Ecological Drivers of Winter Movement and Foraging Behaviour of Brandt's Cormorants (*Urile penicillatus*) in the Salish Sea

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Declaration of Committee

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Ethics Statement

Abstract

Understanding seabird movement and foraging behavior is essential for identifying critical habitats and informing conservation. I used GPS biologging technology to track Brandt's Cormorants from November 2023 to January 2024 across their winter habitat range in British Columbia, Canada. A hidden Markov model integrating movement, dive, and oceanographic data was used to infer behavioural states (resting, foraging, transiting) and assess how oceanographic conditions influence behavioural transitions. Model fit improved with the inclusion of environmental covariates; time of day, bathymetry, and current speed emerged as the strongest predictors of behavioural shifts, especially foraging. Foraging was concentrated around areas of fast currents and shallow bathymetry, such as the mouth of the Fraser River. These findings highlight key drivers of non-breeding habitat use and underscore the species' responsiveness to environmental variability. As mobile marine predators, Brandt's Cormorants may serve as indicators of changing prey distributions in coastal ecosystems.

Keywords: cormorants; Salish Sea; foraging; winter; habitat; hidden Markov models

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Chapter 1. General Introduction

By investigating the causes, mechanisms, and patterns of animal movement, researchers can gain key insights into habitat use and species behaviour and better understand how external environmental factors influence movement dynamics (Nathan et al., 2008). Popular research topics in movement ecology include habitat use, home range estimation, foraging behaviour, migration, activity budgets, and breeding ecology. These areas of study can also reveal how animals are responding to human-driven environmental change (Joo et al., 2020), for example, how movement patterns are increasingly restricted by habitat alteration. These disruptions can have cascading effects beyond individual species, such as limiting nutrient transport and altering ecological interactions (Tucker et al., 2018). In the context of rapid environmental change, recognizing these disruptions is vital for assessing ecosystem resilience, anticipating ecological responses, and mitigating future biodiversity loss. Recent advancements in tracking technologies and computational tools have greatly expanded our ability to collect and analyze high-resolution spatiotemporal data, transforming movement ecology as a field that addresses fundamental questions about how and why animals move (Börger, 2016; Nathan et al., 2008).

Effective wildlife conservation increasingly depends on understanding species' movement patterns, as site-based management alone often fails to capture threats that occur across broader spatial and temporal scales (Allen & Singh, 2016). Seabirds, as highly mobile species inhabiting dynamic coastal and marine ecosystems, offer valuable opportunities to investigate movement patterns in environments that are otherwise difficult to monitor. Importantly, many seabird populations have experienced sharp declines in recent decades, largely due to shifts in oceanic conditions and other changes in the marine environment (Dias et al., 2019; Philips et al., 2023). Studying seabirds offers unique insights into how marine and coastal systems are changing amid climate change and increasing anthropogenic pressures. Monitoring change requires establishing baseline knowledge of their movement and habitat use, which is crucial not only for seabird conservation, but also for understanding broader ecosystem dynamics in marine environments.

Coastal marine waters are highly dynamic environments, shaped by factors such as tidal cycles, currents, and water turbidity, which contribute to the patchy and rapidly changing distribution of prey (Fijn et al., 2022). Seabirds foraging in these habitats have evolved flexible strategies to respond to such variability, adjusting their movements and foraging effort in response to both biotic and abiotic cues across spatial and temporal scales (Fijn et al. 2022; Watanuki et al. 2008; Weimerskirch et al. 1993; Ventura et al. 2020). These strategies involve a range of mechanisms to detect and locate prey, including direct sensory cues (e.g., visual, auditory or olfactory sense) (Hansen et al., 2017; Nevitt, 2000), social information from conspecifics (Monier, 2024; Wakefield et al. 2013), and indirect cues such as oceanographic features or learned experience (Phillips et al., 2017). For instance, Cape gannets were more likely to switch to search-type behaviour near mesoscale fronts (Sabarros et al., 2014), while Manx shearwaters increased foraging activity in areas with elevated chlorophyll-a concentrations (Kane et al., 2020). The variety of cues seabirds use to forage means identifying the drivers of their distribution can be difficult without detailed behavioural data (Darby, 2023). This thesis investigates the environmental drivers influencing the distribution of a pelagic seabird in the coastal waters of British Columbia, Canada.

Bio-logging technologies have rapidly expanded researchers' ability to study animal movement, habitat use, population connectivity, physiological constraints and species-environment relationships (Balance et al., 2019; McGowan et al., 2016). Telemetry data captures the locations of animals at discrete time intervals, but it does not directly reveal the behavioural states driving their movements, presenting a central challenge for behavioural inference. Hidden Markov models (HMMs) are a type of state-space model that address this issue by linking observable movement metrics, such as step lengths and turning angles, to latent (unobserved) behavioural states, such as foraging, transiting, and resting (McClintock et al., 2020). HMMs have become an increasingly popular method for inferring animal movement behaviour from biotelemetry data, due in part to their adaptability to individual datasets and the availability of user-friendly software tailored to complex biotelemetry data (McClintock & Michelot, 2018; Michelot et al., 2016). Additionally, HMMs can be used to explore the ecological drivers of behavioural state transitions by modeling state-switching probabilities as functions of explanatory covariates, such as environmental conditions (McClintock et al., 2020; Patterson et al., 2017). This allows for an understanding of how environmental conditions influence behaviour by linking observed state transitions to external ecological factors.

Cormorants are seabirds that inhabit coastal, pelagic, and inland waters across the globe. Brandt's Cormorants (*Urile penicillatus*) are widely distributed along the Pacific coast of North America, from Alaska to Mexico, with breeding colonies concentrated within the California Current System (Ainley et al., 2018; Jones et al., 2008). In British Columbia, they are Red-listed due to their historically small and highly localized breeding colonies, which remain vulnerable to human disturbance and predation (BC Conservation Status Report). Brandt's Cormorants are considered short-distance migrants, moving north and south of their breeding grounds for winter. Large numbers of Brandt's Cormorants are known to winter in southern British Columbia, with average winter population estimates of 1,800 individuals in Canada, although this estimate is thought to be conservative (Bradford, Birds Canada, pers. comm). While non-breeding populations in the Salish Sea are currently considered stable, there is some uncertainty around this classification (State of Canada's Birds, 2024). In general, piscivorous seabirds that rely on forage fish and do not breed locally are more likely to experience population declines in the Salish Sea (Ethier et al., 2020; de Zwaan et al., 2024; Vilchis et al., 2014), emphasizing the need for improved monitoring during the understudied non-breeding season.

Brandt's Cormorants are pursuit diving foragers that feed on both benthic and pelagic prey (Watanuki et al. 2008). Deep-diving seabirds, such as cormorants, have reduced flight efficiency due to adaptations for underwater foraging, which include their large body mass, small flight muscles, and short wings (Spear & Ainley, 1997a; Watanabe et al., 2011). As a result, they are typically restricted to biologically rich areas where prey is abundant and minimal searching is needed (Ainley et al., 2005). Cormorants' strong dependence on localized prey resources makes them effective indicators of ecosystem productivity and change (Ainley et al., 2005; Orben et al., 2021). They have also been used to study the bioaccumulation of contaminants such as heavy metals (Saeki et al., 2000; Skoric et al., 2012) and to assess changes in forage fish communities through diet analyses (Elliott et al., 2015). Despite their ecological importance, key knowledge gaps remain, particularly regarding their movement patterns and foraging ecology during the non-breeding season, when they are dispersed across a wide and dynamic marine landscape. Collecting data on pelagic seabirds like Brandt's

Cormorants can help address broader challenges in marine monitoring, especially in dynamic coastal environments where fine-scale population data are often lacking (Schmidt et al., 2015).

Coastal British Columbia, Canada, is a region of high biodiversity, complex topography, and significant human settlement being the most densely populated area in the province. Central to the region is the Salish Sea, an inland trans-national sea shared by British Columbia, Washington State, and Coast Salish Indigenous governments. The region's unique oceanography is shaped by glacially derived geology, freshwater inflows from surrounding watersheds, and tidal mixing from the Pacific Ocean. These interacting factors drive high productivity and support a dynamic, interconnected food web that sustains remarkable biological diversity (Sobocinski, 2021). Over 170 bird species and nearly 40 marine mammal species depend on the Salish Sea (Gaydos & Pearson, 2011). This region also plays a critical role along the Pacific Flyway, providing globally significant staging, molting, and wintering habitat for migratory waterbirds (Bower, 2009). Additionally, the Salish Sea area is home to almost nine million people and supports a wide array of ocean-based industries such as commercial fishing and aquaculture, marine transportation and shipping, and tourism and recreation. As a result, the region is subject to intense and complex anthropogenic pressures (Sobocinski, 2021).

In response to these challenges, the early 2000's saw the emergence of more adaptive seabird conservation strategies in British Columbia, including enhanced measures for oil-spill preparedness (Mills et al., 2005), and the implementation of long-term waterbird monitoring programs along the BC coast (Ethier et al., 2020). More recently, national initiatives such as Canada's Ocean Protection Plan have expanded these efforts, emphasizing marine safety, sustainable shipping, ecosystem conservation, and collaboration with Indigenous and coastal communities. Within this evolving framework, seabird research has become increasingly valuable as a tool for assessing ecosystem health and understanding the cumulative impacts of human activity in marine environments like the Salish Sea.

In the following thesis, I have used individual movement data from GPS tracking devices combined with statistical modelling methods to address questions about Brandt's Cormorant winter movement and habitat use in the Salish Sea, British Columbia, Canada. My objectives include understanding critical habitat areas of Brandt's cormorants and how oceanographic variables influence foraging locations. By integrating high-resolution oceanographic data with Brandt's Cormorants movements and dive data, we can better understand this marine species which may guide and inform emergency response planning and habitat protections, a priority under the Canadian federal government's Ocean Protection Plan.

In Chapter 2, I examine the fine-scale movement and foraging behaviour of Brandt's Cormorants in the Salish Sea during the non-breeding season, using GPS tracking data combined with high-resolution oceanographic information[1]. In Chapter 3, I summarize my findings, discuss future directions, and highlight the management and conservation implications of my research.

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[1] Chapter 2 is structured as a stand-alone paper intended for publication, which may result in some repetition of methods and background material across chapters.

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Chapter 2. Ecological Drivers of Winter Movement and Foraging Behavior of Brandt's Cormorants (*Urile penicillatus*) in the Salish Sea

2.1. Introduction

Understanding seabird ecology and developing effective conservation strategies relies on accurate information about their abundance, distribution, and at-sea behaviour. A recently published report on the State of Canada's Birds (Birds Canada & Environment and Climate Change Canada [ECCC], 2024) highlights a gap in data for marine bird populations, especially during their non-breeding season. The report and others also identify that some previously stable marine bird populations have declined in recent decades, which could be in part due to novel threats these birds are facing (Ethier et al., 2020; Stapleton et al., 2025). Ecosystem change linked to ocean-based industries, in combination with climate change effects, are resulting in unprecedented threats to the wildlife that are dependent on these ecosystems (Talloni-Alvarez et al. 2019). This rise in threats has heightened the need for science-based conservation and management strategies to protect coastal marine ecosystems. Studying sentinel species, such as seabirds, can provide valuable insights into ecosystem changes driven by these impacts (Sobocinski, et al., 2021; Vilchis et al. 2015). However, identifying critical habitat areas used by vulnerable marine species remains difficult, particularly during the non-breeding season when many species are more dispersed and more challenging to monitor.

Identifying the environmental conditions shaping movement and foraging behaviour is an important step to gain insight on species' critical habitat. Seabirds often forage in areas where oceanographic features influence prey densities and distributions in predictable ways, such as shelf-edge tidal fronts, bathymetric gradients, and areas of complex topography that drive upwelling (Cox et al., 2013, Cox et al., 2018; O'Hara et al., 2006). As novel climate conditions emerge, species may exhibit new responses that no longer align with previously established environmental cues or relationships, as seen in some seabirds within the U.S. California Current System (Hyrenbach & Veit, 2003; Schmidt et al., 2015). In coastal British Columbia, where such shifts are poorly documented, baseline movement and foraging data linked to species-environment interactions are lacking, hindering our ability to identify critical habitat and how seabirds might adapt to future climate change.

Movement data provides increasingly detailed insight into the mechanisms shaping interactions between animals and their environment. Modern biologging tags have significantly improved the quality and resolution of data we can collect, enabling the collection of both horizontal and vertical dive data for marine predator species (Carter et al., 2016; Ropert-Coudert & Wilson, 2005). Concurrently, the availability of sophisticated statistical models designed to infer animal movement and behaviours from biologging data have also increased. Hidden Markov models (HMMs) are well-suited for such data because they can effectively analyze complex, fine-scale biologging data to accurately identify movement patterns (Conners et al., 2021). They also have the ability to incorporate multiple data streams (Leos-Barajas et al., 2017), assess how predictor variables influence state transition probabilities (McClintock et al., 2017; Patterson et al., 2017), and are becoming increasingly accessible due to open-source software and extensive user guidance (McClintock & Michelot, 2018; Michelot et al., 2016).

Traditional behavioural inference has relied on metrics derived from horizontal location data (e.g., step-length, turning angle), however, relying solely on location data can make it difficult to distinguish between movement behaviours, particularity for diving species whose foraging habitat is vertically structured (Bestley et al., 2015). For instance, periods of rest and intense foraging may both appear to be stationary as both have short horizontal step-lengths (McClintock et al., 2017). Incorporating additional data streams, such as dive metrics, into an integrated approach can refine behavioural classifications and improve the identification of key behaviours like foraging (Carter et al., 2016). While integrated modelling approaches combining multiple biologging data types have been widely used to identify critical marine mammal habitats (Chimienti et al., 2020; McClintock et al., 2017; Nykänen et al., 2025; Russel et al., 2015; van Beest et al., 2019), applying similar methods to highly mobile seabirds offers an opportunity to advance understanding of their behaviour and critical habitats.

Coastal ecosystems worldwide face degrading effects from anthropogenic activities. The coastline and surrounding marine waters of the Salish Sea is one such ecosystem that is experiencing increased anthropogenic activities (Agbayani et al., 2024). Among increased anthropogenic pressures including increased tanker traffic, oil spill risk, climate change, and habitat degradation across the Northeast Pacific, identifying critical foraging habitats is both ecologically informative and essential for mitigating potential impacts in one of the richest and most important ecosystems for migrant and wintering waterbirds in Canada (KBA Canada, 2022). In this study, we apply HMMs to explore how Brandt's Cormorants forage across dynamic oceanographic conditions during the non-breeding season. Based on known linkages between ocean conditions and Brandt's Cormorant breeding success in California (Schmidt et al., 2015) and broader patterns that link foraging seabirds to physical and biological drivers (Ainley et al., 2005; Cox et al., 2018; Fijn et al., 2022; Loredo et al., 2018; Waggitt et al., 2016; Wakefield et al., 2017), we hypothesized that dynamic oceanographic conditions such as variable currents, sea surface temperature, salinity, and bathymetry would influence foraging behaviour. By identifying the environmental cues that increase the likelihood of foraging behaviours in Brandt's Cormorants, our findings contribute to (1) predictive tools for habitat conservation planning in a region of high marine biodiversity that is susceptible to climate change and human disturbance, and (2) spatially-explicit guidance for oil spill response in the non-breeding season where Brandt's Cormorants concentrate their foraging behaviour.

2.2. Methods

2.2.1. Study Species

Brandt's Cormorants are a pelagic seabird found along the Pacific coast of North America, breeding from northwestern Mexico to British Columbia, Canada, with the largest colonies concentrated along the coast of California (Ainley et al., 2018; Jones et al., 2008). Brandt's Cormorants are pursuit-diving piscivores that consume a variety of fish and crustaceans, exhibiting prey-switching when resources shift (Santora et al., 2014). While breeding-season diets are well-documented (Ainley et al., 2018; Couch & Lance, 2004; Elliott et al., 2015), little is known about their non-breeding diet and habitat use in the Salish Sea. Post-breeding, many migrate north to overwinter in British Columbia and Washington (Wallace & Wallace, 1998). Winter foraging occurs in the central Strait of Georgia, influenced by nutrient-rich Fraser River outflow that supports forage fish prey consumed by diving birds and marine mammals (Sobocinski, 2021). Brandt's Cormorants' unique northward winter migration motivates investigation into the environmental and ecological factors influencing this movement. Increased air temperatures and decreased ocean productivity have shown to have impacts on the breeding success of Brandt's Cormorants, suggesting this species is highly vulnerable to warming trends and shifting ocean conditions (Elliott et al., 2015; Schmidt et al., 2015). Their strong reliance on marine habitats, combined with large winter aggregations in the Salish Sea, makes them particularly vulnerable to oil spills and other disturbance events. Brandt's Cormorants have been proposed as useful indicators for monitoring marine ecosystems given their close ecological ties to prey availability and may serve as a proxy for understanding how other marine predators respond to shifting prey dynamics (Ainley et al., 2018). This study investigates the environmental drivers of Brandt's Cormorants habitat use during the non-breeding season, a period during which their at-sea distribution in this region remains poorly documented.

2.2.2. Field methods and Data Collection

Our study focused on the coastal waters of southwestern British Columbia near Vancouver. The GPS tag data covers the south end of the Strait of Georgia, with Burrard Inlet to the north, Nanaimo to the northwest, to Bellingham Bay in the southeast, and as far southwest as San Juan Islands in Washington (Figure 2.1). The tag data overlaps the shallow, productive estuarine waters near the mouth of the Fraser River, particularly in and adjacent to the two main channels and the banks that lie between and south of these channels. The Salish Sea, encompassing the study area, is among the busiest maritime corridors on the west coast of North America (Taylor & Mayer, 2023) and features some of the highest ambient noise levels along the British Columbia coast (Erbe et al., 2014). With ongoing expansion of regional port infrastructure, marine traffic is expected to increase, potentially intensifying anthropogenic disturbance in this ecosystem.

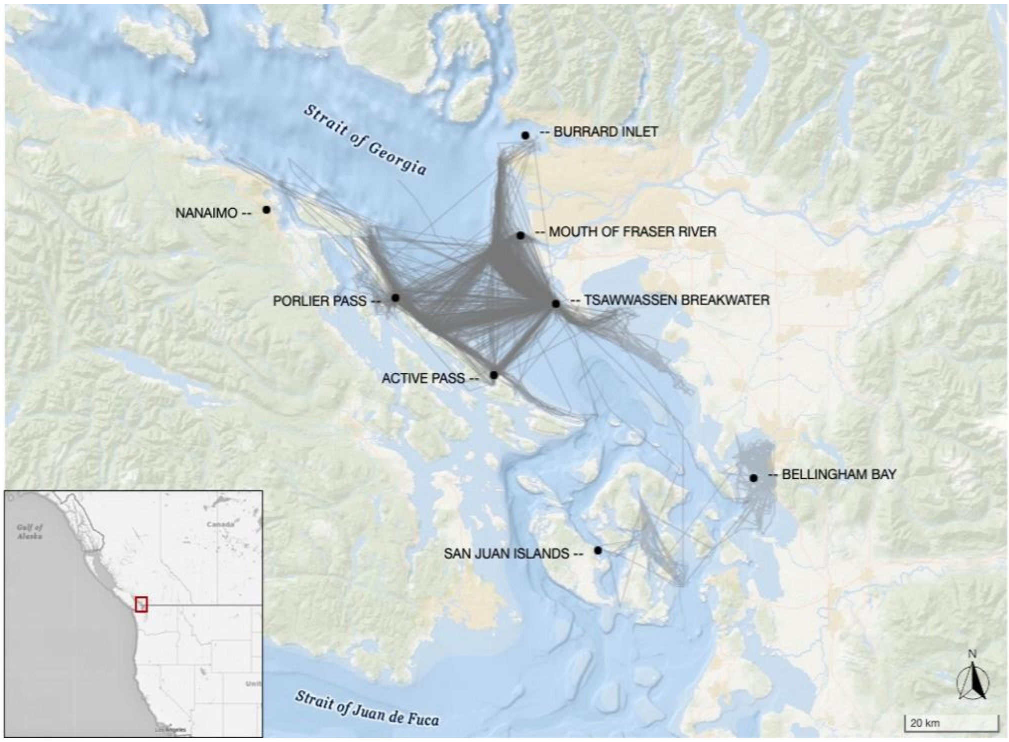

Figure 2.1. **Map of study area including southwestern British Columbia and adjacent bodies of water. Grey lines indicate GPS locations with connected tracks from 25 Brandt's Cormorants collected between November 1, 2023 – January 7, 2024.**

Between October 11 and 26, 2023, 30 adult Brandt's Cormorants were tagged with Ornitela OrniTrack solar powered GPS-GSM/4G transmitter tags. Tagging took place at the Tsawwassen Breakwater in Delta, BC, Canada, a known winter roost site for Brandt's Cormorants. Birds were captured at night by approaching the breakwater in a small zodiac and illuminating part of the roost with a spotlight, prompting birds to flush toward the boat. Individuals were intercepted in flight using a landing net (38" x 38" with a 4-foot handle) and subsequently transported to shore for tagging. Birds were banded with a stainless-steel band, weighed, and morphometric measurements (wing, tarsus, culmen) were taken to aid in sexing. Tags were then attached to each bird via a custom-fitted backpack harness made from Teflon ribbon and mounted on a 2mm thick neoprene pad. Two sizes of loggers were deployed, 24-gram OrniTrack 20D (dimensions 58×25×14 mm) on smaller birds, and 29-gram OrniTrack-30D (dimensions 61×25×20 mm) on larger birds. The weight of the tags including the padding and harness, which added ~12 grams, were less than 2% of the birds' total body mass (mass range of tagged birds: 1830 - 2700 grams). A total of 30 individuals were assessed through molecular sexing: 20 were identified as males, 7 were identified as females, and the sex of 3 individuals could not be determined. All procedures were conducted under British Columbia Wildlife Act Permit MRNA23-799201.

Tags were pre-programmed to account for managing battery life and data resolution and adjusted after deployments as needed. GPS location data were collected at 10-minute intervals under normal conditions. However, to conserve battery life, the fix interval automatically adjusted based on battery percentage. When the battery dropped below 75%, the fix rate decreased to 1-hour intervals. Fluctuating solar charging during the winter resulted in variable GPS fix intervals throughout the season. Additionally, the tags followed a ‘sleep’ schedule from dusk to dawn to further preserve battery life. During this period, GPS fixes were recorded every three hours. To avoid interpolating GPS fixes over these gaps, and because cormorants are known to remain sedentary at night (Quintana et al., 2007), we chose to remove the sleep data from the dataset prior to analysis. Pressure sensors on the tags recorded dive depth at 1-s intervals, which was triggered when the device was submerged below 0.7 m.

2.2.3. GPS and Dive Data Processing

For consistency, we excluded tracking data from October due to variable tag settings during the initial deployment. Movement tracks were visually inspected and when necessary were truncated based on tag movement and sensor patterns that indicated tag loss or mortality events. A small number of tags (n=3) temporarily stopped recording when batteries depleted, resulting in intermittent data gaps before recharging and resuming location fixes. To address this, movement tracks were split when the interval between fixes lasted longer than four hours. This also resulted in the start of a new track for each day, for each individual due to the removal of nighttime location estimates. Finally, tracks with less than 5 locations were removed. After processing, we obtained 655 movement tracks from 25 individuals, covering the period from November 1, 2023, to January 7, 2024. Average daily distances traveled (based on direct travel between GPS points), were calculated for each individual using post-processed data.

As hidden Markov models (HMMs) require observations at regular time intervals, we further processed the data to produce movement and diving metrics on a consistent, discrete time scale. We selected a 30-minute time interval to capture short-term behaviours while also matching the temporal resolution of environmental covariates. To obtain temporally regularized location estimates, we used the crawlWrap function (*momentuHMM* R package) to apply a Kalman filter that interpolates between discrete GPS fixes using a continuous-time movement model (McClintock & Michelot, 2018). For each predicted time step, we used the mean location estimate in the subsequent HMM analyses (single imputation). Given the high temporal resolution of our GPS data and the minimal expected measurement error, this approach is unlikely to differ meaningfully from multiple imputation (McClintock, 2017), while being computationally efficient. Following interpolation, we used the prepData function to compute step lengths (straight-line distance between consecutive interpolated locations), and turning angles (changes in direction between consecutive movement segments).

For diving behaviour, we followed the protocol from similar studies and defined a dive as any submergence to a depth of 1 m and lasting at least 6 seconds (Kokuben et al. 2016; Peck-Richardson, 2017; Shoji et al., 2014). This allows a separation between dive and surface behaviours. Using the *diveMove* R package (Luque, 2007), we extracted individual dive events from the complete depth record for each bird using the getStats function. Dive counts were tallied between consecutive locations and assigned to the second location to align with movement-derived variables for hidden Markov model analysis. We calculated the number of dives for each 30-minute interval, and these dive count values were merged into the dataset. Collectively, there were 14,641 measures of step length, turning angle, and dive count, one for each 30-minute interval serving as potential indicators of Brandt's Cormorant behaviour that can be linked to coastal environment features in their overwintering habitat in the Salish Sea.

2.2.4. Environmental Variables

To test the influence of environmental variables on the probability of the individual (Brandt's Cormorant) switching into a certain movement state (behaviour), we integrated high-resolution static and dynamic oceanographic data with each cormorant movement location. Dynamic variables were extracted from an oceanographic model, the regional SalishSeaCast model (Soontiens et al. 2016). SalishSeaCast is a three-dimensional physical-biological-chemical ocean model that covers the Canadian and US waters of the Salish Sea. Based on the Nucleus for European Modelling of the Ocean (NEMO) framework, the SalishSeaCast NEMO 3.6 offers 500 m spatial and hourly temporal resolution capturing key mesoscale dynamics of the Salish Sea at a finer spatio-temporal resolution than most existing models and satellite-based imagery. Using modified code from the *rerddapXtracto* R package (v1.2.2; Mendelssohn, 2025), we extracted hourly, spatially-indexed modeled values for salinity ($g \cdot kg^{-1}$), current speed ($m \cdot s^{-1}$), and diatom concentration (as a proxy for ocean productivity; $mmol \cdot m^{-3}$) from the SalishSeaCast ERDDAP data server (Olson et al, 2020; Soontiens et al, 2016; Soontiens and Allen, 2017).

Additional environmental variables included bathymetry, downloaded at a 100 m by 100 m horizontal resolution from the British Columbia Marine Conservation Analysis, and a daily Multi-scale Ultra-high Resolution sea surface temperature at 1 km^2 spatial resolution (https://podaac.jpl.nasa.gov/MEaSUREs-MUR). Tide data were extracted from Fisheries and Oceans Canada at tide station Sand Heads (Station 7594, in the Fraser River Estuary). To account for the diurnal cycle in cormorant behaviour, we applied a cosinor model to transform hourly timestamps into sine and cosine components. Environmental variables were matched to each 30-minute cormorant location estimate using nearest-neighbour assignment in both space and time, selecting the closest model grid cell and hourly prediction without interpolation.

2.2.5. Analysis of behaviours using hidden Markov models (HMMs)

HMMs are discrete state-space time-series models comprising two stochastic processes: an observation process, and a latent (hidden) state process. In our HMM framework, the observation process modeled the probability distributions of our 30-minute interval movement data of step lengths, turning angles, and number of dives that are conditional on a hidden behavioural state. The probability distributions are state-dependent, meaning each hidden behavioural state is associated with distinct movement patterns in the observed tag data. The larger the differences in movement patterns, the more likely the hidden states will accurately capture the behaviours. All HMMs assumed a (strictly positive, right skewed) gamma distribution for step length, a (circular) von Mises distribution for turning angle, and an integer valued (overdispersed) negative binomial distribution for dive counts. These choices reflect commonly used distributions for animal movement in HMMs (Michelot et al. 2016).

We followed the HMM analysis workflow described in McClintock and Michelot (2018), including data preparation, visualization, model fitting, and model checking. To determine the appropriate number of behavioural states, we followed the stepwise approach outlined in Pohle et al. (2017), fitting hidden Markov models (HMMs) with an increasing number of states (2-state, 3-state, and 4-state models) using movement-derived variables (step lengths, turning angles, and dive counts). Selecting the correct number of behavioural states can be challenging; while additional states may improve model fit based on information criteria, they can reduce biological interpretability. This trade-off became evident when comparing the 3-state and 4-state models, as the 4-state model produced behavioural states that were difficult to distinguish biologically, whereas the 3-state model provided clear, interpretable states. We visually assessed the state-dependent distributions and Viterbi-decoded sequences to evaluate consistency in behavioural inferences across models and used pseudo-residual analyses to assess model fit (Michelot et al., 2016; Pattison et al., 2022). Ultimately, we selected the 3-state model as the most parsimonious structure, balancing model performance with biological interpretability. This decision was made prior to incorporating environmental covariates.

To select starting values for distributions and ensure numerical convergence, we followed the procedures outlined in Michelot & Langrock (2025), which involved generating random starting parameter values from a distribution of plausible values and fitting 25 models with these different starting points. To verify convergence, we confirmed models had similar maximum likelihood values across runs; we then retained the starting values from the best-fitting model, which was the model with the largest likelihood (i.e., smallest negative log-likelihood) (Michelot & Langrock, 2025).

Although individual-random effect models capture heterogeneity between individuals, accounting for individual variation in the hidden state process introduces additional complexity and computational cost to model implementation (McClintock, 2021). As our focus was to explore population level relationships between movement and environmental covariates (and not to quantify individual variability in behavioural responses), we used a complete pooling method. This makes the strong assumption that environmental variables affect all individuals similarly, which follows evidence that oceanographic features synchronize foraging behaviour across individuals in regional seabird populations (Cox et al. 2016; Wynn et al. 2007), and prioritizes model parsimony by assuming all individuals share common state-dependent distributions, state-switching dynamics, and parameters (Glennie et al., 2022).

To identify environment-driven spatio-temporal state transitions, we evaluated between models with different covariate sets using the Bayesian Information Criterion (BIC; Schwartz, 1978). Although relying on model selection criteria like BIC for state determination in hidden Markov models can be problematic (Pohle et al., 2017), BIC remains useful for comparing models with the same number of states but differing in structure or covariates. Using a BIC-based forward-selection process (Beumer et al., 2020) where covariates were retained only if they provided a substantial improvement in model fit and a biologically interpretable effect on state transition probabilities. We excluded covariates that showed minimal or no influence on BIC values. This approach integrates both model selection criteria and biological interpretability. For example, while primary productivity indicators such as diatoms provided a slight BIC improvement, inspection of the state transition probabilities revealed no consistent or ecologically coherent effects on transitions. In contrast, covariates such as bathymetry and current speed had both strong statistical support and clear biological mechanisms linking them to behaviour. Model fit was further evaluated using visualization and diagnostic steps, including comparison of predicted and raw state distributions, plotting estimated probability distributions, examining state transition probabilities as a function of covariates, and checking pseudo-residuals. Finally, we considered potential correlations among spatio-temporal covariates to avoid multicollinearity. Correlation checks confirmed no strong pairwise correlations that would prevent their simultaneous inclusion. The final model was chosen based on lowest BIC, biological interpretability of state transitions, and uncorrelated environmental covariates (McClintock & Michelot, 2018).

We then applied the Viterbi algorithm to reconstruct the most probably sequence of latent behavioural states (e.g., resting, foraging, transiting) given the covariate-dependent transition probabilities and observed movement data, enabling us to link discrete behavioural states of Brandt's Cormorants to dynamic spatio-temporal habitat in the study region. All data processing and analyses were performed using R Statistical Software (v4.5.0; R Core Team, 2025).

2.3. Results

2.3.1. Behavioural Classification

Based on the previously described model selection procedure, the 3-state HMM was used to characterize Brandt's Cormorant behaviour from movement-derived variables. The parameter estimates for State 1 included the shortest step lengths (mean=27.7 m; sd=24.6 m), and the lowest expected dive count with low dispersion (mean count = 0.13, dispersion = 0.0058), suggesting minimal activity in both horizontal and vertical dimensions, which we interpreted as 'resting' behaviour (Figure 2.2). State 2 was characterised by longer step lengths (mean=461 m; sd=599 m), less concentrated turns (angle conc. = 0.29) and a mean angle of -178° indicating frequent directional changes, and the highest numbers of dives per 30-minute interval (mean count = 9.7, dispersion = 0.39). This suggested intensive dive behaviour, and this state was interpreted as 'foraging' (Figure 2.2). State 3 included the longest mean step length (mean=5541 m; sd=5989 m), and the most concentrated turns (conc. = 0.65), with a mean angle near zero (≈ 2°), indicative of persistent directional travel., and with fewer dives than State 2 (mean count = 7.1, dispersion = 0.24); State 3 was interpreted as 'transiting' (Figure 2.2). Some diving was present in the transiting state as indicated by non-zero mean dive counts, which may be a result of short-term behavioural transitions not captured in the 30-minute interval data. Overall, HMM-predicted behaviours during the day were classified as 36% resting, 41% foraging, and 23% transiting (Figure 2.3).

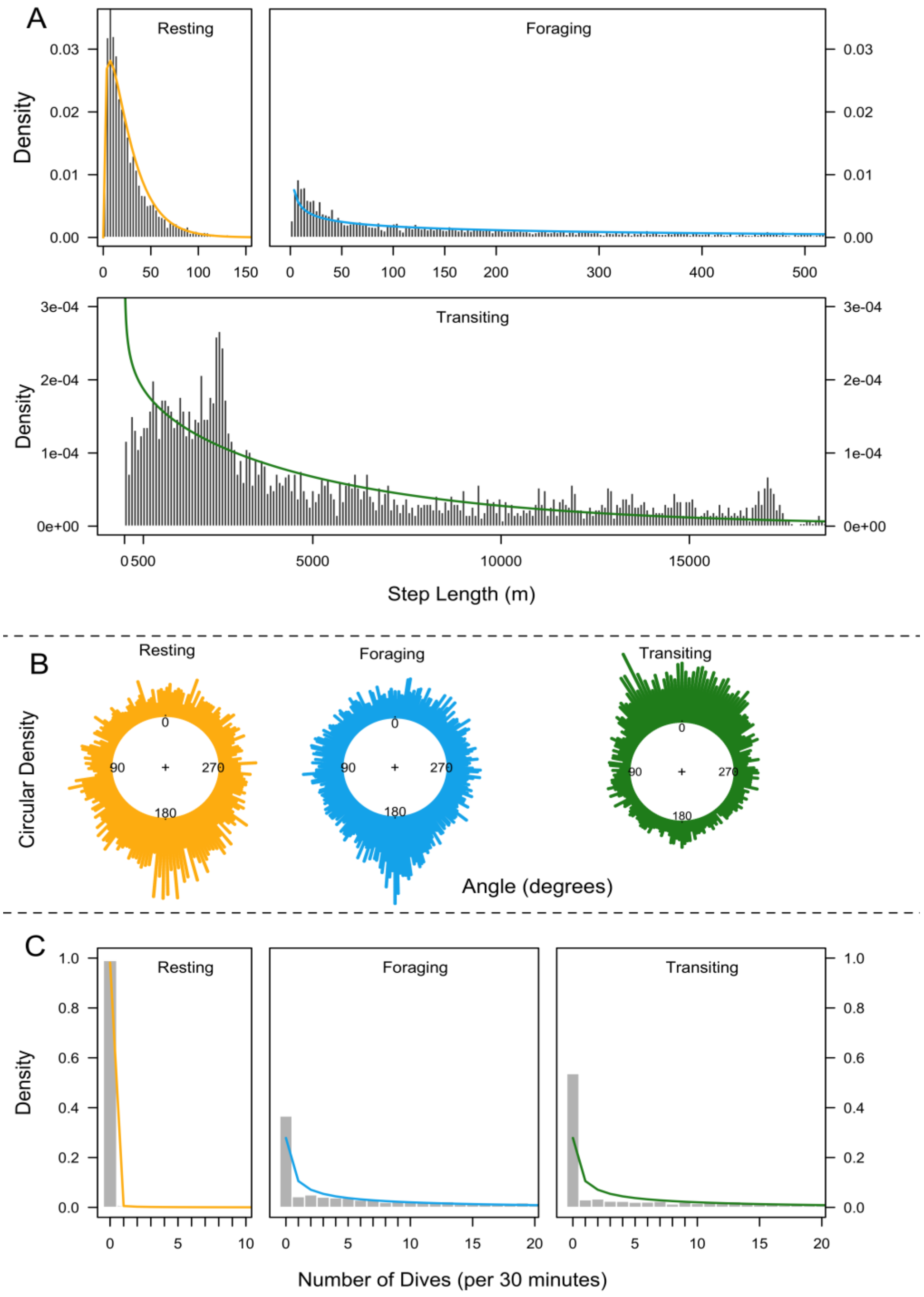

Figure 2.2. **Figure 2: Hidden Markov model state-dependent distributions. Histograms show the raw data for (A) step length (Gamma-distributed), (B) turning angle (von Mises-distributed), and (C) dive count (negative binomial-distributed) from 25 Brandt's Cormorants. The coloured lines represent the probability density functions from the parameter estimates of a three-state HMM (resting, foraging, transiting), selected by BIC, demonstrating how movement patterns differ between behavioural states.**

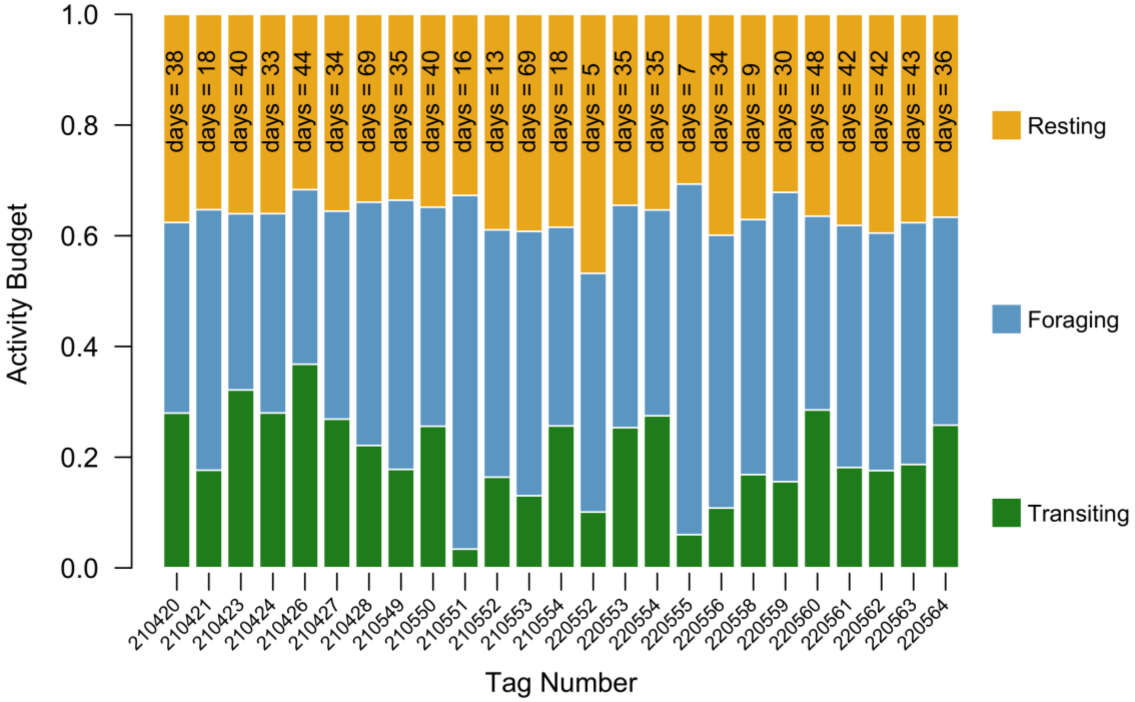

Figure 2.3. **Behavioural activity budget for each of the 25 tagged Brandt's Cormorants contributing to the hidden Markov model. Activity budgets are calculated from post- processed data that exclude nighttime periods; therefore, the budgets represent daytime behavior only. The number of days of tag data is noted for each tagged cormorant.**

2.3.2. GPS and Dive Data

Horizontal movement data from the GPS showed that cormorants traveled widely, including across the coastal waters off mainland southern BC and into Washington State, with most of the activity concentrated in the southern Strait of Georgia. The average daily track distance across all individuals was 34.2 km (95% C.I.; 460 m to 89.7 km). One individual covered at least 167 km in one day, commuting from the mainland across the Strait of Georgia and back, which was a movement pattern common among the tagged birds. Movement paths varied but often included northerly trips from Tsawwassen to the mouth of the Fraser River and cross-strait trips to Porlier and Active Pass, approximately 30 km away. Brandt's Cormorants made on average 125 dives per day (95% C.I.; 0 to 297 dives/day), with a maximum of 82 dives within a single 30-minute interval. Viterbi-state classifications corresponded well with expected behaviors, with birds typically making direct movements from roosts to foraging areas.

All tagged cormorants dispersed from the tagging site at Tsawwassen breakwater, though many frequently returned to this known winter roost. Resting activity was also concentrated at several roost sites across the broader winter range, with foraging density appearing highest near these roosts.

2.3.3. Environmental covariate effects

After forward covariate selection, the most parsimonious model (lowest BIC) included three covariates. This selected model included time of day (as a circular variable), bathymetry (ocean depth), and current speed. This final model outperformed all alternatives, with ΔBIC ≤ 7 BIC units lower than all other candidate models (Table 2.1).

Table 1 **Three-state model selection results from Brandt's cormorant tag data ordered by BIC. The following abbreviations are used: sst = sea surface temperature; BIC = Bayesian Information Criteria; ΔBIC is the difference in BIC between the best model and each of the individual models.**

Model	maximum log-likelihood	Number of estimated parameters	BIC	ΔBIC
time + bathymetry + currents	-154850.9	51	310181.4	-
time + bathymetry + salinity	-155099.6	51	310189	7.6
time + bathymetry	-154902.2	45	310226.3	44.9
time + bathymetry + currents + salinity	-155068	57	310673.2	491.8
time + bathymetry + sst	-154854.7	51	310678.8	497.4
time + salinity	-155162.1	45	310746.3	564.9
time + sst	-155178.7	45	310779.4	598
time + currents	-155182.3	45	310786.6	605.2
time	-155226.1	39	310816.7	635.3
bathymetry	-156228.8	33	312764.6	2583.2
diatoms	-156460.9	33	313228.8	3047.4
salinity	-156470.9	33	313248.7	3067.3
currents	-156477.6	33	313262	3080.6
tidal height	-156492.2	33	313291.3	3109.9
no covariates	-156560.8	27	313371.1	3189.7
sst	-156537.8	33	313382.6	3201.2

Time of day provided the strongest individual improvement in model fit over all other singular covariates (ΔBIC ≤ 1947.9), confirming strong diel patterns in Brandt's Cormorant behaviour. We found additional improvements to BIC values when adding bathymetry as a second covariate (ΔBIC ≤ 590.4 compared to the time-of-day model), outperforming the other two covariate models. However, the best (lowest BIC) fit HMM was the model with three covariates (ΔBIC ≤ 44.9) over the best two covariate model. Expanding the model to a four-covariate formulation uniformly increased the BIC indicating no further improvements to the model.

To isolate the influence of each covariate on state transitions and to understand how these transitions evolve over the course of a day, we held two covariates constant while varying the third. For example, the probability of resting decreases sharply as the morning dawns, and increases sharply at the end of the day for both slack (0.25 m/s) and moderate current (1.2 m/s) conditions (Figure 2.4), at a fixed bathymetry of -7.84 m. There is a strong diel foraging pattern for cormorants with peak activity occurring during the middle of the day across all current conditions. However, this foraging peak was more restricted around noon if currents were weak (0.25 m/s) compared to high (1.2 m/s). In early mornings with weak current conditions (06:00 to 09:00; Figure 4, left panel), cormorants are more likely to be transiting, compared to mornings with moderate currents (1.2 m/s; Figure 2.4, right panel). The model predicted mornings with weak currents (0.25 m/s) may result in a slight increase in likelihood of resting behaviour (i.e., an increase in the stationary state probability of resting at 09:45 in the left panel of Figure 2.4).

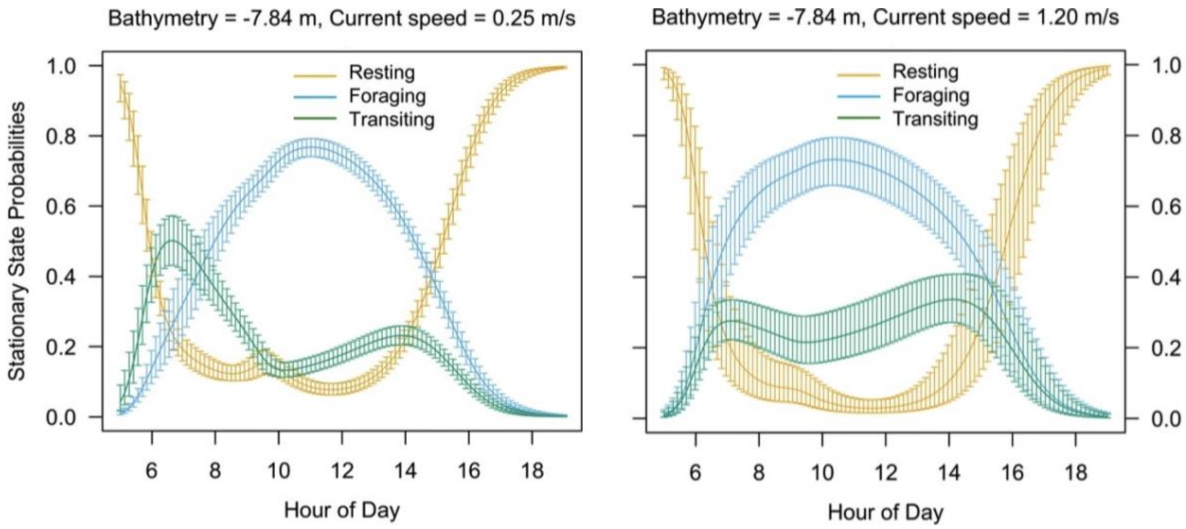

Figure 2.4. **Hidden Markov model stationary state probabilities (with 95% confidence intervals) for Brandt's Cormorant behaviours against time of day. Bathymetry is fixed to the median depth (7.84 m), with low current speeds (0.25 m/s) in the left panel, and higher current speeds (1.20 m/s) in the right panel. These covariates were fixed to isolate the influence of each variable on behavioural state transitions.**

Stationary state probabilities and transition probabilities describe complementary but distinct aspects of the hidden Markov model. Stationary state probabilities reflect the long-term expected proportion of time spent in each state assuming constant transition dynamics (Figure 2.4). The transition probabilities, representing the instantaneous likelihood of moving between behavioural states, were strongly influenced by environmental drivers (Figure 2.5). The probability of transitioning from transiting to foraging (State 3 → State 2) was strongly affected by current speed, indicating birds were more likely to switch into a foraging state in areas with faster currents (Figure 2.5; panel A). Shallower water depths increased the likelihood of the birds transitioning from a transiting state into the foraging state, particularly between 5 to 20 metres depth (Figure 2.5; panel B). Outside of this bathymetric band, the likelihood of foraging steeply drops. Cormorants exhibited a strong diel pattern, increasing the likelihood to switch from transiting to foraging (State 3 → State 2) from dawn to ~11:45, before decreasing to near zero by dusk (Figure 2.5; panel C). Geographically, these conditions aligned with restricted channels of shallow bathymetry where current flows were higher, such as Porlier Pass, Active Pass, and the estuarine mouth of the Fraser River where tidal forces and complex topography created predictable foraging opportunities (Figure 2.6).

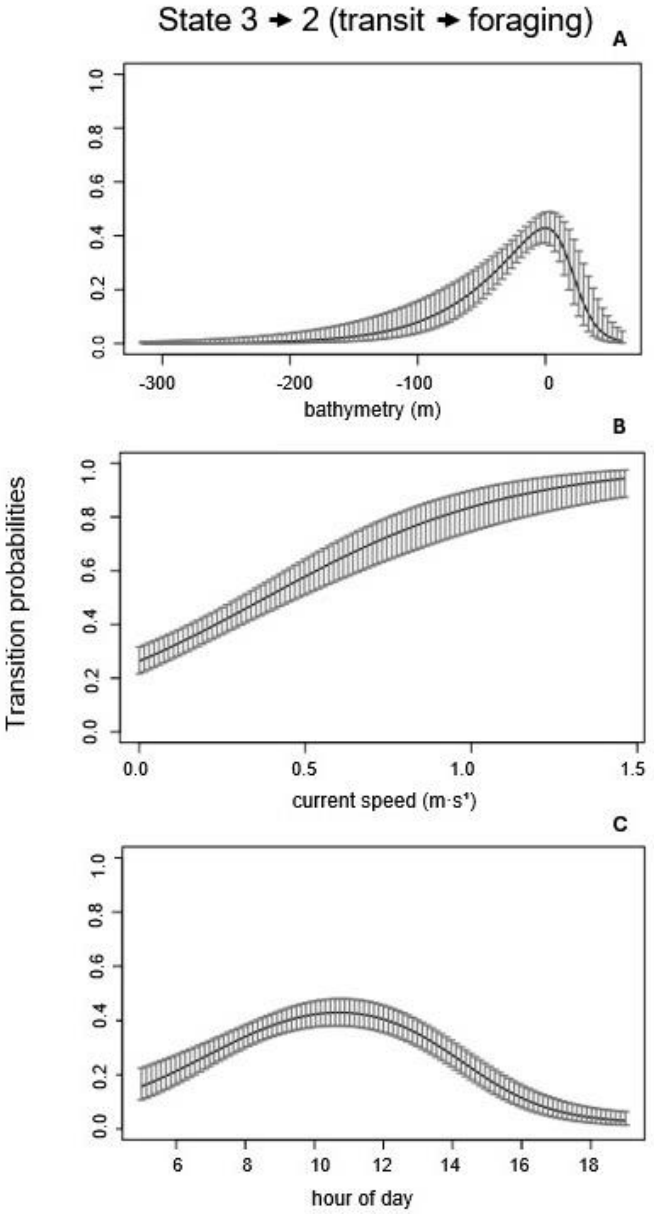

Figure 2.5. **Environmental drivers promoting a transition from Transit to Foraging. The probability of Brandt's Cormorants switching from State 3 (Transit) to State 2 (Foraging) increased in shallower water (A), faster currents (B), and during daylight hours (C). Predictions show the marginal effect of each covariate, with other variables held constant at median values (current speed: 0.25 m/s; bathymetry: 7.84 m; and time of day: 11:45). Shading represents the 95% confidence intervals around the predictions.**

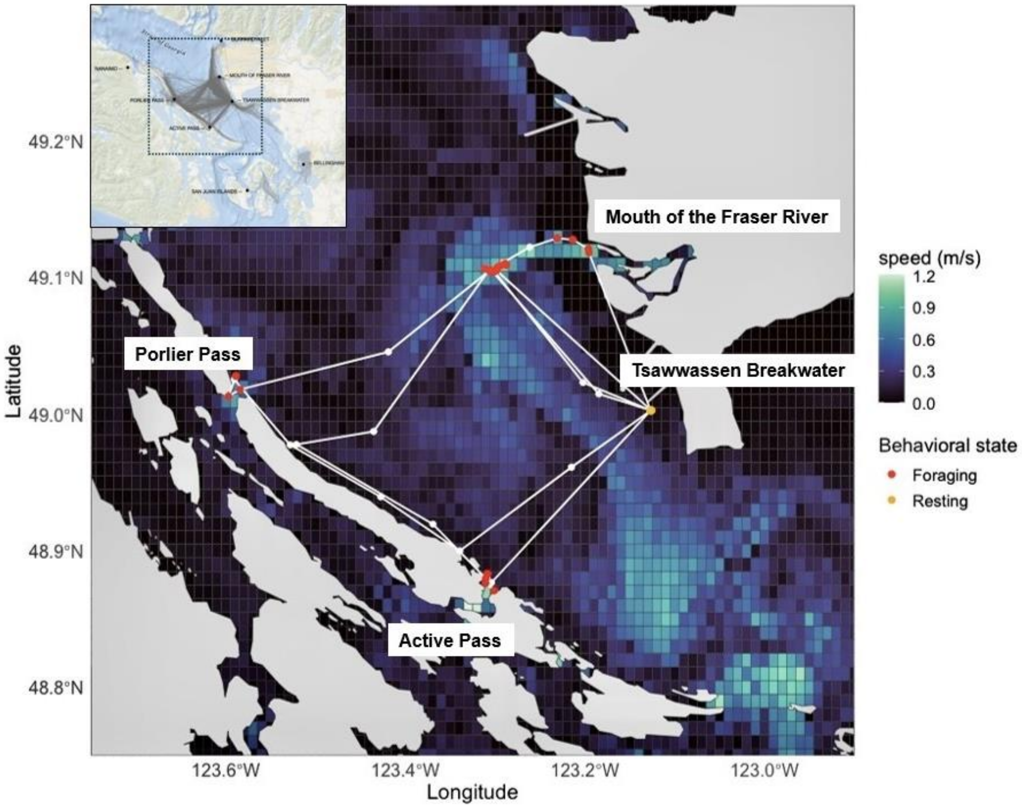

Figure 2.6. Examples of three typical daily movement tracks from Brandt's cormorants. Cormorant movement states were inferred from the HMM. These daily movement tracks illustrate the three behavioural states 1) Resting (yellow points; prolonged stays at discrete locations), 2) Foraging (red points; localised diving behaviour), and 3) Transiting (white points; directed movement between areas). The background shows mean current speed (m/s) during the midpoint of the tracks. These values are shown only for visualization, hourly values were extracted for all analysis.

2.4. Discussion

Our study advances the understanding of marine predator foraging ecology using a hidden Markov model (HMM) framework that links Brandt's Cormorant behavioural states to fine-scale oceanographic cues and identifies critical foraging habitat. Using high-resolution behavioural and environmental data from dynamic coastal waters, our study reveals new insights in to how transitions into and out of foraging behaviours were influenced by time of day, bathymetry, and current speed, with time of day emerging as the strongest predictor of cormorant behaviour. The concentration of diving activity during daylight hours is consistent with findings in other coastal cormorant species (Quintana et al., 2007; White et al., 2008; Zavalaga & Paredes, 2010), suggesting foraging is shaped by visually guided hunting and diel prey movements, as seen in thick-billed murres where light and prey migration interact to influence behaviour (Elliott & Gaston, 2015). Although prey distribution was not assessed in the present study, the observed changes in behavioural patterns may reflect underlying shifts in prey availability and visibility associated with ocean conditions and the diel cycle. A limited understanding of key prey species in this region constrains our ability to interpret the extent to which prey dynamics influence observed behavioural patterns, highlighting a gap that future research could address.

By applying multivariate hidden Markov models to tag-derived movement metrics, we were able to statistically infer latent behavioural states (resting, foraging, transit) directly from movement and dive data. Unlike purely descriptive classifiers, HMM’s provide a full probabilistic framework that models the underlying process generating the observed data, allowing for formal parameter estimation and inference. HMM’s are particularly well-suited to animal movement studies because they formally account for the probabilistic switching between behaviours and the temporal autocorrelation inherent in biologging data, while also separating the observation process from the underlying behavioural processes of interest (Dray et al., 2010; McClintock et al., 2020). In contrast, simpler methods cannot simultaneously capture these dynamics or provide a mechanistic quantification of behavioural state transitions in response to environmental covariates.

The HMM approach makes the assumption that behaviour can be represented as a finite number of discrete states and that the observed data distributions (e.g., step length, turning angles, dive counts) adequately capture behavioural differences. These assumptions are reasonable for our study system but also represent limitations of this approach. For example, further refining the foraging state into sub-states such as searching versus pursuit or incorporating energetic dynamics could provide deeper ecological insight (Pirotta et al., 2018), however adding additional states into the model requires the integration of more observed data resulting in increased model complexity.

This study aggregated the data to a coarser temporal interval than the original sampling frequency. State-space models, including HMMs, can reliably infer behavioural states at these coarser scales, but they cannot distinguish behaviours occurring more frequently than the recorded interval (Beyer et al., 2013; McClintock et al., 2012;

Pattison et al., 2022). While it is possible shorter behavioural switches occurring within the 30-minute interval were not classified, the temporal interval resolution used in this study was suitable for examining behavioural switches in Brandt's Cormorants and provided a practical solution to better match the temporal resolution of the (dynamic) environmental covariates. Additionally, these longer intervals allowed for an understanding of behavioural transitions throughout the entire daily track length, providing insights on activity budgets at a daily scale.

Despite these limitations, HMMs offer a rigorous statistical framework to link behaviour and environmental covariates. This approach allowed for not only the identification of where Brandt's Cormorants were foraging, but also provided insight into why they shifted into or out of a foraging state in response to oceanographic features. In doing so, this analysis provides a direct connection between movement and foraging behaviour in a biologically rich and heavily trafficked marine system, identifying key foraging areas and behavioural responses to environmental variation during a season and region previously understudied for this species.

2.4.1. Response to environmental variables

Brandt's Cormorants exhibited high foraging site fidelity to specific sites within the broader study area, targeting areas with shallow bathymetry and high current speeds that increased the probability of transitioning to and maintaining a foraging behaviour state. This strategy is common in cormorants (Cansse et al 2024; Coleman et al. 2005; Kotzerka et al. 2011) and other pursuit-diving seabirds (Cox et al. 2018; Philips et al. 2017) as interactions between bathymetry and ocean currents predictably influence the density, distribution, behaviours, and accessibility of prey (Embling et al., 2012) resulting in greater foraging efficiency for predators (Cox et al. 2018). The tidal-coupling hypothesis (Zamon 2003) suggests that physical characteristics between topographically complex seafloor contours and currents produce consistent flow features that predictably alter zooplankton distribution, abundance, and transport, in turn creating aggregations of fish that attract piscivorous predators (Zamon, 2003). Brandt's Cormorants in the Salish Sea may be utilizing predictable tidal currents as oceanographic cues of predictable prey hotspots and profitable foraging locations, followed by preferential diving to the seafloor bottom where catch per unit effort is high, a foraging strategy seen in other marine top predators such as King penguins and Elephant seals (Bost et al., 2009). Visual inspection of the raw dive data profiles reveals a strong alignment between foraging depth and seafloor contours (Figure 2.7), further supporting the conclusion from our model that bathymetry is a key driver of dive behaviour. Diet studies in the California Current System confirm that Brandt's cormorants primarily target prey species just above the seafloor (Ainley et al., 1981; Ainley et al., 2018), suggesting their dive behaviour to the seafloor is linked to benthic prey distribution.

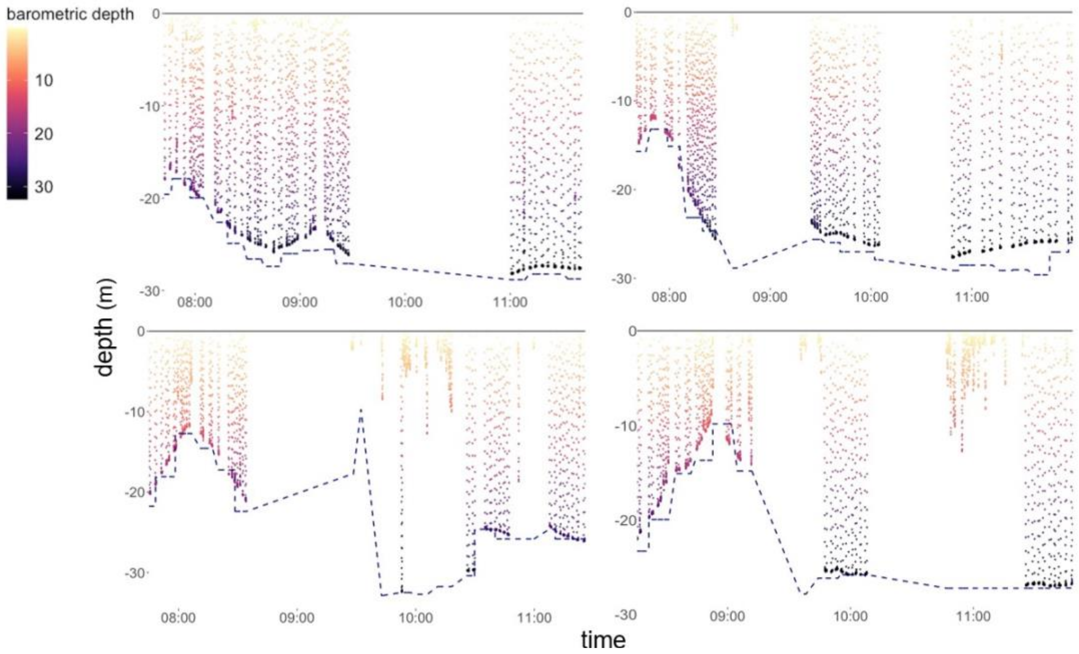

Figure 2.7. Brandt's Cormorants dive profiles from four (>3-hour) foraging bouts showing individual depth measurements against seafloor topography (depth). Coloured points represent individual depth readings, with color intensity indicating barometric depth. The dashed blue line shows the seafloor derived by spatially matching each cormorant location and timestamp to British Columbia Marine Conservation Analysis bathymetric data.

While we did not find diatoms, sea surface temperature, salinity, and tides to be reliable predictors of cormorant foraging areas, this may be due to temporal lags or spatial mismatches between these environmental variables and prey availability. There can be delays between these variables and the underlying factors, like prey accessibility, that influence seabird behaviour in a given area (Boyd et al., 2015; Wakefield et al., 2009). In addition to temporal lags, spatial mismatches can occur due to the complex movement patterns of both prey and predators (O'Hanlon et al., 2024). In Guanay Cormorants, prey availability at shallow, accessible depths has a greater influence on foraging behaviour than overall prey abundance (Boyd et al., 2015), suggesting that cormorants may rely on visual cues, such as elevated surface currents, rather than directly responding to subsurface hydrodynamic features. However, such environmental cues are becoming less reliable, and studies have shown how changing ocean conditions resulting from global climate change have altered previously established environment-species relationships. In other parts of their range, Brandt's Cormorants are no longer responding to local sea surface temperature in the way they had for the last three decades (Schmidt et al. 2015), indicating that sea surface temperature may no longer serve as a reliable proxy for prey availability due to shifting ecosystem dynamics.

Interpreting behavioural states from HMMs requires careful consideration of data resolution and the ecological relevance of the covariates used, both of which influence the accuracy and interpretability of model outputs (Glennie et al., 2022). Foraging clusters were prominent near high current waters and shallow bathymetry of the Fraser River mouth, with dive data supporting expected foraging patterns. The behavioural patterns inferred in this study were influenced by the 30-minute temporal resolution used to match the scale of available oceanographic covariates. This relatively coarse resolution likely increased the probability that multiple behavioural states occurred within a single time step, particularly in the transit state, which exhibited more diving activity than anticipated. A finer time resolution might have captured more variability, possibly reflecting an exploratory phase in which birds assess optimal dive locations before fully transitioning into a foraging state. Additionally, while our analysis relied on proxies such as bathymetry and surface currents to infer foraging habitat, incorporating direct prey field data, stable isotope analysis, or multi-year movement data would allow for more mechanistic insights into predator-prey dynamics. These approaches would strengthen interpretations of how winter foraging behaviour relates to the spatiotemporal variability in prey distribution, especially for mid-trophic species like Brandt's Cormorant that target forage fish. Such insights could inform future studies aimed at linking predator movement to dynamic prey fields under climate-driven ocean changes.

2.5. Conclusion

To our knowledge, this is the first study to document the non-breeding behaviour and movement of Brandt's Cormorants outside of the California Current System. This study identified critical habitat areas for both foraging and resting, revealing new insights into diurnal spatial patterns not previously understood. Furthermore, our study advances the methodological application of hidden Markov models to seabird ecology by integrating multiple data streams with oceanographic data. This work makes use of recent advancements in bio-logging technologies to do fine-scale tracking of Brandt's Cormorants movement and behaviour across fine temporal and spatial scales. The growing investment in these technologies comes with a responsibility to translate the resulting data in a way that is insightful and meaningful for wildlife conservation strategies and management (McGowen et al., 2017). By integrating high-resolution oceanographic data with movement and dive data from Brandt's Cormorants, we have gained a deeper understanding of this species' response to its habitat dynamics, revealing key drivers of behavioural decisions. These findings establish a baseline for monitoring future environmental change, while also directly supporting timely emergency response planning and urgent habitat protection efforts.

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Chapter 3. General conclusion

3.1. Summary of findings

In this thesis, I used GPS tracking technology combined with high-resolution oceanographic data and hidden Markov models to study the at-sea movement and foraging behaviour of Brandt's cormorants in the Salish Sea during the winter season. As an upper trophic level predator and recognized indicator species, the large numbers of Brandt's Cormorants that overwinter in British Columbia highlight the importance of identifying critical habitat areas and patterns of habitat use for effective regional conservation and emergency response planning.

In Chapter 2, I examined fine-scale movement and foraging patterns during the winter of 2023/2024 to assess how oceanographic conditions influence behavioural transitions. Using hidden Markov models applied to GPS tracking data, I identified three behavioural states based on step length, turning angle, and dive count. These behaviours followed a clear diel cycle: birds increased transit and foraging activity with sunrise and began resting prior to sunset. Incorporating depth sensor data from the GPS tags improved the model's ability to accurately classify foraging behaviour.

On average, individuals travelled 34.2 km per day (95% C.I.: 460 m to 89.7 km) and performed 125 dives per day (95% C.I.: 0 to 297 dives/day), with a maximum of 82 dives recorded within a single 30-minute interval. Across the study period, 25 individuals completed a total of 81,973 dives. Importantly, foraging activity occurred consistently in areas characterized by strong water mixing and high current speeds, particularly near the Fraser River mouth, Porlier Pass, and Active Pass. These dynamic environments, often shaped by shallow and uneven bathymetry, likely concentrate prey and enhance feeding opportunities, a pattern also observed in Pelagic Cormorants (Holm & Burger, 2002). Resting behaviour was concentrated at several roost sites across the broader winter range, with foraging density appearing highest near these roosts. The spatial proximity of foraging activity to primary roost sites suggests that cormorants may prioritize foraging efficiency by exploiting areas near known resting locations. This spatial overlap between resting and foraging areas aligns with findings from Brandt's cormorant in the California Current System (Hebshi, 1998; Peck-Richardson, 2017). These roost sites primarily consisted of artificial infrastructure like rocky jetties such as the Tsawwassen breakwater and the Sand Heads breakwater, as well as natural rocky outcrops such as Canoe Islets Ecological Reserve near Porlier Pass. These areas were used for both daytime and nighttime roosting, with exploratory analyses confirming their role as primary nighttime roosts, despite the exclusion of nighttime data from the final models. These high-use foraging areas highlight the importance of both oceanographic features and roost accessibility in shaping foraging behaviour. However, additional factors may also influence their foraging decisions. For example, recent declines of natural breeding colonies of Double-crested Cormorants in the region have been linked to increased predation pressure from Bald Eagles (Broadley, 2024), suggesting that predation risk may play a role in habitat selection. Future research could explore how factors such as prey availability, predation risk, weather conditions, and human disturbance interact with oceanographic dynamics and roost site proximity to influence seabird foraging patterns and space use.

Brandt’s Cormorants consistently revisited key foraging areas throughout the region, demonstrating strong individual fidelity to a limited number of sites. This aligns with previous findings that cormorants typically forage habitually within a narrower individual range nested inside a broader population-level foraging area (Cansse et al., 2024; Morgan & Hassal, 2019). These predictable spatial patterns support the identification of critical marine habitats for targeted seabird conservation and management (Lascelles et al., 2016). This study represents the first known effort to use GPS tracking to examine their winter behaviour in Canada, providing novel insight into this poorly understood season.

3.2. Future Directions and limitations

While our study focuses on how external environmental factors influence cormorant foraging behaviour, a comprehensive understanding of movement ecology also requires consideration of intrinsic and mechanistic drivers. The Movement Ecology Framework (Nathan et al., 2008) outlines three additional components that interact to shape movement behaviour: internal state (e.g., physiological condition, motivation), navigation capacity (i.e., the ability to orient in space and time), and motion capacity (i.e., the biomechanical traits enabling movement). For cormorants and other diving seabirds that utilize benthic habitats, obtaining fine-scale data on prey capture strategies and validating search behaviours is particularly challenging (Bennison et al., 2017). However, such behavioural details are crucial for understanding the sensory and biomechanical capacities that shape movement decisions. For example, Watanuki et al. (2008) used digital camera loggers to reveal that European Shags employ flexible foraging strategies, alternating between visually scanning the seafloor and using tactile probing with the bill, highlighting the diverse mechanisms seabirds may use to detect and capture prey.

Building on this conceptual foundation, our study identified where foraging behaviour occurs in relation to the broader marine environment, providing an important spatial perspective. However, being in a foraging state does not necessarily indicate foraging success or failure. Our dataset provided high-resolution depth data, which can be applied in various ways to infer foraging behaviour (Carter et al., 2016). Further exploration of this dataset could help quantify active search behaviour and patterns, or estimate prey capture attempts, offering insight into the fine-scale drivers of foraging decisions. Similar studies, such as those on Harbour porpoises, have used dive sinuosity (“wiggliness”) as a proxy for prey-chasing behaviour (Leos-Barajas et al., 2017), yielding deeper insights into foraging strategies. Integrating these dimensions is essential for gaining a mechanistic understanding of animal movement (Joo et al., 2020), and future research incorporating these components could yield deeper insights into how movement emerges from the interaction between species traits and their dynamic environment.

3.3. Conservation and management implications

The Salish Sea is a diverse marine ecosystem, characterized by its sediment composition, freshwater inflow from the Fraser River, upwelling, currents, and bathymetric complexity (Sobocinski, 2021). The glacially derived geology of the Salish Sea, combined with freshwater input from surrounding watersheds and marine mixing from the Pacific Ocean, shapes its unique oceanography and ecology, driving productivity and sustaining a dynamic, interconnected food web that supports an incredible diversity of flora and fauna. In British Columbia, there are only a few small breeding colonies of Brandt’s Cormorants (Rodway et al., 2024), meaning the winter population primarily consists of individuals that have migrated north after the breeding season. While the winter diet of this species remains poorly understood, the rich productivity of the Fraser River Estuary and the Salish Sea’s oceanographic complexity are likely major factors influencing their seasonal migration. Our analysis provides a predictive model that identifies areas of fast tidal currents, such as Porlier and Active Pass, and the mouth of the Fraser River as critical habitat areas for this species. High densities of foraging activity near accessible roosts suggest that these sites play a central role in shaping habitat use during the winter season. Notably, several of these roosts are located on artificial structures, such as rock jetties, indicating that both natural and human-made features contribute to habitat availability. Protecting existing natural roosts and ensuring the continued accessibility of artificial ones will be essential for supporting wintering populations. These findings highlight the need for targeted management strategies that preserve both natural and artificial roosting habitats to ensure the long-term viability of wintering populations.

The Salish Sea remains a highly productive marine ecosystem but is under increasing threat from a host of global and local environmental stressors (Johannessen et al. 2021, Sobocinski et al. 2021). The recent approval of the Trans Mountain Pipeline (TMX) is adding up to 30 more tankers per month to the shipping lanes, and the Roberts Bank Terminal 2 (RBT2) expansions are projected to increase container shipping activity by as much as 30% (Vancouver Fraser Port Authority, 2025). Further, the approved expansion of the Roberts Bank Terminal 2 (RBT2) is forecast to alter flow patterns, water depths, sediment transport and, ultimately, the distribution and abundance of forage fish (Environment and Climate Change Canada, 2019). Brandt’s Cormorants critical winter habitat areas identified in this study directly overlaps with the shipping lanes and infrastructure of these developments. In addition to the threat of increased oil pollution, studies have shown that marine mammals can be negatively affected from underwater noise in both their physiology and behaviour (Duarte et al., 2021). However, the effects of noise and disturbance from marine vessel traffic on seabirds remain poorly understood (Blight et al., 2023; Duarte et al., 2021). In particular, the impacts of vessel presence and noise on the behaviour and distribution of Brandt’s Cormorants are not well known, and further investigation through comprehensive impact assessments would be beneficial to better understand these effects. Incorporating oil spill mitigation and chronic pollution management into regional conservation planning is an ongoing effort and is essential to safeguarding the region’s biodiversity and resilience. Effective strategies must prioritize the protection of seabirds and other sensitive marine wildlife from both acute and ongoing contamination threats.

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Appendix A. Supplementary Material for Chapter 2

Table 2.A **Parameter estimates (and their 95% confidence intervals) for the hidden Markov model describing Brandt's Cormorant movement and diving behavior. Estimates are given for each behavioral state: resting (State 1), foraging (State 2), and transiting (State 3). Step lengths were modeled with a gamma distribution, turning angles with a von Mises distribution, and dive counts with a negative binomial distribution. Reported values include the mean and dispersion (for step length and dive count) and the mean direction and concentration (for turning angle).**

		State 1: (Resting)	**State 2 (Foraging)**	**State 3 (Transiting)**
Step length (~Gamma)	Mean step length	26.2 (25.5, 27.0)	448 (417, 478)	5456 (5143, 5768)
	St Dev	22.6 (21.8, 23.5)	580 (539, 621)	5861 (5597, 6124)
Turning angle (~von Mises)	Mean angle	3.08 (2.98, 3.19)	-3.1 (-3.25, -2.96)	0.028 (-0.053, 1.09)
	Concentration	0.43 (0.39, 0.48)	0.29 (0.24, 0.33)	0.65 (0.59, 0.72)
Dive Count (~Negative Binomial)	Mean dive count (per 30 min interval)	0.13 (0.03, 0.23)	9.7 (9.2, 10.1)	7.1 (6.5, 7.6)
	Size (dispersion)	0.006 (0.003, 0.009)	0.39 (0.37, 0.42)	0.24 (0.22, 0.25)