# Evaluating conservation units using network analysis: a sea duck case study

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Conserving migratory wildlife requires understanding how groups of individuals interact across seasons and landscapes. Telemetry reveals individual movements at large spatiotemporal scales; however, using movement data to define conservation units requires scaling up from individual movements to species- and community-level patterns. We developed a framework to define flyways and identify important sites from telemetry data and applied it to long-term, range-wide tracking data from three species (640 individuals) of sea ducks: namely, North American scoters (*Melanitta* spp). Our network of 88 nodes included both multispecies hotspots and areas uniquely important to individual species. We found limited spatial overlap between scoters wintering on the Atlantic and Pacific coasts of North America, with differing connectivity patterns between coasts. Finally, we identified four multispecies conservation units that did not correspond to traditional management flyways. From this approach, we show how individual movements can be used to quantify range-wide connectivity of migratory species and reveal gaps in conservation strategies.

Migratory animals can cover vast distances, with annual-cycle movements spanning biogeographic and geopolitical boundaries. Migratory movements expose species to varying ecological conditions, stressors, and management regimes, making such species challenging to conserve (Dunn *et al.* 2019). In recent decades, management of migratory wildlife has focused on coordinated regional, international, and intercontinental planning efforts (Boere and Stroud 2006). Nevertheless, many species of migratory birds have declined sharply in abundance over the past 50 years despite conservation efforts, even among taxa that have experienced net population increases (Rosenberg *et al.* 2019). This outcome suggests that current conservation measures are inadequate for addressing factors driving trends in migratory populations.

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The challenge of protecting migratory species is compounded by the complexity of defining manageable populations and identifying critical habitat areas across species ranges. Indeed, interlinked single-species populations and multispecies communities may overlap during parts of the annual cycle but diverge widely in others (Webster *et al.* 2002). In these cases, actions targeting specific locations or time periods may be insufficient if limiting factors occur in other locations or periods (Newton 2004). Likewise, interventions that benefit stable segments of the population may not reverse declines in other subpopulations, even if the groups are sympatric during parts of the year (Kramer *et al.* 2018). Identifying and targeting causes of decline therefore requires first quantifying connectivity among population units over time and space (Marra *et al.* 2015).

Advances in tracking technologies have transformed the science of animal movement from single-site studies with small sample sizes to large, continental- and global-scale repositories. These changes make it possible to follow numerous individuals across the annual cycle to understand how breeding, non-breeding, and migratory habitats are interlinked (eg Meattey *et al.* 2018; Lamb *et al.* 2020). However, analysis of telemetry data often emphasizes habitat use rather than population- and community-level connectivity patterns. As larger datasets for multiple species become available, methods that combine telemetry data across individuals, sites, and species are required to identify annual-cycle linkages and optimize conservation actions.

One promising option for integrating large telemetry datasets is network analysis (Xu *et al.* 2020): a branch of graph

theory that quantitatively assesses pairwise relationships among actors, objects, or locations, and uses these relationships to describe the properties of the overall system and its components. Networks have broad applications in biology and ecology, including in genetics (Nacu *et al.* 2007), social-systems ecology (Hasenjager and Dugatkin 2015), cognitive processes (Gray *et al.* 2014), and machine learning (Lek and Guégan 1999). To date, network analysis of animal movement has typically been used to examine relationships among discrete locations (eg Iwamura *et al.* 2013). However, it can also be a powerful tool for using individual movement data to identify key sites and their interconnections in landscape-level migratory networks without predefined habitat patches (Lamb *et al.* 2019).

Our goal was to use network modeling to document community-level, continental-scale migratory connectivity from satellite telemetry data. We evaluated our method based on tracking data for three congeneric species of North American sea ducks—black scoter (*Melanitta americana*), surf scoter (*Melanitta perspicillata*), and white-winged scoter (*Melanitta deglandi*)—across their North American ranges. In contrast to other harvested waterfowl, sea ducks often have uncertain population trajectories, and North American scoters breed in remote boreal habitats where their reproductive success is difficult to measure (Bowman *et al.* 2015; Rosenberg *et al.* 2019). In contrast, their multistage migrations include coastal habitats with intense human activity. Sea ducks are managed using a flyway system developed for mid-continental waterfowl (Nichols *et al.* 1995), which was not designed to capture spatial population structure for sea ducks. Our primary objectives were to identify locations associated with single- and multispecies annual-cycle connectivity at the continental scale and assess alignment of management units with spatial structure of scoter populations.

## Methods

From October to May for 21 consecutive years (1998–2019; target species and locations varied among years), we captured scoters using decoys and net guns, night-lighting, floating mist nets, or gill nets at multiple sites in eastern and western North America (Appendix S1: Table S1). We implanted 26–50-g platform terminal transmitters (PTTs; Microwave Telemetry Inc, Columbia, Maryland, or Telonics, Mesa, Arizona) in 782 individual scoters, of which 538 (143–235 transmitters per species) collected multi-season data suitable for our analysis (Appendix S1: Table S1). Sample sizes for all species were slightly higher in the eastern region (58% of all retained transmitters; 54–60% per species). Capture and implantation methods are fully described in De La Cruz *et al.* (2009), Lamb *et al.* (2019), and Bowman *et al.* (2021).

Transmitters collected location data approximately once every 3–6 days (see De La Cruz *et al.* [2009] and Lamb *et al.* [2019] for duty cycles). Locations were derived from the Doppler shift in transmitter signals, received by polar-orbiting satellites, and compiled through the CLS (Collection & Location by Satellite) America processing center in Lanham, Maryland. We regularly downloaded transmission data, which were filtered through a hybrid Douglas Argos Filter (Douglas *et al.* 2012) to retain the single location with the highest accuracy from each duty cycle and reduce redundant positional information.

We estimated regular movement trajectories using a switching state-space model (Jonsen *et al.* 2005) to account for location error and temporal gaps. Tracks were interpolated to one location per day and daily locations were classified based on their probability of assignment to either resident (shorter step distances, frequent directional change) or transient (longer distances, consistent direction) behavioral states (see Lamb *et al.* [2019] for full model parameterization and state characteristics). We assumed resident birds were actively using habitat, whereas transient birds were flying through. We defined a residency period as ≥2 interpolated resident locations separated before and after by ≥2 transient locations. All models were run using the *bsam* package (Jonsen *et al.* 2005) in R (R Core Team 2018).

Within each residency period, we calculated the occupancy duration and geographic centroid of all locations. Each centroid was assigned to a season based on its phenology within the annual cycle following De La Cruz *et al.* (2009): wintering (November–February), spring migration (February–May), breeding (May–July; inland), or molt and fall migration (May–November for non-breeders and males, July–November for breeding females; primarily coastal). We omitted each individual's first habitat centroid to avoid inflating the relative importance of capture locations and exclude abnormal post-capture movements (Lamb *et al.* 2020).

To define groups of habitat centroids, we selected the optimal number of clusters using the R package *NbClust* (Charrad *et al.* 2014), varying the number of clusters from 20 to 200 and choosing the consensus solution across multiple algorithms. Using the resulting clusters (nodes) and between-cluster movements (edges), we constructed single- and multispecies networks using the R package *igraph* (Csárdi *et al.* 2015). Network analysis evaluates pairwise relationships (here, individual movements) among entities (here, locations) to assess the structure of the community and the roles of its components. We inversely weighted each habitat centroid or edge by the proportion of centroids or edges from that species and region to ensure that each species and region contributed equally to the final network.

Following network construction, we evaluated four node-specific importance metrics using the *igraph* package and Conefor 2.6 software (Saura and Torné 2009): outdegree centrality (number of outgoing edges), indegree centrality (number of incoming edges), betweenness centrality (number of pathways including the target node), and connectivity (dPC [change in probability of connectivity]; here, the change in connectivity after removing the target node) (Appendix S1: Figure S1). To compare interspecific network use and identify opportunities for shared threats or benefits among scoter species, we calculated centrality values across the multispecies

network and for each species individually. We tested the sensitivity of our results to weighting factors by comparing several alternative weighting schemes, including by individual, capture site, duration of use, and combinations of factors (Appendix S1: Figure S2). We found that site rankings were similar regardless of weighting factors (coefficient of variation [CV] of rank: mean = 0.27; range = 0.00–1.64).

To identify groups of linked locations, we assessed network modularity, or the extent to which subgroups of nodes (modules) in a network are more closely connected with one another than expected if linkages were random. We identified modules using propagating labels in *igraph* and evaluated results using the Girvan-Newman algorithm (Appendix S1: Figure S1; Girvan and Newman 2002), which does not require a priori knowledge of the expected number of modules. Under this system, a network with weak migratory connectivity (ie a network in which individuals from different breeding areas are evenly mixed at wintering sites; Webster *et al.* 2002) would score closer to zero, whereas strong connectivity (ie individuals from different breeding sites also segregate on wintering grounds) would score closer to one. A score of one would require all nodes within a module to directly interconnect, which we did not expect because sea ducks use stopover nodes between wintering and breeding. We therefore considered modularity scores closer to fully interconnected modules than random linkages (ie ≥ 0.5) to represent strong connectivity.

## ■ Results

The multispecies North American scoter network consisted of 88 nodes (Appendix S1: Figure S3 and Table S2). Of these, 44 (50%) were used only by scoters captured in eastern North America, 29 (33%) only by scoters captured in western North America, and 15 (17%) by scoters from both groups during spring migration, fall migration, and breeding (Figure 1). Scoters in eastern North America used distinct nodes for wintering, spring migration, breeding, and fall migration/molt, whereas scoters from western North America utilized nodes during multiple seasons. The northernmost terrestrial breeding nodes also included marine coastlines used during molt (Figure 1; Appendix S1: Figure S3).

Several coastal nodes used during migration had high values across all centrality metrics (Figure 2; Appendix S1: Table S2), indicating that they were widely used by tracked individuals and served as points of connection across the
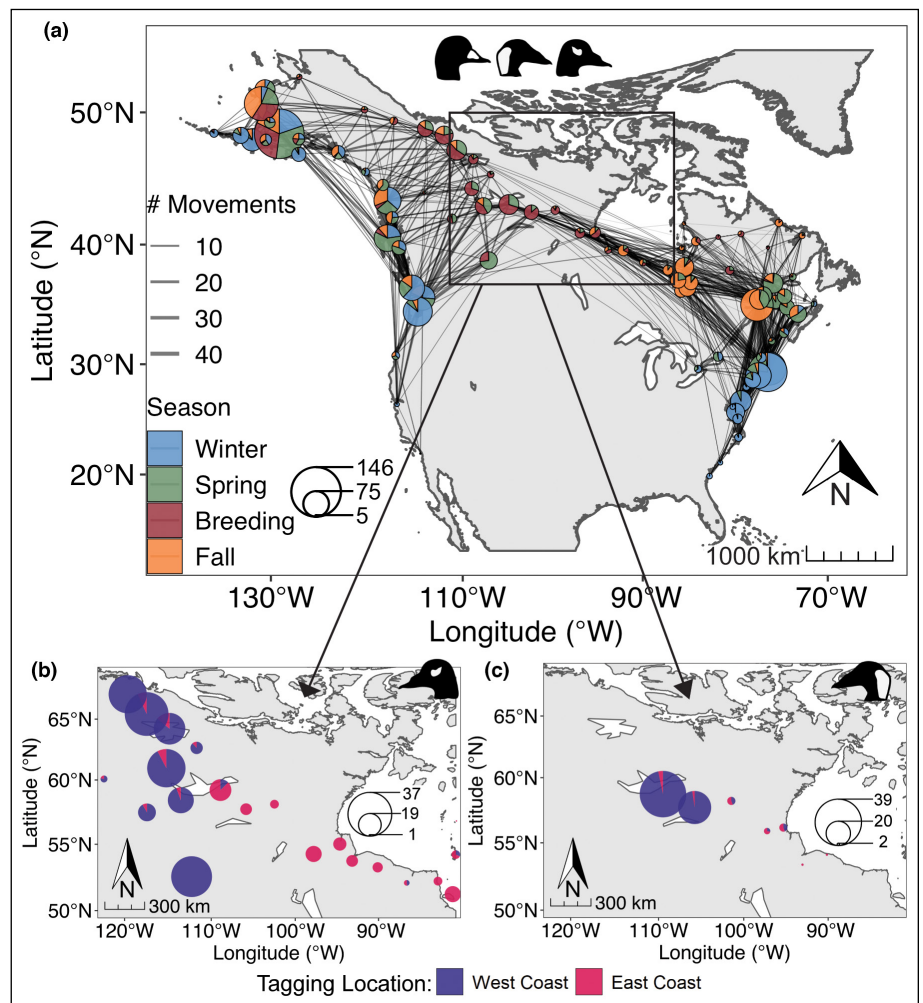


**Figure 1.** (a) Multispecies annual-cycle network for North American black scoter (*Melanitta americana*), surf scoter (*Melanitta perspicillata*), and white-winged scoter (*Melanitta deglandi*) showing seasonal use (blue = winter, green = spring migration, red = breeding, orange = fall migration), 1998–2019. Node sizes correspond to relative intensity of use, with the node size key (nested circles) depicting numbers of centroids for small-, medium-, and large-diameter nodes. Inset maps depict areas of overlap between individuals from western (dark purple) and eastern (dark pink) capture sites for (b) white-winged scoter and (c) surf scoter. Eastern and western black scoter populations did not overlap.

migratory network. Indegree and outdegree centrality and connectivity were highest at coastal staging nodes and wintering nodes on both coasts (Figure 2, a and b, d), and betweenness centrality was also high at breeding and molting nodes where eastern and western scoters overlapped (Figure 2c). Species-specific centrality was comparatively higher in coastal spring and fall migration nodes for black scoters, and in coastal wintering and inland breeding nodes for surf scoters and white-winged scoters (Appendix S1: Figure S4).

The multispecies network was highly modular and contained four interlinked modules (one in the east and three in the west), which did not correspond to existing management units (Figure 3a). Modularity scores were high for single-species networks (Figure 3, b–d), indicating distinct subunits within the continental population for all scoter species. The
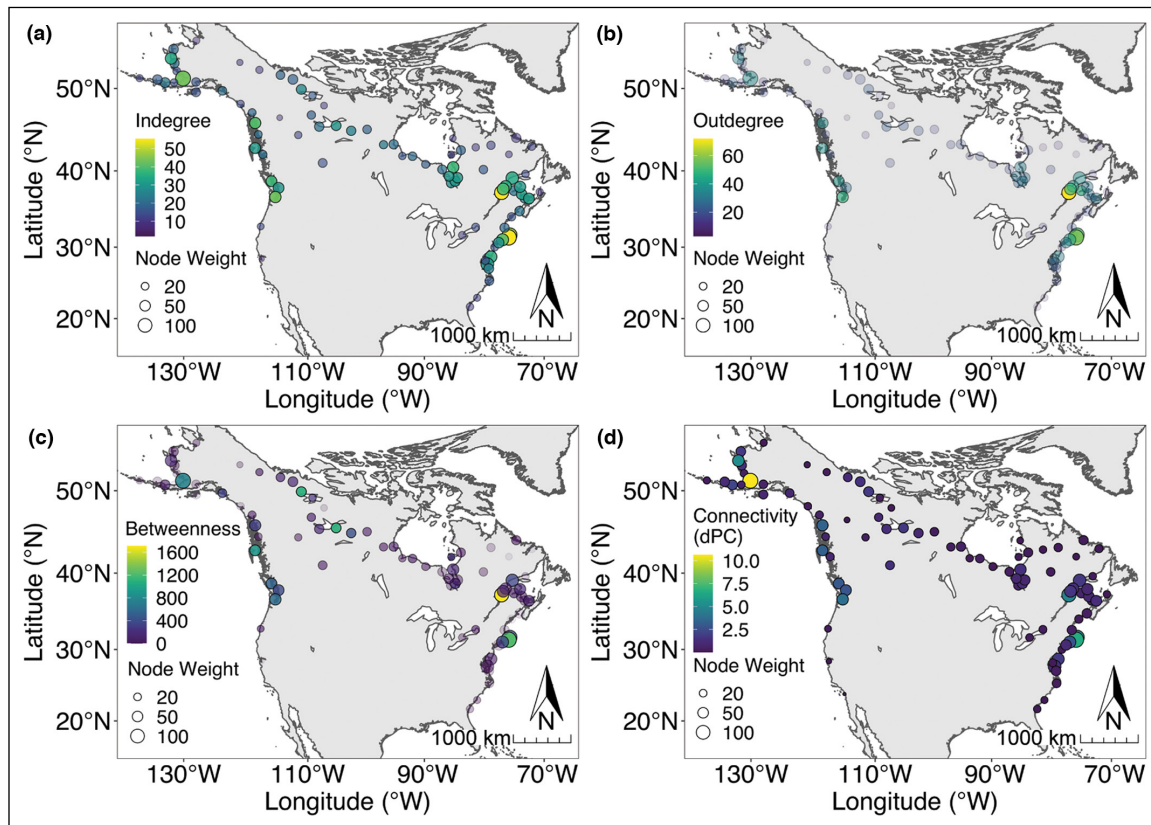
**Figure 2.** Multispecies values for (a) indegree centrality, (b) outdegree centrality, (c) betweenness centrality, and (d) connectivity for North American scoters, 1998–2019. For complete descriptions of the four network centrality metrics, see Appendix S1: Figure S1.

black scoter network consisted of isolated eastern and western modules (Figure 3c), whereas the surf scoter network contained two interlinked modules (Figure 3b) and the white-winged scoter network contained three modules (Figure 3d). Modularity scores were similarly high in all three species (~0.5), suggesting stronger linkages within than between modules. Boundaries between eastern and western subgroups were around 106°W for surf scoters, and 113°W for black scoters and white-winged scoters.

## Discussion

Integrating range-wide telemetry data into a spatial network allowed us to assess the relative importance of sites to annual-cycle movement of migratory birds and identify high-value locations. By measuring and describing patterns of migratory connectivity across the ranges of three scoter species, we highlighted key similarities and differences in network structure among species and regions. In addition, scoter networks were highly modular and spanned multiple management units, highlighting the need for regional coordination.

Our study adds to a growing body of applications of network analysis to movements of migratory species and communities (eg Iwamura *et al.* 2013; Xu *et al.* 2020; Donnelly *et al.* 2021). Like these studies, our application of network analysis reveals the high importance of migratory stopover

sites to overall network connectivity and allows explicit prioritization of sites based on their relationships to other locations within migratory networks. While previous studies often focused on predefined networks of habitat patches, we extended these analyses by using telemetry data rather than habitat to define nodes. Our approach can be flexibly applied to species for which key habitats are not defined a priori. However, it is sensitive to decisions such as clustering methods and weighting, which must be carefully selected. In addition, generating a representative network requires distributing transmitters throughout the population(s) of interest. This study benefited from a coordinated effort to deploy transmitters throughout the populations of interest, resulting in comprehensive coverage of scoter species' ranges (Pearce *et al.* 2019) with sample sizes sufficient to characterize seasonal distributions (ie at least 80–130 individuals per species; Roberts *et al.* 2018). However, low-density wintering areas (eg the Gulf of Mexico for black scoters) were unsampled and are underrepresented in the network. Less common migratory routes could also be underrepresented by chance in our network, which could result in underestimation of connectivity along these routes. Staging sites exhibited high in- and outdegree centrality and population mixing, making them useful targets for increasing sample representativeness, but could still exclude alternative migratory routes. If sampling design is carefully considered, however, our approach offers a straightforward,

repeatable, and transparent mechanism for translating telemetry data into a landscape framework.

Our analysis identified important sites for multispecies connectivity, which could be valuable targets for maximizing conservation benefits across species. For scoters, coastal staging sites in Nantucket Sound, the St Lawrence River, the Salish Sea, and southeast and southwest Alaska had high in- and out-degree centrality, suggesting intermixing of individuals from various breeding and wintering sites. In addition, the white-winged scoter and surf scoter networks each included different breeding nodes with high between-ness centrality values used by individuals from eastern and western wintering areas. Despite similarities in their ranges, migratory patterns, and habitat requirements, however, the three North American scoter species showed differences in breeding and non-breeding habitat selection (Takekawa *et al.* 2011; Lamb *et al.* 2020). Correspondingly, we observed among-species differences in importance of shared sites. In southern Alaska, for instance, Prince William Sound was relatively more central to the white-winged scoter network, whereas southeast Alaska was more central to the surf scoter network. Thus, while it may be optimal to conserve sites with high importance values across multiple species, maintaining a strong migratory network also requires including sites with unique single-species importance.

Our results also highlight regional and species-specific differences in migratory connectivity patterns. While migration of eastern scoters was concentrated along relatively uniform routes consisting of north–south movements to stopover and staging sites followed by east–west breeding or molt-ing migrations, migration of western scoters was diffuse over many routes, with direct movements between inland staging and breeding sites and coastal molt and winter-ing areas. Eastern and western white-winged scoters overlapped over a broad longitudinal range, from Hudson Bay to the Northwest Territories; surf scoters overlapped only in a few nodes; and black scoters did not spatially overlap at all. Furthermore, west-ern black scoters migrated shorter distances than eastern black scoters and the other two scoter species, with a unique migra-tion from multispecies wintering areas in southeast Alaska, British Columbia, and the Salish Sea to southwestern Alaska. Together, these differences suggest that effectiveness of
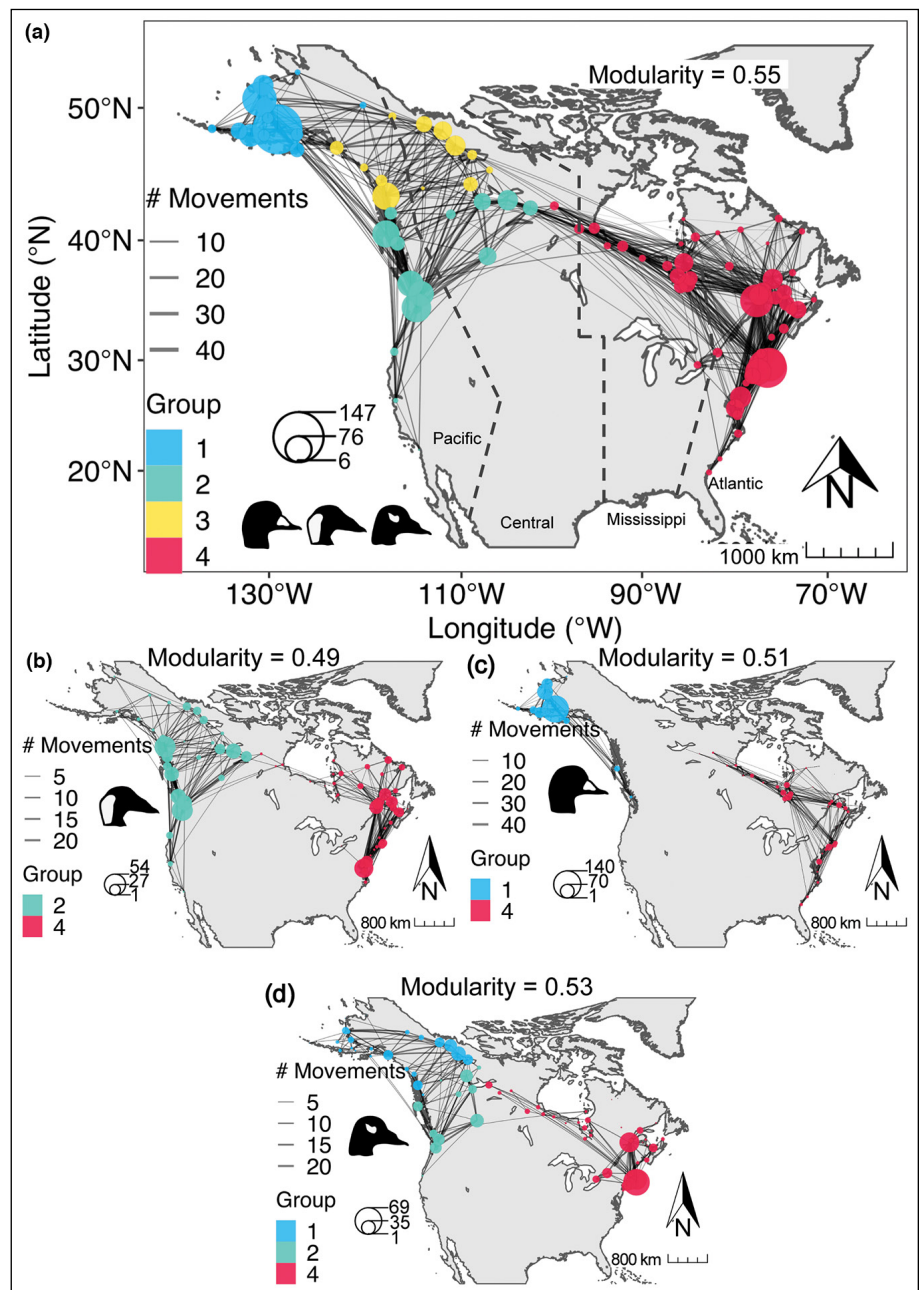


**Figure 3.** Network modularity for North American scoters tracked between 1998 and 2019 for (a) all three scoter species combined, (b) surf scoters only, (c) black scoters only, and (d) white-winged scoters only. Colors indicate groups of nodes (ie modules) that are more interconnected with one another than with the overall network. Modularity values (Girvan-Newman scores) ranged from 0 (random) to 1 (complete interconnection within modules and no connections between modules); we considered values >0.5 to represent high modularity. Dashed lines in (a) show boundaries of traditional waterfowl flyways (Pacific, Central, Mississippi, and Atlantic) in the US and Canada.

multispecies conservation planning may vary by region, with western scoters requiring a more species-specific approach.

Individual movements delineated four groups of scoters that traverse and subdivide existing flyways in North America. All species occupied a single eastern module spanning the Atlantic, Mississippi, and Central flyways (supporting Lamb *et al.* 2019). Three multispecies western modules divided along

a northwest–southeast axis, each spanning the Pacific and Central flyways. Number and configuration of modules varied by species in the western portion of their ranges, with less multispecies overlap. Our results suggest that coordination across North American flyways—and, occasionally, subdivision within flyways—may be needed to distribute management actions across annual-cycle habitats for scoters or species with similarly complex migratory patterns (eg sandhill crane [*Antigone canadensis*]; Donnelly *et al.* 2021). Using individual movements to define management units could offer opportunities to link population trends to relevant demographic rates and external drivers across the annual cycle.

Although our application of network analysis focused on a specific group of sea duck species, similar approaches could be applied to other species and communities of migratory wildlife for which large-scale tracking datasets are available. For example, multispecies tracking data have been compiled across a suite of Arctic wildlife (Davidson *et al.* 2020) and could be analyzed in a network structure to compare modularity among species and to identify migratory pathways and locations vulnerable to habitat loss under future climate scenarios. Telemetry data could also be used to construct or validate spatial networks for identifying populations of mobile wildlife affected by barriers along migratory corridors, such as turtles impacted by road crossings (Pereira *et al.* 2011) or bats exposed to wind energy installations (Erickson *et al.* 2016).

## Conclusions

For North American scoters, our analysis revealed interconnected subgroups that transcend geopolitical management boundaries. Sea ducks spend most of the annual cycle in coastal non-breeding habitats along the Atlantic and Pacific coasts, providing opportunities for conservation and harvest management within these units; however, wintering areas within the same management flyway may be connected to different migratory and breeding habitats. Connectivity-based analyses offer mechanisms for contextualizing varying population trajectories within existing management units and optimizing management decisions across the annual cycle. In addition, although eastern and western populations of surf scoters and white-winged scoters are not genetically distinct (Sonsthagen *et al.* 2019), we found limited spatial overlap between these populations, which could result in separate demographic trajectories. Thus, management and monitoring of eastern and western scoters as distinct subpopulations may be warranted despite genetic overlap.

For scoters and other migratory wildlife, movement networks like ours provide a valuable starting point for further analysis. Integrating survey and demographic data into networks (Studds *et al.* 2017) can help identify differential population trends among modules and assess how vital rates associated with stage-specific habitats propagate throughout the network. Furthermore, assessing relationships between habitat characteristics and node centrality (Donnelly *et al.* 2021) and incorporating predictive modeling provide a basis for evaluating how future changes in habitat will impact migratory movements, and which nodes and pathways may become more important to migratory connectivity under climate warming and habitat loss scenarios. These and other extensions of network analyses could provide valuable insights for conservation of long-distance migrants in a changing world.

## Acknowledgements

## Data Availability Statement

Data and novel code used in this manuscript are available on Zenodo (https://doi.org/10.5281/zenodo.10137095).

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## ◼ Supporting Information

Additional material can be found online at http://onlinelibrary.wiley.com/doi/10.1002/fee.2648/suppinfo

**Appendix S1**



**Supplement to:**



**Evaluating conservation units using network analysis:**
**a sea duck case study**



**JS Lamb *et al*.**



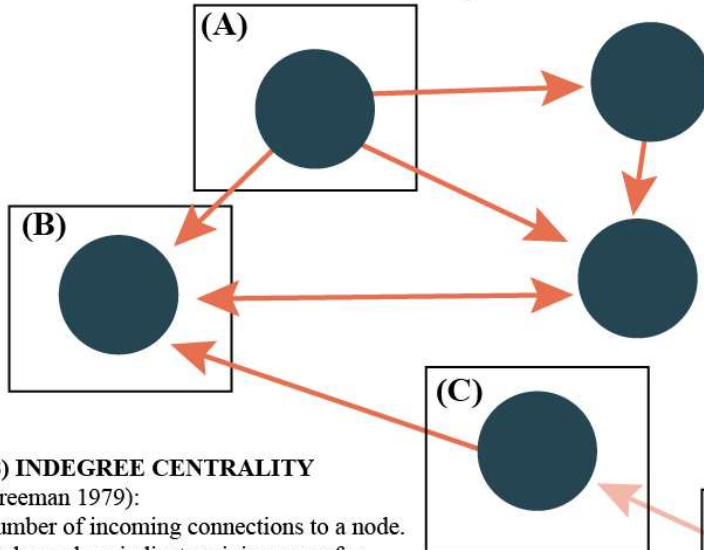**Published in *Frontiers in Ecology and the Environment***

**(A) OUTDEGREE CENTRALITY**
(Freeman 1979):
Number of outgoing connections from a node.
Higher values within our measured range
indicate points of overlap preceding
dispersal events; e.g., a spring staging site used
by individuals that then travel to different breeding areas.

**(E) MODULARITY**
(Girvan and Newman 2002):
Degree (0-1) to which the network
is divided into subgroups of
interconnected nodes. Values
closer to one indicate a higher degree
of separation among subgroups; e.g.,
individuals using the same breeding
areas also use the same wintering sites.

**(B) INDEGREE CENTRALITY**
(Freeman 1979):
Number of incoming connections to a node.
Higher values indicate mixing areas for
individuals from multiple sites or populations;
e.g., a fall staging site used by individuals
from dispersed breeding areas.

**(C) BETWEENNESS CENTRALITY**
(Freeman 1977):
Number of paths including a node. Higher values
indicate locations that connect multiple
incoming and outgoing nodes; e.g., a
stopover where several different
migratory routes overlap.

**(D) CONNECTIVITY (dPC)**
(Saura and Pascual-Hortal 2007):
Change in the number of steps required
to move through the network when a
node is removed. Higher values indicate
locations whose removal interrupts
important pathways through the network;
e.g., a stopover along a migration route
with no comparable stopovers nearby.



**Figure S1.** Complete descriptions of network centrality metrics used to calculate node importance. (a) Outdegree centrality (multispecies network range: 1.75–55.44). (b) Indegree centrality (multispecies network range: 3.02–71.89). (c) Betweenness centrality (multispecies network range: 0–1710). (d) Connectivity (dPC; multispecies network range: 0.01–10.63). (e) Modularity.

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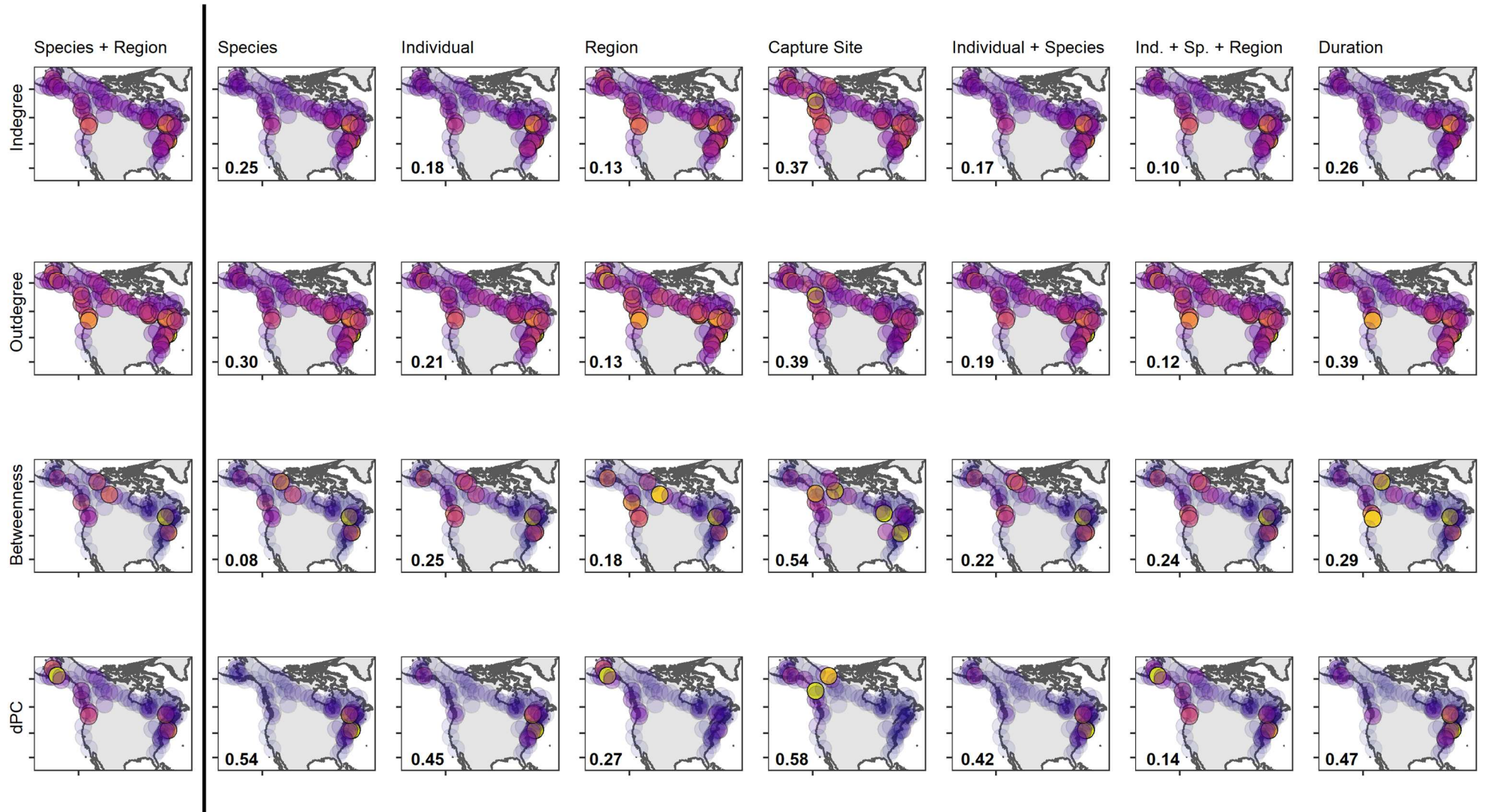
**Figure S2.** Standardized values for indegree centrality (top row), outdegree centrality (second row), betweenness centrality (third row), and change in probability of connectivity (bottom row) obtained using different weighting factors. Yellower and more opaque

colors represent higher centrality values. The leftmost column represents the selected weighting scheme in which each species and region contribute equally to the network. For each alternative scheme the absolute value of the mean change in scaled node weights (ie 1 = one standard deviation) under the alternative scheme compared to the species and region weighting is shown in the lower left corner of the panel.
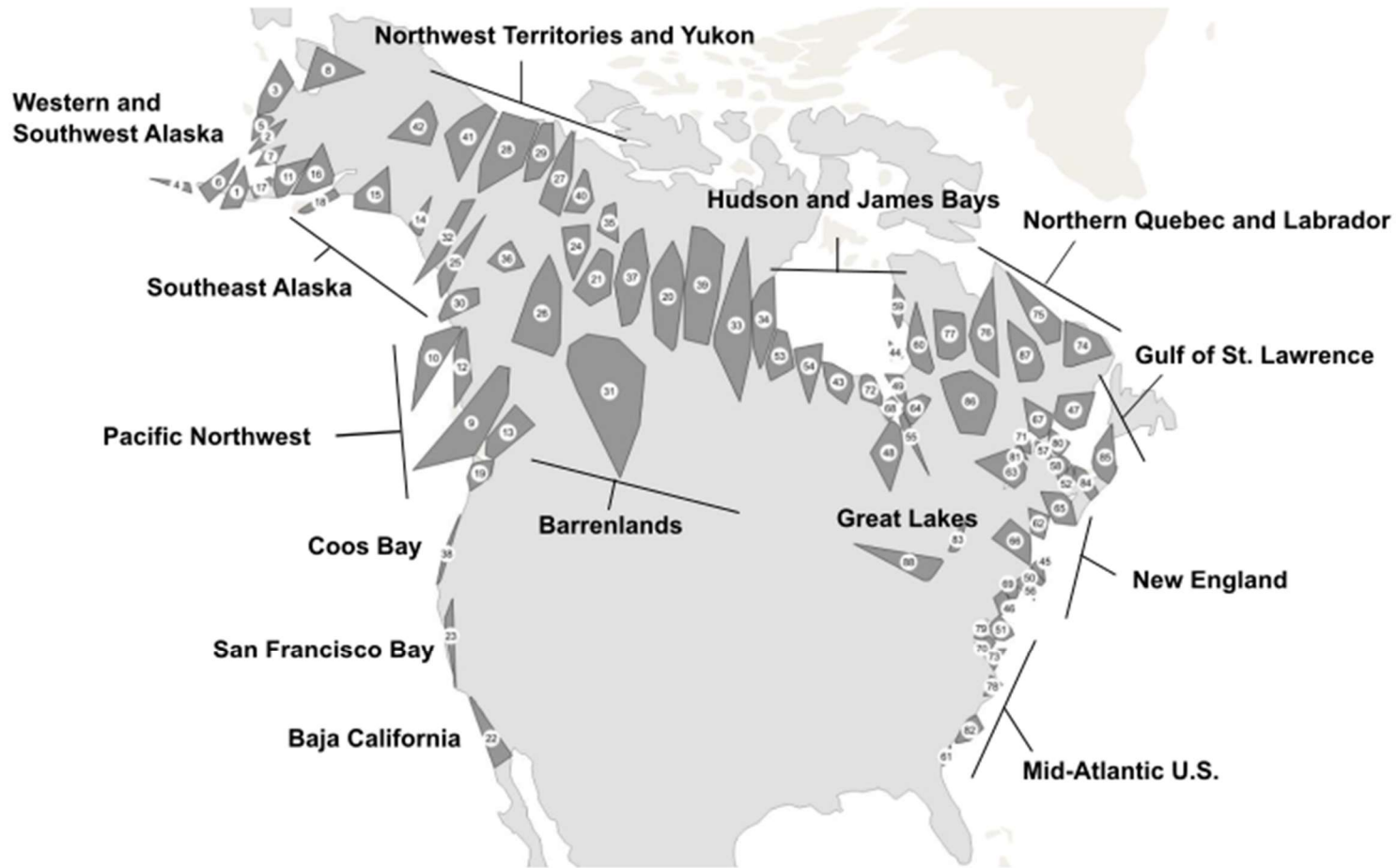
**Figure S3.** Habitat nodes (*n* = 88) determined from unsupervised clustering of satellite telemetry data from North American scoters, 1998–2019. Full location descriptions are provided in Table S2.
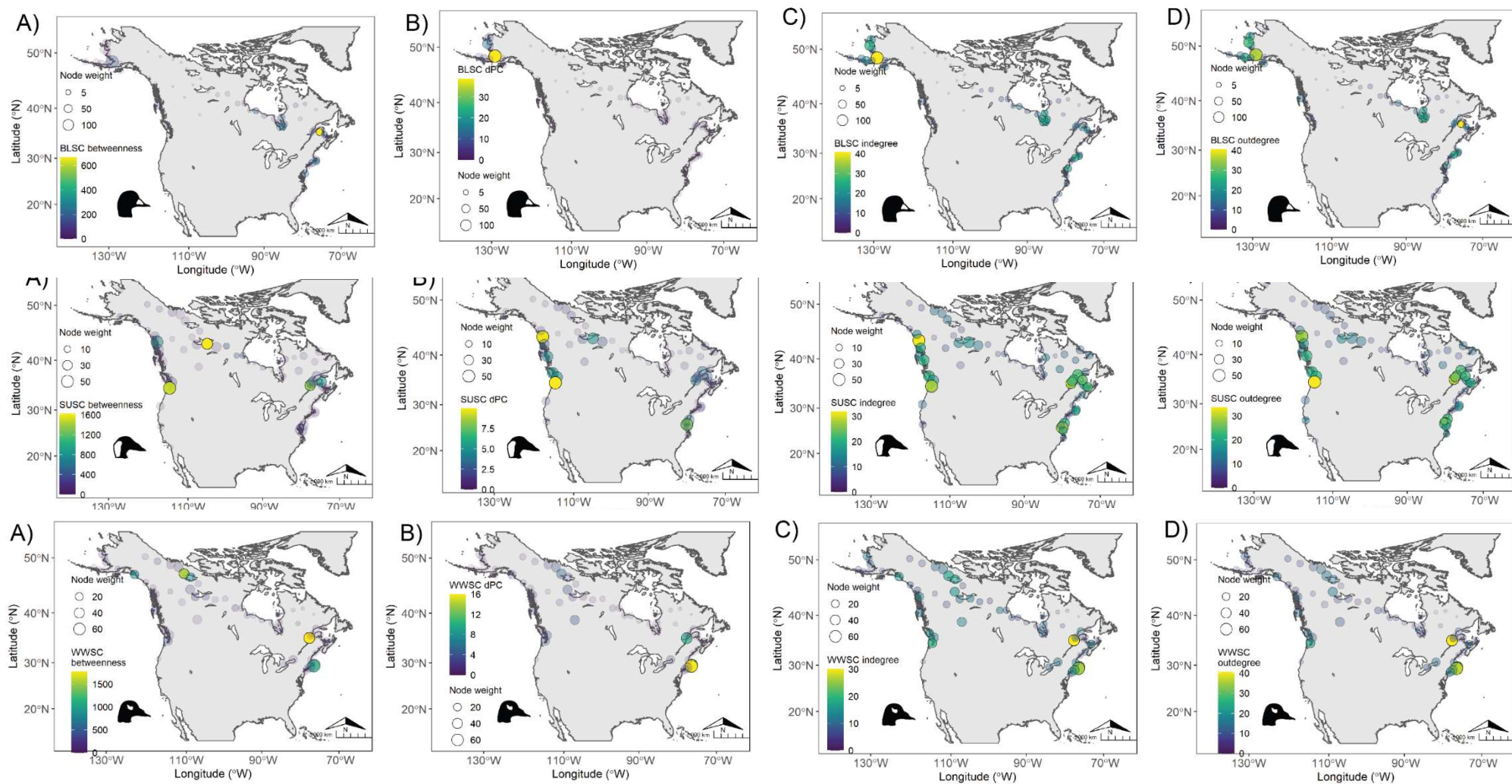
**Figure S4.** Network values for betweenness centrality, connectivity (dPC), indegree centrality, and outdegree centrality for North American (a–d) black scoters (*Melanitta americana*), (e–h) surf scoters (*Melanitta perspicillata*), and (i–l) white-winged scoters (*Melanitta deglandi*), 1998–2019.

**Table S1. Transmitters deployed on scoters in North America from 1998 to 2019 by location, species, year, and season**

| Location | Region | Black Scoter | | Surf Scoter | | White-winged Scoter | | Latitude | Longitude | Deployment season | Deployment years |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Deployed | Retained | Deployed | Retained | Deployed | Retained | | | | |
| **NEWFOUNDLAND & LABRADOR** | | | | | | | | | | | |
| Voiseys Bay | Eastern | 0 | 0 | 14 | 8 | 0 | 0 | 56.28 | -62.03 | Fall molt | 2006 |
| **QUEBEC** | | | | | | | | | | | |
| Forestville, Québec (St. Lawrence River) | Eastern | 0 | 0 | 79 | 41 | 60 | 52 | 48.40 | -69.20 | Fall molt | 2010 – 2016 |
| Chaleur Bay, New Brunswick and Québec | Eastern | 93 | 79 | 6 | 3 | 0 | 0 | 47.87 | -65.40 | Spring migration | 2002 – 2005 2009 – 2010 |
| **GULF OF MAINE** | | | | | | | | | | | |
| Merrimack River | Eastern | 0 | 0 | 0 | 0 | 5 | 3 | 44.73 | -66.49 | Winter | 2011 – 2013 |
| **SOUTHERN NEW ENGLAND / NEW YORK** | | | | | | | | | | | |
| Cape Cod Bay | Eastern | 0 | 0 | 0 | 0 | 22 | 21 | 41.63 | -70.21 | Winter | 2015 – 2016 |
| Rhode Island | Eastern | 17 | 8 | 1 | 1 | 1 | 1 | 41.45 | -71.33 | Winter | 2010 – 2011 |
| Long Island Sound | Eastern | 0 | 0 | 0 | 0 | 7 | 5 | 41.13 | -71.79 | Winter | 2014 – 2016 |
| **GREAT LAKES** | | | | | | | | | | | |
| Lake Ontario | Eastern | 0 | 0 | 0 | 0 | 2 | 1 | 43.29 | -79.48 | Winter | 2013 |
| **MID-ATLANTIC** | | | | | | | | | | | |
| Chesapeake Bay | Eastern | 2 | 2 | 70 | 57 | 0 | 0 | 38.57 | -76.26 | Winter | 2001 – 2005 2011 – 2015 |
| Delaware Bay | Eastern | 0 | 0 | 16 | 11 | 0 | 0 | 38.80 | -75.16 | Winter | 2013 – 2015 |
| **SOUTH ATLANTIC BIGHT** | | | | | | | | | | | |
| Pamlico Sound | Eastern | 0 | 0 | 21 | 18 | 0 | 0 | 35.28 | -76.33 | Winter | 2012 – 2015 |
| **ALASKA** | | | | | | | | | | | |
| Aropuk Lake | Western | 20 | 15 | 0 | 0 | 0 | 0 | 61.13 | -163.89 | Breeding | 2005 – 2006 |
| Canvasback Lake | Western | 0 | 0 | 0 | 0 | 7 | 7 | 66.39 | -146.36 | Breeding | 1999 – 2002 |
| Orca Inlet, Gulf of Alaska | Western | 0 | 0 | 0 | 0 | 20 | 12 | 60.55 | -145.80 | Spring migration | 2000 |
| Juneau | Western | 0 | 0 | 34 | 12 | 19 | 10 | 58.21 | -134.27 | Winter | 2001 2008 – 2019 |
| Kodiak Island | Western | 22 | 15 | 0 | 0 | 0 | 0 | 57.73 | -152.50 | Winter | 2004 – 2006 |
| Montague Strait, Prince William Sound | Western | 0 | 0 | 12 | 5 | 0 | 0 | 60.36 | -147.22 | Spring migration | 1998 |
| Yakutat Bay | Western | 0 | 0 | 8 | 4 | 7 | 3 | 59.63 | -139.72 | Spring migration | 2019 |

| Location | Population | BS Dep | BS Ret | SS Dep | SS Ret | W-WS Dep | W-WS Ret | Lat | Long | Dep season | Dep years |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Fox Islands, Aleutian Islands | Western | 10 | 6 | 0 | 0 | 0 | 0 | 53.85 | -166.57 | Winter | 2007 |
| Nelson Lagoon, Aleutian Islands | Western | 34 | 25 | 0 | 0 | 0 | 0 | 56.00 | -161.08 | Spring migration | 2003 – 2004 2015 – 2016 |
| **BRITISH COLUMBIA** | | | | | | | | | | | |
| Queen Charlotte Sound | Western | 0 | 0 | 28 | 18 | 0 | 0 | 53.93 | -128.72 | Spring migration | 2014 |
| Vancouver Island | Western | 15 | 10 | 9 | 6 | 26 | 11 | 49.30 | -124.50 | Winter | 2003 – 2005 |
| **BAJA CALIFORNIA** | | | | | | | | | | | |
| Baja California | Western | 0 | 0 | 15 | 7 | 0 | 0 | 30.39 | -115.97 | Winter | 2005 – 2006 |
| **CALIFORNIA** | | | | | | | | | | | |
| San Francisco Bay | Western | 0 | 0 | 29 | 15 | 0 | 0 | 37.72 | -122.26 | Winter | 2003 – 2006 |
| **WASHINGTON STATE** | | | | | | | | | | | |
| Puget Sound | Western | 0 | 0 | 32 | 29 | 19 | 17 | 47.50 | -122.40 | Winter | 2003 – 2006 |
| **GRAND TOTAL** | | **213** | **160** | **374** | **235** | **195** | **143** | | | | |

**Notes**: BS = black scoter (*Melanitta americana*), SS = surf scoter (*Melanitta perspicillata*), W-WS = white-winged scoter (*Melanitta deglandi*); Dep = deployed, Ret = retained; Lat = latitude; Long = longitude; Dep season = deployment season; Dep years = deployment years; Spring migr = spring migration.

**Table S2. Location and size of each cluster (*n* = 88) used by North American scoters tracked from 1998 to 2019, calculated from an unsupervised clustering approach (bold text denotes the ten highest-ranked multispecies sites)**

| Cluster ID | Latitude | Longitude | Site name | General area | Country | Habitats | Average rank, all centrality metrics |
|---|---|---|---|---|---|---|---|
| 1 | 55.94 | −160.77 | Nelson Lagoon, Aleutian Islands | SW Alaska | US | Marine | 28.0 |
| 2 | 59.6 | −162.21 | Kuskokwin Bay, Bethel Census Area | SW Alaska | US | Marine | 39.0 |
| 3 | 61.31 | −165.02 | Hooper Bay and Scammon Bay, Kusilvak Census Area | Alaska | US | Terrestrial | 38.4 |
| 4 | 53.75 | −166.62 | Unimak Bight, Aleutian Islands | SW Alaska | US | Marine | 68.9 |
| 5 | 59.82 | −163.81 | Etolin Strait (Cook Strait) | SW Alaska | US | Marine | 20.6 |
| 6 | 55.41 | −162.86 | Bechevin Bay, Aleutian Islands | SW Alaska | US | Marine | 55.3 |
| 7 | 58.75 | −160.31 | Togiak Bay, Iilgayaq (Bristol Bay) | SW Alaska | US | Marine | 63.9 |
| 8 | 65.29 | −161.48 | Kotzebue Sound and Norton Sound, NW Arctic Borough and Nome Census Area | NW Alaska | US | Terrestrial | 75.1 |
| 9 | 49.86 | −124.98 | Strait of Georgia | Vancouver Island, BC | Canada | Marine | 11.9 |
| 10 | 54.06 | −131.59 | Hecate Strait | Haida Gwaii, BC | Canada | Marine | 16.4 |
| 11 | 58.41 | −157.64 | Kvichak Bay and Nushagak Bay, Dillingham Census Area | SW Alaska | US | Marine | 7.3 |
| 12 | 53.54 | −129.12 | Queen Charlotte Sound | Kitimat, BC | Canada | Marine | 50.9 |
| 13 | 49.17 | −122.88 | Salish Sea | Whatcom County, Washington State/ Vancouver, BC | US/ Canada | Marine | 21.1 |
| 14 | 59.94 | −139.98 | Yakutat Bay | SE Alaska | US | Marine | 59.6 |
| 15 | 60.44 | −146.44 | Montague Strait, Prince William Sound | Southcentral Alaska | US | Marine | 34.9 |
| 16 | 59.24 | −154.11 | Cook Inlet (Kamishak Bay, Cungaaciq), Kenai Peninsula | Southcentral Alaska | US | Marine | 48.5 |
| 17 | 56.88 | −158.91 | Aniakchak, Iilgayaq (Bristol Bay) | SW Alaska | US | Marine | 63.6 |
| 18 | 57.81 | −152.49 | Kodiak Island and Kenai Fjords | Southcentral Alaska | US | Marine | 49.5 |
| 19 | 47.61 | −122.99 | Puget Sound | Washington State | US | Marine | 10.5 |
| 20 | 61 | −107.11 | Arctic Ocean Watershed | Northwest Territories/ Saskatchewan | Canada | Terrestrial | 32.4 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 21 | 60.79 | −116.53 | Great Slave Lake (W side), Arctic Ocean Watershed | Northwest Territories/ Alberta | Canada | Terrestrial | 36.8 |
| 22 | 33.19 | −117.61 | Baja California | California/Baja California | US/ Mexico | Marine | 83.9 |
| 23 | 37.6 | −122.17 | San Francisco Bay | California | US | Marine | 76.6 |
| 24 | 62.49 | −119.55 | Willow Lake, Arctic Ocean Watershed | Northwest Territories | Canada | Terrestrial | 42.8 |
| 25 | 57.99 | −134.1 | Taku River, Juneau | Alaska/BC/Yukon | US/ Canada | Marine | 12.6 |
| 26 | 58.47 | −121.72 | Peace River, Arctic Ocean Watershed | BC/Alberta/ Northwest Territories | Canada | Terrestrial | 70.2 |
| 27 | 66.74 | −124.74 | K'áhbamı̧́túé (Colville Lake), Arctic Ocean Watershed | Northwest Territories | Canada | Terrestrial, marine | 21.7 |
| 28 | 68.09 | −132.63 | Inuvik, Mackenzie River, Arctic Ocean Watershed | Northwest Territories/ Yukon (Gwich'in Lands) | Canada | Terrestrial, marine | 47.1 |
| 29 | 68.03 | −128.36 | Fort Good Hope (Charter Community of K'asho Got'ine), Arctic Ocean Watershed | Northwest Territories | Canada | Terrestrial, marine | 34.3 |
| 30 | 56.42 | −132.11 | Zimovia Strait and Stikine River | SE Alaska/BC | US/ Canada | Marine | 53.9 |
| 31 | 54.8 | −113.61 | Lesser Slave Lake, Arctic Ocean Watershed | Alberta/Saskatchewan | Canada | Terrestrial | 57.6 |
| 32 | 59.45 | −136.08 | Glacier Bay and Kusawa Lake | Alaska/BC/Yukon | US/ Canada | Marine | 55.4 |
| 33 | 58.95 | −97.69 | Tadoule Lake, Hudson Bay Watershed | Manitoba/Nunavut | Canada | Terrestrial | 42.2 |
| 34 | 59.02 | −94.86 | W Hudson Bay | Manitoba/Nunavut | Canada | Terrestrial | 32.7 |
| 35 | 64.67 | −116.53 | Ingray Lake, Arctic Ocean Watershed | Northwest Territories | Canada | Terrestrial | 74.3 |
| 36 | 60.4 | −128.2 | Watson Lake, Arctic Ocean Watershed | SE Yukon | Canada | Terrestrial | 81.6 |
| 37 | 61.57 | −111.78 | Lake Claire and Great Slave Lake, Arctic Ocean Watershed | Alberta/ Northwest Territories | Canada | Terrestrial | 28.8 |
| 38 | 42.47 | −124.26 | Coos Bay | N California/ Oregon | US | Marine | 61.9 |
| 39 | 61.51 | −102.59 | Dubawnt Lake, Hudson Bay Watershed | Northwest Territories/ Nunavut/Saskatchewan/ Manitoba | Canada | Terrestrial | 45.5 |

| 40 | 66.11 | −120.74 | Sahtú (Great Bear Lake), Arctic Ocean Watershed | Northwest Territories | Canada | Terrestrial | 52.6 |
|----|-------|---------|--------------------------------------------------|------------------------|--------|-------------|------|
| 41 | 67.16 | −139.55 | Mackenzie Bay, Arctic Ocean and Pacific Ocean Watersheds | Northeastern Alaska/Yukon | US/Canada | Terrestrial | 63.8 |
| 42 | 66.62 | −146.21 | Yukon River, Pacific Ocean Watershed | Alaska | US | Terrestrial | 72.3 |
| 43 | 55.31 | −86.48 | Winisk River, Hudson Bay | Ontario | Canada | Terrestrial | 60.6 |
| 44 | 56.32 | −79.34 | SE Hudson Bay | Sanikiluaq Inuit Land | Canada | Terrestrial | 61.5 |
| 45 | 41.55 | −70.02 | Cape Cod Bay and Eastern Nantucket Sound | Massachusetts | US | Marine | 6.7 |
| 46 | 40.29 | −73.8 | Lower Hudson River and Barnegat Bay | New York/New Jersey | US | Marine | 63.3 |
| 47 | 50.05 | −62.38 | Northern Gulf of St Lawrence | Quebec | Canada | Marine | 70.6 |
| 48 | 51.69 | −80.64 | Moose River, Hudson Bay Watershed | SW James Bay | Canada | Terrestrial | 34.6 |
| 49 | 54.21 | −79.44 | Akimiski Island, Hudson Bay Watershed | Nunavut | Canada | Terrestrial | 15.5 |
| 50 | 41.24 | −70.41 | W Nantucket Sound and Buzzards Bay | Massachusetts | US | Marine | 3.3 |
| 51 | 38.96 | −74.98 | Delaware Bay | New Jersey/Delaware | US | Marine | 20.8 |
| 52 | 46.41 | −64.5 | Northumberland Strait, Gulf of St Lawrence and Bay of Fundy | New Brunswick | Canada | Marine | 37.5 |
| 53 | 56.98 | −92.53 | Nelson River, Hudson Bay | Manitoba | Canada | Terrestrial | 61.1 |
| 54 | 56.85 | −89.79 | SW Hudson Bay | Manitoba/Ontario | Canada | Terrestrial | 39.8 |
| 55 | 51.89 | −79.55 | Hannah Bay, Hudson Bay Watershed | Ontario/Quebec | Canada | Terrestrial | 19.5 |
| 56 | 41.13 | −71.79 | Block Island Sound | Rhode Island/New York | US | Marine | 9.6 |
| 57 | 48.11 | −66.25 | Chaleur Bay, Gulf of St Lawrence | New Brunswick/Quebec | Canada | Marine | 26.0 |
| 58 | 47.18 | −64.85 | Miramichi Bay, Gulf of St Lawrence | New Brunswick | Canada | Marine | 26.8 |
| 59 | 59.04 | −78.1 | E Hudson Bay | Quebec | Canada | Terrestrial | 81.6 |
| 60 | 56.76 | −76.59 | Umiujaq, Hudson Bay | Quebec | Canada | Terrestrial | 44.8 |
| 61 | 31.83 | −80.88 | Blake Plateau | Georgia/South Carolina | US | Marine | 71.6 |
| 62 | 44.25 | −68.58 | Penobscot Bay | Maine | US | Marine | 61.4 |
| 63 | 48.4 | −69.2 | Upper St Lawrence River | Quebec | Canada | Marine | 2.8 |
| 64 | 52.37 | −78.82 | SE James Bay, Hudson Bay Watershed | Quebec | Canada | Terrestrial | 30.3 |
| 65 | 44.73 | −66.49 | Grand Manan Basin, Gulf of Maine | Maine/New Brunswick | US/Canada | Marine | 41.8 |
| 66 | 42.88 | −70.71 | Massachusetts Bay and Casco Bay | Massachusetts/New Hampshire/Maine | US | Marine | 45.0 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| 67 | 50.11 | −65.73 | W Gulf of St Lawrence | Quebec | Canada | Marine | 14.7 |
| 68 | 52.85 | −80.87 | James Bay, Hudson Bay Watershed | Ontario | Canada | Terrestrial | 26.2 |
| 69 | 40.84 | −72.72 | Long Island Sound | New York/Connecticut | US | Marine | 30.5 |
| 70 | 37.94 | −76.03 | Lower Chesapeake Bay | Maryland/Virginia | US | Marine | 29.0 |
| 71 | 49.18 | −67.85 | Upper St Lawrence Estuary | Quebec | Canada | Marine | 18.6 |
| 72 | 54.14 | −82.35 | NW James Bay, Hudson Bay Watershed | Ontario | Canada | Terrestrial | 45.7 |
| 73 | 37.21 | −75.93 | Mouth of Chesapeake Bay | Virginia | US | Marine | 43.7 |
| 74 | 53.86 | −58.42 | Hamilton Bank, Labrador Sea | Newfoundland/Labrador | Canada | Marine | 67.6 |
| 75 | 56.14 | −61.36 | Saglek Bank, Labrador Sea | Newfoundland/Labrador | Canada | Marine | 55.5 |
| 76 | 56.33 | −68.41 | Ungava Bay | Quebec | Canada | Terrestrial, marine | 65.2 |
| 77 | 56.67 | −72.51 | Clearwater Lakes (Lac à l'Eau Claire) | Quebec | Canada | Terrestrial | 77.0 |
| 78 | 35.28 | −76.33 | Pamlico Sound | North Carolina | US | Marine | 50.2 |
| 79 | 38.57 | −76.26 | Upper Chesapeake Bay | Washington, DC, and Maryland | US | Marine | 54.9 |
| 80 | 48.39 | −64.65 | Honguedo Strait, Gulf of St Lawrence | Quebec | Canada | Marine | 21.6 |
| 81 | 48.88 | −68.6 | Lower St Lawrence Estuary | Quebec | Canada | Marine | 12.9 |
| 82 | 33.05 | −79.26 | Long Bay | North Carolina/South Carolina | US | Marine | 70.1 |
| 83 | 44.04 | -76.85 | Lake Ontario | Ontario | Canada | Terrestrial | 54.8 |
| 84 | 46.15 | -63.58 | Northumberland Strait, Gulf of St Lawrence | Nova Scotia/ Prince Edward Island | Canada | Marine | 24.9 |
| 85 | 46.55 | −60.76 | Cabot Strait, Gulf of St Lawrence | Nova Scotia | Canada | Marine | 79.2 |
| 86 | 52.77 | −72 | Lake Mistassini (Lac Mistassini), Hudson Bay Watershed and Atlantic Ocean Watershed | Quebec | Canada | Terrestrial | 53.1 |
| 87 | 53.97 | −64.64 | George River | Quebec/ Newfoundland & Labrador | Canada | Terrestrial | 77.9 |
| 88 | 43.16 | −80.06 | Lake Erie | Ohio | US | Terrestrial | 61.8 |