PACIFIC NORTHWEST HARLEQUIN DUCK (*Histrionicus histrionicus*) HABITAT SUITABILITY AND THE VULNERABILITY OF IDENTIFIED SALISH SEA HABITATS TO OIL SPILLS AND THEIR LEGACY EFFECTS

by

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A Thesis
Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2020

This Thesis for the Master of Environmental Studies Degree

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ABSTRACT

Pacific Northwest Harlequin Duck (*Histrionicus histrionicus*) Habitat Suitability and the Vulnerability of Identified Salish Sea Habitats to Oil Spills and their Legacy Effects

Matthew Hamer

Harlequin ducks (*Histrionicus histrionicus*) are a sea duck species exhibiting life-history traits that increase their vulnerability to external perturbations and restrict their ability to recover from population reductions – they have inherently low productivity, high metabolic requirements, and are highly philopatric. Harlequin duck populations in Prince William Sound, Alaska encountered a substantial perturbation in 1989 when the oil tanker, Exxon Valdez, spilled 10.8 million gallons of crude oil after running aground on a reef. As a result, approximately one-quarter of the local harlequin duck population died from direct oiling immediately after the spill. Surviving individuals philopatric to contaminated habitats were recurrently exposed to residual pollutants, leading to locally depressed survival rates and continued population declines during the following decade. Overall, more harlequin duck losses were caused by persistent exposure to contaminants than the initial oiling event. Harlequin ducks in British Columbia and Washington are also susceptible to oil spills, particularly in the Salish Sea where current tanker traffic is high and projected to increase. In an effort to identify coastal locales that may harbor harlequin ducks, I developed species distribution models (SDMs) depicting potential diurnal and nocturnal harlequin duck use patterns during the nonbreeding period. SDMs were developed using Maxent modeling and occurrence locations collected via satellite telemetry. Satellite telemetry data was supplied by researchers in Alberta, British Columbia, Montana, Washington, and Wyoming. I then utilized an Oil Residence Index (ORI) to identify highly suitable Salish Sea shoreline habitats that could potentially have prolonged oil residence. If oiled, harlequin ducks philopatric to these habitats would likely be subject to continued pollutant exposure. SDMs depicting habitat use patterns were successfully developed and post-model assessment indicated that 90% of identified Salish Sea nearshore harlequin duck habitats may be subject to prolonged oil residence.

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SDM – Species Distribution Model

PTT – Platform Transmitting Terminal

AUC – Area Under the (Receiver Operating Characteristics [ROC]) Curve

AIC – Akaike Information Criterion

AIC_c – Akaike Information Criterion with Correction for Small Sample Sizes

TIN – Triangulated Irregular Network

PSU – Practical Salinity Unit

RMS – Root Mean Square

ACKNOWLEDGMENTS

This study was supported and made possible by an international group of collaborating researchers committed to harlequin duck conservation and research who were graciously willing to share data. I would like to sincerely thank the individuals that were willing to share their satellite telemetry data after working hard to capture, mark, and track harlequin ducks. Captures in British Columbia were undertaken by Sean Boyd, Lisa Bate, Erika Lok, Rian Dickson, Megan Willie, Ken Wright, Kevin Chernoff, Nik Clyde, Jenna Craig, Mark Maftei, Wendy Easton, Shanti Davis, Myron Dundas, and Jesse Bolton under the Science and Technology Branch of Environment and Climate Change Canada. Alberta's capture effort was led by Beth MacCallum of Bighorn Wildlife Technologies Ltd and was supported by the Forest Resource Improvement Association of Alberta and Teck Coal Limited, Cardinal River Operations. Lisa Bate (Glacier National Park) and Chris Hammond (Montana Fish, Wildlife, and Parks) led captures in Glacier National Park and throughout northwest Montana. In Wyoming, captures were undertaken by Lucas Savoy (Biodiversity Research Institute), Susan Patla (Wyoming Game and Fish), John Stephenson (Grand Teton National Park), Sarah Hegg (Grand Teton National Park), and Doug Smith (Yellowstone National Park). Captures in Washington were backed by the Washington Department of Fish and Wildlife, and were undertaken by Joe Evenson, Don Kraege, Kyle Spragens, Matt Wilson, Ruth Milner, Bryan Murphie, Chris Anderson, Mike Smith, Tom Cyra, Paul DeBruyn, Warren Michaelis, Andrew Annanie, Dave Nyesewander, Maynard Axelson, Leah Rensel, Dan Siegner, and Bill Brown. Malcolm McAdie assisted capture efforts at multiple locations and provided expert veterinarian services for PTT marking.

I would also like to thank those that helped me during model development and report writing. John Withey provided thoughtful support and review as my thesis reader and also sponsored earlier independent learning undertaken to develop required spatial analysis skills. Kathleen Moore (Canadian Wildlife Service) and Bruce Harrison (Ducks Unlimited Canada) kindly provided environmental datasets and technical support. Joe Evenson, Sean Boyd, Ruth Milner, and Bryan Murphie reviewed multiple versions of the model and/or provided a review of this thesis report. A special thank you to my supervisors Ruth Milner and Fenner Yarborough for their support of my work towards a master's degree.

Finally, I would like to thank my friends, my family, and especially my wife for their encouragement and support throughout this thesis process and during the previous three years.

INTRODUCTION

On most mornings, Bligh Reef—like other reefs in Prince William Sound, Alaska—served its function as a critical feature of the coastal, nearshore environment. The reef's bathymetric uplifting allowed benthic invertebrates to cling to the reef and feed in the coastal waters. Fish, mammals, and birds all frequented the reef to forage on the invertebrates and other organisms that proliferated there. However, when the sun rose on the morning of March 24th, 1989, it illuminated a scene horrifically unlike the panorama of coastal habitat that had brightened for millennia prior. Sometime shortly after midnight, the Exxon Valdez, a vessel measuring over 300 meters long, collided with the reef, spilling 10.8 million gallons of crude oil, causing profound acute and prolonged harm to Prince William Sound and the Gulf of Alaska (Wolfe et al., 1994).

In the weeks that followed, spilled oil dispersed across 30,000 km^2 of marine waters, a range harboring about a million marine birds (Piatt et al., 1990). Much of the oil descended upon especially productive intertidal, nearshore, and shoreline habitats essential for numerous and diverse taxa. Between one hundred thousand and three hundred thousand marine birds were killed by the immediate effects of oil exposure (Piatt et al., 1990). Loons, grebes, alcids, and sea ducks accounted for most marine bird fatalities in the weeks and months following the spill due to their time spent resting on the water surface and dive foraging (Piatt et al., 1990).

By late April, a month after the spill, the immediate marine bird die-off due to oil exposure had largely concluded; by that point, most of the oil had emulsified into a mousse-like substance less likely to cause acute physical damage to birds (Piatt et al., 1990).

Although the abrupt die-off had subsided, the effects of the spill continued to harm the marine bird inhabitants of the coastal waters for years.

Life-history characteristics of the affected species influenced how populations responded in subsequent years. *Philopatric* species—those exhibiting high fidelity to specific sites—were especially slow to recover. Large proportions of inhabitants philopatric to specific oil affected sites were immediately killed after the spill from acute oil exposure (Esler et al., 2002; Iverson & Esler, 2010). Philopatric individuals that survived the initial oiling event continued to use sites even though habitat quality was greatly diminished. These philopatric individuals were persistently subjected to the legacy impacts of oil pollution, which in turn depressed survival rates, delaying population recovery (Esler et al., 2000, 2002; Iverson & Esler, 2010).

Harlequin ducks (*Histrionicus histrionicus*) are a sea duck species exhibiting life-history traits that increase their vulnerability to environmental perturbations and restrict their ability to recover from population reductions—they are long-lived, slow to reproduce, and highly philopatric (Cooke et al., 2000; Goudie et al., 1994; Robertson et al., 2000a; Smith et al., 2001). Additionally, harlequin ducks must forage more frequently than most sea ducks during winter, due to high metabolic requirements stemming from their small body size (Goudie & Ankney, 1986). The high metabolic requirements of harlequin ducks place them near a survival threshold, especially during winter when metabolic needs increase and foraging opportunities become limited by photoperiod. Perturbations that diminish foraging success and overwinter body condition may severely decrease overwinter survival rates as individuals cross the metabolically established survival threshold.

Approximately one-quarter of the harlequin ducks wintering in oil affected regions of Prince William Sound died immediately as a direct result of oiling from the Exxon Valdez spill (Esler et al., 2000, 2002; Iverson & Esler, 2010). In the decade that followed, the Sound's harlequin duck population continued to decline from long-term exposure to persistent oil pollution and the species' limited ability to recover. More individuals were killed due to chronic exposure and legacy effects of the oil spill than during the initial oiling event (Esler et al., 2000, 2002; Iverson & Esler, 2010; Rosenberg et al., 2005). At its lowest point, female abundance in oiled areas was 55% lower than before the spill (Iverson & Esler, 2010). Harlequin duck populations in oil-affected regions declined until hydrocarbon exposure subsided and survival rates returned to pre-spill levels (Iverson & Esler, 2010; Rosenberg et al., 2005).

Pacific Northwest harlequin duck populations utilizing and philopatric to the coastal waters of British Columbia and Washington State also face substantial and potentially increasing risks from oil spills. Today, approximately 530 oil tankers navigate the waters of the Salish Sea every year, importing crude oil (mostly from Valdez, AK) and exporting petroleum products from local refineries (Washington Department of Ecology, 2019). Oil tanker traffic could increase drastically soon. British Columbia's proposed Trans Mountain Pipeline is expected to increase oil tanker traffic navigating the waters between Vancouver and the Pacific Ocean from 5 to 34 vessels per month (Govt of Canada & National Energy Board, 2016). This increase in tanker traffic signals a major increase in risk to the region's marine life and could have substantial consequences for local harlequin duck populations.

Harlequin duck philopatry necessitates affinity to specific high-quality sites with individuals recurrently occupying particular habitat features and shoreline sections

(Robertson et al., 2000a). In an effort to identify British Columbia, Washington State, and northern Oregon coastal locales likely to support harlequin ducks, I developed species distribution models (SDMs). These models identify areas potentially inhabited during the nonbreeding season at diurnal and nocturnal times and were developed using maximum entropy (Maxent) modeling (Phillips et al., 2006, 2017) and male harlequin duck occurrence locations collected from satellite telemetry. The satellite telemetry data were supplied by researchers in Alberta, British Columbia, Montana, Washington, and Wyoming. I then utilized an established Oil Residence Index (ORI) to identify suitable Salish Sea shoreline habitats with the potential to have prolonged oil residence (Berry et al., n.d.; Howes et al., n.d.). I begin this thesis with a review of literature relevant to harlequin duck natural history and population risks; oil transport in Washington and British Columbia coastal waters; and Maxent species distribution modeling. I then detail my methodology for developing the SDMs and present model results. This thesis concludes with a discussion identifying particular high-quality habitats that may be especially susceptible to oil spills and their legacy effects under current and planned future oil transport scenarios.

LITERATURE REVIEW

Harlequin Ducks

Harlequin ducks (*Histrionicus histrionicus*) exhibit philopatry to sensitive habitats during nonbreeding and breeding periods (Bruner, 1997; Robertson et al., 2000b). From mid-summer to early spring, during their nonbreeding period, harlequin ducks utilize gravel and rock coastlines and nearshore habitats during the day and move farther offshore at night to roost. During the nonbreeding period, Pacific Coast harlequin ducks range from Northern California to the Aleutian archipelago; during the spring breeding season, both sexes migrate inland where they breed and fledge young on fast-flowing, montane streams (Robertson & Goudie, 1999). Pacific harlequin ducks utilize streams from the south throughout Oregon's Cascades, extending north throughout Alaska and the Yukon Territory, and inland to the Northern Rocky Mountains (Robertson & Goudie, 1999).

Harlequin Duck Natural History during the Breeding Period

Harlequin ducks depart coastal habitats during the early spring to migrate inland to montane streams where they spend the breeding period (Cassirer & Groves, 1994; Robertson et al., 2000b). Some populations of harlequin ducks that use streams near the coast—such as those in Prince William Sound, Alaska—continue to use stream estuaries during the breeding period even though they nest at higher elevations along stream corridors (Crowley, 1993). Upon arrival to breeding stream habitats, pairs copulate, and females search for and select nest locations. Males are only present during this early period for ca. 6–7 weeks, returning to the coast soon after females begin incubation, typically by June, although incubation initiation varies by region (Bruner, 1997). Females may initiate nests and begin laying eggs as early as mid-April (Bruner, 1997). A single egg is laid daily or every second day until final clutch formation; final clutches typically consist of five or six eggs (Bengtson, 1972; Bruner, 1997; Crowley, 1993). Incubation is initiated once all the eggs have been laid and lasts for 27–29 days (Bengtson, 1972). After hatching, females and their young remain in stream habitats until the young fledge. Females and young typically depart stream habitats together for the coast during late August and September (Bruner, 1997; Cassirer & Groves, 1994).

Females exhibit philopatry to specific streams and even to particular nesting locations (Bruner, 1997; Cassirer & Groves, 1994; Crowley, 1993). Unpaired young females move more in stream habitats than older, paired females, likely because they are searching for suitable stream and nesting habitats and have not yet established breeding site philopatry (Bruner, 1997). Young females, exhibiting elevated movement and without established site philopatry, are agents of female dispersal into new breeding streams (Bruner, 1997).

Females typically nest upstream from reaches that are used by pairs. In the Cascade Mountains of Oregon, pairs occupied 3rd to 5th order streams while nesting occurred on 1st to 5th order streams (Bruner, 1997). Near Prince William Sound, Alaska, nests are positioned above salmon-bearing stream reaches, near treeline, however, pairs are typically found in lower salmon-bearing stream reaches (Crowley, 1993). Confluences of low-order tributaries and streams are often used by both sexes (Crowley, 1993).

The size of utilized streams may vary by region with availability. In Oregon's Cascade Mountains, Bruner (1997) found that harlequin ducks inhabited stream reaches ranging from 10 to 80 meters in width, averaging 28 meters; however, in Idaho, Cassirer and Groves (1994) found that most harlequin ducks used streams less than 10 meters in width.

Selected stream reaches are typically in mature forest and have ample loafing locations (i.e., places to rest) in the form of instream rocks, wood debris, and islets formed by braided channels (Bruner, 1997; Cassirer & Groves, 1994; Wallen, 1987). Stream reaches with vegetated streambanks are preferred over reaches with unvegetated banks, and rapids, riffles, and runs are preferred over waterfalls and pools by adult birds (Cassirer & Groves, 1994; Goudie & Gilliland, 2008; Wallen, 1987). Broods may use reaches similar to adult pairs or may prefer slower reaches (Cassirer & Groves, 1994; Goudie & Gilliland, 2008); typically, streamflows are lower when broods are present in the summer than when pairs are present. Reach substrate is also a key attribute for harlequin duck utilization; reaches with cobble, boulder, and bedrock substrate are preferred over reaches with sand, gravel, and silt substrates (Bruner, 1997; Cassirer & Groves, 1994; Crowley, 1993; Wright et al., 2000). Areas with increased human disturbance, such as stream reaches adjacent to roads, trails, and logged areas are often avoided (Cassirer & Groves, 1994).

Nests are typically situated on instream islands, in the stream floodplain, or on immediately adjacent streamside slopes and canyon walls (Bruner, 1997; Cassirer & Groves, 1994). Southwest facing slopes with ample sun may be preferred over other aspects and sites free of snow early in the year are often used over sites that remain snow-covered later (Crowley, 1993). Nests may be shallow scrapes on the ground, located on elevated woody debris, perched on canyon walls, or within tree cavities (Bruner, 1997; Cassirer et al., 1993; Cassirer & Groves, 1994; Crowley, 1993). Nests are typically placed under the forest canopy in areas with dense horizontal and vertical vegetative cover (Bengtson, 1972; Bruner, 1997; Crowley, 1993).

Aquatic invertebrate larvae are the primary food source for harlequin ducks while they are in stream habitats (Gardarsson & Einarsson, 2008; Wright et al., 2000). Invertebrate larvae types commonly consumed include caddisfly (*Trichoptera*), mayflies (*Ephemeroptera*), stoneflies (*Plecoptera*), and black flies (*Diptera*; Gardarsson & Einarsson, 2008; MacCallum et al., 2016; Wright et al., 2000). Populations nesting in coastal streams may continue to feed in estuarine areas on invertebrates, juvenile salmonids, and roe (Crowley, 1993). Females nesting away from coastal areas rely solely on freshwater-derived nutrients for egg formation (Bond et al., 2007). Harlequin duck production appears to be limited by food availability in some (Gardarsson & Einarsson, 2008), but not all (Wright et al., 2000) freshwater systems.

<u>Harlequin Duck Natural History during the Nonbreeding Period</u>

Males depart breeding streams and return to coastal habitats after females begin incubating, typically arriving in coastal areas during June and July (Robertson et al., 1997). Females return to coastal regions after nesting and fledging has occurred, typically between late July and September. Nonbreeding and failed nesting females return to coastal sites earlier than successfully nesting females (Robertson et al., 1997). Broods that have survived the summer to fledge depart the breeding stream and return to the coast as a family with their mothers. Once these family groups reach the coast, juveniles of both sexes disperse (Regehr, 2003; Regehr et al., 2001).

Harlequin ducks begin molting soon after they arrive at the coast. Some returning males exhibit interannual philopatry to molting locations which may function as a mechanism to increase survival, developing individual knowledge about specific locations and increasing the likelihood that site characteristics are favorable during the molt period (Robertson et al., 2000b; Robertson & Cooke, 1999). The entire molt period lasts for 2.5-3 months for each individual and results in an approximately 21-day period when birds are flightless. Rapid molting onset likely occurs so that pair-bonds can begin forming early and to ensure flight is regained before winter (Robertson et al., 1997).

Paired individuals also exhibit philopatry to wintering sites which allows for the reunification of pairs and may increase winter survival during periods of stable conditions through developed site knowledge (Robertson et al., 2000b). Most previously formed pairs reunify by December with some pair bonds re-established as early as October. New pair bonds develop later in the winter or spring (Robertson et al., 1998). Males are not territorial on wintering grounds and several male home ranges may overlap; however, males will defend their mate with aggression toward advancing unpaired male suitors (Robertson et al., 2000b).

Exposed, nearshore, intertidal zones with offshore reefs, islands, and islets are preferred coastal habitats during the nonbreeding period (Esler et al., 2000; Rodway et al., 2003). Wide (>100m) intertidal zones provide increased foraging opportunity and are preferred over narrower intertidal areas (Rodway et al., 2003). Areas with cobble, gravel, bedrock, and boulder substrates are often occupied while areas with sand, mud, and silt substrates are generally avoided (Esler et al., 2000; Rodway et al., 2003). Areas near stream mouths may also be preferred (Esler et al., 2000).

In coastal habitats, primary food sources include snails, crabs, bivalves, limpets, chitons, fish roe, and small/juvenile fish (Crowley, 1993; Gaines & Fitzner, 1987; Vermeer, 1983). Wintering harlequin ducks have high metabolic requirements due to their small body size and large surface area to volume ratio; their physiology demands that they feed more frequently than larger-bodied sea ducks during the winter (Goudie & Ankney, 1986). Wide intertidal areas increase feeding opportunities by providing longer periods of suitable foraging conditions during the tidal cycle and more efficient shallow water diving (Esler et al., 2000; Rodway et al., 2003). Herring spawn events that provide access to large amounts of easily acquired roe are frequented by harlequin ducks in the Pacific Northwest. Spawn events typically occur in the early spring, before harlequin ducks depart for breeding areas; harlequin ducks that frequent herring spawn increase endogenous reserves that are used for migration and on the breeding grounds but not for egg production (Bond & Esler, 2006).

Harlequin Duck Population Dynamics

Harlequin duck populations have sex ratios skewed towards males likely as a result of higher female annual mortality (Cooke et al., 2000; Rodway et al., 2003). Counts of wintering Pacific Northwest harlequin ducks indicated that females comprise about 41–45% of the population (Smith et al., 2001; WDFW unpublished data). Female survival is lowest during the breeding period with breeding period survival rates varying by location, ranging from 75% in Alberta to 87% and 89% in British Columbia and Oregon, respectively (Bond et al., 2009). Most female mortalities occur during incubation, and variations in breeding period mortality rates may be due to differences in predator communities and available cover (Bond et al., 2009; Bruner, 1997). Females often attempt to nest during their second year but nest success is generally low; adult-level nest success rates aren't reached until the 4th or 5th year (Hendricks, 1999). Annual recruitment also appears low with hatch-year individuals accounting for less than 10% of wintering abundance in the Pacific Northwest (Smith et al., 2001; WDFW unpublished data).

Male and female survival rates appear to be similar during molting and wintering periods. Annual survival rates of individuals returning to White Rock, Canada varied between juvenile males (56%), adult males (82%), and all age class females (74%; Cooke et al., 2000). Winter survival is higher for philopatric males than non-philopatric males probably because the former have greater success in avoiding predators and exploiting food resources due to their experience with local conditions. (Cooke et al., 2000; Robertson & Cooke, 1999).

Harlequin Duck Population Threats

The resiliency of harlequin duck populations and their ability to recover from external perturbations is reduced by slow reproduction, philopatry, and high overwinter metabolic requirements. Harlequin ducks exhibit delayed sexual maturity and low annual reproduction relative to other ducks (e.g. dabbling ducks [*Anatinae*]), resulting in slow population growth rates (Goudie et al., 1994). Under normal conditions, low productivity typically results in stable populations; however, a population's inherent slow growth rate may hamper recovery when perturbations occur and populations decrease (Esler et al., 2002; Goudie et al., 1994; Iverson & Esler, 2010). Philopatry may increase harlequin duck survival in stable and suitable habitats, but being site faithful means that harlequin ducks may continue the use of an area when environmental conditions degrade and are no longer suitable (Esler et al., 2002). Philopatry also slows immigration to new sites which may hamper population growth in recovering areas (Esler et al., 2000, 2002). The high metabolic demands of wintering harlequin ducks place them near a survival threshold. If foraging conditions or individual physical conditions diminish due to an external perturbation, overwinter survival can decrease drastically as individuals fail to meet their high metabolic needs (Esler et al., 2002).

Catastrophic events like the Exxon Valdez oil spill can immediately reduce local abundance and have long-lasting impacts on future harlequin duck populations. Oil spills are particularly deleterious to philopatric organisms because individuals that survive initial exposure events are routinely re-exposed to remnant hydrocarbons at contaminated sites (Esler et al., 2002; Patten et al., 2000). Following the Exxon Valdez spill, petroleum hydrocarbons persisted in local sediment for years and were present in harlequin duck food sources (Babcock et al., 1996; Carls et al., 2001; Wolfe et al., 1994). As a result, harlequin ducks ingested and absorbed the legacy pollutants. In 1989 and 1990, 74% of Prince William Sound's harlequin duck population had aliphatic (non-aromatic) hydrocarbons present in their liver (Patten et al., 2000).

Female harlequin duck abundance in Prince William Sound fell by one-quarter immediately after the spill due to direct oiling. During the years that followed, female abundance continued to decline in oiled areas until five to ten years after the spill when it hit a low-point 55% below pre-spill abundance (Iverson & Esler, 2010). Nearly a decade after the Exxon Valdez spill, Prince William Sound harlequin duck densities remained lower in oiled areas than unoiled areas, indicating that populations had not recovered from the initial population reduction and continued exposure to persistent environmental toxins (Esler et al., 2000, 2002). Population recovery did not begin until the spill's legacy effects no longer reduced survival rates, 11 to 14 years after the spill (Iverson & Esler, 2010; Rosenberg et al., 2005).

Due to concern over their low productivity, philopatric patterns, and susceptibility to disturbance by human activity, harlequin ducks have been designated a Priority Species for conservation and management and a Species of Greatest Conservation Need (SGCN) by the Washington Department of Fish and Wildlife (Lewis & Kraege, 1999; Washington Department of Fish and Wildlife, 2015). NatureServe, a non-profit organization specializing in independent conservation status assessments, ranks nonbreeding harlequin duck populations as *Vulnerable* in British Columbia and Washington. British Columbia breeding populations are considered *Apparently Secure* while Washington breeding populations are considered *Imperiled* (NatureServe, 2020).

Petroleum Transportation and Oil Spill Risks

Within the Pacific Northwest study area, most oil transport occurs across the straits, sounds, and inlets of the Salish Sea. Presently, there are about 530 tanker transits in the Salish Sea annually. Most tankers transiting the Salish Sea are bound for refineries in Anacortes and Ferndale (Washington State), and Vancouver, British Columbia, Canada (Govt of Canada & National Energy Board, 2016; Washington Department of Ecology, 2019). The Salish Sea also supports more than 10,000 tanker-barge and articulated tug-barge inshore transits annually (Washington Department of Ecology, 2019).

Ocean-going oil tankers traveling to Vancouver via the Strait of Juan de Fuca must navigate three abrupt turns to avoid reefs and negotiate the strong currents of Haro Strait and Boundary Pass. Tankers bound for refineries in Anacortes and Ferndale must travel through the narrow and reef strewed Guemes and Rosario Straits (Washington Department of Ecology, 2019). As a precaution, all tankers must be guided by local pilots and tetherescorted by a tug when traveling past the Strait of Juan de Fuca. Tankers pair with pilots and tugs in Victoria if headed north—through Haro Strait and Boundary Pass—to Vancouver, and in Port Angeles if bound for Ferndale, Anacortes, or Puget Sound.

As recommended by the Canadian National Energy Board, expansions to the Alberta to British Columbia Trans Mountain Pipeline would increase pipeline capacity from 300,000 barrels per day to 890,000 barrels per day of light crude, heavy crude, and diluted bitumen oil (Govt of Canada & National Energy Board, 2016). Diluted bitumen (known as dilbit), is a two-part substance, in which dense and viscous bitumen is diluted with light gas condensates to allow for pipeline transfer (Govt of Canada & National Energy Board, 2016). To facilitate and ship the increased throughput of the pipeline, the Westridge Marine Terminal in Vancouver would be refitted to accommodate three tankers. As a result of the increased oil load, Vancouver-routed tanker vessel traffic is expected to increase from 5 to 34 vessels per month (Govt of Canada & National Energy Board, 2016).

Additional proposed pipeline expansion projects would increase oil transport out of Prince Rupert and Kitimat, British Columbia, however, it is unlikely that these proposals will be completed because the Canadian Government recently enacted a moratorium on oil tanker traffic along the province's northern coast (Transport Canada, 2019). The new moratorium blocks tanker vessels with a capacity greater than 12,500 metric tons from stopping and onloading/offloading oil products at British Columbia north coast communities, north of Vancouver Island. The moratorium still allows for smaller oil shipments to north coast ports to support residential communities and some industrial activities (Transport Canada, 2019).

The anticipated growth of tanker traffic, driven by the Trans Mountain expansion, increases the risk of oil spills in the Salish Sea. The potential for an oil spill is elevated at the

Westridge Marine Terminal in Burrard Inlet during loading and unloading and in navigationally complex Boundary Pass and Haro Strait. The fate of oil spilled at these locations has been modeled using computer particle simulations and drifter device studies (Niu et al., 2017; Pawlowicz et al., 2019). Oil spilled in Burrard Inlet or the Strait of Georgia would be distributed in all directions without a dominant course, whereas, if it was spilled in Boundary Pass, Haro Strait, or the Strait of Juan de Fuca it would be transported oceanward (Johannessen et al., 2020; Niu et al., 2017; Pawlowicz et al., 2019). Most spilled oil would wash ashore within hours or days and relatively little oil would be transported completely through the Strait of Juan de Fuca to the ocean (Johannessen et al., 2020; Pawlowicz et al., 2019).

Being less dense than water, spilled light and heavy crude oil would remain afloat following a spill. Dilbit, however, could potentially sink if its lighter diluting components were to evaporate off, leaving a higher proportion of dense bitumen (Johannessen et al., 2020; Short, 2015). Dilbit would be especially prone to sinking if it was spilled in lower salinity, less dense waters like Burrard Inlet or in turbulent waters such as Haro Strait (Johannessen et al., 2020). If dilbit were to sink some would coat benthic environments, remaining oil would likely refloat as it was transported out of lower salinity waters or as turbulent water conditions ceased (Johannessen et al., 2020). Dilbit would quickly become viscous as the diluting light oils evaporate, greatly increasing its adherence to and retention on shorelines. Spilled dilbit would be resistant to environmental decay because it contains few bioavailable labile compounds (Johannessen et al., 2020; Short, 2015).

Maxent Species Distribution Modeling

Species distribution models (SDMs), also known as ecological niche models, assess associations between species occurrence locations and environmental attributes (Elith & Leathwick, 2009). Established associations are typically projected onto a landscape of interest to estimate species distribution and location suitability. Maxent modeling is an SDM method that analyzes environmental parameter values at presence-only occurrence points against values at pseudo-absence (background) points, using machine learning maximum entropy methodology. This methodology optimizes predicted response distributions to maximize uniformity while meeting constraints inherent within the datasets (Phillips et al., 2006). Continuous and categorical environmental predictors are often depicted across a landscape as raster grids of climatic and habitat attributes. Linear vector features may also be assessed, using the samples-with-data format established by Elith et al. (2011). Occurrence locations and background pseudo-absence locations are represented as points (Phillips et al., 2006).

Within Maxent modeling, species occurrence and prevalence are unknown across the study landscape (Elith et al., 2011; Merow et al., 2013; Phillips et al., 2006). Users can define the study landscape by constraining the spatial extent of sampled parameters at background points. Limiting the spatial extent to areas accessible to and within the dispersal capabilities of the study species helps to reduce sampling bias from irrelevant background sample locations, outside conditions typically encountered by the species of interest (Merow et al., 2013).

During Maxent modeling, predictor variables are transformed using multiple arithmetic functions into *features* that are ultimately used in place of direct covariate measurements. Feature types affect model relationships and imply specific occurrence-covariate relationship assumptions. Because of this, feature types may be defined by the user (Elith et al., 2011). Currently, linear, quadratic, product, hinge, and threshold feature types are available in Maxent modeling software (Merow et al., 2013).

Maxent modeling can produce four result output types: raw, cumulative, logistic, and ‘cloglog’ (complementary log-log). Cumulative, logistic, and cloglog outputs are products of, and scale adjustments to, raw outputs, and are generated by different transformation functions. Across a landscape, raw outputs can be interpreted as relative occurrence rates. Logistic and cloglog outputs are interpreted as the probability of presence of a given cell (Merow et al., 2013; Phillips et al., 2017). Logistic outputs have been criticized due to internal arbitrary estimations of transformation constants that the conversion relies on. As a result, Merow et al. (2013) suggested avoiding logistic outputs entirely. Phillips et al. (2017) introduced the complementary log-log (cloglog) output, with strong statistical justification, as an alternative to logistic output to estimate the probability of presence.

Maxent modeling is especially vulnerable to sampling bias due to its use of presence-only instead of presence-absence occurrence data (Phillips et al., 2009). To lessen the effects of sampling bias, Phillips et al. (2009) suggested restricting the extent of background sampling to areas likely surveyed; however, this approach has since been shown to perform poorly (Fourcade et al., 2014). Other approaches have been tested, and systematic grid sampling appears to have the best results under the widest range of bias types and conditions (Fourcade et al., 2014). Systematic grid sampling reduces bias and spatial autocorrelation by applying a grid across the study landscape with cell sizes larger than the environmental covariate raster grid layers; from each cell, a single observation is randomly selected and retained. Randomized spatial rarefication is a similar process to systematic grid sampling, but instead removes all locations within a defined radius of randomly selected points.

Maxent model overfitting is restricted using model regularization (smoothing). Regularization is controlled within the Maxent software itself using the internal L1-regularization process; the degree of model regularization is governed by the multiplier β (beta), which can be user-defined (Phillips et al., 2006). A range of beta multiplier values may be assessed through model performance using the area under the receiver-operator curve (AUC) metric (Elith et al., 2011; Merow et al., 2013). Alternatively, some spatial statisticians promote regularization selection and model assessment through a model selection approach using Akaike Information Criterion (AIC; Warren et al., 2014; Warren & Seifert, 2011).

Model results are typically assessed using the AUC metric and cross-validation methods where model predictions are verified against a subset of occurrence locations that are withheld for testing (Elith et al., 2011; Merow et al., 2013). The AUC metric establishes the probability that occurrence points are ranked higher than random background samples (Elith et al., 2010; Merow et al., 2013).

Conclusion

The risk of an oil spill in the Salish Sea will grow as expansions to the Trans Mountain pipeline increase Salish Sea tanker traffic. If a spill were to occur, harlequin duck abundance could fall immediately from acute oiling, and abundance could continue to decline during the following years as individuals are repeatedly exposed to remnant hydrocarbons at contaminated sites. The development of a species distribution model would help with the identification of suitable habitats at a high risk of contamination if an oil spill were to occur. Species distribution models could also be useful for identifying suitable habitats that are likely to retain remnant oil contamination for a prolonged period after the contamination event. Maxent modeling is especially well suited for SDM development because it performs well with presence-only occurrence datasets.

MANUSCRIPT

Introduction

Harlequin ducks (*Histrionicus histrionicus*) are a species of sea duck that inhabit exposed rock and gravel shorelines and nearshore marine habitats throughout the Pacific Northwest, during their nonbreeding period. During the breeding season, harlequin ducks migrate inland to breed and fledge young on montane streams (Robertson & Goudie, 1999). Harlequin ducks are highly philopatric to nonbreeding and breeding habitats, they also employ a reproductive strategy with relatively low reproductive rates (Bruner, 1997; Robertson et al., 2000b; Robertson & Goudie, 1999; Smith et al., 2001). Philopatry and low productivity can be beneficial for maintaining stable populations under stable environmental conditions; however, if environmental conditions alter or external perturbations occur, populations displaying philopatry and low productivity can be especially vulnerable to acute and prolonged population reductions (Esler et al., 2002).

Harlequin ducks exhibit an additional trait that makes them particularly vulnerable to population reductions: their small body size and resulting high surface area to volume ratio requires that they feed nearly continuously during cold, short daylight periods in winter to meet their high metabolic requirements (Goudie & Ankney, 1986). To fulfill these metabolic needs, harlequin ducks utilize and are philopatric to high-quality habitats with shallow bathymetry and broad intertidal areas that support rapid dive intervals throughout the tidal cycle (Esler et al., 2000; Rodway et al., 2003). Under typical conditions, these habitats provide ample forage, but the high metabolic requirements of harlequin ducks place them near a survival threshold. If foraging or body conditions diminish due to an external perturbation, overwinter survival can drastically decrease (Esler et al., 2002).

Following the Exxon Valdez oil spill on 24 March 1989, the harlequin duck population in Prince William Sound, AK suffered an immediate and acute impact; abundance declined by approximately one-quarter (>1,000 individuals died) in oiled areas due to direct oil exposure (Esler et al., 2000, 2002; Iverson & Esler, 2010; Piatt et al., 1990). Alone, the loss of one-quarter of a philopatric population with low productivity could have long-lasting suppressive effects, resulting in a slow recovery. However, continued exposure to persistent oil pollution diminished local survival rates, resulting in further losses. More harlequin ducks were lost as a result of prolonged oil pollution exposure than were lost immediately after the spill (Esler et al., 2000, 2002; Iverson & Esler, 2010; Rosenberg et al., 2005). At its lowest point (five to ten years after the spill), female abundance in oiled areas was 55% below pre-spill abundance (Iverson & Esler, 2010). Harlequin duck abundance in oil affected regions did not recover until hydrocarbon exposure waned and survival rates returned to pre-spill levels; this process took at least 11 years (Iverson & Esler, 2010; Rosenberg et al., 2005).

Pacific Northwest harlequin duck populations utilizing and philopatric to the coastal waters of British Columbia and Washington State also face substantial and potentially increasing risks from oil spills. Currently, approximately 530 oil tankers navigate the waters of the Salish Sea every year; this oil tanker traffic is predicted to significantly increase soon (Govt of Canada & National Energy Board, 2016; Washington Department of Ecology, 2019). British Columbia's proposed Trans Mountain Pipeline is expected to increase oil tanker traffic between Vancouver, BC and the Pacific Ocean via the Strait of Georgia, Boundary Pass, Haro Strait, and Strait of Juan de Fuca from 5 to 34 vessels per month (Govt of Canada & National Energy Board, 2016). This increase in tanker traffic signals a major increase in oil spill risk for the region's marine life.

Harlequin duck philopatry necessitates affinity to specific high-quality sites with individuals repeatedly occupying particular habitat features and shoreline sections (Robertson et al., 2000a). In an effort to identify British Columbia, Washington State, and northern Oregon coastal locales likely to support harlequin ducks, I developed species distribution models (SDMs). These models identify areas potentially inhabited during the nonbreeding season at diurnal and nocturnal times, and were developed using maximum entropy (Maxent) modeling (Phillips et al., 2006, 2017) and male harlequin duck occurrence locations collected from satellite telemetry. The satellite telemetry data were supplied by researchers in Alberta, British Columbia, Montana, Washington, and Wyoming. Maxent modeling is an SDM method that analyzes environmental parameter values at presence-only occurrence points against values at pseudo-absence (background) points, using machine learning maximum entropy methodology. This methodology optimizes predicted response distributions to maximize uniformity while meeting constraints inherent within the datasets (Phillips et al., 2006). Maxent modeling was selected for this analysis due to its high performance using few presence-only occurrences relative to other species distribution modeling techniques (Elith et al., 2006, 2011). Following SDM development, I utilized an established shoreline Oil Residence Index (ORI) to identify suitable shoreline habitats in the Salish Sea with potentially prolonged oil residence on the scale of years (Berry et al., n.d.; Howes et al., n.d.).

Methods

Harlequin Duck Capture

Stream Captures – Teams of researchers captured harlequin ducks with mist nets on montane streams during the spring breeding periods of 2016–2018 along the McLeod River, Alberta; in Glacier National Park and elsewhere throughout Northwest Montana; throughout the Cascade and Olympic Mountains of Washington; and in Grand Teton and Yellowstone National Parks, Wyoming. Prior to capture, we assessed and selected streams and potential capture sites through a review of historic survey data and citizen science (i.e., eBird) data (Sullivan et al., 2009). We visited sites before capture efforts to scout for and locate harlequin ducks and to identify sites that permitted safe and effective capture; such sites allowed us to safely and quickly wade or kayak across the stream. Ideal sites typically had vegetation or stream bends which helped conceal the mist net and high streamside banks or vegetation to funnel harlequin ducks toward the net and limit net evasion.

We used two-shelved, 210 denier nylon mist nets (Avinet, Inc., Portland, ME, 04103, USA), that were 1.3 meters tall and 6–18 meters wide with 100mm mesh. The mist nets were suspended between two conduit uprights and hung perpendicular across the stream. To secure the net, we drove a spike into the streambed, placed the lower end of the conduit onto the spike, and blocked the base with rocks to anchor the upright. The top of the upright was stabilized with lines tied to streamside brush and boulders. The method detailed by Smith et al. (2015) was used regularly by the capture team in Montana to safely and effectively capture harlequin ducks in unwadeable, highwater conditions.

During stream captures, we caught harlequin ducks using different approaches. After locating birds, we would attempt to quickly set up the mist net nearby and then drive the targeted harlequin ducks toward the net on foot or in kayaks. If we could not locate harlequin ducks, we would erect the mist net and then drive lengths of the stream on foot or in kayaks toward the net. We also passively caught harlequin ducks that happened to be traveling the stream past the erected net. A person was always positioned near the net to flush rafting harlequin ducks into the net and to immediately remove captured birds.

Coastal Captures – Captures also occurred throughout coastal British Columbia near White Rock, Hornby Island, and Kitimat during March and April of 2014–2015. Coastal captures utilized a floating mist-net technique adapted from the one described by Kasier et al (1995). Mist-nets used during coastal captures were similar to those used on streams but were up to 30 meters wide. Decoys were deployed to lure harlequin ducks close to the net. Captured ducks were recovered from the net via kayaks and inflatable boats.

Marking

Harlequin ducks were marked with Argos platform transmitting terminals (PTTs, 35g; IMPTAV-2630, Telonics, Inc., Mesa, AZ, 85204, USA) using the implant technique of Korschgen (1996). A skilled veterinarian implanted the device into the body coelomic cavity and positioned the external antenna through a dorsal port. After a short recovery period, harlequin ducks were released near the capture location.

Harlequin duck geographic locations were calculated and relayed via the Argos satellite system which estimates locations using the Doppler effect via seven polar-orbiting satellites (Argos, 2016). PTT reporting intervals varied by deployment and by season, but in general, PTTs were programmed to report more frequently during the breeding and molt periods than during the remainder of the year. During the modeled period for this analysis

(August - February), PTTs were programmed to report for three hours every 96–336 hours. PTT locations were uploaded to Movebank.org (Wikelski et al., 2020).

Occurrence Locations

Outlier PTT records were removed from the location dataset using Douglas filtering in Movebank (Douglas et al., 2012). I then subset and retained only Argos location Class 3 records which reflect one standard deviation of error radius at 250 meters or less, as calculated internally within the Argos location estimation algorithm (Argos, 2016). For each Class 3 record, I then calculated the sun angle via the record's timestamp and geographic location through the R-package 'suncalc' (Thieurmel & Elmarhraoui, 2019). Using the sun angle, I classified and subset each retained Class 3 record as either diurnal (sun angle > 0°), crepuscular (0° to -18°), or nocturnal (< -18°). From the diurnal and nocturnal subsets, I then randomly selected one record per tag-day and retained only records that occurred during the harlequin duck nonbreeding period, conservatively defined as August–February. These records were then spatially rarefied to 2500 meters using the 'SDMtoolbox' in ArcGIS (Brown, 2014). Occurrence-only datasets are prone to spatial bias which can result in model overfitting. The spatial rarefication technique has been demonstrated to be a widely applicable approach to reduce inherent spatial bias and model overfitting (Fourcade et al., 2014).

Study Area

I limited the SDM study areas to include all of British Columbia and Washington coastal waters, as well as coastal Oregon waters between the Columbia River and 20 kilometers south of Cape Falcon (Figure 1). Thus, the study area latitudes ranged from 45.70°N to 55.95°N. The diurnal and nocturnal study areas were also limited to ≤6 km and ≤12 km from the shoreline, respectively. These distances reflect the maximum distances from shoreline harlequin ducks were observed using as indicated by the PTT location data. Limiting the spatial extent of the study area to these distances helps reduce spatial bias.

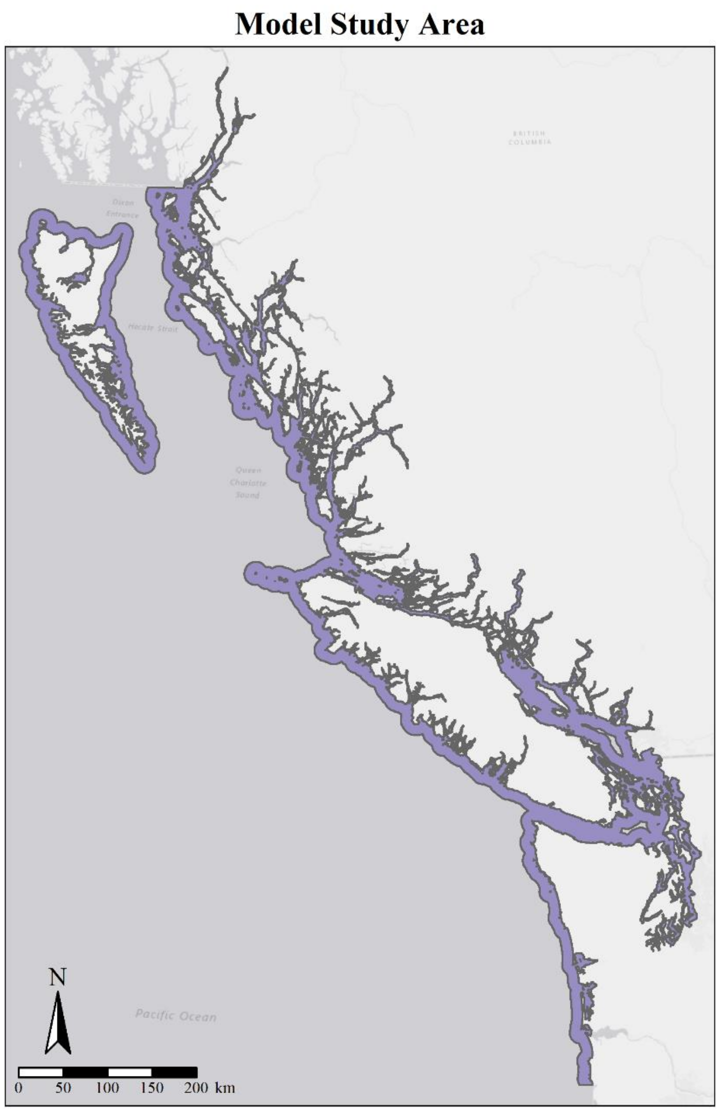

Figure 1: Model study area of northern Oregon, Washington, and British Columbia coastal habitats, approximately 45.70°N to 55.95°N. The nocturnal study area (pictured) extended 12 km from shore while the diurnal study area extended 6 km from shore.

Environmental Predictors

I assembled raster layers depicting various climatic and physical environmental attributes to be considered as predictor variables within the Maxent models (Table 1). Most environmental layers were adapted from preexisting datasets, some were converted from vector data types, and several were developed independently. All environmental layers were developed in or projected to Albers BC projection (Albers; EPSG: 3005) to maintain equal area across the study extent and were developed with or resampled to a cell size of 250 meters.

Atmospheric climate attributes were sourced from the global MERRAClim dataset (Table 1; Vega et al., 2017). MERRAClim utilizes historic land-based weather station data along with remotely sensed satellite data to model global climatic attributes at a 2.5 arcminute (≈4.6 km) resolution. I clipped selected MERRAClim variables by the diurnal and nocturnal study areas, projected them to Albers, and resampled the rasters to 250 meters. I also included several marine climate variables sourced from MARSPEC at a 30 arcsecond (≈0.9 km) resolution (Table 1; Sbrocco & Barber, 2013). MARSPEC rasters were processed similarly to the MERRAClim rasters, differing only in that the 'Nibble' tool—in the ArcGIS Spatial Analyst toolbox—was used to fill small gaps that formed near the shoreline boundaries of the MARSPEC dataset (Esri Inc., 2018).

Bathymetric data were obtained from the National Oceanic and Atmospheric Administration (NOAA, 2020); various bathymetric rasters, ranging in resolution from 1/3 arcsecond (≈10.3 meters) to 3 arcseconds (≈92.6 meters), were mosaicked together, projected to Albers, resampled at 250 meters, and clipped to the study areas to form the bathymetric depth variable. I developed the bathymetric slope variable using the bathymetric depth raster and the ‘Slope’ tool in ArcGIS’s Spatial Analysis toolbox (Esri Inc., 2018).

I projected rasters depicting physical shoreline attributes using Shorezone linear and polygon vector datasets sourced from British Columbia, Washington, and Oregon (Berry et al., n.d.; Harper et al., 2013; Howes et al., n.d.). Shoreline exposure rasters were generated using the exposure value from each dataset; beach substrate and steepness were indexed using British Columbia’s coastal class system. I used ArcGIS’s Feature to Raster conversion tool to develop rasters from the linear and polygon values independently (Esri Inc., 2018). Line and polygon originated rasters were then mosaicked together with the polygon-sourced values taking precedence over the linear-sourced values. Shoreline attributes were then projected to all cells ≤1 km from the shoreline using the ‘Euclidean Allocation’ and ‘Raster Clipping’ tools in ArcGIS (Esri Inc., 2018). An offshore indicator value was then applied to all cells >1 km from the shoreline in the diurnal and nocturnal study areas.

Distance to the shoreline was calculated from the highest resolution state and provincial land boundary polygons that could be located using the ‘Euclidean Allocation’ tool in ArcGIS (Esri Inc., 2018). I also rasterized layers depicting root mean square tidal current from a triangulated irregular network (TIN) sourced from Foreman et al. (2000), and estuary boundaries using polygons sourced from the Pacific Marine and Estuarine Fish Habitat Partnership and the Pacific Birds Habitat Joint Venture (Heady et al., 2014; Pacific Birds Habitat Joint Venture, 2019; Ryder et al., 2007).

Table 1: Assembled environmental predictor variables considered for use in SDM development; unit of measure and native resolution are also detailed.

Assembled Environmental Predictor Variables		
Variable	Unit	Native Resolution
Climatic		
MARSPEC (Marine)		30 arcsecond
Mean Annual Sea Surface Salinity	PSU*	
Annual Range Sea Surface Salinity		
Mean Annual Sea Surface Temperature	°C	
Annual Range Sea Surface Temperature		
MERRAClim (Atmospheric)		2.5 arcminute
Annual Mean Temperature	°C	
Mean Diurnal Range		
Temperature Annual Range		
Isothermality	Mean Diurnal Range/Temp Annual Range	
Temperature Seasonality	Standard Deviation	
Annual Mean Specific Humidity	Kg water/kg air	
Specific Humidity Seasonality	Coefficient of Variation	
Physical		
Bathymetric Depth	Meters	1/3–3 arcsecond
Bathymetric Slope	Degrees	250 meters
Distance to Shoreline (Land Polygons)	Meters	
Estuary	Binary	
Shorezone	Categorical	
Beach Exposure		
Beach Steepness		
Beach Substrate		
Tidal Current	RMS**	Variable (TIN†)

* Practical Salinity Unit
** Root mean square
† Triangulated Irregular Network

Maxent Modeling and Model Evaluation

I used several R-packages to select environmental predictors and appropriate model settings before final diurnal and nocturnal SDM development. First, I used the R-package 'MaxentVariableSelection' (Jueterbock et al., 2016) to select the most influential climatic environmental predictors. MaxentVariableSelection iteratively runs Maxent models using variable numbers and combinations of feature types across a user-defined range of beta multipliers. For each feature type-beta multiplier combination, MaxentVariableSelection reduces the number of environmental predictors based on user-defined contribution and correlation thresholds. I implemented MaxentVariableSelection using the eleven climatic environmental predictors listed in Table 1 and all features types—except threshold—with beta multiplier values ranging from 1 to 15 at intervals of 1.0, for diurnal and nocturnal occurrences independently. I set the variable contribution threshold at 5% and the variable correlation threshold at 0.7. From the resulting statistics, I selected the climatic environmental predictors retained in the model with the lowest AIC_C value and six or fewer variables.

I determined final Maxent model settings using the R-package 'ENMeval' (Muscarella et al., 2014). ENMeval evaluates Maxent model settings by iteratively running models with variable combinations of feature types and beta multipliers; ENMeval does not vary the environmental predictors used. I ran ENMeval using all of the assembled physical environmental predictors and the climatic environmental predictors selected by MaxentVariableSelection (Table 2). I allowed for all feature types—except threshold—and beta multipliers between 1 and 15 at intervals of 0.5. For the final diurnal and nocturnal models, I selected settings that resulted in the highest performing models (highest AUC) according to the ENMEval results.

Final SDMs were produced using the selected settings and environmental predictors in the R-package 'dismo' (Hijmans et al., 2017), which generated outputs that allowed for improved graphical interpretation. Final diurnal and nocturnal Maxent models were then projected to each study area using cloglog transformation to display the probability of presence on a 0–1 scale (Phillips et al., 2017). Final diurnal model performance was also assessed against an independent dataset of diurnal harlequin duck occurrence locations sourced from the Washington Department of Fish and Wildlife's (WDFW) Midwinter Aerial Waterfowl and Seabird Surveys of the Salish Sea (unpublished data), and British Columbia's Coastal Waterbird Survey (Bird Studies Canada, 2008) using the R-package dismo (Hijmans et al., 2017).

Final SDMs were overlaid with tanker vessel transit counts originating from vessel tracking via Automatic Identification Systems (AIS; NOAA, 2017).

Table 2: Environmental predictor variables selected for final diurnal and nocturnal SDM development and their sources.

Modeled Environmental Predictor Variables	
Diurnal Model	
Variable	Source
Climatic	
Specific Humidity Seasonality	MERRAClim – Vega et al. (2017)
Sea Surface Temperature Annual Range	MARSPEC – Sbrocco and Barber (2013)
Physical	
Bathymetric Depth	NOAA (2020)
Bathymetric Slope	Calculated from Bathymetry
Distance to Shoreline	Vector Datasets[*]
Estuary	Vector Datasets[**]
Shorezone – Beach Exposure	Vector Datasets[†]
Shorezone – Beach Steepness	
Shorezone – Beach Substrate	
Tidal Current	Foreman et al. (2000)
Nocturnal Model	
Variable	Source
Climatic	
Temperature Seasonality	MERRAClim – Vega et al. (2017)
Mean Annual Sea Surface Salinity	MARSPEC – Sbrocco and Barber (2013)
Sea Surface Temperature Annual Range	
Mean Annual Sea Surface Temperature	
Physical	
Bathymetric Depth	NOAA (2020)
Bathymetric Slope	Calculated from Bathymetry
Distance to Shoreline	Vector Datasets[*]
Estuary	Vector Datasets[**]
Shorezone – Beach Exposure	Vector Datasets[†]
Shorezone – Beach Steepness	
Shorezone – Beach Substrate	
Tidal Current	Foreman et al. (2000)

[*] Statistics Canada (2019); BLM (2001); WA L&I (2016)
[**] Heady et al., (2014); Pacific Birds Habitat Joint Venture (2019); Ryder et al., (2007)
[†] Berry et al., n.d.; Harper et al., 2013; Howes et al., n.d.

Oil Residency

I identified highly suitable harlequin duck nearshore habitats with prolonged projected oil residence times that may be especially vulnerable to persistent negative impacts following an oil spill. To do this, I projected the ORI to all cells ≤1km from shore (Berry et al., n.d.; Harper et al., 2013; Howes et al., n.d.). I then reclassified the projected ORI layer to a binary where areas with an ORI value of 3–5 were preserved; ORI values between 3 and 5 indicate an oil residence time on the scale of years. I then applied a binary reclassification to the diurnal SDM where predicted cloglog values ≥0.8 were considered suitable. Locales that satisfied both requisites were then identified using raster math.

Results

Occurrence Sampling

A total of 93 male harlequin ducks were captured and tracked with Argos PTTs between March 2014 and October 2019. Of those, 73 generated occurrence locations during the conservatively delineated nonbreeding period (August–February) for a total of 2,416 tag-days (Table 3).

Geographic locations used by tagged harlequin ducks ranged along the Pacific Northwest coast from Glacier Bay, Alaska (58.80°N) southward to Crescent City, California (41.75°N; Figure 2). During the conservatively defined nonbreeding period, 90% of observations occurred between latitudes 48.15°N and 54.89°N, approximately Cape Alava, Washington to Duke Island, Alaska. The maximum distance from the shoreline was 5,553 meters (90% ≤ 717 meters) during diurnal periods and 11,280 meters (90% ≤ 4,427 meters) during nocturnal periods.

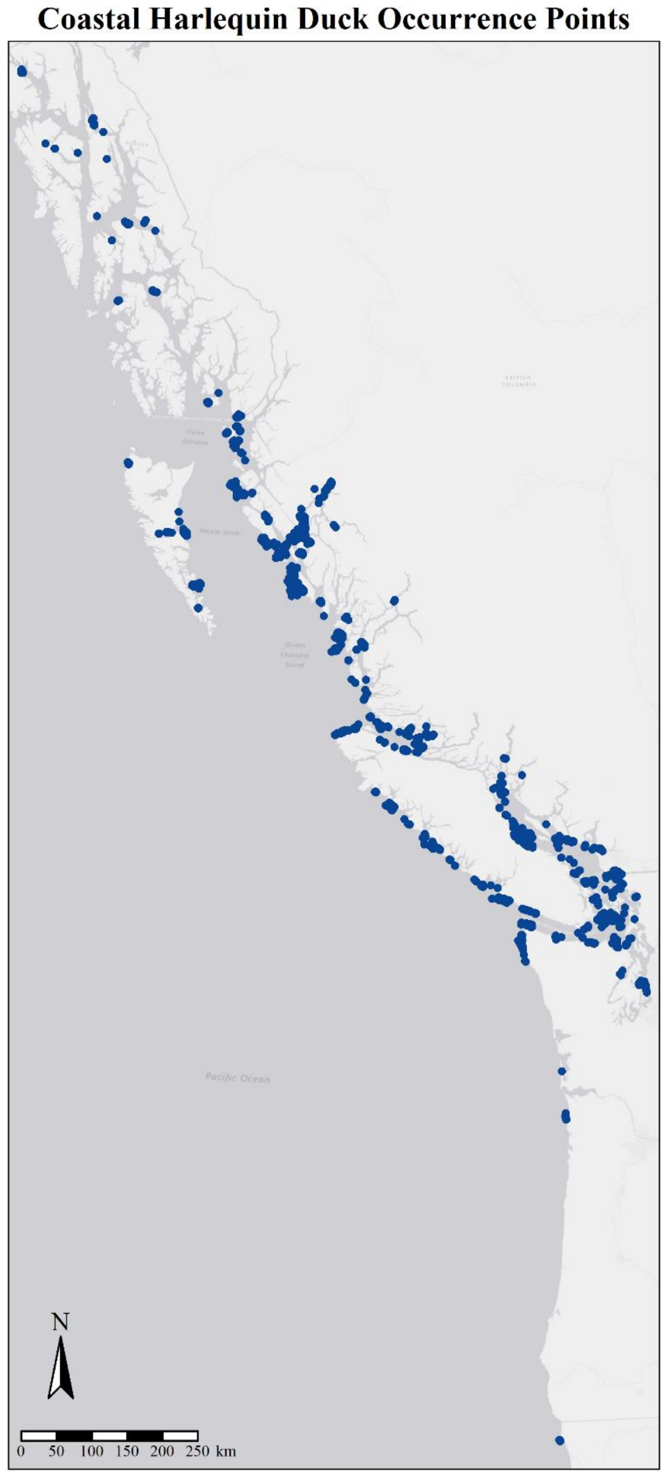

Figure 2: Coastal harlequin duck (*Histrionicus histrionicus*) occurrence points collected via PTT satellite telemetry.

Occurrence filtering to preserve only Argos Class 3 locations (with an error radius ≤250 m) and subsetting by the time of day retained 574 diurnal and 554 nocturnal occurrences. Spatial rarefication (to 2,500 meters) of the filtered and subset occurrences resulted in 119 and 179 occurrences to be used in the development of the diurnal and nocturnal SDMs, respectively.

Additionally, 309 occurrence locations were collected and assembled from WDFW's Midwinter Aerial Waterfowl and Seabird survey of the Salish Sea (unpublished data) and British Columbia's Coastal Waterbirds Survey (Bird Studies Canada, 2008) for an independent evaluation of diurnal SDM performance.

Table 3: Harlequin duck (*Histrionicus histrionicus*) occurrence sampling results.

Harlequin Duck Occurrence Sampling	
Type	Count
PTT Tracking	
HADU Males Tracked	93
AB	10
BC	34
MT	22
WA	18
WY	9
HADU Males w/ Occurrences during Nonbreeding Season	73
Tag-Days during Nonbreeding Season	2416
Class 3 Locations during Nonbreeding Season	1723
Nonbreeding Diurnal Locations	574
Nonbreeding Nocturnal Locations	554
Final Spatially Rarefied Nonbreeding Diurnal Locations	119
Final Spatially Rarefied Nonbreeding Nocturnal Locations	179
Independent Diurnal Locations	
BC Coastal Waterbirds Survey & WA Aerial Winter Survey	309

Observed Environmental Attributes at Occurrence Locations

Diurnal habitat use was restricted to shallow waters that tended to be close to shore with moderate tidal current speeds (Figure 3). Shorelines utilized during the day were typically flat (≤5°) or inclined (5-20°) with rock and/or sediment substrate and moderate to high exposure (Figure 4). Harlequin duck locations were not associated with low exposure shorelines, estuarine areas, or deep-water offshore areas during the day. At night, some harlequin ducks roosted in moderately exposed nearshore habitats within 1km of the shoreline; however, most roosted in offshore waters between 1 and 5km from the coast (Figure 5 & Figure 6).

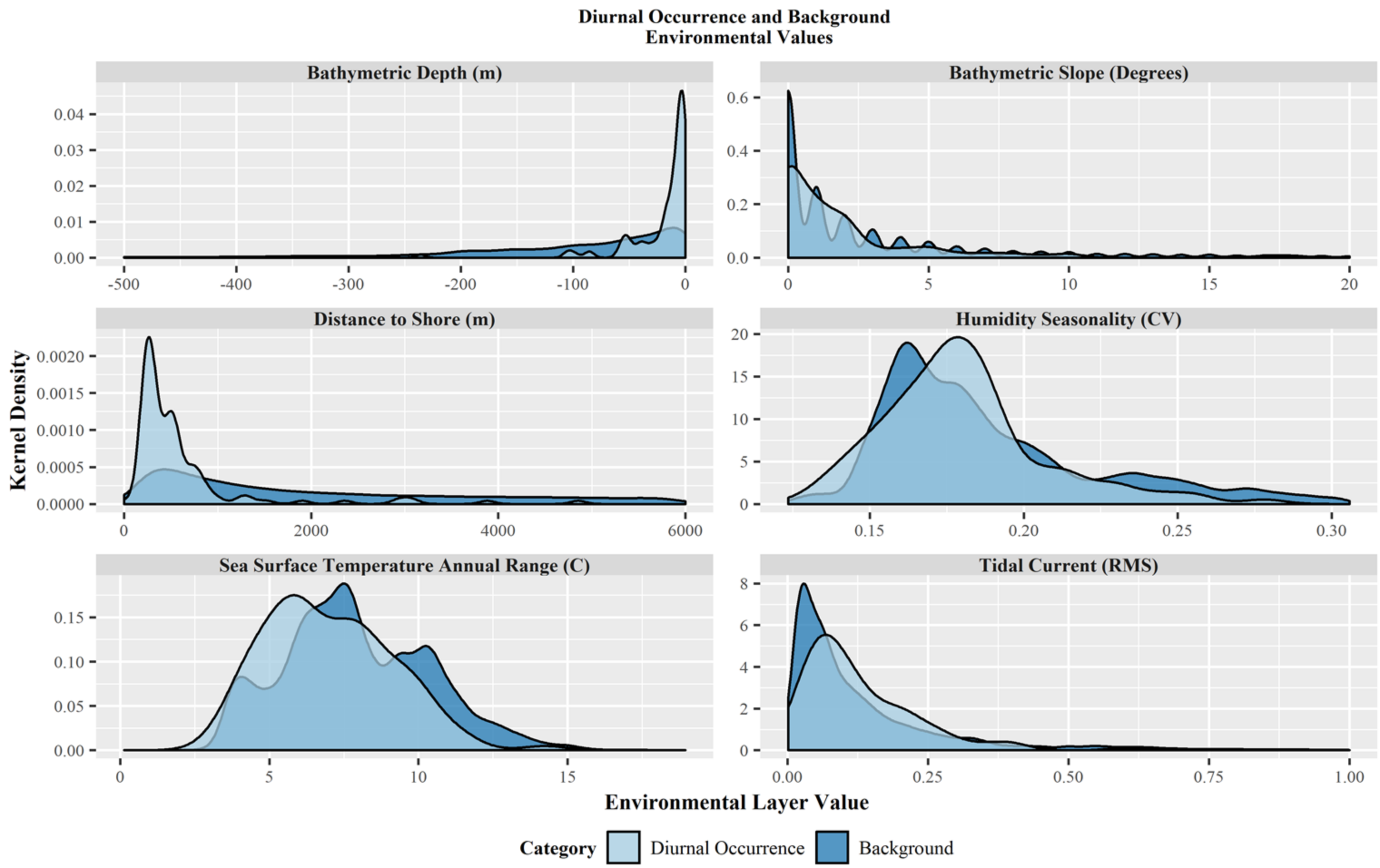

Figure 3: Continuous environmental predictor values at 119 diurnal harlequin duck (*Histrionicus histrionicus*) occurrence points and 30,000 background (i.e. pseudo-absence) points randomly sampled from the study area.

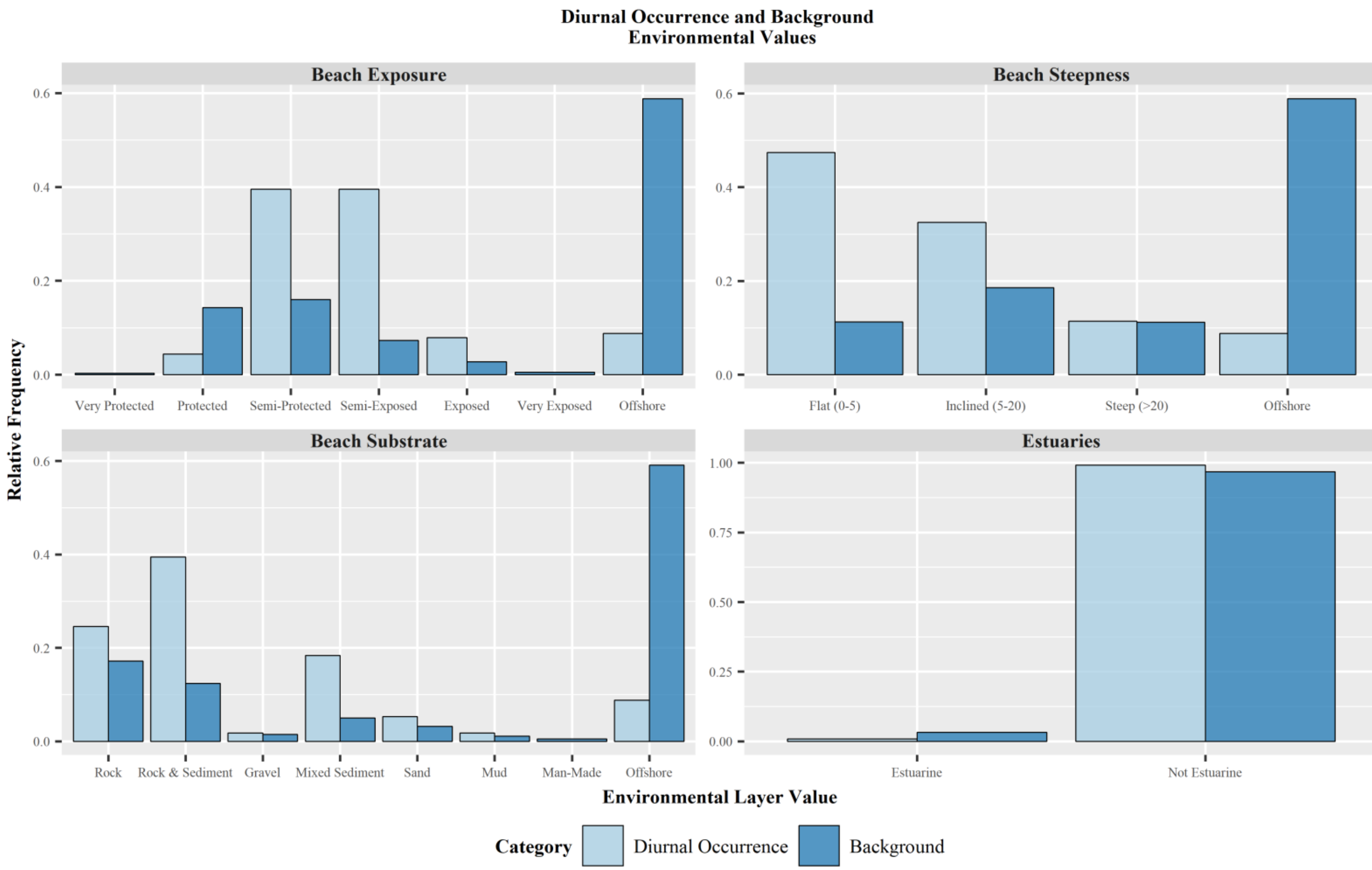

Figure 4: Categorical environmental predictor values at 119 diurnal harlequin duck (*Histrionicus histrionicus*) occurrence points and 30,000 background (i.e. pseudo-absence) points randomly sampled from the study area.

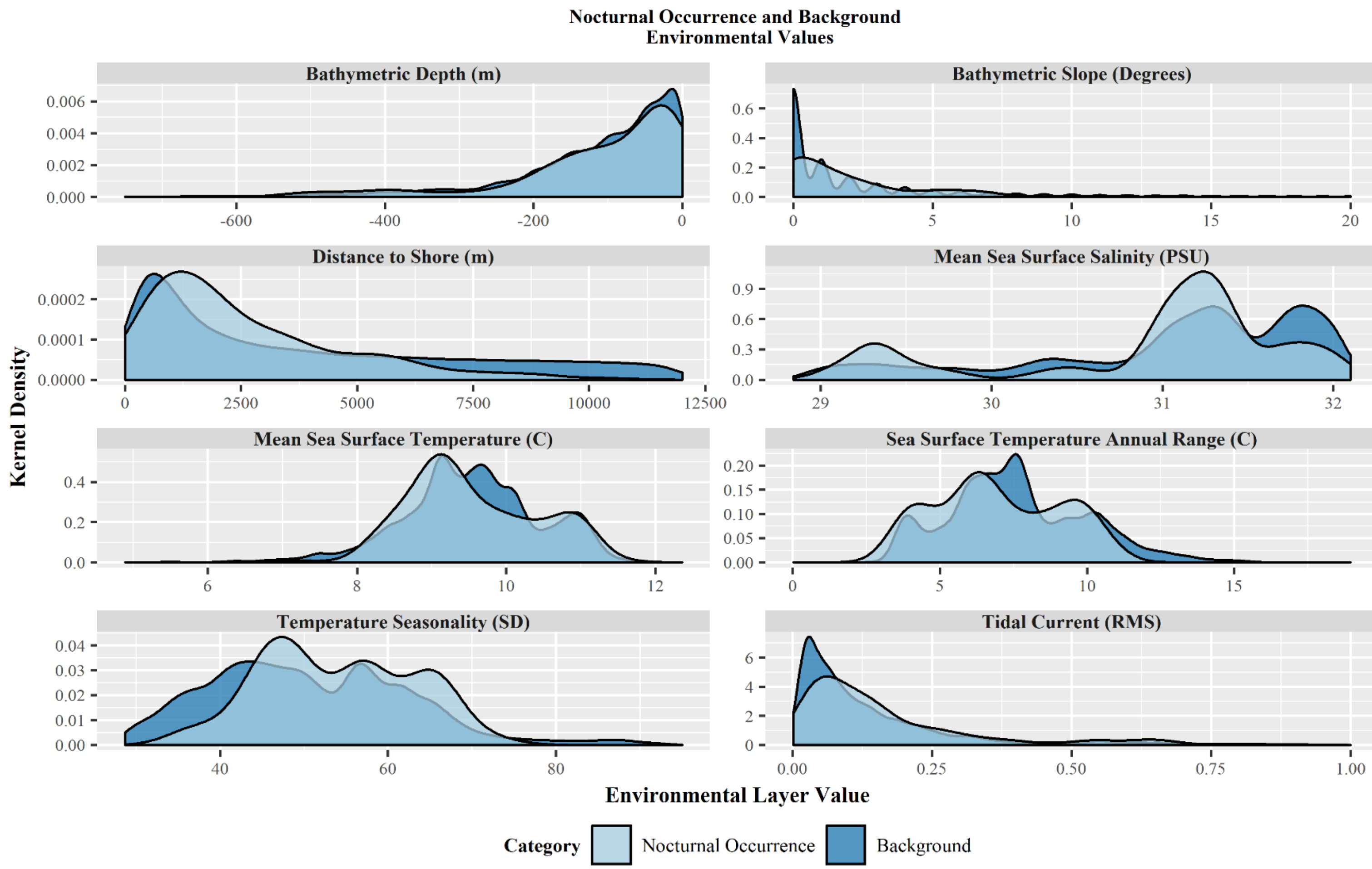

Figure 5: Continuous environmental predictor values at 179 nocturnal harlequin duck (*Histrionicus histrionicus*) occurrence points and 30,000 background (i.e. pseudo-absence) points randomly sampled from the study area.

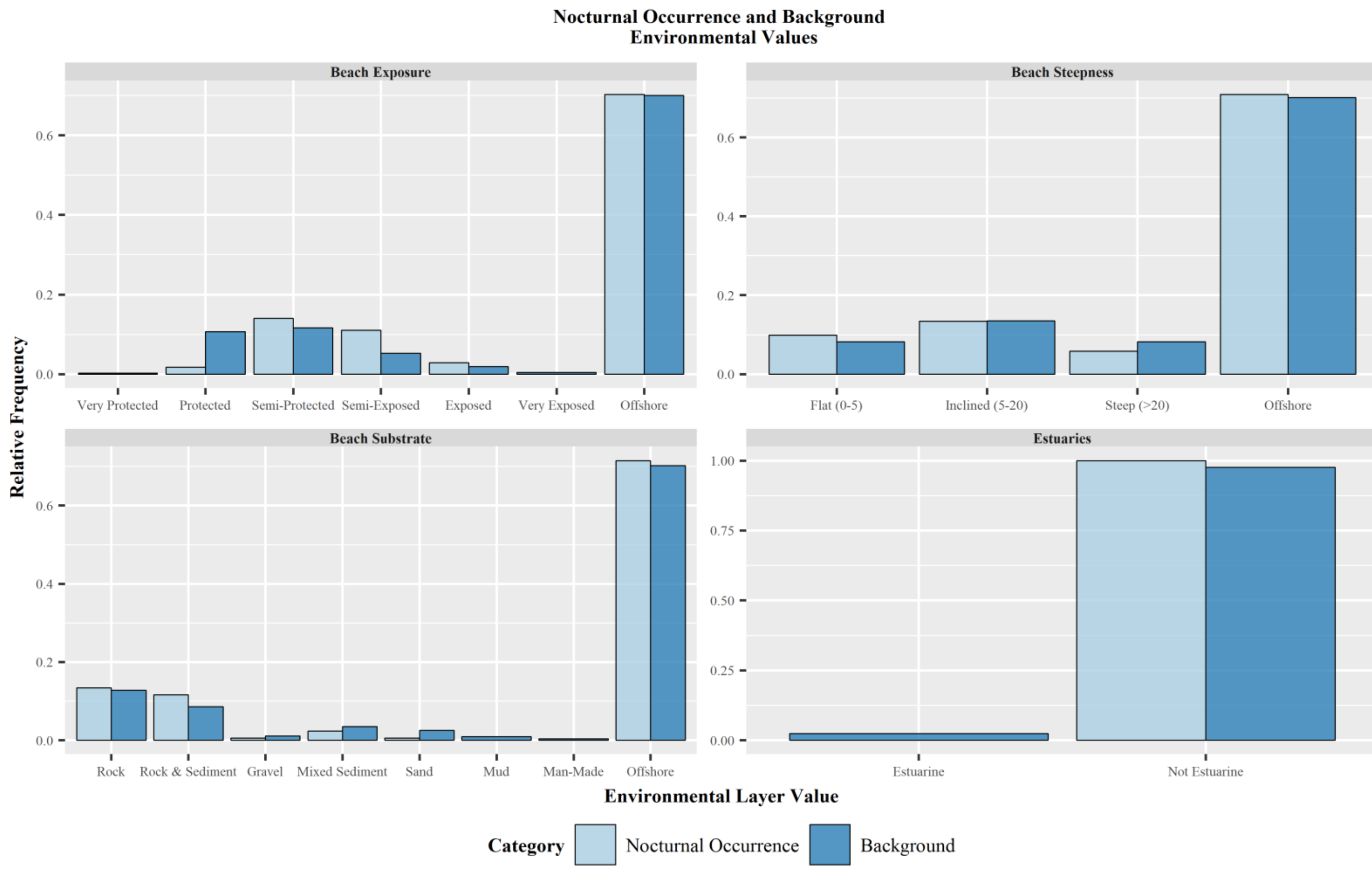

Figure 6: Categorical environmental predictor values at 179 nocturnal harlequin duck (*Histrionicus histrionicus*) and 30,000 background (i.e. pseudo-absence) points randomly sampled from the study area

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Climatic Variable Selection

When climatic environmental predictors were assessed in isolation using a model selection approach, two variables—specific humidity seasonality and sea surface temperature annual range—were retained in the lowest AIC_C diurnal model with six or fewer uncorrelated variables (Table 4). Similarly, four variables—temperature seasonality, mean annual sea surface salinity, mean annual sea surface temperature, and sea surface temperature annual range—were selected when nocturnal occurrences were assessed (Table 5). All selected variables were retained in the first five AIC_C-ranked models, except mean annual sea surface salinity, which was omitted from one of the top nocturnal models. In addition, sea surface salinity annual range was present in one of the top five ranked diurnal models. Most AIC_C variation amongst top-ranked models was due to the beta multiplier value applied. Model performance using only selected climatic environmental variables was low for the diurnal (0.61) and nocturnal models (0.71).

Table 4: Diurnal climatic environmental variable selection results from AIC_C-based selection analysis performed by the R-package MaxentVariableSelection (Jueterbock et al., 2016). Top-ranked models had six or fewer variables, correlations less than 0.7, variable contribution of at least 5%, and the lowest AIC_C values. The absolute AIC_C value of the top-ranked model was 3084.35.

Diurnal Climatic Environmental Variable Selection				
	Lowest AIC_C Models			
# of Variables – Type	# of Parameters	Beta Multiplier	ΔAIC_C	Test AUC
2 Specific Humidity Seasonality Sea Surface Temperature Annual Range	1	9	0.00	0.61
3 Specific Humidity Seasonality Sea Surface Temperature Annual Range Sea Surface Salinity Annual Range	3	4	0.91	0.59
2 Specific Humidity Seasonality Sea Surface Temperature Annual Range	2	6	0.92	0.60
2 Specific Humidity Seasonality Sea Surface Temperature Annual Range	2	7	1.37	0.59
2 Specific Humidity Seasonality Sea Surface Temperature Annual Range	2	8	1.77	0.61

Table 5: Nocturnal climatic environmental variable selection results from AIC_C-based selection analysis performed by the R-package MaxentVariableSelection (Jueterbock et al., 2016). Top-ranked models had six or fewer variables, correlations less than 0.7, variable contribution of at least 5%, and lowest AIC_C values. The absolute AIC_C value of the top-ranked model was 4688.98.

Nocturnal Climatic Environmental Variable Selection				
	Lowest AIC_C Models			
# of Variables – Type	# of Parameters	Beta Multiplier	ΔAIC_C	Test AUC
4 Temperature Seasonality Mean Annual Sea Surface Salinity Mean Annual Sea Surface Temperature Sea Surface Temperature Annual Range	16	2	0.00	0.71
4 Temperature Seasonality Mean Annual Sea Surface Salinity Mean Annual Sea Surface Temperature Sea Surface Temperature Annual Range	9	4	1.39	0.70
3 Temperature Seasonality Mean Annual Sea Surface Temperature Sea Surface Temperature Annual Range	8	3	4.68	0.69
4 Temperature Seasonality Mean Annual Sea Surface Salinity Mean Annual Sea Surface Temperature Sea Surface Temperature Annual Range	13	3	6.07	0.70
4 Temperature Seasonality Mean Annual Sea Surface Salinity Mean Annual Sea Surface Temperature Sea Surface Temperature Annual Range	10	5	7.43	0.69

Beta Multiplier Evaluation

The evaluation of potential beta multipliers indicated that a low degree of regularization was preferential for both diurnal and nocturnal model performance; top-performing beta multiplier values were all less than or equal to three (Table 6 & Table 7). Model performance was similar across top-performing models for each occurrence type.

Table 6: Diurnal beta multiplier evaluation results ranked by model performance (AUC) as determined by the R-package ENMEval (Muscarella et al., 2014). The evaluation tested beta multiplier values between 1 and 15 at increments of 0.5 and allowed linear, quadratic, product, and hinge feature types.

Diurnal Beta Multiplier Evaluation			
	Highest AUC Models		
Rank	Beta Multiplier	Test AUC	# of Parameters
1	1.5	0.894	46
2	2.0	0.894	39
3	2.5	0.895	33
4	3.0	0.893	29
5	1.0	0.893	48

Table 7: Nocturnal beta multiplier evaluation results ranked by model performance (AUC) as determined by the R-package ENMEval (Muscarella et al., 2014). The evaluation tested beta multiplier values between 1 and 15 at increments of 0.5 and allowed linear, quadratic, product, and hinge feature types.

Nocturnal Beta Multiplier Evaluation			
	Highest AUC Models		
Rank	Beta Multiplier	Test AUC	# of Parameters
1	1.0	0.769	71
2	1.5	0.763	48
3	2.0	0.762	38
4	2.5	0.759	30
5	3.0	0.756	31

Final Model Performance

Final diurnal and nocturnal models were implemented with beta multipliers of 1.5 and 1.0, respectively. Final diurnal model performance was high with a test AUC of 0.89, nocturnal model performance was lower with a test AUC of 0.77. When reevaluated against the collection of independent occurrences, diurnal model performance was lower but still fair, with an AUC of 0.85.

Predicted Diurnal Distribution

Along Haida Gwaii's coast, a high probability of diurnal presence was predicted across most of the island's exposed northern, northwest, and southeast coastlines (Appendix A). Harlequin duck presence was also predicted extensively along the exposed, outer shorelines of eastern Hectate Strait, Queen Charlotte Sound, Queen Charlotte Strait, and western Vancouver Island.

In Johnstone Strait, most harlequin duck presence was predicted to occur along the shorelines and inlets to the north and east. In the northern Salish Sea, high suitability was predicted along the Vancouver Island shoreline, between the Campbell River and Cape Lazo, and from Mapleguard Point to south of Qualicum Bay; along the exposed, shallower shorelines of Marina, Savary, Harwood, Hornby, and Denman Islands; at Francisco Point on Quadra Island and Shelter Point on Texada Island; and along the northern end of Lasqueti Island. The eastern mainland shores of the Strait of Georgia were predicted suitable at Sechelt, Point Roberts, White Rock, Birch Point, and from Point Whitehorn south to Lummi Bay.

A high probability of presence was predicted across most exposed, shallower shorelines in the Gulf Islands, especially along northern Gabriola, eastern Valdes, Thetis, eastern Salt Spring, eastern Prevost, Mayne, Pender, and Saturna Islands.

In the San Juan Archipelago, extensive harlequin duck occupation was predicted at Stuart, Flattop, Waldron, Patos, Sucia, Barnes, and Clark Islands. Suitable habitats were also predicted to occur along western Lummi Island; northwest Sinclair Island; northern Orcas Island, east of Point Doughty; eastern Orcas Island, from Lawrence Point south to Deer Point; eastern Obstruction Island; southern and southwest Cypress Island; eastern Decatur

Island; southern and southeast Lopez Island, between Davis Point and Lopez Pass; northern San Juan Island, near Limestone Point; and southern San Juan Island, from south of Deadman Bay around Cattle Point to southern Griffin Bay.

High suitability was predicted to occur continuously along Vancouver Island's shoreline from Sidney, south past Victoria, and west along the entire coastline of the Strait of Juan de Fuca. Continuously suitable habitat was also predicted from Fidalgo head—near Anacortes, WA—south throughout western Deception Pass, along western Whidbey Island into Admiralty Inlet, and along the Olympic Peninsula's north coast along the Strait of Juan de Fuca.

In Puget Sound, high suitability was predicted throughout Admiralty Inlet; along the eastern shoreline of Central Puget Sound, from Edmond to Browns Point; along southeast Blake Island and eastern Bainbridge Island; between Orchard Point and Southworth; and along most of the coastline of Vashon and Maury Islands, except in Colvos Passage. High suitability was predicted sporadically in South Puget Sound.

Along Washington's outer coast, harlequin duck occupancy was predicted continuously from Cape Flattery south to La Push and the Quillayute Needles. Highly suitable habitats were also identified around Hoh Head and Cape Elizabeth. In Oregon, harlequin duck presence was predicted to occur at Tillamook Head and Cape Falcon.

Low diurnal suitability was predicted for most offshore waters >1km from shore and along coastlines with deep water closely adjacent to the shoreline. In the north, interior fjords, passages, and inlets were regularly predicted to be less suitable, likely because of their low exposure and deep nearshore bathymetry. In the Salish Sea, embayments and interior protected coastlines were almost universally predicted to be less suitable. Low suitability was predicted throughout most of Whidbey Basin (Possession Sound, Saratoga Passage, Skagit Bay, and Port Susan) and Hood Canal. Sandy beaches were predicted to be less suitable along the outer coast of Washington and Oregon,

Predicted Nocturnal Distribution

In the northern study area, nocturnal harlequin duck presence was predicted to occur throughout select nearshore waters along the outer islands of Hectate Strait, Queen Charlotte Sound, and Queen Charlotte Strait (Appendix B). High nocturnal suitability was also predicted in Portland Inlet; Wright Sound, northeast of Gill Island; and Finlayson Channel, east of Swindle Island.

A high probability of nocturnal presence was predicted for much of the northern Strait of Georgia, north of Lasqueti Island, except for the most offshore waters. Suitable habitat was predicted throughout Sutil Channel, near Hernando and Savary Island, and along eastern Vancouver Island to south of Hornby Island. High nocturnal suitability was also predicted west of Texada and Lasqueti Islands.

In the central and southern Salish Sea, nocturnal presence was predicted between Point Whitehorn and Point Roberts; north of Orcas Island, near Sucia Island; throughout the interior San Juan Islands and eastern Gulf Islands; throughout nearshore waters along Vancouver Island's coast from Sidney out the Strait of Juan de Fuca; and throughout nearshore waters of the Olympic Peninsula's north coast, along the Strait of Juan de Fuca. Pockets of suitable nocturnal habitat were also predicted to occur in Puget Sound near Blake Island, in Commencement Bay, north of Ketron Island, and north of McNeil Island; in Hood Canal, south of Toandos Peninsula; in Oak Bay, south of Marrowstone Island; and at the mouth of Port Townsend. Large patches of suitable nocturnal habitat stretched far offshore in the eastern Strait of Juan de Fuca, south of San Juan and Lopez Islands, west of Whidbey Island, and north of Sequim and Discovery Bays.

Along Vancouver Island's outer coast, highly suitable nocturnal habitat was predicted to occur near continuously from the Brooks Peninsula south to the Strait of Juan de Fuca. Along Washington's outer coast, highly suitable nocturnal habitats were predicted to occur in the nearshore waters between Cape Flattery and Cape Alava and at La Push and the Quillayute Needles.

Environmental Variable Importance and Response

Post hoc permutation importance analysis indicated that bathymetric depth, distance to shoreline, beach exposure, tidal current, and sea surface temperature annual range were the most consequential variables within the diurnal SDM (Table 8). Jackknife analysis performed internally during SDM development determined that model gain was independently influenced most significantly by beach exposure (Figure 7). Hence, diurnal suitability was predicted to be greatest in nearshore shallow waters closely associated with semi-protected to semi-exposed shorelines (Figure 8 & Figure 9). Diurnal suitability was generally predicted to decrease as tidal current and sea surface temperature annual range increased.

Table 8: Diurnal and nocturnal SDM environmental variable permutation importance as calculated by R-package dismo (Hijmans et al., 2017).

Environmental Variable Permutation Importance			
Diurnal		Nocturnal	
Variable	P.I.	Variable	P.I.
Bathymetric Depth	47.6	Temp Seasonality	31.2
Distance to Shoreline	23.3	Distance to Shoreline	24.0
Beach Exposure	10.0	Sea Surface Temp Annual Range	13.7
Tidal Current	6.8	Bathymetric Depth	7.6
Sea Surface Temp Annual Range	5.8	Mean Sea Surface Temp	5.8
Beach Substrate	2.6	Mean Sea Surface Salinity	5.3
Estuary	1.8	Tidal Current	4.2
Bathymetric Slope	1.4	Beach Exposure	2.7
Beach Steepness	0.4	Beach Substrate	2.7
Humidity Seasonality	0.2	Estuary	2.5
		Bathymetric Slope	0.4
		Beach Steepness	0.0

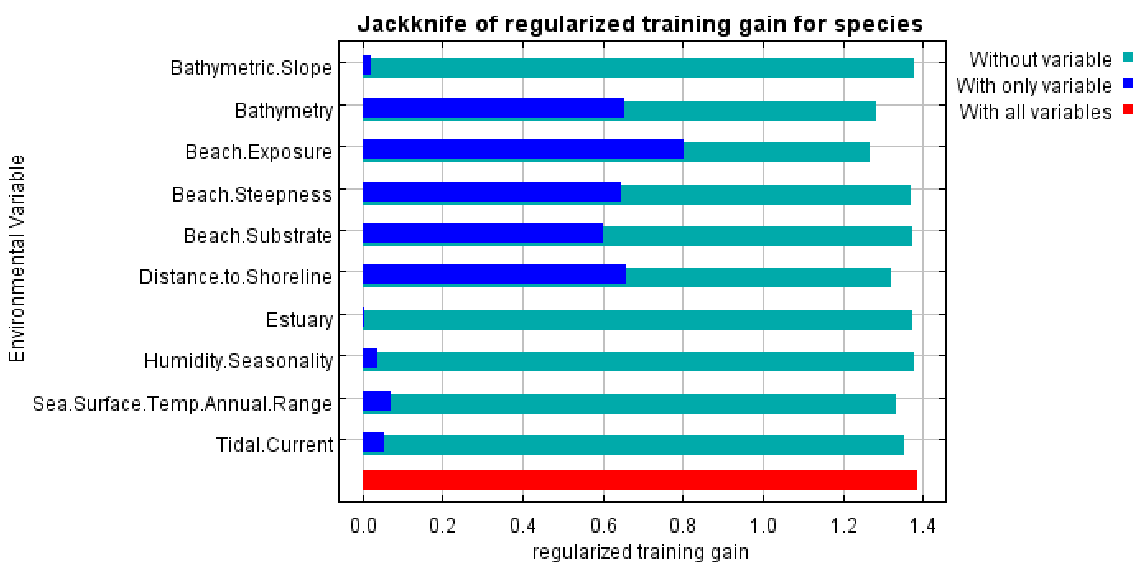

Figure 7: Diurnal variable jackknife analysis results depicting model gain response when each variable is independently modeled and independently withheld from modeling.

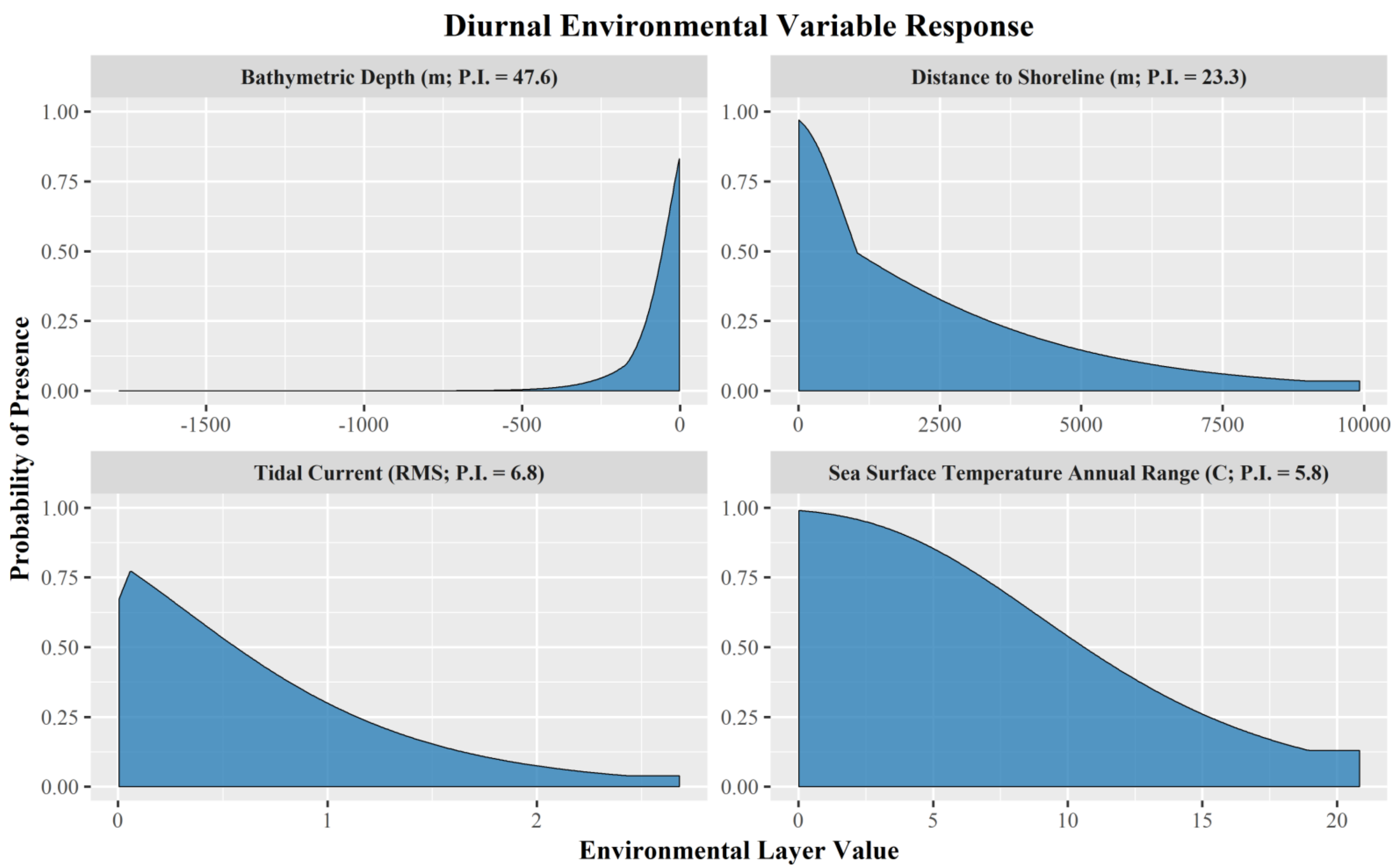

Figure 8: Modeled continuous environmental variable response curves of variables with a permutation importance (P.I.) ≥5% as predicted by the diurnal SDM.

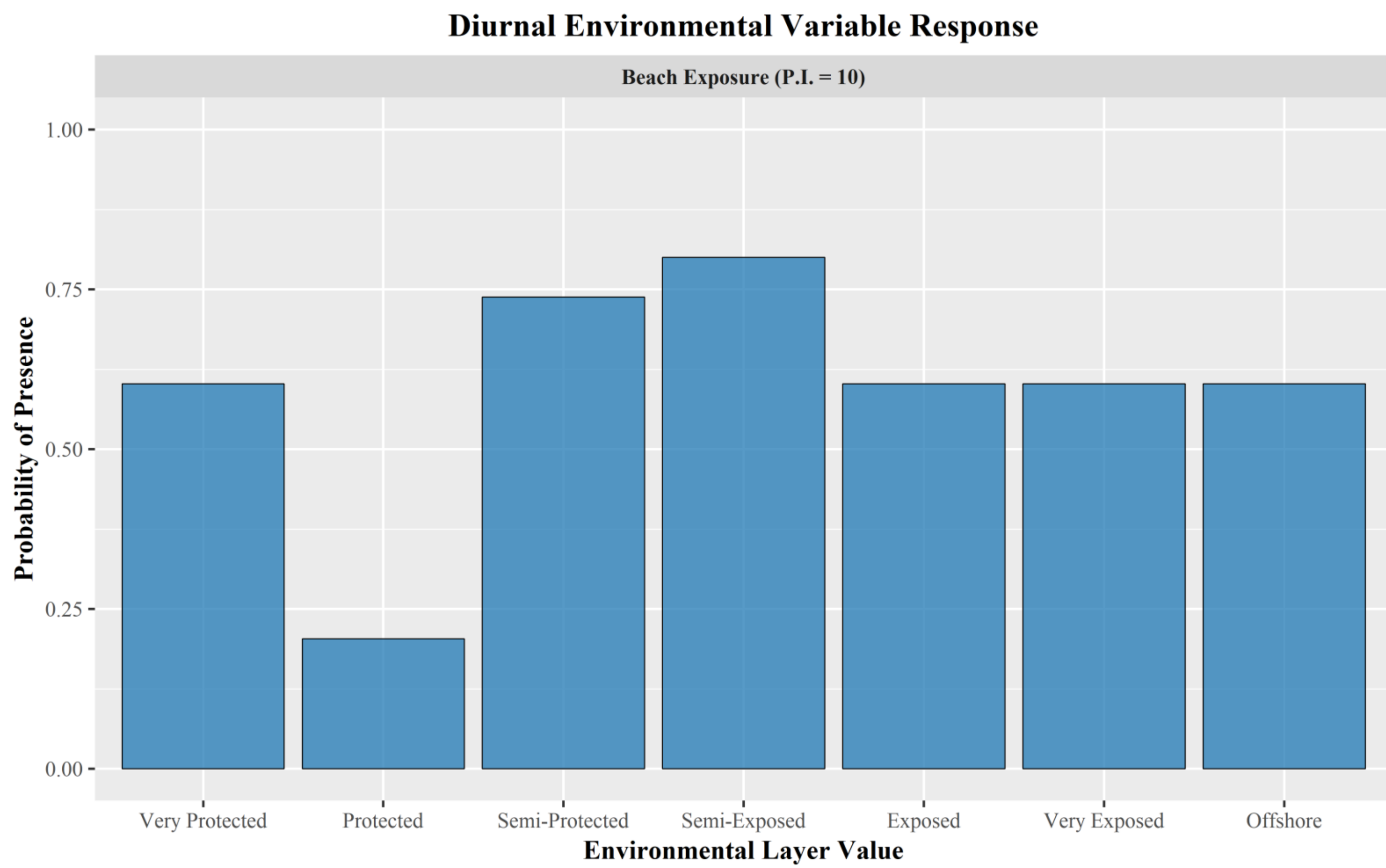

Figure 9: Modeled categorical environmental variable response curves of variables with a permutation importance (P.I.) ≥5% as predicted by the diurnal SDM.

Permutation importance analysis indicated that temperature seasonality, distance to shoreline, sea surface temperature annual range, bathymetric depth, mean sea surface temperature, and mean sea surface salinity were the most significant environmental variables influencing the nocturnal distribution model (Table 8).

Jackknife analysis determined that distance to the shoreline was the most significant variable independently impacting nocturnal model gain (Figure 10). Nocturnal suitability was positively associated with moderate degrees of temperature seasonality, low suitability was projected in regions that experience low and high levels of seasonality (Figure 11). Nocturnal suitability was predicted to sharply increase as the distance to shoreline increased from zero meters to about 1000 meters, after which it was predicted to gradually decrease. Nocturnal suitability was predicted to decrease as sea surface temperature annual range increased and was predicted to be higher in shallower waters and areas with higher mean sea surface temperature. Areas with low salinity were predicted to be of lower suitability.

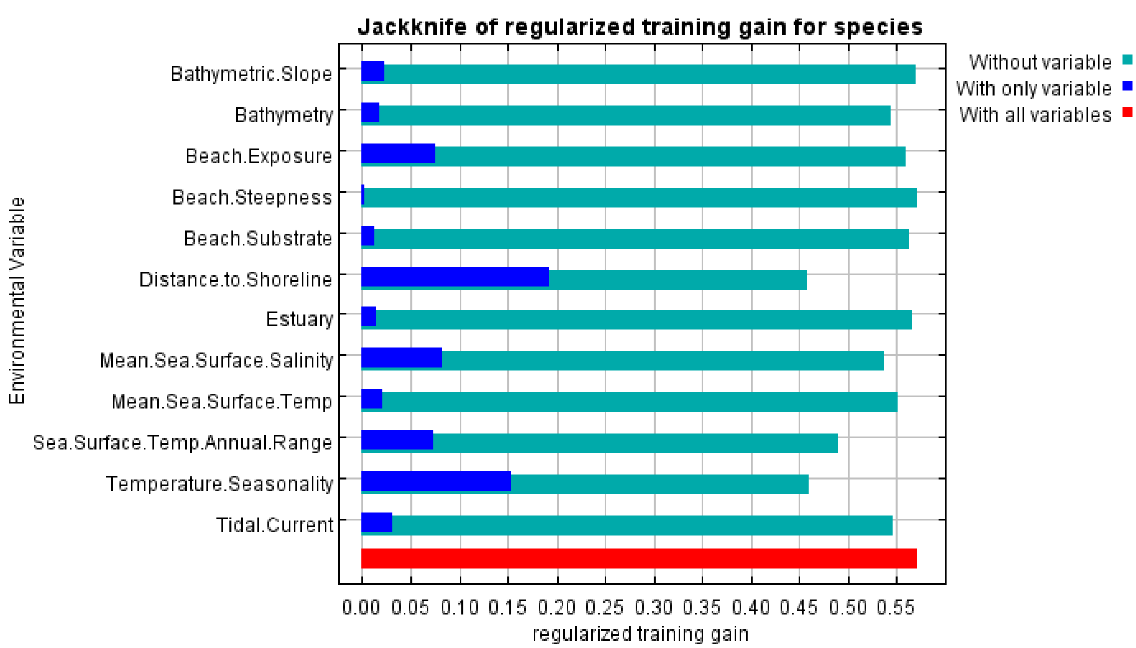

Figure 10: Nocturnal variable jackknife analysis results depicting model gain response when each variable is independently modeled and independently withheld from modeling.

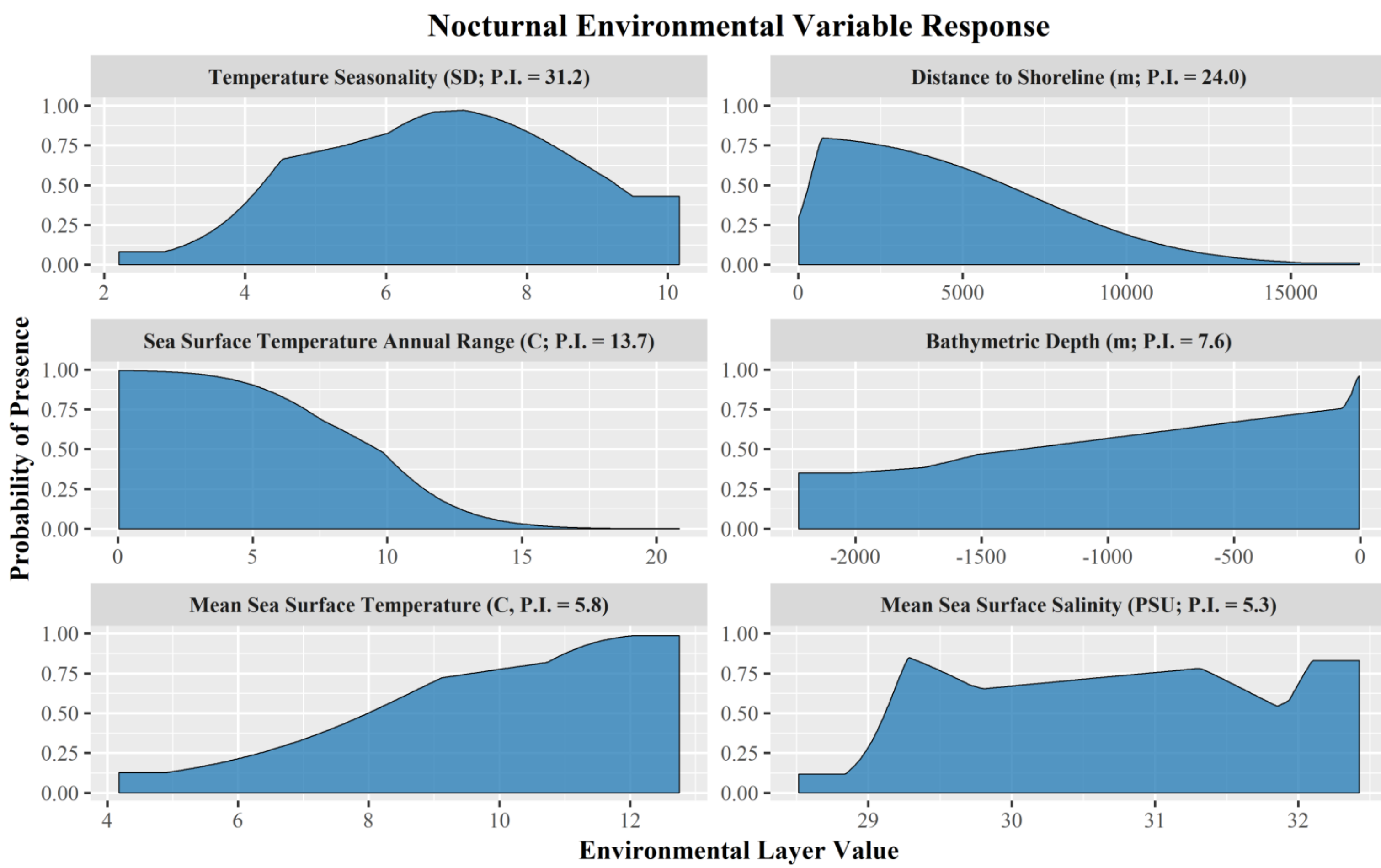

Figure 11: Modeled continuous environmental variable response curves of variables with a permutation importance (P.I.) ≥5% as predicted by the nocturnal SDM.

Salish Sea Habitats near Shipping Lanes

Most suitable diurnal and nocturnal habitats identified in the central and southern Salish Sea are immediately adjacent to oil tanker routes (Appendix C & Appendix D). Tankers leaving Vancouver's Burrard Inlet on route to Victoria via the Strait of Georgia, Boundary Pass, and Haro Strait travel past diurnal habitats at Point Roberts; in the Gulf and San Juan Islands; along Sidney, James, and D'Arcy Islands; and along Vancouver Island between Sidney and Victoria. Vessels departing Cherry Point or Anacortes refineries for Port Angeles transit past diurnal habitats at Point Whitehorn, western Lummi Island, throughout Rosario Strait, and along the coastlines of the eastern Strait of Juan de Fuca. Vessels traveling from Tacoma and Seattle use routes adjacent to habitats in the Central Puget Sound and Admiralty Inlet. All vessels exiting the Salish Sea from Victoria and Port Angeles via the Strait of Juan de Fuca sail past diurnal habitats along the north and south coastlines of the strait.

Oil vessels traveling the same courses also routinely voyage through waters adjacent to nocturnal habitats in the southern Strait of Georgia, Gulf and San Juan Islands, Central Puget Sound, and throughout the Strait of Juan de Fuca. Vessel routes occasionally transect predicted suitable nocturnal habitats, especially when transiting through the eastern Strait of Juan de Fuca to Port Angeles from Cherry Point and Anacortes, and in Central Puget Sound.

Diurnal Habitats with Prolonged Oil Residence

Diurnal habitats with prolonged oil residence (on the scale of years) were identified throughout the Salish Sea and were widely present in regions with oil tanker traffic

(Appendix E). Approximately 90% of the diurnal habitat area identified as suitable (cloglog prediction ≥ 0.8) is projected to experience prolonged oil residence times.

Discussion

This study utilized Maxent species distribution modeling to identify Pacific Northwest locales predicted to be suitable for harlequin ducks during diurnal and nocturnal hours of the nonbreeding period. This study also assessed model predictions to distinguish particular Salish Sea habitats that would be likely to retain oil for a prolonged period if they were contaminated by an oil spill. Prolonged oil retention in these habitats would continually expose local harlequin ducks to contaminates, likely reducing local survival rates.

Unmistakably, the SDMs developed through this study and post-model assessment indicate that harlequin duck populations and their habitats throughout the Salish Sea are subject to a relatively high degree of oil spill risk compared to other regions in the Pacific Northwest. This risk will increase with the future expansion of the Trans Mountain Pipeline that will substantially increase oil tanker traffic traveling through the Strait of Juan de Fuca, Haro Strait, Boundary Pass, and the Strait of Georgia (Govt of Canada & National Energy Board, 2016).

There are multiple locations along Salish Sea shipping routes with the potential for a collision or grounding leading to an oil spill. An incident occurring at Arachne Reef – Turn Point Special Operating Area, at the northern edge of Haro Strait (west of Turn Point, Stuart Island, WA), appears more likely than other areas due to the navigational complexity of the operating area; because of this, Arachne Reef has been used as a hypothetical release site for oil spill simulation models (Niu et al., 2017). Oil released at Arachne Reef would quickly spread throughout Haro Strait, making landfall along the shorelines of the eastern Gulf Islands, the western San Juan Islands, Sidney and James Island, and the Vancouver Island shoreline between Sidney and Victoria. Released oil could also potentially reach the shorelines of the Strait of Juan de Fuca and could travel north, impacting Lasqueti Island (Niu et al., 2017). This area of high impact encompasses extensive lengths of shoreline predicted to be suitable for diurnal harlequin duck use. In addition, floating oil plumes from a spill at Arachne Reef would drift through open water areas neighboring Haro Strait, predicted to be suitable for harlequin ducks during nonbreeding nocturnal periods (Niu et al., 2017).

There is also significant potential for an oil release at the Westridge Marine Terminal in Burrard Inlet or in the Strait of Georgia, west of the Fraser Delta. Spill events in this area were examined using drifter devices released multiple times across the region (Pawlowicz et al., 2019). Subsequent tracking of the drifters indicated that a release in Burrard Inlet or the Strait of Georgia could impact the same regions predicted to be oiled by a release at Arachne Reef; however, a release in the Strait of Georgia or Burrard Inlet could also have the potential to impact regions farther north in the Strait of Georgia (Pawlowicz et al., 2019).

An oil spill in the Salish Sea could result in substantial acute harlequin duck losses immediately after the spill, but numerically more losses could occur during subsequent years from the legacy effects of remnant hydrocarbons (Esler et al., 2002; Iverson & Esler, 2010). Suitable diurnal habitats with prolonged oil residence times were predicted to occur along shorelines in the Strait of Georgia, San Juan Islands, Gulf Islands, and the Strait of Juan de Fuca that would be impacted by an oil release in Burrard Inlet, the Strait of Georgia, or Arachne Reef (Appendix E; Johannessen et al., 2020; Niu et al., 2017; Pawlowicz et al., 2019). Similar habitats occur throughout Central Puget Sound and along Rosario Strait adjacent to tanker routes servicing Ferndale, Anacortes, Seattle, and Tacoma. If oiled, the continued use of these diurnal habitats by philopatric individuals and the ensuing exposure to residual hydrocarbons would result in decreased survival rates and depressed harlequin duck populations similar to what occurred in Prince William Sound following the Exxon Valdez oil spill (Esler et al., 2002; Iverson & Esler, 2010; Rosenberg et al., 2005). Regional population recovery would be delayed until the legacy effects of the oil spill no longer suppressed population survival and growth rates; this process took at least 11 years following the Exxon Valdez oil spill (Iverson & Esler, 2010).

High harlequin duck diurnal and nocturnal habitat suitability was projected throughout British Columbia's remote north coast. Harlequin duck populations in this region should face comparatively low risks of oil spills as a result of existing low tanker traffic densities and the recent moratorium on large tanker vessel north coast port calls (Transport Canada, 2019; BCMCA, 2010). Although the comparative risk is seemingly lower than in the Salish Sea, north coast habitats still face some conceivable degree of oil spill and disturbance risk stemming from smaller oil shipments to north coast communities and large non-tanker vessels (e.g., cruise ships) navigating inside passage routes. Likewise, identified outer coast habitats along the west coast of Vancouver Island should face a comparatively lower risk of an oil spill as a result of British Columbia's Voluntary Tanker Exclusion Zone, which mandates that loaded tankers traveling from Valdez, AK to Puget Sound, WA travel far offshore of British Columbia's outer coast (Transport Canada, 2016, 2019). However, as indicated by the drifter study performed by Pawlowicz et al. (2019), oil spilled within the Salish Sea would have some potential of washing ashore along Vancouver Island's outer coast.

Similarly, significant maritime restrictions are in place to guard the outer coast of Washington's Olympic Peninsula from oil spills. All predicted suitable harlequin duck habitats along Washington's outer coast are within the Olympic Coast National Marine Sanctuary; oil tankers are excluded from transiting near and through the sanctuary by a mandatory designated International Maritime Organization *Area to be Avoided*. Tankers transporting oil along Washington's outer coast are required to follow routes that take them farther than 25km from shore (NOAA, 2017). While these mandatory routing requirements provide strong protection against an oil spill catastrophe along the Olympic Peninsula outer coast, compliance has not been universal in recent years (NOAA, 2018). Routing compliance infractions, crew negligence, and severe weather introduce additional potential for an oil spill disaster along the outer coast.

Limitations

Spatial data acquired from the Shorezone datasets were important for model development and oil residence analysis, but they also presented some challenges. Shorezone coverage of the study area was nearly complete for the data variables used but there were some gaps. Shorezone coverage did not exist for Smith and Minor Islands in the eastern Strait of Juan de Fuca; as a result, both islands and their adjacent nearshore waters were removed from the SDMs. Suitable diurnal habitats are known to exist on both islands as supported by the PTT tracking data utilized in this study and WDFW's Midwinter Aerial Survey of the Salish Sea (unpublished data). Both islands would be highly susceptible to impacts from an oil spill in the Salish Sea. Additionally, the linear aspect of the Shorezone dataset—and shoreline features for that matter—presents challenges when projecting to a raster grid. To overcome this, I arbitrarily applied shoreline features to cells within 1km of the shore. This undoubtedly introduced some spatial bias and an artificial spatial threshold to model predictions. Removal of this spatial bias and arbitrary threshold, through the use of continuous coverage variables, might improve model results.

Very little suitable nocturnal habitat was predicted to occur near Haida Gwaii. This prediction is almost certainly incorrect. I am not sure why this occurred, but it is likely because values for an important environmental covariate (perhaps temperature seasonality) were outside the range typically encountered in other parts of the study area.

The SDMs developed during this study broadly describe coastal use patterns during the nonbreeding period, however seasonal variations in coastal habitat use likely exist. For instance, during the molt, nocturnal occupancy could shift closer to shore as some individuals are flightless and unable to fly to roost areas farther offshore. These seasonal variations would not be discernable in the current models. SDMs that limited occurrence sampling to specific seasons (e.g., molt, winter) may be able to identify seasonal variations in occupied habitats.

Conclusion

The species distribution models (SDMs) developed during this study are fit to inform species distribution and oil spill risk patterns with the data currently available for harlequin ducks. Room for improvement exists and updates to the harlequin duck SDMs should occur to incorporate additional environmental variables and modeling techniques. I had planned to include additional variables of interest, such as vertical tidal range and intertidal width, but was unable to locate data for the entire study area. Future models could be improved if such data becomes available. Future SDMs could also benefit from the utilization of other presence-only distribution modeling methods (e.g., Generalized Additive and Random Forest Models), iterative occurrence point rarefication, and spatial model averaging. Iterative occurrence point rarefication and spatial model averaging could be especially useful when modeling a narrower seasonal range (e.g., molt, winter) since occurrence point sample sizes would be reduced. The diurnal SDM results depict a general linear occupancy pattern along shorelines, the sample-with-data linear modeling technique established by Elith et al. (2011) could be an appropriate method for future nearshore habitat modeling efforts. This linear modeling technique could also be useful for predicting the suitability of stream reaches for harlequin ducks during their breeding season.

The accuracy of these SDMs could be assessed through field surveys at randomly selected cells across a range of predicted suitability values. The surveys could also be used to establish mean harlequin duck densities at given suitability levels. If field surveys were successful in establishing mean densities with reasonable confidence intervals, the estimated densities could be used in conjunction with SDMs to estimate harlequin duck abundance. Similar efforts could also be beneficial for assessing changes in abundance if an oil spill or similar perturbation were to impact modeled areas.

This study is a relatively early attempt to model the spatial distribution of a marine bird species in the Pacific Northwest. Work to refine distribution modeling methods that are widely applicable to other marine bird species should continue. Efforts should also be made to advance approaches that model the characteristics and influences of linear shoreline features across raster coverages.

Other presence-only occurrence datasets—such as aerial survey and citizen science datasets—offer readily available occurrence data for a suite of marine bird species. Presence-only occurrence locations could also be collected by unmanned aerial vehicles (drones) at a high spatial resolution. Much of the work involved in this study went towards the collection and cataloging of environmental covariates and to analysis script preparation. Agencies and institutes interested in the broad application of distribution modeling could simplify future efforts by establishing covariate coverage repositories and common analysis script frameworks.

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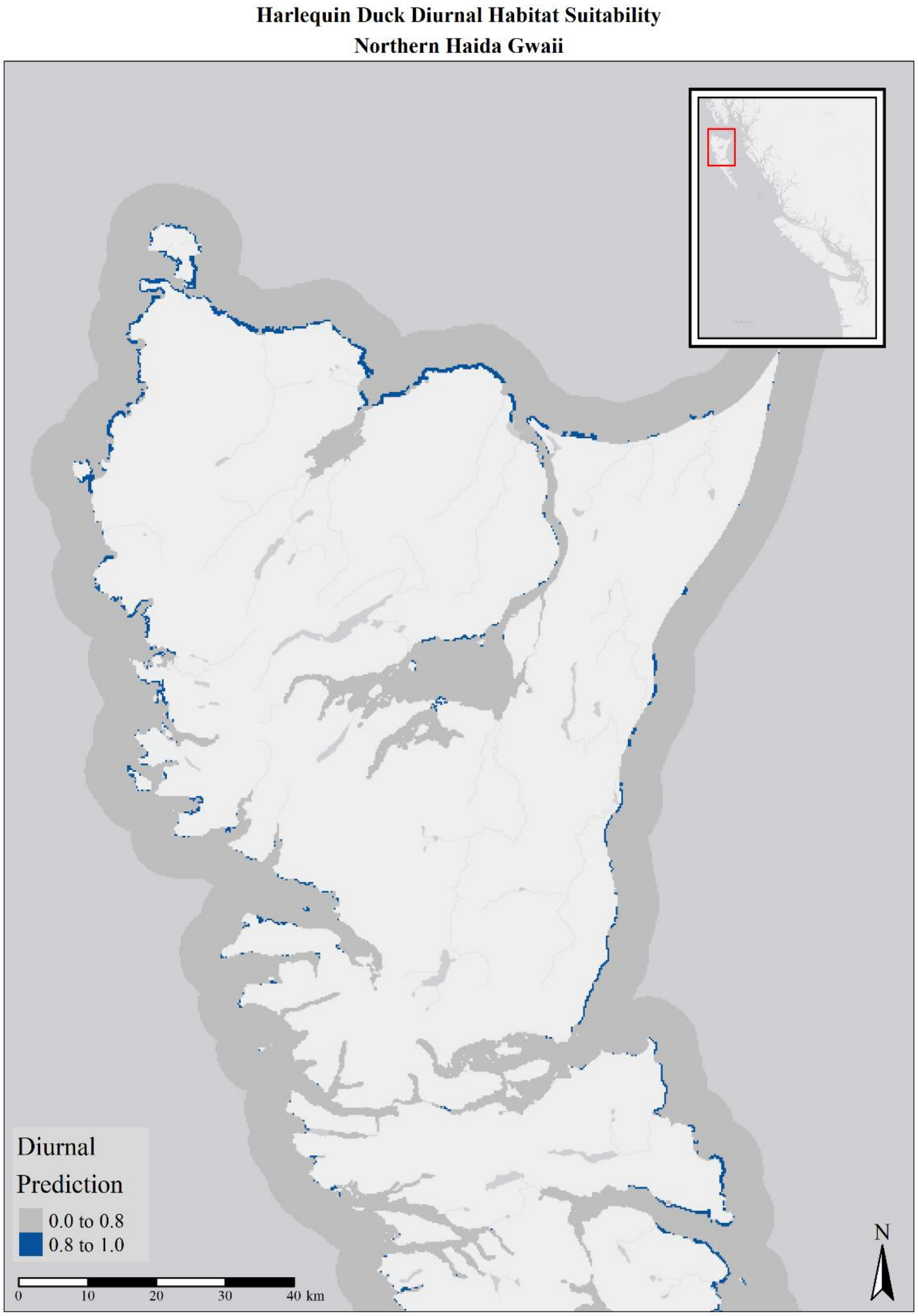
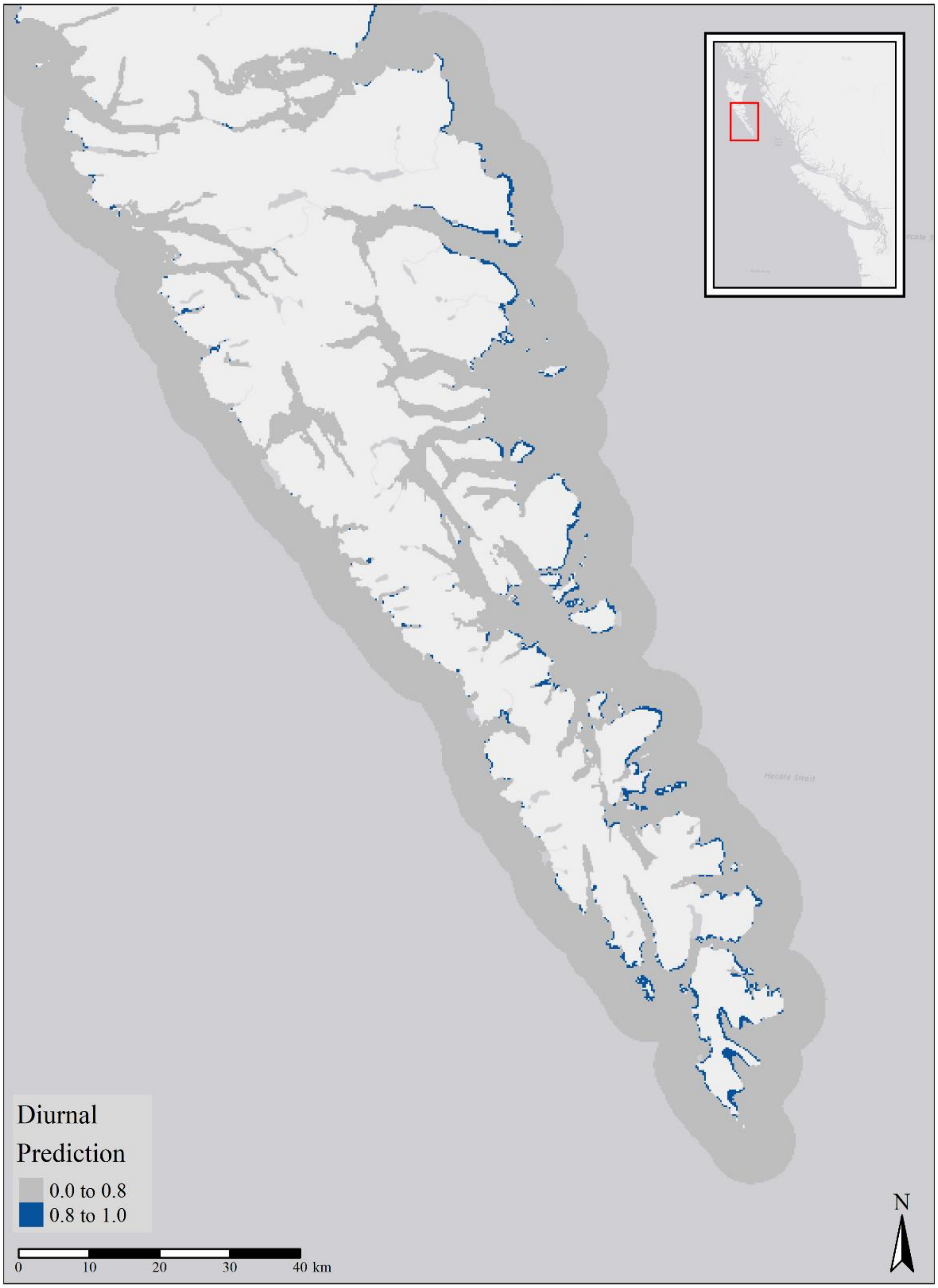
APPENDIX

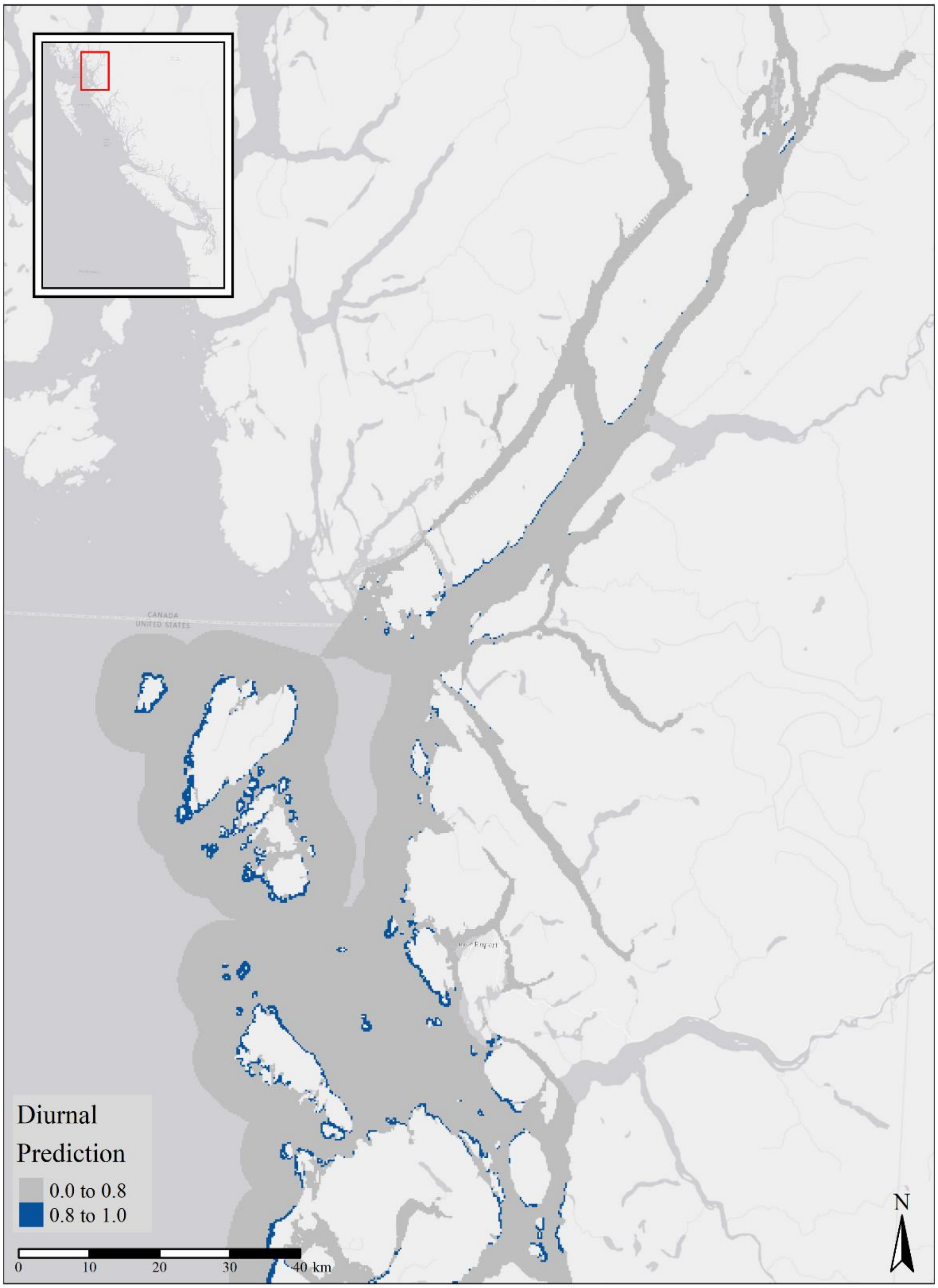
Appendix A: Diurnal harlequin duck (*Histrionicus histrionicus*) species distribution model results, developed using PTT satellite telemetry occurrence points and Maxent SDM methods. Areas in blue indicate high habitat suitability (cloglog prediction ≥ 0.8).



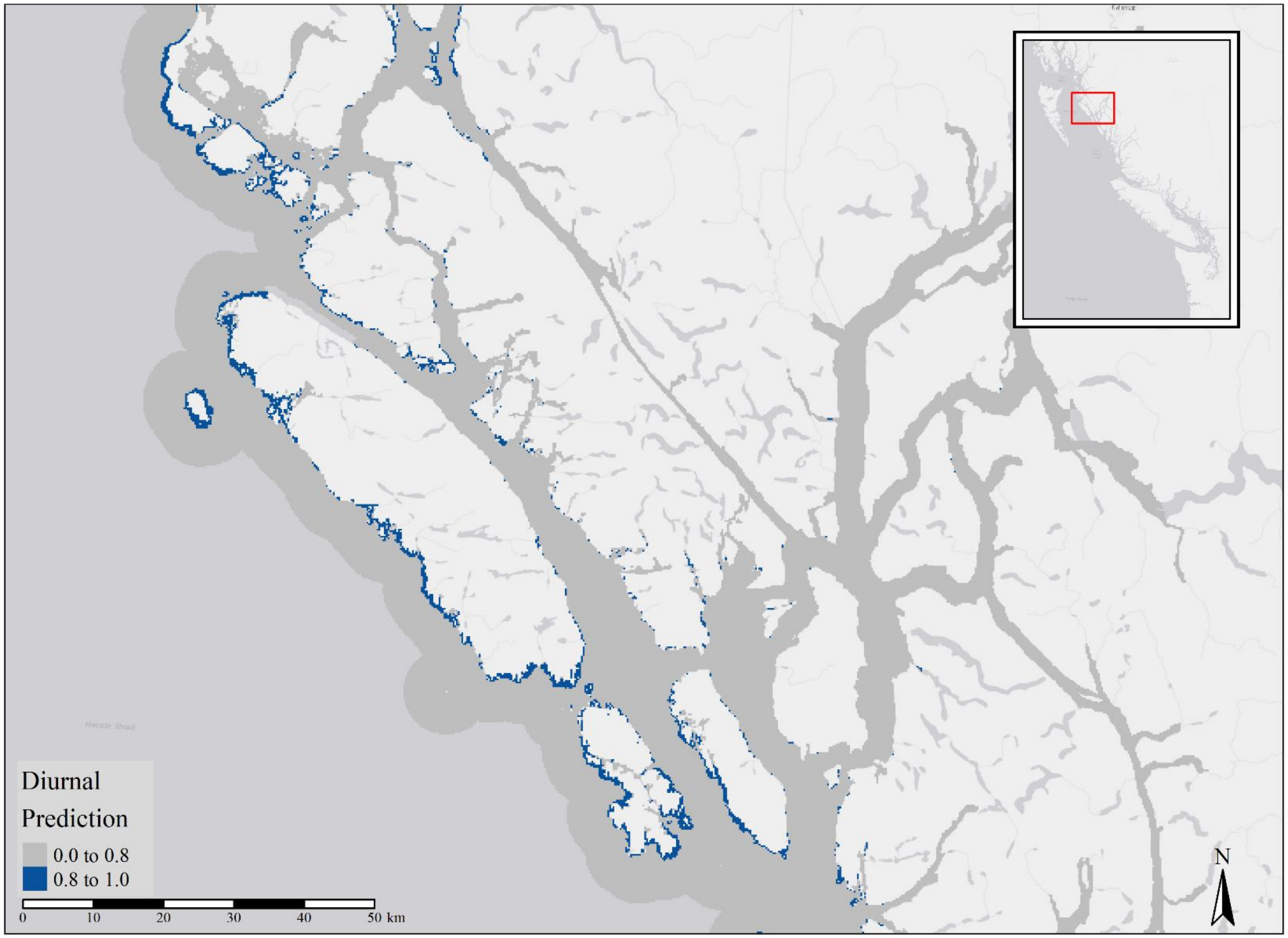
Harlequin Duck Diurnal Habitat Suitability
Southern Haida Gwaii



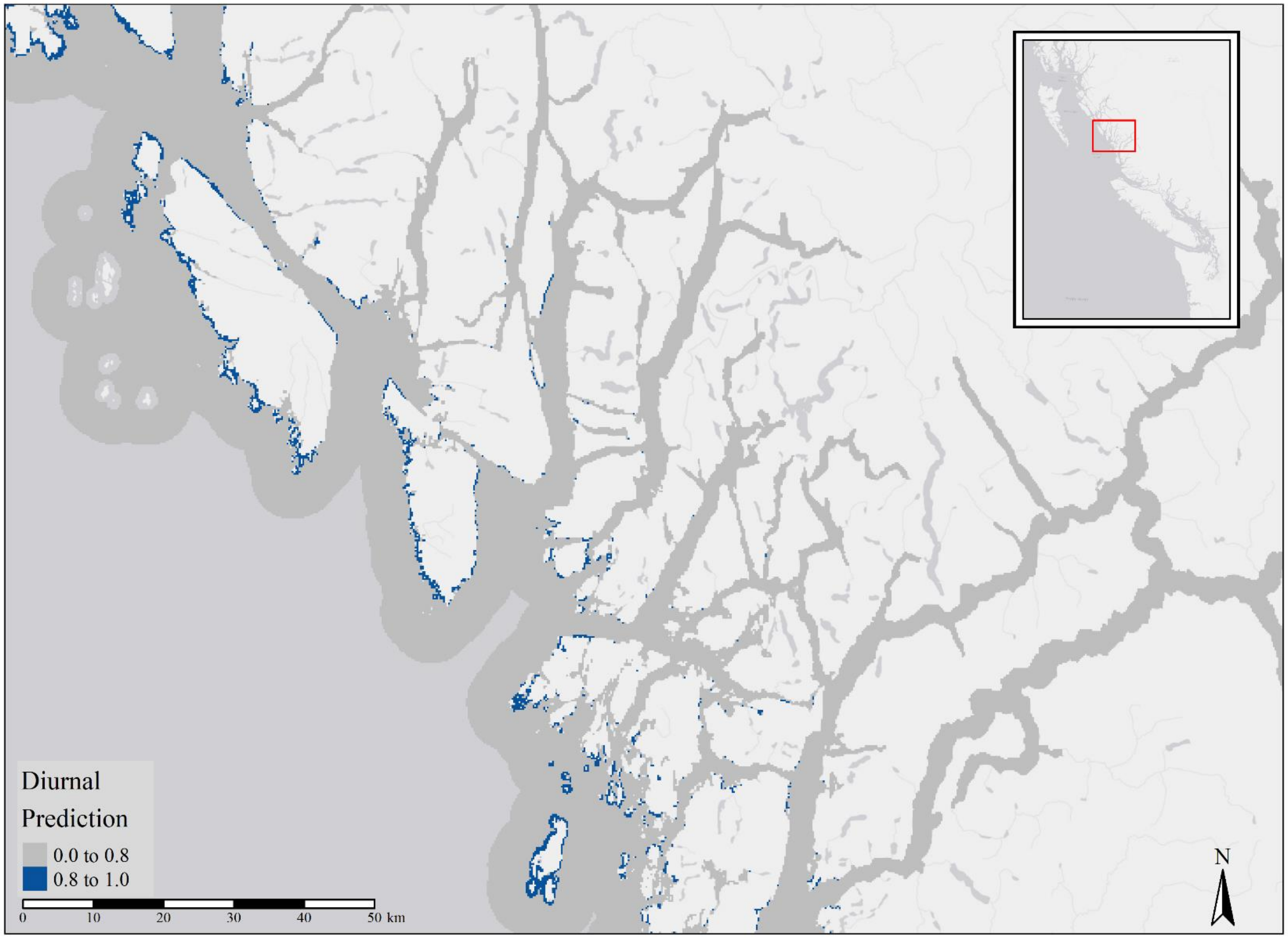
Harlequin Duck Diurnal Habitat Suitability
Northern Hectate Strait



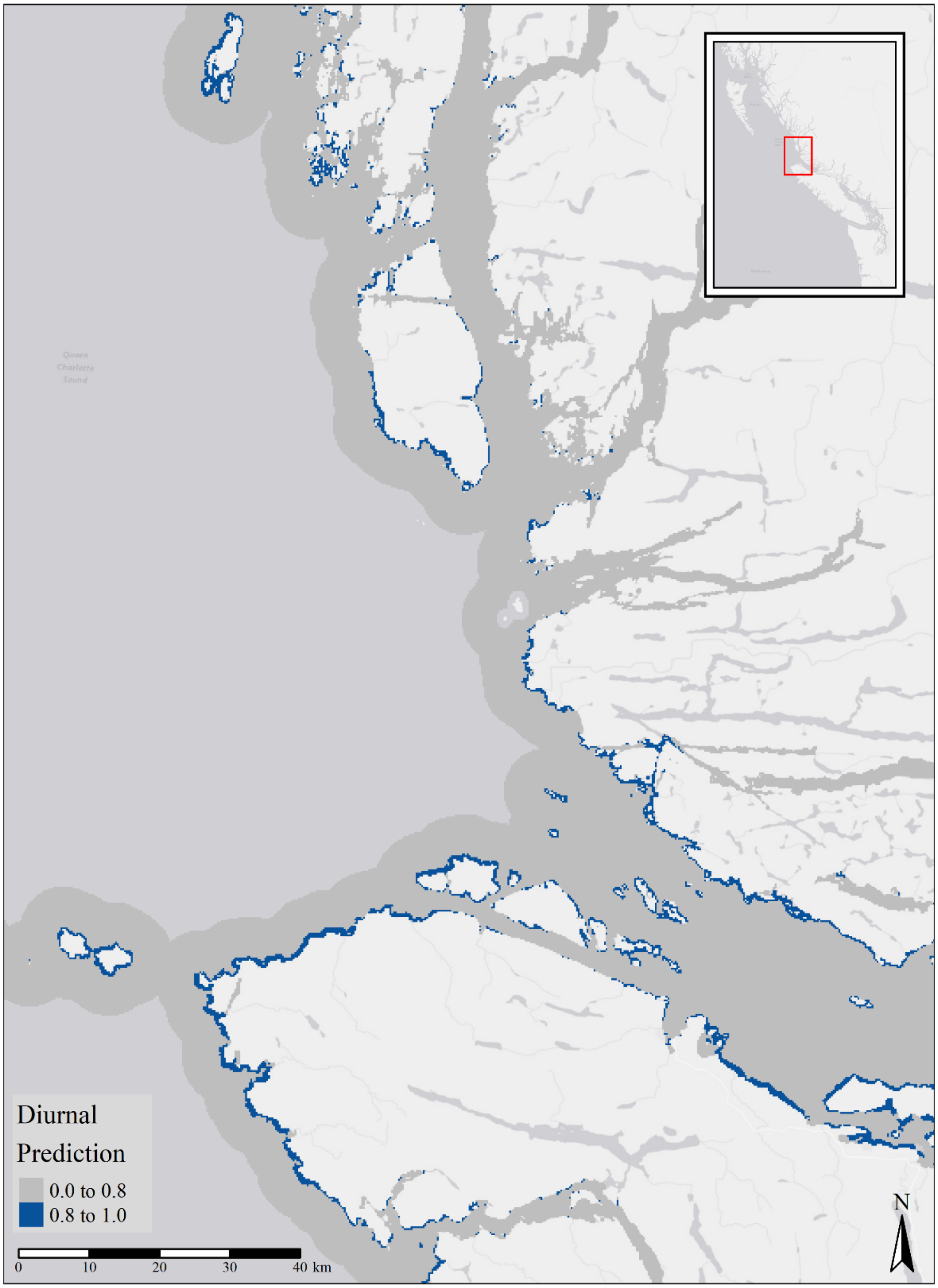
Harlequin Duck Diurnal Habitat Suitability
Central Hectate Strait



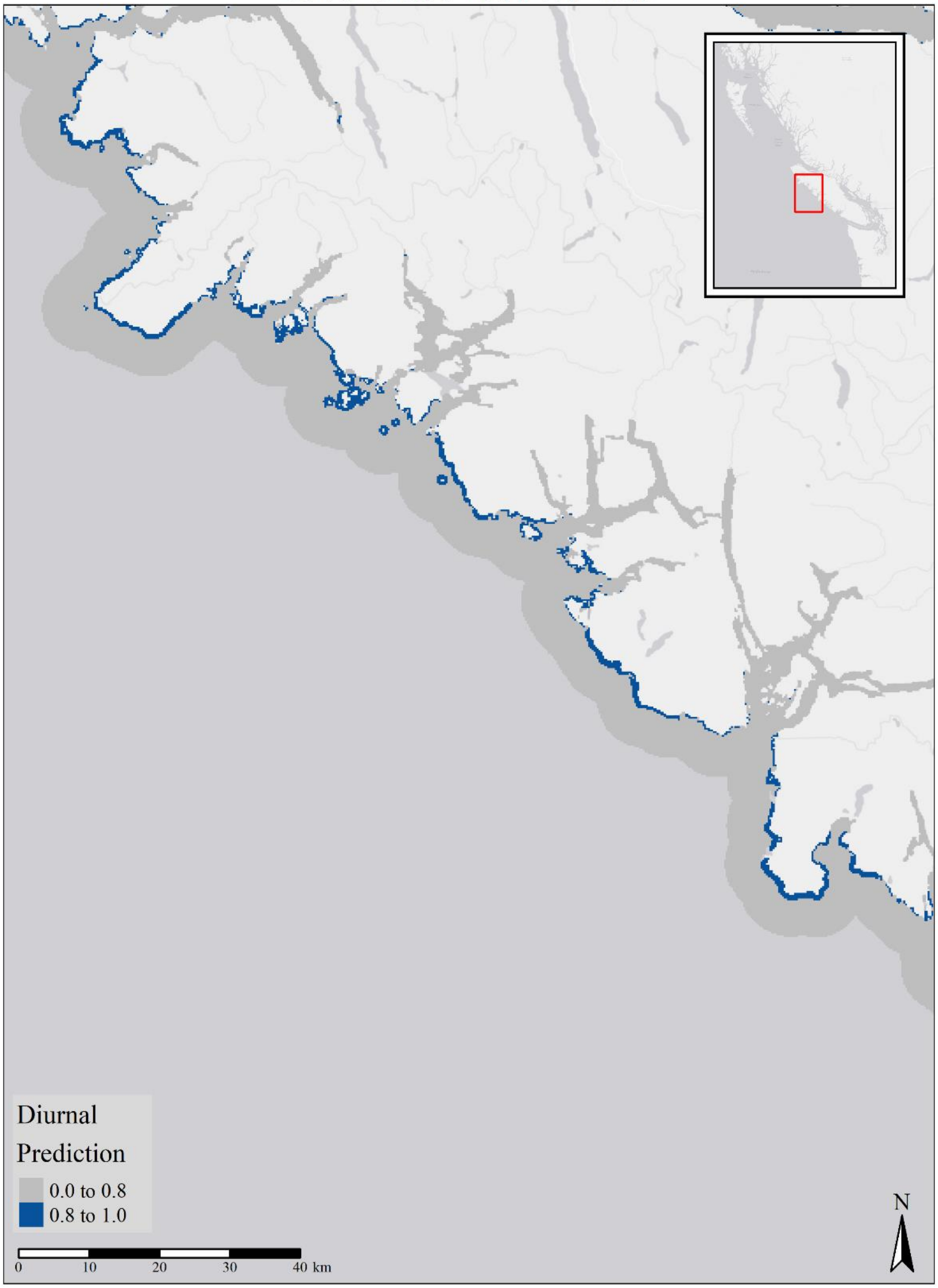
Harlequin Duck Diurnal Habitat Suitability
Southern Hectate Strait



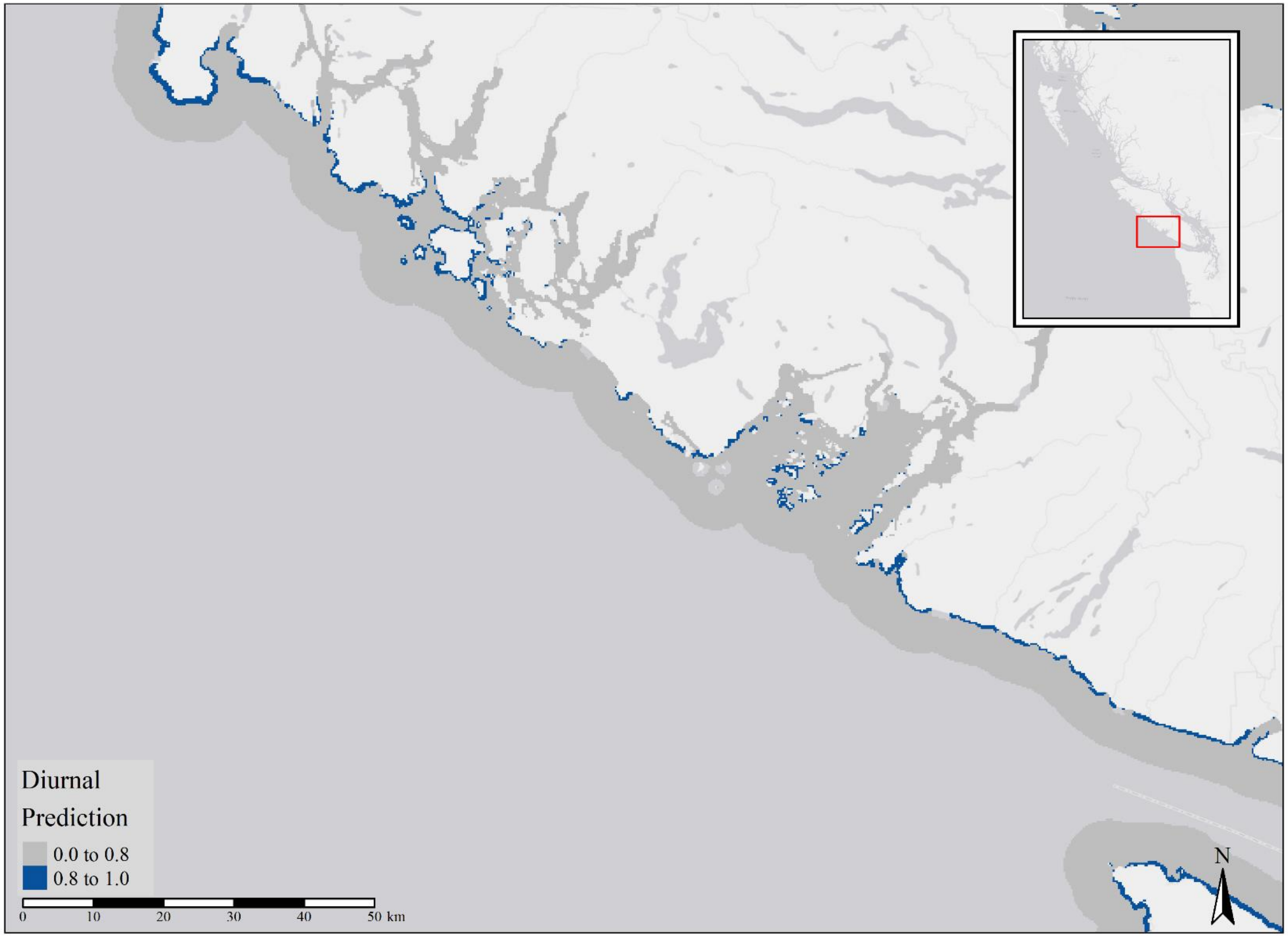
Harlequin Duck Diurnal Habitat Suitability
Queen Charlotte Strait & Northern Vancouver Island



Harlequin Duck Diurnal Habitat Suitability
Central Vancouver Island Outer Coast

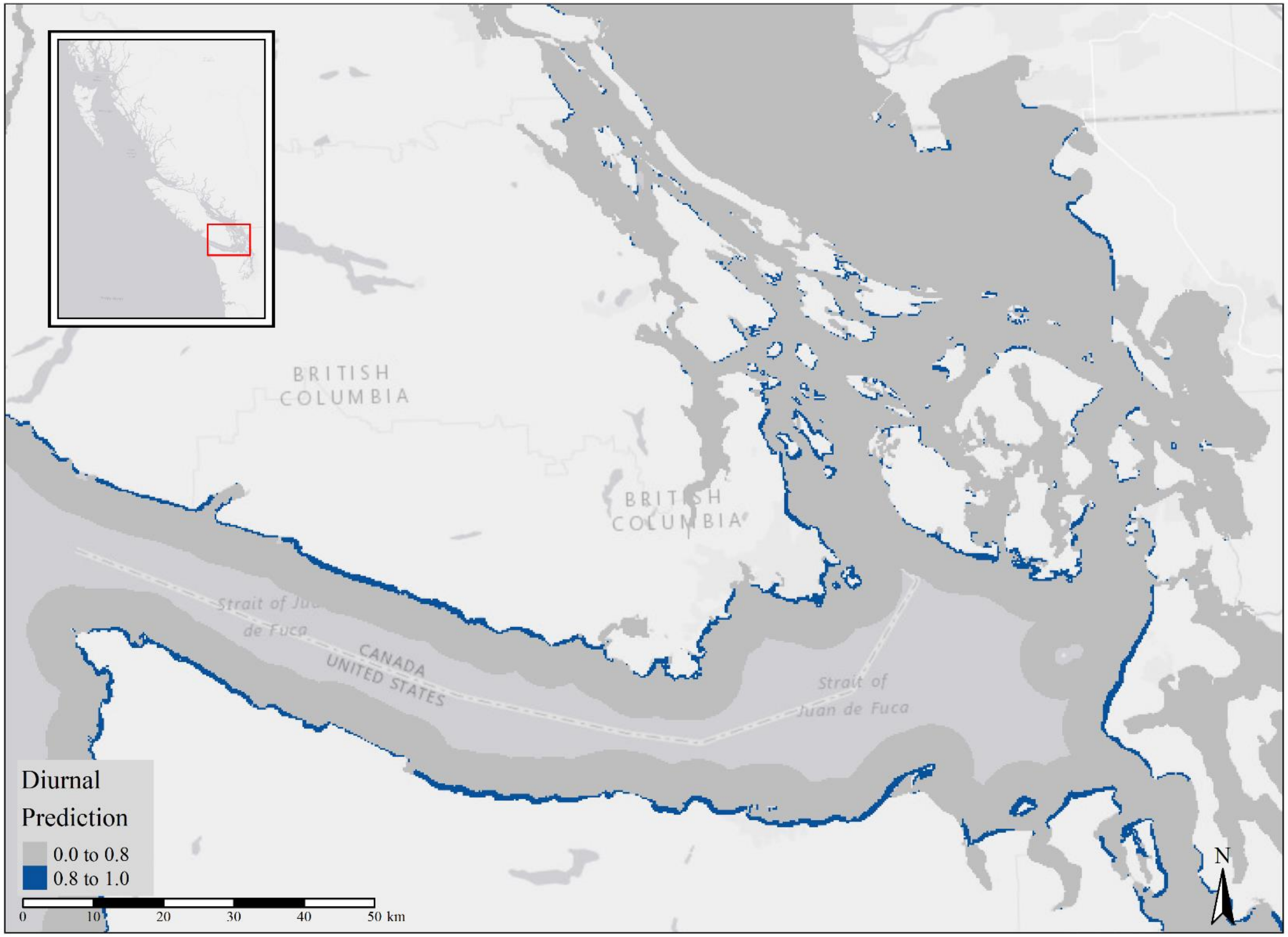


Harlequin Duck Diurnal Habitat Suitability
Southern Vancouver Island Outer Coast

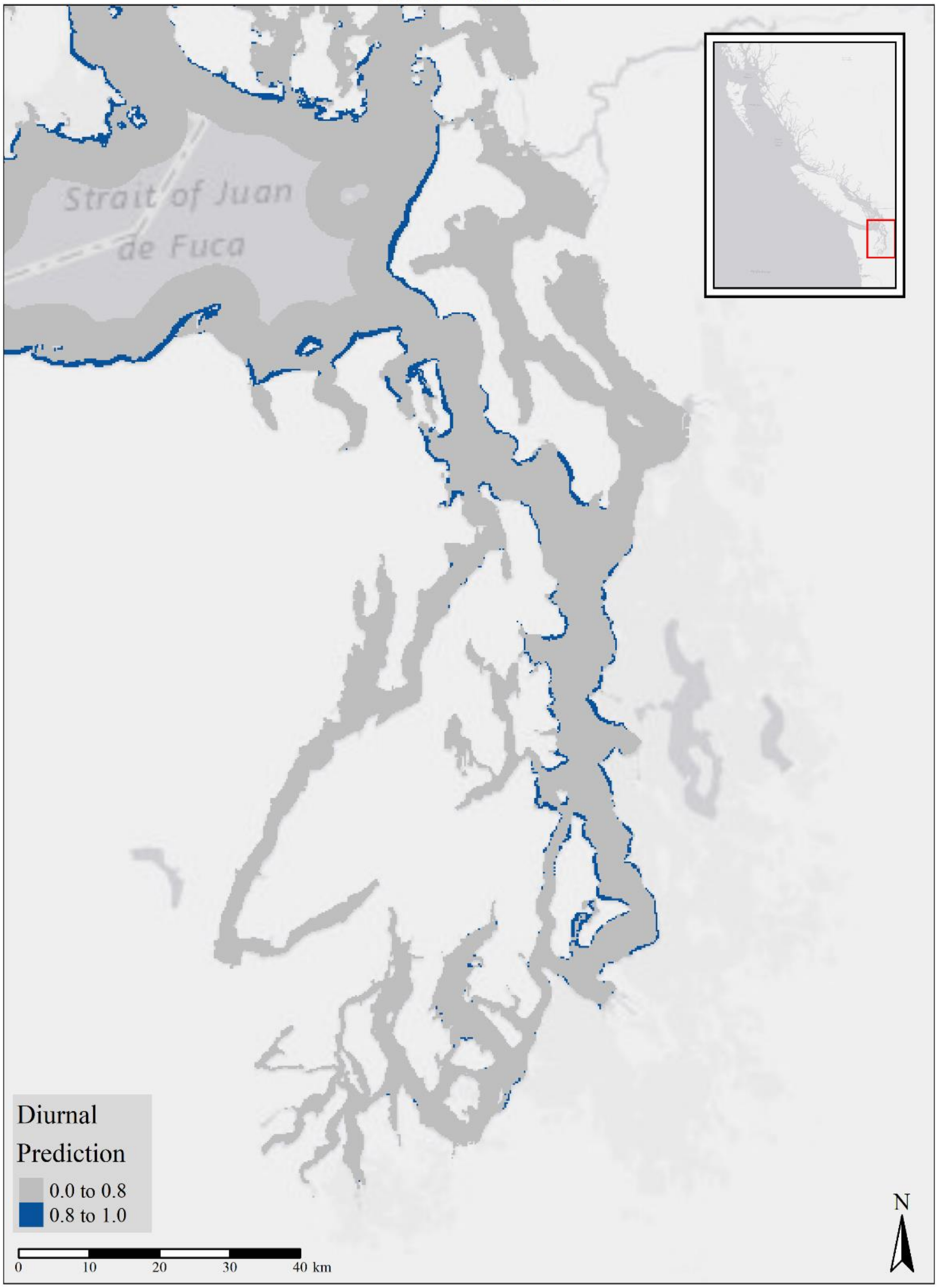


Harlequin Duck Diurnal Habitat Suitability
Northern Salish Sea

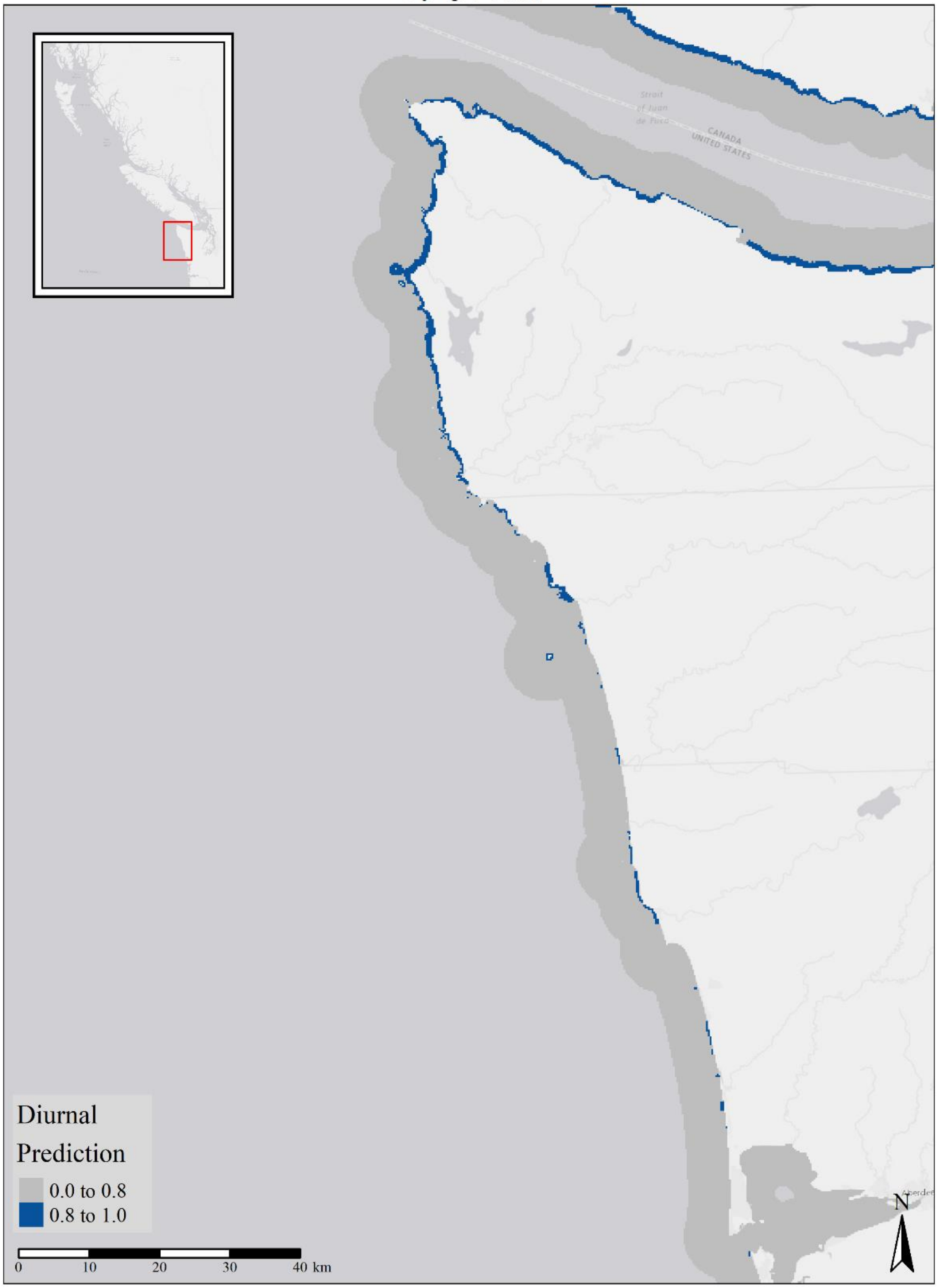
Harlequin Duck Diurnal Habitat Suitability
Central Salish Sea



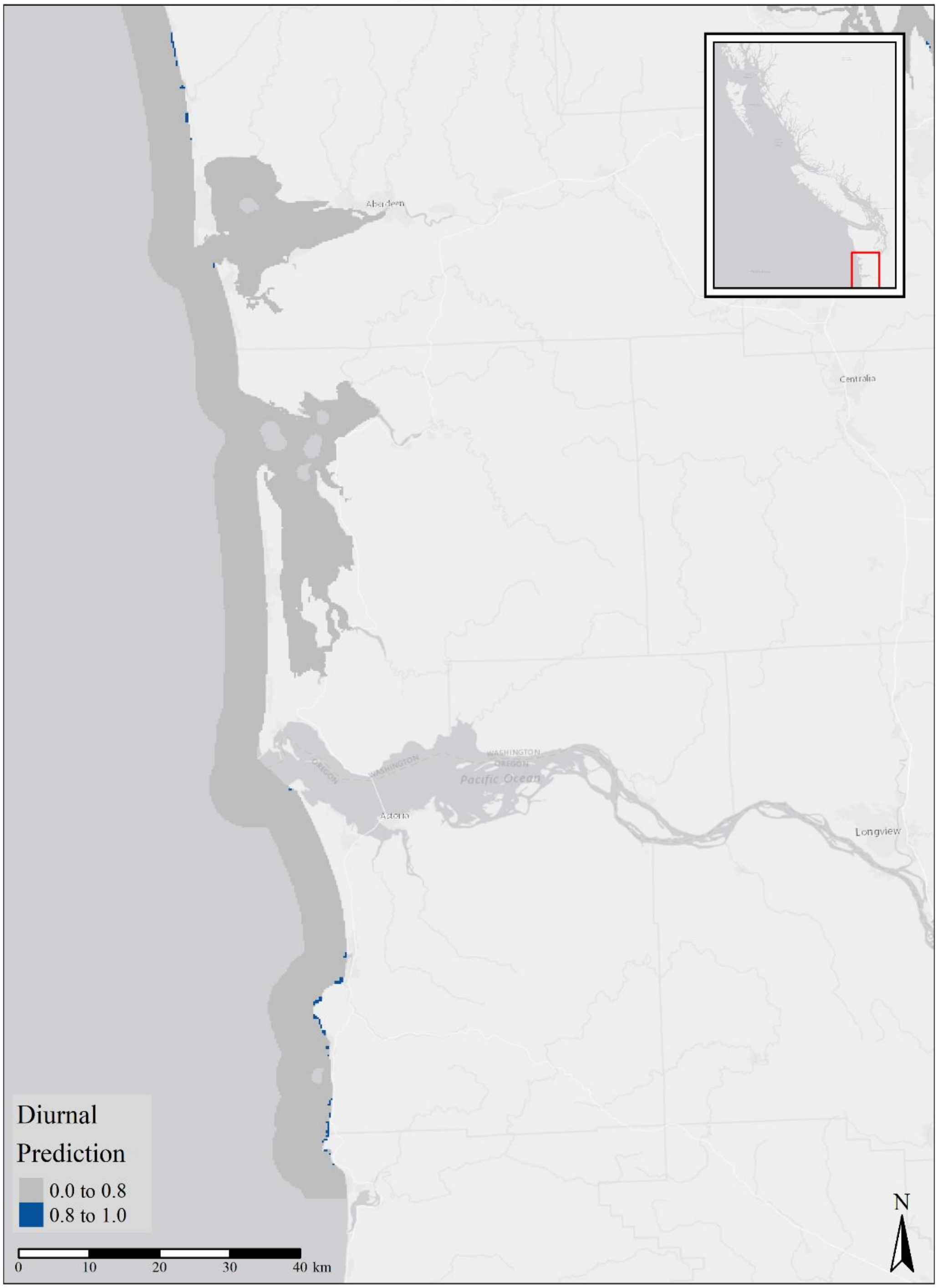
Harlequin Duck Diurnal Habitat Suitability
Southern Salish Sea



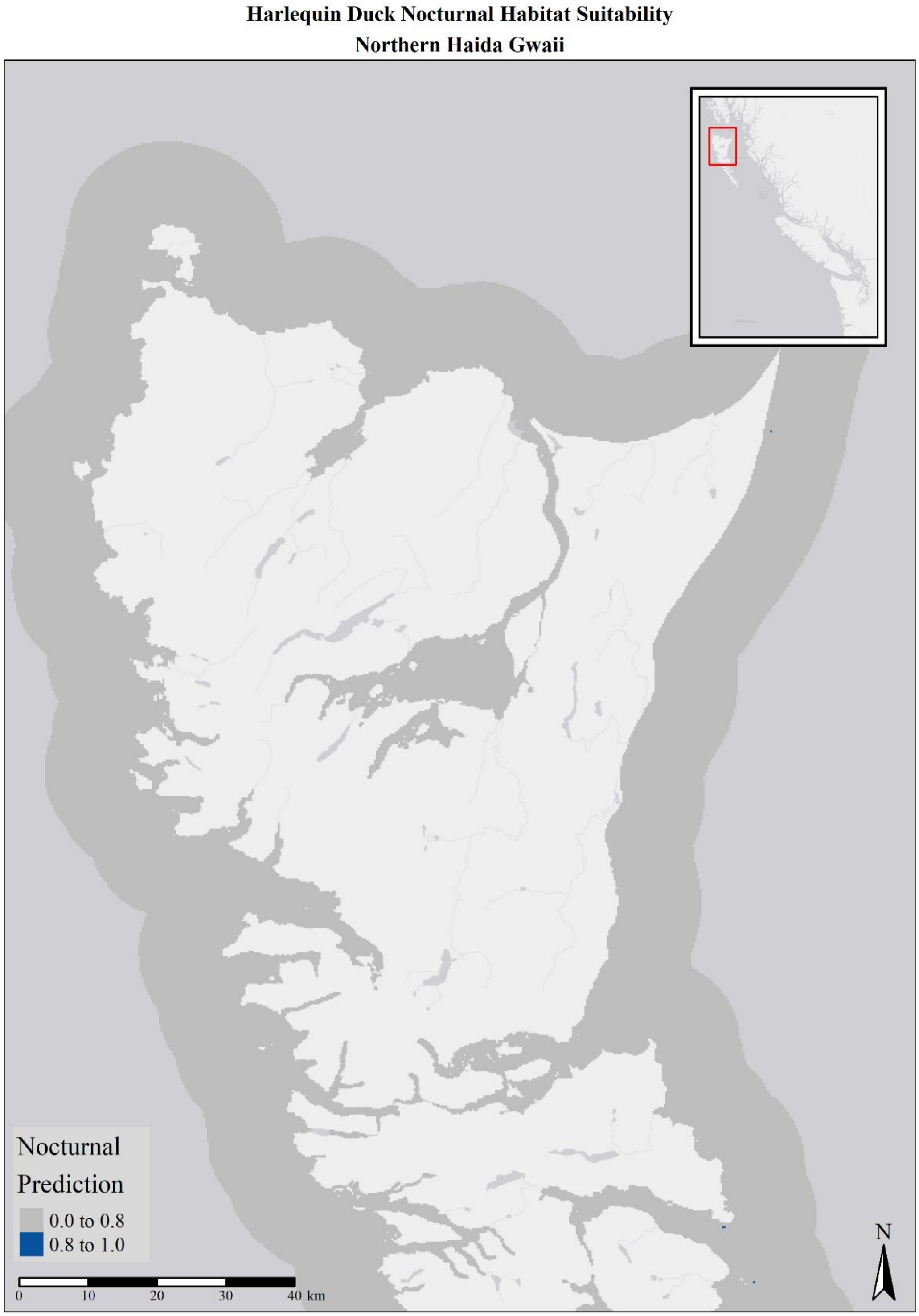
Harlequin Duck Diurnal Habitat Suitability
Olympic Coast



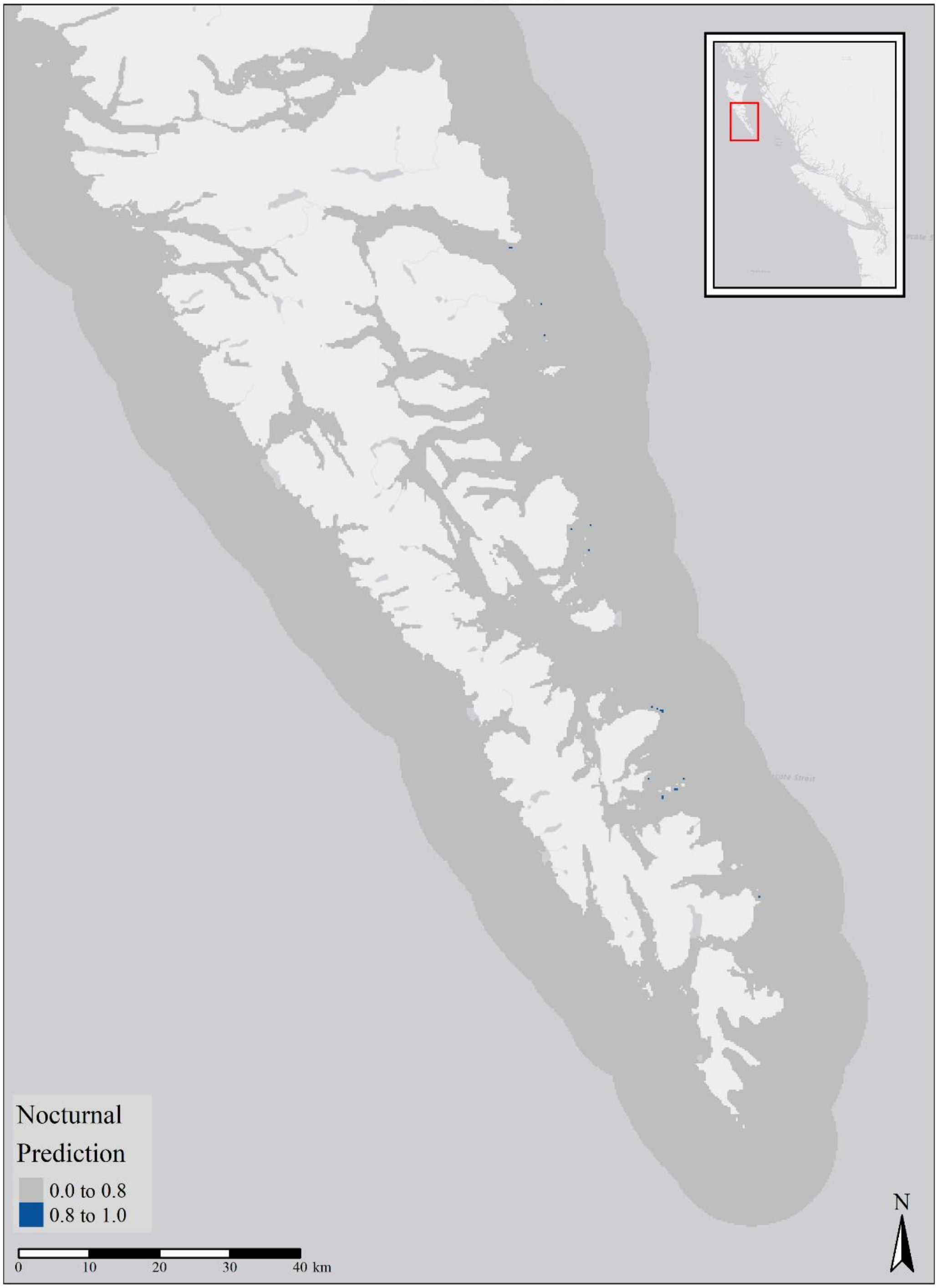
Harlequin Duck Diurnal Habitat Suitability
Southern Coast



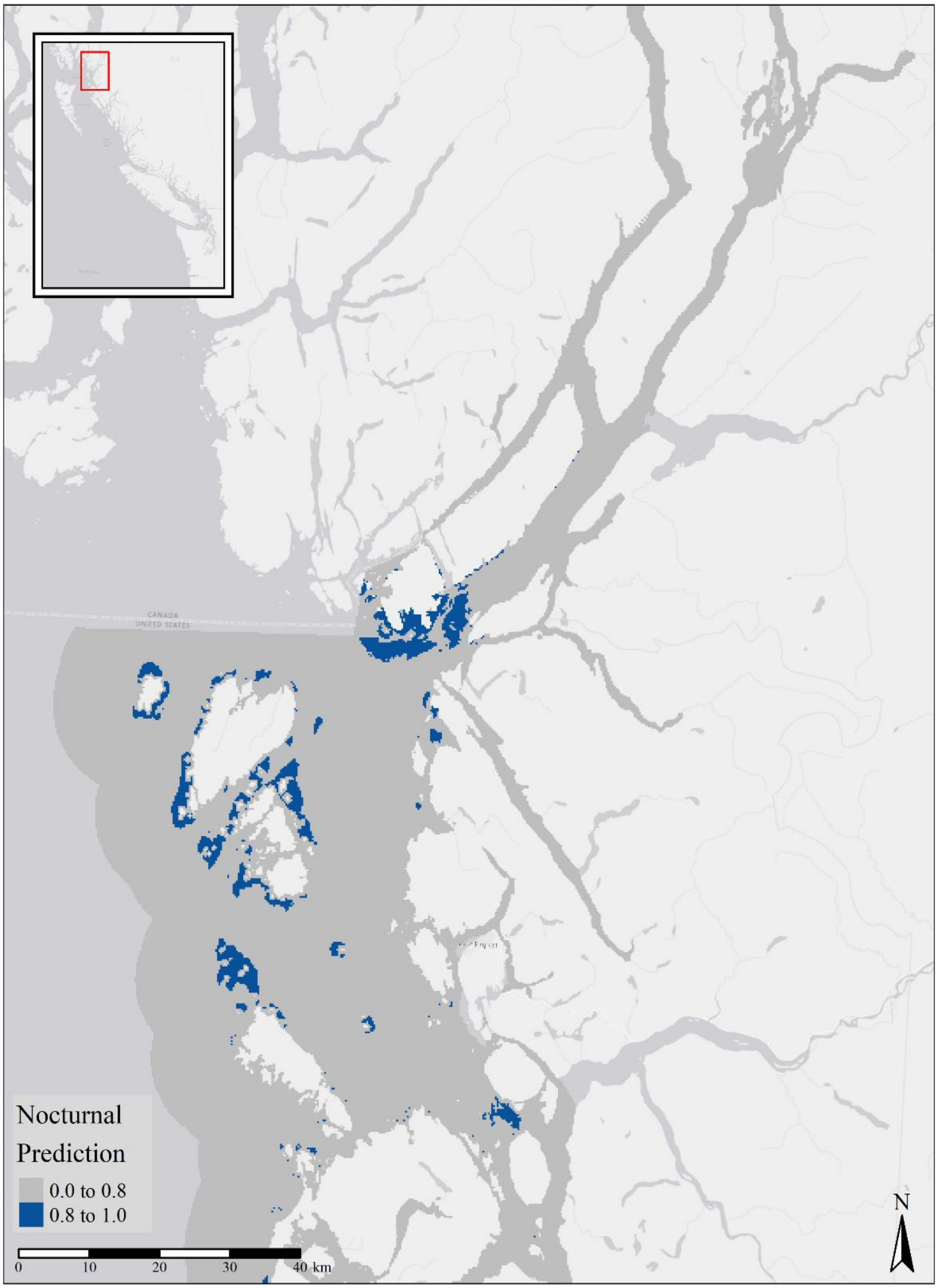
Appendix B: Nocturnal harlequin duck (*Histrionicus histrionicus*) species distribution model results, developed using PTT satellite telemetry occurrence points and Maxent SDM methods. Areas in blue indicate high habitat suitability (cloglog prediction ≥ 0.8).



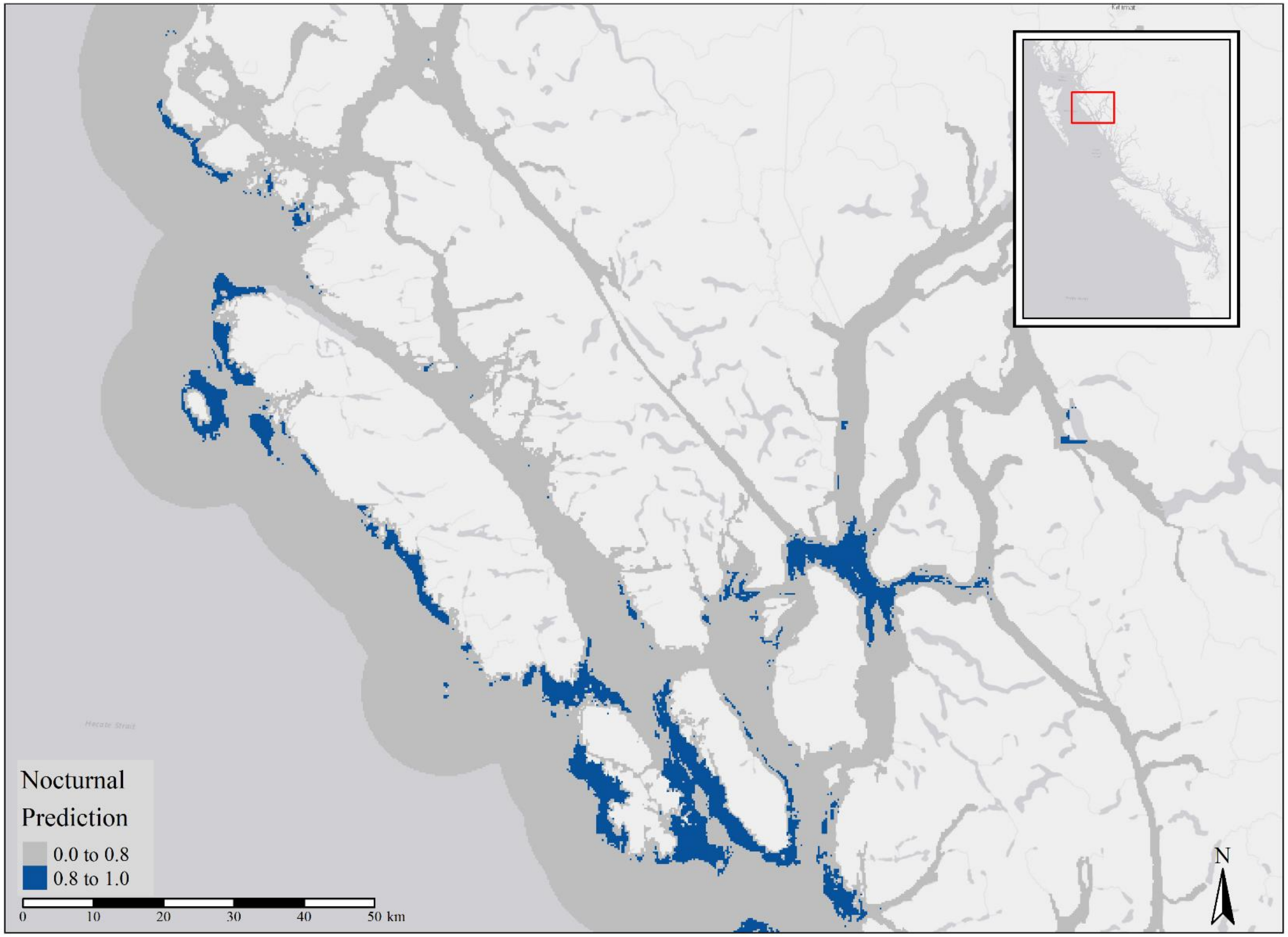
Harlequin Duck Nocturnal Habitat Suitability
Southern Haida Gwaii



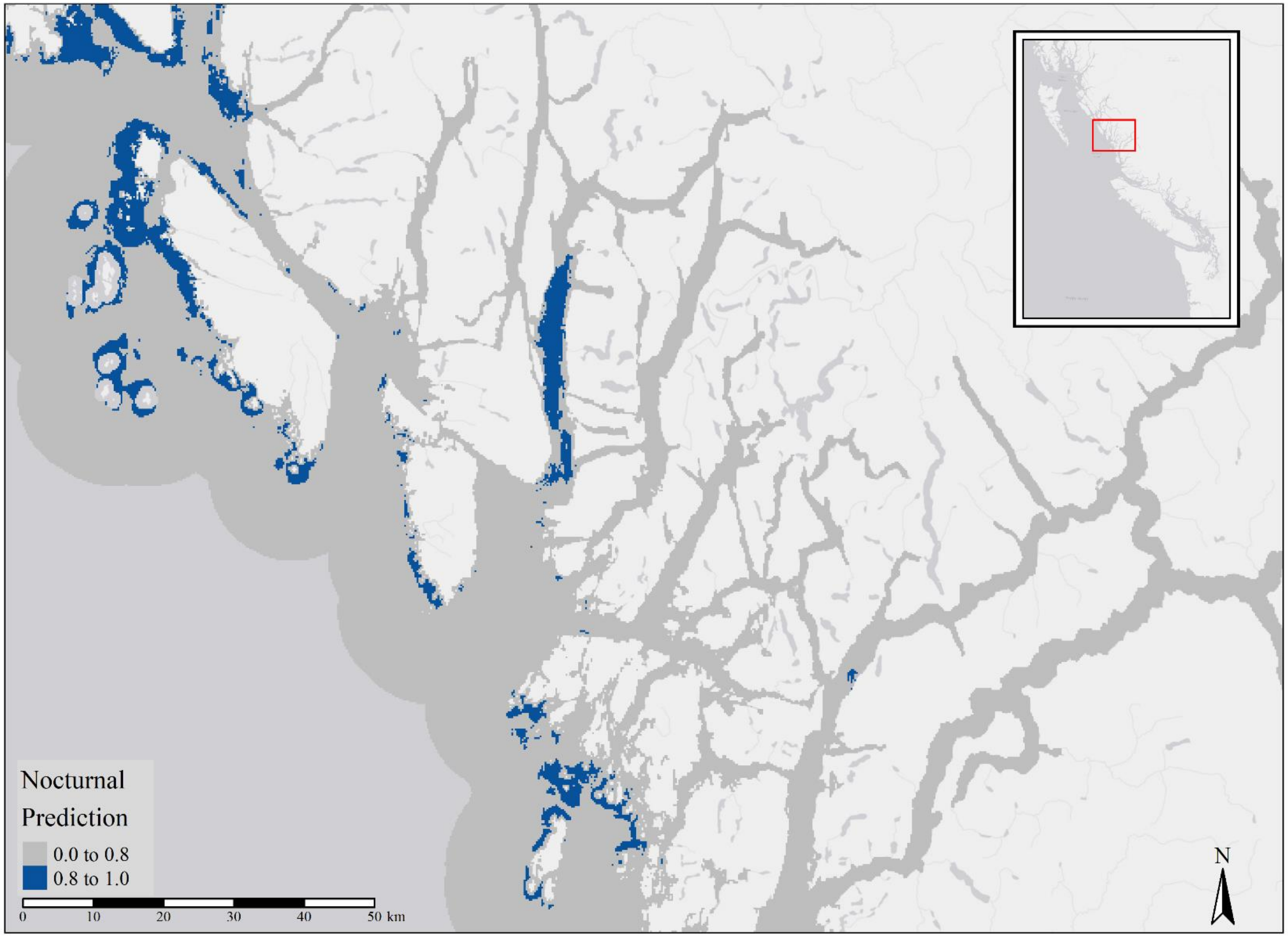
Harlequin Duck Nocturnal Habitat Suitability
Northern Hectate Strait



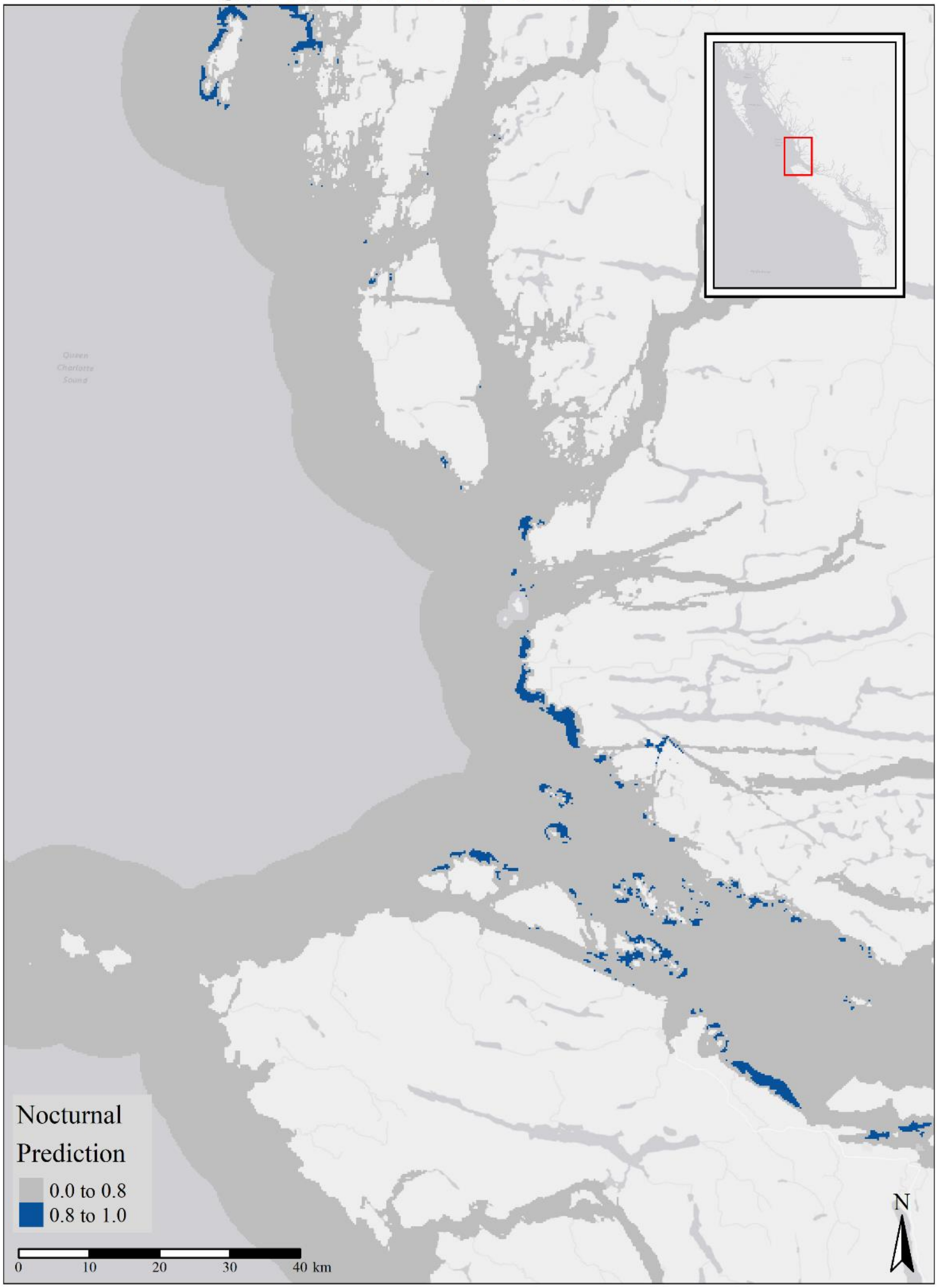
Harlequin Duck Nocturnal Habitat Suitability
Central Hectate Strait



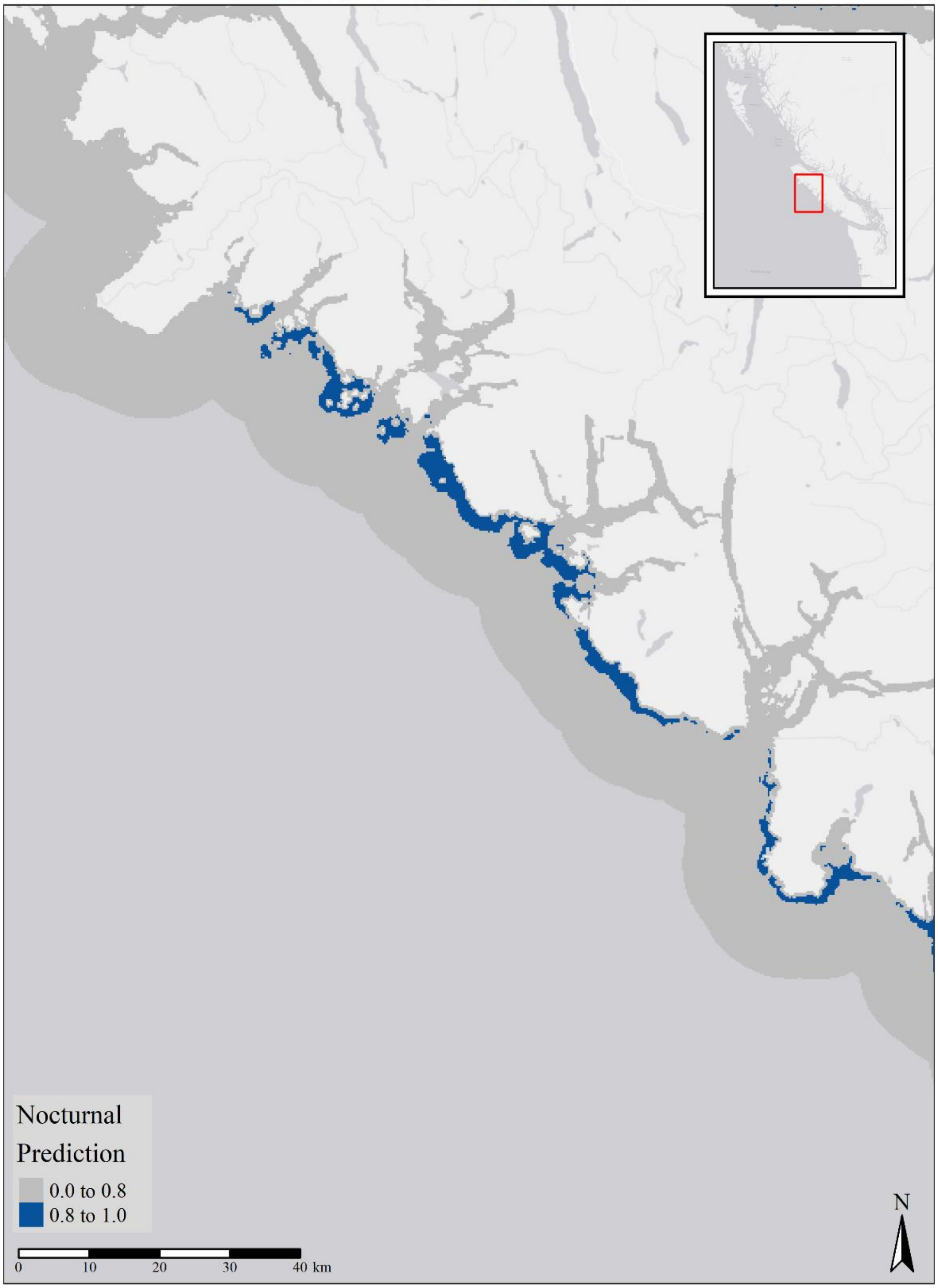
Harlequin Duck Nocturnal Habitat Suitability
Southern Hectate Strait



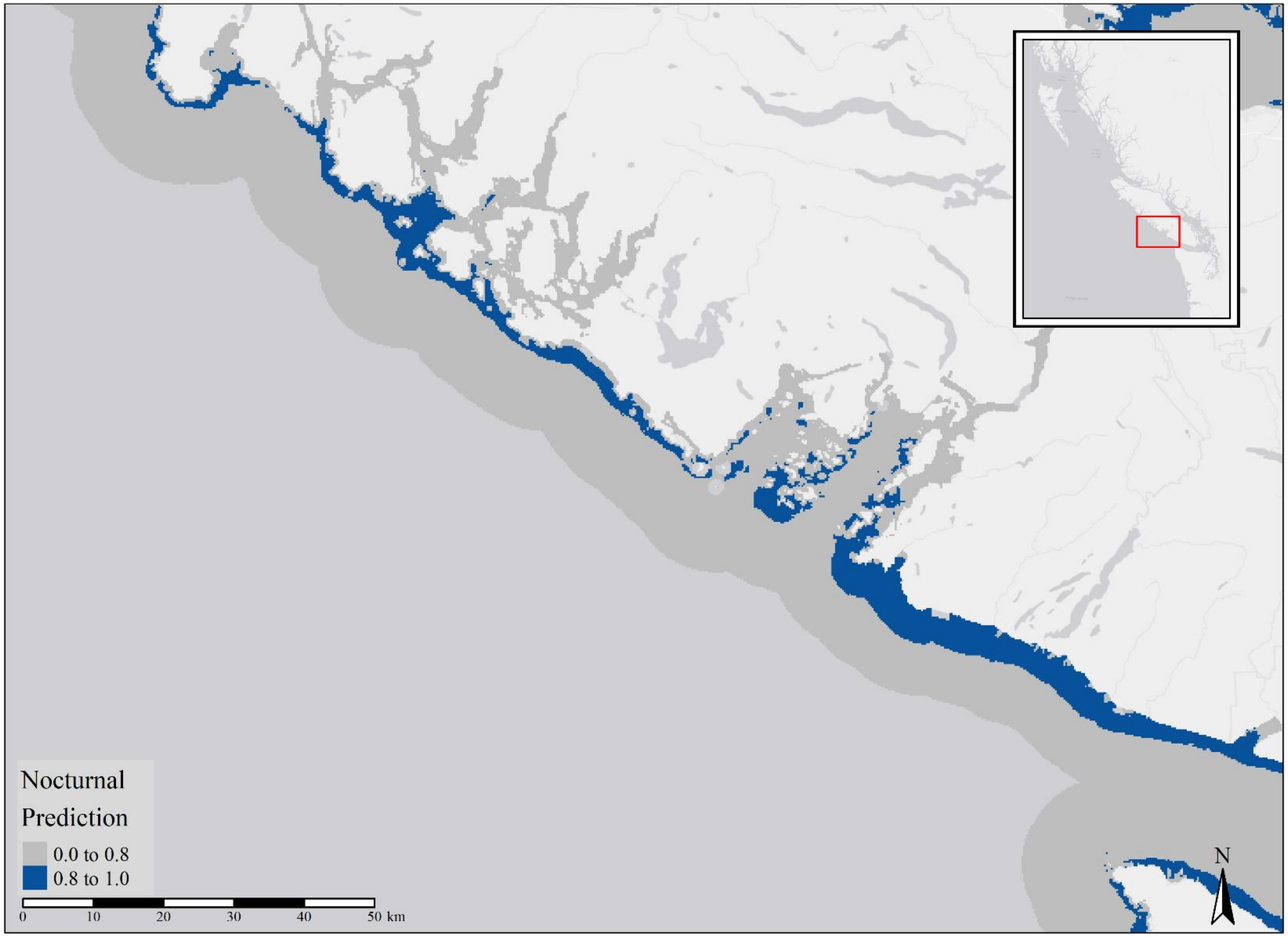
Harlequin Duck Nocturnal Habitat Suitability
Queen Charlotte Strait & Northern Vancouver Island



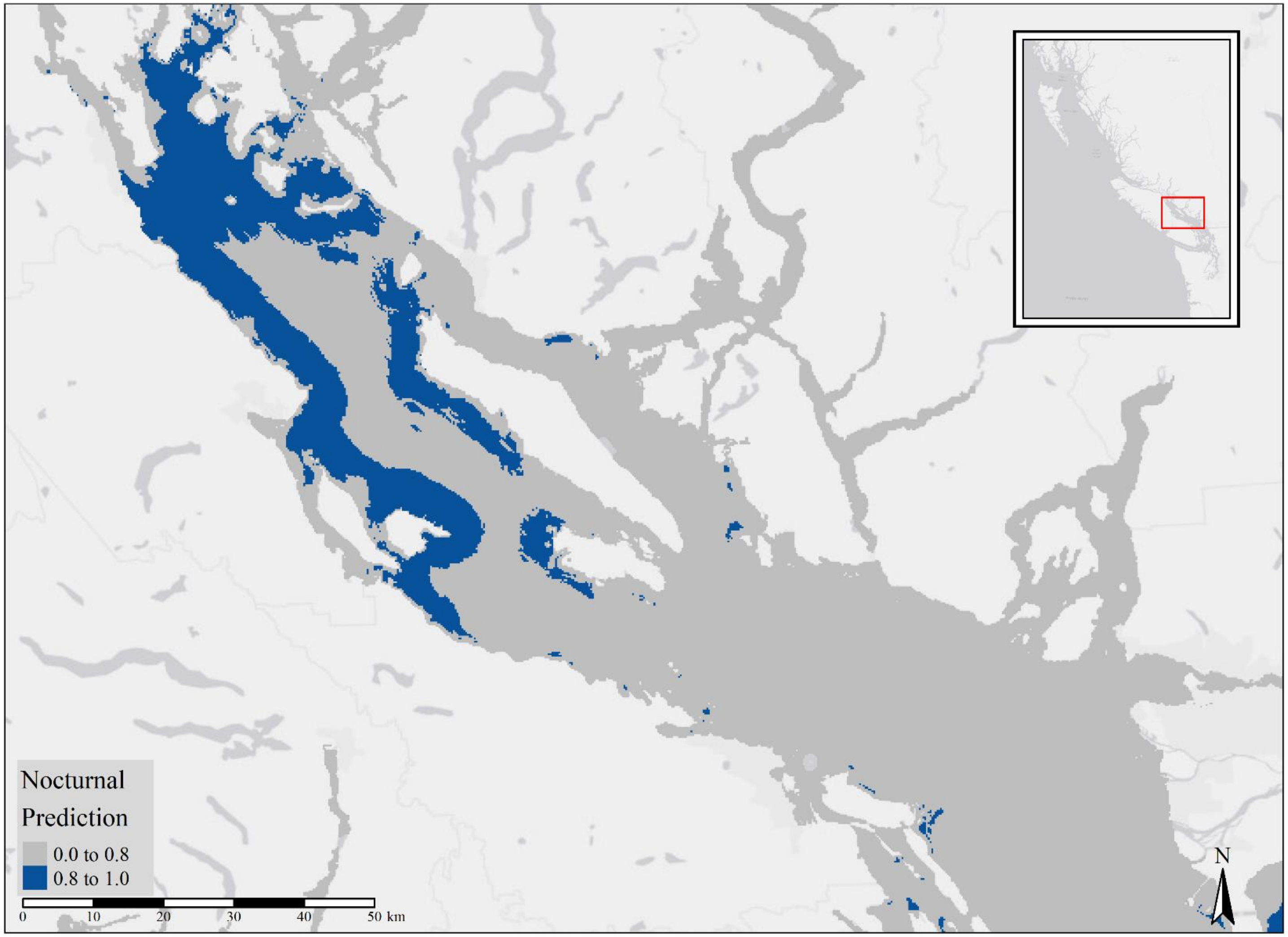
Harlequin Duck Nocturnal Habitat Suitability
Central Vancouver Island Outer Coast



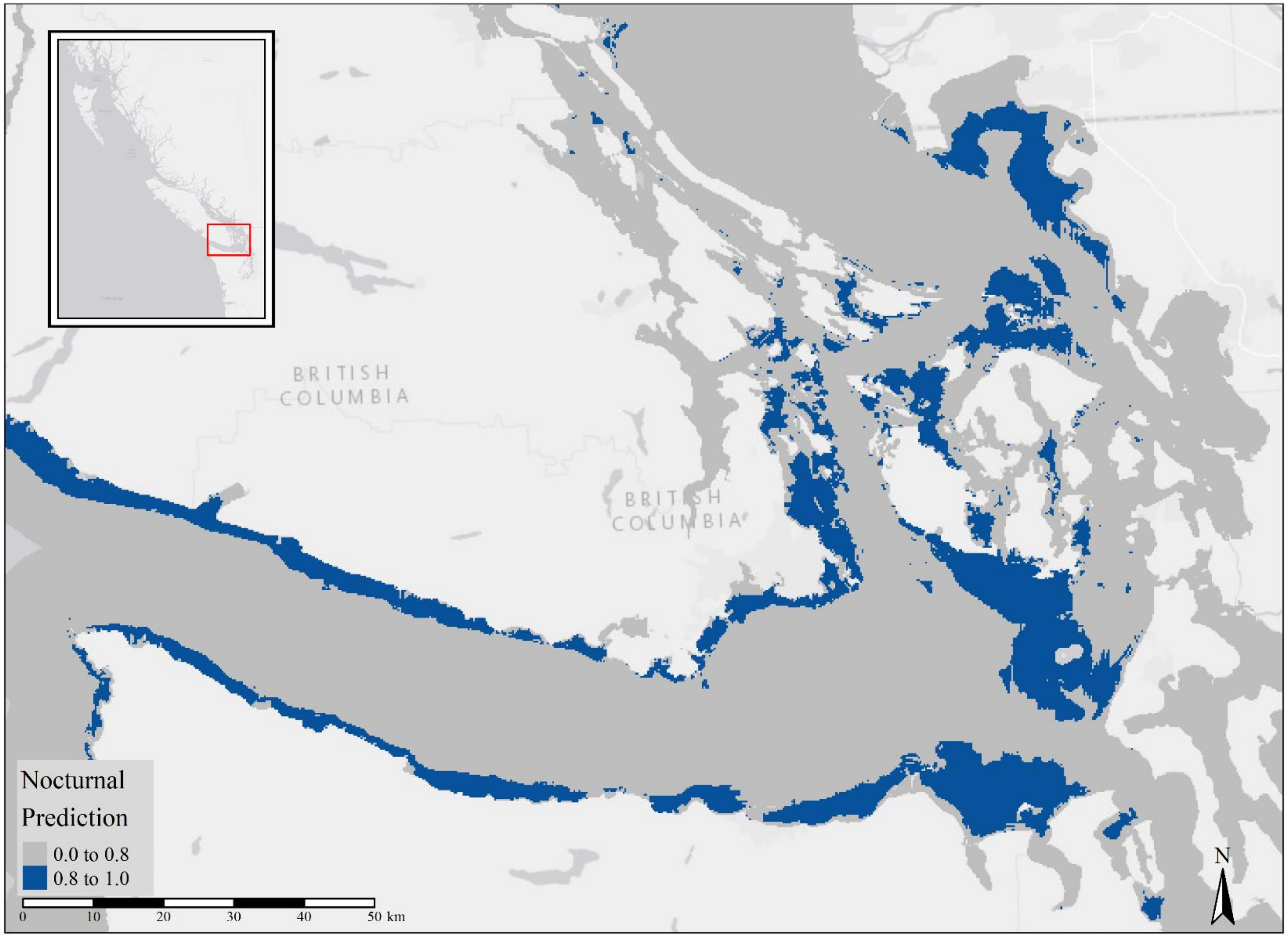
Harlequin Duck Nocturnal Habitat Suitability
Southern Vancouver Island Outer Coast



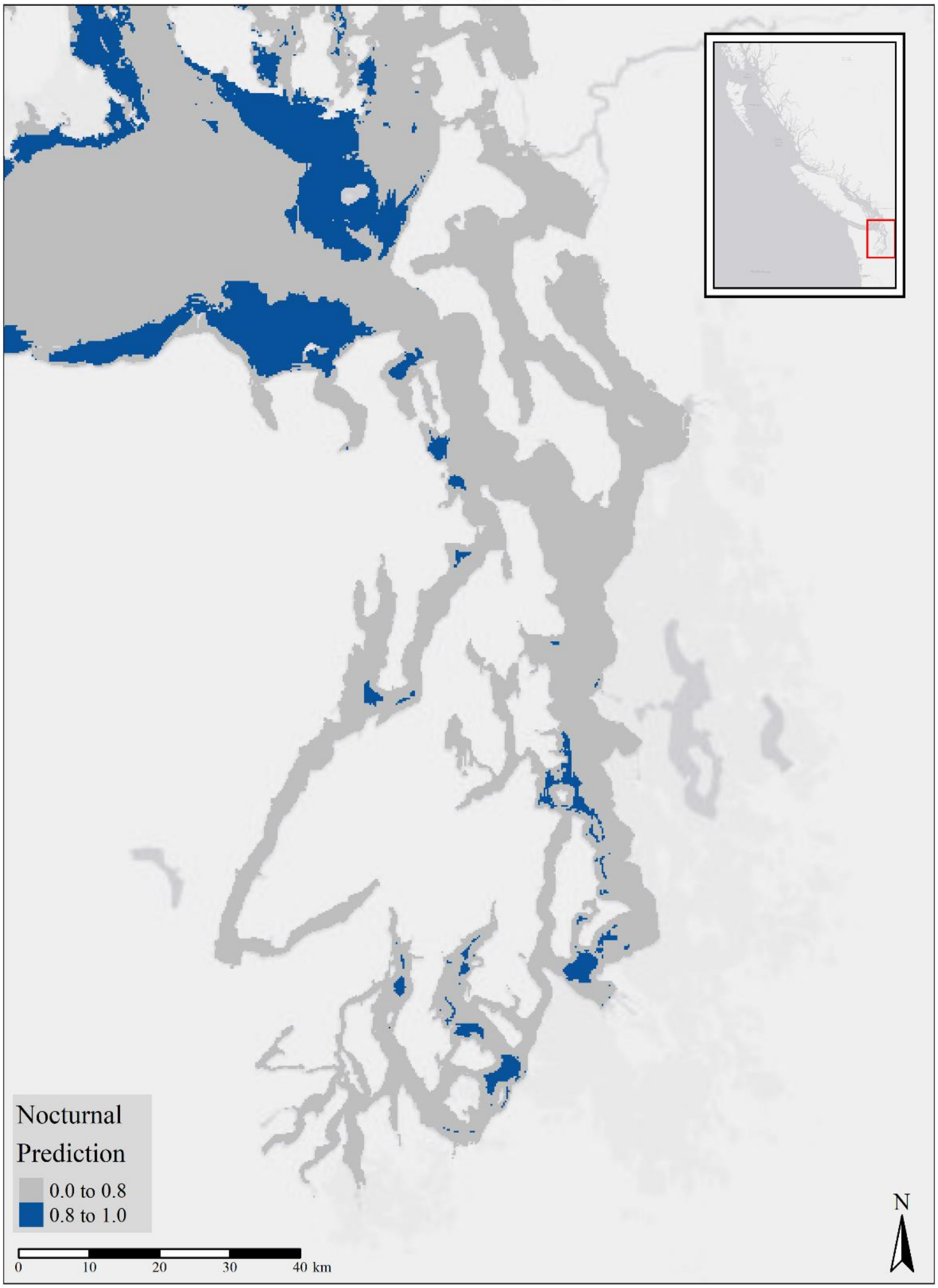
Harlequin Duck Nocturnal Habitat Suitability
Northern Salish Sea



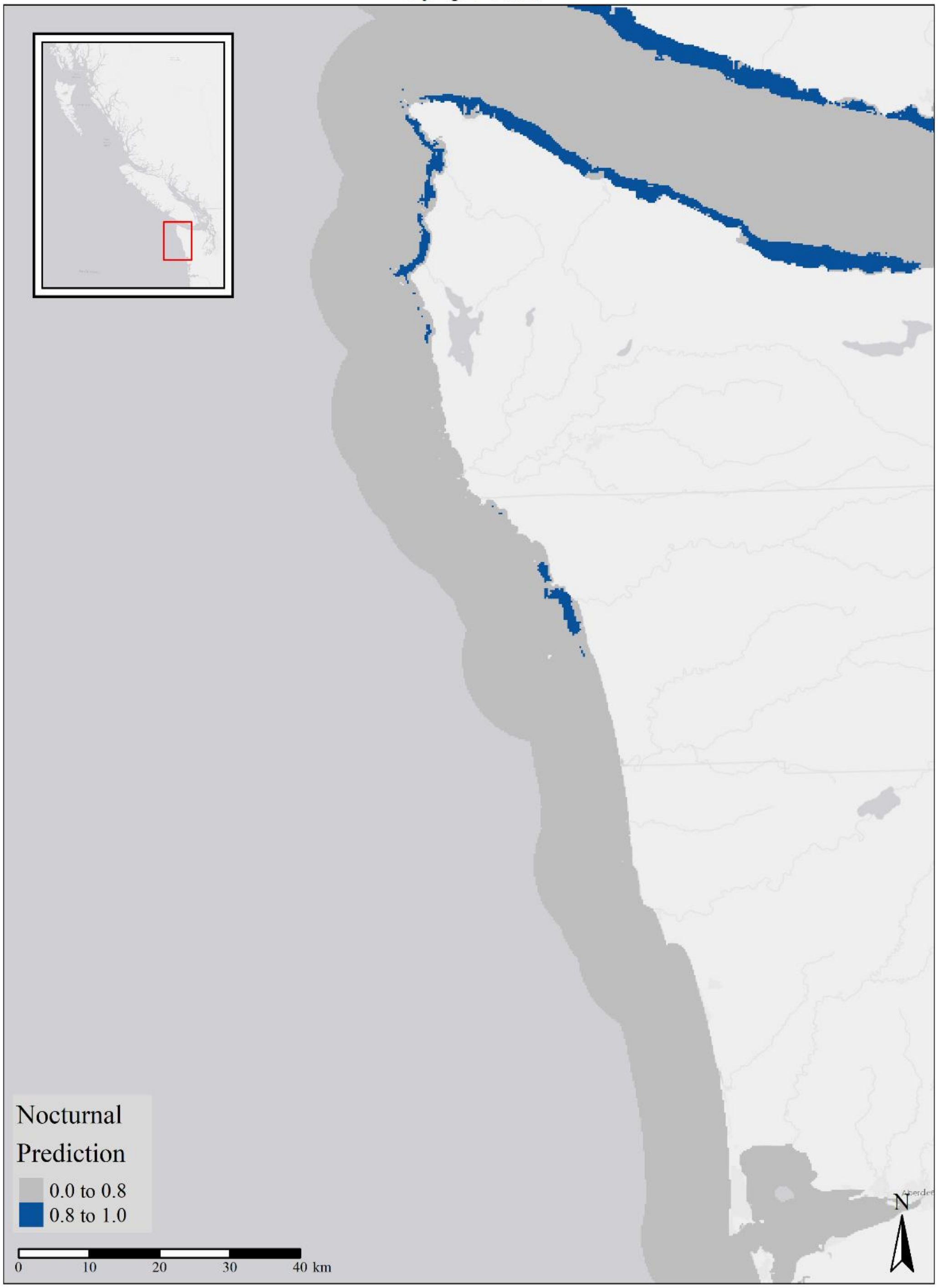
Harlequin Duck Nocturnal Habitat Suitability
Central Salish Sea



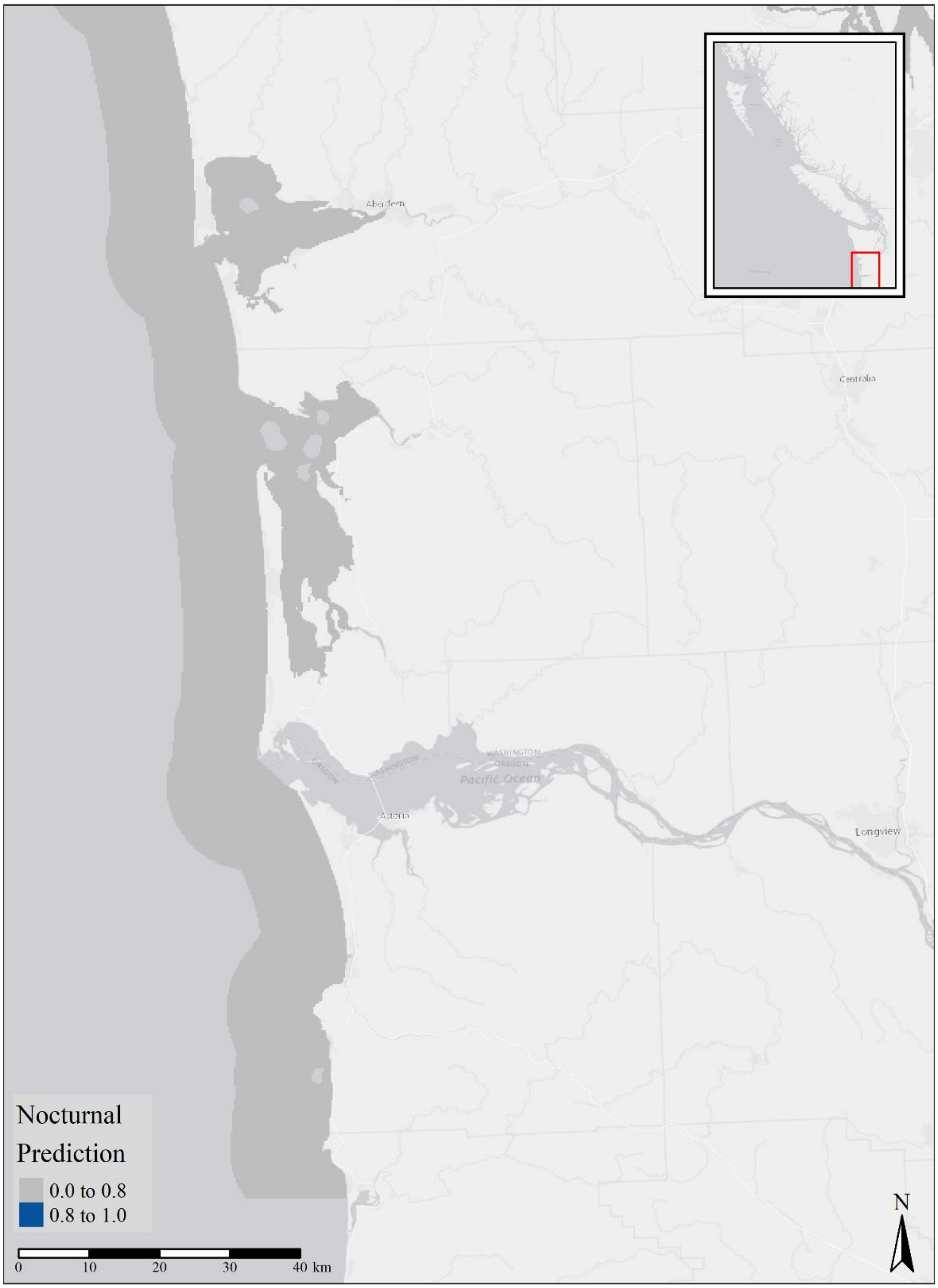
Harlequin Duck Nocturnal Habitat Suitability
Southern Salish Sea



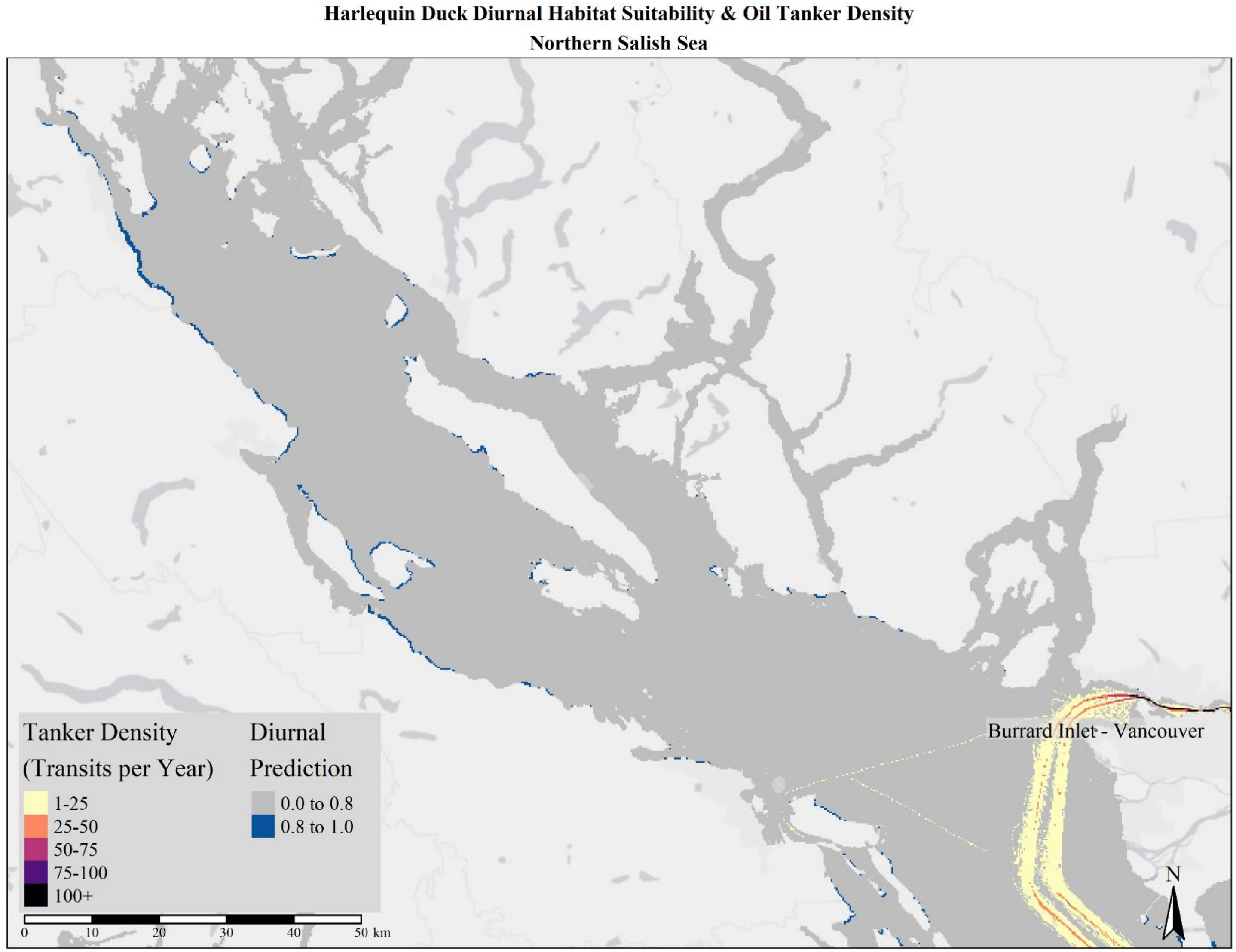
Harlequin Duck Nocturnal Habitat Suitability
Olympic Coast



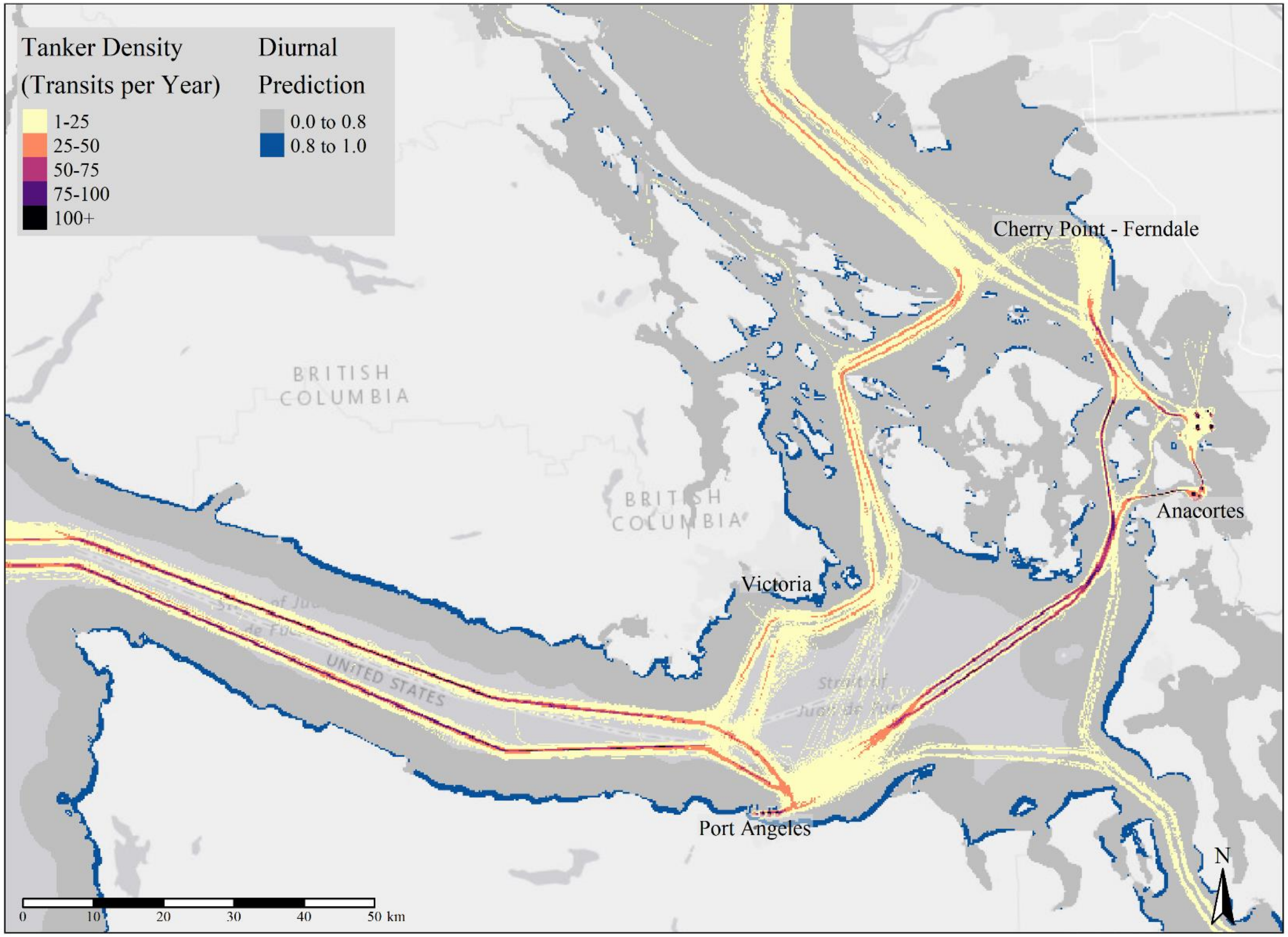
Harlequin Duck Nocturnal Habitat Suitability
Southern Coast



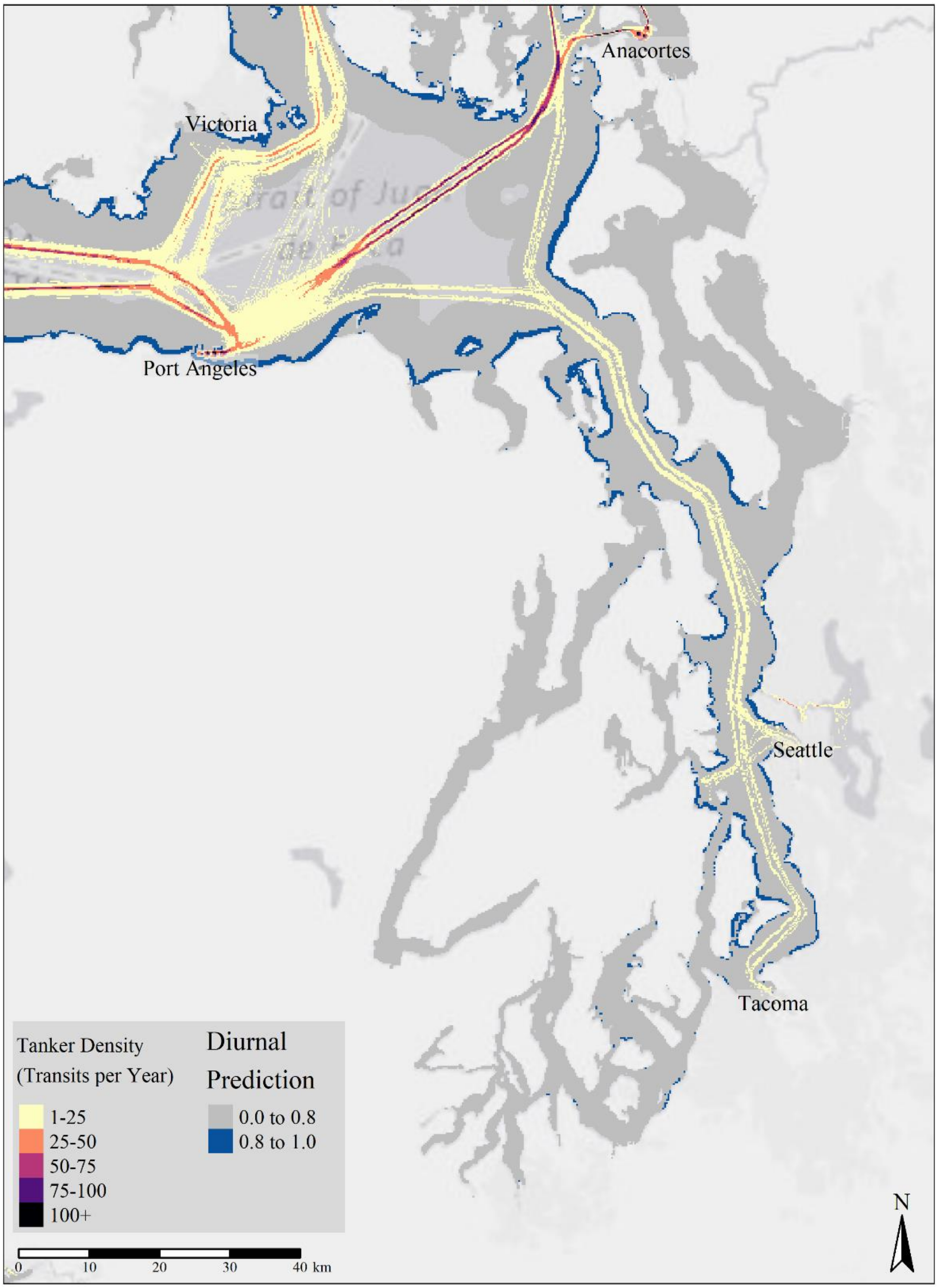
Appendix C: Salish Sea diurnal harlequin duck (*Histrionicus histrionicus*) species distribution model predictions and oil tanker density (transits per year). Areas in blue indicate high habitat suitability (cloglog prediction ≥ 0.8).



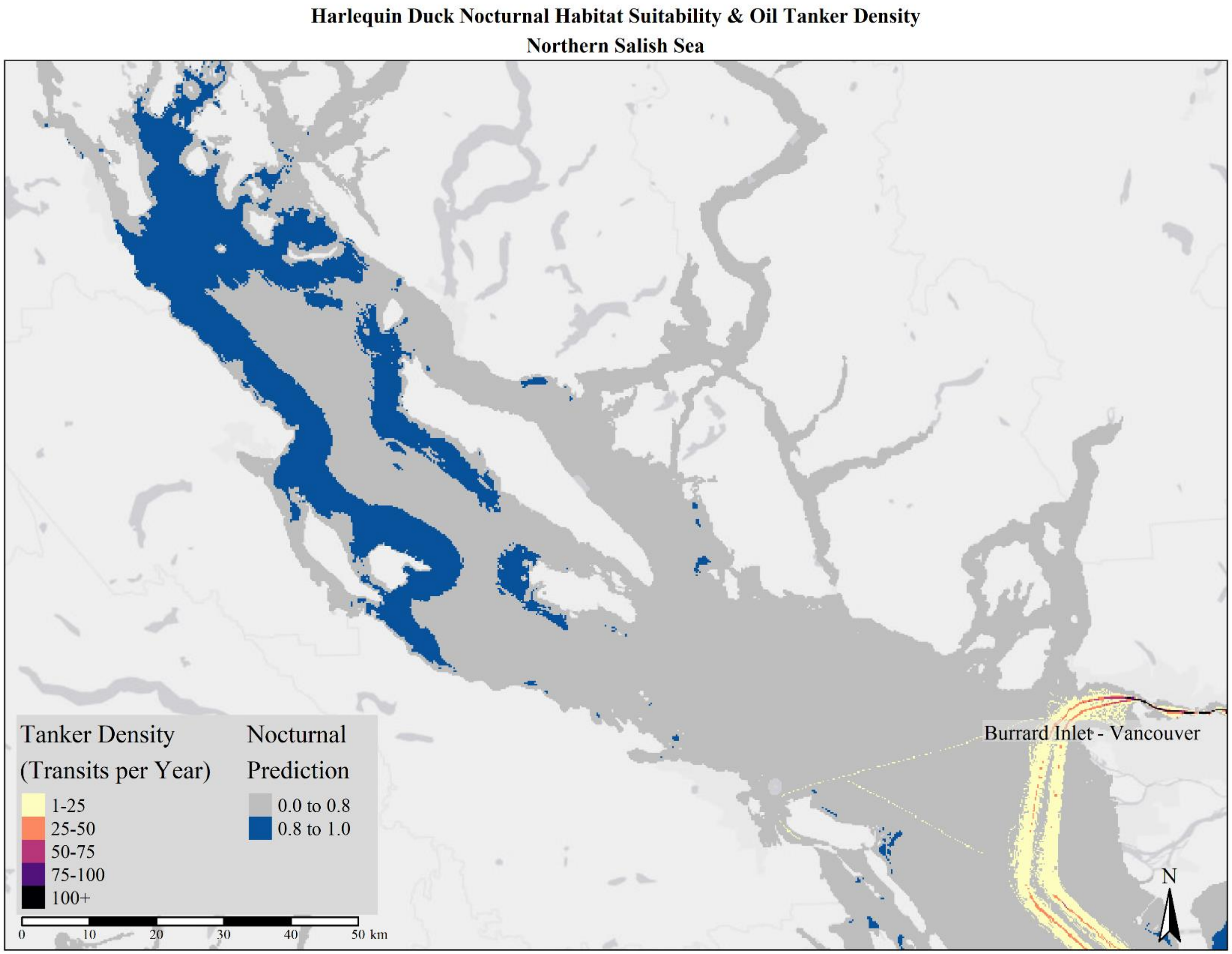
Harlequin Duck Diurnal Habitat Suitability & Oil Tanker Density
Central Salish Sea



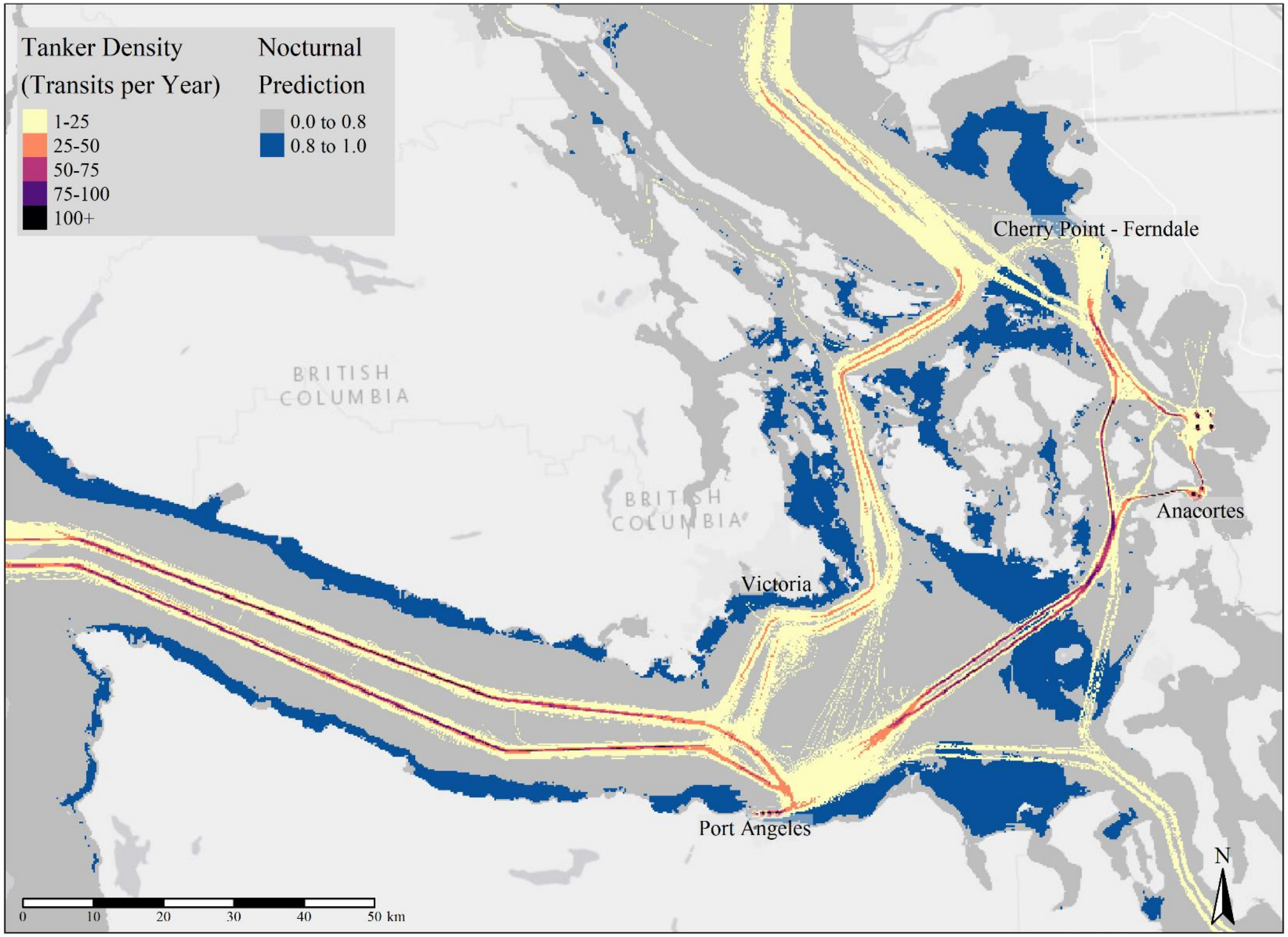
Harlequin Duck Diurnal Habitat Suitability & Oil Tanker Density
Southern Salish Sea



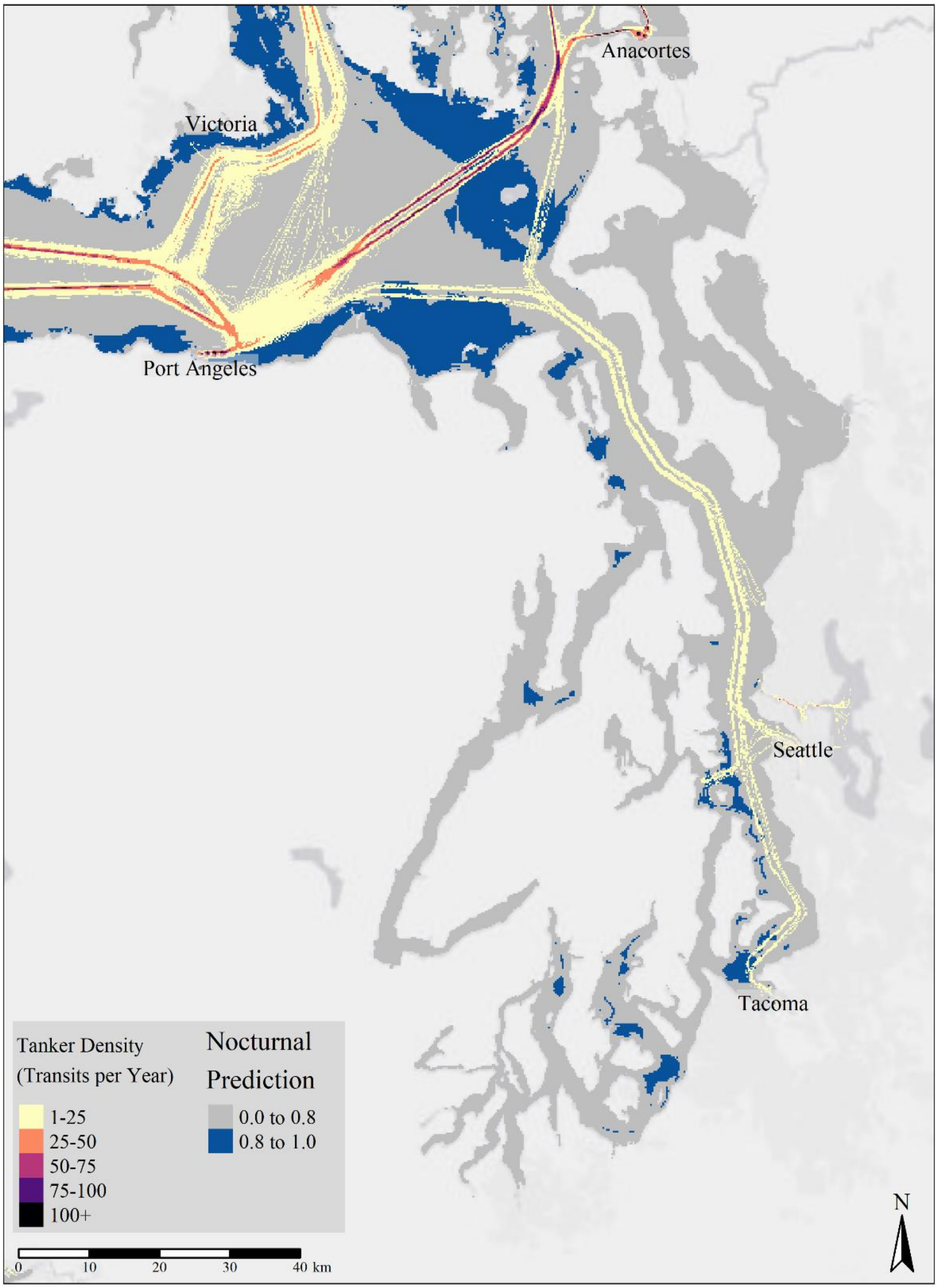
Appendix D: Salish Sea nocturnal harlequin duck (*Histrionicus histrionicus*) species distribution model predictions and oil tanker density (transits per year). Areas in blue indicate high habitat suitability (cloglog prediction ≥ 0.8).



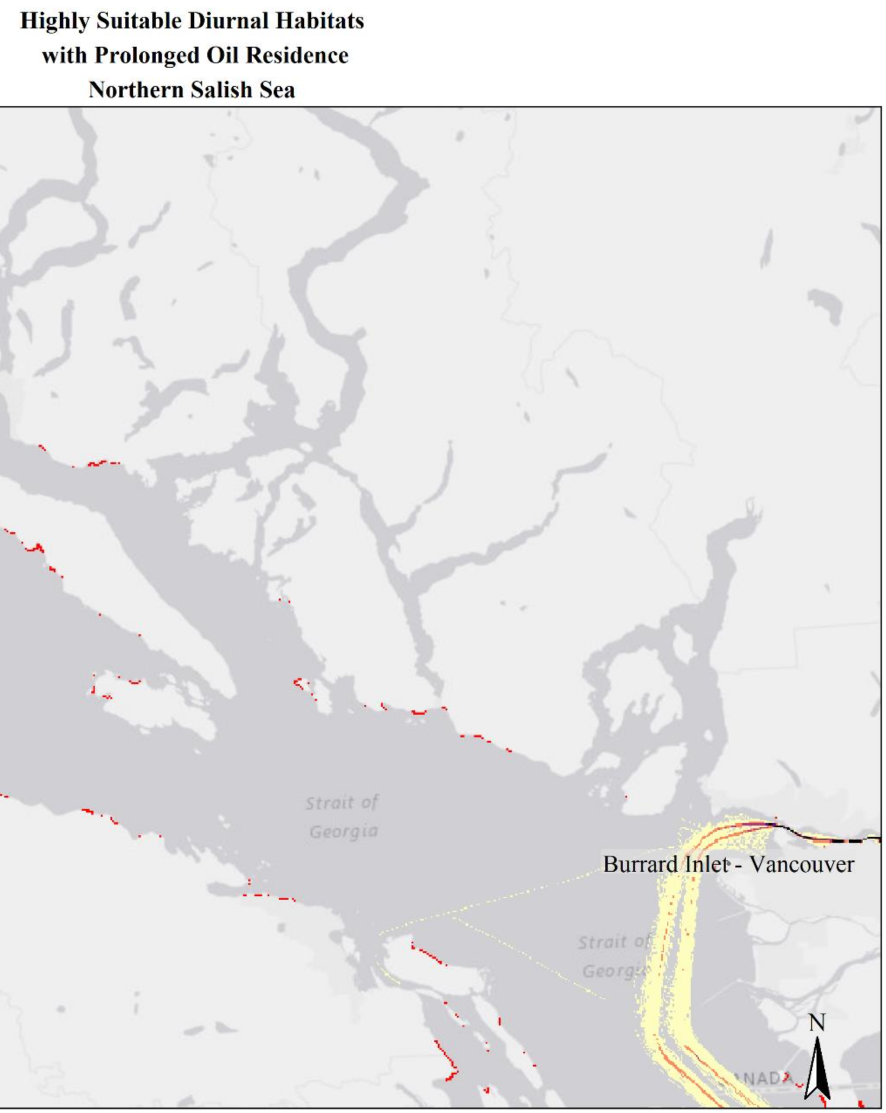
Harlequin Duck Nocturnal Habitat Suitability & Oil Tanker Density
Central Salish Sea



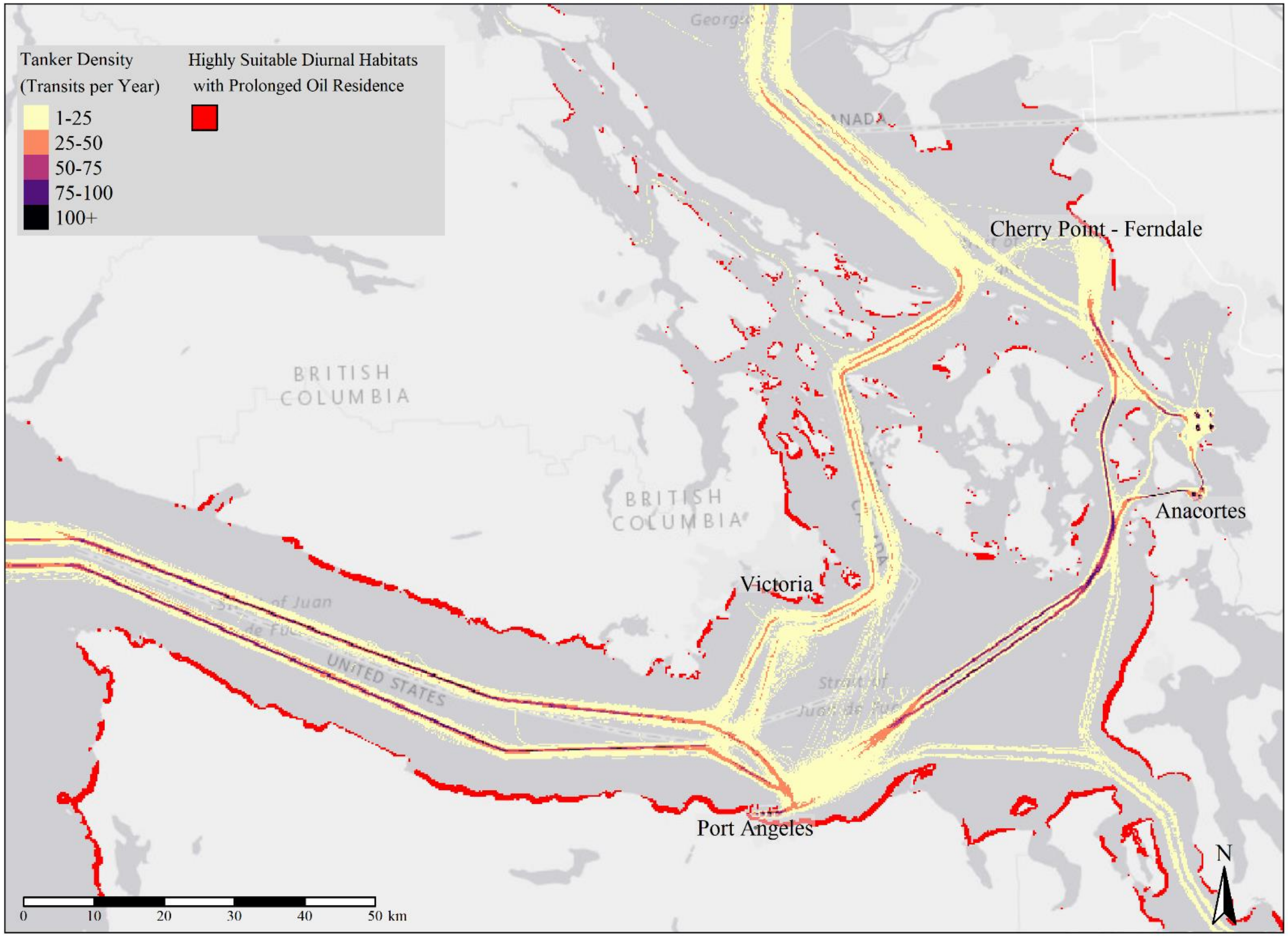
Harlequin Duck Nocturnal Habitat Suitability & Oil Tanker Density
Southern Salish Sea



Appendix E: Suitable (cloglog prediction ≥ 0.8) Salish Sea diurnal harlequin duck (*Histrionicus histrionicus*) habitats with projected oil residence times on the scale of years and oil tanker density (transits per year).



Highly Suitable Diurnal Habitats with Prolonged Oil Residence Central Salish Sea



Highly Suitable Diurnal Habitats with Prolonged Oil Residence Southern Salish Sea