REGIONAL DISTRIBUTION, LIFE HISTORY, AND MORPHOMETRY OF SPAWNING-STAGE CAPELIN *MALLOTUS VILLOSUS*

By

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ABSTRACT

Capelin *Mallotus villosus* is a forage fish that is integral to many Arctic and subarctic marine food webs, but is less thoroughly studied outside the Atlantic Ocean. The goal of this research was to study spawning Capelin in data-poor areas, particularly in waters off the coast of Alaska and the western Canadian Arctic, to enrich baseline data and allude to intraspecies diversity. Chapter one examined the distribution and life history of spawning Capelin in Norton Sound, Alaska, by conducting aerial surveys, collecting sediment samples to characterize beach spawning habitats, and identifying biological attributes of spawners (e.g., body size, age, fecundity, etc.). Chapter two used a geometric morphometric approach (i.e., relative warps) and multiple statistical techniques (i.e., relative warp analysis, Procrustes analysis of variance, estimates of morphological disparity, and canonical variates analysis) to differentiate among and within putative populations of spawning Capelin in the western Canadian Arctic, Newfoundland, Canada, and Alaska. Spawning Capelin in Norton Sound portrayed similar behaviors, occupied similar beach habitats, and encompassed a similar range in biological attributes as fish observed in other regions throughout this species' geographic distribution. However, average spawner body size, age, fecundity, and morphometry differed among regions. These results suggest that Capelin exhibit some similarities in spawning behavior and habitat use across their geographic distribution, but may exhibit population-specific differences in biological attributes among and within regions.

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GENERAL INTRODUCTION

Forage fishes are an integral component of many marine food webs, occupying a key position that has the potential to disproportionately impact the rest of the ecosystem (Libralato et al. 2006; Pikitch et al. 2014). These fishes support piscivorous marine mammals, seabirds, and fishes directly by supplying nutrients through consumption and indirectly by converting energy from plankton into a form accessible to upper trophic levels (Carscadden et al. 2013; Pikitch et al. 2014). Nutrient availability will likely be altered in response to changes in forage-fish distributions and abundance as the climate continues to warm (Andrews III et al. 2016; Siddon and Zador 2018). Arctic fishes, in particular, are expected to respond first to climate change, which makes them important indicator species (Reist et al. 2006). Indicator species help to identify environmental changes that eventually will affect other species in the ecosystem because they are more sensitive to these changes and are therefore affected before other species (McClory and Gotthardt 2005). One important indicator forage-fish species is Capelin *Mallotus villosus*, which is considered a "sea canary" because it responds quickly to environmental fluctuations (Rose 2005).

Capelin is a short-lived (3 – 5 years old) forage fish that has a circumpolar distribution across Arctic and sub-Arctic waters in the northern hemisphere (Carscadden and Vilhjálmsson 2002). This species is thought to have originated in the Pacific Ocean and dispersed to the Atlantic Ocean during two interglacial periods (Rose 2005; Dodson et al. 2007). Despite its distribution, most of our knowledge about this species comes from research conducted in the Atlantic Ocean because there is a large commercial fishery for Capelin in that area (Carscadden and Vilhjálmsson 2002). Based on this research, Capelin spend most of their life offshore where shoals are thought to occupy areas near sea ice and feed on zooplankton (Yang et al. 2005;

McClory and Gotthardt 2005). In the summer, individuals that are ready to spawn undergo a series of changes in morphology, which includes becoming sexually dimorphic, and both sexes actively migrate as a cohort along fairly distinct paths to nearshore waters (Winters 1970; Olafsdottir and Rose 2012; Carscadden et al. 2013). This migration and spawning period is a time of high predation by various fishes, marine mammals, and seabirds because Capelin congregate in dense aggregations in reasonably predictable locations and at predictable times (Arimitsu et al. 2008).

Capelin spawn over a range of water depths, from intertidal beaches (Pahlke 1985) to demersal sites up to 280 m in depth (Nakashima and Wheeler 2002; Davoren 2013); however, only beach-spawners were targeted in this study. Beach-spawning occurs within one wave cycle, a process that takes approximately 30 seconds (Martin et al. 2004). Capelin ride the wave to shore, females deposit their eggs, and males externally fertilize them. The deposited eggs may be partially buried by the male (Huse 1998), but are primarily buried by wave action (Warner and Shafford 1979; Pahlke 1985). The spawners proceed to ride the next wave back out to sea (Warner and Shafford 1979).

The timing and length of the spawning season varies each year, but lasts approximately two to four weeks (Pahlke 1985; Vandeperre and Methven 2007; Maxner 2014). Males spawn multiple times throughout a single spawning season and then typically die, whereas females deposit all their eggs in a single batch and are more likely to survive to spawn in the following season (Huse 1998; Christiansen et al. 2008; Penton 2013). In Newfoundland, female Capelin have been observed to come to the spawning grounds in two distinct groups, whereas males arrived as a single group and remained for the duration of the spawning season (Vandeperre and Methven 2007; Maxner 2014). Capelin that arrived at the spawning grounds first were older and larger, a trend that was especially apparent with females (Vandeperre and Methven 2007; Maxner 2014). Multiple speculations have been made to explain this decline in size and age throughout the spawning season, such as size-dependent maturation rates which are correlated with fish condition and lipid content (Vandeperre and Methven 2007). If larger females spawn first, the beginning of the spawning run may have a disproportionate influence on recruitment in following years because larger, older, and more experienced females tend to be more fecund than their smaller counterparts (Maxner 2014).

Most life history observations and trends for spawning Capelin were acquired through research in the Atlantic Ocean, but these data are limited in the Pacific Ocean. In particular, the eastern Bering Sea is undergoing a transition from Arctic to sub-Arctic conditions which may profoundly affect ecosystem structure and function (Aydin and Mueter 2007). Some baseline data was collected on spawning Capelin in this area, such as in Norton Sound, in the early 1980s (i.e., Pahlke 1985), but these data are over 30 years old and may not be accurate as a result of climate change. Lack of this basic life history data impedes our ability to understand ecosystem function in this rapidly changing region.

Abundance and distribution of important prey resources affect the dynamics of an ecosystem through altered trophic interactions (Aydin and Mueter 2007; Jones et al. 2018; Siddon and Zador 2018). For example, changes in prey quality and distribution during the 2013 – 2015 northeast Pacific Ocean heatwave was thought to have attributed to the starvation and mass mortality of a zooplanktivorous seabird, Cassin's Auklets *Ptychoramphus aleuticus* (Jones et al. 2018). In the eastern Bering Sea, northward shifts have been observed for groundfish since the 1980s (Siddon and Zador 2018) and snow crab *Chionoecetes opilio* since at least 2000 (Aydin and Mueter 2007). In addition, sub-Arctic species, including Pacific salmonids *Oncorhynchus* spp. and juvenile Walleye Pollock *Gadus chalcogrammus*, are more abundant along the northern Bering Sea shelf than they were prior to 2000 (Aydin and Mueter 2007). The distribution of offshore Capelin has also been observed to change when water temperatures fluctuate as little as 1°C, with wider distributions that extend further South in cold years compared to warm years (Andrews III et al. 2016). Since information on spawning Capelin in the North Pacific Ocean is lacking, changes in its distribution could result in ecosystem-level alterations that are poorly understood.

Capelin from certain regions have been identified as genetically distinct from other areas throughout its geographic range. One study identified at least four distinct mtDNA clades of Capelin: 1) Pacific, 2) Arctic, 3) northeast-central Atlantic, and 4) northwest Atlantic (Dodson et al. 2007). Another study used microsatellite analyses to divide offshore Capelin into four slightly different regions: 1) west Pacific, 2) east Pacific, 3) Newfoundland, and 4) northeast Atlantic and west Greenland (Præbel et al. 2008). Additional studies have identified genetic differences for Capelin at smaller spatial scales. For example, along the coast of Alaska, offshore Capelin from the Chukchi Sea were found to genetically differ from those in the Gulf of Alaska (Wildes et al. 2016). In addition, within the Gulf of St. Lawrence and its estuary in Canada, spawning-stage Capelin from the western and eastern regions were genetically distinguishable (Roby et al. 1991). Regional genetic differences suggests there are multiple populations of Capelin throughout its geographic distribution.

Populations (i.e., a genetically distinct group of fish that are reproductively isolated from other groups; Ihssen et al. 1981) can be identified based on differences in genetic structure and/or phenotypic expression (MacLean and Evans 1981; Begg and Waldman 1999). Genes are used to identify reproductively isolated groups of fish, whereas phenotypes express an organism's genotype in its local environment (Chambers 1993). Unfortunately, the results of genetic studies can be challenging to interpret because the function of many genes is unknown, whereas analyzing an organism's morphometry allows differences in shape to be visualized and interpreted in a biologically relevant context (Zelditch et al. 2004; Webster and Sheets 2010). Although it is best to use multiple methods to distinguish populations, such as a combination of genetic and phenotypic traits (Begg and Waldman 1999), the current study focused on quantifying regional phenotypes via variations in morphometry.

Some populations adapt morphological traits that are advantageous in their immediate environment, regardless of whether those traits are advantageous in other habitats (Kawecki and Ebert 2004). For example, some of the variation in fin shape and size among and within species are thought to result from evolutionary strategies that have social purposes (e.g., sexual selection) or benefit swimming ability (Plaut 2000). In addition, in southwest Alaska, body depth of Sockeye Salmon *Oncorhynchus nerka* varied based on whether the fish spawned in stream or lake beach habitats and individual fish had the best reproductive success in the environment for which it was morphologically adapted (Peterson et al. 2014). The potential benefits of these modified phenotypes theoretically outweigh the costs associated with expressing them.

In previous studies, not all morphometric traits were equally effective at differentiating among Capelin populations. Roby et al. (1991) found that the dimensions of the adipose and caudal fins were two of the four components that best accounted for shape variations among Capelin populations in the Gulf of St. Lawrence and its estuary. Sharp et al. (1978) found snout length, eye diameter, head length, and body depth were the most important variables used to distinguish among populations in the Gulf of St. Lawrence and Newfoundland area, whereas Misra and Carscadden (1987) only found snout length (for males only) and body depth useful for differentiating among populations around Newfoundland. These examples of morphometric variation quantitatively support the hypothesis that phenotypic expression can vary by region for Capelin. However, inconsistencies in the effectiveness of a trait for segregating populations further justifies the need to independently measure these traits on Capelin in the Pacific Ocean, where morphometry has not been studied for this species.

This thesis investigated spawning Capelin among and within regions throughout their geographic distribution, including areas lacking extensive baseline data such as Alaska and the western Canadian Arctic. The first chapter of this thesis examined the distribution and life history of spawning Capelin in Norton Sound, Alaska, to update and expand baseline data on Capelin in this region (i.e., Pahlke 1985). The second chapter investigated intraspecies diversity within and among regions throughout this species' geographic distribution in the western Canadian Arctic, Newfoundland, Canada, and Alaska using a geometric morphometric approach to differentiate among putative populations of spawning Capelin. Spawning observations and spawner biological attributes were compared to Capelin from more thoroughly studied areas, such as the North Atlantic Ocean, to evaluate the extent of intraspecific diversity for this species.

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CHAPTER 1: DISTRIBUTION AND LIFE HISTORY OF SPAWNING CAPELIN *MALLOTUS VILLOSUS* IN SUBARCTIC ALASKA[1]

Abstract

Capelin *Mallotus villosus* is a cold-water, marine forage fish that responds quickly to environmental fluctuations; however, little is known about Capelin in Alaskan waters. The objective of the current study was to better understand the distribution and life history of spawning Capelin in northern Norton Sound, Alaska. Surveys were conducted from May through July 2018 to locate and estimate the size of nearshore Capelin aggregations prior to spawning, identify the location and timing of spawning events, characterize spawning habitat, and collect actively spawning fish to examine life-history characteristics (e.g., body size, age, fecundity, etc.). Most (85.9%) nearshore aggregations were less than 12 m^2 in surface area. Spawning Capelin were collected in Norton Sound between 15 and 21 June. At spawning locations, gravel and coarse sand accounted for over 70% of the proportional weight of sediment collected within a beach and all sediment samples contained Capelin eggs. Spawning males were larger than spawning females in total length (mean ± SD = 148.8 ± 6.7 mm versus 137.0 ± 8.4 mm, respectively) and total weight (21.2 ± 2.9 g versus 13.7 ± 3.0 g, respectively), and both sexes were predominately age 3 (range = ages 2 to 4). Absolute fecundity was 9,219 ± 4,529 eggs, and males and females had a gonadosomatic index of 1.09 ± 0.32% and 21.69 ± 8.21%, respectively. In Norton Sound, nearshore aggregation sizes were smaller than reported in Newfoundland, but spawning behavior, timing, and water conditions were similar to observations from other Capelin

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spawning regions (e.g., Greenland), as were size, age, fecundity, and gonadosomatic index estimates. While the results from the current study update baseline information on spawning Capelin in northern Norton Sound, continued research on their distribution and life history is needed to better understand ecosystem function in the North Pacific Ocean.

Introduction

Forage fishes are an integral component of many marine food webs, occupying a key position that has the potential to disproportionately effect the rest of the ecosystem (Pikitch et al. 2014; Andrews III et al. 2016). These fishes provide essential nutrients and energy to predators, including marine mammals, seabirds, and other fish species by converting energy from plankton into a form accessible to upper tropic levels (Carscadden et al. 2013a; Pikitch et al. 2014; Andrews III et al. 2016). Nutrient and energy availability in marine food webs will likely alter in response to changes in forage-fish distributions and abundance as the climate continues to warm (Aydin and Mueter 2007; Andrews III et al. 2016). Fishes that live in Arctic and sub-Arctic waters can be particularly sensitive to environmental change; therefore, they may help identify environmental changes that could have delayed impacts on other species in the ecosystem (Rose 2005). One of these cold-water forage fish is Capelin *Mallotus villosus*, which is considered a "sea canary" because it responds quickly and consistently to environmental fluctuations (Rose 2005).

Capelin is distributed throughout the Arctic, North Atlantic, and North Pacific oceans (Carscadden and Vilhjálmsson 2002; Hedeholm et al. 2011). Capelin live in the open ocean, but migrate to nearshore waters for spawning where fish utilize different habitats than their non-spawning counterparts (Carscadden et al. 2013b). Both offshore and nearshore environments are rapidly warming. For example, the northern Bering Sea, located in the North Pacific Ocean, has experienced only positive sea surface temperature anomalies between 2013 and 2018 and had almost no sea ice in 2018 (Siddon and Zador 2018). Temperature increases as little as 1°C have been associated with large-scale changes in non-spawning stage Capelin distribution in the eastern Bering Sea (Andrews III et al. 2016). In addition, changes in environmental conditions may alter the location and extent of spawning habitat available for beach-spawning Capelin. Warming waters may cause temperatures to exceed this species' thermal optima for spawning (<12°C; Nakashima and Wheeler 2002). Alternatively, the availability of beach spawning areas may be altered due to coastal erosion resulting from a decrease in protective shore ice and an increase in the frequency and intensity of storms (Arthur 2017). Lack of adequate spawning conditions and habitats may reduce Capelin spawning success, larval survival, and overall abundance, which has ecosystem-wide implications (Nakashima and Taggart 2002; Carscadden et al. 2013b).

Collecting baseline data on key species, such as Capelin, is important for understanding ecosystem function; however, this species is not well studied outside the North Atlantic Ocean (Carscadden and Vilhjálmsson 2002). Some life history information is available in the Pacific Ocean for spawning Capelin in Norton Sound, Alaska (Pahlke 1985); although, these data are over 30 years old and may no longer be accurate due to environmental changes. The objective of this study was to better understand spawning Capelin distribution and life history in Norton Sound, Alaska, relative to historical regional data to update and expand baseline knowledge of Capelin in this area (i.e., Pahlke 1985).

Methods

Field data collection

Capelin were surveyed and collected from Norton Sound, located along the western coast of Alaska in the North Pacific Ocean (Figure 1.1). In November 2017, knowledgeable local fishers living in this area were interviewed in Nome and the villages of Brevig Mission and Elim via semi-structured interviews ($N = 8$), and in the village of Teller via informal conversations, to identify candidate Capelin spawning locations. Informational flyers were placed around Nome, and in the villages of Brevig Mission, Elim, and Unalakleet, and an advertisement was aired on the local radio to encourage community members to report information regarding the location of spawning Capelin. In response to community feedback, beaches within driving distance of Nome were occasionally surveyed by driving along the main road (which paralleled the beach from Nome to 30 mi east of Nome) and by using an all-terrain vehicle to drive directly on the beach (from Nome to Penny River ~10 mi west of Nome; see Figure 1.1). Finally, 14 aerial surveys were flown parallel to shore approximately 200 m from the shoreline and at an average altitude of 150 m using a Robinson-R44 or a MD500 helicopter. Surveys were flown at least once weekly from 26 May to 7 July 2018 and spanned from Wales to Golovnin Bay (~490 km of coastline), although the entire area was not surveyed on each flight due to financial limitations (Figure 1.1). Surveys were typically flown in the morning to capitalize on favorable weather conditions and good visibility at that time.

Nearshore and spawning aggregations were observed during the aerial surveys. Nearshore aggregations were characterized by groups of fish that were densely packed, individually identifiable, and located within 400 m of shore. This encompassed the area Capelin were expected to occupy immediately prior to spawning on the beach. The surface area of nearshore aggregations was estimated using a gridded PVC sighting tube, the altitude of the helicopter, and the distance from shore based on the following equation (Lebida and Whitmore 1985):

$$\text{surface area} = \text{survey altitude} * (\text{grid line length}/\text{sighting tube focal length}).$$

The density of nearshore aggregations (regardless of aggregation size) was also determined. The aerial survey area was broken into sections based on geographic landmarks within which nearshore aggregations were tallied (see "Geographic Landmarks" in Figure 1.1). To account for variations in the length of coastline surveyed, aggregation density was calculated for each survey by dividing the number of aggregations observed by the length of shoreline surveyed for that section. Spawning aggregations were characterized by groups of fish located on the beach within the wash zone. Once spawning was observed, the spawning aggregations were monitored as frequently as possible to estimate the length of time that Capelin occupied the site as well as the time of day during which fish were actively spawning. During each aerial survey, nearshore and spawning aggregations were recorded on a map by hand and marked on a handheld GPS.

Actively spawning male and female Capelin were collected using a dip net (square mesh < 3.8 cm). If spawning was observed while driving, samples were collected immediately. If spawning was observed during an aerial survey, the pilot landed the helicopter near the beach (to avoid disturbing spawning) and Capelin were collected before resuming the aerial survey. Fresh mortalities from prior spawning events that were found stranded on the beach were collected opportunistically. Because males outnumbered females on the spawning grounds (e.g., Christiansen et al. 2008), females were actively targeted during collections. As a result, the ratio of males and females collected did not represent the ratio observed at the spawning site. Collected Capelin were euthanized, frozen, and sent to the University of Alaska Fairbanks (UAF) for processing in the laboratory.

Spawning habitat was characterized by measuring the size and physical characteristics of active spawning locations. Seabird presence and active feeding were used to estimate the length of shoreline being used for spawning because birds were easier to see than Capelin when standing on the beach. When possible, GPS waypoints were collected at the edges of a spawning area and the straight distance between the waypoints was measured in Garmin BaseCamp

(Version 4.7.0) to determine the length of beach that was actively used for spawning (Garmin BaseCamp 2018). Wind direction during a spawning event was also noted. Water temperature (°C), dissolved oxygen (mg/L), and salinity (ppt) were collected using a portable YSI meter (Model 85, YSI Incorporated, Yellow Springs, Ohio).

To categorize average beach sediment size and confirm spawner presence (via deposited eggs), sediment was gathered using a clear sediment corer tube (4.8 cm inner diameter). At each spawning site, three replicate cores (each with 10 cm of substrate) were collected at three locations (high, mid, and low) within the tidal wash area on the beach (Figure S1.1.1 in Supplement 1.1). High-, mid-, and low-locations were spaced < 5 m apart at a given site. Replicate cores from each location on the beach were combined into one sample per location on the beach for a total of three sediment samples per beach sample (i.e., high, mid, and low). High-locations were at the highest extent of the wave wash, mid-locations were covered with water as the waves moved on- and offshore, and low-locations were always submerged. Sampling locations were based on the wave action at the time of sampling, not the actual maximum- and minimum-tide levels. Sediment samples were preserved in 4% (vol : vol) formalin : seawater solution buffered with sodium borate (Nakashima and Taggart 2002) and shipped to UAF for laboratory analyses.

Laboratory analyses

Sediment samples were separated from deposited eggs following methods modified from Taggart and Nakashima (1987). Formalin was rinsed and decanted five times from the sediment sample over a 63-µm sieve. The rinsed samples were submerged in a 2% KOH solution for 24 to 36 hours to help remove the eggs from the sediment. The samples were rinsed again and decanted ten times over a 250-µm sieve to collect the eggs and a 63-µm sieve to prevent finer sediments from being lost. Eggs were dried at 80°C for 12 to 24 hours and weighed to the nearest 0.001 g.

Once the sediment was free of eggs, it was processed to categorize spawning substrate. The sediment was dried at 80°C for 24 to 90 hours, allowed to cool in a desiccator for at least one hour, and sieved for one minute by hand through a full set of graded sieving screens (mesh sizes 2000, 1000, 500, 250, 125, and 63 μm plus a base to catch sediment < 63 μm). The sediment was weighed for dry weight (to the nearest 0.1 g), classified using the Wentworth size classes (Wentworth 1922), and reported by proportional weight per size class per location on the beach (i.e., high, mid, and low).

Capelin were thawed in the laboratory immediately prior to measuring TL (to the nearest 1 mm) and total wet body weight (TW; to the nearest 0.001 g). All fish were photographed prior to internal examination. Because Pahlke (1985) measured FL (to the nearest 1 mm) on fresh fish, the FL of 30 males and 30 females were measured from standardized photographs using tpsDig2 (version 2.31; Rohlf 2005). Linear regression was used to establish a relationship between TL and FL for both sexes combined. Fork lengths for the remaining fish were estimated using the following relationship:

$$FL = 0.88 * TL + 6.22 \; (R^2 = 0.97, N = 60, P < 0.001).$$

The calculated FL was then multiplied by 1.03 to account for shrinkage due to freezing (Winters 1982). Only the calculated FLs (not the measured FLs) were compared with FLs reported in Pahlke (1985), whereas all other analyses used TL. Following TW measurements, stomachs were extracted and weighed both full and empty. Stomach content weight only accounted for a mean of 0.5% of the TW (range = 0.0% to 5.5%), so TW was used for the remaining analyses instead of correcting weight estimates based on stomach content weight.

Saggital otoliths were extracted from each Capelin and stored dry. Whole otoliths were submerged in mineral oil to make the translucent bands easier to observe, and four images of the otoliths were captured at 50x magnification (convex and concave sides of the left and right otolith) under a compound light microscope (Leica M165 C, Leica Microsystems, Buffalo Grove, Illinois). Fish were divided into 7-mm length bins, and a subsample of at least five individuals (when available) or 38% of the catch in each length bin per sex were aged from the photographs independently by two readers. Discrepancies were resolved by a concert read. An age–length key for each sex was generated following standard methods to assign ages to the remaining fish based on TL (Ogle 2015).

Capelin gonads were examined to generate fecundity and gonadosomatic index (GSI) estimates. Females that had spawned or partially spawned were not included in these analyses to avoid underestimating fecundity. Conversely, all males were included because they were expected to vary in spawning stage since males are likely to spawn multiple times throughout the season (e.g., Huse 1998). For females, loose eggs were presumed to be from the left ovary because the right ovary in female Capelin is known to be underdeveloped (Winters 1971). In the current study, the right ovary contained few eggs; therefore, all eggs were counted from the right ovary. For the left ovary, 100 eggs were taken from each the anterior, middle, and posterior sections to account for potential egg size differences within the ovary. Mean egg weight was calculated by dividing the total weight of the subsamples by the total number of eggs in the subsamples for each fish. Absolute fecundity was estimated by dividing the total ovary weight by mean egg weight, while relative fecundity was calculated by dividing the absolute fecundity by

TW. For males, the left and right testes were removed and weighed for wet weight. Gonadosomatic index was calculated by dividing total wet gonad weight (total testes weight for males or total ovary weight for females) by TW multiplied by 100.

Current and historic spawning locations for Capelin were mapped using ArcGIS (version 10.5.1; Environmental Systems Research Institute 2017), the software program "R Studio" (version 1.1.463; R Studio Team 2016) operating with "R" (version 3.5.2; R Core Team 2018) was used to conduct analyses (with significance at $\alpha = 0.05$), and graphs were generated with SigmaPlot (version 12.3; Systat Software Inc. 2012). Summary statistics were reported as mean ± SD unless otherwise indicated. Wind direction was qualitatively compared with reported Capelin spawning conditions in other regions. Water conditions during spawning were averaged across all spawning events. Kruskal-Wallis tests were used to determine if differences existed among sites or locations for each sediment size class and for the median total dry egg weight decanted from the sediment samples. All life-history analyses were conducted separately for males and females unless otherwise noted. Female mortalities that were collected were aged but were excluded from remaining analyses. A one-way ANOVA was used to examine relationships among Capelin body size and sex, age class, and collection date. Fisher's exact test was used to determine if age composition differed throughout the spawning season, while a pairwise Kendall's rank correlation test was used to compare relationships among fecundity and GSI estimates to Capelin TL and TW.

Results

Aerial surveys in summer 2018 were 1.60 ± 0.42 hours in duration, with a total of 20.75 hours of aerial survey time. Most nearshore Capelin aggregations (85.9%; 269 of 313 aggregations) covered a surface area of approximately 12 m^2 or less and 13.4% (42/313 aggregations) were approximately 25 m^2. Two larger aggregations were also observed: one approximately 61 m^2 and the other 219 m^2. The highest density of aggregations (4.98 aggregations/km) was observed between Sinuk River and West Mountains (Table 1.1; Figure 1.1). Seals (family Phocidae) were observed actively hunting nearshore fish aggregations during the first aerial survey.

Capelin were collected in Norton Sound from 15 to 21 June 2018 from five active spawning sites (173 males, 105 females) and one site where spawning had occurred (9 female mortalities). Spawning events occurred at beaches between the Nome River mouth and Nome, Nome and Penny River, and 3 km east of the Sinuk River to the Sinuk River mouth (spawning sites hereafter termed “Nome River”, “Penny River”, and “Sinuk River”, respectively; Figure 1.1). Seabirds, including Black-legged Kittiwakes *Rissa tridactyla*, Glaucous Gulls *Larus hyperboreus*, Glaucous-winged Gulls *L. glaucescens*, Herring Gulls *L. argentatus*, Mew Gulls *L. canus*, and Arctic Terns *Sterna paradisaea*, were present and actively feeding on Capelin at spawning sites. Although the time that Capelin spent actively spawning was short, aggregations appeared to be present at spawning areas for two to four days, depending on location. For example, Capelin were reported by community members to be spawning at the Nome River site on 17 June 2018 at 1500 hours and samples were collected while they were actively spawning at 1700 hours the same day. On 18 June, fish were monitored at 1115 hours on the ground, 1400 hours by air, and 1930 hours by ground; however, no spawning activity was observed during these subsequent trips. There were community reports that between those monitoring periods, at approximately 1700 hours, Capelin were actively spawning (see additional examples in Supplement 1.2).

During a spawning event, Capelin congregated within 1 to 2 m of shore, around the area where the waves start breaking, and rode the wave onto shore to spawn. The length of beach used for each spawning event ranged from less than 400 m to approximately 3,500 m. Within each large spawning event there appeared to be smaller aggregations (<4 m^2) that would come onto shore at multiple locations along the beach. Within these smaller spawning aggregations, individuals were sometimes observed forming groups of three (two males with one female) when coming onshore. Capelin were observed spawning at various times throughout the day (0900, 1200–1400, and 1700 hours) and during both on- and offshore winds. Across spawning events, water temperature was 9.0 ± 2.0°C (range = 6.8 – 10.9°C), dissolved oxygen was 9.4 ± 1.0 mg/L (range = 7.6 – 10.4 mg/L), and salinity was 24.3 ± 6.7 ppt (range = 10.6 – 27.7 ppt).

A total of 18 sediment samples (i.e., 6 sediment collection sites x 3 locations within the beach) were collected from four active Capelin spawning sites and one site where spawning had occurred. Two sets of sediment samples were collected from the Sinuk River spawning site approximately 130 m apart from each other (SK1 and SK1.2 in Figure 1.1) to account for potential variability in beach sediment composition because spawning covered nearly 3,500 m of shoreline. All sediment samples contained eggs. Although sediment samples were sorted into seven size classes, the results from a principal components analysis (PCA) and PCA biplot based on percent sediment composition per sediment sample (separated by location) suggested that sediments could be grouped into four size classes: gravel (>2000 μm), coarse sand (500 to 2000 μm), fine sand (63 to 500 μm), and fines (<63 μm). Combining the size classes was corroborated in that the grouped dataset was fully explained by the first two principle components (PC1 and PC2 accounted for > 99.99% variability) and the percent variance explained by PC1 was slightly higher for the grouped dataset (87.0%) than the full dataset (86.3%). Therefore, the grouped dataset was used for all sediment composition analyses.

There was no difference in percent sediment composition among spawning sites for any of the four sediment size classes. The percent sediment composition differed among locations within a beach spawning site (Figure 1.2). Gravel dominated the sediment composition at low-locations whereas fine sand dominated the sediment composition at high-locations. The amount of coarse sand and fine sediments was similar among all locations within the beach (i.e., high, mid, and low). Across all sampled spawning beaches, gravel and coarse sand accounted for nearly all the sediment collected within a beach at high-, mid-, and low-locations (proportional weight of sediment = 73.2, 80.5, and 91.3%, respectively).

Spawning Capelin exhibited a range of sizes and ages. Natural log-transformed TL and TW were positively related for males ($R^2 = 0.85$) and females ($R^2 = 0.61$; Figure 1.3). Males were 8% longer than females based on TL (148.8 ± 6.7 mm versus 137.0 ± 8.4 mm, respectively; ANOVA: $F = 172.50$; $df = 1, 275$; $P < 0.001$; Figure 1.4) and were 35% heavier based on TW (21.2 ± 2.9 g versus 13.7 ± 3.0 g, respectively; ANOVA: $F = 411.00$; $df = 1, 275$; $P < 0.001$). Capelin were predominately age 3 for both males (69.4%, 120/173 fish) and females (63.5%, 66/104 fish; Figure 1.4). There were no differences in Capelin TL among age classes for males (ANOVA: $F = 0.59$; $df = 2, 170$; $P = 0.56$) or females (ANOVA: $F = 1.98$; $df = 2, 101$; $P = 0.14$) or TW among age classes for males (ANOVA: $F = 0.97$, $df = 2, 170$; $P = 0.38$) or females (ANOVA: $F = 0.95$; $df = 2, 101$; $P = 0.39$). Further, sample date was not correlated with TL for males (ANOVA: $F = 1.88$; $df = 3, 169$; $P = 0.13$) or females ($F = 0.22$; $df = 3, 100$; $P = 0.89$) or with age composition of males (Fisher's exact test: $P = 0.65$) or females (Fisher's exact test: $P = 0.98$).

Reproductive structures were assessed on pre-spawn male ($N = 151$) and female ($N = 59$) Capelin. Absolute fecundity was 8,826 ± 4,253 eggs (range = 1,909 to 16,662 eggs), while relative fecundity was 590 ± 236 eggs/g fish weight (range = 158 to 945 eggs/g fish weight). Absolute fecundity was positively correlated with TW (linear regression: $R^2 = 0.42$, $N = 59$, $P < 0.001$; Figure 1.5), but not TL (linear regression: $R^2 = 0.05$, $N = 59$, $P = 0.08$; Figure S1.1.2). Relative fecundity was not correlated with TL (linear regression: $R^2 = 0.02$, $N = 59$, $P = 0.35$; Figure S1.1.3). Male and female Capelin had a GSI of 1.09 ± 0.32% and 21.69 ± 8.21%, respectively. There was a positive correlation between GSI and TL for males (linear regression: $R^2 = 0.05$, $N = 151$, $P < 0.01$; Figure S1.1.4a), but no relationship for females (linear regression: $R^2 < 0.01$, $N = 59$, $P = 0.48$; Figure S1.1.4b).

Discussion

Although Capelin have been extensively studied in the Atlantic Ocean, information on the distribution and life history of spawning-stage adults in the Pacific Ocean is lacking (Pahlke 1985; Carscadden and Vilhjálmsson 2002). Spawning Capelin in Norton Sound had similar spawn timing and behaviors, and water and habitat conditions as Capelin from other regions (e.g., Newfoundland). In addition, Capelin size, age, fecundity, and GSI in the current study were within ranges reported from other areas (e.g., Greenland). Minor discrepancies among Capelin populations (e.g., historic versus current mean age for Norton Sound fish, mean length and weight for Capelin in Norton Sound versus Newfoundland, etc.) were likely due to variations among years or regions (e.g., Maxner et al. 2016; McNicholl et al. 2018). The results from the current study indicate that fundamental ecological aspects of Capelin spawning are similar in multiple marine ecosystems across their geographic range.

Aerial surveys were effective for mapping and estimating the size of nearshore Capelin aggregations in Norton Sound. Most of the nearshore aggregations in Norton Sound were smaller in surface area than the smallest median size of the Capelin aggregations observed in Newfoundland (Table 1.2 [in current study]; Carscadden et al. 1994). Although it is unknown why aggregation size differed between regions, this difference may reflect a lower abundance of Capelin in the Bering Sea relative to Newfoundland. For example, in 2010, Capelin were estimated to have a biomass of 837 t in the eastern Bering Sea and 179 t in the northern Bering Sea based on offshore trawl surveys (Lauth et al. 2019). In contrast, biomass estimates for Capelin on the Newfoundland shelf were estimated at 22,000 t in 2010 and typically ranged from 98 – 200 kt from 2003 – 2017 based on acoustic surveys (Lewis et al. 2019).

Capelin in Norton Sound spawned at the same time of year and were observed on beaches for the same length of time as fish from other locations, but were observed spawning over a shorter duration of time (Table 1.2). Slight variations in the onset of spawn timing likely reflect differences in water temperature and sea ice extent among years and regions (Therriault et al. 1996). For example, in 1981 (i.e., the year Capelin were sampled in Pahlke (1985)), sea ice was present in parts of Norton Sound until August, whereas in 2018, this area was ice-free by May (National Snow and Ice Data Center 2019). In Newfoundland, shorefast sea ice is occasionally present in May and June, but is ice-free by July (National Snow and Ice Data Center 2019). Capelin aggregations were also typically present at a spawning site for multiple days, which is consistent with observations from Newfoundland populations (Maxner et al. 2016). However, the observed spawning season in Norton Sound was shorter in 2018 than in previous years in this region (Pahlke 1985) or in Newfoundland (Vandeperre and Methven 2007; Maxner et al. 2016). Differences in the duration of spawning activities between the current study and previous research likely reflect missed spawning events in Norton Sound. Additional annual spawning evaluations are needed to determine if the discrepancy in spawning duration observed in 2018 was specific to that year or reflect changes in environmental conditions or population dynamics for Capelin in Norton Sound.

Capelin spawning behavior and activity in Norton Sound was generally consistent with reported observations from other areas and studies (Table 1.2). In Norton Sound, Capelin from nearshore aggregations would ride a wave onto shore, spawn between wave cycles (sometimes grouped as two males with one female), and then ride the next wave back to the ocean, which is similar to observations from other researchers (e.g., Martin et al. 2004). The time of day during which Capelin were observed spawning in Norton Sound was broader than some studies that only observed spawning at night (cf. Pahlke 1985; Gjøsæter 1998). This suggests that the onset of Capelin spawning is not necessarily related to or restricted by nocturnal cues and reflects the fact that this region experiences <3 hr of "darkness" (i.e., civil twilight) during the summer (Timeanddate.com 2019). Offshore winds have been suggested to help Capelin access the beach for spawning (Warner and Shafford 1979; Martin et al. 2004), but no discernable qualitative relationship between spawning timing and wind direction was observed in the current study. In addition, compared to other areas, beach-spawning in Norton Sound occurred at similar water temperatures (Carscadden and Vilhjálmsson 2002; Nakashima and Wheeler 2002), dissolved oxygen concentrations (Arimitsu et al. 2008), and salinities (Præbel et al. 2013; Purchase 2017). These observations suggest that beach-spawning Capelin spawn at similar conditions throughout their geographic range.

Sediment sizes in Norton Sound were similar to documented Capelin beach spawning sites in other areas (Table 1.2 [in current study]; Pahlke 1985; Nakashima and Taggart 2002;

Nakashima and Wheeler 2002). Sediment size affects the ability of oxygen to diffuse to the eggs (Martin et al. 2004), so regional similarities in size may imply a sediment size preference or requirement. Despite uniformity among beaches, there was a gradient in sediment sizes within a beach in Norton Sound (Figure 1.2). Sediment sorting is affected by seasonal variations in wind and wave action and intensity, as well as the extent of shorefast ice, which in concert determine and reflect the dynamic nature of beach environments (Reinson and Rosen 1982; Nakashima and Taggart 2002; Arthur 2017). Energy generated by wind and waves erode, deposit, and transport sediments within and among beaches during open-water periods, particularly storm events, whereas shorefast ice preserves beach integrity during ice covered periods (Reinson and Rosen 1982). These factors may limit beach suitability for spawning among locations and years (Nakashima and Taggart 2002), which could result in a mismatch between suitable substrate conditions and other environmental factors that influence Capelin spawning timing (Therriault et al. 1996; Arimitsu et al. 2008).

Length and weight measurements for spawning Capelin were within the reported ranges for this species, but mean values varied among regions (Table 1.3). Regional differences in weight were reduced when females of similar lengths were compared between Norton Sound and Iceland (Jóhannsdóttir and Vilhjálmsson 1999). Previous studies have noted increases in Capelin length with latitude (Hedeholm et al. 2010; McNicholl et al. 2018); yet latitude could not explain differences in fish lengths between populations in Newfoundland (53.1°N), Togiak Bay, Alaska (59.0°N), and Norton Sound (63.8°N). While it is unclear why these size differences existed, they may reflect interannual variations in size structure and growth among cohorts within the same population (Hedeholm et al. 2010; Maxner et al. 2016).

Capelin spawn between ages 2 to 5 (McNicholl et al. 2018), which is consistent with the age range observed in Norton Sound (Table 1.3). However, there was a higher proportion of older Capelin in Norton Sound in 2018 (Figure 1.4b) than in 1981 (Pahlke 1985). The age composition of Capelin spawners can vary annually (e.g., due to environmental factors; Carscadden et al. 1994; Maxner et al. 2016), which may explain the observed differences between studies. Alternatively, older spawners may reflect a change in life-history strategy, such as a switch from primarily semelparity to iteroparity (Christiansen et al. 2008). Capelin are believed to be facultatively semelparous (Christiansen et al. 2008) and lab experiments, using Capelin from Newfoundland (Penton and Davoren 2013a) and the Barents Sea (Christiansen et al. 2008), confirmed that males and females are capable of iteroparity. In Newfoundland, Capelin (primarily females) have been found spawning in subsequent years, confirming this life-history trait is expressed in some wild populations (Winters 1971; Maxner et al. 2016). Populations in highly variable environments, such as the Bering Sea and Norton Sound, or with low spawning success are more likely to exhibit iteroparity than those that reside in stable environments (Aydin and Mueter 2007; Christiansen et al. 2008; Eisner 2019). Iteroparity in Capelin has not been examined for Pacific Ocean populations, but increasing environmental variability in the Bering Sea may be creating conditions that favor an iteroparous life-history strategy and thus lead to changes in age structure of Capelin populations.

Previous research has noted temporal changes in Capelin size and/or age over the duration of a single spawning season. For example, larger, older Capelin have been observed to arrive on the spawning grounds earlier than their smaller, younger conspecifics in Norton Sound and Newfoundland (Pahlke 1985; Vandeperre and Methven 2007; Maxner et al. 2016). However, no change in Capelin size or age composition was observed in Norton Sound during the 2018 spawning period which may be due to the short timeframe during which Capelin were observed spawning compared to other studies (Table 1.2 [in current study]; cf. Pahlke 1985; Maxner et al. 2016). Future studies could examine Capelin size, age, and spawning duration over multiple, successive years in Norton Sound to identify potential intra- and inter-annual variation in reproductive biology.

Absolute and relative fecundity estimates for Capelin varied regionally, but were most similar for females of comparable length and weight (Table 1.3). Regional differences in fecundity may be due to regional differences in environmental conditions, which can affect prey availability and Capelin growth rates (Jóhannsdóttir and Vilhjálmsson 1999; Penton and Davoren 2013b). For example, water temperature can affect prey abundance, composition, and distribution within and among regions, and access to an abundance of high-quality prey may allow Capelin to grow larger and produce more eggs than fish with lower quantity and quality prey (Aydin and Mueter 2007; Hedeholm et al. 2010; Andrews III et al. 2016). Although influenced by many factors, fecundity estimates scaled by fish length and/or weight were more similar among Capelin populations than unscaled absolute fecundity estimates for most regions.

Female Capelin GSI estimates in Norton Sound were similar to females from other regions (Table 1.3). Similarities among GSI estimates in these studies confirm that females were collected at a similar maturation stage and suggest that they were reproductively mature. Female GSI estimates were higher than males in Norton Sound, which were consistent with results from the Barents Sea (Huse 1998). Sex-related differences in GSI reflected differential energy allocation prior to and during spawning, where females invested energy into egg production and males invested in spawning behaviors and frequency (Huse 1998; Hanson et al. 2008). Further, a positive relationship between GSI and TL for males suggested that longer males invested more mass into gonad production than shorter males, while a lack of relationship for females suggested that females of all lengths invest equal mass into egg production. Larger gonads may be more beneficial for males than for females. Males are thought to spawn multiple times throughout the spawning season so large testes may allow larger males to spawn with more females than smaller males (Huse 1998). Each additional spawning mate rapidly increases the potential number offspring for each male. Large ovaries can also increase the number of potential offspring for females due to egg quantity or quality (Hedeholm et al. 2011); however, relative to males, this potential increase in offspring is small. Sex-specific differences in reproductive investment are common (e.g., Hanson et al. 2008), but additional research is required to understand the factors driving these differences.

To understand ecosystem function, it is important to collect baseline information on the distribution and life history of key species that impact the rest of the ecosystem (Rose 2005; Suryan et al. 2009; Pikitch et al. 2014). Baseline measurements have become increasingly important as the Arctic warms, resulting in shifts throughout the food web (Aydin and Mueter 2007; Suryan et al. 2009). For example, recent mass seabird mortality events in the Bering Sea have been occurring at an unprecedented spatial and temporal scales, emphasizing the need to study forage fishes, such as Capelin, to identify changes in prey abundance and availability (Eisner 2019). Although limited to a single sampling season, the information collected during the current study assists in filling our knowledge gap on spawning Capelin in the Pacific Ocean. Additional monitoring of Capelin distribution and abundance may help detect relationships between Capelin and other species in the Bering Sea food web and predict how these relationships may change in altered climate conditions.

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Tables

Table 1.1. Summary of the geographic survey sections (organized from the northwestern to southeastern most extent of the survey range), distance of shoreline covered per section, and the number of nearshore Capelin aggregations observed during the aerial surveys. Survey section numbers correspond with the geographic landmark numbers in Figure 1.1. See Methods for density calculation. Agg = aggregation.

Survey section	Location	Flight date (dd-Mmm)	Start time (24 hr)	End time (24 hr)	Distance (km)	Total number aggs	Agg density (agg/km)
1–2	Past Wales to Wales	29-Jun	11:30	13:15	29.9	0	0.00
		07-Jul	10:15	11:55		2	0.07
2–3	Wales to West Brevig Spit	29-Jun	11:30	13:15	63.6	11	0.17
		07-Jul	10:15	11:55		15	0.24
3–4	West Brevig Spit to Teller	29-Jun	11:30	13:15	33.3	15	0.45
		07-Jul	10:15	11:55		0	0.00
4–5	Teller to inside Port Clarence	29-Jun	13:55	15:00	55.1	2	0.04
		07-Jul	12:40	14:30		1	0.02
5–6	Outside Port Clarence to Cape Douglas	29-Jun	13:55	15:00	38.2	1	0.03
		07-Jul	12:40	14:30		0	0.00
6–7	Cape Douglas to Cape Woolley (Woolley Lagoon)	02-Jun	10:00	11:20	30.5	0	0.00
		07-Jul	12:40	14:30		0	0.00
7–8	Cape Woolley to Cape Rodney	02-Jun	10:00	11:20	17.6	0	0.00
		07-Jul	12:40	14:30		3	0.17
8–9	Cape Rodney to Sinuk	02-Jun	10:00	11:20	10.0	0	0.00
		18-Jun	13:10	14:15		3	0.30
		23-Jun	23:10	23:58		0	0.00
		07-Jul	12:40	14:30		0	0.00

Table 1.1 cont. Summary of the geographic survey sections (organized from the northwestern to southeastern most extent of the survey range), distance of shoreline covered per section, and the number of nearshore Capelin aggregations observed during the aerial surveys. Survey section numbers correspond with the geographic landmark numbers in Figure 1.1. See Methods for density calculation. Agg = aggregation.

Survey section	Location	Flight date (dd-Mmm)	Start time (24 hr)	End time (24 hr)	Distance (km)	Total number aggs	Agg density (agg/km)
9–10	Sinuk to West Mountains	02-Jun	10:00	11:20	9.4	0	0.00
		15-Jun	8:30	11:15		1	0.11
		16-Jun	8:30	10:35		na[a]	na[a]
		18-Jun	13:10	14:15		47	4.98
		23-Jun	23:10	23:58		0	0.00
		07-Jul	12:40	14:30		0	0.00
10–11	West Mountains to Cripple	02-Jun	10:00	11:20	12.8	0	0.00
		15-Jun	8:30	11:15		32	2.51
		16-Jun	8:30	10:35		6	0.47
		18-Jun	13:10	14:15		0	0.00
		23-Jun	23:10	23:58		0	0.00
		07-Jul	12:40	14:30		0	0.00
11–12	Cripple to Nome	02-Jun	10:00	11:20	18.8	0	0.00
		15-Jun	8:30	11:15		11	0.59
		16-Jun	8:30	10:35		8	0.43
		18-Jun	13:10	14:15		17	0.91
		23-Jun	23:10	23:58		0	0.00
		07-Jul	12:40	14:30		0	0.00
12–13	Nome to Cape Nome (continued on next page)	26-May	10:00	11:45	21.2	7	0.33
		02-Jun	10:00	11:20		1	0.05
		08-Jun	10:15	12:20		3	0.14
		13-Jun	9:40	12:44		0	0.00

Table 1.1 cont. Summary of the geographic survey sections (organized from the northwestern to southeastern most extent of the survey range), distance of shoreline covered per section, and the number of nearshore Capelin aggregations observed during the aerial surveys. Survey section numbers correspond with the geographic landmark numbers in Figure 1.1. See Methods for density calculation. Agg = aggregation.

Survey section	Location	Flight date (dd-Mmm)	Start time (24 hr)	End time (24 hr)	Distance (km)	Total number aggs	Agg density (agg/km)
12–13	Nome to Cape Nome cont.	15-Jun	8:30	11:15		0	0.00
		18-Jun	13:10	14:15		7	0.33
		20-Jun	9:20	11:30		0	0.00
		23-Jun	23:10	23:58		0	0.00
		27-Jun	10:20	12:20		0	0.00
13–14	Cape Nome to Solomon	26-May	10:00	11:45	30.9	0	0.00
		08-Jun	10:15	12:20		3	0.10
		13-Jun	9:40	12:44		11	0.36
		15-Jun	8:30	11:15		7	0.23
		20-Jun	9:20	11:30		0	0.00
		27-Jun	10:20	12:20		0	0.00
14–15	Solomon to Topkok	26-May	10:00	11:45	20.9	0	0.00
		08-Jun	10:15	12:20		17	0.81
		13-Jun	9:40	12:44		2	0.10
		15-Jun	8:30	11:15		11	0.53
		20-Jun	9:20	11:30		2	0.10
		27-Jun	10:20	12:20		0	0.00
15–16	Topkok to Bluff	08-Jun	10:15	12:20	15.0	6	0.40
		13-Jun	9:40	12:44		0	0.00
		20-Jun	9:20	11:30		1	0.07
		27-Jun	10:20	12:20		0	0.00

Table 1.1 cont. Summary of the geographic survey sections (organized from the northwestern to southeastern most extent of the survey range), distance of shoreline covered per section, and the number of nearshore Capelin aggregations observed during the aerial surveys. Survey section numbers correspond with the geographic landmark numbers in Figure 1.1. See Methods for density calculation. Agg = aggregation.

Survey section	Location	Flight date (dd-Mmm)	Start time (24 hr)	End time (24 hr)	Distance (km)	Total number aggs	Agg density (agg/km)
16–17	Bluff to Square Rock	08-Jun	10:15	12:20	6.9	3	0.43
		13-Jun	9:40	12:44		1	0.14
		20-Jun	9:20	11:30		0	0.00
		27-Jun	10:20	12:20		0	0.00
17–18	Square Rock to Rocky Point	08-Jun	10:15	12:20	31.6	21	0.66
		13-Jun	9:40	12:44		15	0.47
		20-Jun	9:20	11:30		15	0.47
		27-Jun	10:20	12:20		0	0.00
18–19	West Golovnin Bay	20-Jun	9:20	11:30	19.2	3	0.16
		27-Jun	10:20	12:20		0	0.00
19–20.2	East Golovnin Bay	20-Jun	9:20	11:30	25.2	19	0.75
		27-Jun	10:20	12:20		0	0.00

[a] Capelin were actively spawning along shore and distinct spawning aggregations were not discernable from the helicopter.

Table 1.2. Comparison of behavior and habitat attributes for spawning Capelin from various regions.

Spawning Attribute	Location	Measurement type	Value	Study
nearshore aggregation size	Norton Sound	median	12 m^2	current
	Newfoundland	median	67 m^2	Carscadden et al. 1994
spawning month(s)	Greenland	range	May to July	Hedeholm et al. 2011
	Norton Sound	range	late May to June	Pahlke 1985
	Norton Sound	range	June	current
	Newfoundland	range	June to July	Vandeperre and Methven 2007
spawning season duration	Norton Sound	range	1 wk	current
	Norton Sound	range	3 – 4 wk	Pahlke 1985
	Newfoundland	range	2 – 4 wk	Vandeperre and Methven 2007
	Newfoundland	range	2 – 4 wk	Maxner et al. 2016
spawn timing	Norton Sound	range	day	current
	Barents Sea	range	night	Gjøsæter 1998
	Norton Sound	range	night or cloudy days	Pahlke 1985
wind direction	Norton Sound	range	on- and offshore	current
	Kodiak (AK)	range	offshore	Warner and Shafford 1979
water temperature	Glacier Bay (AK)	range	4.8 – 8.1°C	Arimitsu et al. 2008
	Norton Sound	range	6.8 – 10.9°C	current
	Norton Sound	range	8 – 9°C	Pahlke 1985
	Newfoundland	range	<12°C	Nakashima and Wheeler 2002
dissolved oxygen	Norton Sound	mean ± SD	9.4 ± 1.0 mg/L	current
	Glacier Bay (AK)	mean[a]	~9.8 – 10.2 mg/L	Arimitsu et al. 2008

Table 1.2 cont. Comparison of behavior and habitat attributes for spawning Capelin from various regions.

Spawning Attribute	Location	Measurement type	Value	Study
salinity (during spawning)	Norton Sound	range	10.6 – 27.7 ppt	current
	Norton Sound	mean ± SD	24.3 ± 6.7 ppt	current
	Glacier Bay (AK)	mean[a]	~29 – 30.5 psu	Arimitsu et al. 2008
salinity (lab experiments)	Newfoundland	range[b]	2 – 28 ppt	Purchase 2017
	Barents Sea	range[c]	3.4 – 51 ppt	Præbel et al. 2013
beach sediment size	Norton Sound	mode	>0.5 mm	current
	western Pacific Ocean	mode	1 – 5 mm	Hart and McHugh 1944, cited by Nakashima and Taggart 2002
	Newfoundland	mode	2 – 25 mm	Nakashima and Wheeler 2002

[a] mean ± SD values were reported in a graph for four sample locations. Values reported here were estimated from the graph and are the two locations with the minimum and maximum mean values.

[b] range for best embryo development.

[c] range of tolerances tested for egg incubation (lethal range may be larger).

Table 1.3. Comparison of biological attributes for spawning Capelin from various regions.

Attribute (Units)	Sex	Mean or Range	SD or (SE)	Location	Study
total length (mm)	M	138 – 176	NA	Newfoundland	Penton 2013
		148.8	6.7	Norton Sound	current
		160	NA	Newfoundland	Penton 2013
		170	NA	Newfoundland/Labrador	Maxner et al. 2016
	F	130 – 180[a]	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		137	8.4	Norton Sound	current
		140	NA	Newfoundland/Labrador	Maxner et al. 2016
		144[b]	NA	Newfoundland	Penton 2013
fork length (mm)	M	122	14.6	Greenland (Nuuk)	Hedeholm et al 2010
		141	6.0	Norton Sound	current
		146[c]	13.9	Norton Sound	Pahlke 1985
		154	12.9	Togiak Bay (AK)	Pahlke 1985
	F	121[c]	8.7	Norton Sound	Pahlke 1985
		124	13	Greenland (Nuuk)	Hedeholm et al 2011
		130	7.6	Norton Sound	current
		143	13.9	Togiak Bay (AK)	Pahlke 1985
total weight (g)	M	12.1 – 30.2	NA	Newfoundland	Penton 2013
		21.2	2.9	Norton Sound	current
		22.1	NA	Newfoundland	Penton 2013
		26[c]	8.1	Norton Sound	Pahlke 1985
		28	8.4	Togiak Bay (AK)	Pahlke 1985

Table 1.3 cont. Comparison of biological attributes for spawning Capelin from various regions.

Attribute (Units)	Sex	Mean or Range	SD or (SE)	Location	Study
total weight (g)	F	7.6 – 29.2	NA	Newfoundland	Penton 2013
		9.7 – 28.4	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		11[c]	3.8	Norton Sound	Pahlke 1985
		12.1[d]	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		13.7	3	Norton Sound	current
		17.0[b]	NA	Newfoundland	Penton 2013
		17.7[e]	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		21	6.6	Togiak Bay (AK)	Pahlke 1985
age (yrs)	both	2 – 4	NA	Norton Sound	current
		2 – 5	NA	Newfoundland	McNicholl et al. 2018
		2	NA	Norton Sound	Pahlke 1985
		3	NA	Norton Sound	current
fecundity (# eggs)	F	6,185	2,249	Greenland	Hedeholm et al. 2011
		6,200 – 19,900	NA	Togiak Bay (AK)	Warner and Shafford 1979
		8,826	4,253	Norton Sound	current
		10,600	NA	Togiak Bay (AK)	Warner and Shafford 1979
		12,924	(247)	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		16,878	3,716	Barents Sea	Christiansen et al. 2008
		>21,000	NA	Newfoundland	Penton and Davoren 2013b

Table 1.3 cont. Comparison of biological attributes for spawning Capelin from various regions.

Attribute (Units)	Sex	Mean or Range	SD or (SE)	Location	Study
relative fecundity based on TL (# eggs/mm)	F	62 – 106	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		64	NA	Norton Sound	current
		152 – 171	NA	Newfoundland	Penton and Davoren 2013b
relative fecundity based on TW (# eggs/g fish weight)	F	590	236	Norton Sound	current
		730	NA	Iceland	Jóhannsdóttir and Vilhjálmsson 1999
		760	NA	Barents Sea	Christiansen et al. 2008
		1,286 – 1,575	NA	Newfoundland	Penton and Davoren 2013b
GSI (%)	F	21.6	6.0	Greenland	Hedeholm et al. 2011
		21.69	8.21	Norton Sound	current
		24 – 43	NA	Newfoundland	Penton and Davoren 2013b
		25.4	4.6	Barents Sea	Christiansen et al. 2008
		28.8 – 36.1	NA	Barents Sea	Karamushko and Christiansen 2002
		33	NA	Newfoundland	Penton and Davoren 2013b

[a] range based on length bins

[b] mean of reported means

[c] age-2 and age-3 fish only (excludes age-4 fish which comprised < 3% of fish)

[d] average of average value reported in nearest length bins (i.e., 135 and 140 mm)

[e] reported average based on all lengths

Figures

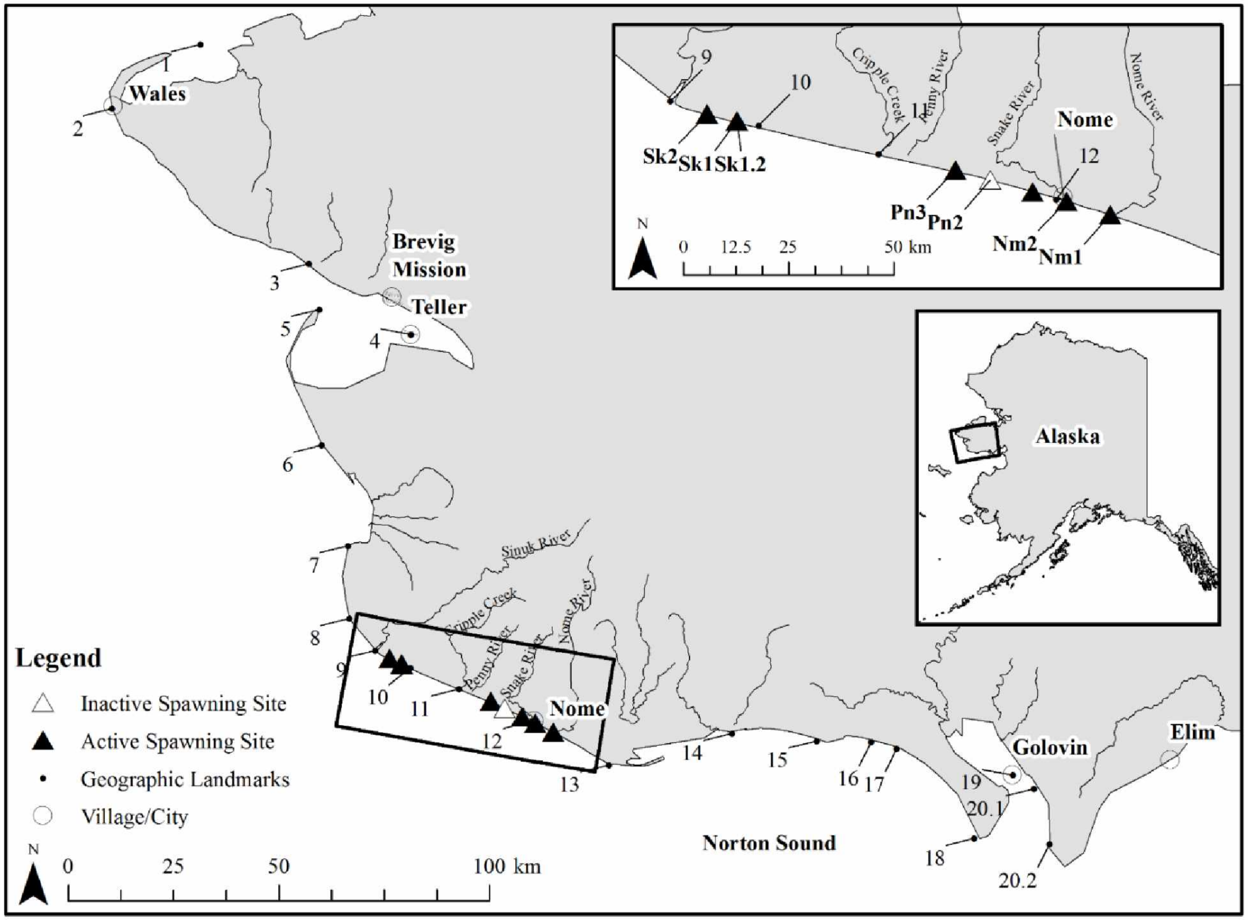

Figure 1.1. Map of the 2018 spawning Capelin spawning sites where Capelin and sediment samples were collected as well as the geographic landmarks (numbered) used to count nearshore fish aggregations during aerial surveys along the coast of Norton Sound, Alaska. Geographic landmark numbers correspond with locations in Table 1.1. Spawning site labels (inset map on top right) correspond to the three broad spawning locations described in-text. Sk = Sinuk River, Pn = Penny River, Nm = Nome River.

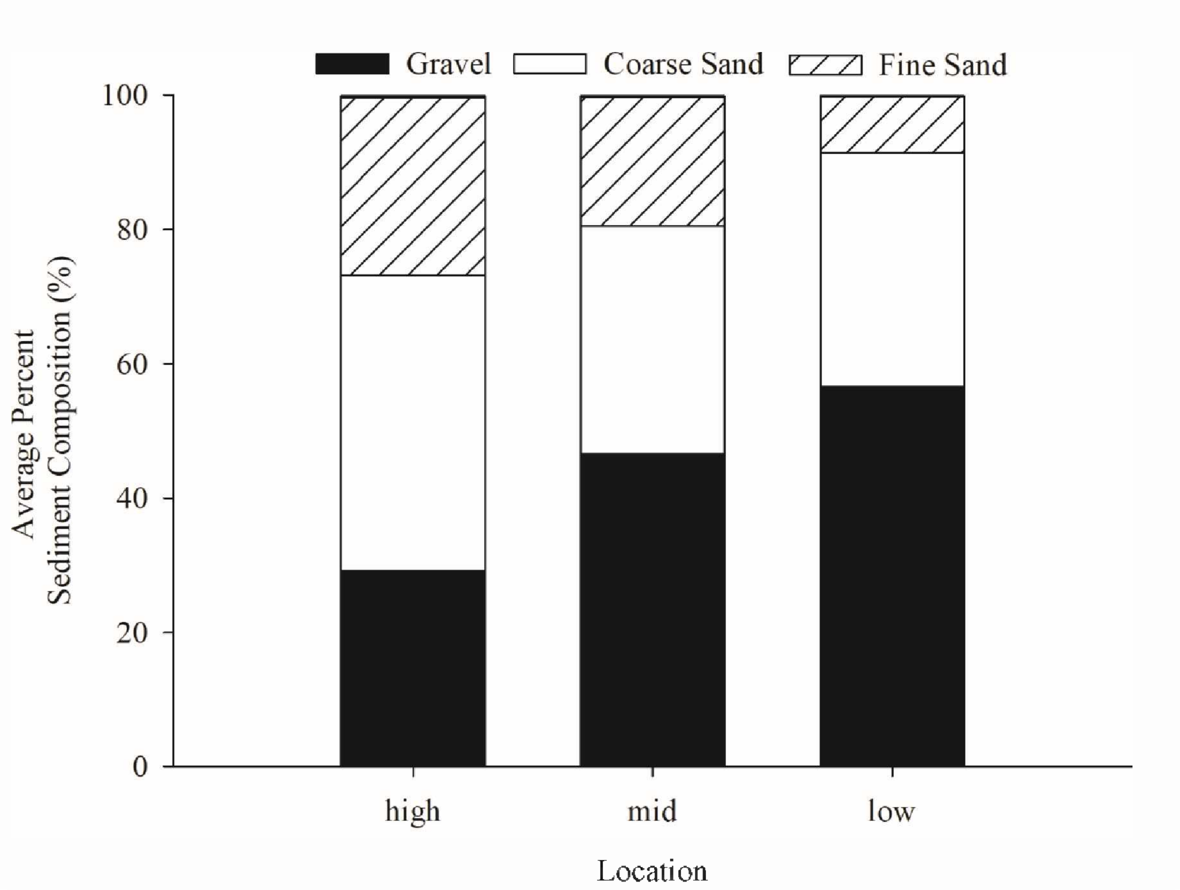

Figure 1.2. Variation in the percent weight of the sediment size classes among locations on the beach at spawning sites (averaged across sites). All locations had < 1% fines. Gravel > 2000 µm, coarse sand = 500 to 2000 µm, fine sand = 63 to 500 µm, fines < 63 µm.

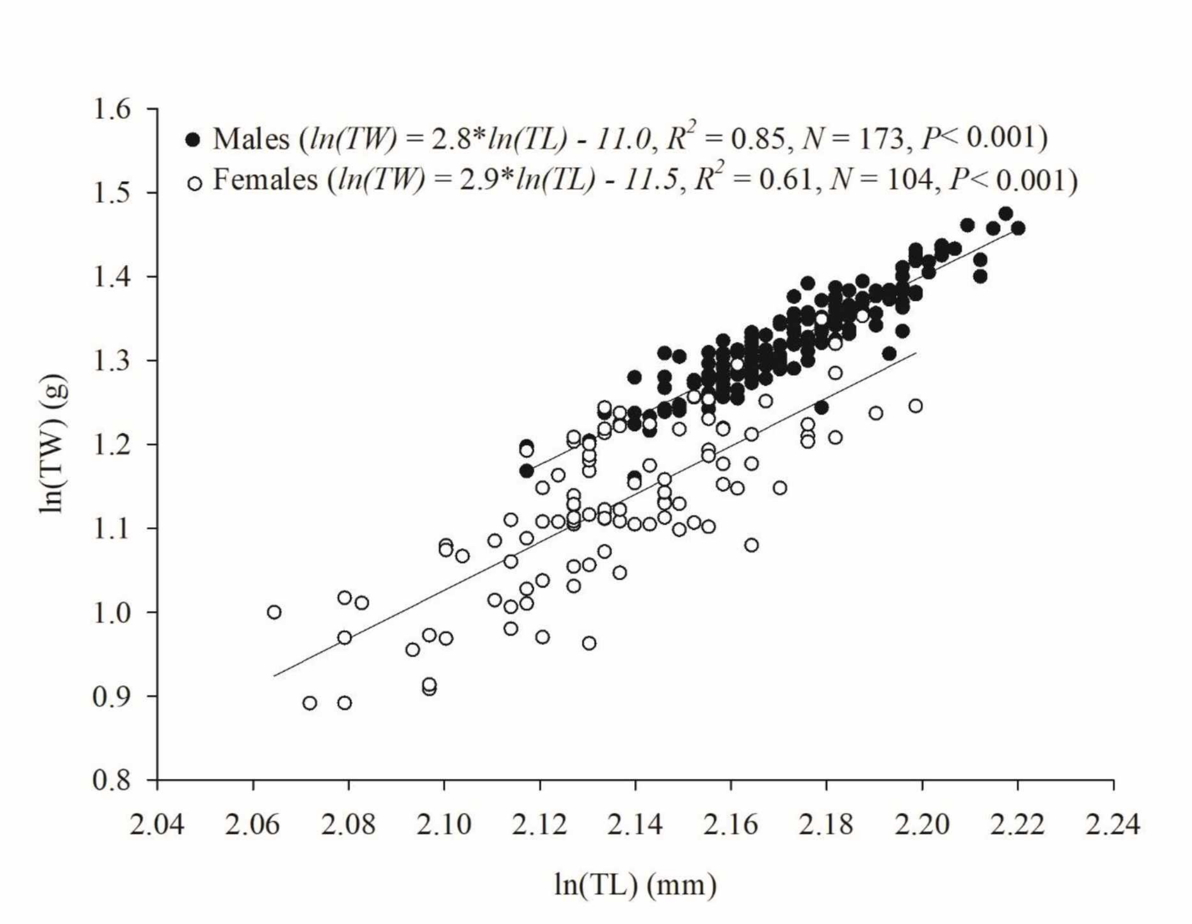

Figure 1.3. Relationship between natural log-transformed TL and total weight (TW) for male and female Capelin.

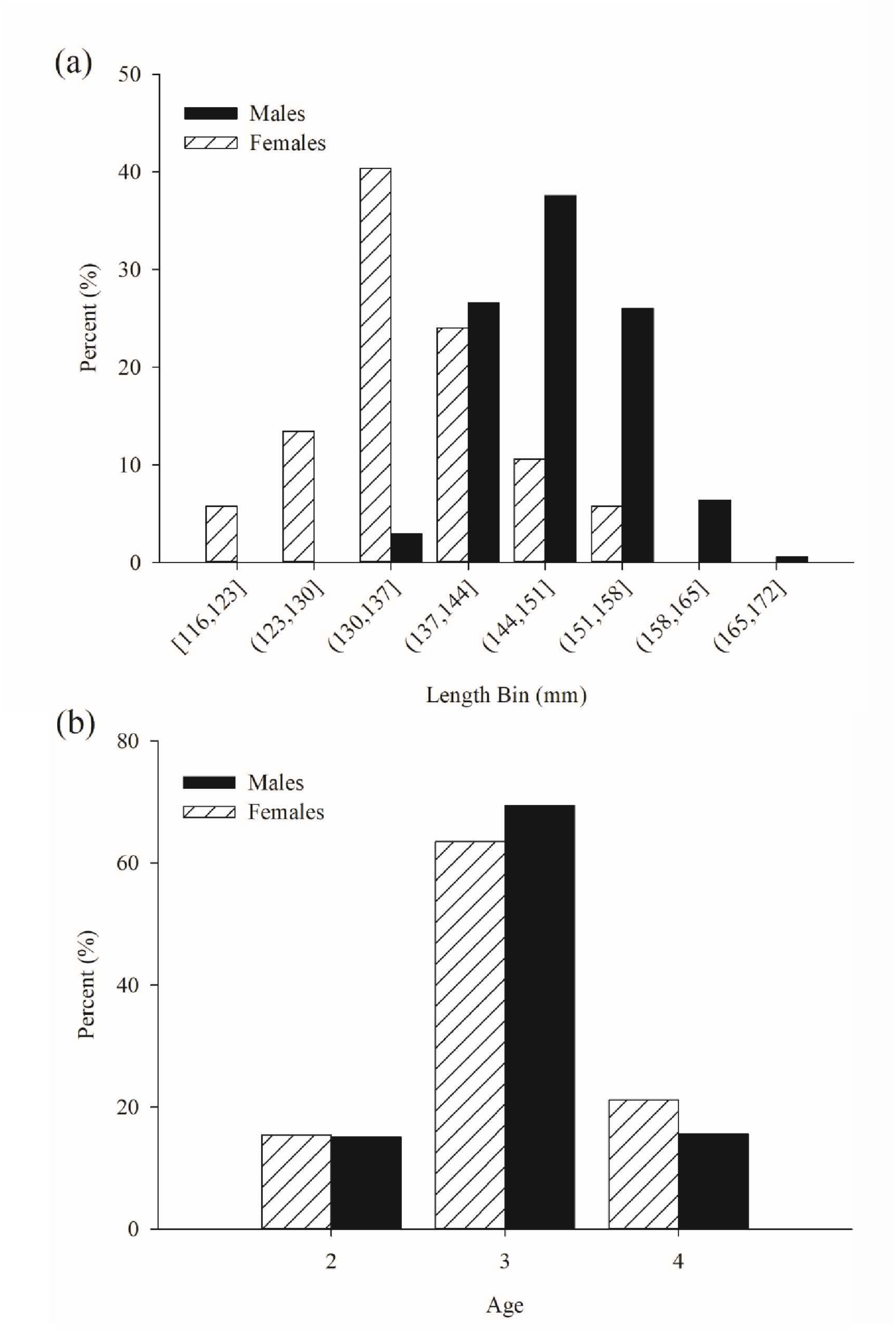

Figure 1.4. Percent frequency distributions for Capelin (a) TL and (b) age.

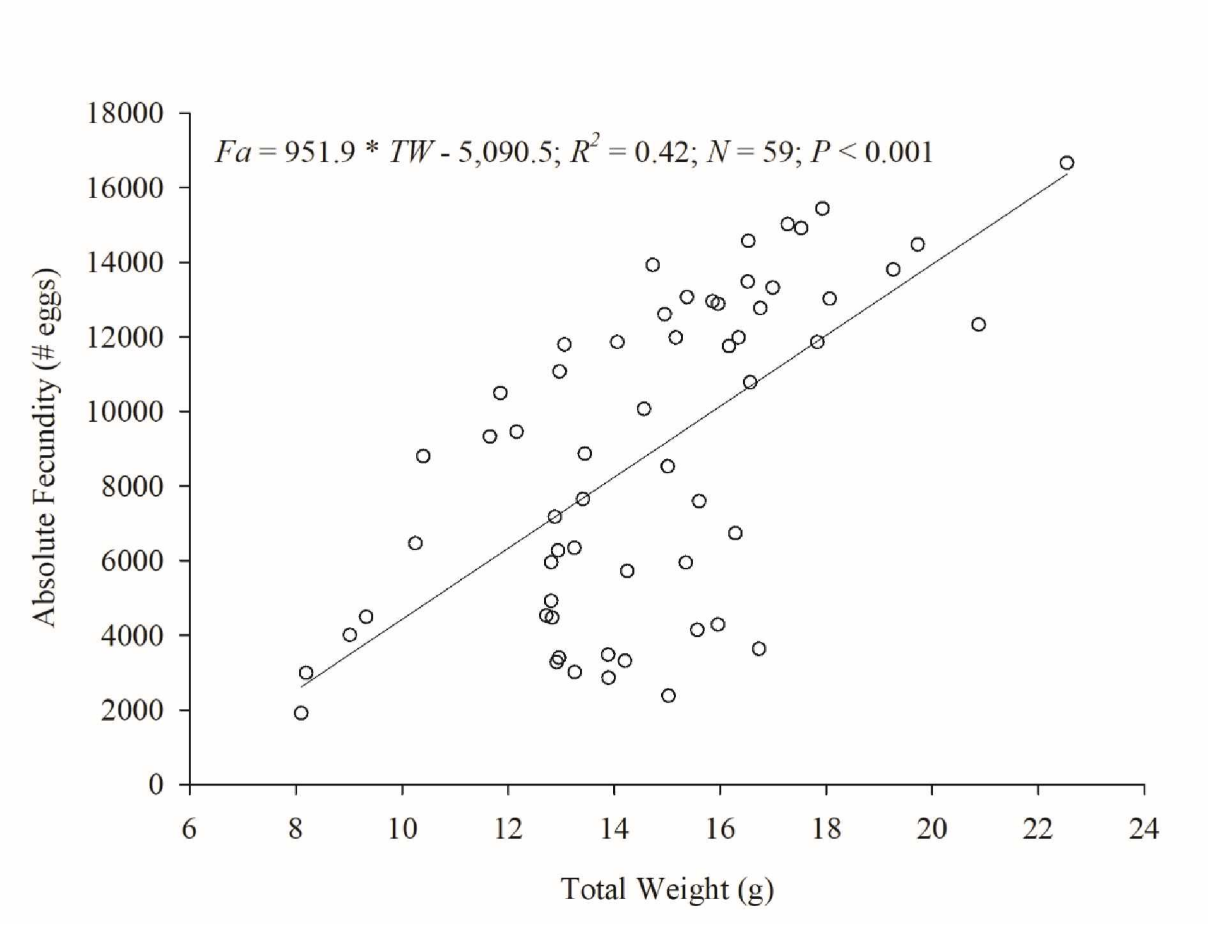

Figure 1.5. Relationship between absolute fecundity (Fa) and total weight (TW) for female Capelin.

Supplement 1.1: Supplemental Figures

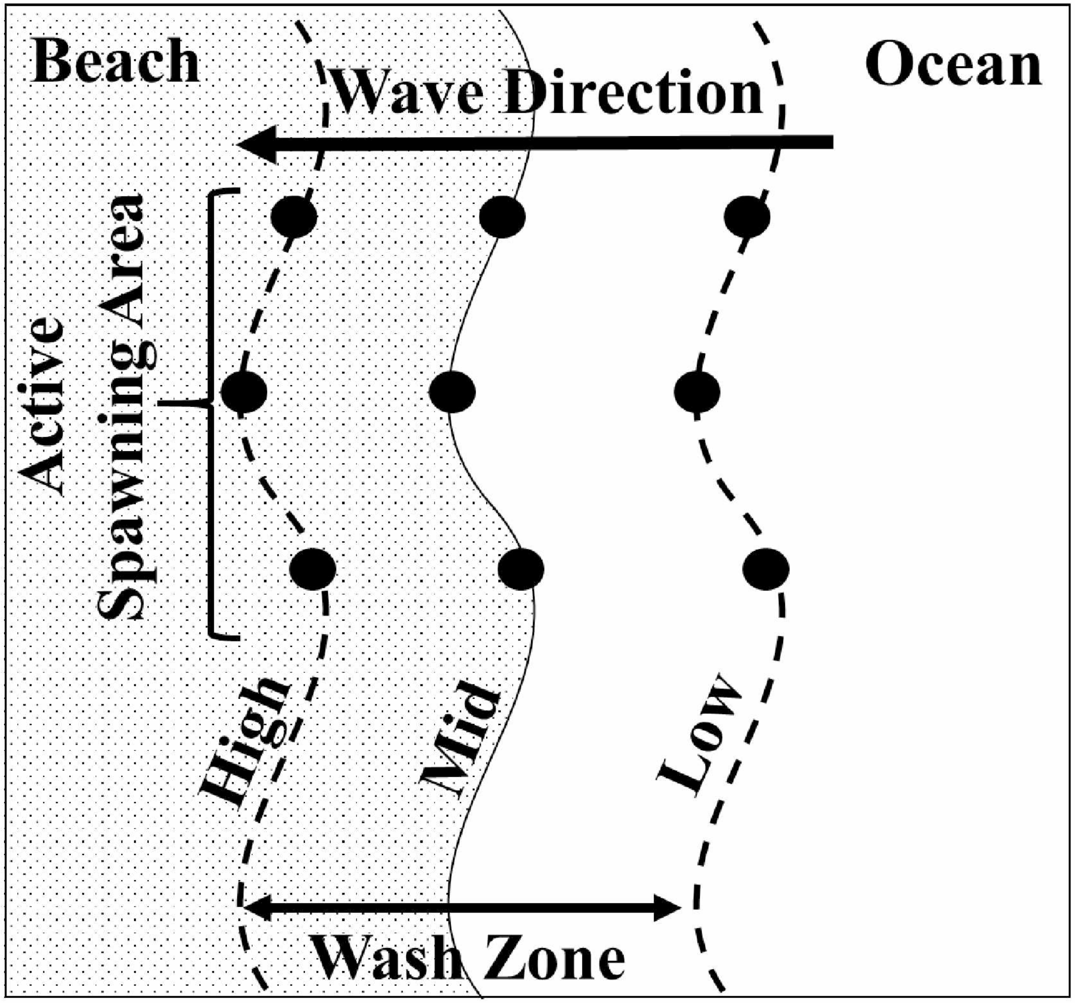

Figure S1.1.1. Schematic of sediment sampling collection locations within the beach wash zone. At each spawning site, three replicate cores (black dots) were collected at three locations (high, mid, and low) within the beach and were combined into one sample per location on the beach. A total of three sediment samples (i.e., high, mid, and low) were analyzed per beach sample.

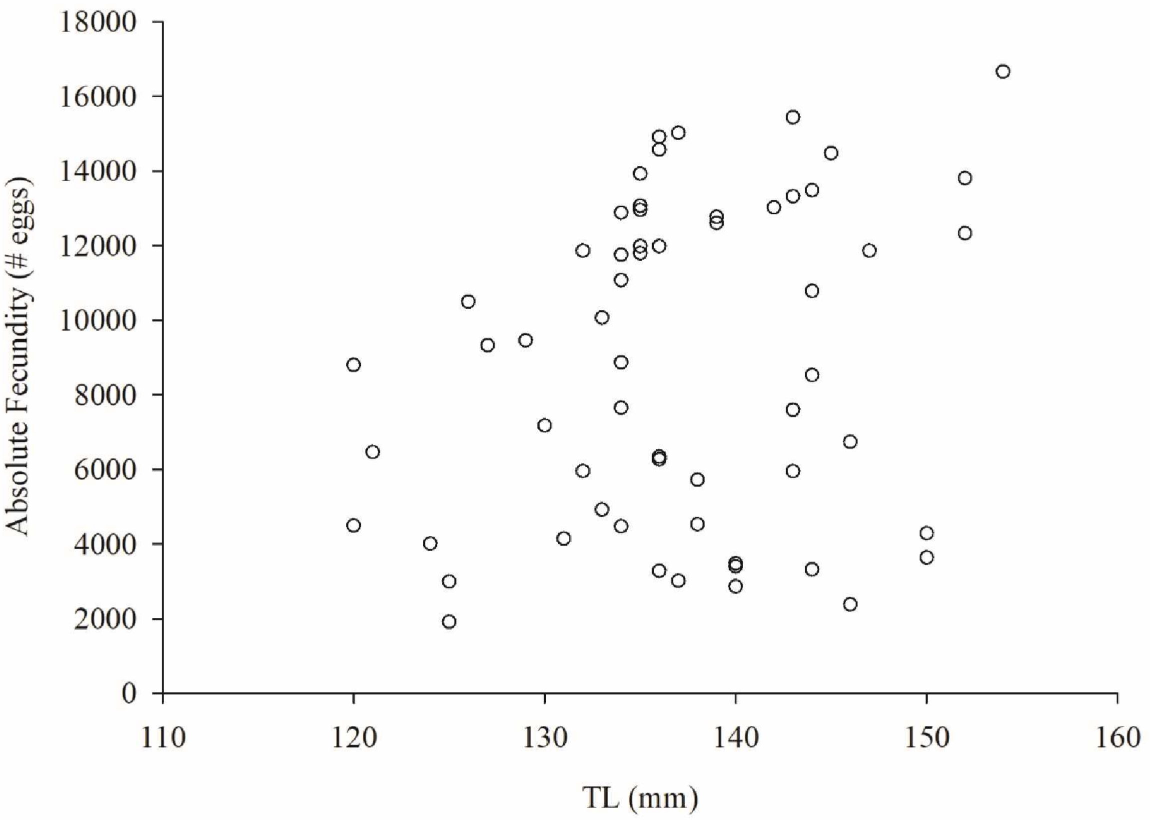

Figure S1.1.2. Relationship between absolute fecundity and TL.

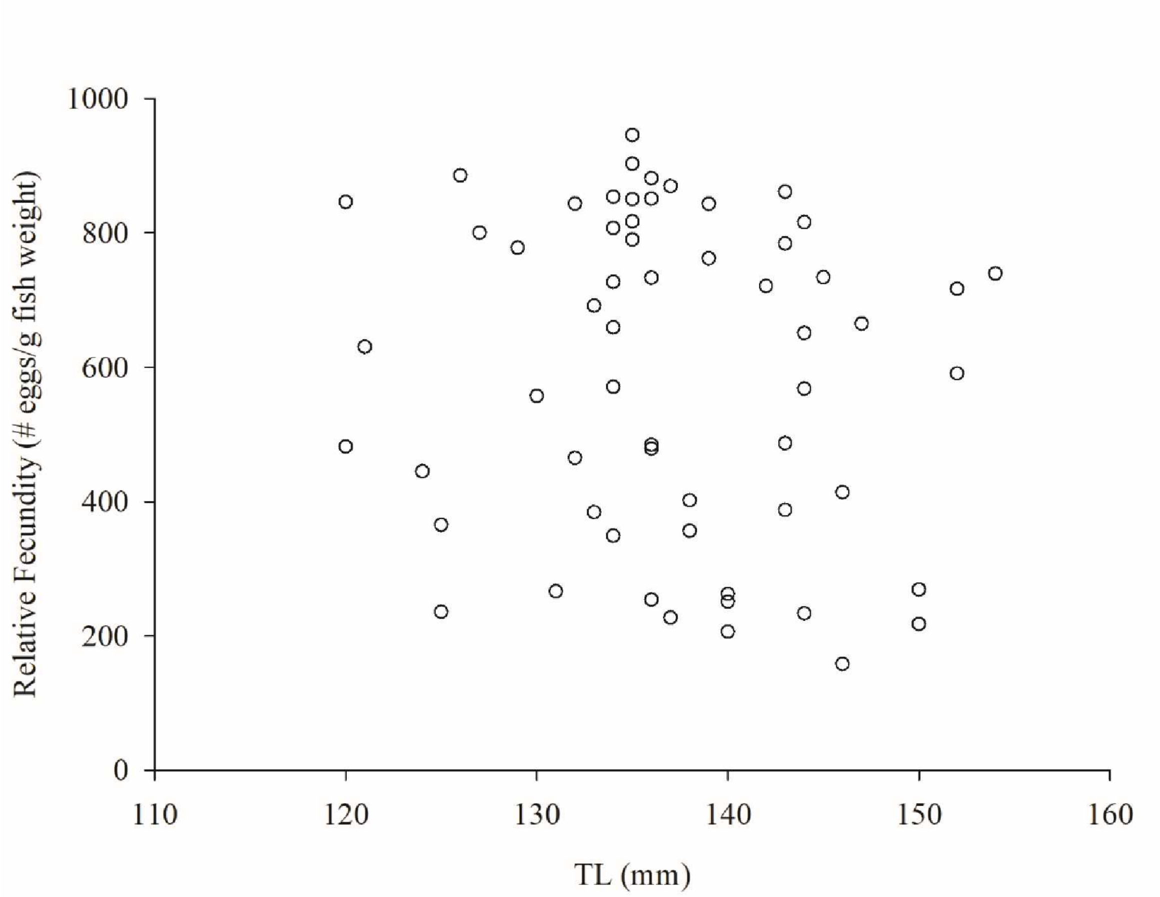

Figure S1.1.3. Relationship between relative fecundity and TL.

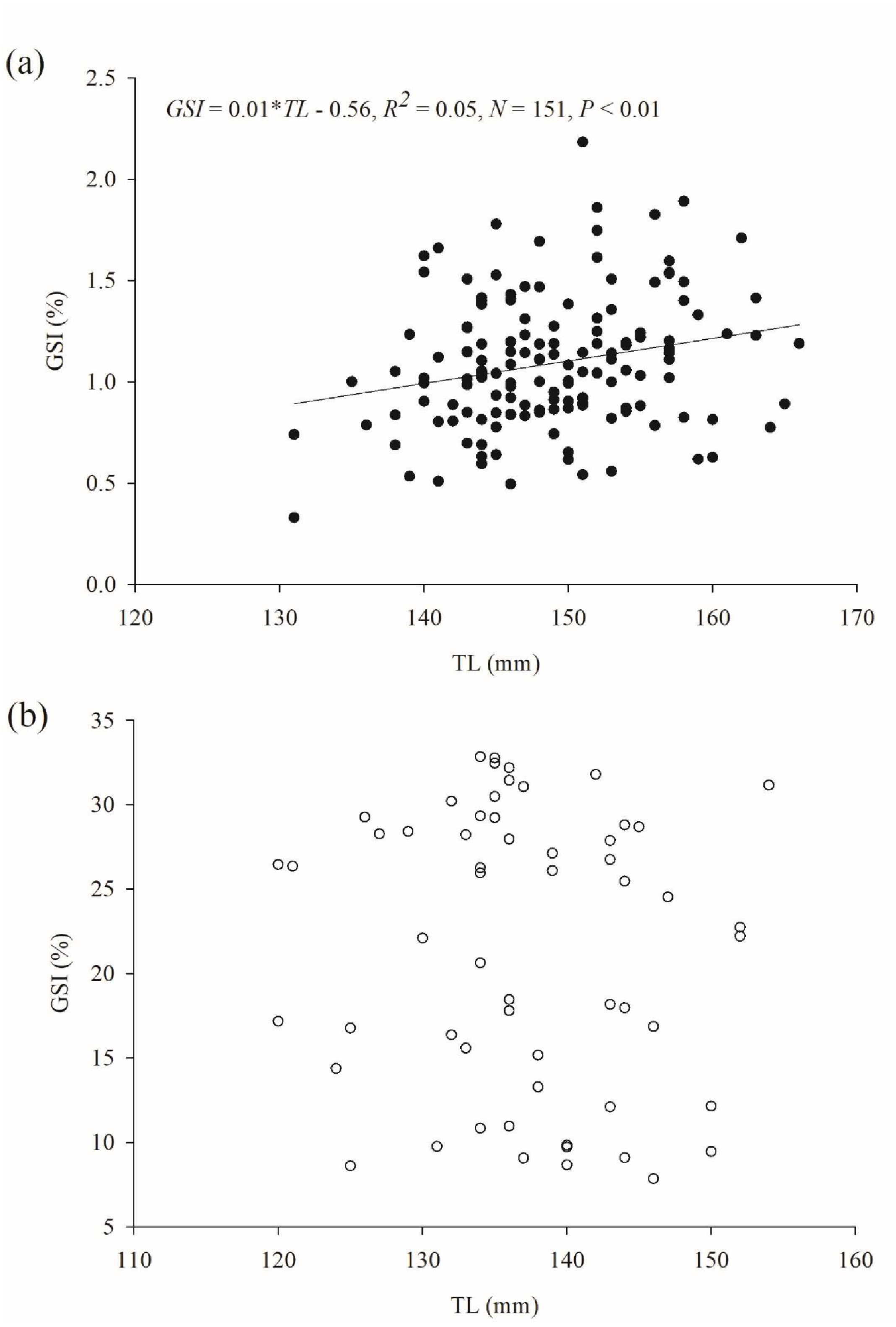

Figure S1.1.4. Relationship between Capelin gonadosomatic index (GSI) and TL for (a) males and (b) females (no correlation). Note scale axes differ.

Supplement 1.2: Observations of monitored Capelin spawning events

Sinuk River Spawning Site

The first Capelin spawning event was observed at the Sinuk River site. Capelin were first seen spawning on 15 June around 0900 hours during an aerial survey. As the helicopter approached, there were hundreds of birds spanning approximately 3,500 m of shoreline. The helicopter landed near the beach so the researchers could collect samples. Birds momentarily flew away when the helicopter and researchers approached the beach, but quickly returned. The researchers walked along the beach from approximately 0900 to 1000 hours, during which time fish were actively spawning. The site was observed the following day at approximately the same time. Fewer birds were observed, but hundreds were still present. Capelin were observed spawning, although the main spawning group covered less shoreline (~1,300 m) and were located closer to Sinuk River. Another aerial survey was flown on 18 June at 1330 hours. Nearshore aggregations and birds were present, but no active beach spawning was observed. Nearshore (<400 m) Capelin aggregations appeared to be disturbing the sediment. This behavior had not been observed on other surveys and plumes of sediment were only observed from some nearshore aggregations. This behavior may be indicative of demersal spawning; however, more research is needed to verify this hypothesis.

Penny River Spawning Site

Community members claimed to have been diving with Capelin near Penny River on 18 June. Additional reports of putative nearshore aggregations seen from a plane were also reported on 20 June. Researchers drove an all-terrain vehicle on the beach from Nome to Penny River to look for spawning Capelin on 21 June from 1145 to 1530 hours. Capelin were found actively spawning at two locations and Capelin mortalities were found at a third location. Birds were observed in all three areas, some of which were actively feeding on Capelin. Each spawning location spanned <400 m of shoreline. Fish were noticed due to the presence of birds because nearshore aggregations were not visible from the beach unless the fish were actively spawning. Researchers stopped at locations with birds to look for Capelin, during which time, fish started spawning. Capelin were collected at 1200 and 1415 hours while actively spawning and mortalities were collected at 1320 hours (each collection was at a different location). Researchers stayed in areas with active bird activity for up to 30 min, during which time Capelin started and/or stopped spawning. All spawning locations (both active and prior) were marked on a handheld GPS. The same length of beach was surveyed again the following day (22 June) from 1100 to 1300 hours but no active spawning was observed. Birds were still present and actively feeding on Capelin in areas where Capelin were collected the previous day (based on the GPS waypoints), but aggregations could not be seen from the beach.

CHAPTER 2: CAPELIN *MALLOTUS VILLOSUS* POPULATION DIFFERENTIATION AMONG AND WITHIN REGIONS USING RELATIVE WARPS[2]

Abstract

Capelin *Mallotus villosus* is a cold-water, marine forge fish preyed upon by many marine predators in the northern Pacific, northern Atlantic, and Arctic oceans. These ecosystems are rapidly changing, but intraspecies diversity (e.g., in morphometry) can increase a species' resilience to these environmental fluctuations. However, this species is less thoroughly studied outside the Atlantic Ocean, which impedes our ability to identify morphometric differences among populations and the functional implications these data can imply. The objective of this study was to use relative warps, a comprehensive geometric morphometric method, to determine if Capelin populations could be distinguished by beach spawning location in the western Canadian Arctic (one location), Newfoundland, Canada (three locations), and Alaska, USA (two locations). Morphometry was examined separately by sex and compared among and within geographic regions using relative warp analysis (RWA), Procrustes ANOVA, estimates of morphological disparity, and canonical variates analysis (CVA). For both sexes, Capelin from the western Canadian Arctic were differentiated from other regions, primarily due to differences in pelvic fin location. Within Newfoundland, Capelin from Witless Bay, Bellevue Beach (males only), and Middle Cove were only distinguishable from each other using CVA. Within Alaska, Norton Sound males were distinct from Prince William Sound males. When all subregions were examined together, evidence for population separation among spawning locations was weaker for both sexes than when regions or subregions were examined separately. These morphological

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[2] Ressel, K. N., D. G. McNicholl, and T. M. Sutton. 2019. Capelin *Mallotus villosus* stock differentiation among and within regions using relative warps. In preparation for submission to Environmental Biology of Fishes.

variations imply diversity throughout this species' geographic distribution. In addition, among and within regions both sexes varied in size and females varied in fecundity. These traits are influenced by multiple environmental factors (e.g., prey availability) and may explain some of the identified morphometric diversity.

Introduction

Capelin *Mallotus villosus* is a cold-water forage fish that serves as an integral component of marine food webs in the northern hemisphere (Carscadden and Vilhjálmsson 2002; Rose 2005). This species is thought to have originated in the Pacific Ocean and dispersed to the Atlantic Ocean during interglacial periods (Carscadden and Vilhjálmsson 2002; Rose 2005; Dodson et al. 2007). Capelin spend most of their life in the open ocean, but migrate inshore to spawn (Carscadden et al. 2013). It is possible that different Capelin populations (i.e., a geographically separated, interbreeding group of fish; Ihssen et al. 1981) occupy similar offshore areas, but segregate for spawning purposes (Carscadden et al. 2013). For Capelin, the spawning season provides an ideal time to differentiate among populations because genetic or morphologic signatures that are unique to one spawning population may not be detectable if samples are collected from offshore shoals that may be comprised of multiple spawning populations (see Ihssen et al. 1981).

Segregation among spawning populations can lead to genetic isolation, when genetic distance (i.e., relatedness) and geographic distance are positively related (Meirmans 2012). Capelin has been separated into at least four broad genetic pools across its circumpolar distribution (Dodson et al. 2007; Præbel et al. 2008). Genetic distinctions have also been identified over smaller spatial scales, such as between Capelin from the Chukchi Sea (Arctic Ocean) and the Gulf of Alaska (Pacific Ocean) as well as between Capelin in the northwest and northeast-central Atlantic Ocean (Dodson et al. 2007; Wildes et al. 2016). These differences in genetic structure suggest that there may be little or no interbreeding within or among Capelin populations in each ocean (Dodson et al. 2007; Præbel et al. 2008).

Genetic analyses are useful for identifying reproductive isolation (Begg and Waldman 1999); however, they can be expensive and require special equipment and chemicals. In addition, the biological importance of genetic differences can be challenging to interpret since the function of many genes is unknown. Morphology, which is influenced by genetic and environmental factors, is another approach that has been used to imply population structure within a species (Begg and Waldman 1999). This method is inexpensive, requires no special equipment, and is often already assessed in many field sampling protocols (e.g., measuring weight and length), or can be easily added (e.g., photographing an organism for later analysis).

An organism's morphometry affects how it functions and how suited it is to its environment (Schindler et al. 2010; Lostrom et al. 2015). For example, morphotypes of Arctic Char *Salvelinus alpinus* vary in the type of prey they consume in Lake Hazen in Canada (Arbour et al. 2011) or their activity level and habitat use in Lake Ellasjøen near Norway (Hawley et al. 2016). Both of these examples decrease intraspecific competition between the morphotypes by segregating the trophic level on which each morphotype feeds in Lake Hazen (Arbour et al. 2011) or utilizing different habitats during spawning and seasons of high foraging (e.g., after ice-break up) in Lake Ellasjøen (Hawley et al. 2016). Some types of morphometric variation can result from adaptations to the organism's local environment (Lostrom et al. 2015). For example, cichlids in East Africa have varying morphologies that allow them to occupy different ecological niches by specializing in the type and size of prey they consume as well as the habitat they occupy (Lostrom et al. 2015). This morphological variation among individuals within a population can help stabilize ecosystem services by filling functional gaps (Schindler et al. 2010).

Multiple studies have differentiated Capelin populations within various subregions of the Atlantic Ocean using traditional (Sharp et al. 1978; Misra and Carscadden 1987) and/or truss-based (Roby et al. 1991; Penton 2013) morphometric approaches. Traditional morphometric methods measure lengths, ratios, and angles of structures, whereas truss-based morphometric methods measure linear distances between sets of landmarks (i.e., discrete, reproducible locations on an organism; Zelditch et al. 2004). However, these types of morphometric approaches may be less effective for analyzing differences in shape and less intuitive for interpreting the results of the analyses than geometric morphometric approaches that examine the relative position of landmarks (e.g., relative warps; Parsons et al. 2003; Zelditch et al. 2004).

Geometric morphometrics, a method to quantitatively study size and shape, transformed traditional morphometric approaches (Cadrin and Friedland 1999; Parsons et al. 2003). Geometric methods overcame a variety of the limitations imposed by traditional methods, such as redundancy in measurements and/or lack of independence between measurements, and provided a powerful tool for visualizing and interpreting biological differences in shape among populations (Parsons et al. 2003; Zelditch et al. 2004; McKeown and Schmidt 2013). One geometric approach is to analyze relative warp scores, which summarize and analyze shape differences among organisms based on the amount of bending energy needed to transform a set of landmark coordinates from one individual or group to another (Zelditch et al. 2004; Webster and Sheets 2010; McKeown and Schmidt 2013). Morphometric analyses have been conducted on spawning-stage Capelin in the Atlantic Ocean but not in the Pacific or Arctic oceans and no relative warp analyses have been conducted on Capelin from any location.

The objective of this study was to determine if putative populations of Capelin can be differentiated based on their spawning location using geometric morphometrics. Relative warps were used to examine putative populations at various geographic scales across the Pacific, Arctic, and Atlantic oceans. Based on previously found genetic and morphometric discrepancies among Capelin from different geographic areas, we expected morphological trait expression to vary by spawning location. Morphological differences could inform the scale at which Capelin segregate (if they mix with other populations in the open ocean) and/or disperse (if they do not mix) when they come nearshore to spawn. High morphological diversity over a small geographic range would suggest there are multiple Capelin populations in that area. Understanding the extent to which Capelin body shape differs among locations will provide insights into the extent of morphometric diversity for this species, which may imply differences in environmental factors, genetic structure, and/or life history traits for Capelin throughout its geographic range (Cooke and Terhune 2015; Lostrom et al. 2015).

Methods

Spawning locations

Spawning-stage Capelin were collected from three regions: 1) the western Canadian Arctic; 2) Newfoundland, Canada; and 3) Alaska, USA (hereafter "CA Arctic", "NFL", and "AK", respectively; Table 2.1; Figure 2.1). Capelin from the CA Arctic were collected from Bennett Point from 14 to 25 July 2014 using a fyke net (1.7 m deep, 15.2-m wings with 2.5-cm nylon stretch mesh) as described in McNicholl (2016). Within NFL and AK, multiple spawning locations were sampled, and each was considered a separate subregion. Within NFL, Capelin were collected from three beaches (i.e., Bellevue Beach, Middle Cove, and Witless Bay; hereafter "BB", "MC", and "WB", respectively) from 11 to 24 July 2018 using a cast net (0.73 m diameter, 1.9-cm stretch mesh). Within AK, Capelin were collected from beaches in Norton Sound (hereafter "NS") from 15 to 21 June 2018 using a dip net (square mesh < 3.8 cm) and from Prince William Sound (hereafter "PWS") on 02 July 2016 using a cast net (1.83 m diameter, 1.9-cm stretch mesh).

Sample preparation

Capelin were processed immediately or frozen and shipped to the University of Alaska Fairbanks. In the laboratory, up to 30 fish per sex were processed from each subregion. Males were available from all subregions, whereas females were available from all subregions except BB and PWS. All fish were measured for TL (mm) and weighed for total weight (g). Capelin were straightened, arranged alongside a ruler for scale, and photographed for morphometric analyses. For all fish except those collected from the CA Arctic, pins were inserted at each landmark to facilitate more reliable landmark digitization and standardized photographs were taken from a mounted camera (Canon PowerShot G10, Canon USA Incorporated, Huntington, New York). Capelin from the CA Arctic were photographed with a non-mounted camera (Nikon Coolpix AW100, Nikon USA Incorporated, Melville, New York) in a similar position as fish from other regions. To explore potential explanations for morphometric variation, estimates of age for AK males as well as absolute fecundity and relative fecundity (fecundity/total weight) for NFL and AK females were opportunistically collected for some Capelin using methods described in Ressel et al. (in Press). Egg density (fecundity/total wet weight of ovary) was also calculated for NFL and AK females to infer potential differences in relative egg size.

Eighteen digital landmarks were applied to each photograph using tpsDig2 (version 2.31; Rohlf 2017) three separate times by a single researcher (Figure 2.2). Landmarks were placed at fin insertion points (landmarks 3 – 4, 5 – 6, 9 – 12), at local maxima or minima of a curve (landmarks 1 and 7 – 8), and at biologically relevant locations such as along the lateral line (landmarks 2 and 13 – 18). To correct for bending along the lateral line, landmarks 1 and 14 – 18 were used to “unbend” specimens using the cubic transformation in the “Unbend Specimens” program in tpsUtil (version 1.78; Rohlf 2019). Landmarks 15 – 17 were excluded from the remaining analyses because they were only digitized to facilitate unbending.

Unbent landmarks were further transformed and analyzed using “R Studio” (version 1.1.463 operating with “R” version 3.5.2; R Studio Team 2016; R Core Team 2018) with the packages “geomorph” (version 3.0.6; Adams et al. 2018) and “Morpho” (version 2.6; Schlager 2017). Males and females were processed separately for all analyses. All three replicates of digitized landmarks for each fish were combined into a single dataset, and transformed using the General Procrustes Analysis (GPA; function: gpagen, package: geomorph; Webster and Sheets 2010; Adams et al. 2018). Consistency in assigning landmark locations was assessed by calculating the Euclidean distances between the landmark location of one fish in a given trial and the mean landmark location from all fish in all three trials combined. The Euclidean distances for each fish in each trial were cube-root transformed to obtain a more normal distribution. The tails of the distribution of landmark distances still departed from normality, so median distances (rather than the mean) were further examined to identify landmarks that were potentially outliers (Zelditch et al. 2004). The median of the cube-root transformed Euclidean distance for each landmark was plotted on a quantile plot to determine if there were any landmarks that deviated from normality. Landmark 12 was identified as an outlier for the females and although no landmarks were identified as outliers for males, landmark 12 was removed from both the male and female datasets for consistency and simplicity. The remaining landmark coordinates for each fish were averaged across all three replicates to obtain mean GPA transformed landmark coordinates that formed the basis for all remaining analyses.

Software and statistical analyses

Capelin were separated by sex, grouped by spawning location, and examined on three geographic scales: 1) among regions (i.e., CA Arctic, NFL, or AK); 2) within a region (i.e., BB, MC, and WB were subregions of NFL, whereas NS and PWS were subregions of AK); and 3) among all subregions combined (i.e., CA Arctic, BB, MC, WB, NS, and PWS). Biological traits (i.e., condition, age, absolute fecundity, relative fecundity, and egg density) were compared among and within groups. Fish condition was reported as the ratio of total weight to total length (hereafter "TW:TL"). Egg density was transformed by taking it's reciprocal to satisfy normality assumptions prior to analysis. Analysis of variance (ANOVA) and Tukey post hoc analyses were used to compare traits when data satisfied normality assumptions and Kruskal–Wallis *H*-test and Dunn's post hoc analyses were used for comparisons when data were not normal.

A relative warp analysis (RWA) was conducted to generate warp scores and reduce the number of variables needed to describe the shape variation between spawning groups (package: Morpho, function: relWarps; Schlager 2017). One RWA was conducted using the entire dataset to determine variation among regions. In contrast, separate RWAs were conducted using only fish from NFL or AK to determine variation within each respective region. In RWA, the variable α can be used to weight bending energy, which describes how much energy is needed to transform one shape into another (Zelditch et al. 2004). Alpha values can range from -1, which emphasizes large-scale variation, to +1, which emphasizes small-scale variation (Zelditch et al. 2004). When $\alpha = 0$, bending energy is unweighted and the RWA is essentially the same as a Principal Components Analysis of warp scores (Zelditch et al. 2004; Webster and Sheets 2010). In the current study, analyses were conducted with $\alpha = -1$, 0, and +1, and the respective results were compared. Warp scores were mathematically computed from a thin-plate spline (TPS) deformation grid for use in standard statistical analyses (Webster and Sheets 2010). The TPS deformation grids were used to visualize how the shape of one individual or group varied from another (Zelditch et al. 2004). The number of relative warp scores reported was determined based on natural breaks in the percent of morphometric variation for which it accounted. Each score was reported as the percent of morphometric variation it explained. The first and second relative warp scores (RW1 and RW2, respectively) were graphed to determine how well the relative warps separated fish by region and/or subregion based on their known spawning location. To interpret the biological relevance of the first few relative warp scores, the difference between the mean shape of all fish and the individuals with the largest and smallest relative warp scores were plotted and compared using a TPS grid.

Three additional tests were conducted to statistically verify if putative visual clusters of fish from the RWA were distinct. First, a Procrustes ANOVA was conducted using 10,000 permutations of the GPA-transformed landmark coordinates (package: geomorph, function: procD.lm; Adams et al. 2018). When significant, the ANOVA was followed by an estimate of morphological disparity, computed with 10,000 permutations, to determine which groups differed based on pairwise comparisons of the Procrustes variance among groups (package: geomorph, function: morphol.disparity; Adams et al. 2018). Finally, a canonical variants analysis (CVA) was conducted on the warp scores to determine if Capelin could be accurately reassigned to groups based on their respective spawning location (Zelditch et al. 2004). A jackknife cross-validation technique was used to classify individuals based on 10,000 permutations (package: Morpho, function: CVA; Schlager 2017), and the overall classification accuracy was reported and graphically depicted using one to two canonical variates.

A map of the study region was created using ArcGIS (version 10.5.1; Environmental Systems Research Institute 2017). The software programs "R Studio" (version 1.1.463 operating with "R" version 3.5.2) was used to conduct analyses with significance at $\alpha = 0.05$ (Sheets 2014; R Studio Team 2016; R Core Team 2018). Graphs were generated with "R Studio" and SigmaPlot (version 12.3; Systat Software Inc. 2012).

Results

Biological traits

Capelin condition, age, fecundity, and egg size varied among and within regions (Table 2.2). Males from NFL had a TW:TL that was 16% larger than males from the CA Arctic and 33% larger than males from AK (Kruskal-Wallis: $H = 56.84$, $df = 2$, $P < 0.001$). Females from the CA Arctic had a TW:TL that was 20% smaller than females from NFL and AK (ANOVA: $F = 20.56$; $df = 2, 113$; $P < 0.001$). Absolute fecundity for NFL females (mean ± SD = 20,662 ± 6,231 eggs) was 134% larger than for AK females (8,826 ± 4,253 eggs). Relative fecundity was also 132% larger for NFL females than AK females (Kruskal-Wallis: $H = 74.14$, $df = 1$, $P < 0.001$), whereas egg density was 46% higher (ANOVA: $F = 186.70$; $df = 1, 111$; $P < 0.001$). Within NFL, males from MC had a TW:TL that was 19% larger than males from BB and 15% larger than males from WB (ANOVA: $F = 15.84$; $df = 2, 83$; $P < 0.001$), but TW:TL was similar for females from MC and WB (ANOVA: $F = 0.69$; $df = 1, 54$; $P = 0.41$). Absolute fecundity did not differ between WB and MC females (Kruskal-Wallis: $H = 3.43$, $df = 1$, $P = 0.06$). However, relative fecundity was 18% larger for females from WB than MC (Kruskal-Wallis: $H = 8.76$, $df = 1$, $P < 0.01$) and egg density was 20% higher (ANOVA: $F = 12.21$; $df = 1, 52$; $P < 0.001$). Within AK, males from NS had a TW:TL that was 58% larger than males from PWS (Kruskal-

Wallis: $H = 44.26$, $df = 1$, $P < 0.001$). Capelin from NS ranged in age from 2 to 4, whereas all PWS males were age 1.

Weighted α comparisons

When the value of α was modified for the RWA, the resulting relative warp scores did not alter which Capelin spawning locations were distinguishable from each other using RWA or CVA. The highest proportion of variance in the first two relative warps was explained by $\alpha = +1$, regardless of which regions or subregions were compared. However, all three α values suggested similar clustering of groups based on the first two relative warps. Conversely, fish were most accurately assigned to their respective spawning groups when $\alpha = 0$, except when females were analyzed for variation among all subregions at which time the percent of correctly classified fish was 86.4% when $\alpha = +1$ versus 85.6% when $\alpha = 0$. More variation was always explained by $\alpha = 0$ or $\alpha = +1$ than by $\alpha = -1$. Because the significance of the statistical analyses and the visual distinctness of Capelin spawning clusters did not vary regardless of the value of α, only $\alpha = 0$ results are reported.

Among region variation

For both male and female Capelin, RWA distinguished CA Arctic fish from NFL and AK fish. The RWA for males was best explained by the first three relative warp scores (RW1 – 3), which accounted for a cumulative variation of 52.9% (RW1 – 3 accounted for 29.2%, 12.5%, and 11.3% of the variation, respectively). The first two relative warp scores appeared to separate CA Arctic males from NFL and AK males, whereas NFL and AK males were indistinguishable from each other (Figure S2.1a in the Supplemental Figures). For females, the first relative warp score best explained variation in shape (37.0%), while the first two scores cumulatively accounted for 49.9% of the variation. The CA Arctic females were also separated from NFL and AK females, which were more clustered (Figure S2.1b).

When TPS grids were used to visualize the minimum (-) and maximum (+) relative warp values, the deformation highlighted by RW1 was driven by the location of the pelvic fin for both sexes, whereas the deformation emphasized by RW2 differed by sex. For males, RW1- corresponded with a more posterior pelvic fin insertion point than males with RW1+ (Figure 2.3a). The second relative warp accounted for extra bending along the lateral line, where RW2- males had a slightly u-shaped curvature and RW2+ males had a more linear or slightly bridge-shaped curvature (Figure 2.3a). For females, RW1- corresponded with a more anterior pelvic fin placement than RW1+ (Figure 2.3b). The variation explained by RW2 appeared to differentiate among head lengths, where the head/body transition point (landmark 2 in Figure 2.2) was more posterior on the body in RW2- females than RW2+ females (Figure 2.3b).

Visual differences identified using the RWA were statistically confirmed with a Procrustes ANOVA and an estimate of morphological disparity, suggesting that at least one region was distinct from the others for males ($F = 6.16$; $df = 2, 174$; $P < 0.001$) and females ($F = 31.88$; $df = 2, 115$; $P < 0.001$). Estimates of morphological disparity indicated that CA Arctic males differed from NFL ($P < 0.01$) and AK ($P = 0.01$) males, while NFL and AK males were similar ($P = 0.62$). The CA Arctic females did not differ from NFL females (morphological disparity: $P = 0.37$), but did differ from AK females (morphological disparity: $P < 0.001$). Females from NFL and AK were also distinct from each other (morphological disparity: $P < 0.001$).

Classification accuracy for Capelin using CVA was 50.3% for males and 94.9% for females. Two canonical variates (CV1 – 2) were identified, where CV1 accounted for 84.1% of the total variation in males and 82.1% of the variation in females. When CV1 and CV2 were graphed, CA Arctic males were partially differentiated from NFL and AK males, which remained a single cluster (Figure 2.4a). In contrast, CV1 – 2 divided females into three spawning regions (Figure 2.4b).

Within region variation

Capelin from NFL were further examined to determine if they could be differentiated among BB (males only), MC, and WB. When males were analyzed using RWA, the largest proportion of the variation was solely accounted for by RW1 (21.7%). Scores for the first two relative warps only accounted for 33.5% of the cumulative variation in shape, but none of the subregions were distinguishable from each other (Figure S2.2a). For females, variations in shape were best explained by the first two relative warp scores. These scores accounted for a cumulative variation of 36.0% (RW1 = 19.5%), and were not adequate for differentiating between subregions (Figure S2.2b). A Procrustes ANOVA supported the visual results of the RWA denoting that subregions were not distinct for males ($F = 1.04$; $df = 2, 84$; $P = 0.41$) or females ($F = 1.70$; $df = 1, 56$; $P = 0.06$). Classification accuracy using CVA was 74.7% for males based on two canonical variates (CV1 explained 62.7% of variation) and 84.5% for females based on one canonical variate (Figure 2.5).

Male Capelin were also examined for differences between spawning subregions in Alaska. The first three relative warp scores best explained the variation in shape and accounted for 53.1% of the variation overall (RW1 – 3 accounted for 27.7%, 14.2%, and 11.1% of the variation, respectively). The first two relative warp scores appeared to separate NS and PWS males primarily along RW1 (Figure S2.3). A Procrustes ANOVA confirmed that the two subregions statistically differed (*F* = 13.34; *df* = 1, 58; *P* < 0.001). Classification accuracy using CVA was 95.0% based on one canonical variate (Figure 2.6).

Variation among all subregions

When all subregions were examined, male Capelin were not well sorted whereas females were distinguishable to their respective regions but not subregions. The CVA classified males into one of six potential subregions (i.e., CA Arctic, BB, MC, WB, NS, and PWS), with an accuracy of 28.8%. Five canonical variates (CV1 – 5) were identified, which accounted for 47.6%, 21.3%, 15.8%, 9.3%, and 6.1% of the overall variance, respectively. However, none of the subregions were distinguishable from each other for males (Figure 2.7a). In contrast, the CVA classified females into one of four subregions (i.e., CA Arctic, MC, WB, and NS), with an accuracy of 85.6%. Three canonical variates (CV1 – 3) were recognized, which accounted for 75.3%, 18.6%, and 6.0% of the overall variance, respectively. For females, CV1 and CV2 only clustered females by region, but did not differentiate between the two NFL subregions (i.e., MC and WB; Figure 2.7b).

Discussion

Morphometry has previously been utilized to distinguish among Capelin populations in the Newfoundland–Labrador area (Sharp et al. 1978; Misra and Carscadden 1987; Roby et al. 1991); however, newer morphometric approaches that analyze relative warp scores offer a more comprehensive approach towards measuring shape for this species (Zelditch et al. 2004; McKeown and Schmidt 2013). The current study utilized relative warps to identify morphometric differences for male and female Capelin on multiple geographic scales across their distribution. Capelin from the CA Arctic were regularly distinguishable from other regions, while distinctions among Capelin at the subregional scale depended on the number of putative populations into which fish could be classified and the statistical technique used to classify them. Because morphology is influenced by genetic and environmental factors, morphological differences suggest that some spawning populations may be genetically and/or geographically isolated from other populations (Begg and Waldman 1999).

Using RWA and TPS grids, Capelin from the CA Arctic were distinguishable from Capelin in other regions primarily based on the location of their pelvic fin, which may reflect regional differences in spawning habitat. Subtle differences in fin shape or position may give some individuals a competitive advantage over others in certain environments (Yamanoue et al. 2010). For example, pelvic fin shape may help reduce drag while swimming in rainbow trout *Oncorhynchus mykiss* and improve turning precision in Arctic Char (Arbour et al. 2011). In addition, anteriorly positioned pelvic fins can help fishes regulate their vertical placement in the water column whereas thoracically placed pelvic fins are more functionally important for swimming (Yamanoue et al. 2010). Additional research is needed to examine the putative relationship between spawning habitat and pelvic fin function for Capelin.

Results from the CVA provided weak support for morphological distinctions among regions for males, but strong support for females. During the spawning season, the body shape of females changes more than males (Friðgeirsson 1976). Because female plumpness varies depending on the quantity and size of eggs in her abdomen (Friðgeirsson 1976), females may have been more accurately separated into their respective spawning locations than males due to regional variation in spawner maturation stage at the time of capture. Absolute fecundity estimates in the current study were consistent with previous estimates for these regions (Carscadden and Vilhjálmsson 2002; Ressel et al. in Press), suggesting that females from both regions were fully fecund and verifying that only spawning-stage adults were analyzed.

However, egg density varied among regions, which may correlate with maturity differences in egg development due to sampling protocols since Capelin were collected while actively spawning on the beach in NS, but were caught nearshore prior to spawning at all other locations. As a result, females captured nearshore may have varied more in how developed their eggs were than females collected during spawning. Alternatively, discrepancies in egg density may reflect a tradeoff between egg quantity and size, which is seen in various fish species (McBride et al. 2015). This reproductive tradeoff can be affected by environmental factors, which could suggest that Capelin from these regions vary in more than just morphometry.

Evidence for morphometric variation within NFL Capelin differed based on the analytical approach used to distinguish among subregions, which likely reflects methodological discrepancies among statistical tests. Both RWA and ANOVA examine variation among individuals in pre-defined groups, whereas CVA pools all individuals together, classifies individuals into groups, and assesses how accurately the classified groups match the pre-defined groups (Zelditch et al. 2004; Webster and Sheets 2010). Therefore, within-group variation (e.g., from the 25% of males and 15% of females that were incorrectly classified using CVA) could have masked morphological differences in the RWA and ANOVA causing the groups to appear similar. Morphometric distinctions within NFL, which were only identified using CVA, corroborated previous research which found evidence for population separation among spawning-stage Capelin in the Newfoundland–Labrador area (Sharp et al. 1978; Misra and Carscadden 1987; Roby et al. 1991). In the current study, Capelin were collected from some of the same areas in NFL as in Misra and Carscadden (1987), and areas were analyzed separately rather than grouped as one region. Because some evidence for population separation by subregion was found in the current study, there may be greater diversity among NFL Capelin than was previously suggested (cf. Misra and Carscadden 1987).

Within AK, strong morphometric variation was detected for males using RWA and CVA, which may have resulted from allometric differences in morphometry among the two subregions. A previous study found that age occasionally affected which Capelin populations could be distinguished within NFL and which morphological traits differed among subregions (Misra and Carscadden 1987). For example, head length differed among two regions in NFL when age-3 and age-4 males were examined together, but not when each age group was assessed independently (Misra and Carscadden 1987). Morphological features, such as growth rate, condition, and/or age, often change as fish mature and are influenced by environmental conditions (Zelditch et al. 2004; McKeown and Schmidt 2013). For example, warmer waters can lead to faster growth rates, earlier maturation, and younger spawning ages than cooler water (Gjøsæter 1999; Hedeholm et al. 2011; McNicholl 2016). Assuming spawners from PWS and NS occupy offshore waters that are adjacent to their spawning sites, warmer water conditions for PWS fish, as is evident by the lack of winter sea-ice in this region compared to the Bering Sea (Niebauer et al. 1994; Aydin and Mueter 2007), may have contributed to the condition and age discrepancy observed between PWS and NS males. Alternatively, PWS males may represent an atypical group of spawners unique to 2016 because Capelin normally spawn between ages 2 – 5 (Misra and Carscadden 1987; McNicholl 2016; Ressel et al. in Press), but all PWS males were age 1. Additional research is necessary to determine if Capelin from PWS were representative of typical spawners in that area and to verify putative morphological division between NS and PWS males.

When all spawning locations were examined together, Capelin could not be distinguished among subregions for either sex; however, females could be differentiated by region. Lack of morphometric distinction among males from each subregion contrasted with results reported in the current study — that RWA and CVA analyses conducted at regional and subregional geographic scales provided some evidence for population segregation for both sexes. Greater putative variation in morphometry, environmental factors, and/or genetic structure within and among fish from all subregions may have concealed morphometric differences that were detectable when subregions were examined individually (Ihssen et al. 1981; MacLean and Evans 1981; Begg and Waldman 1999).

For some species, genetic differences can be identified over smaller spatial scales than what has been examined for Capelin. For example, Atlantic Cod inside the Norwegian fjord were genetically different from those outside the fjord, even though these sampling locations were only ~40 km apart from each other (Knutsen and Andre 2011). Genetic differences for Capelin have been identified at geographic scales slightly broader than the scales explored in the current study. For example, genetic differences have been found between non-spawning Capelin in the Chukchi Sea, immediately north of NS, and the Gulf of Alaska, where PWS samples were collected (Wildes et al. 2016). In addition, two genetic groups of spawning Capelin were identified within the Gulf of St. Lawrence and its estuary in Canada for which the closest genetically distinct sampling locations were ~400 km apart (Roby et al. 1991), which were twice as far apart as the furthest NFL samples collected in the current study (~200 km based on the most direct path a fish could swim estimated from Google Earth). Capelin have also been genetically separated into at least four groups across their circumpolar distribution (i.e., West Pacific, East Pacific, Newfoundland, and Northeast Atlantic/West Greenland; Præbel et al.

2008). These results demonstrate that different geographic scales and analytic approaches impact whether populations can be distinguished from one another (e.g., Roby et al. 1991; Begg and Waldman 1999). Additional metrics, such as genetic structure, would be useful for validating the morphometric variation among putative populations identified in the current study (Ihssen et al. 1981; Begg and Waldman 1999).

Morphology is a tool that can assist with identifying populations of fish when used in concert with other traits such as genetic structure, temporal and/or spatial extent, and/or ecological factors (MacLean and Evans 1981; Cadrin and Friedland 1999). The current study explored Capelin morphometry in areas where data were lacking (i.e., the CA Arctic and AK) and found that CVA was more effective at differentiating among Capelin populations than RWA. Morphological diversity can be found within small geographic scales, such as Arctic Char within Lake Hazen, Canada (area = 542 km^2; Arbour et al. 2011) and Orechromine cichlids (*Alcolapia*) within Lake Natron, Tanzania (area = 81 – 804 km^2 depending on rain; Ford et al. 2016). High diversity within a small geographic range may suggest that fish are locally adapted to their environment. For example, the aforementioned morphometric differences in Arctic Char and cichlids are thought to result from phenotypic plasticity, resource polymorphism, and niche partitioning (Arbour et al. 2011; Ford et al. 2016). Future studies could examine the functional relationship between spawning environment and morphology throughout this species' distribution and use additional techniques (e.g., genetics) to verify Capelin population segregation within regions.

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Tables

Table 2.1 Capelin spawning beach collection locations and sample sizes used for morphometric analyses. CA Arctic = western Canadian Arctic, NFL = Newfoundland, AK = Alaska, BB = Bellevue Beach, MC = Middle Cove, WB = Witless Bay, NS = Norton Sound, and PWS = Prince William Sound.

Region	Subregion	Latitude	Longitude	Collection Date	Net type	Sample Size	
						Males	Females
CA Arctic	Bennett Pt	69.72845	-124.08910	14 – 25 Jul 2014	fyke	30	30
NFL	BB	47.63558	-53.77415	19 – 24 Jul 2018	cast	30	NA
	MC	47.65133	-52.69676	14 Jul 2018	cast	30	30
	WB	47.28138	-52.81036	11 Jul 2018	cast	27	28
AK	NS	64.50110	-165.40640	15 – 21 Jun 2018	dip	30	30
	PWS	60.33836	-146.68371	02 Jul 2016	cast	30	NA

Table 2.2 Biological attributes (mean ± SD) of male and female capelin from each region and subregion. TW:TL = ratio of total weight to total length, CA Arctic = western Canadian Arctic, NFL = Newfoundland, AK = Alaska, BB = Bellevue Beach, MC = Middle Cove, WB = Witless Bay, NS = Norton Sound, and PWS = Prince William Sound. * indicates significant difference among or within regions.

Sex	Region	Subregion	Total weight, g	Total length, mm	TW:TL, g/mm	Fecundity, # eggs	Egg density, # eggs/g ovary
				Among regions			
Males	CA Arctic	NA	19.9 ± 3.4	147 ± 8.1*	0.14 ± 0.02	NA	NA
	NFL	(all)	24.6 ± 4.4*	157 ± 8.3*	0.16 ± 0.02*	NA	NA
	AK	(all)	16.0 ± 6.0	133 ± 17.6*	0.12 ± 0.03	NA	NA
Females	CA Arctic	NA	11.8 ± 2.9*	133 ± 9.6	0.09 ± 0.02*	NA	NA
	NFL	(all)	14.9 ± 3.0	135 ± 8.1	0.11 ± 0.02	20,662 ± 6,231*	4,077 ± 850*
	AK	NA	15.0 ± 3.0	136 ± 8.1	0.11 ± 0.02	8,826 ± 4,253	2,785 ± 292
				Within regions			
Males	NFL	BB	23.1 ± 3.8	158 ± 6.9	0.15 ± 0.02	NA	NA
		MC	27.5 ± 4.3*	159 ± 9.7	0.17 ± 0.02*	NA	NA
		WB	23.0 ± 3.7	152 ± 6.1*	0.15 ± 0.02	NA	NA
	AK	NS	21.5 ± 3.3*	150 ± 6.9*	0.14 ± 0.02*	NA	NA
		PWS	10.6 ± 1.4	117 ± 3.8	0.09 ± 0.01	NA	NA
Females	NFL	MC	15.4 ± 3.2	135 ± 8.8	0.11 ± 0.02	19,719 ± 7,562	3,727 ± 553*
		WB	14.5 ± 2.7	134 ± 7.5	0.11 ± 0.02	21,678 ± 4,299	4,454 ± 957

Figures

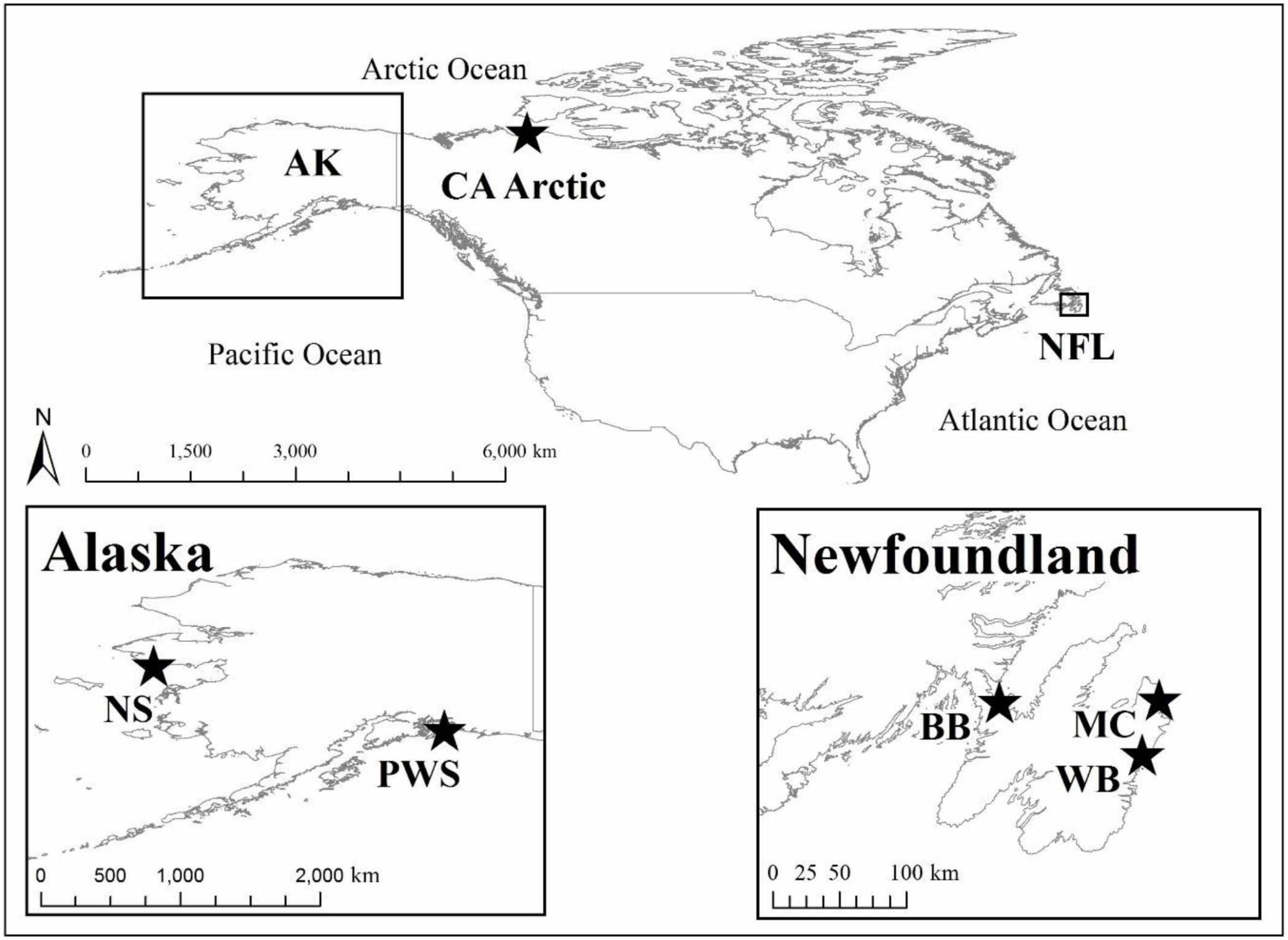

Figure 2.1 Sampling locations for spawning-stage Capelin. Three regions were sampled: 1) western Canadian Arctic (CA Arctic), 2) Newfoundland, Canada (NFL), and 3) Alaska, USA (AK). Additional samples (detailed in inset maps) were collected within NFL (BB = Bellevue Beach, MC = Middle Cove, and WB = Witless Bay) and AK (NS = Norton Sound and PWS = Prince William Sound).

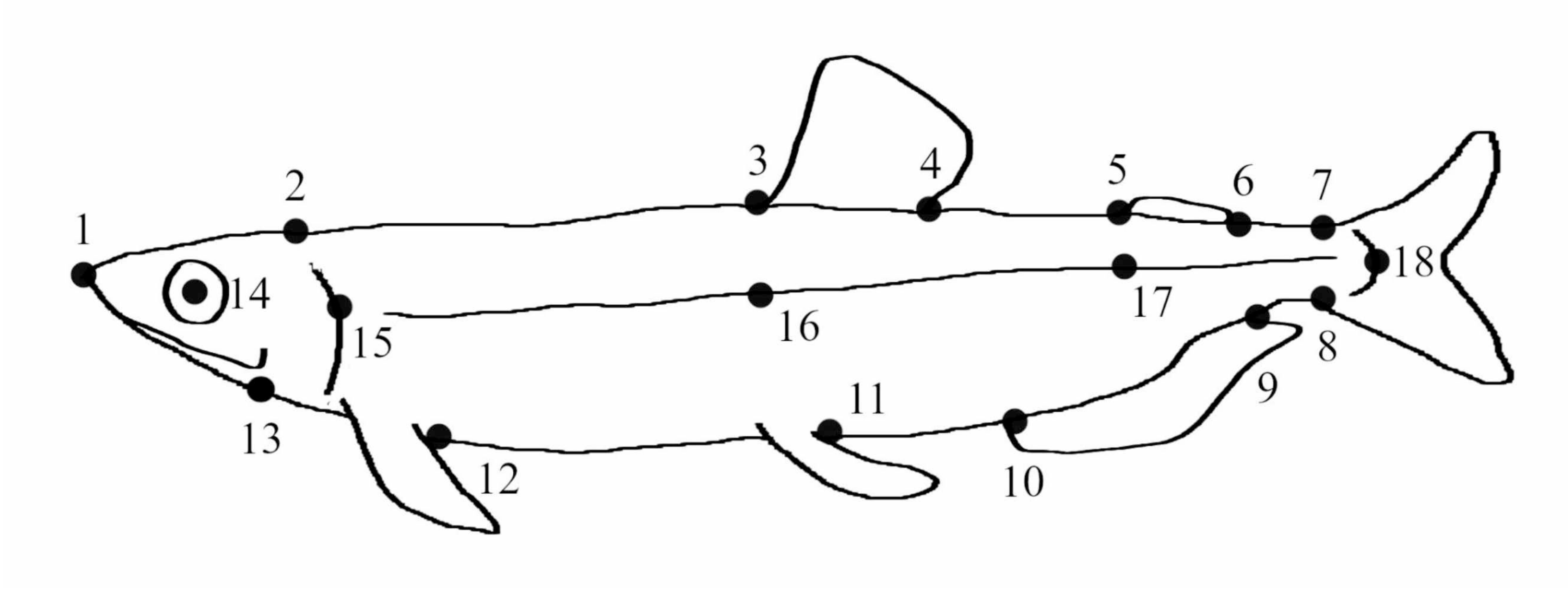

Figure 2.2 Landmark (LM) locations used for geometric morphometric analyses of Capelin: 1) tip of the snout; 2) head/body transition point; 3 – 4) anterior and posterior insertion of the dorsal fin, respectively; 5 – 6) anterior and posterior insertion of the adipose fin, respectively; 7 – 8) local minima of the caudal peduncle; 9 – 10) posterior and anterior insertion of the anal fin, respectively; 11) posterior insertion of the pelvic fin; 12) intersection between the posterior insertion of the pectoral fin and the abdomen; 13) point perpendicular to the posterior tip of the maxilla along the outline of the fish; 14) center of the eye; 15) intersection between the operculum and lateral line; 16 – 17) points perpendicular to LM3 and LM5, respectively, along the lateral line; and 18) final scale along the lateral line. Image created using GIMP (version 2.10.12; GIMP Development Team 2019).

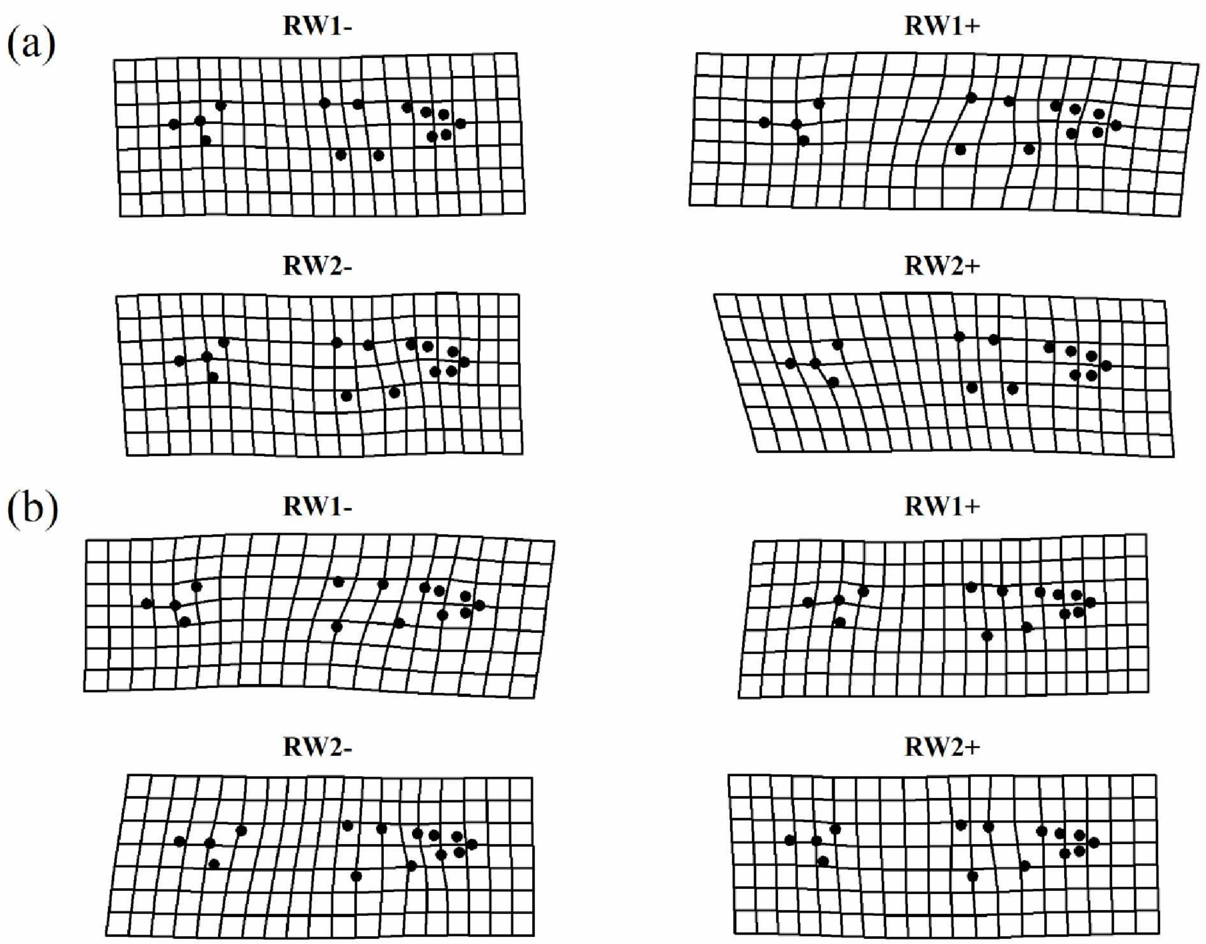

Figure 2.3 Thin-plate spline deformation grids for (a) male and (b) female Capelin. Grids depict the difference between mean landmark configuration and minimum (-) and maximum (+) relative warp (RW) scores (on the left and right, respectively) of the first two RWs.

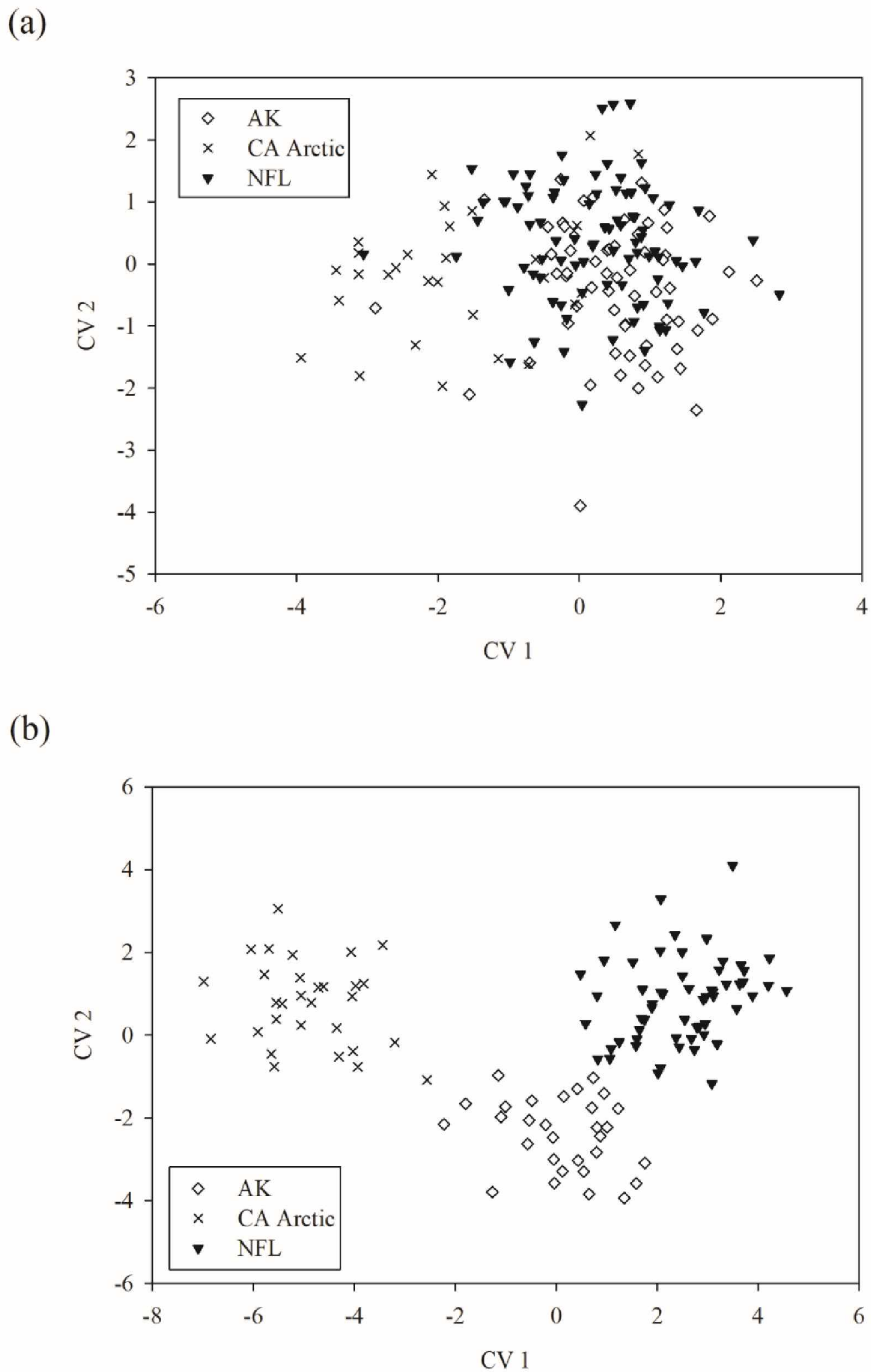

Figure 2.4 Shape variation of Capelin among regions based on the first two canonical variates for (a) males and (b) females. CA Arctic = western Canadian Arctic, NFL = Newfoundland, and AK = Alaska.

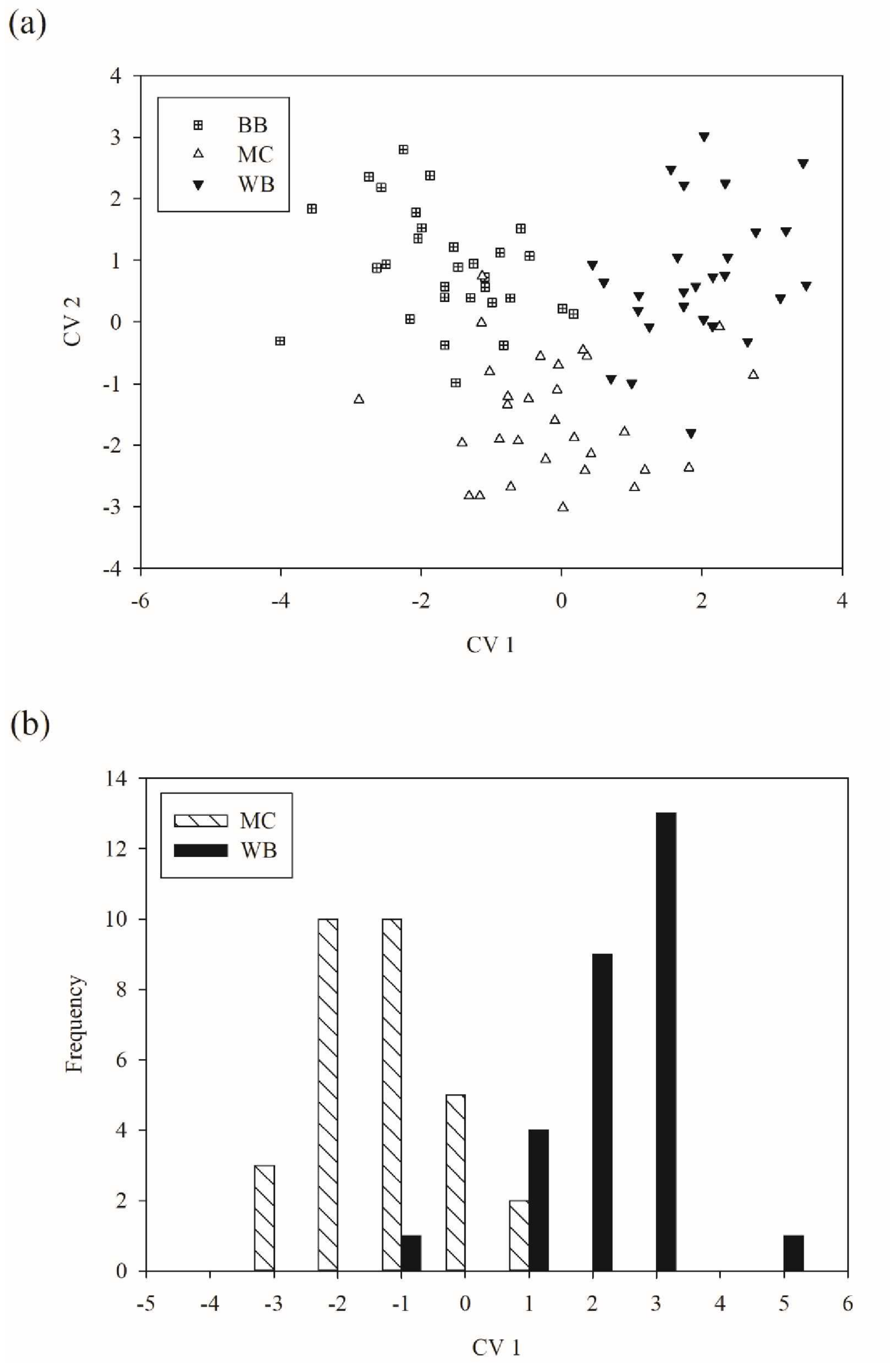

Figure 2.5 Shape variation within Newfoundland Capelin based on (a) the first two canonical variates for males and (b) the first canonical variate for females. BB = Bellevue Beach, MC = Middle Cove, and WB = Witless Bay.

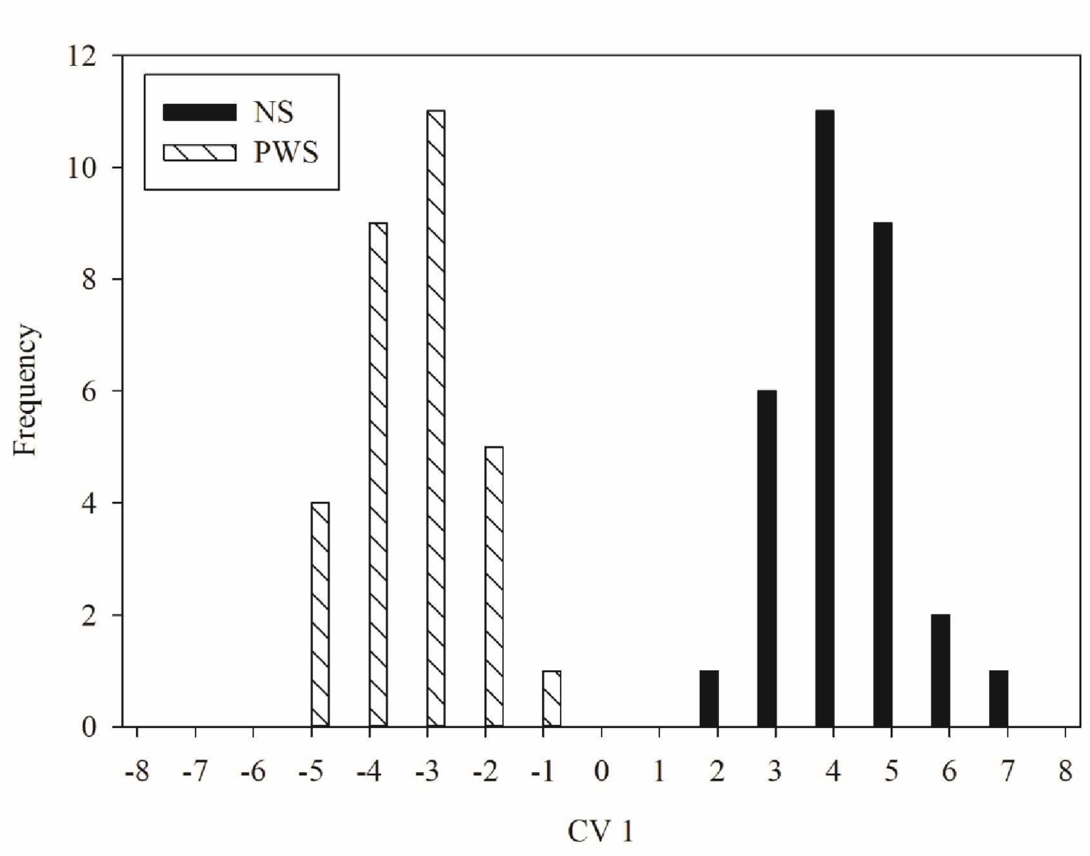

Figure 2.6 Shape variation within Alaskan Capelin based on the first canonical variate for males. NS = Norton Sound and PWS = Prince William Sound.

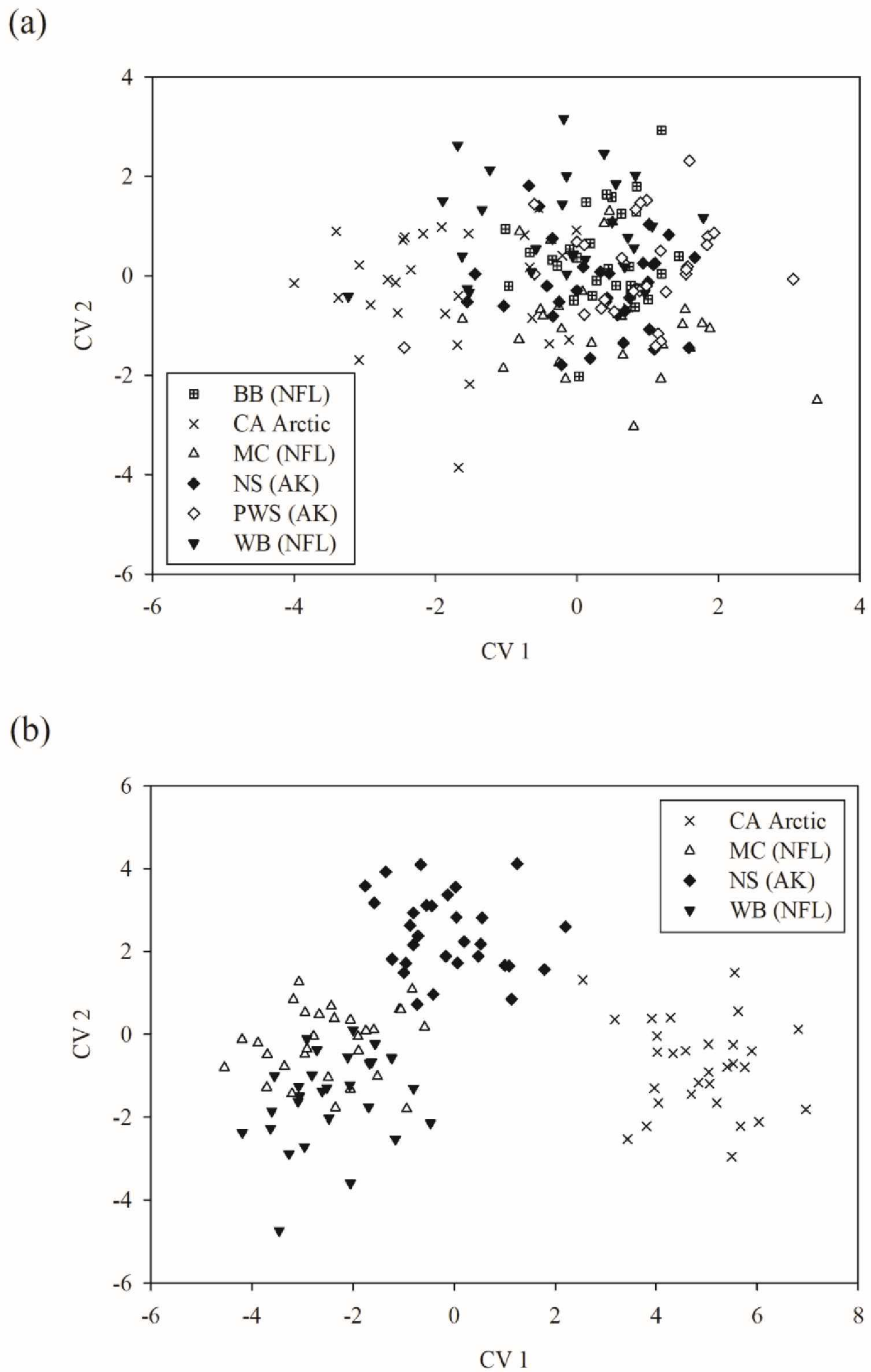

Figure 2.7 Shape variation of Capelin among all subregions based on the first two canonical variates for (a) males and (b) females. Abbreviations indicate region (CA Arctic = western Canadian Arctic, NFL = Newfoundland, and AK = Alaska) and subregion (BB = Bellevue Beach, MC = Middle Cove, WB = Witless Bay, NS = Norton Sound, and PWS = Prince William Sound).

Supplemental Figures

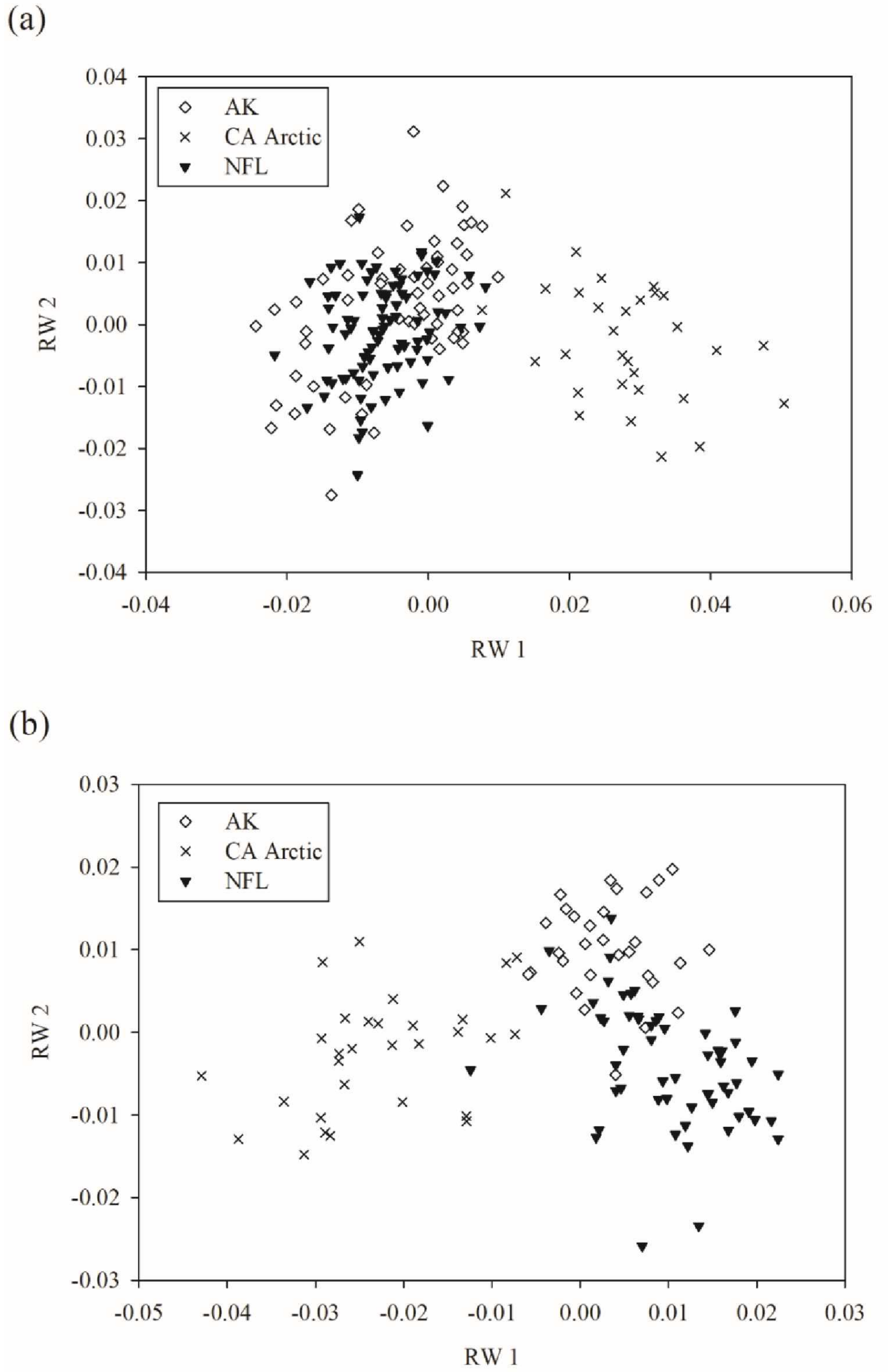

Figure S2.1 Shape variation among regions based on the first two relative warps for (a) male and (b) female Capelin. CA Arctic = western Canadian Arctic, NFL = Newfoundland, and AK = Alaska.

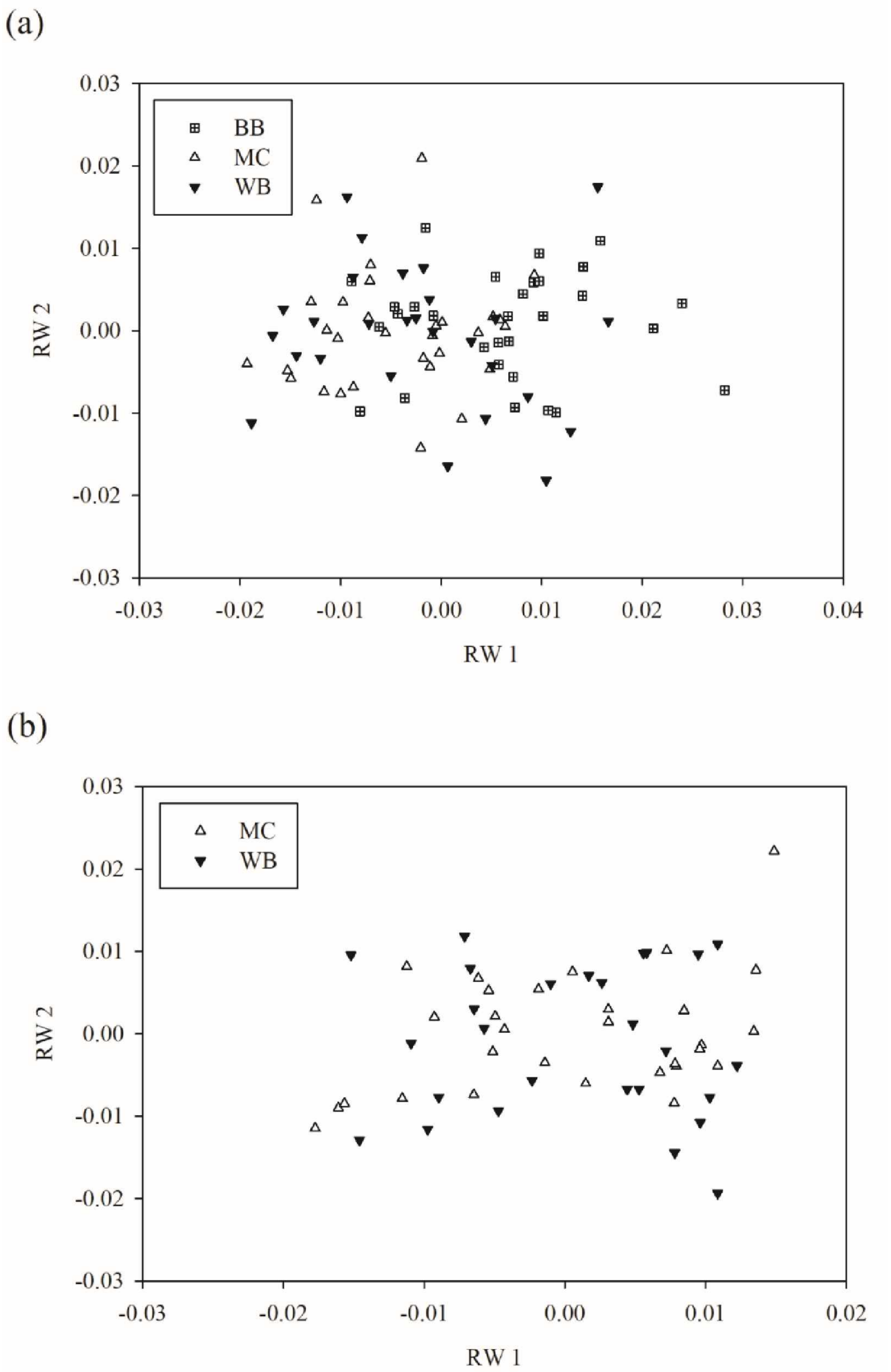

Figure S2.2 Shape variation within Newfoundland Capelin based on the first two relative warps for (a) males and (b) females. BB = Bellevue Beach, MC = Middle Cove, and WB = Witless Bay.

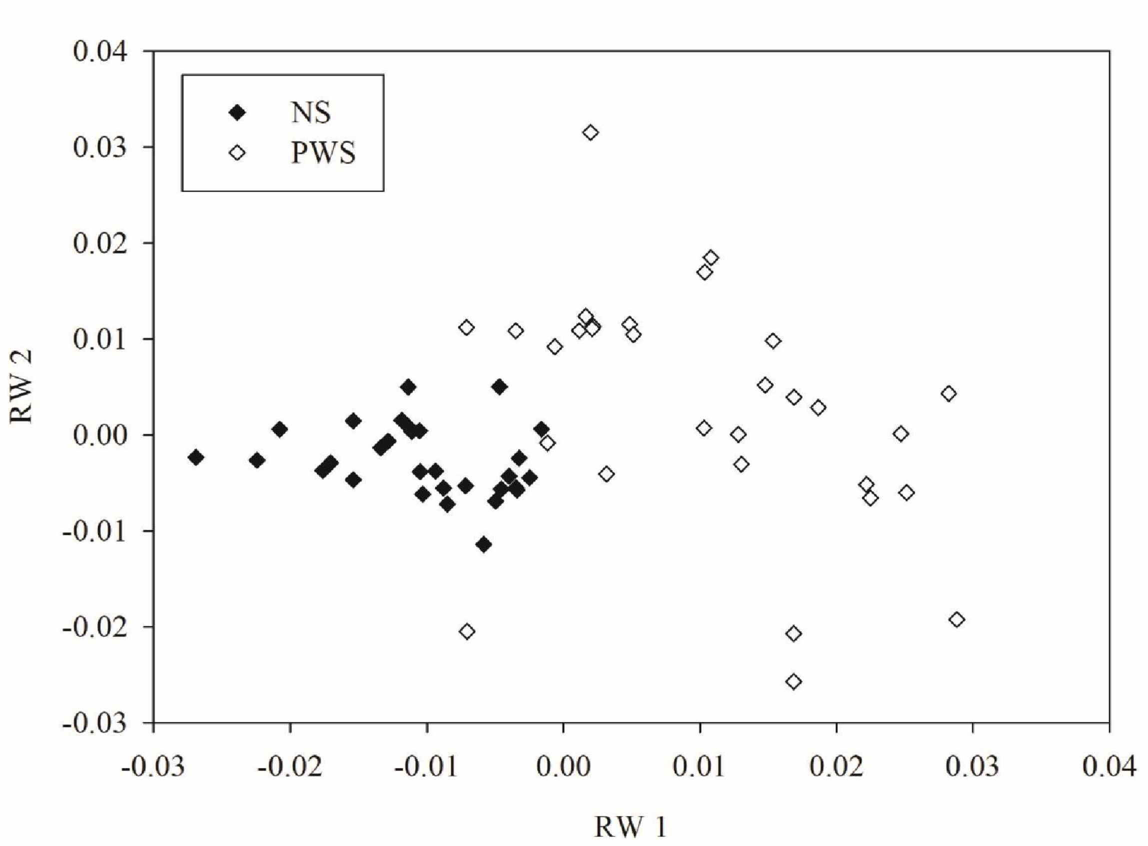

Figure S2.3 Shape variation within Alaskan Capelin based on the first two relative warps for males. NS = Norton Sound and PWS = Prince William Sound.

GENERAL CONCLUSION

The results of the current study increased our understanding of the distribution, biology, and morphology of spawning Capelin *Mallotus villosus* in poorly studied areas in Alaska and the western Canadian Arctic (Carscadden and Vilhjálmsson 2002; Rose 2005). In chapter one, Capelin were observed spawning and collected from five active spawning sites in Norton Sound. Their spawning behavior and environment, including water temperature, salinity, and sediment size, were similar to beach-spawning Capelin in other areas such as Newfoundland (Nakashima and Wheeler 2002; Martin et al. 2004; Purchase 2017). Capelin from Norton Sound had biological attributes within the same range as those documented for other regions, such as Greenland (Hedeholm et al. 2010, 2011), but average values differed among some regions (e.g., average length and weight of Capelin in Norton Sound versus Newfoundland; Penton 2013). In chapter two, male and female Capelin from the western Canadian Arctic were distinguished from fish in Newfoundland and Alaskan waters primarily based on pelvic fin location. There was also some evidence for population separation within Newfoundland and Alaska, although the distinctness of these putative populations varied depending on which regions or subregions were examined as well as which analytic approach was used to distinguish among populations.

The current study found that spawning environment and behavior were similar for beach-spawning Capelin across multiple marine ecosystems throughout their geographic range, which may imply a spawning habitat preference or requirement. Beach-spawning can be considered a type of parental care to provide embryos with proper incubation conditions (e.g., dissolved oxygen concentrations), reduce the predation risk from some marine predators, and/or present offspring with the best environment in which to emerge (Martin et al. 2004). For example, grunion *Leuresthes* spp. spawn on beaches where they deposit their eggs out of water rather than in the water to provide higher oxygen diffusion rates more suitable for their embryos (Martin et al. 2004). Other species, such as Oreochromine cichlids (*Alcolapia* spp.), choose their habitat based on niche availability and then adapt morphological traits that are beneficial to that habitat (Ford et al. 2016). For Capelin, spawning mode (i.e., beach versus demersal spawning) may be a form of local adaptation. Beach-spawning is thought to be the preferred and ancestral mode of spawning for Capelin compared to demersal spawning (Nakashima and Wheeler 2002; Purchase 2017). However, demersal spawning co-occurs with beaching spawning in Newfoundland when water temperatures are adequate, but only occurs in demersal waters when beach water temperatures are too warm (Nakashima and Wheeler 2002). In addition, salinity tolerance differences between eggs deposited by beach versus demersal spawners suggest some embryos may be locally adapted to one mode of spawning over the other (Purchase 2017). It is unclear how changing environmental conditions will affect Capelin spawning, but these changes may affect which spawning mode is used, especially if this trait is locally adaptable.

Different morphological and biological characteristics among and within regions suggested that there were multiple Capelin populations throughout the study area, although genetic analyses would help supplement these phenotypic observations (Begg and Waldman 1999). Even though genetic structure was not directly analyzed in the current study, it may have contributed to some of the phenotypic variation observed since morphometry is influenced by environmental and genetic factors (Begg and Waldman 1999). Utilizing both morphometric and genetic approaches to identify population structure can help identify which underlying factors contribute to the morphometric variation (Begg and Waldman 1999). For example, when groups of organisms are genetically similar, differences in morphology are the result of environmental factors. This has been observed for Arctic Char in Lake Hazen (Arbour et al. 2011), Atlantic

Herring *Clupea harengus* in the northwest Atlantic, Atlantic Cod *Gadus morhua* near Newfoundland, and angler *Lophius vomerinus* off the South African coast (cited in Begg and Waldman 1999). Additional research regarding the genetic signatures of spawning Capelin in the study areas would help support the phenotypic evidence for population segregation identified in the current study and help narrow down the underlying factors driving phenotypic differences among and within regions.

Despite the importance of Capelin as a prey source for many marine organisms, this species has not been well studied outside the Atlantic Ocean. Changes in climatic conditions may alter the geographic distribution of Capelin and/or its ability to respond to environmental fluctuations, which could impact other organisms throughout multiple marine ecosystems (Rose 2005; Andrews III et al. 2016). However, Capelin may demonstrate resilience against impending environmental fluctuations if intraspecies diversity is high (Schindler et al. 2010; Davoren and Halden 2014). The results from the current study suggest Capelin have a level of intraspecies diversity across its geographic range, which may help it adapt to a changing environment.

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