Modelling connectivity among resource wave hotspots: bears and spawning salmon of coastal British Columbia

by

Ilona Mihalik
B.Sc. Honours, University of Victoria, 2018

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We acknowledge and respect the lək̓ʷəŋən peoples on whose traditional
territory the university stands and the Songhees, Esquimalt and WSÁNEĆ
peoples whose historical relationships with the land continue to this day.

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Abstract

Understanding how important landscape features are connected can provide key information for the management of ecological systems, particularly insight into how species move through and interact with their environment. Landscape features and their spatial arrangement can either promote or deter movement among resource patches by individuals. Over microevolutionary time periods, such movement allows for the persistence of population structure via the exchange of genetic material, particularly in metapopulations spatially separated over fragmented landscapes. Over shorter ecological periods, and less understood, the presence and distribution of important food patches can influence habitat connectivity for mobile species, such as large carnivores. In this work, we examined how five species of Pacific salmon (*Oncorhynchus* spp.), which spawn across varying times (~late April to ~late December) and spatial locations throughout coastal British Columbia (BC), might be associated with movement by grizzly bears (*Ursus arctos horribilis*). Following "resource waves", spatial data show how these mobile consumers track salmon spawns as runs become available over space and time throughout the spawning season. In coastal BC, where bears have never been radio-collared, we know little about how landscape features might affect their ability to travel among salmon spawns. Such information is essential to proactive landscape planning for forest management. Following circuit theory, we used Circuitscape to predict movement among these important resource patches within a 17,000km^2 study area. Variables affecting grizzly movement were parameterized during collaborative meetings with the Heiltsuk Integrated Resource Management Department (HIRMD) and incorporated Indigenous and local knowledge. The modelled current flows suggested important areas of high predicted connectivity between salmon spawns *within* and *among* watersheds. Furthermore, we illustrated potential corridors within the unprotected forest matrix for consideration by HIRMD. Broadly, this work unites connectivity modelling and resource waves research to consider movement among food patches, and directly informs conservation planning by an Indigenous government.

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***Disclaimer: For the purposes of this public document, the study area boundary has been reduced to the Heiltsuk bear hair snag study area (not the territory, as the Heiltsuk Nation defines it), owing to overlapping claims of territories among Indigenous Nations in the area. Original figure showing complete study area is available upon request.**

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Dedication

“We need another and a wiser and perhaps a more mystical concept of animals. Remote from universal nature, and living by complicated artifice, man in civilization surveys the creature through the glass of his knowledge and sees thereby a feather magnified and the whole image in distortion. We patronize them for their incompleteness, for their tragic fate of having taken form so far below ourselves. And therein we err, and greatly err. For the animal shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not brethren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the earth."

- Henry Beston, 1928

1. General introduction and research context

1.1 Background

A major threat worldwide to wildlife is the fragmentation and loss of habitat. A decade ago, Barnosky et al., 2012 estimated 50 to 70% of land on earth had been transformed for human use. Generally, such transformations affect the natural landscape for species in four ways: overall habitat loss, increase in habitat fragments, reduction in size of habitat fragments, and increase in isolation of fragments (Bennett, 1999; Fahrig, 2003). Consequentially, large scale disturbances (i.e., agriculture, urban development, forestry, mining, and other resource extractions) are primary drivers of a global reduction in biodiversity (Newbold et al., 2015). Although transforming natural landscapes into a mosaic of cover-types ranging in habitat viability influences species in different ways, mobile species are particularly impacted at varying spatial and temporal scales (Cosgrove et al., 2018; Doherty et al., 2021). Over shorter periods and distances, individuals can face reduced resource availability (i.e., food, water, and habitat; Levin et al., 2009) and increased competition. Over longer periods and distances, migration and dispersal patterns can be affected, which in turn influence population and community structure (Cosgrove et al., 2018; Coulon et al., 2010). Accordingly, this can impede gene flow and ultimately lead to genetic isolation (Cosgrove et al., 2018; Rudnick et al., 2012).

1.2 Landscape connectivity

As a result of growing land-use changes and their myriad of ecological effects, landscape connectivity has become an increasingly important focus of biodiversity conservation. Following theory from island biogeography (MacArthur & Wilson, 1967), landscape connectivity considers both the structure of a landscape and the decision-making by populations or individuals in navigating it to access resources (Levin et al., 2009; Tischendorf & Fahrig, 2000). The concept was first introduced to ecology by

Merriam (1984) as "the degree to which absolute isolation is prevented by landscape elements which allows organisms to move among patches". In 1993, Taylor et al. focussed this definition to "the degree to which the landscape facilitates or impedes movement among resource patches".

Emerging from the literature are two aspects of landscape connectivity: structural and functional. Structural connectivity refers to the physical and spatial components of the landscape's connectivity, rather than the ability and traits of the organism (Auffret et al., 2015; Tischendorf & Fahrig, 2000). Alternatively, functional connectivity focusses on the perception and behavioural responses of the organisms navigating the landscape structure (Auffret et al., 2015; Tischendorf & Fahrig, 2000; Bélisle, 2005). In the past, structural connectivity has often been the focus for measuring habitat disturbance. However, it is now acknowledged that species respond to disturbance in different ways; although altering the spatial composition may pose certain threats to one species, another may benefit or be unaffected (Tischendorf & Fahrig, 2000, Bennett, 1999). As such, methods of measuring landscape connectivity have expanded to include functional aspects (i.e., gene flow, individual habitat preferences) in addition to the physical layout (Baguette & Van Dyck, 2007; Cushman et al., 2006; Rudnick et al., 2012).

1.3 Connectivity analyses tools

Several analytical approaches for measuring connectivity have emerged to confront the above challenges. Approaches following graph theory (Harary, 1969) have become especially popular since the start of the century; to date there are more than 60 graph-based analytical measures for estimating habitat connectivity (Moilanen, 2011; Rayfield et al., 2011; Urban & Keitt, 2001). Based in mathematics, graph theory considers the connectedness of graphs comprised of nodes and edges

(Figure 1). Within landscape connectivity, nodes can represent resource patches, genes, individuals, or populations, whereas edges represent movement or their interaction (Proulx et al., 2005; Urban & Keitt, 2001). Methods following graph theory have since become more advanced, incorporating spatial and ecological information into the configuration of nodes and edges (Rayfield et al., 2011). For example, network theory applies graph theory and weights nodes and edges by including information on the quality of resource patches and costs associated with movement (Figure 2; Rayfield et al., 2011).

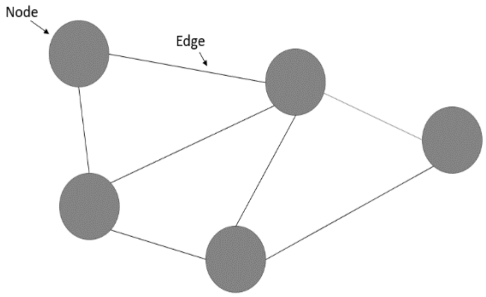


Figure 1: Depiction of a simple graph comprising nodes and edges, following Graph Theory (Harary, 2001).

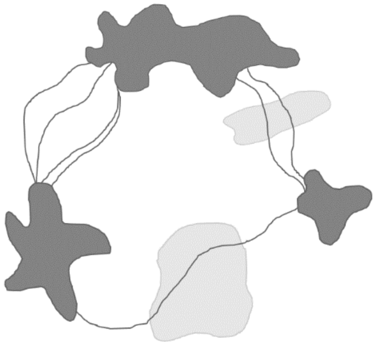
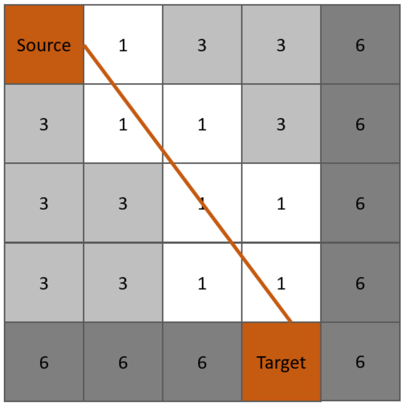


Figure 2: Depiction of a network that includes additional information on the nodes and edges, following Rayfield et al., 2011. Nodes (resource patches) of varying quality are in dark grey. Edges, the dark lines connecting nodes, represent movement and vary in strength as they transverse areas of resistance (light grey).

One of the most used approaches derived from graph and network theories is least cost pathways (LCP) modelling, which identifies the least costly route between two locations (i.e., source and target; Adriaensen et al., 2003; Rayfield et al., 2011). Aside from the source and target spatial data, a raster resistance (to movement) layer is also required (Cushman et al., 2013). The resistance layer is comprised of cells with values reflecting cost to movement for the organism. The least-cost path is estimated as the pathway with the lowest cumulated cost value summed across its cells (Figure 3; Cushman et al., 2013). Therefore, this assumes the organism has complete knowledge of the landscape and can determine the most efficient route.



Source	1	3	3	6
3	1	1	3	6
3	3	1	1	6
3	3	1	1	6
6	6	6	Target	6

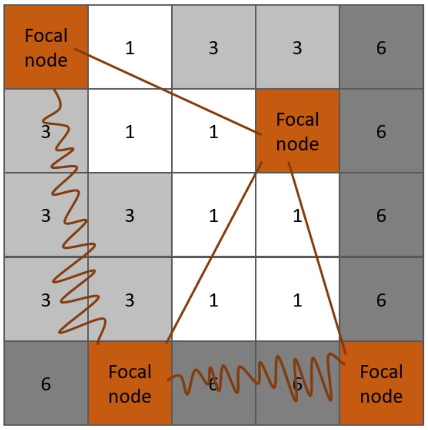
Figure 3: A simple representation of Least Cost Paths (LCP) modelling using a raster resistance layer (grid). Following LCP, the least costly route is estimated between source and target locations.

Recently, approaches incorporating random (unplanned) movement have gained popularity in predicting connectivity for species. For example, drawing on the behaviour of electrical circuits, circuit theory (McRae et al., 2008) models movement similar to current moving through a circuit board. Following Ohm’s Law (Equation 1), current (I) flowing through a system depends on the level of resistance (R) and voltage (V) applied.

(1)

$$I = \frac{V}{R}$$

Circuitscape (Shah & McRae, 2008) is an open-source software that applies circuit theory in an ecological setting to predict connectivity. Focal nodes are connected by resistors (barriers to movement) within a network, and the probability of movement by an individual (i.e., current) is predicted for each pathway (Figure 4). A network or raster layer of resistances is required, which is defined by the user to represent the varying levels of resistance across the landscape for the species in question. All possible movements are predicted among nodes, each varying in strength based on the resistors passed. This approach allows for measuring how well-connected focal nodes are; focal nodes connected by multiple spread-out pathways suggest a highly connected landscape, whereas dense collections of linkages identify bottlenecks where movement is restricted (Cushman et al., 2013; McRae et al., 2008; Rayfield et al., 2011). Defining the bottlenecks, or "pinch points", is particularly useful in this approach, as they represent narrow pathways of high predicted movement navigating a hostile landscape. This provides key information on areas of particular importance to movement for the management of ecological systems.



1.4 Corridors for landscape connectivity

Within land use planning and management, predicting, defining, and protecting corridors has traditionally been one of the most common approaches in preserving landscape connectivity. Forman, 1995 defined corridors in the context of structural connectivity as strips of land differing from the widespread environment (i.e., ‘matrix’) on either side, connecting two habitat patches, and varying in connectivity potential (Tischendorf & Fahrig, 2000; Wade et al., 2015). The effectiveness of corridors, though, has been controversial within the field of landscape connectivity, and largely depends on the species and environment in question, the habitat within and outside the corridor, and their shape (Anderson & Jenkins, 2006; Vogt et al., 2009). Generally, corridors designed for specific species have been found to increase movements between patches across diverse taxa (Gilbert-Norton et al., 2010; Haddad et al., 2003; Resasco, 2019). Indeed, since the concept of corridors first emerged, the idea of focussing solely on the structural components of linkages between patches has instead shifted to focus on species-specific functional connectivity. Functional connectivity models for defining corridors recognize the ability of and requirements for specific species to disperse between patches (Koen et al., 2014; Vogt et al., 2009). Additionally, within the context of functional connectivity, attention has moved from only modelling the single-best corridor between resource patches, to identifying *how well connected* (via multiple corridors) the landscape is between patches (Koen et al., 2014).

1.4.1 Collaborative implementation

Implementing protection for corridors becomes challenging over larger areas. First, there is a disconnect between researchers and managers in general, termed the "research or planning-implementation gap" by Keeley et al., 2018. Although a large body of connectivity literature exists, evidence of successfully translating scientific findings into conservation action alongside land managers is limited (Keeley et al., 2018). Additionally, the management of landscapes involves multiple facets and stakeholders, often balancing ecological, economic, and social interests (Parrott & Meyer, 2012). This becomes even more complicated when corridors cover multiple human systems of governance. Accordingly, successful connectivity conservation which moves past the planning stage requires long-term engagement between researchers, managers, local and Indigenous governments, and other stakeholders involved (Keeley et al., 2018, 2019). Successful implementation may also require foresight; planning corridors important for the functional connectivity of a region early alongside stakeholders may avoid future recovery projects, even for landscapes with relatively low development or human disturbance (Parrott et al., 2019).

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2. Modelling connectivity among resource wave hotspots: bears and spawning salmon of coastal British Columbia

2.1 Introduction

2.1.1 Foraging dynamics and resource waves

Spatial and temporal variation in resource availability can strongly influence the foraging dynamics of wildlife. Movement among food patches by mobile consumers occupying heterogeneous landscapes involves complex trade-offs, as expressed for example in behavioural variation in whether individuals stay at certain patches or travel to exploit others (Stephens & Krebs, 1986; Stephens, 2008). Trade-offs are particularly pronounced when resources are unpredictable and vary across space and time. For example, a key decision for predators is whether to capitalize on food to digestive capacity (i.e., satiation) during periods of abundant prey availability or to alter their functional response and maintain capacity through the exploitation of multiple smaller foraging bouts over space and time (Armstrong & Schindler, 2011).

Emerging theory and data suggest that mobile consumers can maximize their nutritional intake over space and time by following "resource waves". Resource waves represent aggregates of resources that offer ephemeral foraging opportunities at different points across space, displaying spatial variation in resource timing (Armstrong et al., 2016). Whereas pulses of resources can be brief and infrequent in time at certain locations, at a large scale they prolong foraging opportunities for mobile consumers by moving as a wave across a landscape (Armstrong et al., 2016; Service et al., 2019). Indeed, an emergent property of resource waves is the sustained energy provided to mobile consumers tracking pulses of food sources (i.e., "surf the wave") that are otherwise short-lived at small spatial scales (Armstrong et al., 2016). Given that the characteristics of resources vary, many types of resource waves have been specified in the literature, including the "green wave" (i.e., spatiotemporal variation in plant phenology; Fryxell et al., 2005; Sawyer & Kauffman, 2011), the "brown wave" (i.e., spatiotemporal variation of plant roots; Coogan et al., 2012), and "red wave" (i.e., spatiotemporal variation in spawning salmon; Deacy et al., 2018; Service et al., 2019; Van Daele et al., 2013).

2.1.2 Landscape disturbance on consumer movements

To exploit patchy and ephemeral resources, mobile consumers must be able to navigate landscapes that can pose natural and human-caused barriers to movement. Natural features, such as rugged terrain, waterbodies, and glaciers, have long acted as barriers to dispersal for many species and influenced population structures (Lewis et al., 2015; Muñoz-Mendoza et al., 2017; Paetkau et al., 1998). More recently, anthropogenic barriers such as resource extraction and human development have affected movement across taxa (Doherty et al., 2021). In many cases, disturbances act as barriers to consumers and interfere with their ability to migrate and move among resource patches. Disruption of movement in ungulates has been particularly studied. Indeed, Bolger et al., 2008 lists anthropogenic barriers and habitat loss as two of the three human activities (in addition to overhunting), which have resulted in the decline of ungulate migrations around the world. Oil and gas development, for example, has been found to affect the migration patterns of pronghorn (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) by adding detours, limiting stopover opportunities for foraging, and increasing movement rates (Sawyer & Kauffman, 2011; Seidler et al., 2015). Additionally, Holdo et al., 2011 modelled the influence of anthropogenic barriers to wildebeest (*Connochaetes taurinus*) in the Serengeti, as they track seasonal availability of plant resources; results predicted barriers would cause population declines, rendering them increasingly vulnerable to natural disasters.

Large-bodied carnivores (of order Carnivora) are also particularly vulnerable to obstructions to movement. Carnivores often have wide-ranging habitat requirements, large home ranges, and are highly driven in their movements by prey abundance due to their constant energetic requirements (Ripple et al., 2016; Wolf & Ripple, 2016). Mountain lions (*Puma concolor*) within California and the American Southwest, for example, face growing pressures from expanding urban centers and transportation routes (i.e., roads, highways) which impact their movements (Crooks, 2002; McClure et al., 2017). Also within North America, along the borders of British Columbia (BC) and Alberta, Canada, and the United States (US), urban development has affected landscape connectivity for grizzly bears (*Ursus arctos horribilis*; Proctor et al., 2012, 2015). Grizzly bears are especially sensitive to human disturbance compared with other North American carnivore species (i.e., mountain lions, wolves), due to their lower lifetime productivity and dispersal capabilities (Weaver et al., 1996).

Landscape connectivity in the context of resource waves is poorly understood. Although several analytical tools exist for estimating connectivity among resource patches, to our knowledge none have been used on resource wave systems. This is surprising, as many mobile consumers rely on the accessibility and exploitation of pulsed food sources, as mentioned above. Therefore, estimating such functional connectivity among pulses is important for better understanding of these systems, and is currently missing within the connectivity and resource wave literatures.

2.1.3 Study system

Here we address this gap in the literatures via grizzly bear-salmon systems of coastal BC. Grizzly bears, a mobile consumer, occupy a variety of habitats to cover their feeding territory and omnivorous diet, spanning from high alpine meadows to low coastal forests within BC (Hatler et al., 2008; Schwartz et al., 2003). Their diets and foraging behaviour follow seasonal shifts in food availability. After emerging from hibernation in the spring and searching for plant matter, terrestrial meat, and intertidal organisms, most grizzlies on the coast move to feed on pulses of spawning Pacific salmon

(*Oncorhynchus* spp.) during midsummer and fall months (Hilderbrand et al., 1999; Mowat & Heard, 2006; Hatler et al., 2008; Schwartz et al., 2003). Although consumption varies by individuals, salmon provide a major contribution to diet of coastal grizzly bears (median proportion up to 62% of annual diet; Adams et al., 2017), and is associated with increased body size, mobility, cub litter size, and reproductive success and reduced stress hormones (Hilderbrand et al., 1999; Mowat & Heard, 2006; Adams et al., 2017; Bryan et al., 2013). Five species of Pacific salmon inhabit the coastal waters of the Pacific Northwest region: Chinook (*O. tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*; Gende et al., 2002). Each species returns to freshwater systems at differing times throughout the spawning period, which can span from late April to late December (Service et al., 2019). How far upstream salmon migrate to their respective reaches (i.e., spawning and rearing extent) also varies by species and location (Gende et al., 2002; Service et al., 2019). Following resource waves, the spatial and temporal variation in spawning pulses creates opportunities for prolonged access by grizzly bears. Indeed, salmon availability is a major driver of inter-seasonal movement. Studies from Alaska (Deacy et al., 2016; Deacy et al., 2018; Schindler et al., 2013) indicated that brown bears have evolved to track the different spawning events; individuals that spend more time moving among them within and across watersheds consume more salmon overall (Deacy et al., 2018). Within this region, grizzly bears are known to either move among pulses within the same watershed or stream neighbourhood (Wirsing et al., 2018), or move between larger watersheds to access pulses (Barnes, 1990; Deacy et al., 2016).

2.1.4 Objectives

Although the theoretical foundations of resource waves regarding salmon and grizzly bears is now well developed, and empirical movement and diet data exist (Deacy et al., 2016; Deacy et al., 2018; Schindler et al., 2013), to our knowledge no studies have examined or predicted how landscape features and human disturbances might affect the ability of bears to move among salmon reaches during the spawning period. Additionally, although majority of the Pacific Northwest coast of North America is similar ecologically, all resource wave studies on these trophic interactions are within coastal Alaska, and none exist within BC. This is important, as the subspecies of bears within coastal Alaska (Kodiak bears; *Ursus arctos middendorffi*) are generally larger in body size, potentially due to inhabiting ecosystems with more abundant salmon (Hilderbrand et al., 2018). BC's salmon resources by contrast are more spatially discontinuous, including more smaller streams and fewer larger streams (Hyatt et al., 2007; Price et al., 2017). Accordingly, grizzly bears on the BC coast may rely on a larger radius of intact connections among salmon spawns than those in Alaska.

Our objective is to estimate grizzly bear functional connectivity among Pacific salmon reaches, both within and across watersheds, within the central coast of BC. Following circuit theory, we use Circuitscape (Shah & McRae, 2008) to model connections. This work is applied; working by invitation with the Heiltsuk Integrated Resource Management Department (HIRMD), within whose Territory this study occurs, we aimed to not only estimate connectivity, but also identify candidate corridors important to grizzly bears for consideration by HIRMD. Emphasis will be placed on identifying areas of importance around and between some watersheds considered important to the Haíłzaqv (Heiltsuk), who are considering additional forestry protection and solicited research on this culturally important bear-salmon system. Overall, this work will not only add to connectivity and resource wave research by considering dynamic movement among food patches, but also directly inform conservation planning by an Indigenous government.

2.2 Methods

2.2.1 Study area

The study area is located on the Central Coast of BC, Canada (Figure 5). The area spans approximately 17,000km^2 and is within the traditional territories of the Haíłzaqv Nation, as defined by the Nation. We chose to exclude islands within the study area known to have grizzly bears visit too infrequently (i.e., Campbell, Hunter, Denny, Cunningham, Chatfield Islands, etc.), as assessed by local and scientific knowledge (Service et al., 2014). The landscape, described previously (Adams et al., 2017; Bryan et al., 2013; Service et al., 2014, 2019), includes mainland valleys, large inlets, and many other coastal islands known to be consistently occupied by grizzlies. The region is characterised by climatic, biological, and geographic variation, covering the Coastal Western Hemlock, Mountain Hemlock, and Coastal Mountain-heather Alpine biogeoclimatic zones at different elevations (Meidinger & Pojar, 1991). Additionally, the study area covers six ecosections: Kimsquit ranges, Nechako upland, Western Chilcotin ranges, Kitimat ranges, Northern Pacific ranges, and Hecate lowlands. Although the connectivity modelling is conducted across the entire study area, we combined the covered ecosections into two broad regions to separately visualize corridors (Figure 6): "Lowlands" comprised of the Northern Pacific ranges and Hecate lowlands; "Coast mountains", comprised of the Kimsquit ranges, Nechako upland, Western Chilcotin ranges, and Kitimat ranges. We separated the regions in defining areas of highest current because of the extraordinary variation between them in ruggedness, a variable that predicts connectivity. Accordingly, separation allows us to identify and visualize areas of high connectivity relative to each region.

Human and industrial disturbance is lower compared to many other landscapes at these latitudes. Although forestry activity is now present throughout, much of the area lacks connected road systems. The area also has low human density since colonization and associated genocide imposed by Europeans.

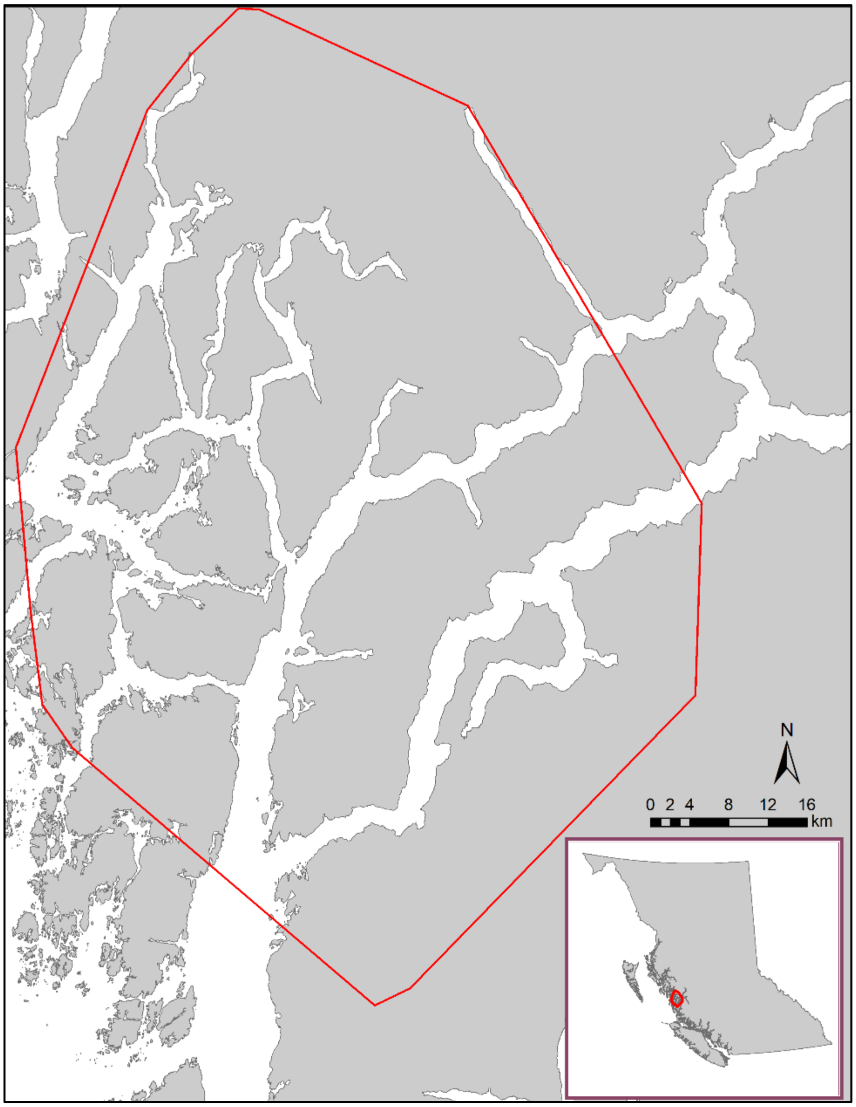


Figure 5: Study area (red; 17000km2) used to model connectivity for grizzly bears. Heiltsuk Territory, as defined by the Heiltsuk Nation, Central coast of British Columbia, Canada. **Disclaimer: For the purposes of this public document, the study area boundary has been reduced to the Heiltsuk bear hair snag study area (not the territory, as the Heiltsuk Nation defines it), owing to overlapping claims of territories among Indigenous Nations in the area. Original figure showing complete study area is available upon request.*

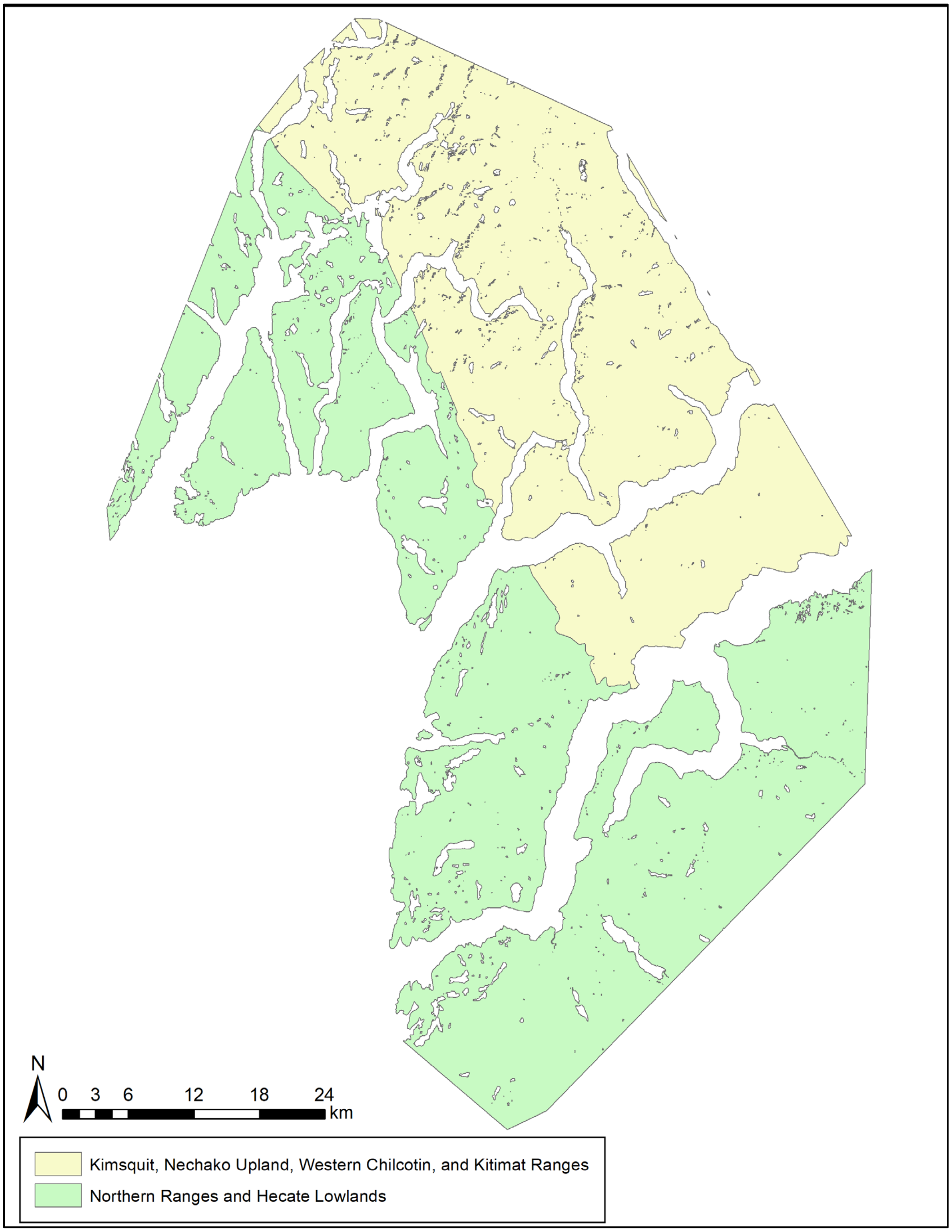


Figure 6: The study area covers six ecosections: Kimsquit ranges, Nechako upland, Western Chilcotin ranges, Kitimat ranges, Northern Pacific ranges, and Hecate lowlands. Following our analyses below, and to visualize connectivity separately within the mountains and lowlands, we combined these into two broad regions: "Lowlands" (in blue) comprised of the Northern Pacific ranges and Hecate lowlands; "Coast mountains" (in green) comprised of the Kimsquit ranges, Nechako upland, Western Chilcotin ranges, and Kitimat ranges. **Disclaimer: For the purposes of this public document, the study area boundary has been reduced to the Heiltsuk bear hair snag study area, owing to overlapping claims of territories among Indigenous Nations in the area. Original figure showing complete study area is available upon request.*

2.2.2 Data sources

We downloaded landcover (including water) and forestry harvest year data (1985 to 2010) from the National Forest Information System (NFIS; Hermosilla et al., 2016, 2018). The landcover data included cover type characterization for all of Canada in 2015 (Hermosilla et al., 2016, 2018). We reclassified the landcovers to represent our habitat variables (below), and separated water into its own spatial layer for analysis. We included additional forestry harvest year data to account for harvests prior to 1985 (Leversee, D., Sierra Club of Canada, unpublished data), which combine provincial "Consolidated Cutblocks", "Reporting Silviculture Updates and Land Status Tracking System" (RESULTS), and "Forest Tenure" (FTEN) datasets that identify cut blocks. We derived the terrain ruggedness index from a digital elevation model (DEM) using the Raster Terrain Analysis plugin in QGIS (which followed methods from Riley et al. 1999).

2.2.3 Resistance surfaces

2.2.3.1 Selection of habitat variables through engagement with the Heiltsuk First Nation's Integration Resource Management Department (HIRMD)

We selected variables likely to affect grizzly bear movement, reasoning that selected and avoided habitats would promote and restrict movements, respectively, and scaled their resistance based on previous literature. We also engaged in depth with HIRMD, whom we have worked with for over a decade to non-invasively monitor grizzly bears within the area (Adams et al., 2017; Bryan et al., 2013; Service et al., 2014, 2019). HIRMD provided their local knowledge and scientific experience in the resistance surface parameterization as part of ongoing forestry and land use planning. William Housty, in particular, provided considerable expertise on movement patterns based on his previous demographic and mark-recapture work within the study area (Housty et al., 2014). In our collaboration meetings, we first explained the analytical approach used (Circuitscape; below) and presented three candidate variables from the literature for discussion: terrain ruggedness, water (by distance), and landcover. We agreed on a straightforward approach to ruggedness and water barriers, although modified our initial suggestion for landcover. HIRMD also suggested two new variables that would influence grizzly movement: forestry age class (i.e., previously logged) and tidal currents. We adopted the forest age class suggestion, but after data preparation we did not pursue tidal currents. There were inadequate spatial data and the velocities of current in the area (0.002-0.572 m/s range) was lower than that shown to influence large semi-aquatic and marine mammals (Williams, 1999). Additionally, there was only one region inside our study area in which currents were near the higher end of variation. We concluded that incorporating the variable was not worth the uncertainty and extra processing required. Overall, we decided to use four variables (Table 1). Further descriptions of the decision processes involved in parameterization and their justification are discussed below for each.

Table 1: Assigned resistance values (unitless, ranging from 1 [very low] to 6 [very high]) for each habitat variable and corresponding classes. Values were used to create the four habitat variable resistance layers.

Habitat variable	Resistance	Resistance value (1-6)
Terrain ruggedness (TRI)		
1-25	Very low	1
25-50	Low	2
50-88	Low-medium	3
88-139	Medium-high	4
139-230	High	5
230-271	Very high	6
Landcover		
Mature forest (non-harvested or harvested over 70 years ago)	Very low	1
Bryoids, shrubland, wetland, treed- wetland, herbs	Very low	1
Barren, exposed, rock	Very low	1
Snow or Ice	Very high	6
Forestry age class		
Previously harvested 10-70 years ago	Low-medium	3
Water (by distance; km)		
<1	Low-medium	3
1-3	High	5
>3	Very high	6

Landcover class: Grizzly bears have been found to use a variety of landscape features, though some act as barriers to movement. Originally, we suggested separating landcover into seven classes, with distinct categories for different forest covers. In discussing the applicability to our study area with HIRMD, we instead combined the different forest covers into one class ("mature forest"), reasoning that stands within the area that were never subject to industrial forestry are very similar in resistance. Accordingly, we identified four landcover types that affect grizzly movement: (1) mature forest, (2) bryoids/shrubland/wetland/treed wetland/herbs (i.e., shrubs) (3) barren/exposed/rock, and (4) snow or ice. We assigned all landcover types, except snow or ice, the lowest resistance score. Grizzly bears have been found to select for habitats with mature forests and shrubs of mixed types/species, as well as avalanche chutes (Apps et al., 2004; McLellan & Hovey, 2001; Nielsen et al., 2002, 2010). In addition, we assumed that bare rock environments, which grizzlies select (Apps et al., 2004; Waller & Mace, 1997; Zager et al., 1983) would not act as a barrier to their movement. We assigned snow or ice environments the highest resistance value, because they provide few food resources, and grizzlies have been found via habitat selection modelling to avoid snow cover (Berman, 2019). Additionally, snow increases energetic costs of movement in ungulates (Parker et al., 1984), which we assumed would apply to grizzly bears as well.

Water: Grizzly bears can be proficient swimmers, but water likely imposes greater cost than terrestrial movement. Grizzlies have been recorded swimming 34km to remote islands in Alaska (Mattson et al., 2005). On the other hand, Bond et al., 2012 found that the Ocmulgee River (width ~50m) in Georgia did often hinder movements by the smaller black bear (*Ursus americanus*), especially females. Similarly, White et al., 2000 found a river 1.6km wide to be a barrier to black bear movement (again prominent in females), whereas another river (width ~200m) was not. Additionally, and although over a longer time-period, Paetkau et al., 1998 suggested water crossings 2-4km and 7km in width are barriers to brown bear dispersal based on the genetic isolation of populations within the Kodiak Archipelago, Alaska. Given these findings, we estimated that smaller crossings (<1km) such as small inlets, rivers, or lakes within our study area would impose moderate resistance, while those greater than

1km would increasingly resist movement. We therefore assigned water areas the following resistance values, based on distance from land: <1km = low/medium, 1-3km = high, and >3km = very high. We used the Multiple Ring Buffer Analysis tool in ArcMap 10.7.1 (ESRI 2019) to estimate waterway width to assign the resistance values.

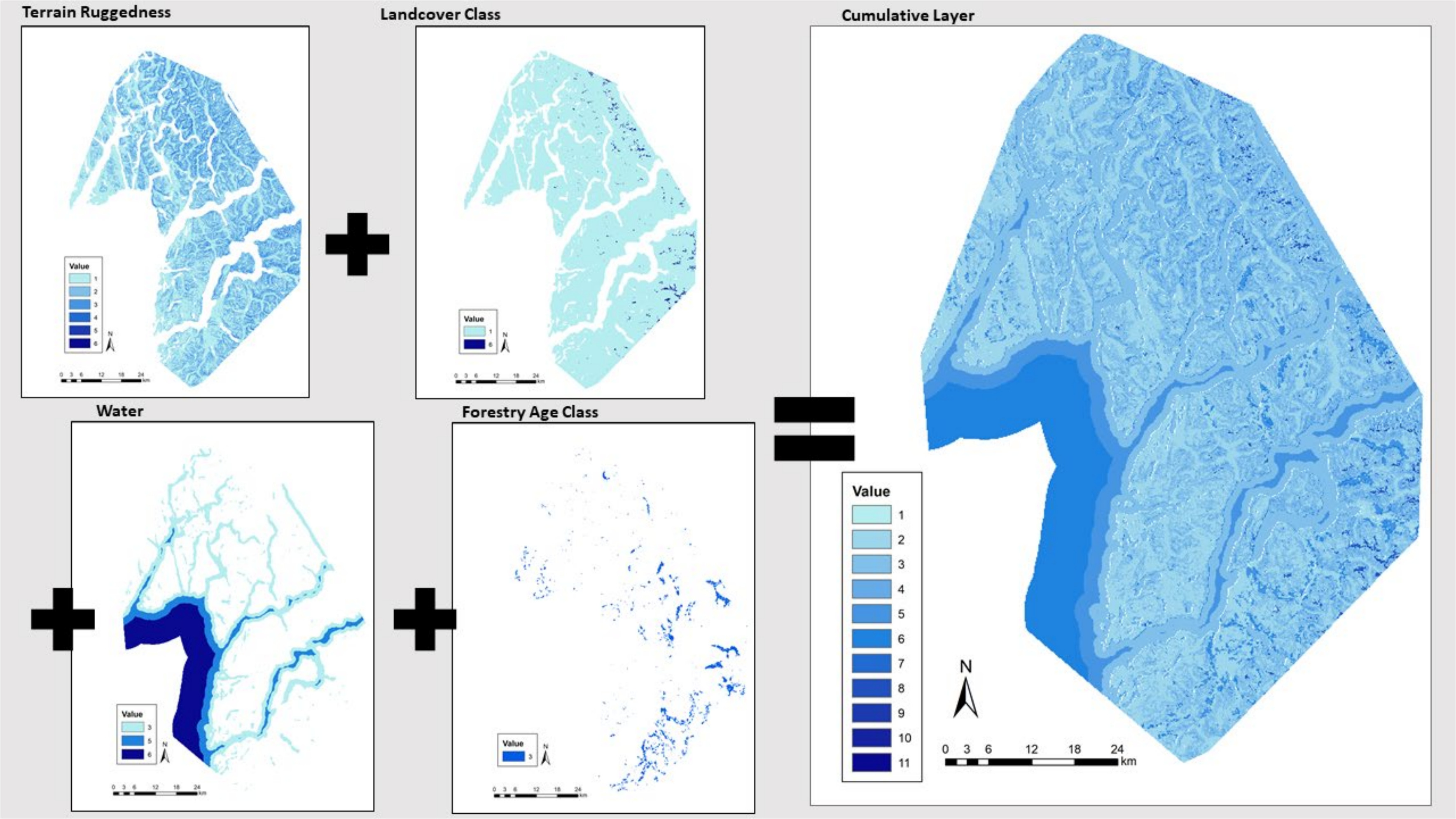
Forestry age class: Discussions with HIRMD and previous literature identified that landscape permeability for grizzly bears likely varies based on post-logging forest age class. During the early regrowth period, pioneer species and shrubs of little resistance colonize the cut blocks. Approximately 10-70 years post harvest, however, cut blocks in productive coastal temperate rainforests progress through a hyper-dense stage comprised of small and medium-diameter trees, before self-thinning occurs (Wells, 1992). We expected this period would act as a moderate barrier to grizzly movement, as well as a window during which few shrub and understory plant resources are available (Wallmo & Schoen, 1980; Alaback, 1982, 1984). We therefore assigned regenerating stands between 10-70 years old a low-medium resistance value.

Terrain ruggedness: Although grizzly bears are known to move up to higher elevations in the area (often scaling steep terrain), we assumed ruggedness would impose resistance to movement during the salmon spawn. Over longer time periods, landscapes with higher ruggedness have been associated with a greater variance in genetic relatedness in grizzly bears (Lewis et al., 2015), suggesting ruggedness imposes costs to movement over the long term. Context also matters. Specifically, at a smaller temporal scale and in areas of increased human activity, grizzly bears have been found to prefer rugged and steep landscapes as they inhibit human access and development (Apps et al., 2004). However, in areas of lower human density grizzly (relevant to our study area and scale) bears were found to prefer lower elevation valley bottoms, particularly during the late summer and fall months (Collins et al., 2005;

McLellan & Hovey, 2001). This could be explained by the seasonal shift in their food sources to lower elevations, as well as the lower energetic costs of traveling over flat terrain (Carnahan et al., 2021; Roever et al., 2008). Given these patterns and details of our study area, we increased resistance values with terrain ruggedness at intervals following Jenks natural breaks. This classification method splits data into clusters of similar (low variation) values, i.e., the natural breaks within the dataset.

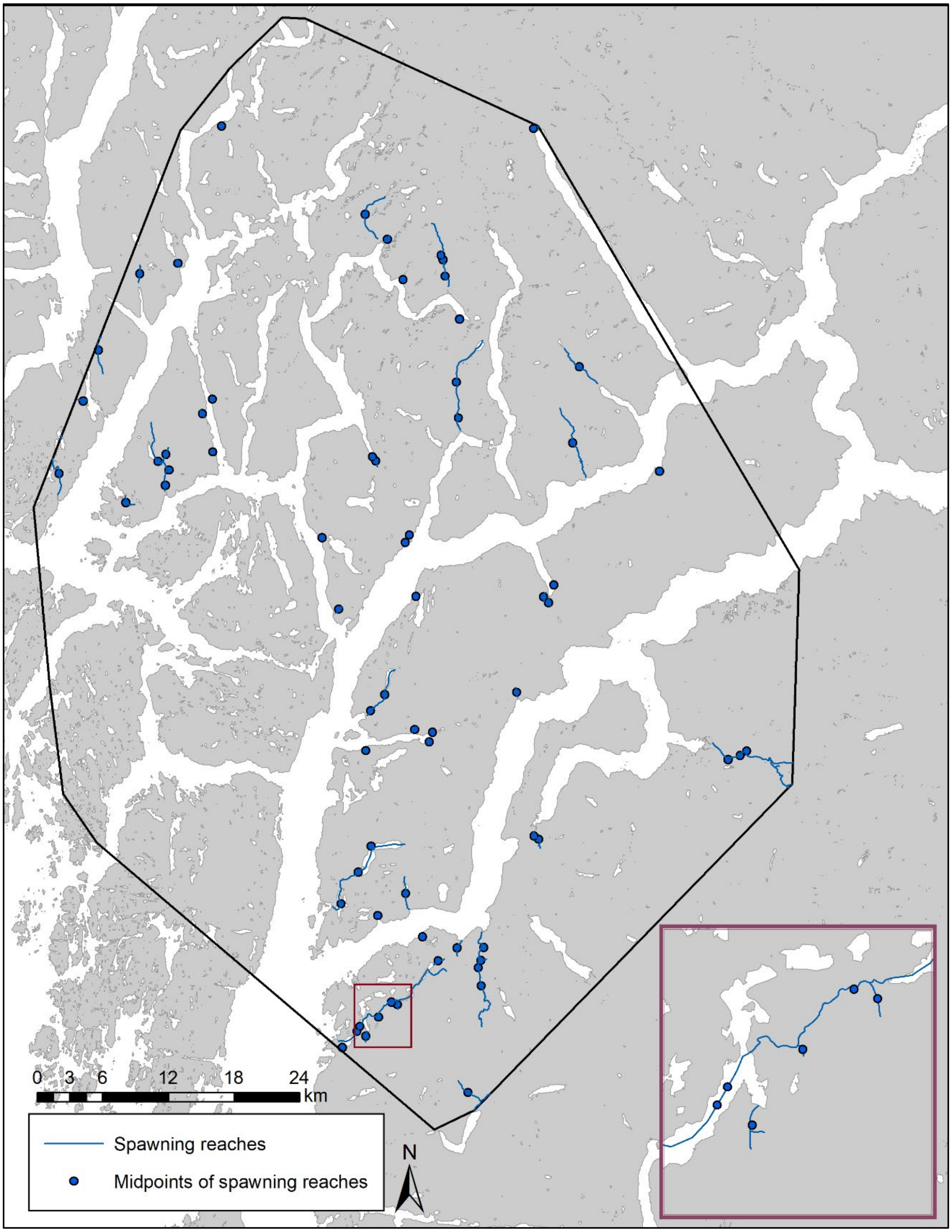
2.2.3.2 Cumulative layer

We summed the four individual resistance layers to identify areas of high and low cumulative resistance. The four resistance layers were created using ArcMap 10.7.1 (ESRI 2019). We converted each raster data layer to EPSG:3005 coordinate system with the NAD83 datum and BC Environment Albers projection. We resampled each layer to a spatial resolution of 150m to balance the computational capacity of running the models. This cell size also follows similar sizes from previous brown bear connectivity and landcover suitability modelling analyses (Almasieh et al., 2019; Falcucci et al., 2008; Henson et al., 2021). After combining the four layers into our cumulative (additive) layer for Circuitscape, our new resistance scale ranged from 1 to 12 (Figure 7). We then clipped the final layer to the study area with a 10km buffer to account for potential edge effects (Koen et al., 2010).


Terrain Ruggedness
Value
1
2
3
4
5
6
Landcover Class
Value
1
6
Water
Value
3
5
6
Forestry Age Class
Value
3
Cumulative Layer
Value
1
2
3
4
5
6
7
8
9
10
11
N
0 3 6 12 18 24
km

2.2.4 Focal nodes

To model connectivity for grizzlies among salmon hotspots, both within and between watersheds, we used the midpoints of each Pacific salmon species reach (hereafter “reach”) per stream as “focal nodes” in Circuitscape. We downloaded and modified the reach spatial data from the BC Data Catalogue. Streams were first distinguished by their “watershed code”, a numeric code unique to each watershed tributary. In many cases, species had multiple reaches within an individual stream. For these, we used the midpoint of all reaches belonging to an individual species per stream. In the cases where multiple reach-midpoints overlapped, we used the mean center of nodes within 150m of one another to simplify, which also recognized the 150m cell resolution of our cumulative resistance layer. In total, we defined 258 focal nodes representing salmon reaches within our study area (Figure 8).


0
3
6
12
18
24
km
Spawning reaches
Midpoints of spawning reaches
N

2.2.5 Circuitscape analysis

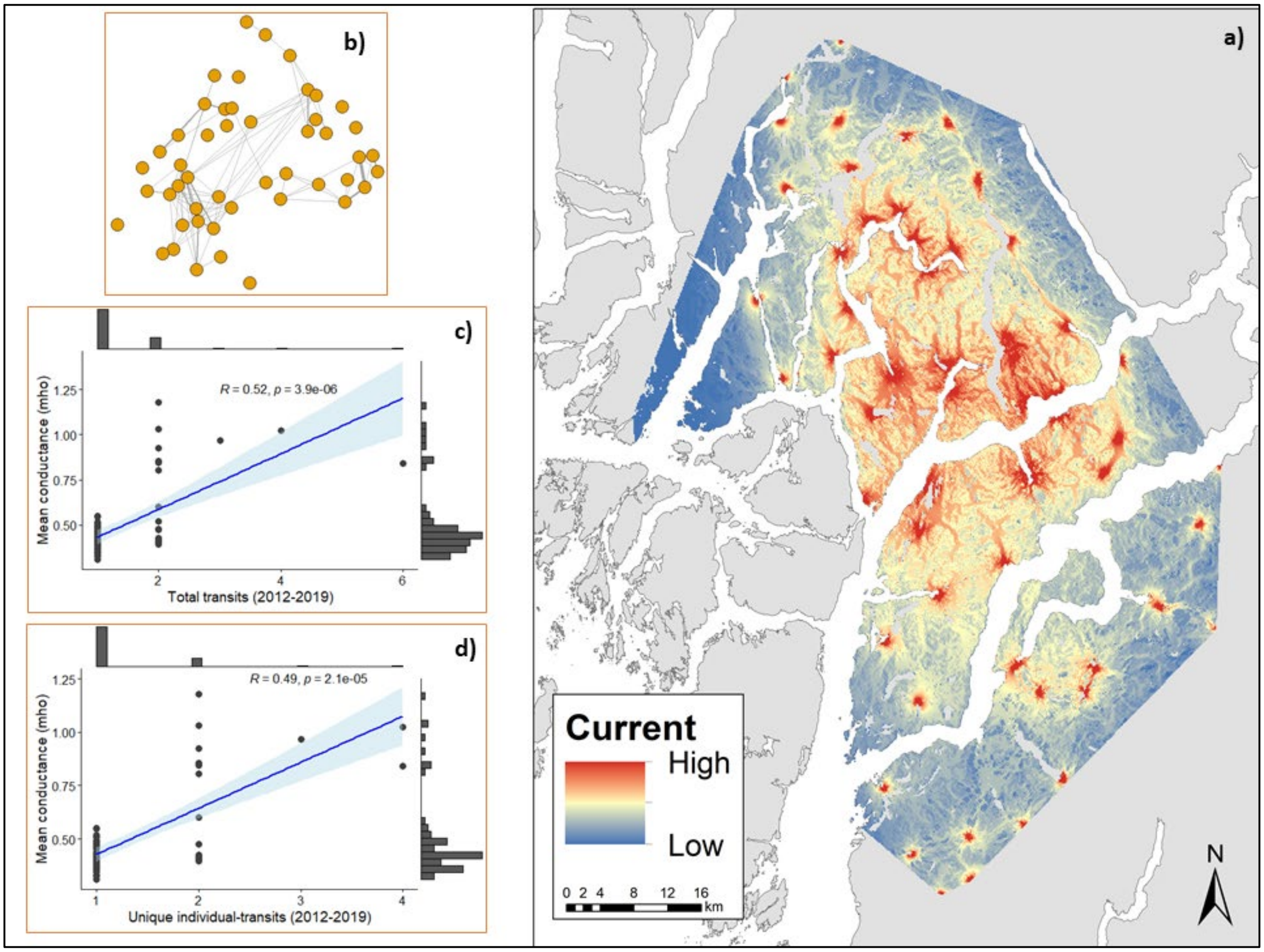
We used Circuitscape 4.0.5 (Shah & McRae, 2008) to model circuit-based connectivity using our cumulative resistance and focal node raster layers as inputs. Using the inputs, Circuitscape generates current maps iteratively for each pair of nodes, with the additional option of creating a map of cumulative current and/or maximum current. Following circuit theory, current displayed in the maps represent the probability of a random walker (in our case an individual bear) to pass each cell as it moves between focal nodes (McRae et al., 2008; Shah & McRae, 2008). Locations of high current density represent areas of higher predicted connectivity with few obstructions. 'Pinch points' are areas of funneled higher current flow, representing landscape corridors (as defined by McRae et al., 2008), and constricted pathways of movement (Laliberté & St-Laurent, 2020; Wade et al., 2015). Rose, 2013 further describes pinch points as analogous to a large volume of water forced through a narrow canyon, resulting in greater velocity. We ran Circuitscape in pairwise mode to estimate connectivity iteratively among each pair of focal nodes (i.e., midpoints of reaches). Cells were connected to their eight immediate neighbours in calculations, both cardinal (first-order) and diagonal (second-order). Our surface contained 3,694,742 cells and current was calculated between 31,878 focal node pairs, which took approximately nine days of computation.

2.2.5.1 Validation of cumulative resistance surface using empirical data from genetic tagging of hair

We used a multi-year dataset of grizzly bear hair samples collected from the same study area to assess *posthoc* the validity of our cumulative resistance surface. Validating the accuracy of connectivity models using empirical data is key, especially those based off resistance parameters set by the user rather than telemetry data (Laliberté & St-Laurent, 2020; Wade et al., 2015). Hair samples identified individual grizzly bears and the date they were detected at each hair snag site (n = 47) during May and June, 2012 to 2019 (see details in Adams et al., 2017, Bryan et al., 2013, and Service et al., 2014, 2019). Briefly, hair samples were collected twice throughout a season (early May to mid-June) from sites baited with a non-reward substance. The two collections (“revisits”) occurred 10-14 days apart after a site was baited (or re-baited). Data from the hair samples not only provided the snag site location and period at which bears were detected, but also the individual identity of a bear via genetics. Therefore, analyzing which sites were visited by individuals, and the number of individuals that have transited between sites within a year, provided empirical information on movement between them. To validate our resistance surface, we examined whether the total number of transits between each snag site pair, over the entire seven-year period, was associated with the average conductance estimated between sites with Circuitscape. If the resistance surface was accurate, we predicted a positive association.

We modelled connectivity using our cumulative resistance surface created above and used the snag site locations (as opposed to the salmon reaches) as focal nodes in this validation step (Figure 9a). We drew upon the average resistance values between each node pair that Circuitscape exports with each model run and converted them to conductance (G) values. Conductance, which is the inverse of resistance (1/R) and equivalent to the permeability of a landscape (McRae et al., 2008; Shah & McRae, 2008), describes how easily current can flow between nodes. For the focal nodes, we grouped hair samples collected from 2012 to 2019 by year, individual, site, and revisit. We then created edge lists (lists of pairs of node connections; Proulx et al., 2005) based on sites visited by individuals for each year. We summed each year’s edge list and counted the total number of connections for each node pair to calculate the total number of transits from 2012-2019. Additionally, we aggregated transits between nodes by individuals to obtain a list of unique “individual bear-transits” that occurred over the period. We then calculated Spearman correlations between the mean conductance calculated from Circuitscape and the total number of transits between node pairs, as well as between the mean conductance and number of unique bear-transits.

We found evidence to support the validation of our estimated resistance surface (Figure 9). The summed edge list results from the hair sample data showed a positive correlation with the conductance values determined from our resistance surface (Figure 9c, d). Although both the total number of transits ($r_s = 0.52$, $p = 3.9e-06$) and number of unique individual transits ($r_s = 0.49$, $p = 2.1e-05$) showed only moderate positive relationships, likely due to positively skewed distributions for both the edge list and conductance data (e.g., few edges had more than two transits), it signalled that our resistance surface was positively and significantly associated with real-world grizzly bear movements. We note, however, that the season from which validation data were derived (spring) differs from the season in which we model connectivity (late summer and fall, during salmon runs). We do not expect, however, that resistance to movement would differ markedly between seasons.



2.2.6 Identifying candidate corridors for consideration in landscape planning

We took an empirical approach to identify candidate corridors, as defined as areas of highest predicted connectivity, using the cumulative current layer from Circuitscape. Although there is no standard threshold for determining candidate corridors or pinch points from the cumulative current maps Circuitscape produces, Rose 2013 and Nordén 2016 have previously used the top 25% of current values, following suggestion from Margules & Pressey, 2000. As suggested, areas meeting this threshold with geometry that lend themselves to corridors outside of existing protected areas could be prioritized in conservation planning (Rose, 2013).

This process had several steps. We first divided our cumulative current layer into the two ecosection regions within the study area (defined above in Figure 6): Coast mountains and Lowlands. These were strikingly different in their predicted connectivity, which compelled us to identify the highest predicted connectivity within each separately. Accordingly, within each region, we converted the cumulative current values to equal area percentiles, each percentile representing 5% of the current flow values within the region. The top 25% of values were defined within the Lowlands, and the top 50% of values were defined within the Coast mountains. Although 50% is higher and more generous than the previously recommended threshold, the top 25% did not include any connections through the rugged mountains.

We then considered protected areas. Accordingly, we mapped existing Conservancies and Ecological Reserves (hereafter "protected areas") within the study area. Conservancies are designated areas that restrict resource extraction (commercial logging, mining, hydroelectric power), while Ecological Reserves prohibit all extractive activities (BC Parks, 2021). To develop some overarching empirical assessments, we calculated the proportion of the top current percentiles that overlapped with -and existed beyond - the protected areas within each region.

Finally, we considered the geometry of potential corridors to support identification of candidate corridors. A consideration in defining corridors from pinch points is the optimal width for grizzly bear movement. In the literature, the recommended width varies based on the level of industrial, residential, and recreational activity in the area. To allow for unrestricted movement of grizzly bears, Ford et al., 2020 recently suggested a corridor width of 1300m in areas that include recreational trails, following a case study within the Bow Valley Provincial Park, Alberta. As such, we suggest 1000m for potential corridors within our study area, owing to its low human density. Using this criterion, and not wishing to be prescriptive before further engagement with HIRMD, we manually identified an illustrative suite of candidate corridors within each region to showcase the possibilities to support local decision-making.

2.3 Results

2.3.1 Cumulative current

Our estimation of cumulative current identified spatial patterns in predicted connectivity among salmon reaches at the inter-watershed and intra-watershed scales. The current map (Figure 10) revealed both areas of higher current density and impeded current flow. Over the entire area, predicted connectivity among reaches was highest towards the southwestern corner (within the Hecate Lowlands), which is closer to the ocean and includes the grizzly-occupied islands. The higher current density observed in this area (depicted in red in Figure 10) indicated multiple linkages between reaches *within* and *across* watersheds with fewer impediments. Current density *across* watersheds was especially high between

Yeo Island and Ocean Falls (Figure 11a), and just south of Burke Channel, including Koeye River, which includes numerous salmon reaches (Figure 11d). The largest island in the area, King Island, which includes rugged terrain and flat valleys, had both pinch points connecting watersheds and expansive areas of high current density (Figure 11b).

By contrast, the northeastern half of our study area, within the Coast mountains, showed far less predicted connectivity *across* watersheds. Overall, current density was relatively lower in this area (range: 0-317.75 amps; mean = 21.51; sd = 10.45) compared with the Lowlands (range: 0-338.30 amps; mean = 35.65; sd = 14.71). In this area, the limited connectivity was mostly comprised of pinch points that connected reaches of the Lowlands with rivers in the Coast mountains (yellow/orange paths in Figure 10; Figure 11c).

In both regions, our current map also identified areas of high predicted connectivity among reaches *within* watersheds (i.e., up and down river systems hosting reaches). Many salmon-bearing watersheds had a high density of greater current adjacent to streams, creating a ‘halo’ effect, such as the rivers north of Ocean Falls (Figure 12a), and Koeye River (Figure 12c). These example watersheds also included areas of lower current between nodes, such as around Upper Koeye Lake (Figure 12c), compared with nodes halfway upstream.

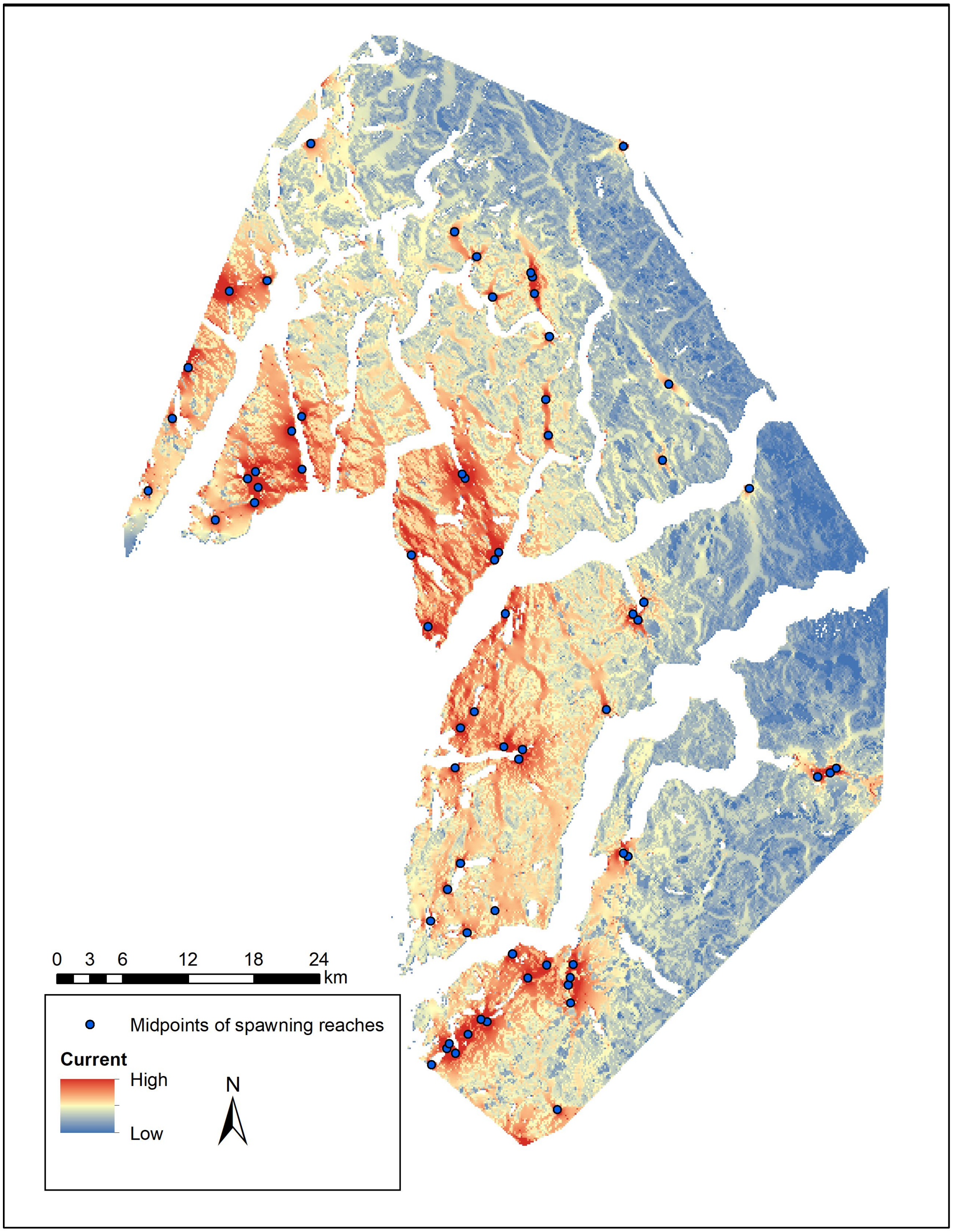


Figure 10: Cumulative current map estimating connectivity for grizzly bears among midpoints of spawning salmon reaches. Red zones depict dense areas of high predicted connectivity. Yellow/orange zones depict narrow corridors of connectivity, referred to as "pinch points". The map was displayed with a percent clip stretch (2%). **Disclaimer: For the purposes of this public document, the study area boundary has been reduced to the Heiltsuk bear hair snag study area, owing to overlapping claims of territories among Indigenous Nations in the area. Original figure showing complete study area is available upon request.*

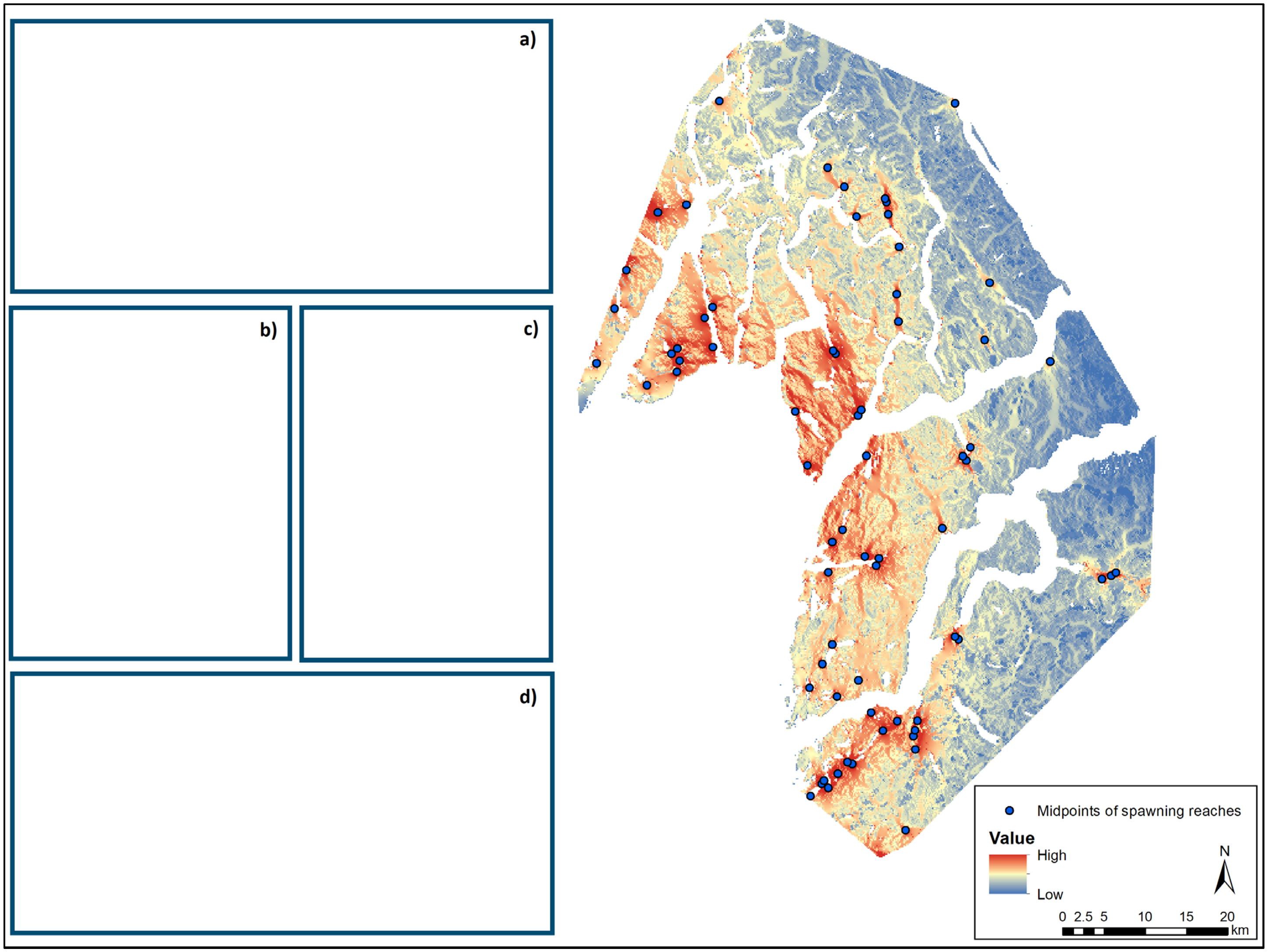
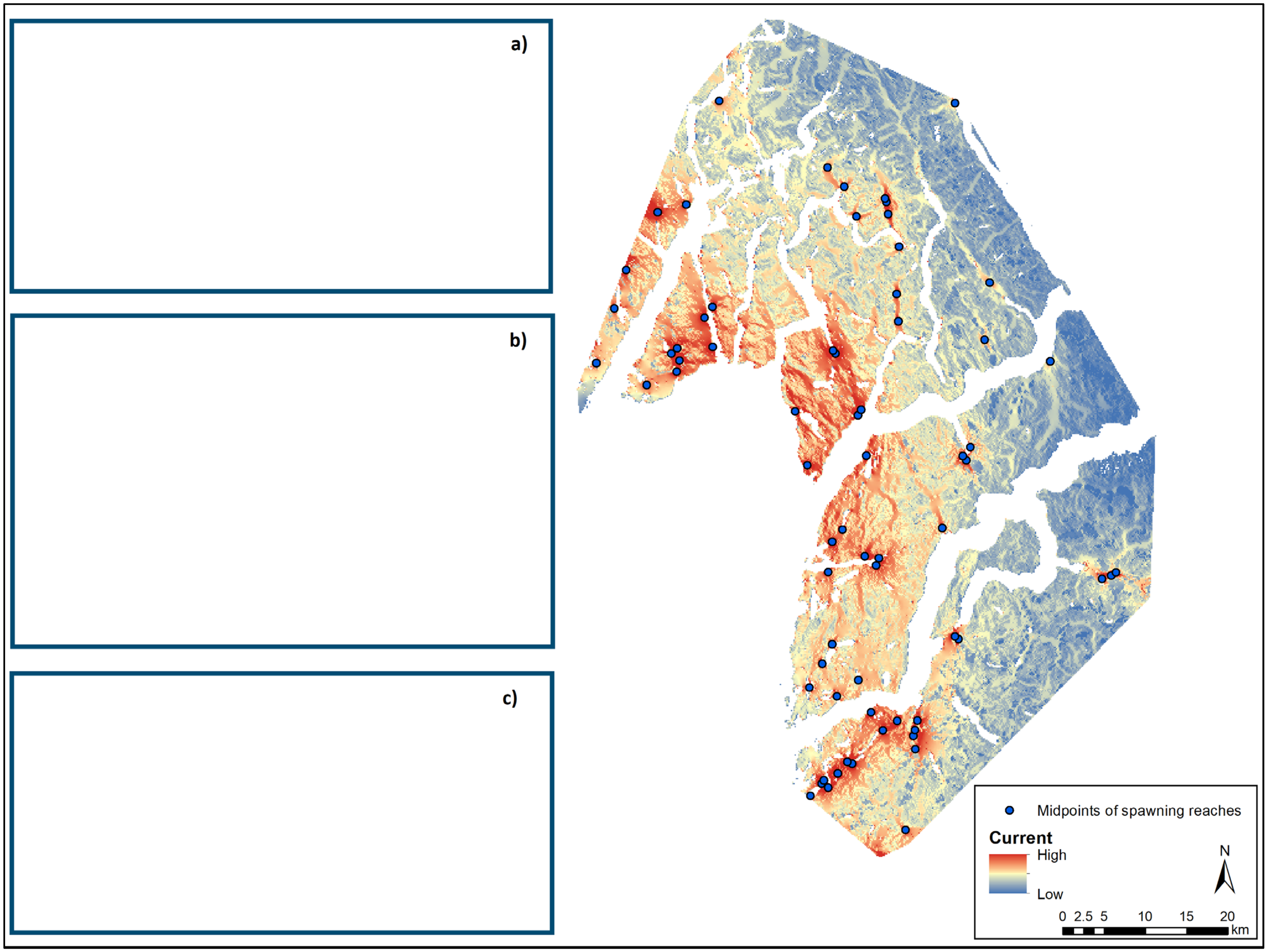


Figure 11: Examples of areas in which predicted connectivity between reaches across watersheds varied. Insets: (a) Yeo Island to Ocean Falls region (b), South King Island (c), Coastal Mountains rivers (d) Southern King Island and south of Burke Channel, including the Koeye and Kwatna Rivers. **Disclaimer: For the purposes of this public document, the study area boundary has been reduced to the Heiltsuk bear hair snag study area, owing to overlapping claims of territories among Indigenous Nations in the area. Original figure showing complete study area is available upon request.*

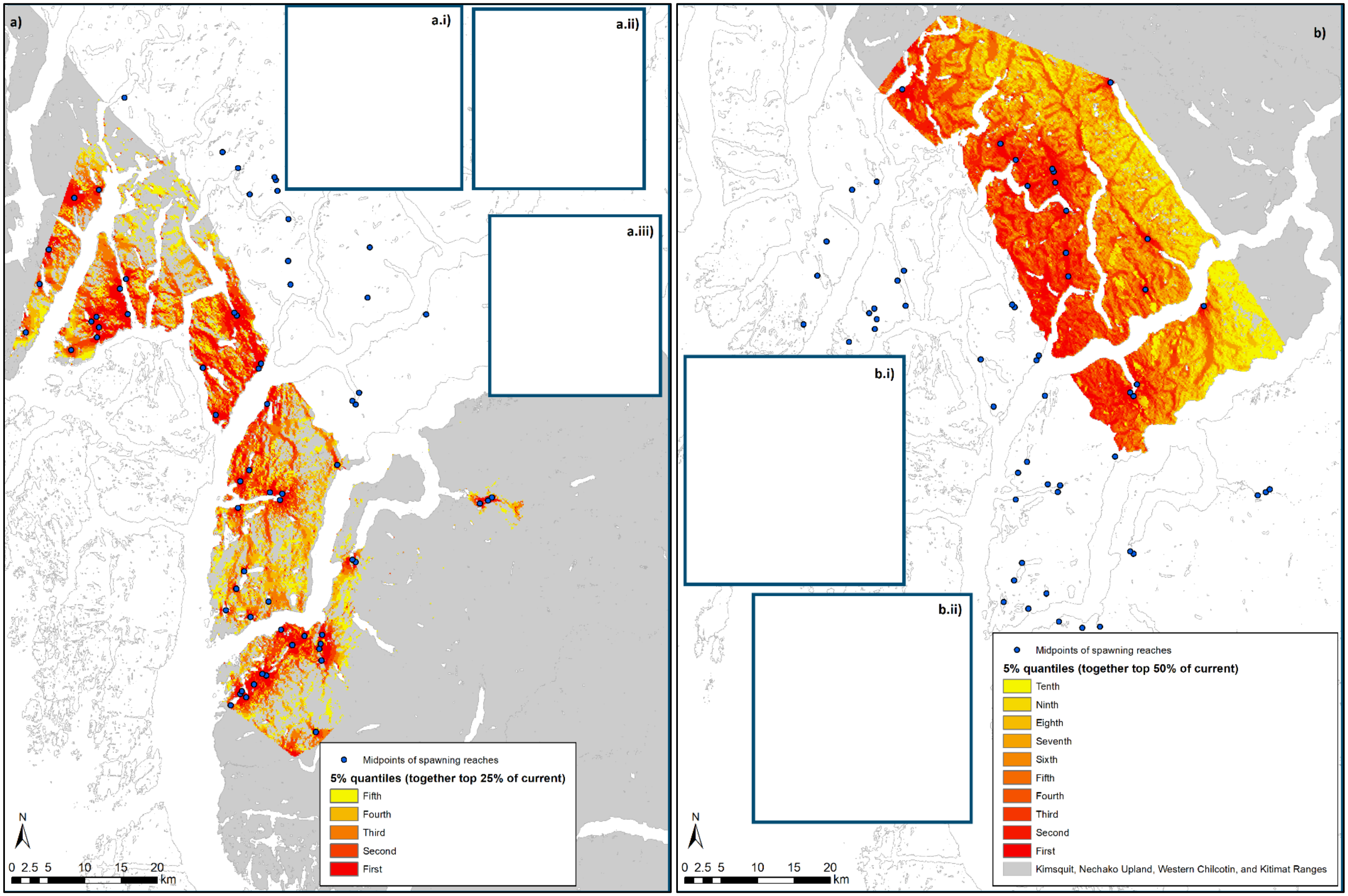

a)
b)
c)
● Midpoints of spawning reaches
Current
High
Low
N
0 2.5 5 10 15 20
km

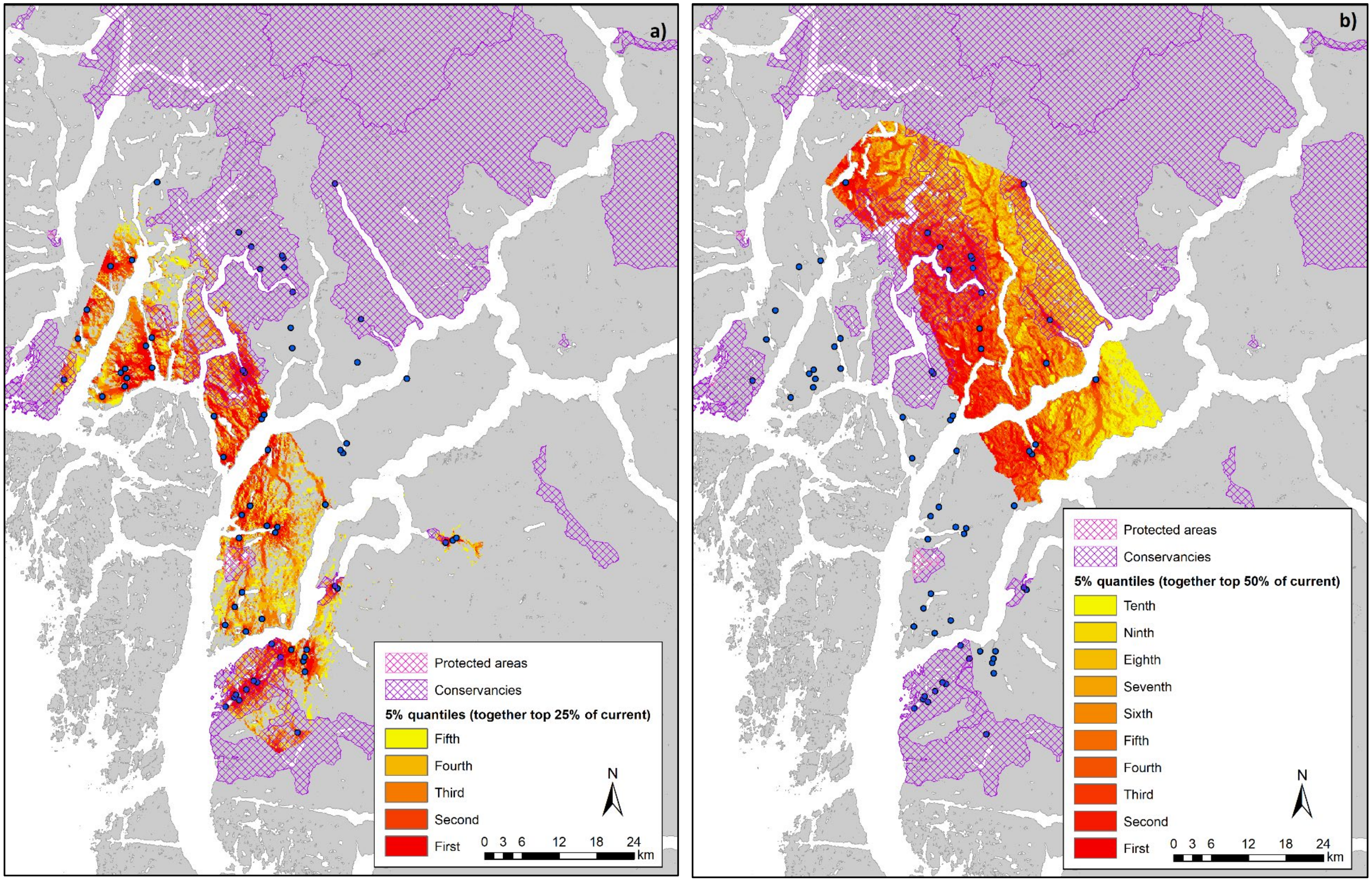
2.3.2 Identification of candidate corridors for further consideration

Areas with the highest predicted connectivity included numerous pinch points between nodes at both scales, most of which are currently unprotected. Most of the top 25th and 50th percentile areas were outside of defined protected areas (Figures 14-16). Indeed, 74% and 51% of the top percentile connections within the Lowlands and Coast mountains, respectfully, are currently outside of the protected areas.

The top 25% current flow within the Lowlands included most of Yeo Island and surrounding area, but further highlighted paths of high predicted movement across watersheds on King Island and south of Burke Channel (Figure 13a). Only the top 50% of current flow within the Coast mountains identified pinch points throughout the rugged mountains (Figure 13b), whereas the top 25% only included a high density of current at lower elevations.

Based on corridor requirements of grizzly bears, we manually defined possible corridors based on our top percentile areas for visualization (Figure 17). Our corridor illustrations, both *within* and *across* watersheds, varied in length and amount of salmon reach midpoints covered. Our aim was to highlight possibilities for connecting as many reach midpoints as possible, while also including areas with the highest current flow. Each illustrated corridor was ~1000m in width.


a)
a.i)
a.ii)
a.iii)
Midpoints of spawning reaches
5% quantiles (together top 25% of current)
Fifth
Fourth
Third
Second
First
N
0 2.5 5 10 15 20
km
b)
b.i)
b.ii)
Midpoints of spawning reaches
5% quantiles (together top 50% of current)
Tenth
Ninth
Eighth
Seventh
Sixth
Fifth
Fourth
Third
Second
First
Kimsquit, Nechako Upland, Western Chilcotin, and Kitimat Ranges
N
0 2.5 5 10 15 20
km


a)
Protected areas
Conservancies
5% quantiles (together top 25% of current)
Fifth
Fourth
Third
Second
First
N
0 3 6 12 18 24
km
b)
Protected areas
Conservancies
5% quantiles (together top 50% of current)
Tenth
Ninth
Eighth
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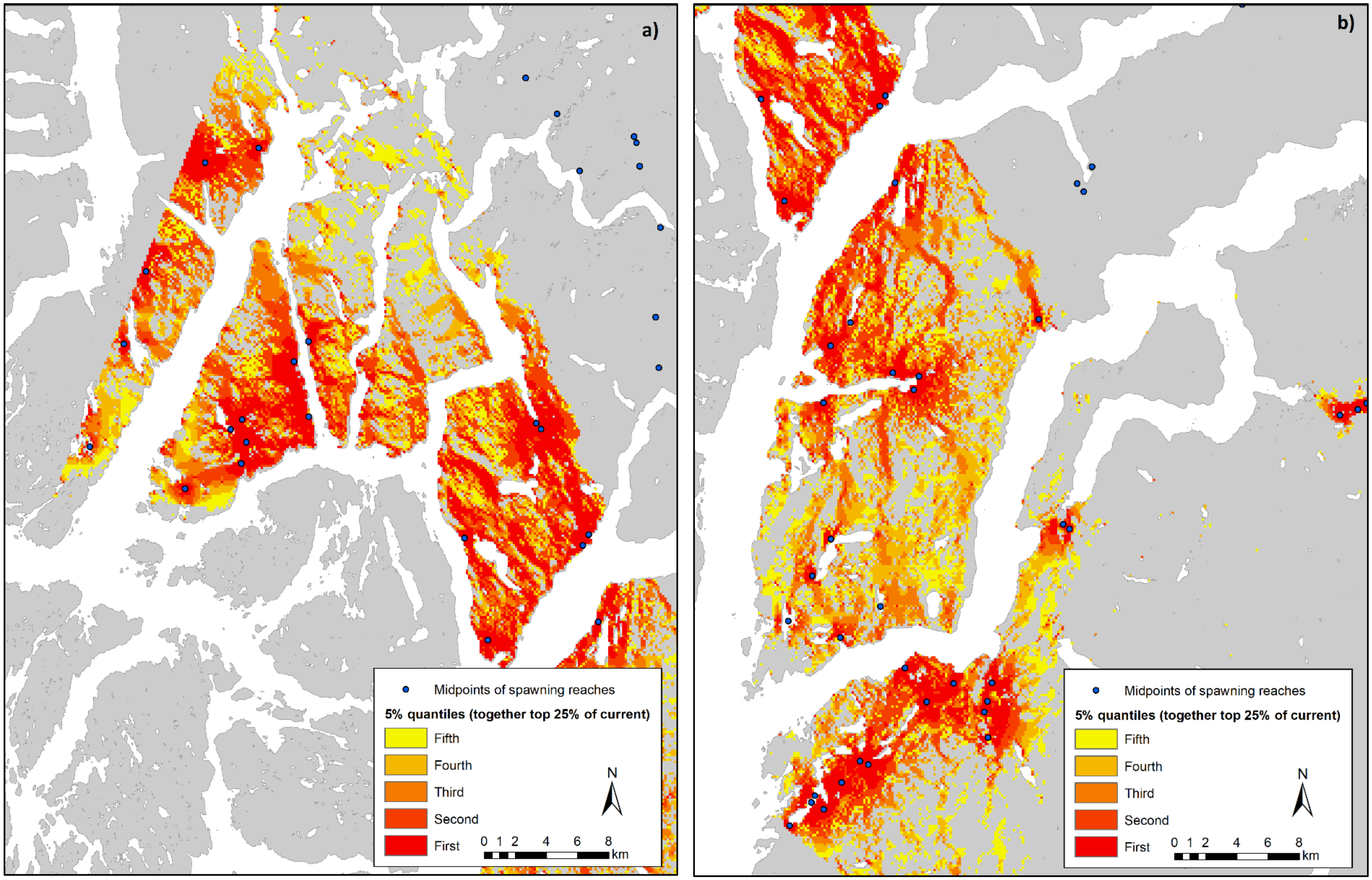
a)
Midpoints of spawning reaches
5% quantiles (together top 25% of current)
Fifth
Fourth
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km
b)
Midpoints of spawning reaches
5% quantiles (together top 25% of current)
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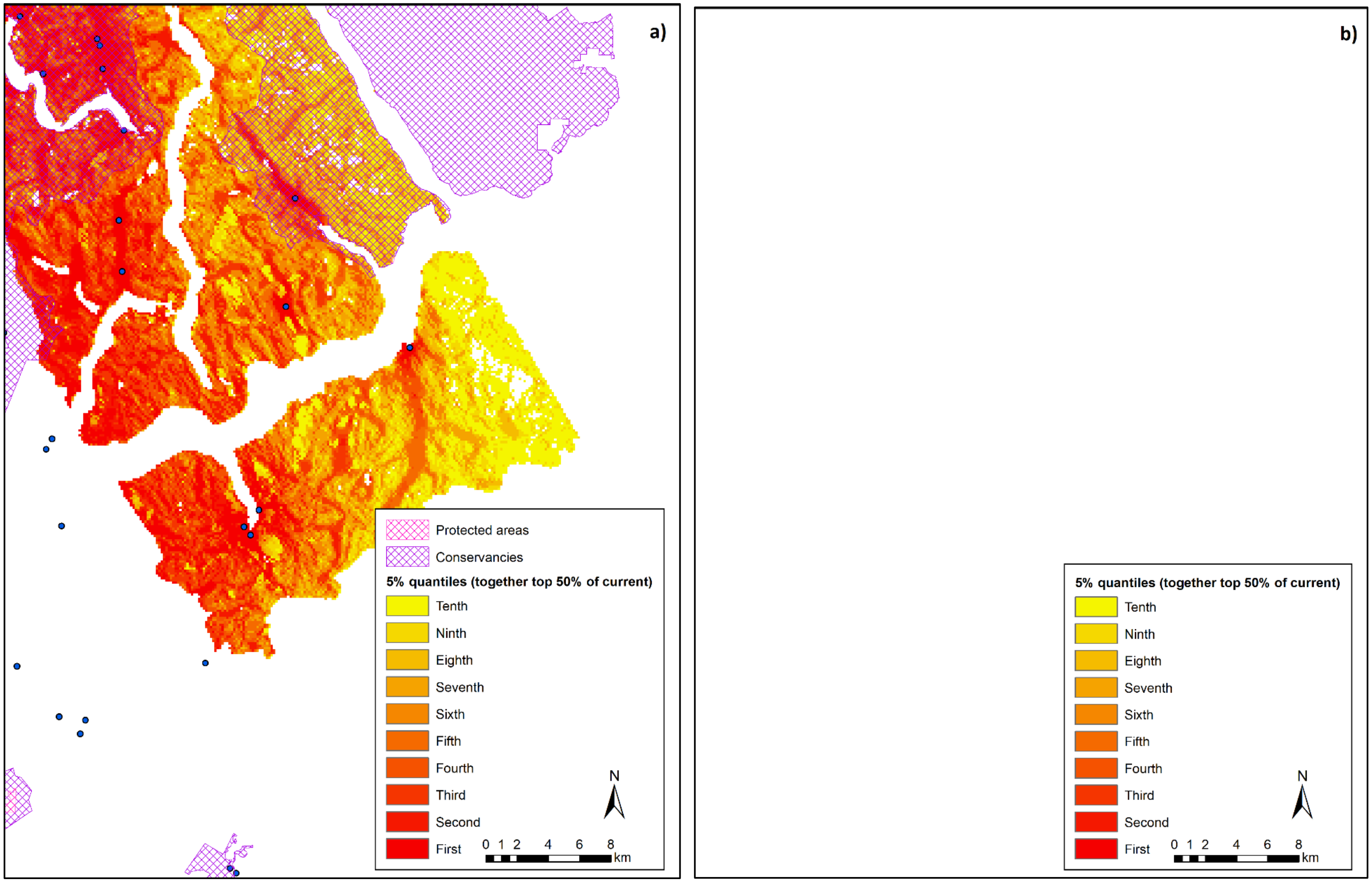
km


a)
Protected areas
Conservancies
5% quantiles (together top 50% of current)
Tenth
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km
b)
5% quantiles (together top 50% of current)
Tenth
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Eighth
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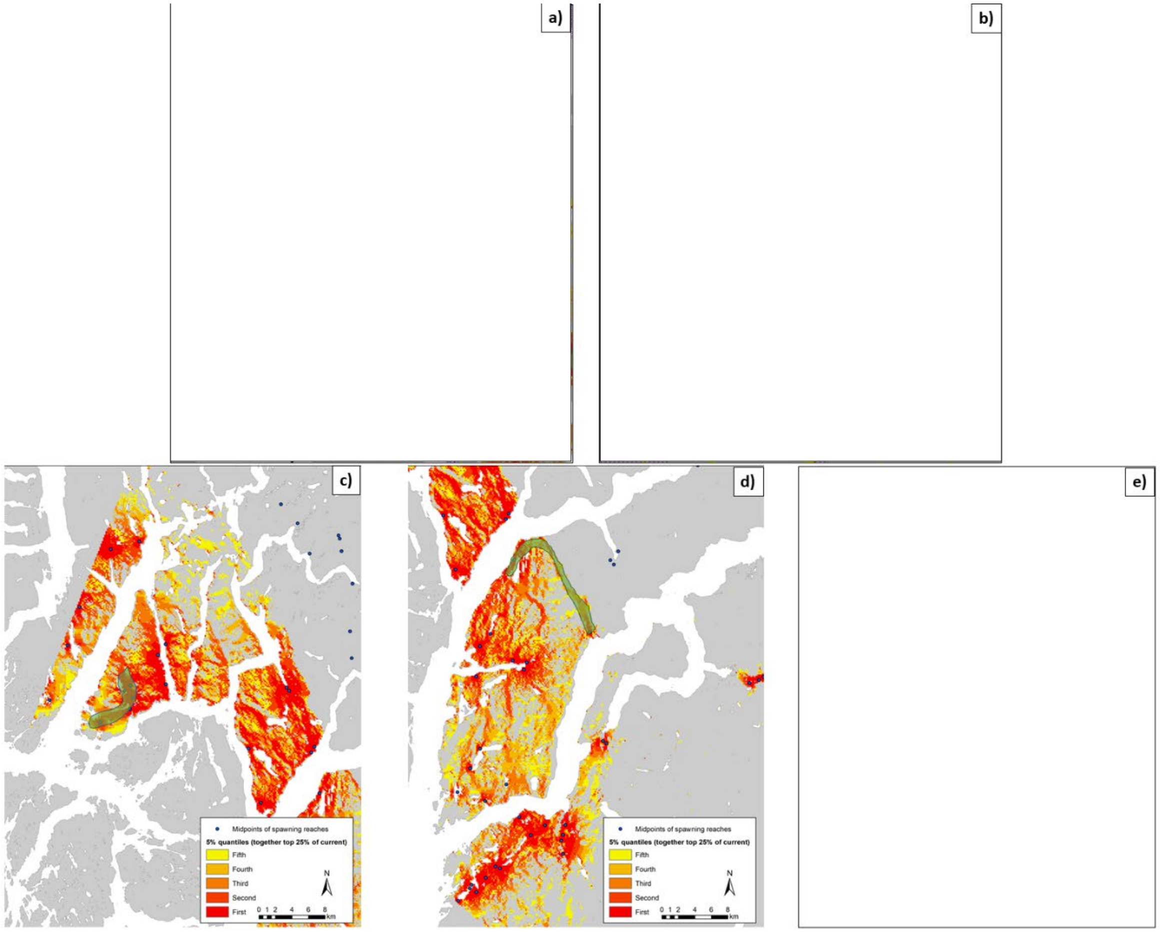
a)
b)
c)
Midpoints of spawning reaches
5% quantiles (together top 25% of current)
Fifth
Fourth
Third
Second
First
N
0 1 2 4 6 8 km
d)
Midpoints of spawning reaches
5% quantiles (together top 25% of current)
Fifth
Fourth
Third
Second
First
N
0 1 2 4 6 8 km
e)

2.4 Discussion

2.4.1 Overview

Our results suggest areas of importance to grizzly bears for movement among salmon reaches during the spawning season. Our work applies circuit-theoretic connectivity modelling to the recent body of work on resource waves, literatures to our knowledge that have not previously been united. Our methods of validating our resistance surface parameters, using empirical data of genetically identified grizzly hair, suggested predictive utility. Working with the Heiltsuk Integrated Resource Management Department (HIRMD), within whose Territory this study took place, our aim was to identify corridors to be considered by HIRMD for future forestry protection. Our results from Circuitscape revealed areas of high current density among reaches at both the inter and intra- watershed scale, including pinch points (i.e. areas where current is high and connectivity could be vulnerable; Grafius et al., 2017). Areas with the most predicted connectivity were located within the Lowlands region of our study area, while the Coast mountains region showed high current density mainly at the base of the mountains leading into the Lowlands. We manually illustrated possible corridors that are not protected via Ecological Reserve or Conservancy designations. Overall, understanding how salmon reaches are connected over the spawning period provides key information for the management of this ecological system, and insight into how grizzly bears move through and interact within this environment.

2.4.2 Model limitations

Our approach to modelling connectivity within this system came with limitations and considerations for future research. These broadly exist in three categories: resistance surface parameterization, placement of nodes, and validation. First, movement data using satellite collars were not available, therefore our habitat variable and resistance parameterization decisions relied on expert local knowledge and the literature. Accordingly, we had to estimate resistance by drawing on habitat quality, as assessed by grizzly occurrence (as observed in the literature and by the Haíłzaqv). Cushman et al., 2013 notes limitations to this approach, primarily that patterns of habitat selection do not necessarily reflect the influence of landscape features on connectivity. Instead, selecting preferred habitat reflects the maximization of fitness in individuals (Cushman et al., 2013). Additionally, our arbitrary resistance scale (1-6 for individual resistance layers; 1-12 for cumulative resistance layer) was subjective, which Sawyer & Kauffman, 2011 emphasises is a limitation in resistance-based connectivity modelling. We encourage future research on this system to re-evaluate our scale. Further work will also require a sensitivity analysis to determine the potential influence of our parametrization scheme on the resistance values in the resulting current map. Finally, the habitat variables we chose are generalized to grizzly bears as a whole and may not accurately represent the factors that affect daily movements by different age and sex classes, as well as individuals.

Second, the methods of validating our cumulative resistance surface also included limitations. Wade et al., 2015 suggested multiple approaches in validating resistance-based connectivity modelling, such as using biogeochemical or genetic markers, or independent occurrence or telemetry data. We used genetically identified samples from hair snag sites and inferred movement based on the association between conductance from our resistance surface and an edge list created from locations of individuals. As these are not directly from movement data, this approach involved assumptions. For example, although we could determine an individual bear travelled in between two sites within a season based on their hair being found at each, we could not determine *how many times* they travelled between the two sites within a season. Therefore, we could only assume a bear moved between each site pair once per year and could not include back-and-forth movements. Finally, our hair samples were collecting during the spring (May and June), rather than during the salmon spawn period in the fall (when our study period is). However, we again note that we do not expect resistance to movement to differ markedly between the two seasons.

Third, modelling connectivity between salmon reaches, some of which extend many kilometers in length, came with challenges. To our knowledge, no other studies have attempted to use river systems as focal nodes in connectivity modelling. We simplified reaches within watersheds into individual midpoints, which reduced accuracy in their overall extent. Additionally, we dissolved overlapping midpoints and those within 150m of one another, therefore generalizing multiple different species-reaches into a single midpoint. The spatial configuration of our midpoints as nodes may also carry limitations. For example, most nodes occurred within the Lowlands region within our study area. This promotes higher connectivity (higher current density) within this area, rather than with reaches farther away (i.e., reaches over the Coast mountains).

2.4.3 Spatial patterns of connectivity

The spatial patterns of modelled connectivity varied across our study area. Broadly, the Lowlands region (including the Northern Pacific ranges and Hecate lowlands ecosections) included the highest predicted connectivity. Pinch points and areas of high current density between reaches were present both *within* and *across* watersheds. This was not a surprise, as topography is less rugged here and reaches are closer to one another. This pattern was also visible in our resistance surfaces (Figure 7); most of the region had very little landcover resistance, and terrain ruggedness resistance values were relatively low. The cumulative resistance layer overall showed most of this area as having little resistance, based on our parameters (Figure 7). Local knowledge and our long-term spring grizzly monitoring work with HIRMD have previously revealed that grizzly bears move great distances within the Lowlands region. Indeed, via genetic tagging of our grizzly hair data, individuals have previously moved between Roscoe Inlet (Figure 11a) and King Island, as well as between King Island and the southern-most tip of our study area (unpublished data). During the salmon spawning season, mean home ranges of coastal grizzly bears are found to vary, from 34 km^2 for females to 85km^2 for males Barnes, 1990. Therefore, conserving high-current connections between reaches at both inter- and intra-watershed scales within the Lowlands is required to facilitate their overall movement.

By contrast, the Coast mountains region (including the Kimsquit ranges, Nechako upland, Western Chilcotin ranges, and Kitimat ranges) included more areas of high resistance, such as rugged terrain, snow, and ice. Valleys of importance were identified throughout the Coast mountains via pinch points (Figure 10) and appeared to offer the primary routes of estimated connectivity. Mountain ranges are a known natural barrier to grizzly bear dispersal, therefore, the limited high-current routes connecting watersheds within the region weren't surprising. Within the Rocky Mountains of BC and Alberta, rugged, glaciated mountains act as natural barriers for grizzly populations and restrict gene flow (Proctor et al., 2012). On the coast of BC, this barrier is apparent in grizzly bear populations via their diet; bears, especially males, on the coast consume more salmon than those found inland (Adams et al., 2017; Mowat & Heard, 2006). Females, who have smaller home ranges than males (Hatler et al., 2008), have especially reduced salmon-rich diets further inland. Therefore, considering the difference in diets among coastal and inland grizzlies, and their seasonal home ranges, migrating from the coastal watersheds at the base of the Coast mountains region to those further inland would be possible but unlikely, especially in females. Accordingly, intra-watershed connections within the Coast mountains region would likely be the priority for conservation, rather than across watersheds. Due to this pronounced trend, further analyses predicting connectivity during the salmon spawn on the BC coast may require separate models for the Coast mountains and Lowlands regions.

2.4.4 Identification of candidate corridors for further consideration

We found that most of the top percentile areas of predicted connectivity were currently unprotected. Most (74%) were unprotected within the Lowlands, including south towards Yeo Island, and south King Island (Figure 15). Top percentile areas within the Coast mountains region included more protected area coverage but were mostly unprotected (51%).

Grizzly bears can benefit from protected corridors or linkages between salmon spawns. By facilitating movement between the different pulses during the spawn season, individuals can exploit the full spatial and temporal extent of this energetically rich resource without bearing the potential costs in energy and risk that could be associated with habitat destruction. Additionally, as umbrella species due to their variety of habitat uses, protected linkages providing functional connectivity for grizzly bears could likely benefit a range of plant and animal species (Nielsen, 2011). While large-scale human disturbances such as forestry are sparsely spread across the area, collaboratively planning networks prior to further development could mitigate future restorative efforts (Parrott et al., 2019; Ament et al., 2014).

We emphasize that our illustrations of potential corridors are not prescriptive. Rather we highlighted them as possibilities to be considered by HIRMD, knowing that decisions will be additionally informed by their spatial and forestry management priorities, as well as other values. However, these candidate corridors illustrate how protected grizzly bear-specific corridors might be designed on the Haíłzaqv landscape, thereby providing a stepping-stone for next steps of engagement.

2.4.5 Relevance and future applications

To our knowledge, this is the first analysis and modelling of connectivity within this or any resource wave system. The rapid growth of functional connectivity modeling tools, such as Circuitscape, creates new opportunities for predicting connectivity within dynamic systems. We demonstrated the applicability of Circuitscape within our study area, using the midpoints from different salmon spawning reaches (which occur over an eight-month period) as nodes. We parameterized our resistance surface using local knowledge and previous literature based not only on landscape structure, but how grizzly bears interact with certain habitat features. Accordingly, this study provides an example of applied connectivity research co-developed with a community to address a real-world issue.

At a local scale, our analysis provided information to HIRMD on important networks for grizzly bears to access spawning salmon within their Territory, and the extent to which these are already protected. HIRMD's Forestry Department oversees forestry management and planning and requested information to guide future landscape planning. In setting the resistance parameters together, we ensured the model was parameterized to reflect functional connectivity and grizzly bear movement within this specific region, as informed by not only the literature but also by local knowledge. Such a "Two-Eyed Seeing" approach, which is informed by both scientific and Indigenous lenses, can provide better insight than any one vantage alone (Reid et al., 2021). Especially in the context of modeling and parameterization, a process that requires "expert opinion", Indigenous knowledge systems hold incredibly detailed past and present information on environmental dynamics (Skroblin et al., 2021). Indeed, millennia of observation have fostered a deep and complex understanding of ecological systems, an understanding that scientific “expert opinion” often cannot compare with but can compliment. Overall, although our models were not based on bear movement data, we believe our collaborative approach defined accurate parameters specific to the region and trophic interaction.

More broadly, we believe this study is an important first step in uniting the connectivity modelling and resource waves or phenological tracking literature. Most of the connectivity modelling literature considers connectivity between stationary resource patches or individual occurrences. In using the location of resource pulses over an extended temporal period, we were able to predict connectivity between resources with phenological diversity. It is well known that grizzly bears that exploit multiple spawning pulses consume more salmon overall (Deacy et al., 2018). Therefore, understanding how accessible multiple reaches at different scales (within and across watersheds) are to individuals is key in promoting grizzly bear fitness. Although we simplified entire salmon reaches to midpoints, which came with limitations, future research within this system could examine using entire reaches and consider actual temporal patterns (i.e., order of species spawns). Our approach is generalizable and could easily be applied to other resource waves interactions. Additionally, connectivity modelling programs such as Circuitscape are relatively simple for users to learn, and “focal nodes” can represent any resource. Future research applying circuit theory could model, for example, ungulate migrations as they track focal nodes of particularly high value in spring green-up (“green wave”) systems. As connectivity models become more sophisticated, modelling such trophic interactions could allow for more accurate predictions.

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3. General Conclusion

3.1 Sustained engagement for planning and implementation

3.1.1 Addressing the disconnect between conservation scientists and land managers

The successful implementation of protected areas for connectivity involves cooperative collaboration among scientists, human governance systems, and multiple stakeholders. Governments and land managers (hereafter "managers") require research to help inform conservation policy and practise (Cook et al., 2013). A major challenge, however, is effective translation of scientific findings into connectivity potential for managers (Githiru et al., 2011; Gray et al., 2020; Keeley et al., 2018). There exists a disconnect. Conservation scientists frequently have compressed timelines of their involvement due to academic norms, thus limiting the long-term engagement on projects required to carry research questions to implementation (Keeley et al., 2018). Additionally, conservation scientists often balance science relevant to local managers with the pressures (via grants and funding) for novel and rigorous science on large systems or broad theoretical topics (Cook et al., 2013). Therefore, managers are left to make decisions based on information not specific to their contextual needs.

To address the gap in connectivity planning and implementation, an integrative approach is required. Enquist et al., 2017 emphasize the need for translational ecology (TE) in addressing complex environmental issues. Following TE, rather than using expert-oriented perspectives of traditional science in confronting issues, scientists work collaboratively from the ground-up to address questions of real concern to resource managers (Enquist et al., 2017). Additionally, conservation scientists must commit to long-term engagement throughout the process. This includes engagement at all steps: (1) initial communication and co-development of problem and goal (common vision); (2) partnership and participation throughout – frequent discussions and consensual adaptations; (3) effective implementation (Burton et al., 2005; Githiru et al., 2011). Successful examples of this approach being applied to connectivity issues exist. For example, Parrott et al., 2019 worked collaboratively alongside multiple stakeholders and local governments to co-develop research and promote connectivity in a multi-use landscape in the Okanagan Valley, BC. Although, as mentioned above, such long-term projects may not align with the norms of traditional science, we argue they provide meaningful case studies and examples which could later be applied to broader connectivity research questions.

3.1.2 Increased collaboration with Indigenous communities and governance

Globally, Indigenous communities are re-asserting their sovereignty to steward natural resources within their Territories. Indigenous peoples have been stewards of their Territories for millennia, maintaining intricate and complex relationships to ecology (Brown & Brown, 2009). Accordingly, scientists are recognizing the importance of engaging with Indigenous communities and their governments, therefore narrowing the gap between the two knowledge systems in conservation efforts (Adams et al., 2014; Reid et al., 2021). Efforts vary in their success, particularly when they are only prescriptive and do not actively engage with communities throughout the entire process (Adams et al., 2014; Atlas et al., 2017). Atlas et al., 2017, who have collaboratively monitored salmon with the Haíłzaqv since 2013, emphasizes, "successful local monitoring should be developed in close partnership with community members, be rooted in existing traditions of management, include a strong education and outreach component, and work to build capacity for ongoing monitoring and implementation".

In chapter two, we illustrate methods of collaborative connectivity research to be further assessed and implemented by an Indigenous government. Working alongside the Heiltsuk Integrated Resource Management Department (HIRMD) and guided by the values and goals of the Haíłzaqv Nation, we co-defined model inputs to predict connectivity within their Territory (as defined by the Nation). HIRMD actively manages and implements forestry initiatives within their Territory and sought additional information on the ability of grizzly bears, a culturally prominent species (Housty et al., 2014), to navigate between resource patches. Our findings suggest there are areas and corridors important for movement by grizzly bears. As such, we illustrated possible corridors, based on the functional requirements of grizzly bears, to facilitate movement between pulses of an important resource. Further work and engagement on this project are ongoing to determine next steps and potential.

3.2 Continued growth of landscape connectivity tools

With more sophisticated functional connectivity modelling tools available, additional information on the ecosystem in question can be included within models. This allows models to be parameterized to localized connectivity questions. For example, in predicting connectivity of large mammals among resource patches collaboratively and/or at a localized scale, models have been used in the US for mountain lions, black bears, desert bighorn sheep (*Ovis canadensis nelsoni*), mule deer (*Odocoileus hemionus*), and pronghorn (*Antilocapra americana*; Dickson et al., 2013; Fleishman et al., 2017), as well as tigers (*Panthera tigris*) in India (Dutta et al., 2016).

We demonstrated in chapter two the ability of our resistance surface to capture changes across the landscape, and how they relate to the movement of grizzly bears at a relatively small spatial scale

(150m). Resistance-based connectivity modelling such as Circuitscape is also relatively simple to use and has minimal computational resources required (Wade et al., 2015). Although our analysis took approximately nine days to run in Circuitscape (owing to a large study area, relatively small spatial scale, and numerous focal nodes), new techniques are emerging for even faster computation. For example, Circuitscape.jl (Anantharaman et al., 2019) is written in Julia programming language, and is suggested to reduce run time from weeks to days, or days to hours.

3.3 Concluding remarks

As natural landscapes continue to be transformed for human use worldwide, collaborative planning is required to retain functional connectivity for species among important resource patches. Land management practises that conserve habitat of importance for species is fundamental in preserving natural processes, especially as landscapes turn into a mosaic of habitat viability for species. Defining species-specific corridors or protected areas, for example, can facilitate movement among resources and mitigate the effects of fragmentation (Gilbert-Norton et al., 2010; Hawn et al., 2018). For conservation practises to be successful, however, strategies should be collaborative, have communal support among stakeholders at each step, and have consideration for sociocultural components (Githiru et al., 2011; Poe et al., 2014).

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