

Sand lance (*Ammodytes* spp) on the Newfoundland Shelf: habitat selection, diel behaviour, and  
synchrony of dynamics with other forage fish

By

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## Table of Contents

Acknowledgments.....	ii
List of Tables.....	iv
List of Figures .....	v
Thesis Format .....	viii
<i>Chapter One. Thesis Introduction.....</i>	<i>1</i>
References .....	10
Tables and Figures .....	27
<i>Chapter Two. Sand lance (<i>Ammodytes spp</i>) and capelin (<i>Mallotus villosus</i>) abundance, distribution, biometrics, and population dynamics on the Newfoundland Shelf.....</i>	<i>28</i>
Abstract .....	28
Introduction .....	30
Methods .....	34
Results .....	39
Discussion.....	41
References .....	47
Tables and Figures .....	64
Supplementary Materials I.....	73
<i>Chapter Three. Habitat characterization and diel patterns of sand lance (<i>Ammodytes spp</i>) in coastal Newfoundland.....</i>	<i>79</i>
Abstract .....	79
Introduction .....	80
Methods .....	83
Results .....	90
Discussion.....	92
References .....	98
Tables and Figures .....	115
Supplementary Materials II .....	124
<i>Chapter Four. Thesis Conclusion .....</i>	<i>126</i>
References .....	130

## List of Tables

### *Chapter Two*

**Table 2.1.** Summary of the dataset from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. The number of sampled capelin were used to calculate mean length ( $\pm$  SE), while the number of sub-sampled capelin were used to calculate mean ( $\pm$  SE) mass and condition. The number of sampled sand lance were used to calculate mean ( $\pm$  SE) length, mass, and condition. The number of immatures was determined from the number of sampled fish.

### *Chapter Three*

**Table 3.1.** Number of sediment grabs, sand lance caught in sediment grabs, hydroacoustic surveys, and camera drift surveys per year from 2013-2021, at the fine-scale region (Gull 3) and our comparison region (Gull 2).

## List of Figures

### **Chapter One: Thesis Introduction**

**Figure 1.1.** Study area on the Newfoundland Shelf showing *NAFO Divisions 3KLNOPs*, where the spring bottom trawl survey was conducted (Chapter 2; *NAFO Divisions 3LNOPs*) from 1996-2015, and Notre Dame Bay (Chapter 3; dashed).

### **Chapter Two**

**Figure 2.1.** Study area on the Newfoundland Shelf showing *NAFO Divisions 3KLNOPs*, where the spring bottom trawl survey was conducted (*NAFO Divisions 3LNOPs*) from 1996-2015.

**Figure 2.2.** Principal component analyses of a) capelin (full dataset), b) sand lance (full dataset), c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015, showing values of PC1 and PC2 along with eigenvectors for abundance, length, mass, and condition. Annual relative indices of abundance, length, mass, and condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models.

**Figure 2.3.** Centre of gravity of a) capelin, b) sand lance, c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. Annual centre of gravity estimates are connected by lines through time, and a composition of spatial variance around these estimates (i.e., inertia) are indicated by the dotted black line. Annual estimates of spatial variance can be viewed at URL. Centre of gravity and spatial variance were calculated using equations found in Woillez *et al.* (2007). The orange area indicates areas poorly covered by the survey

**Figure 2.4.** Relationships between annual relative abundance index and spatial variance (i.e., inertia) of a) capelin, b) sand lance, c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. Annual relative index of abundance was calculated using Bayesian generalized linear mixed models. Spatial variance was calculated using equations for inertia found in Woillez *et al.* (2007).

**Figure 2.5.** Relationships between capelin and sand lance (full dataset) annual relative indices of a) abundance, b) length, c) mass, and d) condition index from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. Annual relative indices of abundance, length, mass, and condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models

**Figure 2.6.** Relationships between immature capelin and sand lance annual relative indices of a) abundance, b) length, c) mass, and d) condition index from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. Annual relative indices of abundance, length, mass, and condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models.

## **Supplementary Materials I**

**Figure S2.1.** a) Latitude of the centre of gravity of capelin, sand lance, and the spring bottom-trawl survey (sand lance versus capelin latitude:  $r^2 = 0.05$ , p-value = 0.34), b) latitude of the centre of gravity of immature capelin, immature sand lance, and the spring bottom-trawl survey (sand lance versus capelin latitude:  $r^2 = 0.13$ , p-value = 0.13), c) longitude of the centre of gravity of capelin, sand lance, and the spring bottom-trawl survey (sand lance versus capelin longitude:  $r^2 = 0.001$ , p-value = 0.91), d) longitude of the centre of gravity of immature capelin, immature sand lance, and the spring bottom-trawl survey (sand lance versus capelin longitude:  $r^2 = 0.003$ , p-value = 0.82). Capelin shown in blue, sand lance shown in green, spring bottom-trawl survey shown in red.

**Figure S2.2.** Centre of gravity (x) and spatial variance (i.e., inertia; ellipse) from the spring multi-species bottom trawl from 1996-2015. Survey shown in red and a) capelin, b) sand lance, c) immature capelin, d) immature sand lance in blue. See all figures at:  
<https://davorenlab.wixsite.com/research/single-post/scott-s-sandlancy-specs>

**Figure S2.3.** Capelin (full dataset) posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

**Figure S2.4.** Sand lance (full dataset) posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

**Figure S2.5.** Immature capelin posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

**Figure S2.6.** Immature sand lance posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

### ***Chapter Three***

**Figure 3.1.** Map of Newfoundland, Canada, indicating capelin spawning beaches (blue circles) and subtidal spawning areas (red diamonds) where camera drift surveys, sediment grabs, and hydroacoustic surveys (line) were conducted. Hydroacoustic surveys were only examined where sand lance were continually present (Gull 3; yellow line). See Figure 3.3 for habitat characteristics for each region.

**Figure 3.2.** Principal component analysis showing values of PC1 and PC2 along with eigenvectors for the ten habitat characteristics (temperature, mean grain size, grain size standard

error, depth, proportion of each grain size category), with sites where sand lance were present indicated in red.

**Figure 3.3.** Mean proportions of different grain size ranges of 7 coastal regions plus one adaptive site (CFB), along with four subtidal capelin spawning areas (Turr, Gull 1, Gull 2, Gull 3). Region-specific mean  $\pm$  SE temperature ( $^{\circ}$ C), depth (m), and sample size (n) are also indicated. All regions were sampled during July-August, 2020, while only AB, SB, and WB were sampled again during July-August, 2021. See Figure 3.11 for locations of each region.

**Figure 3.4.** Acoustic biomass ( $m^2/m^2$ ) of sand lance in the water column ( $y = 4.1e^{-8} - 3.3e^{-13}x$ ,  $r^2 = 0.12$ ) throughout the day during July-August, 2013-2020.

**Figure 3.5.** Proportion of bottom grabs with sand lance present per hour throughout the day from July-August 2013-2021 (circular mean time: 20.5 h after midnight; circular variance: 0.02, Rayleigh test:  $p < 0.0001$ ).

**Figure 3.6.** Number of sand lance caught per sediment grab throughout the day during July-August, 2013-2021 (circular mean time: 19.2 h after midnight; circular variance 0.62; Rayleigh test  $p < 0.0001$ ). Points are jittered to better visualize sampling distribution

**Figure 3.7.** Total length (mm) of sand lance caught in sediment grabs throughout the day during July-August, 2013-2021 (circular mean time: 19.7 h after midnight; circular variance: 0.53; Rayleigh test:  $p < 0.0001$ ). Black: 2013-2018, Gray: 2019, Red: 2020, Blue: 2021. Points are jittered to better visualize sampling distribution.

**Figure 3.8.** Proportion of non-empty sand lance stomachs caught in sediment grabs per hour throughout the day during July-August, 2013-2021 (circular mean time: 19.2 h after midnight; circular variance: 0.03, Rayleigh test:  $p < 0.0001$ ).

## *Supplementary Materials II*

**Figure S3.1.** Mean ( $\pm$  SE) proportions of different grain size ranges of 7 coastal regions plus one adaptive site (CFB), including four subtidal capelin spawning areas (Turr, Gull 1, Gull 2, Gull 3), along with their associated mean ( $\pm$  SE) temperature ( $^{\circ}$ C), depth (m), and sample size (n). All regions were sampled during July-August, 2020, while only AB, SB, and WB were sampled again during July-August, 2021. See Figure 3.1 for locations of each region.

**Figure S3.2.** Sand lance length histograms from *a*) 2013-2018 (n=52), *b*) 2019 (n= 42), *c*) 2020 (n= 45), and *d*) 2021 (n=61).

## **Thesis Format**

This thesis is presented in manuscript format. Both chapters are independent, with their own introduction, methods, results, discussion, conclusions, and references. They are accompanied by an overall general thesis introduction to provide background information, and a synthesis discussion including conclusions and future research. All data analysis and writing were performed by me with guidance from my advisor and committee.

## **Chapter One. Thesis Introduction**

Interactions among species from different trophic levels can alter the abundance, biomass or productivity of species across a food web (Pace et al. 1999), generally taking on three different forms. Top-down control, or trophic cascades, occur when populations of one or more top predators either increase or decrease in an ecosystem, resulting in alternating increased or decreased abundances at each trophic level cascading down the food web through direct and indirect species interactions (Frank et al. 2005). Alternately, bottom-up control occurs when the abundance of primary producers controls the energy at the base of the food web, thereby increasing or decreasing abundance of species at all trophic levels (Frederiksen et al. 2006; Buren et al. 2014; Lynam et al. 2017). Lastly, wasp-waist control refers to mid-trophic levels controlling the abundance of higher and lower trophic levels (Rice 1995; Cury 2000).

Unlike terrestrial ecosystems, the meso-predator trophic level in marine ecosystems is typically dominated by a few forage species. This results in a wasp-waist structure (Pikitch et al. 2012), whereby mid-trophic levels control energy flow from lower to higher trophic levels (Rice 1995; Cury 2000). As such, forage fish play a crucial role transferring energy to higher trophic level predators and, thus, influence population dynamics of these predators (Pikitch et al. 2012). Forage fish species, such as Atlantic herring *Clupea harengus*, anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, capelin *Mallotus villosus* and sand lance *Ammodytes* spp, are small to medium-sized fish species with a short life span, early maturity, and high fecundity (Pikitch et al. 2012). The population dynamics of these species are typically characterized by extreme fluctuations, or ‘boom-bust cycles’. Despite these fluctuations in population size and the short-lived life history traits of forage fish, evidence suggests that density-dependent factors may

influence life history traits (e.g., Icelandic capelin body size and condition, ICES 1999; Carscadden and Frank 2002; Shepherd and Litvak 2004; Jokar et al. 2021; Jourdain et al. 2021). Although predators may also limit forage fish populations (e.g. capelin in the Barents Sea; Huse and Toresen 2000), recruitment is often driven by environmental factors (Essington et al. 2015), with bottom-up processes altering abundance of primary and secondary producers and, thus, mediating forage fish population dynamics (Frederiksen et al. 2006; Buren et al. 2014; Lynam et al. 2017). As fluctuations in forage fish populations can have adverse impacts on top predator reproduction and survival (Cury 2000; Boyd and Murray 2001; Boyd 2002; Piatt et al. 2007; Cury et al. 2011), asynchrony in the population dynamics of a variety of forage fish species can dampen these impacts on top predators within an ecosystem (Arimitsu et al. 2021). Indeed, diversity in forage fish communities increases the stability of marine ecosystems by sustaining their role in key ecosystem processes (e.g., energy flow), creating a portfolio effect (Figge 2004; Schindler et al. 2010; Arimitsu et al. 2021).

Like other animals, forage fish select optimal habitat to maximize growth, reproduction, survival, and, thus, fitness (Morris 2003). The ideal free distribution (IFD) theory predicts how individuals will distribute themselves among available habitat patches, choosing the patches with the most favourable conditions to maximize fitness (Fretwell and Lucas 1970). As abundance increases, intraspecific competition increases within high-quality habitat patches, which results in lower quality patches becoming occupied until organisms have similar fitness within high- and low-quality habitat patches (Svärdson 1949). This expansion of distribution outside of optimal habitat has been associated with increased abundance in many highly mobile marine fish species (Paloheimo and Dickie 1964; Bertrand et al. 2004; Barange et al. 2009), whereby density remains constant within habitat patches while distribution expands (i.e., constant density model;

Iles and Sinclair 1982), or density in expanding habitats varies according to the habitat quality (IDF; Fretwell and Lucas 1970). In contrast, fish distribution may stay constant as abundance increases, resulting in density being proportional to abundance (i.e., proportional model; Petitgas 1997), which maybe more likely for less mobile species with specific habitat requirements.

Fish select habitat based on a number of abiotic and biotic factors. Prey availability and predation risk are among the most important biotic factors for habitat selection (Pyke et al. 1977; Fraser and Huntingford 1986; Gilliam and Fraser 1987; Hugie and Dill 1994). Indeed, fish may choose to forage in habitats with lower prey density to avoid predators or may limit the time spent foraging to increase vigilance to avoid predation when predators are present (Pyke et al. 1977; Fraser and Huntingford 1986). As ectothermic animals, temperature is among the most important abiotic factors for habitat selection, along with oxygen, salinity, turbidity and seabed substrate (Barkley et al. 1978, Perry and Smith 1994). As most of these abiotic factors vary with depth, marine fish often select different depths throughout their diel or annual cycles. Diel vertical movement is a common behaviour exhibited in many aquatic organisms. Multiple hypotheses have been proposed to explain this behaviour, most notably the foraging hypothesis, where fish are known to follow the vertical movement of their zooplankton prey toward the surface at night to increase foraging efficiency (Clark and Levy 1988), while also minimizing predation risk by visual predators. Other fish may feed on benthic organisms at night and display thermotaxis up to warmer waters during the day to aid in digestion (Bacheler et al. 2021). Overall, the optimal habitat of a species will be characterized by a suite of abiotic factors that combine with biotic factors (i.e., prey and predator abundance) to maximize fitness and, thus, multiple hypotheses must be considered to explain habitat selection.

## *The Newfoundland and Labrador Shelf*

The Newfoundland and Labrador Shelf ecosystem is strongly influenced by the seasonal variation of the Labrador Current and the North Atlantic Current (Lilly 1982; Cyr et al. 2019). These currents affect the sea ice extent across the shelf along with the timing of sea ice retreat, which affects the timing and magnitude of primary production (i.e. spring bloom) in the ecosystem (Wu et al. 2007). On the shelf, the primary forage fish species include Atlantic herring and mackerel *Scomber scrombus*, which are primarily found in coastal regions (Moores et al. 1975), and arctic cod *Boreogadus saida*, capelin and sand lance, which reside both in inshore and offshore regions (Templeman 1948; Winters and Dalley 1988).

## *Capelin*

Capelin are commercially fished in an inshore roe fishery in coastal Newfoundland and, thus, the stock status is evaluated annually by Fisheries and Oceans Canada (DFO; DFO 2018). One of the primary indices of capelin abundance is a targeted annual acoustic survey in the spring in NAFO Div. 3L (Fig. 1.1), which is a nursery area for age-1 and age-2 capelin (DFO 2018). Although some age-1 and age-2 capelin remain resident inshore throughout the winter (Templeman 1948, Buren et al. 2019), capelin typically spend the majority of their lives offshore. While in offshore waters, capelin distribution is thought to be determined by multiple factors (e.g., water temperature, density, prey availability) but they are found at a wide range of depths (Mowbray 2002; Rose 2005). In the spring-summer (May-July), the mature stock (age 2-4) migrates inshore to spawn, while immature (age-1 and some age-2) fish remain in offshore areas (Templeman 1948). On the Newfoundland Shelf, capelin recruitment is thought to be

controlled from the bottom up, regulated by the influence of the extent of sea ice and timing of sea ice retreat which influence the timing and magnitude of the spring bloom and ultimately the availability of prey (e.g., copepods; O'Driscoll et al. 2001; Buren et al. 2014; Murphy et al. 2018) for capelin (Carscadden et al. 2013; Buren et al. 2014; Mullowney et al. 2016). In 1991, capelin abundance on the shelf experienced almost an order of magnitude collapse, with a decline from 2-6 Mt to 0.03-1.0 Mt (DFO 2018; Buren et al. 2019). Minimal recovery in the decades since the collapse is hypothesized to have been due to a number of factors (e.g., delayed capelin spawning, earlier sea ice retreat, earlier spring plankton bloom) affecting the recruitment and survival of capelin (Buren et al. 2014; Mullowney et al. 2016; Lewis et al. 2019; Murphy et al. 2021).

### *Sand lance*

In contrast, little is known about the ecology of sand lance on the Newfoundland Shelf, including their abundance, distribution, biometrics, and population dynamics, likely because it is not a commercially fished species and, thus, not assessed by DFO. Most research on this genus is in the Northeast Atlantic Ocean on the lesser sandeel (*A. marinus*) and in the Northeastern Pacific Ocean on the Pacific sand lance (*A. personatus*). Similar to capelin, the abundance of *Ammodytes* in other regions (e.g., Northeast Atlantic Ocean) is thought to be mostly controlled from the bottom-up, primarily regulated by prey abundance (Frederiksen et al. 2006; Lynam et al. 2017). On the Newfoundland Shelf, sand lance feed and grow in the summer months while predominantly consuming *Calanus finmarchicus* (Suca et al. 2021). During the fall, they cease feeding and begin gonad development (Suca et al. 2021) and finally spawn in the winter.

(November–February), in locations they occupy year-round (Winters and Dalley 1988; Robards et al. 1999a). There are two species of sand lance, *A. dubius* and *A. americanus*, on the Newfoundland Shelf, where the distribution of *A. dubius* is thought to be more offshore than *A. americanus*; however, *A. dubius* is occasionally found inshore in deeper and more open regions (Winters and Dalley 1988; Nizinski et al. 1990).

On the Newfoundland Shelf, all age classes of sand lance are non-migratory and have specific habitat requirements (Scott 1968; Reay 1970; Winslade 1974a; Wright et al. 2000; Ostrand et al. 2005). Sand lance are commonly found in cool (1–11°C), shallow (<40 m) and relatively clear water, possibly because they are visual foragers and, thus, require light while foraging (Winslade 1974a). As sand lance lack a swim bladder, individuals burrow into sandy substrate (0.25 – 2 mm; Scott 1968, Reay 1970, Wright et al. 2000, Ostrand et al. 2005) and often remain within 500 m of sandy substrates suitable for burrowing (Hobson 1986; Ostrand et al. 2005; van der Kooij et al. 2008; Robinson et al. 2013). Burrowing is thought to occur when fish are not foraging for shorter parts of the day or longer seasonal periods (e.g. winter) to reduce energy expenditure and the risk of predation (Pinto et al. 1984). They burrow by diving headfirst into the sand and beating their tail to drive their body into the sediment and, thus, have a specialized narrow skull adapted for burrowing in sandy substrates (Gidmark et al. 2011). As such, sand lance can only bury in a specific range of grain sizes, with larger fish burrowing in more coarse sand with larger grain sizes relative to smaller fish (Pinto et al. 1984; Wright et al. 2000; Holland et al. 2005). Overall, their distribution is typically associated with or near sandy substrate and they are typically absent in areas dominated by boulders or bedrock, as well as areas with high silt content (Ostrand et al. 2005; Holland et al. 2005; Haynes et al. 2007).

Sand lance exhibit diel behaviour, where they remain in schools and forage during the day throughout the water column, and remain burrowed in the sediment at night (Winslade 1974a; Hobson 1986; Freeman et al. 2004; Friedlaender et al. 2009). Sand lance appear to primarily seek refuge in sandy sediment at night, presumably to avoid predation under lower efficiency foraging conditions for these visual foragers (Hobson 1986). The tight link between sand lance abundance and sandy substrate habitats for burrowing likely provide predictable areas of high prey abundance for predators, as such, sand lance are vulnerable while burrowing as predators aggregate near sand lance preferred sandy substrates as daylight abates and prey upon sand lance as they burrow (Hobson 1986; Burger 1995; Temming et al. 2004). Not surprisingly, predators exhibit lower reproductive success in years of low sand lance availability (Harris and Wanless 1991; Furness and Tasker 2000; Rindorf et al. 2000). On the Newfoundland and Labrador Shelf, sand lance is a key prey species for many breeding seabirds in coastal Newfoundland before capelin arrive in coastal areas to spawn (Burger and Piatt 1990) and are consistently found in the diet of fin-fish during the summer (DFO 2017; Berard and Davoren 2020).

### *Thesis Objectives*

Similar to forage species in other regions, sand lance and capelin, play an important role in the marine food web on the Newfoundland and Labrador Shelf (Carscadden et al. 2002; Davoren and Montevecchi 2003; Pikitch et al. 2012; Staudinger et al. 2020). Therefore, it is important to examine whether population dynamics of these two species exhibit synchrony to determine if a portfolio effect is present (Arimitsu et al. 2021). My first thesis objective (Chapter 2) is to investigate the synchrony of inter-annual trends in sand lance and capelin abundance,

distribution, and biometrics across the southeastern Newfoundland Shelf (NAFO Div. 3LNOPs; Fig. 1.1), using a 20-year (1996-2015) dataset. I hypothesized that species-specific distribution and biometrics will be influenced by abundance. I predicted density-dependent impacts on life-history traits to be stronger for sand lance than capelin, as sand lance have more specific habitat requirements than capelin and, thus, likely increase density within their current distribution (and do not expand their distribution) as abundance increases. As bottom-up processes drive population dynamics of both forage fish species, I also hypothesize that capelin and sand lance abundance, distribution, and biometrics will exhibit synchronized inter-annual trends.

My second thesis chapter (Chapter 3) investigated sand lance habitat characteristics (i.e., depth, temperature, salinity, seabed grain size range) during July and August in Notre Dame Bay on the northeast coast of Newfoundland (Fig. 1.1). I hypothesized that sand lance would be associated with shallow (<40 m), cool (1-11°C), fine sandy substrate (0.25 – 2 mm), with a salinity of 32-34 ppt, similar to Pacific sand lance and the lesser sandeel (Reay 1970, Wright et al. 2000, Ostrand et al. 2005). Additionally, I aimed to investigate the diel behaviour of sand lance at a fine-scale site of known sand lance presence during July and August (Chapter 3). I hypothesized that sand lance will be in the water column, presumably feeding, during the day and buried in the sediment at night, again similar to other regions (Winslade 1974b; Freeman et al. 2004; Holland et al. 2005).

Overall, a better understanding of sand lance distribution, abundance, density, biomass, diel behaviour and habitat selection on the Newfoundland Shelf will increase our understanding of the ecology of important forage fish, thereby informing population dynamics of top predators. This study will inform future research aimed to determine the mechanisms underlying population dynamics of these forage fish species and will provide insight into the impact of forage fish

population fluctuations on their predators on the Newfoundland Shelf, thereby informing ecosystem-based fisheries management strategies.

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## Tables and Figures

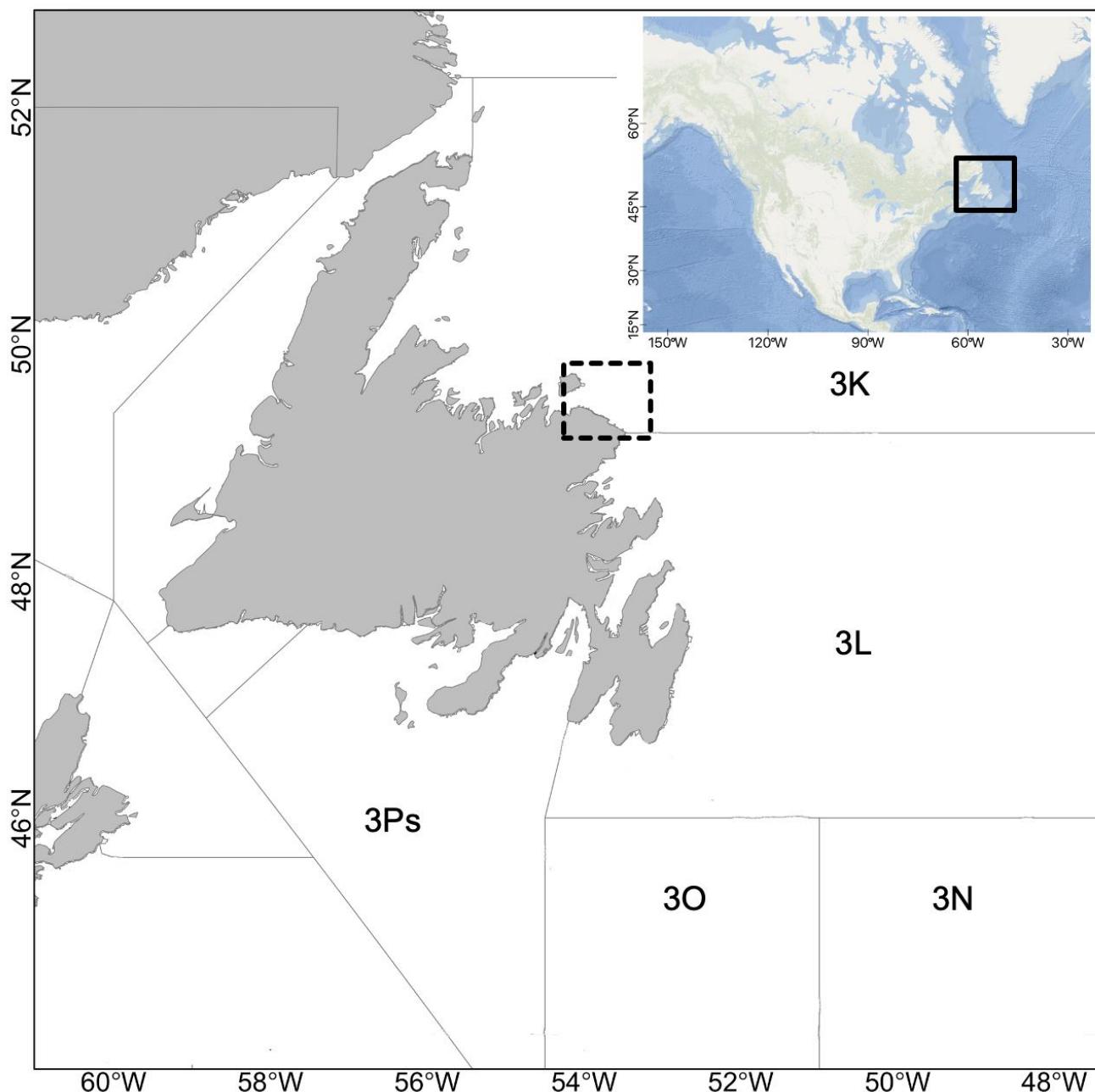


Figure 1.1. Study area on the Newfoundland Shelf showing *NAFO Divisions 3KLNOPs*, where the spring bottom trawl survey was conducted (Chapter 2; *NAFO Divisions 3LNOPs*) from 1996-2015, and Notre Dame Bay (Chapter 3; dashed square).

## **Chapter Two. Sand lance (*Ammodytes* spp) and capelin (*Mallotus villosus*) abundance, distribution, biometrics, and population dynamics on the Newfoundland Shelf**

### **Abstract**

Population dynamics of forage fish species are typically characterized by extreme fluctuations. Therefore, diversity in forage fish communities creates a portfolio effect, whereby the stability of marine ecosystems is increased by sustaining their role in transferring energy between lower and higher trophic levels, a key ecosystem process. The objective of this chapter was to investigate whether inter-annual trends in abundance, distribution, and biometrics (length, mass, condition) were synchronized in key forage fish species, sand lance *Ammodytes* spp and capelin *Mallotus villosus*, across the southeastern Newfoundland Shelf during the spring using a 20-year (1996-2015) bottom-trawl dataset. I also investigated whether species-specific distribution and biometrics were influenced by abundance. Sand lance length, mass and condition decreased with increasing abundance, suggesting density-dependence, but distribution did not expand with abundance. In contrast, capelin length and mass did not decrease with increasing abundance, nor did distribution. Inter-annual variation in abundance, distribution and biometrics were not synchronized in capelin and sand lance, possibly due to species occupying different regions at different life stages. Indeed, capelin were distributed farther north and more inshore than sand lance, possibly because capelin migrate inshore to spawn during the spring and sand lance are resident in the shallower waters of the Grand Banks. These findings support the collapsed state of the Newfoundland capelin population and the lack of predator release at the meso-predator trophic level after the overfishing of a top predator, Atlantic cod, *Gadus morhua*, in the early 1990s. Overall, this study increased the knowledge of forage fish population

dynamics on the Newfoundland Shelf, specifically the understudied sand lance *Ammodytes* species.

## Introduction

Marine ecosystems differ from terrestrial ecosystems in which the marine meso-predator trophic level is typically dominated by a few forage species. This results in a wasp-waist structure (Pikitch et al. 2012), whereby mid-trophic levels control the abundance of higher and lower trophic levels (Rice 1995; Cury 2000). As such, forage fish play a crucial role transferring the bulk of the energy from lower trophic levels to higher trophic level predators (Pikitch et al. 2012). Forage fish species, such as Atlantic herring *Clupea harengus*, anchovy *Engraulis encrasicolus*, sardine *Sardinops sagax*, capelin *Mallotus villosus* and sand lance *Ammodytes* spp, are small to medium-sized fish species with a short life span, early maturity, and high fecundity (Pikitch et al. 2012). The population dynamics of these species are typically characterized by extreme fluctuations, or ‘boom-bust cycles’ (Schwartzlose et al. 1999; Chavez et al. 2003). Despite these fluctuations in population size and the short-lived life history traits of forage fish, evidence suggests that density-dependent factors may influence life history traits (e.g., Icelandic capelin body size and condition, ICES 1999; Carscadden and Frank 2002; Shepherd and Litvak 2004). Although predators may also limit forage fish populations (e.g., capelin in the Barents Sea; Carscadden et al. 2013), recruitment (i.e., to maturity) is often driven by environmental factors (Essington et al. 2015), with bottom-up processes altering abundance of primary and secondary producers and, thus, mediating forage fish population dynamics (Frederiksen et al. 2006; Buren et al. 2014; Lynam et al. 2017). Owing to their important role in food webs, fluctuations in forage fish populations can have adverse impacts on top predator reproduction and survival (Cury 2000; Boyd and Murray 2001; Boyd 2002; Piatt et al. 2007; Cury et al. 2011), but asynchrony in the population dynamics of a variety of forage fish species can dampen these impacts on top predators within an ecosystem (Arimitsu et al. 2021). Indeed, diversity in forage

fish communities increases the stability of marine ecosystems by sustaining their role in key ecosystem processes (e.g., energy flow), creating a portfolio effect (Figge 2004; Schindler et al. 2010; Arimitsu et al. 2021).

Like other animals, forage fish select optimal habitat to maximize growth, reproduction, survival, and, thus, fitness (Morris 2003). The ideal free distribution (IFD) theory predicts how individuals will distribute themselves among available habitat patches, choosing the patches with the most favourable conditions to maximize fitness (Fretwell and Lucas 1970). As abundance increases, intraspecific competition increases within high-quality habitat patches, which results in lower quality patches becoming occupied until organisms have similar fitness within high- and low-quality habitat patches (Svärdson 1949). This expansion of distribution outside of optimal habitat has been associated with increased abundance in many highly mobile marine fish species (Paloheimo and Dickie 1964; Bertrand et al. 2004; Barange et al. 2009), whereby density remains constant within habitat patches while distribution expands (i.e., constant density model; Iles and Sinclair 1982) or density in expanding habitats varies according to the habitat quality (IDF; Fretwell and Lucas 1970). In contrast, fish distribution may stay constant as abundance increases, resulting in density being proportional to abundance (i.e., proportional model; Petitgas 1997), which maybe more likely for less mobile species with specific habitat requirements.

The Newfoundland and Labrador Shelf ecosystem is strongly influenced by the seasonal variation of the Labrador Current and the North Atlantic Current (Lilly 1982; Cyr et al. 2019). These currents affect the sea ice extent across the shelf along with the timing of sea ice retreat, consequently affecting the timing and magnitude of primary production (i.e. spring bloom) in the ecosystem (Wu et al. 2007). On the shelf, the primary forage fish species include herring and mackerel *Scomber scrombus*, which are primarily found in coastal regions (Moores et al. 1975),

and capelin and sand lance, which reside both in inshore and offshore regions (Templeman 1948; Winters and Dalley 1988).

Capelin are commercially fished inshore on the Newfoundland Shelf and, thus, the stock status is evaluated annually by Fisheries and Oceans Canada (DFO). One of the primary indices of capelin abundance is a targeted annual acoustic survey in the spring in NAFO Div. 3L (Fig. 2.1), which is a nursery area for age-1 and age-2 capelin (DFO 2018). Although some age-1 and age-2 capelin remain resident inshore throughout the winter (Templeman 1948, Buren et al. 2019), capelin typically spend the majority of their lives offshore. While in offshore waters, capelin distribution is thought to be determined by multiple factors (e.g., water temperature, density, prey availability) but they are found at a wide range of depths (Mowbray 2002; Rose 2005). In the spring-summer (May-July), the mature stock (age 2-4) migrates inshore to spawn, while immature (age-1 and some age-2) fish remain in offshore areas (Templeman 1948). On the Newfoundland Shelf, capelin recruitment is thought to be controlled from the bottom up, regulated by the influence of the extent of sea ice and timing of sea ice retreat which influence the timing and magnitude of the spring bloom and ultimately the availability of prey (e.g., copepods; O'Driscoll et al. 2001; Buren et al. 2014; Murphy et al. 2018) for capelin (Carscadden et al. 2013; Buren et al. 2014; Mullowney et al. 2016). In 1991, capelin abundance on the shelf experienced almost an order of magnitude collapse, with a decline from 2-6 Mt to 0.03-1.0 Mt (DFO 2018; Buren et al. 2019). Minimal recovery in the decades since the collapse is hypothesized to have been due to a number of factors (e.g., delayed capelin spawning, earlier sea-ice retreat, earlier spring plankton bloom) affecting the recruitment and survival of capelin (Buren et al. 2014; Mullowney et al. 2016; Lewis et al. 2019; Murphy et al. 2021).

In contrast, little is known about the ecology of sand lance on the Newfoundland Shelf, including their abundance, distribution, biometrics, and population dynamics, likely because it is not a commercially fished species and, thus, not assessed by DFO. All age classes of sand lance are non-migratory and have specific habitat requirements (Scott 1968; Reay 1970; Winslade 1974a; Wright et al. 2000; Ostrand et al. 2005). The distribution of sand lance in offshore waters is thought to be determined by similar factors as capelin, but sand lance are more abundant at depths <40 m and are highly associated with suitable sandy seabed substrate in which they burrow as they lack a swim bladder (Scott 1968; Reay 1970; Wright et al. 2000; Ostrand et al. 2005; Bizzarro et al. 2016). Sand lance are thought to spawn in the winter (November-February), in these locations that they occupy year-round (Winters and Dalley 1988; Robards et al. 1999b). Similar to capelin, the abundance of *Ammodytes* in other regions (e.g., Northeast Atlantic Ocean) is thought to be mostly controlled from the bottom-up, primarily regulated by prey (e.g., copepod) abundance (Frederiksen et al. 2006; Lynam et al. 2017). On the Newfoundland Shelf, there are two species of sand lance, *A. dubius* and *A. americanus*, where the distribution of *A. dubius* is thought to be more offshore than *A. americanus*; however, *A. dubius* is occasionally found inshore in deeper and more open regions (Winters and Dalley 1988; Nizinski et al. 1990).

Similar to other forage species, sand lance and capelin, play an important role in the marine food web on the Newfoundland and Labrador Shelf (Carscadden et al. 2002; Davoren and Montevecchi 2003; Pikitch et al. 2012; Staudinger et al. 2020). Therefore, it is important to examine whether population dynamics of these two species exhibit synchrony to determine if a portfolio effect is present (Arimitsu et al. 2021). The objective of this chapter is to investigate trends in sand lance and capelin abundance, distribution, and biometrics across the southeastern Newfoundland Shelf using a 20-year (1996-2015) dataset and determine whether these trends are

synchronized for both species. I hypothesize that species-specific distribution and biometrics will be influenced by abundance. I predict density-dependent impacts on life-history traits to be stronger for sand lance than capelin, as sand lance have more specific habitat requirements than capelin and, thus, likely increase density within their current distribution (i.e., do not expand their distribution) as abundance increases. As bottom-up processes drive population dynamics of both forage fish species, I also hypothesize that capelin and sand lance abundance, distribution, and biometrics will exhibit synchronized inter-annual trends. This will inform future research aimed to determine the mechanisms underlying population dynamics of these important forage fish species and will provide insight into the impact of forage fish population fluctuations on their predators on the Newfoundland Shelf, thereby informing ecosystem-based fisheries management strategies.

## Methods

To test my hypotheses, I used a dataset derived from a depth-stratified random multispecies bottom-trawl survey that has been conducted annually by the Department of Fisheries and Oceans Canada (DFO) on the Newfoundland Shelf (Northwest Atlantic Fisheries Organization (NAFO) Divisions 3LNOPs; Fig. 2.1) during spring (April-June) from 1996-2015. The main objective of the survey is to monitor the distribution, abundance, and biometrics of various groundfish and shellfish species, but forage fish species are also caught. Although I acknowledge inherent biases associated with sampling pelagic fish in a bottom-trawl survey, I anticipate these biases to be consistent across capelin and sand lance as capelin have been distributed near the seabed since the collapse of its population in 1991 (Mowbray 2002) and sand

lance are also likely distributed near the seabed for portions of the day/night due to their burrowing behaviour in seabed sediment and lack of swim bladder (Scott 1968; Hobson 1986; Wright et al. 2000; Bizzarro et al. 2016).

Trawl locations were randomly determined and sampled within each depth-stratum, with the number of trawls proportional to stratum area and a minimum of 2 trawls per stratum. At each station, a Campelen 1800 shrimp trawl was towed along the seabed for 15 min at a constant speed (3 knots). The trawl mouth dimensions are 11.7 m by 4 – 5 m and the trawl is equipped with rockhopper gear (356 mm diameter rubber disks), two 1400 kg polyvalent doors and is constructed with polyethylene twine (2-4 mm diameter) of mesh size (knot centre) varying from 80 mm (wings) to 40-60 mm (bellies) and a codend lined with 12.5 mm knotless nylon mesh (Teigsmark and Oynes 1982; Walsh and McCallum 1997). Each trawl catch was sorted into species (for sand lance to genus *Ammodytes*), then counted and weighed. A random sample of up to 50 fish for sand lance and up to 200 fish for capelin was frozen from one trawl within each superstratum, whereby superstrata were determined by grouping strata based on similar habitat characteristics (e.g., depth, proximity of strata) while respecting NAFO divisions. For capelin, total length (mm), sex and, maturity (maturity index: 1-immature, 2-maturing, 3-ripe, 4-partially spent, 5-spent) were measured and recorded for each fish. Body mass (g), gonad mass (g) and, sagittal otoliths were also removed for ageing on a length-stratified subsample (i.e. 2 fish per sex per 0.5 cm). For sand lance, total length (mm), sex, maturity (same maturity index as capelin), body mass (g) and gonad mass (g) were measured and recorded for all 50 fish. Although sagittal otoliths were removed, sand lance otoliths were not aged. To determine condition, fish were first classified into size/age classes and Le Cren condition (Le Cren 1951) was calculated by first  $\log_{10}$  transforming the length and weights of both sand lance and capelin, and then conducting a

linear regression on the log-transformed data for each species separately. Condition was calculated as the observed weight divided by predicted weight from the length-weight regression equation.

### *Data Analysis*

As the majority of immature capelin remain resident in offshore waters (Buren et al. 2019), while mature fish migrate inshore to spawn during the spring (i.e., survey period), we created subsets of the dataset for each species that included only immature fish to allow more meaningful comparisons between the two species. Capelin were classified as immature based on their maturity index (i.e., maturity index 1 = immature). Due to inconsistencies in visual assessments of sand lance maturity, the maturity index could not be used to classify fish as immature. Instead, the gonadosomatic index (GSI) was calculated [gonad mass/ (body mass – gonad mass) x 100], and immature fish were classified as those with a low GSI (<5%), after which the GSI increased rapidly, likely indicating the onset of maturity. Owing to the likelihood of prey availability regulating recruitment in both species, immature fish of both species were further subset to lengths of <120 mm for capelin and <140 mm for sand lance, based on the presence of larger prey types (e.g., euphausiids) in the diet beyond these sizes in both species (DFO 2012). The proportion of immature fish of each species was then determined from the one subsampled trawl catch in each superstratum. To quantify abundance of immature fish in each trawl, this proportion of immature fish was then applied to all trawl catches in the superstratum for each species, by multiplying the total catch abundance (i.e., number of fish for each species) by the proportion of immature fish estimated to be in each trawl. Note that all analyses described

below were conducted on both the immature capelin and sand lance datasets, along with the full capelin and sand lance datasets.

A centre of gravity analysis was used to assess whether sand lance and capelin on the Newfoundland Shelf have experienced spatial shifts in distribution as well as distributional expansion or contraction. The centre of gravity (CG) represents the mean location of a population, represented by the mean latitude and longitude of each species caught during each annual survey. Due to irregular sampling (i.e., trawl locations not uniformly distributed), mean latitude and longitude were weighted by species-specific abundance and area of influence using the following equation:

$$CG = \frac{\sum_{i=1}^n x_i s_i z_i}{\sum_{i=1}^n s_i z_i}$$

where  $x_i$  represents the latitude or longitude of each trawl,  $z_i$  is species-specific abundance per trawl and  $s_i$  is the area of influence. Area of influence of each trawl was calculated by tessellation, whereby the survey area is broken up into nonoverlapping but adjoining polygons, with each polygon including one trawl. The area within a polygon represents the area of influence of the corresponding trawl (Woillez et al. 2009). The spatial dispersion of the population (i.e., ‘inertia’), or the spatial variance of the location of individuals in the population, was calculated as the mean square distance between an individual fish and the centre of gravity of the population using the following equation:

$$I = \frac{\sum_{i=1}^n (x_i - CG)^2 s_i z_i}{\sum_{i=1}^n s_i z_i}$$

Inertia was used to examine inter-annual expansion/contraction of sand lance and capelin distribution during the study period. Calculations were performed using the *RGeostats* package (Renard et al. 2018) in R (R Core Team 2020). The CG of the survey was also calculated and qualitatively compared to the CG of sand lance and capelin for each year to ensure shifts in fish distributional patterns were not due to shifts in the distribution of the survey.

### *Statistical Analysis*

As the distribution of the number of fish per trawl was highly right skewed (i.e., large number of trawls with zero sand lance or capelin), I used Bayesian generalized linear mixed models (i.e., hurdle models) with an underlying gamma distribution to calculate an annual relative abundance index. Hurdle models are two-part models: a logistic model for whether an observation is zero or not, and a non-zero model. Survey year was a random factor to examine group-level effects (i.e., inter-annual variation in abundance) and was the only factor in the model. Similar to the number of fish per trawl, an annual relative index was calculated for each biometric variable separately (i.e., total length, total mass, and condition) using Bayesian general linear mixed models with an underlying Gaussian distribution. Models were fit using Markov Chain Monte Carlo methods using the following parameters: four chains, 10,000 iterations each, a burn in of 5000 iterations, uninformed priors, and an initial starting value of 0.3 to help the chains initialize. In all models, the chain convergence diagnostic (R-hat) was equal to 1, indicating the chains had converged. The median of the posterior probability distribution for each response variable in each year was used as the relative index. To test the first hypothesis, relative indices generated for both datasets (i.e., immature, full) within each species were used as

response variables in principal component analyses (PCA) to assess the relationships among abundance and biometric variables. General linear regression models were used to investigate relationships between abundance and spatial variance (i.e., inertia) for all four datasets. To test the second hypothesis, capelin and sand lance annual relative indices (i.e., abundance, length, mass, condition) were examined for coherence in inter-annual trends for immature and full datasets separately using general linear regression models. Bayesian statistics were performed using the *brms* package in R (Version 3.6.2) and principal component analyses were performed using JMP (Version 15.2).

## Results

A total of 9622 trawls were performed over the 20-year study period (1996-2015) with an average of  $481 \pm 16.6$  (mean  $\pm$  SE) per year with a depth range of 34-870 m (Table 2.1). During 2006, not all trawls were conducted (Table 2.1) due to technical difficulties with the research vessel and, thus, trends associated with this year should be interpreted cautiously. Capelin were present in 55% of trawls from 1996-2015, whereas immature capelin were present in 25% of the trawls over the same period (Table 2.1). Sand lance were present in 37% of trawls, whereas immature sand lance were present in 10% of trawls over the same period (Table 2.1).

The PCAs for each of the four datasets had two principal components with eigenvalues > 1. For the full capelin dataset, the first two PCs explained a total of 77.3% of the variation (Fig. 2.2a). The variables with the highest positive loadings on PC1 were mass (0.9587) and length (0.8562), while there were no variables with negative loadings on PC1 (Fig. 2.2a). The variable with the highest positive loading on PC2 was condition (0.7753), while the highest negative

loading was abundance (-0.6761; Fig. 2.2a). For the immature capelin dataset, the first two PCs explained more of the variation in the dataset (82.9%; Fig. 2.2c). Similar to the full capelin dataset, the variables with the highest positive loadings on PC1 were mass (0.8779) and length (0.8270), while the variable with highest negative loading was condition (-0.5803; Fig. 2.2c). The variable with the highest positive loading on PC2 was abundance (0.8234), while there were no variables with negative loadings on PC2 (Fig. 2.2c).

The first two PCs for the full sand lance dataset explained a total of 84.8% of the variation (Fig. 2.2b). Similar to the capelin datasets, the variables with the highest positive loadings on PC1 were length (0.9133) and mass (0.9045), but, unlike capelin, the variable with the highest negative loading was abundance (-0.5728; Fig. 2.2b). Similar to the full capelin dataset, the variable with the highest positive loading on PC2 was condition (0.9335), while the highest negative loading was abundance (-0.5431; Fig. 2.2b). For the immature sand lance dataset, the first two PCs explained a total of 86.8% of the variation (Fig. 2.2d). The variables with the highest positive loadings on PC1 were mass (0.9689) and condition (0.9210), while there were no variables with negative loadings on PC1 (Fig. 2.2d). The variable with the highest positive loading on PC2 was abundance (0.7208), while the highest negative loading was length (-0.7152; Fig. 2.2d).

The centre of gravity of capelin (full dataset) was farther north and inshore than that of sand lance (Fig. 2.3, S2.1), as sand lance were associated with the shallow, offshore waters of the Grand Banks in most years (Fig. 2.3b, S2.1). These same patterns were observed in immature datasets for capelin and sand lance, with some anomalous years for immature sand lance (e.g., 1997, 2000; Fig. 2.3d, S2.1), possibly due to a low number of immature fish caught in those years (Table 2.1; Fig. S2.2). There was no indication that survey effort caused these

distributional shifts as the centre of gravity of the survey was constant over the 20-year dataset (excluding 2006; Fig. S2.1). Although capelin and sand lance showed inter-annual variation in abundance (Fig. 2.5a, Fig. S2.3-S2.6) and spatial variance (Fig. S2.2), we found no relationship between abundance and spatial variance in any of the other datasets ( $p$ -values = 0.08 - 0.3; Fig. 2.3b, c, d), except for a significant negative relationship for capelin (full dataset;  $r^2 = 0.47$ ,  $p < 0.001$ ; Fig. 2.3a). Capelin and sand lance relative indices for abundance, length, mass, and condition in both the full and immature datasets did not show synchronized inter-annual trends ( $p$ -values = 0.22 – 0.94; Figs. 2.4, 2.5, S2.3-S2.6). Inter-annual shifts in mean latitude and longitude of capelin and sand lance, in both the full and immature datasets, did not appear to be synchronized ( $r^2 = 0.001 – 0.13$ ,  $p$ -values = 0.13 – 0.91; Fig. S2.1).

## Discussion

As predicted, we found evidence of density-dependence in the full dataset of sand lance but not capelin, whereby sand lance length, mass and condition decreased with increasing abundance while capelin length and mass increased with increasing abundance. Interestingly, the immature datasets for both species showed little evidence of density-dependence, with length, mass and condition all increasing with abundance along the main axis (PC1). Both species did not appear to expand their distribution in years of higher abundance, as was predicted for capelin. Instead, capelin (full dataset) distribution unexpectedly appeared to decrease with increasing abundance (Fig. 2.4). Finally, although bottom-up processes likely drive population dynamics of both forage fish species (Frederiksen et al. 2006; van der Kooij et al. 2008; Buren et al. 2014; Mullowney et al. 2016; Lewis et al. 2019; Murphy et al. 2021), inter-annual variation in

abundance and biometrics (length, mass, condition) of capelin and sand lance were not synchronized. Similarly, both species did not show synchrony for inter-annual shifts in mean latitude and longitude. Capelin were distributed farther north and more inshore than sand lance (Fig. 2.3), possibly because capelin begin their inshore spawning migration during the survey period in the spring (Buren et al. 2014; Murphy et al. 2021) and sand lance mostly reside in the shallower waters of the Grand Banks (Winters 1981, 1983).

In this study, capelin (full dataset) biometrics did not show any evidence of density-dependent variation and capelin did not expand their distribution when abundance was higher; in fact, distribution was more contracted when abundance was higher (Figs. 2.2, 2.4). This unexpected relationship may be due to variation in the timing of inshore spawning migration in relation to the timing of this spring survey. Indeed, great inter-annual variation in the timing of capelin spawning along the coast, a proxy of inshore migration timing, has been documented since the population collapsed in 1991 (Carscadden and Nakashima 1997; Davoren et al. 2012; Crook et al. 2017; Murphy et al. 2021). Capelin migration inshore and out of the survey area at different times each year could be a key driver of inter-annual variation in our annual abundance estimates. This is corroborated by a lack of relationship between our capelin abundance estimates and the primary abundance index of capelin from the spring acoustic survey ( $r^2 = 0.009$ ,  $p = 0.72$ ), which targets the age-2 proportion of the population in NAFO Div. 3L, a known nursery area (DFO 2018). If capelin aggregate in certain areas prior to initiating migration, this may combine with inter-annual variation in the timing of capelin migration out of the survey area to explain lower spatial variance in years of higher abundance. Although no evidence of aggregation prior to migration was observed in this study (Fig. S2.2), further investigation may increase the usefulness of capelin abundance estimates from this spring survey. Unlike the full

dataset, immature capelin do not undergo inshore spawning migration and instead are resident in the survey area. Therefore, our immature capelin abundance estimates would not be affected by migratory behaviour. Immature capelin length, mass and condition appeared to increase with abundance along the main axis (PC1), suggesting a lack of density-dependence. Together with a lack of expansion in distribution under increasing immature capelin abundance, these findings support previous studies showing that inter-annual variability in bottom-up processes simultaneously influence abundance and life history traits (e.g., sea-ice extent, timing of sea-ice retreat, prey availability; Mullowney et al. 2016; Lewis et al. 2019; Murphy et al. 2021) to maintain the collapsed state of the population (Buren et al. 2014, 2019).

Although the biometrics of immature sand lance did not show any signs of density-dependence, the length, mass, and condition in the full dataset decreased as abundance increased, as predicted. The lack of density-dependence in immature sand lance may be due to the much smaller annual sample sizes on which the biometric characteristics were based compared to the full dataset. Although one might not predict forage fish species to reach the carrying capacity of their environment because their population dynamics are characterized by extreme fluctuations (Schwartzlose et al. 1999; Chavez et al. 2003), previous studies have found a strong negative correlation with sand lance growth and abundance in both adult and immature fish (Robards et al. 1999a, 2002; Bergstad et al. 2002). As sand lance have specific habitat requirements, density-dependent effects on growth may occur as fish accumulate within these favourable habitats. Sand lance species require cool (1-11°C), shallow (<40 m) habitat with sandy sediment (0.25 – 2 mm grain size; Scott 1968, Reay 1970, Wright et al. 2000, Ostrand et al. 2005) because they lack a swim bladder, and bury in the sediment when not actively foraging (Winslade 1974a; Hobson 1986; Freeman et al. 2004; Friedlaender et al. 2009). Burrowing in sandy sediment is thought to

reduce the risk of predation, as well as reduce energy expenditure (Pinto et al. 1984). Therefore, sand lance typically remain within 500 m of sandy substrates suitable for burrowing (Hobson 1986; Ostrand et al. 2005). These specific habitat requirements also may explain why the distribution of these resident fish did not expand with increasing abundance, as fish likely aggregated in higher densities within suitable habitat, as predicted. As density was not measured in this study, however, further study on the Newfoundland Shelf will be needed to test whether sand lance density increases within these favourable habitats as abundance increases.

Inter-annual variation in abundance, biometrics (length, mass, condition) and distribution (centre of gravity) were not synchronized in capelin and sand lance, in both the full and immature datasets. The lack of synchrony in the full datasets of capelin and sand lance may be due to the inaccuracies with our annual capelin abundance and biometrics indices due to inter-annual variation of capelin inshore migration during the spring. Although synchrony in the immature annual biometric indices also may not be expected, again due to inaccuracies with the low sample sizes of immature sand lance, we would argue that the abundance estimates of the immature capelin and sand lance datasets are comparable. Although immature capelin and sand lance were subset further by length to ensure variation in diet (i.e., prey size) did not influence biometrics and abundance indices, each species likely experiences different environmental factors that differentially affect growth and survival. In support, capelin and sand lance have different annual cycles and occupy different habitats and regions of the Newfoundland Shelf. For instance, capelin spawn in coastal areas during the summer (July-August; Templeman 1948), whereas sand lance spawn in offshore areas during the winter (November-February; Winters and Dalley 1988; Robards et al. 1999b). Differential timing and location of hatching results in the most vulnerable early life history stages of each species experiencing divergent environmental

conditions immediately upon hatch, likely leading to different selection pressures driving recruitment. Although the main factors influencing capelin larval growth and survival immediately after hatching have been studied (i.e., low predator and high prey abundance; Frank and Leggett 1982), these factors are unknown for sand lance. The growth and survival of age-0 fish (i.e., young of the year) of both species appear to be linked to the spring algal bloom (capelin: Mullowney et al. 2016; Murphy et al. 2018; sand lance: Robards et al. 1999b; van der Kooij et al. 2008), but larvae of each species would be at different stages in their first year during the spring bloom and, thus, likely affected differently.

In conclusion, despite issues mentioned above with my calculated indices (abundance, length, mass, condition) associated with estimating abundance of pelagic species from a bottom-trawl survey, there were no increasing trends in capelin or sand lance abundance over the 20-year study period. These findings suggest little change in the collapsed state of the capelin population and little evidence of predator release at the meso-predator trophic level after the overfishing of Atlantic cod *Gadus morhua*, a key top predator, as seen just south of the study area on the Scotian Shelf (Frank et al. 2005). Owing to the asynchronous inter-annual variation in abundance and biometrics of both forage fish species, which are important prey species for top predators in the offshore waters of the Newfoundland Shelf, predators that consume both of these prey species may not be impacted by this species-specific variation (i.e., portfolio effect; Figge 2004; Schindler et al. 2010; Arimitsu et al. 2021). Indeed, Atlantic cod diet consists of both capelin and sand lance, and prey proportions vary among years (Lilly and Fleming 1981; Lilly 1982; Mello and Rose 2005). Additional diversity in movement patterns (i.e., migration vs. resident), age at maturity, and life stages occurring at different times and locations within a year can further contribute to this portfolio effect (Arimitsu et al. 2021). Overall, my findings increased the

knowledge of forage fish population dynamics on the Newfoundland Shelf, specifically about understudied sand lance *Ammodytes* species.

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## Tables and Figures

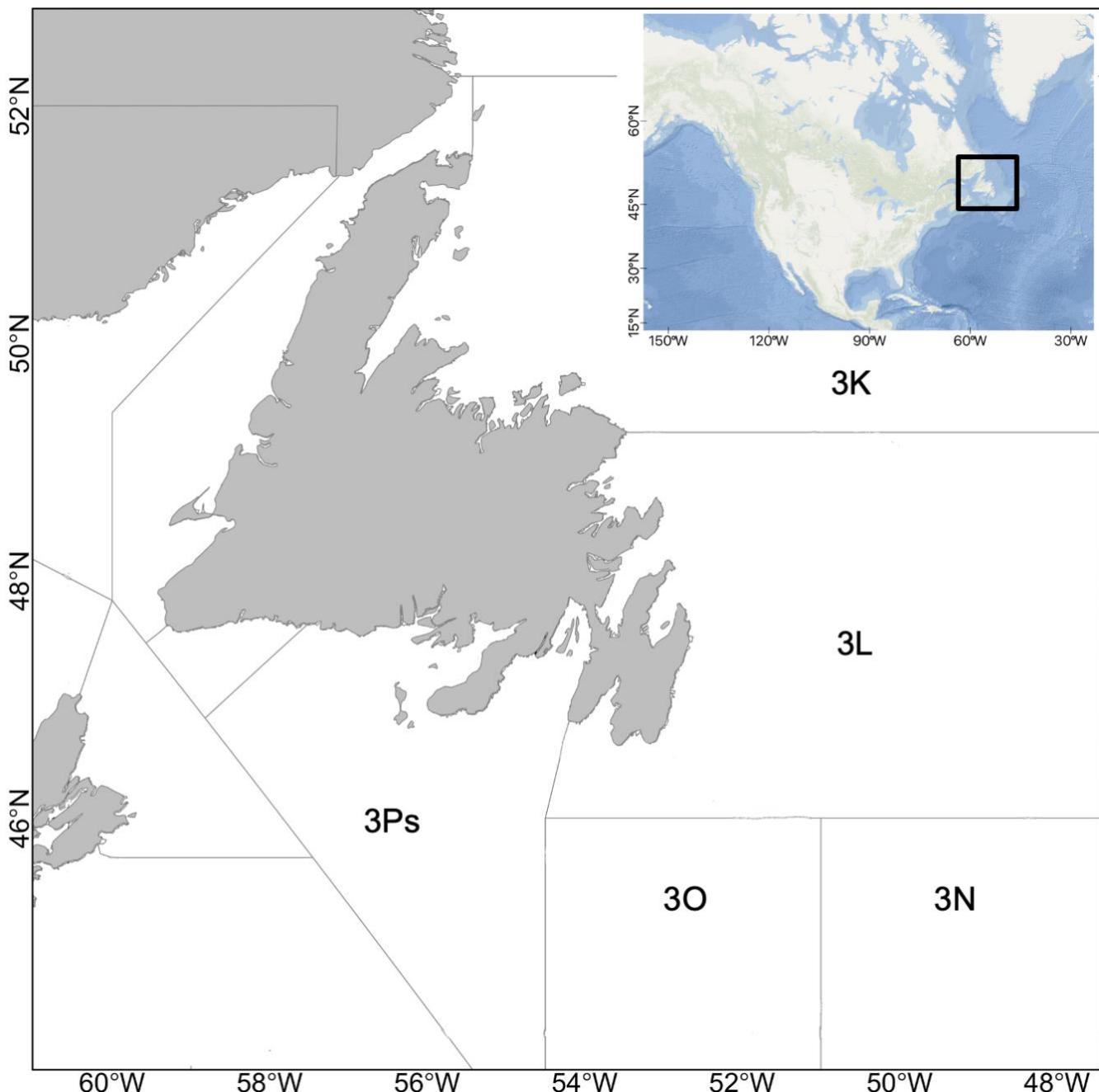


Figure 2.1. Study area on the Newfoundland Shelf showing NAFO Divisions 3KLNOPs, where the spring bottom trawl survey was conducted (NAFO Divisions 3LNOPs) from 1996-2015.

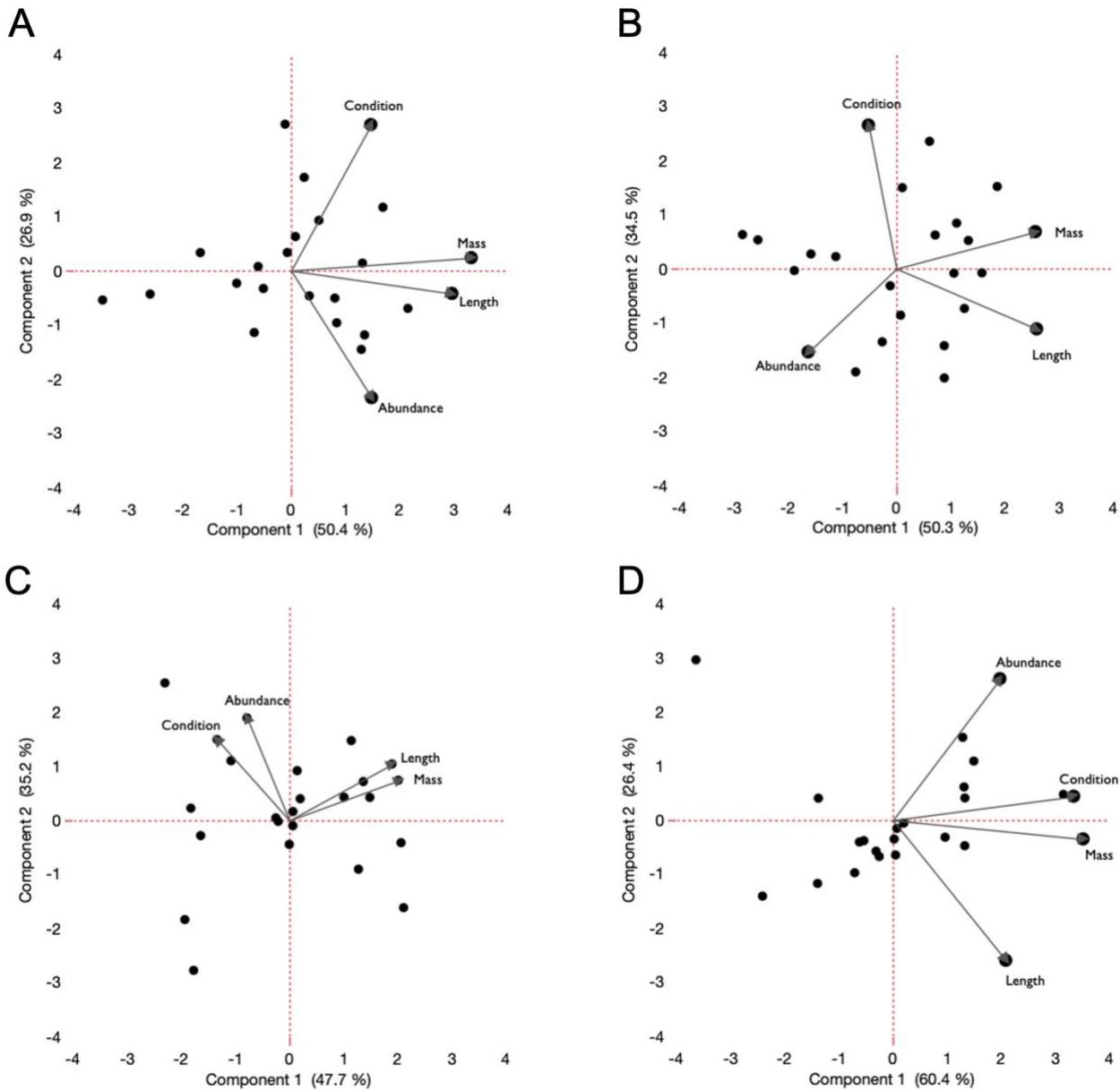


Figure 2.2. Principal component analyses of a) capelin (full dataset), b) sand lance (full dataset), c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in NAFO Divisions 3LNOPs from 1996-2015, showing values of PC1 and PC2 along with eigenvectors for abundance, length, mass, and condition. Annual relative indices of abundance, length, mass, and, condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models.

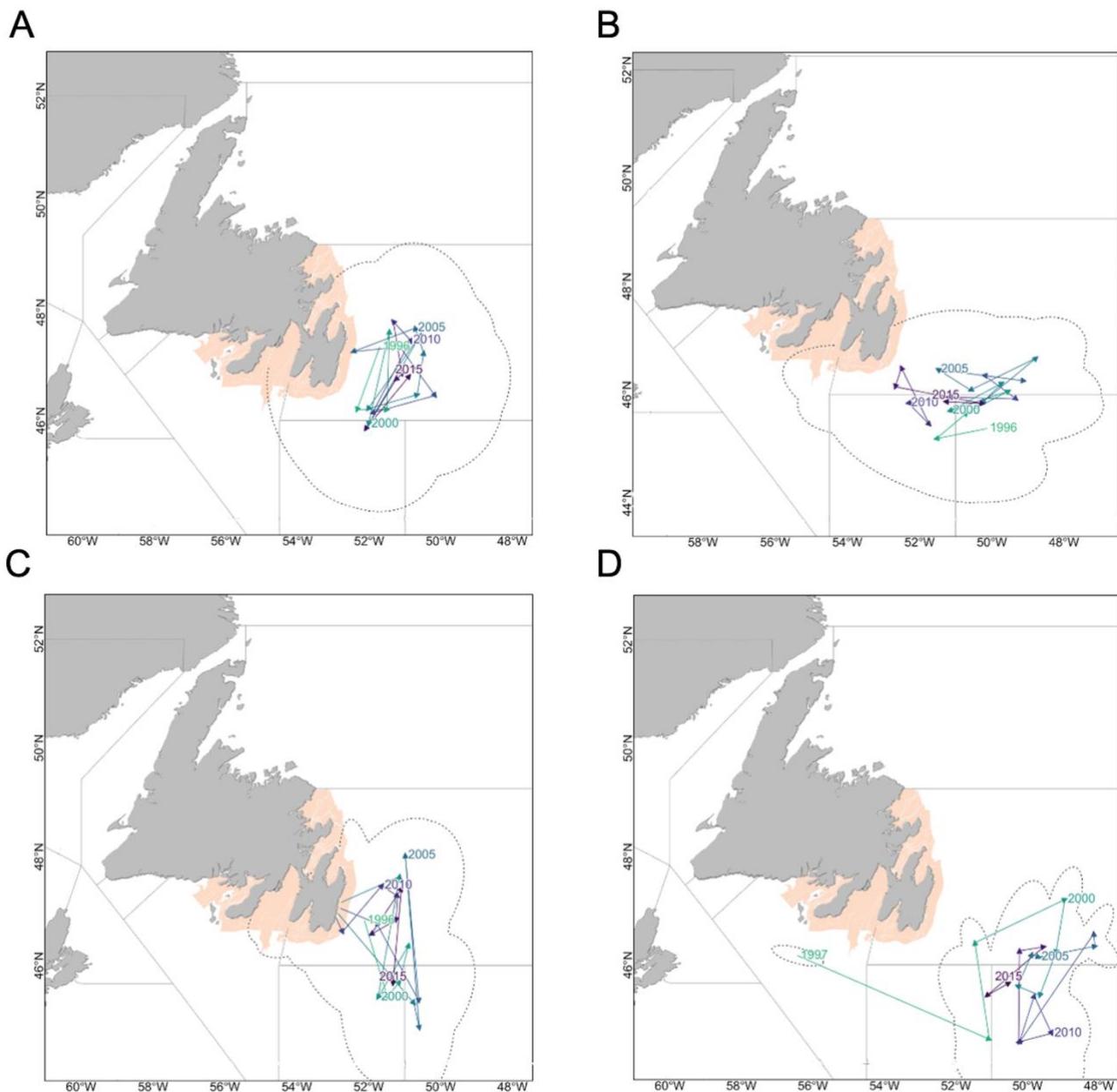


Figure 2.3. Centre of gravity of a) capelin, b) sand lance, c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in NAFO Divisions 3LNOPs from 1996-2015.

Annual centre of gravity estimates are connected by lines through time, and a composition of spatial variance around these estimates (i.e., inertia) are indicated by the dotted black line. Annual estimates of spatial variance can be viewed at URL. Centre of gravity and spatial variance were calculated using equations found in Woillez *et al.* (2007). The orange area

indicates areas poorly covered by the survey.

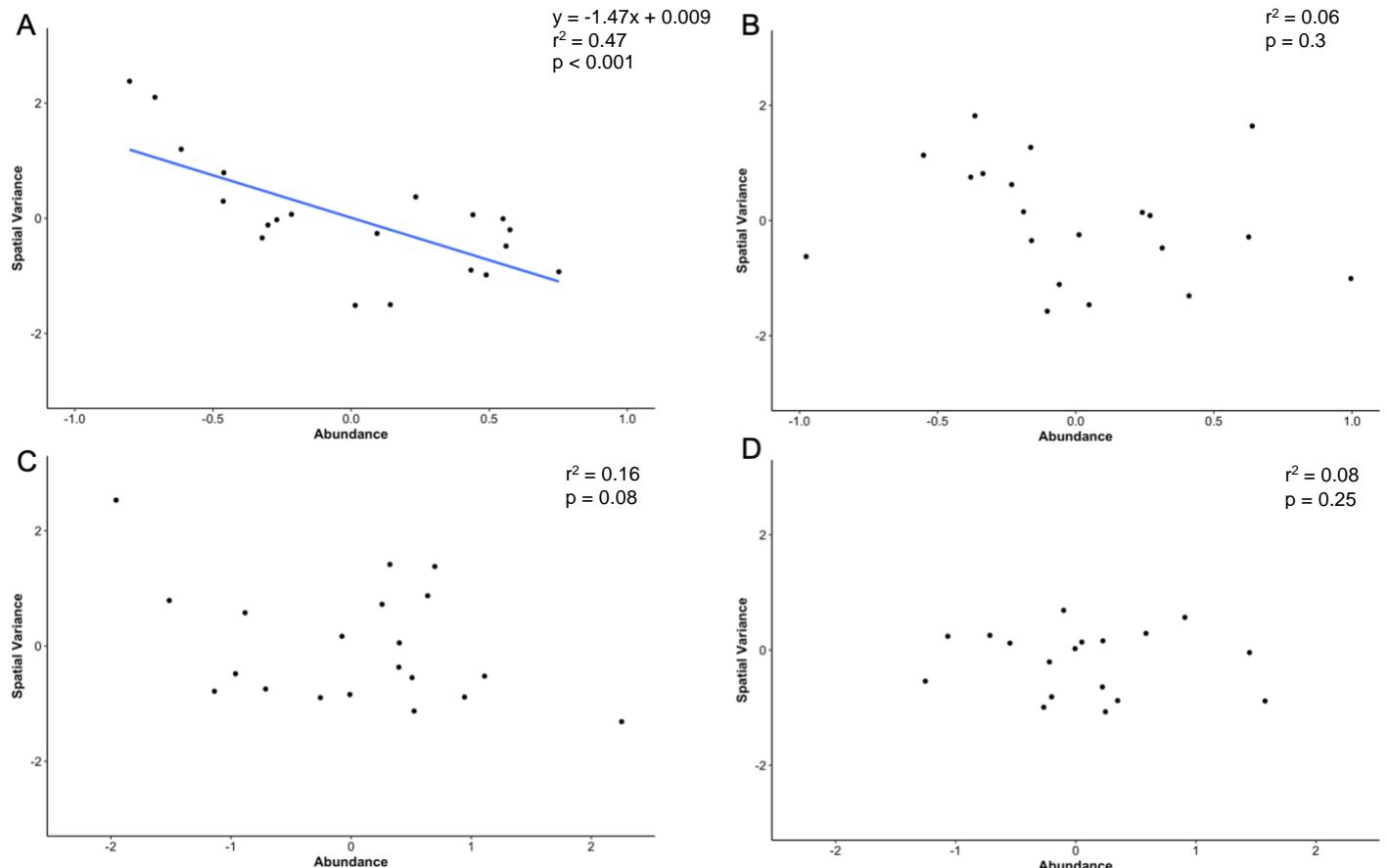


Figure 2.4. Relationships between annual relative abundance index and spatial variance (i.e., inertia) of a) capelin, b) sand lance, c) immature capelin, and d) immature sand lance from the spring bottom trawl survey in *NAFO Divisions 3LNOPs* from 1996-2015. Annual relative index of abundance was calculated using Bayesian generalized linear mixed models. Spatial variance was calculated using equations for inertia found in Woillez *et al.* (2007).

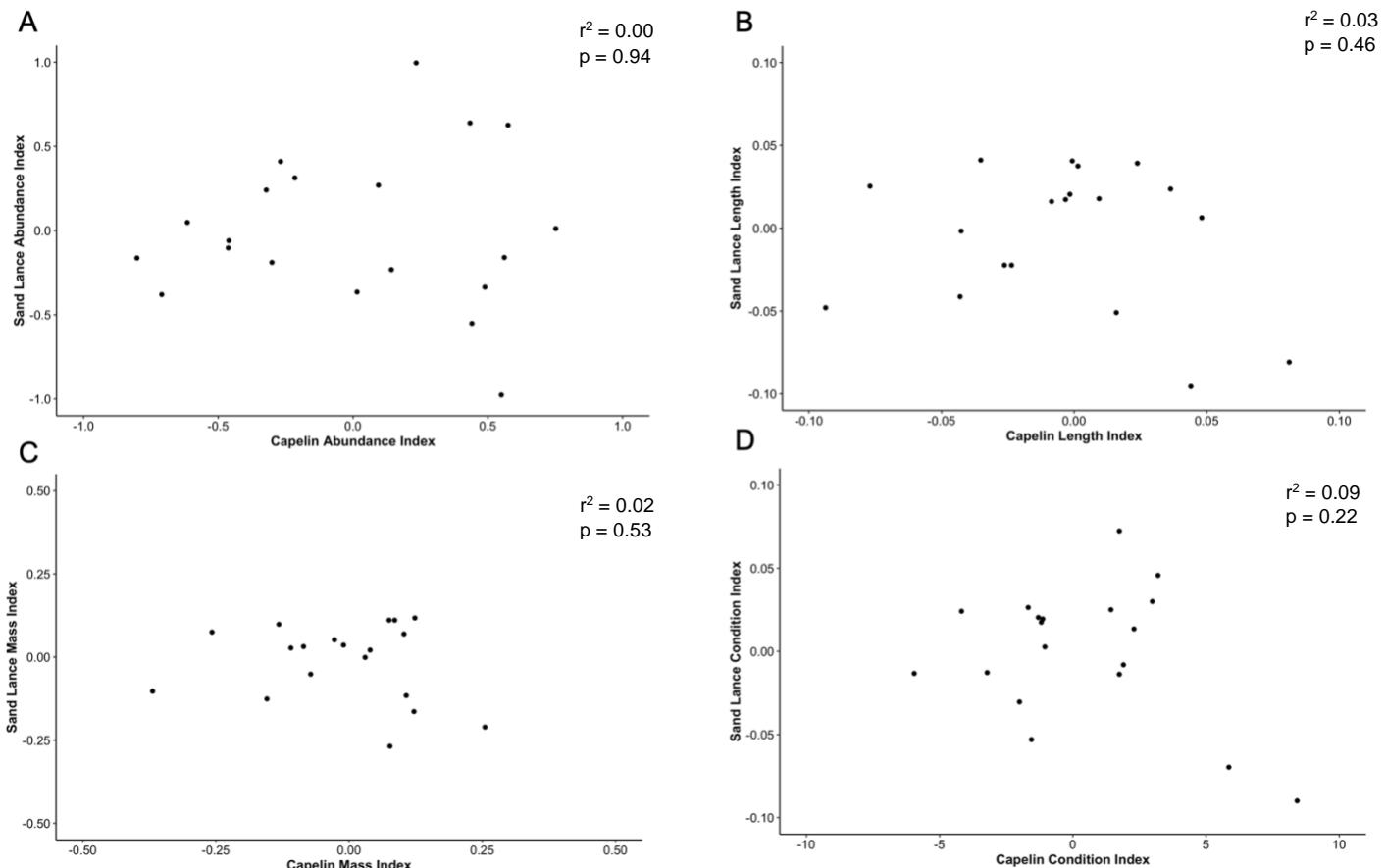


Figure 2.5. Relationships between capelin and sand lance (full dataset) annual relative indices of a) abundance, b) length, c) mass, and d) condition index from the spring bottom trawl survey in NAFO Divisions 3LNOPs from 1996-2015. Annual relative indices of abundance, length, mass, and condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models.

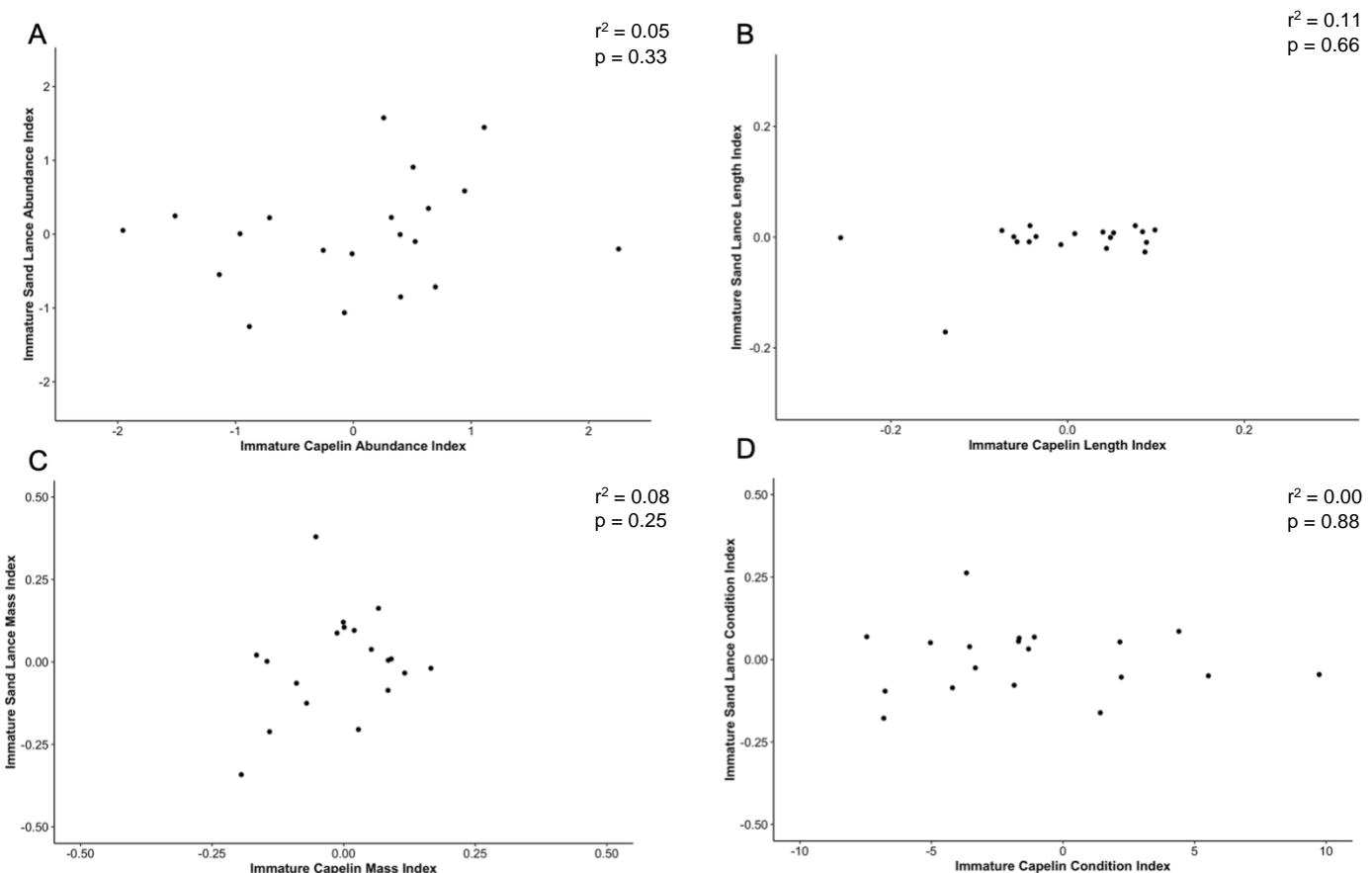


Figure 2.6. Relationships between immature capelin and sand lance annual relative indices of a) abundance, b) length, c) mass, and d) condition index from the spring bottom trawl survey in NAFO Divisions 3LNOPs from 1996-2015. Annual relative indices of abundance, length, mass, and condition were calculated using Bayesian generalized (abundance) and general (length, mass, condition) linear mixed models.

Table 2.1. Summary of the dataset from the spring bottom trawl survey in *NAFO Divisions* 3LNOPs from 1996-2015. The number of sampled capelin were used to calculate mean length ( $\pm$  SE), while the number of sub-sampled capelin were used to calculate mean ( $\pm$  SE) mass and condition. The number of sampled sand lance were used to calculate mean ( $\pm$  SE) length, mass, and condition. The number of immatures was determined from the number of sampled fish.

Year	Capelin								Sand Lance							
	Number of Trawls	Depth Range (m)	Mean Depth (m)	Number of Trawls with Capelin	Number Sampled	Number of Immatures	Number Sub-sampled	Length (mm)	Mass (g)	Condition	Number of Trawls with Sand Lance	Number Sampled	Number of Immatures	Length (mm)	Mass (g)	Condition
1996	484	42 - 664	176	283	5426	141	1156	150 ± 0.2	16.5 ± 0.2	1.0 ± 0.02	208	0	-	-	-	-
1997	449	34 - 681	175	297	21912	1466	1554	143 ± 0.1	13.3 ± 0.2	1.0 ± 0.03	158	519	4	187 ± 1.1	10.5 ± 0.2	0.91 ± 0.00
1998	492	38 - 721	176	278	23406	2127	1466	142 ± 0.1	12.8 ± 0.2	1.0 ± 0.00	190	1386	9	182 ± 0.6	11.3 ± 0.1	0.98 ± 0.00
1999	468	40 - 870	181	250	8627	1605	963	139 ± 0.3	16.3 ± 0.3	1.0 ± 0.03	182	749	5	180 ± 0.7	9.4 ± 0.1	0.93 ± 0.00
2000	537	39 - 681	177	248	5016	1676	1016	131 ± 0.4	12.9 ± 0.3	1.0 ± 0.01	172	918	8	184 ± 0.7	11.5 ± 0.1	0.98 ± 0.00
2001	552	38 - 695	176	291	4284	149	1042	144 ± 0.2	14.5 ± 0.2	1.0 ± 0.00	195	944	15	187 ± 0.7	11.7 ± 0.2	0.97 ± 0.00
2002	545	37 - 710	171	304	4056	574	978	140 ± 0.3	11.6 ± 0.2	0.95 ± 0.02	170	798	14	187 ± 0.7	12.0 ± 0.1	0.98 ± 0.00
2003	456	39 - 698	177	299	4228	220	862	145 ± 0.3	14.4 ± 0.2	0.99 ± 0.01	147	1076	11	189 ± 0.7	11.8 ± 0.2	0.94 ± 0.00
2004	454	36 - 710	175	261	3271	103	722	140 ± 0.2	14.1 ± 0.3	1.0 ± 0.00	159	998	5	183 ± 0.7	11.6 ± 0.2	0.99 ± 0.00
2005	448	37 - 672	177	198	3359	111	689	147 ± 0.3	16.2 ± 0.3	1.0 ± 0.01	194	1369	10	185 ± 0.6	12.7 ± 0.2	1.0 ± 0.00
2006	243	41 - 701	165	157	2977	589	602	142 ± 0.4	15.6 ± 0.4	1.0 ± 0.00	103	911	13	180 ± 0.9	12.3 ± 0.2	1.0 ± 0.00
2007	545	39 - 702	175	307	4372	316	871	144 ± 0.3	15.5 ± 0.3	1.0 ± 0.02	188	1546	24	183 ± 0.5	12.5 ± 0.1	1.0 ± 0.00
2008	516	39 - 684	167	304	5324	271	1236	149 ± 0.3	15.6 ± 0.2	1.0 ± 0.00	194	879	11	181 ± 0.7	12 ± 0.2	1.0 ± 0.00
2009	454	40 - 694	176	259	3105	610	777	131 ± 0.4	10.1 ± 0.2	0.96 ± 0.01	125	899	42	172 ± 0.7	10.2 ± 0.1	1.0 ± 0.00
2010	513	39 - 715	168	256	5060	554	980	139 ± 0.3	12.4 ± 0.2	1.0 ± 0.01	184	717	35	176 ± 0.8	12.3 ± 0.2	1.1 ± 0.00
2011	554	37 - 723	171	296	4511	1021	939	140 ± 0.4	14.7 ± 0.3	1.0 ± 0.03	210	792	13	175 ± 0.7	11.1 ± 0.2	1.0 ± 0.00
2012	552	38 - 723	179	306	5171	233	1135	148 ± 0.2	15.3 ± 0.2	0.99 ± 0.00	233	1008	99	163 ± 0.7	8.5 ± 0.1	1.0 ± 0.00
2013	543	40 - 632	163	308	6604	33	1403	153 ± 0.2	18.2 ± 0.2	0.99 ± 0.00	249	959	32	166 ± 0.6	9.0 ± 0.1	1.0 ± 0.00
2014	390	39 - 702	181	213	4582	522	1253	144 ± 0.3	15.9 ± 0.3	0.99 ± 0.00	143	846	16	170 ± 0.7	9.8 ± 0.1	1.0 ± 0.00
2015	427	38 - 685	170	181	2513	477	669	137 ± 0.5	12.5 ± 0.3	1.0 ± 0.00	154	599	25	172 ± 0.9	9.8 ± 0.2	1.0 ± 0.00
Total/Mean	9622	34 - 870	173.8	5296	127804	12798	20313	142.4	14.4	1.0	3558	17913	391	179.1	11.1	1.0

## Supplementary Materials I

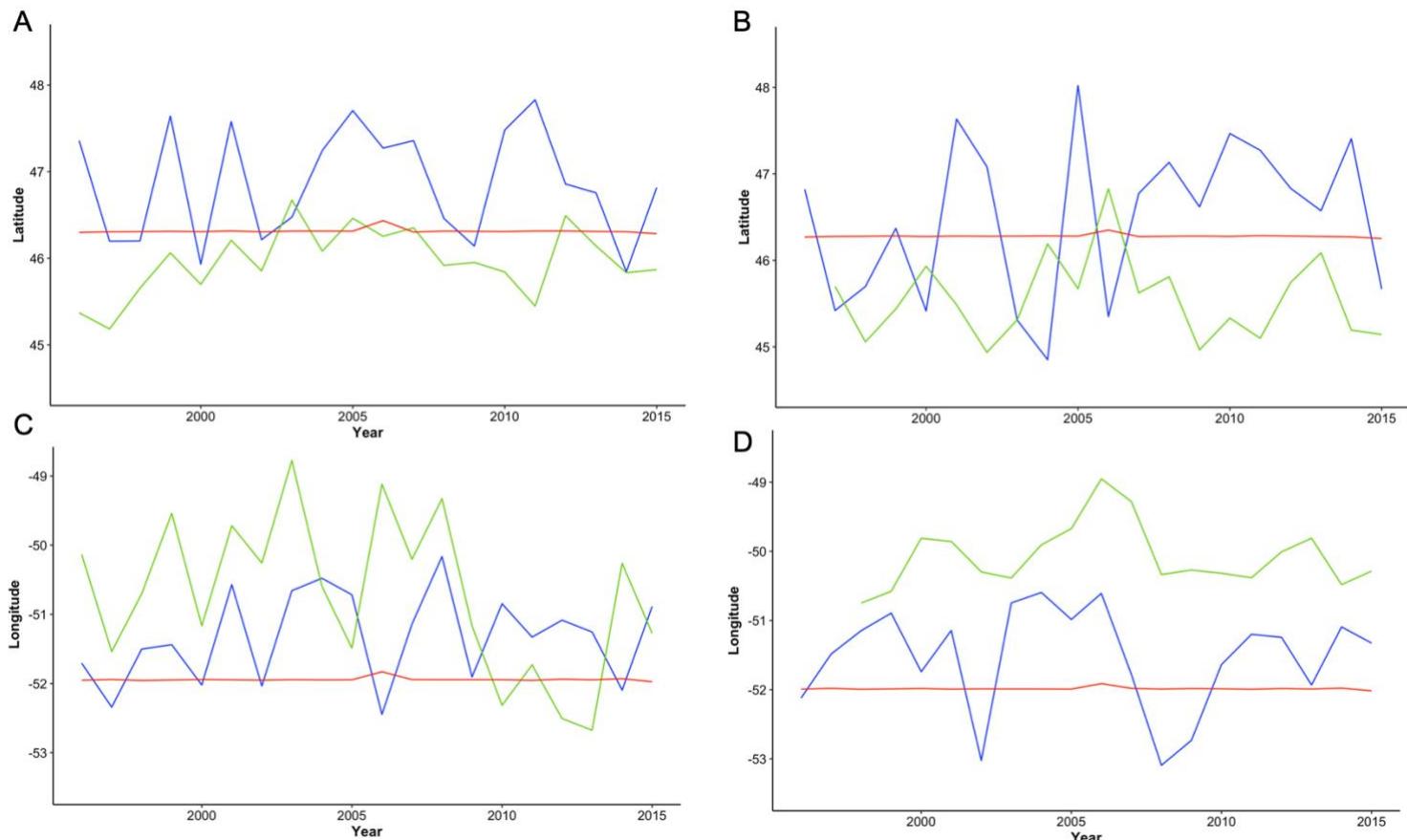


Figure S2.1. a) Latitude of the centre of gravity of capelin, sand lance, and the spring bottom-trawl survey (sand lance versus capelin latitude:  $r^2 = 0.05$ , p-value = 0.34), b) latitude of the centre of gravity of immature capelin, immature sand lance, and the spring bottom-trawl survey (sand lance versus capelin latitude:  $r^2 = 0.13$ , p-value = 0.13), c) longitude of the centre of gravity of capelin, sand lance, and the spring bottom-trawl survey (sand lance versus capelin longitude:  $r^2 = 0.001$ , p-value = 0.91), d) longitude of the centre of gravity of immature capelin, immature sand lance, and the spring bottom-trawl survey (sand lance versus capelin longitude:  $r^2 = 0.003$ , p-value = 0.82). Capelin shown in blue, sand lance shown in green, spring bottom-trawl survey shown in red.

Figure S2.2. Centre of gravity (x) and spatial variance (i.e., inertia; ellipse) from the spring multi-species bottom trawl from 1996-2015. Survey shown in red and a) capelin, b) sand lance, c) immature capelin, d) immature sand lance in blue. See all figures at:

<https://davorenlab.wixsite.com/research/single-post/scott-s-sandlancy-specs>

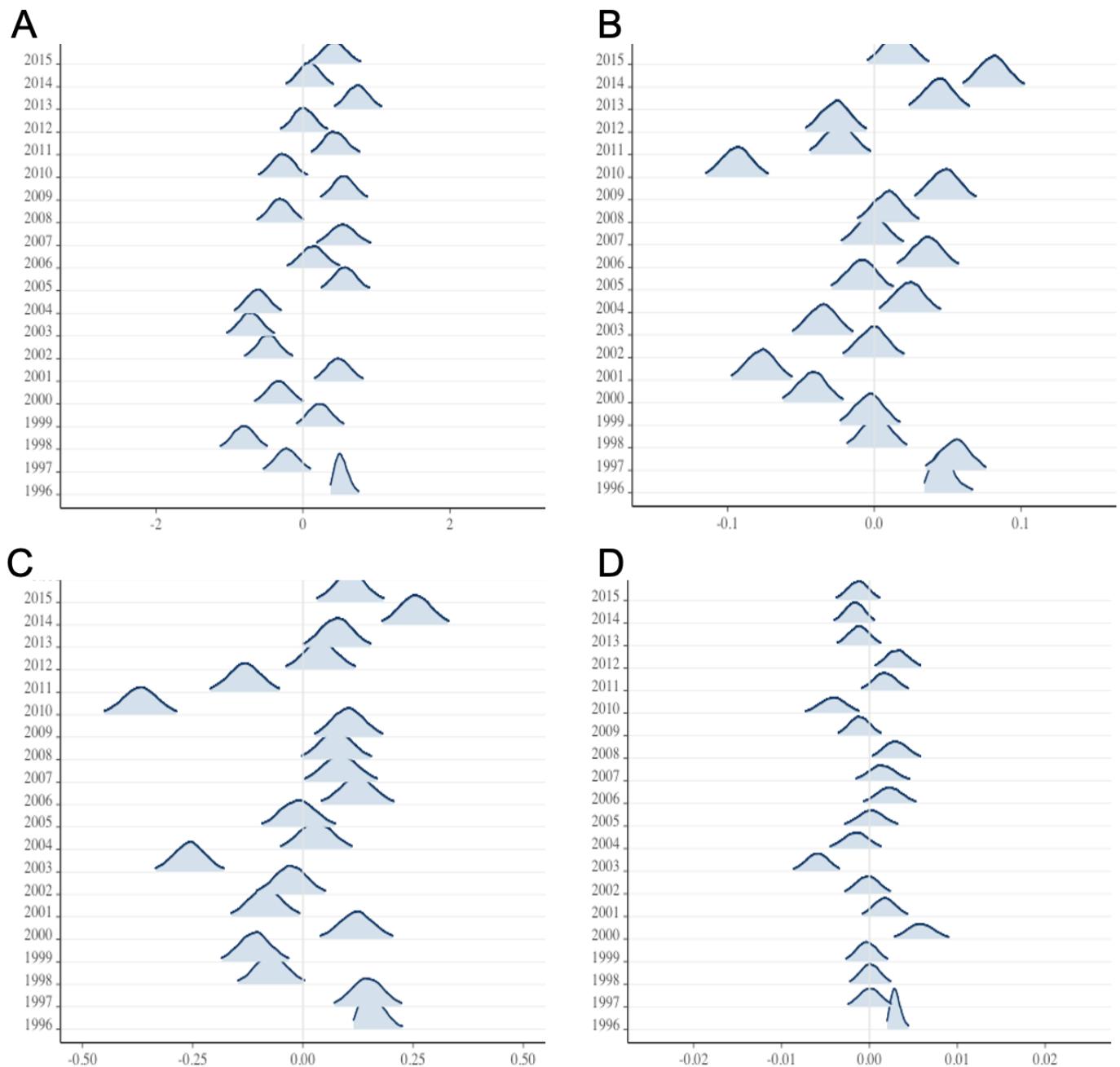


Figure S2.3. Capelin (full dataset) posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

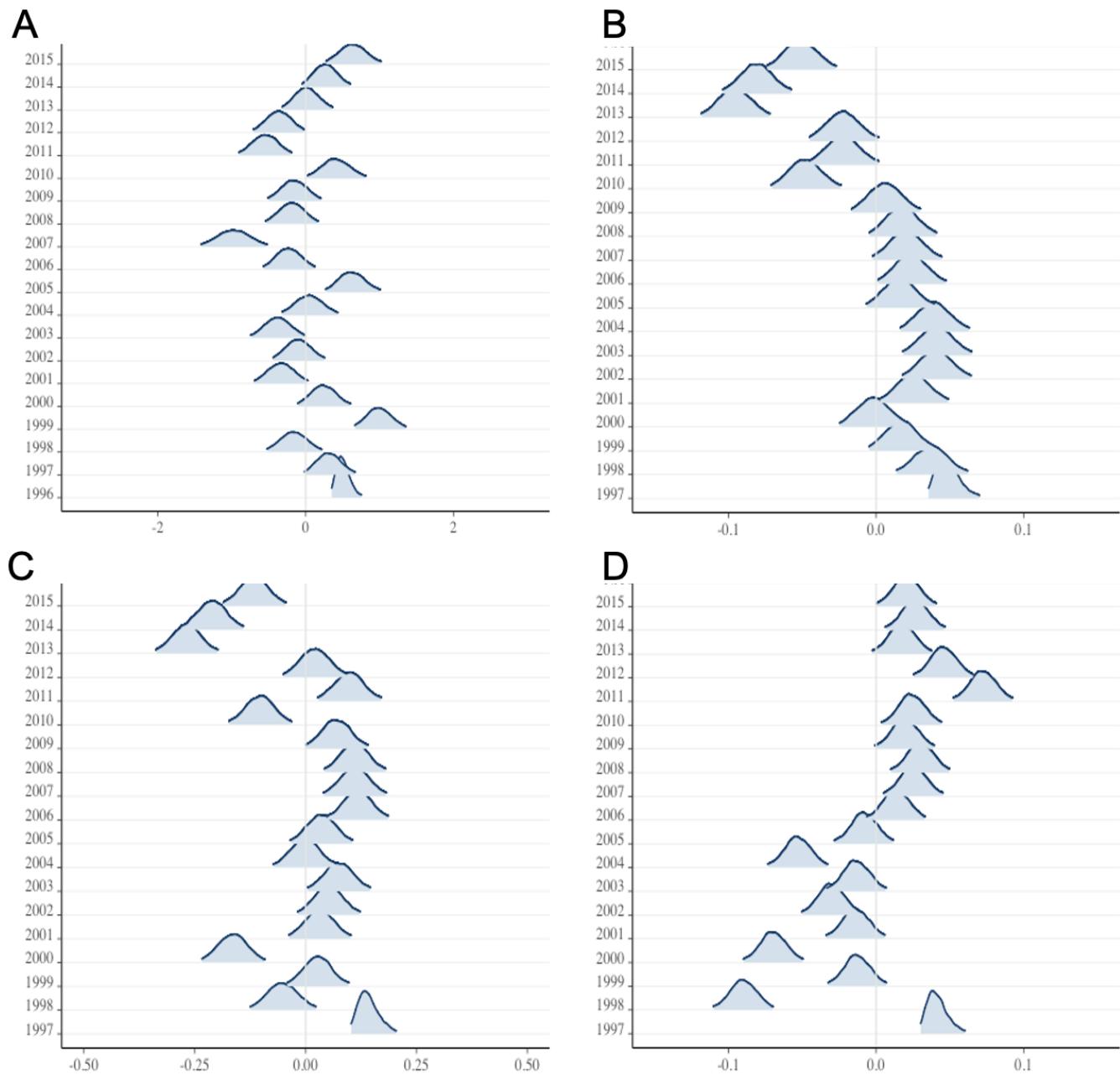


Figure S2.4. Sand lance (full dataset) posterior distributions of relative annual indices of a)

abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

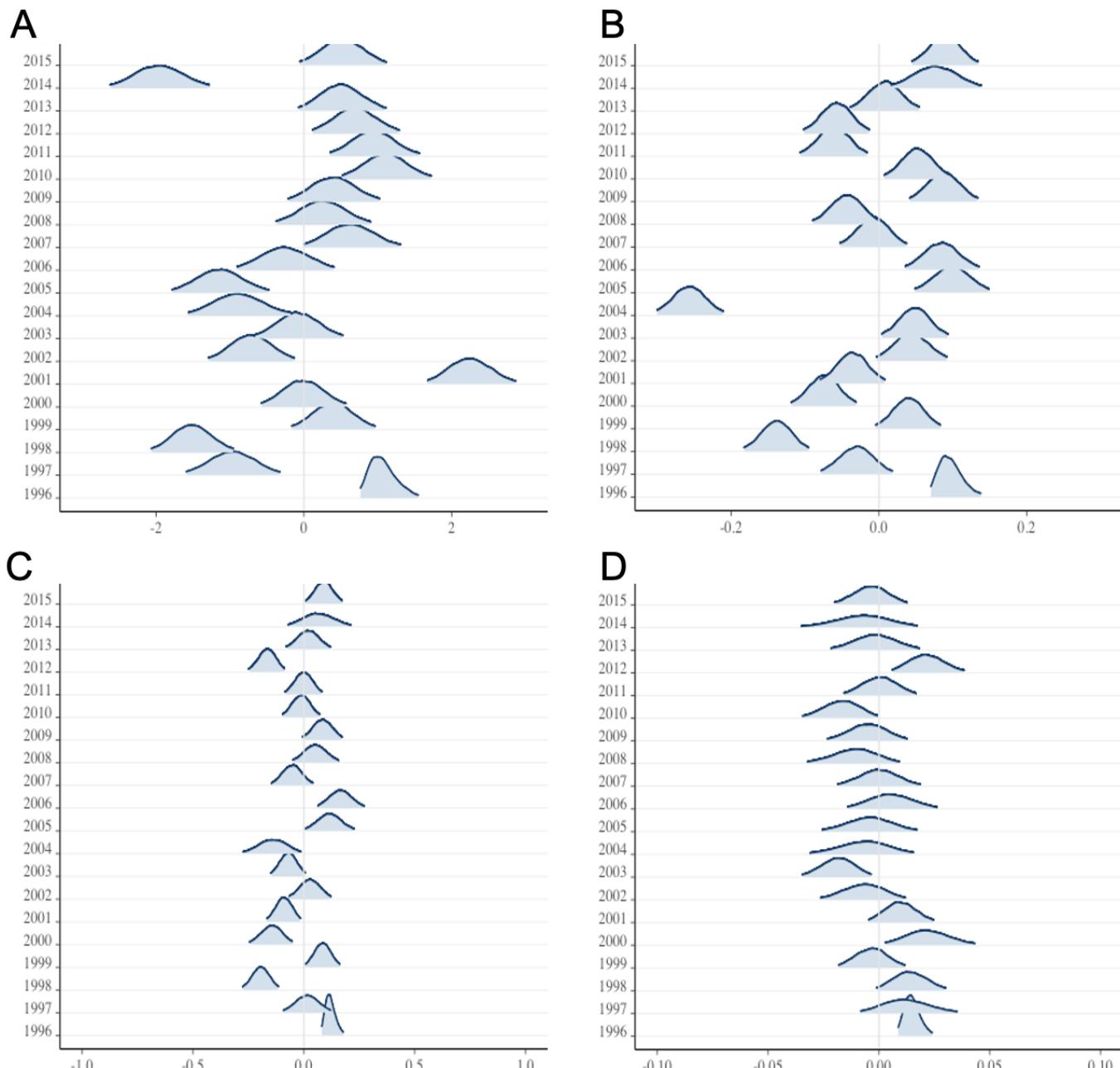


Figure S2.5. Immature capelin posterior distributions of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

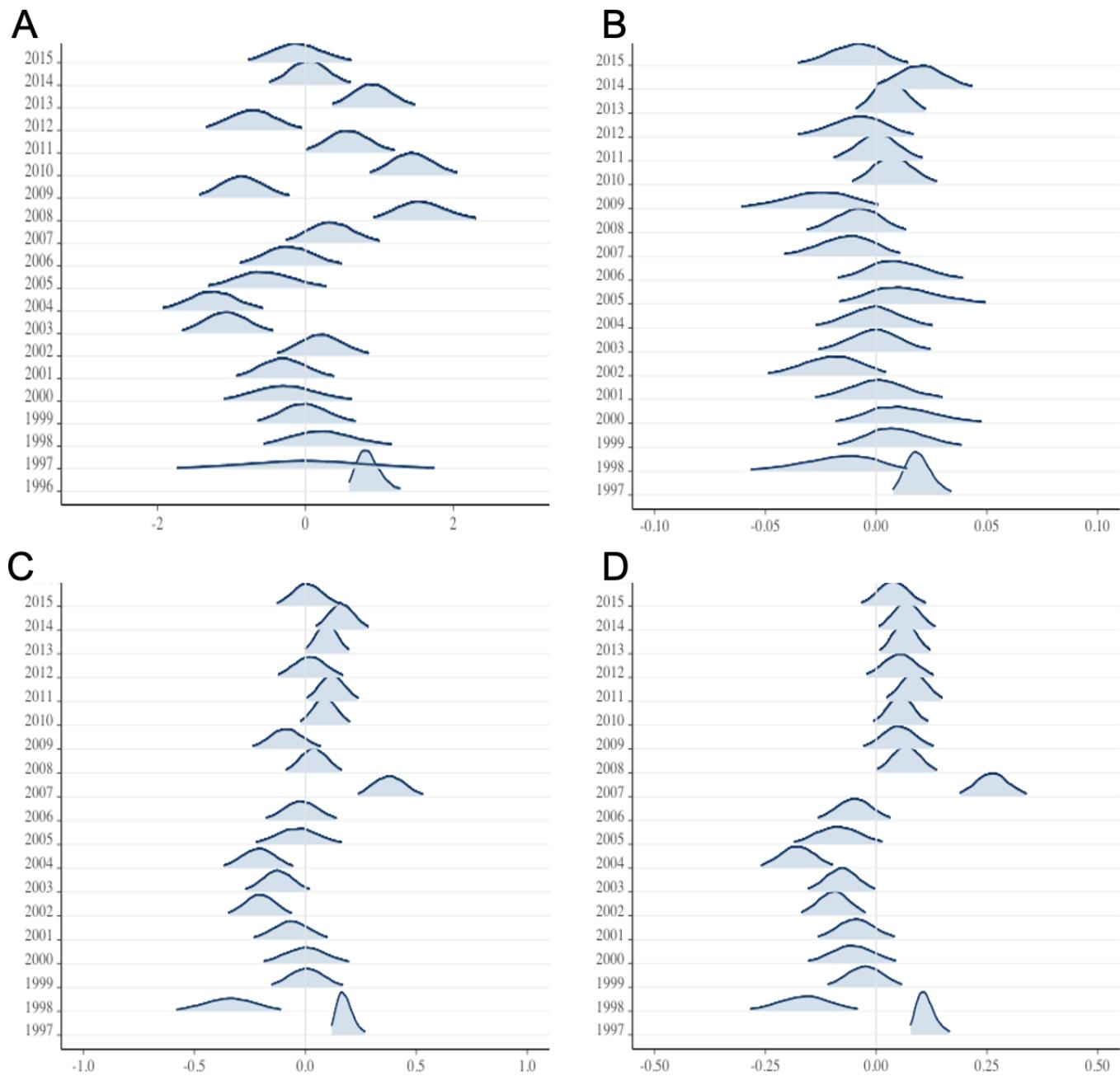


Figure S2.6. Immature sand lance posterior distributions of relative annual indices of a) abundance, b) length, c) mass, and d) condition. Relative annual indices were calculated using Bayesian generalized (abundance) and general (length, mass, and condition) linear mixed models.

## **Chapter Three. Habitat characterization and diel patterns of sand lance (*Ammodytes* spp) in coastal Newfoundland**

### **Abstract**

Non-spawning fish select habitat based on many abiotic and biotic factors. Although prey and predator densities are important biotic factors, many species also have specific abiotic habitat requirements. Sand lance (*Ammodytes* spp) lack a swim bladder and, thus, require sandy substrate for burrowing when not actively feeding to avoid predation and reduce energy expenditure. Although sand lance species in other regions show diel shifts in feeding in the water column and burrowing in seabed substrate, diel patterns for species in the Northwest Atlantic remain unknown. The objectives of this chapter were to investigate sand lance habitat characteristics and diel behaviour during July-August 2013-2021 on the northeast Newfoundland coast. Integrating camera surveys, sediment grabs, and hydroacoustics, I found sand lance were associated with 0.5-4 mm seabed grain sizes that were < 11°C (typically ~2°C). Acoustic sand lance biomass was higher during the morning and afternoon but decreased throughout the day and evening, while densities in sediment grabs simultaneously increased later in the afternoon and evening and buried fish more commonly had non-empty stomachs in the evening. These findings suggest that sand lance were feeding in the water column during the day and burrowed later in the day once stomachs were full. Diel patterns were size-dependent, with more smaller sand lance (<150 mm) caught in sediments throughout the day but primarily only larger sand lance (>150 mm) caught in sediments throughout the night. Findings suggest sand lance species in the Northwest Atlantic exhibit similar habitat requirements and diel patterns to those in other regions. Overall, this study provided a better understanding of *Ammodytes* distribution, abundance, density, biomass, diel behaviour and habitat selection in coastal Newfoundland.

## **Introduction**

Fish select habitat outside of the spawning season based on a number of abiotic and biotic factors. Prey availability and predation risk are among the most important biotic factors for habitat selection (Pyke et al. 1977; Fraser and Huntingford 1986; Gilliam and Fraser 1987; Hugie and Dill 1994). Indeed, fish may choose to forage in habitats with lower prey density to avoid predators or may limit the time spent foraging to increase vigilance to avoid predation when predators are present (Pyke et al. 1977; Fraser and Huntingford 1986). As ectothermic animals, temperature is among the most important abiotic factors for habitat selection, along with oxygen and salinity (Barkley et al. 1978, Perry and Smith 1994). Other physical features, including turbidity, depth (e.g. light), and seabed substrate may also be important as they tend to integrate with prey availability and predation risk (Winslade 1974a; Perry and Smith 1994; Ostrand et al. 2005; Freitas et al. 2016). Overall, the optimal habitat will be characterized by a suite of abiotic and biotic factors that combine to maximize fitness.

Fish of the genus *Ammodytes* have very specific habitat requirements. Most research on this genus is in the Northeast Atlantic Ocean on the lesser sandeel (*A. marinus*) and in the Northeastern Pacific Ocean on the Pacific sand lance (*A. personatus*). Sand lance are commonly found in cool (1-11°C), shallow (<40 m) and relatively clear water, possibly because they are visual foragers and, thus, require light while foraging (Winslade 1974a). As sand lance lack a swim bladder, individuals burrow into sandy substrate (0.25 – 2 mm; Scott 1968, Reay 1970, Wright et al. 2000, Ostrand et al. 2005) when not foraging for shorter parts of the day or longer seasonal periods (e.g. winter) to reduce energy expenditure and the risk of predation (Pinto et al. 1984). They burrow by diving headfirst into the sand and beating their tail to drive their body

into the sediment and, thus, have a specialized narrow skull adapted for burrowing in sandy substrates (Gidmark et al. 2011). As such, sand lance can only bury in a specific range of grain sizes, with larger fish burrowing in more coarse sand with larger grain sizes relative to smaller fish (Pinto et al. 1984; Wright et al. 2000; Holland et al. 2005). Overall, their distribution is typically associated with or near sandy substrate and they are typically absent in areas dominated by boulders or bedrock, as well as areas with high silt content (Ostrand et al. 2005; Holland et al. 2005; Haynes et al. 2007).

Sand lance exhibit diel behaviour, where they remain in schools and forage during the day throughout the water column, and remain burrowed in the sediment at night (Winslade 1974a; Hobson 1986; Freeman et al. 2004; Friedlaender et al. 2009). Diel vertical movement is a common behaviour exhibited in many aquatic organisms. Multiple hypotheses have been proposed to explain this behaviour, most notably the foraging hypothesis, where fish are known to follow the vertical movement of planktonic organisms toward the surface at night to minimize prey pursuit time (Clark and Levy 1988). Some fish feed on benthic organisms at night and display thermotaxis up to warmer waters during the day to aid in digestion (Bacheler et al. 2021). The predator-avoidance hypothesis, however, predicts that organisms choose feeding habitat while minimizing predation risk (Zaret and Suffern 1976; Fraser and Huntingford 1986). At night, sand lance appear to primarily seek refuge in sandy sediment presumably to avoid predation under lower efficiency foraging conditions for these visual foragers (Hobson 1986). However, sand lance are vulnerable while burrowing as predators aggregate near sand lance preferred sandy substrates as daylight abates and prey upon sand lance as they burrow (Hobson 1986; Temming et al. 2004). Overall, one hypothesis taken by itself is inadequate to explain these diel vertical movement patterns and a combination of hypotheses is required.

Similar to other forage species, sand lance are important in many marine systems as they are depredated by a wide variety of marine fishes, seabirds and mammals (Furness 1990; Springer and Speckman 1997). The tight link between sand lance abundance and sandy substrate habitats for burrowing likely provide predictable areas of high prey abundance for predators (Burger 1995). Not surprisingly, predators exhibit lower reproductive success in years of low sand lance availability (Harris and Wanless 1991; Furness and Tasker 2000; Rindorf et al. 2000). On the Newfoundland and Labrador Shelf, sand lance play an important role in the marine food web (Willison et al. 1999), where it is a key prey species for many breeding seabirds in coastal Newfoundland before capelin arrival in coastal areas to spawn (Burger and Piatt 1990) and are consistently found in the diet of fin-fish during the summer (Berard and Davoren 2020). The northern range of sand lance, though under documented, is thought to be 70°N, moving northward with warming temperatures (Winters and Dalley 1988; Staudinger et al. 2020). Despite this species' importance, little is known about the ecology of sand lance on the Newfoundland Shelf, including their distribution, abundance, density, biomass, diel behaviour and habitat selection (Winters 1970, 1981, 1983; Winters and Dalley 1988). In this region, two species of *Ammodytes* are present, *A. dubius* and *A. americanus*, and misclassification of the two species is common. The distribution of *A. dubius* is thought to be more offshore than *A. americanus*; however, *A. dubius* is occasionally found inshore in deeper and more open regions (Winters and Dalley 1988; Nizinski et al. 1990). Historically, meristic structures (e.g., vertebrae) have been used to distinguish between the two species, *A. americanus* tends to have a smaller maximum length (240 mm in fork length [FL]) and have fewer vertebrae (64-69) than *A. dubius* (372 mm FL, 71-78 vertebrae; Scott and Scott 1988; Nizinski et al. 1990). Both species are thought to be non-migratory and spawn in the winter (November-February), in locations they

occupy year-round (Winters and Dalley 1988; Robards et al. 1999b). Sand lance feed and grow in the summer months while predominantly consuming *Calanus finmarchicus*, and then cease feeding and begin gonad development in the fall (Suca et al. 2021).

### *Objectives*

The first objective of this chapter was to investigate sand lance habitat characteristics (i.e., depth, temperature, salinity, seabed grain size range) during July and August on the northeast coast of Newfoundland. I hypothesize that sand lance will be associated with shallow (<40 m), cool (1-11 °C), fine sandy substrate (0.25 – 2 mm), with a salinity of 32-34 ppt, similar to Pacific sand lance and the lesser sandeel (Reay 1970, Wright et al. 2000, Ostrand et al. 2005). The second objective was to investigate the diel behaviour of sand lance at a known area during July and August. I hypothesize that sand lance will be in the water column, presumably feeding, during the day and buried in the sediment at night, again similar to other regions (Winslade 1974b; Freeman et al. 2004; Holland et al. 2005). Overall, a better understanding of sand lance distribution, abundance, density, biomass, diel behaviour and habitat selection on the Newfoundland Shelf will increase our understanding of the ecology of this forage fish, thereby forming an important basis for studying interactions with predators.

### **Methods**

To characterize sand lance habitat on the northeast coast of Newfoundland, I investigated sand lance distribution and presence on a meso-scale in Notre Dame Bay, Newfoundland,

Canada (Fig. 3.1), during the non-spawning season (July-August, 2020-2021) using underwater camera drift surveys and sediment grabs. Additionally, I investigated the diel behaviour of sand lance during July-August, 2013-2021 at one area (i.e., Gull 3; Fig. 3.1) using hydroacoustic surveys (2013-2020) and sediment grabs (2013-2021) to estimate sand lance densities in the water column and burrowed in sediments, respectively, throughout the day. This area is a regularly monitored subtidal spawning area of capelin, where sand lance has consistently been present since 2013. Indeed, sand lance habitat has similar characteristics as subtidal capelin spawning habitat, including temperature (2 - 12°C), depth (15-40 m), and sediment size (0.5 - 16 mm; Penton and Davoren 2012; Crook et al. 2017). The data collected during the fine-scale diel study (2019-2021) were supplemented with archived data collected at this area during July-August, 2013-2018.

#### *Meso-scale Study: Distribution and Habitat Characterization*

We sampled seven inshore regions (Fig. 3.1) for sand lance from July 11-22, 2020 and three of these regions (AB, SB WB; Fig. 3.1) were sampled again from July 14-17, 2021. Region selection was based on nearby capelin spawning beaches with presumed suitable sediment characteristics along with foraging areas of tracked breeding seabirds (i.e., razorbills *Alca torda*, common murres *Uria aalge*) when primarily capturing sand lance to provision chicks (2016-2018; Gulka and Davoren 2019; Gulka et al. 2019). During 2020, within each region, two lines parallel to the coast were established ~300 m and 600 m from shore that covered the length of a sandy beach, or up to 1 km. Up to five sites, spaced 250 m apart, along each line were then visited to conduct camera drift surveys. During 2021, ten randomly generated sites within a

rectangle spanning the length of the beach and ~750 m from shore in each region were similarly visited.

During 2020 and 2021 at each site, latitude and longitude were recorded at the start and end of camera deployment using a handheld Global Positioning System (GPS) to later calculate the distance of each camera survey. During each camera survey, a metal frame with 2 GoPro cameras (Hero 7 black with underwater casing) attached, positioned away from each other and toward the seabed, was lowered to ~ 1 m off the seabed and the research vessel (~7 m) was allowed to drift for 5 min. The metal frame was dropped to the seabed every 1 min during the survey to disturb the sediment, with the aim to reveal buried sand lance. A Star-Oddi DST also was attached to the metal frame to record conductivity (salinity), temperature and depth near the seabed every 5 s throughout the camera survey. Sediment samples were collected using a Petite Ponar Grab (152 x 152 mm, 2.4 L) at the centre point of each line (~300 m/600 m from shore) per region during 2020, and both sediment samples were retained for grain size analysis. During 2021, sediment grabs were performed at all sites prior to each camera drift survey and four sediment samples were retained from each region for grain size analysis. An additional site was opportunistically sampled during 2020, which included a camera drift survey and a sediment grab, as an aggregation of sand lance predators (e.g., seabirds) was observed. In addition to the seven and three inshore regions sampled during 2020 and 2021, respectively, sediment was also sampled from four regularly monitored subtidal capelin spawning areas in 2020 for sand lance presence/absence and grain size analysis. All sampling and surveys were only undertaken when sea conditions were favorable (e.g., low swell and wave height).

During 2020, I further explored the importance of sediment characteristics to sand lance presence/absence and density (i.e., number of sand lance per sediment grab) by conducting

sediment grabs and camera drift surveys at one spawning area with suitable sediment characteristics of sand lance (Gull 3; Fig. 3.1) and another area < 1 km away with less suitable sediment characteristics (Gull 2; Fig. 3.1) where most other variables (i.e., temperature, salinity, depth) were similar (Penton and Davoren 2012; Crook et al. 2017). Both areas were regularly monitored subtidal spawning areas of capelin. Four replicate camera drift surveys (described above) were performed at each area per day on six days from July 23 – August 15, 2020. Site locations were based on locations where sediment was previously sampled successfully and to maximize the area surveyed. Given the depths of these areas (25-40 m), the metal frame with the camera array was modified to be heavier, whereby three ~ 1 m ropes, each with 12 x 227 g lead weights, were attached to the metal frame to drag along the seabed while drifting. This modification also provided a greater surface area of disturbed sediment to reveal buried sand lance. Latitude and longitude were recorded at the start and end of each camera survey and depth, salinity, and temperature were recorded every 5 s near the seabed throughout each survey with a Star-Oddi DST CTD. Additionally, 10 sediment grabs that successfully collected sediment were performed at each of the two areas on nine days using a Ponar sediment grab (229 x 229 mm, 8.2 L) from July 16 – August 17, 2020, during the diel study (see below). These data were supplemented with archived sediment grab data at both areas during July-August, 2013-2019 and 2021. Again, surveys were only undertaken when sea conditions were favorable (e.g., low swell and wave height).

#### *Grain size analysis*

Sediment samples were processed using a dry sieving technique. First, sediment was dried in an oven for 2 h at 300°C, stirred every 15 min, and then poured onto a stack of 6 sieve mesh sizes (in mm; 0.063, 0.125, 0.25, 0.5, 2.0, 4.0) and agitated for 5 min. After agitation, the mass that each grain size fraction contributed to the total sample was measured using a Pesola® scale (2500 g). This resulted in six grain size categories: (in mm;  $\leq 0.063$ ,  $\geq 0.125 - < 0.25$ ,  $\geq 0.25 - < 0.5$ ,  $\geq 0.5 - < 2$ ,  $\geq 2 - < 4$ ,  $\geq 4$ ), which hereafter are referred to as the minimum mesh size (e.g.,  $\geq 0.125 - < 0.25 = \geq 0.125$ ). The proportions of each size fraction were calculated per sample and mean grain size and grain size standard error were quantified using the Microsoft Excel spreadsheet package GRADISTAT (Blott and Pye 2001).

#### *Statistical analysis*

The meso-scale dataset consisted of habitat characteristics (i.e., bottom temperature, depth, mean grain size, grain size standard error, proportion of each grain size) at each sediment grab sample site within each region/area on each day. Habitat characteristics were examined for normality using histograms, quantile-quantile plots and Shapiro-Wilk tests. A principal component analysis (PCA) was used to combine all habitat characteristics into a smaller set of uncorrelated variables that simultaneously characterized the habitat where sand lance was present. Statistical analyses were performed using JMP (Version 15.2). Components were orthogonally rotated (Quartimax) to increase correlations of response variables with the newly derived variables to increase interpretation (Quinn and Keough 2002).

#### *Fine-scale: Diel Behaviour*

To assess diel behaviour of sand lance, I focused research at one regularly monitored subtidal capelin spawning area ( $37.5 \pm 3.3$  m depth; Penton and Davoren 2012) located in a bathymetric depression during July-August, 2019-2021, where sand lance had been present annually in the sediment (i.e., Gull 3; Fig. 3.1) since 2013. Acoustic biomass in the water column was assessed through hydroacoustic surveys, while sediment grabs (Ponar sediment grab: 229 x 229 mm, 8.2 L) estimated sand lance densities in the sediment. During 2019 and 2020, hydroacoustic surveys were performed at different times of the day to assess diel variation in sand lance biomass in the water column (Table 3.1). During 2019 only, hydroacoustic surveys were targeted during three periods: daylight (<20:00), nautical twilight (21:30-22:30) and dark (>22:30; Table 3.1), on six days from July 12 – August 14 (Table 3.1). In 2019-2021, 10 sediment grabs that successfully collected sediment were performed at our fine-scale area (Gull 3; Fig. 3.1) from a 13.4 m commercial fishing vessel (*Lady Easton III*) as well as from a small boat (7 m; 2020 only). Sand lance caught in sediment grabs were counted and frozen immediately. In the lab, total length (snout to tip of tail, mm) and stomach fullness (empty, not empty) were recorded. This dataset was supplemented with archived data from July-August, 2013-2018 from the same hydroacoustic survey (0-5/yr) and sediment grabs (1-3 grabs/day, 3-6 days/yr), which were primarily conducted during early afternoon to evening (Table 3.1).

Following methods outlined in Davoren et al. (2006), acoustic biomass ( $s_a$ , area backscattering coefficient,  $m^2 m^{-2}$ ), as a proxy for sand lance biomass, was quantified during hydroacoustic surveys from a 13.4 m commercial fishing vessel. The ~1200 m survey included ~600 m across the sandy substrate area with an additional 300 m on either side of the area, where the seabed rises 5-10 m onto bedrock. During each survey, a BioSonics DTX 6000 (BioSonics Inc., Seattle, Washington, USA) scientific echosounding system with a transducer (70 kHz split-

beam) was towed at ~1 m below the surface of the water. Echoview software (Version 4, SonarData, Myriax Software Pty. Ltd., Hobart, Tasmania) was used to omit acoustic signals indistinguishable from the seafloor. Additionally, raw high-resolution hydroacoustic data ( $s_v$ , volume backscattering coefficient) was examined and acoustic signals with  $s_v > -60$  dB were omitted as they are likely due to fish with higher target strengths (e.g., capelin) compared to sand lance at the surveyed depth range (0-40 m), based on previously published target strength estimates of sandeels (-68.9 to -72.9 dB; Mackinson et al. 2005). Acoustic biomass was quantified using a minimum threshold of raw high-resolution hydroacoustic data ( $s_v$ , volume backscattering coefficient) of -80 dB in each 100 m segment along each survey, which was then averaged over all 100 m segments to estimate the mean acoustic biomass due to sand lance in the water column per survey.

#### *Statistical analysis*

Continuous response variables (i.e., acoustic biomass, number of sand lance per sediment grab, total fish length) were examined for normality using histograms, quantile-quantile plots and Shapiro-Wilk tests. A general linear mixed model was used to test whether acoustic biomass varied with time of day between 0900-2300 h, where time of day was a continuous fixed predictor variable and year and date were categorical random variables to account for repeated surveys within a day (2019 only) and year. As sediment grabs were performed throughout the diel cycle, a Rayleigh test for uniformity was used to test if the number of sand lance per sediment grab, total fish length, fish presence (i.e., proportion of bottom grabs where sand lance were present per hour), and stomach fullness (i.e., proportion of sand lance with non-empty

stomachs per hour) were concentrated in a particular part of the diel cycle. Statistical analyses were performed using the *lme4* and *circular* packages in R (Version 3.6.2) and analyses were considered statistically significant at  $P < 0.05$ .

## Results

### *Meso-scale Study: Habitat Characterization*

A total of 60 camera drift surveys were conducted at the seven inshore regions during 2020 ( $n=2-10/\text{region}$ ), with another 30 camera surveys conducted at three of these inshore regions again during 2021 ( $n=10/\text{region}$ ). Additionally, another 48 camera surveys were conducted during 2020 at the two subtidal spawning areas of capelin (Gull 3:  $n=26$ ; Gull 2:  $n=22$ ; Table 3.1). During 2020, sand lance were observed twice during camera surveys at only one area (Gull 3; Fig. 3.1) either schooling ( $n=1$  survey) or buried in the sediments ( $n = 1$  survey). Sediment samples were collected from a total of seven regions (1-8 samples/region) during 2020, with three regions resampled during 2021, along with four subtidal capelin spawning areas ( $n=4$  samples/area), and one adaptive site (i.e., sand lance predators present;  $n=1$ ; Fig. 3.1) in 2020. Sand lance was only sampled in sediments at one area (Gull 3; Fig. 3.1) in both years. The PCA including all habitat characteristics had three principal components with eigenvalues  $> 1$ , explaining a total of 78.4% of the variation (PC1: 44.8%; PC2: 19.7%; PC3: 13.9%). The habitat characteristics with the highest positive loadings on PC1 were depth (0.8406), proportion of  $\geq 2$  mm grain size (0.7180), and grain size standard error (0.7003), while the highest negative loadings were temperature (-0.8500), proportion of  $\geq 0.25$  mm grain size (-0.7192), and proportion of  $\geq 0.125$  mm grain size (-0.6698; Fig. 3.2). The habitat characteristics with the

highest positive loadings on PC2 were the proportion of  $\geq 4$  mm grain size (0.7338) and mean grain size (0.6759), while the highest negative loading was the proportion of  $\geq 0.5$  mm grain size (-0.8418; Fig. 3.2). PC3 was not further explored, as it represented a high proportion of  $\leq 0.063$  mm grain size (0.8278), which is unsuitable sand lance habitat. Overall, sand lance was only present at one deeper, cooler area with a high proportion of 0.5 - 2 mm grain size (Figs. 3.2, 3.3, S3.1).

From July-August 2013-2021, a total of 532 sediment grabs successfully collected sediment at our fine-scale area (Gull 3; n=405) and our comparison area (Gull 2; n=127; Table 3.1), which were  $< 1$  km part. A total of 229 sand lance (56 – 209 mm;  $149 \pm 1.8$  mm) were collected from these two areas, only four of which were collected at Gull 2 over the nine years (Table 3.1). Sediment grain size composition sampled during 2020 was the main difference in habitat characteristics at these two areas, while other characteristics were similar, although Gull 3 was slightly deeper ( $41 \pm 0.7$  m) and cooler ( $2.1 \pm 0.2^\circ\text{C}$ ) than the other area (Gull 2:  $24 \pm 1.1$  m,  $6.0 \pm 0.8^\circ\text{C}$ ).

#### *Fine-scale: Diel Behaviour*

At our fine-scale area (Gull 3) from 2013-2021, acoustic biomass in the water column tended to decrease from 0900 to 2300 h (Fig. 3.4), but this relationship was not significant (linear mixed effect model,  $t_{28} = -1.8$ ,  $p = 0.07$ ). In contrast, sand lance were more commonly present in sediments in the evening (circular mean time: 20.5 h after midnight; circular variance: 0.02; Rayleigh test:  $p < 0.0001$ ; Fig. 3.5). Similarly, the number of sand lance in sediment grabs also showed a significant departure from uniformity, whereby a higher number was observed during

the evening (circular mean time: 19.2 h after midnight; circular variance 0.62; Rayleigh test  $p < 0.0001$ ; Fig. 3.6). Sand lance length also showed a significant departure from uniformity, with a higher number of smaller sand lance (100-150 mm) caught in sediment grabs during the evening (circular mean time: 19.7 h after midnight; circular variance: 0.53; Rayleigh test:  $p < 0.0001$ ; Fig. 3.7), during which time non-empty stomachs were more common (circular mean time: 19.2 h after midnight; circular variance: 0.03; Rayleigh test:  $p < 0.0001$ ; Fig. 3.8).

## Discussion

Sand lance was only present at one area where sediment grain size primarily ranged between 0.5 – 4 mm and temperatures were  $\sim 2^\circ\text{C}$ , which reflects similar preferred sediment size ranges (0.25-2 mm) and temperatures (1-11°C) published for Pacific sand lance (Ostrand et al. 2005; Robinson et al. 2013) and lesser sandeels (Reay 1970; Wright et al. 2000; Holland et al. 2005). Owing to their burrowing behaviour, studies have reported that suitable sediment is the primary habitat characteristic determining sand lance presence (Wright et al. 2000; Holland et al. 2005; van der Kooij et al. 2008). Indeed, sand lance appear to avoid sediments containing  $> 10\%$  silt ( $< 0.063$  mm; Reay 1970; Wright et al. 2000; Holland et al. 2005), as fine particles may clog their gills, inhibiting respiration (Meyer et al. 1979; Pinto et al. 1984). Sand lance also appear to avoid sediments containing large grain sizes ( $> 16$  mm), as they are unable to successfully burrow (Wright et al. 2000; Holland et al. 2005; Haynes et al. 2007). In support, sand lance in this study were absent from regions with unsuitable sediment, either primarily  $> 4$  mm (Gull 2, Turr) or  $< 0.5$  mm (CFB, DB, LB, SB, WB). It is possible that sand lance may have been present at these regions, or others with more suitable sediment (AB, CC, MS), but not detected on our camera

drift surveys or in sediment grabs, as most sampling was performed during the day when sand lance appear to be feeding up in the water column (see below). Alternately, Haynes et al. (2007) found that grain size heterogeneity within suitable ranges (0.25-8 mm), was an important sediment characteristic influencing sand lance presence and density. As larger sand lance (>65 mm TL) are able to burrow in coarser sand (0.5-16 mm) than smaller sand lance (<65 mm TL in 0.125-1 mm; Wright et al. 2000; Holland et al. 2005), which may be linked to greater oxygen availability and requirements of larger fish (Holland et al. 2005), grain size heterogeneity may have allowed the wide size range of fish (56 - 205 mm) to bury in the sediment at our fine-scale area.

Temperature also appeared to influence sand lance presence in this study, as evidenced by being absent from regions with primarily suitable sediment (0.5 - 2 mm) but temperatures > 11°C (12.3 – 13.5 °C at AB, CC). In support, bottom temperature in areas of suitable sediment best explained *Ammodytes* distribution and abundance in the northeast Atlantic, rather than zooplankton abundance (van der Kooij et al. 2008). In contrast, although temperature positively influences growth within regions, *A. hexapterus* grew faster and were more abundant in cooler (7.9 - 9.7 °C), more productive regions relative to warmer (10.1 - 12.0 °C; Robards et al. 2002), less productive regions. This study suggests that prey availability and temperature are likely linked during habitat selection. Indeed, fish generally appear to occupy warmer regions when there is high zooplankton (food) abundance to increase growth but may avoid warmer regions with low zooplankton abundance to reduce the risk of starvation (Crowder and Magnuson 1983). Although the optimal temperature range of sand lance is unknown, habitat selection within the published temperature range likely results from a trade-off between high growth and starvation risk.

Acoustic biomass was higher in the water column during the morning and afternoon but declined throughout the day until 2300. Concurrently, the density of sand lance burrowed in sediments increased later in the afternoon and evening and buried fish more commonly had non-empty stomachs in the evening. These findings suggest that sand lance were feeding in the water column during the day and burrowed later in the day once stomachs were full, similar to diel patterns previously shown for Pacific sand lance and the lesser sandeel (Winslade 1974b; Hobson 1986; Friedlaender et al. 2009). Diel vertical movement patterns are common in other small pelagic fish (e.g., Hays 2003; Davoren et al. 2006) and are thought to be driven by a trade-off between foraging (Clark and Levy 1988) and predator avoidance (Pinto et al. 1984), along with other factors (e.g. thermotaxis; Bacheler et al. 2021). For instance, capelin in the study region exhibit diel vertical movements, wherein fish remain in cold ( $<0^{\circ}\text{C}$ ), deep ( $>240\text{ m}$ ) water during daylight and move into warmer surface waters to feed at night, presumably to follow vertical movements of their prey (Record and Young 2006), while avoiding predation by air-breathing, visual predators (Davoren et al. 2006). In this study, sand lance may forage up in the water column during the day in shallow waters ( $< 50\text{ m}$ ) because they are visual foragers and, thus, require light to forage efficiently (Winslade 1971; Winslade 1974a). Although occupying shallow water during the day may increase the risk of predation from visual, air-breathing predators (e.g., seabirds, marine mammals), this risk is likely minimized by forming schools (Magurran 1990; Pavlov and Kasumyan 2000; Hoare et al. 2000). Predation risk may instead be highest for individuals as they break off from schools to burrow in the sediments, as predators appear to aggregate near preferred sandy substrates of sand lance as daylight abates and prey upon sand lance (Hobson 1986; Temming et al. 2004). Friedlander et al (2009) found the highest biomass of sand lance in the water column between 0300 – 0500 h, which may suggest sand

lance also feed during this time, under limited light, to avoid visual predators. Future research will be required to further examine the relative importance of foraging and predator avoidance throughout the diel cycle to determine the primary mechanisms underlying sand lance diel behaviour.

Diel patterns appeared to be size-dependent in this study. Indeed, a higher number of smaller sand lance (<150 mm) were caught in the sediments throughout the day but primarily only larger sand lance (>150 mm) were caught in sediments throughout the night. Night sampling (0000-0800 h), however, primarily occurred during 2021 and, thus, the larger fish size at night may indicate a potential year effect. Indeed, sand lance caught during 2021 were on average 21 mm longer than fish caught across the nine-year study period (Fig. S3.2). Unfortunately, few sand lance were caught at other times of day during 2021 and, thus, it is difficult to determine if fish were just larger during 2021. Alternately, fish size has been found to modify the trade-off between predation risk and foraging (Busch and Mehner 2012) and, thus, size-dependent variation in diel behaviour has been shown in freshwater fishes (e.g., *Coregonid* spp, Busch and Mehner 2012; *Salvelinus confluentus*, Gutowsky et al. 2013), as well as marine species (e.g., *Scolopsis bilineatus*, Boaden and Kingsford 2012; *Lutjanus campechanus*, Bacheler et al. 2021). Additionally, there is some evidence from other studies that diel behaviour in *Ammodytes* may be size-dependent and follow a pattern similar to our findings. For instance, Bizzarro et al. (2016) found smaller fish (65-123 mm in total length [TL]) burrow more during the day, while larger fish (> 123 mm TL) may follow the typical pattern of primarily burrowing at night. In this study, smaller sized fish (<150 mm) may limit time spent in the water column during the day relative to larger fish (>150 mm) to avoid abundant air-breathing predators. Although fish typically school with other fish of similar size (Magurran 1990; Hoare et al. 2000),

body size-segregation in fish schools occurs, possibly due to differential size-dependent swim speeds (Hoare et al. 2000). As smaller sand lance tend to be located on the periphery of school, with the larger sand lance occupying the centre of the school (Meyer et al. 1979), smaller sand lance may have a higher predation risk while schooling during the day. Therefore, this pattern of smaller sand lance burrowing more during the day may be an adaptive trade-off between predation risk and foraging during periods of daylight.

In conclusion, sand lance preferred sediment with a mixture of grain sizes between 0.5 – 4 mm within a temperature range of ~2°C, which was similar to other species of *Ammodytes* in other regions (Reay 1970; Wright et al. 2000; Holland et al. 2005; van der Kooij et al. 2008). Although I successfully detected sand lance using sediment grabs and camera surveys, I recommend combining these techniques with others, such as sampling environmental DNA (eDNA) in sediments, to enhance detection probability of sand lance especially when sampling during the day (Berger et al. 2020; Staudinger et al. 2020; Ratcliffe et al. 2021). Sand lance appeared to feed in the water column during the day, and then burrow in sandy sediments at night again similar to *Ammodytes* in other regions (Winslade 1974a; Hobson 1986; Friedlaender et al. 2009), possibly to maximize foraging efficiency while minimizing predation risk. The total length of sand lance caught in this study ranged between 56-209 mm and, thus, never ranged above the maximum reported fork length of *A. americanus* (240 mm; Scott and Scott 1988). As *A. americanus* is reported to have more of an inshore distribution (Scott 1968, 1972; Winters 1970; Winters and Dalley 1988), we suggest that we primarily collected *A. americanus*, but we cannot rule out the inclusion of smaller/younger individuals of *A. dubius*. Further research examining morphometrics/meristics (Winters 1970; Winters and Dalley 1988; Nizinski et al. 1990) along with eDNA and DNA sequencing will help distinguish between species of this

genus (Berger et al. 2020; Ratcliffe et al. 2021). *Ammodytes* are integral in many ecosystems as they transfer energy from lower to higher trophic levels. This study contributes to the growing body of literature of northwest Atlantic sand lance (Staudinger et al. 2020), but more research is needed. In particular, a better understanding of *Ammodytes* distribution, abundance, density, biomass, diel behaviour and habitat selection in coastal Newfoundland will help form a basis to study interactions with predators.

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## Tables and Figures

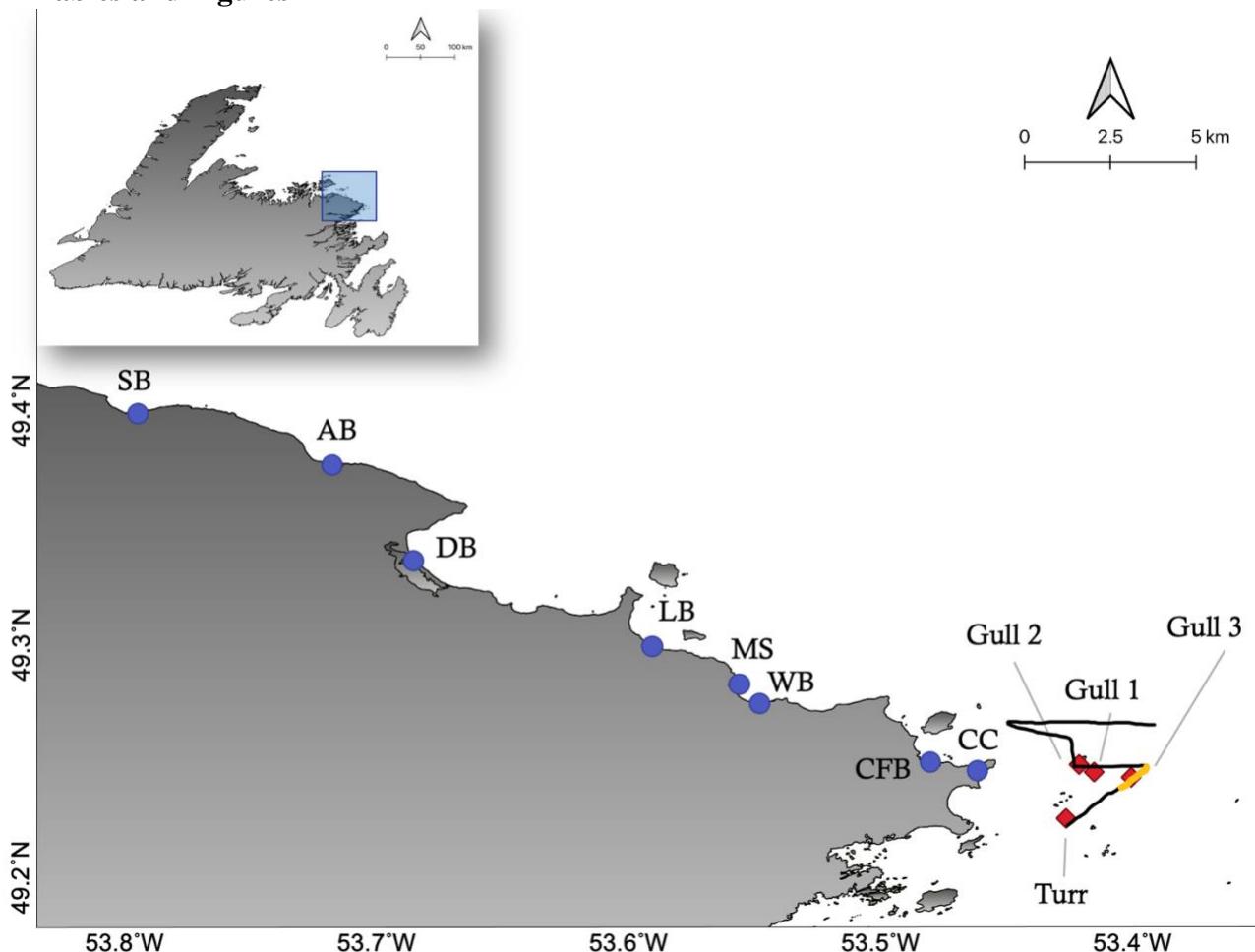


Figure 3.1. Map of Newfoundland, Canada, indicating capelin spawning beaches (blue circles) and subtidal spawning areas (red diamonds) where camera drift surveys, sediment grabs, and hydroacoustic surveys (line) were conducted. Hydroacoustic surveys were only examined where sand lance were continually present (Gull 3; yellow line). See Figure 3.3 for habitat characteristics for each region.

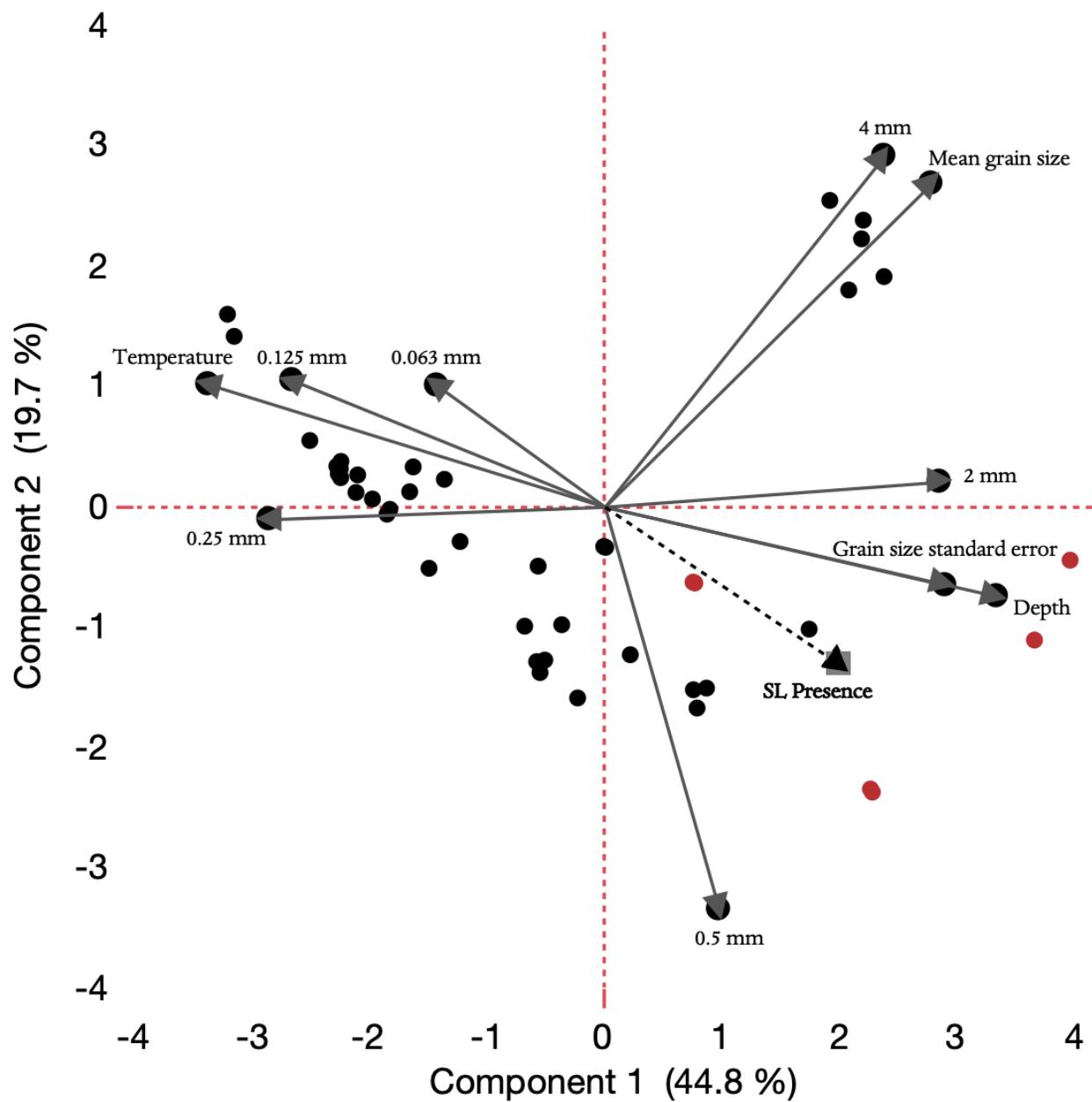


Figure 3.2. Principal component analysis showing values of PC1 and PC2 along with eigenvectors for the ten habitat characteristics (temperature, mean grain size, grain size standard error, depth, proportion of each grain size category), with sites where sand lance were present indicated in red.

Site	AB	CC	CFB	DB	LB	MS	SB	WB	Turr	Gull 1	Gull 2	Gull3
Temperature (°C)	13±0.7	13±0.5	14	13±0.2	9±0.25	8.3±0.75	13±0.4	9.6±1.6	6.0±0.6	3.6±1.4	6.0±0.8	2.1±0.2
Depth (m)	7.6±0.8	8.0±1.0	4	6.0±1.0	6.5±1.5	7.5±2.5	7.7±0.9	6.0±1.1	17±0.9	34±0.8	24±1.1	41±0.7
n	6	1	1	2	2	1	5	6	4	4	4	4

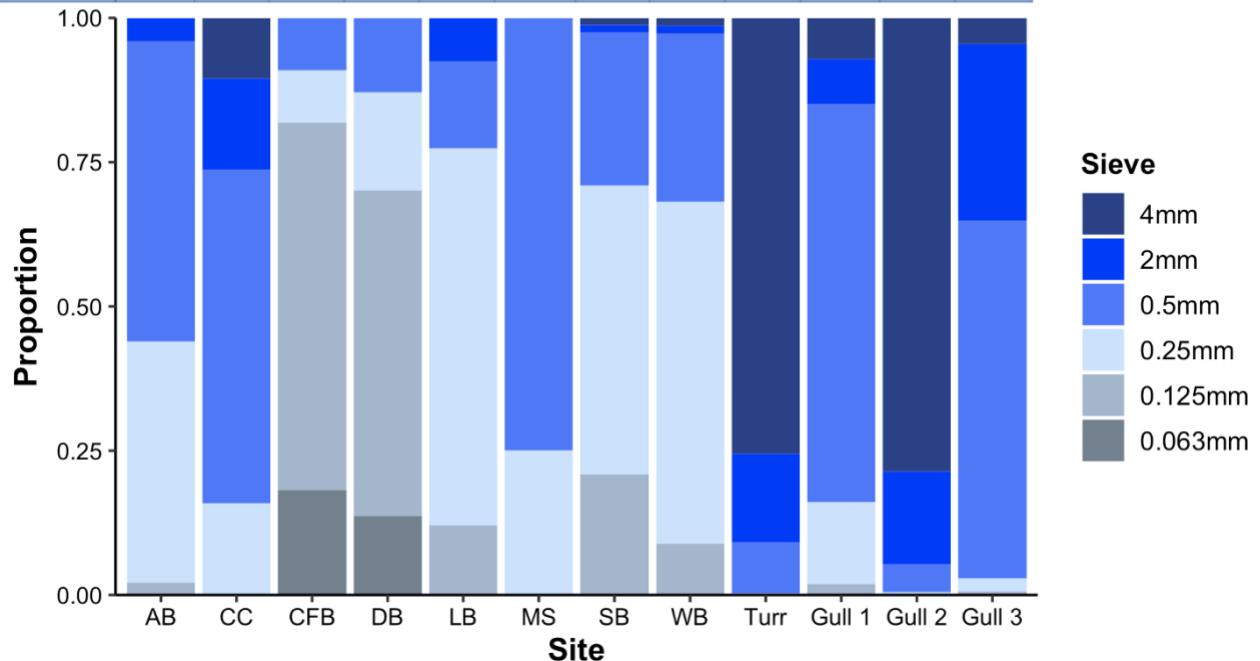


Figure 3.3. Mean proportions of different grain size ranges of 7 coastal regions plus one adaptive site (CFB), along with four subtidal capelin spawning areas (Turr, Gull 1, Gull 2, Gull 3).

Region-specific mean  $\pm$  SE temperature (°C), depth (m), and sample size (n) are also indicated.

All regions were sampled during July-August, 2020, while only AB, SB, and WB were sampled again during July-August, 2021. See Figure 3.1 for locations of each region.

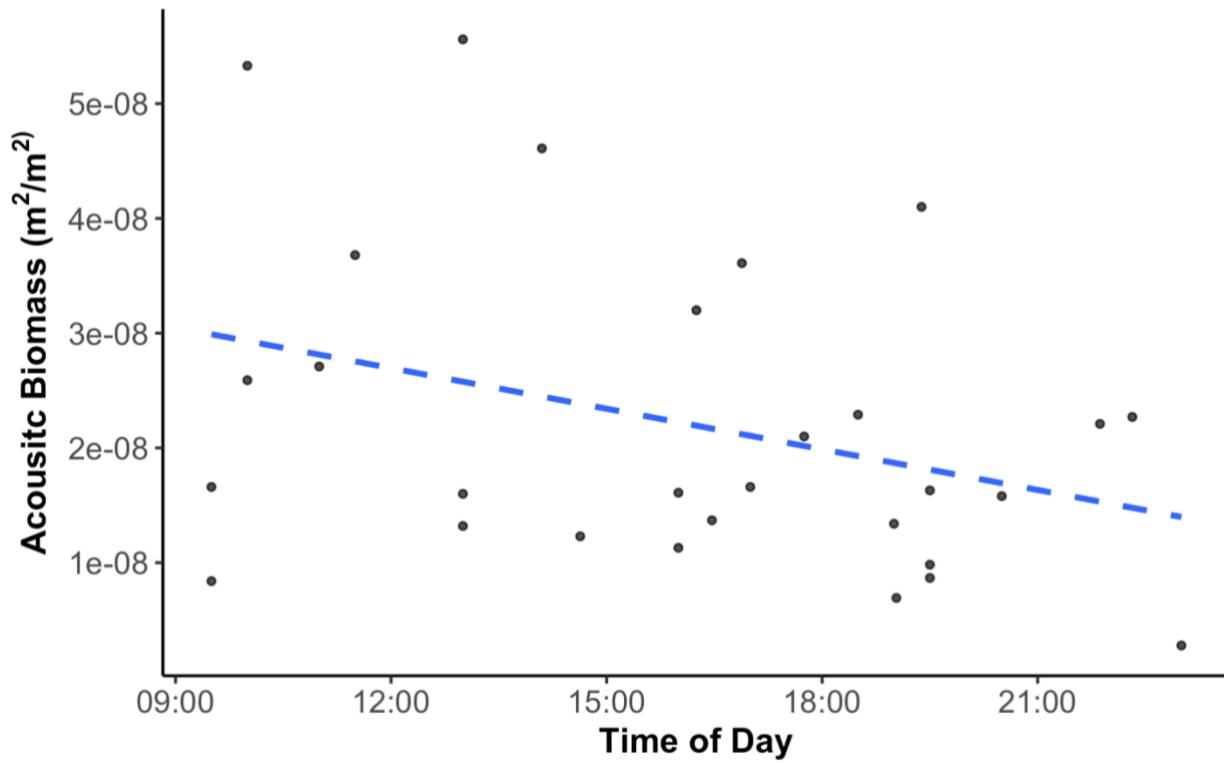


Figure 3.4. Acoustic biomass ( $\text{m}^2/\text{m}^2$ ) of sand lance in the water column ( $y = 4.1\text{e}^{-8} - 3.3\text{e}^{-13}x$ ,  $r^2 = 0.12$ ) throughout the day during July-August, 2013-2020.

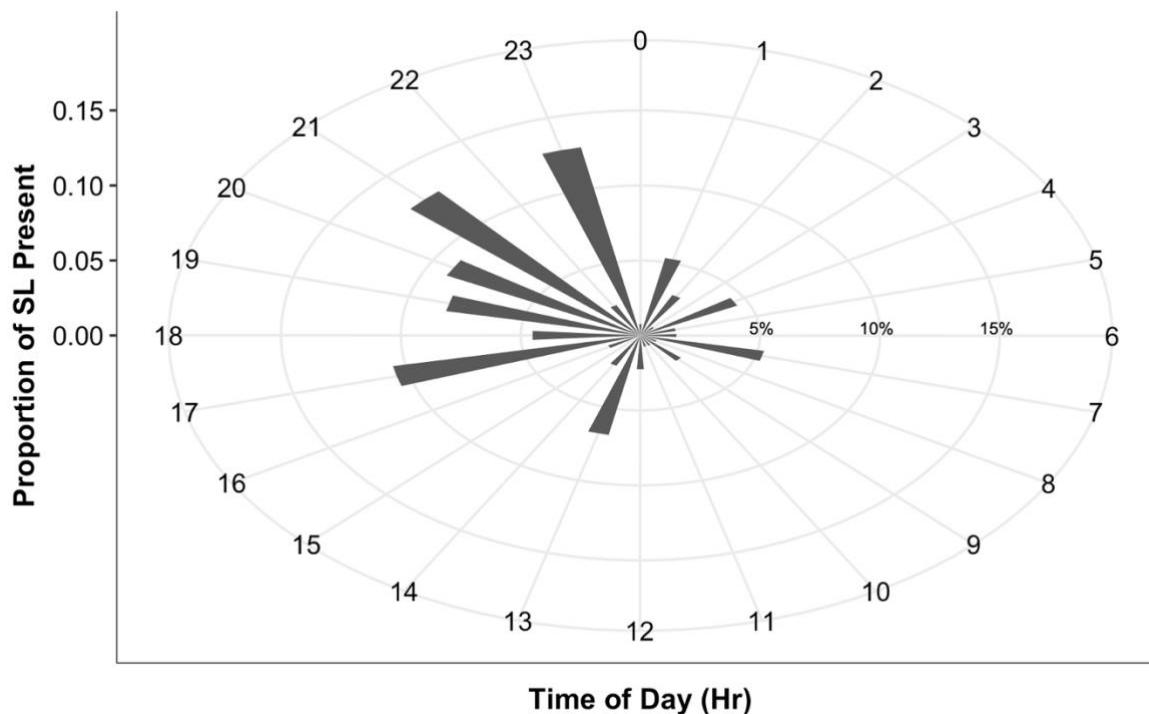


Figure 3.5. Proportion of bottom grabs with sand lance present per hour throughout the day from July-August 2013-2021 (circular mean time: 20.5 h after midnight; circular variance: 0.02, Rayleigh test:  $p < 0.0001$ ).

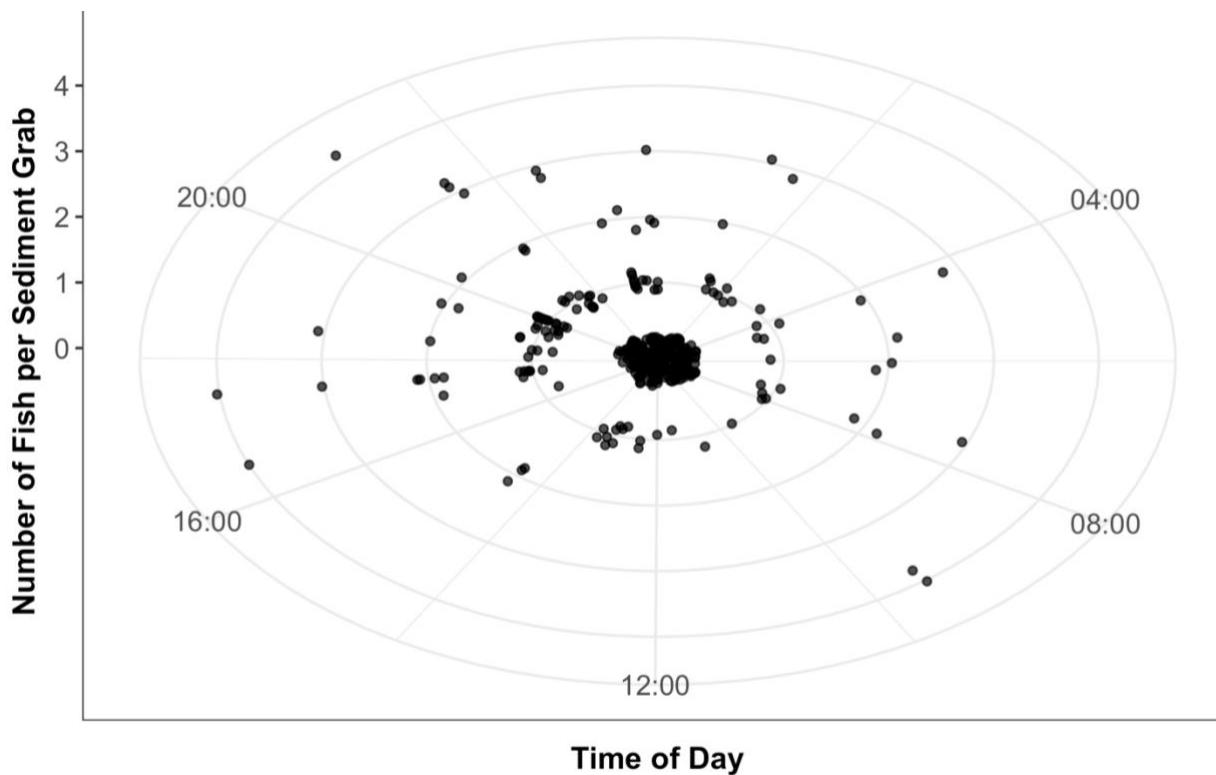


Figure 3.6. Number of sand lance caught per sediment grab throughout the day during July-August, 2013-2021 (circular mean time: 19.2 h after midnight; circular variance 0.62; Rayleigh test  $p < 0.0001$ ). Points are jittered to better visualize sampling distribution.

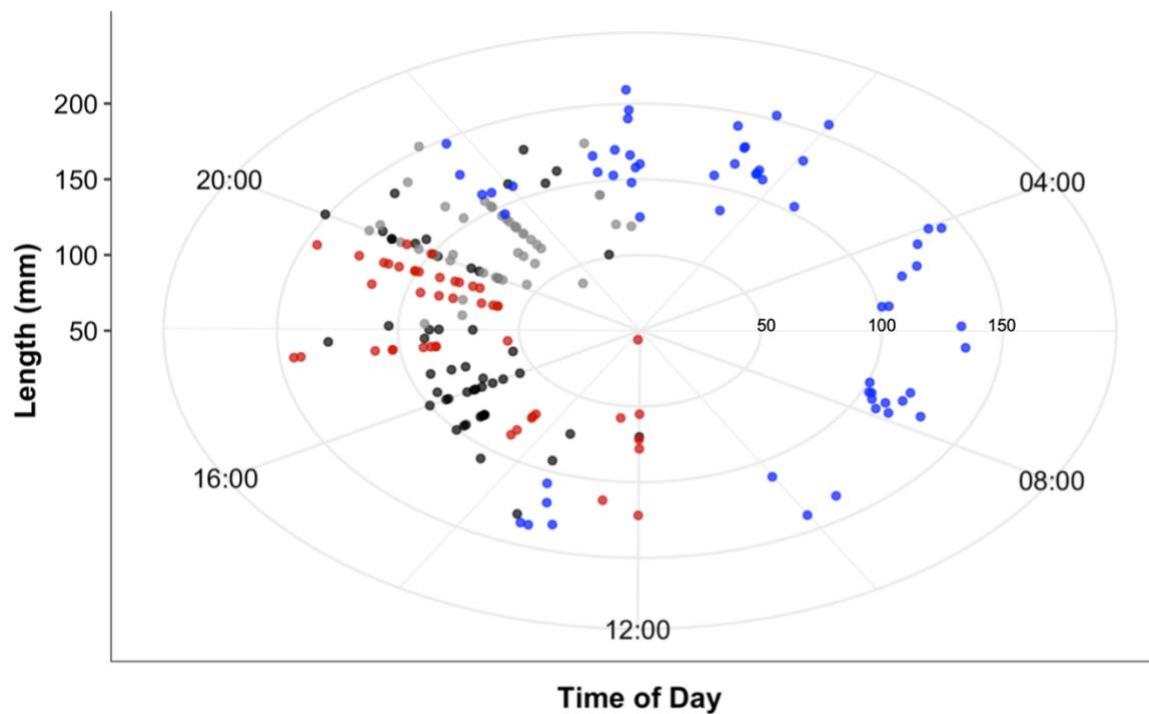


Figure 3.7. Total length (mm) of sand lance caught in sediment grabs throughout the day during July-August, 2013-2021 (circular mean time: 19.7 h after midnight; circular variance: 0.53; Rayleigh test:  $p < 0.0001$ ). Black: 2013-2018, Gray: 2019, Red: 2020, Blue: 2021. Points are jittered to better visualize sampling distribution.

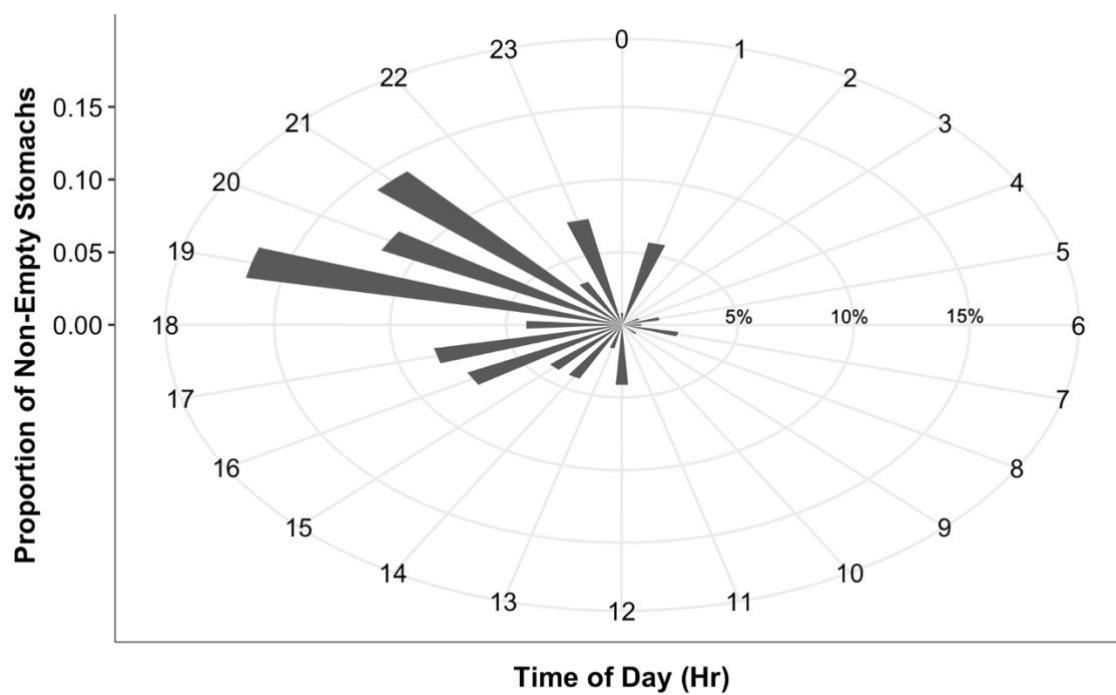


Figure 3.8. Proportion of non-empty sand lance stomachs caught in sediment grabs per hour throughout the day during July-August, 2013-2021 (circular mean time: 19.2 h after midnight; circular variance: 0.03, Rayleigh test:  $p < 0.0001$ ).

Table 3.1. Number of sediment grabs, sand lance caught in sediment grabs, hydroacoustic surveys, and camera drift surveys per year from 2013-2021, at the fine-scale region (Gull 3) and our comparison region (Gull 2).

	<b>Year</b>	<b>Sediment grabs</b>	<b>No. Sand lance Caught</b>	<b>Hydroacoustic Surveys</b>	<b>Camera Drift Surveys</b>
<b>Gull 3</b>	2013	10	24	0	-
	2014	9	9	3	-
	2015	10	6	4	-
	2016	9	0	1	-
	2017	7	9	5	-
	2018	16	5	5	-
	2019	72	48	9	-
	2020	80	50	2	26
	2021	192	74	-	-
<b>Gull 2</b>	2013	15	4	-	-
	2014	10	0	-	-
	2015	13	0	-	-
	2016	6	0	-	-
	2017	3	0	-	-
	2018	11	0	-	-
	2019	14	0	-	-
	2020	46	0	-	22
	2021	9	0	-	-

## Supplementary Materials II

Site	AB	CC	CFB	DB	LB	MS	SB	WB	Turr	Gull 1	Gull 2	Gull3
Temperature (°C)	13±0.7	13±0.5	14	13±0.2	9±0.25	8.3±0.75	13±0.4	9.6±1.6	6.0±0.6	3.6±1.4	6.0±0.8	2.1±0.2
Depth (m)	7.6±0.8	8.0±1.0	4	6.0±1.0	6.5±1.5	7.5±2.5	7.7±0.9	6.0±1.1	17±0.9	34±0.8	24±1.1	41±0.7
n	6	1	1	2	2	1	5	6	4	4	4	4

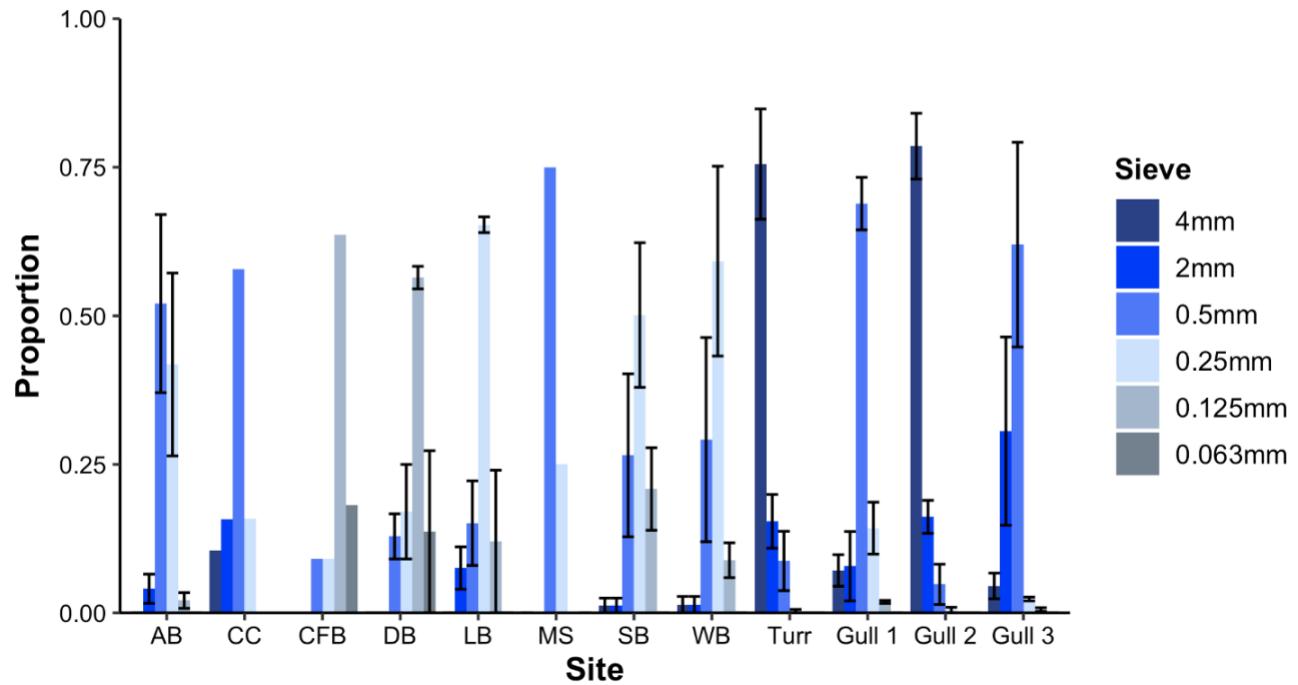


Figure S3.1. Mean ( $\pm$  SE) proportions of different grain size ranges of 7 coastal regions plus one adaptive site (CFB), including four subtidal capelin spawning areas (Turr, Gull 1, Gull 2, Gull 3), along with their associated mean ( $\pm$  SE) temperature (°C), depth (m), and sample size (n). All regions were sampled during July-August, 2020, while only AB, SB, and WB were sampled again during July-August, 2021. See Figure 3.1 for locations of each region.

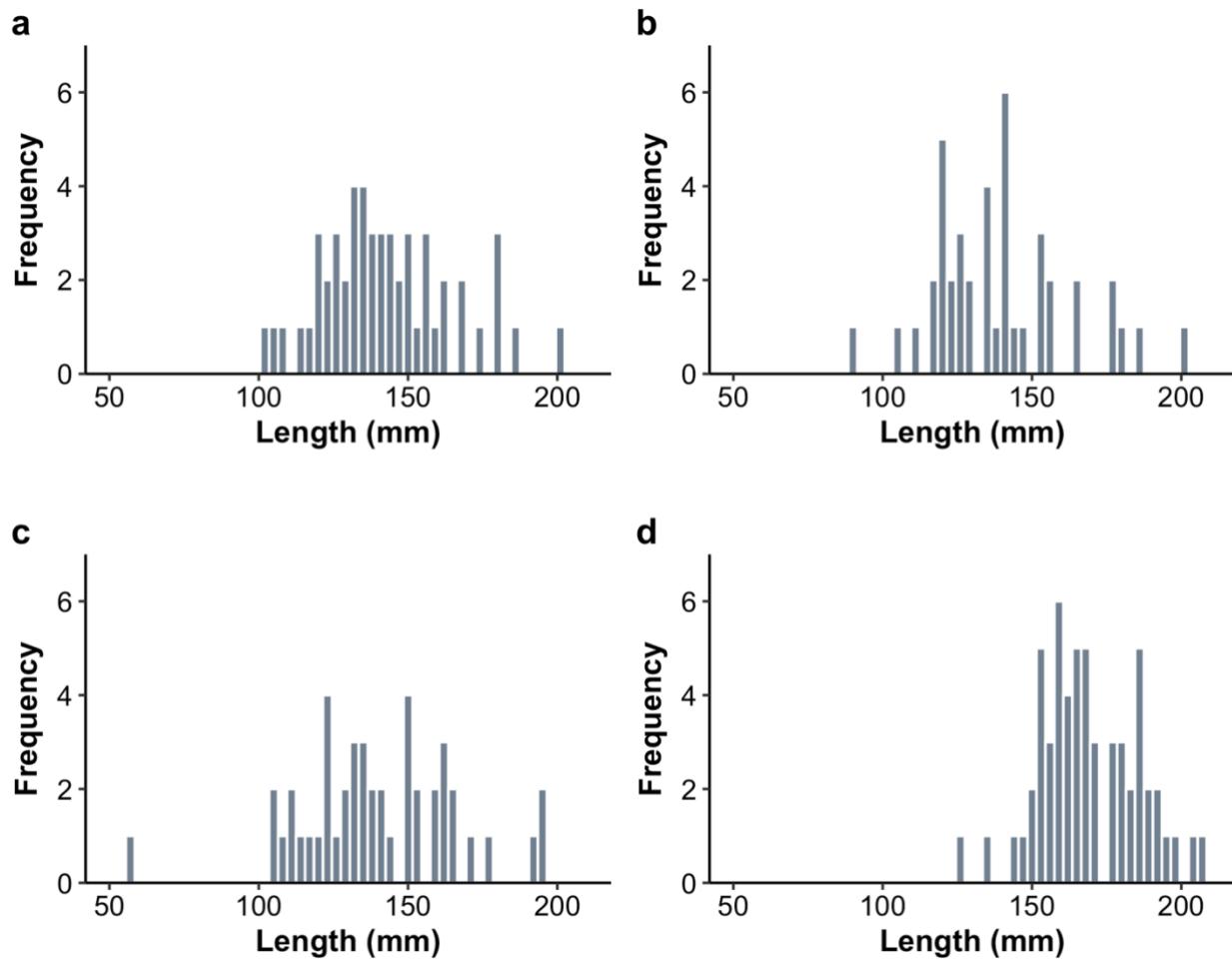


Figure S3.2. Sand lance length histograms from *a*) 2013-2018 (n=52), *b*) 2019 (n= 42), *c*) 2020 (n= 45), and *d*) 2021 (n=61).

## **Chapter Four. Thesis Conclusion**

Sand lance are an understudied species in the northwest Atlantic, and little is known about their ecology, including their abundance, distribution, biometrics, population dynamics, habitat characteristics and diel behaviour, likely because it is not a commercially fished species and, thus, not assessed by DFO. By investigating trends in sand lance *Ammodytes* spp and capelin *Mallotus villosus* abundance, distribution, and biometrics across the southeastern Newfoundland Shelf during the spring using a 20-year (1996-2015) dataset, I was able to show evidence of density-dependent growth for sand lance, but not capelin. Indeed, sand lance length, mass and condition decreased with increasing abundance, while capelin length and mass increased with increasing abundance. Neither sand lance nor capelin appeared to expand their distribution in years of higher abundance. For sand lance, this lack of expansion was likely due to the specific habitat requirements, but may be related to the collapsed state of the population for capelin. Importantly, I also showed that inter-annual variation in abundance, distribution and biometrics (length, mass, condition) were not synchronized in capelin and sand lance. The lack of synchrony in the full datasets of capelin and sand lance may have been due to the inaccuracies with our capelin abundance and biometrics estimates, but the abundance estimates of the immature capelin and sand lance datasets were comparable. Although bottom-up processes altering the abundance of primary and secondary producers are thought to mediate the population dynamics of these forage fish species (Frederiksen et al. 2006; Buren et al. 2014; Lynam et al. 2017), the different regions of the Grand Bank occupied (capelin farther north and more inshore than sand lance) likely have divergent prey types and abundance, and thus, differentially affect biometrics and abundance in each species. Overall, the observed diversity in population dynamics, distribution and biometrics of the forage fish species on the Newfoundland Shelf

likely increases the stability of this marine ecosystem by sustaining the role of these meso-predators in key ecosystem processes (e.g., energy flow), thereby creating a portfolio effect.

Although my calculated abundance indices do not provide absolute values, due to issues associated with estimating abundance of pelagic species from a bottom trawl survey, there were no increasing trends in capelin or sand lance abundance in any datasets over the 20-year study period. These findings suggest little change in the collapsed state of the capelin population and little evidence of predator release at the meso-predator trophic level after the overfishing of Atlantic cod, a key top predator, in the early 1990s. Interestingly, a trophic cascade was evident just south of the study area on the Scotia Shelf, where the biomass of the meso-predator trophic level increased in response to the decline in cod stocks (Frank et al. 2005). This cascade may be due to the ecosystem on Scotian Shelf being regulated more from the top-down in comparison to the primary bottom-up regulation of the Newfoundland Shelf ecosystem (Buren et al. 2014; Lewis et al. 2019; Murphy et al. 2021).

Findings of this study suggest sand lance species in the Northwest Atlantic have similar habitat requirements and diel patterns to *Ammodytes* species in other regions. Most research on *Ammodytes* is from the Northeast Atlantic Ocean on the lesser sandeel (*A. marinus*) and from the Northeastern Pacific Ocean on the Pacific sand lance (*A. personatus*). In these regions, sand lance are commonly found in cool (1-11°C), shallow (<40 m) regions with suitable burrowing sandy seabed substrate (0.25 – 2 mm; Scott 1968, Reay 1970, Wright et al. 2000, Ostrand et al. 2005). By integrating camera surveys, sediment grabs, and hydroacoustics, I found that sand lance in coastal Newfoundland was associated with similar habitat characteristics, including 0.5–4 mm grain sizes that were < 11°C (typically ~2°C). Pacific and Northeast Atlantic sand lance species show diel shifts in feeding and burrowing, where they remain in schools and forage

during the day throughout the water column, and remain burrowed in the sediment at night (Winslade 1974a; Hobson 1986; Freeman et al. 2004; Friedlaender et al. 2009). In my study, acoustic sand lance biomass was higher during the morning and afternoon but decreased throughout the day and evening, while densities in sediment grabs simultaneously increased later in the afternoon and evening and buried fish more commonly had non-empty stomachs in the evening. These findings suggested that sand lance were feeding in the water column during the day and burrowed later in the day once stomachs were full. Diel patterns were size-dependent, with more smaller sand lance (<150 mm) caught in sediments throughout the day but primarily only larger sand lance (>150 mm) caught in sediments throughout the night. Overall, my study increased our understanding of *Ammodytes* distribution, abundance, density, biomass, diel behaviour and habitat selection in coastal Newfoundland. This new information will help form the basis of future research on the interactions between sand lance and top predators in coastal Newfoundland.

Overall, these studies contributed to the growing body of literature on *Ammodytes* in the northwest Atlantic (Staudinger et al. 2020), but more research is needed. For instance, although I successfully detected the presence of sand lance using sediment grabs and seabed camera surveys, I recommend combining these techniques with others, such as sampling environmental DNA (eDNA) in sediments, to enhance detection probability of sand lance (Berger et al. 2020; Staudinger et al. 2020; Ratcliffe et al. 2021). This technique would be especially important during daytime sampling, when sand lance may be more likely foraging in the water column and, thus, not present in sediments. Another approach may be to use predators to locate sand lance habitats. Indeed, sand lance are an important food source of Atlantic puffins in other regions (Harris and Wanless 1986; Barrett and Furness 1990), therefore, foraging locations of puffins may

provide a further understanding of sand lance habitat requirements in coastal Newfoundland.

Additionally, on the Newfoundland Shelf, there are two species of sand lance, *A. dubius* and *A. americanus*, and misclassification between the two species is common. Owing to issues distinguishing these species, it was unclear which species was being studied in both my coastal and offshore study areas. Further research examining morphometrics/meristics (Winters 1970; Winters and Dalley 1988; Nizinski et al. 1990) along with eDNA and DNA sequencing will help distinguish between species of this genus (Berger et al. 2020; Ratcliffe et al. 2021). For instance, a comparison of genetic markers from sand lance tissues collected both inshore and offshore may provide insight into the differentiation of these two species. Finally, future research should be aimed at determining the mechanisms underlying population dynamics of this important forage fish. Such research would provide insight into the impact of forage fish population fluctuations on their predators on the Newfoundland Shelf, thereby informing ecosystem-based fisheries management strategies.

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