

**Identifying important habitat of forage fish and their seabird predators in coastal
Newfoundland, Canada**

by

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Thesis Abstract

The ecological niche is the set of environmental characteristics required for a species to grow, survive, and reproduce. Although individuals are predicted to select habitat within a range of conditions that maximize fitness throughout their annual cycle, information regarding the availability of suitable habitat or species-specific differences in habitat use are often limited. Here, I identified important habitat for forage fish, critical energy links between lower and upper trophic levels of marine food webs, and their seabird predators in coastal Newfoundland, Canada. I developed habitat suitability models for three forage fish species/groups to predict the location and extent of suitable coastal habitat for each species in two bays during spawning (Atlantic herring *Clupea harengus*, spring; capelin *Mallotus villosus*, summer) or year-round (sand lance *Ammodytes* spp.; Chap. 2). Suitable habitat was more limited for all species during summer (Notre Dame Bay; 8.1–73.3% of surveyed area) relative to spring (Fortune Bay; 25.2–100%) and sand lance burying habitat was more limited and patchier (8.1–25.2%) in both bays relative to capelin (35–97.6%) and herring (73.3–100%), suggesting sand lance are most vulnerable to habitat loss. 2.1°C ocean warming resulted in predicted decreases in the extent of suitable habitat for all species during summer. I also examined the foraging habitat of three breeding seabird species in coastal Newfoundland by quantifying species-specific prey patch characteristics in foraging hotspots (derived from archived GPS tracking datasets) during at-sea surveys (Chap. 3). Foraging hotspots for each species differed based on community and environmental variables. Atlantic puffins *Fratercula arctica* foraged at deeper, colder sites with lower prey densities compared to razorbills *Alca torda*, suggesting puffin displacement from high-quality prey patches. Common murre *Uria aalge* foraged at higher conspecific densities and at a broader range of prey densities and depths relative to puffins and razorbills. Together,

these findings revealed persistent seabird foraging areas where forage fish complete important parts of their annual cycle (e.g., spawning), identified limited suitable habitat for forage fish, and elucidated divergent foraging habitat characteristics among breeding seabird species, informing conservation and management decisions (e.g., spatial planning) for important species in coastal Newfoundland, Canada.

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Thesis Format

This thesis is presented in grouped manuscript format. Chapter 1 provides a general introduction, with theoretical background information relevant to Chapters 2 and 3, which present independent research, with individual abstract, introduction, methods, results, discussion, conclusion, and references sections, with their own associated tables, figures, and supplementary materials. These are followed by a concluding chapter (Chapter 4) that synthesizes the results of Chapters 2 and 3, providing further recommendations for conservation, management, and future research.

Contribution of Authors

Gibson Rieger conducted all field work, data analysis, and wrote this thesis. Gail Davoren (thesis advisor) acquired funding for the projects in Chapters 2 and 3. Gibson Rieger and Gail Davoren were both involved in determining appropriate data analyses, manuscript structure, editing, and revising the manuscript, and Dr. Hannah Murphy and Dr. Patricia Ramey-Balci (thesis committee) provided input.

Chapter One: Introduction.

The ecological niche concept refers to the set of environmental characteristics evolved over time that are required for a species to grow, survive, and reproduce (Vandermeer 1972, Alley 1982). Although a species may thrive under a wide set of environmental characteristics (fundamental niche; Hutchinson 1957), individuals of a species are often restricted to a smaller set in nature (realized niche; Hutchinson 1957, Melo-Merino *et al.* 2020), possibly due to environmental limitations or to limit competition through niche partitioning (e.g., partitioning of habitat, prey types). As such, by examining the range of environmental characteristics where individuals are present, we can begin to understand their species' realized niche and, thus, typical habitat requirements. After characterizing a species' niche, we can then use these environmental characteristics to predict the location and extent of suitable habitat for that species (habitat suitability modelling; Hirzel and Le Lay 2008) to support management or conservation efforts (e.g., Robinson *et al.* 2013, Huard *et al.* 2022).

Species are predicted to select habitat within a range of environmental conditions that maximize fitness (i.e., survival and reproduction), but these environmental characteristics may vary throughout a species' annual cycle. During reproductive events, species are predicted to select habitat with environmental conditions that favour offspring survival. Adult fish whose eggs become adhesive after fertilization select spawning habitat based on multiple physical and biological variables (e.g., sediment grain size, vegetation cover, salinity, temperature) within ranges that maximize incubation and hatching success (i.e., reproductive success; Dahlberg 1979, Tripp *et al.* 2023). Early life history stages (i.e., egg and larval stages) of fishes are characterized by high mortality (type III survivorship; Dahlberg 1979) and, thus, spawning habitat quality is a particularly important determinant of fitness. As such, the current or future lack of suitable

spawning habitat could result in lower recruitment and, ultimately, population bottlenecks.

During foraging, animals are predicted to maximize fitness in part by selecting habitat that maximizes their net energy intake (MacArthur and Pianka 1966). For instance, the marginal value theorem (“MVT”) predicts that predators should maximize their net energy intake when foraging in a patchy environment by selecting high density prey patches, where the rate of energy intake is greater than the mean across the environment (Charnov 1976; Tome 1988). Central place foraging theory, a further extension of MVT, predicts that animals that must return to a central place following foraging excursions (e.g., a breeding bird returning to a nest) will factor patch distance from the central place into patch selection decisions, whereby closer patches are prioritized if the forager can achieve the same net energy intake relative to distant patches (Orians and Pearson 1979). When multiple species use the same central place (e.g., a multi-species breeding colony), high numbers of competitors may forage nearby, and competitor density may also influence patch selection decisions. Under these circumstances, the ideal free distribution model predicts that an animal’s rate of energy intake in a prey patch decreases with increasing conspecific and allospecific densities when individuals compete for prey (Fretwell and Lucas 1970, assumptions and modifications reviewed in Kennedy and Gray 1993, Tregenza 1995). Thus, patch selection is informed by a trade-off between prey and competitor densities.

Marine food webs are under “wasp-waist” control (Rice 1995; Bakun *et al.* 2009), where energy is typically funnelled through only a few species at the intermediate trophic level. Forage fish, generally characterized as small, short-lived pelagic species (Pikitch *et al.* 2012, 2014), occupy this intermediate trophic level and, thus, play a key role in converting energy from lower trophic levels (zooplankton) into prey for a diversity of top predators, including piscivorous fish, marine mammals, and seabirds (Pikitch *et al.* 2012, Buren *et al.* 2014, Richardson *et al.* 2014).

During spawning, forage fish often form large, high-density aggregations to ensure high fertilization success (Pikitch *et al.* 2012), attracting high predator densities (see Pikitch *et al.* 2012, Davoren *et al.* 2025) which, in turn, allows high foraging success for predators. Therefore, conservation strategies targeting forage fish, and their spawning habitat in particular, are at the core of ecosystem-based approaches to fisheries management, allowing the conservation of culturally and economically important predator species (Smith *et al.* 2011, Pikitch *et al.* 2012, 2014, Dickey-Collas *et al.* 2014) along with the maintenance of key ecosystem processes (i.e., energy flow through food webs; Pikitch *et al.* 2012).

Study Area: Coastal Newfoundland, Canada

Coastal marine habitat (mean low tide to 50 m depth) in Newfoundland, Canada, is dominated by steep bedrock (Forbes 1984, Eamer *et al.* 2020), with dense nearshore kelp (brown algae) beds divided by green sea urchin *Strongylocentrotus droebachiensis* (hereafter “urchins”) barrens (i.e., bedrock where urchin grazing has removed macroalgae; Keats 1986, Keats *et al.* 1987, Konar 2000). Both cold- and warm-water adapted macroalgae are present at the extremes of their respective ranges along Newfoundland’s coast, which represents an interface between subarctic and boreal biogeographic regions (Adey and Steneck 2001, Merzouk and Johnson 2011). Nearshore kelp beds are often dominated by brown alga *Desmarestia viridis* (seabed cover increasing from 2 to 8 m depth; Blain and Gagnon 2014), a primary succession species which is resistant to urchin grazing (Keats 1986, Konar 2000, Gagnon *et al.* 2003, 2006, Blain and Gagnon 2014). By contrast, kelp beds at deeper sites (10–30 m) typically include other brown algae species (e.g., *Agarum* spp.; Cote *et al.* 2001, Bliss and Davoren 2021). Other common macroalgae in coastal Newfoundland include *Laminaria*, *Alaria*, and *Saccharina* spp. (Merzouk and Johnson 2011). Beds of eelgrass *Zostera marina*, the predominant seagrass species

in the northwest Atlantic (Wilson and Lotze 2019), are also present to 12 m depth across coastal Newfoundland (DFO 2009), likely owing to the species' tolerance of broad salinity and temperature ranges. Marine vegetation provides important structural fish habitat both for predator evasion (e.g., juvenile Atlantic cod *Gadus morhua*, Pacific herring *Clupea pallasii*; Keats *et al.* 1987, Cote *et al.* 2001, Thedinga *et al.* 2011, Lazzari 2013, Dunlop *et al.* 2022) and spawning (Haeghele and Schweigert 1985; Blain and Gagnon 2014, Bliss and Davoren 2021). As coastal regions are disproportionately impacted by increasing warming trends (Varela *et al.* 2023), changes in the distribution and density of this biogenic structural habitat are likely (e.g., Wilson and Lotze 2019, Wilson *et al.* 2018).

Due to an immediate increase in depth nearshore, depths typically exceed > 50 m within 5 km of shore in most Newfoundland bays (e.g., Fortune Bay), with some exceptions (e.g., Notre Dame Bay; Fig. 1.1, Shaw and Potter 2015, Eamer *et al.* 2020). Intertidal (i.e., beach) and shallow subtidal sites of fine grain size sediment (e.g., sand, gravel) are limited coastwide (Forbes 1984) but, where they occur, these sites often form a thin, unstable layer of sediment atop bedrock or deeper, stable deposits within bedrock depressions (Forbes 1984, Eamer *et al.* 2020; Penton and Davoren 2012). Subtidal sandy sediments are most common along Newfoundland's west coast, as well as the Burin and Avalon peninsulas, and in Notre Dame Bay (Eamer *et al.* 2020). Indeed, bare bedrock is relatively rare on the extensive shallow inner shelf (< 50 m depth up to 20 km from the shoreline in some areas) of the Straight Shore region (i.e., eastern Notre Dame Bay; Fig. 1.1, Eamer *et al.* 2020).

Study Species: Forage Fish

Key forage fish species in coastal Newfoundland include capelin *Mallotus villosus*, Atlantic herring *Clupea harengus* (hereafter “herring”), and two sand lance species, Northern

sand lance *Ammodytes dubius* and American sand lance *A. americanus* (Staudinger *et al.* 2020). Herring are managed as multiple stocks throughout Northwest Atlantic Fisheries Organization (NAFO) Divisions 3K (White Bay–Notre Dame Bay), 3L (Bonavista Bay–Trinity Bay, Conception Bay), and 3Ps (St. Mary’s Bay–Placentia Bay, Fortune Bay) with ranging statuses (from uncertain to “cause for concern”; Bourne *et al.* 2023), while two capelin stocks (NAFO Divisions 2J3KL and 3Ps) have yet to recover from a collapse associated with a cold-water event in the early 1990s (Colbourne *et al.* 1997, Buren *et al.* 2019) and sand lance population status in the region is largely unknown as *Ammodytes* spp. are not commercially fished (Staudinger *et al.* 2020). While the habitat associations of these species are relatively similar during spring–summer in coastal Newfoundland and other regions for the same or similar species, there are key differences in their use of coastal subtidal habitat.

Capelin are a small (12–23 cm adult size; DFO 2018), short-lived (2–6 years; Olsen 1968) fish that typically spawn only once (semelparous) after reaching sexual maturity (3–4 years pre-collapse, 2–3 years post-collapse; Winters 1982, DFO 2018, Buren *et al.* 2019), although repeat spawning has been recorded (more common in female capelin; Maxner *et al.* 2016). Changes in capelin biology, including smaller size at maturity (Carscadden *et al.* 2001, DFO 2024) and delayed spawning timing (Carscadden *et al.* 1997, Murphy *et al.* 2021, Murphy 2022) are associated with the 2J3KL stock collapse (Colbourne *et al.* 1997). Capelin migrate inshore each summer (June–August; Carscadden *et al.* 1997, Davoren *et al.* 2025) to spawn at beach or shallow (≤ 50 m) subtidal sites (Nakashima and Wheeler 2002, Penton and Davoren 2012) on suitable grain size sediment (sand or pebble, 0.5–25 mm grain size; Nakashima and Wheeler 2002, Davoren *et al.* 2008, Penton and Davoren 2012) or marine vegetation (*D. viridis*; Bliss and Davoren 2021). The retention of suitable sediment in bedrock depressions is an important feature

of annually persistent subtidal spawning sites, where a deeper, more stable layer of suitable sediment is present relative to a thin ephemeral layer on flat, exposed bedrock (Penton and Davoren 2012). Additionally, capelin spawn within a temperature range (2–12°C) that is optimal for offspring survival (Carscadden *et al.* 1989, Nakashima and Wheeler 2002, Davoren *et al.* 2008, Crook *et al.* 2017), along with a relatively broad range of salinities (14–33 psu; Rose 2005).

Relative to capelin, herring in coastal Newfoundland are larger (24–40 cm adult size), longer-lived fish (aged to 11+; Bourne *et al.* 2023, Randall *et al.* 2022) that spawn annually (iteroparous) after reaching sexual maturity (Wheeler *et al.* 2009). Following a population decline associated with overfishing in the 1970s and the same cold-water event that led to the collapsed capelin stock, herring have been reaching sexual maturity earlier at smaller sizes than historically (Wheeler *et al.* 2001, 2009, Bourne *et al.* 2015, Beaudry-Sylvestre *et al.* 2024). Herring stocks in eastern Newfoundland are comprised of both spring (April–June) and fall spawners (August–September; Parsons 1973) which overwinter on the southwest and northeast coasts (Moore and Winters 1984, Wheeler and Winters 1984) and aggregate at summer feeding grounds in the Strait of Belle Isle (Wheeler and Winters 1984; Moore and Winters 1984). Less is known of the movement of southern Newfoundland stocks as few fish have been tagged in Division 3Ps (e.g., no tagging in Fortune Bay) relative to western and eastern Newfoundland (Wheeler and Winters 1984). Although their spawning habitat associations in coastal Newfoundland are not well characterized, fertilized herring eggs in the northeast and northwest Atlantic, along with those of Pacific herring, adhere to a range of sediment grain sizes (pebble to cobble, ~4–150 mm; Runnstrom 1941, de Groot 1980, Munro *et al.* 1998) and an array of marine vegetation (e.g., eelgrass *Zostera marina*, *Desmarestia* spp., red algae including Irish moss

Chondrus crispus, rockweeds *Ascophyllum* and *Fucus* spp.; Tibbo *et al.* 1963, Messieh *et al.* 1983, Hourston *et al.* 1984, Haegele and Schweigert 1985, Munro *et al.* 1998, Shelton *et al.* 2014, Burbank unpublished data). Spring spawning in the Atlantic has been recorded between 2–12°C at shallow (< 20 m; Scattergood 1959, Parsons 1973, Haegele and Schweigert 1985) and deeper sites (< 80 m; Runnstrom 1941, de Groot 1980, Haegele and Schweigert 1985), and herring are known to spawn at a broad range of salinities (10–35 psu; de Groot 1980) which may have varying impacts on egg development and/or post-hatch mortality rates (e.g., Alderdice and Velsen 1971, Alderdice *et al.* 1979).

Sand lance (*Ammodytes* spp.) reach maturity at 20–30 cm in the northwest Atlantic (Winters 1981, Staudinger *et al.* 2020) as early as 2 years of age (Winters 1981) and are characteristically shallow-bodied. In contrast to capelin and herring, sand lance are non-migratory and spawn annually (iteroparous) outside of the spring-summer months in the northwest Atlantic (typically during fall–winter; Staudinger *et al.* 2020), although information on age at maturity and lifespan in coastal Newfoundland are lacking (Staudinger *et al.* 2020). Sand lance lack a swim bladder and research on Pacific sand lance *A. hexapterus* (Pinto *et al.* 1984, Robinson *et al.* 2013, Robinson *et al.* 2022) and *Ammodytes* spp. in the northeast Atlantic (Reay 1970, Wright *et al.* 2000) has shown that sand lance bury themselves in silt-free, coarse sand (0.5–4 mm grain size) during parts of the day year-round to reduce energy expenditure and minimize predation. Adults are typically associated with cool (1–11°C), shallow waters (<20–80 m; Reay 1970, Wright *et al.* 2000, Robinson *et al.* 2013). Sand lance are known to be patchily distributed typically within ~2 km of suitable sediment patches year-round (Haynes and Robinson 2011, Robinson *et al.* 2013), showing inter-annual site fidelity to areas with persistent suitable burying habitat (Haynes and Robinson 2011, Morrison and Davoren 2024). Limited

research has recently shown that sand lance in coastal Newfoundland are associated with similar habitat characteristics to *Ammodytes* spp. in other regions (Morrison and Davoren 2024).

Additionally, capelin (Vesin *et al.* 1981, Davoren *et al.* 2008) and herring (Stacey and Hourston 1982, Taylor 1964, Nøttestad *et al.* 1996) typically cease feeding during summer and spring spawning, respectively, while sand lance actively feed during this period on a pelagic planktivorous diet including primarily marine copepods (*Calanus* spp.; Staudinger *et al.* 2020).

Study Species: Seabirds

Chick-rearing seabirds are central place foragers and, thus, must travel out from nests to forage for themselves and their offspring at sea and return with prey to provision chicks. Most seabird species are colonial breeders (Danchin and Wagner 1997), and seabirds frequently nest in large numbers, often at multi-species colonies (Brown *et al.* 1990). Large numbers of birds foraging within limited foraging ranges of multispecies colonies may result in prey limitation through mechanisms such as local displacement, as prey become wary of predation (“landscape of fear”, an extension of MVT; Brown *et al.* 1999, Laundré *et al.* 2010), or local depletion (“Ashmole’s halo”; Ashmole 1963) resulting from predation rates that exceed replacement (Weber *et al.* 2021). Although prey limitation within colony foraging ranges is often unknown, previous studies have shown behavioural, spatial, and/or temporal segregation during foraging by breeding seabirds (Piatt 1990, Linnebjerg *et al.* 2015, Pratte *et al.* 2017, Jenkins and Davoren 2020, Weber *et al.* 2021, Symons and Diamond 2022), possibly indicating intra- and interspecific competition.

The largest populations of breeding common murre *Uria aalge* (hereafter “murre”) and Atlantic puffins *Fratercula arctica* (hereafter “puffins”) in the northwest Atlantic are found in coastal Newfoundland, Canada (Lowther *et al.* 2020, Ainley *et al.* 2021). Razorbills *Alca torda*

are also present in this region, albeit in smaller numbers (Lavers *et al.* 2020). All three species are members of the Family Alcidae (hereafter “alcids”), characterized as wing-propelled pursuit-divers, that breed in large numbers at multiple colonies on the northeast coast of Newfoundland, often forming multi-species colonies (Fig. 1.2). Alcids are characterized by high wing loading (body mass to wing surface area ratio), with high energetic costs of flight (Elliott *et al.* 2013, Winkler *et al.* 2020). During summer on the northeast Newfoundland coast, breeding pairs of each species lay one egg and rely primarily on forage fish as key prey to successfully provision and raise their chicks (Gulka and Davoren 2019, Gulka *et al.* 2019, Montevecchi *et al.* 2019, Gulka *et al.* 2020, Jenkins and Davoren 2020). Provisioning duties are shared between maternal and paternal parents during chick-rearing, although male murres and razorbills tend to spend more time at the colony with their chick (Linnebjerg *et al.* 2015). Puffins are multi-prey loaders, carrying multiple prey items at one time back to feed their chicks (Lowther *et al.* 2020), whereas murres and razorbills are typically single-prey loaders in the study area (Linnebjerg *et al.* 2015, Lescure *et al.* 2023). These alcids rely on a diet of sand lance *Ammodytes* spp., small crustaceans (e.g., northern shrimp *Pandalus borealis*), and juvenile fish of other species (e.g., Atlantic cod) during incubation and early chick-rearing and typically shift to capelin when they arrive inshore to spawn, resulting in decreased dietary diversity and increased trophic position during chick-rearing (Gulka *et al.* 2017, 2020, Jenkins and Davoren 2020, Lescure *et al.* 2023). Capelin are high-quality prey (i.e., calorically dense; Vonderbank 2024) that act as a pulsed resource, representing a ~150 times increase in forage fish biomass in coastal waters when they migrate inshore to spawn during the summer (Davoren *et al.* 2025). Additionally, the peak in capelin biomass during the summer typically coincides with alcid chick-rearing (July–August) on the northeast Newfoundland coast (Davoren 2024).

While parental puffins, razorbills, and murres all rely on forage fish to varying degrees during breeding to feed themselves and their chicks, physiological differences among these alcids may influence prey patch selection decisions. Puffins are the smallest of the three species (~300–550 g; Lowther *et al.* 2020), with the lowest energetic cost of flight (i.e., lowest wing loading; Pennycuik 1987) and, thus, may travel farther from colonies during foraging trips compared to the mid-sized razorbills (~500–900 g; Lavers *et al.* 2020) and larger murres (the largest extant alcid, ~800–1,100 g; Ainley *et al.* 2021). Indeed, puffins have been shown to travel farther during foraging trips from colonies where they breed sympatrically with razorbills in other regions (Symons and Diamond 2022) and, though the effect of additional mass of bill loads appears minimal in other birds (e.g., passerines; Cuthill and Kacelnik 1990, Wright *et al.* 1998, Hinsley 2000), this additional mass may result in increased energetic costs of flight for larger alcids (i.e., murres and razorbills) due to their high wing loading (Elliott *et al.* 2013, Winkler *et al.* 2020). Alcids also have differing physiological dive capabilities; puffins have a shallower maximum dive depth (~60 m; Piatt and Nettleship 1985, Burger and Simpson 1986) relative to razorbills (~120 m; Piatt and Nettleship 1985) and murres (~180 m; Piatt and Nettleship 1985, Burger and Simpson 1986, Hedd *et al.* 2009, Regular *et al.* 2010). While murres tend to dive deeper for prey than puffins and razorbills where the species co-occur (Piatt 1990, Linnebjerg *et al.* 2015), all three alcids tend to forage on shallow (< 50 m) prey aggregations when they are available in coastal Newfoundland (Piatt 1990, Gulka *et al.* 2019). In support, puffins (Dalton unpublished data), razorbills (Lesure *et al.* 2023), and murres (Hedd *et al.* 2009) have shallow mean dive depths (~10–30 m) compared to species-specific maxima when they forage at capelin spawning sites on the northeast Newfoundland coast.

Murres may be competitively dominant relative to puffins and razorbills, a relationship

observed in other pursuit- and plunge-diving seabird species of varying body size (e.g., shearwaters *Ardenna* spp.; Carvalho *et al.* 2020). Piatt (1990) found that murres were associated with larger, more dense prey aggregations than puffins in coastal Newfoundland. In support, recent studies indicate puffins tend to forage at a lower trophic level relative to razorbills and murres during chick-rearing where foraging ranges of all three species overlap (Pratte *et al.* 2017, Jenkins and Davoren 2020). While prey are not typically expected to be limiting during alcid chick-rearing on the northeast Newfoundland coast and foraging in areas of high conspecific and/or allospecific densities may minimize energetic costs of searching (e.g., local enhancement, as demonstrated for murres and puffins; Bairos-Novak *et al.* 2015), puffins and razorbills may be excluded from high density prey patches due to their smaller body and lower dive depth capability relative to murres. These competitive differences among alcids may result in the formation of species-specific foraging “hotspots”, where each species makes trade-offs between foraging at higher/lower prey and competitor densities to attain similar net energy gain (Tregenza 1995).

Objectives

Overall, the objective of my thesis was to investigate important habitat for forage fish and seabird species during the spring–summer in coastal Newfoundland, Canada. In my second chapter, I aimed to (i) develop simple habitat suitability models for the three dominant forage fish species/groups in coastal Newfoundland (capelin, Atlantic herring, and sand lance) by interpolating species-specific environmental optima and (ii) determine the spatial extent of suitable habitat for each species in coastal regions of Newfoundland (≤ 50 m). To meet these objectives, I performed at-sea coastal habitat surveys in two bays during summer 2023 (Notre Dame Bay) and spring 2024 (Fortune Bay; Fig. 1.1), employing a systematic survey design to

measure key characteristics of forage fish habitat through paired sediment sampling and underwater video at regularly spaced sites, and overlaid spatially interpolated habitat characteristics to calculate the predicted extent of suitable habitat for each species. I hypothesized that the spatial extent of suitable subtidal habitat for spawning (capelin, herring) and burying (sand lance) would differ among species and predicted that sand lance habitat would be most limited due to their narrow habitat requirements for burying. Additionally, I predicted that the extent of suitable habitat would be greater for all species in Notre Dame Bay, where low relief beaches and an extensive shallow inner shelf are present and the seabed is characterized to a greater extent by fine grain size sediment (e.g., sand and gravel).

The objectives of my third thesis chapter were to examine coastal prey patch characteristics used by three alcid species (Atlantic puffins, common murre, and razorbills) breeding on the northeast Newfoundland coast (Fig. 1.2). I performed at-sea surveys at foraging “hotspots” of each species in Notre Dame Bay during alcid chick-rearing, where I paired bird and hydroacoustic surveys along standard transects to characterize competitor and prey densities, respectively, measured temperature and depth, and collected underwater video to identify prey species present. I hypothesized that breeding alcids select different prey patch characteristics at the population level such that alcids are distributed in an ideal free manner (i.e., based on prey and competitor densities at patches). Additionally, I predicted that, in accordance with their differing physiological attributes, common murre use patches with the greatest prey and competitor densities, while razorbills use less dense prey patches with lower competitor densities, and puffins use patches with the lowest prey and competitor densities, relative to murre and razorbills, during foraging.

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Figures

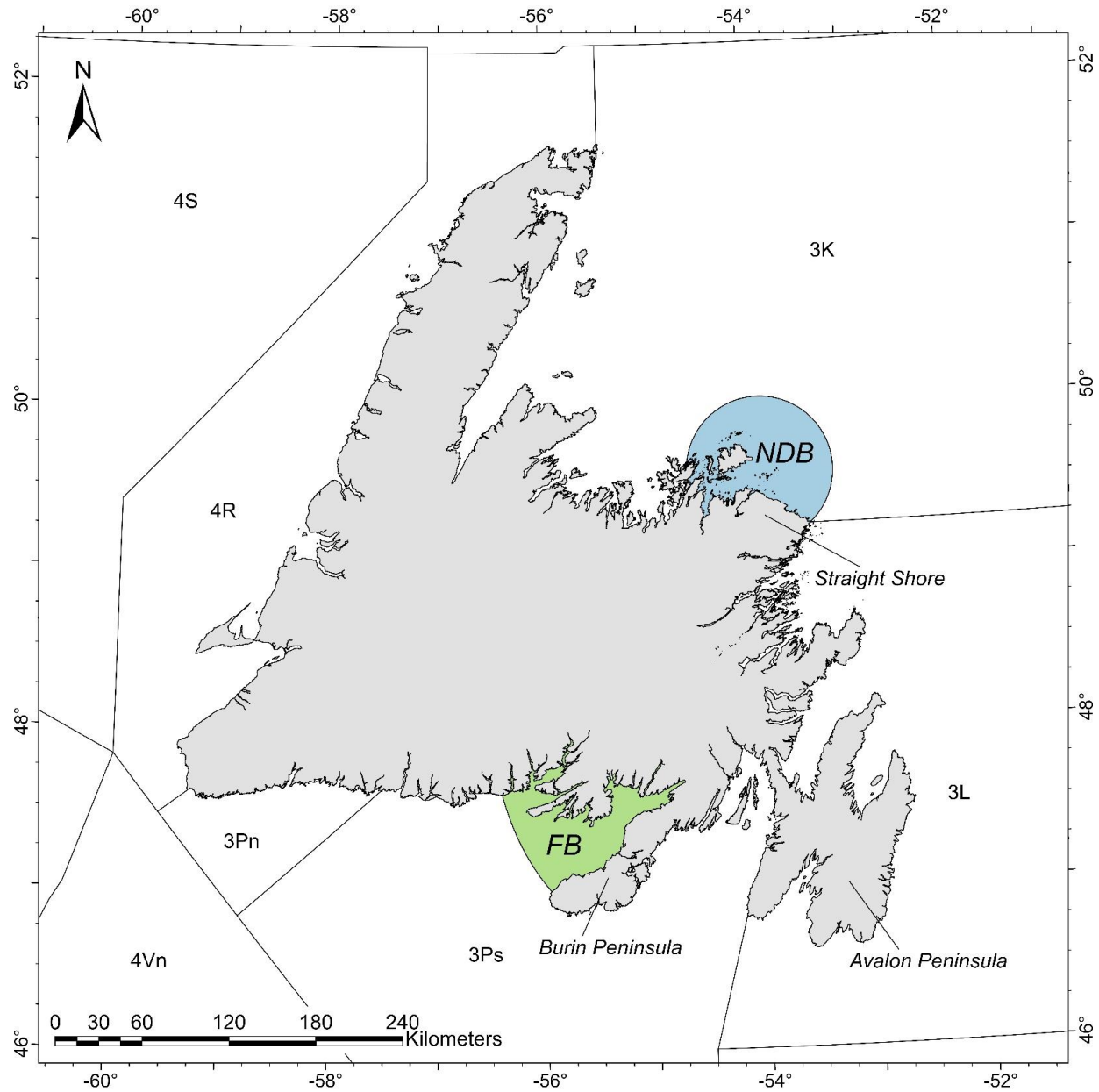


Figure 1.1. Location of the study areas on the northeast (Notre Dame Bay, NDB) and south (Fortune Bay, FB) coasts of Newfoundland, Canada. Black lines indicate the boundaries of Northwest Atlantic Fisheries Organization (NAFO) Divisions in the region.

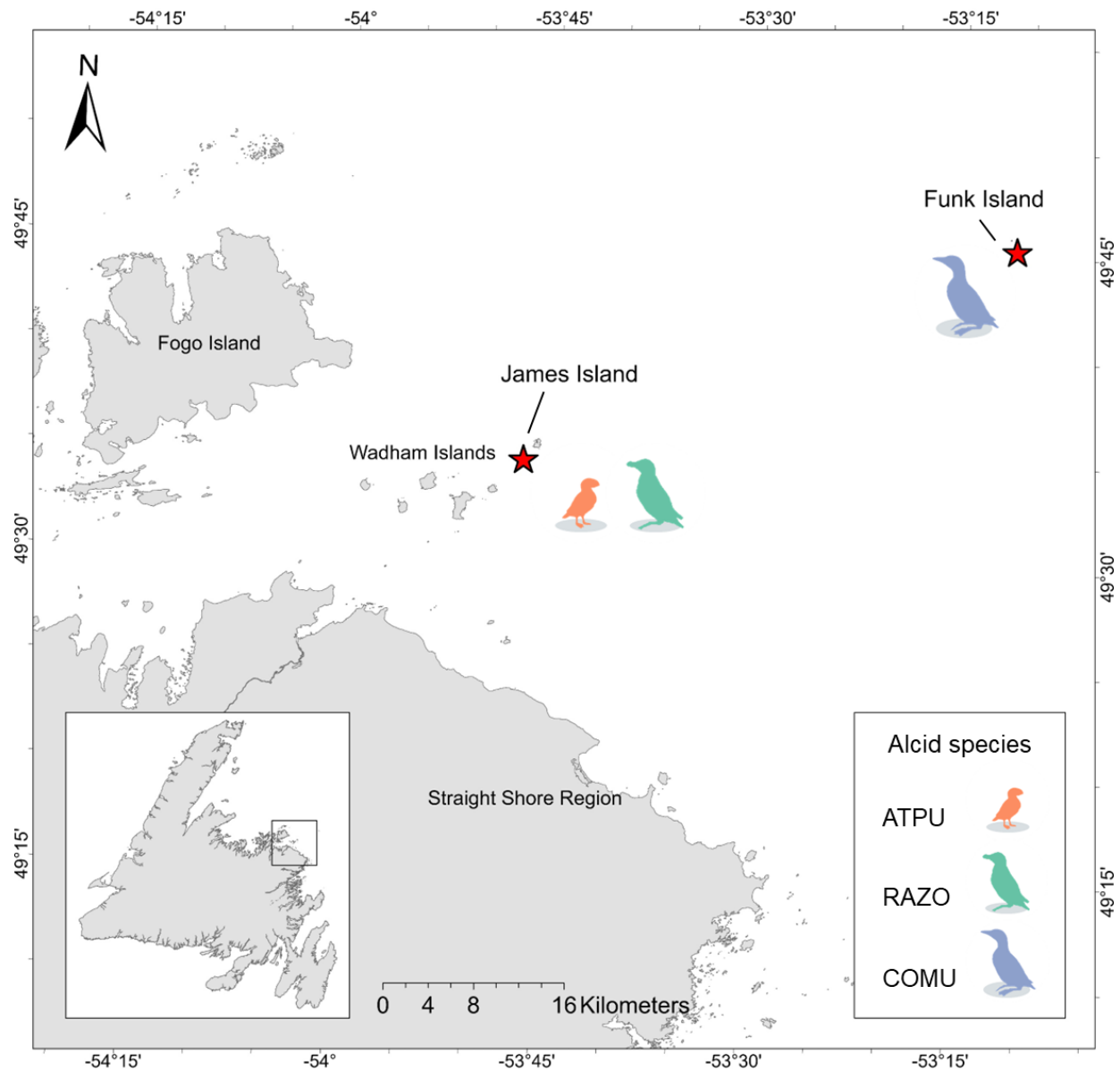


Figure 1.2. Location of coastal breeding colonies (red stars) where bird-borne GPS tags were deployed on breeding Atlantic puffins (orange), razorbills (green), and common murre (purple). Location on northeast Newfoundland coast shown in inset.

Chapter Two: Habitat suitability for key coastal forage fish in Newfoundland, Canada.

Abstract

Habitat suitability models (HSM) use the ecological niche concept to estimate the extent of suitable habitat for a species based on its habitat requirements. In marine food webs, forage fish act as critical energy links between lower and upper trophic levels and, thus, their conservation and management are essential to ecosystem-based fisheries management. Important forage fish species in coastal Newfoundland, Canada include capelin *Mallotus villosus*, Atlantic herring *Clupea harengus*, and sand lance *Ammodytes* spp. These fish share similar subtidal habitat associations either during spawning (herring, spring; capelin, summer) or year-round (sand lance burying habitat). We aimed to build simple HSMs using published species-specific environmental optima and quantify the spatial extent of suitable habitat for each species in coastal Newfoundland (≤ 50 m) under current conditions and future climate change scenarios (0.4°C and 2.1°C increase). HSMs were built by interpolating and overlaying important suitable habitat characteristics (i.e., seabed sediment grain size, marine vegetation, temperature) measured through systematic sampling/video surveys in two bays (Notre Dame Bay, July 2023; Fortune Bay, May 2024). Suitable habitat was more limited for all species in Notre Dame Bay (8.1–73.3% of surveyed area) relative to Fortune Bay (25.2–100%). Suitable herring spawning habitat was abundant (73.3–100%), while sand lance burying habitat was limited and patchy (8.1–25.2%) in both bays, suggesting sand lance are most vulnerable to coastal habitat degradation or destruction. The 2.1°C warming scenario resulted in the greatest predicted decrease in the extent of suitable habitat for all forage fish species during summer in Notre Dame Bay (14.2–35.2% decrease). Although we identified key knowledge gaps needed to refine these simple HSMs (e.g., documenting region- and species-specific habitat associations), our HSMs

directly inform spatial planning and management to protect habitat of these important species in coastal Newfoundland.

Introduction

An ecological niche encompasses the full set of resources and environmental characteristics required for a species to grow, survive, and reproduce (fundamental niche; Hutchinson 1957, Vandermeer 1972, Alley 1982). Individuals of a species are often restricted to a smaller set of environmental characteristics (realized niche; Hutchinson 1957, Melo-Merino *et al.* 2020), possibly due to environmental limitations or through niche partitioning to limit competition (e.g., partitioning of habitat, prey types). When species-specific niches are characterized, information about the range of physical and environmental characteristics in a region can be used to predict the location and extent of suitable habitat for a species (habitat suitability modelling; Hirzel and Le Lay 2008). Habitat suitability models (HSM) can then be used to support management or conservation efforts to protect species against current and future anthropogenic threats (e.g., Robinson *et al.* 2013, Huard *et al.* 2022).

Marine food webs are under “wasp-waist” control (Rice 1995; Bakun *et al.* 2009), where energy is typically funnelled through only a few species at the intermediate trophic level. Forage fish, generally characterized as small, short-lived, pelagic species (Pikitch *et al.* 2012, 2014), occupy this intermediate trophic level and, thus, play a key role in converting energy from lower trophic levels (e.g., zooplankton) into prey for a diversity of top predators, including piscivorous fish, marine mammals, and seabirds (Pikitch *et al.* 2012, Buren *et al.* 2014, Richardson *et al.* 2014). Conservation strategies targeting this critical link in marine food webs are at the core of ecosystem-based approaches to fisheries management and the conservation of culturally and economically important species (Smith *et al.* 2011, Pikitch *et al.* 2012, 2014, Dickey-Collas *et al.* 2014). One such strategy may involve protecting important forage fish habitat. Adults of forage fish species whose eggs become adhesive after fertilization typically select spawning habitat

based on multiple physical and biological variables (e.g., sediment grain size, vegetation cover, salinity, temperature) within ranges that maximize incubation and hatching success (i.e., reproductive success; Dahlberg 1979, Tripp *et al.* 2023). As early life history stages (i.e., egg and larval stages) of fish are characterized by high mortality (type III survivorship; Dahlberg 1979), current or future lack of suitable spawning habitat could result in population bottlenecks.

Dominant forage fish species in coastal regions on the Newfoundland Shelf during the spring and summer include capelin *Mallotus villosus*, Atlantic herring *Clupea harengus* (hereafter “herring”), and two sand lance species, northern sand lance *Ammodytes dubius* and American sand lance *A. americanus* (Staudinger *et al.* 2020). In coastal Newfoundland, herring are managed as multiple stocks throughout Northwest Atlantic Fisheries Organization (NAFO) Divisions 3K (White Bay–Notre Dame Bay), 3L (Bonavista Bay–Trinity Bay, Conception Bay), and 3Ps (St. Mary’s Bay–Placentia Bay, Fortune Bay) with ranging statuses (from uncertain to “cause for concern”; Bourne *et al.* 2023), while two capelin stocks (NAFO Divisions 2J3KL and 3Ps) have experienced minimal recovery from a collapse associated with a cold-water event in the early 1990s (Colbourne *et al.* 1997, Buren *et al.* 2019) and sand lance population status in the region is largely unknown as they are not commercially fished (Staudinger *et al.* 2020).

The subtidal habitat associations of these species are relatively similar during spring–summer in coastal Newfoundland, Canada, and elsewhere (i.e., for the same species in the northwest and/or northeast Atlantic or similar species in the Pacific), with some key differences (Table 1.1). Capelin spawn during the summer (June–August; Carscadden *et al.* 1997, Davoren *et al.* 2025) at beach or shallow (≤ 50 m) subtidal sites (Nakashima and Wheeler 2002, Penton and Davoren 2012) on suitable grain size sediment (sand or pebble, 0.5–25 mm grain size; Nakashima and Wheeler 2002, Davoren *et al.* 2008, Penton and Davoren 2012) or marine

vegetation (brown alga *Desmarestia viridis*; Bliss and Davoren 2021), within an optimal temperature range for offspring survival (2–12°C; Carscadden *et al.* 1989, Nakashima and Wheeler 2002, Davoren *et al.* 2008, Crook *et al.* 2017). By contrast, herring spawn in the spring (April–June) and fall (August–September; Parsons 1973) and, although their spawning habitat associations in coastal Newfoundland are not well characterized, fertilized herring eggs in the northeast and northwest Atlantic, along with those of Pacific herring *Clupea pallasii*, adhere to a range of sediment grain sizes (pebble to cobble, ~4–150 mm; Runnstrom 1941, de Groot 1980, Munro *et al.* 1998) and many types of marine vegetation (e.g., eelgrass *Zostera marina*, *Desmarestia* spp., red algae including Irish moss *Chondrus crispus*, and rockweeds *Ascophyllum* and *Fucus* spp.; Tibbo *et al.* 1963, Messieh *et al.* 1983, Hourston *et al.* 1984, Haegele and Schweigert 1985, Munro *et al.* 1998, Shelton *et al.* 2014, Burbank unpublished data). Spring spawning in the Atlantic has been recorded between 2–12°C at shallow sites (< 20 m; Scattergood 1959, Parsons 1973, Haegele and Schweigert 1985) and deeper sites (< 80 m; Runnstrom 1941, de Groot 1980, Haegele and Schweigert 1985). During spawning, capelin and herring typically cease feeding (Vesin *et al.* 1981, Stacey and Hourston 1982, Taylor 1964, Nøttestad *et al.* 1996, Davoren *et al.* 2008). Sand lance *Ammodytes* spp. spawn outside of the spring-summer months in the northwest Atlantic (typically during fall–winter; Staudinger *et al.* 2020). Unlike capelin and herring, sand lance lack a swim bladder and research on Pacific sand lance *Ammodytes hexapterus* (Pinto *et al.* 1984, Robinson *et al.* 2013, Robinson *et al.* 2022) and *Ammodytes* species in the northeast Atlantic (Reay 1970, Wright *et al.* 2000) has shown that sand lance bury themselves in silt-free, coarse sand (0.5–4 mm grain size) at 1–11°C, typically in shallow waters (~20–60 m; Reay 1970, Wright *et al.* 2000, Robinson *et al.* 2013), during parts of the day to reduce energy expenditure and minimize predation. Sand lance often remain within ~2

km of these rare suitable sediment patches year-round (Haynes and Robinson 2011, Robinson *et al.* 2013). Recently, Morrison and Davoren (2024) found sand lance associated with habitat characteristics similar to capelin spawning habitat (0.5–4 mm grain size, $\sim 2^{\circ}\text{C}$, ~ 40 m) in coastal Newfoundland.

Coastal marine habitat (i.e., mean low tide to 50 m depth) in Newfoundland, Canada, is dominated by steep bedrock increasing in depth immediately from the shoreline (Forbes 1984, Eamer *et al.* 2020), with kelp (brown algae) beds or green sea urchin *Strongylocentrotus droebachiensis* (hereafter “urchin”) barrens (i.e., bedrock where urchin grazing has removed macroalgae; Keats 1986, Konar 2000). With some exceptions (e.g., Notre Dame Bay, Avalon Peninsula; Fig. 2.1), depths exceed 50 m within 5 km of shore in most bays (e.g., Fortune Bay; Shaw and Potter 2015, Eamer *et al.* 2020) and shallow subtidal sites of fine grain size sediment (e.g., sand, gravel) are limited coastwide (Forbes 1984). Where they occur, they typically form a shallow, unstable layer of sediment atop bedrock or deeper deposits within depressions in bedrock (Forbes 1984, Eamer *et al.* 2020, Penton and Davoren 2012). Subtidal sandy sediments are most common along Newfoundland’s west coast, the Burin and Avalon peninsulas, and in Notre Dame Bay, where subtidal sediment is typically dominated by sand and gravel (Shaw and Potter 2015, Eamer *et al.* 2020). Trends in the northwest Atlantic reflect increasing global average temperatures, with predicted increases in seabed temperatures ranging $+0.4$ – 2.1°C by 2060 (see Han *et al.* 2015). Recently, high sea surface and seabed temperatures have been recorded on the Newfoundland Shelf. The second highest bottom temperature anomaly recorded across the shelf from 1980 to present occurred in 2021 (Cyr *et al.* 2022), record high mean sea surface temperatures were recorded during May–November 2022 in NAFO Divisions 3K, 3L, and 3Ps, and record high seabed temperatures were recorded during spring 2022 in 3Ps (DFO

2023a, Fig. 2.1). Globally, coastal regions are disproportionately impacted by increasing warming trends (Varela *et al.* 2023) which are likely to drive changes in the biogenic structural habitat present (e.g., eelgrass and macroalgae distribution; Wilson and Lotze 2019, Wilson *et al.* 2019).

Objectives

While bathymetric features and typical seabed substrate types have been broadly characterized in coastal Newfoundland (Forbes 1984, Eamer *et al.* 2020), a lack of detailed fine-scale bathymetry, seabed substrate type, and temperature and ocean current models limits our knowledge on the availability and extent of suitable coastal habitat for forage fish. Following other studies (e.g., Robinson *et al.* 2013), we aimed to develop simple HSMs through interpolation of species-specific environmental optima for key forage fish species (capelin, herring, sand lance) and to determine the spatial extent of suitable habitat for each species in coastal regions (≤ 50 m) of Newfoundland, Canada. We focused on two Newfoundland bays with uncharacteristically high presence of fine grain size sediment but contrasting habitat features, including an extensive sloping inner shelf with low relief shorelines in Notre Dame Bay and a narrow shelf with high marine terraces in Fortune Bay (Shaw and Potter 2015, Eamer *et al.* 2020). Long-term monitoring and local ecological knowledge indicated the importance of subtidal capelin spawning during summer (July) in Notre Dame Bay (Penton and Davoren 2012, Davoren *et al.* 2025) relative to herring dominance during spring (May) in Fortune Bay (recent commercial fisher interviews following Bliss *et al.* 2023, Davoren unpublished data), and the presence of sand lance in both bays (Morrison and Davoren 2024, Davoren unpublished data). We hypothesized that the spatial extent of suitable subtidal habitat for spawning and/or burying would differ among species in each bay. We predicted that the availability of suitable habitat

would be most limited for sand lance across bays due to their narrow habitat requirements for burying in the seabed. We also predicted that the extent of suitable habitat would be more limited for all species in Fortune Bay as the more extensive shallow inner shelf present along the Straight Shore region in Notre Dame Bay (Fig. 2.1), characterized by its low relief sandy beaches (Smallwood *et al.* 1984, Shaw and Potter 2015), may retain more coastal deposits of fine grain size sediment. Overall, this project will address knowledge gaps on the availability of suitable forage fish habitat in the northwest Atlantic, a potential population bottleneck (e.g., rare sand lance burying habitat; Robinson *et al.* 2013) for these ecologically important species.

Methods

Study design

To coincide with the spawn timing of the predominant forage fish species in each bay, we conducted at-sea surveys to collect contemporary coastal habitat data during July 2023 in Notre Dame Bay (NAFO Division 3K) and May 2024 in Fortune Bay (NAFO Division 3Ps; Fig. 2.1). Surveys were conducted in Notre Dame Bay near multiple capelin beach and subtidal spawning sites (49.32–49.49 °N, 53.59–53.96 °W; Davoren *et al.* 2025) and on the east coast of Fortune Bay, where fisher interviews indicated potential herring and capelin spawning sites, sand lance burying habitat, and marine predator hotspots (47.11–47.27 °N, 55.34–55.77 °W; Fig. 2.2). Surveys were conducted aboard the *Lady Easton III* (10 m commercial fishing vessel) and a 6 m open boat in Notre Dame Bay and an 8 m open boat in Fortune Bay. A systematic survey design was established within the 50 m depth contour, where sites were sampled in duplicate every ~1 km along a series of 1 km-spaced lines parallel to the coast, starting ~100 m away from shore (four lines in Notre Dame Bay, three in Fortune Bay; Fig. 2.2). This design resulted in a grid of equidistant sampling points and allowed assessment of both fine- (within-site) and large-scale

(whole coastline) spatial variation in environmental conditions (i.e., spatial autocorrelation; Mitchell and Griffin 2021). In Notre Dame Bay, additional lines were added to increase coverage of a small bay (Deadman's Bay; Fig. 2.2).

Habitat Characteristics

At each site, a Ponar Grab (15.2 or 22.9 cm² sample area; hereafter, “grab”) was deployed twice to collect samples of the seabed substrate. When sediment was present, grain size composition of each sample was visually characterized in the field using a grain size card (Leicester University Grain Card), with grain size classifications (silt, sand, granule, pebble, cobble, boulder, and bedrock) following the Wentworth scale (Wentworth 1922). Forage fish adults, fish eggs, and marine vegetation that were sampled were identified to the lowest taxonomic level possible. An underwater camera (GoPro Hero 7/8 in waterproof casing) was attached to the grab to continuously collect video of the water column and seabed to supplement grab samples. From the video, we recorded the presence/absence and number of forage fish observed at each site along with their identity to lowest taxonomic level possible and presence/absence of fish eggs. Additionally, bio-physical characteristics were visually characterized within ~1 m of the grab, including the presence/absence of each sediment grain size category and marine vegetation to the lowest taxonomic level possible. A conductivity-temperature-depth logger (Star-Oddi DST CTD; Star-Oddi Ltd, Skeiðarás, Iceland) was also attached to the grab to quantify bottom depth, temperature, and salinity.

At each site, sediment grain size presence/absence was primarily assigned from grab samples. If sediment was not sampled (i.e., “water haul”), the underwater video was used, when available, to assign the presence/absence of each sediment grain size category. Sites where video was missing (due to equipment failure) and the grab sample was a water haul were assigned

absence of all suitable grain sizes, indicating the likely presence of bedrock, boulder, and/or large cobble. Our assignment of the presence/absence of marine vegetation (seagrass and/or macroalgae) was informed by both grab samples and underwater video, where available, as vegetation was often not sampled by the grab when visibly present on the video (e.g., vegetation was sampled at only 38% of sites where presence was confirmed with video in Fortune Bay). At all sites, presence/absence of forage fish adults and eggs were also assigned using grab samples and underwater video. For analyses, grain size data were summarized into presence/absence of four discrete categories: medium–coarse grain sand, granule, pebble, and cobble (see Table 1.2 for grain sizes in mm). Within-site variation in structural habitat was summarized as the percentage of duplicate samples with the same presence/absence of sediment grain size categories and vegetation (Table 1.2).

Habitat Suitability Modelling

Geostatistical analyses and HSM construction were performed in ArcGIS Pro v3.2.0 (Esri Inc, Redlands, California). To determine appropriate interpolation methods, we first used the Spatial Autocorrelation (Global Moran's I) tool to explore spatial patterns in our sediment grain size and marine vegetation presence/absence data and continuous seabed temperature data across three spatial scales (5, 15, and 25 km). Seabed depth was not investigated as sampling was restricted to ≤ 50 m, which was within the depth range of spawning and/or burying for all species (see Table 1.1). Additionally, we did not include salinity in our HSMs as it has not been identified as a key habitat variable, did not vary markedly across our survey, and fell within the relatively broad suitable ranges for capelin spawning (Rose 2005), herring spawning (de Groot 1980), and sand lance burying (Reay 1970) within both bays. Moran's I compares the difference between values (e.g., seabed temperature) at nearby sites within a specified neighbourhood to the

mean of differences across the entire survey area, wherein positive spatial autocorrelation (i.e., clustering) occurs if the difference between neighbours is less than the mean of differences across all measures (Mitchell and Griffin 2021). Most sediment grain size presence/absence, vegetation presence/absence, and seabed temperature measures in both bays were spatially autocorrelated with clustered distribution (i.e., nearby sites were more similar relative to distant sites; Mitchell and Griffin 2021) across all spatial scales (exception: granules in Notre Dame Bay; Table S2.1, S2.2). Therefore, we explored interpolation methods that assumed spatial autocorrelation to determine the optimal method for each habitat variable.

Common interpolation methods were explored using the Geostatistical Wizard in ArcGIS Pro, including one deterministic model (inverse distance weighted, IDW) and one geostatistical model (ordinary Kriging) which are appropriate for use with data collected at regular spatial intervals (Li and Heap 2014). Deterministic and geostatistical interpolation methods differ in that deterministic interpolation makes predictions based simply upon distance from measured values, whereas geostatistical interpolation adjusts predictions based on the distance and spatial pattern of measured points (Li and Heap 2014), and such methods are frequently compared (e.g., Li *et al.* 2009, Li and Heap 2011, 2014, Sahlin *et al.* 2014, Biernacik *et al.* 2023). IDW interpolation assigns the greatest power (i.e., influence of value measured at a site on the predicted value at a non-measured site) to nearby sites, with decreasing influence with increasing distance (Mitchell and Griffin 2021). Additionally, ordinary Kriging assumes stationarity (i.e., spatial homogeneity) and an unknown but constant mean value across the surveyed area (Sahlin *et al.* 2014), such that no underlying trend produces differences in measured values across the area. IDW interpolation was performed using two power values, two (the default in ArcGIS Pro) and one; lower power values increase the influence of more distant measurements on predicted values. Ordinary

Kriging interpolation was performed using the default parameters in ArcGIS Pro. As spatial autocorrelation was generally strongest at low distances (i.e., the influence of neighbouring values on that measured at a site decreased with increasing distance; Table S2.1, S2.2, Mitchell and Griffin 2021), all interpolation models were specified to incorporate a minimum and maximum of 10 and 15 nearest neighbours in predictions, respectively, such that model predictions were influenced by the surrounding grid of nearby measured sites (see Fig. 2.2). We then assessed the results of cross validation (i.e., comparing measured values at survey sites to predicted values on the interpolated surface) for each model by comparing root-mean-square prediction errors to choose the “best” interpolation model for each habitat variable within each bay. Ordinary Kriging consistently resulted in the most accurate model predictions (Table S2.3, S2.4). Indeed, Kriging interpolation methods typically provide better models than deterministic methods (Li and Heap 2011, 2014) and, thus, we used interpolated surfaces produced through this method to map the presence/absence of suitable sediment grain sizes, vegetation, and seabed temperature for each forage fish species (outlined in Table 1.1).

Suitable habitats for each species within each bay were mapped by overlaying interpolated surfaces for the presence of species-specific suitable sediment grain sizes (Fig. S2.1). Presence/absence data were assigned values of one (presence) or zero (absence) and interpolated surfaces were summarized as the presence of suitable features (i.e., sediment, vegetation) indicated by an interpolated (i.e., predicted) presence threshold value > 0.3 . The presence of suitable sediment grain sizes (capelin: sand, granule, pebble; herring: pebble, cobble; sand lance: sand, granule) were summarized into a single layer (Fig. S2.1). Interpolated surfaces for the presence of *D. viridis* and all vegetation were summarized as suitable biogenic structure for capelin and herring spawning, respectively (Fig. S2.2). Finally, we summarized the overlap of

suitable sediment grain sizes and/or marine vegetation and seabed temperature into a single layer representing current species-specific suitable habitat (Fig. 2.3; following Robinson *et al.* 2013). The estimated total area (km²) of current suitable habitat for each forage fish species/bay combination was then quantified by calculating the area of the polygon(s) formed by overlapping layers for interpolated habitat variables in each bay using the Calculate Geometry Attributes tool (Fig. 2.3, Table 2.3). We also determined the percentage of the total surveyed area within each bay that was suitable for each species. To determine the change in the extent of species-specific suitable habitat within each bay, this process was repeated using seabed temperatures adjusted under two Newfoundland ocean climate change projections, specifically a 0.4°C and 2.1°C increase in seabed temperatures (see Han *et al.* 2015; Fig. 2.3, Table 2.3). Finally, we used the presence of forage fish adults and/or eggs either sampled with the grab or observed in videos during surveys to qualitatively validate our predicted suitability models.

Results

We quantified habitat variables at 131 sites in Notre Dame Bay (n = 262 grab samples, n = 194 videos) during 9–20 July 2023 in Notre Dame Bay and at 112 sites (n = 224 grab samples, n = 219 videos) during 15–25 May 2024 in Fortune Bay (Fig. 2.2, Table 1.2). On average, duplicate grab samples were 34.9 m and 18.0 m apart in Notre Dame and Fortune bays, respectively. Within-site variation (i.e., fine-scale patchiness) in sediment grain size presence was similar in Notre Dame Bay and Fortune Bay, as indicated by a generally high percentage of duplicate samples at each site having the same presence of each sediment grain size category (Table 1.2). By contrast, within-site variation in marine vegetation presence was greater in Notre Dame Bay than Fortune Bay (Table 1.2), but this may be related to the greater number of sites with missing underwater video in Notre Dame Bay (Fig. 2.2). Subtidal capelin spawning was

recorded at five sites in Notre Dame Bay. We sampled eggs adhered to macroalgae species other than *D. viridis* at two sites and adhered to urchins at one site. While we did not sample eggs at the other two sites, their presence was visually confirmed from the video as a thick layer that obscured parts of the seabed, such that the presence of eggs and spawning capelin precluded sediment grain size categorization. Additionally, adult capelin were observed at a single site where capelin eggs were not present (Fig. 2.3). In Fortune Bay, herring eggs were recorded at two sites and we sampled eggs adhered to macroalgae including *D. viridis* and red algae, and adults were observed aggregated at two sites where herring eggs were not present (Fig. 2.3). Sand lance were not sampled/observed during surveys in either bay. Seabed temperatures ranged more widely in Notre Dame Bay during July and the mean temperature was nearly double that recorded in Fortune Bay during May (Table 1.2). Marine vegetation was present at most sites in both bays and sand was present in similar proportions in both bays, but granules and pebbles were approximately twice as common at sites in Fortune Bay compared to Notre Dame Bay (Table 1.2). Marine vegetation recorded during surveys included eelgrass, red algae (e.g., Irish moss *Chondrus crispus*), and brown algae (e.g., *D. viridis*, *Agarum clathratum*, *Chorda filum*, *Laminaria saccharina*, *L. digitata*, and *L. longicruris*).

The spatial extent of suitable habitat was more limited for all species in Notre Dame Bay relative to Fortune Bay despite a similar survey area (Table 2.3). Fine grain size sediment (i.e., sand, granule, and pebble, 0.5–64 mm) was more rare in Notre Dame Bay and seabed temperatures ranged 0.8–19.9°C during July in this bay compared to 2.1–8.0°C in Fortune Bay during May, which is within the suitable temperature range for these forage fish species (Table 1.2). Salinity ranges were similar in both bays (Table 1.2). Suitable herring spawning habitat was most prevalent in both bays relative to suitable subtidal spawning habitat for capelin and burying

habitat for sand lance, due in part to the large interpolated areas of pebble, cobble, and all marine vegetation presence (Table 2.3, Fig. S2.2). By contrast, suitable sand lance burying habitat (i.e., sand, granules) was more limited and patchier (i.e., forming more distinct polygons within surveyed areas) in both bays relative to capelin and herring spawning habitat (Table 2.3, Fig. 2.3).

Cooler seabed temperatures during May in Fortune Bay meant neither seabed warming scenario resulted in a change in the proportion of suitable spawning/burying habitat for forage fish (Fig. 2.3, Table 2.3). During July in Notre Dame Bay, the 0.4°C warming scenario resulted in minimal reductions in the extent of predicted suitable habitat for capelin (-1.3 km²) and sand lance (-0.5 km²) and a small increase in area for herring (+1.2 km²; Table 2.3). The 2.1°C increase in seabed temperatures, however, generally resulted in a shift toward more offshore suitable habitat and a larger reduction in the spatial extent of suitable habitat within our survey area (3.2–11.6 km²; Fig. 2.3), with sand lance having the greatest proportional decrease in the extent of suitable spawning habitat (-35.2% of current suitable area; Table 1.2).

Discussion

We used published information on habitat associations to predict the extent of suitable subtidal spawning and/or burying habitat for capelin, herring, and sand lance within two bays during spring and summer in coastal Newfoundland, Canada. Given knowledge gaps regarding species-specific habitat associations in coastal Newfoundland, we created HSMs based on habitat characteristics from Newfoundland, where possible, and biological data from the same species or genus in other regions, to inform the spatial extent of species-specific suitable habitat in both bays. Suitable habitat was present for each species in both bays and, as predicted, suitable sand lance burying habitat was more limited compared to capelin and herring spawning habitat (Table

2.3). We documented spawning by the predominant species in each bay (i.e., capelin in Notre Dame Bay, herring in Fortune Bay; Fig. 2.3), but sand lance were not sampled/observed during surveys in either bay despite knowledge of their presence (Morrison and Davoren 2024, Davoren unpublished data). Interestingly, contrary to our prediction, suitable habitat was more limited for all species in Notre Dame Bay relative to Fortune Bay (Table 2.3). Our survey area in Fortune Bay, however, was located at the lowest relief and widest area of the otherwise narrow shallow inner shelf present in the eastern part of this bay (Shaw and Potter 2015, Eamer *et al.* 2020) and, thus, our results may primarily represent an anomalous area of suitable habitat for these forage fish in this bay. Finally, the predicted extent of suitable habitat generally decreased for all species under ocean warming scenarios during July in Notre Dame Bay but did not change during May in Fortune Bay (Fig. 2.3), due to the lower water temperatures recorded during spring (Table 1.2). As capelin typically do not typically spawn in May in NAFO Division 3Ps and herring do not spawn in July, our climate-driven predicted changes in the spatial extent of suitable habitat should be considered cautiously for capelin in Fortune Bay and herring in Notre Dame Bay.

Interestingly, there was a lower spatial extent of suitable subtidal habitat for capelin spawning in Notre Dame Bay, where capelin is the dominant forage fish during the summer (Davoren *et al.* 2006, 2025), relative to Fortune Bay (Fig. 2.3, Table 2.3). This was unexpected due to the apparently low abundance of the 3Ps stock since the 2J3KL capelin stock collapse in the early 1990s (Davoren unpublished data), which is supported by a lack of commercial landings in recent years despite a quota allotted to 3Ps (Fig. 2.1; DFO 1993, 2023b, 2024). However, our HSM for subtidal capelin spawning habitat in Fortune Bay may become important baseline information if the 3Ps stock recovers in the future. The unexpected lower spatial extent of suitable subtidal spawning habitat in Notre Dame Bay appeared to be primarily due to the

lower percentage of sites with suitable sediment grain sizes for capelin spawning, especially pebbles, and lower presence of *D. viridis*, an important macroalgae species for capelin spawning (Bliss and Davoren 2021), relative to Fortune Bay (Fig. S2.1, S2.2, Table 1.2). While Notre Dame Bay is generally characterized by low relief sandy beaches and high presence of fine sediment grain sizes (Smallwood *et al.* 1984, Shaw and Potter 2015, Eamer *et al.* 2020), these results highlight the importance of collecting fine-scale baseline subtidal habitat data in coastal Newfoundland. Additionally, seabed temperature was unsurprisingly warmer during summer in Notre Dame Bay than in Fortune Bay during spring, and the majority of the area adjacent to the shoreline in Notre Dame Bay was too warm for spawning capelin (Fig. S2.2). High ($> 12^{\circ}\text{C}$) temperatures nearshore partly resulted in three of the five documented capelin spawning sites in Notre Dame Bay being outside the current area of suitable subtidal spawning habitat predicted by our HSM (Fig. 2.3). As capelin spawning in the bay began on 12 July 2023, approximately one week prior to our surveys, it is possible that temperatures at these subtidal sites were within the optimal range ($2\text{--}12^{\circ}\text{C}$) when capelin spawned but increased post-spawning (i.e., during our survey; see Tripp *et al.* 2023). Documented capelin spawning sites outside of predicted suitable habitat also may be due in part to capelin eggs found adhered to previously undescribed structures (i.e., urchins, macroalgae species other than *D. viridis*) in grab samples paired with a lack of supplemental habitat information from video due to an equipment failure (see Fig. 2.2). As subtidal capelin spawning sites have been well-documented in this bay (Davoren and Penton 2012) and other bays in coastal Newfoundland (Nakashima and Wheeler 2002, Bliss and Davoren 2021), these findings likely highlight the importance of pairing grab samples with video to improve characterizations of fish habitat.

Increasing temperatures during summer spawning may cause subtidal capelin spawning

habitat to shift farther offshore, as indicated by our model in Notre Dame Bay (Fig. 2.3). In support, capelin are predicted to increasingly select cooler habitat for spawning (e.g., shift from generally warmer beach to cooler subtidal habitat) under future climate warming scenarios (Templeman 1948, Nakashima and Wheeler 2002, Crook *et al.* 2017, Tripp *et al.* 2023). However, as indicated by our survey, the temperatures capelin encounter at shallow subtidal spawning sites are also likely to become higher than optimal during the summer with predicted ocean warming (Han *et al.* 2015) and as 2J3KL and 3Ps capelin stocks continue to delay spawning (i.e., spawning is up to four weeks later relative to historic, associated with the stock collapse in the early 1990s; Carscadden *et al.* 1997, DFO 2024, Buren *et al.* 2019, Murphy *et al.* 2021, Murphy 2022, Tripp *et al.* 2023). Additionally, as *D. viridis* releases sulphuric acid upon senescence under consistently warm ($> 12^{\circ}\text{C}$) temperatures (Gagnon *et al.* 2013, Blain and Gagnon 2013, 2014), high egg mortality could occur if warm temperatures result in the die-off of *D. viridis* while incubating capelin eggs are adhered. Overall, baseline information on the location and extent of suitable subtidal spawning habitat provided by our HSM will be important for future monitoring of capelin in Notre Dame Bay, and future surveys pairing sediment sampling and video are recommended to build HSMs in other regions.

Our HSMs for suitable herring spawning habitat suggest that this habitat is abundant in both bays (Fig. 2.3, Table 2.3), likely due to the broad habitat requirements of spawning herring. In Fortune Bay, we recorded herring spawning at two sites within the area of suitable spawning habitat predicted by our model (Fig. 2.3) and herring also spawned in Notre Dame Bay at sites in which our model predicted the presence of suitable structural spawning habitat during May 2024 and 2025 (49.46°N, 53.96°W; Davoren unpublished data). However, unlike the well-characterized habitat associations that result in high hatching success at subtidal capelin

spawning sites in coastal Newfoundland (Table 1.1; Tripp *et al.* 2023), optimal spawning habitat characteristics for herring in this region are largely unknown. Therefore, it is possible that our models provide an overestimate of the extent of suitable herring spawning habitat and likely could be refined through the development of HSMs which focus on characteristics representing habitat quality. For instance, we included the predicted location of all marine vegetation species as suitable structural habitat for herring spawning in our HSMs and, while adhered herring eggs have been documented on a breadth of marine vegetation species (Tibbo *et al.* 1963, Messieh *et al.* 1983, Hourston *et al.* 1984, Haegele and Schweigert 1985, Munro *et al.* 1998, Shelton *et al.* 2014), some studies have shown varying egg survival rates when reared on different macroalgae species for both Pacific herring (Shelton *et al.* 2014) and Atlantic herring (Aneer 1987, Burbank unpublished data). Future studies examining hatching success on different substrate types (sediment grain size, vegetation) in coastal Newfoundland could help refine our models and provide a more realistic estimate of the spatial extent of high-quality (i.e., high offspring survival) spawning habitat.

Predicted areas for suitable sand lance burying habitat were more limited (Table 2.3) and patchier (Fig. 2.3) relative to capelin and herring spawning habitat in both bays, likely due to their narrow habitat requirements. Although sand and granule presence were spatially autocorrelated (Table S2.1, S2.2) and less patchy at a fine scale (i.e., low within-site variability) relative to larger sediment grain sizes (Table 1.2), the large-scale patchiness of suitable habitat in coastal Newfoundland may result in generally lower sand lance abundance. This large-scale patchiness also may increase sand lance vulnerability relative to other forage fish species to coastal habitat degradation through warming and anthropogenic activities that alter their limited habitats (e.g., dredging, aquaculture, and noise from boat traffic, pile driving, wind farms;

Staudinger *et al.* 2020, Huard *et al.* 2024, Carlson *et al.* 2025). In support, our HSM predicted a 35.2% decrease in the area of suitable sand lance burying habitat under a 2.1°C increase in seabed temperature (Fig. 2.3, Table 2.3). Alternatively, the limited areas of rare patchy sand lance burying habitat predicted by our HSMs in each bay provide discrete localized areas for focused protection of sand lance if these patches are temporally stable. As Pacific sand lance are restricted to forage in areas immediately surrounding (i.e., within 2 km) suitable sediment patches year-round (Haynes and Robinson 2011, Robinson *et al.* 2013), the spatial extent of suitable habitat may be even more restricted than predicted by our HSMs to areas with suitable sediment that overlap with high zooplankton densities. Although sand lance distribution may be driven to a greater degree by the presence of suitable burying habitat than zooplankton density (van der Kooij *et al.* 2008), sand lance abundance may be further limited if prey densities are low within foraging ranges of suitable burying habitat patches. Therefore, quantifying zooplankton densities nearby suitable sediment patches could refine our burying HSMs during spring–summer, when sand lance are actively feeding, in contrast to capelin and herring which cease feeding during spawning (Vesin *et al.* 1981, Stacey and Hourston 1982, Taylor 1964, Nøttestad *et al.* 1996, Davoren *et al.* 2006). Additionally, as most habitat associations used to build our sand lance HSMs were based on those characterized for different *Ammodytes* species in the Pacific and northeast Atlantic, our study highlights the importance of characterizing the understudied habitat associations of sand lance in coastal Newfoundland (see Staudinger *et al.* 2020). While the distributions of two *Ammodytes* species in Newfoundland are thought to differ (i.e., shallow nearshore versus deeper offshore habitat; Staudinger *et al.* 2020), recent studies characterizing sand lance habitat do not differentiate between these two species (e.g., Morrison and Davoren 2024). While we did not sample/observe sand lance in either bay and sand lance can evade

typical fish sampling methods (e.g., acoustics, trawling) by burying, a combination of these and alternative methods, such as environmental DNA sampling, could serve to validate our HSM predictions (see Robinson *et al.* 2022).

Future studies should consider performing similar habitat surveys across multiple years, allowing us to assess inter-annual variability in the extent of suitable forage fish habitat (e.g., variation in cover of annual macroalgal species, coastal deposits of fine grain sizes). Indeed, the retention of suitable sediment in bedrock depressions is an important feature of annually persistent subtidal capelin spawning sites in coastal Newfoundland, where a deeper, more temporally stable layer of suitable sediment is present relative to a thin ephemeral layer on flat, exposed bedrock (Davoren *et al.* 2008, Penton and Davoren 2012). Similarly, sand lance show inter-annual site fidelity to areas with persistent suitable burying habitat (Haynes and Robinson 2011, Morrison and Davoren 2024). Pairing hydroacoustic surveys and sediment sampling on an annual basis could inform fine-scale bathymetry and the location of important persistent suitable sediment patches. Additionally, investigating interannual differences in the distribution of marine vegetation would provide information on the temporal stability of our HSM predictions, as vegetation likely provides important biogenic structure (e.g., capelin spawning on *D. viridis*; Bliss and Davoren 2021) where suitable sediment grain sizes are absent (i.e., barren bedrock or boulder habitat). To illustrate, our HSMs predicted a decrease in the extent of suitable subtidal habitat for all forage fish in Notre Dame Bay under a 2.1°C increase in seabed temperature (Fig. 2.3, Table 2.3) and, as Newfoundland's coast presents an interface between subarctic and boreal biogeographic regions, where both cold- and warm-water adapted macroalgae species are present at the extremes of their respective ranges (Adey and Steneck 2001, Merzouk and Johnson 2011), the distributions of some species are likely to change with ocean warming (Wilson and Lotze

2019, Wilson *et al.* 2019). High inter-annual variation in seabed temperatures also may influence density and distributional patterns of annual macroalgae species on shorter temporal scales (i.e., between years). For example, *D. viridis*, a structural habitat-forming annual brown alga, experiences senescence-related mortality at extended periods $> 12^{\circ}\text{C}$ (Gagnon *et al.* 2013, Blain and Gagnon 2013, 2014), resulting in inter-annual variation in site-specific presence (Bliss and Davoren 2021). As this species is typically restricted to nearshore sites where high wave action aids in resistance to urchin grazing (Gagnon *et al.* 2006), it is unlikely to undergo an offshore distributional shift as nearshore waters warm. Therefore, warming in coastal Newfoundland is likely to result in the loss of this important structure-forming species, reducing spawning habitat availability for capelin and herring (Fig. 2.3).

Conclusion

Overall, our HSM predictions are only as accurate as the habitat associations that inform them. Therefore, we recommend studies in coastal Newfoundland further characterize the species-specific habitat associations of these forage fish species, which may differ throughout their ranges, to improve model predictions. For example, while capelin appear to primarily select spawning habitat based on the presence of fine grain size sediment in coastal Newfoundland (Penton and Davoren 2012), capelin eggs have also been recorded adhered to larger substrates (e.g., boulder, bedrock, anthropogenic structures) in the eastern Canadian Arctic (Ogloff *et al.* 2020). While subtidal capelin spawning habitat is generally well-documented in coastal Newfoundland (e.g., Nakashima and Wheeler 2002, Davoren *et al.* 2008, Penton and Davoren 2012, Crook *et al.* 2017, Bliss and Davoren 2021), we relied to a greater extent on habitat associations from the Pacific and elsewhere in the Atlantic for herring spawning and sand lance burying habitat, as habitat characteristics of these species are generally understudied in coastal

Newfoundland. Future studies could refine our HSMs by including additional habitat characteristics in models (e.g., macroalgal density). Similar calls for further defining forage fish habitat associations in the northwest Atlantic have been made (e.g., Staudinger *et al.* 2020). For example, refining models by incorporating a narrower range of depth and salinity could further inform habitat quality. Indeed, a recently described annually persistent sand lance burying site in coastal Newfoundland (Morrison and Davoren 2024) has a documented narrow salinity range (31.1–31.3 psu; Loeppky and Davoren 2018), the interaction between temperature and salinity is known to influence herring egg development and/or post-hatch mortality rates (e.g., Alderdice and Velsen 1971, Alderdice *et al.* 1979), and salinity may also indirectly impact spawning habitat by influencing the distribution of biogenic structure (e.g., high *D. viridis* mortality < 29 psu; Gagnon *et al.* 2013).

As detailed fine-scale bathymetry, seabed substrate type, and temperature and ocean current models are lacking in coastal Newfoundland, funding programs that promote the collection of baseline coastal habitat information (e.g., Fisheries and Oceans Canada’s Coastal Environmental Baseline Program, <https://www.dfo-mpo.gc.ca/science/partnerships-partenariats/research-recherche/cebp-pdecr/index-eng.html>) will also be critical for building HSMs for these and other species in other regions of coastal Newfoundland, and for other understudied areas. These baseline data could also validate our HSM predictions by confirming species presence. Refining the simple HSMs presented here will directly inform spatial planning and management to protect important forage fish habitat (e.g., avoiding dredging, armouring, and aquaculture siting within limited areas identified as suitable for spawning and/or burying; Dugan and Hubbard 2006, Wenger *et al.* 2017, Huard *et al.* 2024) and allow us to predict changes in the extent of suitable habitat due to changing ocean conditions. As forage fish represent critical

energy links in marine food webs, their protection will ultimately promote ecosystem-based approaches to fisheries management (Smith *et al.* 2011, Pikitch *et al.* 2012, 2014, Dickey-Collas *et al.* 2014).

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Tables

Table 2.1. Summary of published forage fish habitat associations for spawning during spring–summer (herring) and summer (capelin) and for burying year-round (sand lance) in subtidal habitat. Where possible, habitat associations in Newfoundland, Canada, are listed; habitat associations documented for the same species or other species within the same genus outside the northwest Atlantic are indicated by *.

	Capelin <i>Mallotus villosus</i>	Herring <i>Clupea harengus</i>	Sand lance <i>Ammodytes</i> spp.
Spawn timing	Summer (June–August) ^{1,2}	Spring–summer (April–June) ⁹	Fall–winter ¹⁹
Sediment (mm)	Silt-free sand, granules, pebbles (0.5–25) ^{3,4,5}	Pebbles, gravel, cobbles (4–150) ^{10,11*,12}	Silt-free sand, granules (0.5–4) ^{20*,21,22*}
Marine vegetation	<i>Desmarestia viridis</i> ⁶	Various genera ^{10,13,14,15*,16}	N/A
Depth (m)	≤ 50 ^{4,7}	< 20–80 ^{9,11*,14,17*}	~20–60, up to 80 ^{19,20*,21,22*,23*}
Temperature (°C)	2–12 ^{3,4,7,8}	2–12 ^{9,18}	1–11 ^{21,22*}

¹Carscadden *et al.* 1997, ²Davoren *et al.* 2025, ³Nakashima and Wheeler 2002, ⁴Davoren *et al.* 2008, ⁵Penton and Davoren 2012, ⁶Bliss and Davoren 2021, ⁷Carscadden *et al.* 1989, ⁸Crook *et al.* 2017, ⁹Parsons 1973, ¹⁰Munro *et al.* 1998, ¹¹Runnstrom 1941, ¹²de Groot 1980, ¹³Tibbo *et al.* 1963, ¹⁴Haegle and Schweigert 1985, ¹⁵Shelton *et al.* 2014, ¹⁶Messieh *et al.* 1983, ¹⁷Thompson 2005, ¹⁸Scattergood 1959, ¹⁹Staudinger *et al.* 2020, ²⁰Wright *et al.* 2000, ²¹Morrison and Davoren 2024, ²²Reay 1970, ²³Ostrand *et al.* 2005

Table 2.2. Summary of coastal marine habitat survey results, indicating the number of sites (number of sediment grabs in brackets) and date range of sampling in Notre Dame Bay (NDB) during July 2023 and Fortune Bay (FB) during May 2024. The percentage of the total number of surveyed sites with the presence of each sediment type (grain size in mm indicated in table header) and marine vegetation, with *Desmarestia viridis* indicated separately, confirmed via sediment grab and/or video, and the mean (range) bottom temperature and salinity measured in both bays are provided. The percentages of sites that had the same presence of each sediment grain size and marine vegetation in duplicate samples at the same site is indicated in brackets.

Bay / No. sites (sediment grabs)	Survey date range	Sand (0.5–2)	Granule (2–4)	Pebble (4–64)	Cobble (64–150)	Marine vegetation	<i>D. viridis</i>	Seabed temp. (°C)	Salinity (psu)
NDB / 131 (262)	9–20 July	14.9 (85)	4.2 (90)	25.6 (74)	36.6 (75)	63.4 (78)	16.8 (82)	8.4 (0.8–19.9)	27.8 (24.4–31.6)
FB / 112 (224)	15–25 May	17.9 (81)	9.4 (89)	52.7 (66)	48.7 (69)	93.3 (97)	34.8 (91)	4.3 (2.1–8.0)	29.1 (24.8–30.3)

Table 2.3. Total area surveyed (km²) along with the estimated total area (percentage of total surveyed area) of current suitable habitat for capelin subtidal spawning, herring subtidal spawning and sand lance burying based on interpolation of suitable habitat variables during July 2023 in Notre Dame Bay (NDB) and May 2024 in Fortune Bay (FB), Newfoundland. The change in the extent of suitable habitat (+ indicating increase, - indicating decrease) under two predicted ocean warming scenarios (see Han *et al.* 2015) is indicated (percentage change from current suitable area).

Bay (survey area km ²)	Species	Suitable spawning/burying area (current)	Change in suitable spawning/burying area (+0.4°C)	Change in suitable spawning/burying area (+2.1°C)
NDB (111.5)	Capelin	39.0 (35.0)	-1.3 (-3.3)	-7.6 (-19.5)
	Herring	81.8 (73.3)	+1.2 (+1.5)	-11.6 (-14.2)
	Sand lance	9.1 (8.1)	-0.5 (-5.5)	-3.2 (-35.2)
FB (92.4)	Capelin	90.2 (97.6)	0 (0)	0 (0)
	Herring	92.4 (100)	0 (0)	0 (0)
	Sand lance	23.2 (25.2)	0 (0)	0 (0)

Figures

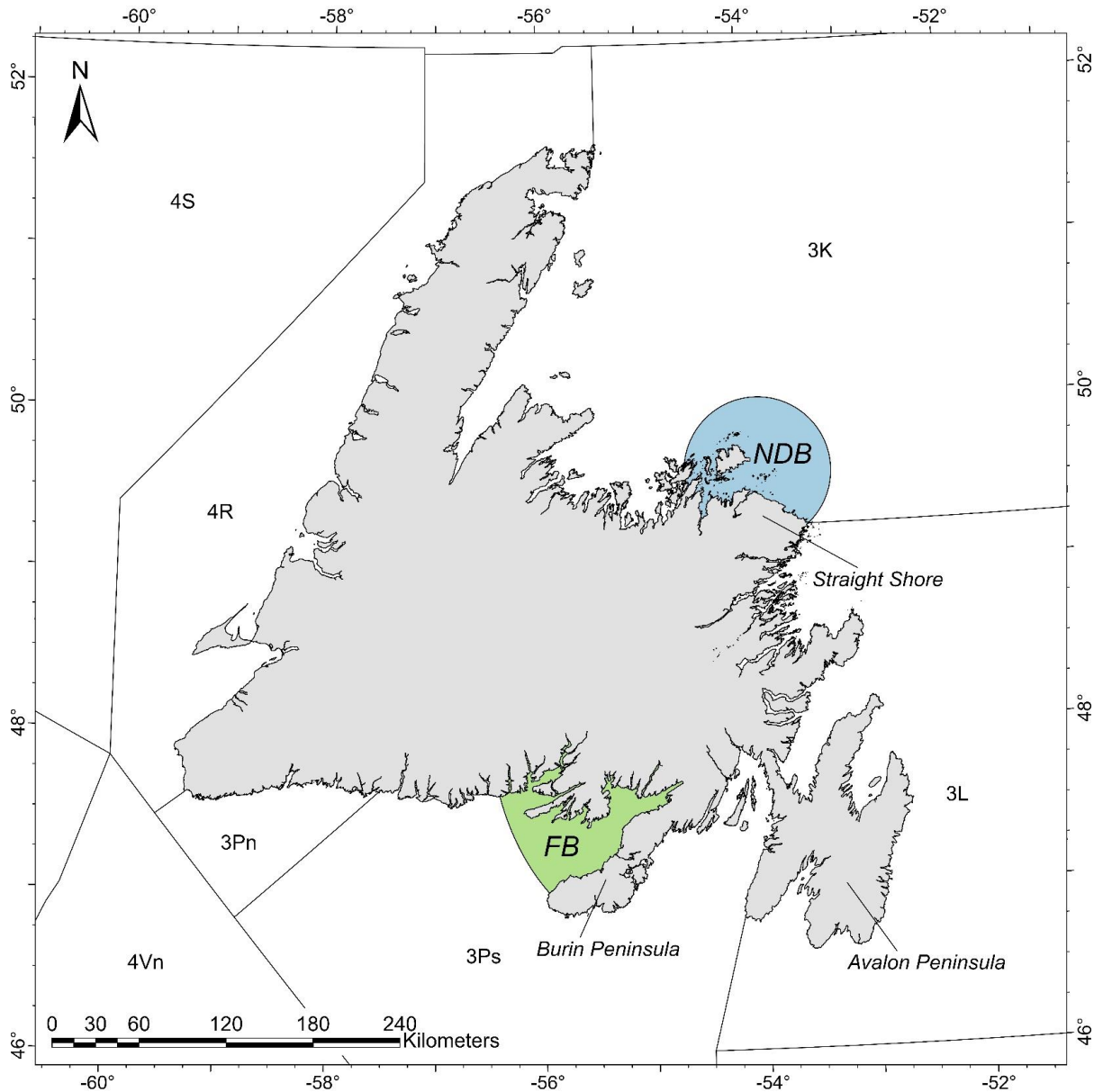


Figure 2.1. The location of the study areas on the northeast (Notre Dame Bay, NDB) and south (Fortune Bay, FB) coasts of Newfoundland, Canada. Black lines indicate the boundaries of Northwest Atlantic Fisheries Organization (NAFO) Divisions in the region.

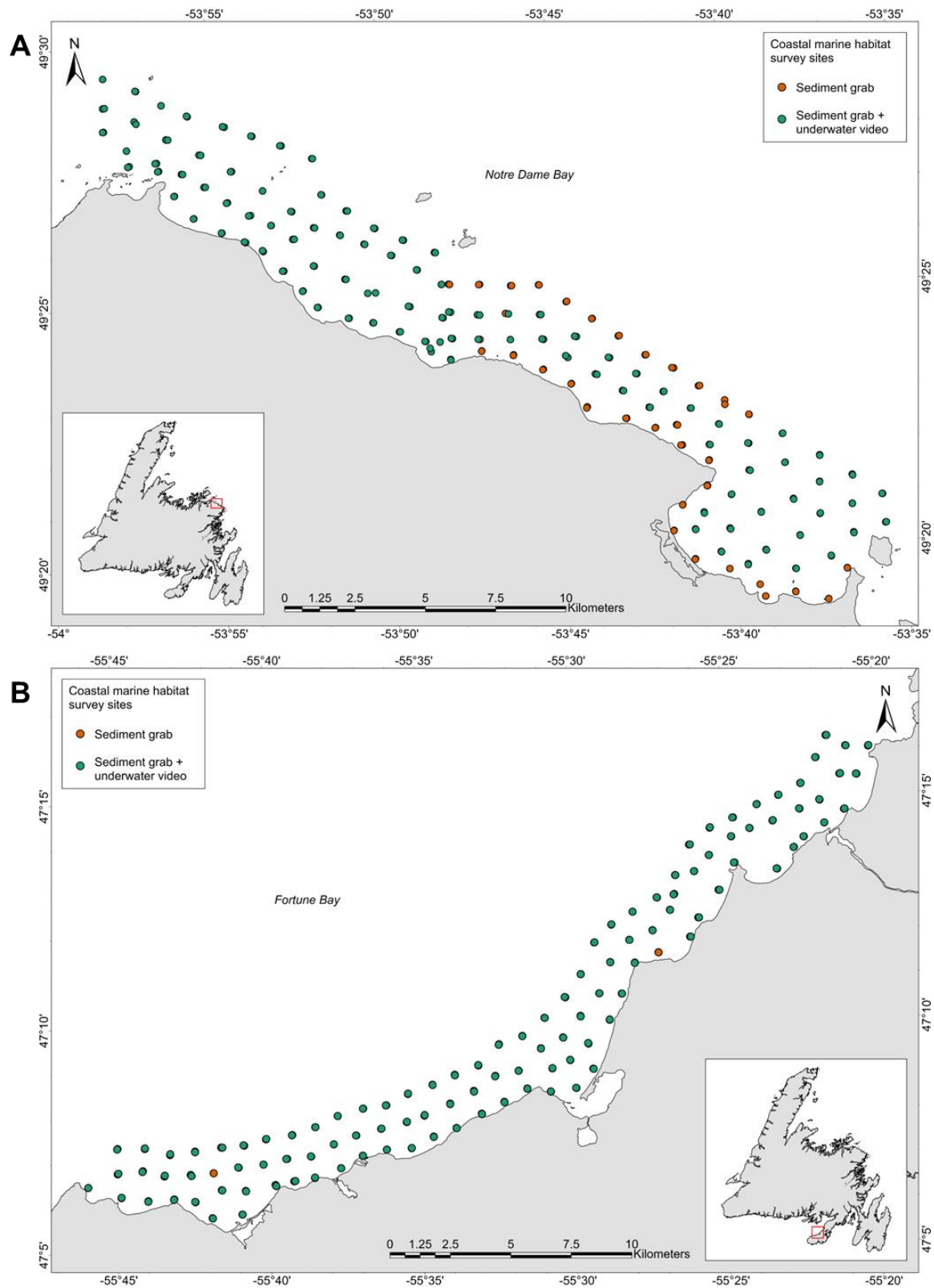


Figure 2.2. The survey design showing sites sampled for forage fish presence and coastal marine habitat characteristics during July 2023 in Notre Dame Bay (A) and during May 2024 in Fortune Bay (B) in Newfoundland, Canada.

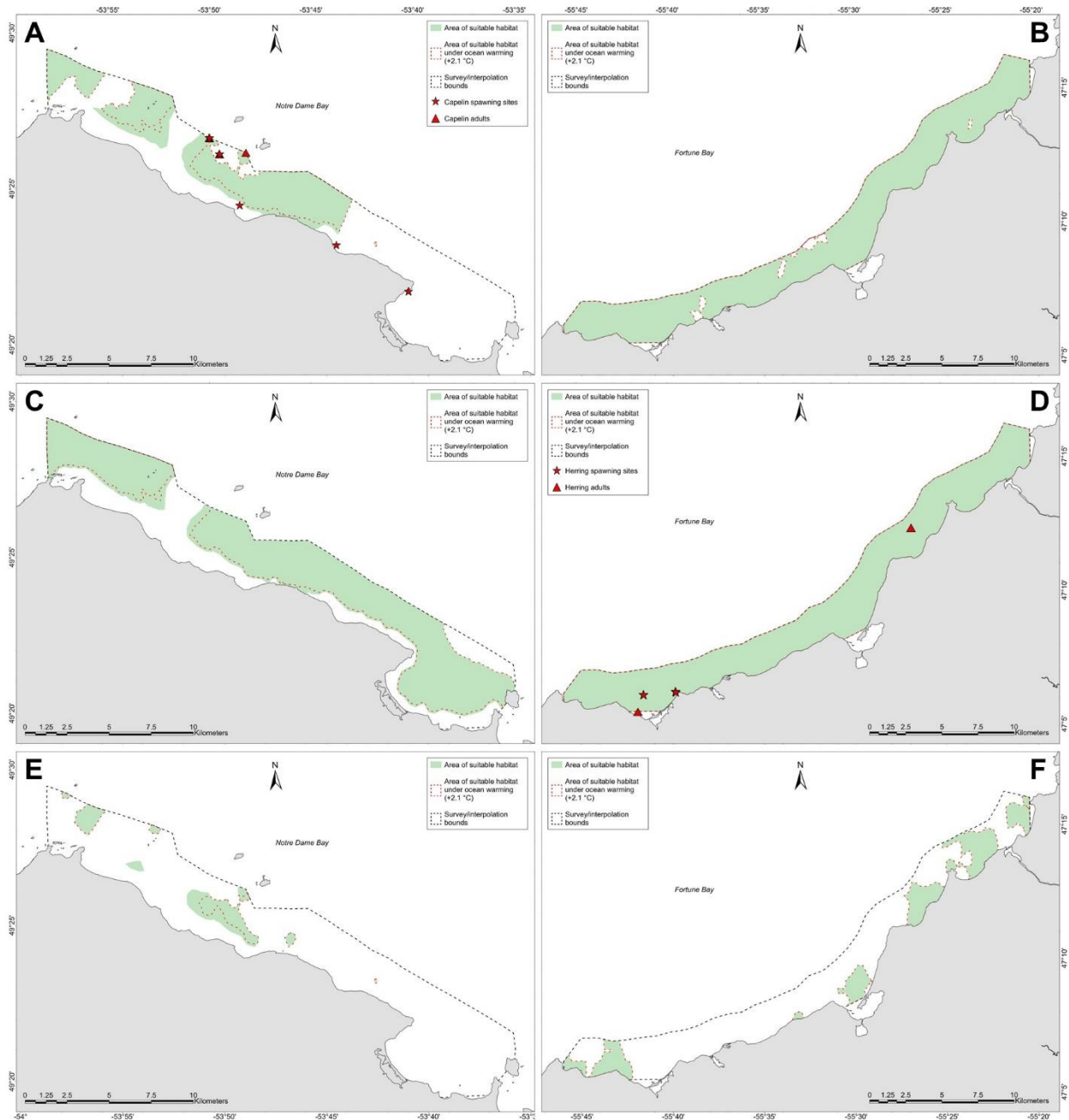


Figure 2.3. Results of Ordinary Kriging interpolation of suitable coastal (≤ 50 m) marine structural habitat (i.e., presence of suitable seabed sediment grain size ranges and marine vegetation) and environmental conditions (seabed temperature) as outlined in Figures S1 and S2, showing the area of suitable habitat for capelin spawning (A, B), herring spawning (C, D), and sand lance burying (E, F) in Notre Dame Bay (July) and Fortune Bay (May), Newfoundland. Current suitable area based on contemporary survey data shown in green, with the area of suitable habitat based on a 2.1°C increase in seabed temperature shown by the dashed red line. The locations of observed forage fish eggs and/or adults during surveys are shown.

Supplementary Materials

Table S2.1. Summary of Global Moran's I tests for spatial autocorrelation of coastal marine environmental data (presence/absence of sediment grain sizes and marine vegetation species, continuous seabed temperature measures collected in Notre Dame Bay during July 2023) using inverse Euclidean distance with row standardization, where: $p > 0.05$ = random spatial distribution, $p < 0.05$ and $z > 0$ = spatially clustered feature, and $p < 0.05$ and $z < 0$ = spatially dispersed feature (typically reflecting a competitive process). Moran's Index nearing 1 indicates clustering, -1 indicates dispersal/repellence, and 0 indicates random distribution.

Variable	Distance threshold (km)	Moran's Index	z-score	p-value	Interpretation
Sand	5	0.229	4.578	< 0.001	Clustered
	15	0.183	4.209	< 0.001	Clustered
	25	0.171	4.071	< 0.001	Clustered
Granule	5	0.006	0.199	0.842	Random
	15	0.005	0.213	0.831	Random
	25	0.004	0.190	0.849	Random
Pebble	5	0.277	5.480	< 0.001	Clustered
	15	0.246	5.592	< 0.001	Clustered
	25	0.232	5.458	< 0.001	Clustered
Cobble	5	0.325	6.420	< 0.001	Clustered
	15	0.271	6.141	< 0.001	Clustered
	25	0.258	6.049	< 0.001	Clustered
<i>Desmarestia viridis</i>	5	0.369	7.309	< 0.001	Clustered
	15	0.314	7.156	< 0.001	Clustered
	25	0.297	6.986	< 0.001	Clustered
Marine vegetation	5	0.453	8.914	< 0.001	Clustered
	15	0.399	8.999	< 0.001	Clustered
	25	0.374	8.733	< 0.001	Clustered
Temperature	5	0.680	13.307	< 0.001	Clustered
	15	0.579	12.997	< 0.001	Clustered
	25	0.554	12.875	< 0.001	Clustered

Table S2.2. Summary of Global Moran's I tests for spatial autocorrelation of coastal marine environmental data (presence/absence of sediment grain sizes and marine vegetation species, continuous seabed temperature measures collected in Fortune Bay during May 2024) using inverse Euclidean distance with row standardization, where: $p > 0.05$ = random spatial distribution, $p < 0.05$ and $z > 0$ = spatially clustered feature, and $p < 0.05$ and $z < 0$ = spatially dispersed feature (typically reflecting a competitive process). Moran's Index nearing 1 indicates clustering, -1 indicates dispersal/repellence, and 0 indicates random distribution.

Variable	Distance threshold (km)	Moran's Index	z-score	p-value	Interpretation
Sand	5	0.218	3.208	0.001	Clustered
	15	0.196	3.181	0.001	Clustered
	25	0.187	3.126	0.002	Clustered
Granule	5	0.186	2.781	0.005	Clustered
	15	0.162	2.666	0.007	Clustered
	25	0.154	2.617	0.009	Clustered
Pebble	5	0.235	3.431	< 0.001	Clustered
	15	0.209	3.375	< 0.001	Clustered
	25	0.204	3.375	< 0.001	Clustered
Cobble	5	0.340	4.933	< 0.001	Clustered
	15	0.312	4.996	< 0.001	Clustered
	25	0.300	4.939	< 0.001	Clustered
<i>Desmarestia viridis</i>	5	0.600	8.662	< 0.001	Clustered
	15	0.543	8.638	< 0.001	Clustered
	25	0.527	8.631	< 0.001	Clustered
Marine vegetation	5	0.546	8.095	< 0.001	Clustered
	15	0.486	7.960	< 0.001	Clustered
	25	0.467	7.871	< 0.001	Clustered
Temperature	5	0.645	9.520	< 0.001	Clustered
	15	0.571	9.309	< 0.001	Clustered
	25	0.555	9.299	< 0.001	Clustered

Table S2.3. Comparison of cross validation results from exploratory analysis of deterministic (Inverse Distance Weighted, “IDW”) and geostatistical (Ordinary Kriging) spatial interpolation methods for coastal marine environmental data (presence/absence of sediment grain sizes and marine vegetation species, continuous seabed temperature measures collected in Notre Dame Bay during July 2023). Lowest root-mean-square error (RMSE) value indicates the best interpolation model fit. All interpolation models constructed with a minimum of ten and maximum of 15 neighbours within a single 360° sector.

Habitat variable	Method	Power	RMSE
Sand	IDW	1	0.323
	IDW	2	0.347
	Ordinary Kriging	N/A	0.308
Granule	IDW	1	0.232
	IDW	2	0.273
	Ordinary Kriging	N/A	0.209
Pebble	IDW	1	0.424
	IDW	2	0.475
	Ordinary Kriging	N/A	0.407
Cobble	IDW	1	0.413
	IDW	2	0.451
	Ordinary Kriging	N/A	0.396
<i>Desmarestia viridis</i>	IDW	1	0.329
	IDW	2	0.373
	Ordinary Kriging	N/A	0.323
Marine vegetation	IDW	1	0.398
	IDW	2	0.435
	Ordinary Kriging	N/A	0.385
Temperature	IDW	1	1.895
	IDW	2	1.465
	Ordinary Kriging	N/A	1.454

Table S2.4. Comparison of cross validation results from exploratory analysis of deterministic (Inverse Distance Weighted, “IDW”) and geostatistical (Ordinary Kriging) spatial interpolation methods for coastal marine environmental data (presence/absence of sediment grain sizes and marine vegetation species, continuous seabed temperature measures collected in Fortune Bay during May 2024). Lowest root-mean-square error (RMSE) value indicates the best interpolation model fit. All interpolation models constructed with a minimum of ten and maximum of 15 neighbours within a single 360° sector.

Habitat variable	Method	Power	RMSE
Sand	IDW	1	0.415
	IDW	2	0.442
	Ordinary Kriging	N/A	0.385
Granule	IDW	1	0.321
	IDW	2	0.340
	Ordinary Kriging	N/A	0.289
Pebble	IDW	1	0.539
	IDW	2	0.581
	Ordinary Kriging	N/A	0.481
Cobble	IDW	1	0.514
	IDW	2	0.558
	Ordinary Kriging	N/A	0.439
<i>Desmarestia viridis</i>	IDW	1	0.287
	IDW	2	0.298
	Ordinary Kriging	N/A	0.283
Marine vegetation	IDW	1	0.164
	IDW	2	0.164
	Ordinary Kriging	N/A	0.157
Temperature	IDW	1	0.581
	IDW	2	0.604
	Ordinary Kriging	N/A	0.579

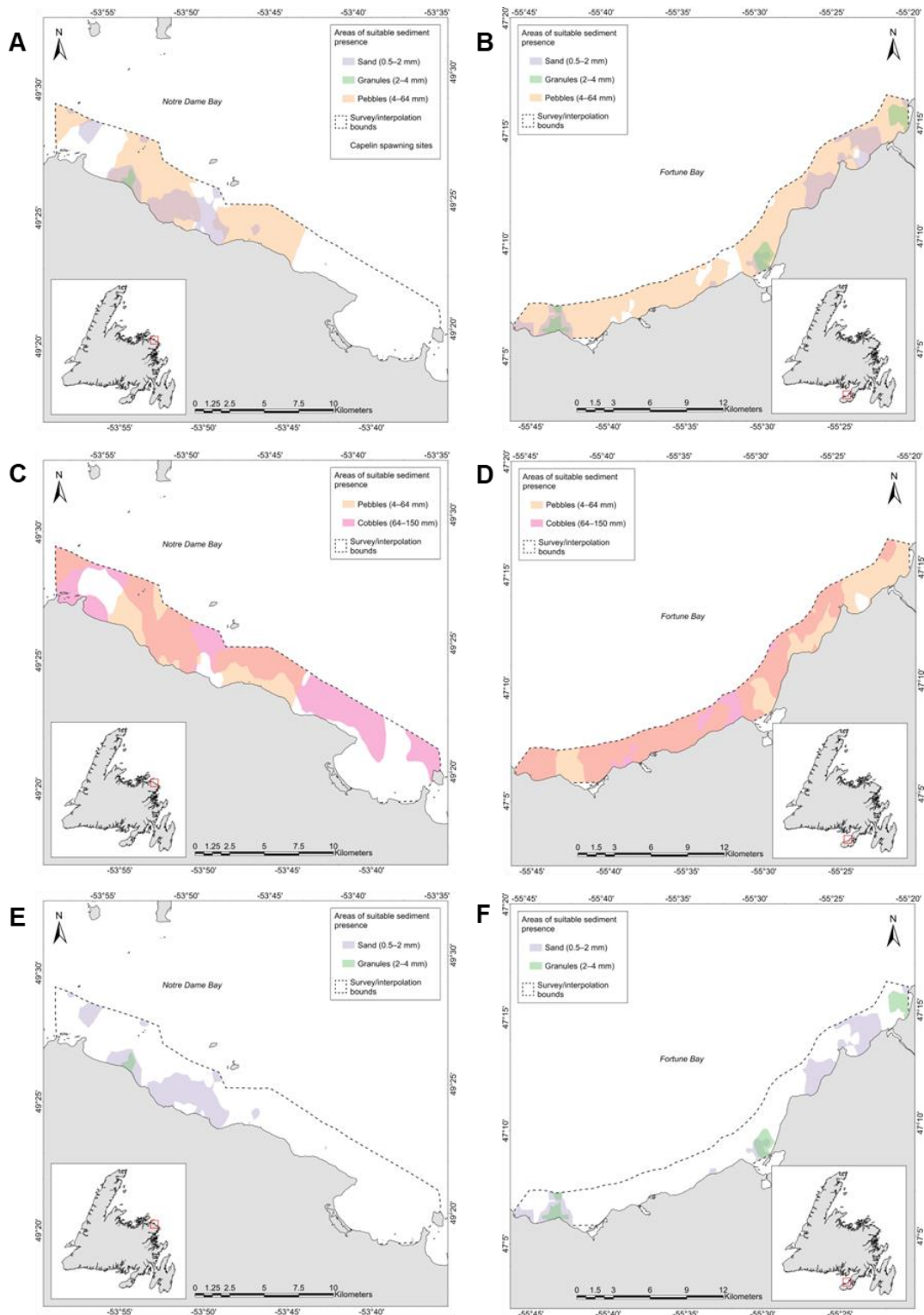


Figure S2.1. Results of Ordinary Kriging interpolation showing the overlap of suitable sediment grain sizes for capelin spawning (A, B), herring spawning (C, D), and sand lance burying (E, F) in Notre Dame (July) and Fortune Bay (May), Newfoundland.

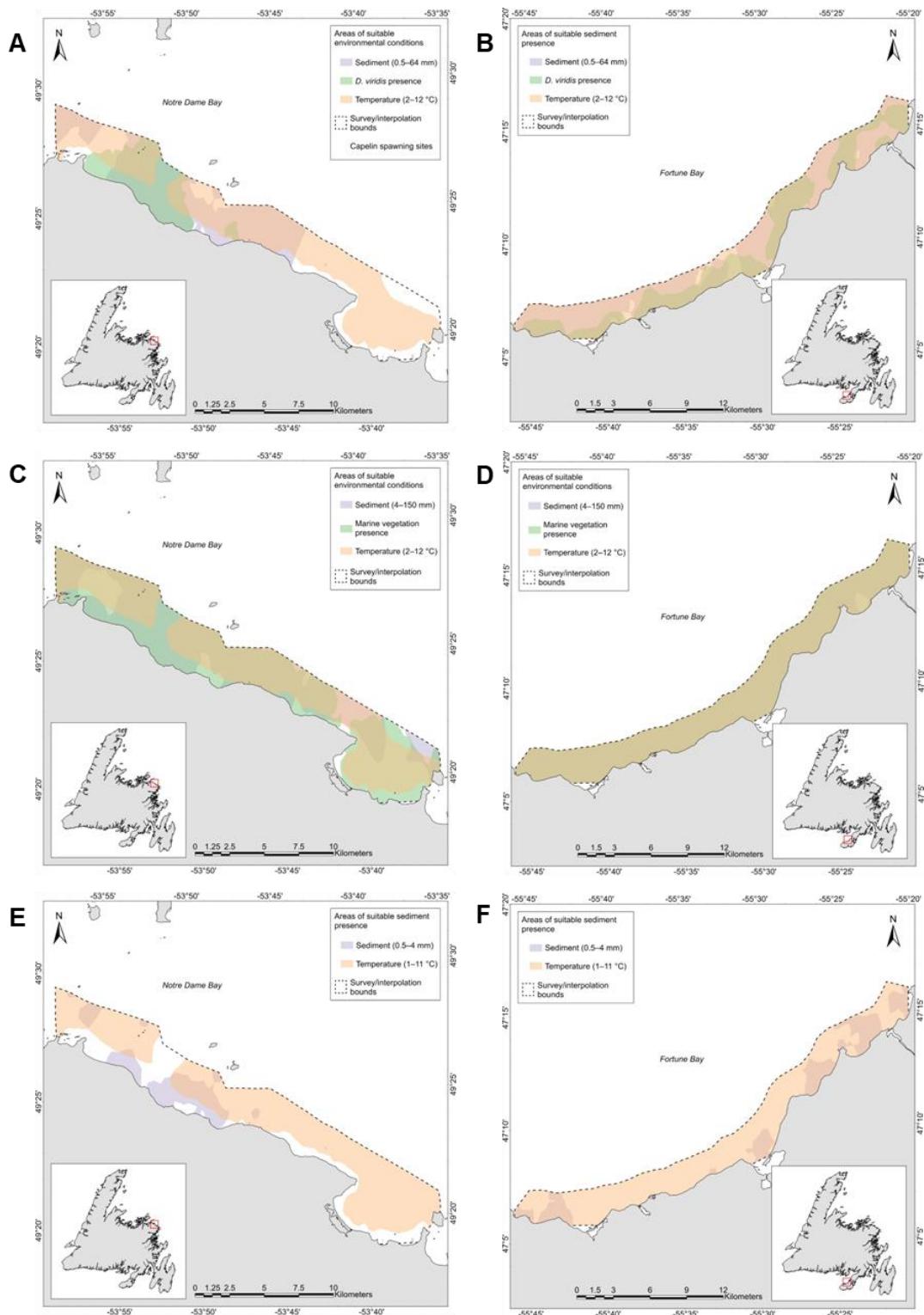


Figure S2.2. Results of Ordinary Kriging interpolation showing the overlap of suitable sediment grain sizes, marine vegetation, and seabed temperatures for capelin spawning (A, B), herring spawning (C, D), and sand lance burying (E, F) in Notre Dame (July) and Fortune Bay (May), Newfoundland.

Chapter Three: Chick-rearing alcids use divergent prey patch characteristics during foraging in Newfoundland, Canada.

Abstract

Central place foragers in patchy environments should maximize their net energy intake by targeting nearby prey patches with high densities of accessible prey, but high competitor densities may also influence species-specific patch selection decisions among species with varying competitive ability. Atlantic puffins *Fratercula arctica*, razorbills *Alca torda*, and common murre *Uria aalge* breed in large numbers on multi-species colonies in the northwest Atlantic. In coastal Newfoundland, Canada, these species in the family Alcidae (alcids) rely primarily on forage fish as prey during the summer breeding season to provision their chicks but may target prey patches with different characteristics as body size and dive capability confer varying competitive abilities. We aimed to quantify species-specific prey patch characteristics and predicted that the small-bodied Atlantic puffin would forage at lower prey and competitor densities than the mid-sized razorbill and large-bodied common murre. Using archived GPS tagging data collected from each species during chick-rearing, we determined species-specific foraging hotspots (i.e., 50% and 95% volume contours) and conducted paired hydroacoustic and seabird surveys to quantify prey accessibility (i.e., depth, m) and density, site temperature, and relative abundances of competitors. Non-metric multidimensional scaling revealed that alcid hotspots differed based on community and environmental variables and generalized linear models revealed that Atlantic puffins foraged at deeper, colder sites with lower prey densities compared to razorbills, suggesting puffins may be displaced from higher quality prey patches. By contrast, common murre foraged at higher conspecific densities than smaller-bodied alcids (i.e., Atlantic puffins and razorbills) at a wide range of prey densities and depths, showing that

common murres distribute across a broader range of patch qualities during foraging likely due to their higher breeding population. This study elucidates divergent species-specific prey patch characteristics among these three alcid species, while revealing temporally persistent foraging areas and predictable locations where their prey complete important parts of their annual cycle (e.g., spawning sites), informing important conservation targets within this marine ecosystem.

Introduction

The marginal value theorem predicts that predators should maximize their net energy intake when foraging in a patchy environment by selecting high density prey patches, where the rate of energy intake is greater than the mean across the environment (Charnov 1976; Tome 1988). Central place foragers, animals that must return to a central place following foraging excursions (e.g., a breeding bird returning to a nest), are predicted to make patch selection decisions based on patch distance from the central place, where nearby patches are prioritized if the forager can achieve the same net energy intake relative to distant patches (Orians and Pearson 1979). When multiple species use the same central place (e.g., a multi-species breeding colony), high numbers of competitors may forage near the central place and competitor density may also influence patch selection decisions. The ideal free distribution model assumes that energy intake rates in a prey patch decrease with increasing conspecific and allospecific densities when individuals compete for prey and, thus, competitor density should also be considered during patch selection (Fretwell and Lucas 1970, assumptions and modifications reviewed in Kennedy and Gray 1993, Tregenza 1995). Therefore, assuming prey are equally available at each patch, this model predicts that a predator foraging at a high prey density patch with more competitors will have a rate of energy intake equal to that of a predator foraging at a low prey density patch with fewer competitors (Tregenza 1995).

Chick-rearing seabirds are central place foragers and, thus, must travel out from nests to forage for themselves and their offspring at sea and return with prey to provision chicks. Most seabird species are colonial breeders (Danchin and Wagner 1997), and seabirds frequently nest in large numbers, often at multi-species colonies (Brown *et al.* 1990). Large numbers of birds foraging within limited foraging ranges of multispecies colonies may result in prey limitation

through mechanisms such as local prey displacement, as prey become wary of predation (“landscape of fear”; Brown *et al.* 1999, Laundré *et al.* 2010), or local prey depletion (“Ashmole’s halo”; Ashmole 1963) resulting from predation rates that exceed replacement (Weber *et al.* 2021). Although prey limitation within colony foraging ranges is often unknown, previous studies have shown behavioural, spatial, and/or temporal segregation by seabirds during foraging (Piatt 1990, Linnebjerg *et al.* 2015, Pratte *et al.* 2017, Jenkins and Davoren 2020, Weber *et al.* 2021, Symons and Diamond 2022), possibly indicating intra- and interspecific competition.

The largest populations of breeding common murres *Uria aalge* (hereafter “murres”) and Atlantic puffins *Fratercula arctica* (hereafter “puffins”) in the northwest Atlantic are found in coastal Newfoundland, Canada (Lowther *et al.* 2020, Ainley *et al.* 2021), and razorbill *Alca torda* populations are increasing in this region (Lavers *et al.* 2020). All three species are members of the Family Alcidae (hereafter “alcids”), characterized as wing-propelled pursuit-divers, that breed at multiple colonies on the northeast coast of Newfoundland (Fig. 3.1). Due to their high wing loading (body mass to wing surface area ratio), alcids have high energetic costs of flight (Elliott *et al.* 2013, Winkler *et al.* 2020). During the summer on the northeast Newfoundland coast, breeding pairs of each species lay one egg and rely primarily on forage fish as key prey to successfully provision and raise their chicks (Gulka and Davoren 2019, Gulka *et al.* 2019, Montevecchi *et al.* 2019, Gulka *et al.* 2020, Jenkins and Davoren 2020). These alcids rely on a variable diet of sand lance *Ammodytes* spp., small crustaceans (e.g., northern shrimp *Pandalus borealis*), and juvenile fish of other species (e.g., Atlantic cod *Gadus morhua*) during incubation and early chick-rearing and typically shift to capelin *Mallotus villosus* when capelin arrive inshore to spawn, resulting in decreased dietary diversity and increased trophic position during chick-rearing (Gulka *et al.* 2020, Jenkins and Davoren 2020, Lescure *et al.* 2023). Capelin are

high-quality prey (i.e., calorically dense; Vonderbank 2024) that act as a pulsed resource, representing a ~150 times increase in forage fish biomass in coastal waters when they migrate inshore to spawn during the summer (Davoren *et al.* 2025). Additionally, the peak in capelin biomass during the summer typically coincides with alcid chick-rearing (July–August) on the northeast Newfoundland coast (Davoren 2024).

While parental murres, puffins, and razorbills all rely on forage fish to varying degrees during breeding to feed themselves and their chicks, physiological differences among these alcids may influence patch selection decisions. Puffins are the smallest of the three species (~300–550 g; Lowther *et al.* 2020), with the lowest energetic cost to flight (i.e., lowest wing loading; Pennycuik 1987) and, thus, may travel farther from colonies during foraging trips compared to the mid-sized razorbills (~500–900 g; Lavers *et al.* 2020) and larger murres (the largest extant alcid, ~800–1,100 g; Ainley *et al.* 2021), which have greater energetic costs of flight. Indeed, puffins have been shown to travel farther during foraging trips from colonies where they breed sympatrically with razorbills in other regions (Symons and Diamond 2022). Alcids also have differing physiological dive capabilities; puffins have a shallower maximum dive depth (~50–60 m; Piatt and Nettleship 1985, Burger and Simpson 1986, Dalton unpublished data) relative to razorbills (~120 m; Piatt and Nettleship 1985) and murres (~180 m; Piatt and Nettleship 1985, Burger and Simpson 1986, Hedd *et al.* 2009, Regular *et al.* 2010). While murres tend to dive deeper for prey than puffins and razorbills where the species co-occur (Piatt 1990, Linnebjerg *et al.* 2015), all three alcids tend to forage on shallow (< 50 m) prey aggregations when they are available in coastal Newfoundland (Piatt 1990, Gulka *et al.* 2019). In support, all three species have shallow mean dive depths (~10–30 m) compared to species-specific maxima when they forage at coastal capelin spawning sites on the northeast Newfoundland coast (Hedd

et al. 2009, Lesure *et al.* 2023, Dalton unpublished data).

Murres may be competitively dominant relative to razorbills and puffins, a relationship observed in other pursuit- and plunge-diving seabird species of varying body size (e.g., shearwaters *Ardenna* spp.; Carvalho *et al.* 2020). Piatt (1990) found that murres were associated with larger, more dense prey aggregations than puffins in coastal Newfoundland, and puffins tend to forage at a lower trophic level relative to razorbills and murres during chick-rearing where foraging ranges of all three species overlap (Pratte *et al.* 2017, Jenkins and Davoren 2020). Therefore, while prey are not typically expected to be limiting during alcid chick-rearing on the northeast Newfoundland coast and foraging in areas of high conspecific and/or allospecific densities may minimize energetic costs of searching (e.g., local enhancement, as demonstrated in murres and puffins; Bairos-Novak *et al.* 2015), puffins and razorbills may be excluded from high density prey patches due to their smaller body and lower dive depth capability relative to murres, resulting in the formation of species-specific foraging “hotspots” where each species makes trade-offs to attain similar net energy gain (e.g., between prey and competitor densities; Tregenza 1995).

Objectives

The objective of this thesis chapter was to examine prey patch characteristics used by three alcid species in coastal Newfoundland, Canada, during chick-rearing. We hypothesized that breeding alcids (puffins, razorbills, and murres) select prey patches with different characteristics at the population level such that they distribute themselves based on prey and competitor densities (i.e., in an ideal free manner) in accordance with their differing physiological attributes. Specifically, we predict that murres use patches with the greatest densities of prey, while razorbills use less dense prey patches with lower competitor densities, and puffins use the lowest

prey and competitor densities relative to murres and razorbills. Characterizing prey patches used by chick-rearing alcids on the northeast Newfoundland coast will increase our understanding of the factors that drive observed dietary and spatial differences among seabird species while foraging near colonies during breeding, a highly energetically taxing stage in their annual cycle.

Methods

Experimental Design

To identify the location of prey patches used by breeding alcids (puffins, razorbills, and murres), we used archived tracking data collected across four years (2016–2018, 2023) in Notre Dame Bay (Fig. 3.1) during previous studies (Gulka and Davoren 2019, Gulka *et al.* 2019, 2020, Lescure *et al.* 2023, Legard *et al.* 2025, Dalton unpublished data). In brief, global positioning system (GPS) tracking devices with a wet/dry sensor were deployed on chick-rearing birds at two multi-species breeding colonies. Tagging occurred on James Island, where ~16,900 pairs of puffins and ~2,800 pairs of razorbills breed (Jenkins *et al.* 2018), and on Funk Island, where ~472,300 pairs of murres breed (Wilhelm *et al.* 2015; Table S3.1). Additionally, ~10,000 pairs of northern gannets *Morus bassanus* breed alongside murres on Funk Island during the same period (Chardine *et al.* 2013). Devices collected location data (latitude and longitude) every 10 min and dive duration continuously when wet. We subset all tracking datasets to include locations of foraging dives, defined as the location recorded immediately preceding dives lasting > 4 s and occurring > 250 m from breeding colonies (see Gulka *et al.* 2020 for details). Following Gulka *et al.* (2020), we randomly subsampled the same number of dive locations from individuals within each species to ensure all tracked individuals in each year had equal influence on identifying core foraging areas. We then combined data for species with multiple years of tracking data (i.e., razorbills and murres; Table S3.1) to indicate the location of persistently used prey patches (e.g.,

capelin spawning and sand lance burrowing sites; Penton and Davoren 2012, Morrison and Davoren 2024). Next, we used kernel density estimation to determine the locations of species-specific foraging dive “hotspots”. Planar kernel density estimation (0.05° search radius, output cell size 2.89×10^{-3} dd) was performed in ArcGIS Pro v3.2.0 (Esri Inc, Redlands, California) using the Kernel Density geoprocessing tool, with input barrier features of the Wadham Islands Archipelago, Fogo Island, and the Notre Dame Bay coastline (“Straight Shore Region”; Fig. 3.1) to restrict density estimation to the marine environment. Finally, we summarized the output to the 50% (core) and 95% (total) volume contours for each alcid species to define foraging dive hotspots (Fig. S3.1). These hotspots were used to select locations for boat-based surveys to quantify species-specific prey patch characteristics (see below).

Boat-based Surveys

To match the timing of our surveys with tracking efforts in previous years, at-sea surveys were conducted during summer 2024 aboard the *Lady Easton III* (10 m commercial fishing vessel) after the onset of chick-rearing, defined as hatching in $> 25\%$ of regularly monitored nests (every 2–3 d) of puffins and razorbills on James Island (Fig. 3.1). Due to limited ship time, we selected a subset of 6–10 spatially distinct foraging hotspots of each species to maximize the ratio of survey to travel time. We prioritized surveys within core foraging hotspots (50% volume contours) that did not overlap with other species, but we also conducted surveys within total foraging hotspots (95% volume contours) and some areas where species-specific hotspots overlapped to increase sample size (Fig. S3.1). Within these hotspots, we established two parallel 1 NM (1.852 km) transect lines spaced 0.5 km apart (Fig. 3.1). Continuous hydroacoustic data were recorded along each transect using a Biosonics DT-X 6000 scientific echosounder with a 70 kHz split-beam transducer (BioSonics, Inc., Seattle, Washington) towed at ~ 1 m depth off the

ship's starboard side to offset wave action and vessel movement (see Davoren *et al.* 2025). Hydroacoustic data were visualized in real-time on a laptop computer onboard the ship (BioSonics, Inc., Visual Acquisition v6.4 software), allowing researchers to monitor and record the location of potential prey aggregations. Simultaneously, one to two observers conducted continuous counts of bird and marine mammal species, along with their behaviour (i.e., on the water, flying, flight direction, foraging), within 300 m on the ship's port side (90° field, perpendicular to boat to the bow) using standard strip transect methods following Davoren (2013) and Davoren *et al.* (2025, adapted from Tasker *et al.* 1984). Another person recorded these counts in a laptop computer in real-time using Birds & Beastly Counter v1.12 software (D. Senciall, 1998, Fisheries and Oceans Canada, St. John's, Canada).

Immediately following the paired transects within each hotspot, we returned to (a) the location where the largest prey aggregation was observed on each transect line or (b) the midpoint of the transect line if prey were not observed. At these locations, we attempted to determine prey species composition by deploying a Ponar Grab (30 cm²) with an attached underwater camera (GoPro Hero 8 in waterproof casing) that continuously recorded video. The underwater camera was not deployed with the grab at sites > 60 m depth as they exceeded the depth rating of the waterproof casing. From the grab sample, we determined the presence of forage fish adults and eggs associated with the seabed, which typically include sand lance buried in sediment (Morrison and Davoren 2024), capelin eggs adhered to sediment or vegetation, and adult capelin spawning near the seabed during summer in the study area. We used underwater video to determine the presence and identity of any observed prey in the water column and/or associated with the seabed. Finally, we deployed a SBE 19plus V2 SeaCAT Profiler CTD (Sea-Bird Scientific, Bellevue, Washington) to quantify the temperature profile of the water column.

Data Processing

We quantified patch characteristics including prey density, site depth, sea surface and seabed temperature, and species/group-specific seabird and marine mammal abundance along each transect. Following methods in Davoren *et al.* (2025), we visualized and processed the hydroacoustic survey data using Echoview v4.90.81.19054 software (Myriax Software Pty., Ltd., Hobart, Tasmania) to estimate prey density and accessibility (i.e., prey depth). In brief, acoustic signals from ~3 m below the water surface to ~0.5 m above the seabed were included in analyses to prevent inclusion of surface “noise” (e.g., bubbles from wave action) and seabed features in prey density calculations. The volume backscattering coefficient (s_v) was visualized with a minimum threshold of -80 dB and all acoustic targets with unusual visual characteristics or depth-specific s_v values greater than those expected for small pelagic species typically encountered in the study area were manually removed (see Davoren *et al.* 2006, 2025). This eliminated acoustic targets that could not be consumed by alcids, such as large predatory fish (e.g., Atlantic cod) and whales, along with non-biological targets (e.g., bubble trails of diving birds) from further analyses. As prey species present could not be identified from hydroacoustic data and prey species were often not observed on underwater video, we quantified the area backscattering coefficient (s_a , m^2/m^2 ; Maclellan *et al.* 2002) as a proxy of prey density in the water column (s_a is referred to as prey density hereafter). We first quantified prey density in 10 m depth by 100 m distance intervals along each transect. We then produced two prey density metrics: (i) average prey density within the upper 50 m (a proxy for accessible prey for alcids) for each 100 m distance interval and (ii) average prey density throughout the water column for each 100 m interval, and both measures were then averaged across the entire length of each transect. Additionally, we recorded the presence/absence (visual) of prey aggregations during

hydroacoustic surveys along each transect as a proxy for prey availability. Minimum, maximum, and mean depth (m) along each transect was quantified in Echoview software and point measures of sea surface temperature (SST) and temperature at the seabed (°C) were obtained from the CTD data.

Species/group-specific seabird abundance was quantified for each transect by summing counts for each species within each behavioural category. Following methods in Davoren (2013) and Davoren *et al.* (2025), we focused analyses on the total number of murres, puffins, and razorbills on the water and actively diving as these behaviours most likely indicate the use of a patch for foraging by alcids relative to flying birds. We also summed the counts of other numerically dominant species in the study area. We summed great shearwaters *Ardenna gravis* and sooty shearwaters *A. grisa* on the water and actively diving into “shearwaters”, great black-backed gulls *Larus marinus* and American herring gulls *L. argentatus smithsonianus* on the water and flying into “gulls”, and northern gannets on the water and flying into “gannets”. These species were included in our analyses because they are potential competitors (shearwaters, gannets) and/or kleptoparasites (gulls) of alcids when present in multi-species foraging aggregations (Hoffman *et al.* 1981). We also included summed counts of marine mammals, which were primarily comprised of humpback whales *Megaptera novaeangliae*, with relatively fewer minke whales *Balaenoptera acutorostrata* and dolphins *Lagenorhynchus* spp.

Data Analysis

We used multivariate analyses to explore and test whether patch characteristics differed among species-specific alcid foraging hotspots. Patch characteristics included a variety of data types with differing measurement scales and underlying distributions and, thus, were split into two major groups for analysis in R v4.2.3 software (R Core Team 2023): community

characteristics (i.e., seabird and marine mammal species/group-specific abundances) and environmental characteristics (i.e., prey density, prey aggregation presence, temperature, and depth).

For the community patch characteristics, summed species/group counts per transect included many zeros (i.e., many transects where one or more species/groups were absent) and were non-normally distributed (Fig. 3.2, Table S3.3). Therefore, we first explored pairwise correlations between species/group-specific abundances using Spearman's rank correlation (see Fig. 3.2). We also explored several transformations to minimize skewness in our data (i.e., raw counts, square and fourth root transformed counts, presence/absence) and found that fourth root transformation resulted in the greatest reduction of skewness across species/groups, but did not impact normality. This transformation also has the advantage of emphasizing rare or low abundance species/groups (Quinn and Keough 2002) and, in our case, helped account for considerably greater numbers of murres and shearwaters relative to other species/groups in the study area (see also Davoren *et al.* 2025). Next, to determine whether the community (i.e., species/group-specific abundances) differed among each hotspot type (puffin, razorbill, murre), we used the *vegdist* function from the *vegan* package (Oksanen *et al.* 2022) to calculate a Bray-Curtis dissimilarity matrix, a dissimilarity measure typically used for species abundance data (Quinn and Keough 2002).

We performed non-metric multidimensional scaling (NMDS) using the *metaMDS* function from the *vegan* package (Oksanen *et al.* 2022) and then visualized the Bray-Curtis dissimilarity matrix based on fourth root transformed abundances by placing transects on an ordination plot using the *ggplot2* package (Wickham 2016). NMDS is an iterative process that converges on an arrangement of objects (i.e., transects) which most accurately depicts dissimilarity between

objects as physical distance in an ordination plot (Quinn and Keough 2002). This plot visually illustrated whether transects formed separate groups based on differences in the seabird and marine mammal community by hotspot type. A non-linear relationship between observed dissimilarity (Bray-Curtis dissimilarity values) and ordination distance (inter-object distances on the ordination plot) indicated that NMDS was suitable for our community data. As the assumption of homogeneity of multivariate dispersion was met, indicated by similar object-centroid distances among hotspot types, we performed a permutational multivariate analysis of variance test (perMANOVA) using the *adonis2* function from the *vegan* package (Oksanen *et al.* 2022) and calculated Benjamini-Hochberg adjusted pairwise *p*-values (post-hoc) to determine whether the communities differed among hotspot types. Finally, to assess whether individual species/group-specific abundances differed among hotspot types, we performed generalized linear models (GLM) on each species/group-specific abundance (response variable), using hotspot type as the fixed predictor variable. The best underlying distribution for each response variable was determined using the *descdist* and *denscomp* functions from the *fitdistrplus* package (Delignette-Muller and Dutang 2015) and negative binomial (log link function) GLMs were performed using the *glm.nb* function from the *MASS* package (Venables and Ripley 2002; Table S3.3). Post-hoc tests were performed using the *emmeans* function from the *emmeans* package (Lenth 2025).

We followed similar analysis steps for our environmental patch characteristics. Most metrics were correlated (Spearman's rank correlation; Fig. S3.2) and several represented similar environmental variables. Therefore, we selected a subset of these metrics to represent each environmental variable measured (i.e., mean depth, SST, seabed temperature, and overall prey density; Fig. 3.3) for our multivariate analysis. After exploring the same transformations as

above to minimize skewness, data were log transformed (with no impact on normality). We calculated a Canberra dissimilarity matrix (appropriate for continuous measurement data; Quinn and Keough 2002) and performed NMDS to illustrate whether transects formed separate groups based on differences in environmental site characteristics by hotspot type. Finally, we performed a perMANOVA to determine whether site characteristics differed among hotspot types and, after selecting the best underlying distributions for each response variable, performed GLMs using the best underlying distribution for each response variable (Table S3.3) to assess whether each environmental site characteristic differed among hotspot types.

Results

We conducted a total of 48 transects within 24 alcid foraging hotspots (puffin: 8 hotspots; razorbill: 6; murre: 10; Fig. 3.1) in Notre Dame Bay on five days from 21–31 July 2024. Of these transects, one quarter represented core (50% volume contour), single species foraging areas (puffin: two; razorbill: two; murre: eight), while other transects represented or overlapped with other species' total (95% volume contour) foraging areas (Fig. S3.1). Murres overwhelmed seabird counts during transects, accounting for nearly one third of all birds recorded. We collected underwater video at 30 transects and detected prey species at four transects within three hotspots (razorbill: two; murre: one; Fig. S3.3). Of these four transects, we observed adult capelin and evidence of capelin spawning (e.g., eggs adhered to sediment or vegetation, dead adult fish at site) at two transects, capelin eggs with no adult capelin at one transect, and adult capelin schooling with no evidence of spawning at one transect. Nearly half of the transects had a mean depth ≤ 50 m (puffin: six; razorbill: ten; murre: 12), with a mean depth range of ~11–138 m across all transects (Table S3.2). SST and temperature at the seabed measured at hotspots ranged 14.5–18.3°C and -1.3–9.9°C, respectively (Table S3.2). Murres tended to forage farther

from the Funk Island breeding colony than puffins and razorbills from the James Island breeding colony, traveling up to ~130 km to core foraging areas (Fig. S3.1). From James Island, puffins tended to forage farther north of the colony, offshore and to the east of Fogo Island (farthest core foraging area ~52 km), while razorbills primarily foraged within the Wadham Islands archipelago (single core foraging area within ~8 km of James Island; Fig. S3.1).

Positive correlations were found between puffin and gull, razorbill and gannet, and murre and shearwater abundances, the latter having the strongest correlation (Fig. 3.2). Seabird species/group abundances were not correlated with marine mammal abundance. NMDS with four dimensions ($k = 4$) resulted in a Kruskal's stress value < 0.1 , allowing for visual interpretation of the ordination plot (Quinn and Keough 2002), and a strong non-linear relationship between measured dissimilarity and ordination distance (non-metric $R^2 > 0.95$) was observed. An ordination plot produced using the first two axes ($k = 2$) from NMDS of the Bray-Curtis dissimilarity matrix of species/group-specific abundances (fourth root transformed) revealed that the transects grouped by alcid species (i.e., puffin, razorbill, or murre hotspot; Fig. 3.4). A perMANOVA test confirmed that the community present at each hotspot type differed significantly ($F_{(2,45)} = 6.088$, $p = 0.001$), with post-hoc tests revealing significant pairwise differences among puffin, murre, and razorbill hotspots (p -value range: 0.003–0.012). GLMs on species/group-specific abundances showed that puffin abundances were significantly greater at puffin hotspots relative to murre and razorbill hotspots and murre abundances were significantly greater at murre hotspots relative to puffin and razorbill hotspots, but razorbill abundance did not differ across hotspot types (Fig. 3.5, Table S3.3). Similarly, abundances of other seabird species/groups and marine mammals did not differ across hotspot types, except for greater abundances of gannets at puffin hotspots relative to murre hotspots (Fig. 3.5, Table S3.3).

Mean depth along each transect was negatively correlated with SST, seabed temperature, and prey density (Fig. 3.3). Additionally, prey density was positively correlated with seabed temperature (Fig. 3.3). Although SST tended to increase with seabed temperature, the correlation was not significant. NMDS with three dimensions ($k = 3$) resulted in a Kruskal's stress value < 0.1 and there was a strong non-linear relationship between measured dissimilarity and ordination distance (non-metric $R^2 > 0.95$). An ordination plot produced using the first two axes ($k = 2$) from NMDS of the Canberra dissimilarity matrix of environmental measures (log transformed) revealed that transects grouped by alcid species (Fig. 3.4). A perMANOVA confirmed that environmental characteristics differed significantly among hotspot types ($F_{(2,44)} = 3.339$, $p = 0.006$), with post-hoc tests revealing that environmental characteristics differed between puffin and murre hotspots ($p = 0.045$) and puffin and razorbill hotspots ($p = 0.009$), but not between murre and razorbill hotspots ($p = 0.165$). GLMs revealed mean depth and seabed temperature differed among hotspot types, with razorbill hotspots being shallower and warmer at the seabed compared to puffin hotspots and warmer at the seabed compared to murre hotspots (Fig. 3.6, Table S3.3). Additionally, prey density averaged across the water column was greater at razorbill hotspots compared to puffin hotspots, but did not differ between razorbill and murre hotspots (Fig. 3.6, Table S3.3).

Discussion

We found support for our hypothesis that three alcid species foraged in areas with different prey patch characteristics, including competitor and prey densities, during chick-rearing in coastal Newfoundland, Canada. In the context of community characteristics, puffin hotspots had lower murre densities, suggesting that the smaller-bodied puffin forages in patches with lower densities of larger-bodied murres, as predicted. This prediction was also supported by

greater puffin abundance at puffin hotspots than at hotspots of larger-bodied murres and razorbills. Razorbill hotspots also had lower murre densities, suggesting this mid-sized alcid may have been displaced from murre hotspots, as predicted. Higher mean conspecific abundance at murre hotspots (> 30 murres) than at puffin (~ 3 puffins) and razorbill (~ 1 razorbill; Fig. 3.5) hotspots suggests that murres forage at greater conspecific densities, possibly due to their numerical dominance in the study area (Davoren 2007, 2013, Davoren *et al.* 2025). Despite positive correlations between the abundance of some species/groups across all surveys (e.g., murre–shearwater; Fig. 3.2), the abundance of most other species/groups did not differ among hotspot types, apart from greater northern gannet abundance at puffin hotspots, suggesting that conspecific densities were the main drivers of community differences among hotspot types. In the context of environmental characteristics, these characteristics differed primarily between puffin and razorbill hotspots, while murre hotspots typically had intermediate characteristics to those of puffins and razorbills. Specifically, razorbill hotspots were shallower, warmer at the seabed, and had greater prey densities than puffin hotspots, suggesting that smaller-bodied puffins may be displaced from higher quality prey patches by larger-bodied razorbills, as predicted.

Puffins foraged at deeper and colder sites with lower prey densities compared to razorbills (Fig. 3.6). Additionally, core (50% volume contour) puffin hotspots were farther than core razorbill hotspots from James Island (Fig. S3.1), where both species breed. Paired with the lesser physiological dive capability of puffins relative to razorbills (Piatt and Nettleship 1985) and lower abundance of razorbills breeding on James Island (Fig. 3.1, Jenkins *et al.* 2018), this evidence supports razorbills displacing puffins from higher quality prey patches (i.e., shallow, high prey density, low competitor density; Fig. 3.5, 3.6) close to the colony. Indeed, razorbills

tend to forage close to breeding colonies under moderate–high prey availability, as predicted by central place foraging theory, despite large maximum foraging ranges (~80 km; Linnebjerg *et al.* 2015, Lescure *et al.* 2023). Similar to our findings, Pratte *et al.* (2017) found that razorbills breeding in the northwest Atlantic foraged more in coastal habitats, while puffins tagged on the same colony tended to forage offshore. Foraging in offshore areas might place puffins at depths exceeding their maximum dive capability (Piatt and Nettleship 1985, Burger and Simpson 1986), as found in this study (Table S3.2). Despite higher energetic costs of traveling farther to deeper offshore foraging areas, puffins have lower wing loading than razorbills and murres (Pennycuik 1987) and, thus, flying farther may have relatively lower energetic costs for puffins. Puffins are also multi-prey loaders, carrying multiple prey items at one time back to feed their chicks (Lowther *et al.* 2020), which may also offset the energetic cost of traveling farther and, thus, potentially lower frequency of chick provisioning (Orians and Pearson 1979) relative to razorbills which are typically single-prey loaders in the study area (Lescure *et al.* 2023). Travelling farther to forage at patches with lower prey densities but also lower allospecific competitor densities may also ensure higher net energy gain by puffins than foraging closer to the colony at higher prey densities alongside razorbills, as predicted for species with lower competitive ability by the ideal free distribution model (Tregenza 1995). Selecting patches with divergent characteristics may also result in observed dietary differences between breeding puffins and razorbills. Indeed, breeding puffins tend to forage at a lower trophic level than razorbills (Pratte *et al.* 2017, Jenkins and Davoren 2020) and, in the study area, the isotopic niche breadth of razorbills contracts more during high capelin availability relative to puffins, indicating that razorbills rely on capelin to a greater extent than puffins during breeding (Jenkins and Davoren 2020). In support, puffin hotspots were often colder at the seabed (mean < 2°C; Table

S3.2) than sites capelin typically select for subtidal spawning (Nakashima and Wheeler 2002, Penton and Davoren 2012, Crook *et al.* 2017). This finding suggests that offshore puffin hotspots identified north of the breeding colony may represent persistent patches of alternative, lower-quality prey (e.g., sand lance; Jenkins and Davoren 2020, Vonderbank 2024).

Although puffins typically foraged at low allospecific competitor abundances, the abundance of northern gannets, a common species at sea in the study area (Davoren 2007, 2013) that breeds on nearby Funk Island (Chardine *et al.* 2013), was greater at puffin hotspots relative to murre hotspots (Fig. 3.5). Additionally, gannet abundance was positively correlated with razorbill abundance across hotspot types (Fig. 3.2). The association of gannets with puffins and razorbills was unexpected due to dietary preferences of breeding gannets for larger-bodied pelagic fish (e.g., Atlantic herring *Clupea harengus*) and squid (Montevecchi 2007) relative to puffins and razorbills (Jenkins and Davoren 2020, Davoren 2024), although all three species feed on capelin to some degree. Alternatively, it was unsurprising that gannet abundance was comparatively lower at murre hotspots as gannets typically do not forage alongside high densities of murres in the study area (Davoren 2013) and due to conspecifics at sea but not higher densities of murres (Bairos-Novak *et al.* 2015). In the study area, pursuit-diving murres typically exploit high-density aggregations of spawning capelin by attacking and chasing solitary capelin near the seabed from above (Crook and Davoren 2014) and, thus, may make capelin inaccessible to shallow, plunge-diving gannets (mean-maximum dive depth ~11 m for gannets tagged on Funk Island; Garthe *et al.* 2007, Mowbray 2020), thereby acting as a “suppressor” species at multi-species foraging aggregations (Hoffman *et al.* 1981). While puffins and razorbills are also pursuit divers and may drive prey into deeper water out of dive range of gannets, the average abundance of murres present at murre hotspots (>30 murres) was greater than that of puffins and

razorbills at their respective hotspots (< 5 birds; Fig. 3.5), suggesting that these two species likely would not influence prey accessibility at their hotspots to the same degree as higher densities of murres. Interestingly, puffin and gull abundance were also positively correlated (Fig. 3.2). While this association may indicate gull attraction to puffins, as alcids are susceptible to kleptoparasitism (theft of prey caught by another individual, typically associated with limited prey availability or accessibility; Lavers and Jones 2007, Ashbrook *et al.* 2011, Veitch *et al.* 2016) while holding fish in their bills for chick provisioning at multi-species assemblages with gulls (Hoffman *et al.* 1981, Davoren and Burger 1999), it may also indicate the presence of accessible prey high in the water column where puffins are foraging.

Contrary to our prediction, prey density was not greater at murre hotspots than at hotspots of puffins and razorbills (Fig. 3.6). Instead, prey density (and depth) was intermediate between higher-density, shallower razorbill and lower-density, deeper puffin hotspots, likely a result of the order of magnitude greater number of murre breeding pairs in the study area compared to puffins and razorbills (Wilhelm *et al.* 2015, Jenkins *et al.* 2018). While we would expect murres to target prey patches nearby the Funk Island breeding colony as central place foragers (Orians and Pearson 1979), the ideal free distribution model predicts that some birds may maximize net energy gain by foraging at lower conspecific competitor densities (Fretwell and Lucas 1970, Tregenza 1995) likely found farther from the colony even if prey densities are lower. In support, previous studies have shown that murres overwhelm the at-sea community in the study area during the summer (Davoren 2007, 2013, Davoren *et al.* 2025) and murre foraging ranges during chick-rearing are known to increase with colony size in the study area (Gulka *et al.* 2020) and throughout the species' range (Patterson *et al.* 2022). Therefore, high conspecific densities of murres dispersing from Funk Island, the largest murre colony in the Atlantic (Ainley *et al.* 2021),

may explain observed intermediate prey densities at murre hotspots as well as greater travel distances of murres to forage offshore and near the coast (Fig. 3.1, S3.1) compared to puffins and razorbills. Indeed, although within the species' maximum documented foraging range (Patterson *et al.* 2022), the farthest core murre foraging area occurred ~130 km from the Funk Island breeding colony, while the farthest core puffin foraging area was closer to James Island (~50 km) and razorbills primarily foraged within ~8 km of James Island (Fig. S3.1). While dispersing across a larger area to forage at a broader range of prey densities may minimize foraging at high conspecific competitor densities at murre hotspots, comparatively larger foraging distances of murres to occasionally lower prey density patches might be costly, as murres have the greatest wing loading of the three species (Pennycuik 1987) and, thus, the greatest energetic cost of flight (Elliott *et al.* 2013). Additionally, as single-prey loaders (Linnebjerg *et al.* 2015), murres have a reduced ability to adjust their prey load to offset longer foraging trips, and, thus, flying to farther prey patches may reduce prey deliveries to the nest during chick-rearing. In support, Davoren and Montevecchi (2003) showed that murres breeding on Funk Island performed longer foraging trips, resulting in lower provisioning rates relative to murres breeding at a smaller colony in another region.

Alternatively, murres may not target high prey densities during foraging, but rather predictable prey aggregations (e.g., annually persistent capelin spawning sites; Davoren *et al.* 2025). In support, we found evidence of recent capelin spawning at a core murre hotspot that was the farthest we surveyed from Funk Island (Fig. S3.3) and multiple core foraging areas of murres overlapped with known annually persistent subtidal and beach capelin spawning sites (Fig. S3.1; Davoren *et al.* 2025). These sites represent predictable sources of easily accessible prey (spawning capelin show reduced predator avoidance behaviour; Davoren *et al.* 2006), which may

allow murres to rely largely on memory to minimize energetic costs of search during foraging (Davoren *et al.* 2003, Regular *et al.* 2013, Bairos-Novak *et al.* 2015). Greater prey densities likely occurred at some of these murre hotspots prior to our surveys as peak capelin spawning in the study area (measured annually at persistent subtidal spawning sites; see Davoren *et al.* 2025) occurred on 13 July 2024, approximately one week prior to the onset of our surveys.

Additionally, murre abundance was positively correlated with the abundance of shearwaters (Fig. 3.2), another numerically dominant group in the study area (Davoren 2007, 2013, Davoren *et al.* 2025) which, unlike murres, are non-breeding during the summer and, thus, may indicate recent capelin spawning as shearwaters increase in abundance at-sea near peak capelin spawning (Davoren *et al.* 2025) along migratory paths and at predictable shallow (< 50 m) sites of capelin spawning (Carvalho and Davoren 2019).

Conclusion

Species-specific alcid abundance tended to be greatest at each species' hotspots (Fig. 3.5), indicating that foraging locations estimated from multiple previous years of tracking data (Table S3.1) continued to represent important foraging areas. As tagging data used in this study were from years of moderate or above-average capelin abundance and peak capelin biomass during 2024 (0.132 g/m²; Davoren unpublished data) was near the long-term average (0.150 g/m², 2009–2024; Davoren *et al.* 2025, Davoren unpublished data), we expect that the seabird communities and environmental conditions we described at alcid hotspots are representative of those within a typical year. Therefore, these tracking-derived foraging locations not only revealed the location of temporally persistent alcid foraging areas but also predictable locations where their prey complete important parts of their annual cycle (e.g., spawning sites; Fig. S3.3). These findings suggest that monitoring the foraging locations of different seabird species,

combined with known dietary information, may present a reliable alternative method of locating and sampling prey species which evade typical fish surveying and sampling techniques (e.g., burrowing sand lance; Morrison and Davoren 2024). As seabird species may rely in part on memory during foraging, as shown for alcids (Davoren *et al.* 2003, Regular *et al.* 2013, Bairos-Novak *et al.* 2015, Regan *et al.* 2024) and gannets (Montevecchi *et al.* 2009, Wakefield *et al.* 2015), and, thus, show foraging site fidelity (e.g., alcids; Regan *et al.* 2024), offshore development poses the risk of displacing seabirds from such persistent prey aggregations (e.g., razorbills and murre are displaced in response to wind farm construction in coastal regions; Petersen 2005, Dierschke *et al.* 2016; risks reviewed in IAAC 2025). Multi-year tracking data from previous or future studies in other regions have the potential to identify novel prey aggregations and, when combined with at-sea surveys, could provide insight into persistent multi-species hotspots, where energy flow through ecosystems is maximized (e.g., subtidal capelin spawning sites; Davoren 2013). Identifying the location of these important, temporally persistent hotspots will provide valuable information for marine spatial planning (e.g., informing the designation of marine protected areas, locations to protect against resource exploration and development; Osmond *et al.* 2010, Requena *et al.* 2020) to maintain key ecosystem processes.

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Figures

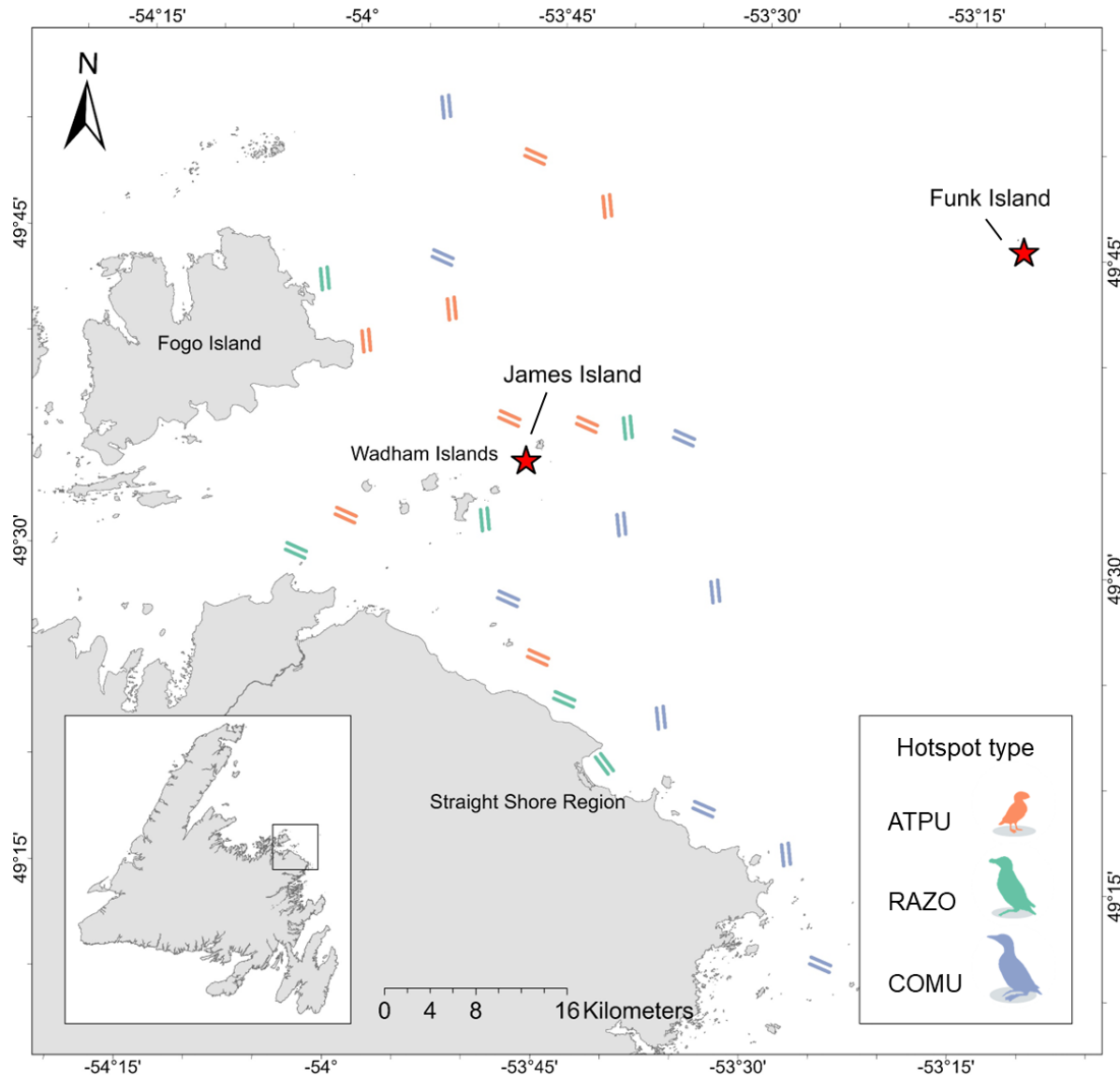


Figure 3.1. Location of boat-based surveys to determine differences in prey patch characteristics at species-specific alcid foraging dive hotspots. The locations of paired transect lines surveyed during summer 2024, with line colours indicating the hotspot type (orange = Atlantic puffin, green = razorbill, purple = common murre). Breeding colonies where bird-borne tags were deployed are indicated by red stars. Location on northeast Newfoundland coast shown in inset.

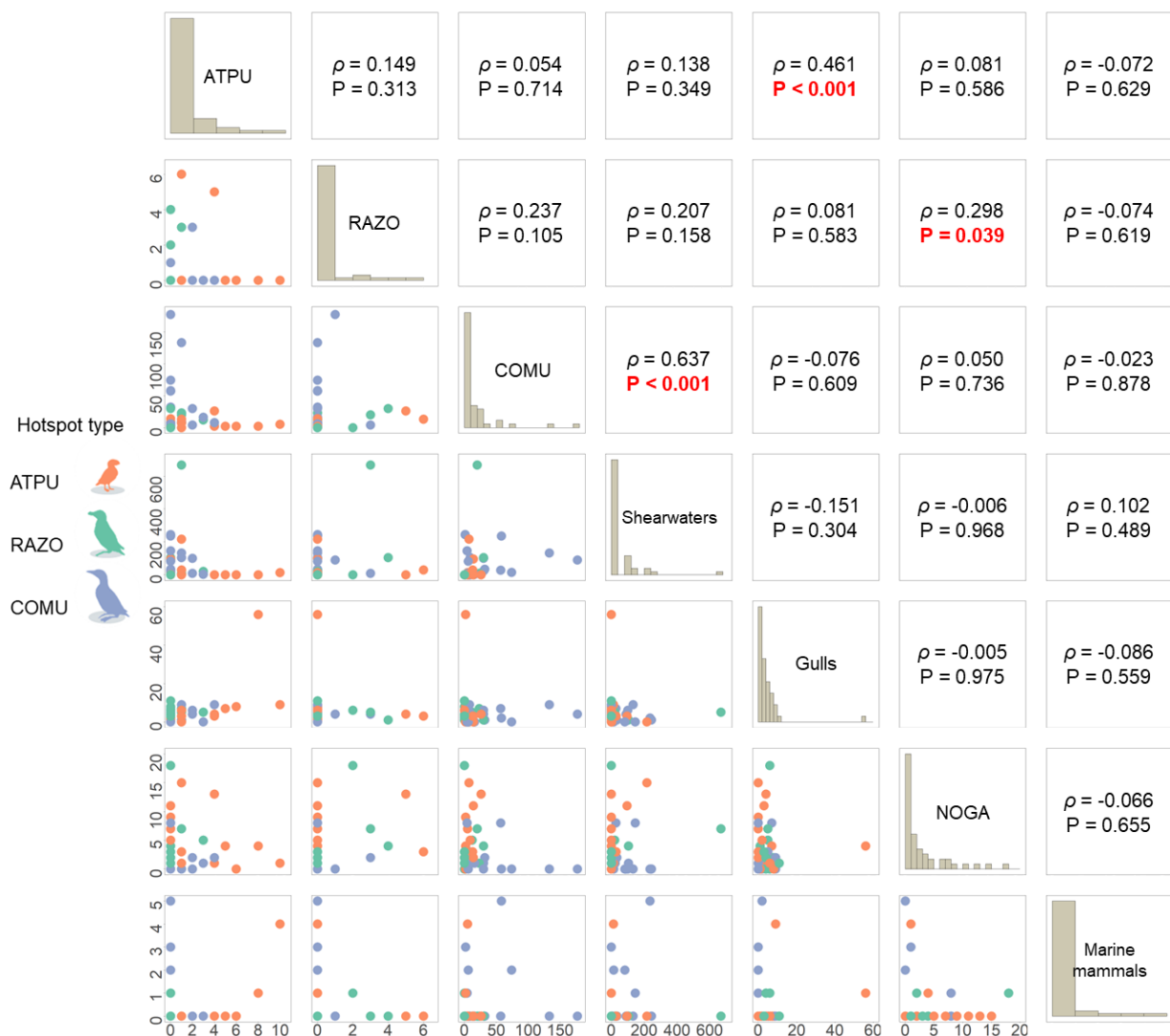


Figure 3.2. Correlation matrix of species/group-specific abundances at alcid foraging dive hotspots (orange = Atlantic puffin, green = razorbill, purple = common murre). ATPU = Atlantic puffins on the water; RAZO = razorbills on the water; COMU = common murre on the water; shearwaters = great and sooty shearwaters on the water; gulls = great black-backed and American herring gulls; NOGA = northern gannets; marine mammals = dolphins, humpback and minke whales. Spearman's rank correlation coefficient (ρ) and P-value included in upper right, with significant correlations ($P < 0.05$) shown in red.

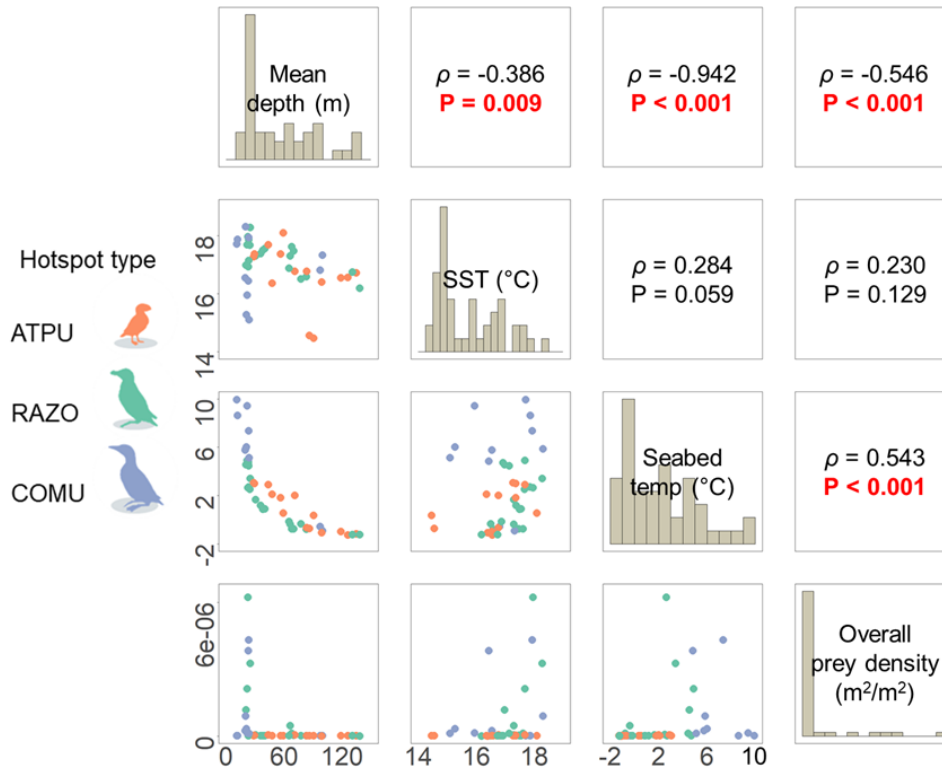


Figure 3.3. Correlation matrix of environmental patch characteristics (depth, sea surface temperature, seabed temperature, prey density) measured at alcid foraging dive hotspots (orange = Atlantic puffin, green = razorbill, purple = common murre). Spearman's rank correlation coefficient (ρ) and P-value included in upper right, with significant correlations ($P < 0.05$) shown in red.

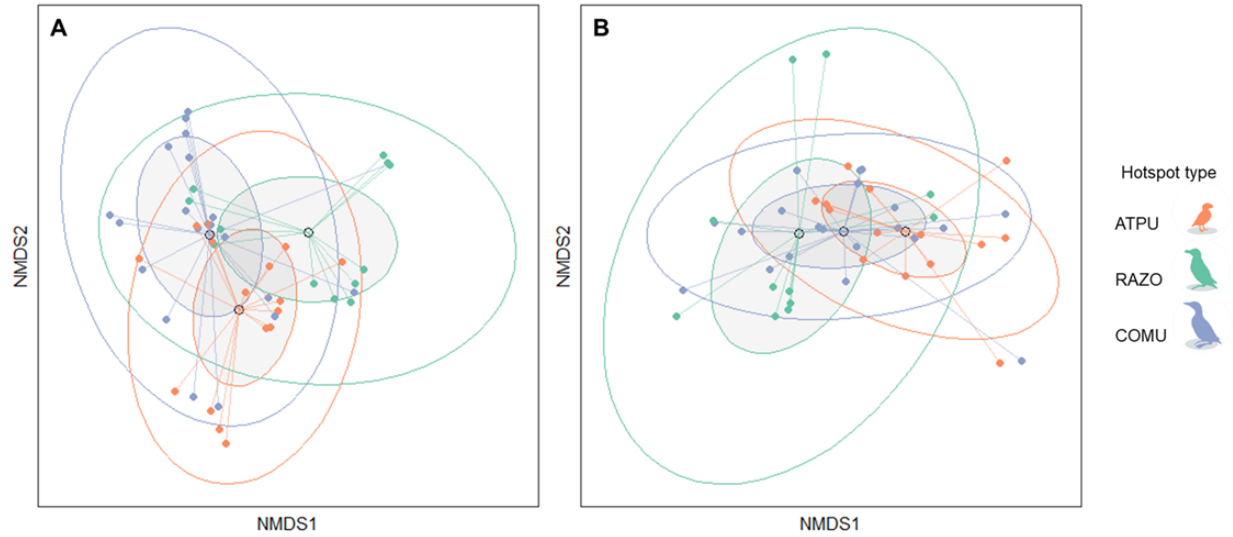


Figure 3.4. Non-metric multidimensional scaling (NMDS) ordination plots of transects (filled circles coloured by hotspot type; orange = Atlantic puffin, green = razorbill, purple = common murre) based on (A) a Bray-Curtis matrix of dissimilarities in fourth root transformed species/group-specific abundances (see Fig. 3.2) and (B) a Canberra matrix of dissimilarities in log transformed mean depth, sea surface and seabed temperatures, and overall prey density averaged along transects (see Fig. 3.3). The first two axes ($k = 2$) from NMDS ordination are shown, with lines indicating distances from group centroids (open circles) by hotspot type. Ellipses enclose 50% (shaded) and 95% of transects from each hotspot type.

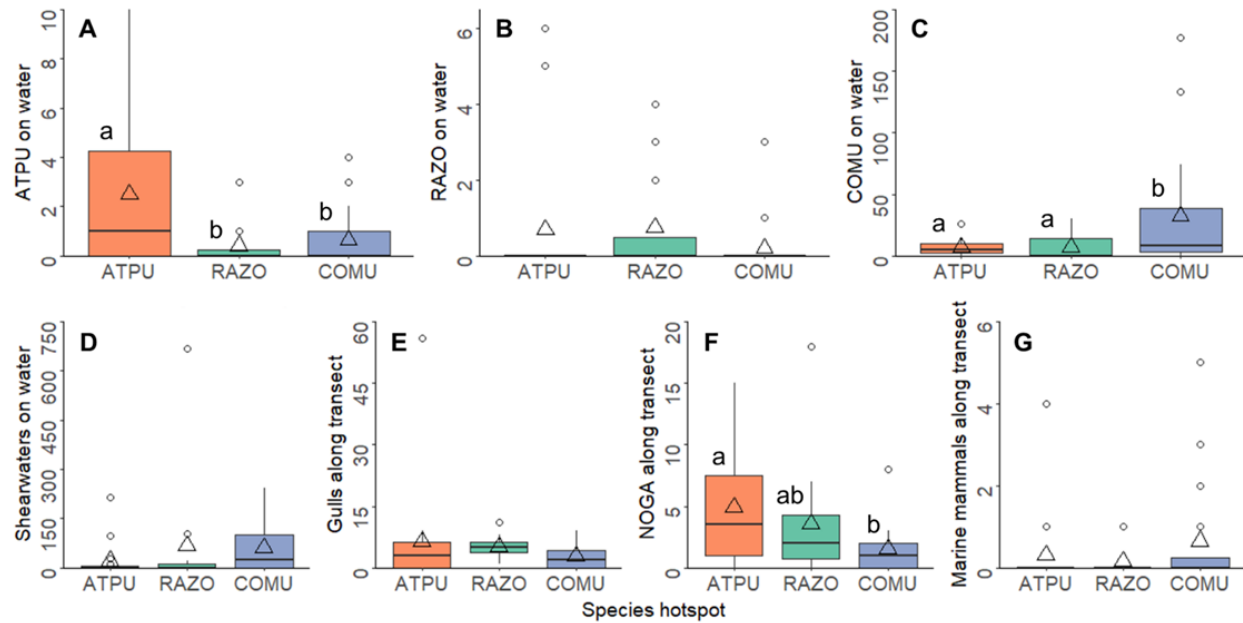


Figure 3.5. Abundance of (A) Atlantic puffins, (B) razorbills, (C) common murre, and (D) shearwater spp. (great shearwaters, sooty shearwaters) on the water and (E) gull spp. (American herring gulls, great black-backed gulls), (F) northern gannets, and (G) marine mammal spp. in all behaviour categories by alcid foraging dive hotspot type. Boxes represent the median (bold line), Q1 and Q3. Triangles show the mean by hotspot type; open circles show outliers. Lowercase letters show post-hoc test results where significant differences occur, with groups that differ sharing no letters in common. Note that y-axis scales differ across species/groups.

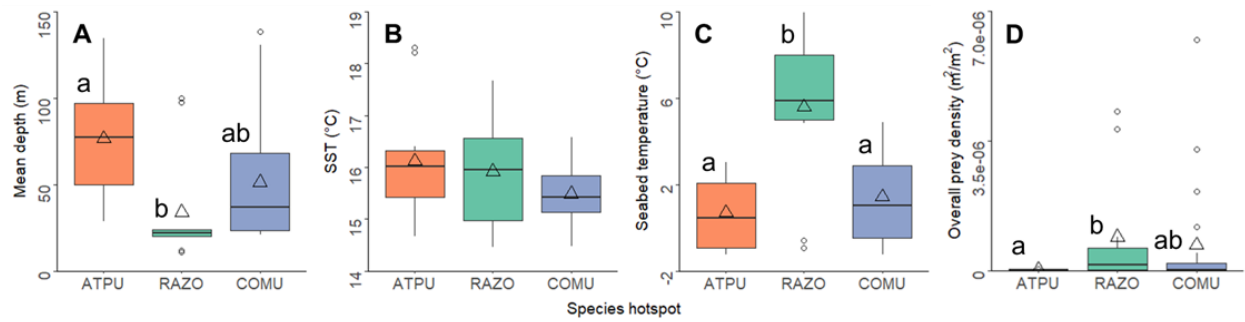


Figure 3.6. (A) Mean depth, (B) sea surface temperature, (C) seabed temperature, and (D) prey density averaged across the entire water column by alcid foraging dive hotspot type. Boxes represent the median (bold line), Q1 and Q3. Triangles show the mean by hotspot type; open circles show outliers. Lowercase letters show post-hoc test results where significant differences occur, with groups that differ sharing no letters in common.

Supplementary Materials

Table S3.1. Summary of archived tracking data used to derive species-specific alcid foraging hotspots. The number of tagged individuals by species and year and the number of foraging dives per individual subsampled from the tracking data are provided. Ecotone GPS tracking devices recorded latitude and longitude and included built-in saltwater switches to determine foraging dive locations.

	ATPU	RAZO		COMU	
	2023	2017	2023	2016	2018
No. individuals	5	7	20	6	5
No. foraging dives subsampled per individual	250	65		75	
Tag deployment date range	1–8 August	28 July–13 August	17 July–4 August	18–31 July	16–21 July
Tag model	URIA-60 TDR	URIA-300	URIA-300 TDR	URIA-300	URIA-300 TDR, URIA-60
Associated publication(s)	Dalton unpublished data	Lescure <i>et al.</i> 2023	Legard <i>et al.</i> 2025	Gulka and Davoren 2019, Gulka <i>et al.</i> 2019, 2020	

Table S3.2. Mean (min–max) values of environmental patch characteristics measured at transects representing species-specific Atlantic puffin (ATPU), razorbill (RAZO), and common murre (COMU) foraging hotspots.

Hotspot	Depth (m)	SST (°C)	Seabed temperature (°C)
ATPU	71.43 (28.83–134.60)	16.64 (14.46–18.10)	0.70 (-1.26–3.05)
RAZO	33.14 (11.02–99.85)	16.80 (15.10–18.30)	5.59 (-0.92–9.94)
COMU	51.44 (20.80–138.42)	17.28 (16.18–18.29)	1.44 (-1.25–4.89)

Table S3.3. Statistical output for response variables used in univariate analyses and results of generalized linear models to determine differences in species composition and environmental factors between alcid dive hotspots. Normality and homogeneity of variance were examined for each variable using Shapiro-Wilk and Levene's tests, respectively. Underlying distribution used in each generalized linear model included. Note: seabed temperatures were adjusted to positive values by adding a constant (+1.5°C) to fit assumptions of the Gamma distribution.

Response variable	Shapiro-Wilk	Levene's	Underlying distribution	χ^2	df	P
ATPU on water	< 0.001	0.006	Negative binomial	8.445	2, 45	0.015
COMU on water	< 0.001	0.036	Negative binomial	12.448	2, 45	0.002
RAZO on water	< 0.001	0.445	Negative binomial	1.297	2, 45	0.523
Shearwaters on water	< 0.001	0.498	Negative binomial	1.251	2, 45	0.535
Gulls along transect	< 0.001	0.355	Negative binomial	3.972	2, 45	0.137
NOGA along transect	< 0.001	0.131	Negative binomial	8.034	2, 45	0.018
Marine mammals along transect	< 0.001	0.423	Negative binomial	1.728	2, 45	0.421
Mean depth	< 0.001	0.318	Gamma	4.001	2, 42	0.017
SST	0.005	0.088	Gamma	0.013	2, 42	0.093
Seabed temperature	0.001	0.278	Gamma	10.012	2, 42	< 0.001
Upper 50 m s_a	< 0.001	< 0.001	Lognormal	21.801	2, 42	0.021
Overall s_a	< 0.001	< 0.001	Lognormal	25.299	2, 42	0.017

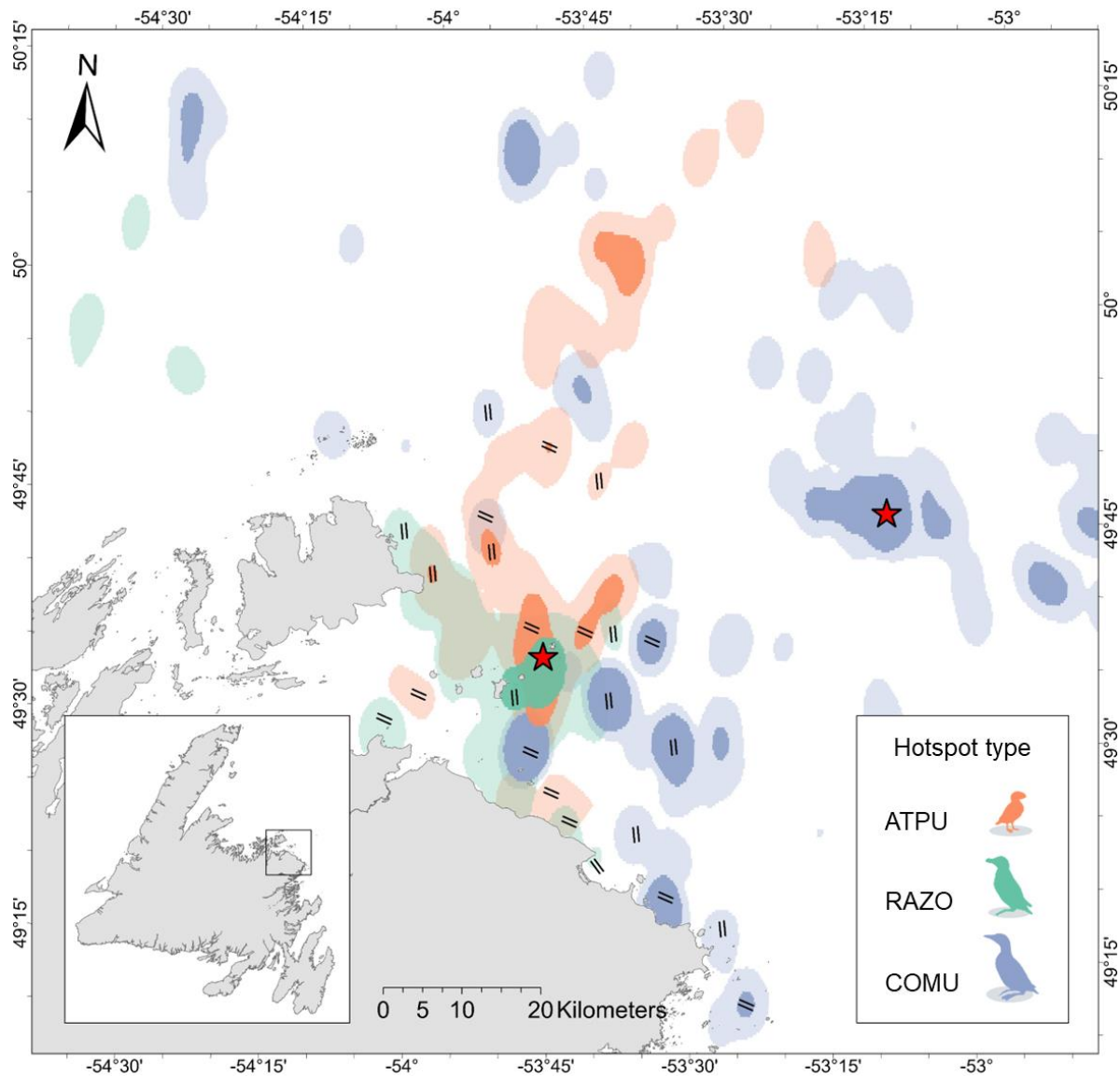


Figure S3.1. Location of species-specific foraging dive hotspots (orange = Atlantic puffin, green = razorbill, purple = common murre) determined through kernel density estimation (KDE). Core (50%) and total (95%) use areas indicated by shaded and translucent contours, respectively, and the locations of paired transect lines surveyed during summer 2024 indicated by black lines. Breeding colonies where tag deployments occurred indicated by red stars. Location on northeast Newfoundland coast shown in inset.

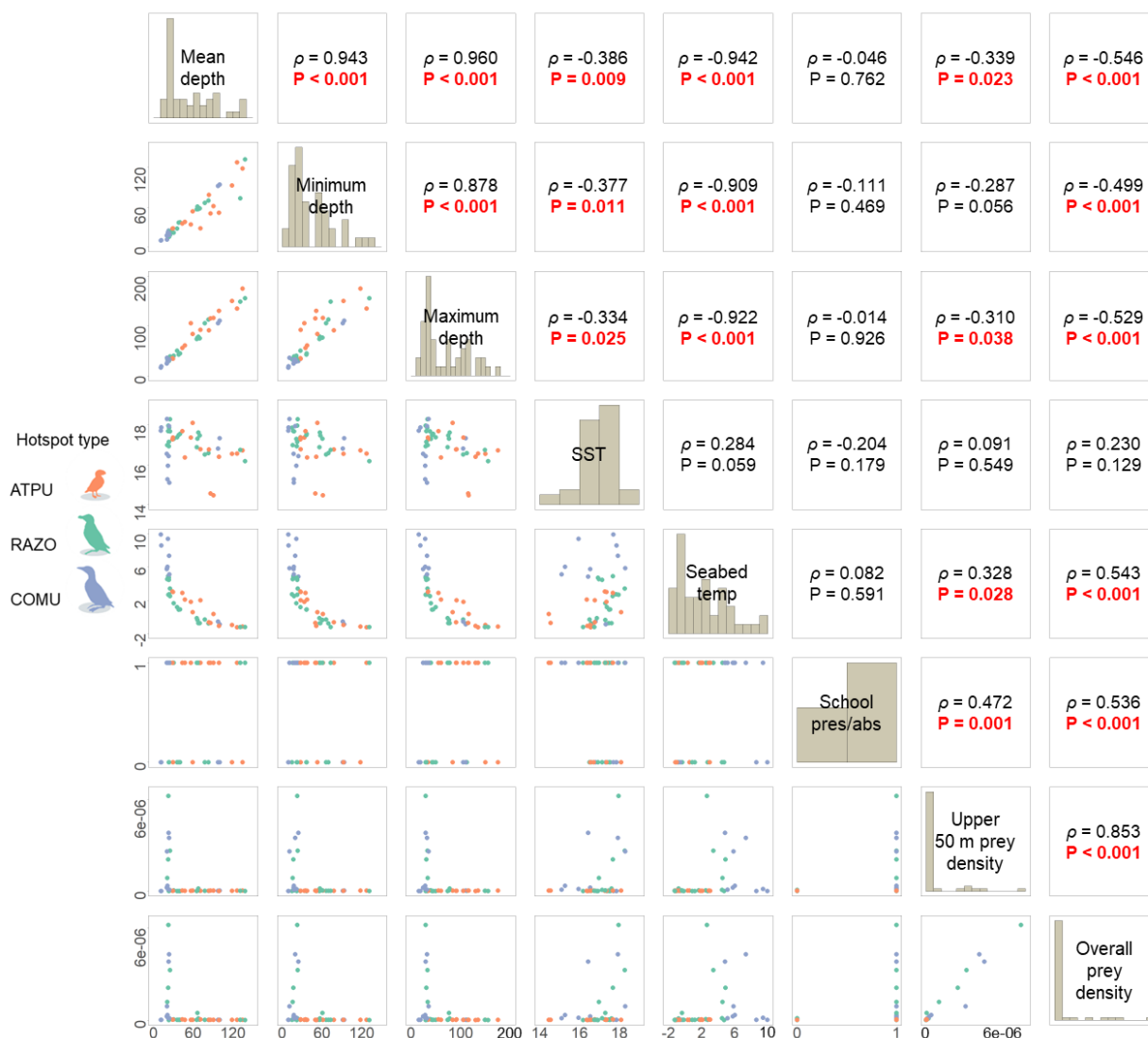


Figure S3.2. Correlation matrix of environmental patch characteristics measured at alcid foraging dive hotspots (orange = Atlantic puffin, green = razorbill, purple = common murre). Spearman's rank correlation coefficient (ρ) and P-value included in upper right, with significant correlations ($P < 0.05$) shown in red.

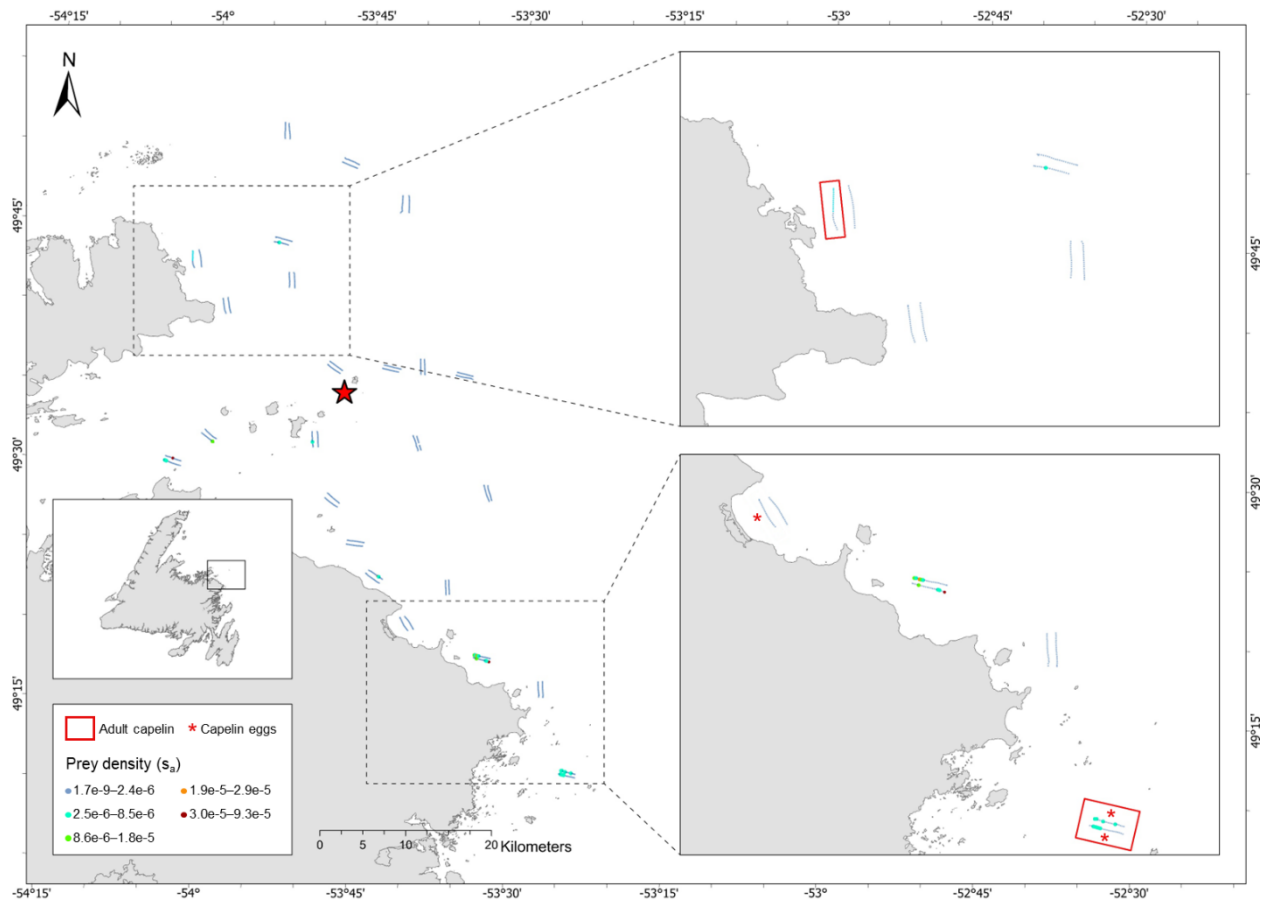


Figure S3.3. Prey density (s_a) within 100 m bins along transects within alcid foraging dive hotspots surveyed during summer 2024. Transects where adult capelin or capelin spawning were recorded are indicated by red rectangles and asterisks, respectively, and the James Island breeding colony is indicated by a red star. Location on northeast Newfoundland coast shown in inset.

Chapter Four: Conclusions.

The aim of my thesis was to investigate important habitat for forage fish and their seabird predators in coastal Newfoundland, Canada. In my second chapter, I quantified previously determined important environmental characteristics for forage fish at coastal (≤ 50 m) subtidal sites in two Newfoundland bays (Notre Dame and Fortune bays) and used habitat suitability modelling (HSM) to predict the current and future extent of suitable habitat for forage fish spawning (capelin, summer; Atlantic herring, spring) and burying (sand lance *Ammodytes* spp., spring–summer). My HSMs predicted suitable habitat is more limited for all species in Notre Dame Bay (8.1–73.3% of surveyed area) relative to Fortune Bay (25.2–100%) and demonstrated a decline in coastal habitat availability for these species by up to 35.2% of the current predicted suitable area under a 2.1°C ocean warming scenario during summer in Notre Dame Bay. Additionally, I identified limited patchy suitable burying habitat for sand lance species across bays (8.1–25.2%) in contrast to more abundant capelin (35–97.6%) and herring (73.3–100%) spawning habitat. This finding is similar to Robinson *et al.* (2013) who showed similarly limited habitat for Pacific sand lance *Ammodytes hexapterus* (6% of model area) and suggests sand lance are more vulnerable to coastal habitat degradation or destruction relative to capelin and herring. Such limited habitat may present a population bottleneck, as the year-round distribution of sand lance, which require this habitat for burying to reduce energy expenditure and evade predation, is limited to within ~2 km of these small patches of suitable sediment (Haynes and Robinson 2011, Robinson *et al.* 2013).

In my third chapter, I characterized prey patch characteristics used by alcid species (Atlantic puffins, razorbills, common murre) during the summer breeding season on the northeast Newfoundland coast. I performed paired bird and hydroacoustic surveys at tracking-

based alcid foraging dive “hotspots” and used non-metric multidimensional scaling and generalized linear models to identify prey patch characteristics used by each alcid species. My results demonstrated that puffins, the smallest of the three species, foraged at lower conspecific densities than the larger common murres and at deeper sites farther from their breeding colony with lower prey densities than mid-sized razorbills, suggesting that puffins are displaced from higher quality prey patches (i.e., shallow, high prey density, close to the colony). Common murres foraged at higher conspecific densities and at a breadth of prey densities and depths relative to puffins and razorbills, demonstrating a broader range of patch characteristics used during foraging likely due to the high murre population breeding in the region (Ainley *et al.* 2021). Murre foraging hotspots tended to have the greatest shearwater *Ardenna* spp. and marine mammal abundance, suggesting murre hotspots represent important multi-species predator foraging aggregations. Additionally, I identified previously undocumented subtidal capelin spawning sites at razorbill and murre hotspots and both species foraged at or near known annually persistent capelin spawning sites (Davoren *et al.* 2025, Chap. 2). One such novel site fell within the area surveyed in my second chapter (in predicted unsuitable habitat) and was used as a spawning site during summers 2023 and 2024, indicating this may be an annually persistent spawning site. Overall, species-specific alcid abundance tended to be greatest at each species’ respective hotspots, demonstrating that seabird foraging hotspot locations can be used to (i) quantify the prey patch characteristics of breeding seabirds and (ii) identify temporally stable important locations for energy transfer within ecosystems (e.g., capelin spawning sites; Davoren 2013).

Implications and Future Research

My HSMs provide important baseline data indicating the locations and spatial extent of

suitable subtidal spawning habitat for capelin and herring in two Newfoundland bays, which could inform the siting of future annual monitoring efforts. In Newfoundland, capelin and Atlantic herring are monitored by Fisheries and Oceans Canada (“DFO”), which provides science-based recommendations to managers to inform management decisions, including setting species- and/or stock-specific total allowable catch (“TAC”) limits. Monitoring for capelin includes an offshore spring acoustic biomass survey and an inshore larval abundance index (collected near annually persistent spawning sites) that are both used to forecast capelin biomass (DFO 2024a). This forecasted biomass is then compared to a limit reference point (based on capelin’s role as prey for Atlantic cod; DFO 2024a) for Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J+3KL (3Ps is not monitored but is allotted a TAC) to inform a TAC. For Atlantic herring, monitoring includes spring research gillnet abundance indices and fall–winter inshore acoustic biomass surveys in multiple bays in NAFO Divisions 3KLPs, which will be used in the development of future limit reference points (DFO 2024b). As fish experience high mortality during early life stages (type III survivorship; Dahlberg 1979) and forage fish recruitment is often determined in early life history stages (e.g., Murphy *et al.* 2018), my HSMs could aid in forecasting the strength of future year classes by predicting changes in the spatial extent of subtidal spawning habitat (e.g., under varying ocean temperatures). Areas predicted as suitable habitat for capelin spawning could also be used as new locations for capelin larval abundance indices and my HSMs could inform the siting of similar herring larval abundance indices if they reveal persistent herring spawning sites. Indeed, as climate change is predicted to drive consistent temperature increases in coastal regions globally (Varela *et al.* 2023) including in Newfoundland (Han *et al.* 2015), capelin will likely shift to deeper, cooler subtidal habitat farther from shore to spawn (Templeman 1948, Nakashima and Wheeler 2002, Crook *et al.* 2017,

Tripp *et al.* 2023), emphasizing the need for greater monitoring of subtidal spawning site locations and site-specific productivity (e.g., Tripp *et al.* 2023).

Baseline information on coastal habitat characteristics in Newfoundland are lacking, including detailed fine-scale bathymetry, seabed substrate type, and marine vegetation presence and abundance. This limited my ability to predict the availability and extent of species-specific suitable coastal habitat in regions beyond my surveyed areas. I recommend the collection of similar baseline coastal habitat information in other regions to apply similar HSMs throughout coastal Newfoundland. I also echo Staudinger *et al.* (2020) in recommending further characterization of forage fish habitat associations in coastal Newfoundland to allow my HSMs to be refined by including more species- and region-specific habitat characteristics (e.g., to model high hatching success habitat) and additional characteristics in models (e.g., macroalgal density, salinity). In particular, sand lance species are not commercially fished nor monitored under a similar framework to capelin or herring by DFO and, thus, these species are data limited in Newfoundland (see Staudinger *et al.* 2020). My HSMs for *Ammodytes* spp. provide a starting point for future studies to characterize *Ammodytes* spp. density and distributional patterns in coastal Newfoundland (e.g., through environmental DNA sampling; Robinson *et al.* 2022) and further characterize habitat associations to inform more region-specific HSMs.

The results of my third chapter revealed temporally persistent alcid foraging hotspots and predictable locations where their prey aggregate, supporting the use of multi-year archived seabird tracking datasets to identify important forage fish habitat (e.g., spawning sites) associated with critical ecosystem processes (e.g., food web energy flow; Davoren 2013) and the use of seabirds as indicators of marine ecosystem health (Cairns 1987). BirdLife International, a partnership of non-government organizations with a common goal of bird conservation, has

designated several Important Bird and Biodiversity Areas (“IBA”) in coastal Newfoundland. IBAs are typically established on breeding colonies, migratory routes, or immediately adjacent marine areas (e.g., the Wadham Islands Archipelago, NF0013; IBA Canada 2024) in Notre Dame Bay. However, designating seabird foraging aggregations near breeding colonies as IBAs could aid in the protection of a wide variety of seabird species and their prey. For example, despite growing seabird populations following the Atlantic cod moratorium in Newfoundland (Regular *et al.* 2013), pursuit-diving seabirds (e.g., alcids, shearwaters) are highly vulnerable to gillnet by-catch related mortality (Piatt *et al.* 1982, Benjamins *et al.* 2008) and Davoren (2007) identified murre as particularly vulnerable when they forage at annually persistent capelin spawning sites targeted by commercial cod fisheries. Thus, my results could inform the limited designation of marine protected areas (i.e., no take zones where commercial fishing activities are prohibited) at annually persistent murre foraging hotspots to achieve the greatest reduction in by-catch rates of multiple top predator species. These hotspots could also be considered during future siting of resource exploitation and development (Osmond *et al.* 2010, Requena *et al.* 2020). For example, razorbills and murre are vulnerable to displacement from persistent prey aggregations during the construction and operation of wind farms in other coastal regions (Petersen 2005, Dierschke *et al.* 2016; risks reviewed in IAAC 2025).

Finally, I described predicted decreases in the extent of suitable habitat for forage fish spawning (capelin, herring) and burying (sand lance) during the summer in Notre Dame Bay under climate change, where a 2.1°C increase from contemporary temperatures resulted in loss of suitable habitat based on species-specific optima for successful egg development or burying. Further indirect effects of climate change on forage fish habitat, not considered in my thesis, are also anticipated. For example, brown alga *Desmarestia viridis*, is dominant in coastal

Newfoundland (Blain and Gagnon 2014) and provides important spawning habitat for capelin (Bliss and Davoren 2021) and herring (Chap. 2, Davoren unpublished data) in the region. Extended periods above 12°C (Gagnon *et al.* 2013, Blain and Gagnon 2013, 2014) and in low salinity (< 29 psu; Gagnon *et al.* 2013) induce mortality in this annual species. As such, warming temperatures (Han *et al.* 2015, Varela *et al.* 2023) and decreased salinity from melting sea ice (Han *et al.* 2017) may influence the abundance of *D. viridis* and, thus, alter the extent of available forage fish spawning habitat. Additionally, *D. viridis* relies on wave action at shallow sites to resist urchin grazing (Gagnon *et al.* 2006) and, thus, is unlikely to shift to deeper, cooler subtidal habitat. My HSMs suggest nearshore warming is likely to drive forage fish into deeper water for spawning, indicating a potential population bottleneck for capelin and herring (i.e., limited habitat for reproduction). As persistent forage fish spawning sites can provide predictable locations of high-density prey (Davoren *et al.* 2006) where predators that use memory can maximize net energy intake (e.g., alcids; Davoren *et al.* 2003, Regular *et al.* 2013, Bairos-Novak *et al.* 2015, Regan *et al.* 2024), climate change will likely result in wide ranging impacts on marine ecosystems including distributional shifts in forage fish species and reduced foraging success for predators.

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