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RESEARCH ARTICLE

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Network analysis of sea turtle movements and connectivity: A tool for conservation prioritization

Connie Y. Kot[1] | Susanne Åkesson[2] | Joanna Alfaro-Shigueto[3,4,5] | Diego Fernando Amorocho Llanos[6] | Marina Antonopoulou[7] | George H. Balazs[8] | Warren R. Baverstock[9] | Janice M. Blumenthal[10] | Annette C. Broderick[11] | Ignacio Bruno[12] | Ali Fuat Canbolat[13,14] | Paolo Casale[15] | Daniel Cejudo[16] | Michael S. Coyne[17] | Corrie Curtice[1] | Sarah DeLand[1] | Andrew DiMatteo[18] | Kara Dodge[19] | Daniel C. Dunn[1,20] | Nicole Esteban[21] | Angela Formia[22] | Mariana M. P. B. Fuentes[23] | Ei Fujioka[1] | Julie Garnier[24] | Matthew H. Godfrey[25] | Brendan J. Godley[11,26] | Victoria González Carman[27,28] | Autumn-Lynn Harrison[29] | Catherine E. Hart[30,31] | Lucy A. Hawkes[11] | Graeme C. Hays[32] | Nicholas Hill[24] | Sandra Hochscheid[33] | Yakup Kaska[34,35] | Yaniv Levy[36,37] | César P. Ley-Quiñónez[38] | Gwen G. Lockhart[39,40] | Milagros López-Mendilaharsu[41] | Paolo Luschi[15] | Jeffrey C. Mangel[3,4] | Dimitris Margaritoulis[42] | Sara M. Maxwell[43] | Catherine M. McClellan[44] | Kristian Metcalfe[4] | Antonio Mingozzi[45] | Felix G. Moncada[46] | Wallace J. Nichols[47,48] | Denise M. Parker[8] | Samir H. Patel[49,50] | Nicolas J. Pilcher[51] | Sarah Poulin[1] | Andrew J. Read[44] | ALan F. Rees[11,42] | David P. Robinson[9] | Nathan J. Robinson[52] | Alejandra G. Sandoval-Lugo[38] | Gail Schofield[53] | Jeffrey A. Seminoff[54] | Erin E. Seney[55] | Robin T. E. Snape[11] | Doğan Sözbilen[34,35] | Jesús Tomás[56] | Nuria Varo-Cruz[16,57,58] | Bryan P. Wallace[59,60] | Natalie E. Wildermann[61] | Matthew J. Witt[11] | Alan A. Zavala-Norzagaray[38] | Patrick N. Halpin[1]

[1]Marine Geospatial Ecology Lab, Duke University Nicholas School of the Environment, Beaufort, North Carolina, USA

[2]Lund University, Lund, Sweden

[3]ProDelphinus, Lima, Peru

[4]University of Exeter, Penryn, UK

[5]Universidad Cientifica del Sur, Lima, Peru

[6]Research Center for Environmental Management and Development—CIMAD, Bogotá, Colombia

[7]Emirates Nature—World Wildlife Fund, Dubai, United Arab Emirates

[8]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Pacific Islands Fisheries Science Center, Honolulu, Hawaii, USA

[9]The Aquarium and Dubai Turtle Rehabilitation Project, Dubai, United Arab Emirates

[10]Cayman Islands Department of Environment, George Town, Cayman Islands

[11]Centre for Ecology and Conservation, University of Exeter, Penryn, UK

[12]Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina

[13]EKAD (Ecological Research Society), Ankara, Turkey
[14]Hacettepe University, Ankara, Turkey
[15]University of Pisa, Pisa, Italy
[16]Biology Department of the University of Las Palmas de Gran Canaria, Las Palmas, Gran Canaria, Spain
[17]seaturtle.org, Durham, North Carolina, USA
[18]CheloniData, LLC, Berthoud, Colorado, USA
[19]New England Aquarium, Boston, Massachusetts, USA
[20]University of Queensland, Brisbane, Queensland, Australia
[21]Swansea University, Swansea, UK
[22]Wildlife Conservation Society, Bronx, New York, USA
[23]Florida State University, Tallahassee, Florida, USA
[24]The Zoological Society of London, London, UK
[25]North Carolina Wildlife Resources Commission, Beaufort, North Carolina, USA
[26]Marine Turtle Research Group
[27]Instituto de Investigaciones Marinas y Costeras (CONICET - UNMdP), Mar del Plata, Argentina
[28]Instituto de Investigación y Desarrollo Pesquero, Buenos Aires, Argentina
[29]Smithsonian Institute, Washington, District of Columbia, USA
[30]Grupo Tortuguero de las Californias A.C., La Paz, Mexico
[31]Investigacion, Capacitacion y Soluciones Ambientales y Sociales A.C., Tepic, Mexico
[32]School of Life and Environmental Sciences, Deakin University, Warrnambool, Victoria, Australia
[33]Stazione Zoologica Anton Dohrn, Portici, Italy
[34]Dekamer—Sea Turtle Rescue Center, Muäÿla, Turkey
[35]Pamukkale University, Denizli, Turkey
[36]Israel Nature and Parks Authority, Mikhmoret, Israel
[37]University of Haifa, Haifa, Israel
[38]Instituto Politécnico Nacional, CIIDIR- SINALOA, Guasave, Mexico
[39]Naval Facilities Engineering Command, Norfolk, Virginia, USA
[40]Virginia Aquarium Marine Science Foundation, Virginia Beach, Virginia, USA
[41]Projeto TAMAR, Salvador, Brazil
[42]ARCHELON, The Sea Turtle Protection Society of Greece, Athens, Greece
[43]University of Washington, Seattle, Washington, USA
[44]Duke University Marine Laboratory, Beaufort, North Carolina, USA
[45]University of Calabria, Arcavacata di Rende, Italy
[46]Biologo Pesquero y Jefe Programa de Tortugas Marinas Centro de Investigaciones Pesqueras (CIP), Ciudad de La Habana, Cuba
[47]California Academy of Sciences, San Francisco, California, USA
[48]Center for the Blue Economy, Monterey, California, USA
[49]Drexel University, Philadelphia, Pennsylvania, USA
[50]Coonamessett Farm Foundation, East Falmouth, Massachusetts, USA
[51]Marine Research Foundation, Kota Kinabalu, Malaysia
[52]Fundación Oceanogràfic, Valencia, Spain
[53]Queen Mary University, London, UK
[54]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Science Center, La Jolla, California, USA
[55]Marine Turtle Research Group, University of Central Florida, Orlando, Florida, USA
[56]Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, Valencia, Spain
[57]Instituto Canario de Ciencias Marinas, Telde, Gran Canaria, Spain
[58]ADS Biodiversidad, Arinaga, Gran Canaria, Spain
[59]Ecolibrium, Boulder, Colorado, USA
[60]Duke University, Durham, North Carolina, USA
[61]Texas Sea Grant at Texas A&M University, College Station, Texas, USA

Correspondence
Connie Y. Kot, Duke University, 135 Duke Marine Lab Road, Beaufort, NC 28516, USA.
Email: connie.kot@duke.edu

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Abstract

Aim: Understanding the spatial ecology of animal movements is a critical element in conserving long-lived, highly mobile marine species. Analyzing networks developed from movements of six sea turtle species reveals marine connectivity and can help prioritize conservation efforts.

Location: Global.

Methods: We collated telemetry data from 1235 individuals and reviewed the literature to determine our dataset's representativeness. We used the telemetry data to develop spatial networks at different scales to examine areas, connections, and their geographic arrangement. We used graph theory metrics to compare networks across regions and species and to identify the role of important areas and connections.

Results: Relevant literature and citations for data used in this study had very little overlap. Network analysis showed that sampling effort influenced network structure, and the arrangement of areas and connections for most networks was complex. However, important areas and connections identified by graph theory metrics can be different than areas of high data density. For the global network, marine regions in the Mediterranean had high closeness, while links with high betweenness among marine regions in the South Atlantic were critical for maintaining connectivity. Comparisons among species-specific networks showed that functional connectivity was related to movement ecology, resulting in networks composed of different areas and links.

Main conclusions: Network analysis identified the structure and functional connectivity of the sea turtles in our sample at multiple scales. These network characteristics could help guide the coordination of management strategies for wide-ranging animals throughout their geographic extent. Most networks had complex structures that can contribute to greater robustness but may be more difficult to manage changes when compared to simpler forms. Area-based conservation measures would benefit sea turtle populations when directed toward areas with high closeness dominating network function. Promoting seascape connectivity of links with high betweenness would decrease network vulnerability.

KEYWORDS
betweenness, centrality, closeness, graph theory, marine turtle, migratory, satellite telemetry, tracking

1 | INTRODUCTION

Long-lived migratory species often traverse vast areas, making them vulnerable to multiple anthropogenic and environmental threats throughout their lives (Alerstam et al., 2003; Dingle & Drake, 2007; Heppell et al., 2005; Maxwell et al., 2013; Musick, 1999). Understanding the spatial ecology of animals, particularly how movements of migratory animals link different areas, is a critical element in conserving highly mobile species (Dunn et al., 2019; Webster et al., 2002). For example, unfavorable conditions on adult foraging grounds can alter the phenology of migration and body condition, which influence reproductive frequency and success (Marra et al., 2006). Ecological connectivity between areas can shape the genetic variation that manifests in migratory behavior and, in turn, can influence population resilience (e.g., the ability to respond quickly to change; Bernhardt & Leslie, 2013; Carr et al., 2017; Olds et al., 2015; Webster et al., 2002). Describing and quantifying the spatial ecology of animal movements contributes to understanding the overall network of habitats and the specific roles that areas and connections have during various life-stages. These areas and connections (network components) can control the dynamics of area use, resource flow, and other ecological patterns (Cohen et al., 2018; Dunn et al., 2019; Treml & Halpin, 2012).

Scientific research on connectivity can guide conservation within a network of habitats (Hays et al., 2019; Orellana, 2004; Pendoley et al., 2014). Data on marine species movements have typically been collected with capture–mark–recapture, tracking, genetic, and stable isotope analytical methods (Bradshaw et al., 2017; Ceriani et al., 2017; Godley et al., 2010; Nishizawa et al., 2018; Rees et al., 2017). However, these techniques are limited in identifying all suitable and unsuitable habitats and, with the exception of tracking data, will not describe the "corridors" (pathways used to connect high use areas). Tracking data can be used to reconstruct animal movements, though a common constraint occurs when small sample sizes are used to represent the corridor (Mazor et al., 2016). Additionally, information on the spatial connectivity can be difficult to apply to management measures at the appropriate scale, especially for highly migratory species utilizing areas across ocean basins (Balbar & Metaxas, 2019; Dunn et al., 2019; Shuter et al., 2011). Incorporating knowledge of connectivity in marine conservation is challenging due to (1) limited understanding of the scale and extent of connectivity necessary for population survival (Cowen et al. 2006; Foley et al., 2010; Sale et al. 2005), (2) a shortage of empirical data to conduct robust analyses (Mumby et al., 2011), and (3) non-standard ways to measure and define the ideal level of connectivity to maintain or conserve (Almany et al., 2009; Balbar & Metaxas, 2019; Keeley et al., 2021). Meanwhile, connectivity remains a core principle for improved management measures (Convention on Biological Diversity, 2010; Foley et al., 2010; Helsinki Commission, 2010), and efforts continue to increase to describe and integrate connectivity information into the design of marine protected networks (e.g., Andrello et al., 2015; Dunn et al., 2018; Friesen et al., 2019; Kininmonth et al., 2011; Magris et al., 2016; Smith & Metaxas, 2018).

Networks are graphs that can display spatial connectivity within a structure composed of nodes (vertices that can represent available habitat) and links (edges that can represent landscape connectivity; Kindlmann & Burel, 2008). Functional connectivity within spatial networks can be displayed by animal movements represented as links between nodes that are high-use areas (Jacoby et al., 2012; Jacoby & Freeman, 2016; Kindlmann & Burel, 2008; Olds et al., 2015). As a first step, examining the topology or pattern within the structure of the network can be a qualitative way to visualize the role of individual nodes and links based on their position and how changes would affect functional connectivity (Bisht & Singh, 2015; Santra & Acharjya, 2013). Evaluating differences in topology could provide quick comparisons on conservation and maintenance needs across multiple networks (Bisht & Singh, 2015; Santra & Acharjya, 2013).

Graph theoretical methods can also use mathematical applications to study modeled relationships between node pairs within a network (Bunn et al., 2000; Rayfield et al., 2011; Urban & Keitt, 2001). Network metrics are used to quantitatively compare centrality (dominance or influence of an area or connection) and connectivity (the movement of organisms within paths) between and among the network node and link positions (Schick & Lindley, 2007; Treml & Halpin, 2012; Urban & Keitt, 2001). Standardized network metrics applied in a variety of other disciplines (e.g., engineering, social science, and chemistry) have been leveraged in ecology to determine flow of resources and identify sources, sinks, and isolated areas (Rayfield et al., 2011; Urban et al., 2009). These methods can also facilitate a better understanding of ecological connectivity on a global and local scale, such as evaluating the amount of resources transferred among key habitats of highly migratory species in marine environments (Jacoby & Freeman, 2016). Graph theory has a large potential to help prioritize conservation measures within or across key areas at different spatial and temporal scales.

Spatially explicit networks can distil complex movement patterns into "connections" that are more easily communicated to policymakers, helping bridge the knowledge gap in ecological connectivity for the implementation of appropriate conservation measures. The number of satellite tracking studies is increasing for marine species (Hussey et al., 2015), along with the ability to synthesize data across large spatial extents (Block et al., 2011; Davidson et al., 2020; Ropert-Coudert et al., 2020; Sequeira et al., 2019), but graph theory applications have not yet been common practice for examining movements (Jacoby et al., 2012; Jacoby & Freeman, 2016). Here, we applied graph theory to spatial networks constructed from the movements of 1235 individual sea turtles from six species to highlight marine connectivity in support of conservation prioritization. Using this large dataset, we described and compared the structure and function among several networks. Last, we proposed recommendations on (1) how graph theory concepts can facilitate analyses on emerging connectivity patterns in networks created by highly migratory species, (2) applications for the prioritizing conservation efforts within and across regions and species, and (3) collaborative methods for gathering existing data to support the synthesis of knowledge on connectivity in the ocean.

2 | METHODS

2.1 | Sea turtle movement and connectivity data

We conducted a formal literature review on sea turtle movements and connectivity and summarized the common methods presented in publications (see Appendix S1). Relevant references from the literature review were used to determine how representative the telemetry dataset was that was collated for this study compared to the published studies. From March 2018 to April 2019, telemetry tracking data on sea turtle movements were requested from data providers for the State of the World's Sea Turtles (SWOT), the seaturtle.org tracking listserv, and the CTURTLE listserv. Most of the data collated for this study originated from online data archives (e.g., Coyne & Godley, 2005; Halpin et al., 2006; Kot et al., 2018). No telemetry data on flatback sea turtle (*Natator depressus*) were directly contributed.

A total of 1235 individuals, from six sea turtle species, included in this study were tracked with Advanced Research and Global Observation Satellite (ARGOS) tags receiving ARGOS doppler or global positioning satellite (GPS) locations (Table 1; see Appendix S2). For all ARGOS doppler and global GPS data, points on land (using Global Administrative Areas, 2018), erroneous or low-accuracy locations, and animals with only one location recorded were removed.

TABLE 1 Tracking data summarized by species, sex, age class, number of locations, and temporal coverage. Species: *Cc* = Caretta *caretta*, *Cm* = Chelonia *mydas*, *Dc* = *Dermochelys coriacea*, *Ei* = Eretmochelys *imbricata*, *Lk* = Lepidochelys *kempii*, *Lo* = Lepidochelys *olivacea*. Number of animals per basin: Atl = Atlantic Ocean, Ind = Indian Ocean, Med = Mediterranean Sea, Pac = Pacific Ocean; sex: F = female, M = male, U = unknown; age class: A = adult, S = sub-adult, J = juvenile, U = unknown. Unknown sex and age class numbers are the sum of number of animals that were both "unknown" at the time of tagging and animals that did not have any available information contributed. For more information, see Appendices S1 and S2

	Basin					Sex			Age class				Tracking data				
Species	All	Atl	Ind	Med	Pac	F	M	U	A	S	J	U	Locations	Days	Years	Year (min)	Year (max)
All	1235	473	197	257	308	607	99	529	642	46	256	291	140,524	7661	23	1996	2018
Cc	608	179	11	208	210	172	72	364	222	138	28	220	76,064	6692	22	1997	2018
Cm	230	70	49	47	64	156	18	56	145	71	12	2	17,475	5102	21	1997	2017
Dc	102	64	29	0	9	80	4	18	75	8	4	15	12,825	3626	20	1996	2017
Ei	159	46	99	0	14	123	5	31	124	17	2	16	24,634	4267	20	1996	2018
Lk	57	55	0	2	0	7	0	50	7	22	0	28	1931	1082	12	2004	2018
Lo	79	59	9	0	11	69	0	10	69	0	0	10	7595	2070	13	1997	2016

For locations that were not estimated using a state-space model, a speed, distance, and angle (SDA) filter was applied using the R package argosfilter (Freitas, 2012; Freitas et al., 2008; R Core Team, 2019), where all GPS data were assigned the highest location quality value (LC = 3, estimated error <250 m), following Thums et al. (2017) and Wildermann et al. (2019). We applied a conservative speed filter of 10 km/h as the maximum speed for all six species (see Eckert, 2002; Luschi et al., 1998; Walcott et al., 2012; Wirsing et al., 2008). Finally, to better normalize data with timestamp irregularities and tags programmed to record locations on different schedules, we subsampled each track to retain just one location per day (De Solla et al., 1999). The highest quality record of the day was chosen; the first occurrence of the high-quality points was retained if multiple locations of the same highest quality level was recorded for one day (per Metcalfe et al., 2020; Witt et al., 2010). All types of sea turtle movements from one point to another were used in this study, such as those described by Dingle and Drake (2007) as short- and long-distance migrations, ranging, foraging, commuting, or seasonal movements "between habitat regions."

2.2 | Sea turtle movement and connectivity networks

We used all collated tracking data to create ten spatial networks: one global network for all data, three regionally connected networks (herein called the "Atlantic-Indian," "Mediterranean," and "Pacific" components), and six species-specific networks (loggerhead [*Caretta caretta*], green [*Chelonia mydas*], leatherback [*Dermochelys coriacea*], hawksbill [*Eretmochelys imbricata*], Kemp's ridley [*Lepidochelys kempii*], and olive ridley [*Lepidochelys olivacea*]). We a priori used the centroids of marine regions that were frequently used for management purposes as network nodes (points within the graph; see Appendix S3). Marine regions included high seas (areas beyond national jurisdiction), exclusive economic zones (EEZs), and sub-regions of EEZs (Flanders Marine Institute, 2018a, 2018b). Each tracking data point was assigned to the intersecting marine region polygon that varied greatly in size (i.e., high-seas region, EEZ, or sub-region of an EEZ), which was then represented by the polygon's centroid using ESRI ArcMap 10.6.1 (ESRI, 2019). Marine region centroids were not the same as specific locations of animals, and nodes could fall outside of known geographic extents of sea turtles. Tracking data network links (arcs within the network) were created representing connectivity between two nodes when at least one animal moved from one marine region to another (see Appendix S4); links within one node (self-loops) were eliminated. Links were not representative of the specific path sea turtles travelled, and lines could be longer or shorter than distance travelled. Rather, mapping the nodes and links helped visualize their geographic arrangement within each network for qualitative comparisons on structure and function among different networks.

We also created four "neighbor networks" based on the relative geographic location of nodes, following Bange and Hoefer (1976), to serve as a baseline network of structural connectivity when assuming that neighboring areas sharing borders were connected. Neighbor networks were created using all possible nodes (*n* = 227 marine regions with at least one tracking data point) and links that represented connections between marine regions that shared a border (ESRI ArcMap 10.6.1 Polygon Neighbors Tool; ESRI, 2019). The structural connectivity of one global neighbor network and three regional neighbor networks (Atlantic-Indian, Mediterranean, and Pacific components) was compared directly with the functional connectivity of networks created using tracking data (herein called “tracking data networks”).

2.3 | Network metrics selection and analyses

We selected centrality metrics within the current literature that quantified how important an area or connection was within the network, which is related to how specific nodes or links dominated the connectivity of the network. This translated to how animals moved within the physical structure of the network on a local level (nodes and links), contributing to the spatial network properties on a global level (functional connectivity and centrality). Network metric calculations and statistical analyses were all conducted using R software (R Core Team, 2019) on three levels: (1) global or whole network (connected nodes AND isolated nodes or nodes without links to any other node), (2) sub-network (connected nodes OR isolated nodes), and (3) local (individual node OR link; Lau et al., 2017). Metrics were calculated without any assumptions of the effect from including isolated nodes.

Based on previous studies analyzing animal ecology, behavior, and movement strategies using biologically relevant network centrality metrics (e.g., Bastille-Rousseau et al., 2018; Brodie et al., 2018; Farine & Whitehead, 2015; Minor & Urban, 2008; Ospina-Alvarez et al., 2020; Webber & Vander Wal, 2019; Wu et al., 2018), 46 widely used metrics were calculated using the R packages igraph and CePa (see Appendix S5; Csardi & Nepusz, 2006; Gu & Wang, 2013) from which a subset was then selected for further application to our study. For tracking data networks, node weights (based on the number of animals at each node), link weights (based on the number of routes observed), and link direction were applied whenever possible in calculating metrics. Routes were counted as the number of times animals travelled from one marine region to the other. High numbers of animals were assumed to represent high flow, and abundances were normalized within five categories using the Jenks natural breaks classification method (Jenks, 1963, 1967) for all data and within species. For the neighbor networks, marine regions and connections were normalized to minimize potential differences due to weight and direction by treating links as undirected and attributing the overall average number of animals, average number of routes, and median weight to individual nodes and links.

To refine our set of metrics, principal component analysis (PCA; Hotelling, 1933; Pearson, 1901) was first used to determine a subset of metrics that contributed significantly to the total variance of the tracking data network using the 80% cumulative sum as a threshold (R packages factoextra and FactoMineR; Kassambara & Mundt, 2016; Lê et al., 2008). Second, uncorrelated metrics (Spearman's rho <0.80) from the subset were retained to test for significant differences among region and species-specific networks using the Kruskal–Wallis (KW) test and post hoc Dunn's test with Bonferroni adjustment for multiple comparisons ($\alpha = .05$; R package FSA; Bonferroni, 1936; Dunn, 1964; Kendall, 1938; Kruskal & Wallis, 1952). These nonparametric tests were used because metrics were not normally distributed (Shapiro–Wilk normality test, $p > .05$; Shapiro & Wilk, 1965) or comparisons were made with a small sample size. Finally, the 14 node and link centrality metrics that showed the greatest differences (lowest KW test *p*-value) among networks were selected to describe network properties (see Appendix S5).

Global-level metrics were calculated to give an overall connectivity metric that would take into account all components, including disconnected sub-networks and isolated nodes. Node degree (number of links, in all directions, connected to the node) and the number of links (calculated using links with direction) were the global level metrics that were retained to describe global connectivity because they contributed significantly (PCA sum >80%) and were uncorrelated with other metrics (Spearman's rho <0.80). In general, both degree and the number of links related positively to overall network connectivity, where greater values corresponded to higher levels of network flux or movement (Borgatti, 2005; Rayfield et al., 2011). However, these global metrics could not be statistically compared among the whole region or whole species networks because of low statistical power (only one network per species and region was created, and not enough data were available for a longitudinal analysis).

Local-level metrics that displayed the greatest difference among regions were node “closeness” and link “betweenness.” The node closeness metric is related to “how close a node is to all the other nodes in the network beyond ones that are directly connected to” where the distance is the shortest path; a node with greater closeness that can reach all other nodes quickly is more independent than other nodes (Kim et al., 2011). Node closeness is ecologically significant to determine areas that are relatively central that may be more critical to conserve to maintain the network (Estrada & Bodin, 2008; Jacoby & Freeman, 2016; Ospina-Alvarez et al., 2020). The link betweenness metrics is related to “the number of shortest paths between pairs of vertices that run along it”; links that are highly relied upon to connect different communities or at the borders of communities can have greater betweenness (Girvan & Newman, 2002). Link betweenness is ecologically significant to determine links acting as stepping stones that may be more critical to conserve to maintain the network (Estrada & Bodin, 2008; Jacoby & Freeman, 2016; Ospina-Alvarez et al., 2020). Node closeness and link betweenness metrics were used here as proxies for measuring two network properties, respectively: connectedness (the ability to spread resources using short distances to other nodes; Muller & Peres, 2019) and vulnerability (the network's ability to continue functioning given changes to network structure, such as the removal of links; Aytaç

& Öztürk, 2018). These metrics were complementary because the node closeness metric is limited to only calculating relationships and distances within connected components, while link betweenness can be calculated over networks that contain connected and disconnected components (Baranyi et al., 2011; Borgatti, 2005; Wasserman & Faust, 1994).

3 | RESULTS

3.1 | Sea turtle movement and connectivity data

There was a considerable amount of information on global sea turtle movements and connectivity presented within the relevant literature ($n = 969$ references), and very little overlap with references attributed to the telemetry data collated for this study. About 92% of the references presenting relevant telemetry data were unique to the literature review, and 40% of references attributed to the telemetry data used in this study were found within the literature review. Over 64% of all relevant publications from the literature review presented data from telemetry or capture–mark–recapture methods, though a diversity of methods were used (see Appendix S1).

Differences in sampling effort highly influenced the number of nodes and links contributing to the network structure within each region, resulting in more tagged individuals representing more nodes and links in the Atlantic–Indian component, a moderate number of nodes in the Pacific component, and the fewest numbers in the Mediterranean component (Figures 1 and 2, Tables 1 and 2). Marine regions with the largest numbers of animals were within the United States of America North Atlantic EEZ, the North Pacific Ocean high seas, and the Japanese North Pacific EEZ (see Appendix S2). Additionally, the median node degree, representing a measure of global network connectivity, was the greatest within the Mediterranean component. Nearly 80% of marine regions were connected to other marine regions with links in both directions; the largest number of routes were in the Indian Ocean (Persian Gulf: Qatari and Bahraini part), Pacific Ocean (Sulu Sea: Malaysian and Philippines part), and Mediterranean Sea (Eastern Mediterranean Basin: Libyan and Tunisian part; see Appendix S4).

When comparing by species, there was an uneven number of individuals tagged, a large difference in the number of days tracked, and a varying number of marine regions used (Tables 1 and 2; see Appendix S2). These factors may have also influenced the variability in the number of nodes and links within networks, where loggerhead sea turtles had the greatest numbers, followed by leatherback sea turtles (Table 2; Figure 2). The fewest number of links and nodes were within the Kemp's ridley sea turtle network, which also had the greatest median node degree resulting from a small number of highly central nodes and links in the Mediterranean Sea where this species was rarely found.

Most networks exhibited complex arrangements of nodes and links within connected components, typically described as “hybrid topologies” (Figures 3 and 4). These networks contained a combination of node and link patterns that can involve point-to-point (nodes connected along a single path), ring (nodes connected within a circular path), star (a single centere node acts as a hub when connecting to several different nodes), and mesh formations (multiple nodes are connected in multiple ways; Bisht & Singh, 2015; Santra & Acharjya, 2013). The Mediterranean component exhibited a hybrid topology closer to a mesh; the Atlantic–Indian, Pacific, most species networks included star topologies within their hybrid form with high-sea marine regions as highly connected hubs (Figure 3). Nodes identified as hubs have relatively high number of links and can act as “super-spreaders.” On the other hand, the Kemp's ridley sea turtle network was the only one that displayed a single connected component displaying a point-to-point topology, the simplest structure that has a relatively low number of links (Figure 4e).

3.2 | Regionally connected networks

Comparisons among regionally connected networks showed that the tracking data network had significantly higher node closeness within the Mediterranean component (maximum in the Greek part of the eastern basin; KW test, $p < .01$) and the lowest node closeness in the Atlantic–Indian component (minimum in the Andaman and Nicobar Islands, Bay of Bengal; Table 2; see Appendix S5). Median link betweenness was significantly higher within the tracking data network in the Atlantic–Indian component (maximum in the North Atlantic high-sea link to Brazilian part of the North Atlantic; KW test, $p < .001$), while the lowest link betweenness was in the Mediterranean (minimum in the Libyan part of the Mediterranean Sea; Table 2; see Appendix S5).

Comparisons of structural and functional connectivity across regionally connected networks showed the same trend: higher levels of node closeness in the Mediterranean (maximum node was the Italian part of the eastern basin for the neighbours network) and higher levels of link betweenness in the Atlantic–Indian component (maximum link for the neighbor network was the South Atlantic Ocean high seas to the Indian Ocean high seas). The Atlantic–Indian and Pacific network components developed with tracking data had significantly lower node closeness and higher link betweenness than corresponding neighbor networks (KW test, $p < .05$; see Appendix S5). Neighbor networks showed the highest values in node closeness in the Italian and Greek parts of the Mediterranean Sea; the minimum link betweenness was found in the Mediterranean (minimum 1.0 for multiple links). In the Mediterranean, median link betweenness was not significantly different between tracking data and neighbor networks (KW test, $p > .05$), though the overall minimum link betweenness of 0 was found in the Libyan part of the Mediterranean Sea within the tracking data network. Compared to neighbor networks, tracking networks in the Atlantic–Indian and Pacific components showed lower efficiency among marine areas with less path redundancy among links, which could make these networks more vulnerable to potential network changes.

3.3 | Species-specific networks

Compared to other sea turtle species, the closeness of marine region nodes was significantly higher within hawksbill, Kemp's ridley, and olive ridley sea turtle networks (KW test, $p < .05$, see Appendix S5). Maximum closeness was found for the Italian part of the Mediterranean eastern basin node within the Kemp's ridley sea turtle network, the network with the smallest number of individuals tracked and nodes with the lowest link betweenness, resulting from a minimal number of links along a straight path (Figure 4). On the other hand, the loggerhead sea turtle network with the largest number of individuals tracked created a network with the largest

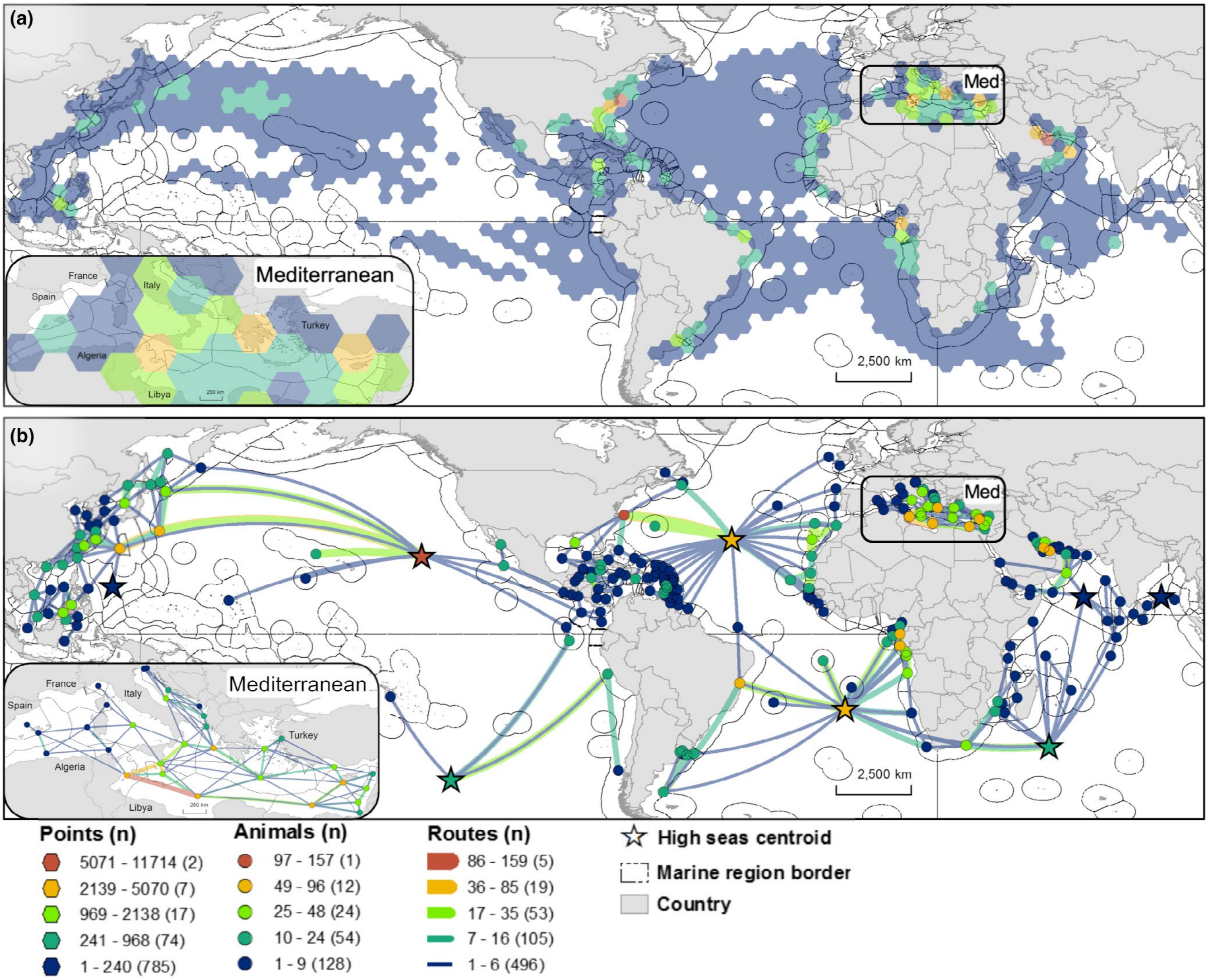

FIGURE 1 Tracking data for six sea turtle species summarized by (a) number of locations within a hexagonal grid, and (b) number of animals per marine region and number of routes taken between marine regions within a network diagram using marine region centroids as nodes. Grid cell = 1.62×10^5 km hexagon; stars symbolize the centroid of individual high-sea marine regions, not animal point location; circles symbolize the centroid of individual marine regions within national jurisdictions, not animal location; links represent connections, not animal paths; two overlapping links between nodes represent connections in both directions. Data were classified using natural breaks (Jenks) within each panel; warmer colors represent higher values and cooler colors represent lower values; number of map features in parenthesis. For more information, see Appendices S1-S4

FIGURE 2 Summary of tracking data for six sea turtle species within a hexagonal grid (left) and within a network diagram using marine region centroids and connecting links (right) for (a–b) *Caretta caretta*, (c–d) *Chelonia mydas*, (e–f) *Dermochelys coriacea*, (g–h) *Eretmochelys imbricata*, (i–j) *Lepidochelys kempii*, and (k–l) *Lepidochelys olivacea*. Grid cell = 1.62×10^5 km hexagon; stars symbolize the centroid of individual high-sea marine regions, not animal point location; circles symbolize the centroid of individual marine regions within national jurisdictions, not animal location; links represent connections, not animal paths; two overlapping links between nodes represent connections in both directions. Data classified using natural breaks (Jenks) within each panel; warmer colors represent higher values and cooler colors represent lower values; number of map features in parenthesis. For more information, see Appendices S1-S4

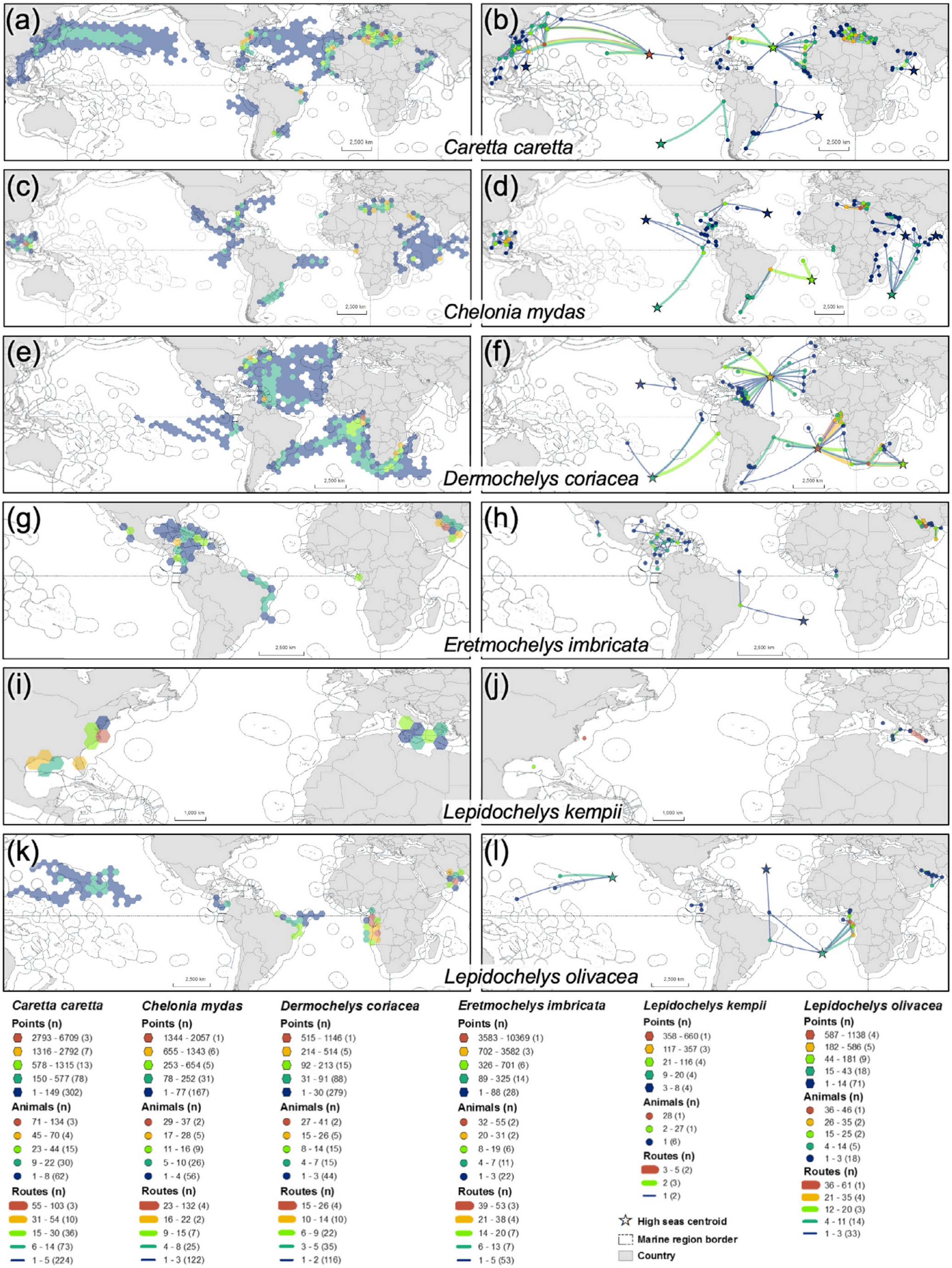
(a)
(b)
Caretta caretta
(c)
(d)
Chelonia mydas
(e)
(f)
Dermochelys coriacea
(g)
(h)
Eretmochelys imbricata
(i)
(j)
Lepidochelys kempii
(k)
(l)
Lepidochelys olivacea
2,500 km
1,000 km
Caretta caretta
Points (n)
2793 - 6709 (3)
1316 - 2792 (7)
578 - 1315 (13)
150 - 577 (78)
1 - 149 (302)
Animals (n)
71 - 134 (3)
45 - 70 (4)
23 - 44 (15)
9 - 22 (30)
1 - 8 (62)
Routes (n)
55 - 103 (3)
31 - 54 (10)
15 - 30 (36)
6 - 14 (73)
1 - 5 (224)
Chelonia mydas
Points (n)
1344 - 2057 (1)
655 - 1343 (6)
253 - 654 (5)
78 - 252 (31)
1 - 77 (167)
Animals (n)
29 - 37 (2)
17 - 28 (5)
11 - 16 (9)
5 - 10 (26)
1 - 4 (56)
Routes (n)
23 - 132 (4)
16 - 22 (2)
9 - 15 (7)
4 - 8 (25)
1 - 3 (122)
Dermochelys coriacea
Points (n)
515 - 1146 (1)
214 - 514 (5)
92 - 213 (15)
31 - 91 (88)
1 - 30 (279)
Animals (n)
27 - 41 (2)
15 - 26 (5)
8 - 14 (15)
4 - 7 (15)
1 - 3 (44)
Routes (n)
15 - 26 (4)
10 - 14 (10)
6 - 9 (22)
3 - 5 (35)
1 - 2 (116)
Eretmochelys imbricata
Points (n)
3583 - 10369 (1)
702 - 3582 (3)
326 - 701 (6)
89 - 325 (14)
1 - 88 (28)
Animals (n)
32 - 55 (2)
20 - 31 (2)
8 - 19 (6)
4 - 7 (11)
1 - 3 (22)
Routes (n)
39 - 53 (3)
21 - 38 (4)
14 - 20 (7)
6 - 13 (7)
1 - 5 (53)
Lepidochelys kempii
Points (n)
358 - 660 (1)
117 - 357 (3)
21 - 116 (4)
9 - 20 (4)
3 - 8 (4)
Animals (n)
28 (1)
2 - 27 (1)
1 (6)
Routes (n)
3 - 5 (2)
2 (3)
1 (2)
High seas centroid
Marine region border
Country
Lepidochelys olivacea
Points (n)
587 - 1138 (4)
182 - 586 (5)
44 - 181 (9)
15 - 43 (18)
1 - 14 (71)
Animals (n)
36 - 46 (1)
26 - 35 (2)
15 - 25 (2)
4 - 14 (5)
1 - 3 (18)
Routes (n)
36 - 61 (1)
21 - 35 (4)
12 - 20 (3)
4 - 11 (14)
1 - 3 (33)

TABLE 2 Network, node, and link metrics calculated for networks created with sea turtle tracking data. Region networks: Atl–Ind = Atlantic–Indian component, Med = Mediterranean component, Pac = Pacific component. Species-specific networks: *Cc* = Caretta *caretta*, *Cm* = Chelonia *mydas*, *Dc* = *Dermochelys coriacea*, *Ei* = Eretmochelys *imbricata*, *Lk* = Lepidochelys *kempii*, *Lo* = Lepidochelys *olivacea*. All nodes were used to calculate closeness within region networks; nodes with links going out, only, were used to calculate closeness within species-specific networks. For more information, see Appendices S3-S5

	Sub-networks (all)	Nodes	Isolate nodes	Animals per node (mean)	Links (directed)	Links (undirected)	Animals per link (mean)	Degree centrality (all)	Node closeness†	Link betweenness†
Region										
All	3	227	0	14.93	678	426	4.65	0.08	0.00004	182.72
Atl–Ind	1	140	0	12.24	389	250	4.15	0.13	0.00026	283.94
Med	1	31	0	26.45	132	74	5.95	0.17	0.00270	21.15
Pac	1	56	0	15.27	157	102	4.80	0.10	0.00095	67.75
Species										
Cc	8	114	1	14.84	346	202	4.74	0.07	0.00009	23.43
Cm	10	98	1	5.99	160	122	2.84	0.04	0.00011	13.13
Dc	4	81	0	5.85	187	124	2.83	0.18	0.00023	42.17
Ei	8	43	3	7.84	74	50	3.93	0.08	0.00064	19.42
Lk	4	8	3	7.63	7	4	1.00	0.21	0.01929	3.57
Lo	4	28	0	8.46	55	35	4.25	0.10	0.00158	6.83

†Significant node and link metric retained for comparisons (PCA sum >80%; Spearman's rho <0.80; KW test $p < .01$).

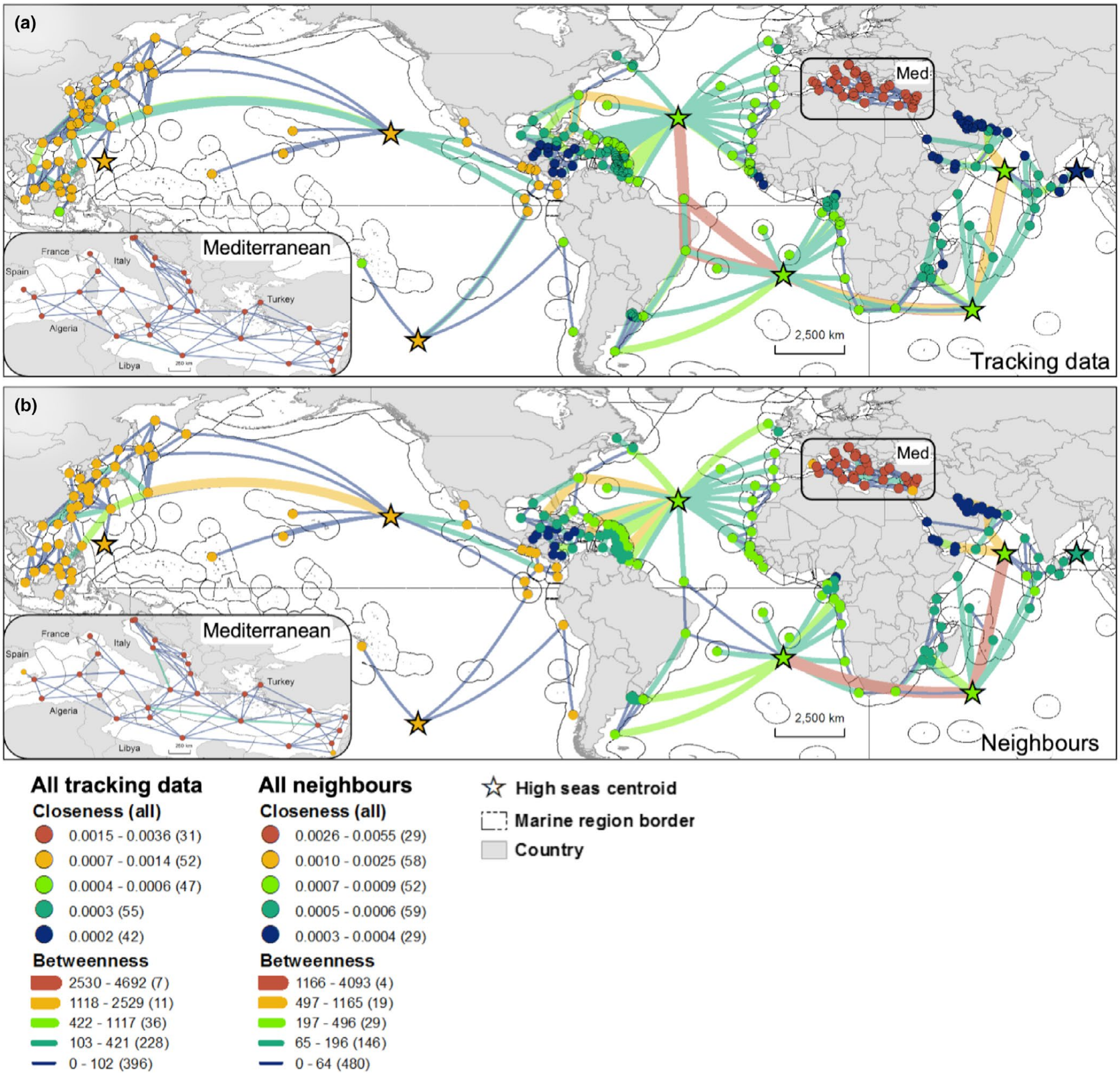

FIGURE 3 Marine region closeness (reciprocal of the average distance between one node to all other nodes) and link betweenness (number of shortest paths connecting a link) within network diagrams created with (a) all tracking data, and (b) marine region neighbors (shared borders). Med = see Mediterranean Sea inset. Stars symbolize the centroid of individual high-sea marine regions, not animal point location; circles symbolize the centroid of individual marine regions within national jurisdictions, not animal location; links represent connections, not animal paths; two overlapping links between nodes represent connections in both directions. Data classified using natural breaks (Jenks) within each panel; warmer colors represent higher values and cooler colors represent lower values; number of map features in parenthesis. For more information, see Appendices S3 and S4

number of nodes and significantly lower node closeness than all other species networks (KW test, $p < .001$; Table 2; see Appendix S5). Compared to other species, link betweenness was significantly higher within the leatherback sea turtle network, and the lowest link betweenness was within the Kemp's ridley sea turtle network (KW test, $p < .001$; Table 2; see Appendix S5). The loggerhead and green sea turtle networks were among the lowest in node closeness and link betweenness, which may infer relatively low connectedness and lower overall vulnerability than other species networks.

Within sea turtle species networks, regions with relatively high node closeness also had high link betweenness, but these regions differed across species (Figure 4). The loggerhead sea turtle network was the only species that showed high node closeness and link betweenness in the Pacific Ocean, specifically in the Japanese EEZs,

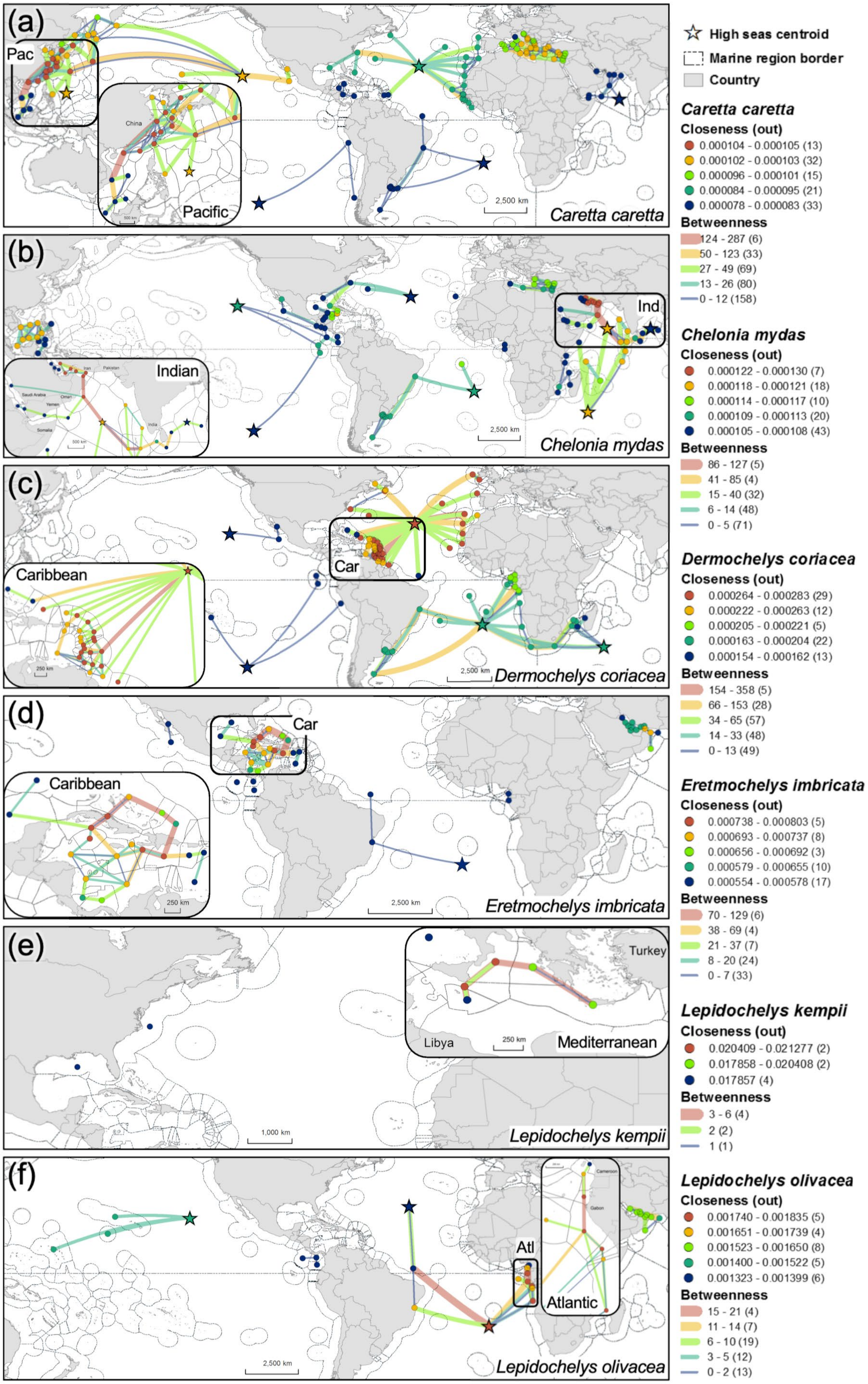
(a)
Pac
Pacific
China
2,500 km
Caretta caretta
(b)
Ind
Indian
2,500 km
Chelonia mydas
(c)
Car
Caribbean
2,500 km
Dermochelys coriacea
(d)
Car
Caribbean
250 km
2,500 km
Eretmochelys imbricata
(e)
Turkey
Libya
250 km
Mediterranean
1,000 km
Lepidochelys kempii
(f)
Atl
Atlantic
2,500 km
Lepidochelys olivacea
High seas centroid
Marine region border
Country
Caretta caretta
Closeness (out)
0.000104 - 0.000105 (13)
0.000102 - 0.000103 (32)
0.000096 - 0.000101 (15)
0.000084 - 0.000095 (21)
0.000078 - 0.000083 (33)
Betweenness
124 - 287 (6)
50 - 123 (33)
27 - 49 (69)
13 - 26 (80)
0 - 12 (158)
Chelonia mydas
Closeness (out)
0.000122 - 0.000130 (7)
0.000118 - 0.000121 (18)
0.000114 - 0.000117 (10)
0.000109 - 0.000113 (20)
0.000105 - 0.000108 (43)
Betweenness
86 - 127 (5)
41 - 85 (4)
15 - 40 (32)
6 - 14 (48)
0 - 5 (71)
Dermochelys coriacea
Closeness (out)
0.000264 - 0.000283 (29)
0.000222 - 0.000263 (12)
0.000205 - 0.000221 (5)
0.000163 - 0.000204 (22)
0.000154 - 0.000162 (13)
Betweenness
154 - 358 (5)
66 - 153 (28)
34 - 65 (57)
14 - 33 (48)
0 - 13 (49)
Eretmochelys imbricata
Closeness (out)
0.000738 - 0.000803 (5)
0.000693 - 0.000737 (8)
0.000656 - 0.000692 (3)
0.000579 - 0.000655 (10)
0.000554 - 0.000578 (17)
Betweenness
70 - 129 (6)
38 - 69 (4)
21 - 37 (7)
8 - 20 (24)
0 - 7 (33)
Lepidochelys kempii
Closeness (out)
0.020409 - 0.021277 (2)
0.017858 - 0.020408 (2)
0.017857 (4)
Betweenness
3 - 6 (4)
2 (2)
1 (1)
Lepidochelys olivacea
Closeness (out)
0.001740 - 0.001835 (5)
0.001651 - 0.001739 (4)
0.001523 - 0.001650 (8)
0.001400 - 0.001522 (5)
0.001323 - 0.001399 (6)
Betweenness
15 - 21 (4)
11 - 14 (7)
6 - 10 (19)
3 - 5 (12)
0 - 2 (13)

FIGURE 4 Marine region closeness (reciprocal of the average distance between one node to all other nodes) and link betweenness (number of shortest paths connecting a link) within network diagrams created by tracking data for (a) *Caretta caretta* (Pac = see Pacific inset), (b) *Chelonia mydas* (Ind = see Indian Ocean inset), (c) *Dermochelys coriacea* (Car = see Caribbean inset), (d) *Eretmochelys imbricata* (Car = see Caribbean inset), (e) *Lepidochelys kempii* (with Mediterranean inset), and (f) *Lepidochelys olivacea* (Atl = see Atlantic Ocean inset). Stars symbolize the centroid of individual high-sea marine regions, not animal point location; circles symbolize the centroid of individual marine regions within national jurisdictions, not animal location; links represent connections, not animal paths; two overlapping links between nodes represent connections in both directions. Data classified using natural breaks (Jenks) within each panel; warmer colors represent higher values and cooler colors represent lower values; number of map features in parenthesis. For more information, see Appendices S3 and S4

Chinese EEZs, and North Pacific high seas. High node closeness and link betweenness occurred in marine regions in the eastern Indian Ocean (Gulf of Oman and Persian Gulf) for green sea turtles, North Atlantic Ocean for leatherback sea turtles, Caribbean Sea for hawksbill sea turtles, Mediterranean Sea for Kemp's ridley sea turtles, and South Atlantic for olive ridley sea turtles (Figure 4).

Node closeness and link betweenness were not significantly correlated to the numbers of individuals tracked or locations recorded (Spearman's rho < 0.80). However, a pattern of high node closeness and link betweenness and relatively low numbers of individuals within a region occurred with all species in this study except for olive ridley sea turtles. The South Pacific had the least amount of data contributing to relatively low numbers of nodes, node closeness, links, and link betweenness.

4 | DISCUSSION

4.1 | The relationship between movement ecology and spatial networks

Spatial networks enabled a modeled, coordinate-free representation of detailed and complex data, contributing to the suite of methods used to examine area use, connections, and animal movement ecology. Within the tracking data used for this study, we found that the number of marine regions used per individual was greatest for leatherback, green, and loggerhead sea turtles (see Appendix S2). Hays and Scott (2013) also found from tracking data that adult leatherback, green, and loggerhead sea turtles travelled the greatest distances, in decreasing order, compared to other sea turtle species. These migration differences may have also influenced the differences in spatial connectivity among networks. Compared to other species-specific networks, areas within the hawksbill, Kemp's ridley, and olive ridley sea turtle networks were closer (shorter paths), and critical connections of high betweenness (stepping-stones) may contribute to greater vulnerability within the network. Therefore, effects on areas or connections for species that tended to have shorter movements may also show higher levels of impact within the network and greater vulnerability to changes that may affect the population. Taking into account movement ecology, network analyses have the potential to further support different management strategies and priorities by highlighting which regions and populations may be most vulnerable.

Spatial network patterns generally agreed with the observed variability in sea turtle ecology and their habitats when summarized within specific marine regions. Leatherback and olive ridley sea turtles rely more on oceanic habitats than other sea turtle species (Bolten, 2013; Luschi et al., 2003). In contrast, marine regions and links within EEZs were highly centralized within the loggerhead, green, hawksbill, and Kemp's ridley sea turtle networks. These comparisons underscored the importance of developing separate networks to inform decisions involving distinct communities (Cerdeira et al., 2010) because species ecology can affect measurable network characteristics. Additionally, investigating these patterns and network metrics by species can contribute to greater understanding of the relationship between sea turtles and other ecosystem factors influencing their distribution, such as prey availability, presence or absence of predators, conspecific distribution, seasonal environmental conditions, or oceanic currents.

4.2 | Conservation recommendations

Progress has been slow in the explicit use and application of connectivity research for managing the marine ecosystem (Balbar & Metaxas, 2019; Carr et al., 2020). However, our results provided a better understanding on connectivity to further any advances and contribute to future conservation proposals that can appropriately cover sea turtle movements throughout their life cycle, following the success of others using tracking data to influence marine policy (see Davies et al., 2021; Hays et al., 2019). As international efforts continue in the development of spatial management plans in the high seas, areas that lack the most data (Ardron et al., 2008; Dunn et al., 2019; Wright et al., 2021), our results are the first to quantify the important role of the high seas in connecting coastal areas for multiple sea turtle species on a global scale. Additionally, our results could be applied to any post hoc assessment of how existing management measures account for connectivity related to marine species movements (see Casselberry et al., 2020; Friesen et al., 2019; Ospina-Alvarez et al., 2020).

The topology (underlying spatial arrangement of nodes and links) provided a direct way to visualize network vulnerability and the requirements for maintaining or conserving connectivity across different networks. For example, areas and connections within simpler network patterns containing low numbers of links relative to nodes (e.g., Kemp's ridley sea turtle point-to-point topology) may be more vulnerable to any network changes without the availability of alternative nodes or links as a backup. However, changes such as loss of a node or link within a point-to-point network would be relatively easy to detect and manage, and given that network changes would be within a more direct path, effects could be easier to predict, and the needs to restore network function could be quickly addressed (Bisht & Singh, 2015; Forouzan & Fegan, 2007; Santra & Acharjya, 2013). Conversely, complex network topology containing many links relative to nodes may be less vulnerable to changes, given the options for alternate paths, but can require more effort to identify where resources should be applied to best conserve network function. It may be more difficult to prioritize among multiple nodes with relatively high numbers of links (hub centres) or several links identified as bottlenecks (connections without alternative paths). Examining the roles of nodes within node sets or multiple nodes within the network can also provide support for the most efficient selection of priority areas necessary within reserve networks after identifying habitats and omitting redundant nodes from conservation efforts (Pereira, 2018; Pereira et al., 2017). Many critical hubs in the high seas were identified within the loggerhead (North Pacific and Philippine Sea), green (Arabian and Indian Oceans), and leatherback (North Atlantic) sea turtle networks, emphasizing the need to include areas beyond national jurisdictions in conservation and prioritization efforts for these species.

Network node and link metrics can also facilitate conservation strategies on a more regional or local level (Beger et al., 2015; Mazor et al., 2013). Networks with higher node closeness may indicate that benefits from area-based conservation measures within marine regions could spread to other highly connected marine regions, especially when directed toward important areas. Examples of priority marine regions included those overlapping EEZs in the northwest Pacific for the loggerhead sea turtle network and within EEZs in the Persian Gulf/Gulf of Oman areas for the green sea turtle network. On the other hand, networks with relatively high link betweenness may benefit more from preserving seascape connectivity among marine regions (e.g., protecting migratory corridors) to increase overall stability within populations that rely on connections. Policies to conserve network structure and function may be more critical for these populations, such as leatherback sea turtles across the Atlantic.

The notion that marine geographic proximity generally relates to similar ecological habitats that drive species area-use (Spalding et al., 2007) was confirmed by the agreement in relative levels of connectivity among regions in this study. For example, the geography and sea turtle movements within Mediterranean marine regions resulted in a network with relatively high node closeness and link betweenness, contributing to high connectedness and vulnerability. In other regions, tracking data networks were less connected (lower median closeness) and more vulnerable (higher median link betweenness), indicating that dependence on sea turtle movements to inform connectivity may be more critical than relying on geography alone. Because of these network differences, empirical data on sea turtle movements need to be directly incorporated into marine network conservation and management.

4.3 | Methods considerations

Our approach was to include as much of the available telemetry data as possible, providing a greater overview of spatial connectivity through networks on a global and regional scale, even when our dataset was not fully representative of all published studies. Therefore, the resulting maps and networks were developed using the best available data, and many details on the individual sea turtles included in this study were unknown or unavailable. Characteristics such as sex, age-class, life-history stage, health condition, core area utilized, amount of time spent in a specific area, the availability of habitats, or movement types (e.g., foraging, inter-nesting, migrating, ranging), were likely to be highly variable within our study sample.

We also recognized that the extent and distribution of our study sample cannot be used to describe all populations because results were heavily influenced by tagged population (most individuals were nesting females), location (disproportionate number of tracks found within the Northwest Atlantic and North Pacific Oceans), limitations on tracking durations (which may not show the true extent of individual movements), and uneven species sample sizes (minimum sample of 57 for Kemp's ridley sea turtles, maximum sample of 608 for loggerhead sea turtles). Increased heterogeneity of tracked movements was also necessary for a more comprehensive assessment (Mazor et al., 2016). Future research is needed to properly correct for sampling biases or appropriately weigh data (e.g., according to location from tagging site, distinct research methods, groups of individuals, activities, or habitat quality) to evaluate network patterns based on ecological niches, specializations, and biological traits (Block et al., 2011; Brodie et al., 2018; Hays et al., 2020; Jacoby et al., 2012; Queiroz et al., 2019). Network analysis methods developed in our study were applicable at various scales, allowing future comparisons at finer resolutions or longitudinal analysis, given the appropriate data.

Lédée et al. (2015) found that network analysis added valuable information to kernel-based methods, revealing important movements within and between core habitats. However, within the current study, node closeness and link betweenness values that were scaled within global or species-specific networks were not directly related to the number of individuals or abundance of locations recorded within marine regions. Furthermore, high seas nodes represented relatively large marine regions (e.g., North Atlantic Ocean, South Atlantic Ocean, North Pacific Ocean, and South Pacific Ocean) compared to EEZs, and false connections between coastal EEZ marine regions *via* the high seas may be revealed or overemphasized due to higher probability of falling within a larger area. For example, olive ridleys in this analysis appeared connected across the South Atlantic, but tracking data from Pikesley et al. (2013) indicated that they spend limited time in the high seas and have fidelity to either side of the Atlantic. Therefore, we recommend supplementing results from more traditional approaches (e.g., abundance and density estimates) or higher-resolution animal movement data with network analyses to identify important high-use areas.

4.4 | Datasets for "big data" analyses

Many studies reviewed within the literature were limited to describing areas used for specific behaviors (e.g., female nesting), lacking details on how multiple marine areas were connected by individual animal movements. Among the relevant data types, data from telemetry tags were most effective in describing core area use, spatial patterns, networks, and migratory connectivity, especially when studies incorporated capture–mark–recapture, stable isotope, or genetic analyses (e.g., Godley et al., 2008; Hart et al., 2015; Hays & Hawkes, 2018; Haywood et al., 2020; McClellan et al., 2010; Rees et al., 2017; Stewart et al., 2013). While a small proportion (about 5%) of the reviewed literature combined telemetry data with another research method (e.g., capture–mark–recapture, genetic, stable isotope analyses), the trend in integrating approaches has increased in recent years. A better understanding of the geographic extent of global sea turtle movements and area use could result from future studies that either include a combination of approaches or encourage data sharing to compare with data collected by different tools.

Benefits of collating primary datasets for "big data" animal movement analyses have been widely recognized and can be a major driver for standardizing data collection, analyses, and archiving methods (Sequeira et al., 2019, 2021; Thums et al., 2018). Even with a largely inclusive approach for gathering data, the number of sea turtle tracks contributed to this study was <18% of what has been reported in the literature, according to Hays and Hawkes' (2018) estimation of over 7000 tracked sea turtles up until 2017. Furthermore, datasets used in this study may show data where species were relatively rare (e.g., Kemp's ridley tracks in the Mediterranean), exclude data where species were known to be present (e.g., South Pacific), or had unique references and information not found within the formal literature review. This study emphasized that synthesizing large-scale sea turtle movements needed a collaborative approach to gather data directly from data owners, especially when prompt publication in a peer-reviewed journal was not always the final research product.

Many limitations to data sharing still exist that continue to hinder scientific advancement (see Jeffers & Godley, 2016; Nguyen et al., 2017). As of 2014, around 140 unpublished sea turtle tracks within the Mediterranean Sea were publicly viewable on seaturtle.org/STAT (Luschi & Casale, 2014), a large online collection of ARGOS-tagged animals (Coyne & Godley, 2005). Collections of unpublished tracking data likely exist in other similar databases or archives, but these numbers are unknown. Leveraging large databases that have aggregated global knowledge on species distributions and ecological connectivity, published or unpublished, greatly expedites analyses, collaboration, and integration of scientific research into policies (Coyne & Godley, 2005; Halpin et al., 2009; Harcourt et al., 2019; Hays et al., 2019; Jeffers & Godley, 2016). In addition to careful reporting of data sources within publications, collaboration and data sharing were essential to this study for an overview of sea turtle movements and have contributed to highlighting the importance of marine connectivity among EEZs and the high seas (Davidson et al., 2020; Dunn et al., 2019). Future collective efforts to share and synthesize available information on all of the marine areas and linkages that populations depend upon will continue to be valuable for both scientists and resource managers (Halpin et al., 2009; Hampton et al., 2013; Hays et al., 2016; Kot et al., 2014).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13485.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supplementary Material of this article and Zenodo (https://doi.org/10.5281/zenodo.5898578). Details for all animals included in this study are provided in Appendices S1 and S2. Data used to create the spatial networks are listed in the Appendices S3 and S4. The geospatial files for all networks are available on the Migratory Connectivity in the Ocean Project website (https://mico.eco) and Dryad (https://doi.org/10.5061/dryad.j3tx95xg9). Additional data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Connie Y. Kot https://orcid.org/0000-0002-4900-5289
Mariana M. P. B. Fuentes https://orcid.org/0000-0002-2789-824X
Victoria González Carman https://orcid.org/0000-0002-6603-1753
Sandra Hochscheid https://orcid.org/0000-0002-8103-2236
Yakup Kaska https://orcid.org/0000-0001-5169-8216
Erin E. Seney https://orcid.org/0000-0002-4153-7379

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BIOSKETCH

Connie Y. Kot is an Associate in Research with the Marine Geospatial Ecology Lab at Duke University (https://mgel.env.duke.edu). Her research focuses on analyzing species distributions, spatial and temporal patterns, linkages among animals, fisheries effort and bycatch, and relationships between protected species and the environment. She uses complex biogeographic data to better understand marine megafauna for conservation. Recent collaborative initiatives include the Migratory Connectivity in the Ocean (MiCO; https://mico.eco), the State of the World's Sea Turtles (SWOT; http://seamap.env.duke.edu/swot), and the Ocean Biodiversity Information System - Spatial Ecological Analysis of Megavertebrate Populations (OBIS-SEAMAP; http://seamap.env.duke.edu).

Author contribution: CYK, CC, SD, DCD, A-LH and PNH conceptualized the study; CYK, MSC, CC, SD, EF, SP, AFR, BPW and PNH contributed to the curation of the data; CYK performed the formal analysis, investigation and visualization, and prepared the original draft; DCD and PNH acquired funding and support; CYK, CC, SD, DCD, EF, BJG, A-LH, GCH, SMM, SP, BPW and PNH contributed to the methodology; CC, DCD and PNH provided project administration; SA, JA-S, DFAL, MA, GB, WRB, JMB, ACB, IB, AFC, PC, DC, MSC, AD, KD, NE, AF, MMPBF, JG, MHG, BJG, VGC, CEH, LAH, GCH, NH, SH, YK, YL, CPL-Q, GGL, ML-M, PL, JCM, DM, SMM, CMM, KM, AM, FGM, WJN, DMP, SHP, NJP, AJR, AFR, DPR, NJR, AGS-L, GS, JAS, EES, RTES, DS, JT, NV-C, NEW, MJW and AAZ-N contributed satellite tracking data resources and metadata; and all authors reviewed and edited the manuscript.

SUPPORTING INFORMATION

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