Marine turtle regional management units 2.0

an updated framework for conservation and research of wide-ranging megafauna species

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Marine turtle regional management units 2.0: an updated framework for conservation and research of wide-ranging megafauna species

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ABSTRACT: Delineating spatial boundaries that accurately encompass complex, often cryptic, life histories of highly migratory marine megafauna can be a significant conservation challenge. For example, marine turtles range across vast ocean basins and coastal areas, thus complicating the evaluation of relative impacts of multiple overlapping threats and the creation of coherent conservation strategies. To address these challenges, spatially explicit 'regional management units' (RMUs) were developed in 2010 for all marine turtle species, globally. RMUs were intended to provide a consistent framework that organizes conspecific assemblages into units above the level of nesting rookeries and genetic stocks, but below the species level, within regional entities that may share demographic trajectories because they experience similar environmental conditions and other factors. From their initial conception, RMUs were intended to be periodically revised using new information about marine turtle distributions, life history, habitat use patterns, and population structure. Here, we describe the process used to update the 2010 RMU framework by incorporating newly published information and inputs from global marine turtle experts who are members of the IUCN Marine Turtle Specialist Group. A total of 48 RMUs for 6 of 7 marine turtle species and 166 distinct genetic stocks for all 7 species are presented herein. The updated RMU framework reflects a significant advance in knowledge of marine turtle biology and biogeography, and it provides improved clarity about the RMU concept and its potential applications. All RMU products have been made open access to support research and conservation initiatives worldwide.

KEY WORDS: Marine turtle · Conservation priorities · Population boundaries · Population delineation · Spatial distribution

1. INTRODUCTION

Widespread megafauna often travel large distances and experience variations in threats and environmental conditions across their geographic ranges, which can manifest in differential life histories and population dynamics. This makes it challenging, yet critical, to identify appropriate units for monitoring, conser-

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vation, and management. This is particularly true for widely distributed marine species with life cycles that span multiple ecosystems and which thus face different anthropogenic threats at different scales (Dulvy et al. 2014, Lascelles et al. 2014). Therefore, a fundamental step in designing effective conservation strategies is to accurately define boundaries for conspecific marine megafauna populations that may experience similar biological and demographic processes and thus could be appropriate population-level targets for management below the species level.

Marine turtles exemplify the challenges associated with monitoring, assessing, and managing migratory megafauna taxa across multiple scales. The world's 7 species (loggerhead *Caretta caretta*, green turtle *Chelonia mydas*, leatherback *Dermochelys coriacea*, hawksbill *Eretmochelys imbricata*, Kemp's ridley *Lepidochelys kempii*, olive ridley *L. olivacea*, flatback *Natator depressus*) are widely distributed across marine and coastal biomes, and they rely on habitats spanning geopolitical and ecological boundaries to fulfill their life history requirements (Wallace et al. 2010, 2011, Havice et al. 2018). Further, marine turtle population dynamics are complex, with multiple overlapping generations, expansive dispersal of hatchlings from natal sites (i.e. nesting beaches), migrations of juveniles to successive developmental habitats, long-distance migrations by adults between feeding and breeding areas, polygyny and polyandry, and multi-decadal lifespans (Bowen & Karl 2007). This combination of complex life histories and multiple threats operating at different scales and life stages warrants a cohesive approach to defining conspecific marine turtle assemblages at a broad scale to facilitate conservation and research prioritization.

Resolving marine turtle population structure below the species level requires defining population-appropriate conservation goals and interpreting results from different kinds of tools (see Wallace et al. 2010 for summary). The use of matrilineally inherited mitochondrial DNA (mtDNA) markers is particularly useful for defining genetically independent nesting stocks of adult females, often termed 'management units' (MUs) in the marine turtle research community (e.g. Moritz 1994, FitzSimmons et al. 1997a, Bowen & Karl 2007, FitzSimmons & Limpus 2014, Shamblin et al. 2014, Komoroske et al. 2017). When MUs in a region have been characterized, they can be used to assess the natal origins of turtles in shared marine habitats, providing essential information about the connectivity between nesting and marine habitats (Jensen et al. 2016, Shamblin et al. 2017). However, multiple MUs may be linked demographically by processes in shared marine habitats (e.g. foraging grounds, migratory pathways), or through male-mediated gene flow (FitzSimmons et al. 1997b, Bowen & Karl 2007, Shamblin et al. 2014), as well as threats. Therefore, to enhance conservation effectiveness, it is vital that specific management objectives reflect threats and other factors affecting the populations being studied (Taylor & Dizon 1999).

The concept of the marine turtle 'regional management unit', or RMU, was developed in 2010 to provide a globally consistent, biologically relevant framework for defining conspecific marine turtle assemblages below the level of species but above the level of individual MUs or breeding rookeries that share marine habitats (Wallace et al. 2010). These RMUs integrated biogeographical information from multiple scales and tools, including nesting sites, MUs, satellite telemetry, and geographic distributions based on monitoring research (i.e. mark-recapture). The initial effort to delineate RMUs highlighted the importance of having a flexible approach to characterizing marine turtle population complexity and to enable its use for all species and regions globally, despite significant variations in available data. RMUs also allow for the development of holistic conservation strategies to address threats to all life stages across geographic scales (Pakiding et al. 2020, Squires et al. 2021). Further, RMUs were an attempt to help the International Union for Conservation of Nature Marine Turtle Specialist Group (IUCN MTSG) move beyond debates about technical challenges in applying the IUCN's Red List criteria to disparate data (and data availability) on geographically widespread, long-lived marine turtles (Mrosovsky 2003, Godfrey & Godley 2008). Additionally, the RMU concept provides a consistent global framework to provide appropriate targets for conservation status assessments and actions in which IUCN MTSG members could be active participants (Seminoff & Shanker 2008, Wallace et al. 2010, Havice et al. 2018). As such, RMUs were intended to avoid biasing *a priori* the interpretations of RMU applications, thereby facilitating scale-appropriate assessments, priority setting, and actions. For example, RMUs were used to develop a global 'conservation priorities portfolio' that highlighted the wide variation in conservation status among marine turtle RMUs that warrant case-specific conservation and management approaches, rather than solely focusing on RMUs with the most threatened conservation status and limited conservation measures (Wallace et al. 2011). For priorities and strategies that emerge from RMU-based applications to be useful, they should also incorporate local cultural and governance systems so that the appropriate conservation or management action can be taken.

The original paper describing RMUs has been cited widely within and beyond the marine turtle literature, often in reference to the need to define population structure and evaluate conservation status at levels below species for widespread taxa (e.g. Lascelles et al. 2014, de la Torre et al. 2018). The RMUs have provided geographic structure with which to compare natural history features of populations across the global range of a species (Esteban et al. 2020) and have been used in numerous analyses of relative effects of widespread threats to marine turtles, such as fisheries bycatch (Wallace et al. 2013a, Clarke et al. 2014, Burgess et al. 2018), climate change (Fuentes et al. 2013), illegal exploitation (Senko & Burgher et al. 2022), marine debris (Schuyler et al. 2016, Senko et al. 2020), inorganic contaminants (Cortés-Gómez et al. 2017), and oil spills (Wallace et al. 2020). RMUs have also been used to structure analyses of spatial overlaps between marine turtle distributions and protections (Mazaris et al. 2014), conservation status (Mazaris et al. 2017, Valdivia et al. 2019), enforcement capacity (Barrios-Garrido et al. 2020), and priority setting (Wallace et al. 2011). Further, RMUs have been used as the basis for IUCN 'subpopulations' in Red List assessments for several of the 7 marine turtle species (e.g. Pilcher et al. 2012, Wallace et al. 2013b, Casale & Tucker 2017).

Given the widespread application of RMUs in marine turtle conservation research and planning, the IUCN MTSG determined that updates and improvements to RMU boundaries were needed to reflect new information that had become available in the ensuing years since 2010. In addition, concerns about confusion and inconsistency between RMUs and other MU concepts (e.g. FitzSimmons & Limpus 2014) provided further motivation for updating RMUs. To address this issue, organizers of the IUCN MTSG's 7th 'Burning Issues Initiative' (MTSG-BI7) facilitated an inclusive, multi-stage process to collate and share new information with IUCN MTSG members to update all RMUs across species globally. This paper describes in detail the process of defining 'RMUs 2.0,' and presents and discusses the updated RMUs and their potential applications.

2. METHODS

As in the first iteration, the process of defining RMUs began with a comprehensive analysis of peer-reviewed publications, reports, abstracts, and other resources that provided biological information on nesting sites, population genetics, tag returns, and satellite telemetry, as well as other relevant aspects of marine turtle natural history and biogeography published since 2009 (Supplement 1; all supplements available at www.int-res.com/articles/suppl/n052p209_supp/). For clarity, the factors used to delineate RMUs were purely biological; no spatial threats information was used to draw boundaries. Generally, we followed similar methods to those described in Wallace et al. (2010), except where noted below. However, in the update described herein, MTSG-BI7 organizers also facilitated a prolonged, inclusive review by the IUCN MTSG's global membership by using an online platform to display and edit spatial information (i.e. turtle movements, spatial habitat use, and distributions, as well as RMU boundaries), as well as other methods to allow participants to make suggested edits to RMUs (i.e. digitally drawing lines on image files). Significant efforts were made to ensure broad participation of global experts regardless of their access or abilities to use the online platform. Participants who contributed comments during the review period were invited to be co-authors on the present paper.

2.1. Definition of RMU concept

Despite the broad uptake of RMUs for various applications, several valid points have been raised since their initial development about whether the RMU concept and delineation process had been defined clearly enough to ensure globally consistent implementation, particularly when considering how RMUs compared to other conservation unit frameworks (e.g. MUs, or evolutionary significant units [ESUs]; see FitzSimmons & Limpus 2014 for review). Thus, before embarking on a time-intensive process of updating RMUs, we revisited the definition of the RMU concept to provide clear guidance for the update process.

RMUs are assemblages of marine turtles from the same species that share areas critical to life history requirements such as breeding, foraging, and juvenile development. These turtles are exposed to similar drivers of population dynamics (e.g. *environmental factors*) *across their overlapping geographic distributions, which places them on similar demographic and potentially evolutionary trajectories. These spatially explicit marine turtle RMUs, which include all life history stages, are similar to IUCN 'subpopulations'* (*IUCN 2019*) *because they are directly below the level of global species and can* *encompass finer-scale population structuring (e.g. unique genetic stocks/MUs).*

In practice, RMUs provide a globally applicable assessment framework that (1) can account for influences of environmental and anthropogenic factors on geographically widespread, complex marine turtle assemblages and (2) allows for conservation and management priorities to be designed for appropriate geographic scales.

We applied the above definition in deciding where to draw initial updated boundaries, which were then further adjusted based on comments received during the review process.

2.2. RMUs updated since 2010

Previously, the MTSG-BI working group recognized that IUCN Red List assessments of marine turtle subpopulations, which were to be based on RMUs, might provide opportunities to review and update RMUs, given the information available at the time of the assessments. Since the introduction of RMUs in 2010, Red List assessments have been performed on all subpopulations of leatherbacks (Wallace et al. 2013b) and loggerheads (Casale & Tucker 2017) and on some subpopulations of green turtles (e.g. Pilcher et al. 2012, Broderick & Patricio 2019). While the process of conducting detailed assessments for loggerheads and leatherbacks did not alter the original 2010 RMU boundaries for those species, RMUs changed significantly for green turtles through the redlisting process. These changes occurred because the US National Oceanic and Atmospheric Administration (NOAA) Fisheries and US Fish and Wildlife Service (USFWS) performed a global status review for green turtles to determine 'distinct population segments' (DPSs) and evaluate the status of each DPS under the US Endangered Species Act (Seminoff et al. 2015).

As noted when RMUs were first developed, DPSs and RMUs are conceptually similar and their determinations rely on similar types of information. An important difference, however, is that RMUs are spatially explicit, whereas geographic boundaries of DPSs are generalized, if at all defined. To determine DPSs for green turtles, the NOAA Fisheries-USFWS status review synthesized new information on turtle movements and connectivity (via satellite telemetry and tag returns) as well as genetic population structure, much of which became available after RMUs were originally developed. This NOAA Fisheries-USFWS status review resulted in designation of 11 (non-spatially explicit) DPSs (Seminoff et al. 2015). In response, the 17 original green turtle RMUs (Wallace et al. 2010) were initially reduced to 11 RMUs, and thus subpopulations for redlisting. Thus, for green turtles, we used these 11 updated DPSs/RMUs as the basis for the RMU update described herein.

2.3. Inclusive, virtual review process

The original plan to update RMUs included an in-person workshop of the MTSG-BI7 working group to efficiently generate and incorporate revisions, similar to the process used to develop RMUs initially (Wallace et al. 2010). However, when the COVID-19 pandemic rendered such in-person meetings impossible, we developed a fully virtual process to engage the global MTSG membership (~300 people, 112 countries). Briefly, this process consisted of the following steps, which are described below in greater detail: (1) information collation and organization; (2) a virtual, participatory expert review process via online platform; and (3) review periods and incorporation of suggested edits.

2.3.1. Information collation and organization

First, MTSG-BI7 organizers reviewed resources published since 2009, when the first RMUs were developed, based on a similar review of >1000 sources. This literature review focused first on peer-reviewed publications but also included grey literature (e.g. technical reports, symposium abstracts) presenting biological information as described below. Publications were categorized by species, region, life history stage, and type of information presented that would be relevant to informing the development of RMUs, focusing primarily on satellite telemetry and genetic analyses. Through this process, we compiled and reviewed nearly 500 additional references (279 tracking papers; 194 genetics papers), published between 2009 and August 2022.

In addition, MTSG-BI7 organizers generated an updated spatial layer of known genetic stocks for all marine turtle species globally. In the initial iteration, published genetic stocks were georeferenced and mapped within RMUs by species (Wallace et al. 2010). In this iteration, genetics experts among the MTSG-BI7 organizers collated published genetic stocks determined using various mitochondrial (mt) DNA markers. Genetic stocks were collated as defined in the most recent published literature, with a few exceptions. For example, data on olive ridleys in Indonesia were reanalyzed using a longer fragment of the mtDNA control region (~670 bp) than was presented in the original paper (Madduppa et al. 2021). Pairwise comparisons were performed using F_{ST} and exact tests, and identified a total of 7 genetic stocks for Indonesia. Altogether, the full, combined mtDNA dataset presents a globally consistent perspective of marine turtle genetic stock structure for each species. It is important to note that the stocks were purely defined by mtDNA data. For some species and populations nuclear DNA (nDNA) (e.g. microsatellites and/or single nucleotide polymorphisms) has provided additional resolution to stock structure (e.g. leatherbacks in the Atlantic, see Dutton et al. 2013). While fine-scale stock structure and its application is complicated and constantly evolving, these distinctions currently do not change the current RMU designations. These genetic stock layers were also made available to IUCN MTSG members to inform their review and recommendations about updated RMU boundaries.

2.3.2. Information review platforms

Compiling references from a literature review is a useful exercise, but we wanted to present this information in a way that would facilitate a robust, inclusive review of existing information. Because spatial distribution data are most important for delineating RMU boundaries, we focused on summarizing information from published maps and providing this information (e.g. Eckert & Eckert 2019) via a platform that would facilitate review and comments by the MTSG's global membership.

First, all papers collated during the previous step were reviewed, and papers that presented spatial data in published maps were prioritized (Supplement 2). Next, spatial data were georeferenced and digitized to generate generic polygons that broadly represented the static spatial patterns presented in the original maps. This resulted in digitization of 934 marine turtle biogeography maps (Table 1). For each feature class (i.e. shapefile) created, relevant information was provided in attribute tables, including georeferenced projection, relevant RMUs affected, and citations. MTSG-BI7 organizers generated draft, updated RMUs based on an initial review of the georeferenced maps, collated literature, public data repositories (e.g. Ocean Biodiversity Information System Spatial Ecological Analysis of Megavertebrate Populations [OBIS-SEAMAP]; Halpin et al. 2009), and grey literature maps published by the State of the World's Sea Turtles (SWOT, a program of the Oceanic Society), and included these in the expert review. IUCN MTSG members had access to the full list of papers (and the papers themselves) reviewed for both spatial and genetics information for review and updates of RMUs. These bibliographies are provided in Supplements 1 (spatial data and genetics) and 2 (papers used to generate maps).

Digitized spatial information, shapefiles of the existing 2010 RMUs as well as the draft, updated RMUs, and accompanying citations were then shared with the global MTSG membership via an ArcGIS Online (AGOL) platform through The George Washington University server (Fig. 1). This platform provided all available spatial information (and accompanying citation information; Supplement 2) by species and allowed users to make, save, and share suggested edits with the MTSG-BI7 organizers. Participating MTSG members were provided access to the AGOL system starting in September 2021, following introductory instructional webinars. We also provided video and written tutorials as well as webinars on how to use the AGOL system. For the remainder of 2021, the AGOL system operated largely under a trial basis to work out technical challenges

Table 1. Numbers of papers published since 2009 that were used to update global marine turtle regional management units. Some papers contained multiple maps that were georeferenced, resulting in more maps than papers. See Supplement 1 for full list of papers

	Loggerhead *Caretta caretta*	Kemp's ridley *Lepidochelys kempii*	Green *Chelonia mydas*	Flatback *Natator depressus*	Olive ridley *Lepidochelys olivacea*	Hawksbill *Eretmochelys imbricata*	Leatherback *Dermochelys coriacea*	Total across all species
Papers that contained relevant maps	80	11	77	12	19	54	34	287
Total number of digitized maps across all papers	284	50	266	29	37	210	58	934

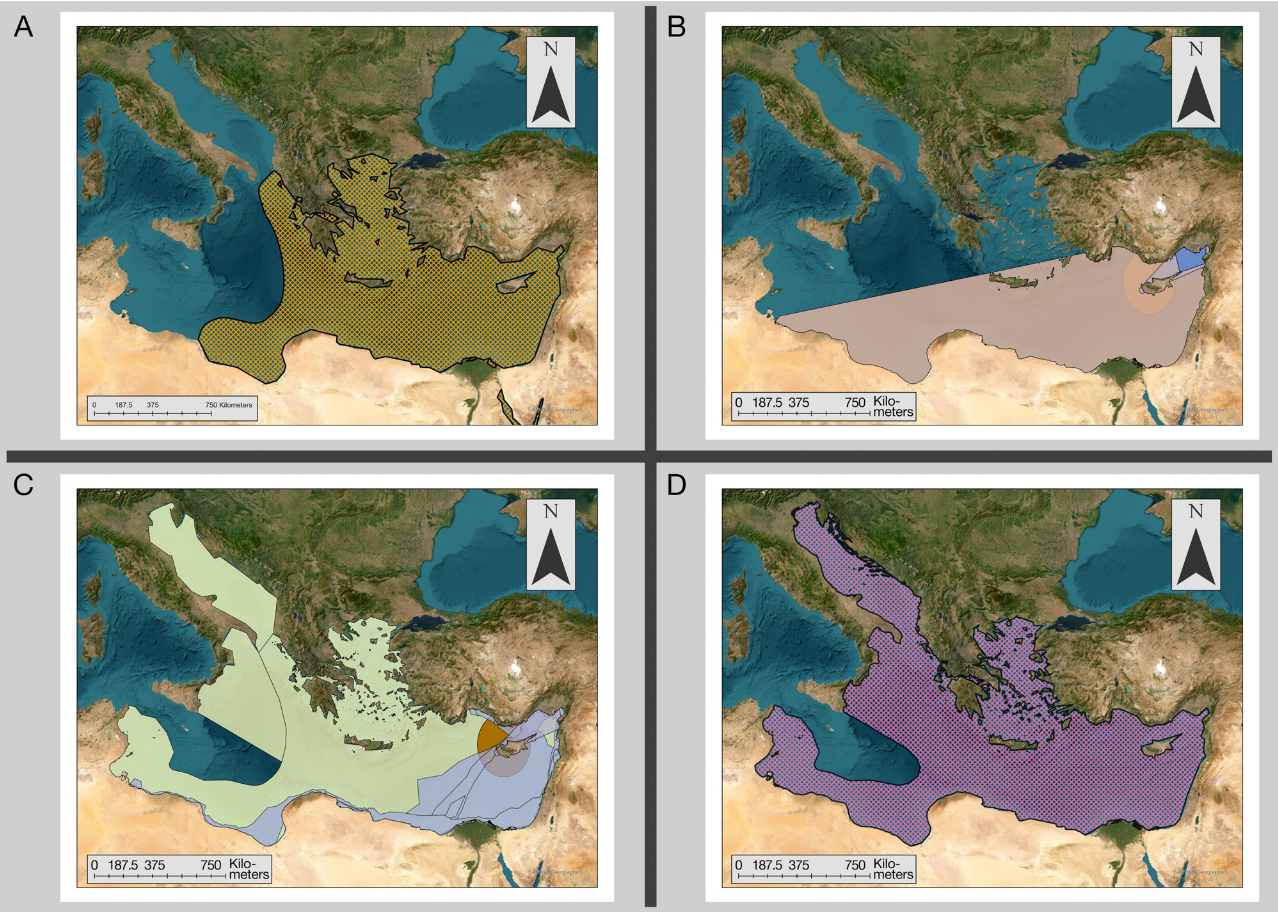

Fig. 1. An example of the process used to update marine turtle regional management units (RMUs) using an online mapping platform. (A) The starting point for the update of 1 RMU: the original Mediterranean green turtle RMU (Wallace et al. 2010). (B) Component files of green turtle data in the Mediterranean Sea were georeferenced from the literature review and provided to participants via an ArcGIS Online platform served by George Washington University. (C) Participants then reviewed original RMU and georeferenced component files, demarcated additional areas, and provided references for any data not included in our literature review. (D) The final product: an adjusted RMU, which was synthesized from contributions of multiple participants and data sources. See Section 2 for additional details. Polygons of different colors were different spatial layers identified and georeferenced in review by the BI-7 organizers or MTSG experts

and make it more user-friendly. For people who could not access the AGOL platform, we provided static map files (.png, .jpeg) of draft updated RMUs as well as the list of references reviewed. We invited review and recommendations via whatever means available (e.g. email, Microsoft Paint or PowerPoint, Mac Preview) to facilitate as much participation by as many experts as possible.

2.3.3. Multiple review periods, incorporation of edits

Two formal review periods, each approximately 1 mo in duration, occurred in March and August 2022, though comments were received throughout the year. We received comments from 49 experts — many of whom provided multiple comments — including simple confirmations of agreement with proposed boundaries, text descriptions of suggested edits via email, suggested edits to the static map image files, and edits to maps in AGOL. We also received additional publications or other resources that had not been included in our initial compilation that either supported draft RMU boundaries or justified changes to the RMU boundaries. We responded to each message to confirm receipt and then engaged participants in clarifications and discussions about proposed changes as needed. Proposed changes were collated, and if conflicting proposals were received either within or between review rounds, relevant experts were engaged, and a group decision was made on how to proceed.

The experts who provided comments were generally biologists whose technical expertise about specific data types, species, and regions aligned with the goal of interpreting biogeographical data to define RMU boundaries. Thus, each expert's input was weighted equally. In these ways, our methods were similar to key informant and expert elicitation approaches, though not formally structured as such. No survey instruments were used to update RMU boundaries. We acknowledge that, despite efforts to make the review as inclusive and accessible as possible — i.e. regular email reminders to the MTSG listserv inviting participation, multiple accepted methods for providing comments — the pool of experts who ultimately provided comments may not reflect the diverse technical, cultural, or geographical expertise among the full MTSG membership (~300 people, 112 countries). This could have resulted in disproportionate contributions of expertise from some regions, and underrepresentation from others.

When considering suggested changes, we aimed to consistently apply the above RMU definition in making decisions. We considered each suggested change separately and tried to apply consistency as appropriate across species. In general, we included areas within RMUs by relying on empirical evidence for turtles using that area to support their life history needs. In contrast, we did not include areas that included only scant or isolated observations (e.g. sightings or strandings of a few individuals), particularly if the natal origins of those individuals were unknown. In addition, we did not delineate RMUs based on dispersal modeling that infers trajectories of hatchling turtles away from nesting beaches into oceanic nursery habitats. While we appreciate that hatchlings may be widely dispersed by ocean currents and might be carried to areas outside the updated RMUs (e.g. Scott et al. 2014), no areas outside the RMUs have yet been identified as key development habitat for these young turtles. Likewise, RMU boundaries were not changed on the sole basis of a single satellite track, or a small number of rehabilitated or head-started turtles that might not exhibit representative movement behaviors. However, we did adjust RMU boundaries to include areas important for juvenile development if those areas were determined by empirical data (e.g. genetic analyses, satellite tracking, flipper tag returns) to be consistently used by individuals from an RMU. When needed, we discussed specific RMU boundaries with relevant IUCN MTSG members to ensure clarity of proposed and finalized boundaries. Because some records at range extremes (e.g. leatherbacks sighted off northern Norway) that were previously included in the global distribution of this species (Wallace et al. 2010) were likely vagrants rather than being within the normal species ranges, the updated RMUs better reflect the normal distributions based on empirical documentation of turtle presence. Along these lines, we also updated global distribution maps for all 7 species in order to capture all observations of where marine turtle species occur, not just those areas defined by RMU boundaries (Supplement 3). Maps and metadata describing the final accepted changes for each RMU compared to the original RMUs, as well as the sources used to support the changes and a brief text description, are available in Supplements 3 & 4, respectively.

We did not develop RMUs for flatback turtles *Natator depressus*, which nest only in Australia and have a relatively restricted geographic range (Limpus 2007). MUs defined by mtDNA and nDNA serve as the basis for marine turtle management in Australia, and 7 distinct MUs have already been identified for the flatback turtle and are the focus of management in Australia (Department of the Environment and Energy 2017, FitzSimmons et al. 2020). Although 2 flatback RMUs had been identified previously (Wallace et al. 2010), after consulting Australia MTSG members, it was decided to not define updated RMUs for flatback turtles to avoid potential confusion with the existing MU structure in official use (Department of the Environment and Energy 2017).

All edits were performed in ArcGIS Pro 2.9 (Esri).

3. RESULTS AND DISCUSSION

3.1. Updated RMUs and genetic stocks

We defined 48 RMUs among 6 species (excluding flatbacks) (Table 2, Fig. 2), ranging from a single RMU for Kemp's ridleys to 13 RMUs for hawksbills. Of the 58 original RMUs, only 9 remained unchanged, while the rest were altered in some way, either being combined with others or having adjustments made to boundaries (Supplements 3 & 4).

The total number of RMUs remained the same for 4 of the 6 species included in this update. Green turtle RMUs were reduced in number from 17 to 11 (Fig. 2C), as described in Section 2.2. The initial number of olive ridley RMUs was reduced from 8 to 6 in the present RMU update for the following reasons. Within some regions (i.e. East Pacific Ocean and North Indian Ocean), olive ridleys can display 2 types of nesting behaviors — synchronous mass

Table 2. Numbers of marine turtle regional management units (RMUs) and genetic stocks by species. Assumed: assumed RMUs; undefined: undefined genetic stocks; –: not defined

Species	RMU (assumed)	Defined genetic stocks (undefined)
Loggerhead *Caretta caretta*	10 (1)	26
Green turtle *Chelonia mydas*	11	73 (1)
Leatherback *Dermochelys coriacea*	7	9 (2)
Hawksbill *Eretmochelys imbricata*	13 (3)	32 (6)
Kemp's ridley *Lepidochelys kempii*	1	1
Olive ridley *Lepidochelys olivacea*	6	18 (5)
Flatback *Natator depressus*	–	7

nesting at particular beaches, termed 'arribadas', and dispersed, asynchronous or solitary nesting at the rest of the species' nesting beaches (Wallace et al. 2010). The initial RMU framework had assigned separate RMUs for each behavior in the regions where both behaviors exist. In this update (Fig. 2K), however, we defined a single, consolidated RMU that includes all olive ridleys in the same regions because they overlap completely in geography, some individuals nest in arribadas as well as solitarily, and environmental and anthropogenic factors affect all individuals in a region. This resulted in 6 olive ridley RMUs in the current update.

As in the initial RMU framework, we designated RMUs as 'putative' in regions where nesting sites and general presence were known for certain species, but no other biological information (e.g. genetics or distributions) was available (Wallace et al. 2010). These 'putative RMUs' — hereafter renamed 'assumed RMUs' for clarity — were intended to ensure that no region–species combination was excluded. As with all RMUs, these assumed RMUs will require modification as new information becomes available, but in the meantime, they represent obvious research and reporting priorities. In this update, assumed RMUs were identified for only 2 species: loggerheads (Fig. 2A) and hawksbills (Fig. 2G). The only assumed RMU for loggerheads was in the Northeast Indian Ocean (Fig. 2A); this was also an assumed RMU in the initial framework. Three hawksbill RMUs remained assumed, a decrease from 8 in the original framework, showing improved data availability for several hawksbill RMUs in the Pacific Ocean and Southwest Indian Ocean (e.g. Hays et al. 2022, van de Crommenacker et al. 2022, Madden Hof et al. 2023) (Fig. 2G).

We also identified at least 166 distinct genetic stocks among all species based on mtDNA, ranging from a single stock for Kemp's ridleys to 73 for green turtles (Table 2). Importantly, no MU is displayed in more than 1 RMU, but, as before, multiple MUs are identifiable within single RMU boundaries (Fig. 2). This illustrates both the fine-scale population structure determined by genetic markers as well as the extent to which the shared geographic distributions of these stocks will likely subject them to similar threats and environmental conditions. While knowledge on stock-specific distributions across life stages are critical to support MU-specific management per-

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Fig. 2. (A,C,E,G,I,K) Regional management units (RMUs) and (B,D,F,H,J) mtDNA genetic stocks for marine turtles. Species RMUs are displayed in different color series to easily discriminate between species. Diagonal lines represent areas of overlap between more than one RMU. Genetic stocks are presented using a repeating color palette to allow discrimination between adjacent stocks, as there were too many to label individually. Genetic stocks of different species are displayed as different shapes to facilitate discrimination between species. Assumed RMUs and genetically sampled sites unassigned to stocks are displayed in shades of grey. Detailed metadata for all RMUs and genetic stocks are provided in Supplement 4. (A) Loggerhead turtle *Caretta caretta* RMUs. 1: Northwest Atlantic, 2: Southwest Atlantic, 3: Northeast Atlantic, 4: Mediterranean, 5: Northwest Indian, 6: Southwest Indian, 7: Northeast Indian (assumed), 8: Southeast Indian, 9: North Pacific, 10: South Pacific. (B) Loggerhead turtle genetic stocks (● n = 26). (C) Green turtle *Chelonia mydas* RMUs. 11: North Atlantic, 12: South Atlantic, 13: Mediterranean, 14: Northwest Indian, 15: Southwest Indian, 16: East Indian and Southeast Asia, 17: Southwest Pacific, 18: North Central Pacific, 19: West Central Pacific, 20: South Central Pacific, 21: East Pacific. (D) Green turtle genetic stocks (■ n = 73, 1 unassigned). (E) Leatherback turtle *Dermochelys coriacea* RMUs. 22: Northwest Atlantic, 23: Southwest Atlantic, 24: Southeast Atlantic, 25: Southwest Indian, 26: Northeast Indian, 27: West Pacific, 28: East Pacific. (F) Leatherback turtle genetic stocks (▲ n = 9, 2 unassigned). (G) Hawksbill turtle *Eretmochelys imbricata* RMUs. 29: Northwest Atlantic, 30: Southwest Atlantic, 31: East Atlantic, 32: Northwest Indian (assumed), 33: Southwest Indian, 34: Northeast Indian (assumed), 35: Southeast Indian (assumed), 36: Southeast Asia, 37: Southwest Pacific, 38: North Central Pacific, 39: West Central Pacific, 40: South Central Pacific, 41: East Pacific. (H) Hawksbill turtle genetic stocks (⬟ n = 32, 6 unassigned). (I) Kemp's ridley turtle *Lepidochelys kempii* RMU. 42: Northwest Atlantic. (J) Kemp's ridley turtle genetic stocks (✚ n = 1). (K) Olive ridley turtle *Lepidochelys olivacea* RMUs. 43: West Atlantic, 44: East Atlantic, 45: West Indian, 46: Northeast Indian, 47: West Pacific, 48: East Pacific. (L) Olive ridley turtle genetic stocks (♦ n = 18, 5 unassigned). See Supplements for more details

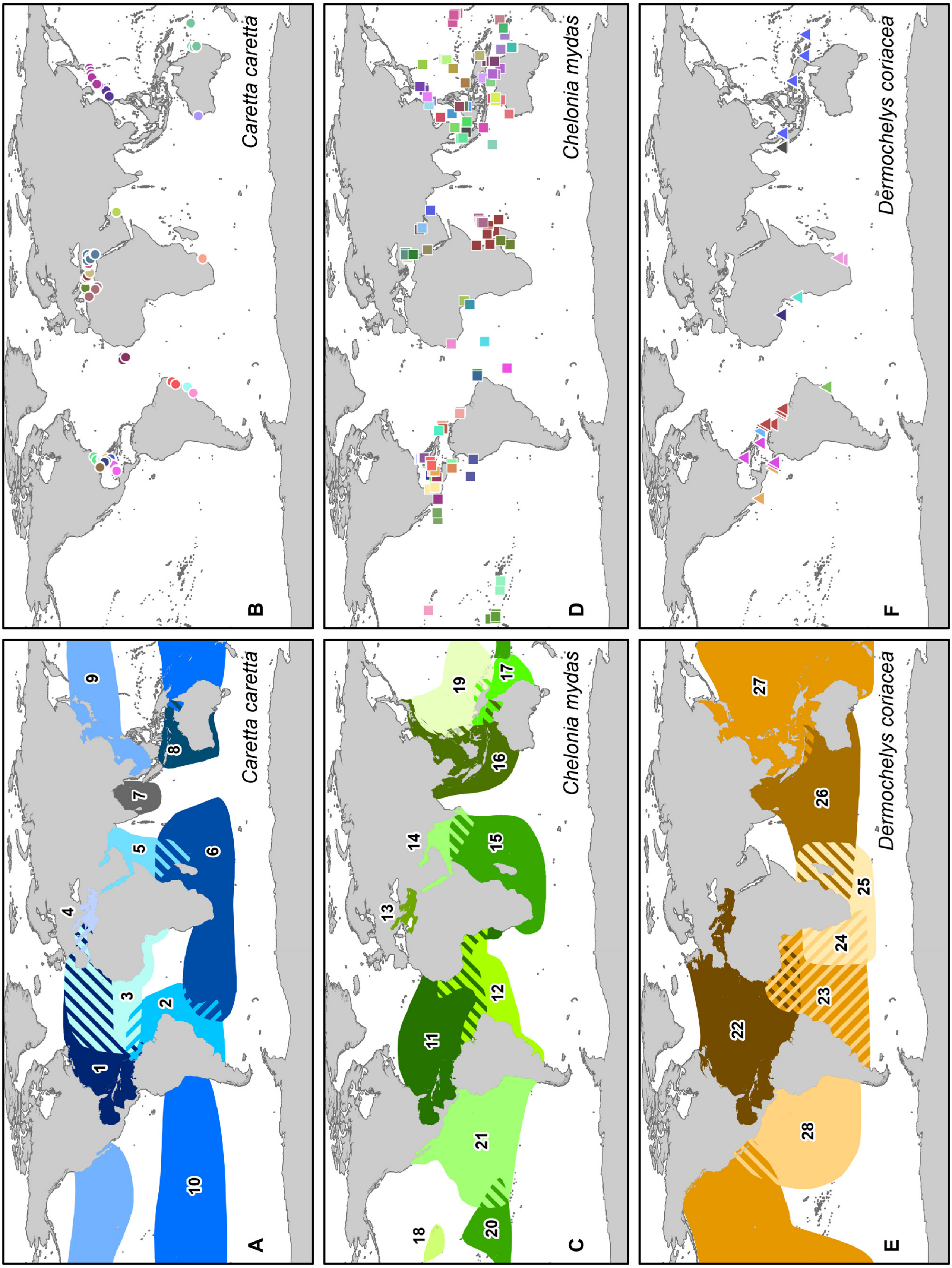

Fig. 2 (continued on next page)

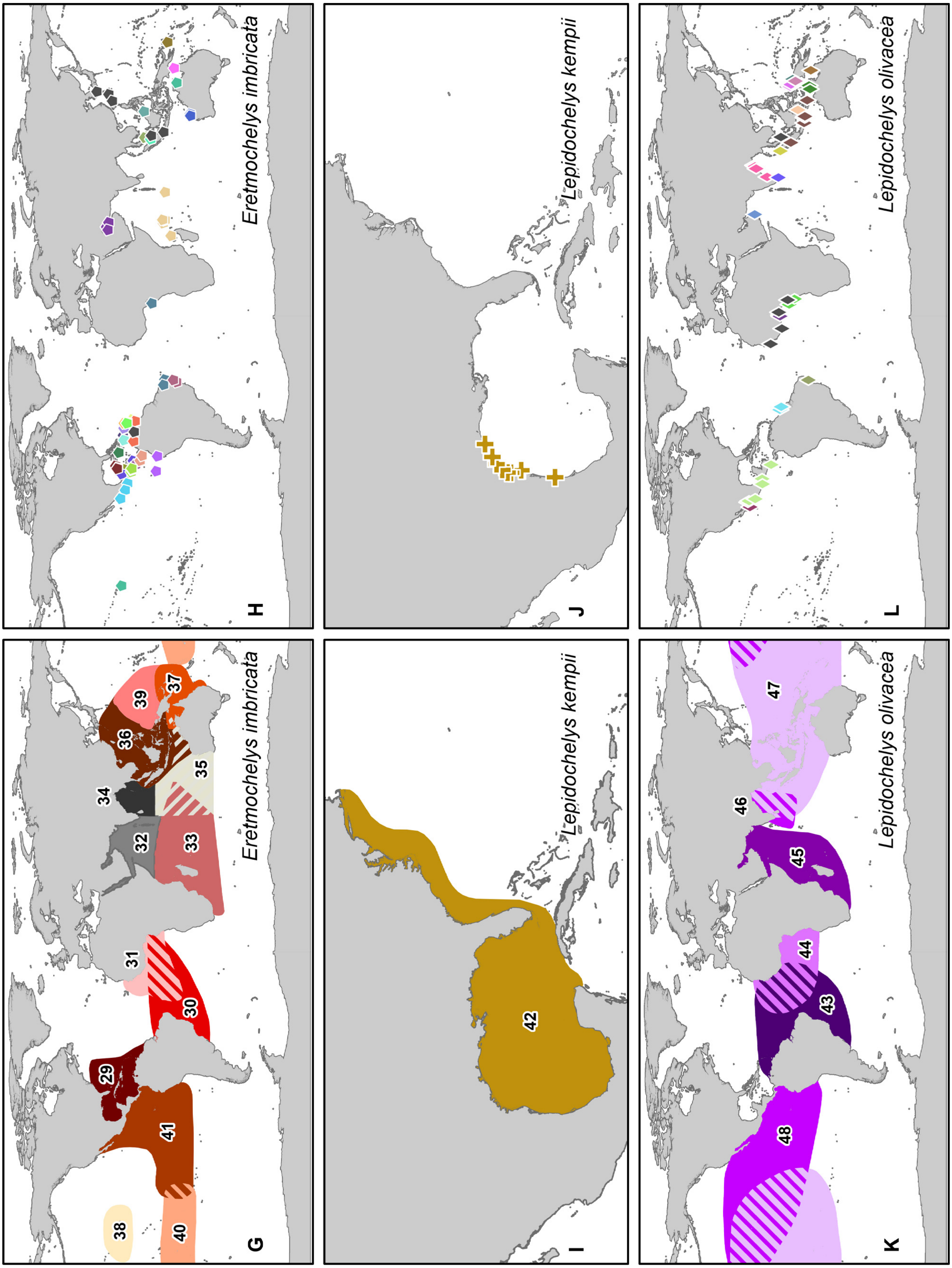

Fig. 2 (continued)

spectives, such as in the Recovery Plan for Marine Turtles in Australia, which is based on genetic stock designations (Department of the Environment and Energy 2017), it is not possible at present to classify all marine turtle populations among all species worldwide in this way because of persistent gaps in sampling and resources. Therefore, this RMU characterization of marine turtle assemblages — from nesting sites to genetic stocks to shared geographic distributions — offers flexibility to managers and researchers, whether the conservation objective is understanding fine-scale population structure or evaluating and addressing impacts of threats affecting multiple stocks (Taylor & Dizon 1999).

3.2. Applications and implications of the updated RMU framework

RMUs have provided a biology-based framework for evaluating threats impacts (e.g. Fuentes et al. 2013, Wallace et al. 2013a, Senko et al. 2020, Eckert & Hart 2021, Senko & Burgher et al. 2022) as well as conservation status and priorities for marine turtles (e.g. Wallace et al. 2011, Mazaris et al. 2014, 2017, Barrios-Garrido et al. 2020) below the species level and above the scale of individual nesting sites and genetic stocks (where appropriate). Further, RMUs were developed to address perennial challenges faced by the IUCN MTSG when performing Red List assessments by providing a basis for subpopulation-level assessments, which has been widely recognized as more appropriate from a biological and demographic perspective, as well as for targeting strategies to improve conservation status, than global scale assessments (Seminoff & Shanker 2008, Wallace et al. 2010). Whether RMUs — a purely technical tool — have helped IUCN MTSG solve significant differences of opinions among members about conservation status assessments, values, and priorities remains an open and important question (Havice et al. 2018). This is particularly true in cases where, according to Red List criteria, some marine turtle subpopulations are determined not to be in imminent risk of extinction (i.e. Red List category 'Least Concern'; e.g. Northwest Atlantic loggerheads, South Atlantic green turtles), triggering important debates within the IUCN MTSG about the implications of these results for support for marine turtle conservation among funders, managers, and the broader public. Nonetheless, the development of the RMU framework has improved marine turtle Red List assessments by focusing on more biologically appropriate and conservation-relevant units of assessment.

The updated RMU definition presented above clarifies that RMUs are spatially explicit marine turtle distributions that focus on where conspecific assemblages of turtles share areas to meet life history requirements and are thus exposed to environmental conditions and other factors, which may place them on similar demographic trajectories. Thus, RMUs are unique among — and complementary to — other frameworks specifically because they are spatially explicit and encompass multiple life stages of conspecific assemblages. For example, genetic analyses can indicate that population structure exists, but usually cannot resolve the boundaries of that structure, which is particularly important in marine areas where individuals from multiple genetic stocks are present and affected by the same drivers of population trends (e.g. sources of mortality, resource availability). Combining genetic analyses and other tools, such as mark-recapture and satellite telemetry, is essential for drawing population boundaries (Wallace et al. 2010, FitzSimmons & Limpus 2014, Madden Hof et al. 2023).

Another promising application of RMUs is delineation of Important Marine Turtle Areas (IMTA), which were defined by the IMTA Working Group of the MTSG-BI7 initiative as follows:

> '[IMTAs] are discrete areas within RMUs that are of particular biological significance for the persistence of marine turtles, and/or where the contributions of marine turtles to traditions and cultures of local people are particularly significant'

(IMTA Working Group 2021, p. 6). IMTAs should provide a robust, globally consistent framework to support conservation and management of areas important to marine turtles at multiple scales, in parallel to similar initiatives for seabirds (Important Bird Areas; BirdLife International 2010) and marine mammals (Important Marine Mammal Areas; IUCN Marine Mammal Protected Areas Task Force 2022), thus ensuring that biodiversity assessment and prioritization processes are comprehensive and comparable across multiple taxa of marine megafauna.

3.3. Conclusion

RMUs spatially integrate biogeographical information across life stages and are used to determine spatial overlaps between marine turtle distributions, threats, and environmental conditions. This integration permits evaluation of relative impacts and identification of conservation priorities for marine turtles within and among global regions. RMUs leverage publicly available biological information collected by various research tools, and — particularly in the present iteration — rely on inputs and recommendations from dozens of marine turtle experts worldwide. Depending on available data, future efforts might employ more sophisticated ecological modeling to define RMU boundaries and/or IMTAs within RMU boundaries. Further, we hope that the collaborative approach to synthesizing widely dispersed information described herein, as well as the resulting products, might be useful for other species specialist groups confronting similar challenges posed by widely distributed species with complex population structures that face multiple and varied threats and environmental conditions at various spatial scales. However, we recognize that RMUs are just one 'conservation unit' framework that might not be useful at all spatial scales; we encourage researchers, managers, and conservationists to identify and use the framework that best addresses their unique priorities. For situations where RMUs are deemed appropriate, we have provided open, public access to all products of this update via the SWOT online application on OBIS-SEAMAP (https://seamap.env.duke.edu/swot) — the RMU maps, spatial files, and accompanying metadata — which we hope will be used widely to support and stimulate research and conservation priority setting for marine turtles worldwide.

Data availability. The full suite of updated RMUs, and list of accompanying references used in the review and update process, are publicly available for download via the SWOT online application on OBIS-SEAMAP (https://seamap.env.duke.edu/swot), after completing a brief, online prospectus and agreeing to the data use terms of OBIS-SEAMAP and SWOT.

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