine ecosystems by top-down regulation. Because of their status as ecosystem engineers (Roman et al. 2014), their long lifespans, our shared anatomy, susceptibility to certain diseases, and sources of food, (essentially, they are our marine counterparts), they are often regarded as sentinel species for ocean and human wellbeing (Bossart 2006, 2011, Maxwell et al. 2013).

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Overall, marine mammals are disproportionately facing more threats than terrestrial mammals, yet we also know a lot less about them and their extinction risk (Schipper et al. 2008, Jarić et al. 2014). There are currently about 134 recognized species of marine mammals listed in the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species. Of those, about one third (45 species) are listed as LC (least concern), meaning that their populations are not currently facing major extinction risks when considered globally (local populations might still be threatened). Another third (45 species) are listed as DD (data deficient), meaning that we currently lack sufficient information to determine their extinction risk (it is likely that an important number of these species belong to one of the threatened categories). The last third of marine mammals are either in one of the threatened categories (38 species), extinct (3 species), or have not yet been evaluated by the IUCN (3 species), given that they have only recently been recognized (figure 1.1).
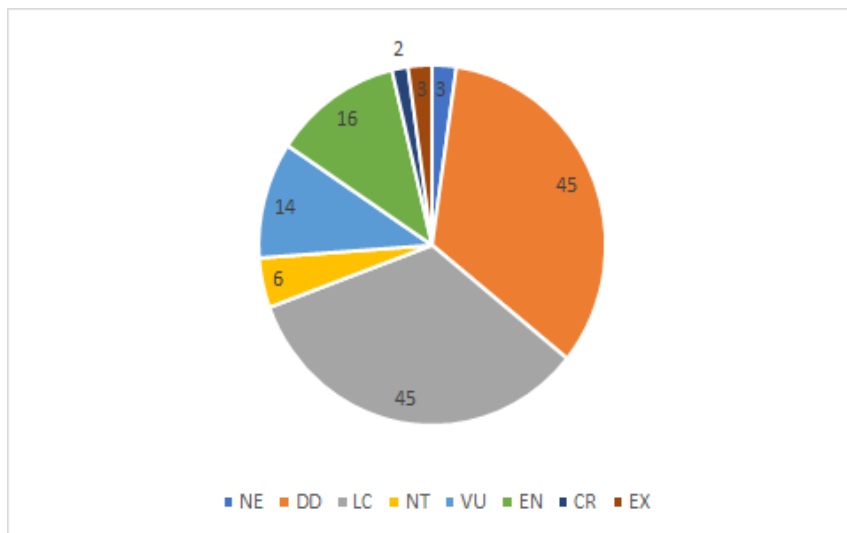
Figure 1.1. Number of marine mammal species per IUCN category (based on global assessments). NE=Not Evaluated; DD=Data Deficient; LC=Least Concern; NT=Near Threatened; VU=Vulnerable; EN=Endangered; CR=Critically Endangered; and EX=Extinct (*Source: IUCN as of summer 2017*).

1.4 Challenges in Marine Mammal Research and Conservation

The vast majority of the marine mammal species listed as DD by IUCN are cetaceans (whales, dolphins and porpoises). Cetaceans are fully aquatic mammals, meaning that unlike other taxa such as sea otters, polar bears and pinnipeds (seals and sea lions), they do not share their time between land and sea. Spending all of their time in the water (and most especially pelagic species) makes them harder to study given the resources required to access them. They are also the biggest group of marine mammals with approximately 92 species (about 69% of marine mammal species listed in IUCN; IUCN 2018), which in part explains why data available for marine mammals are overall scarcer compared to terrestrial mammals.

Because data available for marine mammals are not as comprehensive as those for terrestrial mammals (Tittensor et al. 2010), determining conservation status of these species and key biodiversity areas for marine mammal conservation represent an overall bigger challenge than equivalent studies for terrestrial mammal conservation. Therefore, more studies that address these issues are currently needed in marine areas, especially when those studies address ways to make conservation planning more accessible. This is important given the uncertainty that exists about how human-caused threats and climate change might impact marine biodiversity in the coming years (Tittensor et al. 2010).

1.5 About this Dissertation

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be

considered. These analyses are analytical exercises that represent one small piece toward those considerations.

This research is not about species-specific conservation, and therefore results are not ready for applied MPA implementation. This research is about spatial prioritization optimization. Therefore, the following assumptions are being made: (1) Resources are limited (which is often the case in conservation planning); (2) Resource allocation is to be applied to protection of space; and (3) Spatial optimization can be achieved by solving the minimum-set coverage problem (representation of the greatest number of species in the least number of sites). This work represents a proof of concept based on surrogates of biodiversity that have been previously tested successfully in terrestrial systems, but to the best of our knowledge, have not been tested in global marine systems for marine mammals.

The objectives of this dissertation are to: (1) Evaluate the effectiveness of alternative surrogates of marine mammal species representation; and (2) investigate the extent to which current marine protected area (MPA) coverage represents marine mammal species, and elucidate the extent to which unprotected areas are exposed to anthropogenic activities. To this end, in chapters 2 and 3 I assess the effectiveness of alternative biotic surrogates of marine mammals; namely, the use of complementarity and rarity indices, respectively. In chapter 4, I present the first maps of global marine mammal complementarity, and study which environmental variables most correlate to areas of high conservation priority for marine mammals. This assessment of the relationship between marine mammal complementarity and environmental conditions leads into chapter 5, where I evaluate the effectiveness of environmental diversity as another

alternative (abiotic) surrogate of marine mammal species representation. Lastly, in chapter 6 I perform a gap analysis comparing the current extent of global MPA networks against complementarity-based hotspots of marine mammals and global indices of cumulative human impacts. Altogether, this dissertation presents a series of assessments of the effectiveness of biodiversity surrogates that have been previously tested successfully in terrestrial systems, but that to this day, had not yet been tested in marine systems at the global scale. My work represents the first steps in the exploration of how these surrogates can be later implemented in conservation actions of marine mammals and possibly other marine taxa.

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CHAPTER 2

IS SPECIES RICHNESS THE BEST SURROGATE FOR SOLVING THE MINIMUM-

SET COVERAGE PROBLEM IN MARINE MAMMAL CONSERVATION

PLANNING?

2.1 Abstract

Species richness has been largely used for determining site conservation values when solving the minimum-set coverage problem, but this has not been assessed in the context of marine mammal conservation. In our study, we assessed the effectiveness of species richness as a surrogate of marine mammal species representation, and compared it to the use of complementarity as an alternative approach, at the global scale. We obtained 134 marine mammal distribution maps from the IUCN Red List database, and used the complementarity algorithms to calculate conservation priorities. To determine the effectiveness of species richness as a surrogate, we calculated the Species Accumulation Index (SAI) scores for marine mammal groups. Our findings indicate that both complementarity approaches are consistently more effective surrogates when solving the minimum-set coverage problem for marine mammal species representation across all groups and grains tested. Our study strongly supports the use of complementarity as supposed to richness as the preferred method to select sites conservation values for marine mammals when solving the minimum-set coverage problem. To the best of our knowledge, we are the first to assess the effectiveness of richness and compare it to results obtained by the use of complementarity in global marine mammal species representation.

2.2 Introduction

To increase the feasibility of conservation efforts and given that biodiversity inventories are incomplete for most parts of the world, surrogates of species representation are often used to determine which sites to select for the implementation of protected areas or reserves (Rodrigues and Brooks 2007). These surrogates be either biotic (e.g., species richness; Rodrigues and Brooks 2007) or abiotic (e.g., environmental variables; Albuquerque and Beier 2015c), and determining which is the most effective surrogate for biodiversity representation is a goal of conservation planning.

In the last decades, many studies have used surrogates of diversity patterns (e.g., species richness - sites with the highest number of species or threatened species in a given area) to select the least number of sites for a potential reserve, that collectively represent all or nearly all the species (minimum set coverage, Moilanen et al. 2009 and references therein). The selection of sites based on species richness is one of the most traditional ways of prioritizing sites for conservation (see for example Roberts et al. 2002, Brooks et al. 2004, Rodrigues et al. 2004, Kaschner et al. 2011, Pompa et al. 2011, Jenkins et al. 2013, Ramírez et al. 2017). When the goal of conservation planning is to address ecosystem function based on the presence of a determined number of species, and/or the presence of specific species of interest, species richness is an appropriate measure to identify the sites that are the most important candidates for protection (Fleishman et al. 2006). Previous studies have found that there is a positive correlation between species richness and ecosystem function, and that in some cases the identity of certain species can have an equal or greater effect on the magnitude of an ecosystem

process compared to the effects of species richness by and of itself (Griffin et al. 2009 and sources therein).

However, when the goal of conservation planning is to represent the greatest number of species in a small number of sites (such as could be the case under criteria C(iii) and D(ii) of the Important Marine Mammal Areas (IMMA) Selection criteria [MMPATF n.d.]), then site selection based on species richness is seldom the most effective approach (references Albuquerque and Beier 2015a and b). According to Veach et al. (2017 and references therein), species richness can fail to account for endemism and rarity, and it can result in a decreased number of protected species. This is also because the most species rich sites will not necessarily represent different species, but can instead consist of a series of sites that all represent only a subset of all species present in an area, some of which could be already protected elsewhere (Langhammer et al. 2007). Additionally, because species richness does not reflect complementarity - a site-based measure of conservation values that ensures that sites selected for inclusion in a reserve network complement those already selected - species richness is not always a good indicator of conservation priority (Kirkpatrick 1983, Albuquerque and Beier 2015a and b).

Complementarity is an alternative site selection approach that has consistently performed better than species richness when tested in terrestrial systems (e.g., Williams et al. 1996, Albuquerque and Beier 2015, Veach et al. 2017, and Albuquerque and Gregory 2017). This approach selects sites that are complementary to each other (each site is not necessarily the most species rich but sites all differ in species composition), producing a solution that consists of sites that collectively include all or nearly all of the species. Accordingly, sites that are candidates for conservation efforts are selected by

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first assessing the presence/absence or abundance of each species per site, and subsequently selecting the best sites in terms of importance (i.e., species representation). Complementarity algorithms such as Zonation (Moilanen et al. 2014), also account for rarity of species because they test all possible scenarios of site-selection, giving a higher priority to those species with a limited range (see methods). The effectiveness of complementarity over that of species richness has been known by conservation biologists for over three decades; however, it has yet to become a mainstream approach in biodiversity conservation studies (Albuquerque and Beier 2015 and references therein), perhaps because this concept is yet to be well understood.

Despite its importance, complementarity has been largely ignored in spatial prioritization studies in marine ecosystems, perhaps because the ocean landscape represents a much greater area compared to the terrestrial landscape, and information on species distributions and habitats is not as accurate. Diversity patterns of terrestrial species are overall better known than those of marine species (Tittensor et al. 2010). While mammals have been studied in terrestrial and marine ecosystems, there is still an important knowledge gap problem, although we do know that marine mammals face a disproportionally higher level of threats compared to their land counterparts (Schipper et al. 2008). Marine mammals are an important taxon due to their status as ecosystem engineers (they can alter ecosystem structure and function due to their large-scale movement, prey-consumption, and non-consumptive behaviors; Kiszka et al. 2015), and are also considered sentinel species for ocean and human wellbeing (Bossart 2011). Of the 134 marine mammal species listed in the IUCN Red List of Threatened Species (www.iucnredlist.org), about one third are listed as Least Concern (LC), another third as

Data Deficient (DD; not sufficient information to determine extinction risk), and the last third belong to one of the imperiled categories (Near Threatened - NT, Vulnerable - VU, Endangered - EN, Critically Endangered - CR, or Extinct - EX), or has not yet been evaluated (NE; IUCN listings as of summer 2017).

Several studies that identify important global areas for marine mammals have used species richness to determine the sites with the highest conservation priority (e.g., Tittensor et al. 2010, Pompa et al. 2011, and Ramírez et al. 2017). However, given the results obtained by other studies that specifically compared the effectiveness of species richness vs. complementarity in selecting sites with the highest conservation values for terrestrial vertebrates (e.g., Williams et al. 1996 and Albuquerque and Gregory 2017), here we address three questions: (1) Is species richness a good surrogate for marine mammal species representation when solving the minimum-set coverage problem; (2) Are the results scale-dependent (i.e., grain/site size-dependent); and (3) What is the minimum number of cells (minimum-set coverage) required to represent all marine mammal species in each scenario? We hypothesize that species richness is not the best surrogate for marine mammal representation when solving the minimum-set coverage problem, regardless of the grain (cell size), and predict that complementarity will outcompete species richness as a more effective surrogate in all the scenarios that we test. To the best of our knowledge, we are the first to test complementarity algorithms to determine global marine mammal sites conservation priorities, as well as to perform a global assessment of the effectiveness of species richness as a surrogate of marine mammal representation.

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations.

2.3 Materials and Methods

2.3.1 Data source and preparation. We obtained maps of 134 global marine mammal species distributions from the IUCN Red List Spatial Data database (IUCN, Gland, Switzerland; available at: http://www.iucnredlist.org/technical-documents/spatial-data) and used the *letsR* (Vilela and Villalobos 2015) package in R to obtain presence/absence values for each grid cell at 1° (N = 47,283), 1.5^o (N = 21,346), 2° (N = 12,168), 2.5^o (N = 7,891), and 3° (N = 5,548). This process was completed for 123 of the 134 marine mammal species (we excluded species listed as extinct (EX), not evaluated (NE), and those that live strictly in freshwater environments). IUCN generalized species distribution maps are created by connecting all known, expert-verified, distribution points, but may include locations where species have not formally been recorded. They also do not indicate life history relevant areas such as for example where there are higher population densities and/or key breeding sites (Red List 2018).

2.3.1.1 Groups. Marine mammals were classified into seven groups to account for differences in life histories (five groups) as well as extinction risk levels based on IUCN listings (two groups). The groups are: 1) fully aquatic (FA; n=87) species (those that spend all of their time in the water; cetaceans and sirenians); 2) non-fully aquatic (NFA;

n=36) species (those that share their time between land and sea; pinnipeds and fissipeds); 3) migratory (MI; n=37) species; 4) non-migratory (NMI; n=52) species; 5) species with unknown (UNK; n=29) migratory status; 6) threatened (TR; n=79) species (those listed as CR, EN, VU, NT, and DD – for the purposes of this study we are treating DD species as potentially threatened given that the impact of a significant threat is unknown); and 7) non-threatened (NTR; n=44) species (those listed as LC). While all species were included in general analyses (ALL; n=123), nomad species were excluded from group analyses because the small number of species does not allow for reliable complementarity studies for that group.

2.3.2 Data analysis.

2.3.2.1 Global conservation priority. To determine global conservation priority of marine mammal habitats we compared the Core Area Zonation (CAZ) and Additive Benefit Function (ABF) forms of the reserve-selection software Zonation (Moilanen et al. 2014), which are complementarity-based algorithms that hierarchically prioritize cells (at 1°, 1.5^o, 2°, 2.5^o, and 3° for our study), based on their importance for each taxon. ABF determines importance of a site (cell) based on the sum of important features in that area (meaning that cells with higher species richness are assigned a higher priority), while CAZ selects core areas of importance for species, resulting in cells with lower species richness that receive high priority if those areas have rare species (Moilanen et al. 2014). In both cases, Zonation begins by assuming all cells are potentially important, and progressively removes cells that are least important after each iteration (based on the criteria described). By minimizing the proportional loss of important geographical sites (number of cells selected), the Zonation approach also minimizes biodiversity loss in the

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current tentative solution for species with the most reduced geographical range remaining. The resulting hierarchy allows for smaller 'reserved' number of sites to be contained within larger ones (e.g., the most important 5% is a subset of the most important 10% and so forth) (Moilanen et al. 2014).

2.3.2.2 Congruence of species-rich cells and high-priority conservation cells. For each of the seven marine mammal groups created, and for all species combined, we evaluated the effectiveness of species richness as a surrogate for marine mammal species representation in solving the minimum-set coverage problem (i.e., how well it represents the greatest number of species in the smallest number of sites). To determine this, all cells were initially selected and iteratively cells were removed such as to cause the lowest marginal loss in the overall conservation score values of the remaining landscape (Moilanen et al. 2014). We calculated the number of species represented by at least one cell at each step. For each pair of independent groups' conservation priority scores we calculated the Spearman rank correlation coefficients. To verify potential effect of the grain, these analyses were repeated at five different grains (1º, 1.5º, 2º, 2.5º, and 3º).

We measured the efficiency of species richness as a surrogate for marine mammal representation using the species accumulation index (SAI; Rodrigues and Brooks 2007). SAI is formally defined as SAI $= (S - R) / (O - R)$, where S is the number of species represented at least once in the group of sites selected by the surrogate, O is the optimum value or greatest number of species that can be represented in the same number of sites, and R is the mean number of species represented at least once within the same number of sites selected at random. We obtained the O values from running the Zonation algorithms, which generate true conservation priority values. To obtain the R values we

selected cells at random and during each iteration calculated the number of species represented in at least one cell. This process was repeated 1000 times to calculate the 95% confidence interval and assign the mean values as the R values. While we used 'representation in at least one cell' as our metric to define species representation for the purposes of this study, it might not be a suitable metric for applied species conservation efforts.

SAI values can range from $-\infty$ to 1, where negative values are indicative of results that are worse than random, 0 is a result equal to a result obtained by random site selection, and positive values represent a measure of efficiency. Therefore, a SAI value of 0.5 means that a result is 50% as efficient as the optimal solution in terms of improving site selection when compared to results obtained based on random site selection. Instead of calculating SAI for the entire area under each of the curves (O, S and R), we calculated SAI for targets between 0-15% at 0.1% intervals. We chose these values given that current marine protected areas (MPAs) encompass approximately 3.27% of the global oceans out of the targeted 10% by the year 2020 (Boonzaier and Pauly 2016).

2.4 Results

Overall results for marine mammal groups and all species combined at all grains tested demonstrate that species richness is a poor surrogate for marine mammal species representation when solving the minimum-set coverage problem. Based on SAI target results, species richness was outperformed by both complementarity solutions (CAZ and ABF) in all cases, and outperformed by the random solution in all cases except for the group UNK at 2.5° and 3° scales (figures 2.1, 1A-4A in appendix, table 2.1). Additionally, the number of sites (cells) required to represent all marine mammal species

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when using complementarity is significantly less than when using species richness. For example, to represent all marine mammal species using complementarity the minimum number of cells required are 23 (0.05%) and 100 (0.21%) for CAZ and ABF respectively, while the species richness approach requires 46,964 (99.33%) cells out of the total 47,283 cells at 1° resolution (table 2.2).

Spearman correlation values for pairwise groups tests indicated that, between groups, CAZ solutions yielded higher correlation scores than ABF. In general, the correlation scores were slightly correlated, irrespective of the grain of analysis (table 2.3). The highest correlation value at 1° was observed for TR and NTR species for CAZ (0.381), followed by FA and NFA for CAZ (0.308). The lowest correlation score was observed for NMI and UNK for ABF (-0.003).

2.4.1 Complementarity performance of CAZ vs. ABF. Both complementarity algorithms, produced median SAI scores that are identical to each other (table 2.1; see also overlapping curves in figures 2.1, 1A-4A). However, for the metric of calculating the minimum number of cells required to represent all species in a group (minimum set coverage), CAZ consistently performed better at all grains tested (table 2.2).
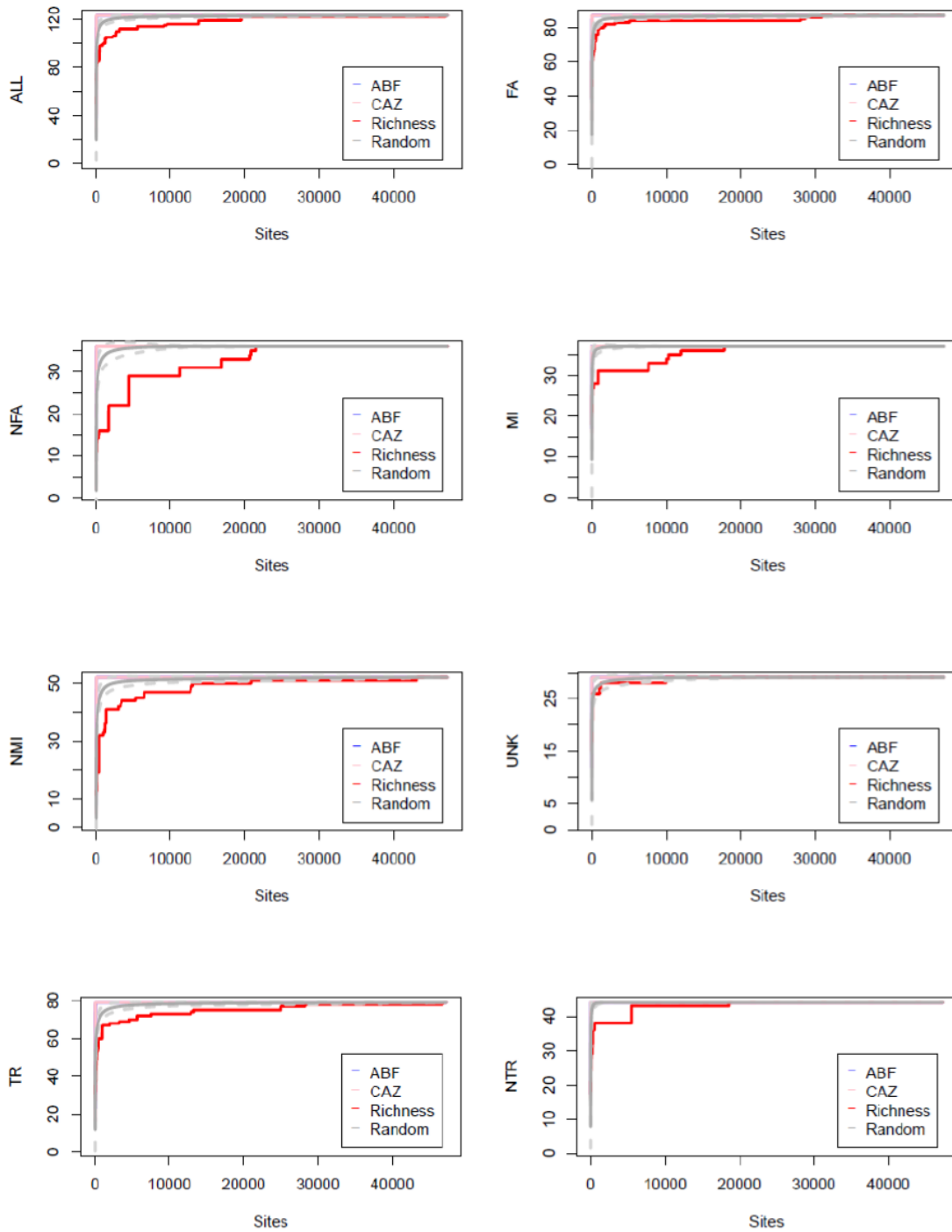
Figure 2.1. Species accumulation curves for 1° cells for all marine mammal species (ALL), and groups: fully aquatic species (FA; cetaceans and sirenians), non-fully aquatic species (NFA; pinnipeds and fissipeds), migratory (MI) species, non-migratory (NMI) species, and species with unknown (UNK) migratory status. ABF = Additive Benefit Function, and CAZ = Core Area Zonation (both complementarity algorithms). Richness represents species richness and Random is the random solution with 95% C.I.

2.5 Discussion

To the best of our knowledge, we are the first to provide an assessment of the effectiveness of species richness versus complementarity as approaches for optimizing global marine mammal species representation across a minimum number of "sites" at different cell sizes or scales. The species accumulation curves (figures 2.1, 1A-4A) and the SAI scores (table 2.1) all indicate that species richness is a poor surrogate for marine mammal species representation when solving the minimum-set coverage problem, and that complementarity is a more effective approach for determining sites conservation values for marine mammals at the global scale, supporting our hypothesis. This was consistent for all marine mammal species combined and for all the groups accounting for differences in marine mammal life histories and IUCN risk category listings. Our results are congruent with previous studies (Williams et al. 1996, Albuquerque and Beier 2015b, Veach et al. 2017), all of which found that complementarity outperformed species richness when determining sites conservation values for terrestrial mammals and other taxa. The reason for the increased effectiveness of complementarity is due to its algorithms being non-greedy (as supposed to the greedy species richness approach). This means that while species richness selects the sites with the highest number of species, complementarity instead selects sites that are different in terms of species composition (site are not necessarily the most species rich but collectively represent nearly all or all species; Moilanen et al. 2014).

Table 2.1. Species accumulation index (SAI) median scores calculated for 151 targets (from 0-15% at 0.1% intervals), for all scales and groups tested: all marine mammal species (ALL), fully aquatic species (FA), non-fully aquatic species (NFA), migratory species (MI), non-migratory species (NMI), species with unknown migratory status (UNK), threatened species (TR), and non-threatened species (NTR). Complementarity algorithms used are Core Area Zonation (CAZ) and Additive Benefit Function (ABF). Negative score = solution worse than random; score of 0 = result equal to random; and positive score = measure of efficiency (e.g., SAI score of 0.5 = surrogate – in this case species richness – is 50% as good as the Zonation/complementarity solution). Both algorithms have equal medians in all cases. Results with -∞ scores were omitted in median calculations.

	1 degree		1.5 degree		2 degrees		2.5 degrees		3 degrees	
	CAZ	ABF	CAZ	ABF	CAZ	ABF	CAZ	ABF	CAZ	ABF
ALL	-5.31	-5.31	-3.26	-3.26	-12.81	-12.81	-1.27	-1.27	-1.13	-1.13
FA	-1.95	-1.95	-1.41	-1.41	-0.66	-0.66	-0.45	-0.45	-0.33	-0.33
NFA	-23.73	-23.73	-12.16	-12.16	-5.41	-5.41	-3.88	-3.88	-3.29	-3.29
MI	-239.00	-239.00	-65.67	-65.67	-28.13	-28.13	-15.57	-15.57	-13.18	-13.18
NMI	-5.01	-5.01	-4.03	-4.03	-2.17	-2.17	-1.71	-1.71	-1.19	-1.19
UNK	-1.33	-1.33	-0.46	-0.46	-0.30	-0.30	0.36	0.36	0.13	0.13
TR	-4.58	-4.58	-2.95	-2.95	-1.48	-1.48	-0.92	-0.92	-0.70	-0.70
NTR	-129.43	-129.43	-125.67	-125.67	-110.11	-110.11	-54.05	-54.05	-23.15	-23.15

Resources allocated to conservation planning are usually limited, calling for conservation actions that are the most efficient possible to maximize biodiversity protection (Moilanen et al. 2009). Median SAI scores were identical for both complementarity approaches (table 2.1), indicating that both CAZ and ABF are equally effective at outperforming species richness for marine mammals. The results for the minimum set coverage problem (a metric that determines the minimum number of cells required to represent all the species in the study by at least one cell), also show that complementarity methods far surpass the effectiveness of species richness, but in this case the values do differ (table 2.2). The increased effectiveness for CAZ ranges from 10.94% to 99.28% across all groups and grains, and for ABF it ranges from 10.91% to 99.11%, also across all groups and grains tested (table 2.2). While CAZ and ABF algorithms are highly effective, the former is still a better solution to minimize conservation costs while maximizing effective protection coverage for marine mammal species (Moilanen et al. 2009). In the context of the current extent of marine protected areas (3.27%) and the targeted 10% for the year 2020 (Boonzaier and Pauly 2016), complementarity could make effectively meeting those targets a more reasonable goal if these results also apply to other taxa.

The group of species with unknown migratory status (UNK) was the only one to show that species richness outperformed the random solution at the 2.5° (SAI score = 0.36) and 3° (SAI score = 0.13) grains, although it still performed worse than the complementarity solutions by a significant margin (table 2.1). However, the great majority of species in the UNK group are data deficient cetacean species, and distribution

maps for these species are often generated based on predictions based on oceanographic conditions and where species have "not been recorded for all the states within the hypothetical range as shown on the map[s]" (Bearzi et al. 2012, Hammond et al. 2012). These distributions may over represent the presence of these species in their projected geographical range, which means that their use as a potential surrogate for marine mammal representation would be unreliable. Nevertheless, results suggest that given the same distribution data, complementarity is still a better option than species richness.

Correlation scores for the conservation priorities values between independent groups' pairwise comparisons were consistent across grains for both complementarity algorithms, suggesting that the effect of grain is negligible (table 2.3). Additionally, the values for most of these group comparisons show low correlations, with the exception of TR/NTR, which were moderately correlated. The implications of these results for management indicate that different marine mammal species groups, based on their life histories or IUCN listings, might require different approaches in their conservation planning, as a plan that is suitable for one group might not be suitable for another.

Effective representation of species for the purposes of applied conservation action does not only refer to having species represented by at least one site for the sake of inclusion in the solution, but that the selected site(s) are enough to increase the probability for those species to persist (Moilanen et al. 2009). The results of our research are in a theoretical framework and as such are not ready for the implementation of marine reserves, as we have not yet considered specific species needs (e.g., the minimum number of sites needed to guarantee the persistence of a species, as supposed to just being

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Table 2.2. Minimum number of cells (n) required to represent all marine mammal species by at least one cell, and the % of the total number of cells (N). Table shows all groups and scales tested (ALL = all marine mammal species; FA = fully aquatic species; NFA = non-fully aquatic species, MI = migratory species; NMI = non-migratory species; UNK = species with unknown migratory status; TR = threatened species; and NTR = non-threatened species). CAZ = Core Area Zonation; ABF = Additive Benefit Function; and Ri = species richness.

	1 degree (N=47,283)		1.5 degree (N=21,346)		2 degrees (N=12,168)		2.5 degrees (N=7,891)		3 degrees (N=5,548)	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
ALL_CAZ	23	0.05	21	0.10	23	0.19	23	0.29	23	0.41
ALL_BAF	100	0.21	100	0.47	98	0.81	373	4.73	95	1.71
ALL_Ri	46964	99.33	21172	99.18	7424	61.01	7811	98.99	5495	99.04
FA_CAZ	14	0.03	14	0.07	14	0.12	14	0.18	14	0.25
FA_BAF	33	0.07	30	0.14	29	0.24	30	0.38	32	0.58
FA_Ri	30893	65.34	13958	65.39	7966	65.47	5158	65.37	3626	65.36
NFA_CAZ	11	0.02	11	0.05	11	0.09	11	0.14	11	0.20
NFA_BAF	27	0.06	26	0.12	28	0.23	29	0.37	29	0.52
NFA_Ri	21433	45.33	9832	46.06	5698	46.83	3771	47.79	2668	48.09
MI_CAZ	9	0.02	9	0.04	9	0.07	9	0.11	9	0.16
MI_BAF	31	0.07	28	0.13	25	0.21	21	0.27	19	0.34
MI_Ri	17837	37.72	8259	38.69	3610	29.67	2385	30.22	1741	31.38
NMI_CAZ	16	0.03	16	0.07	17	0.14	18	0.23	17	0.31
NMI_BAF	46	0.10	45	0.21	47	0.39	45	0.57	45	0.81
NMI_Ri	43028	91.00	19542	91.55	11231	92.30	7303	92.55	5161	93.02
UNK_CAZ	6	0.01	6	0.03	6	0.05	6	0.08	6	0.11
UNK_BAF	18	0.04	18	0.08	19	0.16	8	0.10	14	0.25
UNK_Ri	9891	20.92	4615	21.62	2736	22.49	869	11.01	1324	23.86
TR_CAZ	19	0.04	18	0.08	19	0.16	19	0.24	19	0.34
TR_BAF	64	0.14	60	0.28	59	0.48	57	0.72	57	1.03
TR_Ri	46793	98.96	21088	98.79	12011	98.71	7770	98.47	5467	98.54
NTR_CAZ	7	0.01	8	0.04	7	0.06	7	0.09	7	0.13
NTR_BAF	16	0.03	17	0.08	17	0.14	17	0.22	14	0.25
NTR_Ri	18579	39.29	2752	12.89	1700	13.97	1194	15.13	917	16.53

Table 2.3. Spearman correlation scores for pairwise comparisons of complementarity values between independent groups tested at all scales (FA = fully aquatic species; NFA = non-fully aquatic species; MI = migratory species; NMI = non-migratory species; UNK = species with unknown migratory status; TR = threatened species; and NTR = non-threatened species). The complementarity algorithms are CAZ (Core Area Zonation) and ABF (Additive Benefit Function).

		1 degree	1.5 degree	2 degrees	2.5 degrees	3 degrees
CAZ	FA - NFA	0.3084	0.3134	0.3971	0.3784	0.3948
	MI - NMI	0.0170	0.0438	0.0264	0.1637	0.1499
	MI - UNK	0.2105	0.2171	0.2179	0.1972	0.2053
	NMI - UNK	0.2528	0.2398	0.2297	0.2360	0.2839
	TR - NTR	0.3818	0.4116	0.4333	0.4272	0.3608
ABF	FA - NFA	0.0864	0.0998	0.0754	0.0621	0.0762
	MI - NMI	0.0139	0.0151	0.0296	-0.0051	0.0379
	MI - UNK	0.2764	0.2903	0.2740	0.3310	0.3336
	NMI - UNK	-0.0030	0.0003	-0.0313	-0.0543	-0.0205
	TR - NTR	0.2429	0.2542	0.2421	0.2401	0.2564

represented by at least one site). Nonetheless, species-specific information is required in conservation planning regardless of the approach, and we believe that our work as it stands still supports the use of complementarity as a more efficient approach for determining sites conservation priorities.

For complementarity results to be applicable in conservation planning, species inventories at finer resolutions are required. Future work must thus account for the life histories of species, as well as logistical parameters including conservation costs (e.g., costs associated with implementing a marine reserve), and the likelihood of success (Joseph et al. 2008), among other things. Complementarity maps created with this information (as supposed to more redundant species richness maps), can help managers and stakeholders develop more efficient conservation plans.

As stated in the introduction, this is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations. There are few global marine mammal datasets that are available. The IUCN distribution maps are the most complete but they currently lack information on critical factors needed for spatial conservation assessments at this scale. Two of the most important factors are species specific density estimates and minimum home range data. Without this information it is difficult to fully evaluate how different areas would be at protecting the community of marine mammal species within.

It is important to highlight that our intention is not to criticize previous works done using species richness as the method to determine sites conservation values for marine mammals (such as could be the case for local marine mammal protected areas, under criterion D(ii) of the IMMA (MMPATF n.d.). Instead, we seek to test alternative conservation tools with the aim to increase effectiveness of conservation efforts given the current rate of biodiversity loss and a decrease in available resources committed to conservation actions in some areas of the world. As previously mentioned, species richness has its own ecological importance when it comes to its role in ecosystem structure and function (Griffin et al. 2009); however, we find that for the sake of species

representation it is not the most effective approach for solving the minimum set coverage problem for marine mammals.

In the future, we plan to test cross-taxon surrogacy at a finer grain to see if any particular group or sets of groups in our study can effectively represent all others. Global analyses like ours are important because biodiversity conservation initiatives can first assess species distributions across the globe before centering their efforts at the regional scale. This first step can help minimize redundancy such as focusing resources on species that might be rare in one location, but abundant and/or already protected elsewhere, as suggested by Langhammer et al. (2007). We believe that the use of complementarity in solving the minimum set coverage problem for marine mammals (and possibly other taxa) can significantly increase the effectiveness of marine conservation planning outcomes. This is strongly supported by our results, which is why we recommend it as the preferred approach in future studies that aim to determine sites conservation priorities to maximize marine mammal species representation.

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CHAPTER 3

EVALUATING THE PERFORMANCE OF RARITY AS A SURROGATE OF

MARINE MAMMAL SPECIES REPRESENTATION IN BIODIVERSITY

CONSERVATION PLANNING

3.1 Abstract

In conservation planning, surrogates of biodiversity are often used to prioritize sites based on their conservation values. Traditionally, species richness has been widely used to determine the conservation value of sites, but previous studies have shown that this is not the most effective method when solving the minimum-set coverage problem (determining the least number of sites that represent the greatest number of species). An alternative surrogate that has proven more effective in terrestrial systems is rarity. Here we test several rarity indices to determine if they are good surrogates for marine mammal biodiversity when solving the minimum-set coverage problem. Our results indicate that rarity could be a good surrogate for marine mammals, but most especially for cetaceans, as most results showed a median of 100% effectiveness. Given that cetaceans are the most understudied marine mammal group due to the difficulty of reaching them in pelagic waters, our results justify the need for further studies to elucidate how conservation action of cetaceans can be improved with the use of rarity. To the best our knowledge, we are the first to assess the performance of these rarity indices as surrogates of marine mammal representation at the global scale.

3.2 Introduction

The need for surrogates in conservation planning has become an important way of preserving biodiversity because generally, species' spatial and demographic information is not fully known and described (Rodrigues and Brooks 2007, Beier et al. 2015 and references therein). While spatial information relating to species distribution may be hard to obtain, land classes, environmental variables, well-known taxa (e.g., birds), and community composition are all examples of biodiversity surrogates that have been used in previous studies that seek to determine the location of the most relevant areas for conservation action (see e.g., Myers et al. 2000, Albuquerque and Beier 2015a, Sutcliffe et al. 2015, Beier and Albuquerque 2016). The basis for using surrogates in conservation, is that the selection of sites based on the presence of surrogates will result in the representation of additional species with unknown distributions, such as marine mammals (Rodrigues and Brooks 2007, IUCN 2018).

According to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2018), about one third of marine mammals are currently listed as data-deficient (DD), meaning that there is insufficient information to determine their extinction risk level. Distribution maps for all species are often overrepresentations or under-representations of species presence created with expert knowledge and predictions based on oceanographic conditions (Red List 2018). Potentially, the great majority of DD species (if not all of them) could belong to one of the imperiled categories because marine mammals are exposed to a disproportionally greater number of threats (e.g., accidental deaths due to fisheries bycatch and vessel strikes, and pollution),

compared to terrestrial mammals (Schipper et al. 2008). In addition, all DD species are cetaceans. Because of the costs associated with studying cetaceans, especially in pelagic habitats, we tend to know less about marine mammal distributions than about their terrestrial counterparts (Tittensor et al. 2010). Therefore, an important challenge for conservationist scientists is to identify and evaluate the efficiency of potential surrogates of marine mammals, especially for cetacean representation (Hoyt 2011).

Although the need for surrogates in conservation planning is widely recognized, there is not a "silver-bullet" surrogate that will work in all conservation planning scenarios, and testing of different solutions on a case-by-case basis is required to determine the most effective one (Rodrigues and Brooks 2007). Efficient surrogates should maximize the occurrence level of all species represented by a reserve network while meeting a set of biodiversity targets, such as minimizing the cost by finding a subset of candidate reserves that achieves all conservation targets (minimum set coverage [Moilanen et al. 2009]). One example of an efficient surrogate are complementarity-based algorithms (e.g., Zonation [Moilanen et al. 2014]). Complementarity solutions work by adding sites already selected for a reserve, based on the presence of species that have yet to be represented in the result (Haight and Snyder 2002, Pressey et al. 2009, Ardron et al. 2010, Moilanen et al. 2014). While powerful, complementarity solutions require relevant spatial information, such as complete map layers, produced by geographical information systems, remote sensing, or species distribution modelling (Moilanen et al. 2014).

The presence of rare species can also be used to identify areas for developing conservation actions (Gaston 1994). Previous studies show that rarity is a highly efficient

surrogate of plants and vertebrates in temperate and tropical terrestrial environments

(Csuti 1997, Albuquerque and Beier 2015c). However, determining rarity is not a one-

size-fits-all process, since many metrics can be used to calculate distribution frequencies

of species (Leroy et al. 2013). Rarity algorithms can be based on discontinuous or

continuous methods. In the former, rarity is expressed by the number of rare species per

site, while continuous methods consider levels of rarity of each species at the site (Gaston

1994). One example of a continuous rarity metric is rarity weighted richness (RWR),

where rarity of a site is defined by the sum of the inverse of the number of sites where

each species is present (see Williams et al. 1996 for details). In this context, rarity is

defined as rarity of a site, which is determined based on the number of species with

restricted ranges and not on population density. RWR selects sites where the

concentration of limited range species is high, based on the resulting rarity score values

(Stein et al. 2000). Other more recent examples of rarity metrics have been proposed by

Leroy et al. (2012, 2013) to measure the rarity of sets of species assemblages, and include

the index of summed rarity (ISR), and the index of relative rarity (IRR). ISR defines

rarity by the sum of weights of all species, whereas IRR defines rarity of a site by the

proportion of species that are rare, and the cut-off threshold (Leroy et al. 2012, 2013). As

the occurrence of species decreases below the threshold, rare species' weights are

expected to increase exponentially (Leroy et al. 2012). The IRR approach provides an

accurate description of the rarity patterns of assemblages (Leroy et al. 2013). It is

important to highlight that rarity is not synonymous with endemism. A species can be

endemic to a large geographic area, and therefore not rare (Gaston 1994).

Rarity algorithms themselves do not require extensive analytic or programming skills and are easy to implement. Results can be produced by using a spreadsheet or open source software (e.g., R; R Core Team 2017). In the context of marine mammal biodiversity conservation, rarity indices could be considered affordable and feasible surrogates of species representation, with the greatest benefit to those areas of the world that are in most need to accessible alternative tools, such as developing countries in tropical areas known to host the most biodiversity while having the least resources.

Previous conservation prioritization studies reported that areas with high rarity scores tend to be correlated with sites that have high species richness (Gaston 1994). Species richness has been used extensively in previous marine mammal conservation studies (e.g., Tittensor et al 2010, Kaschner et al. 2011, Pompa et al. 2011, Ramírez et al. 2017). However, studies that assessed the use of richness as a surrogate found that richness is not the most effective approach (Albuquerque and Beier 2015b and references therein). Because tests of its efficiency have focused on terrestrial realms, the ability of species richness to efficiently represent marine mammal biodiversity still awaits confirmation.

In our study, we assessed the effectiveness of rarity as a surrogate of marine mammal biodiversity. Our objectives were to: (1) determine if the rarity indices RWR, ISR, and IRR can be used as surrogates of marine mammal biodiversity by representing the greatest number of species in the smallest number of sites (i.e., solve the minimum-set coverage problem); (2) calculate the specific values (i.e., number of sites required) to solve the minimum-set coverage problem in each case; (3) evaluate the effectiveness of species richness and rarity in representing marine mammal biodiversity; and (4)

determine if the metric used to define rarity impacts the effectiveness of rarity indices. Solving the minimum-set coverage problem is one of the most popular approaches in site prioritization because it minimizes costs associated with the implementation of reserves, while maximizing biodiversity conservation efforts by increasing species representation in a limited number of sites. Results that support rarity as an effective surrogate for marine mammal species representation in this case would justify the need for further investigation as to the applicability of rarity as a surrogate in applied conservation planning (e.g., studies that include species-specific needs). Moreover, identifying how different indices perform under different scenarios can significantly increase our understanding and use of the available knowledge of surrogates in applied conservation planning, and provide better guidelines for future data collection. To the best of our knowledge, we are the first to assess the effectiveness of these rarity indices as surrogates of marine mammal species at the global scale.

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations.

3.3 Materials and Methods

3.3.1 Data sources and preparation. We acquired distribution maps from the IUCN Red List Spatial Database (IUCN, Gland, Switzerland; available at:

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http://www.iucnredlist.org/technical-documents/spatial-data) for 134 marine mammal species, and used the R package *letsR* (Vilela and Villalobos 2015) to obtain presence/absence information for each 1º grid cell of ocean surface (N = 47,283). We repeated this process for 123 marine mammals. We excluded species (n=11) that are listed as extinct (EX), not evaluated (NE), and those that live in freshwater-only habitats. Generalized species distribution maps from IUCN are produced by creating polygons that connect and/or surround data from all known expert-verified distribution points, and thus may potentially include areas where there have been no formal record of species presence. Additionally, these maps do not specify which areas are more relevant to species-specific needs (e.g., population density information, important sites for feeding and breeding, etc.) (Red List 2018).

We grouped marine mammals into several categories according to their use of habitat and IUCN listing. Our analyses were done for all marine mammal species together (group ALL; n=123), for fully aquatic species (cetaceans and sirenians, group FA; n=87), non-fully aquatic species (pinnipeds and fissipeds, group NFA; n=36), migratory species (group MI; n=37), non-migratory species (group NMI; n=52), species with unknown migratory status (group UNK; n=29), and threatened (group TR; n=79) and non-threatened species (group NTR; n=44). TR species we designated as those belonging to an imperiled category (NT or near threatened, VU or vulnerable, EN or endangered, and CR or critically endangered), as well as the DD (data deficient) species. We are treating DD species as potentially imperiled in this study because it is not known how a significant threat could affect these species (i.e., we do not currently know their

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extinction risk levels), as has been done in previous studies (Rey Benayas and De La Montaña 2003). We acknowledge the subjectivity of this choice, yet other choices for group analyses would also be considered subjective. NTR species are those listed as LC (least concern). Species with nomadic migration status (n=5) were included in the ALL group but were not analyzed separately because this group has such a small number of species that reliable results cannot be obtained from our tests.

3.3.2 Estimating rarity. We calculated five rarity indices and compared the results to those obtained by using species richness and complementarity. The first rarity index we used was the rarity-weighted richness (RWR) algorithm (Williams et al. 1996), which calculates rarity scores for a particular site by summing the rarity scores of all species present at that site (Stein et al. 2000). Each species' rarity score is defined as the inverse of the number of sites where it is present; therefore, species with the most limited ranges are given higher scores (e.g., score of 1.0 for a species present in one site only).

We also measured the index of relative rarity (IRR) and index of summed rarity (ISR), as described by Leroy et al. (2012, 2013). These indices calculate rarity of an assemblage, resulting in a selection of sites for each taxon, organized in hierarchical order. To calculate results for IRR and ISR, we designated the first quartile of species occurrences (the lowest 25 percent) as the threshold or cutoff point below which a species is considered rare (Gaston 1994, Leroy et al. 2013). We used the *rWeights* function in R to determine rarity weights using the weighted functions *W* (ISR1 and IRR1) and *invQ* (ISR2 and IRR2) (Leroy et al. 2012). In the *W* function, species that fall below the threshold are expected to have an exponential increase in their rarity scores while species

that fall above the threshold are expected to have scores closer to zero (Leroy et al. 2013).

W is formally defined as:

$$\exp\left(-\left(\frac{Q_i - Q_{min}}{r_j \times Q_{max} - Q_{min}} \times 0.97 + 1.05\right)^2\right)$$

Where Q_i is the occurrence of species i, Q_{min} and Q_{max} are the minimum and maximum occurrences respectively, and r represents the chosen rarity threshold. The inv$Q$ function is defined by the inverse of the occurrence.

We calculated ISR by summing the species' rarity weights produced by W and inv$Q$, and calculated IRR by using the species richness and rarity weights (also as produced by W and inv$Q$). We calculated ISR and IRR using the following formula:

$$ISR = (\sum w_i); \quad IRR = \frac{\frac{\sum w_i}{S} - w_{min}}{w_{max} - w_{min}}$$

Where w_i is the weight of the i_{th} species, S is species richness, and w_{min} and w_{max} represent the minimum and maximum weights.

3.3.3 Evaluating the performance of rarity surrogates. To determine if the rarity indices RWR, IRR and ISR are effective at representing biodiversity, we added sites to a hypothetical "reserve" by first selecting sites with the highest rarity scores, and subsequently added sites with the next highest rarity scores after each iteration, calculating the number of species represented in at least one cell at each step. To evaluate the efficiency of the indices, we used the Species Accumulation Index (SAI), as suggested by Rodrigues and Brooks (2007), defined as:

$$SAI = (S\text{-}R)/(O\text{-}R)$$

Where *S* represents the number of species present in the selected set of sites (selected for each rarity index). *O* is an optimum value (the greatest number of species that can be represented in that same number of sites). *O* values were obtained by using Zonation to generate priority ranks (Moilanen et al. 2014). *R* is the mean number of species represented in 100 sites selected at random. We calculated the number of represented species (by at least one site) in the sites selected at random (*R*) by using species accumulation curves (SAC), and calculated the 95% confidence interval. We also used the SAC to calculate the results for the minimum-set coverage problem (i.e., determining the minimum number of sites required to represent all species in each group, by at least one cell).

SAI values can range from $-\infty$ to 1. Negative SAI scores represent results that are worse than random, while values that are near 0 are comparable to those obtained by the random solutions. Positive SAI scores represent a measure of efficiency by the surrogate. For example, a SAI score of 1.0 indicates that a rarity index is 100% as effective as the optimal solution (*O*) in improving random site selection. SAI scores were calculated for 151 targets, which represent the percentages of the area of our hypothetical "reserve". Targets ranged from 0% to 15% at 0.1% intervals. We selected these targets because currently the world's oceans only have approximately 3.27% of area protected by a reserve, yet the goal is that by the year 2020 that number should increase to 10% (Boonzaier and Pauly 2016). Therefore, the lower targets are comparable to the current extent of marine protected areas (MPAs), while the higher targets represent the potential

for expansion. We used the median of these 151 SAI scores to obtain an estimate of the overall performance of each rarity index surrogate.

3.4 Results

Minimum-set coverage problem results using rarity indices RWR, ISR, and IRR were not consistent across all marine mammal groups tested. Based on median SAI scores, RWR and ISR were effective for fully aquatic mammals (group FA), imperiled and data-deficient species (threatened group or TR), and species with unknown migratory status (group UNK); whereas IRR was effective for UNK and TR species only (figure 3.1, table 3.1). Instances where rarity indices were effective show that their median efficiency scored at 100%, meaning that those results can be 100% as good as the optimum solution (calculated using Zonation) at improving on random results. The exceptions are for the TR group, with a RWR median score of 15.8%, and an ISR (calculated using the *invQ* method) with a median score of 24.8% (table 3.1). In all cases, species richness was consistently the most ineffective surrogate (figure 3.1, tables 3.1-3.2).

Values that measure the minimum number of cells required to represent all marine mammal species at least once (minimum-set coverage problem results) also indicate that species richness is not a good surrogate for marine mammal species representation, as all targets tested (up to 15%) are insufficient to cover 100% of marine mammal species in this study (table 3.2). In the case of the rarity indices, RWR was the most consistent at representing all marine mammals within the tested targets, because it was able to produce results for all marine mammal groups, except for the group combining all species (ALL) (table 3.2). ISR and IRR also failed to produce results within the tested targets for group

ALL, as well as for the non-migratory species (NMI) group (table 3.2). ISR calculated using the *invQ* method was the only one to produce results within the targets for the non-threatened (NTR) group along with RWR, whereas neither IRR index, or the ISR index calculated using *W*, produced results within the target for the non-fully aquatic (NFA) group (table 3.2). IRR calculated using *invQ* was also the only rarity index unable to produce results within the targets for the migratory (MI) species group. Groups FA, UNK, and TR were the only ones where all rarity indices produced results within the targets (table 3.2).

3.5 Discussion

Our results show that rarity can be used as a surrogate of marine mammal species biodiversity for solving the minimum-set coverage problem but only in some instances, as not all indices performed equally across all marine mammal groups tested. Trends in the data suggest that rarity indices calculated based on the sum of the inverse of species occurrence (i.e., RWR and ISR calculated using the *invQ* method) might perform more effectively for more groups of marine mammals, as compared to those indices calculated using the *W* method (figure 3.1, tables 3.1-3.2). Further studies are warranted to elucidate the sources of these differences. Our findings also suggest that rarity indices are, for the most part, either not effective as marine mammal biodiversity surrogates, or extremely effective, depending on the group. In our study, 80% of instances where rarity indices where effective show a 100% efficiency rate, according to median SAI scores (table 3.1). These findings are consistent with the results from the minimum-set coverage problem (table 3.2).
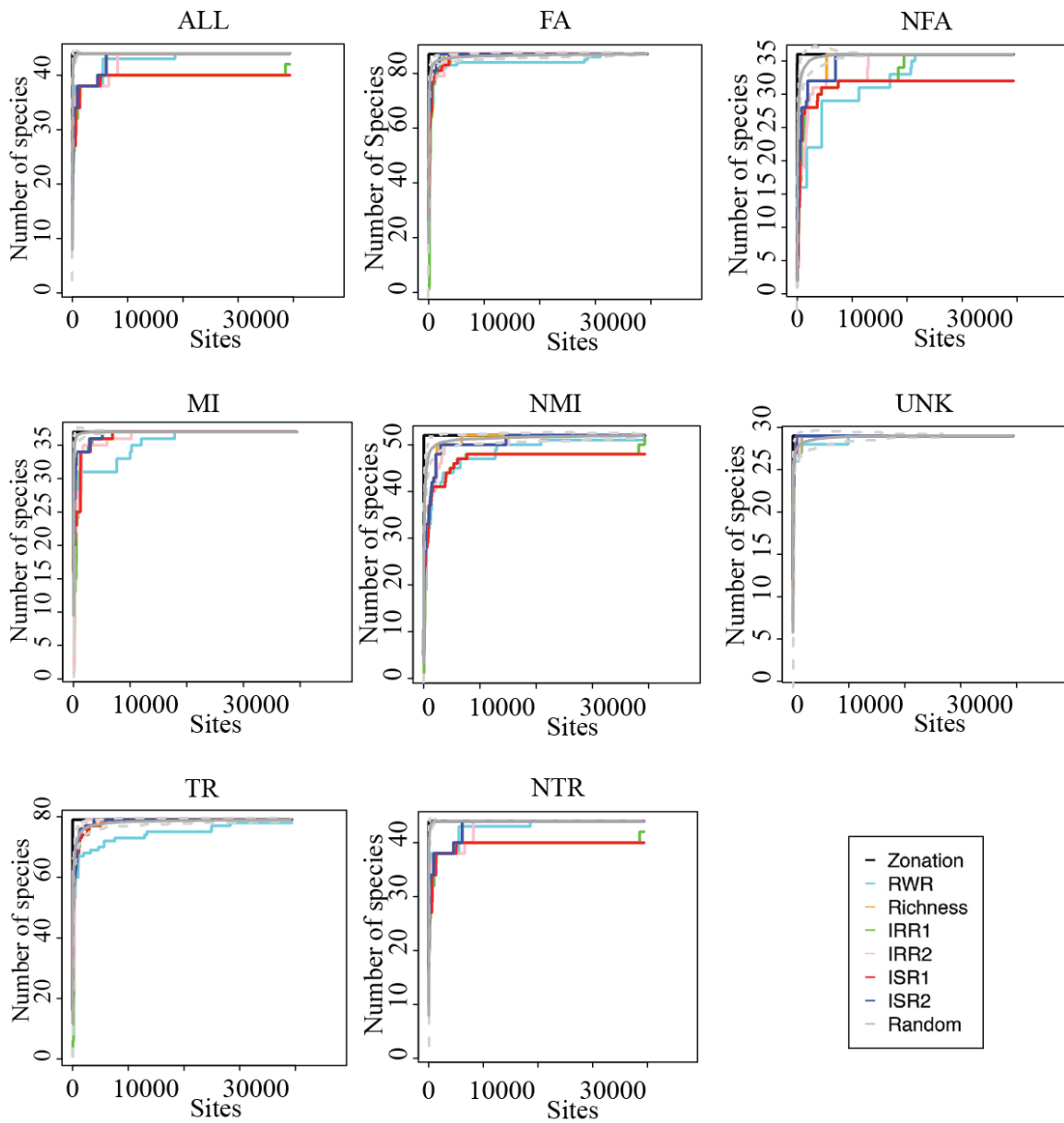
Figure 3.1. Species accumulation curves for all marine mammal species (ALL) and groups (FA = fully aquatic; NFA = non-fully aquatic; MI = migratory; NMI = non-migratory; UNK = unknown migratory status; TR = threatened species; and NTR = non-threatened species). Zonation represents the optimum solution as calculated by complementarity and Richness represents the species richness solution. Rarity indices are: RWR = rarity-weighted richness; IRR1 = index of relative rarity calculated using *W*; IRR2 = index of relative rarity calculated using *invQ*; ISR1 = index of summed rarity calculated using *W*; and ISR2 = index of summed rarity calculated using *invQ*. Random solution is represented with the 95% confidence interval.

Marine mammal taxa for which rarity indices were most effective were fully aquatic species (FA), species with unknown migratory status (UNK), and threatened/data deficient species (TR). FA species are approximately 97% cetaceans and 3% sirenians, UNK species are 100% cetaceans (with approximately 79% listed as DD and 21% listed as LC), and TR species are approximately 78% cetaceans, 14% pinnipeds, 4% sirenians, and 4% fissipeds. In all cases, groups consisted in either mostly or all cetaceans. With a few exceptions of coastal-dwelling species, cetacean species in these groups have a mostly oceanic distribution with spread-out ranges.

In the context of the results, the above values indicate that rarity indices might be the most effective surrogates for cetaceans, as compared to other mammal groups (e.g., pinnipeds). More studies are required to elucidate the drivers of the patterns observed. These findings are highly relevant because cetacean species, especially those living in pelagic waters, are difficult to study due to the logistics required to reach them, and therefore are the marine mammal species we know the least about. Our results indicate that the use of rarity indices as surrogates for conservation of these species could be a promising approach, especially in cases when high biodiversity and low resources combine, such as in tropical developing countries (approximately 55% of UNK species occur in these areas, all of which are listed as DD).

As supported by previous studies (Albuquerque and Beier 2015c, Veach et al. 2017), species richness was the poorest of all surrogates when solving the minimum-set coverage problem (figure 3.1, tables 3.1-3.2). The use of species richness as a surrogate of species representation in this context is often inadequate because it fails to represent

Table 3.1. Median species accumulation index (SAI) scores for 151 targets (0-15% by 0.1% increments) per each group (ALL = all species; FA = fully aquatic; NFA = non-fully-aquatic; MI = migratory; NMI = non-migratory; UNK = species with unknown migratory status; TR = threatened species; and NTR = non-threatened species). Negative values indicate solutions worse than random. Positive values (in bold) are a measure of effectiveness (e.g., a value of 1.0 means a result is 100% as effective as the optimum solution, as calculated by Zonation). Richness represents the species richness solution. Rarity indices are: RWR = rarity-weighted richness; IRR1 = index of relative rarity calculated using *W*; IRR2 = index of relative rarity calculated using *invQ*; ISR1 = index of summed rarity calculated using *W*; and ISR2 = index of summed rarity calculated using *invQ*.

	Richness	RWR	ISR1	ISR2	IRR1	IRR2
ALL	-5.400	-1.051	-1.842	-1.808	-2.575	-1.726
FA	-1.874	**1.000**	-0.987	**1.000**	-1.055	-0.409
NFA	-24.926	-3.336	-14.152	-6.846	-14.152	-9.875
MI	-199.000	-26.270	-40.379	-26.273	-39.000	-65.667
NMI	-5.098	-0.952	-5.024	-1.151	-4.976	-1.575
UNK	-1.198	**1.000**	**1.000**	**1.000**	**1.000**	**1.000**
TR	-4.263	**0.158**	-0.227	**0.248**	-0.226	**1.000**
NTR	-∞	-∞	-∞	-∞	-∞	-∞

Table 3.2. Results for the minimum-set coverage problem for each marine mammal group (ALL = all species; FA = fully aquatic; NFA = non-fully-aquatic; MI = migratory; NMI = non-migratory; UNK = species with unknown migratory status; TR = threatened species; and NTR = non-threatened species) and surrogate (Zonation = optimum solution as calculated by complementarity; and Richness = species richness. Rarity indices are: RWR = rarity-weighted richness; IRR1 = index of relative rarity calculated using W; IRR2 = index of relative rarity calculated using $invQ$; ISR1 = index of summed rarity calculated using W; and ISR2 = index of summed rarity calculated using $invQ$). Values show the minimum number of grid cells (n) required to represent all marine mammal species in each case, and the percentage from the total number of grid cells (N = 47,283). Entries denoting a ">" sign indicate that the result is a value higher than the maximum target (i.e., the minimum number of cells required to represent all marine mammal species at least once is higher than 15%).

	Richness		RWR		ISR1		ISR2		IRR1		IRR2	
	n	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**	**n**	**%**
ALL	>	>	>	>	>	>	>	>	>	>	>	>
FA	>	>	2742	0.058	3735	0.079	1986	0.042	4019	0.085	4776	0.101
NFA	>	>	5343	0.113	>	>	6998	0.148	>	>	>	>
MI	>	>	5201	0.110	6903	0.146	5107	0.108	6903	0.146	>	>
NMI	>	>	6809	0.144	>	>	>	>	>	>	>	>
UNK	>	>	662	0.014	662	0.014	662	0.014	1560	0.033	1277	0.027
TR	>	>	4208	0.089	6100	0.129	3877	0.082	6100	0.129	2506	0.053
NTR	>	>	6147	0.130	>	>	6147	0.130	>	>	>	>

the largest number of species in the least number of sites (Kirkpatrick 1983). This happens because species richness assigns the highest conservation priority to sites that have the highest number of species and regardless of the identity of the species. This approach almost always results in a collection of sites that share the same species composition, excluding rarest species if they are found in sites with low species richness (Veach et al. 2017). For this reason, it is recommended to avoid the use of species richness as the surrogate for species representation in this conservation-planning context.

On the other hand, rarity appears to be more effective as a surrogate of species representation when solving the minimum-set coverage problem because it accounts for the rarity of species, giving sites with rare species higher conservation values than sites with common species (Ratcliffe 1977). The intuitive approach of rarity algorithms does not assign the same conservation value weights to all species alike, and instead guarantees that those species considered rare are prioritized (Justus and Sarkar 2002). Rarity indices are also advantageous when it comes to computing time, as shown by the fact that we obtained our results using R in a matter of seconds (real time decision). When results are needed within a short amount of time, other approaches that involve computations incurring longer waiting times may hinder the process of conservation planning (Pressey et al. 1996).

In some instances, rarity results were comparable to those obtained by the complementarity approach (table 3.1). One of the main advantages of using rarity as a surrogate would then be the ability to select high-quality sites that complement sites already selected (Justus and Sarkar 2002). While complementarity algorithms start by

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also favoring sites with high species richness, the difference is that subsequent site selection is done by adding sites with new species (as supposed to continuing to select sites with high species richness even when they contain the same species already covered) (Pressey et al. 1996, Moilanen et al. 2014). Rarity also does not prioritize sites according to species richness, but instead on the weight assigned to species given their level of rarity. This results in species with limited ranges having priority over common, widespread species (Leroy et al. 2012, 2013).

Our results are in a theoretical framework and thus not ready to be directly applied to conservation planning of marine mammals. Information specific to these species, such as life history (e.g., related to breeding, feeding, and migration) and place-specific (e.g., adjacency of selected sites or avoiding sites with poor conditions) requirements, as well as logistical information (e.g., feasibility and costs associated with the implementation of a future reserve or protected area) must be incorporated to effectively apply this knowledge to the conservation planning process (Pressey et al. 1996, Hoyt 2011). Additionally, species might need more than the "representation by at least one cell" approach to make conservation efforts meaningful. Nevertheless, this information is always needed for applied conservation action regardless of the approach used to prioritize sites for conservation. Therefore, we believe that our results justify further studies on how rarity indices can be used in conservation of marine mammals, especially in cases when resources are limited, by incorporating the information that will make results be more meaningful to applied conservation planning. Studies such as ours would also benefit from more detailed marine mammal spatial data to increase the accuracy of

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the results. However, this data shortage problem is also the reason why we perform studies such as this one, i.e., to determine which surrogates of marine mammal biodiversity are more appropriate to increase species representation when there is insufficient knowledge of species distributions.

Rarity has been extensively used in past studies as the metric to prioritize sites for conservation, making it one of the most popular approaches in this context (Gaston 1994 and references therein). Vellak et al. (2008) investigated the effectiveness of protected areas for rare plant species in Estonia, and found that for the most part, conservation efforts based on this metric for those rare plant species were considered successful. Given the previous success of rarity-based conservation efforts and scientific studies, it is likely that managers in charge of the conservation planning of cetaceans stand to benefit the most from the use of rarity and our findings. Our results also indicate that not all marine mammal species should be managed in the same way, and that different surrogates might be needed for different marine species groups or taxa, as suggested by previous findings (Sutcliffe et al. 2015). Further understanding of rarity as a surrogate of marine mammal representation will enhance our toolbox for dealing with the biodiversity loss of the sixth mass extinction (Ceballos et al. 2015).

As stated in the introduction, this is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that

represent one small piece toward those considerations. There are few global marine

mammal datasets that are available. The IUCN distribution maps are the most complete

but they currently lack information on critical factors needed for spatial conservation

assessments at this scale. Two of the most important factors are species specific density

estimates and minimum home range data. Without this information it is difficult to fully

evaluate how different areas would be at protecting the community of marine mammal

species within.

We found that rarity could be an effective surrogate for cetacean species, to the extent

that distribution maps accurately represent their distributions. Results also demonstrate

that when rarity indices here tested were effective, their effectiveness was as high as the

optimal solution. This is the first study assessing the performance of RWR, ISR, and IRR

in marine mammals at the global scale in this context, and we believe that our results

justify further studies to elucidate how rarity of assemblages can be used as a surrogate in

conservation planning of marine mammals and potentially other marine species. This is

especially the case when species-specific information such as population abundance and

density are unavailable but spatial prioritization can still be pursued when the lack of

access to more sophisticated methods can hinder biodiversity protection. Increasing our

knowledge and use of alternative conservation tools can thus greatly increase our ability

to counteract the current biodiversity loss crisis.

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CHAPTER 4

GLOBAL PATTERNS AND ENVIRONMENTAL CORRELATES OF HIGH-

PRIORITY CONSERVATION AREAS FOR MARINE MAMMALS

4.1 Abstract

Traditionally in conservation planning, reserve design will utilize biotic surrogates

such as patterns of complementarity to determine site importance and thus prioritize areas

for conservation. Surrogates are used because knowledge of species and their

distributions are usually limited for most species. While biotic surrogates of biodiversity

are extremely useful in this context, they are still limited by the amount of species

information available. In this study, we investigated how abiotic factors such as

environmental variables (water chemistry, temperature, and topography) relate to patterns

of marine mammal complementarity (i.e., site importance). Global distribution maps for

123 marine mammals were obtained from the IUCN Spatial Database to determine

presence/absence of species at the global scale. Oceanographic variables (n=30) were

obtained from NOAA (water chemistry) and GEBECO (bathymetry) and analyzed using

Varimax-rotated PCA to reduce the dimensionality of the data, and investigate the

relationship between abiotic variables and patterns of complementarity-based marine

mammal site importance, which we calculated using the software Zonation. We found

that oceanographic variables (e.g., water chemistry) and bathymetry have a strong

relationship with patterns of marine mammal site importance, and therefore can be used

to help predict species presence (i.e., can be used as a surrogate for marine mammals).

More specifically, our findings show that sea surface temperature, water density, and

bathymetry, are among the top three variables that are most associated with areas of high conservation priority for marine mammals at the global scale. Our findings support the idea that abiotic factors are associated with patterns of species presence, and suggest that the use of abiotic factors, and especially when combined with biotic data, can greatly increase the effectiveness of surrogates in representing sites conservation priorities, and justify future studies that will help further elucidate this relationship. Ours is the first study to represent global maps of marine mammal complementarity.

4.2 Introduction

In conservation planning, one of the goals is to maximize the use of limited resources by prioritizing sites to increase the effectiveness of spatially-based conservation efforts (e.g., establishing a protected area that will benefit the most species/habitats within the constraints of the available funds/resources). One of the most common ways to accomplish this is by solving the minimum-set coverage problem, or representing the greatest number of species in the fewest number of sites (Moilanen et al. 2009). To this end, an approach known as complementarity has been used for approximately three decades as an effective metric to prioritize sites for conservation purposes. Complementarity is a type of 'scoring' algorithm that analyzes the available biotic information for each spatial unit in a study (e.g., a grid cell), to determine its level of importance by comparing it against a set of criteria (e.g., level of threat, species geographical range, or presence/absence of species) and subsequently comparing it to the rest of the spatial units in the study to rank them all in order of importance (Moilanen et al. 2009). When applied, complementarity algorithms select sites (spatial units) for a

potential reserve such that the new sites added complement those already chosen; in other words, new sites added will contain new species that are not already represented in the original set of sites, regardless of the number of species present in each site. The result is a collection of sites that together represent the greatest number of species, including those that have restricted ranges (Moilanen et al. 2009, 2014).

Modeling complementarity is important in conservation planning because it provides a more accurate representation of conservation priorities of sites in a study, compared to other approaches such as the use of species richness. The species richness (the number of species present in a site) approach focuses on consistently selecting sites based on the highest number of species present. While this approach is still used in some studies (see e.g., Roberts et al. 2002, Tittensor et al. 2010, Ramírez et al. 2017), it is not the best surrogate to conserve species biodiversity, because it often over-represents common widespread species while underrepresenting those that are endemic or rare (Albuquerque and Beier 2015a, 2015b, Veach et al. 2017 and references therein). For example, Albuquerque and Beier (2015b) compared patterns of high-priority conservation areas for terrestrial mammals, amphibians and birds, that were generated by using both the species richness and the complementarity methods. They found that complementarity-based conservation priority and species richness were only moderately correlated, and that often species-rich sites were not among the areas with top conservation priority (as measured by complementarity).

Complementarity is among the best approaches for site prioritization in conservation planning, but is still limited by the amount of biotic information available for a study site

(Albuquerque and Beier 2015c). Because our knowledge of species and their distributions is limited in most cases (Moilanen et al. 2009, Lomolino et al. 2010), alternative methods are required to complement the information about which geographical sites might be important for conservation. There have been several hypotheses that address the geographical patterns of biodiversity distributions, such as for example biological interactions (e.g., competition, predation, and mutualism), community composition, population growth rate, and primary productivity, among others (Lomolino et al. 2010 and references therein). These factors provide useful information, but any knowledge gaps of these topics limit our ability to accurately represent biodiversity in conservation.

Alternatively, abiotic information or environmental factors can be used to determine site importance. For over three decades, conservation biogeographers have been studying biodiversity distribution patterns and the geographical characteristics associated with key biodiversity areas, on the premise that only when we understand those geographical drivers can we successfully conserve biodiversity (Lomolino et al. 2010). More specifically, biogeographers have focused on creating predictive biogeographic models that can identify areas that are likely biodiversity hotspots and could be later surveyed and considered for future conservation efforts (Lomolino et al. 2010). One example of an abiotic variable used to describe species distributions is topography. Along with other environmental variables, topography is an important driver of terrestrial species (Currie 1991), presumably because it drives primary productivity patterns which in turn affect animal species distributions. In a study by Tittensor et al. (2010), the authors studied patterns of species richness of 13 marine taxa (including marine mammals), as well as the

associated environmental variables, and found that sea surface temperature was the variable that correlated best with high species-rich areas (areas with higher temperatures). Their findings support the kinetic energy hypothesis, which states that higher metabolic rates, which are a result of higher temperatures, promote diversity (Tittensor et al. 2010). Other studies examined the relationship between areas of complementarity-based high-conservation priority of terrestrial mammals and other vertebrates, and the associated environmental variables, and found that environmental factors related to energy and water explained 78% to 85% of the variance observed, making them good predictors of areas with high-conservation priority (Albuquerque and Beier 2015b, c). These authors also reported that complementarity of sites modeled as a function of available abiotic variables can then be used as a surrogate to prioritize all sites (Albuquerque and Beier 2015c).

Despite its ability to produce more accurate site-prioritization results in terms of species representation, complementarity has not been used in studies that seek to determine global patterns of site importance for marine mammals, or the environmental variables associated with those patterns. Therefore, the objectives of this study are to: (1) provide the first maps of complementarity-based global conservation priority for marine mammals at the 1º cell resolution level; (2) identify which environmental variables (water chemistry and temperature) are most strongly associated with these high conservation priority patterns; and (3) test the hypothesis that topography (bathymetry) is an important driver not only of species richness but also of complementarity patterns of marine mammal site importance. Identifying top conservation priority global areas for marine

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mammals, as well as environmental variables that are associated with these areas, would provide important insight into best management approaches for these species, especially in the context of climate change. Additionally, marine mammals are top predators and ecosystem engineers (Roman et al. 2014). Consequently, their conservation can indirectly affect sympatric species that require the same environmental conditions to thrive.

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations.

4.3 Materials and Methods

4.3.1 Data sources. Shape-file maps of 134 marine mammal species global distributions were obtained from the IUCN Red List Spatial Data database (IUCN, Gland, Switzerland; available at: http://www.iucnredlist.org/technical-documents/spatial-data) and the R package *letsR* (Vilela and Villalobos 2015) was used to determine values of presence/absence for each 1° grid cell (N = 47,283) for 123 of the 134 species (species listed as extinct, not evaluated, and those living exclusively in freshwater environments were excluded).

For more detailed analyses, marine mammal species were assigned to groups that account for life history differences and IUCN extinction risk listings. The groups are: 1) FA (fully aquatic species; n=87), comprised of cetaceans and sirenians; 2) NFA (non-

fully aquatic species; n=36), comprised of pinnipeds and fissipeds; 3) MI (migratory species; n=37); 4) NMI (non-migratory species; n=52); 5) Unknown (species with unknown migratory status; n=29); 6) TR (threatened and data deficient species; n=79 – those listed as CR, EN, VU, NT, and DD); and 7) NTR (non-threatened species; n=44 – those listed as LC). For the purposes of our study, DD species were included under the TR category because we are currently unaware as to the extinction risk of these species, and as stated by Schipper et al. (2008), marine mammals are exposed to a disproportionate greater number of threats compared to terrestrial mammals. Therefore, it is likely that an important number of DD species might fall under one of the threatened categories. Nomadic species were included in analyses for the group ALL (n=123); however, the limited number of species in this category (n=5) was insufficient to conduct the tests performed in this study as its own group.

Environmental variables were obtained from the National Oceanic and Atmospheric Administration's World Ocean Atlas database (NOAA, WOA 2013), and were converted into 1° cell raster files using ArcMap 10.5 (ESRI 2011). These oceanographic data are provided for monthly, seasonal, and annual timelines. In our analyses, we used annual, minimum and maximum values of the available oceanographic data, totaling 30 variables (see table S1). Two bathymetry variables also at the 1° cell resolution (mean and range) were also used in this study, and were obtained from Global Ocean and Land Terrain Models (GEBECO 30 arc-second grid, GEBCO 2014).

4.3.2 Determining global conservation priority. The core area form of the Zonation software (Moilanen et al. 2014) was used to measure global conservation priority.

Zonation is a reserve-selection software that uses the complementarity approach to hierarchically prioritize cells based on their conservation importance for each taxon. Zonation works by first assuming that all cells are potentially 'reserved', and after each iteration removes those cells that are least important. This process conserves the core areas for each species and minimizes biodiversity loss by minimizing proportional area loss for those species that have the most restricted ranges in the current tentative solution. The result is a hierarchy of cells where the smallest number of 'reserved' sites are contained within larger sets. For example, the top 1% of sites are a subset of the top 5% and so on (Moilanen et al. 2014). A separate model of conservation priority was calculated using species richness (the number of species present at each site or cell) for comparison.

4.3.3 Environmental variables and conservation priority relationship. Varimax-rotated principal component analysis (PCA) was used to identify sets of the least correlated water chemistry variables and thus reduce the dimensionality of the environmental data. To determine the number of dimensions, we used the Kaiser rule (Kaiser 1960) to conserve those components that were the most meaningful. To test the hypothesis that topography is an important driver of marine mammal species distributions, bathymetry variables were omitted from the PCA analyses and added separately to one set of environmental correlation (random forest) tests, and omitted during a second set of tests to compare the level of importance in results. Random forest models (Breiman 2001) were used to elucidate the relationship between the environmental predictors (PCA factors and bathymetry variables) and conservation

priority of marine mammals. Random forest works by randomly selecting bootstrap

samples from the original data and performing 500 regression trees, at each step selecting

the best split among the number of predictors chosen. During each iteration, trees were

built using approximately 66% of the original data and the leftover ~33% were used to

estimate the rate of error of the training data (the first ~66%). This error rate is referred to

as the out-of-bag- error (OOB), and was subsequently used to estimate the relative

importance of each predictor by noticing any changes in the OOB values every time the

values of a predictor from the training set were permuted (leaving other predictor values

unaltered). OOB predictor errors were calculated for each tree and each variable, and the

mean difference in OOB error values before and after permutations were assigned as the

importance score for each variable. Random forest models with the environmental

variables (PCA factors related to water chemistry and temperature, and bathymetry) were

applied as the independent variables to each marine mammal taxon, and conservation

priority as the dependent variable. All analyses were performed in R using the packages

dismo (Hijmans et al. 2017) and *randomForest* (Breiman et al. 2018).

4.4 Results

   PCA models produced 8 groups of environmental data, which explained between

17% and 83% of the variance observed (figure 1B, table S1 in appendix). The most

representative environmental variables were annual density, minimum density, annual

nitrate, minimum phosphate, minimum and maximum percent oxygen saturation, annual

temperature, and annual apparent oxygen utilization (tables 1B, 4.1-4.2).

Maps depicting the conservation priority of the world's oceans, using complementarity to prioritize sites, show a clear contrast between areas of least (dark blue, figure 4.1) *versus* most (red, figure 4.1) importance. On the other hand, maps created using species richness show less contrast between least and most important sites (figure 4.2), making it more difficult to determine which sites are truly irreplaceable. For example, the complementarity map for all marine mammal species (ALL) shows a gradient of increasing importance from pelagic towards coastal areas, with patches of high priority in the Southern, North Pacific, and Arctic Oceans (figure 4.1A). Opposite of this is the map for ALL based on species richness, where none of these areas is marked as high-priority, but instead as low to moderately important for the Southern and North Pacific Oceans, and low to least important for the Arctic Ocean (figure 4.2A).

Random forest models produced a hierarchy of variable importance for the 10 variables (8 water chemistry and temperature variables from the PCA analysis, plus the 2 bathymetry variables, mean and range; table 4.1). For the complementarity study, annual temperature was the most important variable for most groups, with the exception of NFA and UNK, for which the most important variables were mean bathymetry and annual density, respectively (table 4.1). Annual temperature was the second most important variable for those two groups, and mean bathymetry and annual density were the second or third most important variables for groups where those variables were not already the most important ones. For the species richness study, annual temperature was the most important variable for all groups, followed by annual density and then mean bathymetry, also for all groups (table 4.1). Correlation values of random forest models ranged from

55.6 to 65.2 across marine mammal groups for the complementarity study, and from 57.4 to 84.2 for the species richness study (table 4.1).

When bathymetry variables were omitted, random forest models produced results that include annual temperature (top variable for all groups except MI, for which it was the second most important variable), annual density (top variable for group MI and secondary for all others), maximum percent oxygen saturation (third most important variable for all groups except for NFA and UNK), and annual nitrate (third most important variable for groups NFA and UNK) as the top variables in the species richness study (table 4.2). For the complementarity study, annual temperature was the top variable for all groups except FA, UNK and TR, for which annual density was the top variable, as well as the second most important variable for the rest of the groups, and maximum percent oxygen saturation was the third most important variable for all groups in the study (table 4.2). Correlation values ranged from 32.9 to 56.1 for the complementarity study, and from 45.6 to 77.6 for the species richness study (table 4.2).

4.5 Discussion

Results for species richness and complementarity studies show a consistent, shared selection of top environmental variables, even though the specific values per marine mammal group vary with each study (tables 4.1, 4.2). With and without bathymetry included, mean annual sea surface temperature (SST) was the most important variable in most cases (tables 4.1, 4.2), followed by a combination of mean annual density and mean bathymetry as either the second or third most important variables in most cases whenever bathymetry was included as an environmental variable (table 4.1). When bathymetry was

Complementarity
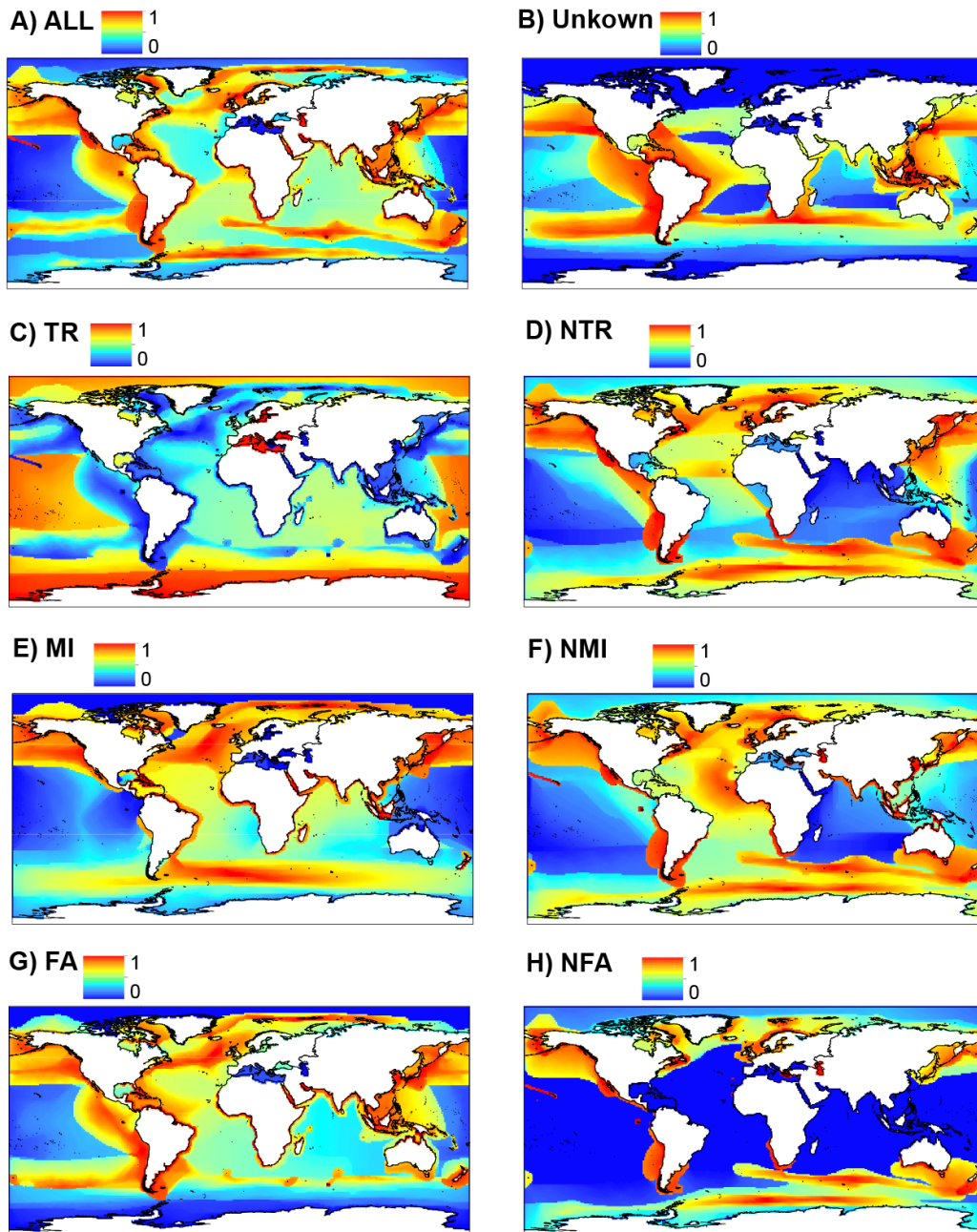
Figure 4.1. Global marine mammal species representation priorities of 1° cells, calculated using Zonation's core-area form (reserve-selection software; complementarity approach), scaled from 0 (dark blue, least important) to 1 (red, most important) for each marine mammal group. Groups are: ALL = all species; TR = threatened species; NTR = non-threatened species; MI = migratory species; NMI = non-migratory species; Unknown = species with unknown migratory status; FA = fully aquatic species; and NFA = non-fully aquatic species.

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excluded, the most common second and third top variables were either mean annual density, mean maximum percent oxygen saturation, or mean annual nitrate (this one only in a couple of cases in the species richness study; table 4.2). These trends show that as expected, results depend on the environmental variables that are included in the analyses (e.g., variables that are not included cannot possibly be listed as important); however, this also means that trial and error of several environmental variable tests should be run to determine the best group of variables to represent species distribution and sites importance on a case-by-case basis. In addition, since we reported evidence that marine sites complementarity is strongly correlated with abiotic drivers, our results support the tenet that site importance can be modeled and predicted as a function of environmental variables (Albuquerque and Beier 2015c).

The higher correlation values for the species richness results compared to the complementarity results are expected, as species richness is an important ecological descriptor of a site, and complementarity does not have a homogeneous distribution (its purpose is to clearly define areas of least to most importance). Correlation values in this case do not determine which approach is better, but instead indicate the level of correlation between each distribution pattern (species richness or complementarity) and the corresponding set of environmental variables.

Temperature data have been associated with species distributions in previous studies. For example, Albuquerque and Beier (2015b) found that the main variables associated with distribution of complementarity patterns for terrestrial mammals, birds, and

Species richness
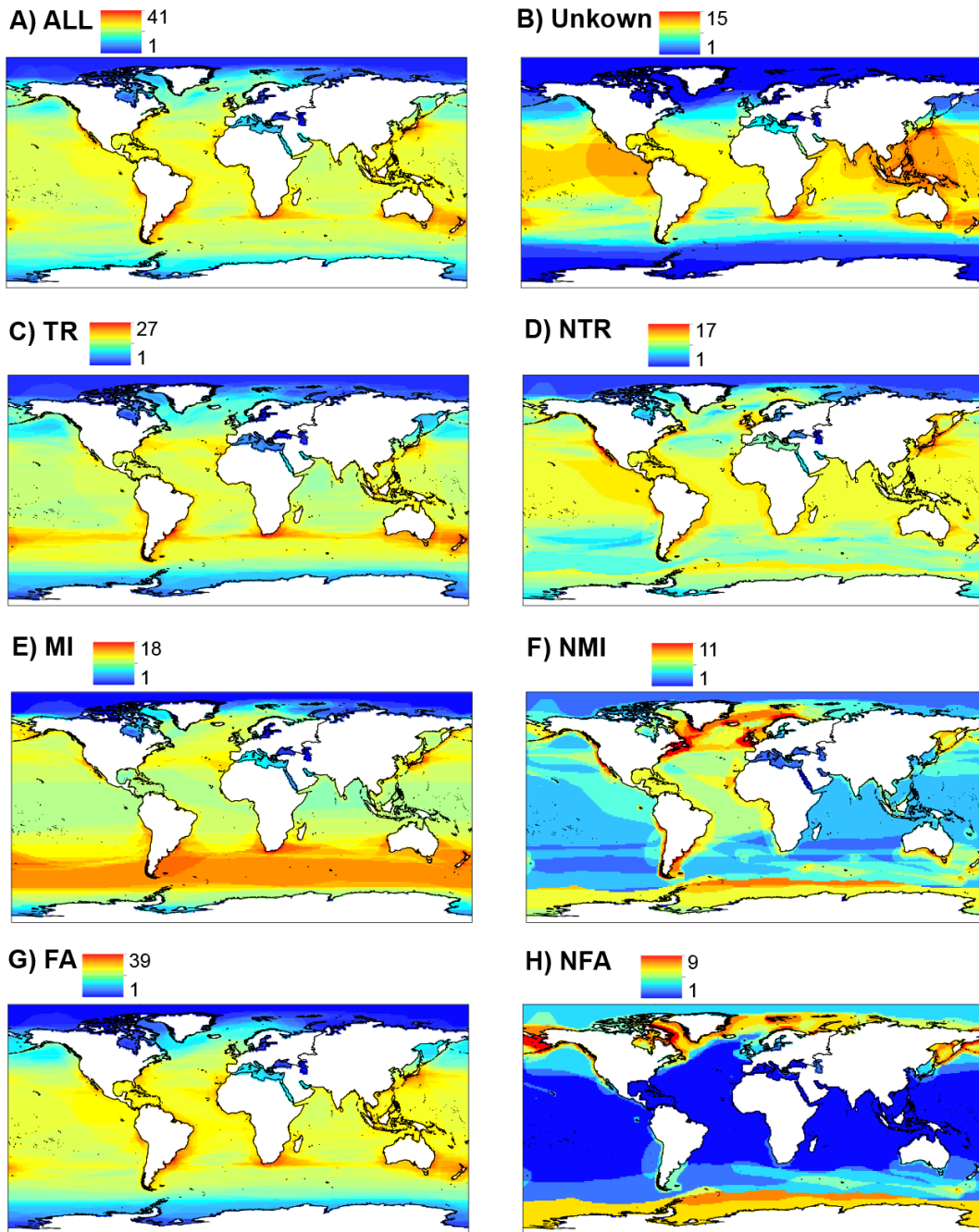
Figure 4.2. Global marine mammal species representation priorities of 1° cells, calculated using species richness, scaled from 0 (dark blue, least important) to 1 (red, most important) for each marine mammal group. Groups are: ALL = all species; TR = threatened species; NTR = non-threatened species; MI = migratory species; NMI = non-migratory species; Unknown = species with unknown migratory status; FA = fully aquatic species; and NFA = non-fully aquatic species.

amphibians, were variables associated with energy (i.e., evapotranspiration as an indirect measurement of temperature), and water availability (a relevant variable for terrestrial species). Climate, and specially temperature, has also been strongly associated with diversity patterns determined by species richness in terrestrial systems (e.g., Currie 1991, Francis and Currie 2003, Hawkins et al. 2003, Rodríguez et al. 2005), and marine systems (e.g., Tittensor et al. 2010). Our results are consistent with these findings, as SST was often the top predictor of marine mammal species distributions both for species richness and complementarity patterns (tables 4.1, 4.2). Kaschner et al. (2011) also found that when models of marine mammal species richness distributions are compared to environmental variables, temperate waters in both hemispheres are strongly associated with higher species presence. This suggests that temperature preference by marine mammals shows a bimodal distribution, with colder waters at the poles being associated with less marine mammal species richness than in tropical areas (Kaschner et al. 2011).

Results also support the hypothesis that topography, as represented by bathymetry in our study, is an important environmental variable strongly associated with patterns of marine mammal species distributions for both the species richness and the complementarity cases (compare results on tables 4.1 and 4.2). Whenever bathymetry variables were included in the study, mean bathymetry outcompeted other first, second, and third variables, as determined by the studies omitting bathymetry, and altogether displaced maximum percent oxygen saturation and annual nitrate as possible top three variables (tables 4.1, 4.2). This is perhaps because bathymetry might be acting as a proxy for distance from shore, or of upselling (i.e., how productive an ecosystem is), or both. In

Table 4.1. Relative importance of environmental variables including bathymetry, based on random forest models (decreasing level of importance with 1 = most important and 10 = least important), and corresponding R^2 values per group. Shaded boxes highlight the top three values/surrogates for each group, and bolded values represent the most important surrogate for each marine mammal group. Groups are: ALL = all species; TR = threatened species; NTR = non-threatened species; MI = migratory species; NMI = non-migratory species; Unknown = species with unknown migratory status; FA = fully aquatic species; and NFA = non-fully aquatic species.

					Groups				
	Surrogates	ALL	FA	NFA	MI	NMI	UNK	TR	NTR
Complementarity	Apparent oxygen utilization (annual)	7	7	6	6	6	7	7	7
	Bathymetry (mean)	2	2	1	3	3	3	3	3
	Bathymetry (range)	4	5	4	5	5	4	5	5
	Density (annual)	3	3	3	2	2	1	2	2
	Density (min)	8	8	8	8	8	8	8	8
	Nitrate (annual)	6	6	7	7	7	6	6	6
	Phosphate (min)	10	10	10	10	10	10	10	10
	% oxygen saturation (max)	5	4	5	4	4	5	4	4
	% oxygen saturation (min)	9	9	9	9	9	9	9	9
	Temperature (annual)	**1**	**1**	2	**1**	**1**	2	**1**	**1**
	R^2	57.3	65.0	55.6	64.0	59.4	65.2	62.8	58.4
Richness	Apparent oxygen utilization (annual)	7	7	7	7	8	8	7	7
	Bathymetry (mean)	3	3	3	3	3	3	3	3
	Bathymetry (range)	4	4	4	4	5	4	4	4
	Density (annual)	2	2	2	2	2	2	2	2
	Density (min)	8	8	8	8	7	7	8	8
	Nitrate (annual)	6	6	5	6	6	5	6	6
	Phosphate (min)	10	10	10	10	10	10	10	10
	% oxygen saturation (max)	5	5	6	5	4	6	5	5
	% oxygen saturation (min)	9	9	9	9	9	9	9	9
	Temperature (annual)	**1**	**1**	**1**	**1**	**1**	**1**	**1**	**1**
	R^2	73.2	78.5	77.5	76.6	57.4	84.2	75.7	66.8

either case, this result indicates a correlation, and further studies are required to determine causation. Pineda and Caswell (1997) simulated northwest-Atlantic gastropod and polychaete diversity patterns against bathymetric data, and found that distribution patterns follow a parabolic shape: highest species distributions occur within the mid-ranges of bathymetric values and lower diversity occurs towards the minimum and maximum extremes in the study. In another study, by Dolan et al. (2008) determined how coral distributions in Ireland correlates with bathymetric and terrain type data (an important aspect for coral communities), and found that these variables are important predictors of coral species distributions. This is presumably because bathymetry and terrain type will affect the ability of coral to attach themselves to a particular area.

The third top variable in this study was mean annual density. Density is calculated by combining salinity, depth, and temperature data for each site (NOAA, WOA 2013). Therefore, density values are strongly associated with temperature and bathymetry data, the other two top variables in this study (tables 4.1, 4.2). It is important to note that because these variables resulted from the PCA, we do not believe that they can be auto-correlated. Results suggest that salinity is indirectly responsible for some of the site importance patterns for both species richness and complementarity models, but more importantly, that bathymetry is also indirectly accounted for in the studies that omitted it, as density was one of the top two variables associated with patterns of species richness and complementarity, along with SST (table 4.2). This observation further supports the hypothesis that bathymetry is an important variable driving patterns of marine mammal

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Table 4.2. Relative importance of environmental variables excluding bathymetry, based on random forest models (decreasing level of importance with 1 = most important and 8 = least important), and corresponding R^2 values per group. Shaded boxes highlight the top three values/surrogates for each group, and bolded values represent the most important surrogate for each marine mammal group. Groups are: ALL = all species; TR = threatened species; NTR = non-threatened species; MI = migratory species; NMI = non-migratory species; Unknown = species with unknown migratory status; FA = fully aquatic species; and NFA = non-fully aquatic species.

	Surrogates	ALL	FA	NFA	MI	NMI	UNK	TR	NTR
Complementarity	Apparent oxygen utilization (annual)	5	5	4	4	5	5	5	5
	Density (annual)	2	**1**	2	2	2	**1**	**1**	2
	Density (min)	6	6	6	6	6	6	6	6
	Nitrate (annual)	4	4	5	5	4	4	4	4
	Phosphate (min)	8	8	8	8	8	8	8	8
	% oxygen saturation (max)	3	3	3	3	3	3	3	3
	% oxygen saturation (min)	7	7	7	7	7	7	7	7
	Temperature (annual)	**1**	2	**1**	**1**	**1**	2	2	**1**
	R^2	39.2	51.4	32.9	54.5	48.1	56.1	46.9	47.9
Richness	Apparent oxygen utilization (annual)	4	4	5	5	6	6	4	4
	Density (annual)	2	2	2	**1**	2	2	2	2
	Density (min)	6	6	6	6	5	5	6	5
	Nitrate (annual)	5	5	3	4	4	3	5	6
	Phosphate (min)	8	8	8	8	8	8	8	8
	% oxygen saturation (max)	3	3	4	3	3	4	3	3
	% oxygen saturation (min)	7	7	7	7	7	7	7	7
	Temperature (annual)	**1**	**1**	**1**	2	**1**	**1**	**1**	**1**
	R^2	59.9	68.4	72.1	65.1	45.6	77.6	65.1	50.5

species distributions. The UNK group and the UNK and TR groups were those for which density was the top driver under the bathymetry-included and bathymetry-excluded models, respectively (tables 4.1, 4.2). Group UNK is composed of 100% cetaceans, many of which are pelagic-dwelling species with a few coastal species. Group TR is composed of approximately 78% cetaceans, also many of which are mostly oceanic species that overlap with group UNK. Beaked whales include deep diving species, several of which are included in both groups. For example, Cuvier's beaked whales can dive as deep as 3,000 m (Schorr et al. 2014). A study by Mauritzen et al. (2012) addressed the role of density on temperature regulation in the deep North Atlantic Ocean and found that density mediates heat uptake of deeper oceans. These findings, along with ours, suggest that the importance of temperature for some species depend more on several factors combined (e.g., salinity, depth, temperature) than on temperature alone, as for other species. Nonetheless, temperature is included as an important factor, whether its influence is direct or indirect.

Oxygen variables, represented in our study as either mean annual apparent oxygen utilization, or minimum and maximum percent oxygen saturation, do not seem to have a particularly significant impact on the results, except when bathymetry was excluded (max % oxygen saturation; table 4.2). Marine mammals obtain oxygen by breathing air and not through gills. This may explain why oxygen is a somewhat important driver, as oxygen dissolved in water is required by marine mammal prey (e.g., fish, as they breathe through gills), but not for these mammals themselves). Dissolved oxygen concentrations can also vary depending on temperature and depth, and further studies are needed to determine

how specifically these concentrations can impact marine mammals. Annual nitrate was found to be only moderately correlated to marine mammal site importance and minimum phosphate was consistently the least impactful variable. Together, oxygen, nitrate and phosphate may be directly correlated to distribution patterns of primary productivity and taxa lower in the food chain. Many marine mammals follow seasonal migration patterns and their distribution maps do not account for seasonality of presence. This may explain why these three variables do not show their full importance in our study, but further studies on this subject are warranted.

The above discussion indicated that including different variables in the study alters the results (as seen with the presence/absence of bathymetry variables on tables 4.1 and 4.2). It is important to note that the approach used to determine distribution patterns of site importance for marine mammal species (e.g., by using species richness or complementarity), also alters the results (tables 4.1, 4.2). For example, the bathymetry-included models using species richness show that SST is consistently the most important variable, but for the complementarity model, SST is the most important variable for all but two groups, NFA and UNK (table 4.1). This difference suggests that not all environmental variables are created equal for all groups, and that as with the use of surrogates for species representation in conservation planning, some approaches are more appropriate than others, depending on the set of taxa considered (see e.g., Sutcliffe et al. 2015). The implication of these findings for applied species management is that the quality or effectiveness of the conservation efforts depends on the drivers selected as indicators of sites conservation priorities.

The importance of the approach used to determine site importance patterns for species distributions is further supported by comparing the results produced using the complementarity and species richness approaches. In this study, we present the first complementarity-based site importance patterns for marine mammal species distributions at the global scale. These maps are more detailed than those of species richness as to the conservation priorities of sites, and with regard to highlighting sites that are irreplaceable (red areas; figure 4.1). By contrast, the species richness approach produces maps that are more homogeneous, making it more difficult to discern areas that require the most attention (figure 4.2). More specifically, complementarity maps show a gradient of site importance from the dark blue (least important) to the red (most important), also highlighting regions with low species richness that are important areas for rare or endemic species (see for example the North Pacific, Southern Ocean, and Arctic Ocean regions for all marine mammal species combined; figure 4.1A). The species richness map for this same group (ALL) fails to show these areas as having high conservation priorities, especially the Arctic Ocean region (figure 4.2A). This difference in patterns is observed across all marine mammal groups in this study (figures 4.1, 4.2; B-H), and suggests that using complementarity as the distribution model to determine environmental variables associated with these patterns provides a more accurate foundation over which to build more effective conservation actions than does the species richness approach. These results are congruent with the findings by Albuquerque and Beier (2015b), showing that complementarity maps outperformed species richness maps

for terrestrial mammals and other vertebrates, by providing true conservation values of sites at the global scale.

It is important to highlight that our study is one of association and not causation. Further studies are required to elucidate the relationship between patterns of site importance distributions and environmental variables, such that causation can be established. Additionally, future studies need to incorporate distribution patterns of other taxonomic species, as the use of a single dataset (i.e., marine mammal species distributions) is insufficient to determine if the observed patterns in our results can be generalized and applied to other marine species. We are also not suggesting that biotic information is less important than biotic information when determining site conservation values. On the contrary, in a previous study the addition of biotic information produced more accurate site prioritization results than abiotic information alone (Sutcliffe et al. 2015). However, when biotic information is limited, abiotic information, which is usually easier and more affordable to obtain, can complement and/or provide the information necessary to spatially prioritize sites for conservation actions and increase their effectiveness (see e.g., Albuquerque and Beier 2015c).

As stated in the introduction, this is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations. There are few global marine

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mammal datasets that are available. The IUCN distribution maps are the most complete but they currently lack information on critical factors needed for spatial conservation assessments at this scale. Two of the most important factors are species specific density estimates and minimum home range data. Without this information it is difficult to fully evaluate how different areas would be at protecting the community of marine mammal species within.

Our results are especially meaningful in the context of climate change. Two of the most important variables in this study were temperature and density (also related to temperature). Ramírez et al. (2017) found that marine biodiversity hotspots, including those for marine mammals, are located in areas that will be most impacted by climate change. However, these hotspots of biodiversity were determined by using the species richness approach. Future studies should therefore elucidate how biodiversity hotspots of marine species, based on complementarity patterns, will be affected by climate change. The study by Mauritzen et al. (2012) also suggests that climate change will directly impact density-compensated temperature changes in the deep oceans.

Climate change processes such as changes in SST and density-related dynamics that help regulate deep ocean water temperatures, suggest that the distribution of marine mammal species is already changing and will continue to change in the future (Moilanen et al. 2009 and references therein). Our results show that climate variables are as important drivers of marine sites complementarity as they are in terrestrial systems. Unavoidably, conservation efforts must use this information to plan for potential future scenarios requiring remediation and preventive conservation actions. One example of

how this can be accomplished is by identifying and understanding how abiotic variables

impact species distributions in order to predict complementarity patterns that can be

applied to the implementation of future reserves (see e.g., Sutcliffe et al. 2015,

Albuquerque and Beier 2015c). Our study provides evidence that complementarity-based

species distributions and abiotic variables can be combined to inform contingency plans

that will help mitigate the biodiversity loss crisis.

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CHAPTER 5

ENVIRONMENTAL DIVERSITY AS A SURROGATE OF MARINE MAMMAL

DIVERSITY

5.1 Abstract

Surrogates of biodiversity have been used for several decades in conservation
planning to represent species whenever information about their geographical distributions
is insufficient. Until recently, the majority of surrogates of biodiversity have been biotic,
such as for example species richness, site complementarity and well-known taxa (cross-
taxon surrogacy). While biotic information is relevant and imperative in determining
conservation priorities of sites, conservation efforts are still limited by the amount of
biotic information available. To offset this issue, an alternative surrogate known as
environmental diversity (ED) can be incorporated. Environmental diversity uses readily
available abiotic data to help determine site conservation importance because it accounts
for the environmental variables usually associated with the presence of species. In this
study, I investigated the use of ED as a surrogate of global marine mammal species
representation and tested it with and without bathymetry to determine the importance of
topography on species distributions, as previously proposed in terrestrial realms. Results
indicate that ED is an effective surrogate, as in general it increased species representation
by 65%, compared to solutions based on random site selection. Results also show that
bathymetry does play an important role in how marine mammal species are
geographically distributed. While the effectiveness of ED has been demonstrated in
previous studies of terrestrial vertebrates, this is the first time ED is assessed as a

surrogate in marine systems at the global scale. These findings suggest that ED can be

used in combination with known biotic data to increase the effectiveness of site

prioritization for conservation of marine mammals, and potentially other marine taxa.

5.2 Introduction

Because of the limited knowledge about species and their distributions, conservation

scientists, stakeholders, and biogeographers often use surrogates, such as well-known

taxa and species richness – the number of species present in a site (Jenkins et al. 2013) or

environmental factors (Faith and Walker 1996) in order to determine which sites have

higher conservation priorities. Among these surrogates, species richness has been the

most popular metric to define the biodiversity of sites, including defining rates of global

biodiversity loss (Ladle and Whittaker 2011, Sala and Knowlton 2006, Ramírez et al.

2017). Species richness is an important characteristic when it comes to the structure and

function of an ecosystem and the role each species or number of species play in it (e.g.,

Griffin et al. 2009 and references therein), but is not an effective measure of site

importance in the context of conservation. Indeed, widespread species overlap at sites

containing a high number of species, resulting in sites with limited range species, which

tend to occur in areas with lower species richness, being underrepresented (Kirkpatrick

1983, Csuti et al. 1997, Albuquerque and Beier 2015a & b, and papers cited therein). To

address this issue, for the last three decades conservation scientists and biogeographers

have turned to an alternative surrogate known as complementarity. The complementarity

approach prioritizes sites for conservation in a way that accounts for those limited range

species by giving them priority when adding new sites to complement an already

established reserve network. The result is a set of sites that together represent a higher number of species than if they had all been selected using species richness alone. Several methods can be used to calculate complementarity values. For example, these values can be calculated using integer programming (Haight and Snyder 2009) or by using heuristic algorithms such as Zonation - a reserve-selection software (Moilanen et al. 2014).

Abiotic variables (e.g., temperature, topography, and rainfall) have been used in previous studies as alternative surrogates for terrestrial (Faith and Walker 1996, Beier and Albuquerque 2015, Albuquerque and Beier 2018) and marine (Sutcliffe et al. 2015) biodiversity. There is a strong relationship between environmental data and biotic factors like sites complementarity, community composition (beta diversity), and species richness (alpha diversity), according to previous findings (Albuquerque and Beier 2015, 2018). One specific type of environmental factors approach is environmental diversity, or ED (Faith and Walker 1996). ED is defined by the relative diversity of the abiotic characteristics of an area and how the relative abiotic composition of that area compares to that of other geographical areas (Faith and Walker 1996). ED is not defined as geographical space, but instead, a multidimensional environmental space that is quantified by non-metric multidimensional scaling (i.e., ordination; Faith and Walker 1996). This environmental space represents the various combinations of environmental conditions that are associated with species distributions, and therefore serves as a predictor of species presence by linking the biotic and abiotic information (Faith et al. 2003). Two algorithms are commonly used to define the environmental space. The first is p-median ED, which creates a hypothetical grid of demand points (reference points)

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uniformly distributed across the ordination space, so that equal distribution of site selection can be guaranteed (Faith 2003). ED uses a minimum framework to select sites that represent the greatest variety of environment types, therefore maximizing environmental space coverage. This algorithm selects p number of sites such that the sum of distances (in ordination space) between them can be minimized, from each demand point to the closest site selected. The premise is that this method for site selection produces a group of sites that collectively represent different types of environments, and so also includes a greater number of species than if site selection had occurred with a reduced number of environment types (Faith and Walker 1996, Hortal et al. 2009, Beier and Albuquerque 2015). The second commonly used algorithm to define ED is Maxdisp. This approach works in much the same way as p-median, but Maxdisp does not use demand points. Instead, it calculates the inverse of the square of distances between sites in order to uniformly place them through the ordination space. Research by Engelbrecht et al. (2016) and Albuquerque and Beier (2018) compared the performance of both approaches on empirical sets of biotic data and concluded that Maxdisp is as effective as continuous p-median in representing ED.

Previous studies have reported that ED is a highly effective surrogate of plants and vertebrates in tropical and temperate regions (Beier and Albuquerque et al. 2015, Albuquerque and Beier 2018). These findings justify further studies as to the effectiveness of ED as a surrogate to determine conservation priority of sites. ED can be particularly meaningful in areas of the world where knowledge of species geographical distributions is most limited due to a lack of resource availability (e.g., developing

countries in tropical regions that host the highest biodiversity but have the poorest reserve network implementation), and which might be experiencing rapid biodiversity loss (Pimm 2000). If ED proves to be as effective for marine mammals as it is for terrestrial mammals and other species, this affordable surrogate would be useful to determine site prioritization of ocean areas, which remain largely unexplored (NOAA 2018a). Therefore, the objective of this study is to calculate ED using oceanographic variables such as sea surface temperature, density, and other factors (n=30, see methods), and assess how effective it is in representing site importance for marine mammal biodiversity at the global scale. To date, only terrestrial environmental factors have been used to calculate and assess ED (e.g., Faith et al. 2004, Beier and Albuquerque 2015, Albuquerque and Beier 2017). In marine systems, Sutcliff et al. (2015) studied how well abiotic variables represented species belonging to a network of reserves in an Australian inter-reef system, and found that abiotic information can be used to identify areas for potential marine reserves. If my hypothesis that ED is an effective surrogate for marine mammal representation is supported, the idea that ED can also be an efficient surrogate for other marine taxa would be strengthened. If this hypothesis is not supported, this would suggest that although ED is an effective surrogate in the terrestrial context, it could not be equally applied to the marine landscape.

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be

considered. These analyses are analytical exercises that represent one small piece toward those considerations.

5.3 Materials and Methods

5.3.1 Data preparation. I obtained 123 range maps depicting the distribution of marine mammals form the International Union for the Conservation of Nature (IUCN) Red List Spatial Data database (IUCN, Gland, Switzerland; http://www.iucnredlist.org/technical-documents/spatial-data). I processed these range maps in R (*letsR*, Vilela and Villalobos 2015) to generate presence/absence values for each 1° grid cell (N = 46,130). I excluded species that occurred only on freshwater because environmental data specific to the land areas within the 1° cells where these species occur are not available. I also excluded species listed as extinct (EX) or not evaluated (NE) because distribution maps for these species are not available.

Based on differences in life histories and extinction risk levels according to IUCN, I grouped marine mammals into seven groups: 1) fully aquatic (FA; n=87) species (cetaceans and sirenians); 2) non-fully aquatic (NFA; n=36) species (pinnipeds and fissipeds); 3) migratory (MI; n=37) species; 4) non-migratory (NMI; n=52) species; 5) species with unknown (UNK; n=29) migratory status; 6) threatened (TR; n=79) species; and 7) non-threatened (NTR; n=44) species. Species in the TR group are those listed as critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT), and data deficient (DD). For the purposes of this study, I am treating DD species as potentially threatened given that their actual conservation risk has not been assessed. Additionally, marine mammal species are disproportionally more threatened compared to

terrestrial mammals (Schipper et al. 2008), suggesting that an important number of DD species might belong to one of the imperiled IUCN categories. Species in the NTR group are those listed as least concern (LC). I also performed analyses for all marine mammals together (group ALL), which includes species with nomadic movement patterns. However, those nomad species were excluded from life history movement-based groups (i.e., MI, NMI, and UNK), because the number of species (n=5) was insufficient for reliable analyses as their own group.

I selected 33 oceanographic variables associated with patterns of species distribution at the global extent (table 1C). I obtained temperature, salinity, density, conductivity, dissolved oxygen, percent oxygen saturation, apparent oxygen utilization, silicate, phosphate, and nitrate from the National Centers for Environmental Information (NOAA, WOA 2013). WOA is a set of oceanographic variables in each 1° square, which contains values for annual, seasonal, and monthly periods. I calculated the mean or range of each oceanographic variable across each 1° cell. I also calculated the mean and range of depth values for each 1° cell. I obtained gridded bathymetric data from Global Ocean and Land Terrain models (GEBCO 30 arc-second grid, GEBCO 2014).

5.3.2 Measuring complementarity. I used the core-area form of the reserve-selection software Zonation (Moilanen et al., 2014) to estimate the complementarity of every 1° marine cell on Earth for each marine mammal group. Zonation is known for its ability to identify the best part of a landscape, and for suggesting the optimal balanced expansion of an existing reserve network, to solve the minimum set coverage problem (i.e., achieve conservation targets at a minimum cost; Di Minin et al. 2014). Zonation is deterministic

and produces a complementarity-based ranking of conservation values over the entire landscape.

5.3.3 Measuring environmental diversity (ED). I used principal component analysis (PCA) to reduce data dimensionality and the Kaiser rule (Kaiser 1960) to retain the meaningful components, i.e., to select the number of dimensions of the reduced space. I adopted a Varimax-rotated PCA to maximize the variance of the loadings across the PCA factors, thus making their interpretation easier and more reliable (i.e., easier to replicate with different data samples). The Varimax rotation allows a clearer identification of major environmental gradients, as well as those showing higher loadings in the main rotated PCA factors. For each factor, I selected the oceanographic variable with highest loadings, to select a subset of oceanographic variables. I used the most correlated variables with each factor and the bathymetry variables to calculate environmental Euclidean distances among sites. I did not include bathymetry in the PCA because I wanted to investigate depth influences on the ability of ED to select sites that represent species efficiently. Based on the type of environmental variables used to define environmental space, I created two environmental diversity models: 1) ED_{ob} - derived from oceanographic variables and bathymetry, and 2) ED_o -based on oceanographic variables only. Then, I used the Maxdisp ED approach (Engelbrecht et al. 2016) and the variables for selecting environmentally diverse sites. In this approach, I first used the set of selected variables (with and without bathymetry) to produce an Euclidean distance matrix among the grid cells (sites). Then, I used the inverse of the square of distances

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between sites to produce sites more evenly distributed in environmental space
(Engelbrecht et al., 2016).

I used the Species Accumulation Index, SAI (Ferrier & Watson 1997, Rodrigues &
Brooks 2007, Beier *et al.* 2015b; Beier & Albuquerque 2015, 2016; Albuquerque & Beier
2015a, 2015b, 2015c, Engelbrecht et al. 2016) to evaluate the ability of ED_{ob} and ED_o to
identify sites that most efficiently represent species across 96 targets, ranging from 0.1 to
10% (by 0.5%) of the most environmental diverse sites. SAI is expressed by: $(S\text{-}R)/(O\text{-}R)$,
where S is the number of species represented in sites with the highest predicted
complementarity ranks, O is the maximum number of species that can be represented in
the same number of sites (based on complementarity values), and R is the number of
species represented in the same number of randomly selected sites. SAI is scaled $-\infty$ to
1; negative SAI indicates a worse than random result, 0 indicates random performance,
and positive SAI is a measure of surrogate efficiency. For example, SAI of 0.6 indicates
the ED is 60% as effective as having full knowledge of where species occur in its ability
to improve on random selection of sites.

5.4 Results

According to the Kaiser criterion, major environmental trends were captured by the
eight first factors of the PCA, which jointly described 82% of the variance in
oceanographic variables (table 1B in appendix). The highest factor loadings for the eight
first factor corresponded to density - annual and minimum, nitrate - annual, phosphate -
minimum, percent oxygen saturation -maximum and minimum, temperature - annual,

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apparent oxygen utilization - annual. I also selected bathymetry - range and mean, for further ED modeling.

For all eight groups and all percentages of sites prioritized (targets), Zonation solutions represented many more species than the same number of randomly-selected sites (figure 5.1). In general, sites prioritized by both ED approaches represented more species than occurred in randomly selected sites for most datasets and combinations of environmental variables (figure 5.1). ED_{ob} represented substantially more species than ED_o for seven datasets (figure 5.1). For the threatened dataset (TR), ED approaches performed approximately equally (figure 5.1). In 447 (58%) and 250 (32%) instances, ED_{ob} and ED_o solutions were respectively better (closer to the true optimum) than Zonation (figure 5.1). In 355 (46%) instances, ED_{ob} provided better solutions than ED_o. In the other 145 (19%) instances, ED_o represented more mammals than ED_{ob}.

The effectiveness of ED as a surrogate for species representation varied across the two sets of environmental variables used to define environmental space. As expected, ED_{ob}, as defined by oceanographic variables and bathymetry, consistently produced higher (better) SAI values than ED_o (consisting of oceanographic variables excluding bathymetry; table 5.1). On average across all marine mammal groups and targets, ED_{ob} solutions were 61% as effective as Zonation solutions in improving on random selection of sites (table 5.1). ED_{ob} and ED_o represented significantly more species than randomly selected sites for groups TR and UNK, respectively (mean SAI 1.00). This indicates that on average, ED is 100% effective at representing our current knowledge of where threatened and data deficient marine mammals occur (given ED's ability to improve on

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random selection of sites; table 5.1). The ED_o approach poorly represented fully aquatic and migratory marine mammals (negative SAI), which indicates that water chemistry alone (no bathymetry information) in insufficient to describe the importance of a site.

5.5 Discussion

Over the last two decades, a number of publications have demonstrated that ED is a reliable surrogate to represent plant and animal species in terrestrial realms (Faith and Walker 1996, Faith 2003; 2011, Faith et al. 1996; 2004, 2011, Beier and Albuquerque 2015, Engelbrecht et al. 2016, Albuquerque and Beier 2018). This study reinforces the finding that ED is as good as complementarity-based models for two of the datasets I tested (TR including bathymetry, and UNK excluding bathymetry), even though it was worse for two other datasets (FA and MI, both excluding bathymetry; table 5.1). Further studies are required to elucidate the cause of these patterns. The efficiency of ED_{ob} was consistent regardless of the fraction of the landscape prioritized, across the eight marine mammal datasets, supporting the idea that bathymetry improves the efficiency of ED as a surrogate of marine mammal diversity.

As expected, Zonation was a remarkably good surrogate for conservation priority of all marine mammal groups, indicating that conservation planning based on biotic data is effective in representing a set of target species (Rodrigues and Brooks 2007). Biotic surrogates allow conservation managers to prioritize sites for biodiversity representation based on complementarity, define target choices (e.g., population size), and identify irreplaceable areas such that future biodiversity loss can be minimized (Rodrigues and Brooks 2007, Moilanen et al. 2009). However, as only a small fraction of biodiversity has

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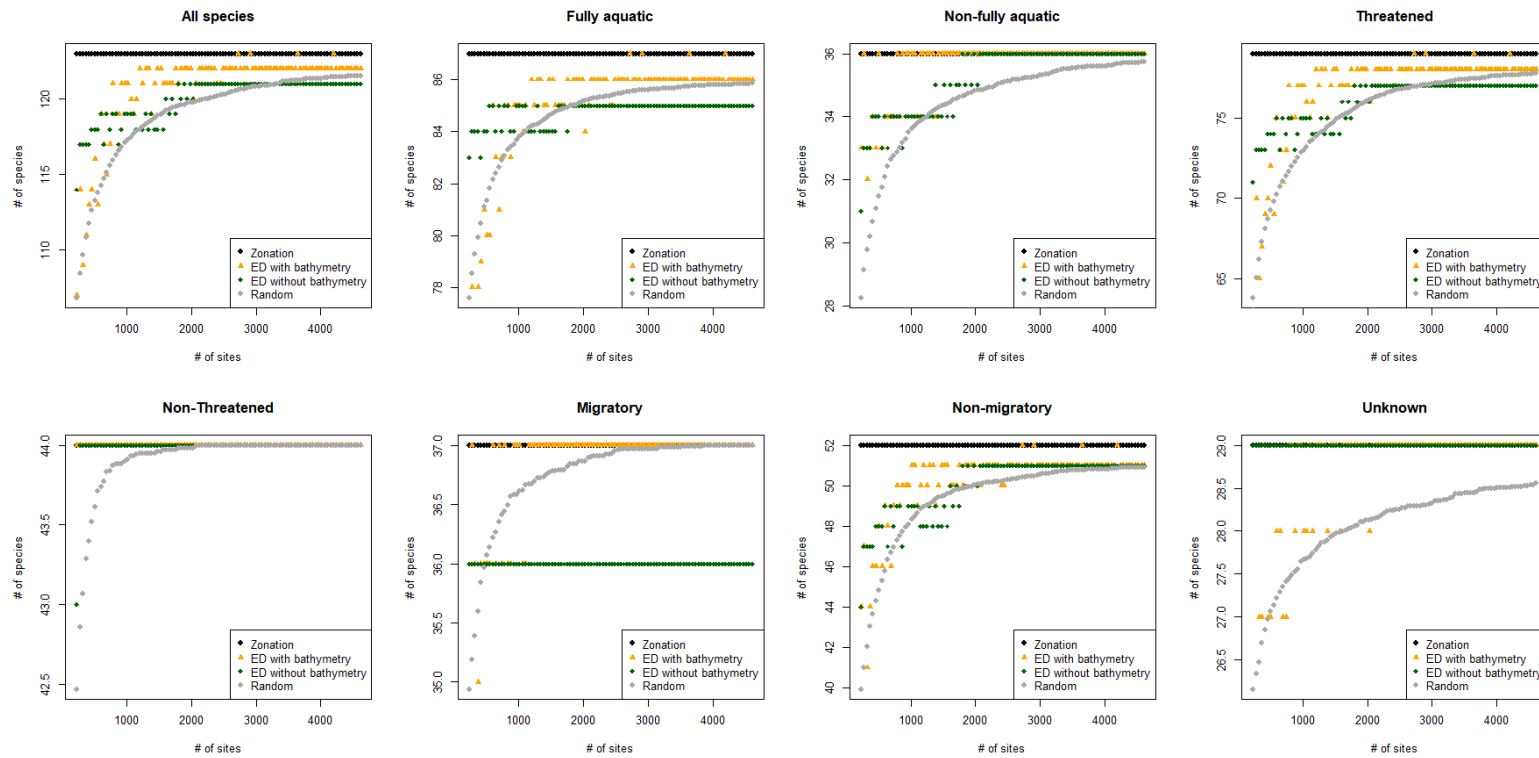
Figure 5.1. Number of marine mammal species represented at least once in sites selected by the two environmental diversity (ED) approaches, and species represented at least once in sites selected by Zonation, compared to the number of species represented in an equal number of randomly-selected sites. ED selects environmentally diverse sites and was calculated from two sets of variables: (1) oceanographic variables and bathymetry (with bathymetry) and (2) oceanographic variables (without bathymetry).

been described or inventoried (Brown and Lomolino 1998), the use of biotic data for surrogates imposes a serious limitation on real world conservation planning.

One way to overcome the biotic data limitation may be to collect comprehensive abiotic data for a subset of sites. This expectation is well supported by my evidence, since ED is on average 65% as effective as biotic data. In a recent meta-analysis, Beier et al. (2015) reviewed 622 evaluations of the effectiveness of abiotic surrogates in representing species in terrestrial ecosystems and reported that the use of abiotic surrogates represented plants and vegetation types relatively well. Beier and Albuquerque (2015) tested the efficiency of ED in eight terrestrial datasets and showed that ED was 42% as effective as having knowledge of species locations (median SAI 0.42), and 7 of 8 SAI values were significantly positive. Sutcliffe et al. (2015) evaluated the use of abiotic domains to measure the efficacy of different marine reserve systems in representing species for conservation purposes, and reported that abiotic domains performed substantially better than random solutions.

I believe that abiotic data, and particularly ED, is an efficient surrogate of biotic representation because it selects sites to optimally span environmental space without the arbitrary constraints of binning methods, and because abiotic conditions are often associated with biogeographical patterns of plant and animal species richness, beta diversity, and patterns of sites complementarity (e.g., Currie 1991, Hawkins et al. 2003, Field et al. 2005, Orme et al. 2007, Albuquerque and Beier 2015a). These studies suggest that energy and climate limit species richness over broad geographic extents (Hawkins et al., 2003 and references therein). An important assumption of using ED is that the values

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Table 5.1. Species accumulation indices (SAI) values for two approaches of environmental diversity (ED) calculated from oceanographic variables with and without bathymetry. SAI is expressed by (S-R)/(Z-R) and describes the effectiveness of ED to that of Zonation in terms of their ability to improve on random selection of sites. SAI values are represented by the mean across 96 spatial prioritization targets. The confidence level (CI) is also displayed.

ED approach	Mammal group	SAI	CI
With bathymetry	All species	0.48	0.05
	Fully aquatic	0.23	0.06
	Non-fully aquatic	0.91	0.05
	Non-threatened	0.43	0.05
	Threatened	1.00	0.00
	Migratory	0.73	0.15
	Non-migratory	0.32	0.05
	Unknown	0.80	0.09
Without bathymetry	All species	0.10	0.05
	Fully aquatic	-0.13	0.07
	Non-fully aquatic	0.72	0.08
	Non-threatened	0.09	0.05
	Threatened	0.98	0.04
	Migratory	-31.85	7.94
	Non-migratory	0.24	0.05
	Unknown	1.00	0.00

of oceanographic variables in a site reflect conditions experienced by marine species. For example, Tittensor et al. (2010) investigated the global patterns and predictors of marine biodiversity and reported that temperature or kinetic energy plays a key role in structuring cross-taxon marine biodiversity. As indicated by the high efficiency of ED in identifying sites that represented species efficiently, my results show that variables related to diversity and complementarity can be used as abiotic surrogates to represent species in the marine realms. This follows the premise that areas with higher

environmental diversity can host a greater diversity of species by providing a wider range of environmental conditions or niche space.

I observed that the choice of variables to include in each study affected the performance of both approaches to ED. Albuquerque and Beier (2018) used 38 environmental variables to calculate ED, and they reported that the use of all variables was not consistently better than using different sets of variables. I suggest that the strong performance of ED_{ob} relative to ED_o reflects the fact that marine biodiversity is strongly correlated with depth in the ocean (Costello and Chaudhary 2017), and more specifically, that the number of marine species is negatively correlated with depth (Cartes and Sardà 1992). The lowest efficiency of ED_o may mean that the standard (i.e., 2D) oceanographical variables fail to capture the intricacies of the marine mammal diversity. However, the density variable is calculated using depth (NOAA, WOA 2013), and therefore indirectly accounts for some bathymetric information. This might help explain why models that excluded bathymetry were still generally effective. However, further studies (e.g., the removal of the density variables) might be needed to corroborate this idea. Regardless of the approach, the complementary nature of this study (with and without bathymetry) strongly supports the inference that using depth information improves surrogate performance.

Additionally, these findings suggest that different species ought to be managed separately, and that trial and error of marine mammal groupings and environmental variables must be performed before settling on the best abiotic surrogates to represent each species. For example, results show that TR species are the best represented by the

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ED$_{ob}$ model (mean SAI 1.00), while the worst group represented by this model was FA (mean SAI 0.23; table 5.1). TR species are approximately 18% non-fully aquatic species and 82% fully aquatic species, several of which are coastal dwellers (approximately 4% are sirenians, and some cetacean species also live in coastal areas). Combined, those species that live in shallower waters will have their distributions impacted by bathymetric patterns. Conversely, the FA group excludes all the non-fully aquatic species that are coastal-dwellers, making this group primarily composed of pelagic species. Pelagic species might not necessarily be as affected by bathymetry after a certain depth, which would justify the results obtained for this group. This idea is further supported by the results for the ED$_o$ model. In this case, the best-represented group is Unknown (mean SAI 1.00), which is composed 100% of cetaceans that are predominantly pelagic species. However, this model also shows that group FA is one of the worst represented (FA mean SAI-0.13; table 5.1), but this could be explained because of the combination of coastal and pelagic species. Future work that separates coastal-dwelling FA species from pelagic ones will most likely provide more accurate results that show to which extent bathymetry is a good surrogate for cetaceans and sirenians.

I highlight that support for ED as a surrogate of biodiversity is a necessary but insufficient condition for ED to serve as a good surrogate in marine conservation planning. Nonetheless, I found that ED could be an effective surrogate of marine mammals, especially when bathymetry is used to define the environmental space and select the most diverse environmental sites. This is the first study assessing the performance of ED as a surrogate of marine mammal biodiversity representation at the

global scale. I propose that my results justify further studies on how ED can be used in applied conservation of marine species by complementing the available biotic information and thus increasing the overall effectiveness of the surrogates. This is in alignment with the findings by Rodrigues and Brooks (2007) and Sutcliff et al. (2015), who reported that biologically informed environmental surrogates, those that incorporated biological variables to develop their models, improved the efficiency of abiotic data as a surrogate of biodiversity.

As stated in the introduction, this is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations. There are few global marine mammal datasets that are available. The IUCN distribution maps are the most complete but they currently lack information on critical factors needed for spatial conservation assessments at this scale. Two of the most important factors are species specific density estimates and minimum home range data. Without this information it is difficult to fully evaluate how different areas would be at protecting the community of marine mammal species within.

In the future, multivariate procedures such as gradient forests (Ellis et al. 2012) can be used to identify the variables that most affect species distributions, therefore increasing the accuracy of ED as a surrogate. Additionally, increasing our knowledge of

marine mammal species distributions would help increase the accuracy of abiotic

surrogates. Unfortunately, this is challenging to do for marine mammals given the

logistics and expenses associated with survey efforts, especially for pelagic species. This

lack of detailed distribution data is also what justifies studies such as this one. Indeed,

determining if ED is an effective surrogate of marine mammal biodiversity and thus

appropriate to identify priority areas for conservation, can aid conservation actions when

there is a lack of knowledge of species distributions (e.g., UNK species), as well as when

resources are limited, because abiotic data are easier and more affordable to obtain.

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CHAPTER 6

THE GEOGRAPHY OF GLOBAL HOTSPOTS OF MARINE MAMMAL

BIODIVERSITY, THEIR EXPOSURE TO ANTHROPOGENIC STRESSORS, AND

THEIR COVERAGE BY MARINE PROTECTED AREA NETWORKS

6.1 Abstract

Global studies that measure the gap in protected area coverage compared to hotspots of marine biodiversity and cumulative human impacts, are necessary to assess the effectiveness that conservation actions are having on the protection of species biodiversity. In this study, I investigated the overlap of marine mammal biodiversity hotspots, as determined by complementarity, against hotspots of cumulative human impacts and current marine protected area coverage. I found that marine mammals are overall poorly protected, although they are exposed to a series of anthropogenic stressors across their most important habitats. My findings are similar to previous studies that also show that current MPA coverage is insufficient given the current rate of biodiversity loss. However, mine is the first study to determine gaps based on marine mammal biodiversity hotspot maps generated using complementarity, which has been previously shown to improve the accuracy of species area prioritization in the context of conservation planning.

6.2 Introduction

The world's biodiversity (diversity of species on the planet) has been rapidly declining in recent years due to human activities, which continue without abatement and are driving the sixth mass extinction at an unprecedented rate (Butchart et al. 2010,

Ceballos et al. 2015). In marine ecosystems, some of the most common human impacts include the pressure from overfishing from different types of fisheries, both artisanal and commercial, as well as the bycatch of species, animal mutilations, and habitat destruction that result from several types of fishing gear and techniques used (Davidson et al. 2011, Halpern et al. 2015a). Other pressures on marine areas include, but are not limited to, organic and inorganic pollution, vessel traffic (causes environmental noise and collisions with marine mammals), oilrigs (also produce underwater noise and pollution when there is an oil spill), and one of the most impactful pressures on marine life: climate change (Halpern et al. 2015a, 2015b, Avila et al. 2018). Halpern et al. (2008) assessed the various anthropogenic stressors that affect marine ecosystems and found that these stressors affect virtually all oceans, with 41% of the study areas strongly affected by several drivers. They reached this conclusion by developing a global map that indicates the level of threat each area is exposed to when accounting for the different combinations and intensities of anthropogenic stressors present (Halpern et al. 2008).

Preserving biodiversity is important because biodiversity directly impacts ecosystem structure and function (Duffy 2009). This is why in response to the biodiversity loss crisis, conservation scientists have continued to implement conservation actions (e.g., establishing protected areas or reserves) that help mitigate the impacts of human activities. Research shows that these actions are somewhat effective (Hoffmann et al. 2010, Butchard et al. 2012). In the ocean, marine protected areas (MPAs) have different levels of protection, as they can be any reserve, sanctuary, or refuge that helps protect, conserve, and manage marine wildlife (NOAA 2018b). However, contrary to terrestrial

protected areas, how effective MPAs are at protecting marine biodiversity is not well understood (Klein et al. 2015). MPAs can have each a different focus depending on what needs to be preserved. For example, marine mammal protected areas (MMPAs) focus specifically on the protection of areas that are of high importance to the welfare of marine mammals (see e.g., Hoyt 2011 and MMPATK n.d.). However, any protected area can benefit all species present and not only those that are the focus of the MPA.

The specific focus on marine mammal protection stems from their importance in marine ecosystems. Marine mammals are sentinel species of ocean and human health because they are indicators of how changes in their environment can impact their ecosystems and human wellbeing (Bossart 2006, 2011). Some marine mammals are also known as ecosystem engineers, because they fertilize oceans with fecal matter and their large size and movement patterns can drive nutrient cycles that ultimately impact the entire food network (Roman et al. 2014). Marine mammals are impacted by anthropogenic activities and are relatively more threatened than their terrestrial counterparts (Schipper et al. 2008). According to the International Union for the Conservation of Nature (IUCN), approximately one third of the 134 species of marine mammals are globally listed in one of the threatened categories, one third is listed as data deficient (meaning we do not have enough information to determine their risk of extinction), and the last third is listed as least concern, or not currently threatened at the global scale (IUCN 2018).

Because not all biodiversity can be protected by a reserve due to limitations in resources and logistics, focusing conservation efforts on hotspots of biodiversity (i.e.,

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areas with the highest biodiversity concentrations) maximizes effectiveness of conservation actions (Mittermeier et al. 2011). Several studies have thus focused on elucidating the distribution patterns and hotspots of marine mammal biodiversity and other marine taxa (e.g., Roberts et al. 2002, Sala and Knowlton 2006, Renema et al. 2008, Tittensor et al. 2010, Kaschner et al. 2011, Pompa et al. 2011, Ramírez et al. 2017). However, many of these studies have determined site importance for species based on the use of species richness, i.e., the number of species present at each study site. While this is a popular, straightforward metric to determine site importance for the purposes of conservation planning, other studies have shown that this approach is not effective because species richness usually fails to maximize species representation (Brooks et al. 2006, Rodrigues and Brooks 2007, Albuquerque and Beier 2015a, Veach et al. 2017).

An alternative and more effective approach for site prioritization can be achieved using complementarity (see methods). Complementarity outperforms species richness in site prioritization because it accounts for species that have restricted ranges, something that species richness often fails to do (see chapter 2 and also Williams et al. 1996, Moilanen et al. 2009, Albuquerque and Beier 2015b). For example, in a study by Albuquerque and Beier (2015b), the authors compared the use of species richness and complementarity in determining global hotspots of terrestrial vertebrate diversity and found that complementarity is more effective at representing hotspots of species biodiversity than species richness.

To date, no global gap analysis study has been performed to compare MPA coverage and hotspots of marine mammal biodiversity, as determined by complementarity.

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Therefore, the goals of this study are to: (1) map the complementarity-based hotspots of marine mammal biodiversity; (2) compare those hotspots to current MPA coverage to determine the extent and location of gaps; (3) compare the distribution of hotspots within groups of marine mammals to determine level of overlap; and (4) compare these factors against hotspots of cumulative human impacts (CHI) to determine the level of threat to which marine mammals are exposed in their most important areas. Given the increased effectiveness of complementarity at representing hotspots of species biodiversity and if my results show that its effectiveness applies to marine mammals, this study would represent a step further in fine-tuning methods for area prioritization in conservation planning of marine mammals these organisms.

This is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations.

6.3 Materials and Methods

6.3.1 Data. I obtained global marine mammal distribution maps from the IUCN Red List Spatial Database (IUCN n.d.) and determined presence/absence of species for each 1° cell (N = 47,283) using the R package *letsR* (Vilela and Villalobos 2015). I repeated this process for 123 of the 134 marine mammal species because I omitted those species that reside exclusively in freshwater habitats, as well as those species listed as extinct

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(EX), or not evaluated (NE; these species do not yet have distribution maps available). Generalized distribution maps by IUCN are generated by combining all the known distribution points that have been verified by experts, and then drawing a polygon connecting these known distribution points. Note that the resulting maps could over-represent species distributions if these species are not present in sections within the polygon (Red List 2018).

To increase the accuracy of my results, marine mammals were divided into groups that accounted for life history-based use of habitat, as well as their IUCN extinction risk listings. A total of 8 groups were analyzed, as follows: (1) ALL group, consisting of all marine mammal species combined (n=123); (2) FA group, consisting of fully aquatic species such as cetaceans and sirenians – these species spend all of their time in the water (n=87); (3) NFA group, consisting of pinnipeds and fissipeds – these species share their time between land and water (n=36); (4) MI group, consisting of species that are migratory (n=37); (5) NMI group, consisting of species that are not migratory (n=52); (6) Unknown group, consisting of species that have unknown migratory status (n=29); (7) NTR group, consisting of species that are not threatened – these species are listed as least concern (LC) by the IUCN (n=44); and (8) TR group, consisting of species that are either threatened (one of the following categories: critically endangered or CR, endangered or EN, vulnerable or VU, and near threatened or NT), as well as data deficient species (DD), as listed by the IUCN (n=79). For the purposes of this study, I include DD species in the group TR because we are unaware of their extinction risk levels. Given that marine mammals are exposed to an increased amount of threats compared to terrestrial mammals

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(Schipper et al. 2008), they could likely belong to one of the threatened categories. A previous study combined species with unknown risk levels with those that are endangered (Rey Benayas and De La Montaña 2003). Nomadic species were included in group ALL analyses, but were not analyzed as its own group because the small number of species (n=5) was not sufficient to guarantee reliable results.

   6.3.2 Identification of marine mammal biodiversity hotspots. To first determine complementarity-based global conservation priorities of marine mammal habitats, I used the core-area algorithm of the reserve-selection software Zonation (Moilanen et al. 2014). Zonation evaluates each site or area (in our case, each 1° cell) and compares it against a set of criteria (e.g., species presence and range) and subsequently against all other areas in the study to determine their level of importance and produce a hierarchy of areas that depict their conservation priorities. This approach allows for areas containing rare species to receive priority over other areas that have widespread species. Zonation being a complementarity approach, it also adds new sites to an existing hypothetical reserve in a way that guarantees that these sites contain those species that are not already represented. This results in maximizing species representation regardless of the number of species present in the new sites (Moilanen et al. 2014). For each above group, I calculated the 15% most important areas or hotspots of biodiversity (i.e., the top 15% of cells with the highest conservation priorities). I selected the top 15% because the current global oceans coverage by protected areas is of 5.1% (UNEP-WCMC and IUCN 2016), and the goal is to increase this coverage to at least 10% in the near future (Klein et al. 2015, Boonzaier and Pauly 2016). Also, I overlapped the complementarity-based hotspots of marine

mammal biodiversity (Hotspots), and gaps in coverage between biodiversity hotspots and marine protected areas (Gaps), among all groups used in this study.

6.3.3 Gap analyses. To investigate the extent to which current MPAs cover hotspots of marine mammal biodiversity, I overlapped the complementarity maps against a global map of current MPAs obtained from the World Database on Protected Areas, which contains the most comprehensive and up-to-date records of global marine and terrestrial protected areas (WDPA n.d.). To determine the level of threats marine mammals are exposed to in their hotspot areas, I also overlapped a map depicting the current cumulative human index (CHI), which I obtained from the Knowledge Network for Biocomplexity database (Halpern et al. 2015a). This map combines all known anthropogenic pressures on marine habitats worldwide, producing an index that portrays the level of threat for each area. Some anthropogenic activities represented in this map include different types of fisheries, bycatch, pollution, night lights, ocean acidification, oilrigs, fertilizer and pesticide runoff, vessel traffic, and sea surface temperature, among others (Halpern et al. 2015a). For CHI, I also selected the top 15% most threatened cells (CHI hotspots) that overlapped with biodiversity hotspot cells for each group of marine mammals in this study in order to elucidate the impact of threat levels on the different species.

6.4 Results

The global map for current MPA coverage shows that MPAs are highly biased towards coastal areas, whereas pelagic areas are overall poorly protected (figure 6.1). Maps depicting complementarity-based hotspots of marine mammal biodiversity show

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that hotspots are located mostly around continental areas with some areas of high importance in pelagic waters (e.g., Southern Ocean; figure 6.2). Complementarity-based hotspots of marine mammal biodiversity are highly concentrated along the North and eastern South Pacific Oceans, Southern Ocean, and some North Atlantic and Arctic Ocean areas (figure 6.2).

The map that shows gaps in coverage between biodiversity hotspots and MPAs (figure 6.3) has similar distributions to those of the hotspots (figure 6.2), indicating that most areas of high priority for marine mammal biodiversity are not currently covered by MPAs. Overlap of CHI and hotspots of marine mammal biodiversity ranged from 10.4% to 25.3% of the top 15% of cells/areas across groups, and overlap between the gaps in coverage and CHI ranged from 6.9% to 22.0% (table 6.1). When comparing overlap among marine mammal groups, hotspots overlapped between 18.2% and 77.6%, and gaps overlapped between 12.9% and 56.7% (table 6.2).

6.5 Discussion

Results for the complementarity-based maps of marine mammal hotspots and the gaps in MPA coverage show great similarity, which suggests that the current extent of MPA coverage is insufficient to protect hotspots of marine mammal biodiversity (figures 6.2, 6.3). In general, current MPA coverage of the world's oceans is of 5.1% (UNEP-WCMC and IUCN 2016), whereas the selected hotspots of marine mammal biodiversity represent the top 15%. While marine mammal species distributions might not cover all of the area of the world's oceans, they are still significantly widespread, and therefore the difference in magnitude between the hotspots area and MPA coverage is expected. This

lack of sufficient coverage is not exclusive to marine mammals, as other marine species

are also experiencing significant gaps in coverage. For example, a previous study that

performed a gap analysis of several marine taxa's generalized distributions and MPA

coverage (including marine mammals) found that 97.4% of species have their

distributions covered by an MPA by less than 10% (Klein et al. 2015).

Overlap between marine mammal hotspots and CHI ranged from 10.4% (group NFA)

to 25.3% (group Unknown; table 6.1). The groups with lowest overlap (NFA, ALL,

NTR) all contain an important number of non-fully aquatic species, which share their

time between land and sea (table 6.1). This means that this study only addressed CHI

overlap in part of their habitat, which would explain the lower overlap. On the other

hand, groups with the highest overlaps (Unknown, TR, FA) are groups that are composed

of all or mostly of fully-aquatic species (table 6.1). These species would therefore

experience an increased exposure to the CHI addressed in this study. Of the hotspots that

are not covered by MPAs (GAPs), overlap with CHI hotspots ranged from 6.9% (group

NFA) to 22.0% (group Unknown; table 6.1). These values also follow the same patterns

as the values for CHI exposure of marine mammal hotspots, indicating that increased

aquatic ranges positively correlate with increased exposure to marine CHI, as would be

expected (table 6.1, figures 6.2, 6.3). These findings suggest that overall, fully aquatic

species (cetaceans and sirenians) are more exposed to CHI than non-fully aquatic species

(pinnipeds and fissipeds), but it is important to note that this study only addressed CHI in

marine systems. Missing threats that are not accounted for in this study may affect the

terrestrial habitats of non-fully aquatic species. Further studies that account for CHI in

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terrestrial coastal areas are required to better define the level of threat to which these species are exposed.

Within-group analyses showed that hotspots of marine mammal biodiversity have overlaps that range from 18.2% (NFA and Unknown groups) to 77.6% (TR and FA groups; table 6.2). In the case of gaps in coverage between hotspots and MPAs, the range was from 12.9% (MI and Unknown groups) to 56.7% (TR and FA groups; table 6.2). In both cases, the lower overlaps represent two groups with different species each (i.e., species within both groups do not overlap), whereas the higher overlap represents groups that share some species. The range in overlap in both cases is indicative of the level of species overlap among groups and can be used by managers to assess and determine the best strategy to adopt when planning for marine mammal conservation actions.
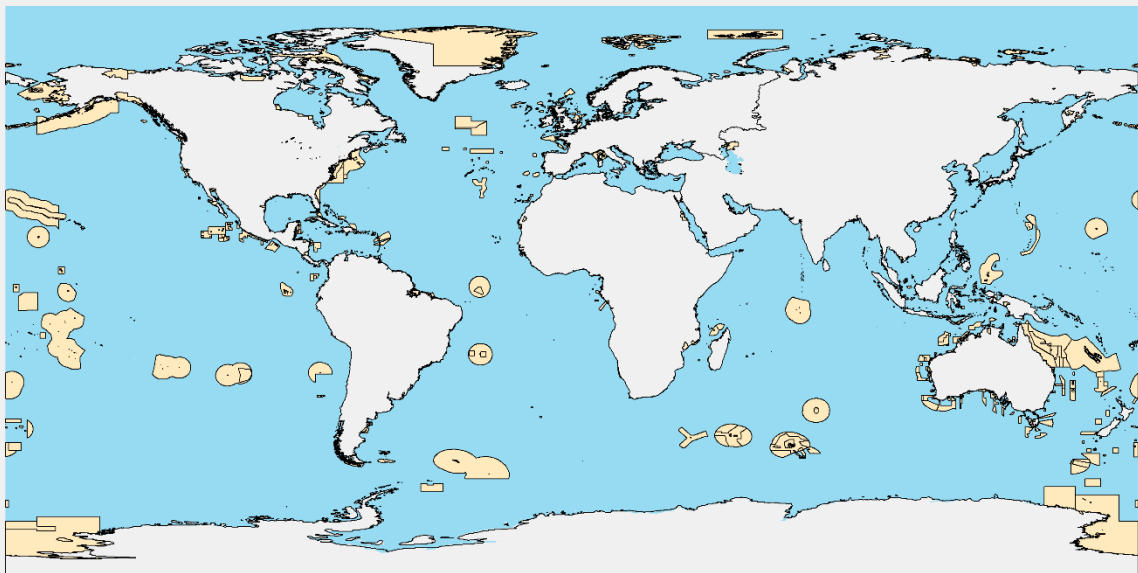
Figure 6.1. Map of global marine protected area networks (*Source: WDPA*).

Hotspots
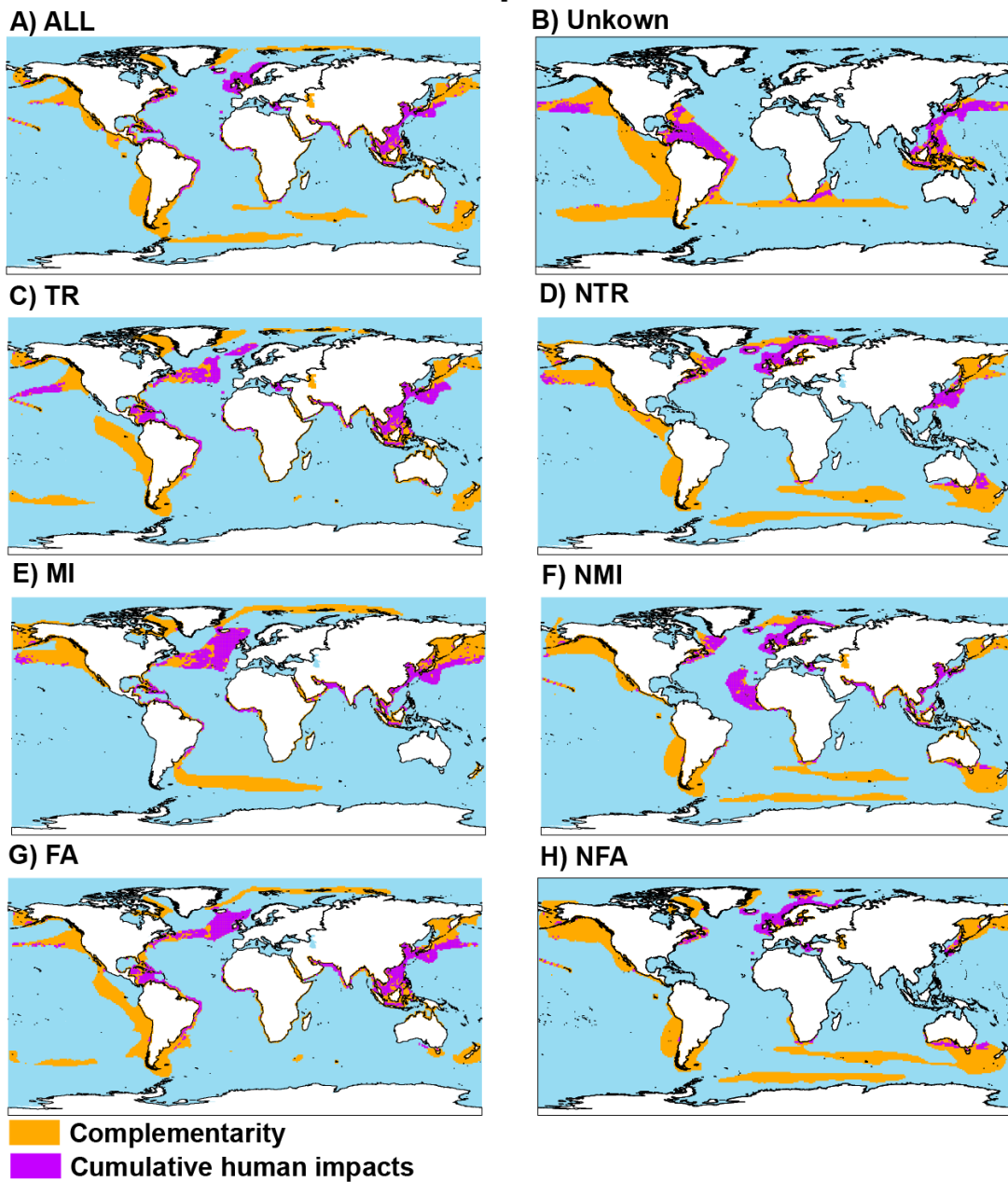
Figure 6.2. Maps depicting the global distribution of complementarity-based hotspots of marine mammal biodiversity (yellow) and areas with highest cumulative human impacts (magenta). Groups are: ALL = all marine mammal species; Unknown = species with unknown migratory status; TR = threatened and data deficient species; NTR = non-threatened species (least concern); MI = migratory species; NMI = non-migratory species; FA = fully-aquatic species (cetaceans and sirenians); and NFA = non-fully aquatic species (pinnipeds and fissipeds).

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GAPS

A) ALL

B) Unkown

C) TR

D) NTR

E) MI

F) NMI

G) FA

H) NFA

■ Complementarity
■ Cumulative human impacts
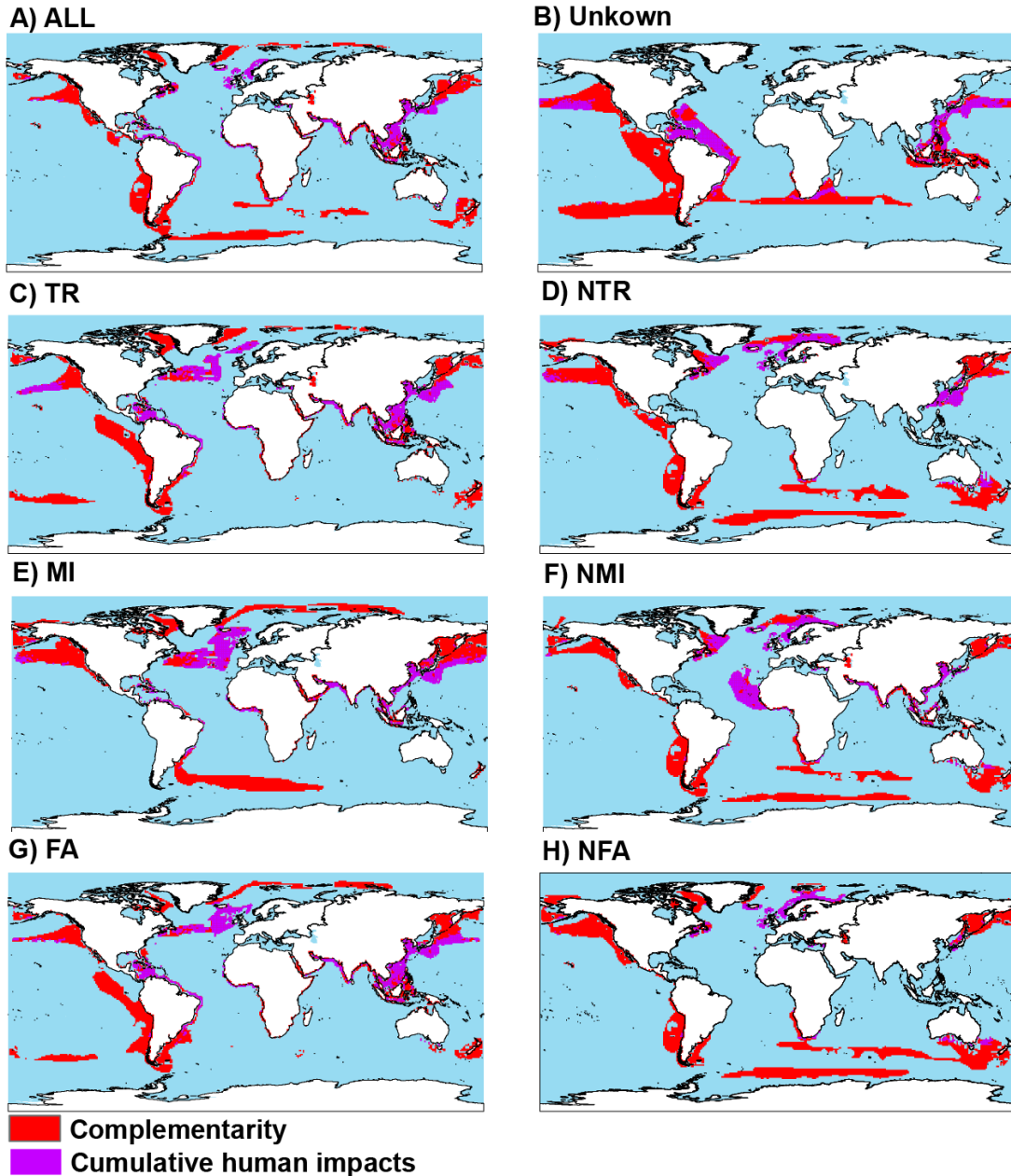
Figure 6.3. Maps depicting the global distribution of gaps in coverage between complementarity-based hotspots of marine mammal biodiversity and marine protected areas (red), and areas with highest cumulative human impacts (magenta). Groups are: ALL = all marine mammal species; Unknown = species with unknown migratory status; TR = threatened and data deficient species; NTR = non-threatened species (least concern); MI = migratory species; NMI = non-migratory species; FA = fully-aquatic species (cetaceans and sirenians); and NFA = non-fully aquatic species (pinnipeds and fissipeds).

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Complementarity-based hotspots of marine mammal biodiversity coincide with areas of high primary productivity in the world's oceans (NASA n.d.), which would help explain why these areas are of high importance to marine mammals. Hotspots of CHI overlap these areas to a certain extent (table 6.1, figures 6.2, 6.3), with other important areas located along the mid-Atlantic (figures 6.2, 6.3). In many cases, pockets of CHI hotspots are located along the coast of highly populated developing countries (e.g., Southeast Asia, Latin America, West Africa; figures 6.2, 6.3). The combination of low resources (e.g., to process waste or incorporate sustainable systems) in countries with high population density (e.g., high demand for marine resources) could also help explain the location of these CHI hotspots. Along these, the North Pacific Garbage Patch is another important CHI hotspot. This hotspot is not adjacent to land but it consists of a high concentration of human-originated debris that creates a vortex in the North Pacific due to the action of wind and ocean currents (Howell et al. 2012).

The distribution of current MPA coverage shows a distinct bias towards coastal areas, which are mostly within the exclusive economic zones (EEZ) of countries (figure 6.1). It is beneficial to have more MPAs in areas of greatest human activities (compare figure 6.1 with magenta coverage in figures 6.2 and 6.3), but current MPA coverage is still insufficient to represent marine biodiversity, as 99.8% of the least represented species (less than 2% representation) occur within EEZs (Klein et al. 2015). Additionally, MPAs also show a bias towards countries that are more affluent. It is often the case that tropical countries, which tend to have the most biodiversity, also have the most limited resources

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Table 6.1. Overlap of hotpots of cumulative human index (CHI) and complementarity-based hotspots of marine mammal biodiversity (Hotspots), and overlap of CHI and gaps in coverage between biodiversity hotspots and marine protected areas (GAPs). Groups are: ALL = all marine mammal species; Unknown = species with unknown migratory status; TR = threatened and data deficient species; NTR = non-threatened species (least concern); MI = migratory species; NMI = non-migratory species; FA = fully-aquatic species (cetaceans and sirenians); and NFA = non-fully aquatic species (pinnipeds and fissipeds).

	Mammal Groups							
CHI	**ALL**	**FA**	**NFA**	**MI**	**NMI**	**TR**	**NTR**	**Unknown**
Hotspots	1012(16.8%)	1459(24.2%)	625(10.4%)	1443(24.0%)	1295(21.5%)	1505(25.0%)	1098(18.2%)	1523(25.3%)
GAPs	753(12.5%)	1235(20.5%)	414(6.9%)	1256(20.8%)	1066(17.7%)	1302(21.6%)	890(14.2%)	1368(22.0%)

and poorest protection coverage due to poor species inventories (Albuquerque and Beier 2015c and references therein). For example, Southern Africa and Patagonia both have highly biodiverse marine ecosystems, yet protection coverage is poor to non-existent, whereas Australia is virtually surrounded by a network of MPAs (figure 6.1).

While the CHI hotspots map used in this study represents indices of threats produced by the combination of all the anthropogenic activities, spatial distribution of threats are different in different areas, and might thus affect species differently. For example, CHI surrounding coastal areas will most likely consist of fisheries-related threats, night lights, and pollution runoff from land, among others (Halpern et al. 2015a). These threats are more likely to affect mostly non-fully aquatic species and those fully aquatic species that inhabit coastal areas (see e.g., figures 6.2-6.3 D, F, H). On the other hand, pelagic species (in groups FA, MI, NMI, TR, Unknown; figures 6.2, 6.3) are more likely to be mostly affected by stressors such as shipping traffic noise and collisions, which have become a major problem for large cetaceans (see e.g., Houghton et al. 2015, Rockwood et al. 2017, Peel et al. 2018). Other anthropogenic stressors, such as plastic pollution, and climate change-related stressors (e.g., sea surface temperature, ocean acidification) currently affect all species due to their widespread distribution (Davidson et al. 2011, Ramírez et al. 2017). Lastly, I must emphasize that this study focused on the top 15% of threats in marine systems and therefore it does not mean that areas where CHI are not mapped are free of threats to marine mammals. CHI are still present in other areas that are important to marine mammals and other species, only to a lesser degree that might still negatively affect them significantly.

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Table 6.2. Overlap percentage matrices of complementarity-based hotspots of marine mammal biodiversity (Hotspots), and gaps in coverage between biodiversity hotspots and marine protected areas (Gaps), among all groups used in this study. Groups are: ALL = all marine mammal species; Unknown = species with unknown migratory status; TR = threatened and data deficient species; NTR = non-threatened species (least concern); MI = migratory species; NMI = non-migratory species; FA = fully-aquatic species (cetaceans and sirenians); and NFA = non-fully aquatic species (pinnipeds and fissipeds).

Groups	ALL	MI	NMI	TR	NTR	FA	NFA	Unknown
Hotspots								
ALL	1							
MI	45.5	1						
NMI	67.1	28.8	1					
TR	64.7	52.0	43.4	1				
NTR	54.8	29.8	66.3	28.5	1			
FA	64.1	57.6	41.5	77.6	35.6	1		
NFA	59.5	31.0	72.4	36.5	75.1	34.6	1	
Unknown	32.0	18.9	19.5	39.3	25.1	43.4	18.2	1
Gaps								
ALL	1							
MI	29.2	1						
NMI	43.5	19.4	1					
TR	41.2	35.8	27.5	1				
NTR	38.8	22.7	48.4	20.4	1			
FA	42.8	40.0	27.7	56.7	25.8	1		
NFA	39.3	22.1	49.8	23.3	55.0	23.5	1	
Unknown	22.6	12.9	13.9	30.1	19.8	33.3	13.6	1

The complementarity maps of marine mammal hotspots are based on generalized species distribution maps, and therefore do not account for seasonality of species presence (i.e., breeding vs. feeding areas for migratory species). Future studies will need to incorporate species-specific information based on life history needs to produce more accurate maps of important marine mammal areas per group of species. Nonetheless, this study already adds to previous findings that used species richness to determine importance of sites for marine mammals and showed the distributions of these mammals

to be more homogeneous (this makes it harder to define hotspots of marine mammal biodiversity; see e.g., Pompa et al. 2011). Additionally, species-specific needs would need to be addressed regardless of the approach used to determine hotspots of marine mammal biodiversity. To the best of my knowledge, this is the first global gap analysis study performed based on complementarity maps of marine mammal biodiversity hotspots in the context of MPA coverage and CHI exposure.

As stated in the introduction, this is one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations. There are few global marine mammal datasets that are available. The IUCN distribution maps are the most complete but they currently lack information on critical factors needed for spatial conservation assessments at this scale. Two of the most important factors are species specific density estimates and minimum home range data. Without this information it is difficult to fully evaluate how different areas would be at protecting the community of marine mammal species within.

Studies similar to this one have been done at the regional scale (e.g., Coll et al. 2012). However, marine mammals require a global strategy approach for their protection given their widespread distributions and the migratory lifestyle of some species (Rondinini et al. 2011, Lascelles et al. 2014). This need further justifies global studies such as this one

that identify global marine mammal hotspots, and the use of complementarity further

increases accuracy as to the location of those hotspots, as shown by Albuquerque and

Beier (2015b). It is also important to mention that the presence of MPAs do not

automatically guarantee the protection of species. MPAs that are not properly managed

can become paper parks (i.e., protected areas in paper only; Boonzaier and Pauly 2016).

Additionally, the boundaries of MPAs cannot protect them against the spread of pollution

and climate change effects. However, while they are not infallible, these areas provide a

certain level of protection for species, which is necessary given the current biodiversity

loss crisis. I therefore recommend the continued expansion of MPA implementation to

increase worldwide protection of marine mammals and other species.

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CHAPTER 7

CLOSING REMARKS

The research work in this dissertation was pursued to evaluate the use of alternative biotic and abiotic surrogates of biodiversity, using methods that had until now been successfully tested in terrestrial systems but not in marine systems at the global scale. I assessed how well these alternative surrogates performed when representing marine mammal biodiversity, as well as investigated the extent to which currently established conservation actions (i.e., current extent of marine protected area coverage) represent marine mammal species, and how threatened unprotected marine mammal habitats are. For this purpose, in chapters 2, 3, and 5 I evaluated the use of complementarity, rarity, and environmental diversity (respectively) as surrogates of marine mammal species in the context of conservation planning and solving the minimum-set coverage problem. In chapter 4, I presented the first global maps of marine mammal complementarity, and determined which environmental variables best correlate to those areas of high conservation priority. Finally, in chapter 6 I studied how well current marine protected area (MPA) coverage represents complementarity-based marine mammal hotspots, and estimated the level of anthropogenic threats unprotected marine mammal habitats are exposed to.

My findings demonstrate that complementarity and environmental diversity represent effective surrogates of marine mammal biodiversity, and that rarity can also be a good surrogate in certain cases, supporting my hypotheses. Additionally, these alternative surrogates consistently outcompeted species richness, which has been the most widely

used surrogate of biodiversity used to date. These findings are congruent with previous terrestrial vertebrate studies (see chapters) that also found these surrogates to be effective for biodiversity representation. I also found that bathymetry (depth), sea surface temperature, and water density, are the top variables best associated with patterns of global marine mammal complementarity. Furthermore, areas of high conservation priorities for marine mammals, as determined by complementarity, are concentrated along the coast in tropical and subtropical areas, as well as oceanic regions of the Southern Ocean, Arctic Ocean, and North Pacific Ocean, with some variations observed among the different marine mammal groups. Lastly, my research also shows that based on marine mammal complementarity hotspots, current MPA coverage is insufficient, and that unprotected are exposed to moderate levels of anthropogenic threat.

As stated in the introductory chapter and throughout this dissertation, this work represents one of the very first efforts in assessing how existing spatial biodiversity conservation tools might work at a global scale to protect marine mammal species. Because spatial usage patterns, life history strategies, and ecological characteristics differ enormously between different marine mammal species, many factors still need to be considered. These analyses are analytical exercises that represent one small piece toward those considerations. There are few global marine mammal datasets that are available. The IUCN distribution maps are the most complete but they currently lack information on critical factors needed for spatial conservation assessments at this scale. Two of the most important factors are species specific density estimates and minimum home range

data. Without this information it is difficult to fully evaluate how different areas would be at protecting the community of marine mammal species within.

The work here presented is therefore a proof of concept and as such, it is not ready for applied MPA implementation. Life history information for each marine mammal species, such as population density per site, important reproductive and feeding areas, and important migration routes must be incorporated to make this work more comprehensive and therefore applicable to actual conservation actions. Additionally, the logistical information required to implement an MPA must be included, such as for example the cost of implementation, feasibility, stakeholder input, and maintenance and enforcement protocols, to prevent established MPAs to turn into paper parks.

These findings nonetheless support the idea that alternative surrogates of biodiversity, which are found to be significantly more effective than species richness, can eventually be used as spatial prioritization methods in conservation planning to increase the effectiveness of conservation actions for marine mammals, and potentially other marine taxa. Results justify continued studies of these surrogates, where they can be combined with relevant planning information (as described above), and eventually incorporated in MPA implementation. Global studies such as those presented here are important because marine mammal distributions are widespread, and strategies for their conservation must therefore be addressed from a global perspective. My findings are particularly relevant in the context of climate change, and the impact that changes in environmental conditions and human activities can have on marine mammal species populations around the world. Given the current biodiversity loss crisis, conservation scientists must continue to work

on improving methods used in conservation action. The work here presented provides preliminary test results for methods that can potentially become important conservation action tools, and which will help us improve our efforts when mitigating the impact humans are having on biodiversity and habitats.

More specifically, the work here presented can be applied to some of the criteria used for the establishment of marine mammal protected areas. IUCN's Marine Mammal Protected Areas Task Force has defined a set of criteria for selecting locations that are considered Important Marine Mammal Areas (IMMA). For example, one or more of the approaches here described can be applied to criteria A (species or population vulnerability), B(ii) (distribution and abundance – aggregations), C(iii) (key life cycle activities – migration routes), and D (ii) (special attributes – diversity) (MMPATF n.d.).

Future directions for this work include testing cross-taxon surrogacy, to see how well each of the marine mammal groups represents the others. This would further help us understand which taxa have overlapping spatial characteristics that would facilitate conservation planning, as well as which species require different management approaches. Additionally, testing these approaches on other marine taxa besides marine mammals would also help us better understand marine ecosystem spatial dynamics and maximize spatial prioritization across expanded species communities. Besides incorporating species-specific needs (life history information), these approaches can also be further tested by assessing their performance through a downscaling approach (see Albuquerque and Beier 2016), as well as performing local case studies with distribution and abundance data at finer resolutions. Combined, these future directions would allow

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us to better understand which species would benefit the most by each of these approaches, so that species-driven conservation actions can be undertaken to guarantee efficient conservation outcomes.

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APPENDIX A

SUPPLEMENTAL MATERIALS FOR CHAPTER 2
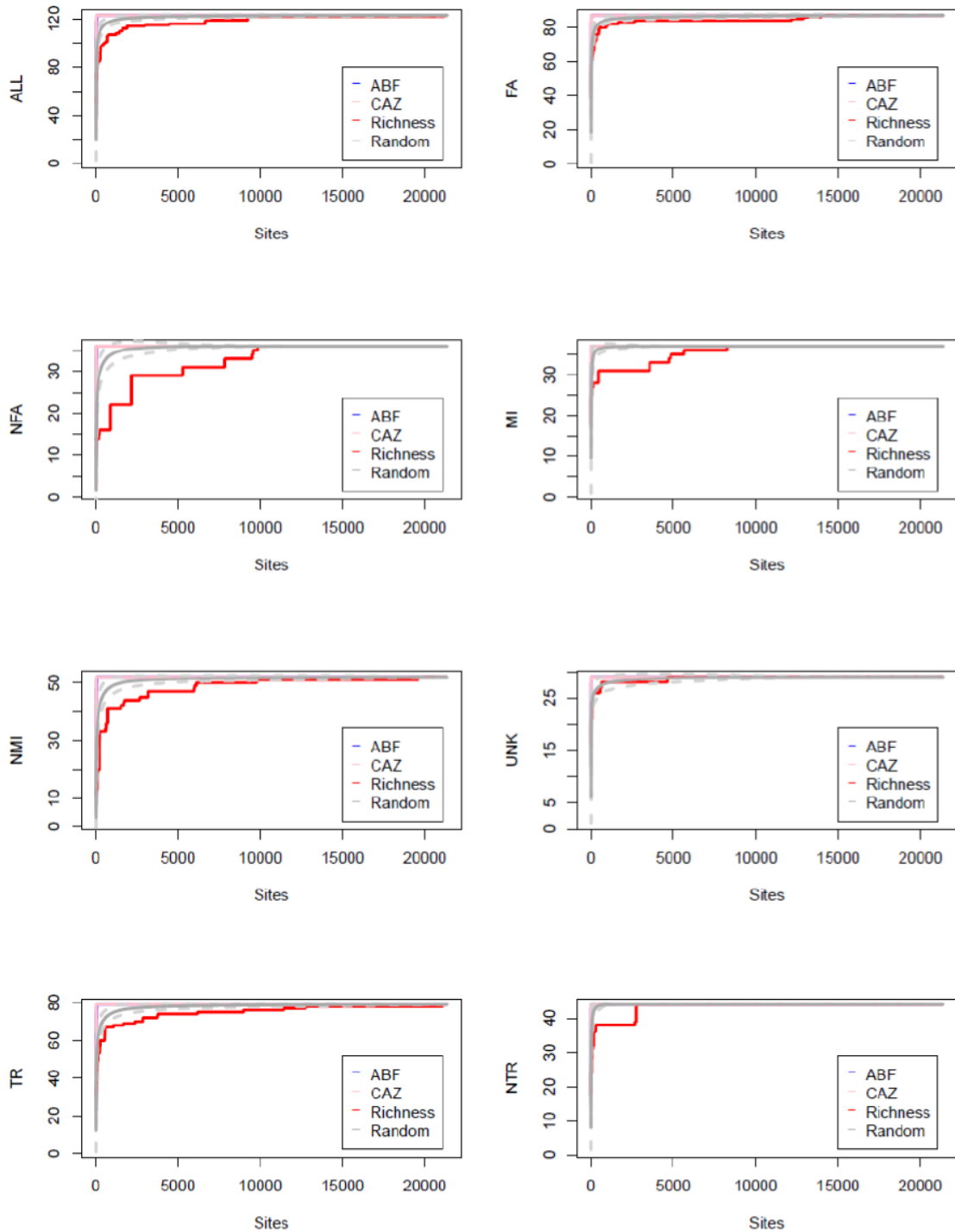
Figure 1A. Species accumulation curves for 1.5° cells for all marine mammal species (ALL), and groups: fully aquatic species (FA; cetaceans and sirenians), non-fully aquatic species (NFA; pinnipeds and fissipeds), migratory (MI) species, non-migratory (NMI) species, and species with unknown (UNK) migratory status. ABF = Additive Benefit Function, and CAZ = Core Area Zonation (both complementarity algorithms). Richness represents species richness and Random is the random solution with 95% C.I.
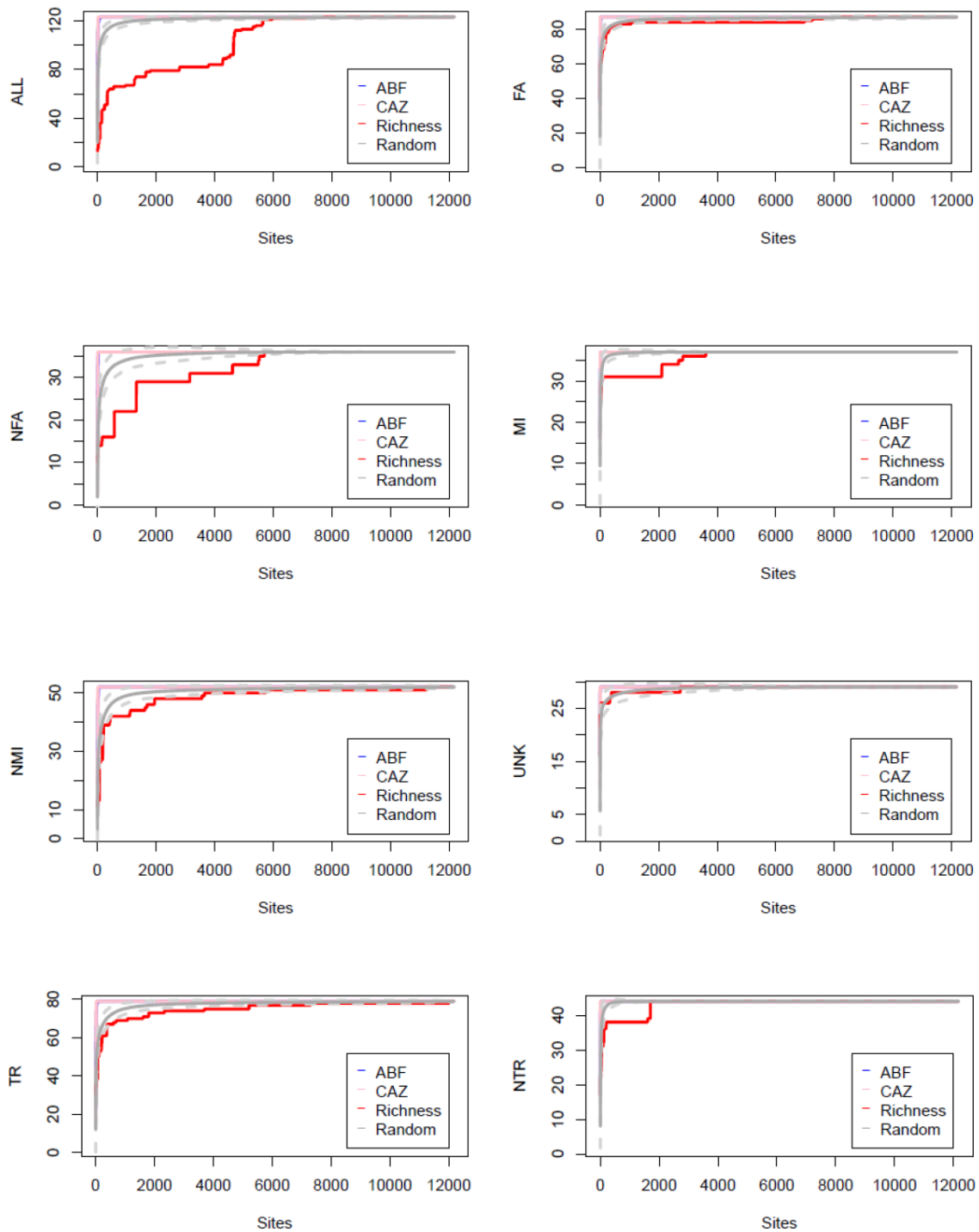
Figure 2A. Species accumulation curves for 2º cells for all marine mammal species (ALL), and groups: fully aquatic species (FA; cetaceans and sirenians), non-fully aquatic species (NFA; pinnipeds and fissipeds), migratory (MI) species, non-migratory (NMI) species, and species with unknown (UNK) migratory status. ABF = Additive Benefit Function, and CAZ = Core Area Zonation (both complementarity algorithms). Richness represents species richness and Random is the random solution with 95% C.I.
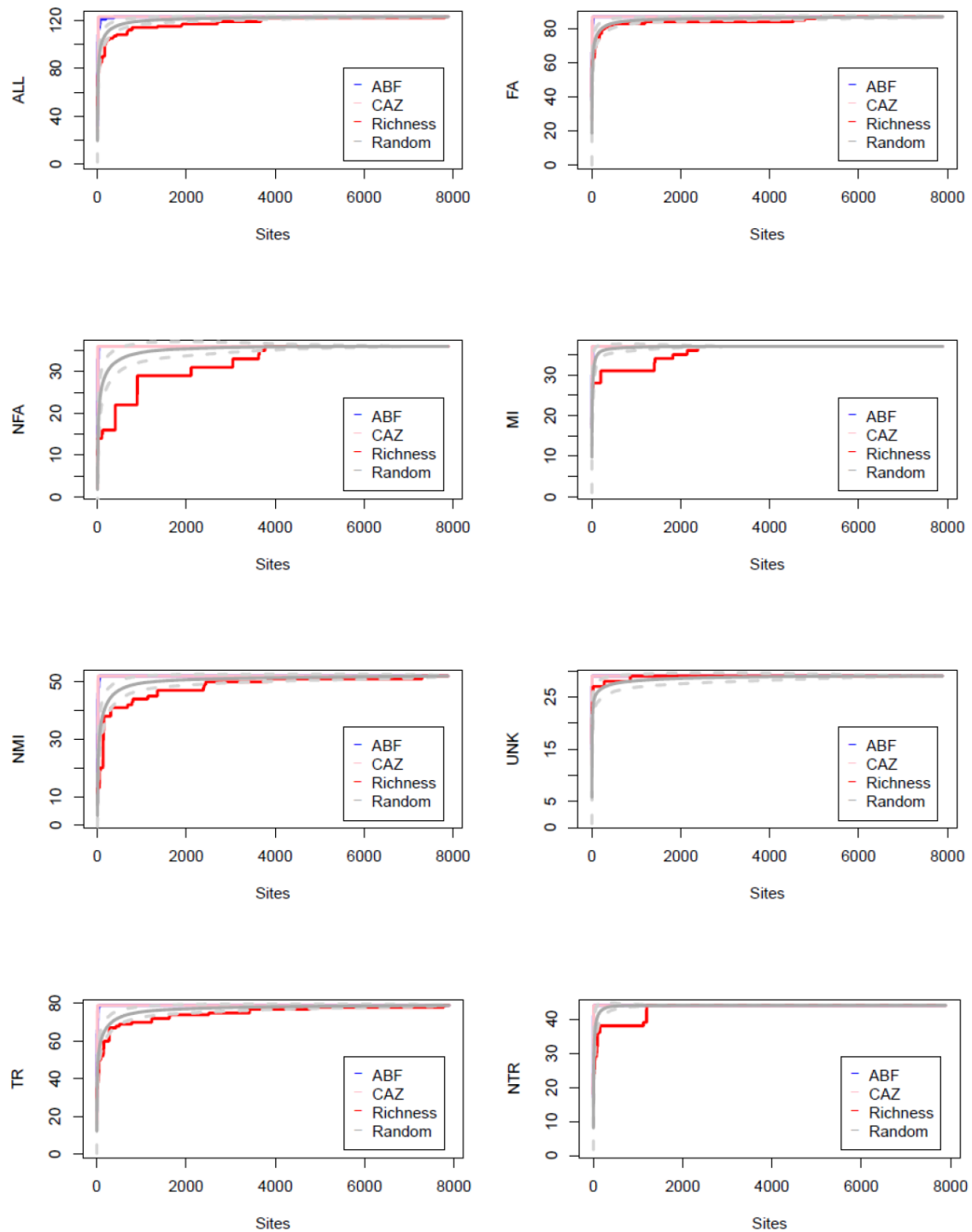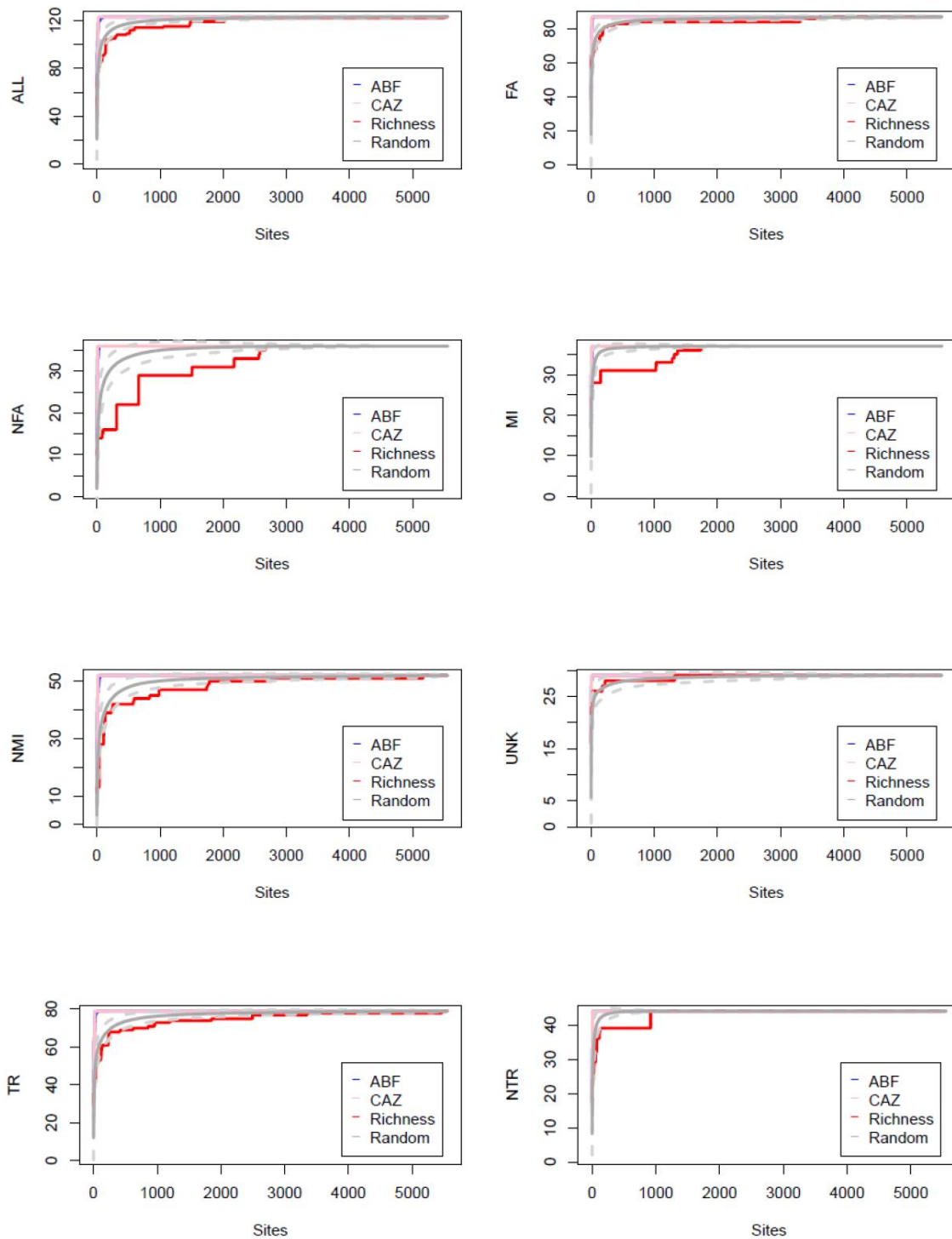
Figure 3A. Species accumulation curves for 2.5º cells for all marine mammal species (ALL), and groups: fully aquatic species (FA; cetaceans and sirenians), non-fully aquatic species (NFA; pinnipeds and fissipeds), migratory (MI) species, non-migratory (NMI) species, and species with unknown (UNK) migratory status. ABF = Additive Benefit Function, and CAZ = Core Area Zonation (both complementarity algorithms). Richness represents species richness and Random is the random solution with 95% C.I.

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Figure 4A. Species accumulation curves for 3° cells for all marine mammal species (ALL), and groups: fully aquatic species (FA; cetaceans and sirenians), non-fully aquatic species (NFA; pinnipeds and fissipeds), migratory (MI) species, non-migratory (NMI) species, and species with unknown (UNK) migratory status. ABF = Additive Benefit Function, and CAZ = Core Area Zonation (both complementarity algorithms). Richness represents species richness and Random is the random solution with 95% C.I.
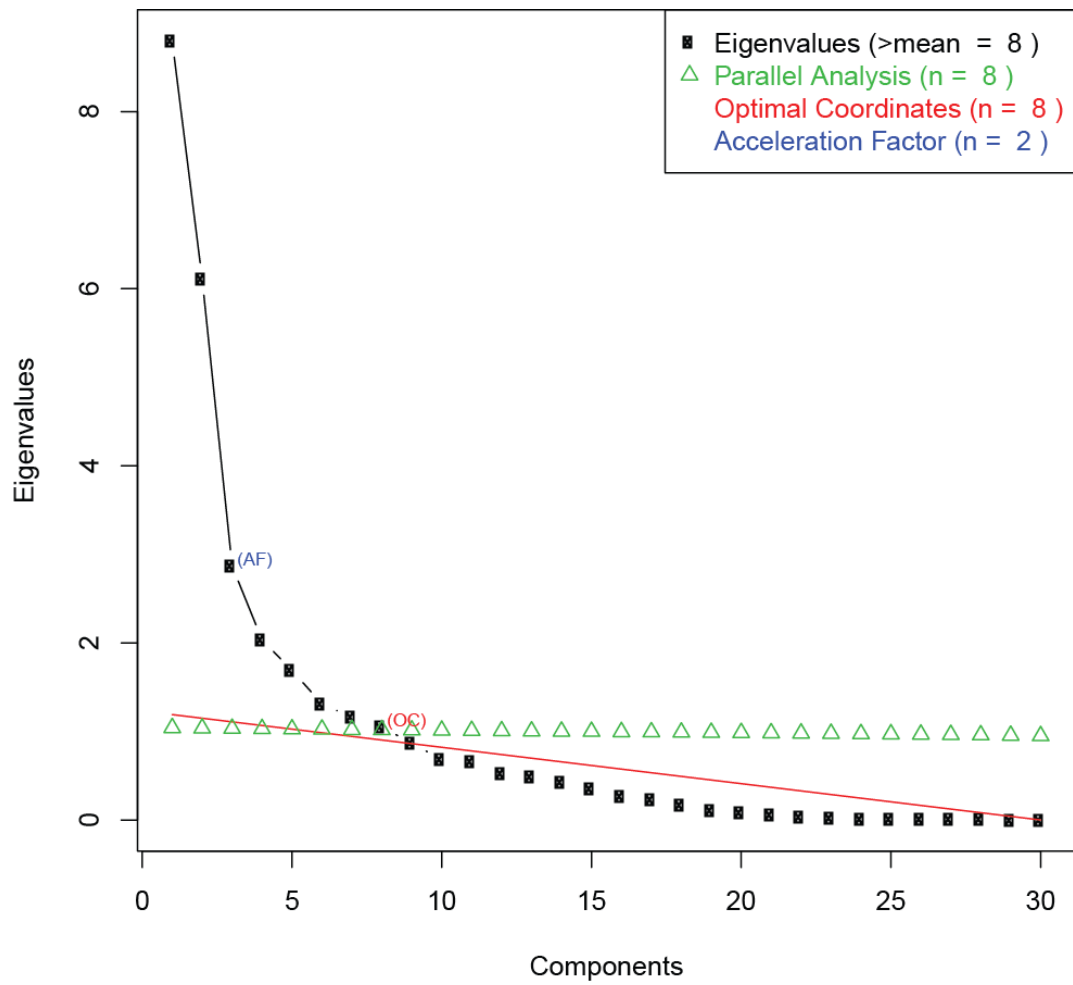
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APPENDIX B

SUPPLEMENTAL MATERIALS FOR CHAPTER 4

Figure 1B. Scree plot depicting the eigenvalues of the principal component analysis (PCA).

Table 1B. List of environmental variables used (excluding bathymetry variables) for the principal component analysis (PCA). Bold entries are the representative variables for each axis and corresponding loading values. Shaded boxes highlight values with high correlation.

Environmental Variables	Orthogonal axes							
	PCA2	PCA1	PCA4	PCA7	PCA5	PCA3	PCA8	PCA6
Conductivity (annual)	-0.07	0.54	0.03	0.76	0.13	0.01	0	-0.08
Conductivity (max)	-0.05	0.52	0.06	0.73	0.17	0.03	0	-0.08
Conductivity (min)	-0.01	0.05	-0.03	0.12	0.81	-0.04	-0.02	0.01
Density (annual)	0.15	**0.95**	0.21	0.14	0.05	0.01	0	0.01
Density (max)	0.16	0.9	0.27	0.21	0.08	0.02	0	0.01
Density (min)	0.01	0.09	0.2	0.11	**0.86**	0.22	0.05	-0.01
Dissolved oxygen (annual)	0.36	0.34	0.78	0.03	0.05	0.01	-0.01	0.05
Dissolved oxygen (max)	0.35	0.29	0.81	0.04	0.06	0.03	0	0.05
Dissolved oxygen (min)	0.03	0.02	0.1	0.02	0.14	0.93	0.17	0.01
Nitrate (annual)	**0.91**	0.06	0.06	-0.07	0	-0.01	0.03	-0.03
Nitrate (max)	0.88	0.05	0.1	-0.07	0.03	0.05	0.07	-0.04
Nitrate (min)	0.04	0.01	-0.02	0	0.03	0.03	0.62	-0.07
Phosphate (annual)	0.84	0.16	0.27	-0.14	-0.01	-0.03	0.02	0.04
Phosphate (max)	0.82	0.13	0.34	-0.12	0.04	0.04	0.04	0.03
Phosphate (min)	0.03	0.01	0.04	0	0.03	0.31	**0.76**	0.06
% oxygen saturation (annual)	0.2	0.22	0.85	0.28	0.1	0.03	0	0.03
% oxygen saturation (max)	0.19	0.18	**0.87**	0.26	0.1	0.05	0.01	0.03
% oxygen saturation (min)	0.02	0.01	0.08	0.03	0.12	**0.94**	0.14	0.01
Salinity (annual)	0.09	0.89	0.19	0.32	0.05	0	0	0.01
Salinity (max)	0.11	0.88	0.24	0.35	0.07	0.01	0	0.01
Salinity (min)	-0.02	0.08	0.2	0.3	0.79	0.16	0.05	0
Silicate (annual)	0.84	0.05	0.11	-0.1	-0.05	-0.01	-0.01	0.22

Silicate (max)	0.83	0.03	0.15	-0.09	-0.03	0.03	0	0.21
Silicate (min)	0.02	-0.02	0.05	0	-0.01	0.01	0.76	0.09
Temperature (annual)	-0.23	0.24	0.07	**0.9**	0.06	0	0	-0.01
Temperature (max)	-0.19	0.3	0.15	0.88	0.09	0.03	0	-0.01
Temperature (min)	-0.13	0.03	0.14	0.82	0.26	0	0	0.03
Apparent oxygen utilization (annual)	0.15	-0.03	-0.35	-0.02	-0.05	-0.03	0	**0.88**
Apparent oxygen utilization (max)	0.27	0.05	0.39	-0.07	0.08	0.11	0.11	0.71
Apparent oxygen utilization (min)	-0.1	-0.07	-0.71	0.06	-0.15	-0.2	-0.1	0.34
Cumulative variance	*0.17*	*0.31*	*0.45*	*0.58*	*0.66*	*0.72*	*0.78*	*0.83*

APPENDIX C

SUPPLEMENTAL MATERIALS FOR CHAPTER 5

Table 1C. Principal Component Analysis (PCA) of the database of 33 oceanographic variables. Higher loadings are highlighted in bold.

Oceanographic variables		PCA1	PCA2	PCA3	PCA4	PCA5	PCA7	PCA8	PCA8
					PCA Factors				
Conductivity	Annual	0.55	-0.07	0.01	0.03	0.13	0.76	0	-0.08
	Maximum	0.52	-0.04	0.03	0.06	0.17	0.73	0	-0.08
	Minimum	0.05	-0.01	-0.04	-0.03	0.81	0.12	-0.02	0.01
Density	**Annual**	**0.94**	0.15	0.01	0.21	0.05	0.14	0	0.01
	Maximum	0.9	0.16	0.02	0.27	0.08	0.21	0	0.01
	Minimum	0.09	0.01	0.22	0.2	**0.86**	0.11	0.05	-0.01
Dissolved oxygen	Annual	0.34	0.36	0.01	0.78	0.05	0.03	-0.01	0.05
	Maximum	0.29	0.35	0.03	0.81	0.06	0.04	0	0.05
	Minimum	0.02	0.03	0.93	0.1	0.14	0.02	0.17	0.01
Nitrate	**Annual**	0.06	**0.91**	-0.01	0.06	0	-0.07	0.03	-0.03
	Maximum	0.05	0.88	0.05	0.1	0.03	-0.07	0.07	-0.04
	Minimum	0.01	0.04	0.03	-0.02	0.03	0	0.62	-0.07
Phosphate	Annual	0.16	0.84	-0.03	0.27	-0.01	-0.14	0.02	0.04
	Maximum	0.13	0.82	0.04	0.34	0.04	-0.12	0.04	0.03
	Minimum	0.01	0.03	0.31	0.04	0.03	0	**0.76**	0.06
Percent oxygen saturation	Annual	0.22	0.2	0.03	0.85	0.1	0.28	0	0.03
	Maximum	0.18	0.19	0.05	**0.87**	0.1	0.27	0.01	0.03
	Minimum	0.01	0.02	**0.94**	0.08	0.12	0.03	0.14	0.01
Salinity	Annual	0.89	0.1	0	0.19	0.05	0.32	0	0.01
	Maximum	0.88	0.11	0.01	0.24	0.07	0.35	0	0.01
	Minimum	0.08	-0.02	0.16	0.2	0.79	0.3	0.05	0
Silicate	Annual	0.05	0.84	-0.01	0.11	-0.05	-0.1	-0.01	0.22

	Maximum	0.03	0.83	0.03	0.15	-0.03	-0.09	0	0.21
	Minimum	-0.02	0.02	0.01	0.05	-0.01	0	0.76	0.09
	Annual	0.24	-0.23	0	0.07	0.06	**0.9**	0	-0.01
Temperature	Maximum	0.3	-0.19	0.03	0.16	0.09	0.88	0	-0.01
	Minimum	0.03	-0.13	0	0.14	0.26	0.82	0	0.03
Apparent	**Annual**	-0.03	0.15	-0.03	-0.35	-0.05	-0.02	0	**0.88**
Oxygen	Maximum	0.05	0.27	0.11	0.39	0.08	-0.07	0.11	0.71
Utilization	Minimum	-0.07	-0.1	-0.2	-0.71	-0.15	0.06	-0.1	0.34
SS loadings		**4.35**	**4.99**	**1.99**	**4.13**	**2.25**	**1.54**	**4.01**	**1.63**
Proportion Var		**0.14**	**0.17**	**0.07**	**0.14**	**0.07**	**0.05**	**0.13**	**0.05**
Cumulative Var		**0.14**	**0.31**	**0.38**	**0.52**	**0.59**	**0.64**	**0.77**	**0.82**

APPENDIX D

STATEMENT OF CO-AUTHORS PERMISSION

I hereby declare that I have my co-authors' permission (Fábio Suzart de Albuquerque and Beth Polidoro) to use our work, for which I am the first listed co-author, and which is considered publishable as per ASU's guidelines, as chapters 2-4 of this dissertation.