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PRELIMINARY STUDIES OF CAPELIN (*Mallotus villosus*) IN ALASKAN WATERS

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ABSTRACT

Capelin, *Mallotus villosus,* are distributed throughout coastal Alaska with substantial populations spawning in northern Norton Sound, Bristol Bay, and near Kodiak Island. Spawning behavior is similar to that of Atlantic capelin. They concentrate near the coast in the spring and spawn on gravel beaches. Time of spawning varies with location and water temperature, ranging from April to August at 5-10°C and often overlaps that of Pacific herring, *Clupea harengus pallasi*. Spawning capelin were collected in Bristol Bay in 1979, 1981, 1982, and 1983, in Norton Sound in 1981 and in Kodiak in 1982. Lengths, weights, and ages were analysed and compared with Atlantic and other Pacific data. Size and age at maturity are less than those for Atlantic stocks. Age ranged from II to IV; the predominate class is age III. Age composition, average length, and average weight were significantly different between the study areas and varied from year to year. Males were larger, ranging from average lengths of 115 mm in Kodiak (1982) to 168 mm in Togiak (1981). Females ranged from 109 mm in Kodiak (1982) to 153 mm in Togiak (1981). Survival of spawners is very low. Abundance fluctuates widely due to natural causes.

KEY WORDS: Capelin, *Mallotus villosus*, spawning behavior, length, weight, age, distribution.

INTRODUCTION

Capelin, *Mallotus villosus*, are an abundant Alaskan resource and the small smelt-like fish is the focus of a developing fishery. The available literature on Pacific capelin is extremely scarce and information on the life history and distribution of a species is essential for sound management of a fishery.

Background

Capelin are an arctic-boreal osmerid found along the Atlantic coast of North America, Iceland, and Norway; along the Arctic coast of Canada and the Soviet Union; and along the Pacific coast in the Bering Strait, Kamchatka Peninsula waters, the Sea of Okhotsk, and the Sea of Japan as far south as Korea (Walters 1955; McAllister 1963; Prokhorov 1968). Capelin are distributed along the entire coastline of Alaska and extend south through British Columbia to the Strait of Juan de Fuca in Washington (Hart 1973). Most of the available information on capelin is from the North Atlantic where there has been a large commercial fishery (total harvest during 1981 of 2,787,911 mt) during the last decade (FAO 1983).

Shultz (1937) compared the capelin of the North Pacific and North Atlantic. On the basis of meristic characters he concluded that the two forms were separate species; the name *Mallotus catervarious* (Pennant) was revived for the Pacific form and the name *Mallotus villosus* (Muller) was retained for the Atlantic form. Examination of further material including Arctic specimens showed that Arctic capelin had meristic indices intermediate to those of Pacific and Atlantic capelin (McAllister 1963). Consequently *Mallotus villosus* is generally regarded as a monotypic species, however some Japanese literature still refers to two species of capelin and Soviet literature refers to a Pacific subspecies, *M. villosus socialis* (Okada and Kobayashi 1968; Velikanov 1984).

The spawning behavior of Atlantic capelin has been extensively studied (Jeffers 1931; Templeman 1948; Winters 1969). The time of spawning varies greatly with location, ranging from April to October.

Details of overwintering and migratory habits of western Atlantic capelin are described by Winters (1969). From January through March, capelin are concentrated in large inactive schools near the bottom at depths of 140 to 200 m and bottom temperatures of less than 0°C. By April these large schools break up into smaller feeding schools which move off the bottom to begin their migrations to the spawning grounds. Spawning takes place in May or June.

Segregation of schools by sex prior to spawning has been frequently reported (Templeman 1948; Pitt 1958; Trumble 1973). Schools composed of males stay closer to shore and are larger in size than female schools. Vertical segregation of sexes with males in dense schools near the bottom and females in low density pelagic schools has also been reported in Atlantic capelin (Bakke and Bjorke 1973; Winters 1974; Saetre and Gjøsaeter 1975). This segregation often results in highly disproportionate sex ratios in individual samples;

however the sex ratio of two-year-old virgin capelin on the feeding grounds was 1:1 (Prokhorov 1968).

At the time of spawning, gonads occupy most of the female's body cavity and may represent up to 30% of total body weight. Fecundity varies greatly with geographic location ranging from 5,000 to 61,500 eggs/female (Table 1). Male gonads are relatively small and represent only 1.5% of total body weight of Barents Sea capelin (Prokhorov 1968). Fecundity estimates of Northwest Atlantic capelin revealed the left ovary to be up to nine times more fecund than the right (Winters 1971).

Spawning capelin are characterized by distinctive sexual dimorphism. Males are longer than the females and develop enlarged pectoral, anal, and pelvic fins. Several weeks prior to spawning a ridge of elongated scales appears above the lateral line. On mature capelin captured during the spawning season, the epidermis is much thicker on males than on females. The thickening of the epidermis and formation of the spawning ridges probably helps to protect the males during the spawning act, a much longer and more damaging event for males than females (Templeman 1948).

Spawning takes place on gravel beaches or offshore in deeper water and is limited to a narrow range of water temperature (Table 2). The preferred water temperature range for beach spawning Atlantic capelin is 5 to 10°C. Offshore spawning has been reported to depths of 280 m but usually occurs in less than 75 m of water (Templeman 1948; Saetre and Gjøsaeter 1975). Pitt (1958) stated that it was well known that when waters become too warm on the beach, spawning continues in deeper coastal waters. Temperatures for offshore spawning range from 2 to 4.2°C (Pitt 1958; Bakke and Bjorke 1971). Preferred beaches generally have gravel substrate of grain size from 2.5 to 25 mm (Templeman 1948; Jangaard 1974). The demersal and adhesive eggs are buried further by wave action.

Spawning occurs primarily at night or on heavily overcast days. Leggett et al. (1984) predicted the spawning date in Newfoundland capelin within 3 days from an empirical relationship between observed spawning date and cumulative growing degree days. Spawning activity is usually greatest just after high tide and increased surf action (Pitt 1958; Trumble 1973). Older, larger fish ripen and spawn earlier, resulting in a decrease in average size of spawners over the four to six weeks spawning period (Templeman 1968). Lanman (1874) gives a colorful and fairly accurate description of the behavior of Atlantic beach spawning capelin:

> The manner in which the capelin deposits its spawn is one of the most curious circumstances attending its natural history. The male fishes are somewhat larger than the female, and are provided with a sort of ridge projecting on each side of their back-bones, similar to the eaves of a house, in which the female capelin is deficient. The latter, on approaching the beach to deposit its spawn, is attended by two male fishes, who huddle the female between them, until the whole body is concealed under the projecting ridges, and her head only is visible. In this position all three run together, with great swiftness, upon the sands, when the males,

Table 1. Literature values for fecundity ranges of capelin populations.

Location	Fecundity	Source
Barents Sea	5,800 - 19,090	Gjøsaeter and Monstad 1973
Barents Sea	5,256 - 48,336	Galkin and Kovalev 1975
White Sea	6,200 - 13,400	Altukhov 1977
Newfoundland	15,000 - 52,000	Templeman 1968
Newfoundland	16,550 - 61,500	Winters 1971
Sea of Japan	15,000 - 57,000	Andriyashev 1954
British Columbia	5,000 - 6,000	Clemens and Wilby 1961
Bering Sea	6,000 - 22,000	Warner and Shafford 1978

Table 2. Locations, dates, water temperatures, and sources of information on spawning Atlantic capelin populations.

Location	Date	Water Temp (°C)	Source
Barents Sea	March - April	2 - 4	Bakke and Bjorke 1973
Norway	Feb. - March	1.5 - 5	Olsen 1968
Iceland	March - June	6 - 7	Winters 1969
Greenland	May - June	2 - 6	Winters 1969
Newfoundland	June - July	5.5 - 8.5	Templeman 1948
Grand Banks	June - July	2.8 - 4.2	Pitt 1958

> by some inherent imperceptible power, compress the body of the female, between their own, so as to expel the spawn from the orifice and the tail. Having thus accomplished its delivery, the three capelins separate and paddling with their whole force through the shallow water of the beach, generally succeed in regaining once more the bosom of the deep; although many fail to do so, and are cast upon the shore, especially if the surf be at all heavy.

Capelin populations periodically fail to arrive at traditional spawning grounds (Templeman 1948). Turner (1886) hypothesized that Pacific capelin exhibit a three-year cycle. Spawning activity varies in location from year to year due to different temperature regimes (Prokhorov 1968; Olson 1968; Dunbar 1970). Many dead capelin, mostly males, are washed onshore during and immediately following spawning. Many of the males are at the spawning grounds constantly throughout the season and towards the end of the season these fish have ragged fins and are emaciated with little chance of survival (Jangaard 1974). The mortality rate of spawning capelin is undoubtedly high and most investigators believe post-spawning survival and repeated spawning is, for all practical purposes, negligible (Olsen 1968; Prokhorov 1968).

Incubation period for capelin eggs varies with temperature. Hatching occurs in about 30 days at 5° and 15 days at 10°C (Jeffers 1931). Newly hatched larvae are from 3 to 6 mm long and soon start a pelagic life near the surface. The rate of fertilization appears to be very close to 100% (Saetre and Gjøsaeter 1975). Capelin eggs are hardy and will tolerate wide ranges of temperature, salinity, and exposure to air (Jeffers 1931 and Davenport et al. 1979). Predation by fish is often the most significant cause of mortality in demersal eggs (Saetre and Gjøsaeter 1975). In the Atlantic, haddock may consume a significant percentage of capelin eggs spawned deeper than 100 m but are insignificant predators on shallow spawned eggs.

Many fish, including herring feed upon the larvae. Fluctuations in the abundance of capelin larvae off the coast of Iceland were directly related to water temperatures. When the water temperatures were above normal during summer months, the larvae were very abundant in the area (Magnusson 1968).

Capelin usually do not develop scales during their first year of growth; consequently, otoliths are generally used for age determination. Atlantic capelin may mature at age two but maturation does not normally occur until age three (Prokhorov 1968). Age three and four fish dominate the spawning stocks, with ratios between three-, four-, and five-year-old varying from year to year.

During their first year, males and females are the same size, but during the second year males grow at a faster rate (Jangaard 1974). An examination of the average length and age class composition of spawning Norwegian capelin over a five-year period indicated that these parameters varied considerably from year to year (Olsen 1968). Lengths of males ranged from 144 to 204 mm and females ranged from 128 to 185 mm.

Capelin feeding activity is highly seasonal. Feeding is most intense in summer and autumn and decreases in the winter when feeding almost ceases.

Feeding increases in the pre-spawning period of late winter and early spring and then ceases again during the actual spawning period. The oil content reflects this pattern; ranging from 25% at the end of the summer to 1% in spent fish (Prokhorov 1968 and Winters 1969). Capelin are planktivorous, feeding primarily on copepods and euphausiids (Prokhorov 1968; Viljalmsson 1968). Although the food habits of capelin and young herring are quite similar there is no marked competition (Prokhorov 1968). Lambert et al. (1982) found that capelin larvae and herring larvae of the same size were rarely found at the same depth, decreasing the likelihood of competition.

Capelin are an important food supply for many other fish, marine mammals, and birds. During the spawning migration schools of Atlantic capelin are closely followed by large schools of cod. In Newfoundland, from June to early August, cod feed almost exclusively on capelin (Templeman 1965). Capelin are a major food item in the diet of Atlantic salmon in the northwest Atlantic (Lear 1972).

Objectives

Information on capelin in Alaskan waters, and the Pacific Ocean in general, is scarce and incomplete. A solid data base is needed to form management policies and decisions. If an intensive capelin fishery were to develop quickly it is conceivable that local stocks could be seriously damaged before sufficient information was available to manage the fishery. Data on unexploited stocks would become difficult to collect. The objectives of this study are to:

1) Describe the distribution, spawning timing, and spawning behavior of Northeast Pacific capelin.

2) Determine whether age, weight, length (AWL), and sex ratio vary spatiotemporally in the Bering Sea.

3) Test the hypothesis that the AWL and sex ratio characteristics of the spawning populations in the Bering Sea and Gulf of Alaska are different.

4) Determine if capelin in Alaskan waters spawn more than once.

5) Discuss capelin abundance.

MATERIALS AND METHODS

Sampling Locations

After completion of one field season and a literature review, I selected study areas at Kodiak, Togiak, and Nome (Figure 1). These areas were selected for three reasons: (1) they are known to have large spawning populations of capelin; (2) they are geographically distinct; and (3) they have existing Alaska Department of Fish and Game (ADF&G) research projects which could be modified to include capelin research. The Kodiak area includes all the bays and inlets of the Kodiak Island group. The Togiak area consists of the coastline from Kulukak Bay to Cape Newenham, including Summit Island and

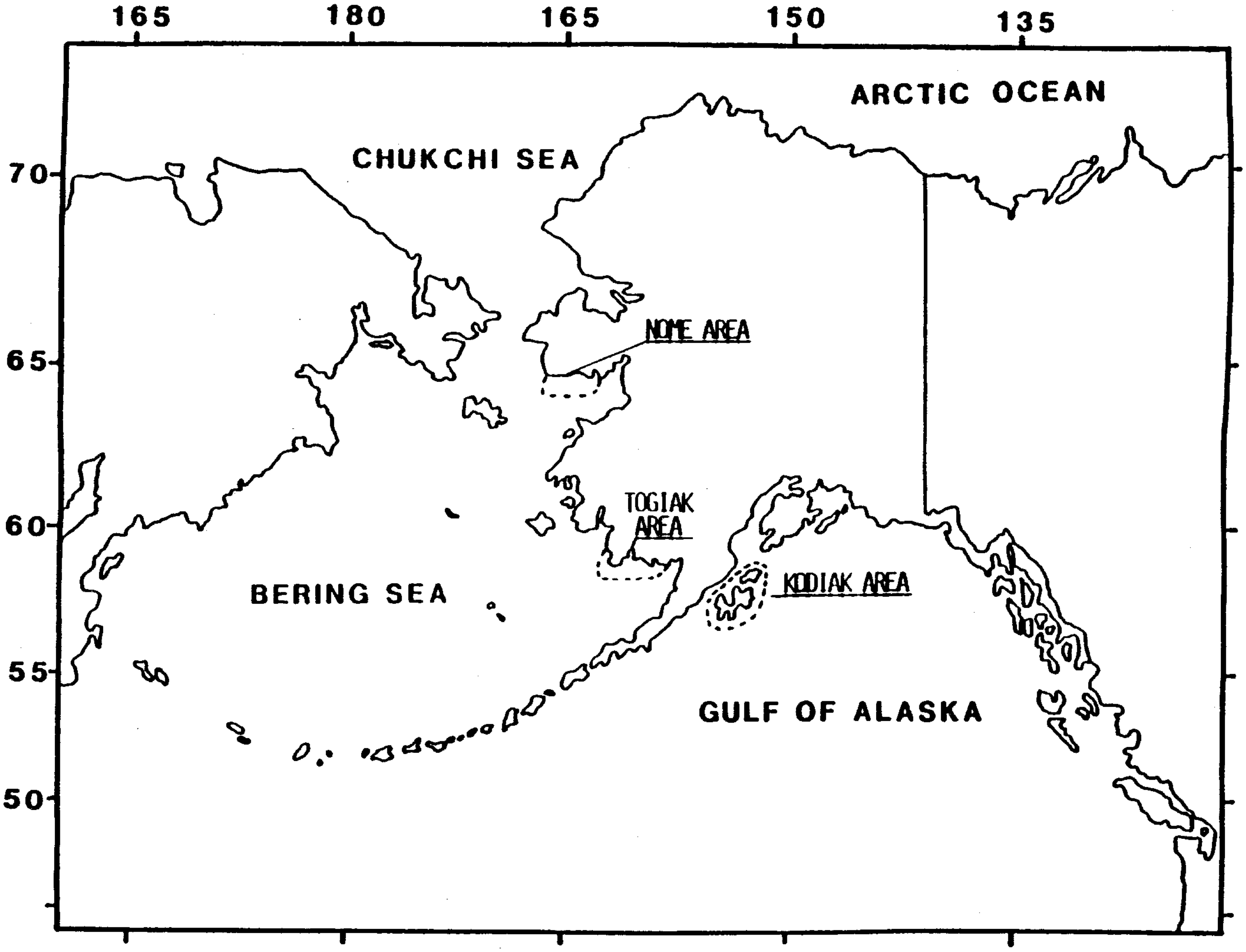

Figure 1. Locations of study areas in Alaska.

Security Cove. The Nome area encompasses the northern portion of Norton Sound from Golovin Bay to Cape Rodney (Appendix 1).

Samples of spawning fish were collected in the Togiak area in 1979, 1981, 1982, and 1983, in the Nome area in 1981, and in the Kodiak area in 1982. These samples were analyzed along with information from several other investigations. The length frequency data and otoliths from 1977, 1978, and 1979 were obtained from either the ADF&G or the Outer Continental Shelf Environmental Assessment Program (OCSEAP). Many different investigators collected these data using different techniques and various gear which likely introduced small errors and/or biases to the data. In order to reduce length measurement biases, the data were grouped into 5 mm classes and population differences of less than 5 mm were discounted. Over 6,000 fish were examined over six different years from three major areas (Table 3).

Distribution

Distribution of spawning and nonspawning populations was determined through the use of historical references, incidental catch records, troll log books, stomach contents of predators, research and management agency publications, interviews, and in-field observations. The same references and sources, in combination with data collected in the field, were used to compile biological information relating to each study area.

Sampling Techniques

Samples were collected with multifilament variable mesh gillnets, dipnets, a small trawl, a cast net, and commercial purse seines and otter trawls. Spawning mortalities were collected by hand. The majority of fish sampled were collected by variable mesh gillnet, dipnet or were spawning mortalities. The gillnets had six 3.1 x 3.1 m (10 ft x 10 ft) panels with mesh sizes of 10, 7.5, 6.25, 5.0, 3.75, 2.5 cm (4, 3, 2.5, 1.5, 1 in). Dipnets were used to catch fish in the surf and shallow water. The 3.1 m diameter, 2.5 cm mesh cast net was also tried in shallow water when fish were not plainly visible. The small (3.1 m opening) otter trawl had 5 cm mesh in the wings and 1.3 cm mesh in the cod end, and was pulled behind a skiff to sample further offshore.

When sufficient time and personnel were available, length and weight measurements were taken on fresh fish and two otoliths (sagittae), were collected and stored in 50% ethanol in a vial labeled to identify the specific fish. Snout to fork lengths were measured to the nearest millimeter and weights to the nearest gram. When many fish were being sampled where freezer facilities were not available, only one otolith per fish was taken. It was placed in a vial containing otoliths from other fish from that sample of the same sex and length range (5 mm). When many fish were being sampled and freezers were available, some fish were labeled and frozen for examination at a later date.

Table 3. Summary of all capelin samples examined in this study including numbers of males and females sampled, numbers of lengths, weights, and otoliths collected, gear type, and source of data.

Location	Year	Males (n)	Females (n)	Lengths (n)	Weights (n)	Otoliths (n)	Gear[1]	Source
Kodiak	1977	80	16	96	96	0	6	OCSEAP
Togiak	1977	411	446	857	613	0	4	OCSEAP
Togiak	1978	355	14	369	365	0	1	ADFG
Security Cove	1978	233	15	248	248	0	1	ADFG
Kodiak	1979	425	122	583	508	0	5,3	ADFG
Togiak	1979	727	309	1036	238	930	1,4,5	ADFG
Kodiak[2]	1981	3	2	326	316	308	3	this study
Togiak	1981	492	466	958	530	511	1,2,5	this study
Security Cove	1981	143	22	165	137	165	1	this study
Nome	1981	714	535	1249	1166	1249	5	this study
Kodiak	1982	170	0	170	169	170	5	this study
Kodiak[2]	1982	84	111	243	241	232	5	this study
Togiak	1982	431	65	498	475	498	1,5	this study
Security Cove	1982	581	172	581	577	451	1	ADFG
Kodiak[2]	1983	11	47	146	57	138	5	this study
Togiak	1983	164	206	370	370	370	4,5	this study
totals		5024	2548	7895	6106	5022		

[1] Gear: (1) variable mesh gillnet; (2) 3.1 m beam otter trawl; (3) commercial shrimp trawl; (4) commercial purse seine; (5) dipnet; and (6) hand.

[2] Non-spawning fish, sample totals: 1981, 326; 1982, 243; 1983, 146.

Age Estimation

Cleaned otoliths were mounted on plastic trays, immersed in 50% ethanol solution and allowed to clear for up to one hour. They were then examined under reflected light with a binocular microscope at 10-20 X magnification. Ages were determined from the lateral convex face of the otoliths and were recorded as age groups with an arbitrary birthdate of 1 January (Winters and Campbell 1974). Terminology used is that described by Jensen (1965).

In aging the otoliths in this study, the opaque central ring is considered the first annulus and the hyaline zone at the outer edge is considered the last annulus (Templeman 1968). Otoliths without clearly defined annuli were omitted from age determinations. Two hundred otoliths representing the complete range of sampling locations and lengths of fish sampled were sent to the Department of Fisheries and Oceans in Newfoundland, Canada for verification of technique. Age agreement was 96% for spawning fish and 88% for post-spawning fish displaying recent plus growth. Since post-spawning fish have no distinct outer hyaline zone, the outermost hyaline zone was counted as the last annulus and further growth recorded as plus growth from the sampling year (Jearld 1983). Examining fresh otoliths in the field was found to be the simplest method of aging fish and in 1983 otoliths were aged immediately after sampling in the Togiak area.

Analysis

Data on location, date, length, weight, sex, and age of each fish were entered into the University of Alaska Honeywell computer and analyzed using the Statistical Package for the Social Sciences (SPSS) (Nie et al. 1975). Fish were separated by sex and grouped into five millimeter length increments. Length-frequency histograms were plotted for each sample. The variation of length at age between years and between locations was tested using a one-way analysis of variance (ANOVA). Significant differences were identified by using the Student-Newman-Keuls (SNK) test (Zar 1974). The SNK procedure is a multiple range test that was used to compare differences among sets of means after arranging them in rank order from smallest to largest. The null hypothesis tested is that the difference between two means is zero. Contingency tables (not shown) were used to determine the observed age-at-length proportions for the years in which otoliths were aged (Nie et al. 1975; Sokal and Rohlf 1981). These values were then used to estimate age composition in 1977 and 1978 in the Togiak area (Ricker 1975).

RESULTS

Spawning Behavior

The onset of spawning ranged from mid-May to late June with nearshore water temperatures between 5 and 9°C (Table 4).

Togiak Area:

Spawning began in mid-May in 1979 and continued for more than three weeks. Capelin were not collected in the Togiak area in 1980. In 1981, environmental

Table 4. Locations, dates, water temperatures, and sources of information on Pacific spawning capelin.

Location	Date	Water Temp (°C)	Source
Vancouver Is.	Sept.-Oct.	10-13	Hart and McHugh 1944
Kodiak	June 1977	-	Warner and Shafford 1978
Kodiak	May 28,1979	-	Warner and Shafford 1978
Kodiak	June 1982	-	This study
Port Moller	May 1977	6-8	Warner and Shafford 1978
Togiak	June 1977	7.8	Warner and Shafford 1978
Togiak	May 1978	6.0	ADF&G
Togiak	May 1979	-	ADF&G
Togiak	May 19,1981	5.0	This study
Togiak	June 1982	5-9	This study
Togiak	mid-May 1983	6.0	This study
Nome	June 1981	8-9	This study
Nome	June 1983	-	ADF&G
Point Lay	Aug.1,1983	8-10.6	Craig (personal com.)
Prudhoe Bay	Aug. 1975	6-10	Bendock 1977
Sea of Japan	April-May	2-4	Linberg and Legaza 1965
Sakhalin Is.	May-July	1-14	Velikanov 1984

conditions were closely observed from the onset of spawning on 19 May. There had been high winds for the previous two days and the seas were still rough. The fish were first observed at 6:30 AM at high tide with water temperature of 5°C. There was a full moon, overcast sky and an onshore wind. The spawning continued all day, through periods of bright sunshine and the full range of tidal stages. The substrate on the beaches was a mixture of fine sand and small gravel.

Capelin were scarce in Bristol Bay in 1982, a few were caught on 2 June at a water temperature of 5°C. No spawning was observed until 22 June when the water temperature was over 9°C.

The 1983 capelin spawning run began in mid-May at a water temperature of 6°C. Once again the spawning started after three days of high winds and rough seas. Most of the spawning occurred at night.

Sex ratio of individual samples ranged from 25%-99% males, varying with location and gear type (Table 5). Spawning mortalities found onshore were always predominately males.

Security Cove fish displayed characteristics similar to other Togiak area fish. They spawned in mid to late May each year from 1978-1983. Capelin were more abundant in Security Cove in 1980 and 1982 than in the rest of the Togiak area.

Nome Area:

Capelin spawned on the beaches of northern Norton Sound throughout June 1981 at water temperatures of 8-9°C. Spawning was predominately at night, which in this northern latitude begins about midnight and ends about 2:00 AM in June. The sex ratio of individual samples caught in the surf varied from 24%-86% male. The beaches in the area are very narrow and very few spawning mortalities were observed. Tidal fluctuations in Norton Sound and the Chukchi and Beaufort Seas are very small and do not seem to affect capelin spawning. No capelin were observed in the Nome area in 1982. In 1983 spawning began 29 May and continued to 22 June.

Age-Weight-Length

Mature male capelin are consistently larger than females of the same age class (t-test $p<.001$). Therefore, whenever sexes were determined, samples were split into sex categories (Tables 6 and 7). The length-weight relationship of mature capelin was nearly identical for both sexes (Table 8). The correlation between length and weight was significant ($r^2 = .90$) so most analysis was carried out only on length data. The age of spawning Alaskan capelin ranged from age II to IV with age IV being extremely rare.

Togiak Area:

The length frequencies of Togiak area spawners varied considerably from year to year (Figure 2). Average lengths ranged from a high in 1981 of 168 mm for males and 153 mm for females to a low in 1977 of 143 mm for males and

Table 5. Sex ratio of capelin samples by date, location, and gear.

Area	Date	Gear[1]	Sample Size	Male (%)	Female (%)
Togiak	5/19/81	1	4,394	52	48
Togiak	5/20/81	5a	145	99	1
Togiak	5/20/81	5a	517	94	6
Togiak	5/20/81	5b	64	89	11
Togiak	5/20/81	5c	55	85	15
Togiak	5/20/81	5d	59	54	26
Togiak	5/20/81	6	377	78	22
Togiak	5/21/81	5a	108	99	1
Togiak	5/21/81	2	211	25	75
Togiak	5/22/81	1	240	96	4
Togiak	5/26/81	1	261	95	5
Togiak	5/17/83	4	240	36	64
Togiak	5/22/83	6	334	84	16
Nome	6/21/81	5	192	86	14
Nome	6/22/81	5	553	24	76
Kodiak[2]	5/ /82	3	195	57	43
Kodiak[2]	7/ /83	3	58	19	81

[1] Gear: (1) variable mesh gillnet; (2) 3.1 m beam otter trawl; (3) commercial shrimp trawl; (4) commercial purse seine; (5) dipnet; a - in surf; b - 3 m from shore; c - 10 m from shore; d - 16 m from shore; and (6) hand.

[2] Non-spawning fish.

Table 6. Annual average lengths (mm) and weight (gm) of age II, III, and IV spawning capelin in the Togiak area[1].

	Male													
	Age II				Age III				Age IV				total	
	no.	%	L (sd)	W (sd)	no.	%	L (sd)	W (sd)	no.	%	L (sd)	W (sd)	L (sd)	W (sd)
1977[2]	347	84	-	-	64	16	-	-	0	0	-	-	143 (7.8)	21(4.4)
1978[2]	221	62	-	-	134	38	-	-	0	0	-	-	149 (6.2)	24(3.0)
1979	230	36	144(7.6)	23(3.6)	417	64	162(7.0)	34(5.6)	1	0	174(0)	46(0)	158(11.4)	31(7.4)
1981	3	1	145(5.0)	24(1.7)	245	99	166(7.1)	40(5.8)	0	0	-	-	168 (7.3)	40(5.9)
1982	309	73	138(8.3)	19(4.1)	115	27	154(7.5)	27(5.2)	1	0	152(0)	24(0)	144(10.5)	21(5.7)
1983	0	0	-	-	164	100	160(6.5)	32(4.8)	0	0	-	-	160 (6.5)	32(4.8)
Average		43	141(8.5)	20(4.4)		57	162(8.0)	34(7.4)	0	0	163(11)	35(15.6)	154(12.9)	28(8.4)

	Female													
	Age II				Age III				Age IV				total	
	no.	%	L (sd)	W (sd)	no.	%	L (sd)	W (sd)	no.	%	L (sd)	W (sd)	L (sd)	W (sd)
1977[2]	362	81	-	-	84	19	-	-	0	0	-	-	130 (9.1)	15(3.5)
1978[2]	1	7	-	-	13	93	-	-	0	0	-	-	149 (5.8)	25(5.3)
1979	135	48	130(9.2)	15(4.2)	128	49	150(8.1)	25(5.4)	8	3	166(2.3)	36(0)	142(13.8)	19(6.6)
1981	11	4	139(5.3)	20(4.4)	244	93	152(7.6)	26(5.5)	8	3	167(6.4)	35(6.5)	153 (9.2)	26(5.8)
1982	31	49	122(10.8)	11(3.8)	31	48	146(6.3)	23(3.0)	2	3	164(12.0)	32(5.7)	137(15.6)	17(7.6)
1983	4	2	139(7.5)	18(5.3)	201	98	147(7.2)	22(3.9)	1	0	158 (0)	26(0)	148 (7.3)	22(3.9)
Average		32	129(10.1)	16(5.0)		67	150(7.8)	24(5.2)		2	164(5.5)	34(6.2)	143(13.9)	21(6.6)

[1] L = average length (mm); W = average weight (gm); (sd) = standard deviation; no. = sample size.

[2] Age estimation by length frequencies, all others by otoliths.

Table 7. Annual average lengths (mm) and weights (gm) of age II and III spawning capelin in the Kodiak and Nome areas[1].

	Male										
	Age II				Age III				Total		
area	no.	%	L (sd)	W (sd)	no.	%	L (sd)	W (sd)	no.	L (sd)	W (sd)
Kodiak 1977$	-	-	-	-	-	-	-	-	80	118 (4.4)	10(1.7)
Kodiak 1979$	-	-	-	-	-	-	-	-	425	118 (4.4)	11(3.1)
Kodiak 1982	217	85	114(8.3)	12(3.2)	30	15	122(5.6)	14(2.1)	254	115 (8.4)	12(3.2)
Nome 1981	242	64	134(6.6)	18(2.9)	224	36	157(8.0)	32(5.6)	714	146(13.9)	26(8.1)
	Female										
Kodiak 1977$	-	-	-	-	-	-	-	-	16	94 (4.9)	6(1.2)
Kodiak 1979$	-	-	-	-	-	-	-	-	122	113 (7.7)	9(2.5)
Kodiak 1982	55	54	101(8.8)	7(2.4)	47	46	118(6.7)	12(2.2)	111	109(11.8)	9(3.3)
Nome 1981	230	91	121(6.3)	10(2.2)	23	9	141(10.1)	19(6.3)	535	121 (8.7)	11(3.8)

[1] L = average length (mm); W = average weight (gm); (sd) = standard deviation; no. = sample size.

[2] From Warner and Shafford 1978.

Table 8. Length-weight parameters of male and female capelin for years 1977-1983, excluding 1980, all areas combined.

	a	b	no.
Male	0.0000025	3.213	3595
Female	0.0000023	3.213	1582

From $W = aL^b$ W=weight, L=length. $r^2 = .90$

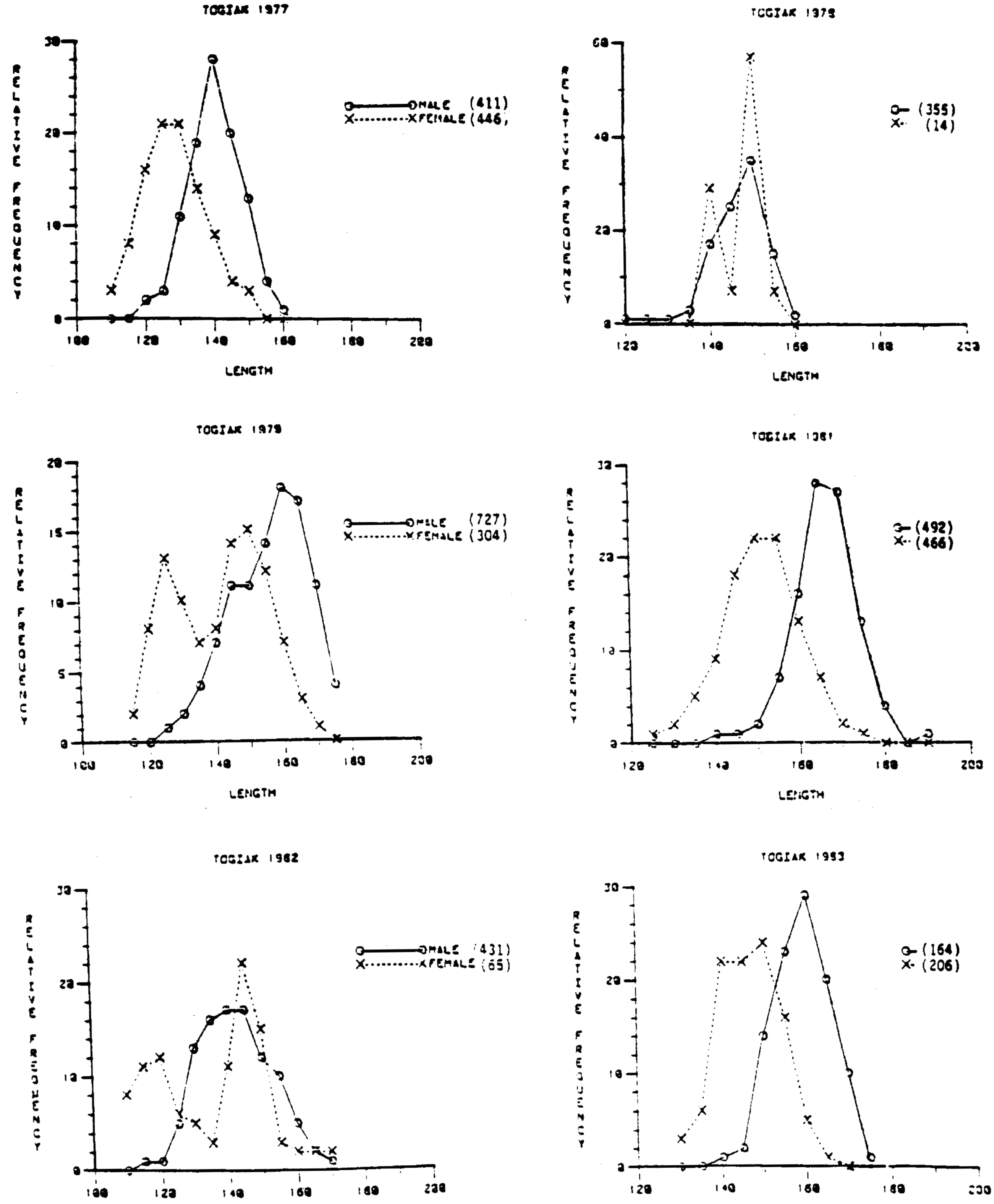

Figure 2. Length frequencies (mm) of male and female capelin in the Togiak area, 1977, 1978, 1979, 1981, 1982, and 1983.

130 mm for females. The changes in length frequency were caused in part by differences in the age composition of the spawners, which ranged from over 90% to less than 30% age III fish (Figure 3). The average length at age varied little with averages ranging from 140 to 146 mm for age II males and 155 to 168 mm for age III males (Figures 4 and 5). Differences were sometimes significant at $p<0.05$ (Table 9).

Analysis of the 1982 run to the Togiak area indicated a decrease in age composition over a four-week period. Male fish sampled early in the run were 40% age III with average lengths of 150 mm, these parameters decreased to 8% age III and average lengths of 136 mm in fish sampled near the end of the spawning run (Figure 6). Although sample sizes were smaller, females showed a similar pattern, with age composition decreasing from 83% age III and 3% age IV early in the run to 100% age II late in the run. Age-length data collected simultaneously at Summit Island and Metervik Bay in 1981 showed small but statistically significant differences (SNK 0.05, Table 10). Security Cove samples were intermediate and not distinguishable from either group.

AWL and sex ratio characteristics of Nome area capelin were sampled in 1981 only. No fish were observed in 1982. In 1981, 1,240 fish were collected by dipnet over a five-week period. The age composition and average lengths of Nome area fish were consistently less than those of Togiak area fish in 1981 (Figure 7 and Table 11). The average length and age of fish sampled decreased over the duration of the spawning run (Figure 8).

Kodiak Area:

Spawning runs to the Kodiak area were sampled in 1977, 1979, and 1982. The average ages and lengths at age of fish from the three years were consistently lower than averages for the Togiak area (Table 7). Males averaged 118, 119, and 115 mm and females 94, 114, and 110 mm for 1977, 1979, and 1982, respectively (Figure 9). The low average of 94 mm for 1977 females resulted from a sample size of only 16 fish and the 1982 female sample came from fish collected two to four weeks prior to spawning. The actual spawning sample consisted of 170 fish, all males, 85% age II, 15% age III.

Non-spawning Capelin

Three samples of non-spawning capelin were collected from the Kodiak area in 1981, 1982, and 1983 (Table 3). The samples were from trawl surveys targeting on shrimp and the selectivity of the gear on capelin is unknown. A sample of 326 immature capelin of undetermined sex was collected by shrimp trawl in September 1981. Apparently two age classes were present, although plus growth and incomplete formation of the hyaline zone made aging of these fish difficult. Lengths ranged from 84-121 mm with an average of 104 mm. At this range there is no difference in size between sexes and the average length of age I+ fish (102.5 mm sd 6.8) overlapped those of age II+ fish (108.4 mm sd 6.2).

In May 1982, a mixture of 243 pre-spawning and immature capelin were collected by shrimp trawl in the Kodiak area. The fish were still feeding and the transition to spawning morphology was incomplete in most individuals. The sex of 48 fish could not be determined because of their immaturity. All 46 of the

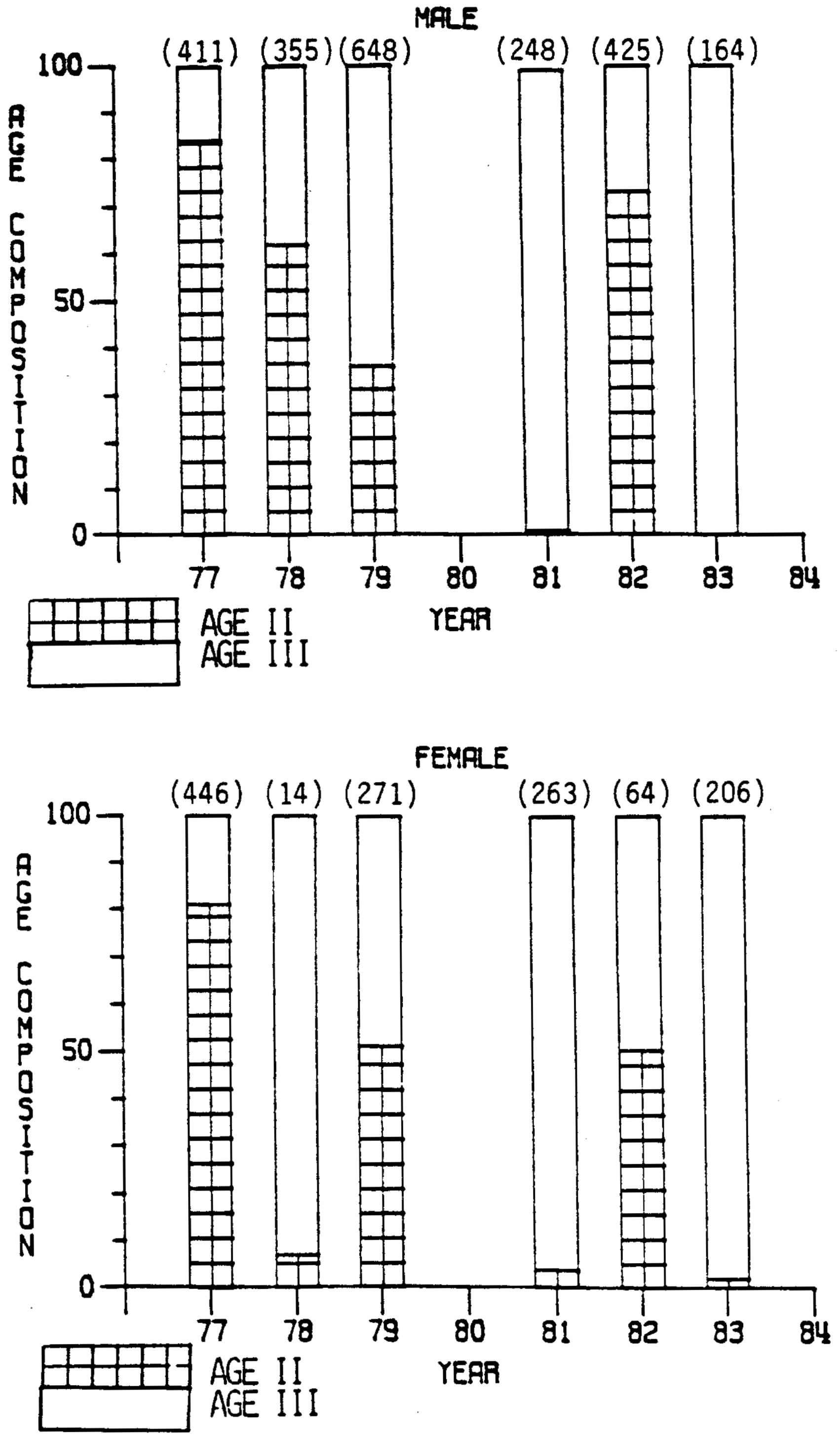

Figure 3. Age composition of Togiak area capelin in 1977, 1978, 1979, 1981, 1982, and 1983[1].

[1] Ages in 1977 and 1978 from length-frequencies, all others from otoliths. Sample sizes in parentheses.

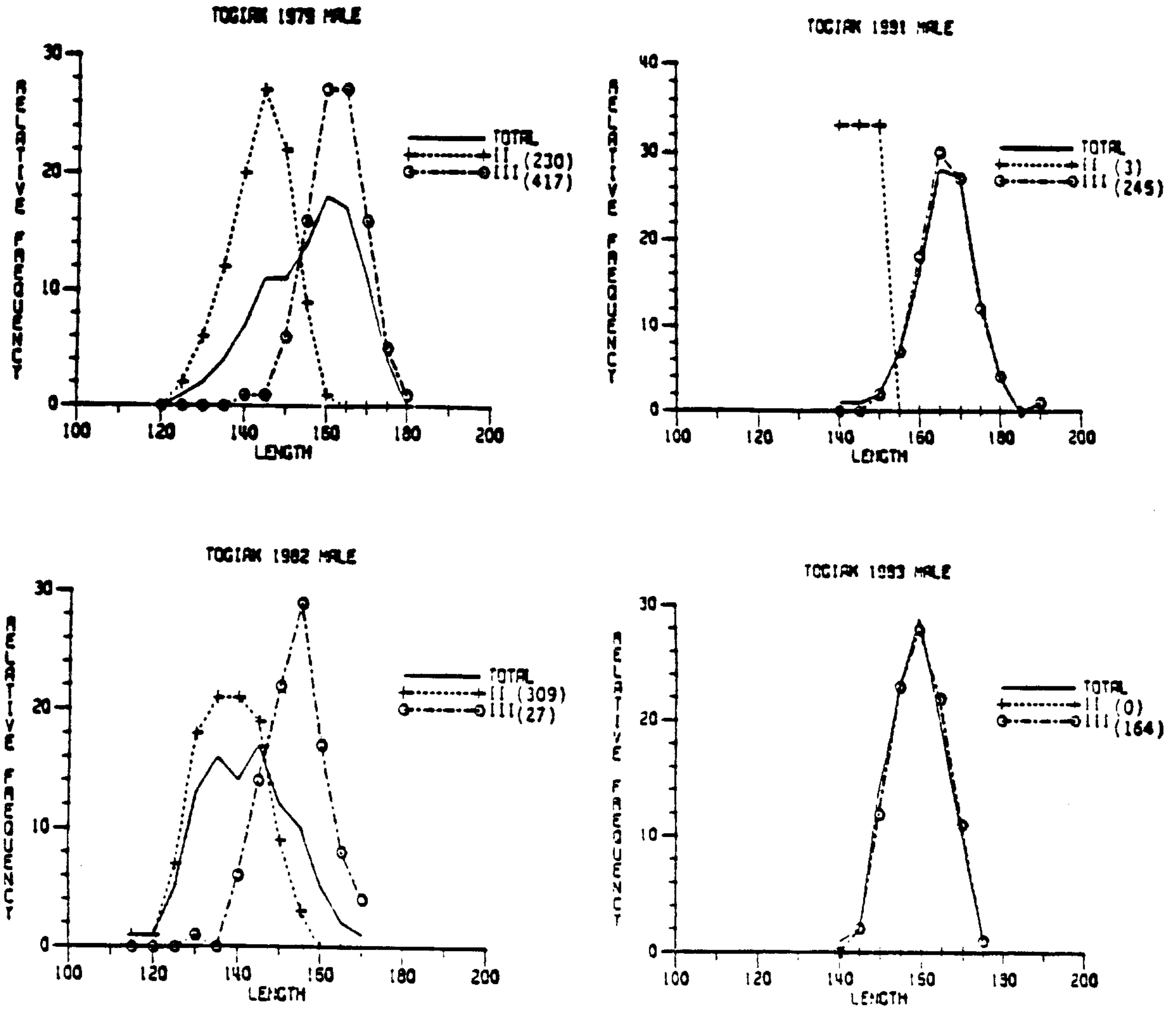

Figure 4. Length frequencies (mm) of age II and age III male capelin in the Togiak area, 1979, 1981, 1982, and 1983.

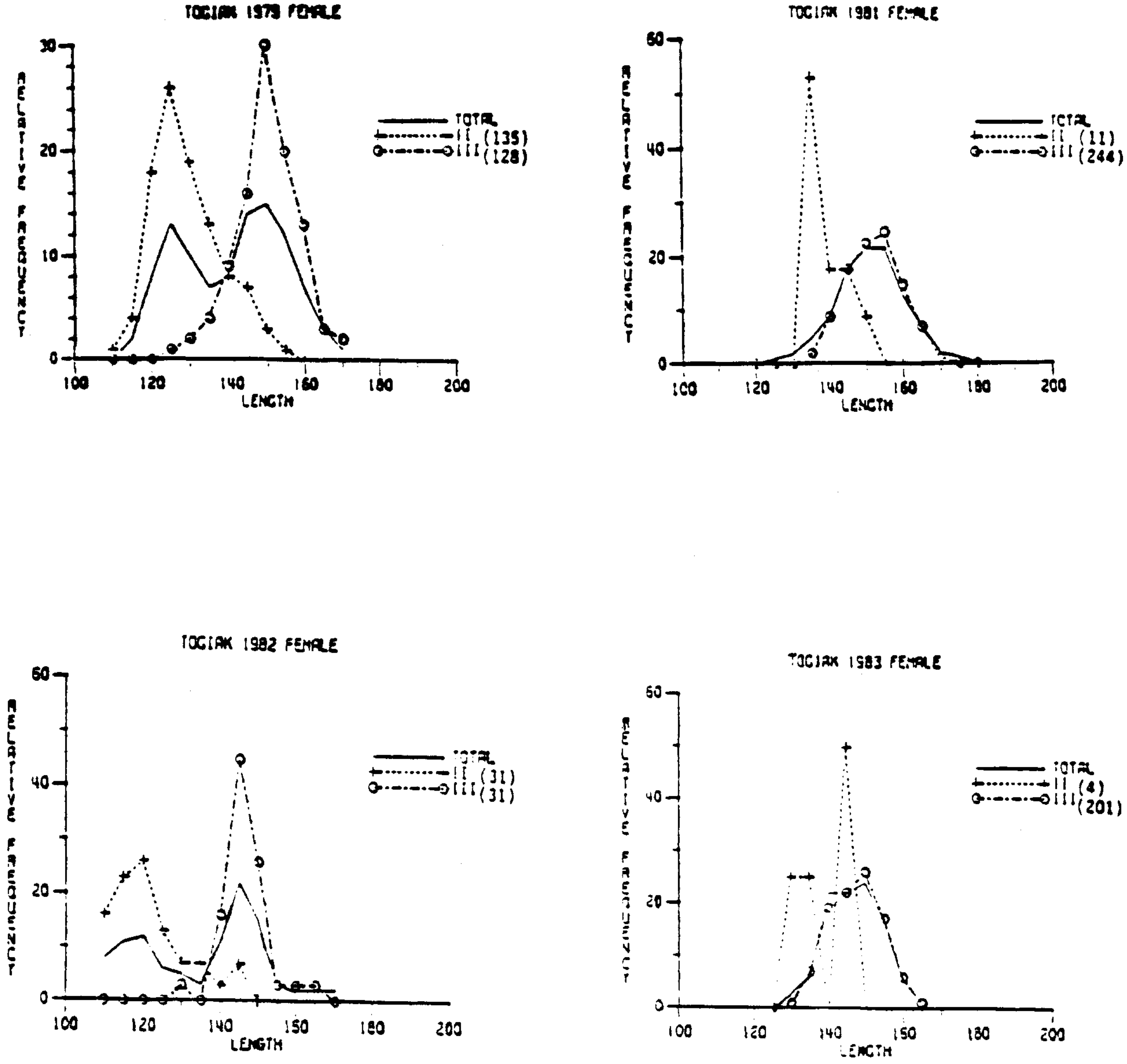

Figure 5. Length frequencies (mm) of age II and age III female capelin in the Togiak area, 1979, 1981, 1982, and 1983.

Table 9. Results of SNK tests of average length by age and year of spawning Togiak area capelin[1].

Males

Age II	1982	1979	1981	1983
Length (sd)[2]	138.2 (8.4)	143.7 (7.7)	145.0 (5.0)	-
sample size	309	230	3	0

Age III	1982	1983	1979	1981
length (sd)[2]	153.6 (7.5)	159.7 (6.5)	162.1 (7.1)	166.3 (7.1)
sample size	115	148	417	245

Females

Age II	1982	1979	1983	1981
length (sd)[2]	122.1 (10.8)	129.7 (9.2)	138.8 (7.5)	139.1 (5.4)
sample size	31	135	4	11

Age III	1982	1983	1979	1981
length (sd)[2]	146.5 (6.4)	147.3 (7.2)	150.3 (8.1)	152.0 (7.6)
sample size	31	167	128	244

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[1] Non-significantly different means are underlined (p=0.05).

[2] Length = average length (mm); (sd) = standard deviation.

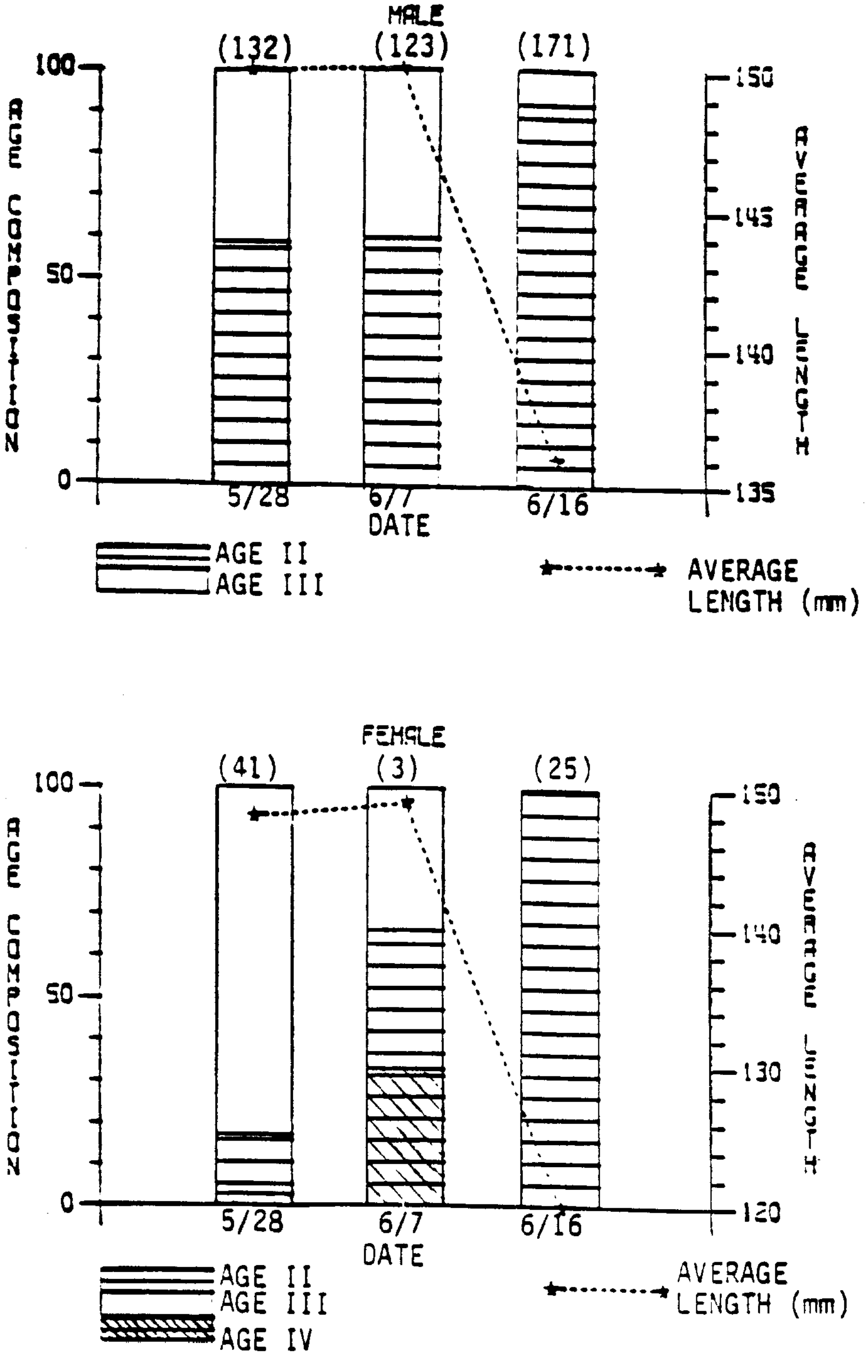

Figure 6. Change in age composition and average length of capelin in the Togiak area, 1982[1].

[1] Sample sizes in parentheses.

Table 10. Results of SNK tests of average length at age between locations within the Togiak area in 1981[1].

		Males	
Age II	**Metervik Bay**	**Security Cove**	**Summit Island**
length (sd)[2]	142.5 (3.5)	148.4 (1.7)	151.0 (0)
sample size	2	5	1
Age III	166.8 (6.7)	165.3 (6.3)	170.1 (6.3)
sample size	146	93	99
		Females	
Age II	141.2 (6.0)	145.7 (3.1)	137.0 (0)
sample size	10	3	1
Age III	152.2 (7.1)	154.6 (6.8)	156.4 (7.5)
sample size	147	17	97

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[1] Non-significantly different means are underlined (p=0.05).

[2] Length = average length (mm); (sd) = standard deviation.

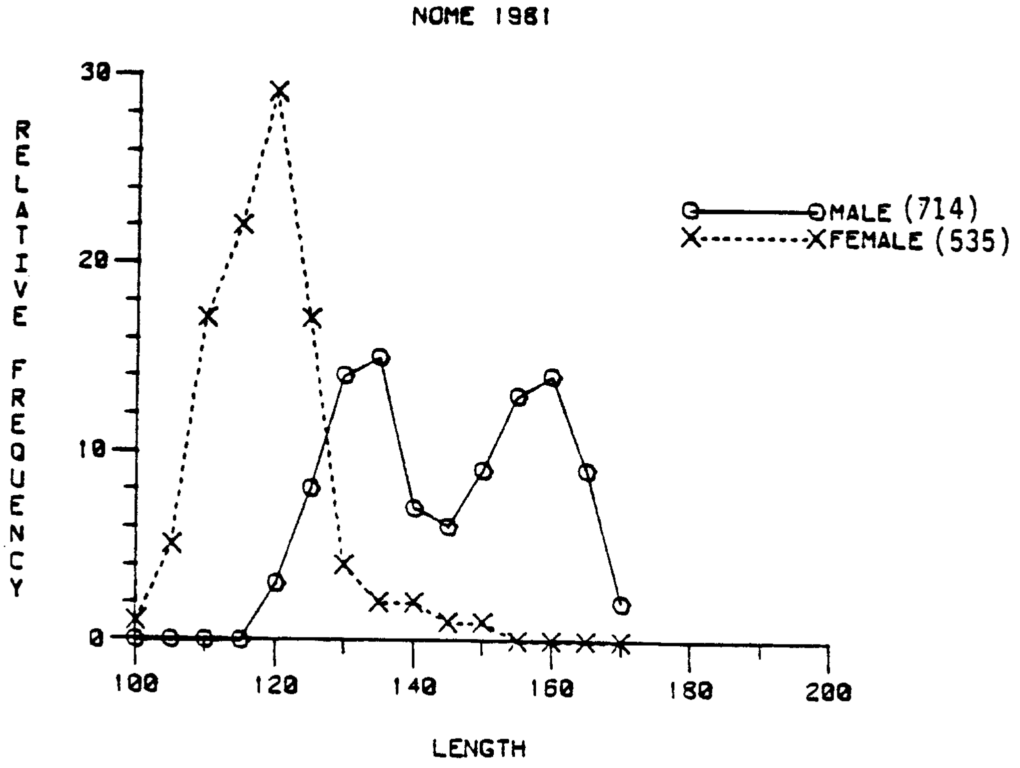

Figure 7. Length frequencies (mm) of spawning capelin in the Nome area, 1981.

Table 11. Results of SNK tests of average length by location and age[1].

1981

	Age	Togiak length (sd)	Security Cove length (sd)	Kodiak length (sd)	Nome length (sd)[2]
Male	III	168.2 (6.7)	165.3 (6.3)	-	157.5 (8.1)
no.		245	93	0	224
Female	III	153.9 (7.5)	154.6 (6.8)	-	141.3 (10.1)
no.		244	17	0	23
Male	II	145.3 (5.5)	148.4 (1.7)	-	133.6 (6.6)
no.		3	5	0	243
Female	II	140.8 (5.8)	145.7 (3.1)	-	121.0 (6.3)
no.		11	3	0	231
			1982		
Male	III	155.4 (7.3)	157.0 (6.7)	122.8 (5.6)	-
no.		115	54	26	0
Female	III	139.9 (8.2)	144.9 (5.3)	117.8 (6.7)	-
no.		309	43	47	0
Male	II	148.2 (6.3)	150.4 (6.1)	114.0 (8.3)	-
no.		31	57	217	0
Female	II	123.8 (10.8)	145.4 (4.6)	101.1 (8.8)	-
no.		31	8	55	0

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[1] Non-significantly different means are underlined (p=0.05).

[2] Length = average length (mm); (sd) = standard deviation; no. = sample size.

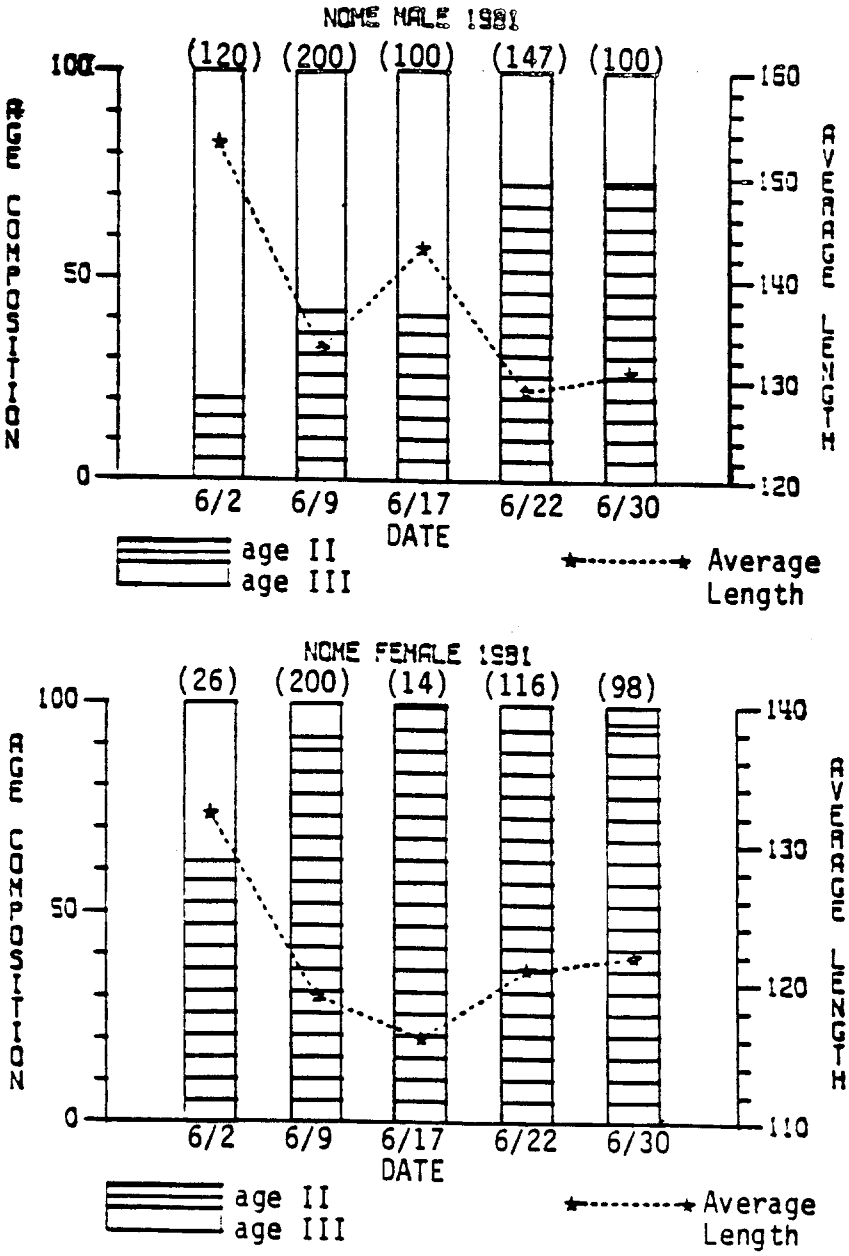

Figure 8. Change in age composition and average length (mm) over time of capelin from the Nome area, 1981[1].

[1] Sample sizes in parentheses.

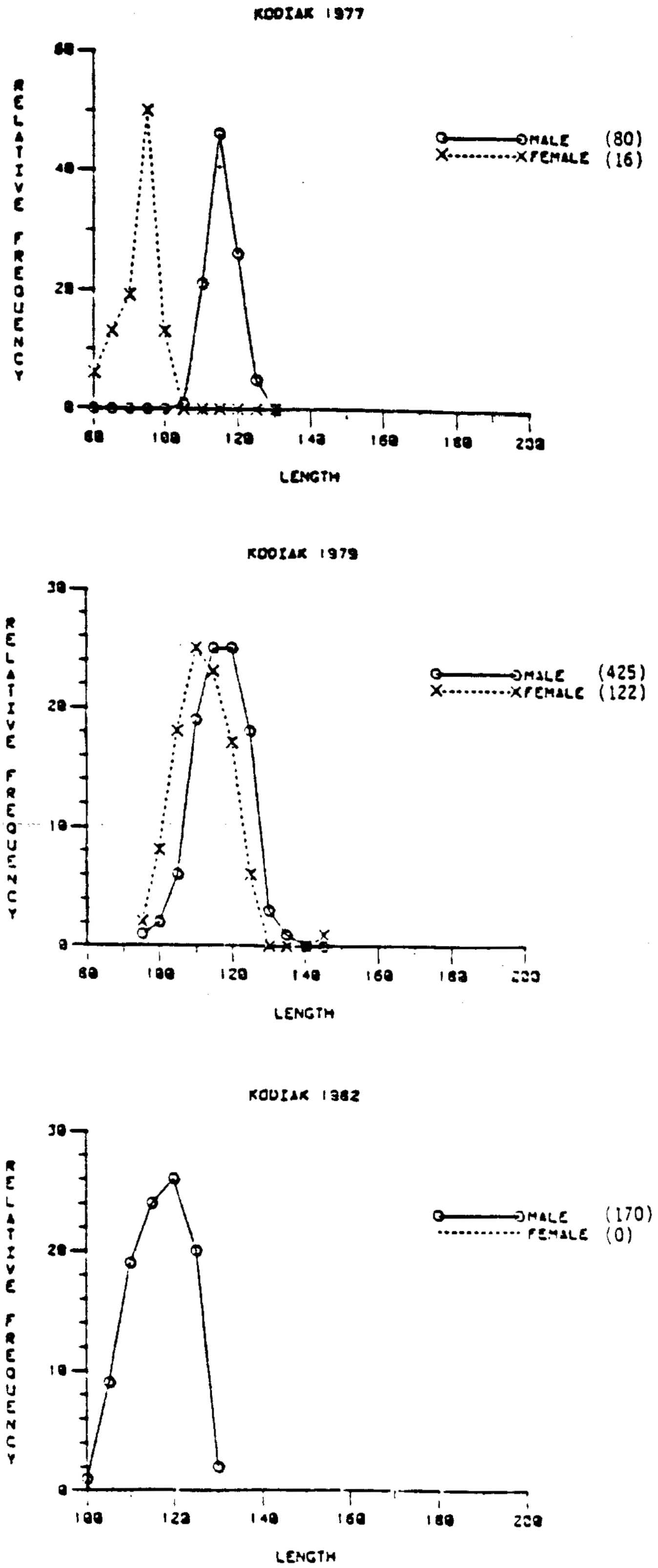

Figure 9. Length frequencies (mm) of spawning capelin in the Kodiak area, 1977, 1979, and 1982.

fish that could be aged were age II and probably did not spawn that year. The average length of the immature fish was 91 mm. The sex ratio of the 195 pre-spawning fish was 57% female, not statistically different from 50:50 (binomial test, $p<0.05$).

Post-spawning capelin were collected by shrimp trawl in July 1983. The secondary sex characteristics were resorbed and sex determination was difficult. Of 50 fish examined microscopically, 47 were determined to be females by the presence of residual eggs in the gonads. Of the total sample of 146 fish, 9 fish were definitely recovering males, with ragged caudal and anal fins. Overall age composition was 64% age II, 36% age III. All fish examined had been feeding on euphausids.

In the sample of 195 pre-spawning capelin captured in May 1982, ten fish were parasitized in the gill area with a copepod parasite *(Haemobaphes* spp.*)*.

DISCUSSION

Distribution and Timing of Spawning

The earliest records of capelin in Alaskan waters are from the Bering Strait, Cape Lisburne, and Point Belcher on the Arctic Ocean (Bean 1882). Murdoch (1885) reported spawning capelin on the beaches of Point Barrow in 1882. Recently Bendock (1977) reported capelin spawning in Prudhoe Bay in mid-August of 1975. South of Point Barrow spawning has been reported at Pt. Lay, Shishmaref, and Port Clarence on the Seward Peninsula (Scofield 1899; Craig, personal communication). Reports of spawning are more frequent in Northwestern Norton Sound, Cape Romanzoff, Nelson Island, Goodnews Bay, Security Cove, Togiak Bay, Southern Bristol Bay, and Atka and Attu Islands. In the Gulf of Alaska spawning occurs in the many bays in the Kodiak archipelago, and in Kachemak Bay (Warner and Shafford 1978; Blackburn 1978b) (Figure 10).

Reports of spawning capelin southeast of Kodiak Island are much rarer. Blackburn et al. (1981) and Rogers et al. (1980) mention reports of capelin spawning in Prince William Sound in August and in the Yakutat area in July to mid-August. Spawning was reported in Sitka in September of 1897 (Jordan and Gilbert 1899), and October 1908 (Marsh and Cobb 1908) and near Juneau in the mid 1960s (Wing, personal communication).

South of Alaska, Hart and McHugh (1944) reported capelin spawning near Vancouver Island in late September and October. Garrison and Miller (1982) report capelin spawning along the west side of Sequim Bay and the southern shore of the Strait of Juan de Fuca in Washington State.

On the Asian side of the Pacific Ocean spawning commences in the Sea of Japan in April-May and continues through June along the Kamchatka Peninsula and into July in the Sea of Okhotsk (Schmidt 1950; Andriyshev 1954; Lindberg and Legeza 1965; Churikov 1975; Velikanov 1984).

Spawning commences in late May along the Alaska Peninsula, Kodiak area, and in Togiak Bay and continues northward until the late July, early August spawning

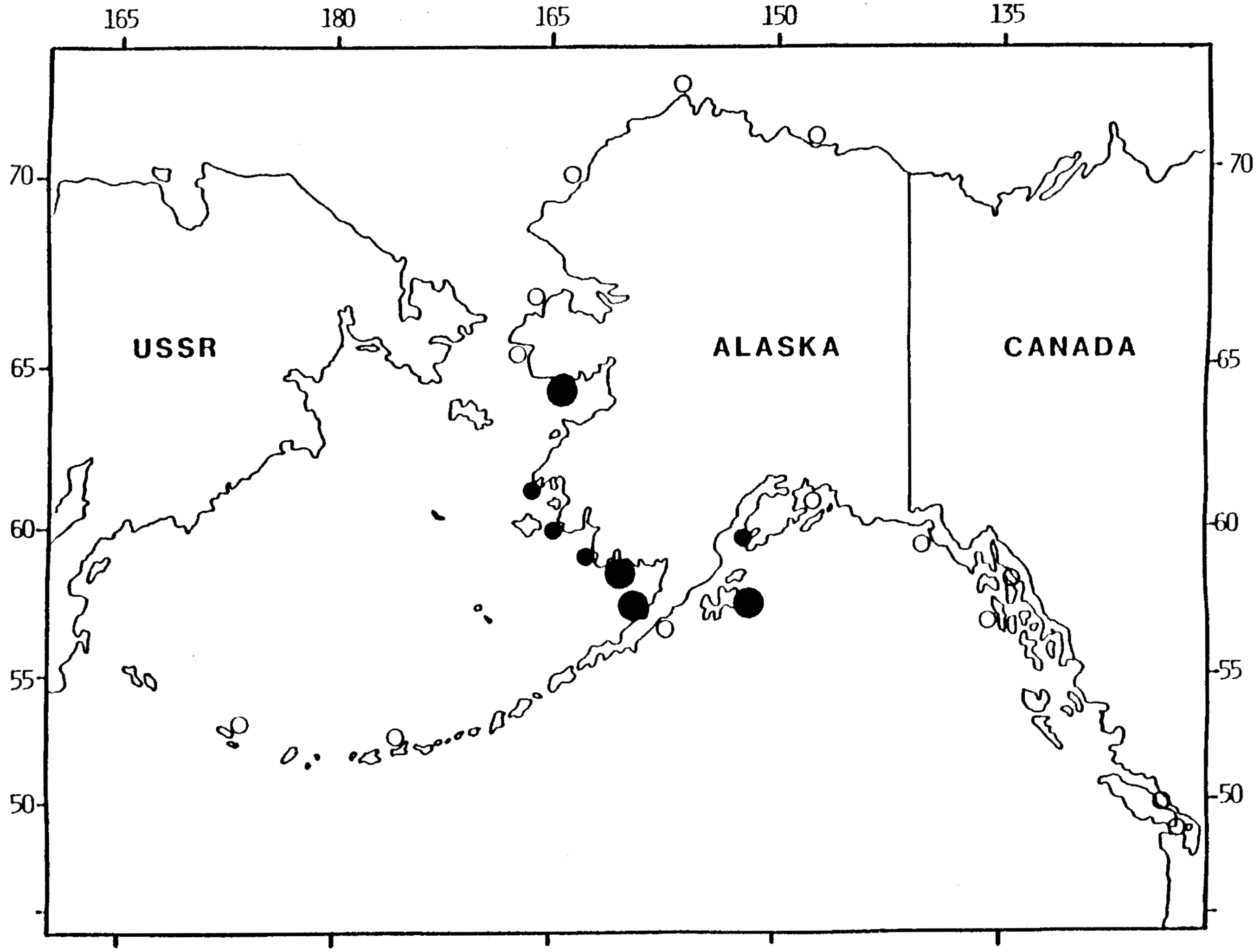

Figure 10. Locations of capelin spawning in the Northeast Pacific Ocean[1].

[1] ● = large recurring populations, ● = small recurring populations, ○ = infrequently reported spawning.

at Pt. Barrow. The trend for capelin to spawn later in more northern waters coincides with the breakup of the icepack and the warming of nearshore waters. The rare reports of capelin spawning in Prince William Sound, Sitka, and British Columbia late in the year are exceptions to this trend.

Spawning Behavior

Substantial variations in the physical circumstances surrounding spawning behavior have been reported for many different localities.

Hart and McHugh (1944) reported spawning in the evening at high tide with water temperatures of 50-55°F (10-13°C) near Vancouver Island. More extensive accounts of spawning are available from the Kodiak area. In 1977, capelin spawned on 4-14 June on beaches near the city of Kodiak (Warner and Shafford 1978). Male capelin began to appear in the surf an hour before the 2:00 AM high tide with females not appearing until the highest wave of the tide series. Hundreds of fish (over 99% males) were stranded on the beach (Warner and Shafford 1978). Warner and Shafford noted that the substrate on Pillar Beach, although not densely packed was definitely sandy in texture, not small gravel which is the preferred substrate for Atlantic beach spawners (Jangaard 1974). They also noted that there was a slight offshore wind, a factor also mentioned by Atlantic biologists (Winters 1969; Campbell 1973). Capelin were not sampled in the Kodiak area in 1978.

In a later observation from the Kodiak area in 1979, several samples of spawning or mature fish were collected between 26 April and 23 June in Monashka Bay. Spawning capelin were observed at 11:45 PM on 28 May 1979 at the high tide. A slight offshore wind blew at a 45° angle to the shore and the surf was less than half a meter in height. Spawning continued for four hours, past high tide and until dawn (Blackburn et al. 1981). The next morning eggs were observed 1-3 meters seaward from where spawning had been observed the previous night. The gravel substrate was 2-20 mm in diameter and the eggs had been buried by wave action to a depth of up to 240 mm. Blackburn et al. noted intense predation on the eggs by amphipods. No spawning mortalities were noted at Monashka beach, however at a similar spawning site five kilometers away approximately 1,000 male capelin were observed along the high tide line.

In samples from trawl catches in June 1979, immature capelin and ripe eulachon, *Thaleichthys pacificus*, were mixed with catches of mature capelin. Capelin were not collected between 1979 and June 1982 when spawning fish were sampled. Details of spawning timing and behavior for these years are not available.

In 1977 capelin spawning began in early June in Nunavachak Bay in Northwestern Bristol Bay at a water temperature of 7.8°C. In 1978 spawning began in mid-May at a water temperature of 6°C.

Craig (personal communication) observed capelin spawning at Pt. Lay on the Chukchi Sea in early August 1983 at water temperatures of 8-10.6°C. Spawning occurred in Prudhoe Bay in mid-August at water temperatures of 6-10°C (Bendock 1977).

In the Sea of Japan, capelin schools spawn near the coast of Peter the Great Bay in April and May at water temperatures of 2-4°C (Lindberg and Legaza 1965).

The conditions necessary for the onset of spawning appear to be less specific than previously reported. The offshore wind mentioned by Warner and Shafford (1978) and Blackburn et al. (1981) in the Pacific and by Winters (1966) and Campbell (1973) in the Atlantic was not observed in the Togiak or Nome areas. Spawning did often occur at high tide as reported by these researchers, but it also occurred at low and intermediate stages of the tide. In Norton Sound, the Chukchi Sea, and Beaufort Sea, the tides are extremely small, from less than 1 meter at Nome to essentially zero at Point Barrow. On the other hand, in Bristol Bay and the Gulf of Alaska the tides can vary as much as 8 meters (-3.7 to 23.1 ft) (Hartman and Johnson 1978). The condition of the tide is therefore not an important factor in the onset of spawning in Norton Sound and the Chukchi and Beaufort Seas. In the Togiak area and Gulf of Alaska it appears that even though spawning can occur at all stages of the tide, the initial onset is generally near high tide. The same is true of the light conditions; while capelin do spawn on clear days, spawning usually starts at night or on cloudy days.

Some wave action was observed during spawnings in the Togiak and Nome areas and two spawnings (1981, 1983 in the Togiak area) occurred after several days of high winds and stormy seas. In 1981 capelin spawned continuously for the next several days on every available beach for many kilometers. The storm may have prevented fish from spawning in the usual manner and forced fish that had been ripe prior to the storm to spawn under unusual conditions.

Water temperatures observed during capelin spawning were all within the range of 5-10°C reported by Atlantic researchers (Winters 1969). Water temperature in the shallow northern waters of Alaska can fluctuate very quickly with changes in the weather. During the early August spawning at Pt. Lay on the Chukchi Sea, Craig (personal communication) reported temperatures ranging from 6-10.6°C in a five-day period.

Segregation of sexes prior to spawning occurred in all cases observed. Gear fished near shore usually caught a much higher percentage of males than females. It was possible to target on females by fishing a trawl offshore beyond the schools of males (Table 5). The segregation of sexes will become an extremely important aspect of capelin behavior should a fishery develop on roe-bearing females. Such a fishery presently occurs on Pacific herring, *Clupea harengus pallasi*, which has a distribution and run timing often overlapping those of capelin.

Distribution of Non-spawning Fish

The distribution of Pacific capelin prior to and subsequent to spawning has not been studied. The largest source of information is the survey data-base system developed at the Northwest and Alaska Fisheries Center (NWAFC) for multiple, large-scale groundfish trawl surveys conducted by the Resource Assessment and Conservation Engineering (RACE) Division of the National Marine Fisheries Service (NMFS) (Mintel and Smith 1981). Macy et al. (1978) summarized not only trawl surveys but gillnet, seine, and plankton surveys and commercial fishing records. While capelin were seldom, if ever, the target species in these surveys the data does provide some information on distribution. Lowry and Frost (personal communication) conducted trawl surveys of the Bering Sea during 1976-1978 in which forage fish were the target species of a marine mammal feeding study. Other sources of information were studies on the stomach contents of salmon (Krygier 1981 and Krygier 1982), sea birds (Divoky 1978; Springer and Roseneau 1978; Hunt et al. 1981), and marine mammals (Fiscus et al. 1964; NMFS 1979; Kajimura et al. 1980; Harry and Hartley 1981; Bukhtiyarov et al. 1983).

In the Bering, Chukchi, and Beaufort Seas, adult capelin are only found nearshore during the months surrounding the spawning run. In the fall and early spring, capelin have been found far offshore in the vicinity of the Pribilof Islands and the continental shelf break (Divoky 1978; Harry and Hartley 1981; NMFS unpublished). The stability of the ice-edge region initiates a spring bloom of phytoplankton. Marine birds and mammals utilize the ice-edge extensively. Divoky (1978), reported capelin in the stomachs of sea birds from the ice-front in March, April, and May.

In contrast, the Alaska current keeps the Gulf of Alaska ice free and the average winter water temperature several degrees warmer than the Bering Sea (Hartman and Johnson 1978). Capelin overwinter in the bays of Kodiak Island and in Kachemak Bay (Blackburn 1978a; Blackburn 1978b; Blackburn et al. 1981).

Krygier (1982) reported capelin in the stomachs of salmon caught in Southeast Alaska from April through September. Immature capelin were abundant in Glacier Bay in the summer of 1982, but were not present in 1983 (B. Wing, personal communication). Between December 1967 and February 1968, capelin were found in the stomach contents of fur seals and Dall porpoises off the coast of Washington State (Kajimura et al. 1980; NMFS 1980).

Larval capelin are found near the spawning areas in the summer and fall and are widely distributed by the end of their first year (Waldron 1981; Dunn et al. 1980; Musienko 1963). Catches of larval capelin were greater at night indicating a diurnal vertical migration. The young reach lengths of 40-60 mm during their first winter (Blackburn 1978b).

The monthly distribution of capelin as determined from available sources is plotted in Appendix 2. Obviously there is no information for the northern areas from months in which they are ice-covered and information from the winter months is scarce for all areasl Lack of data should not be interpreted as non-occurrence of fish.

Age-Weight-Length

Age of spawning capelin was less than ages reported for Atlantic capelin. Atlantic capelin may mature at age II, but predominately spawn at age III or IV with sometime significant survival to age V (Prokhorov 1968; Winters and Campbell 1974). Capelin in this study spawned at age II or III with less than 3% spawning at age IV.

Problems in Age Estimation

A debate over the otolith aging techniques for Atlantic capelin has been resolved. Hyaline zones are deposited annually in the late fall and winter and thus can be used in age determination (Bailey et al. 1977). The otolith method of aging Atlantic capelin has been validated by length frequency distribution and back calculation of mean length at hyaline zone formation (Bailey et al. 1977). At least two different procedures were used in the past. Templeman (1968) compared "Greenland" and "Newfoundland" methods. In the process of validating the otolith technique, Bailey, et al. (1977) reported that the length at which the second hyaline zone was deposited corresponded precisely with the length at which capelin undergo a profound metamorphosis. They proposed that these morphological changes, occurring at between 50 and 80 mm total length, resulted in the formation of the second hyaline zone (metamorphic check). The absence of a metamorphic check on some otoliths may result from its deposition simultaneously with the first or second annulus. Differences in first year growth rates resulting in different frequencies of overlapping the metamorphic check with the first or second annulus, could significantly influence the frequency with which the metamorphic check is observed. Bailey et al. (1977) concluded that the "Greenland" method, which correctly interpreted the first annulus but apparently considered the metamorphic check to be the second winter zone, results in ages that are one year too old. The "Newfoundland" method considered the metamorphic check to be the first annulus and misinterpreted the first annulus as a "larval check". This method gave correct age estimates, but overestimated length at first annulus formation.

Warner and Shafford (1978) reported up to 15% age I spawners from two sites in Bristol Bay. They apparently considered the first annulus embryonic growth, resulting in age estimates for some fish which were one year less than my interpretation. An age-length key using the 1979, 1981, 1982, and 1983 Togiak otolith data and Warner and Shafford's length frequencies resulted in slightly higher estimates of age II and III fish and removed the age I fish from the age composition for 1977 and 1978.

All graphical and most statistical methods of age determination assume that size distribution within each cohort is normally distributed and that there is some discernible separation between year-class size distributions (Jearld 1983). Given sufficient sample sizes, length frequency plots of capelin sampled by sex and cohort satisfy these assumptions (Figures 4 and 5). Age-length keys must be determined using fish from the same stock, during the same season (Ricker 1975), so this test only indicates the unlikeliness of age I fish being found in a spawning population. The average total length of Atlantic capelin was 76 mm for age I and 112 and 115 mm for age II females and males, respectively (Winters 1974). Only one fish sampled by Warner and Shafford (1978) had a fork length of less than 110 mm.

Blackburn et al. (1981) apparently used the same technique as Warner and Shafford, as they also reported age I fish in samples of mature capelin from Alitak Bay. They could find no length-age relationship and suggested that spawning may occur over an extended time period. Blackburn (1978a), collected larval capelin in October displaying a bimodal length distribution with peaks at 2 to 3 cm and at 5 cm and he suggested a prolonged spawning period or two distinct spawning times.

Lambert et al. (1982) reported the occurrence of polymodal length frequency distributions in larval capelin and herring in Nova Scotia. These modes were the results of the regular release of larval cohorts. Cohorts of capelin showed a mean spacing of 10.1 days, whereas, herring cohorts were separated by 21.5 days on the average. They did not describe the mechanism controlling cohort separation. Frank and Leggett (1981) reported a pattern of larval emergence with intermittent abrupt increases in the numbers of larvae in the nearshore waters strongly correlated with onshore wind induced wave action. The regular release of successive cohorts of larvae is thought to be a "hedged bet" spawning strategy which help ensure survival of slow growing larvae (Lambert et al. 1982).

Aging difficulties due to extended spawning periods or metamorphic checks were not a problem in this study. In the Togiak and Kodiak areas, the majority of spawning takes place over a short period, usually less than two weeks. In the Nome area spawning continued for over four weeks in 1981 and 1983 but otolith ages and length frequencies clearly showed only two age classes.

Otoliths are a time consuming but accurate method of aging capelin once the investigator is proficient in the proper technique. Any errors made are likely to result from obscured annuli in older fish and fish diaplying plus growth since the formation of the most recent annuli.

Possible Sampling Problems

The sampling design for this project was based on the assumption that a specific population of capelin spawns over a short period, of one to two weeks, without significant spawning before or after the peak of nearshore abundance. In several cases capelin were observed nearshore for up to four weeks and Blackburn et al. (1981) suggested the possibility of a prolonged spawning period in the Kodiak area. Periodic samples of Nome and Togiak area capelin indicated some differences in size and age composition of spawners over time. If the relative abundance of early spawning fish was greatly different from that of late spawning fish, the trends indicated in the samples could be insignificant. On the other hand, in 1981 capelin sampling in the Togiak area was discontinued while spawning was still in progress thereby missing any fish which may have spawned later. Because the population mean depends more on the means of large units than on those of small units, weighted means are usually used to account for difference in sample or unit sizes (Sokal and Rohlf 1981). As I had no good method of estimating spawner abundance, samples were regularly collected and treated equally. Therefore the possibility of the sampling program under or over sampling a significant portion of a population must be realized before any discussion of differences within or between areas and years.

Gear selectivity may affect any estimates that assume random sampling. The differences in behavior of male and female spawning capelin make gear selectivity difficult to assess but variable mesh gillnets are reported to underestimate the abundance of the smallest fish collected, in this case predominately age II females (Hamley 1975). This would explain the apparent differences in age composition between sexes observed in Togiak and Security Cove in 1978 and 1982 in gillnet samples (Table 3). Dipnets are assumed to accurately sample the surf spawners and whenever possible dipnet samples were used in the analysis. The gear selectivity of trawls or purse seines on capelin is unknown. The trawl samples of non-spawning Kodiak area capelin were collected on shrimp surveys which are fished near the sea bottom and may not accurately represent the size and age of the pelagic population. Therefore, until information on the selectivity and efficiency of shrimp trawls on capelin is available, capelin data from trawl surveys should be used cautiously.

AWL Differences Within a Season

Larger, older fish matured and spawned earlier in the Togiak area in 1982, and in the Nome area in 1981 (Figures 6 and 9). The overall abundance in the Togiak area in 1982 was far below average and the spawning schools were small enough to have been overlooked completely on an average year. Spawning in the Togiak and Kodiak area is usually completed in less than two weeks so it is unlikely that a sampling program would miss a significant portion of the run. The earlier maturing of older fish has been frequently reported for female Atlantic capelin (Templeman 1948; Winters and Campbell 1974), but male capelin are generally reported to mature as a group and spawn repeatedly over the duration of the spawning period. In the Nome area in 1981 newly arrived males, determined by the condition of their fins, continued to arrive throughout the spawning period. The change in the composition of the spawners were gradual, and distinct schools of different ages were not observed.

AWL Differences Within an Area

Age-weight-length data for capelin simultaneously sampled at three locations within the Togiak area showed small differences (Table 9). The significant differences were in average lengths between Metervik Bay and Summit Island, sites within 20 km of each other, while samples from Security Cove, about 100 km distant, showed measurements indistinguishable from either site. The differences are all less than 5 mm which, although statistically significant (SNK 0.05) should probably be discounted due to some measuring bias on the part of independent investigators.

The age compositions of the three stocks were also indistinguishable with over 94% of all fish age III.

As can be seen in Tables 9 and 10 SNK analysis can give suprising results when used with small samples sizes. In Table 9 the conclusion is that the average lengths of age II females in 1979 and 1983 do not differ and that those in 1983 and 1981 do not differ while at the same time, the lengths in 1979 and 1981 are significantly different. The analysis warns that a larger sample size is required to detect clear patterns of differences (Underwood 1981).

Differences in Age Composition Between Years

Age composition of the Togiak area spawning run varied greatly between age II and III from year to year (Figure 3). Age composition of Atlantic capelin also varies greatly from year to year between ages II to VI (Olsen 1968; Winters and Campbell 1974). Age composition is dependent upon the survival, growth rate, and maturation of a year-class and upon the contribution of repeat-spawners. Survival, growth rate, and age of maturation are variable and the contribution of repeat-spawners is thought to be low (Prokhorov 1968; Winters and Campbell 1974).

AWL Differences Between Areas

Atlantic capelin mature at somewhat younger ages in southern waters (Winters 1974). The north-south gradient of age at maturity described for Atlantic capelin breaks down in Pacific waters north of the Togiak area. The largest capelin occur in the Togiak area with the mean lengths at age less in the Nome and Kodiak areas. Nome and Kodiak area fish mature at smaller lengths and younger ages than Togiak area fish. The 1981 age composition varied greatly between the Togiak and Nome areas. The smaller sizes of Pacific capelin in the Kodiak areas and British Columbia agree with the cline reported in Atlantic stocks (Hart and McHugh 1944). Hart and McHugh reported spawning fish of scale age I and standard lengths of 95-100 mm for females and 102-108 mm for males from Vancouver Island. The standard lengths convert to fork lengths of 101-106 mm and 108-115 mm respectively (Templeman 1948). As capelin scales generally give age estimates of one year too young, the converted lengths and ages agree with those of age II Kodiak area capelin.

The oceanography of the North Pacific Ocean is very different from that of the North Atlantic. Also within the North Pacific there are great differences between the Gulf of Alaska and the Bering Sea. The North Atlantic is characterized by a central anticyclonic gyre with an intense, warm, western boundary current which generally turns northeastward at middle latitudes, modifying the climate in the high latitudes of Europe to the extent that sea ice is not present at or even north of 60°N. The Aleutian-Commander Island system prevents a similar occurrence in the North Pacific by restricting the northward flow of water (Favorite et al. 1977). The Beaufort and Chukchi Seas are completely covered with the ice during the fall, winter, and spring months and the Bering Sea is partly covered with ice during those months. The ice reaches its maximum extent in early spring, and its southerly extent has great significance to the biology of the southeast Bering Sea shelf region (Alexander 1981).

In contrast, the Alaska current keeps the Gulf of Alaska ice free and the average winter water temperature several degrees warmer than the Bering Sea (Hartman and Johnson 1978).

Nome area capelin appear to compensate for the shorter growing season by maturing sooner than more southern stocks. This contrasts with the life history strategies of Arctic populations of rainbow smelt, *Osmerus mordax*, and Arctic char, *Salvelinus alpinus*, which live longer, mature later, and grow more slowly than their southern and Atlantic counterparts (Haldorson and Craig 1984). The small size at maturity of Kodiak capelin cannot be explained by water temperature or growing season. Growth of Pacific herring, *Clupea harengus pallasi*, from the three areas is similar to capelin in that the largest fish occur in the Togiak area and the mean lengths at age decrease north and south of there (Wespestad and Fried 1983). Herring and capelin have similar early life histories and the growth trends indicate similar responses to differences in the environment. In contrast to capelin, in 1981 herring displayed similar year class strengths for all major spawning groups in the eastern Bering Sea (Wespestad and Fried 1983). This indicates that although the eggs of the two species hatch within a few weeks of each other, their survival rates are not necessarily correlated.

Repeat Spawning

Spawning mortality is high in the Togiak and Kodiak areas particularly for males. Males tend to remain on the spawning grounds for prolonged periods and frequently large numbers of spawning mortalities are observed. Females do not display this behavior and are seldom observed in spawning mortalities. In the Nome area fresh males appeared to arrive throughout the spawning period and few mortalities of either sex were observed. The fact that females survive the spawning period is generally accepted but survival to the next spawning season is believed in Atlantic populations to be negligible (Olsen 1968; Prokhorov 1968; Winters and Campbell 1974). At least some females survive to spawn again, as females have been collected containing retained eggs from a previous spawning along with maturing eggs (Templeman 1948; Warner and Shafford 1978). In the single sample of post-spawning fish observed in this study the sex of 59 fish was determined, 47 were female, 12 were male. Of 146 fish aged, 64% were age II, 36% age III, and 1 fish was age IV. The fish had resumed feeding and, with the exception of 9 males with ragged fins, appeared healthy. The fact that no age V fish and virtually no age IV fish spawn in the Kodiak area indicates that while age III fish may survive the spawning period, they probably do not survive to spawn again. The evidence against the survival of age II spawners is less conclusive. In the Nome area in 1981, 91% of the females and 64% of the males were age II. If a significant number of these two-year-old spawners survived they would have returned as age III spawners in 1982, instead no capelin of either age were observed in 1982.

Schaefer (1936) indicated repeat spawning in surf smelt, *Hypomesus pretiosus*, by microscopic observations of immature eggs in post-spawning females. In a cursory microscopic examination of post-spawning female capelin a few unspawned eggs were common but no immature eggs were observed in this study.

If substantially more females than males survived to spawn again the sex ratio would be skewed toward females. This was not observed in a sample of 195 pre-spawning fish in which the sex ratio was 57% female, not significantly different from 50:50 at $p<0.05$.

Winters and Campbell (1974) developed a further indication of the magnitude of spawning survival by comparing the cumulative mean age composition of mature pre-spawning fish with the percentage mature at age. If spawning survival were negligible then the two sets of data should agree. This has been done in Table 12 and compared with Winters and Campbell's data from Newfoundland. The single sample appears to follow the same pattern as Winters and Campbell's data and agrees with their conclusion that spawning survival is not a significant contributor to the age composition of mature fish.

Growth

Mean lengths at age suggest that there is considerable annual variation in growth in both sexes with the variation being consistent in direction for both sexes. Growth and yield models cannot be constructed without catch and catch per unit effort (CPUE) records or more information on sizes of immature, pre-spawning, and post-spawning fish from the same areas for consecutive years.

Table 12. Comparison of mean age compositions of mature capelin with the cumulative age composition of mature fish, both sexes combined.

Age	imm	mat	%mat	accum % mean age comp	imm	mat	%mat	accum % mean age comp
II	838	12	1.4	1.6	46	142	76	72
III	1075	765	41.6	45.1	0	53	100	100
IV	87	1037	92.2	91.6				
V	-	168	100.0	99.2				
VI	-	18	100.0	100.0				
from Winters and Campbell (1974).					this study, Kodiak 1982.			

The Kodiak area would be the easiest location in which to collect the necessary time-series of samples, as capelin of all sizes are found near shore throughout the year in that area.

Winters (1974) back-calculated lengths of fish from otolith radii. He could not find any convenient mathematical relationship between length and otolith radii and resorted to reading off fish lengths from the empirical curve of the otolith radii, body length relationship. Even this technique requires a complete set of length and age data for a population.

Abundance

The actual magnitude of the capelin resource in the Northeast Pacific is uncertain although several rough estimates have been made. The lowest estimate of 190 mt by Wolotira et al. (1977), was made only for Norton Sound and the southeast Chukchi Sea. It was based on trawl data taken in the fall when capelin are not common in nearshore waters.

Trumble (1973) used an analogy to the Atlantic fishery to obtain a rough estimate of abundance of capelin in the Northeastern Pacific. He thought that 25 to 50% of the Atlantic catch was not excessive. At that time the Atlantic catch was about one million tons giving an estimate of 250,000 to 500,000 tons. It should be noted that the Atlantic capelin harvest since 1973 increased to over two million tons per year (FAO 1983).

Aerial surveys are used extensively to estimate abundance of herring in the Bering Sea. Species identification is always a problem with aerial surveys and unless actual spawning is observed or samples are collected by ground crews or fishermen, the observed schools are often recorded as unknown species. Habitat type (i.e., rocky shores or gravel beaches) is also used as a species indicator. In surveys flown over the Togiak district in 1978, 849 large schools were seen of which 636 were classified as unknown species (ADF&G, unpublished). Many capelin schools may not be counted by aerial survey because of their preference for spawning at night or on overcast days. Diurnal vertical migrations and offshore spawning have been reported in Atlantic capelin which would also affect aerial surveys (Luka and Ponomarenko 1983). Citing the phenomenal numbers of spawning capelin observed in 1977, Warner and Shafford (1978) conjectured a higher biomass of capelin than other forage fish species including herring.

Using a ecosystem simulation model, Laevastu and Favorite (1978) estimated the biomass of herring and other pelagic species in the eastern Bering Sea. Their estimate of the equilibrium biomass of other species, primarily capelin and sand lance was 4.3 million tons. Their model, which incorporated knowledge of interactions in the marine ecosystem as well as empirical data, found that although the biomass of different species and ecological groups varied from year to year due to several influencing factors, the sum of the biomass of pelagic and semi-demersal species changed little.

The relative abundance of spawning capelin varied greatly over the years studied. The fluctuations are all assumed to be due to natural causes, as the populations were not subject to any known fishing mortality. Year-class strength in Newfoundland stocks of capelin was strongly influenced by onshore wind frequency during the period immediately following hatching and water temperatures experienced during the subsequent period of larval drift (Legget et al. 1984). Collection of similar data could be easily included in an Alaskan management program.

Atlantic capelin periodically fail to arrive at traditional spawning grounds (Templeman 1948). Prokhorov (1968) reported that Barents Sea capelin change their spawning area depending on the temperature regime. In cold years, capelin spawn in the western parts of the spawning area and in warm years they spawn to the east. He suggested that the temperature regime of the Barents Sea observed for the last three months of the previous calendar year determines which area the capelin approach. Olsen (1968) also noted that temperature was an important factor in determining spawning site. Dunbar (1970) reported that North Atlantic capelin are usually rare in northern Labrador and Ungava Bay, but sometimes appear in large numbers, probably due to sudden upswings in the marine climate and inflow of Atlantic water from the east. Temperature also influences growth and maturation (Winters 1974).

The water temperature of the Bering Sea is influenced greatly by the extent of the winter ice-edge which varies with winter temperature and wind direction (Hartman and Johnson 1978). Between years the temperature may vary as much as 6°C for the same month (Straty and Haight 1979). In May 1982, when capelin abundance was low in the Togiak and Nome areas, conditions were unusually cold. Water temperatures in May were never above 5°C and large pieces of ice were blown upon the beaches on 27 May and remained for several days. Togiak area capelin may have been diverted to other areas, some spawning was reported in Security Cove in May and large numbers were reported along the northern coast of the Alaska Peninsula (J. Skrade, personal communication). Those areas have regular spawning populations so it is unknown whether the spawning fish were in fact displaced Togiak fish. On 22 June, a limited spawning did take place in the Togiak area at water temperature of 9°C. The Nome area water temperatures in early June are unknown but by 28 June the water temperature was over 13°C, above the preferred spawning range.

Olsen (1968), found a positive correlation between growth and abundance in Norwegian capelin, indicating that the number of capelin which survive to maturity is dependent on the environmental conditions during the juvenile phase as well as the initial year-class strength. In contrast, density dependence has been suggested as a factor in that large year-classes may exert a heavy demand on the available food supply resulting in poor growth and later maturity (Ulltang 1975; Carscadden 1977).

Pearcy (1983) summarized the environmental variables which affect herring stocks:

> Environmental variables that affect year-class success of herring range from single, short-term events such as a storm or freshet that affect the survival of a cohort in an isolated inlet to large-scale events that affect the productivity and circulation of large areas of the northeastern Pacific for a year or more. The synchrony of strong

year classes in distant stocks during El Ninos, supports the idea that large-scale ocean events are important.

The same variables must affect capelin stocks but conclusions about the importance of large scale events can't be made without more annual data from all three study areas.

"Ecological theory on r and K selection has proven to be a useful tool in conceptualizing different extremes in life history strategy" (Gunderson 1980). An r-strategist is a species which is exposed to a large component of nonselective mortality and continually colonizes habitats of a temporary nature. Such a species would be selected for characteristics that would increase productivity, such as early maturity, rapid growth rates, production of larger numbers of offspring at a given parental size and maximum production of offspring at an early age (Gadgil and Bossert 1970; Adams 1980). Other characteristics would be small body size, high mortality rates, and short life span (Adams 1980). Adams expresses the r-strategist in terms of commonly measured fishery population parameters as: (1) a low age at first maturity, (2) a high value of k from the von Bertalanffy growth equation, (3) a small L from the von Bertalanffy growth equation, (4) high rates of instantaneous natural mortality (M), and (5) low maximum age. A K-strategist would have the opposing combination of parameters. Gunderon (1980), compared the life history parameters of twelve species of marine fish and found Atlantic capelin to be the most r-selected species. They had the highest value for M (1.30), and k (0.48) and the lowest values for age at first maturity (3), maximum age (7), and L (19.50 cm). The values for Pacific capelin should be similar with an even lower maximum age. The fluctuating abundance of Pacific capelin is consistent with the naturally alternating "booms" and "busts" in population size of an r-strategist.

Fisheries on r-selected species will be more productive, can be fished at higher levels of fishing mortality, and have quicker recovery time from overfishing than K-selected species. They will be more likely to be influenced strongly by the environment and be characterized by erratic production and "boom and bust cycles" (Adams 1980).

This was seen in the North Atlantic fishery which expanded rapidly in the early 70's to peak in 1977 and then decline sharply as stocks were overfished. The North Atlantic Fisheries Organization (NAFO) now does an annual stock assessment in order to set total allowable catches (TACs). Their main survey technique is acoustics in offshore areas. This technique is not too useful for inshore areas so a sequential capelin abundance model (SCAM), which resembles cohort analysis, was developed to use data from the fishery (Carscadden; personal communication). Although Pacific capelin have fewer cohorts in the population than Atlantic capelin, a similar model might still be useful in estimating stock sizes.

By monitoring the environmental conditions and the age composition and relative abundance of spawning populations, biologists can estimate the recruitment success and expected run strength. Aerial surveys, in conjunction with herring management programs, may prove to be the earliest survey technique to implement in Alaskan waters.

Summary

1) Capelin are widely distributed in Alaskan waters. Spawning behavior is similar to that of Atlantic stocks but size and age at maturity are less.

2) Because the age of maturity varies between age II and age III, monitoring the age composition of a spawning stock is important for estimation of recruitment by brood year.

3) The age compositions and correspondingly, the average lengths and weights of capelin populations in the three study areas were significantly different.

4) Growth rates varied from year to year and between locations resulting in different sizes at age.

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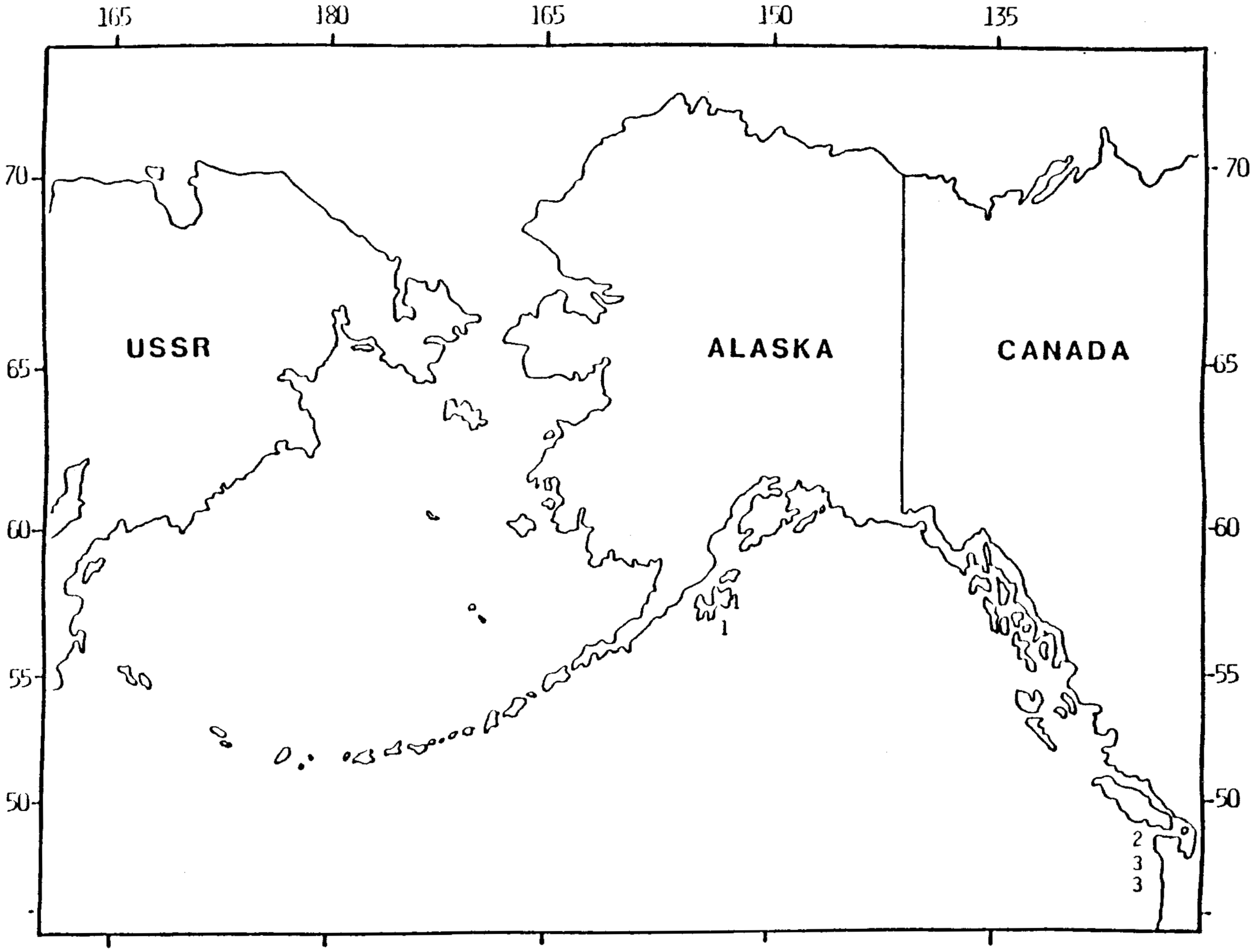
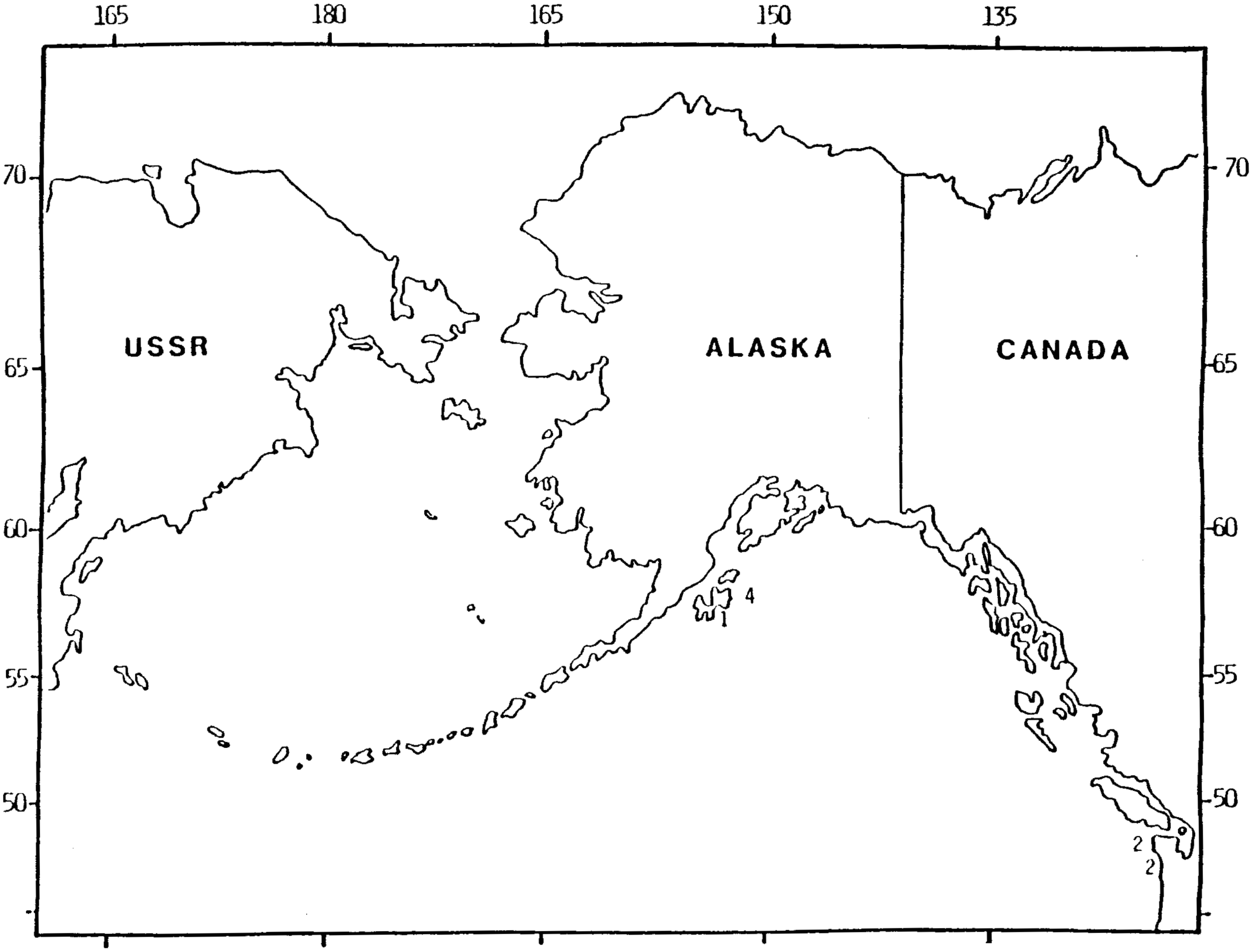
Appendix 1. General locations and approximate latitudes and longitudes of the places mentioned in the text.

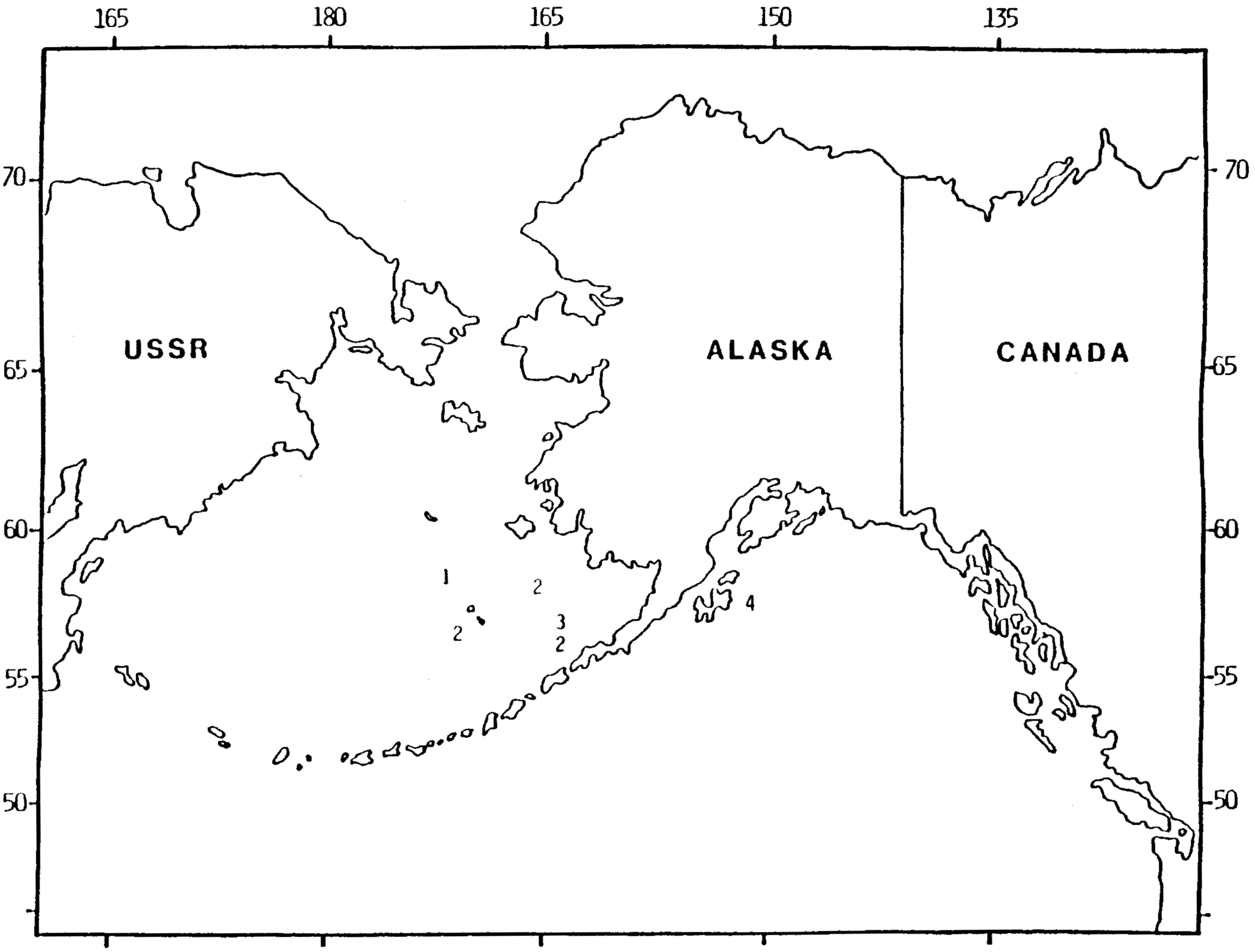
Place name	General location	latitude and longitude	
Akta Island	Western Aleutians	52.15N	174.30W
Attu Island	Western Aleutians	52.55N	173.00E
Alitak Bay	Southwest Kodiak Island	56.50N	154.10W
Barents Sea	North of Finland	75.00N	40.00E
Beaufort Sea	Northeast coast of Ak.	71.00N	150.00W
Bering Strait	Between USSR and Alaska	65.20N	169.00W
Cape Newenham	West Togiak Bay	58.45N	162.10W
Cape Lisburne	Chukchi Sea	68.50N	166.10W
Cape Rodney	Northwest Norton Sound	64.50N	166.50W
Cape Romanzoff	West Yukon River Delta	61.50N	166.10W
Glacier Bay	Northern southeast AK.	58.20N	136.00W
Goodnews Bay	Northwest of Togiak Bay	59.07N	161.36W
Golovin Bay	Northern Norton Sound	64.30N	163.00W
Kachemak Bay	Southeast Cook Inlet	59.35N	151.30W
Kulukak Bay	Togiak Bay	58.55N	159.36W
Metervik Bay	Kulukak Bay	58.52N	160.00W
Monashka Bay	Northeast Kodiak Island	57.53N	152.25W
Nelson Island	Kuskokwim River Delta	60.40N	165.00W
Newfoundland	Eastern Canada	52.00N	56.00W
Nunavachak Bay	Togiak Bay	58.52N	160.02W
Okhotsk Sea	Pacific USSR	55.00N	150.00E
Pillar Beach	Northeast Kodiak Island	57.51N	152.28W
Point Barrow	Artic Ocean	71.32N	156.30W
Point Belcher	Southwest of Pt. Barrow	70.55N	159.40W
Point Lay	Chukchi Sea	69.45N	163.10W
Point Moller	Northern Alaska Peninsula	55.52N	160.42W
Port Clarence	Seward Peninsula	65.15N	167.00W
Pribilof Islands	Bering Sea	57.00N	170.00W
Peter the Great Bay	Pacific USSR	42.40N	132.00E
Prince William Sound	Northern Gulf of Alaska	60.30N	147.00W
Prudhoe Bay	Arctic Ocean	70.30N	148.30W
Sakhalin Island	East Asia	51.00N	143.00E
Security Cove	Northeast of Cape Newenham	58.38N	161.55W
Shismaref	North Seward Peninsula	66.15N	160.01W
Summit Island	Togiak Bay	58.51N	160.14W
Vancouver Island	Southern British Columbia	50.00N	126.00W
White Sea	Northwestern USSR	66.00N	40.00E
Yakutat	Gulf of Alaska	59.40N	139.50W



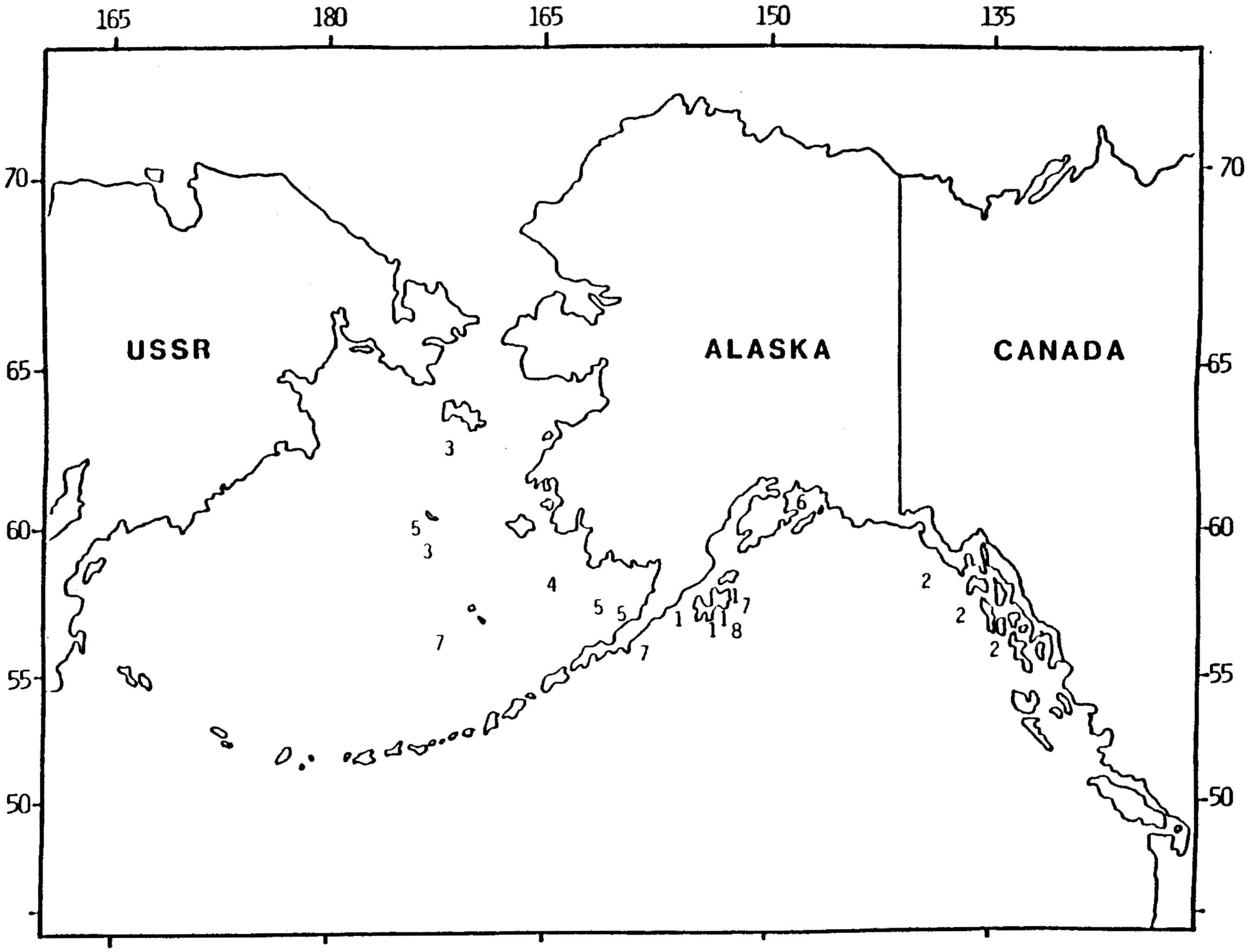
Appendix 2. Monthly location in the northeast Pacific Ocean in which non-spawning capelin have been collected, 1948-1983, and sources of information. A2-1 January 1: Jackson (personal communication), 2: Kajimura et al. (1980), 3: NMFS (1970).



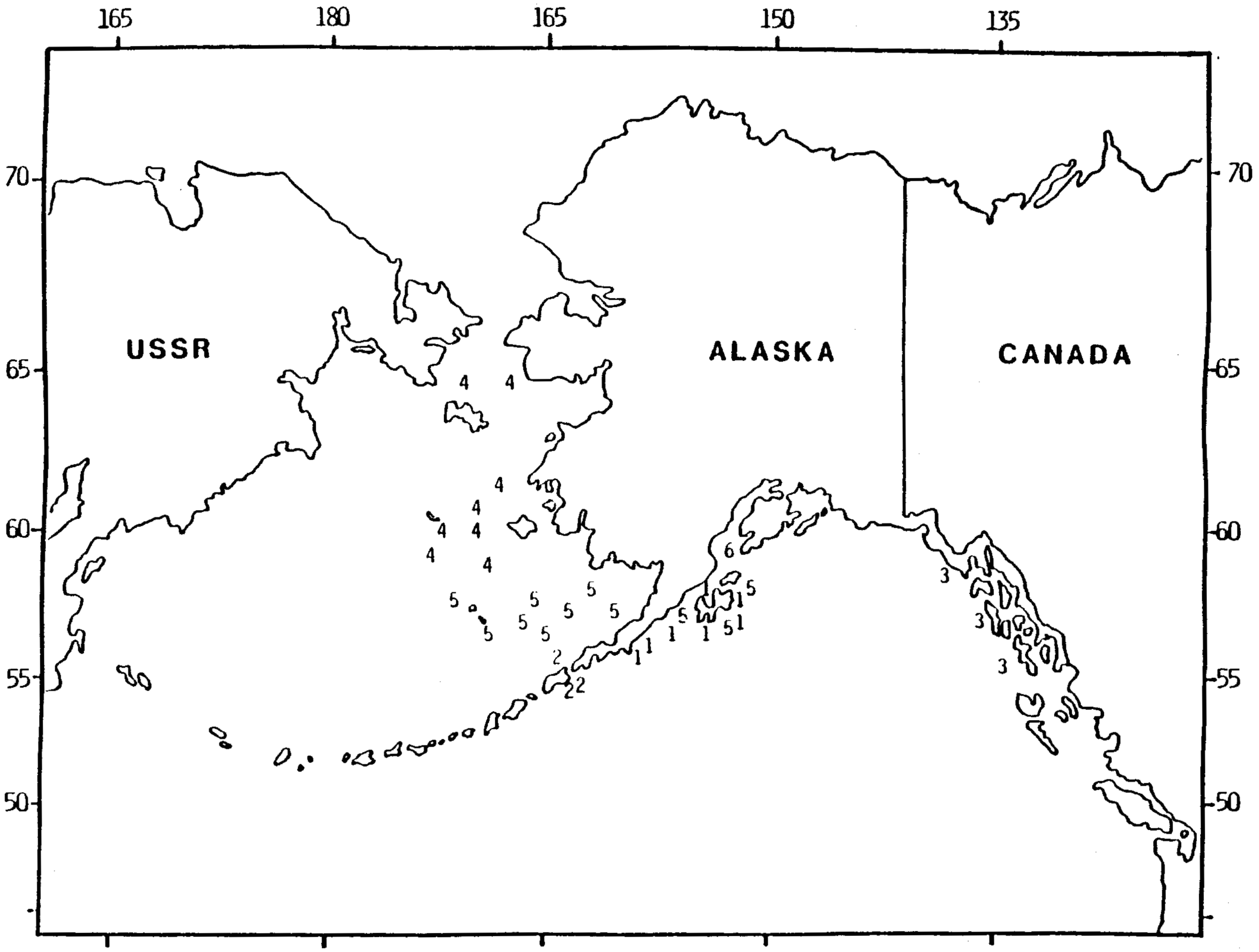
A2-2 February capelin distribution and sources of information. 1: Jackson (personal communication), 2: NMFS (unpublished RACE data), 3: Pitcher (1980), 4: Dunn et al. (1981).



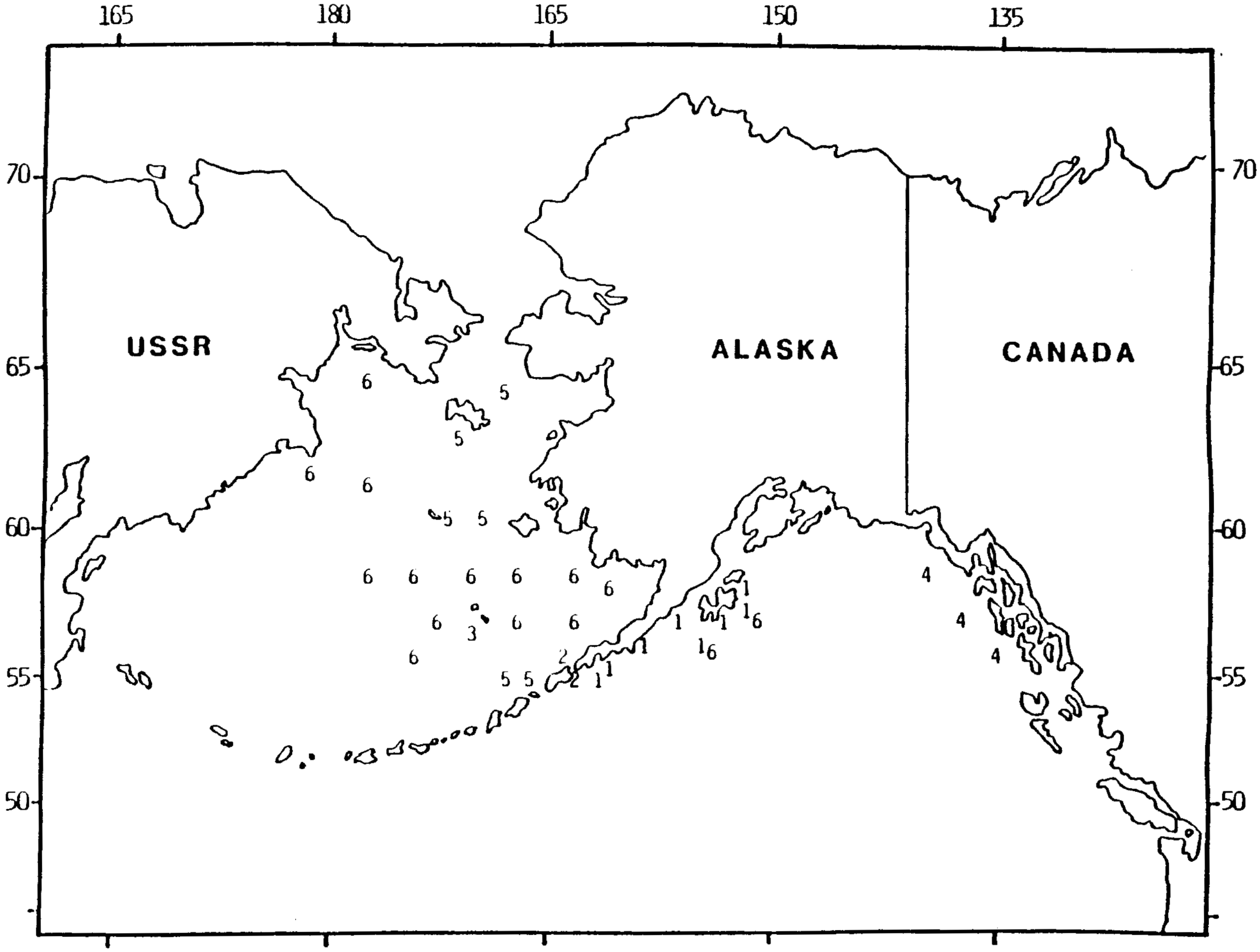
A2-3 March capelin distribution and sources of information. 1: Lowry and Frost (personal communication), 2: Lowry and Frost (1981), 3: Frost and Lowry (1980), 4: Dunn et al. (1981).



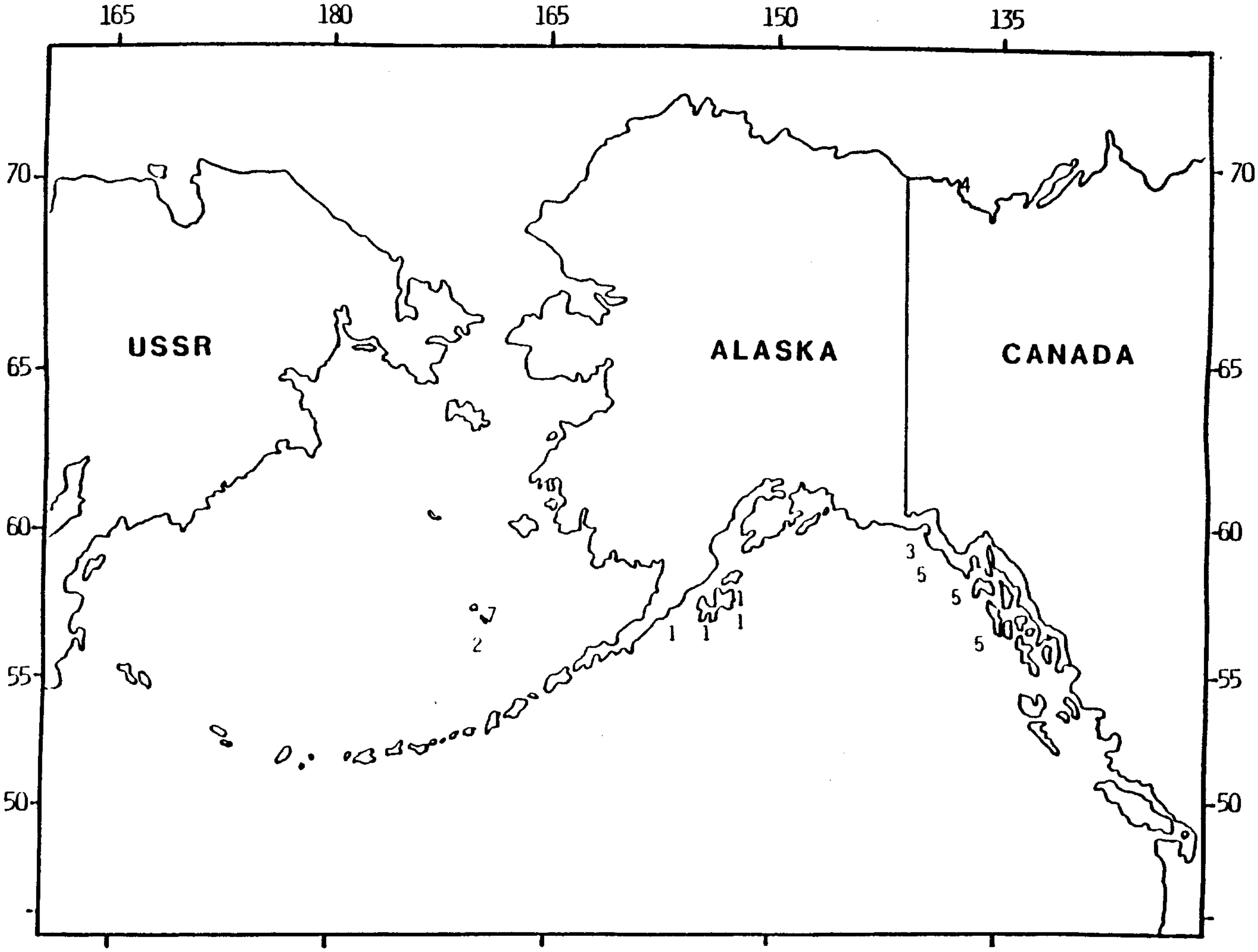
A2-4 April capelin distribution and sources of information. 1: Jackson (personal communication), 2: Krygier (1981), 3: Frost and Lowry (1980), 4: Bukhtiyarov et al. (in press), 5: Lowry and Frost (personal communication, 6: Parks and Zenger (1979), 7: NMFS (unpublished RACE data), 8: Dunn et al. (1981).



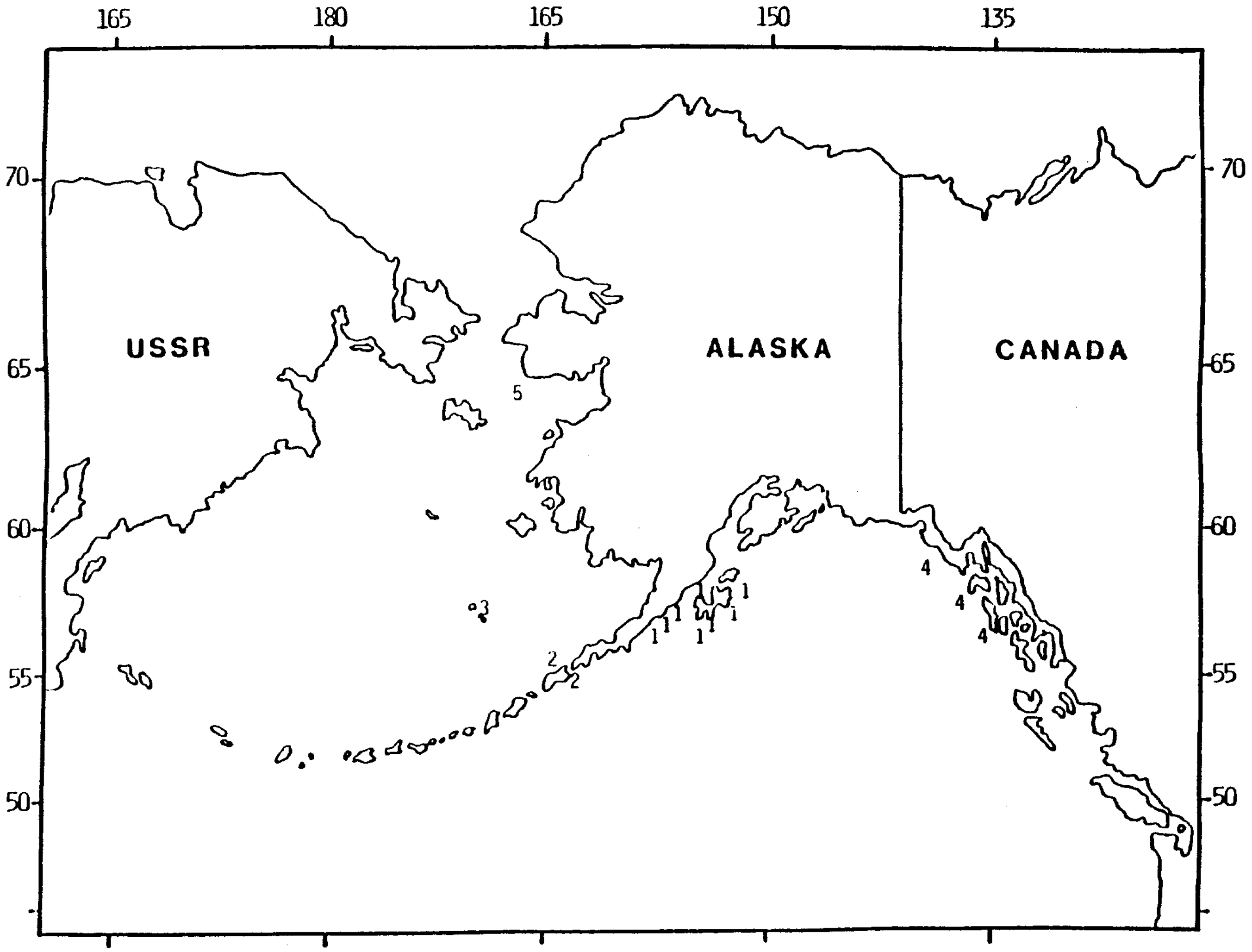
A2-5 May capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: Krygier (1982), 4: Lowry and Frost (personal communication), 5: NMFS (unpublished RACE data), 6: Blackburn (1978b).



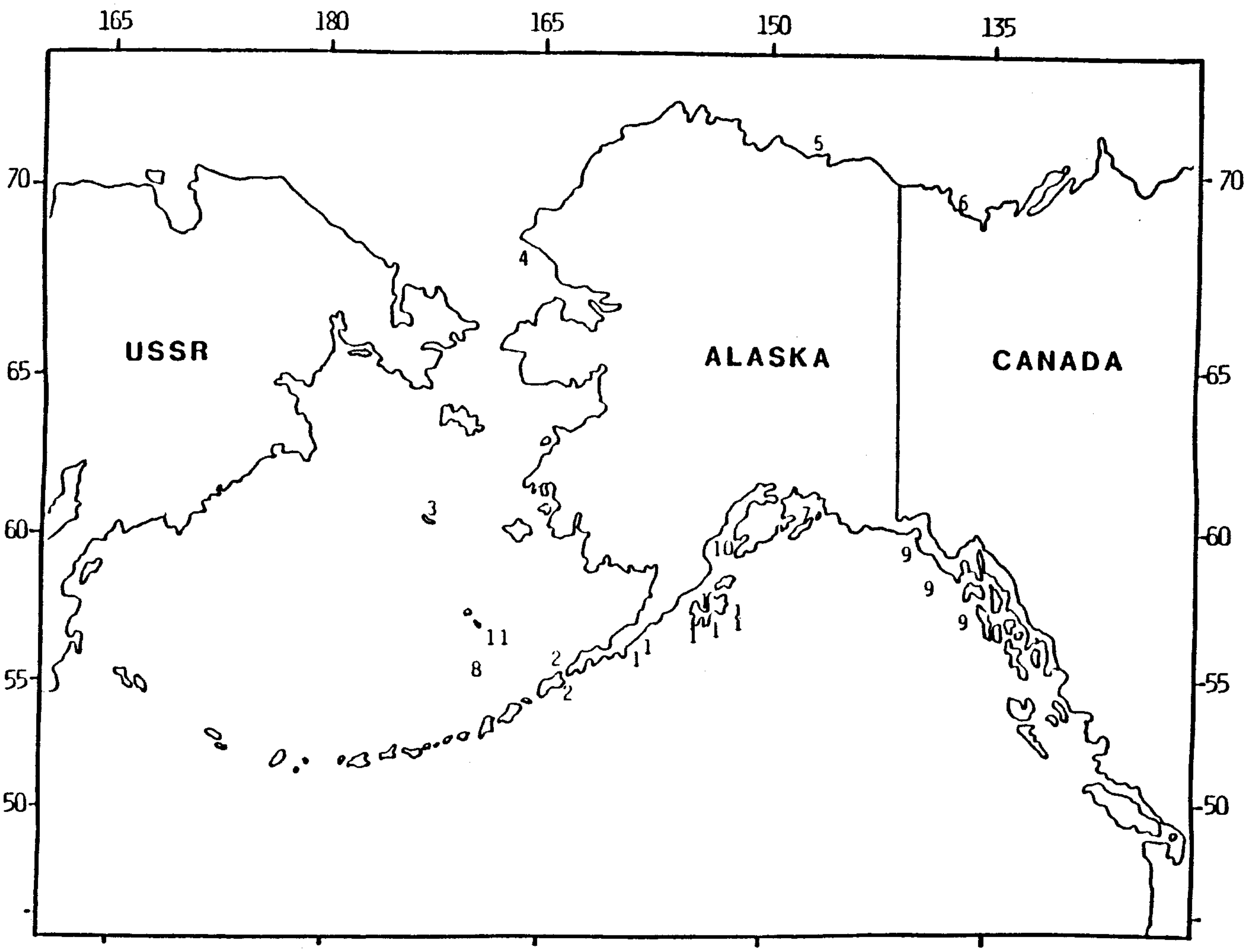
A2-6 June capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: Harry and Hartley (1981), 4: Krygier (1982), 5: Lowry and Frost (personal communication), 6: NMFS (unpublished).



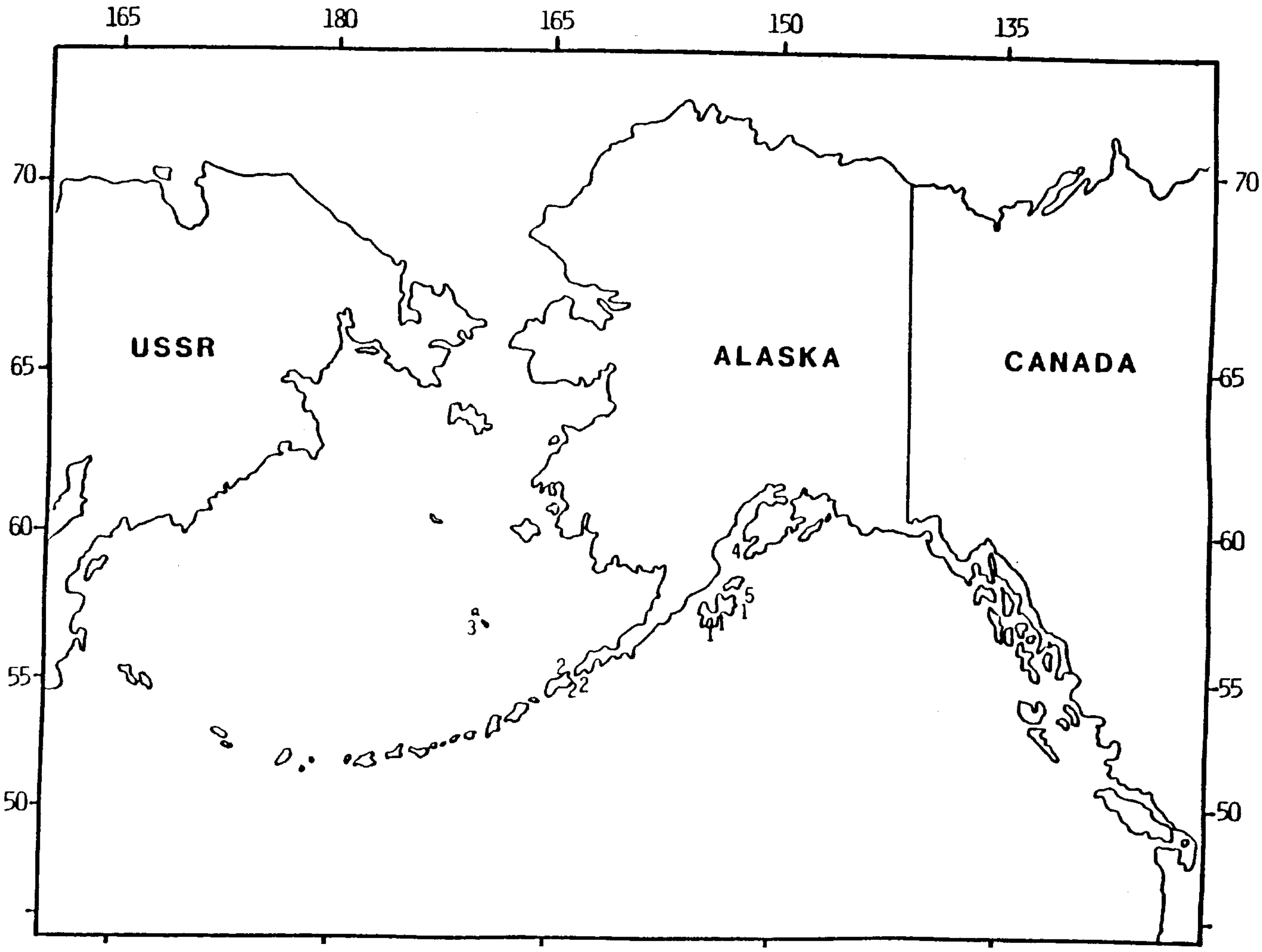
A2-7 July capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: Rogers et al. (1980), 4: Kendel et al. (1974), 5: Krygier (1982), 6: NMFS (unpublished), 7: Hunt et al. (1981).



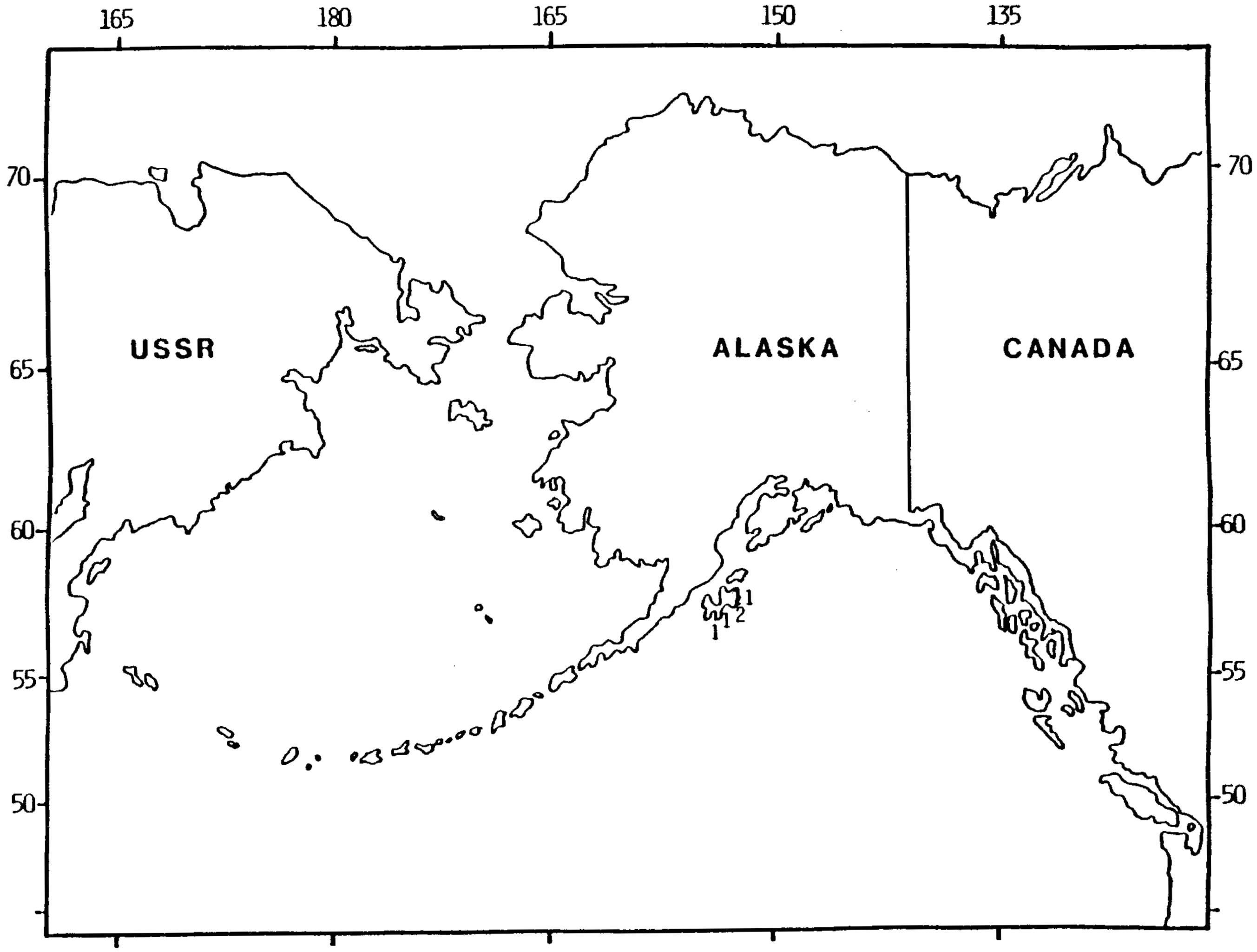
A2-8 September capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: Hunt et al. (1981), 4: Krygier (1982), 5: Wolotira et al. (1977).



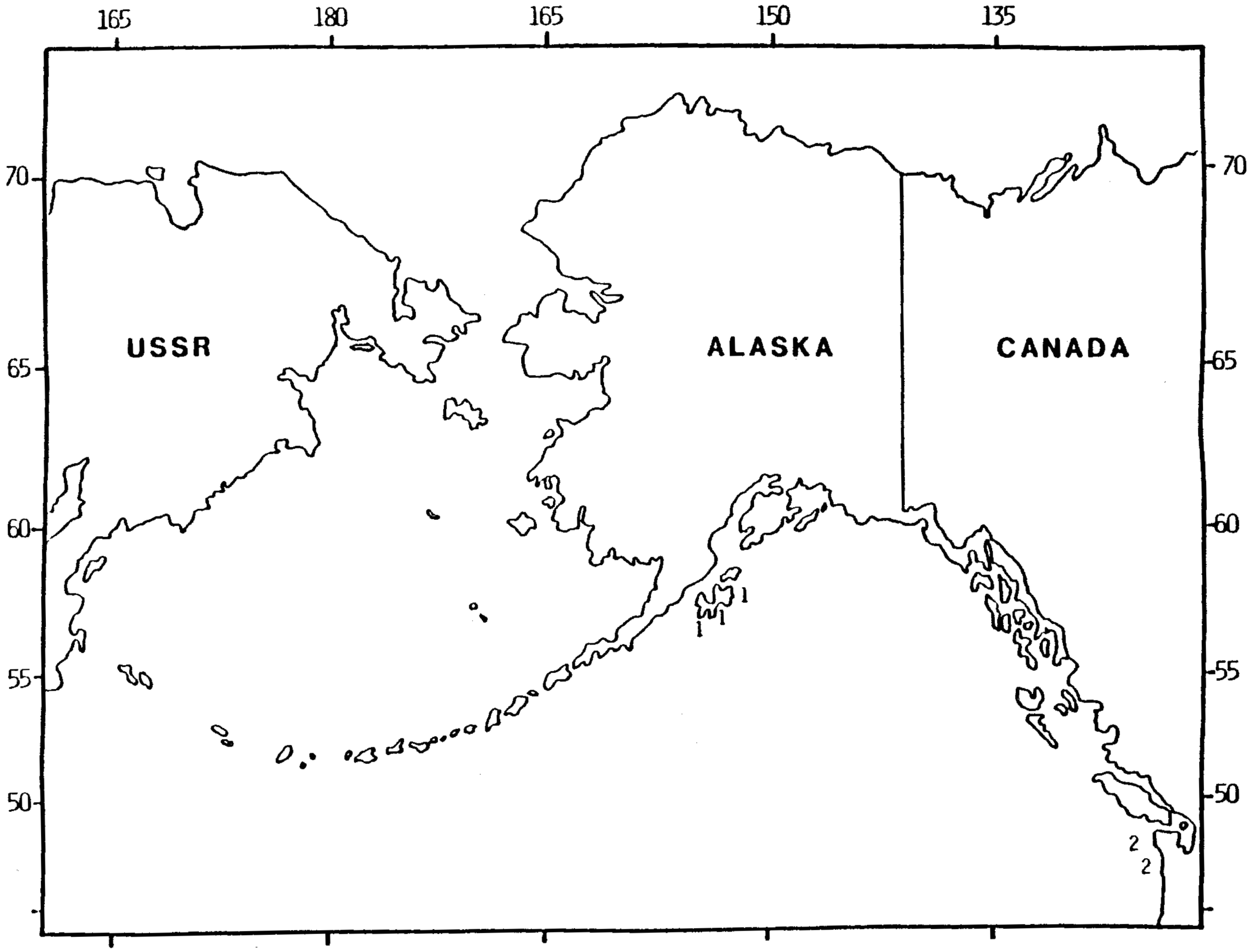
A2-8 August capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: NMFS (unpublished), 4: Springer and Roseneau (1978), 5: Bendock (1977), 6: Kendel et al. (1975), 7: Pitcher (1980), 8: Harry and Hartley (1981), 9: Krygier (1982), 10: Blackburn (1978b), 11: Hunt et al. (1981).



A2-10 October capelin distribution and sources of information. 1: Jackson (personal communication), 2: Fiscus et al. (1964), 3: Harry and Hartley (1981), 4: Blackburn (1978b), 5: Dunn et al. (1981).



A2-11 November capelin distribution and sources of information. 1: Jackson (personal communication), 2: Dunn et al. (1981).



A2-12 December capelin distribution and sources of information. 1: Jackson (personal communication), 2: NMFS (1970).