# NICHE PARTITINOING AND BEHAVIOUR OF MIGRATORY SHOREBIRDS IN IN THE NORTHUMBERLAND STRAIT AND BAY OF FUNDY

BY

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**Abstract**

Animal populations take advantage of environmental heterogeneity to partition themselves into microhabitat niches. Such partitioning plays an important role in determining interspecific competition and community structure by allowing multiple species to coexist. Many species of shorebirds use stopover sites in Atlantic Canada to fuel their annual southbound migration in late summer and early fall. The Bay of Fundy is recognized as a landscape of hemispheric importance for migratory shorebirds, and hosts hundreds of thousands of Semipalmated Sandpipers annually. Other stopover sites on the eastern coast of New Brunswick, Canada, host smaller but more diverse shorebird populations. There is a lack of research on stopover ecology of whole shorebird communities in New Brunswick, especially at small coastal stopover sites. We examined stopover ecology at staging areas in the Bay of Fundy and Northumberland Strait to examine niche dynamics relative to shorebird behaviour and habitat use. Foraging strategies and rates varied among shorebird species at stopover sites on the Northumberland Strait and also between Semipalmated Sandpipers in the Bay of Fundy and Northumberland Strait. We found that Short-billed Dowitchers primarily forage by probing, and Semipalmated Plovers forage by pecking. Semipalmated Sandpipers, White-rumped Sandpipers, Least Sandpipers, and Yellowlegs used a combination of pecking and probing. Diets also varied between species and sites. We found that Semipalmated Sandpipers and Semipalmated Plovers consume generalist diets, while the diets of Short-billed Dowitchers and White-rumped Sandpipers were more specialized for specific food sources. Different taxa face foraging constraints based on morphological features, which creates both spatial and behavioural segregation. This was evident on the Northumberland Strait, probably because greater environmental heterogeneity in small coastal sites created more dimensions for segregation than large mudflat sites. As a result, a wider diversity of species can co-exist. Small coastal sites constitute important stopover habitat for migratory shorebirds outside of the Bay of Fundy. These findings broaden our understanding of stopover ecology of multi-species flocks and indicate that conservation of small coastal sites is also important for success of migratory shorebirds in Atlantic Canada.

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## Chapter 1: Introduction

### *Niche Partitioning*

Ecologists have long understood that animal populations take advantage of environmental heterogeneity to partition themselves into microhabitat niches, and thus avoid competitive exclusion of ecologically similar species (MacArthur, 1958). Niche partitioning occurs when resources are limiting, and species compress their realized niche to limit overlap with heterospecifics. A greater degree of partitioning in species-rich communities allows the fulfillment of more functional roles, which increases total resource consumption (Finke and Snyder 2008). Studying this niche partitioning can help us understand the influences of interspecific competition on community structure.

Niche complementarity predicts that species similar in one niche dimension should differ from each other in another dimension (Schoener 1974). Individuals from allopatric species consume more prey items of similar size and taxa than those from species that co-exist (Schoener 1968). Food and habitat are common resource complements, meaning species foraging in the same habitat tend to have different diets (Schoener 1974). However, niche dimensions are rarely independent, therefore, species are likely to overlap in more than one niche dimension (Schoener 1974). If two niche dimensions are strongly correlated, species overlapping in one may also show some degree of overlap in the other. Niche complementarity also predicts that communities with many species should have segregation in more niche dimensions than simpler communities, as interspecific competition is the main driver of segregation (Wiens 1992). This results in species inhabiting more diverse communities exhibiting more niche specialization and segregation than those in less diverse communities (Quevedo et al. 2009).

### *Stopover Ecology*

Many shorebirds (order Charadriiformes) undertake long-distance migrations from Artic breeding habitat to southern wintering grounds (O'Reilly and Wingfield 1995). The probability of survival is much lower during migration than stationary periods (Sillett and Holmes 2002), however, migration allows shorebirds to take advantage of seasonally abundant resources across their latitudinal range (Faaborg et al. 2010). The costs of long and potentially dangerous migration are outweighed by the benefits of breeding and wintering during productive periods at harsh locations (O'Reilly and Wingfield 1995). Long-distance migrations have an extremely high energetic cost. Therefore, most migratory birds replenish fat stores by foraging at stopover sites along their migration route (Schaub and Jenni 2000). Stopover sites must provide seasonally abundant and predictable resources if migrants are to effectively refuel and complete their migration (Warnock 2010). Changing resource conditions, competition, weather, and predation are all factors that can determine success of migrants at stopover sites (Lyons and Haig 1995).

The Bay of Fundy is a well-studied stopover site for migratory shorebirds and is recognized as a Western Hemisphere Shorebird Reserve Network (WHSRN) landscape of hemispheric importance (Western Hemisphere Shorebird Reserve Network 2019). Semipalmated Sandpipers (*Calidris pusilla*) congregate by the hundreds of thousands in the upper Bay of Fundy during fall migration (Neima 2017) and make up 95% of the shorebird population in the area (Hicklin 1987). Other shorebird species are far outnumbered by Semipalmated Sandpipers in the Bay of Fundy in late summer and early fall, however, shorebird diversity increases after the Semipalmated Sandpipers have departed for the last leg of their migration (Atlantic Canada Shorebird Survey 2017). Some shorebirds tagged with radio trackers earlier along their fall migration route do not stop in the Bay of Fundy (Neima 2017), and we know that some shorebirds use other stopover sites in Atlantic Canada during fall migration and avoid the Bay entirely (Geldart 2018). These sites outside the Bay of Fundy can provide shorebirds with sufficient fuel to finish their migration (Davis 2019). Many shorebirds outside of the Bay of Fundy use small coastal stopover sites in New Brunswick and Nova Scotia, such as those on the Northumberland Strait (Atlantic Canada Shorebird Survey 2017). Stopover ecology at these smaller sites is less studied than the Bay of Fundy, however, recent studies have revealed the importance of these stopover sites for successful shorebird migration (Geldart 2018; Mackellar 2018; Davis 2019).

*Resource availability*

The ability to build sufficient fat stores at stopover sites influences migratory success of shorebirds. Therefore, it is very important to have suitable habitat and abundant food resources at stopover sites (Skagen 2006). Shorebirds rely on an abundance of invertebrate prey at stopover sites, such as amphipods, bivalves, and various worms (Smith et al. 2012; Rose et al. 2016).

While prey abundance is critical, it in turn is influenced by factors such as sediment particle size, water content, and resistance (VanDusen et al. 2012). These factors also affect the ability of birds to access prey. When particle size is small and substrate resistance low, prey are more accessible, and shorebirds are more efficient at consuming buried prey items (Finn et al. 2008). Small sediment particle size is also characteristic of poor drainage, which allows puddles or pools to persist on the surface longer after the tide has uncovered the sediment (VanDusen et al. 2012). This may lead to greater penetrability for tactile foragers, or prolonged surface activity of invertebrate prey items (VanDusen et al. 2012). Sediments in the Bay of Fundy have greater water content and smaller particle size than coastal sites on the Northumberland Strait in Eastern New Brunswick (Davis 2019).

The mudflats of the Bay of Fundy are home to high densities of the amphipod *Corophium volutator*. *C. volutator* is considered the most abundant macrofaunal invertebrate on the mudflats (Hicklin and Smith 1979). However, infauna (animals living in sediment) abundance has varied considerably from year to year, and other invertebrates, such as ostracods, have been known to dominate when *C. volutator* density is low (MacDonald et al. 2012). In 2018, stopover sites in the Bay of Fundy were characterized by high densities of *C. volutator*, copepods, and ostracods (Davis 2019). Conversely, coastal stopover sites are more characterized by shelled invertebrates, such as bivalves and gastropods (Mackellar 2018; Davis 2019). Petit-Cap, a stopover site on the Northumberland Strait in New Brunswick, had highest densities of bivalves, gastropods, and ostracods in 2018, and had little to no amphipods (Davis 2019).

### *Diet*

*Corophium volutator* is a common diet item of many shorebird species stopping in the Bay of Fundy, such as the Semipalmated Sandpiper, Semipalmated Plover (*Charadrius semipalmatus*), Least Sandpiper (*Calidris minutilla*), and Short-billed Dowitcher (*Limnodromus griseus*) (Hicklin and Smith 1979). Polychaete worms are also common diet items in the Bay of Fundy (Hicklin and Smith 1979) and often replace *C. volutator* as the most common prey item in the diets of shorebirds at other stopover sites (Weber and Haig 1997; Rose et al. 2016). Although shorebirds are known predators of invertebrates (e.g. Hicklin and Smith 1979; Quammen 1984; Weber and Haig 1997), recent evidence shows that many small-bodied Calidrid shorebirds also consume biofilm (Elner et al. 2005; Kuwae et al. 2008; Mathot et al. 2010; Quinn and Hamilton

2012; Jardine et al. 2015; Gerwing et al. 2016). Biofilms are communities of microbes within a mucilaginous matrix of extracellular polymeric substances that can form on nearly all surfaces (Characklis and Marshall 1990; Lopez et al. 2010). Biofilm found in the intertidal zone can make up substantial proportions of shorebird diets (Quinn and Hamilton 2012; Jardine et al. 2015; Davis 2019), and it contains an assortment of lipids and fatty acids that are essential for weight gain during migratory stopover (Schnurr et al. 2020).

*Foraging Behaviour*

Shorebirds exhibit a variety of foraging strategies, most of which are highly dependent on morphological characteristics (Barbosa and Moreno 1999; Dit Durell 2000; Norazlimi and Ramli 2015). Bill morphology is especially important in determining the most efficient foraging strategy (Dit Durell 2000). Short bills are often indicative of a surface-feeding strategy, such as pecking (Dit Durell 2000). Pecking is a visual tactic where shorebirds forage for prey items on the sediment surface (Barbosa and Moreno 1999). Longer bills are adapted for probing (Barbosa and Moreno 1999) where shorebirds consume prey buried deeper in the sediment (Dit Durell 2000). Probing is a tactile foraging strategy facilitated by sensory pits located on the bill tip (Nebel et al. 2005).

Skimming and grazing are more recently recognized foraging strategies observed in the Semipalmated Sandpiper (MacDonald et al. 2012) and Western Sandpiper (Kuwae et al. 2008). These strategies are facilitated by spines on the tongues of Calidrid shorebirds, which help scrape biofilm off the sediment surface (Kuwae et al. 2012). Biofilm consumption is often observed at night when visibility of invertebrate prey is low (Quinn 2011).

*Niche partitioning in shorebirds*

Because most shorebirds spend time in mixed-species flocks, it is likely that differences in morphology, foraging strategy, and diet are driven by competition (Burger et al. 1977). Shorebirds have a variety of morphological features that are adapted for particular diets and foraging strategies (Chandler 2009). These inter- and intraspecific differences enhance resource partitioning by limiting the niches of shorebirds even when competition does not occur (Bocher et al. 2014). Increasing habitat heterogeneity increases species richness by fulfilling the niche requirements of more species (Danufsky and Colwell 2003). Many shorebirds exhibit preference for wet areas (Burger et al. 1977), however, standing water can reduce food availability when it is too deep for birds to use (Isola et al. 2000). This can cause spatial segregation between small and large species as shorebirds need long enough bills and legs to forage in standing water (Danufsky and Colwell 2003). Differences in sediment characteristics can also lead to segregation as tactile foragers show preference for fine sediments through which they can move their bills (Quammen 1982; Danufsky and Colwell 2003). There is much variability in the degree of diet segregation between shorebird species (Bocher et al. 2014). However, when shorebird species have overlapping diets, morphology or foraging strategy often causes segregation of size or depth of prey to compensate for competition for prey taxa (Bocher et al. 2014). To support multi-species shorebird assemblages, stopover sites should have spatial variation in water content, sediment particle size, and type of available prey.

*Population declines*

Shorebird populations have declined by 37% since the 1970s, however, some species have done better or worse than average (North American Bird Conservation Initiative Canada 2019). There is a lack of understanding about where these declines are originating, which makes it difficult to implement effective conservation strategies (Morrison et al. 2012). Some factors that may be contributing to shorebird declines include increases in raptor population since the ban of DDT use in the 1980s (Morrison et al. 2012), hunting on South American wintering grounds (Ottema and Spaans 2008; Morrison et al. 2012), or habitat changes at stopover sites as a result of climate change (Galbraith et al. 2014). Although it is suggested that conditions on wintering grounds contribute greatly to shorebird declines (Morrison et al. 2012), degradation of stopover habitat – such as that at sites on the Yellow Sea – can have severe consequences for species that greatly rely on them (Studds et al. 2017). Many shorebird species rely heavily on stopover sites in Atlantic Canada during fall migration, especially those refuelling for non-stop flights over the Atlantic Ocean, such as the Semipalmated Sandpiper (Hicklin and Gratto-Trevor 2010). Therefore, understanding stopover ecology of shorebirds in Atlantic Canada is important if we hope to pinpoint the causes of shorebird declines.

*Study Objectives and Significance*

Small coastal sites in Atlantic Canada host diverse shorebird populations in late summer and early fall, but see less abundant populations than stopover sites in the Bay of Fundy. Recent studies show that small coastal sites also provide suitable stopover habitat for migratory shorebirds (Mackellar 2018; Davis 2019), and that these sites need to be studied more extensively to integrate them into large conservation plans. Coastal stopover sites on the Northumberland Strait in eastern New Brunswick host a large diversity of shorebird species including White-rumped Sandpipers (*Calidris fusicolis*), Semipalmated Plovers, Black-bellied Plovers (*Pluvialis squatarola*), Least Sandpipers, and Short-billed Dowitchers (Atlantic Canada Shorebird Survey 2017). Whereas in the Bay of Fundy, Semipalmated Sandpipers dominate the mudflats during their stay.

It is yet unclear how smaller coastal sites in Atlantic Canada support such diverse populations of shorebirds. Recent studies have demonstrated the importance of these sites to two specific shorebird species – the Semipalmated Plover and Semipalmated Sandpiper (Mackellar 2018; Davis 2019), however, there is a lack of research on whole community ecology at coastal stopover sites. The diversity of shorebirds and limited space available at coastal sites suggest that the effects of interspecific competition are strong. If resources are not in excess at these sites, niche partitioning must occur for diverse assemblages of shorebirds to coexist.

To address these knowledge gaps we are addressing the following research questions: 1) Is niche partitioning present in shorebird populations at coastal sites on the Northumberland Strait?, 2) If niche partitioning is present, on what niche dimensions do shorebird species partition themselves to avoid interspecific competition?, and 3) Why are shorebird assemblages more diverse in small coastal stopover sites than the Bay of Fundy? We hypothesize that niche partitioning is present between shorebird species at stopover sites in the Northumberland Strait, and that this partitioning allows diverse assemblages of shorebirds to coexist in small coastal sites. To answer these questions, we observed shorebird foraging behaviour at stopover sites in the Bay of Fundy and on the Northumberland Strait during fall migration to determine if shorebird species are partitioned by variation in foraging strategy. We measured prey availability, sediment characteristics, and biofilm abundance to examine how different habitat characteristics are segregated between shorebird species in the Northumberland Strait. Stable isotope analysis of shorebird blood and prey samples was used to map diet niches of each species.

Habitat degradation and steady declines in shorebird populations could have a profound effect on coastal sites where interspecific interactions span multiple trophic levels. Understanding niche partitioning among species with a similar prey base helps us predict the impacts of ecosystem changes (Friedlaender et al. 2011). Comparing habitat use of multiple species may also provide insights into how some species have maintained stable populations, while others are experiencing steep declines. To preserve stopover sites for all shorebird species that use them, it is important to understand how whole populations of shorebirds use these sites. Conservation efforts aimed at helping one species run the risk of hindering others if we do not have a better understanding of whole community ecology. It is therefore important to consider not only the interactions between shorebirds and their environment, but also the interactions between different shorebird species.

## Chapter 2: Methods

### *Study Area*

We examined stopover ecology of shorebirds at four sites in New Brunswick, Canada: Johnson's Mills ($45.81^{o}$N, $-64.50^{o}$N) and Pecks Cove ($45.73^{o}$W, $-64.49^{o}$N) in the Bay of Fundy, and Petit-Cap ($46.19^{o}$N, $-64.15^{o}$W) and Cape Jourimain ($46.15^{o}$N, $-63.85^{o}$W) in the Northumberland Strait. Behavioural observations and prey availability samples were taken at all four sites, but shorebirds were captured at only Johnson's Mills and Petit-Cap (Figure 2.1).

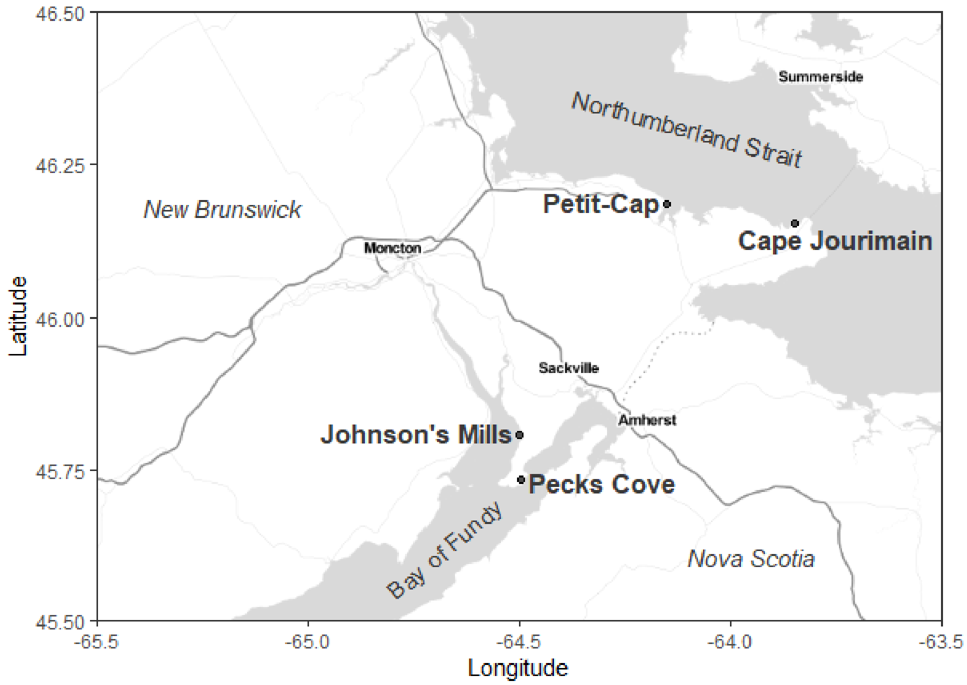


**Figure 2.1** Map of the two study sites in the Bay of Fundy and two sites in the Northumberland Strait in New Brunswick, Canada.

*Prey Availability*

We sampled mud- and sandflats in the Bay of Fundy and the Northumberland Strait to obtain estimates of invertebrate and biofilm abundance during early migration (July 17-19, 2019) and late migration (September 9-29, 2019). We took samples along transects perpendicular to shore at each site, starting 50 m from the end of the salt marsh at Pecks Cove, at the start of the mudflat at Johnson's Mills, and at the high tide line at Petit-Cap and Cape Jourimain. In the Bay of Fundy, we had two 500 m transects at each site, which were spaced 500 m apart. At Cape Jourimain, we had three 300 m transects, each spaced 100 m apart. At Petit-Cap we had five 300 m transects, with two facing the open side of the barrier beach, which were 400 m apart, and three facing the interior flats, which were 100 m apart. All transects were stratified into 100 m sections, and we collected samples from two randomly selected points in each stratum. A different set of random points were sampled in early- and late-season.

We collected invertebrate samples by pushing a 5.5 cm diameter core into the sediment until there was resistance at the point where the sediment consolidates. We sieved samples from the Bay of Fundy through 250 μm mesh, and samples from the Northumberland Straight through

500 µm mesh. The larger sieve size was needed for Northumberland Strait samples as the sediment particles are large and too much gets trapped by 250 µm mesh. Invertebrates retained by the sieve were stored in 95% ethanol until they could be sorted by taxon (lowest possible classification) and size. Only invertebrates alive at the time of sampling were sorted, which we determined by ensuring shelled invertebrates were not fragile enough to break easily, and that other invertebrates were not decomposed and/or missing heads. Individual invertebrates were sorted into 2 mm size classes, except polychaete worms, which were measured lengthwise in 10 mm size classes. Invertebrates, organized by site, size class, and taxa, were dried in an oven (40GC Gravity Convection Oven, Quincy Lab Inc., Chicago, IL) at 90°C for at least 24 hours, and then weighed. Following weighing, shelled invertebrates (phylum *Mollusca*) were then ashed at 550°C in a muffle furnace (Isotemp Programmable Muffle Furnace 650-750 Series, Fisher-Scientific, Waltman, MA) for 2 hours to remove consumable biomass. They were then reweighed, and the difference between pre- and post-ashing mass was calculated to determine the consumable biomass. Average invertebrate biomass was calculated for each taxon to estimate the mass of a single prey item. These average values were used to calculate the biomass of samples which were too light for the balance to weigh. This was achieved by multiplying the number of individuals in a light sample by the average mass of the taxon.

We collected two samples of the top 2 mm of sediment using a modified 10cc syringe at each sampling point to measure Chlorophyll *a* concentration, a proxy for biofilm standing crop. The syringe was pushed into the sediment, and the sampler used their thumb to trap air and sediment in the syringe before removing it. The syringe was then inverted, and we used the plunger to push up the top 2 mm of the sediment, which we sliced off using a metal spatula into a 20mL glass scintillation vial. The samples were kept in the dark at -20°C until further processing. They were later freeze dried at -50°C and 0.05mBar (FreeZone one-liter benchtop freeze drier, Labconco Corporation, Kansas City, MO) for a minimum of 5 hours. We used a fluorometry technique based off the methods of Welschmeyer (1994) to measure Chlorophyll *a* concentration of a 0.002-0.003 mg subsample of each biofilm sample. We added 5 mL of 3:2 mixture of 90% acetone to dimethyl sulfoxide (DMSO) extraction solvent to each sample. We mixed the samples by inverting them several times or mixing them for 2-3 seconds in a vortex mixer, then we placed the samples in a dark room on ice for 20 minutes. We repeated the mixing, then placed the samples back in the dark for another 10 minutes before mixing again and centrifuging for 20 minutes at 2500 rpm (Thermo Fisher Scientific Model no. 225A, Waltam MA; Hettick MIKRO 120, Beverly MA) to complete the extraction. Working with one sample at a time, we transferred ~4 mL of sample extract to a glass test tube. This test tube was placed in a fluorometer (10AU Chl *a* Fluorometer, Turner Designs, San Jose, CA), which provided a concentration reading in Relative Fluorescence Units (RFU). Samples reported over the standard curve (>2500 RFU) were diluted with extraction solvent and measured again. We converted Chlorophyll *a* concentration to µg/L, then calculated concentration of Chl *a* per gram of sediment using the following formula:

$$\frac{[Chl\ a](\mu g/L) * Extraction\ volume\ (L)}{Mass\ of\ sediment\ (g)} = \frac{\mu g\ Chl\ a}{g\ sediment}$$

We collected a sediment sample from each sampling point in a 45 mL plastic vial to analyze sediment particle size. We sieved samples through a cascade of 850 µm, 500 µm, 250 µm, 125 µm, and 63 µm mesh sizes, and collected the remaining sediment in each sieve in aluminum weigh boats. We collected the water and suspended sediment that flowed through all mesh sizes in a bucket under the 63 µm sieve (termed the pan fraction). We measured the volume of the pan fraction, mixed it well, and put 20 mL of it into a weigh boat. We dried all samples for at least 24 hours at 90$^{o}$C before weighing them. We then scaled the amount of sediment in 20 mL to the total amount of sediment in the pan fraction. These weights were used to calculate the proportion of each sediment size class in each sample.

*Foraging Behaviour*

We collected data on foraging behaviour of shorebirds between June 17$^{th}$ and October 9$^{th}$, 2019 at Johnson's Mills and Pecks Cove in the Bay of Fundy, and Petit-Cap and Cape Jourimain on the Northumberland Strait. We used focal animal sampling to estimate pecking and probing rates of foraging shorebirds. We also recorded date, time of observation, flock size, tide height, ground saturation, temperature, and weather conditions before sampling each flock. Behavioural observations took place during the day, and time of observations varied with tide height. Observations took place at a range of tide heights from 1.1 to 0.2 m in the Northumberland Strait and 10 to 3.8 m in the Bay of Fundy. We only observed foraging behaviour of flocks with more than 5 individuals, and flocks were considered separate if the distance between groups of birds was greater than the area taken up by the largest group.

Focal animal sampling was completed by recording the number of times an individual shorebird pecked or probed for a maximum of one minute. If a shorebird skimmed during a focal observation, we recorded the length of time they spent skimming. One or two observers collected data on 30 different birds each, or until focal samples had been collected for all birds in the flock. Movement of birds or observer error could have resulted in the same bird being sampled twice, however, by observing birds from left to right across the flock, we assumed that different individual birds were observed for each focal sample. Data from focal animal sampling were compiled to calculate an average pecking and probing rate per minute for each shorebird species.

After collecting behavioural observations, we took two prey samples, two sediment samples, and four biofilm samples from the location at which each flock was seen foraging. Methods and types of data collected are as described above for transect sampling. We took GPS coordinates at each sampling location and measured the penetrability of the sediments. These samples were taken to examine the habitat and prey characteristics at the locations different shorebird species chose to forage. Samples were taken once behavioural observations were finished for the day to prevent human disturbance from interfering with shorebird behaviour.

*Catching and Sampling Shorebirds*

We captured shorebirds between July 31 and September 13, 2019 at Johnson's Mills in the Bay of Fundy, and Petit-Cap on the Northumberland Strait. Semipalmated Sandpipers were captured at Johnson's Mills using a Fundy pull trap (Hicklin et al. 1989). We used mist nets at Petit-Cap to capture Semipalmated Sandpipers, White-rumped Sandpipers, Semipalmated Plovers, Short-billed Dowitchers, and Least Sandpipers. Mist nets were set up in arrays across the intertidal zone, and capturing took place at night, when visibility was low. This made the nets more difficult for flying shorebirds to see and evade. Shorebirds were weighed upon capture, and we collected blood from those that met species-specific minimum weight requirements (Table 2.1). We assume shorebirds arrive at stopover sites light and become heavier over time as they forage (Quinn and Hamilton 2012). Therefore, these minimum weight requirements ensure plasma samples are taken from shorebirds that have been feeding in the area, which allows for more accurate estimates of their diet during migratory stopover. We pricked the brachial vein with a 27.5-gauge needle and collected blood in two 70 µL capillary tubes, which were used to transfer the blood to 200 µL Eppendorf tubes. Blood samples were kept on ice until they could later be centrifuged for one minute at 10,000 rpm (mySPIN12 Mini Centrifuge, Thermo Scientific) to separate plasma and red blood cells. We held each bird and applied pressure to puncture wounds until the bleeding had stopped. Captured shorebirds were then fitted with aluminum USGS bands on the upper left leg and field-readable alphanumeric flags on the upper right leg. We took morphometric measurements from each bird, measuring flattened straightened wing cord, tarsus length, bill length (culmen to tip), and age before releasing them.

**Table 2.1.** Details of shorebird capture and blood sampling for stable isotope analysis at Petit-Cap and Johnson's Mills in 2019.

| Species (common name) | Captured (N) | Minimum weight for stable isotope analysis (g) | Blood samples for analysis (N) |
|---|---|---|---|
| Semipalmated Sandpiper | 232 | 30 | 82 |
| White-rumped Sandpiper | 57 | 45-48 | 20 |
| Least Sandpiper | 3 | 25 | 3 |
| Semipalmated Plover | 20 | 50 | 20 |
| Short-billed Dowitcher | 16 | no minimum | 15 |

*Diet*

We collected blood samples from 53 Semipalmated Sandpipers at Johnson's Mills, and 87 shorebirds of various species at Petit-Cap for analysis of stable isotopes of $^{15}N$ and $^{13}C$. These birds met the minimum weight requirements, indicating that they had gained weight since arrival and had been foraging in the area for some time. Stable isotope ratios in bird blood plasma reflect diet over the last six days; bird plasma has a half-life of three days (Hobson and Clark 1993).

Prey samples were collected from Johnson's Mills, Pecks Cove, Petit-Cap, and Cape Jourimain where birds were observed foraging. We sieved these samples and sorted live invertebrates by taxa from each site. We collect one to three samples of each taxon from each site. When possible, three samples were made, however, some taxa were not abundant enough to make three full samples. We kept the live-sorted invertebrate samples at -20°C in glass scintillation vials until processing. Excess sediment from three biofilm samples at each site was used to analyze the stable isotope signatures of biofilm. We dissected *Macoma* spp. and *Mya* spp. to remove soft tissue from shells. Then all samples were dried in an oven at 70°C for at least 24 hours. We then ground the dehydrated samples individually into a fine powder using a mortar and pestle. We cleaned the mortar and pestle with 90% ethanol between samples to prevent contamination. We acid treated a portion of each sample of *Corophium volutator*, *Gemma gemma*, *Hydrobia* spp., and biofilm to remove inorganic carbon and prevent it from interfering with $\delta^{13}C$ values (Kennedy et al. 2005). Acid treatment was performed by adding 0.5M hydrochloric acid to samples in glass centrifuge tubes. We stirred each sample with a glass rod until we saw no more $CO_2$ bubbles being released. We then let the samples sit for one hour before centrifuging them and pipetting off excess acid. We repeated this process until there was no visible calcareous material in the samples and the addition of acid no longer produced $CO_2$ bubbles. We rinsed the acid treated samples with Milli-Q water, then let them sit for 20 minutes to settle before pipetting off the excess water. We then rinsed the samples once more with Milli-Q water and centrifuged them before pipetting off excess water and placing them in the oven at 70°C for 24 hours to re-dry.

We pre-weighed dried samples for stable isotope analysis using a Mettler-Toledo MX5 microbalance with readability to 0.001mg. Target weights for invertebrate samples were 1.000mg, plasma samples were 0.800mg, and biofilm samples were 45mg for both $\delta^{13}C$ and $\delta^{15}N$ from Cape Jourimain and Pecks Cove, 45mg for $\delta^{15}N$ and 10mg for $\delta^{13}C$ from Johnson's Mills, and 45mg for $\delta^{15}N$ and 20mg for $\delta^{13}C$ from Petit-Cap. Samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ signatures at the Environmental Analytics and Stable Isotope Laboratory at Mount Allison University using an Elementar PyroCube Elemental Analyzer (EA)(Elementar Analysensysteme GmbH, Hanau, Germany) and an Isoprime Precision Isotope Ratio Mass Spectrometer (IRMS) (Elementar UK Ltd, Cheadle, UK). Isotope signatures are represented as delta values, which are a relative isotope ratio of the sample to international standards based on the following formula:

$$\delta^{a} X_{(Sample)} = \left[\left(\frac{R_{(Sample)}}{R_{(Standard)}}\right) - 1\right] * 1000$$

where a = the heavier isotope, X = the element of interest (Nitrogen or Carbon), and R = the ratio of heavy to light isotope. We applied diet-tissue fractionation coefficients to the isotope signatures of shorebird plasma to account for differential uptake of dietary isotopes by different organs, and to position plasma nearer to prey signatures for use in Bayesian mix models (Quinn and Hamilton 2012). We applied fractionation coefficients of 3.3±0.3 (mean ± SD) for $\delta^{15}N$ signatures, and 0.5±0.3 for $\delta^{13}C$ signatures, which are derived from Dunlin (*Calidris alpina;* Ogden et al. 2004). Diet-tissue fractionation coefficients have not been calculated for most shorebird species, therefore, the Dunlin-derived coefficients were applied to all species in this study. Fractionation is constant across varying diets for bird blood plasma (Caut et al. 2009), and the coefficients from Dunlin have been used for closely related species, such as the Semipalmated Sandpiper. The accuracy of these values for less closely related species is not known, but they are the closest approximation available for this study.

*Statistical Analyses*

*Overview*

Analyses were performed using R (version 3.6.2) with R Studio interface (RStudio Team 2018). Parametric assumptions were tested with Levene's test of homogeneity of variance, Box's M test for equivalence of covariance matrices, and Shapiro-Wilk normality test. Transformations were applied to data that did not meet assumptions, and non-parametric tests were used when transformed data also failed to meet assumptions. Data were plotted using the 'ggplot2' package (Wickham 2016), 'simmr' package (Parnell 2019), and 'SIBER' package (Jackson et al. 2011).

*Prey availability*

We pooled prey items from Johnson's Mills and Pecks Cove to estimate prey abundance in the Bay of Fundy, and we pooled prey from Petit-Cap and Cape Jourimain to estimate prey abundance in the Northumberland Strait. We grouped prey items into the following taxonomic groups: amphipods, bivalves, gastropods, polychaetes, and meiofauna. Amphipods, bivalves, and gastropods were further organized in 4 mm size classes, and polychaetes in 10 mm size classes. Meiofauna were not size classed. All sizes of polychaetes were included in analyses, however, shelled prey items > 12mm in length were excluded as they are too large for most shorebird to consume. Many samples did not contain prey items from each taxon, which resulted in a large number of zeros in the data set. This created a non-normal distribution of points as well as heterogeneous multivariate variances, therefore, we used a non-parametric permutational multivariate analysis of variance (PERMANOVA) to compare invertebrate biomass between the Bay of Fundy and Northumberland Strait. This was performed with the 'adonis' function in the 'vegan' package (Oksanen et al. 2019; permutations = 999, dissimilarity matrix = Bray-Curtis), with biomass of each taxon as dependent variables and stopover location as the independent variable. Size classes were pooled for this analysis to test only differences in taxa, rather than sizes of taxa. Pairwise Kruskal-Wallis rank sum tests were performed to contrast the biomass of each taxon between stopover locations. Bonferroni correction was used to adjust the alpha value for 5 pairwise comparisons (adjusted $a = 0.01$).

Samples of Chlorophyll *a* concentration failed normality assumptions, and this was not remedied by application of a $\log_{10}$ transformation. Therefore, we compared Chlorophyll *a* concentration between sites by performing a non-parametric Kruskal-Wallis rank sum test with Chlorophyll *a* concentration as the dependent variable and stopover location as the independent variable.

We performed a principal component analysis (PCA) with a varimax rotation using the 'principal' function in the 'GPA rotation' package (Bernaards et al. 2005) on sediment penetrability and particle size data to reduce the number of variables for analysis. The rotated solution was used to make the results more easily interpretable. The resulting two orthogonal components were sediment resistance (low to high) and sediment particle size (small to large). The sediment resistance component failed to pass normality assumptions after $\log_{10}$ transformation, therefore, a non-parametric PERMANOVA was performed using the 'adonis' function (permutations = 999, dissimilarity matrix = Bray-Curtis), with both sediment components as the dependent variables and stopover location as the independent variable. Pairwise Kruskal-Wallis rank sum tests were performed to contrast each sediment component separately between stopover locations.

*Foraging behaviour*

We included foraging rates of 7 shorebird species in the analyses, however, Greater Yellowlegs and Lesser Yellowlegs were pooled together as "Yellowlegs". Shorebird species are abbreviated using the following four-letter codes: Semipalmated Sandpiper = SESA, White-rumped Sandpiper = WRSA, Least Sandpiper = LESA, Semipalmated Plover = SEPL, Short-billed Dowitcher = SBDO, and Yellowlegs = YELL. Foraging rate data were biased for abundant shorebird species, which created an unbalanced design. Therefore, we performed a non-parametric PERMANCOVA using the 'adonis' function to compare the pecking and probing rates of different shorebird species in the Northumberland Strait (permutations = 999). We specified that a Bray-Curtis matrix be used to compute dissimilarity indices between individual shorebirds. We used pecking and probing rates as the dependent variables and species as the independent variable. We controlled for 25 habitat covariates, which included the biomass of 4mm size classes of invertebrate taxa, both sediment principal components, and Chlorophyll *a* concentration. However, non-significant covariates were not included in the final PERMANCOVA. This resulted in 4 significant covariates in the design – the sediment particle size component and biomass of 4-8mm amphipods, 4-8mm bivalves, and meiofauna. We tested the homogeneity of multivariate group dispersions (variances) using the 'permutest' function in the 'vegan' package (Oksanen et al. 2019; dissimilarity matrix = Bray-Curtis). We plotted a non-metric multidimensional scaling (NMDS) plot to visualize the foraging strategy of each species.

We compared the foraging strategies of each shorebird species using 15 pairwise PERMANCOVAs (permutations = 999, dissimilarity matrix = Bray-Curtis). We then used 15 pairwise Kruskal-Wallis rank sum tests to compare the pecking rates of each species, and another 15 Kruskal-Wallis tests to compare probing rates. Bonferroni correction was used to adjust the alpha value for these pairwise comparisons (adjusted $\alpha = 0.0033$).

We used the methods outlined above to perform a PERMANCOVA to compare the foraging strategies of Semipalmated Sandpipers in the Bay of Fundy and the Northumberland Strait. We used pecking and probing rates of Semipalmated Sandpipers as the dependent variables and stopover location as the independent variables. We removed non-significant habitat variables to control for only significant covariates. We used the 'permutest' function to test the homogeneity of multivariate group dispersions (variances), and Kruskal-Wallis rank sum tests to compare pecking and probing rates separately between stopover locations.

*Diet*

Blood samples were collected from Semipalmated Sandpipers, White-rumped Sandpipers, Least Sandpipers, Semipalmated Plovers, and Short-billed Dowitchers. However, too few Least Sandpipers were sampled to be included in diet analyses. Stable isotope signatures of shorebird plasma failed normality and homogeneity of variance assumptions. We compared stable isotope signatures of shorebird species in the Northumberland Strait using a non-parametric PERMANOVA with $\delta^{13}C$ and $\delta^{15}N$ signatures as the dependent variables and species as the independent variable. This was done using the 'adonis' function (permutations = 999, dissimilarity matrix = Bray-Curtis). The 'pairwise.adonis' function in the 'vegan' package (Oksanen et al. 2019) was used to contrast diets between species. We performed six pairwise Kruskal-Wallis rank sum tests to compare the $\delta^{13}C$ isotope signatures of each species, and another six Kruskal-Wallis tests to compare $\delta^{15}N$ isotope signatures. Bonferroni correction was used to adjust the alpha value for these pairwise comparisons (adjusted $\alpha = 0.0083$).

We repeated these methods to compare stable isotopes signatures of plasma samples from Semipalmated Sandpipers captured in the Bay of Fundy and the Northumberland Strait. We used a PERMANOVA with $\delta^{13}C$ and $\delta^{15}N$ signatures of Semipalmated Sandpipers as the dependent variables and stopover location as the independent variable. We used Kruskal-Wallis rank sum tests to compare the $\delta^{13}C$ and $\delta^{15}N$ signatures separately between stopover locations.

We used Bayesian mixing models to estimate contributions of available prey taxa to shorebird diets with the 'Stable Isotopes in R' (SIAR) package (Parnell and Jackson 2013). This mixing model calculates potential diet proportions based on plasma isotope signatures and the mean isotope values of each food source included in the model. We included potential food sources in the model based on the available prey base at each site, including biofilm. We included the prey base from the Northumberland Strait in estimates of the diets of shorebirds captured at Petit-Cap, and we included the prey base from the Bay of Fundy for Semipalmated Sandpipers captured at Johnson's Mills. We did not include prior distribution in the mixing models. Because assumptions about diet-tissue fractionation coefficients generate error that may influence results, statistical analyses were not performed on these data and results should be considered to be estimates only, with the true values falling somewhere within the confidence intervals of those estimates.

## Chapter 3: Results

### *Prey availability*

Invertebrate community composition varied between the Bay of Fundy and Northumberland Strait (Figure 3.1; Table 3.1). We found that the Bay of Fundy had more amphipods and meiofauna than the Northumberland Strait, but less gastropods (Table 3.1). There is not a significant different in the biomass of bivalves or polychaetes at stopover sites in the Bay of Fundy and Northumberland Strait (Table 3.1).

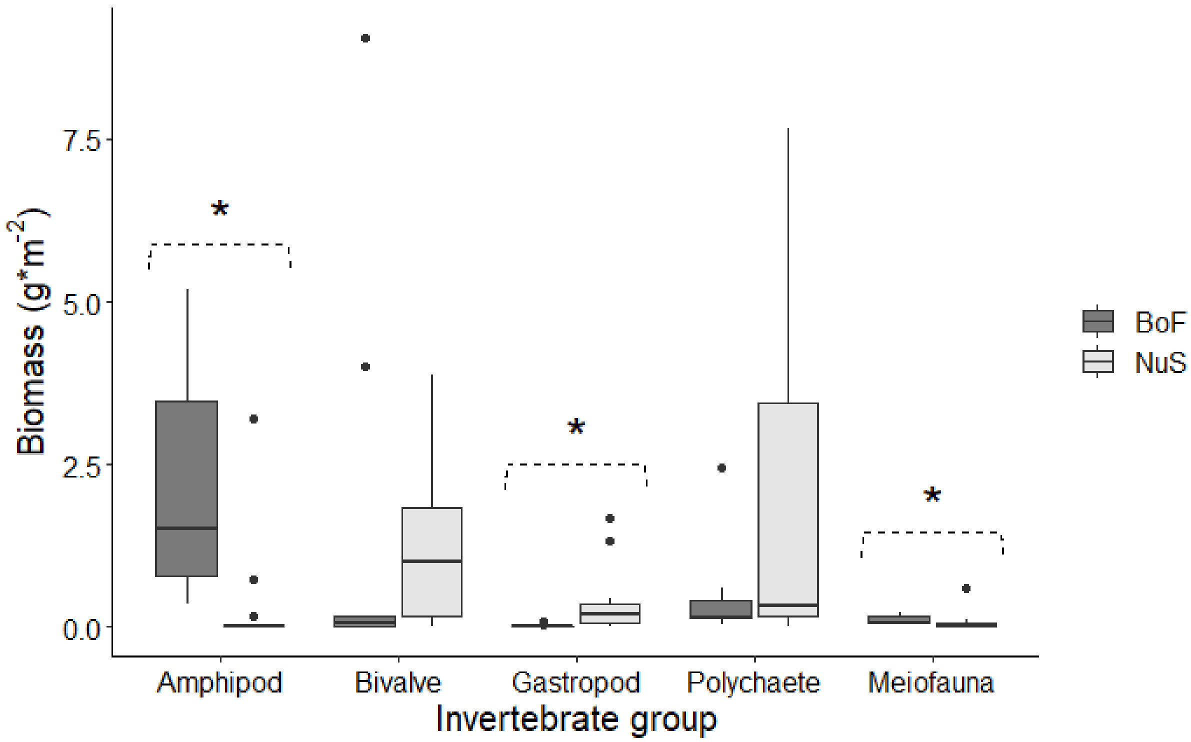


**Figure 3.1.** Biomass ($g*m^{-2}$) of invertebrate taxonomic groups from stopover sites in the Bay of Fundy (BoF, dark grey) and Northumberland Strait (NuS, light gray). Boxes represent 1st and 3rd quartiles around the median line at box centers, and whiskers represent interquartile range. Points represent statistical outliers. Statistically significant differences between BoF and NuS are denoted with asterisks (*). $N_{NuS} = 90$, $N_{BoF} = 45$.

**Table 3.1.** Results from PERMANOVA of the effect of stopover location on prey availability, and the results of pairwise Kruskal Wallis tests comparing the available biomass of invertebrate taxa between the Bay of Fundy (BoF) and Northumberland Strait (NuS). Statistically significant p-values are indicated with an asterisk (*).

| **Contrast** | **Multivariate Effect** | | **Pairwise Comparison** | |
|---|---|---|---|---|
| | F value | p value | Prey item | p value |
| Location | 5.64 | 0.005* | Amphipod | < 0.0001* |
| | | | Bivalve | 0.067 |
| | | | Gastropod | 0.002* |
| | | | Polychaete | 0.123 |
| | | | Meiofauna | 0.027* |

There was no significant difference in the concentration of Chlorophyll *a* in the Bay of Fundy and Northumberland Strait (Figure 3.2; Kruskal-Wallis $\chi^2_1 = 3.06$, $p = 0.080$).

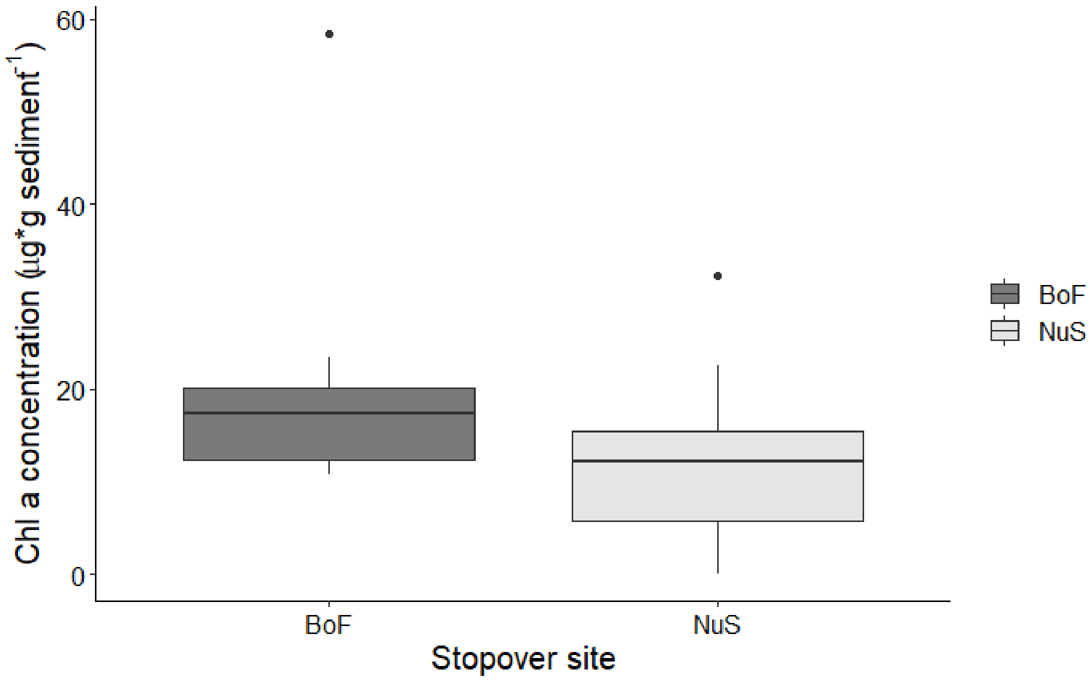


**Figure 3.2.** Chlorophyll a concentration (µg*g sediment $^{-1}$) in the Bay of Fundy (BoF, dark grey) and Northumberland Strait (NuS, light grey). See figure 3.1 for boxplot interpretation. $N_{NuS}$ = 18, $N_{BoF}$ = 9.

A rotated principal component analysis (PCA) of the proportions of sediment particle sizes and penetrability data resulted in two eigenvalues greater than one (Figure 3.3). Rotated component one (RC1; low to high sediment resistance) accounted for 45% of the variability, and rotated component two (RC2; small to large sediment particle size) accounted for 33% of the variability.

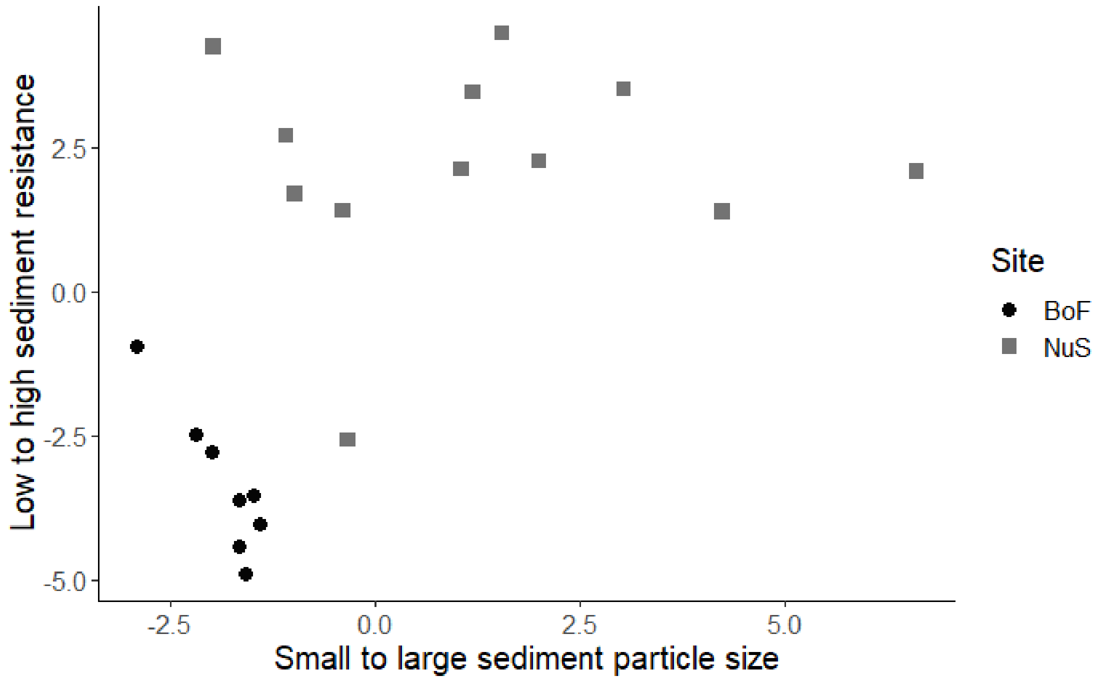


**Figure 3.3.** Rotated component 2 on the x-axis against rotated component 1 on the y-axis for sediment characteristics in the Bay of Fundy (BoF) and Northumberland Strait (NuS). Axes are labelled to reflect loadings from principal components analysis. RC1 accounts for 45% of variability, and RC2 accounts for 33% of variability.

We found a significant difference between the sediment characteristics in the Bay of Fundy and Northumberland Strait (Figure 3.4; PERMANOVA $F_{1,25} = 724.73$, $p = 0.001$). The sediments in the Bay of Fundy are finer (Kruskal-Wallis $\chi^2_1 = 10.544$, $p = 0.001$) and less resistant (Kruskal-Wallis $\chi^2_1 = 15.74$, $p < 0.0001$) than those in the Northumberland Strait (Figure 3.4).

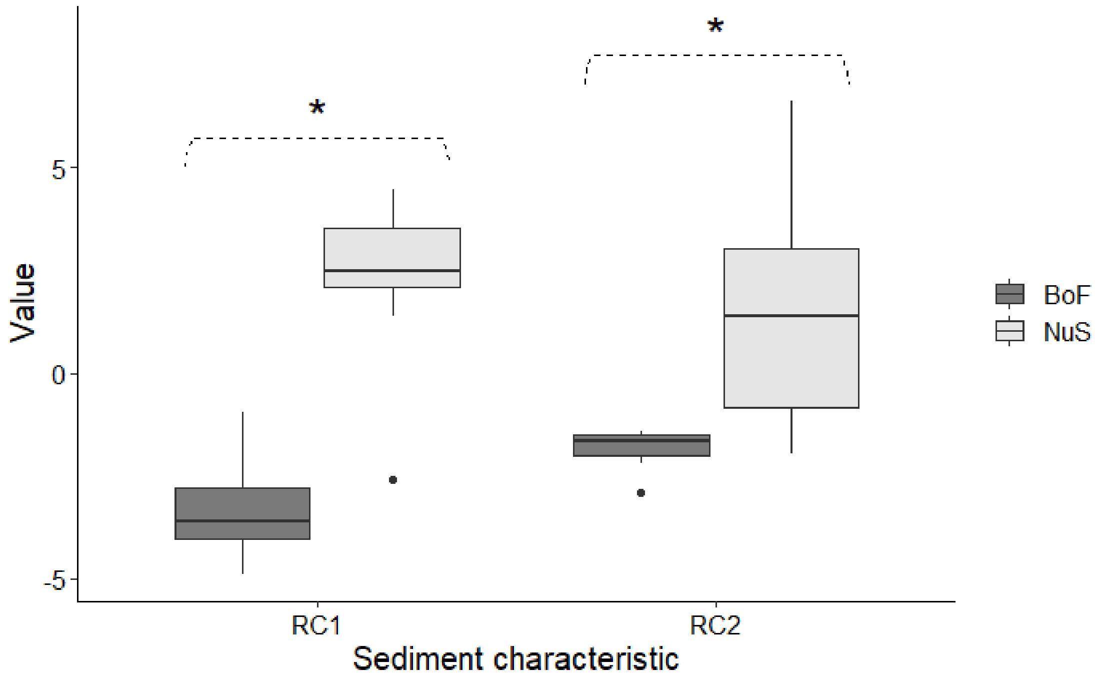


**Figure 3.4.** Values of rotated components of sediment characteristics in the Bay of Fundy (BoF, dark grey) and Northumberland Strait (NuS, light grey). RC1 = sediment resistance and RC2 = sediment particle size. Statistically significant differences between BoF and NuS are denoted with asterisks. (*). See figure 3.1 for boxplot interpretation. $N_{NuS} = 36$, $N_{BoF} = 18$.

*Foraging behaviour*

Species composition of flocks in the Northumberland Strait was influenced by sediment particle size and resistance (Table 3.2). Availability of invertebrate prey taxa and Chlorophyll *a* concentration did not have a significant effect on flock species composition (Table 3.2).

**Table 3.2.** Results from PERMANOVA of the effect of habitat characteristics on the abundance of different shorebird species in a flock on the Northumberland Strait. Significant p-values are denoted with and asterisk (*).

| Factor | Df | F-value | p-value |
|---|---|---|---|
| Sediment particle size | 1 | 3.15 | 0.015* |
| Sediment resistance | 1 | 2.51 | 0.026* |
| Amphipod availability | 1 | 1.51 | 0.165 |
| Bivalve availability | 1 | 1.57 | 0.155 |
| Gastropod availability | 1 | 0.29 | 0.938 |
| Polychaete availability | 1 | 0.11 | 0.99 |
| Chl *a* concentration | 1 | 0.82 | 0.569 |
| Residuals | 10 | | |
| Total | 17 | | |

The multivariate dispersions of shorebird foraging strategies differ between species ($F_{5,430} = 7.63$, $p = 0.001$). We detected a significant effect of species on multivariate foraging strategies in the Northumberland Strait when controlled for significant ($p < 0.05$) covariates (Figure 3.5; Table 3.3). Short-billed Dowitchers and Semipalmated Plovers use significantly different foraging strategies than all other species (Figure 3.5; Table 3.4). The foraging strategy of Yellowlegs is significantly different from all species except the White-rumped Sandpiper (Figure 3.5; Table 3.4). Semipalmated Sandpipers, Least Sandpipers, and White-rumped Sandpipers do not use significantly different foraging strategies (Figure 3.5; Table 3.4).

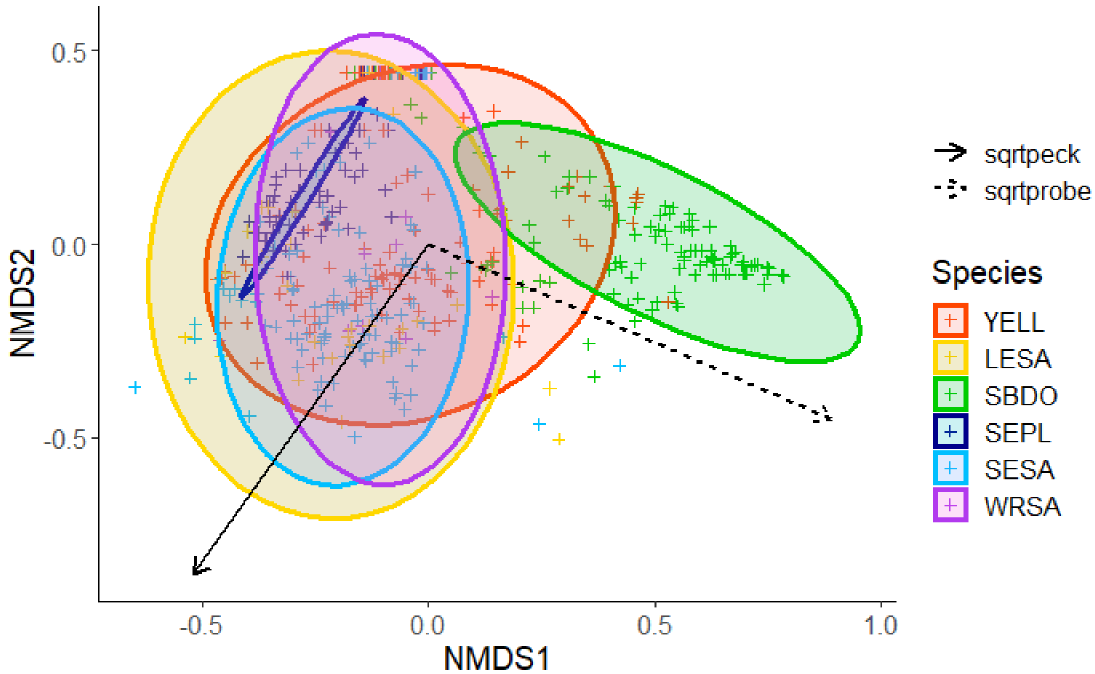


**Figure 3.5.** Non-metric multidimensional scaling (NMDS) plot of shorebird foraging strategies in the Northumberland Strait. Size, shape, and location of ellipses within the plot represent foraging strategies. Arrows indicate the direction of the two significant factors: square root transformed pecking rate (solid arrow) and probing rate (dotted arrow). Two-dimensional stress = 0.065. N = 436.

**Table 3.3** Results of PERMANCOVA of effect of species on foraging strategies at stopover sites in the Northumberland Strait controlled for significant habitat covariates.

| Factor | Df | F-value | p-value |
|---|---|---|---|
| Species | 5 | 96.16 | 0.001 |
| Sediment particle size | 1 | 7.43 | 0.004 |
| Amphipods 4-8 mm | 1 | 4.34 | 0.015 |
| Bivalves 4-8 mm | 1 | 4.17 | 0.026 |
| Meiofauna | 1 | 9.41 | 0.001 |
| Residuals | 426 | | |
| Total | 435 | | |

**Table 3.4.** P-values from pairwise PERMANCOVAs between multivariate foraging strategies of shorebird species controlled for significant covariates. P-values smaller than the adjusted alpha value ($\alpha = 0.003$; corrected for 15 comparisons with Bonferroni correction) are marked with asterisks (*). SESA = Semipalmated Sandpiper, WRSA = White-rumped Sandpiper, LESA = Least Sandpiper, SEPL = Semipalmated Plover, YELL = Yellowlegs, SBDO = Short-billed Dowitcher.

| | SESA | WRSA | LESA | SEPL | YELL |
|---|---|---|---|---|---|
| WRSA | 0.181 | | | | |
| LESA | 0.209 | 0.254 | | | |
| SEPL | 0.001* | 0.002* | 0.001* | | |
| YELL | 0.001* | 0.242 | 0.001* | 0.001* | |
| SBDO | 0.001* | 0.001* | 0.001* | 0.001* | 0.001* |

There is a significant effect of species on pecking rates (Kruskal-Wallis $\chi^2_5 = 192.31$, $p < 0.0001$) and probing rates (Kruskal-Wallis $\chi^2_5 = 211.5$, $p < 0.0001$). Short-billed Dowitchers have significantly lower pecking rates than all other species (Figure 3.6; Table 3.5). There is not a significant difference between the pecking rates of Semipalmated Sandpipers, Least Sandpipers, and White-rumped Sandpipers, or between Yellowlegs, Semipalmated Plovers, and White-rumped Sandpipers (Figure 3.6; Table 3.5). Short-billed Dowitchers have significantly higher probing rates than all other species, while Semipalmated Plovers have significantly lower probing rates than all other species (Figure 3.6; Table 3.5). The probing rates of Semipalmated Sandpipers, Least Sandpipers, White-rumped Sandpipers, and Yellowlegs do not differ (Figure 3.6; Table 3.5).

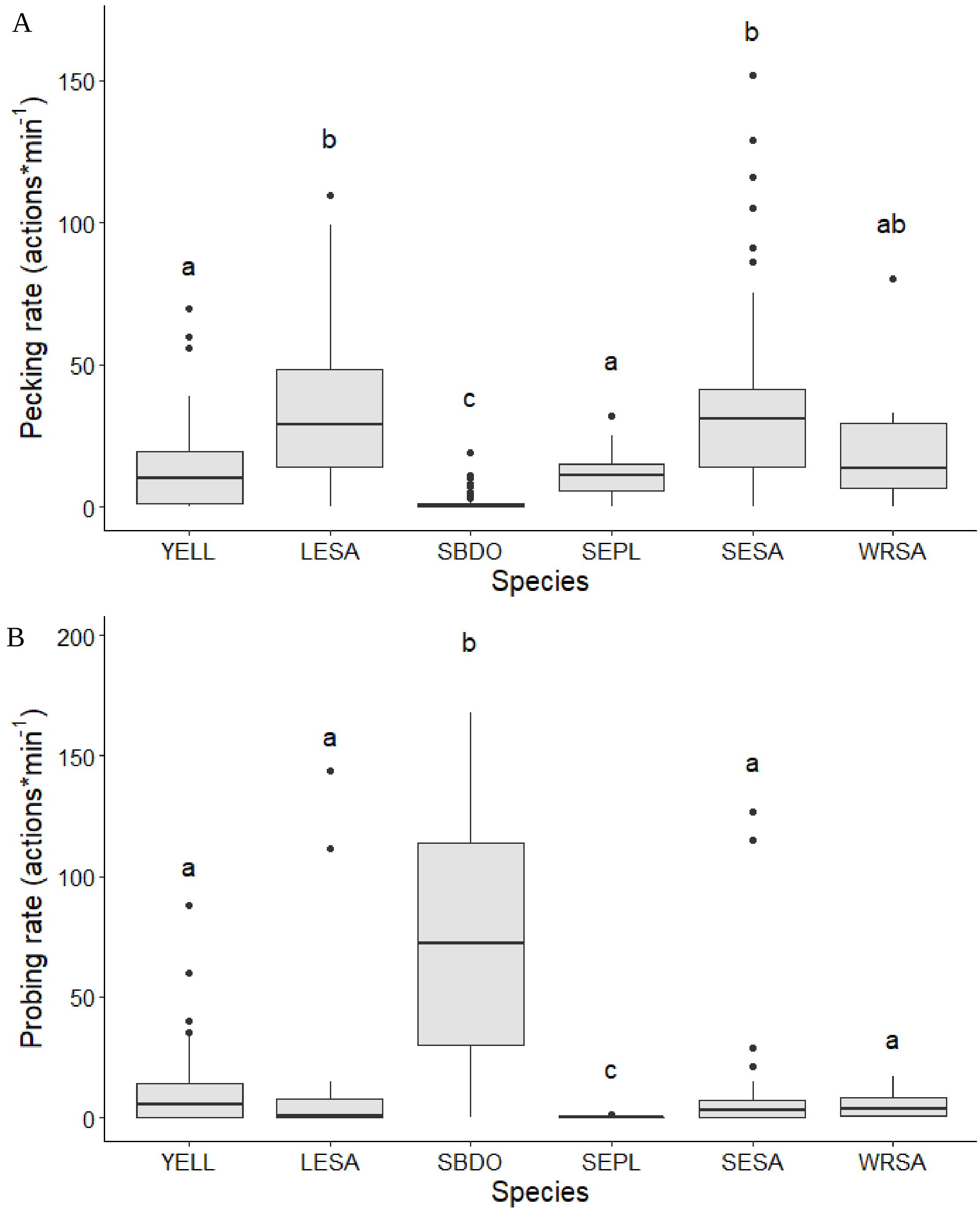


**Figure 3.6.** Boxplots of A) pecking rates (actions*min$^{-1}$) and B) probing rates (actions*min$^{-1}$) of shorebird species in the Northumberland Strait. Statistically significant differences are denoted with letters. Boxes labelled with different letters represent significantly different foraging rates. See figure 3.1 for boxplot interpretation. $N_{YELL}$ = 29, $N_{LESA}$ = 30, $N_{SBDO}$ = 109, $N_{SEPL}$ = 63, $N_{SESA}$ = 115, $N_{WRSA}$ = 10.

**Table 3.5.** P-values from pairwise Kruskal-Wallis rank sum tests between pecking and probing rates of shorebird species. P-values smaller than the adjusted alpha value ($\alpha = 0.003$; corrected for 15 comparisons with Bonferroni correction) are marked with asterisks (*).

| Foraging rate | | SESA | WRSA | LESA | SEPL | YELL |
|---|---|---|---|---|---|---|
| Pecking rate | SESA | | | | | |
| | WRSA | 0.103 | | | | |
| | LESA | 0.965 | 0.184 | | | |
| | SEPL | < 0.0001* | 0.251 | < 0.0001* | | |
| | YELL | < 0.0001* | 0.192 | < 0.0001* | 0.815 | |
| | SBDO | < 0.0001* | < 0.0001* | < 0.0001* | < 0.0001* | < 0.0001* |
| Probing rate | SESA | | | | | |
| | WRSA | 0.653 | | | | |
| | LESA | 0.397 | 0.422 | | | |
| | SEPL | < 0.0001* | < 0.0001* | < 0.0001* | | |
| | YELL | 0.006 | 0.445 | 0.025 | < 0.0001* | |
| | SBDO | < 0.0001* | < 0.0001* | < 0.0001* | < 0.0001* | < 0.0001* |

The multivariate dispersions of foraging strategies of Semipalmated Sandpipers differ between the Bay of Fundy and the Northumberland Strait ($F_{1, 372} = 9.22$, $p = 0.005$). We found a significant effect of stopover location on multivariate foraging strategies when controlling for significant ($p < 0.05$) covariates (Figure 3.7; Table 3.6; PERMANCOVA, $F_{1, 363} = 102.80$, $p = 0.001$).

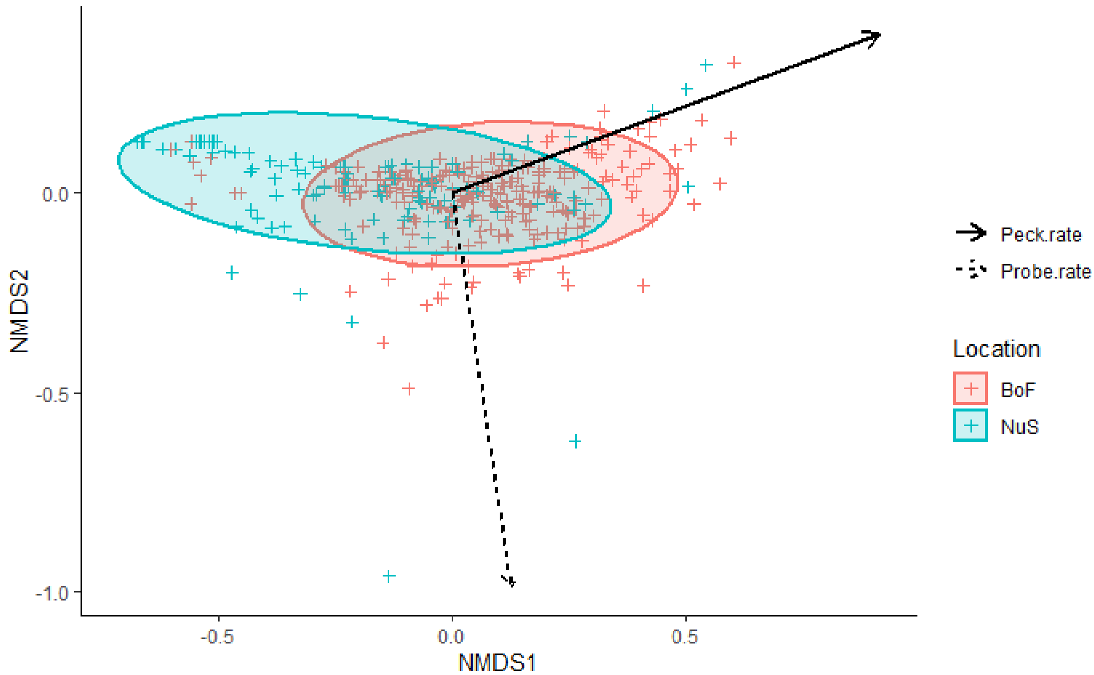


**Figure 3.7.** Non-metric multidimensional scaling (NMDS) plot of Semipalmated Sandpiper foraging strategies in the Bay of Fundy (BoF, red) and the Northumberland Strait (NuS, blue). Size, shape, and location of ellipses within the plot represent foraging strategies. Arrows indicate the direction of the two significant factors: pecking rate (solid arrow) and probing rate (dotted arrow). Two-dimensional stress = 0.046. N = 748.

**Table 3.6.** Results of PERMANCOVA of the effect of stopover location (Bay of Fundy versus Northumberland Strait) on foraging strategies of Semipalmated Sandpipers, controlling for significant habitat covariates.

| Factor | Df | F-value | p-value |
|---|---|---|---|
| Location | 1 | 102.80 | 0.001 |
| Sediment resistance | 1 | 24.01 | 0.001 |
| Sediment particle size | 1 | 5.43 | 0.011 |
| Amphipods <4 mm | 1 | 14.30 | 0.001 |
| Bivalves 4-8 mm | 1 | 16.41 | 0.001 |
| Bivalves 8-10 mm | 1 | 14.26 | 0.001 |
| Gastropods 4-8 mm | 1 | 5.15 | 0.007 |
| Meiofauna | 1 | 16.57 | 0.001 |
| Polychaetes <10 mm | 1 | 9.56 | 0.001 |
| Polychaetes 20-30 mm | 1 | 17.18 | 0.001 |
| Residuals | 363 | | |
| Total | 373 | | |

Semipalmated Sandpipers in the Bay of Fundy have significantly higher pecking rates (Kruskal-Wallis $\chi^2_1 = 80.24$, $p < 0.0001$) and probing rates (Kruskal-Wallis $\chi^2_1 = 40.91$, $p < 0.0001$) than Semipalmated Sandpipers in the Northumberland Strait (Figure 3.8).

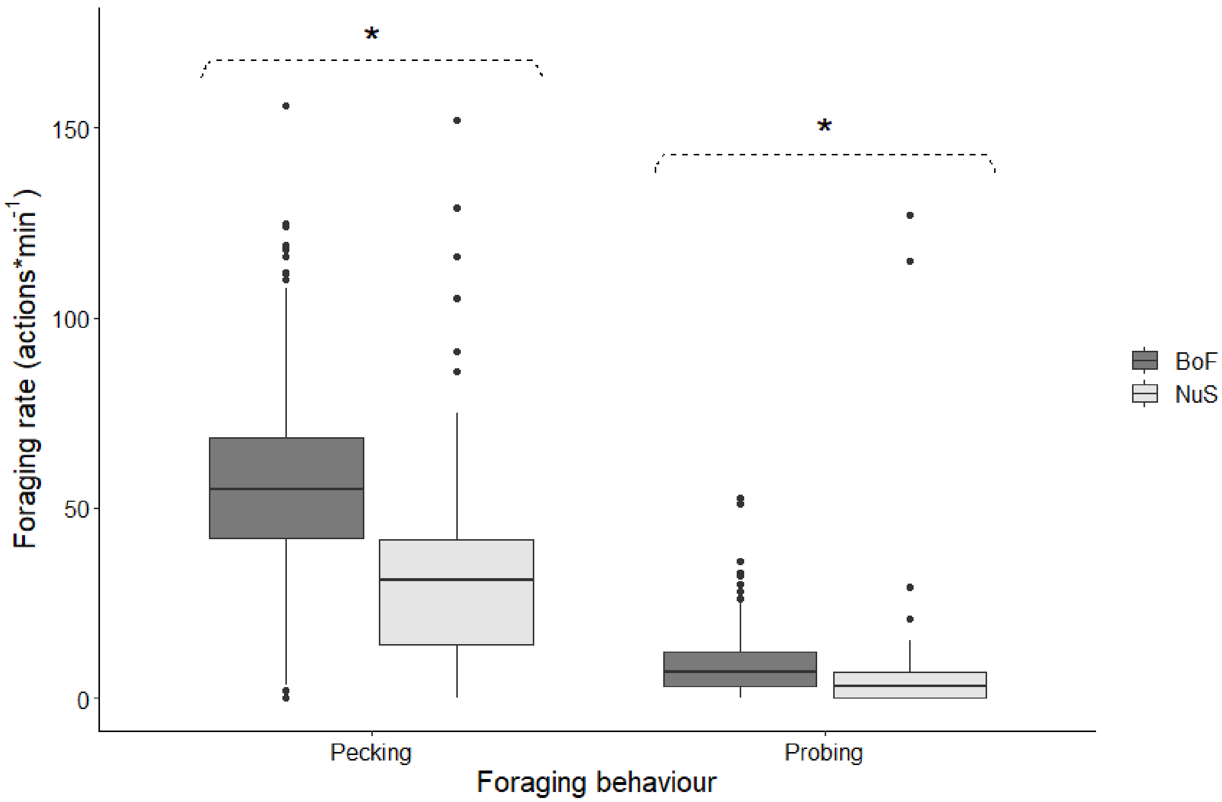


**Figure 3.8.** Pecking and probing rates (actions*min$^{-1}$) of Semipalmated Sandpipers in the Bay of Fundy (BoF, dark grey) and Northumberland Strait (NuS, light grey). Statistically significant differences between BoF and NuS are denoted with asterisks (*). See figure 3.1 for boxplot interpretation. $N_{NuS}$ = 230, $N_{BoF}$ = 518.

*Diet*

There is a significant effect of species on plasma isotope signatures of shorebirds in the Northumberland Strait (Table 3.7; PERMANOVA, $F_{3,80}$ = 13.65, p = 0.001). The diet of White-rumped Sandpipers, estimated from stable isotope signatures, is significantly different than that of all other species (Table 3.8). Semipalmated Sandpipers and Short-billed Dowitchers have significantly different diets, however, neither is significantly different from the Semipalmated Plover (Table 3.8).

**Table 3.7.** Results from PERMANOVA of the effect of species on diets of shorebird captured at Petit-Cap in the Northumberland Strait, estimated with $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures.

| **Factor** | **Df** | **F-value** | **p-value** |
|---|---|---|---|
| Species | 3 | 13.65 | 0.001 |
| Residuals | 80 | | |
| Total | 83 | | |

**Table 3.8.** P-values from pairwise PERMANOVAs between diets of shorebird captured at Petit-Cap in the Northumberland Strait, estimated from plasma $\delta^{15}N$ and $\delta^{13}C$ isotope signatures. P-values smaller than the adjusted alpha value ($\alpha = 0.0083$; corrected for 6 comparisons with Bonferroni correction) are marked with asterisks (*).

| | SESA | WRSA | SEPL |
|---|---|---|---|
| SESA | | | |
| WRSA | 0.006* | | |
| SEPL | 0.780 | 0.006* | |
| SBDO | 0.006* | 0.006* | 0.012 |

Pairwise comparisons of plasma $\delta^{15}N$ and $\delta^{13}C$ isotope signatures show that Short-billed Dowitchers have significantly lower $\delta^{15}N$ and $\delta^{13}C$ isotope signatures than all other species (Figure 3.9; Table 3.9). Semipalmated Sandpipers, White-rumped Sandpipers, and Semipalmated Plovers do not have significantly different $\delta^{15}N$ isotope signatures, but White-rumped Sandpipers have higher $\delta^{13}C$ isotope signatures (Figure 3.9; Table 3.9).

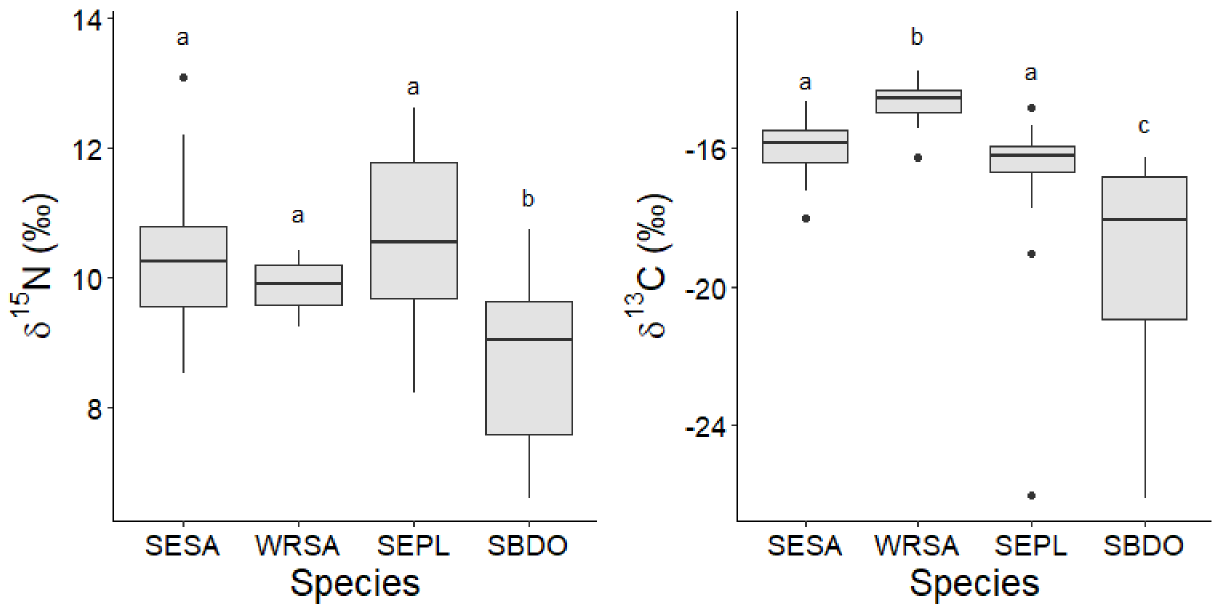


**Figure 3.9.** Boxplots of $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of plasma from shorebirds captured at Petit-Cap in the Northumberland Strait. Statistically significant differences are denoted with letters. See figure 3.1 for boxplot interpretation. $N_{SESA} = 29$, $N_{WRSA} = 20$, $N_{SEPL} = 20$, $N_{SBDO} = 15$.

**Table 3.9.** P-values from pairwise Kruskal-Wallis rank sum tests between $\delta^{13}C$ and $\delta^{15}N$ of shorebirds captured at Petit-Cap in the Northumberland Strait. P-values smaller than the adjusted alpha value ($\alpha = 0.0083$; corrected for 6 comparisons with Bonferroni correction) are marked with asterisks (*).

| Isotope signature | | SESA | WRSA | SEPL |
|---|---|---|---|---|
| $\delta^{13}C$ | SESA | | | |
| | WRSA | < 0.0001* | | |
| | SEPL | 0.0193 | < 0.0001* | |
| | SBDO | < 0.0001* | < 0.0001* | 0.0007* |
| $\delta^{15}N$ | SESA | | | |
| | WRSA | 0.113 | | |
| | SEPL | 0.483 | 0.042 | |
| | SBDO | 0.0005* | 0.004* | 0.0008* |

There is overlap between the isotopic diet niches of all species in the analyses (Figure 3.10). The multivariate dispersions of isotopic signatures are significantly different between species ($F_{3, 80} = 7.37$, $p = 0.001$), which tells us diet niche breadth differs between species. The Semipalmated Plover and Short-billed Dowitcher have broad diet niches, and the Short-billed Dowitcher's niche contains lower $\delta^{15}N$ isotopes than the other species (Figure 3.10). The White-rumped Sandpiper has the narrowest diet niche, and the niche of the Semipalmated Sandpiper is slightly broader (Figure 3.10).

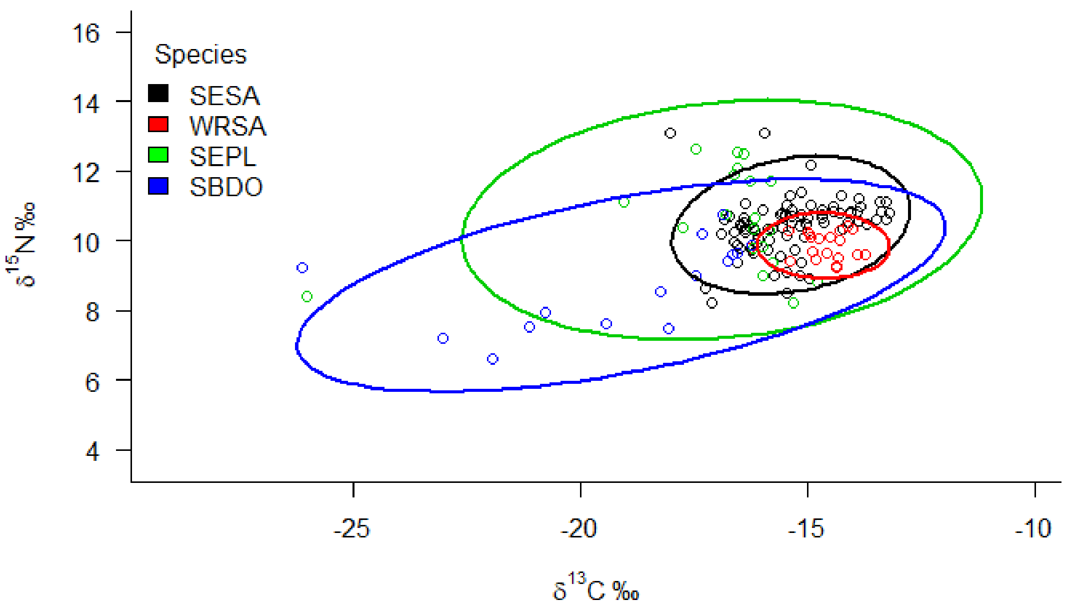


**Figure 3.10.** Isotopic diet niches of shorebirds captured at Petit-Cap in the Northumberland Strait, estimated using $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of blood plasma in parts per thousand. $N_{SESA} = 29$, $N_{WRSA} = 20$, $N_{SEPL} = 20$, $N_{SBDO} = 15$.

Bayesian mixing models estimated that the diet of Semipalmated Sandpipers and White-rumped Sandpipers contains mainly gastropods and polychaetes, while Short-billed Dowitchers and Semipalmated Plovers consume more bivalves and biofilm (Figure 3.11). The Semipalmated Sandpipers' diet includes small proportions of biofilm and bivalves, and the White-rumped Sandpipers appear to consume far less biofilm or bivalves than gastropods (Figure 3.12). The diet of Semipalmated Plovers contains similar proportions of biofilm, gastropods, and polychaetes, with slightly a higher proportion of bivalves (Figure 3.12). Short-billed Dowitchers consume less invertebrate prey items, and their diet mainly consists of biofilm (Figure 3.12).

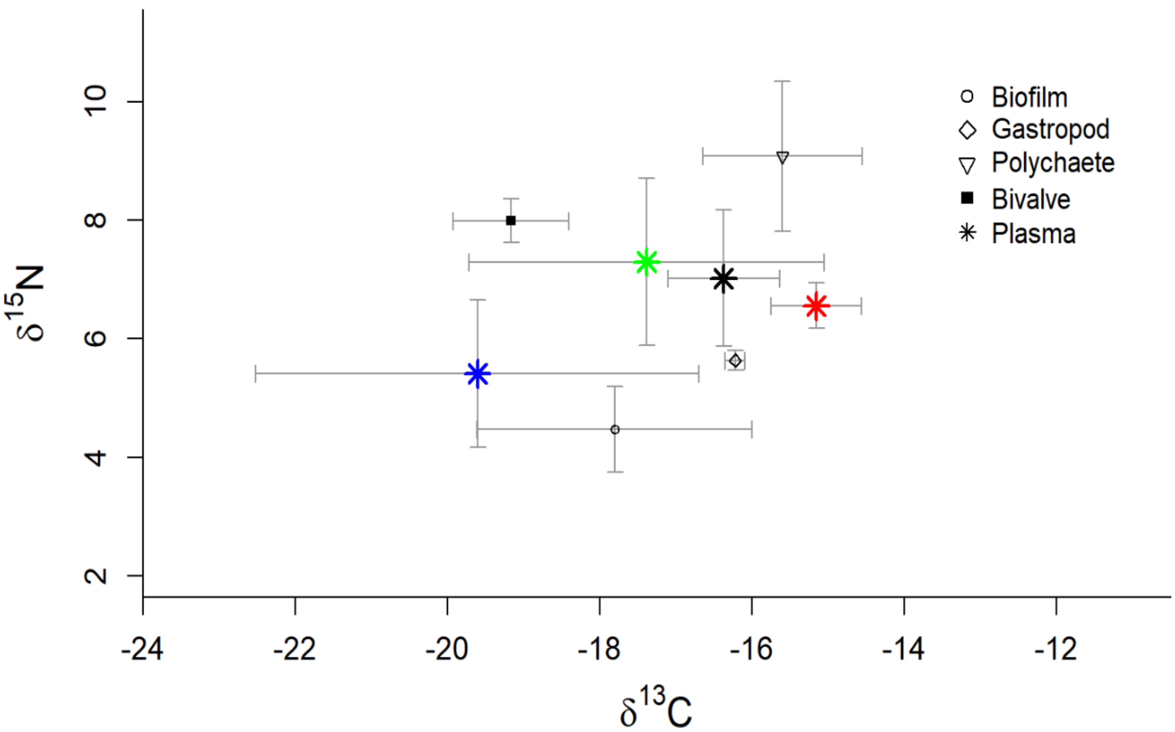


**Figure 3.11.** Average $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of prey and plasma from Semipalmated Sandpipers (black star), White-rumped Sandpipers (red star), Semipalmated Plovers (green star), and Short-billed Dowitchers (blue star) captured at Petit-Cap in the Northumberland Strait. Fractionation coefficients of 3.3 and 0.5 were applied to $\delta^{15}N$ and $\delta^{13}C$ respectively. Error bars represent standard deviation.

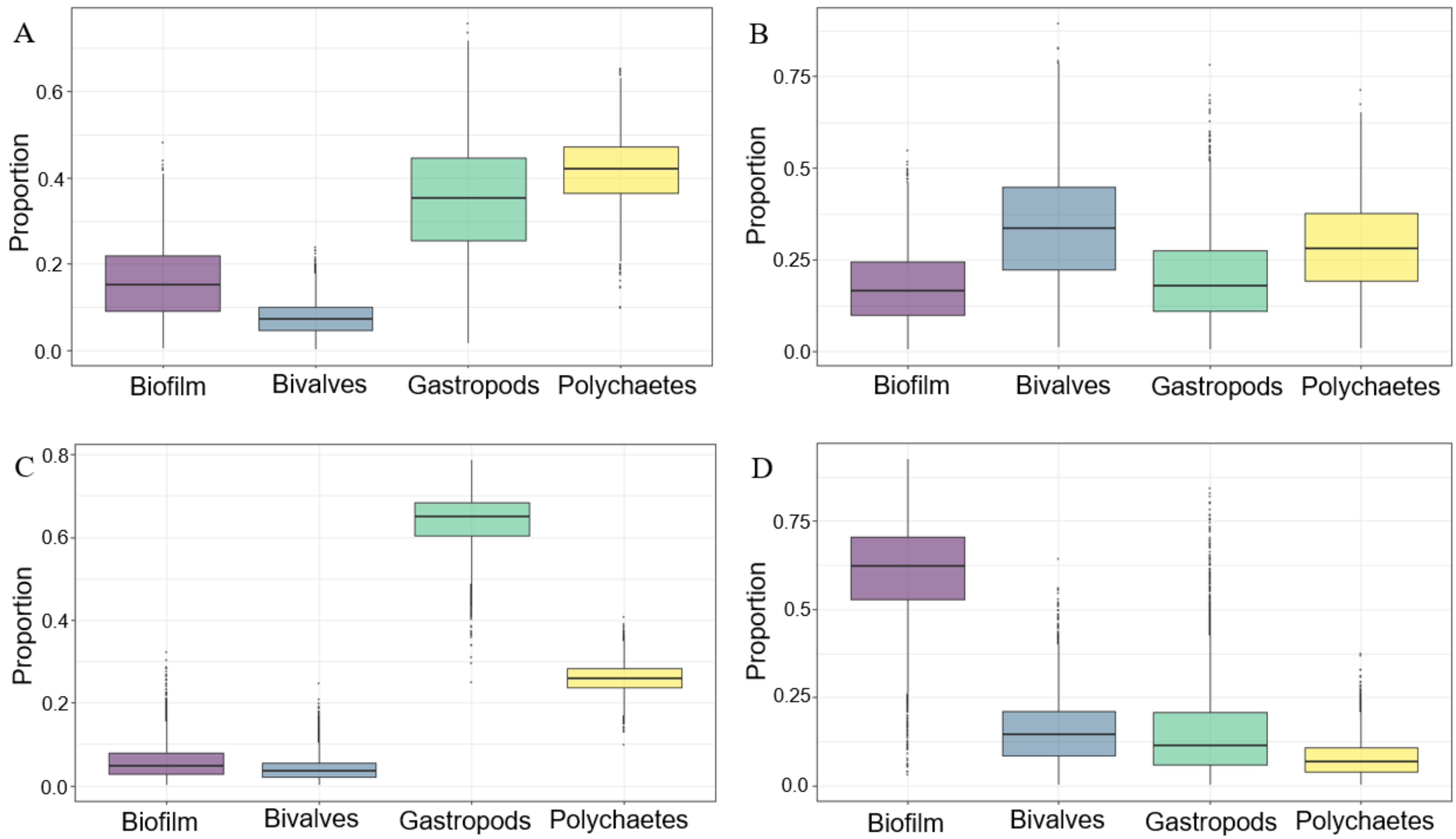


**Figure 3.12.** Estimated proportion of potential prey items in the diets of A) Semipalmated Sandpipers, B) Semipalmated Plovers, C) White-rumped Sandpipers, and D) Short-billed Dowitchers captured at Petit-Cap in the Northumberland Strait. See figure 3.1 for boxplot interpretation.

We found a significant difference between the plasma isotope signatures of Semipalmated Sandpipers in the Bay of Fundy and Northumberland Strait (Table 3.10; PERMANOVA, $F_{1, 78} = 8.65$, $p = 0.002$).

**Table 3.10.** Results of PERMANOVA of the effect of stopover location on diets of Semipalmated Sadnpipers captured at Johnson's Mills in the Bay of Fundy (BoF) and at Petit-Cap in the Northumberland Strait (NuS), estimated with $\delta^{15}N$ and $\delta^{13}C$ isotopic signatures.

| Factor | Df | F-value | p-value |
|---|---|---|---|
| Location | 1 | 8.65 | 0.002 |
| Residuals | 78 | | |
| Total | 79 | | |

The isotopic diet niche of Semipalmated Sandpipers in the Bay of Fundy has a broader distribution of $\delta^{13}C$ signatures, and narrower $\delta^{15}N$ signatures than that of Semipalmated Sandpipers in the Northumberland Strait (Figure 3.13). However, the multivariate dispersions of isotopic signatures do not differ between Semipalmated Sandpipers in the Bay of Fundy and the Northumberland Strait ($F_{1, 78} = 0.68$, $p = 0.387$), which tells us diet niche breadth is not significantly different between stopover locations.

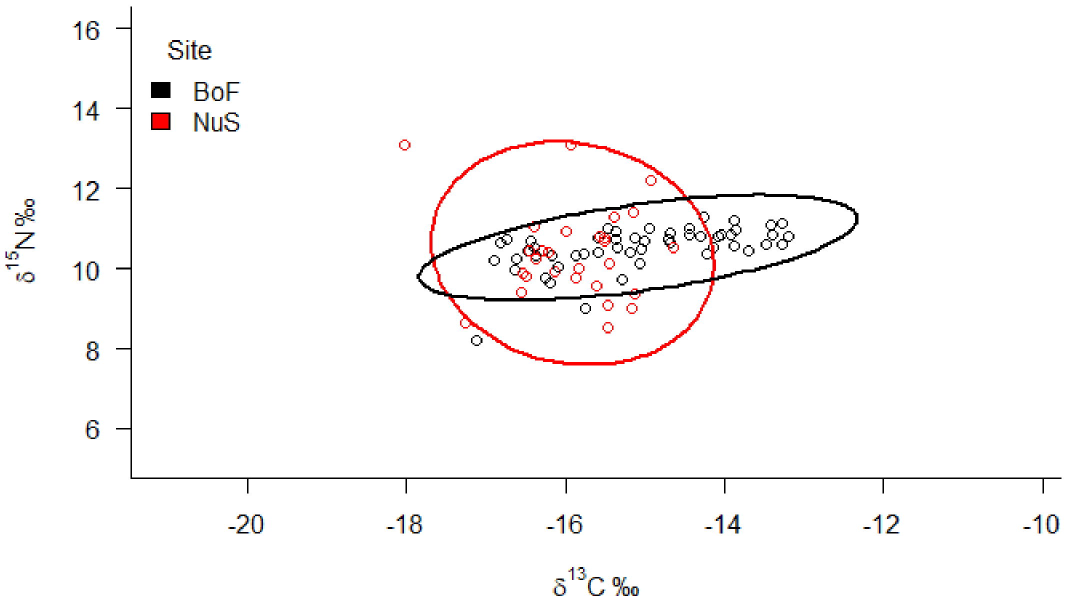


**Figure 3.13.** Isotopic diet niche of Semipalmated Sandpipers captured at Johnson's Mills in the Bay of Fundy (BoF, black) and at Petit-Cap in the Northumberland Strait (NuS, red), estimated using $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of blood plasma in parts per thousand. $N_{NuS} = 28$, $N_{BoF} = 52$.

Semipalmated Sandpipers captured in the Bay of Fundy have significantly higher $\delta^{13}C$ isotope signatures than Semipalmated Sandpipers in the Northumberland Strait (Figure 3.14; Kruskal-Wallis $\chi^2_1 = 9.31$, $p = 0.002$). There is not a significant different between the $\delta^{15}N$ isotope signatures of Semipalmated Sandpipers at the different stopover locations (Figure 3.14; Kruskal-Wallis $\chi^2_1 = 2.46$, $p = 0.117$).

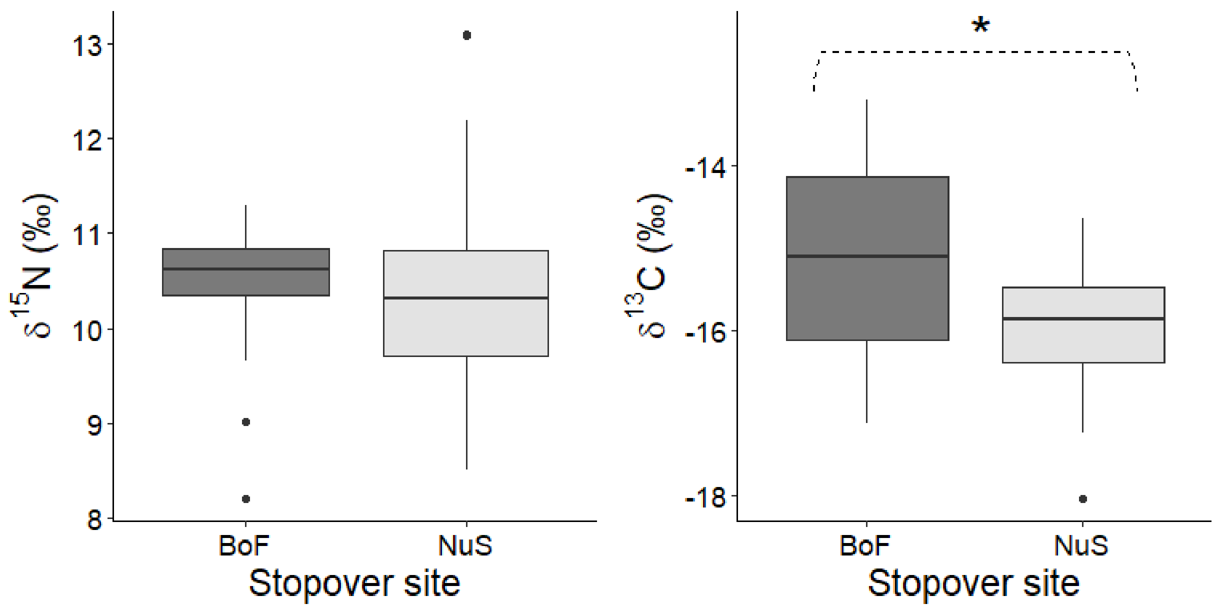


**Figure 3.14.** Boxplots of $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of plasma from shorebirds captured at Johnsons Mills in the Bay of Fundy (BoF, dark grey) and at Petit-Cap in the Northumberland Strait (NuS, light grey). Statistically significant differences between BoF and NuS are denoted with asterisks (*). See figure 3.1 for boxplot interpretation. $N_{NuS} = 28$, $N_{BoF} = 52$.

Using Bayesian mixing models, we estimated that the diet of Semipalmated Sandpipers in the Bay of Fundy is more enriched in $\delta^{13}C$ than those in the Northumberland Strait (Figure 3.15). In the Bay of Fundy, Semipalmated Sandpipers' diet consists of high proportions of bivalves and polychaetes and lower proportions of amphipods and biofilm (Figure 3.16). Semipalmated Sandpipers consume a similar proportion of polychaetes and biofilm at both locations, however, their diet has of a higher proportion of gastropods and no amphipods in the Northumberland Strait (Figure 3.16).

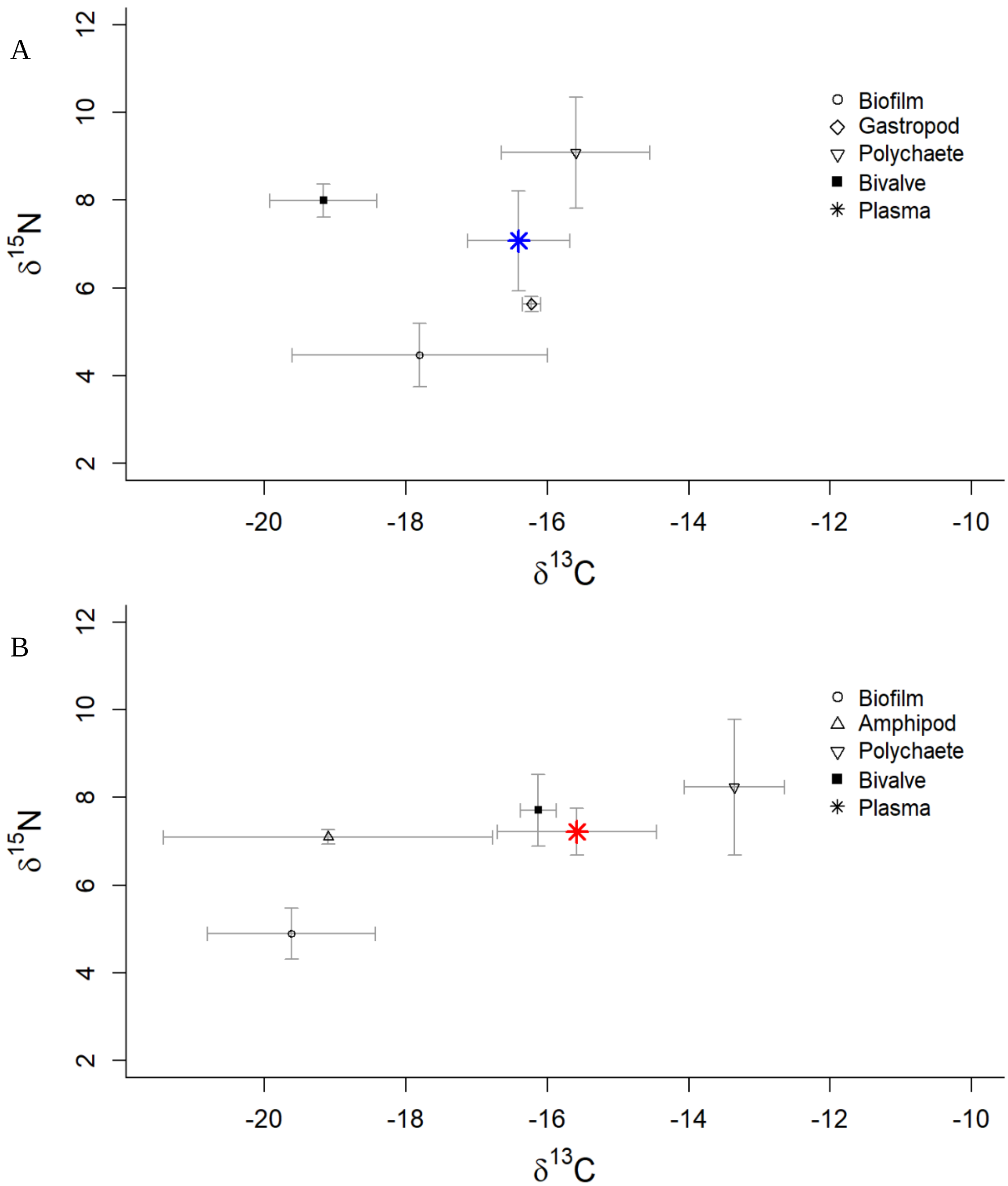


**Figure 3.15.** Average $\delta^{15}N$ and $\delta^{13}C$ isotope signatures of prey and plasma from Semipalmated Sandpipers (blue and red stars) at A) Petit-Cap in the Northumberland Strait and B) Johnson's Mills in the Bay of Fundy. Fractionation factors of 3.3 and 0.5 were subtracted from $\delta^{15}N$ and $\delta^{13}C$ respectively. Error bars represent standard deviation.

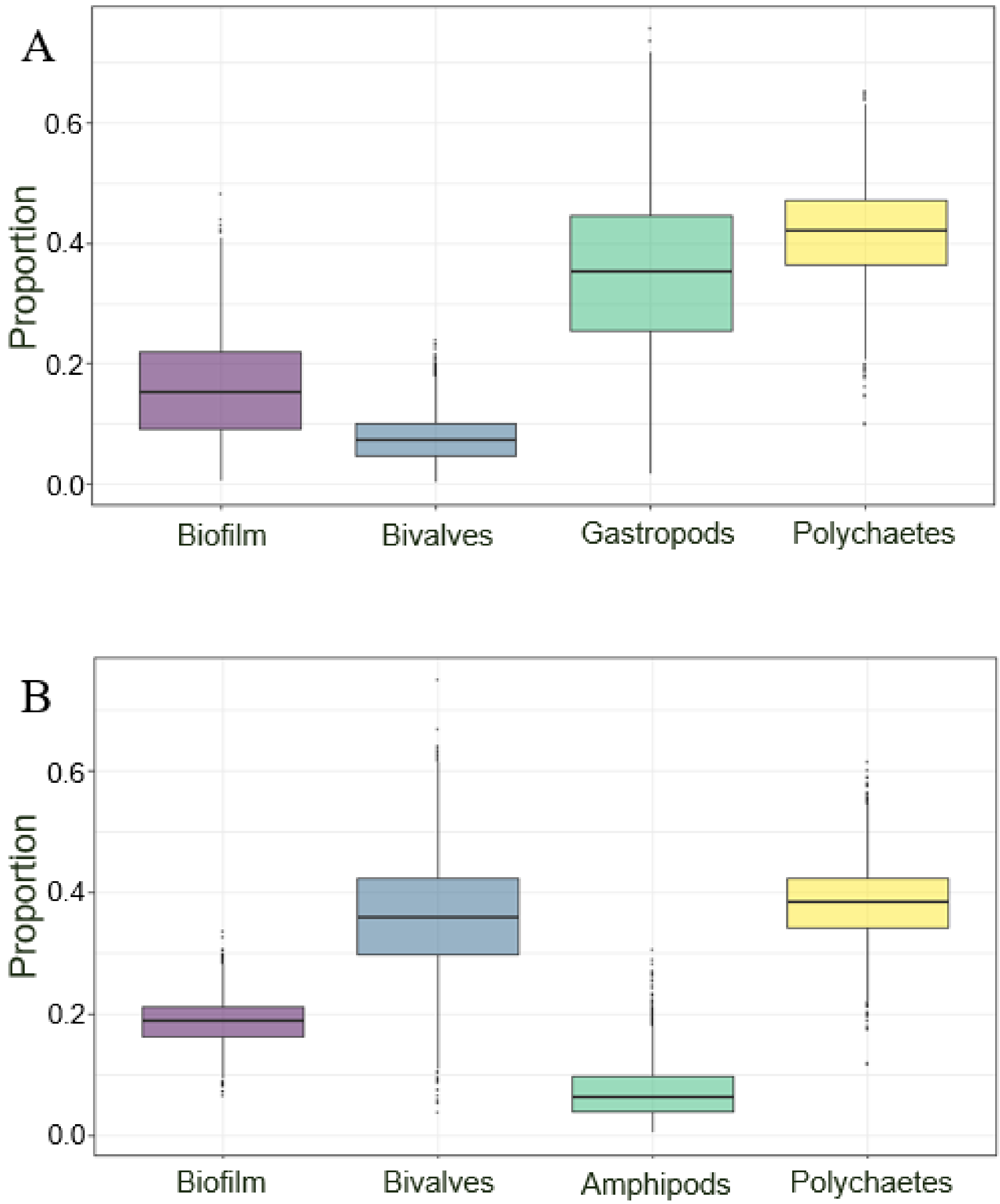


**Figure 3.16.** Estimated proportions of potential prey items in the diets of Semipalmated Sandpipers captured in A) the Northumberland Strait and B) the Bay of Fundy. See figure 3.1 for boxplot interpretation.

## Chapter 3: Discussion

Migratory shorebirds stop in the Bay of Fundy and at smaller coastal sites in Atlantic Canada on their fall migration to South American wintering grounds. Their stopover ecology in the Bay of Fundy has been extensively studied (Morrison 1977; Hicklin 1987; Quinn and Hamilton 2012; Neima et al. 2020), however, less in known about nearby coastal stopover sites in the Northumberland Strait. Shorebird research in New Brunswick has primarily focused on the Semipalmated Sandpiper. Therefore, there is a lack information on whole community ecology of migratory shorebirds, particularly at coastal stopover sites. To fill this gap in knowledge, we examined foraging behaviour and habitat use of migratory shorebirds in the Northumberland Strait to better understand the niche interactions of diverse shorebird communities in small coastal sites. We compare this information to shorebird behaviour in the Bay of Fundy to consider the potential reasons for differences in shorebird diversity at these two stopover locations.

### *Foraging behaviour*

We found that the different shorebird species in the Northumberland Strait use different foraging strategies, and these differences appear to be related to each species' morphology. Baker and Baker (1973) described shorebirds as having specialist foraging strategies if they used a small repertoire of foraging behaviours, whereas generalist foragers exhibit a variety of behaviours. Our results show that Short-billed Dowitchers have a unique foraging strategy out of the six species analyzed, which suggests that they may be more specialist foragers than the other species. They have significantly higher probing rates and lower pecking rates than the other species. This is unsurprising, as long-billed shorebird species, like the Short-billed Dowitcher, are better adapted for probing strategies (Barbosa and Moreno 1999). Novcic (2016) found similar results, reporting that the foraging strategy of Short-billed Dowitchers is a primarily probing strategy and has little overlap with other shorebird species during spring stopover in Delaware Bay.

Semipalmated Plovers also use a unique foraging strategy, however, they primarily peck and rarely probe, which is likely related to their short bill size. Although Semipalmated Plovers in our study did not have significantly lower pecking rates than the Calidrid sandpipers (Semipalmated Sandpipers, White-rumped Sandpipers, and Least Sandpipers), their probing rates were significantly lower than all other species. Small coastal sites on the Acadian Peninsula on the northeastern coast of New Brunswick also host populations of Semipalmated Plovers and Calidrid Sandpipers (Atlantic Canada Shorebird Survey 2017). MacKellar (2018) found that both pecking and probing rates of Semipalmated Plovers on the Acadian Peninsula were slower than those of Semipalmated Sandpipers. The run-and-catch strategy employed by Semipalmated Plovers makes their average foraging rates low, as they spend more time moving and looking for prey items (Nol 1986), whereas other species tend to peck or probe while walking. Alternatively, Thomas et al. (2006) suggest there is an evolutionary relationship between nocturnal behaviour and large eye size. Semipalmated Plovers have large eyes and excellent vision (Nol 1986). Therefore, it is possible that they exhibit higher pecking rates at night when we were not observing foraging behaviour. Temporal segregation of foraging behaviour is often related to tide cycles (Novcic 2016), however, daily cycles of foraging behaviour may reduce competition, especially in areas with coarse sediments where tactile probing strategies are less effective.

The foraging strategy of Greater and Lesser Yellowlegs is not significantly different from that of White-rumped Sandpipers. However, their foraging strategy appears to be more generalist, as they peck and probe at similar rates and were often observed skimming biofilm. This generalist behaviour causes the foraging strategy of the Yellowlegs to overlap with many other species. Niche complementarity predicts that Yellowlegs should be more specialized on another niche dimension to compensate for this overlap (Schoener 1974). Differences in tarsal length can facilitate microhabitat segregation between shorebird species wherein taller shorebirds can exploit a range of water depths, while shorter birds are restricted to shallow water (Davis and Smith 2001). Yellowlegs are relatively tall shorebirds, and in this study and others (Danufsky and Colwell 2003) they were often observed foraging in standing water where smaller shorebirds, such as Calidrid sandpipers and Semipalmated Plovers, cannot access prey (Novcic 2016). This spatial segregation may make up for overlapping foraging strategies.

We found that Semipalmated Sandpipers, Least Sandpipers, and White-rumped Sandpipers do not use significantly different foraging strategies. Morphology of these shorebirds is more similar than the other species, which likely plays a part in their similar foraging strategies. All three sandpiper species use a combination of pecking and probing, but have higher pecking rates than probing rates. We often observed Semipalmated, Least, and White-rumped Sandpipers foraging in the same flocks, which suggests they experience interspecific competition for resources. Within a foraging area, Least Sandpipers tend to stay closer to shore, while spatial overlap between Semipalmated Sandpipers and White-rumped Sandpipers is more complete. Competition may be intensified by their overlapping foraging strategies, however, differences in diet breadth compensate for spatial and behavioural overlap (see below). Additionally, the time of passage through Atlantic Canada varies between these species (Turcotte et al. 2017). Least Sandpipers arrive first, followed Semipalmated Sandpipers, then White-rumped Sandpipers, however, they overlap for most of their stopover (Turcotte et al. 2017). Although all three species reach peck abundance in Atlantic Canada in August, Semipalmated Sandpipers depart earlier, while some Least Sandpipers and White-rumped Sandpipers stay in the area into October or November (Atlantic Canada Shorebird Survey 2017). This creates a degree of temporal segregation early in the stopover period, and again near the end that may relieve competition between the Calidrid sandpipers.

Semipalmated Sandpipers in the Bay of Fundy have higher pecking and probing rates than those foraging in the Northumberland Strait. Davis (2019) found similar results comparing pecking rates of Semipalmated Sandpipers in the Bay of Fundy and Northumberland Strait, however, probing rates did not differ between locations. Sediment particle size and penetrability were significant covariates when testing the effect of stopover location on Semipalmated Sandpiper foraging strategies. The coarser, more resistant sediments in the Northumberland Strait likely reduce the ability of shorebirds to penetrate the substrate with their bills. This may lead Semipalmated Sandpipers to use a more visual foraging strategy, such as that used by the Semipalmated Plover, which is characterized by slower foraging rates.

Although these differences in foraging rates between Semipalmated Sandpipers in the Bay of Fundy and Northumberland Strait result in statistically different foraging strategies, the ratio of pecks to probes in both locations is similar. Semipalmated Sandpipers in the Bay of Fundy peck approximately 6 times for every probe, while in the Northumberland Strait the ratio is approximately 5 pecks for every probe. This suggests that Semipalmated Sandpipers do not make large modifications to their foraging strategy at different locations besides changing their overall foraging rate. Semipalmated Sandpipers are generalist feeders (Gerwing et al. 2016; see below) and their ability to exploit resources in different stopover sites emphasizes the effectiveness of the pecking and probing strategy for generalist diets.

*Prey availability and habitat associations*

Amphipods and polychaetes are the most abundant potential prey items at stopover sites in the Bay of Fundy, while availability of gastropods is very low. The mudsnail *Tritia obsoleta* is abundant in the Bay of Fundy, however, adults are too large for shorebirds to consume and were not included in the pool of available prey. Mudshrimp (*Corophium volutator*) are extremely abundant at Pecks Cove, which makes them the most abundant invertebrate prey item in the Bay of Fundy overall. However, the mudshrimp population at Johnson’s Mills was far lower than reported by Davis (2019) the year before. Depressions in mudshrimp abundance have been previously observed at Johnson’s Mills, and Semipalmated Sandpipers in the area are known to exhibit opportunistic foraging behaviour in such situations (MacDonald et al. 2012). In the Northumberland Strait, the most abundant prey items are polychaetes and bivalves. Although some amphipods are found in the Northumberland Strait, they are mainly *Gammarus* spp., as *Corophium volutator* does not inhabit the sand flats in this area.

We found not only a difference in the relative abundance of prey groups among sites, but also in the abundance of different taxa within those group. Bivalves in the Bay of Fundy were primarily *Macoma* spp., whereas in the Northumberland Strait, *Gemma gemma* were most abundant, followed by *Mya* spp.. Gastropods are diverse in the Northumberland Strait, and we found the highest abundance of *Hydrobia* spp., *Turbonille* spp., and *Melampus* spp.. Only *Hydrobia* spp. and *Littoria* spp. that were small enough for shorebirds to consume were found in the Bay of Fundy, however, they were very rare. Polychaetes are diverse in both the Northumberland Strait and Bay of Fundy, however, they are generally larger in the Northumberland Strait, and were found in samples up to 7 cm long. The largest polychaetes we found in the Bay of Fundy are approximately 2 cm long. The variation in prey taxa made the use of broader taxonomic groups necessary, otherwise overlap in prey taxa between sites would have been far lower, and it is unlikely shorebirds target one species versus another at these sites.

Sediment characteristics at foraging sites are also important factors influencing prey availability. Sediment resistance reduces the depth to which shorebirds can probe for prey (Finn et al. 2008). This decreases prey availability if invertebrates can burrow deeper than shorebirds can probe. VanDunsen et al. (2012) found assemblages of only surface feeding, pecking shorebirds on tidal flats with coarse, resistant sediment, as probing shorebirds could not access buried prey. Although environmental heterogeneity creates microhabitats of wet and dry sediments in the area, overall the Northumberland Strait has significantly coarser and more resistant sediment that the Bay of Fundy. This suggest that sediment characteristics in dry areas of the Northumberland Strait are not ideal for accessing buried prey, whereas the Bay of Fundy sediments have a larger depth of prey availability. However, in areas where the penetrable layer of sediment is deeper than the average shorebird bill length, prey may also be able to burrow deeper to avoid predation (Stillman et al. 2000; MacDonald et al. 2014).

Cyr and Morton (2006) suggest that Chlorophyll *a* concentration is higher in wet sediments than dry, but sediment particle size does not influence Chlorophyll *a* concentration. We found that the concentration of Chlorophyll *a* did not differ between the Northumberland Strait and Bay of Fundy, despite differences in sediment characteristics. These results agree with the findings of Davis (2019) at similar stopover sites in New Brunswick, and may be associated with the formation of wet and dry microhabitats due to environmental heterogeneity. Both stopover locations had outlying samples of high Chlorophyll *a* concentration, which suggest there is also spatial heterogeneity of biofilm abundance at both sites.

*Effects of habitat on shorebird assemblages in the Northumberland Strait*

There was not a significant effect of prey abundance or Chlorophyll *a* concentration on flock species composition in the Northumberland Strait, however, the effects of both sediment resistance and particle size were significant. Previous studies on Eastern Curlew (*Numenius madagascariensis*) agree with these results, suggesting that substrate resistance is the best predictor of shorebird density as it is a better indicator of prey availability than abundance alone (Finn et al. 2008). The resistance of sediments in the Northumberland Strait suggests it is not an ideal foraging location for tactile, probing shorebirds. However, Short-billed Dowitchers, which use a probing strategy, were only seen in the Northumberland Strait. Sediment resistance and particle size in the Northumberland Strait are variable, and in some places are comparable to conditions in the Bay of Fundy. This environmental heterogeneity at Northumberland Strait sites creates microhabitats of standing water, which increases sediment penetrability (VanDunsen et al. 2012). These wetter microhabitats often attract multi-species flocks of foraging shorebirds and are the only places Short-billed Dowitchers were observed foraging. Smaller shorebirds, such as the Calidrid sandpipers and Semipalmated Plovers, were restricted to the edges of wet microhabitats, and sandpipers were occasionally observed skimming in the shallow water. This creates spatial segregation based on water depth within these microhabitats that can reduce interspecific overlap. Foraging shorebirds often followed the receding tide at Petit-Cap, and taller shorebirds, such as Short-billed Dowitchers and Yellowlegs, were observed foraging in the water across a range of tide heights. We did not see shorebirds foraging in the receding tide at Cape Jourimain, instead they targeted microhabitats with standing water in the intertidal zone.

While taller Short-billed Dowitchers and Yellowlegs were primarily observed foraging in standing water, we frequently saw smaller shorebirds in both wet and dry microhabitats. Semipalmated Sandipers, White-rumped Sandpipers, and Least Sandpipers were often observed foraging in microhabitats with resistant, sandy sediments as well as wetter, more penetrable sediments. We also saw Semipalmated Plovers foraging in areas with resistant sediments more often than near wet microhabitats. The pecking strategy used by the Semipalmated Plover makes them better equipped to forage in resistant sediments, while the pecking and probing strategies of the Calidrid sandpipers allows them to exploit a greater range of microhabitats. Because multiple species use wet microhabitats (also see Novcic 2016), this suggests interspecific competition is lower in dry microhabitats with resistant sediments. However, this poses a trade-off between competition and prey availability. Small shorebirds foraging in dry microhabitats avoid competition with larger, probing shorebirds, however, dry microhabitats have coarse, resistant sediments where prey availability is often reduced. Partitioning of microhabitats has been reported in similar communities of shorebirds during migratory stopover in Delaware Bay (Novcic 2016). Microhabitat segregation may compensate for overlap on other niche dimensions, such as foraging strategy between Calidrid sandpipers and Yellowlegs, or diet between Semipalmated Sandpipers and Semipalmated Plovers (see below).

*Diet*

There are notable differences in diet, estimated by stable isotopes of C and N, among species. These differences reduce interspecific competition for food resources when shorebird species overlap on other niche dimensions, such as foraging strategy or microhabitat use. Plasma samples from Short-billed Dowitchers in the Northumberland Strait have very low $\delta^{15}N$ isotope signatures compared to other shorebird species in the analyses. This suggests they consume lower trophic level food sources, such as biofilm. Most shorebirds that consume biofilm use a skimming or grazing strategy (MacDonald et al 2012; Kuwae et al. 2008), however, we did not observe this behaviour in Short-billed Dowitchers. Other studies of shorebird foraging behaviour also report that Short-billed Dowitchers do not use the skimming strategy (Novcic, 2016). Additionally, studies on Short-billed Dowitcher diet suggest that they generally consume high proportions of invertebrate prey, such as amphipods (Novcic et al. 2016) and polychaetes (Weber and Haig 1997). We propose several possible explanations for this surprising result. First, skimming behaviour is associated with nocturnal foraging in Semipalmated Sandpipers, possibly because it is a tactile method of feeding, and therefore more effective at night when visual acuity is lower (Quinn 2011). Our behavioural observations took place during the day, and therefore may have missed the Short-billed Dowitchers skimming if it is a nocturnal behaviour in this species. However, the probing strategy used by Short-billed Dowitchers is a tactile one (Barbosa and Moreno 1999), which should not need to be modified for low visibility at night. This suggests it is unlikely that Short-billed Dowitchers switch from a probing to a skimming strategy at night. Skimming is also not a nocturnal foraging strategy in all shorebirds, as Western Sandpipers frequently forage on biofilm during the day (Kuwae et al. 2008), and we observed skimming in other species during daytime observations.

Short-billed Dowitchers were only observed foraging in standing water where they would probe their bills in and out of the water. We categorized this behaviour as probing, however, we could not see their bills penetrate the sediment underwater, nor could we detect successful prey captures. Therefore, a second possibility is that Short-billed Dowitchers are using a method of consuming biofilm when their bills are underwater that we did not notice. Alternatively, there are often algae or macrophytes in wet microhabitats where Short-billed Dowitchers forage, and they may be picking up biofilm or other low trophic level food sources as a result of probing in these areas.

A final possibility is that our Bayesian mixing model may be overestimating the importance of biofilm in the diet of Short-billed Dowitchers. The diet-tissue fractionation coefficient used to estimate shorebird diets is derived from Dunlin (*Calidris alpina*), which may lead to inaccurate diet estimates for more distantly related species, such as the Short-billed Dowitcher. Given the bill morphology and foraging strategy of these shorebirds, it seems unlikely that they are consuming such a high proportion of biofilm. However, including biofilm as a potential food source in the model with uninformative priors will lead to an estimation based on their isotopic signatures, and not morphology. More research is needed to examine the importance of biofilm in the diets of shorebirds other than *Calidris* spp. and to understand its role as a source of fuel for these migratory birds.

We estimated a generalist diet for Semipalmated Plovers, while previous studies on these shorebirds suggest they exhibit opportunistic specialization for abundant prey sources (Rose et al. 2016; MacKellar 2018). Our diet estimates suggest Semipalmated Plovers consume marginally higher proportions of bivalves and polychaetes than other food sources, which are the most abundant prey at stopover sites in the Northumberland Strait. However, these proportions are not high enough to suggest they are specializing for abundant prey items. The breadth of the Semipalmated Plover's diet niche causes them to overlap with all three other species. It is unlikely this overlap increases interspecific competition for food resources as the specialized foraging strategy of the Semipalmated Plover compensates for its general diet. Realistic diet overlap between the Semipalmated Plover and Short-billed Dowitcher is minimal, as their foraging strategies are not adapted for the same microhabitats or depth of prey. Overlap between Semipalmated Plovers and the Calidrid sandpipers is likely more realistic, as they all peck to some degree for surface invertebrates and often forage in the same microhabitats.

Semipalmated Sandpipers, White-rumped Sandpipers, and Semipalmated Plovers consume prey items from similar trophic levels in the Northumberland Strait, however, White-rumped Sandpipers appear to have a more specialized diet than the others. Our results suggest that nearly 75% of their diet is made up of gastropods. The remainder is mainly polychaetes, and they consume only small proportions of biofilm and bivalves. According to niche theory, this specialization reduces interspecific competition between the White-rumped Sandpiper and more generalist species, such as the Semipalmated Sandpiper and Semipalmated Plover, by causing them to compete for fewer prey items. On their wintering grounds, White-rumped Sandpipers consume high proportions of polychaetes and bivalves, and forage in areas with the highest abundance of these prey items (de los Angeles Hernandez and Bala 2007). This suggests White-rumped Sandpipers modify their diet to target abundant prey items at different staging areas across their migratory range.

Semipalmated Sandpipers are generalist foragers with broad diets (Gerwing et al. 2016). Biofilm is known to be an important contributor to their diet (Quinn 2011; Davis 2019), and we found that Semipalmated Sandpipers in both the Bay of Fundy and Northumberland Strait consume similar proportions of biofilm. Semipalmated Sandpipers also consume similar proportions of polychaetes in both locations, however, their $\delta^{13}C$ isotope signatures are significantly different. This likely has to do with differences in abundance of invertebrate prey items between locations. We estimated that the diet of Semipalmated Sandpipers in the Northumberland Strait contains high proportions of gastropods. However, because gastropod abundance was low in the Bay of Fundy, these prey were excluded from the mixing model of Semipalmated Sandpipers' diets in the Bay of Fundy. Similarly, amphipods are not estimated as a potential prey item for Semipalmated Sandpipers in the Northumberland Strait because of their low abundance. Additionally, the isotope signatures of the same prey taxa vary between sites. The $\delta^{13}C$ isotope signatures of polychaetes and bivalves in the Bay of Fundy are higher than those in the Northumberland Strait, which would raise the $\delta^{13}C$ signatures of shorebirds consuming them.

Diet estimates of Semipalmated Sandpipers in the Bay of Fundy do not contain high proportions of amphipods, which is likely a result of low *Corophium volutator* abundance at Johnson's Mills where plasma samples were taken. Instead, bivalves make up a large proportion of the diet estimate for Semipalmated Sandpipers. The *Macoma* spp. bivalves found in the Bay of Fundy are often larger than *Gemma gemma* or *Mya* spp. in the Northumberland Strait, and the soft sediments would make these burrowing prey more available to Semipalmated Sandpipers. However, these bivalves often grow too large for Semipalmated Sandpipers to consume, which reduces their availability. In the Northumberland Strait, small *Hydrobia* spp. gastropods are often found on the sediment surface where they are available for pecking shorebirds. This may explain their high proportion in the diet of Semipalmated Sandpipers in the area given their tendency to peck more than probe.

Previous studies show that some Semipalmated Sandpipers move between the Bay of Fundy and Northumberland Strait during their stopover in New Brunswick (Davis 2019). Only available prey from the location each shorebird was captured was included as a potential prey item in their diet estimates. This presents a potential source of error for diet estimates if shorebirds captured in one location had been recently foraging in the other location. The half-life of dietary-derived $\delta^{13}C$ in blood plasma is 2.9 days (Hobson and Clark 1993), which suggests we can estimate the diet of shorebirds from the week before they were captured and sampled. This gives shorebirds enough time to make the short flight between stopover locations before capture. However, the incidence of flyover between sites was very low, and most flew from the

Northumberland Strait to the Bay of Fundy and stayed for the remainder of their stopover (Davis 2019). Therefore, it is unlikely our captured shorebirds flew between sites, which allows us to confidently interpret their diet estimates. Future research on movement of other shorebird species between stopover sites in New Brunswick would give us a better understanding of shorebird diets during their migration through the area. Given the variation in available prey between stopover sites, it is likely that shorebirds must show some degree generalization to cope with differences in prey throughout their migratory range. However, the generalization or specialization they exhibit at each different stopover site will play a role in determining the amount of interspecific competition they encounter during their stay.

*Conclusions*

Migratory shorebirds in the Northumberland Strait exhibit partitioning in three niche dimensions: microhabitat use, foraging behaviour, and diet. Species that use similar foraging strategies, such as the Semipalmated Sandpiper and White-rumped Sandpiper, have different diets, whereas species with broad diet niches, such as the Semipalmated Plover, have more specialized foraging strategies. Shorebird species also experience spatial segregation based on their ability to exploit different microhabitat niches, which eliminates the competitive effects of overlap in other niche dimensions. This is an excellent example of niche complementarity and emphasizes the intricate ways shorebirds are adapted for life in multi-species flocks. Niche partitioning and complementarity is observed in shorebird populations at other stopover sites throughout their range (Baker and Baker 1973; VanDunsen et al 2012; Bocher et al. 2014; Novcic 2016). Niche partitioning in multi-species shorebird populations reduces interspecific competition and may be especially important at stopover locations where resources are limited as a result of climate change or other habitat disturbances.

Biofilm is an available resource for migratory shorebirds at many stopover sites, and shows up in the diet estimates of most species. This is consistent with other studies of stopover ecology in New Brunswick (Quinn and Hamilton 2012; MacKellar 2018; Davis 2019) and other locations across North America (Jardine et al. 2009; Mathot et al. 2010). It is yet unknown if some of these shorebird species are equipped with bill structures or behavioural adaptations for biofilm consumption, which highlights a need for more research. If biofilm is a reliable source of fuel for migratory shorebirds, it may become a more important part of their diet in stopover sites that are at risk of disruptions to the invertebrate prey base. Overall, it seems that niche partitioning is present between shorebird species at stopover sites in the Northumberland Strait, and may be a determinant of their ability to put on fat stores and successfully complete their long migration.

It remains unclear why Semipalmated Sandpipers dominate the mudflats of the Bay of Fundy. Given their generalist foraging strategy and diet, Semipalmated Sandpipers are able to put on sufficient fat stores at both stopover locations (Davis 2019), and do not show a specialization for specific habitat characteristics. Interestingly, conditions in the Bay of Fundy appear to be more favourable than those in the Northumberland Strait for most shorebird species. Soft sediments and a high abundance of invertebrate prey make the Bay of Fundy a good habitat for tactile, probing foragers, such as Short-billed Dowitchers. At low tide when the mudflats are exposed, the fine sediment particles retain more water and invertebrates are more active at the sediment surface. This creates an abundance of available prey for pecking shorebirds, such as Semipalmated Plovers. These conditions also appear to make an excellent habitat for shorebirds using the generalist pecking and probing strategy. This raises the question, once again, of why diverse assemblages of shorebirds are seen at stopover sites in the Northumberland Strait but not the Bay of Fundy during the time of the Semipalmated Sandpiper's migration? The results of this study and previous work suggest that there is considerable annual variation in prey abundance in the Bay of Fundy, and that the dominant shorebird species in the Bay of Fundy exhibits opportunistic and generalist stopover ecology. Predictable abundant resources at stopover sites are key to successful migration (Warnock 2010). Perhaps this large annual variation reduces the predictability of resources and makes the Bay of Fundy unappealing to less flexible shorebird species.

These results add to the growing pool of research suggesting small coastal stopover sites are important for the success of migratory shorebirds in Atlantic Canada. Given the widespread declines in shorebird populations, it is important to consider whole shorebird communities and their interactions with habitat conditions to better understand how we can preserve stopover sites. Climate change and human disturbance can drastically alter stopover habitat, and being able to predict the effects of these changes on stopover ecology is crucial for conservation of shorebird populations.

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