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Distribution and life history of spawning Capelin *Mallotus villosus* in subarctic Alaska

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<A> 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 m² 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 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.

47 <A> Introduction

48 Forage fishes are an integral component of many marine food webs, occupying a key
49 position that has the potential to disproportionately effect the rest of the ecosystem (Pikitch et al.
50 2014; Andrews III et al. 2016). These fishes provide essential nutrients and energy to predators,
51 including marine mammals, seabirds, and other fish species by converting energy from plankton
52 into a form accessible to upper trophic levels (Carscadden et al. 2013a; Pikitch et al. 2014;
53 Andrews III et al. 2016). Nutrient and energy availability in marine food webs will likely alter in
54 response to changes in forage-fish distributions and abundance as the climate continues to warm
55 (Aydin and Mueter 2007; Andrews III et al. 2016). Fishes that live in Arctic and sub-Arctic
56 waters can be particularly sensitive to environmental change; therefore, they may help identify
57 environmental changes that could have delayed impacts on other species in the ecosystem (Rose
58 2005). One of these cold-water forage fish is Capelin *Mallotus villosus*, which is considered a
59 “sea canary” because it responds quickly and consistently to environmental fluctuations (Rose
60 2005).

61 Capelin is distributed throughout the Arctic, North Atlantic, and North Pacific oceans
62 (Carscadden and Vilhjálmsón 2002; Hedeholm et al. 2011). Capelin live in the open ocean, but
63 migrate to nearshore waters for spawning where fish utilize different habitats than their non-
64 spawning counterparts (Carscadden et al. 2013b). Both offshore and nearshore environments are
65 rapidly warming. For example, the northern Bering Sea, located in the North Pacific Ocean, has
66 experienced only positive sea surface temperature anomalies between 2013 and 2018 and had
67 almost no sea ice in 2018 (Siddon and Zador 2018). Temperature increases as little as 1°C have
68 been associated with large-scale changes in non-spawning stage Capelin distribution in the
69 eastern Bering Sea (Andrews III et al. 2016). In addition, changes in environmental conditions
70 may alter the location and extent of spawning habitat available for beach-spawning Capelin.
71 Warming waters may cause temperatures to exceed this species’ thermal optima for spawning
72 (<12°C; Nakashima and Wheeler 2002). Alternatively, the availability of beach spawning areas
73 may be altered due to coastal erosion resulting from a decrease in protective shore ice and an
74 increase in the frequency and intensity of storms (Arthur 2017). Lack of adequate spawning
75 conditions and habitats may reduce Capelin spawning success, larval survival, and overall

76 abundance, which has ecosystem-wide implications (Nakashima and Taggart 2002; Carscadden
77 et al. 2013b).

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

86 <A> Methods

87 *Field data collection.*—

88 Capelin were surveyed and collected from Norton Sound, located along the western coast
89 of Alaska in the North Pacific Ocean (Figure 1). In November 2017, knowledgeable local fishers
90 living in this area were interviewed in Nome and the villages of Brevig Mission and Elim via
91 semi-structured interviews ($N = 8$), and in the village of Teller via informal conversations, to
92 identify candidate Capelin spawning locations. Informational flyers were placed around Nome,
93 and in the villages of Brevig Mission, Elim, and Unalakleet, and an advertisement was aired on
94 the local radio to encourage community members to report information regarding the location of
95 spawning Capelin. In response to community feedback, beaches within driving distance of Nome
96 were occasionally surveyed by driving along the main road (which paralleled the beach from
97 Nome to 30 mi east of Nome) and by using an all-terrain vehicle to drive directly on the beach
98 (from Nome to Penny River ~10 mi west of Nome; see Figure 1). Finally, 14 aerial surveys were
99 flown parallel to shore approximately 200 m from the shoreline and at an average altitude of 150
100 m using a Robinson-R44 or a MD500 helicopter. Surveys were flown at least once weekly from
101 26 May to 7 July 2018 and spanned from Wales to Golovnin Bay (~490 km of coastline),
102 although the entire area was not surveyed on each flight due to financial limitations (Figure 1).
103 Surveys were typically flown in the morning to capitalize on favorable weather conditions and
104 good visibility at that time.

105 Nearshore and spawning aggregations were observed during the aerial surveys.
106 Nearshore aggregations were characterized by groups of fish that were densely packed,
107 individually identifiable, and located within 400 m of shore. This encompassed the area Capelin
108 were expected to occupy immediately prior to spawning on the beach. The surface area of
109 nearshore aggregations was estimated using a gridded PVC sighting tube, the altitude of the
110 helicopter, and the distance from shore based on the following equation (Lebida and Whitmore
111 1985):

112
$$\text{surface area} = \text{survey altitude} * (\text{grid line length} / \text{sighting tube focal length}).$$

113 The density of nearshore aggregations (regardless of aggregation size) was also determined. The
114 aerial survey area was broken into sections based on geographic landmarks within which
115 nearshore aggregations were tallied (see “Geographic Landmarks” in Figure 1). To account for
116 variations in the length of coastline surveyed, aggregation density was calculated for each survey
117 by dividing the number of aggregations observed by the length of shoreline surveyed for that
118 section. Spawning aggregations were characterized by groups of fish located on the beach within
119 the wash zone. Once spawning was observed, the spawning aggregations were monitored as
120 frequently as possible to estimate the length of time that Capelin occupied the site as well as the
121 time of day during which fish were actively spawning. During each aerial survey, nearshore and
122 spawning aggregations were recorded on a map by hand and marked on a handheld GPS.

123 Actively spawning male and female Capelin were collected using a dip net (square mesh
124 < 3.8 cm). If spawning was observed while driving, samples were collected immediately. If
125 spawning was observed during an aerial survey, the pilot landed the helicopter near the beach (to
126 avoid disturbing spawning) and Capelin were collected before resuming the aerial survey. Fresh
127 mortalities from prior spawning events that were found stranded on the beach were collected
128 opportunistically. Because males outnumbered females on the spawning grounds (e.g.,
129 Christiansen et al. 2008), females were actively targeted during collections. As a result, the ratio
130 of males and females collected did not represent the ratio observed at the spawning site.
131 Collected Capelin were euthanized, frozen, and sent to the University of Alaska Fairbanks
132 (UAF) for processing in the laboratory.

133 Spawning habitat was characterized by measuring the size and physical characteristics of
134 active spawning locations. Seabird presence and active feeding were used to estimate the length
135 of shoreline being used for spawning because birds were easier to see than Capelin when
136 standing on the beach. When possible, GPS waypoints were collected at the edges of a spawning
137 area and the straight distance between the waypoints was measured in Garmin BaseCamp
138 (Version 4.7.0) to determine the length of beach that was actively used for spawning (Garmin
139 BaseCamp 2018). Wind direction during a spawning event was also noted. Water temperature
140 (°C), dissolved oxygen (mg/L), and salinity (ppt) were collected using a portable YSI meter
141 (Model 85, YSI Incorporated, Yellow Springs, Ohio).

142 To categorize average beach sediment size and confirm spawner presence (via deposited
143 eggs), sediment was gathered using a clear sediment corer tube (4.8 cm inner diameter). At each
144 spawning site, three replicate cores (each with 10 cm of substrate) were collected at three
145 locations (high, mid, and low) within the tidal wash area on the beach (Figure S1.1 in
146 Supplement 1). High-, mid-, and low-locations were spaced < 5 m apart at a given site. Replicate
147 cores from each location on the beach were combined into one sample per location on the beach
148 for a total of three sediment samples per beach sample (i.e., high, mid, and low). High-locations
149 were at the highest extent of the wave wash, mid-locations were covered with water as the waves
150 moved on- and offshore, and low-locations were always submerged. Sampling locations were
151 based on the wave action at the time of sampling, not the actual maximum- and minimum-tide
152 levels. Sediment samples were preserved in 4% (vol : vol) formalin : seawater solution buffered
153 with sodium borate (Nakashima and Taggart 2002) and shipped to UAF for laboratory analyses.

154 *Laboratory analyses.*—

155 Sediment samples were separated from deposited eggs following methods modified from
156 Taggart and Nakashima (1987). Formalin was rinsed and decanted five times from the sediment
157 sample over a 63- μ m sieve. The rinsed samples were submerged in a 2% KOH solution for 24 to
158 36 hours to help remove the eggs from the sediment. The samples were rinsed again and
159 decanted ten times over a 250- μ m sieve to collect the eggs and a 63- μ m sieve to prevent finer
160 sediments from being lost. Eggs were dried at 80°C for 12 to 24 hours and weighed to the nearest
161 0.001 g.

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

169 Capelin were thawed in the laboratory immediately prior to measuring TL (to the nearest
170 1 mm) and total wet body weight (TW; to the nearest 0.001 g). All fish were photographed prior
171 to internal examination. Because Pahlke (1985) measured FL (to the nearest 1 mm) on fresh fish,
172 the FL of 30 males and 30 females were measured from standardized photographs using tpsDig2
173 (version 2.31; Rohlf 2005). Linear regression was used to establish a relationship between TL
174 and FL for both sexes combined. Fork lengths for the remaining fish were estimated using the
175 following relationship:

$$176 \qquad \qquad \qquad FL = 0.88 * TL + 6.22 (R^2 = 0.97, N = 60, P < 0.001).$$

177 The calculated FL was then multiplied by 1.03 to account for shrinkage due to freezing (Winters
178 1982). Only the calculated FLs (not the measured FLs) were compared with FLs reported in
179 Pahlke (1985), whereas all other analyses used TL. Following TW measurements, stomachs were
180 extracted and weighed both full and empty. Stomach content weight only accounted for a mean
181 of 0.5% of the TW (range = 0.0% to 5.5%), so TW was used for the remaining analyses instead
182 of correcting weight estimates based on stomach content weight.

183 Sagittal otoliths were extracted from each Capelin and stored dry. Whole otoliths were
184 submerged in mineral oil to make the translucent bands easier to observe, and four images of the
185 otoliths were captured at 50x magnification (convex and concave sides of the left and right
186 otolith) under a compound light microscope (Leica M165 C, Leica Microsystems, Buffalo
187 Grove, Illinois). Fish were divided into 7-mm length bins, and a subsample of at least five
188 individuals (when available) or 38% of the catch in each length bin per sex were aged from the
189 photographs independently by two readers. Discrepancies were resolved by a concert read. An

190 age–length key for each sex was generated following standard methods to assign ages to the
191 remaining fish based on TL (Ogle 2015).

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

207 Current and historic spawning locations for Capelin were mapped using ArcGIS (version
208 10.5.1; Environmental Systems Research Institute 2017), the software program “R Studio”
209 (version 1.1.463; R Studio Team 2016) operating with “R” (version 3.5.2; R Core Team 2018)
210 was used to conduct analyses (with significance at $\alpha = 0.05$), and graphs were generated with
211 SigmaPlot (version 12.3; Systat Software Inc. 2012). Summary statistics were reported as mean \pm
212 SD unless otherwise indicated. Wind direction was qualitatively compared with reported Capelin
213 spawning conditions in other regions. Water conditions during spawning were averaged across
214 all spawning events. Kruskal-Wallis tests were used to determine if differences existed among
215 sites or locations for each sediment size class and for the median total dry egg weight decanted
216 from the sediment samples. All life-history analyses were conducted separately for males and
217 females unless otherwise noted. Female mortalities that were collected were aged but were
218 excluded from remaining analyses. A one-way ANOVA was used to examine relationships
219 among Capelin body size and sex, age class, and collection date. Fisher’s exact test was used to

220 determine if age composition differed throughout the spawning season, while a pairwise
221 Kendall's rank correlation test was used to compare relationships among fecundity and GSI
222 estimates to Capelin TL and TW.

223 <A> Results

224 Aerial surveys in summer 2018 were 1.60 ± 0.42 hours in duration, with a total of 20.75
225 hours of aerial survey time. Most nearshore Capelin aggregations (85.9%; 269 of 313
226 aggregations) covered a surface area of approximately 12 m² or less and 13.4% (42/313
227 aggregations) were approximately 25 m². Two larger aggregations were also observed: one
228 approximately 61 m² and the other 219 m². The highest density of aggregations (4.98
229 aggregations/km) was observed between Sinuk River and West Mountains (Table 1; Figure 1).
230 Seals (family Phocidae) were observed actively hunting nearshore fish aggregations during the
231 first aerial survey.

232 Capelin were collected in Norton Sound from 15 to 21 June 2018 from five active
233 spawning sites (173 males, 105 females) and one site where spawning had occurred (9 female
234 mortalities). Spawning events occurred at beaches between the Nome River mouth and Nome,
235 Nome and Penny River, and 3 km east of the Sinuk River to the Sinuk River mouth (spawning
236 sites hereafter termed "Nome River", "Penny River", and "Sinuk River", respectively; Figure 1).
237 Seabirds, including Black-legged Kittiwakes *Rissa tridactyla*, Glaucous Gulls *Larus*
238 *hyperboreus*, Glaucous-winged Gulls *L. glaucescens*, Herring Gulls *L. argentatus*, Mew Gulls *L.*
239 *canus*, and Arctic Terns *Sterna paradisaea*, were present and actively feeding on Capelin at
240 spawning sites. Although the time that Capelin spent actively spawning was short, aggregations
241 appeared to be present at spawning areas for two to four days, depending on location. For
242 example, Capelin were reported by community members to be spawning at the Nome River site
243 on 17 June 2018 at 1500 hours and samples were collected while they were actively spawning at
244 1700 hours the same day. On 18 June, fish were monitored at 1115 hours on the ground, 1400
245 hours by air, and 1930 hours by ground; however, no spawning activity was observed during
246 these subsequent trips. There were community reports that between those monitoring periods, at
247 approximately 1700 hours, Capelin were actively spawning (see additional examples in
248 Supplement 2).

249 During a spawning event, Capelin congregated within 1 to 2 m of shore, around the area
250 where the waves start breaking, and rode the wave onto shore to spawn. The length of beach
251 used for each spawning event ranged from less than 400 m to approximately 3,500 m. Within
252 each large spawning event there appeared to be smaller aggregations ($<4 \text{ m}^2$) that would come
253 onto shore at multiple locations along the beach. Within these smaller spawning aggregations,
254 individuals were sometimes observed forming groups of three (two males with one female) when
255 coming onshore. Capelin were observed spawning at various times throughout the day (0900,
256 1200–1400, and 1700 hours) and during both on- and offshore winds. Across spawning events,
257 water temperature was $9.0 \pm 2.0^\circ\text{C}$ (range = $6.8 - 10.9^\circ\text{C}$), dissolved oxygen was $9.4 \pm 1.0 \text{ mg/L}$
258 (range = $7.6 - 10.4 \text{ mg/L}$), and salinity was $24.3 \pm 6.7 \text{ ppt}$ (range = $10.6 - 27.7 \text{ ppt}$).

259 A total of 18 sediment samples (i.e., 6 sediment collection sites x 3 locations within the
260 beach) were collected from four active Capelin spawning sites and one site where spawning had
261 occurred. Two sets of sediment samples were collected from the Sinuk River spawning site
262 approximately 130 m apart from each other (SK1 and SK1.2 in Figure 1) to account for potential
263 variability in beach sediment composition because spawning covered nearly 3,500 m of
264 shoreline. All sediment samples contained eggs. Although sediment samples were sorted into
265 seven size classes, the results from a principal components analysis (PCA) and PCA biplot based
266 on percent sediment composition per sediment sample (separated by location) suggested that
267 sediments could be grouped into four size classes: gravel ($>2000 \mu\text{m}$), coarse sand (500 to 2000
268 μm), fine sand (63 to 500 μm), and fines ($<63 \mu\text{m}$). Combining the size classes was corroborated
269 in that the grouped dataset was fully explained by the first two principle components (PC1 and
270 PC2 accounted for $> 99.99\%$ variability) and the percent variance explained by PC1 was slightly
271 higher for the grouped dataset (87.0%) than the full dataset (86.3%). Therefore, the grouped
272 dataset was used for all sediment composition analyses.

273 There was no difference in percent sediment composition among spawning sites for any
274 of the four sediment size classes. The percent sediment composition differed among locations
275 within a beach spawning site (Figure 2). Gravel dominated the sediment composition at low-
276 locations whereas fine sand dominated the sediment composition at high-locations. The amount
277 of coarse sand and fine sediments was similar among all locations within the beach (i.e., high,
278 mid, and low). Across all sampled spawning beaches, gravel and coarse sand accounted for

279 nearly all the sediment collected within a beach at high-, mid-, and low-locations (proportional
280 weight of sediment = 73.2, 80.5, and 91.3%, respectively).

281 Spawning Capelin exhibited a range of sizes and ages. Log transformed TL and TW were
282 positively related for males ($R^2 = 0.85$) and females ($R^2 = 0.61$; Figure 3). Males were 8% longer
283 than females based on TL (148.8 ± 6.7 mm versus 137.0 ± 8.4 mm, respectively; ANOVA: $F =$
284 172.50 ; $df = 1, 275$; $P < 0.001$; Figure 4) and were 35% heavier based on TW (21.2 ± 2.9 mg
285 versus 13.7 ± 3.0 mg, respectively; ANOVA: $F = 411.00$; $df = 1, 275$; $P < 0.001$). Capelin were
286 predominately age 3 for both males (69.4%, 120/173 fish) and females (63.5%, 66/104 fish;
287 Figure 4). There were no differences in Capelin TL among age classes for males (ANOVA: $F =$
288 0.59 ; $df = 2, 170$; $P = 0.56$) or females (ANOVA: $F = 1.98$; $df = 2, 101$; $P = 0.14$) or TW among
289 age classes for males (ANOVA: $F = 0.97$, $df = 2, 170$; $P = 0.38$) or females (ANOVA: $F = 0.95$;
290 $df = 2, 101$; $P = 0.39$). Further, sample date was not correlated with TL for males (ANOVA: $F =$
291 1.88 ; $df = 3, 169$; $P = 0.13$) or females ($F = 0.22$; $df = 3, 100$; $P = 0.89$) or with age composition
292 of males (Fisher's exact test: $P = 0.65$) or females (Fisher's exact test: $P = 0.98$).

293 Reproductive structures were assessed on pre-spawn male ($N = 151$) and female ($N = 59$)
294 Capelin. Absolute fecundity was $8,826 \pm 4,253$ eggs (range = 1,909 to 16,662 eggs), while
295 relative fecundity was 590 ± 236 eggs/g fish weight (range = 158 to 945 eggs/g fish weight).
296 Absolute fecundity was positively correlated with TW (linear regression: $R^2 = 0.42$, $N = 59$, $P <$
297 0.001 ; Figure 5), but not TL (linear regression: $R^2 = 0.05$, $N = 59$, $P = 0.08$; Figure S1.2).
298 Relative fecundity was not correlated with TL (linear regression: $R^2 = 0.02$, $N = 59$, $P = 0.35$;
299 Figure S1.3). Male and female Capelin had a GSI of $1.09 \pm 0.32\%$ and $21.69 \pm 8.21\%$,
300 respectively. There was a positive correlation between GSI and TL for males (linear regression:
301 $R^2 = 0.05$, $N = 151$, $P < 0.01$; Figure S1.4A), but no relationship for females (linear regression:
302 $R^2 < 0.01$, $N = 59$, $P = 0.48$; Figure S1.4B).

303 <A> Discussion

304 Although Capelin have been extensively studied in the Atlantic Ocean, information on
305 the distribution and life history of spawning-stage adults in the Pacific Ocean is lacking (Pahlke
306 1985; Carscadden and Vilhjálmsson 2002). Spawning Capelin in Norton Sound had similar
307 spawn timing and behaviors, and water and habitat conditions as Capelin from other regions

308 (e.g., Newfoundland). In addition, Capelin size, age, fecundity, and GSI in the current study were
309 within ranges reported from other areas (e.g., Greenland). Minor discrepancies among Capelin
310 populations (e.g., historic versus current mean age for Norton Sound fish, mean length and
311 weight for Capelin in Norton Sound versus Newfoundland, etc.) were likely due to variations
312 among years or regions (e.g., Maxner et al. 2016; McNicholl et al. 2018). The results from the
313 current study indicate that fundamental ecological aspects of Capelin spawning are similar in
314 multiple marine ecosystems across their geographic range.

315 Aerial surveys were effective for mapping and estimating the size of nearshore Capelin
316 aggregations in Norton Sound. Most of the nearshore aggregations in Norton Sound were smaller
317 in surface area than the smallest median size of the Capelin aggregations observed in
318 Newfoundland (Table 2 [in current study]; Carscadden et al. 1994). Although it is unknown why
319 aggregation size differed between regions, this difference may reflect a lower abundance of
320 Capelin in the Bering Sea relative to Newfoundland. For example, in 2010, Capelin were
321 estimated to have a biomass of 837 t in the eastern Bering Sea and 179 t in the northern Bering
322 Sea based on offshore trawl surveys (Lauth et al. 2019). In contrast, biomass estimates for
323 Capelin on the Newfoundland shelf were estimated at 22,000 t in 2010 and typically ranged from
324 98 – 200 kt from 2003 – 2017 based on acoustic surveys (Lewis et al. 2019).

325 Capelin in Norton Sound spawned at the same time of year and were observed on
326 beaches for the same length of time as fish from other locations, but were observed spawning
327 over a shorter duration of time (Table 2). Slight variations in the onset of spawn timing likely
328 reflect differences in water temperature and sea ice extent among years and regions (Therriault et
329 al. 1996). For example, in 1981 (i.e., the year Capelin were sampled in Pahlke (1985)), sea ice
330 was present in parts of Norton Sound until August, whereas in 2018, this area was ice-free by
331 May (National Snow and Ice Data Center 2019). In Newfoundland, shorefast sea ice is
332 occasionally present in May and June, but is ice-free by July (National Snow and Ice Data Center
333 2019). Capelin aggregations were also typically present at a spawning site for multiple days,
334 which is consistent with observations from Newfoundland populations (Maxner et al. 2016).
335 However, the observed spawning season in Norton Sound was shorter in 2018 than in previous
336 years in this region (Pahlke 1985) or in Newfoundland (Vandeperre and Methven 2007; Maxner
337 et al. 2016). Differences in the duration of spawning activities between the current study and

338 previous research likely reflect missed spawning events in Norton Sound. Additional annual
339 spawning evaluations are needed to determine if the discrepancy in spawning duration observed
340 in 2018 was specific to that year or reflect changes in environmental conditions or population
341 dynamics for Capelin in Norton Sound.

342 Capelin spawning behavior and activity in Norton Sound was generally consistent with
343 reported observations from other areas and studies (Table 2). In Norton Sound, Capelin from
344 nearshore aggregations would ride a wave onto shore, spawn between wave cycles (sometimes
345 grouped as two males with one female), and then ride the next wave back to the ocean, which is
346 similar to observations from other researchers (e.g., Martin et al. 2004). The time of day during
347 which Capelin were observed spawning in Norton Sound was broader than some studies that
348 only observed spawning at night (cf. Pahlke 1985; Gjørseter 1998). This suggests that the onset
349 of Capelin spawning is not necessarily related to or restricted by nocturnal cues and reflects the
350 fact that this region experiences <3 hr of “darkness” (i.e., civil twilight) during the summer
351 (Timeanddate.com 2019). Offshore winds have been suggested to help Capelin access the beach
352 for spawning (Warner and Shafford 1979; Martin et al. 2004), but no discernable qualitative
353 relationship between spawning timing and wind direction was observed in the current study. In
354 addition, compared to other areas, beach-spawning in Norton Sound occurred at similar water
355 temperatures (Carscadden and Vilhjálmsson 2002; Nakashima and Wheeler 2002), dissolved
356 oxygen concentrations (Arimitsu et al. 2008), and salinities (Präbel et al. 2013; Purchase 2017).
357 These observations suggest that beach-spawning Capelin spawn at similar conditions throughout
358 their geographic range.

359 Sediment sizes in Norton Sound were similar to documented Capelin beach spawning
360 sites in other areas (Table 2 [in current study]; Pahlke 1985; Nakashima and Taggart 2002;
361 Nakashima and Wheeler 2002). Sediment size affects the ability of oxygen to diffuse to the eggs
362 (Martin et al. 2004), so regional similarities in size may imply a sediment size preference or
363 requirement. Despite uniformity among beaches, there was a gradient in sediment sizes within a
364 beach in Norton Sound (Figure 2). Sediment sorting is affected by seasonal variations in wind
365 and wave action and intensity, as well as the extent of shorefast ice, which in concert determine
366 and reflect the dynamic nature of beach environments (Reinson and Rosen 1982; Nakashima and
367 Taggart 2002; Arthur 2017). Energy generated by wind and waves erode, deposit, and transport

368 sediments within and among beaches during open-water periods, particularly storm events,
369 whereas shorefast ice preserves beach integrity during ice covered periods (Reinson and Rosen
370 1982). These factors may limit beach suitability for spawning among locations and years
371 (Nakashima and Taggart 2002), which could result in a mismatch between suitable substrate
372 conditions and other environmental factors that influence Capelin spawning timing (Therriault et
373 al. 1996; Arimitsu et al. 2008).

374 Length and weight measurements for spawning Capelin were within the reported ranges
375 for this species, but mean values varied among regions (Table 3). Regional differences in weight
376 were reduced when females of similar lengths were compared between Norton Sound and
377 Iceland (Jóhannsdóttir and Vilhjálmsón 1999). Previous studies have noted increases in Capelin
378 length with latitude (Hedeholm et al. 2010; McNicholl et al. 2018); yet latitude could not explain
379 differences in fish lengths between populations in Newfoundland (53.1°N), Togiak Bay, Alaska
380 (59.0°N), and Norton Sound (63.8°N). While it is unclear why these size differences existed,
381 they may reflect interannual variations in size structure and growth among cohorts within the
382 same population (Hedeholm et al. 2010; Maxner et al. 2016).

383 Capelin spawn between ages 2 to 5 (McNicholl et al. 2018), which is consistent with the
384 age range observed in Norton Sound (Table 3). However, there was a higher proportion of older
385 Capelin in Norton Sound in 2018 (Figure 4B) than in 1981 (Pahlke 1985). The age composition
386 of Capelin spawners can vary annually (e.g., due to environmental factors; Carscadden et al.
387 1994; Maxner et al. 2016), which may explain the observed differences between studies.
388 Alternatively, older spawners may reflect a change in life-history strategy, such as a switch from
389 primarily semelparity to iteroparity (Christiansen et al. 2008). Capelin are believed to be
390 facultatively semelparous (Christiansen et al. 2008) and lab experiments, using Capelin from
391 Newfoundland (Penton and Davoren 2013a) and the Barents Sea (Christiansen et al. 2008),
392 confirmed that males and females are capable of iteroparity. In Newfoundland, Capelin
393 (primarily females) have been found spawning in subsequent years, confirming this life-history
394 trait is expressed in some wild populations (Winters 1971; Maxner et al. 2016). Populations in
395 highly variable environments, such as the Bering Sea and Norton Sound, or with low spawning
396 success are more likely to exhibit iteroparity than those that reside in stable environments (Aydin
397 and Mueter 2007; Christiansen et al. 2008; Eisner 2019). Iteroparity in Capelin has not been

398 examined for Pacific Ocean populations, but increasing environmental variability in the Bering
399 Sea may be creating conditions that favor an iteroparous life-history strategy and thus lead to
400 changes in age structure of Capelin populations.

401 Previous research has noted temporal changes in Capelin size and/or age over the
402 duration of a single spawning season. For example, larger, older Capelin have been observed to
403 arrive on the spawning grounds earlier than their smaller, younger conspecifics in Norton Sound
404 and Newfoundland (Pahlke 1985; Vandeperre and Methven 2007; Maxner et al. 2016). However,
405 no change in Capelin size or age composition was observed in Norton Sound during the 2018
406 spawning period which may be due to the short timeframe during which Capelin were observed
407 spawning compared to other studies (Table 2 [in current study]; cf. Pahlke 1985; Maxner et al.
408 2016). Future studies could examine Capelin size, age, and spawning duration over multiple,
409 successive years in Norton Sound to identify potential intra- and inter-annual variation in
410 reproductive biology.

411 Absolute and relative fecundity estimates for Capelin varied regionally, but were most
412 similar for females of comparable length and weight (Table 3). Regional differences in fecundity
413 may be due to regional differences in environmental conditions, which can affect prey
414 availability and Capelin growth rates (Jóhannsdóttir and Vilhjálmsson 1999; Penton and Davoren
415 2013a). For example, water temperature can affect prey abundance, composition, and
416 distribution within and among regions, and access to an abundance of high-quality prey may
417 allow Capelin to grow larger and produce more eggs than fish with lower quantity and quality
418 prey (Aydin and Mueter 2007; Hedeholm et al. 2010; Andrews III et al. 2016). Although
419 influenced by many factors, fecundity estimates scaled by fish length and/or weight were more
420 similar among Capelin populations than unscaled absolute fecundity estimates for most regions.

421 Female Capelin GSI estimates in Norton Sound were similar to females from other
422 regions (Table 3). Similarities among GSI estimates in these studies confirm that females were
423 collected at a similar maturation stage and suggest that they were reproductively mature. Female
424 GSI estimates were higher than males in Norton Sound, which were consistent with results from
425 the Barents Sea (Huse 1998). Sex-related differences in GSI reflected differential energy
426 allocation prior to and during spawning, where females invested energy into egg production and
427 males invested in spawning behaviors and frequency (Huse 1998; Hanson et al. 2008). Further, a

428 positive relationship between GSI and TL for males suggested that longer males invested more
429 mass into gonad production than shorter males, while a lack of relationship for females
430 suggested that females of all lengths invest equal mass into egg production. Larger gonads may
431 be more beneficial for males than for females. Males are thought to spawn multiple times
432 throughout the spawning season so large testes may allow larger males to spawn with more
433 females than smaller males (Huse 1998). Each additional spawning mate rapidly increases the
434 potential number offspring for each male. Large ovaries can also increase the number of
435 potential offspring for females due to egg quantity or quality (Hedeholm et al. 2011); however,
436 relative to males, this potential increase in offspring is small. Sex-specific differences in
437 reproductive investment are common (e.g., Hanson et al. 2008), but additional research is
438 required to understand the factors driving these differences.

439 To understand ecosystem function, it is important to collect baseline information on the
440 distribution and life history of key species that impact the rest of the ecosystem (Rose 2005;
441 Suryan et al. 2009; Pikitch et al. 2014). Baseline measurements have become increasingly
442 important as the Arctic warms, resulting in shifts throughout the food web (Aydin and Mueter
443 2007; Suryan et al. 2009). For example, recent mass seabird mortality events in the Bering Sea
444 have been occurring at an unprecedented spatial and temporal scales, emphasizing the need to
445 study forage fishes, such as Capelin, to identify changes in prey abundance and availability
446 (Eisner 2019). Although limited to a single sampling season, the information collected during the
447 current study assists in filling our knowledge gap on spawning Capelin in the Pacific Ocean.
448 Additional monitoring of Capelin distribution and abundance may help detect relationships
449 between Capelin and other species in the Bering Sea food web and predict how these
450 relationships may change in altered climate conditions.

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476 <A> References

477 Andrews III, A. G., W. W. Strasburger, E. V Farley Jr., J. M. Murphy, and K. O. Coyle. 2016.
478 Effects of warm and cold climate conditions on Capelin (*Mallotus villosus*) and Pacific
479 Herring (*Clupea pallasii*) in the eastern Bering Sea. Deep-Sea Research II 134:235–246.

480 Arimitsu, M. L., J. F. Piatt, M. A. Litzow, A. A. Abookire, M. D. Romano, and M. D. Robards.
481 2008. Distribution and spawning dynamics of Capelin (*Mallotus villosus*) in Glacier Bay,

- 482 Alaska: a cold water refugium. *Fisheries Oceanography* 17:137–146.
- 483 Arthur, L. 2017, December. An analysis of Arctic coastal resilience in response to erosion.
484 Science Buzz. [https://www.sciencebuzz.com/analysis-arctic-coastal-resilience-response-](https://www.sciencebuzz.com/analysis-arctic-coastal-resilience-response-erosion/)
485 [erosion/](https://www.sciencebuzz.com/analysis-arctic-coastal-resilience-response-erosion/)
- 486 Aydin, K., and F. Mueter. 2007. The Bering Sea - a dynamic food web perspective. *Deep-Sea*
487 *Research Part II* 54:2501–2525.
- 488 Carscadden, J. E., H. Gjørseter, and H. Vilhjálmsson. 2013a. A comparison of recent changes in
489 distribution of Capelin (*Mallotus villosus*) in the Barents Sea, around Iceland and in the
490 Northwest Atlantic. *Progress in Oceanography* 114:64–83.
- 491 Carscadden, J. E., H. Gjørseter, and H. Vilhjálmsson. 2013b. Recruitment in the Barents Sea,
492 Icelandic, and Eastern Newfoundland/Labrador Capelin (*Mallotus villosus*) stocks. *Progress*
493 *in Oceanography* 114:84–96.
- 494 Carscadden, J., B. Nakashima, and D. S. Miller. 1994. An evaluation of trends in abundance of
495 Capelin (*Mallotus villosus*) from acoustics, aerial surveys and catch rates in NAFO Division
496 3L, 1982-89. *Journal of Northwest Atlantic Fishery Science* 17:45–57.
- 497 Carscadden, J., and H. Vilhjálmsson. 2002. Capelin – what are they good for? *ICES Journal of*
498 *Marine Science* 59:863–869.
- 499 Christiansen, J. S., K. Præbel, S. I. Siikavuopio, and J. E. Carscadden. 2008. Facultative
500 semelparity in Capelin *Mallotus villosus* (Osmeridae) - an experimental test of a life history
501 phenomenon in a sub-arctic fish. *Journal of Experimental Marine Biology and Ecology*
502 360:47–55.
- 503 Eisner, L. 2019. The Bering Sea: current status and recent trends. *PICES Press* 27:33–35.
- 504 Environmental systems research institute. 2017. ArcGIS (Version 10.5.1). [Computer Software].
505 Redlands, California.
- 506 Garmin BaseCamp. 2018. Norton Sound. (Version 4.7.0). [https://www.garmin.com/en-](https://www.garmin.com/en-US/shop/downloads/basecamp)
507 [US/shop/downloads/basecamp](https://www.garmin.com/en-US/shop/downloads/basecamp).

- 508 Gjørseter, H. 1998. The population biology and exploitation of Capelin (*Mallotus villosus*) in the
509 Barents Sea. *Sarsia* 83:453–496.
- 510 Hanson, K. C., M. A. Gravel, A. Graham, A. Shoji, and S. J. Cooke. 2008. Sexual variation in
511 fisheries research and management: when does sex matter? *Reviews in Fisheries Science*
512 16:421–436.
- 513 Hedeholm, R., P. GrønkJær, and S. Rysgaard. 2010. Variation in size and growth of West
514 Greenland Capelin (*Mallotus villosus*) along latitudinal gradients. *ICES Journal of Marine*
515 *Science* 67:1128–1137.
- 516 Hedeholm, R., P. GrønkJær, and S. Rysgaard. 2011. Energy content and fecundity of Capelin
517 (*Mallotus villosus*) along a 1,500-km latitudinal gradient. *Marine Biology* (158):1319–1330.
- 518 Huse, G. 1998. Sex-specific life history strategies in Capelin (*Mallotus villosus*)? *Canadian*
519 *Journal of Fisheries and Aquatic Sciences* 55:631–638.
- 520 Jóhannsdóttir, S., and H. Vilhjálmsson. 1999. Fecundity of Icelandic Capelin *Mallotus villosus*
521 (Müller). *Rit Fiskideildar* 16:263–270.
- 522 Karamushko, L. I., and J. S. Christiansen. 2002. Aerobic scaling and resting metabolism in
523 oviferous and post-spawning Barents Sea Capelin *Mallotus villosus villosus* (Müller, 1776).
524 *Journal of Experimental Marine Biology and Ecology* 269:1–8.
- 525 Lauth, R. R., E. J. Dawson, and J. Conner. 2019. Results of the 2010 eastern and northern Bering
526 Sea continental shelf bottom trawl survey of groundfish and invertebrate fauna. National
527 Oceanic and Atmospheric Administration. NMFS-AFSC-396, Seattle, Washington.
- 528 Lebida, R. C., and D. C. Whitmore. 1985. Bering Sea Herring aerial survey manual. Alaska
529 Department of Fish and Game, Bristol Bay Data Report No. 85–2, Anchorage.
- 530 Lewis, K. P., A. D. Buren, P. M. Regular, F. K. Mowbray, and H. M. Murphy. 2019. Forecasting
531 Capelin *Mallotus villosus* biomass on the Newfoundland shelf. *Marine Ecology Progress*
532 *Series* 616:171–183.
- 533 Martin, K. L. M., R. C. Van, W. J. E. Draais, and H. Lakisic. 2004. Beach-spawning fishes,

- 534 terrestrial eggs, and air breathing. *Physiological and Biochemical Zoology* 77:750–759.
- 535 Maxner, E., N. M. Halden, J. D. Roth, and G. K. Davoren. 2016. Intrinsic factors influence the
536 timing of arrival of Capelin (*Mallotus villosus*) to spawning grounds in coastal
537 Newfoundland. *Fisheries Research* 179:202–212.
- 538 McNicholl, D. G., G. K. Davoren, and J. D. Reist. 2018. Life history variation across latitudes:
539 observations between Capelin (*Mallotus villosus*) from Newfoundland and the eastern
540 Canadian Arctic. *Polar Biology* 41:643–651.
- 541 Nakashima, B. S., and C. T. Taggart. 2002. Is beach-spawning success for Capelin, *Mallotus*
542 *villosus* (Müller), a function of the beach? *ICES Journal of Marine Science* 59:897–908.
- 543 Nakashima, B. S., and J. P. Wheeler. 2002. Capelin (*Mallotus villosus*) spawning behaviour in
544 Newfoundland waters – the interaction between beach and demersal spawning. *ICES*
545 *Journal of Marine Science* 59:909–916.
- 546 National Snow and Ice Data Center. 2019. Sea ice index. Available:
547 https://nsidc.org/data/seaice_index/archives/image_select. (September 2019).
- 548 Ogle, D. 2015. Age-length keys. Pages 87–106 in *Introductory fisheries analyses with R*, 1st
549 edition. Chapman and Hall/CRC, Boca Raton, Florida.
- 550 Pahlke, K. A. 1985. Life history and distribution of Capelin, *Mallotus villosus*, in Alaskan
551 waters. Master's thesis. University of Alaska Juneau, Juneau.
- 552 Penton, P. M. 2013. Life history variation in Capelin (*Mallotus villosus*) - a forage fish in the
553 North Atlantic. Doctoral dissertation. University of Manitoba, Winnipeg, Canada.
- 554 Penton, P. M., and G. K. Davoren. 2013a. A common garden experiment on Capelin (*Mallotus*
555 *villosus*) early life history stages to examine use of beach and deep-water spawning habitats.
556 *Journal of Experimental Marine Biology and Ecology* 439:54–60.
- 557 Penton, P. M., and G. K. Davoren. 2013b. Capelin (*Mallotus villosus*) fecundity in post-1990s
558 coastal Newfoundland. *Marine Biology* 160:1625–1632.

559 Pikitch, E. K., K. J. Rountos, T. E. Essington, C. Santora, D. Pauly, R. Watson, U. R. Sumaila, P.
560 D. Boersma, I. L. Boyd, D. O. Conover, P. Cury, S. S. Heppell, E. D. Houde, M. Mangel, É.
561 Plagányi, K. Sainsbury, R. S. Steneck, T. M. Geers, N. Gownaris, and S. B. Munch. 2014.
562 The global contribution of forage fish to marine fisheries and ecosystems. *Fish and*
563 *Fisheries* 15:43–64.

564 Præbel, K., J. S. Christiansen, A. Kettunen-Præbel, and S. E. Fevolden. 2013. Thermohaline
565 tolerance and embryonic development in Capelin eggs (*Mallotus villosus*) from the
566 Northeast Atlantic Ocean. *Environmental Biology of Fishes* 96:753–761.

567 Purchase, C. F. 2017. Low tolerance of salt water in a marine fish: new and historical evidence
568 for surprising local adaption in the well-studied commercially exploited Capelin. *Canadian*
569 *Journal of Fisheries and Aquatic Sciences* 75:673–681.

570 R Core Team. 2018. R: A language and environment for statistical computing (Version 3.5.2).
571 [Computer Software]. R Foundation for Statistical Computing, Vienna, Austria.

572 R Studio Team. 2016. RStudio: integrated development environment for R (Version 1.1.463)
573 [Computer Software]. RStudio Inc., Boston.

574 Reinson, G. E., and P. S. Rosen. 1982. Preservation of ice-formed features in a subarctic sandy
575 beach sequence: geologic implications. *Journal of Sedimentary Petrology* 52:463–471.

576 Rohlf, F. J. 2005. tpsDig2, Digitize landmarks and outlines [Computer Software]. State
577 University of New York, Stony Brook.

578 Rose, G. A. 2005. Capelin (*Mallotus villosus*) distribution and climate: a sea “canary” for marine
579 ecosystem change. *ICES Journal of Marine Science* 62:1524–1530.

580 Siddon, E., and S. Zador. 2018. Ecosystem status report 2018: Eastern Bering Sea. Stock
581 Assessment and Fishery Evaluation Report, North Pacific Fishery Management Council,
582 Anchorage, Alaska.

- 583 Suryan, R. M., V. S. Saba, B. P. Wallace, S. A. Hatch, M. Frederiksen, and S. Wanless. 2009.
584 Environmental forcing on life history strategies: evidence for multi-trophic level responses
585 at ocean basin scales. *Progress in Oceanography* 81:214–222.
- 586 Systat Software Inc. 2012. SigmaPlot (Version 12.3). [Computer Software]. San Jose, California.
- 587 Taggart, C. T., and B. S. Nakashima. 1987. The density of Capelin (*Mallotus villosus* Müller)
588 eggs on spawning beaches in Conception Bay, Newfoundland. Canadian Technical Report
589 of Fisheries and Aquatic Sciences, No. 1580. St. John's, Newfoundland, Canada.
- 590 Therriault, T. W., D. C. Schneider, and D. A. Methven. 1996. The timing of spawning in Capelin
591 (*Mallotus villosus* Müller) at a coastal location in eastern Newfoundland. *Polar Biology*
592 16:201–207.
- 593 Vandeperre, F., and D. A. Methven. 2007. Do bigger fish arrive and spawn at the spawning
594 grounds before smaller fish: cod (*Gadus morhua*) predation on beach spawning Capelin
595 (*Mallotus villosus*) from coastal Newfoundland. *Estuarine, Coastal and Shelf Science*
596 71:391–400.
- 597 Warner, I. M., and P. Shafford. 1979. *Forage fish spawning surveys: southern Bering Sea*.
598 Alaska Department of Fish and Game, Research Unit No. 19, Project Completion Report,
599 Kodiak, Alaska.
- 600 Wentworth, C. K. 1922. A scale of grade and class terms for clastic sediments. *The Journal of*
601 *Geology* 30:377–392.
- 602 Winters, G. H. 1971. Fecundity of the left and right ovaries of Grand Bank Capelin (*Mallotus*
603 *villosus*). *Fisheries Research Board of Canada* 28:1029–1033.
- 604 Winters, G. H. 1982. Life history and geographical patterns of growth in Capelin, *Mallotus*
605 *villosus*, of the Labrador and Newfoundland areas. *Journal of Northwest Atlantic Fishery*
606 *Science* 3:105–114.

607 <A> Tables

608 TABLE 1. Summary of the geographic survey sections (organized from the northwestern to southeastern most extent of the survey
609 range), distance of shoreline covered per section, and the number of nearshore Capelin aggregations observed during the aerial
610 surveys. Survey section numbers correspond with the geographic landmark numbers in Figure 1. See Methods for density calculation.

611 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
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

10-11 West Mountains to Cripple

07-Jul	12:40	14:30		0	0.00
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

11-12 Cripple to Nome

07-Jul	12:40	14:30		0	0.00
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

12-13 Nome to Cape Nome

07-Jul	12:40	14:30		0	0.00
26-May	10:00	11:45	21.2	7	0.33
02-Jun	10:00	11:20		1	0.05

13–14 Cape Nome to Solomon

08-Jun	10:15	12:20		3	0.14
13-Jun	9:40	12:44		0	0.00
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
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
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

612 ^aCapelin were actively spawning along shore and distinct spawning aggregations were not discernable from the helicopter.

613 TABLE 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	Gjørseter 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
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

614 ^amean \pm SD values were reported in a graph for four sample locations. Values reported here were estimated from the graph and are the
615 two locations with the minimum and maximum mean values.

616 ^brange for best embryo development.

617 ^crange of tolerances tested for egg incubation (lethal range may be larger).

618 TABLE 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
	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
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	F	590	236	Norton Sound	current
based on TW (# eggs/g fish weight)		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

619 ^arange based on length bins

620 ^bmean of reported means

621 ^cage-3 and age-4 fish only (excludes age-4 fish which comprised < 3% of fish)

622 ^daverage of average value reported in nearest length bins (i.e., 135 and 140 mm)

623 ^ereported average based on all lengths

624 <A> Figure Captions

625 FIGURE 1. Map of the 2018 spawning Capelin spawning sites where Capelin and sediment
626 samples were collected as well as the geographic landmarks (numbered) used to count nearshore
627 fish aggregations during aerial surveys along the coast of Norton Sound, Alaska. Geographic
628 landmark numbers correspond with locations in Table 1. Spawning site labels (inset map on top
629 right) correspond to the three broad spawning locations described in-text. Sk = Sinuk River, Pn =
630 Penny River, Nm = Nome River.

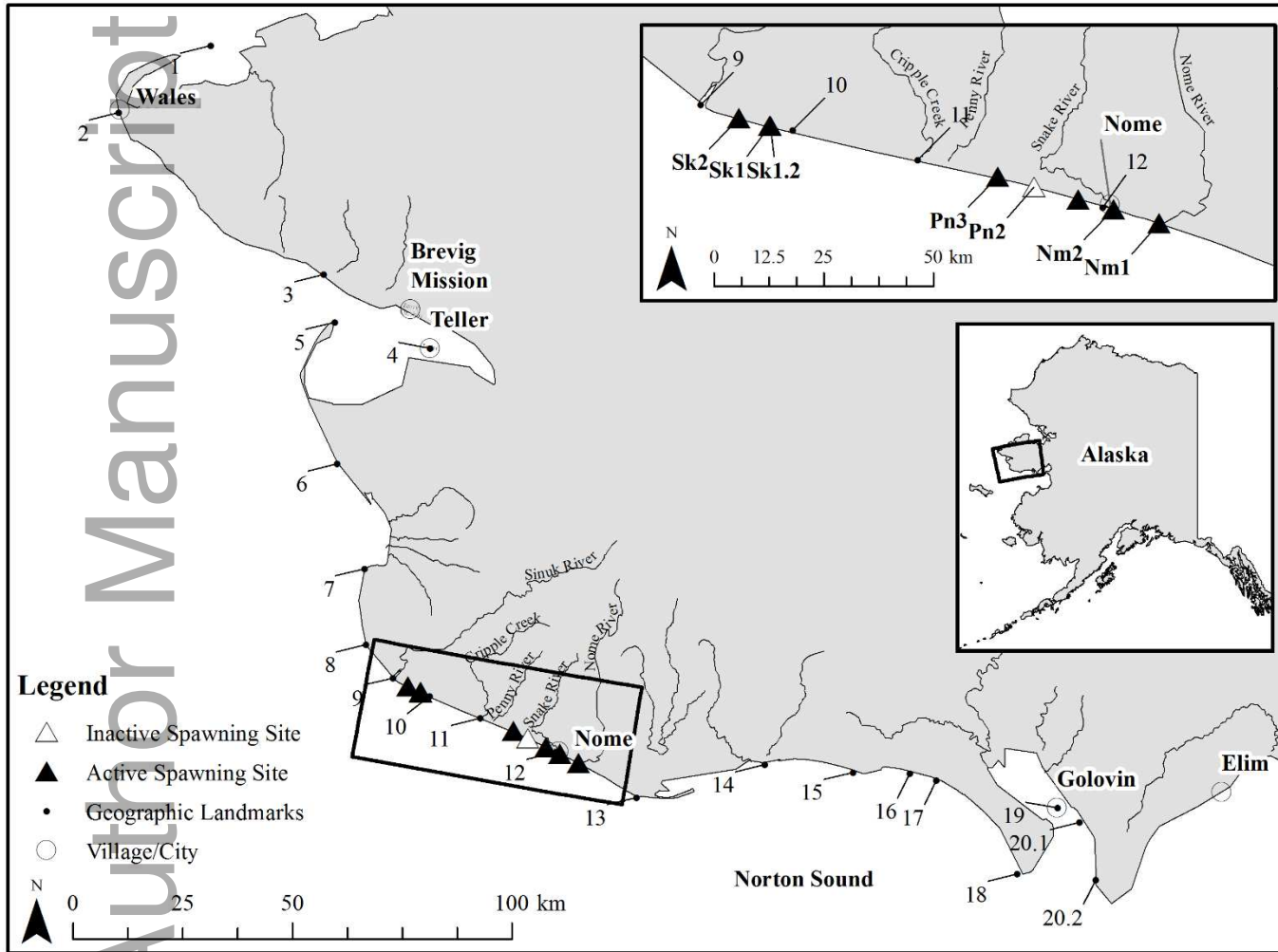
631 FIGURE 2. Variation in the percent weight of the sediment size classes among locations on the
632 beach at spawning sites (averaged across sites). All locations had < 1% fines. Gravel > 2000 μm ,
633 coarse sand = 500 to 2000 μm , fine sand = 63 to 500 μm , fines < 63 μm .

634 FIGURE 3. Relationship between log-transformed TL and total weight (TW) for male and
635 female Capelin.

636 FIGURE 4. Percent frequency distributions for Capelin **(A)** TL and **(B)** age.

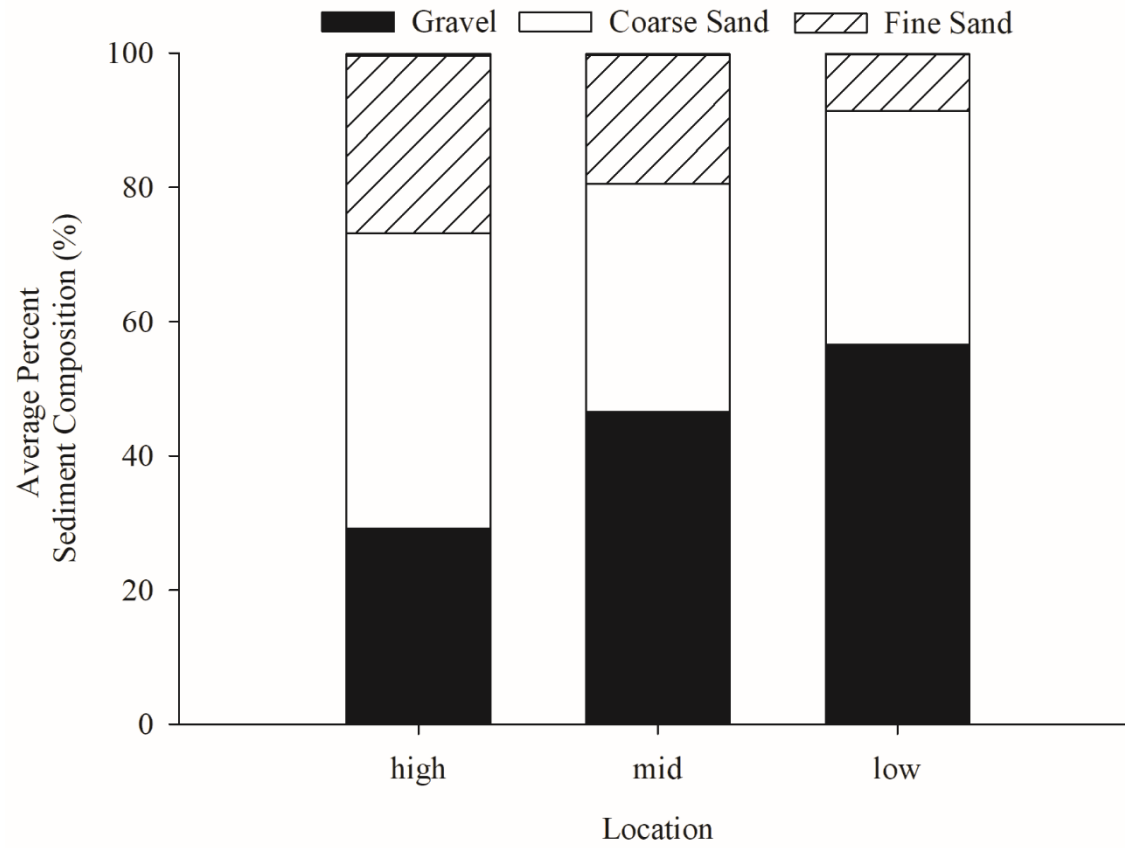
637 FIGURE 5. Relationship between absolute fecundity (Fa) and total weight (TW) for female
638 Capelin.

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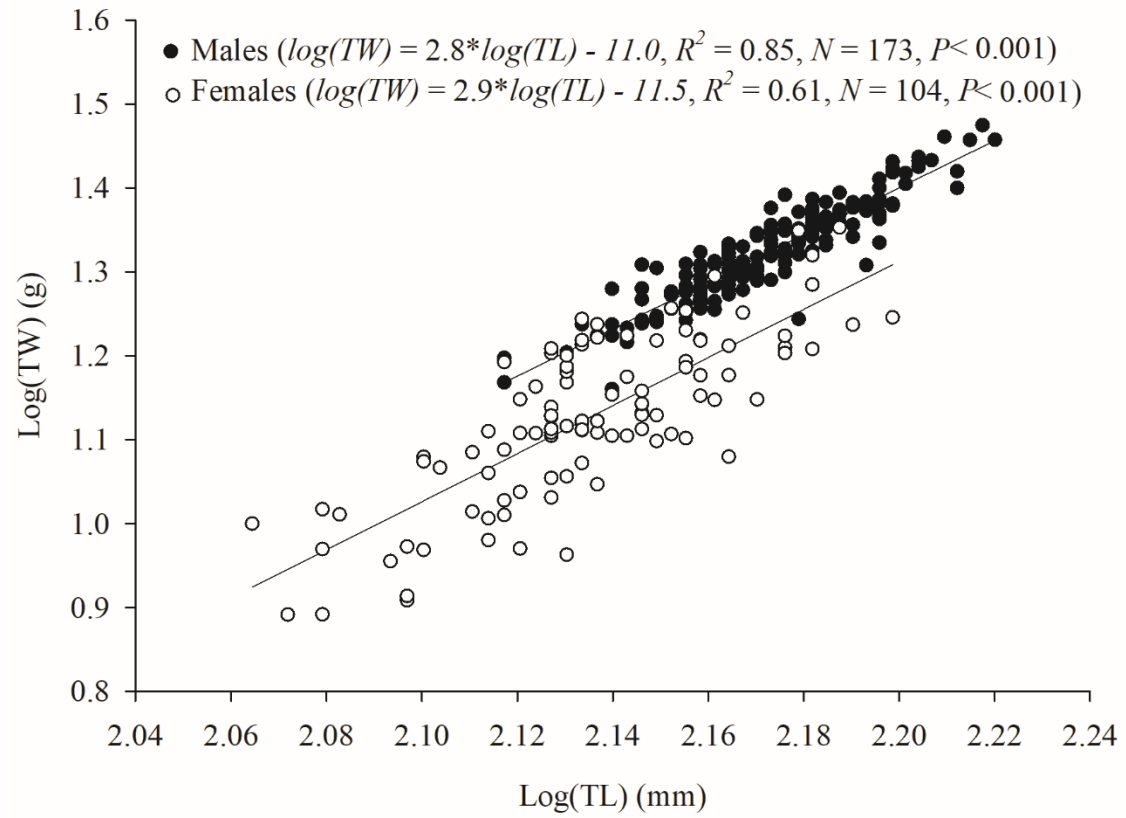


640

641 FIGURE 1

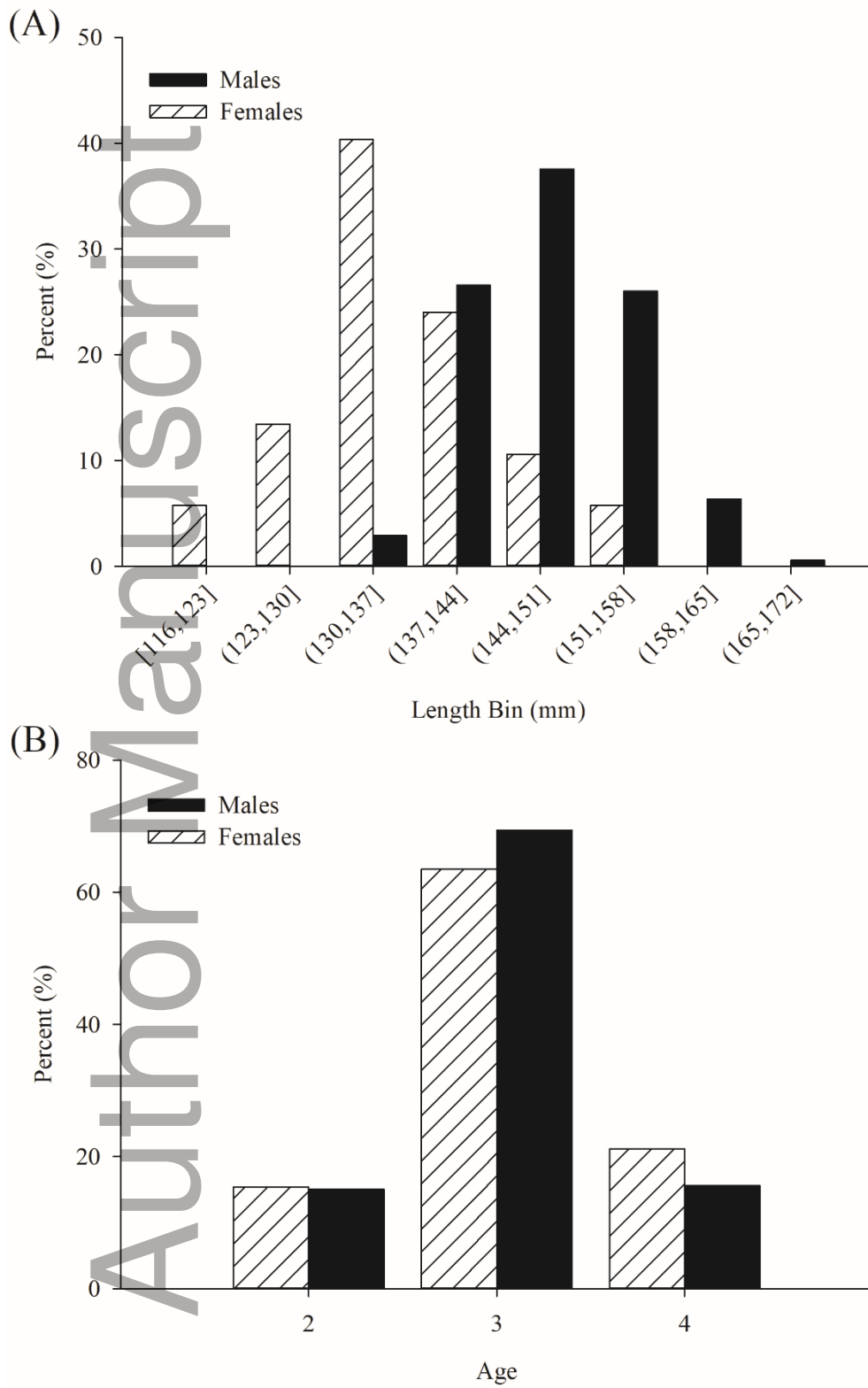


642 FIGURE 2



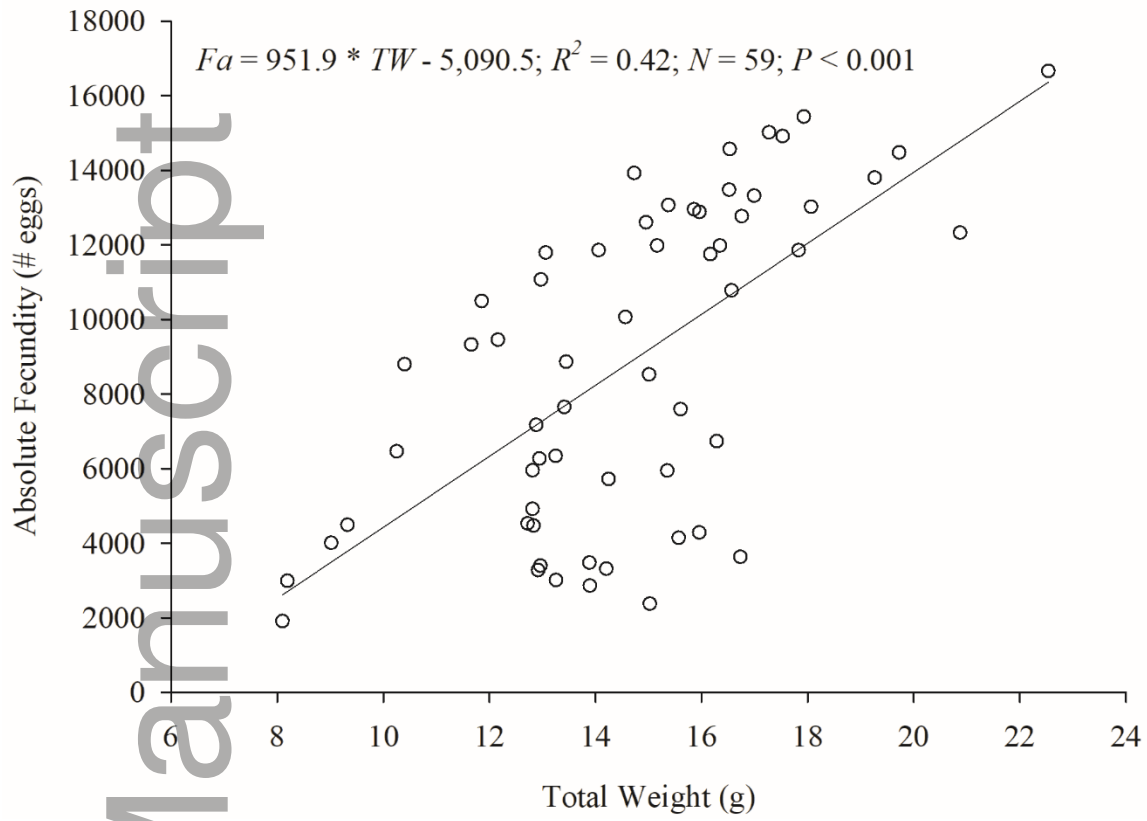
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644 FIGURE 3



645

646 FIGURE 4



647

648 FIGURE 5

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