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Habitat Partitioning by Ice-Associated Pinnipeds: Distribution and Density of Seals and Walruses in the Bering Sea, April 1976

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ABSTRACT

Aerial surveys were conducted over the Bering Sea pack ice in April 1976 to assess the distribution and density of five ice-associated pinnipeds. Results from those surveys support the hypothesis that walruses, ringed, ribbon, spotted, and bearded seals partition the available ice habitat by distributing themselves differentially according to north-south and east-west gradients. Partitioning is believed to be the result of selection for specific ice types and, perhaps, availability of different prey. All species exhibited a clumped distribution. Walruses were most abundant near St. Lawrence Island and in outer Bristol Bay, as had been observed in previous surveys during April. Ringed seals were widely dispersed, and their presence in considerable numbers in the southeastern sector of the pack is reported for the first time. Ribbon seals were most abundant in the west-central ice front. Densities of spotted seals were highest in the ice front, east and west of the major concentration of ribbon seals as well as in outer Bristol Bay. Bearded seals were nearly ubiquitous on the pack ice but with higher densities in the northern than in the southern sectors. The pack ice in April 1976 extended nearly to its southern maximum, hence the data collected during this study allowed a comparison of the spatial relationship among the ice-associated pinnipeds in a year of maximal dispersal.

РЕЗЮМЕ

В апреле 1976 г. были проведены аэровизуальные наблюдения за распределением и плотностью залегания пяти видов ластоногих на льдах Берингова моря. Результаты этих наблюдений подкрепляют гипотезу дифференцированного распределения моржа, акибы, крылатки, ларги, и лахтак соответственно с севера на юг и с востока на запад.

Предполагается, что такое распределение обусловлено выбором определенного типа льда, а также доступностью предпочтительной пищи.

Распределение всех видов имело пятнистый характер. Наибольшая численность моржей отмечалась близ острова Св. Лаврентия и по периферии зал. Бристоль, как, и в предыдущие годы. Кольчатая нерпа широко распространена и впервые в изобилии отмечалась в юго-восточной части ледового покрова. Наибольшее количество крылатки отмечено в западно-центральной части ледового фронта. Самая высокая плотность ларги была вдоль ледового фронта к востоку и западу от основных сосредоточений крылатки, а также в зал. Бристоль. Лохтак встречался почти повсеместно на паковом льду и плотность его скоплений была выше на севере, чем на юге.

Поскольку лёд в апреле 1976 г. простирался на юг до максимальных значений, полученные данные по распределению ластоногих характерны для года с максимальной ледовитостью моря.

INTRODUCTION

In winter and early spring, much of the Bering Sea is covered with ice floes, which are used as haul out areas by several species of pinnipeds: The Pacific walrus, *Odobenus rosmarus divergens*; the ringed seal, *Phoca hispida*; the ribbon seal, *Phoca fasciata*; the spotted or larga seal, *Phoca largha*; and the bearded seal, *Erignathus barbatus*. These pinnipeds use the ice as a substrate on which to give birth to their young, to molt, and to rest. To some extent also, the moving ice serves as a means for passive dispersal of these mammals into seasonal feeding areas, especially during its southward advance in autumn and its northward retreat in spring (Burns 1970; Fay 1974). Harbor seals, *Phoca vitulina*, and northern sea

lions, *Eumetopias jubatus*, also rest on floes in the southern edge of the pack during the spring, particularly when it extends far into the southwestern and southeastern Bering Sea. The centers of abundance for those two pinnipeds, however, lie farther to the south, in ice-free areas such as the Aleutian and Commander Islands and the Alaska and Kamchatka Peninsulas. Their use of the pack ice, therefore, is irregular and opportunistic.

Pack ice generally is present over most of the continental shelf of the Bering Sea from December to June (Shapiro and Burns 1975; McNutt 1981). In most years, the pack reaches its maximum in extent during late March, when its extreme southern limit coincides approximately with the 200 m isobath (Burns and Harbo 1977⁴). In years of extreme icing, however, the maximum is attained in April

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⁴Burns, J. J., and S. J. Harbo, Jr. 1977. An aerial census of spotted seal, *Phoca vitulina largha*, and walruses, *Odobenus rosmarus* in the ice front of Bering Sea. In Environmental assessment of the Alaskan continental shelf. Quarterly reports of principal investigators, April-June 1977, Vol. 1, p. 58-132. NOAA Environ. Res. Lab., Boulder, Colo.

and extends farther south. This was its condition in April 1976 (Fig. 1).

The spring distribution of pinnipeds in parts of the Bering Sea pack ice had been investigated previously, for example by Kenyon (1960⁵, 1972⁶), Krylov et al. (1964), Tikhomirov (1964), Fedoseev (1965), Shustov (1965, 1969), Kosygin (1966), Burns (1970), and Fay (1974), but no single study had investigated distribution throughout the pack ice, as we were able to do in April 1976. April is the optimal month for such an investigation, for the greatest proportion of the species occurring there at that time is likely to be lying out on the ice, where they can be seen from the survey aircraft.

Three separate aerial surveys were conducted over the Bering Sea pack ice in April 1976, with the common objective of describing the distribution and density of the several species of pinnipeds residing there. Surveys were conducted over 1) the eastern Bering Sea by the National Marine Fisheries Service (H. W. Braham), 2) the ice front in the southeastern and southcentral Bering Sea by the Alaska Department of Fish and Game (J. J. Burns), and 3) the western Bering Sea by the Pacific Institute of Fisheries and Oceanography (G. A. Fedoseev). Although these surveys were conducted independently of each other, they were coordinated for purposes of obtaining maximal areal coverage and compatible data. Because the ice cover was more extensive than normal, we hypothesized that the distribution of the pinnipeds also would be near its maximum in extent. The aerial surveys conducted at that time offered an unusual opportunity to test that hypothesis. The purpose of this paper is to report on the combined results.

NATURAL HISTORY OF THE SPECIES SURVEYED

The distribution and movements of the ice-associated pinnipeds in the study area are closely linked with the advance and retreat of the pack ice (Burns 1970; Fay 1974). A major part of the Pacific walrus population migrates from the Bering Sea into the Chukchi Sea from April to June; they return to the Bering Sea in October to December (Belopol'skii 1939; Nikulin 1941; Fay 1982). In winter, the entire population is distributed throughout the Bering pack ice, but tends to concentrate in outer Bristol and Kuskokwim Bays and in the north-central Bering Sea near St. Lawrence Island (Kenyon footnotes 5, 6). Because they feed mainly on bivalve mollusks, walrus normally remain in waters <100 m deep, which coincides with the usual distribution of pack ice over the continental shelf. The young are born mainly in May, during the northward migration.

Ringed seals occur throughout the pack in the Bering Sea, with highest densities in areas of shore-fast ice (Fedoseev 1965; Johnson et al. 1966; Burns 1970, 1973⁷). This is the smallest of the ice-associated pinnipeds and it generally is solitary, congregating only during the molt in May-June. The subadults which have wintered in the Bering Sea begin to migrate northward in April; the adults and pups migrate later (Burns 1970, unpubl. data). During the winter, the highest concentrations of breeding adults occur 5-40 km offshore in the fast ice zone; juveniles and subadults tend to occur farther offshore (Tikhomirov 1966a; Burns 1970, footnote 7). The pups usually are born in the first week of April in snow lairs on fast

ice, stable pack, or in pressure ridges (McLaren 1958; Burns 1970; Smith and Stirling 1975), hence the pups and attendant adults generally are not visible from the air during April.

Ribbon seals are unique to the North Pacific, occurring mainly in the Bering and Okhotsk Seas (Shustov 1965). Two "reproductive groups" in the Bering Sea were identified tentatively by Fedoseev and Shmakova (1976⁸), one in the western and the other in the eastern zone. Nevertheless, Fedoseev's (1984) craniological comparison suggests that considerable intermixing of these groups takes place. In April, ribbon seals characteristically occur on floes in the ice front, where they give birth to their pups from western Bristol Bay to within 50 km of the Soviet coast (Shustov 1965; Tikhomirov 1966a, b; Burns footnote 7; Fay 1974). Late spring concentrations have been reported in Anadyr Gulf and near St. Lawrence Island (Tikhomirov 1966a).

The spotted or larga seal, an ice-associated relative of the coastal harbor seal, frequents the ice front during winter and spring, with the greatest numbers within 25 km of the irregular southern edge of the pack. This seal is the most abundant species of the ice front in southeastern Bering Sea (Tikhomirov 1964). Although present throughout the front, the adults tend to congregate in eastern, central, and western zones. During April, the adults occur as isolated pairs, each with a single pup (Tikhomirov and Kosygin 1966; Burns et al. 1972); later, during the molt, they congregate in small herds and move northward to coastal and estuarine habitats in the northern Bering and Chukchi Seas.

Bearded seals are widely distributed throughout the Bering Sea pack ice in winter and spring, occurring principally in waters <200 m deep, wherever polynyas, leads, and thin ice persist (Burns 1970). In April, most bearded seals are solitary, except for females with pups; occasionally several seals may rest on the same floe. Highest densities in the pack ice have been reported near St. Lawrence Island, southeast of St. Matthew Island, south of Nunivak Island, and in Anadyr Gulf (Kosygin 1966). Local abundance may be related to availability of food (Tikhomirov 1964). The northward migration of bearded seals is underway in April (Burns 1967⁹); they later move northward into the Chukchi Sea with the retreating ice.

METHODS

Eastern Bering Sea Pack Ice Survey

The National Marine Fisheries Service (NMFS) survey covered the northeastern Bering Sea on 13, 15, 19-23 April and southeastern Bering and Bristol Bay on 6, 8, 9, 12, 13, 15, 17-19 April 1976 (Fig. 2). Strip census methods were applied, as described in Eberhardt (1978). Initially, the survey was stratified using randomly selected strips along lines of latitude 3 nmi (5.6 km) apart. Subsequently, strips were chosen systematically and the surveys flown to delineate further the areas of animal abundance (Krogman et al. 1978¹⁰). Stratification methods were used in the analysis to reduce the variance when estimating abundance.

⁵Kenyon, K. W. 1960. Aerial surveys of marine mammals in the Bering Sea, 23 February to 2 March 1960 and 25-28 April 1960. Unpubl. rep., 39 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

⁶Kenyon, K. W. 1972. Aerial surveys of marine mammals in the Bering Sea, 6-16 April 1972. Unpubl. rep., 79 p. U.S. Bur. Sport Fish. Wildl., Seattle, WA 98115.

⁷Burns, J. J. 1973. Marine mammal report. Project report, Fed. Aid Wildl. Restor., Vol. XIII, 44 p. Alaska Dep. Fish Game, Juneau, AK 99802.

⁸Fedoseev, G. A., and G. G. Shmakova. 1976. Some results of investigations of spatial structure of ribbon and larga seals of the Bering Sea. Unpubl. rep., 9 p. Special Meeting Marine Mammal Project, US-USSR Environmental Protection Agreement, Moscow.

⁹Burns, J. J. 1967. The Pacific bearded seal. Alaska Dep. Fish Game, Juneau, 66 p.

¹⁰Krogman, B. D., H. W. Braham, R. M. Sonntag, and R. G. Punsly. 1978. Early spring distribution, density, and abundance of the Pacific walrus (*Odobenus rosmarus*) in 1976. Final report, R.U. 14, 47 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

The survey aircraft were the turbo-jet powered Grumman Goose¹¹ (N780) and the long-range Lockheed Neptune P2V (N48347). The P2V was used only on 13 and 15 April. Airspeed generally was 120-140 kn at survey altitudes of 100-350 m; most surveys were flown at about 135 m. A crew of four people was used for most surveys; there were two observers, one recorder, and one alternate. Crew members changed jobs hourly to reduce observer fatigue. The alternate observer periodically surveyed from the rear of the aircraft to test for observer bias (e.g., for the number of animals missed by forward observers or to validate species identification).

Information recorded included species, number of adults and pups, local time of sighting, position to 1 nmi² (obtained from an onboard Global Navigation System, model GNS500), perpendicular angular distance from aircraft to animal (taken with an optical clinometer, model Pm-5/360 PC, Suunto Instruments, Helsinki), animal activity, and environmental conditions, including weather, visibility, ice type, and ice cover.

Sighting angles were recorded during surveys and were later converted to distance of the animal from the aircraft. When large concentrations of animals were encountered, their occurrence within different "sectors" of a strip transect were noted. Each of those sectors was 0.25 statute mile wide (0.4 km), as follows: A = 0-0.25 mi; B = 0.25-0.5 mi; C = 0.5-0.75 mi; D = >0.75 mi. Since observers could not see directly below the aircraft, sector boundaries were offset to each side of the aircraft (approximately 15°) during flights made in the Grumman Goose. Sector boundaries for all flights were delineated by the clinometer. In this report, density estimates of pinnipeds other than walrus were based upon only those sightings made within the first 0.25 mi strip on each side of the aircraft; total strip width therefore equaled 0.5 mi (0.8 km). For walrus, strip width equaled 1 mi (1.61 km).

Southern Bering Sea Ice Front Survey

The Alaska Department of Fish and Game (ADF&G) surveys were restricted to the ice front (Fig. 3). Their primary purpose was to determine the distribution and relative abundance of spotted seals. Flights were conducted on 8, 9, 11, 17, 19, 20, 21, and 23 April 1976. The aircraft used was the P2V which had a large Plexiglas observation compartment in the nose. A crew of three persons usually occupied this compartment during the surveys; two were primarily observers, but one also recorded. The third person acted as a back-up observer whose function was to determine the proportion of seals not seen by the primary observers, to verify inclusion or omission of animals at the limit of transects, and to replace primary observers when fatigued. On most flights, a primary observer counted on one side of the aircraft for 2 h, then counted on the other side for 2 h, then rested for up to 1 h. Forward, lateral, and downward visibilities from the observation compartment were excellent.

Survey procedures involved use of strip transects 0.5 nmi (0.93 km) wide on each side of the aircraft, for a total strip width of 1 nmi (1.85 km). Angle indicators were mounted on each side of the observation compartment to limit the outer boundaries of the strip. The survey aircraft was equipped with a GNS500. To the extent possible, survey altitude in the P2V was maintained at 91 m. Lower altitudes were flown when necessitated by weather. Flight speed averaged 160 kn.

Information recorded included species and number of animals sighted, group size, animal activities, ice types, weather, local time, and navigational information. Animal sightings were recorded continuously in 1 min time intervals.

The P2V flight strips on 8, 9, and 11 April were selected at random. Those surveys on 17 and 19 April were along preselected flight lines designed to achieve a replicate, stratified, random sample in the recognized area of highest seal density. Systematic surveys, flown mainly in an east-west direction, covered the southern portion of the ice front on 20 April and the northern part on 21 April.

Western Bering Sea Survey

The Pacific Institute of Fisheries and Oceanography (TINRO) surveys involved extensive flights over the ice-covered regions of north-central and northwestern Bering Sea. Survey lines generally were oriented north-south and covered all ice types from the front to Bering Strait. Surveys were flown on 12-15, 17, 19, and 21-26 April 1976. The aircraft employed was a Soviet UL-14 equipped with standard navigation instruments.

Marine mammals were observed from the left side of the aircraft by a single observer (Fedoseev) viewing through a bubble-type window installed in the compartment aft of the flight deck. This bubble window provided both vertical and horizontal visibility. The observer also was the recorder.

Flight altitude was 200 m, with occasional descents to 100 m. A strip transect equal in width to the altitude of the aircraft was used. The outer limit of the transect was maintained by sighting a 45° angle from the observation window. All animals observed were recorded, but only those animals sighted within the strip were included in the analysis.

Observation periods varied in duration, usually lasting 1 to 1.5 h, followed by a short rest period. Information recorded for each 5-min survey period included start and end time, start and end coordinates, distance covered, transect width, area surveyed, and kind and number of animals sighted. Ice type was recorded by a hydrologist, also on board the aircraft.

Accuracy of the Counts and Identifications

Only the animals sighted on the ice were included in the analyses, since pinnipeds in the water are difficult to identify from aircraft. Because the ability of the observers to sight animals on the ice was recognized as being impaired by fog and snow, the segments of survey strips covered during such periods of poor visibility were routinely deleted from the analyses.

Walrus are easier to see from low-flying aircraft than are any of the other pinnipeds surveyed, but because they tend to congregate on the ice in dense herds, they are more difficult to count. In these surveys, most of the small groups (< 20) were believed to have been counted accurately, but the numbers in the larger groups mostly were estimated in round numbers.

The sightings of ringed seals probably were the least precise because these seals are the smallest and the most shy (i.e., most disturbed by aircraft) of any of the pinnipeds surveyed. Even under the best of conditions, the numbers sighted on the ice in April probably will be only a very small fraction of the numbers present, since many of the animals (particularly females and pups) at that time haul out in lairs under the snow, where they cannot be seen from the air.

Ribbon seals usually react only slightly to the presence of aircraft, frequently remaining on the ice, even when the plane passes

¹¹Reference to trade names does not imply endorsement by any agencies represented by the authors.

directly overhead. They are easily identified by their characteristic method of locomotion, as well as by their distinctive coloration. During April, most of the ribbon seals sighted on the ice probably are adult females and pups; adult males tend to remain in the water at that time. The pups are more difficult to sight than are the adults because of their small size and white coloration.

Spotted seals also are easily identified by their locomotion, coloration, and the fact that the adults in April generally occur as pairs on the ice, usually with a white-coated pup. These seals are more disturbed by the aircraft than are the ribbon seals, hence tend to move more rapidly and in a straight line to the water. Because of this motion, the pups usually can be seen, despite their small size and coloration.

Bearded seals are readily seen and identified from the air, because of their large size. They usually are not frightened, often remaining on the ice even when the aircraft passes directly over them. Most of those sighted in April probably are subadults, which occur singly, and adult females with pups; adult males tend to be in the water at that time.

Analytical Methods

Data from the TINRO surveys were computer-plotted directly as numbers of animals sighted per 5-min time segment of each transect. Data from the NMFS and ADF&G surveys were plotted as numbers of animals sighted per 1-min of time within each 10' × 10' (0.3 km × 0.3 km) block of latitude and longitude. Where more than one survey strip crossed a 10' × 10' (0.3 km × 0.3 km) block, the data were averaged to give equal weight to the survey effort in all blocks.

The data were stratified by the method developed experimentally by Krogman et al. (footnote 10). Estimates of regional density and abundance were computed only from the NMFS surveys by "Method I" of Estes and Gilbert (1978):

$$(1) \hat{R} = \Sigma y_i / \Sigma x_i$$

where $\hat{R}$ = density of animals per square nautical mile
 y_i = number of animals in the i th survey strip
 x_i = area of the i th survey strip

$$(2) S_R^2 = [\Sigma (y_i^2 / x_i) - \hat{R} \Sigma y_i] / (n-1) (\Sigma x_i)$$

where S_R^2 = variance of $\hat{R}$
 n = number of survey strips

$$(3) \hat{T}_y = \hat{R}A$$

where $\hat{T}_y$ = animal abundance in stratum
 A = total area of stratum

$$(4) V(\hat{T}_y) = A(A - \Sigma x_i) S_R^2$$

where $V(\hat{T}_y)$ = variance of $\hat{T}_y$.

Average group size was calculated as:

$$(5) \bar{G} = \Sigma y_i / \Sigma O_i$$

where $\bar{G}$ = average group size in stratum
 O_i = number of observations (= groups in the i th survey strip)

$$(6) S^2 = \Sigma (y_i - \bar{G})^2 / \Sigma O_i - 1$$

where S^2 = group size variance.

Abundance estimates with 95% confidence intervals were generated for each region covered by the NMFS surveys. Confidence intervals were calculated as:

$$(7) \hat{T} \pm t_{.05(2)V} \sqrt{V(\hat{T})}$$

The notation $t_{.05(2)V}$ refers to the critical value of t where alpha (α) = .05 ($1 - \alpha = .95$) based upon a two-tailed test with V degrees of freedom. Degrees of freedom were calculated as the total number of survey strips minus the number of strata.

RESULTS

Walrus

In the northern Bering Sea, walrus were concentrated to the west and north of St. Lawrence Island, in a pattern suggesting movement through Anadyr Strait (between St. Lawrence Island and the Chukchi Peninsula), toward Bering Strait (Figs. 4, 5). The numbers north of St. Lawrence Island apparently were greater than had been reported previously in this month by Kenyon (footnotes 5, 6). Kenyon's April surveys showed the highest concentrations in this region to be southwest of St. Lawrence Island and in Anadyr Strait. The overall density of animals in the St. Lawrence Island area in April 1976 was 2.77 ± 0.77 (mean $\pm$ SD) individuals/nmi² (Table 1, unstratified estimate). Data from the TINRO surveys in that area suggest that the abundance estimate from the NMFS surveys of $25,320 \pm 9,744$ (mean $\pm$ 95% confidence interval) animals was conservative (Krogman et al. footnote 10).

Walrus were conspicuously absent in the central Bering Sea from lat. 59° to 63°N, as well as in Norton Sound and north of lat. 65°N. The ice in those areas was considerably more compact than it was to the north and west of St. Lawrence Island and in Bristol Bay.

Walrus were found in the southeastern part of the Bering Sea, particularly from the Pribilof Islands to Bristol Bay. Highest densities were found 1) around the Pribilof Islands, 2) east of the Pribilofs, approximately 10-40 km north of the ice front, 3) southwest of Cape Newenham, and 4) in outer Bristol Bay (Figs. 4, 6). Walrus were nearly absent from inner Bristol Bay, including Round Island, a traditional summer haulout site. Densities also were lower along the ice front than deeper in the pack, indicating that walrus prefer the heavier pack.

Walrus were most dispersed in Bristol Bay (Table 2) than near St. Lawrence Island (Table 1). The density estimate (unstratified) for Bristol Bay was 0.82 ± 0.22 animals/nmi². An abundance estimate of $30,358 \pm 13,933$ (95% CI) was derived from the NMFS survey area (Table 2), to which an additional 1,319 animals should be added for the areas covered exclusively by the ADF&G surveys (Krogman et al. footnote 10).

Ringed Seals

In the northern Bering Sea, ringed seals were found to be most closely associated with shorefast and dense pack ice, except just west of St. Lawrence Island (Figs. 7, 8). Along the Soviet coast, they were most abundant in the ice of the eastern Chukchi Peninsula and were numerous also in the southwestern Anadyr ice massif, where the pack ice is characteristically very dense, and in

Table 1.—Walrus statistics from NMFS aerial surveys conducted 13-23 April 1976 in northern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum ¹ area (nmi ²)	Percent of area sampled	No. of transects	No. of walrus counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance	Animals per group	Variance	No. groups	Variance	No. of walrus	Variance (× 10 ⁶)
1	6,683	5.00	12	32	0.10	>0.00	6.40	21.71	0.03	>0.00	641	0.12
2	394	14.57	6	12	0.21	0.01	3.00	1.83	0.07	>0.00	82	>0.00
3	315	19.28	3	66	1.09	0.59	4.13	3.03	0.26	0.03	342	0.05
4	3,945	10.90	13	698	1.62	0.20	8.13	3.12	0.20	>0.00	6,401	2.74
5	1,343	5.44	3	267	3.66	0.82	20.54	124.92	0.18	>0.00	4,908	1.40
6	133	14.63	2	254	13.09	195.59	18.14	88.27	0.72	0.45	1,736	2.94
7	86	8.69	2	250	33.30	1,102.89	125.00	625.00	0.27	0.07	2,876	7.51
8	44	17.40	2	451	59.39	3,522.23	56.37	1,765.64	1.05	1.11	2,592	5.54
9	87	13.06	3	750	65.69	425.86	83.33	600.00	0.79	0.07	5,742	2.83
Total stratified	13,030		46	2,780							25,320	23.13
Unstratified	12,878	7.80	17	2,780	2.77	0.60	17.94	12.05	0.15	>0.00	35,622	91.96

¹Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 2.—Walrus statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum ¹ area (nmi ²)	Percent of area sampled	No. of transects	No. of walrus counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance	Animals per group	Variance	No. groups	Variance	No. of walrus	Variance (× 10 ⁶)
1	1,472	5.32	3	0	0.00	0.00	—	—	0.00	0.00	0	—
2	1,772	5.62	7	1	0.01	>0.00	1.00	—	>0.00	—	18	>0.00
3	8,037	6.27	15	13	0.03	>0.00	1.86	0.31	0.01	>0.00	207	0.00
4	18,063	8.82	37	298	0.19	>0.00	5.05	1.83	0.04	>0.00	3,378	1.54
5	3,895	14.09	36	712	1.30	0.06	3.61	0.21	0.36	>0.00	5,054	0.81
6	652	9.67	4	124	1.97	0.65	2.70	0.18	0.73	0.07	1,282	0.25
7	272	6.97	2	81	4.28	13.20	4.05	1.38	1.06	2.15	1,163	0.91
8	556	5.02	2	273	9.80	46.46	21.00	120.21	0.47	0.05	5,441	13.64
9	370	6.22	2	302	13.12	37.72	20.13	73.20	0.65	0.05	4,854	4.84
10	167	8.71	2	344	23.99	284.42	10.42	35.85	2.30	0.78	3,947	7.03
11	110	5.78	2	290	45.72	1,791.72	18.13	27.59	2.52	5.45	5,014	20.30
Total stratified	35,364		112	2,438							30,358	49.32
Unstratified	35,230	8.40	32	2,438	0.82	0.05	5.99	0.63	0.14	>0.00	29,014	58.80

¹Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Karaginskii Gulf (Fig. 8). Ringed seals were not numerous offshore, except to the west of St. Lawrence Island (Fig. 7), where many were seen in a rather narrow band associated with thin ice. The mean group size ($\pm$ 95% CI) north of lat. 60°N was 1.20 ± 0.08 (Table 3).

In southeastern Bering Sea, ringed seals were present from north of the Pribilof Islands to outer Bristol Bay, mainly well north of the ice front (Figs. 7, 8, 9). Densities were low and group size south of lat. 60°N was 1.04 ± 0.02 (Table 3). Those seen 15 to 50 km offshore probably were immature or nonbreeding animals. These animals

probably move southward with the advancing pack ice in late winter, away from the preferred breeding habitat in the north.

Ribbon Seals

Apparently, ribbon seals were absent north of lat. 61°N, except in one location southwest of St. Lawrence Island (Figs. 10, 11) but were abundant from the Pribilof Islands west to Olyutorskii Bay (Fig. 12). Most of these were situated from the ice edge to about 100 km north. The distribution appears to have been continuous, with

Table 3.—Comparative statistics for ribbon and ringed seals from NMFS aerial surveys conducted 6-23 April in northern and southeastern Bering Sea.

Species and stratum	Stratum area (nmi ²)	Percent of area sampled	No. of transects	No. of seals counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance	Seals per group	Variance	No. groups	Variance	No. of seals	Variance
Ribbon seals, southeastern	35,441	4.21	32	9	0.006	>0.00	1.13	0.016	0.005	>0.00	214	5,236
Ribbon seals, northern	13,547	3.76	18	0	0.000	0.00	—	—	—	—	0	0.000
Ringed seals, southeastern	35,441	4.21	32	25	0.017	>0.00	1.04	0.002	0.016	>0.00	594	66,549
Ringed seals, northern	13,547	3.76	18	30	0.059	0.002	1.20	0.040	0.049	0.01	799	326,959

no major clumping of breeding groups into eastern and western segments, as suggested by Fedoseev and Shmakova (footnote 8).

Density estimates generated from the NMFS surveys were extremely low (Table 3). No estimates were generated for areas covered by the ADF&G and TINRO surveys.

Spotted Seals

Although virtually absent from the northern Bering Sea, spotted seals were widely distributed in the ice front from Bristol Bay to Karaginskii Gulf (Figs. 13, 14, 15). The highest densities were in 1) outer Bristol Bay, 2) central Bering Sea from about long. 175°W to 180°, and 3) Karaginskii Gulf. Density estimates (stratified) from the NMFS surveys in the Bristol Bay region ranged from about 0.05 to 6.3 seals/nmi², with a mean (not stratified) of 0.37 ± 0.06 (Table 4). Densities clearly were greatest in the ice front, decreasing northward into the pack ice. Seals collected by Burns (unpubl. data) in the Bristol Bay concentration in March 1976 were principally subadults, suggesting that there is some age-segregation at that time. The larger groups there also included a few harbor seals, which are abundant in the nearshore zone of that area.

Bearded Seals

These seals were nearly ubiquitous in the Bering Sea pack ice but apparently were concentrated in three or four areas: 1) To the west and north of St. Lawrence Island, 2) in southwestern Anadyr Gulf, 3) about 40 to 60 km north of the ice front in the central Bering Sea, and 4) in the area between the Pribilof Islands and Bristol Bay (Figs. 16, 17, 18). A few were sighted also along the Koryak coast and in Karaginskii Gulf. Densities computed from the NMFS surveys were higher in the northern than in the southern areas (Tables 5, 6).

Overall Relative Abundance

As is apparent from the foregoing descriptions of the distribution of each species, the pinnipeds of the Bering Sea pack ice were not uniformly distributed. Each species tended to be most abundant in a slightly to extremely different part of the pack ice than did the others, presumably because of different habitat requirements and, perhaps, interspecific competition for food or space. For walrus, ringed seals, and bearded seals, the centers of abundance were well

Table 4.—Spotted seal statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum ¹ area (nmi ²)	Percent of area sampled	No. of transects	No. of spotted seals counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance ($\times 10^{-3}$)	Seals per group	Variance ($\times 10^{-3}$)	No. groups	Variance ($\times 10^{-3}$)	No. of seals	Variance ($\times 10^6$)
1	5,872	3.34	12	9	0.046	0.1	1.50	11.7	0.03	>0.0	269	0.02
2	8,475	4.03	22	18	0.053	>0.0	1.20	1.1	0.04	>0.0	446	0.03
3	14,762	4.02	30	41	0.069	>0.0	1.58	1.6	0.04	>0.0	1,020	0.08
4	382	5.05	3	2	0.121	1.0	1.00	0.0	0.12	1.0	40	>0.00
5	217	17.08	6	7	0.189	0.8	1.40	6.0	0.14	0.4	41	>0.00
6	581	3.41	2	7	0.354	4.8	1.75	22.9	0.20	0.9	206	0.02
7	240	4.55	2	4	0.366	1.7	1.33	11.1	0.28	0.3	88	>0.00
8	214	8.60	4	7	0.380	2.7	1.40	6.0	0.27	1.1	81	>0.00
9	2,530	6.45	19	84	0.515	1.0	1.59	1.0	0.33	0.3	1,302	0.06
10	733	3.74	2	27	0.985	1.0	1.23	0.8	0.80	0.2	722	>0.00
11	108	9.60	4	12	1.161	54.2	2.40	6.0	0.48	7.3	125	>0.00
12	476	2.97	3	27	1.909	106.9	2.08	5.7	0.92	11.2	909	0.24
13	385	3.92	2	54	2.577	241.9	1.46	2.0	2.45	113.6	1,377	0.34
14	666	6.06	8	254	6.290	492.4	4.62	74.6	1.36	15.9	4,190	2.05
Total stratified	35,587		119	553							10,876	2.84
Unstratified	35,441	4.21	32	552	0.370	3.3	2.21	4.4	0.17	0.3	13,125	39.79

¹ Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 5.—Bearded seal statistics from NMFS aerial surveys conducted 12-23 April 1976 in northern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum ¹ area (nmi ²)	Percent of area sampled	No. of transects	No. of bearded seals counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance ($\times 10^{-3}$)	Seals per group	Variance ($\times 10^{-3}$)	No. groups	Variance ($\times 10^{-3}$)	No. of seals	Variance ($\times 10^3$)
1	3,580	5.66	18	7	0.035	>0.0	1.00	0.0	0.04	>0.0	124	1.6
2	6,642	2.13	9	11	0.078	0.1	1.10	1.0	0.07	0.1	516	43.3
3	2,738	3.96	8	14	0.129	0.3	1.17	1.3	0.11	0.2	354	26.6
4	189	2.40	2	2	0.440	407.8	1.00	0.0	0.44	407.8	83	142.3
5	43	8.70	2	2	0.537	0.0	1.00	0.0	0.54	0.0	23	0.0
6	221	8.80	2	8	0.822	6.6	2.00	100.0	0.41	1.7	182	3.1
7	86	6.53	3	5	0.893	3.1	1.67	11.1	0.54	0.0	77	0.2
8	131	5.81	3	7	0.918	41.6	1.75	22.9	0.53	13.6	120	6.8
9	129	4.34	2	6	1.067	>0.0	1.50	8.3	0.71	1.6	138	>0.0
10	43	8.70	2	10	2.682	260.2	2.00	10.0	1.34	65.0	115	4.4
Total stratified	13,802		51	72							1,732	228.3
Unstratified	13,547	3.76	18	72	0.141	0.1	1.35	1.0	0.10	>0.0	1,917	186.6

¹ Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

Table 6.—Bearded seal statistics from NMFS aerial surveys conducted 6-15 April 1976 in southeastern Bering Sea. Data were treated by stratified and unstratified methods.

Density stratum	Stratum ¹ area (nmi ²)	Percent of area sampled	No. of transects	No. of bearded seals counted			Average group size		Groups/nmi ²		Estimated total/stratum	
				Total	Individuals per nmi ²	Variance ($\times 10^{-3}$)	Seals per group	Variance ($\times 10^{-3}$)	No. groups	Variance ($\times 10^{-3}$)	No. of seals	Variance ($\times 10^2$)
1	14,040	4.07	34	12	0.021	>0.0	1.20	1.8	0.02	>0.0	295	29.4
2	5,974	3.71	27	5	0.023	>0.0	1.00	0.0	0.02	>0.0	135	2.7
3	5,883	3.44	19	5	0.025	>0.0	1.00	0.0	0.03	>0.0	145	5.6
4	4,586	4.15	18	9	0.047	>0.0	1.13	1.6	0.04	>0.0	217	6.6
5	382	11.45	11	4	0.091	0.2	1.00	0.0	0.09	0.2	35	0.3
6	269	14.01	6	6	0.159	0.3	1.20	4.0	0.13	0.2	43	0.2
7	165	5.90	2	2	0.205	4.0	2.00	—	0.10	—	34	1.0
8	1,535	7.40	18	24	0.211	0.3	1.09	0.8	0.19	0.3	324	7.4
9	471	3.87	2	4	0.219	0.7	1.00	0.0	0.22	0.7	103	1.4
10	218	6.34	2	4	0.289	7.4	1.33	11.1	0.22	2.7	63	3.3
11	322	7.28	4	7	0.298	0.4	1.17	2.8	0.26	0.3	96	0.4
12	110	4.98	2	2	0.365	10.3	1.00	0.0	0.37	10.3	40	1.2
13	641	8.19	11	21	0.400	1.5	1.17	0.8	0.34	1.1	256	5.7
14	495	4.35	2	9	0.418	2.2	1.00	0.0	0.42	2.2	207	5.1
15	374	4.35	6	8	0.491	1.1	1.14	2.0	0.43	1.4	184	1.5
16	157	2.91	2	8	1.748	308.4	2.67	277.8	0.66	43.4	275	71.8
Total stratified	35,622		166	130							2,452	145.9
Unstratified	35,441	4.21	32	124	0.083	>0.0	1.16	0.3	0.07	>0.0	2,948	367.6

¹Areas were approximated by straight line integration, thus minor discrepancies exist between sum of strata and total unstratified region.

inside of the pack ice; those of the ribbon and spotted seals were in the ice front itself.

Within the ice front, the spotted seals showed essentially three centers of abundance, in the southeastern, central, and southwestern sectors, whereas the ribbon seals were centered primarily in the west-central front zone (Fig. 19). In the inner pack ice, walrus were centered in the southeastern and north-central sectors, as had been shown previously by Kenyon (footnotes 5, 6).

The ringed seals were abundant in patches in the southwestern, northern, and southeastern sectors, mainly outside of the areas inhabited by the walrus. Bearded seals were most abundant in the southeastern, central, and northern sectors in and around the areas occupied by both the walrus and the ringed seals.

Compartmenting the surveyed area into six sectors, in which the survey effort was approximately comparable, we find that the ringed and bearded seals and walrus all showed their greatest abundance within the same (north-central) sector, and that both the ribbon and the spotted seal were most abundant in the west-central sector (Table 7). Although walrus and spotted seals were the two most frequently sighted species in the southeastern sector, each was more abundant in another part of the Bering Sea pack ice; similarly,

ribbon and ringed seals showed centers of abundance in the southwestern sector, but each was more abundant elsewhere.

DISCUSSION

The winter pack ice of the Bering Sea is by no means a uniform covering over the water, nor is the marine environment beneath it of uniform physical or biotic composition (Hood and Calder 1981). A wide variety of ice and aquatic habitats is available here, as is indicated by the unusual diversity of marine mammals inhabiting this region (Fay 1974). Because the margin of the ice was exceptionally far south in April 1976, extending to the edge of the continental shelf in the eastern Bering Sea and well beyond it in the west, the variety of habitats available to these mammals was even greater than normal. The partitioning of those habitats among the five species of ice-associated pinnipeds, therefore, probably was about maximal at that time.

The actual densities of pinnipeds in each sector of the ice certainly were greater than could be estimated from the counts along the survey strips, for only the animals that were lying on the ice were included in the computations. At all times, some proportion of the animals is in the water, swimming, feeding, or courting, where only a small proportion of them can be seen from the air. For this reason, each of the estimates of abundance certainly is very conservative, and the degree of conservatism differs greatly between species. For example, the probability is very high that a much lower proportion of the ringed seals than of any other species was on the ice, and a much higher proportion of walrus and spotted seals. Therefore, comparison of estimated densities among the five species within any given region or overall is not a reliable indicator of their relative abundance. Nevertheless, the estimated densities of a given species in different areas probably can be relied on as approximations of that species' relative abundance in each area.

Nearly all of the walrus which were sighted during the several aerial surveys described in this and earlier reports were situated in the north-central sector near St. Lawrence Island, and in the southeastern sector, between Bristol Bay and the Pribilof Islands. During the winter, these are major areas of ice formation and divergence,

Table 7.—Comparative abundance of pinnipeds sighted (no./min.) in relation to location in the Bering Sea pack ice, April 1976.¹

Pinniped	Sector of pack ice ²					
	South-eastern	East-central	West-central	South-western	North-central	North-western
Walrus	1.2-76.0	1.2-8.2	0.2- 1.0	0	0.6-197.5	0.4-1.3
Ringed seal	0.2- 1.6	0.2-0.8	0.2	0.2- 1.0	0.2- 4.4	0.2-0.6
Ribbon seal	0.2- 0.6	0.2-0.9	0.2- 6.0	0.2- 1.2	3.0	0
Spotted seal	0.4-22.0	0.4-7.0	0.4-24.5	0.5-11.9	0	0.4
Bearded seal	0.2- 2.2	0.2-0.9	0.2- 3.0	0.5- 1.0	0.2- 5.0	0.2-3.0

¹Data from all surveys, combined.

²Southeastern = long. 160° to 168°W, south of lat. 61°N; East-central = long. 168° to 174°W, south of lat. 61°N; West-central = long. 174°W to 176°E, south of lat. 61°N; Southwestern = long. 176° to 162°E; North-central = long. 168° to 176°W, north of lat. 61°N; Northwestern = long. 176°W to 178°E, north of lat. 61°N.

where leads and polynyas are plentiful (Burns et al. 1980¹²), and the benthic food supply presumably is adequate. Ringed and bearded seals, like the walruses, also were situated for the most part well north of the southern border of the pack ice, but they were more widely distributed, presumably because of their greater ability to make and maintain breathing holes in even the denser parts of the pack. The distribution of the bearded seals, in general, overlapped those of both the walruses and the ringed seals to a high degree but extended also into a broad sector of the western ice where neither of the other two species was sighted. Earlier, Braham et al. (1977¹³) had indicated that the mean group size of bearded seals in the northern Bering Sea was significantly larger than in the southeastern sector, implying that more of the northern animals were pairs of adults. Reevaluation of those data, however, indicates no difference between sectors.

Most of the ringed seals sighted during our surveys probably were immature or nonbreeding individuals, for the breeding adults in this month (April) mainly inhabit the shorefast ice and haul out only in lairs beneath the drifted snow (Fedoseev 1965; Burns 1970; Smith and Stirling 1975). The presence of these seals in considerable numbers in the southeastern sector of the Bering Sea pack ice is reported here for the first time. Previous information from that region by Kosygin (1966) from shipboard surveys in April 1962 and 1963, indicated that they were absent there. Their regular presence was confirmed, however, by several shipboard sightings from the icebreaker CGC *Glacier* in April 1971 (J. J. Burns, unpubl. data) and by numerous shipboard sightings from the ZRS *Zvyagino* in February-March 1981, during joint Soviet-American investigations of marine mammals.¹⁴

The predominant inhabitants of the outer 200 km of the pack, all across the Bering Sea, were the ribbon and spotted seals, whose preferred pupping habitat appears to be in the "front" zone, just inside the southern edge of the pack ice (Burns et al. 1972, footnote 12). The front is made up of more or less rectangular floes, about 10 to 20 m in diameter, which are formed from larger fields of ice by the action of sea swells. Ribbon seals were found throughout the front, from Bristol Bay to Karaginskii Gulf, but were most abundant in the west-central sector, over deep waters south of the continental shelf. Spotted seals also were widely distributed in the front but tended to be concentrated only in those parts which were situated over waters about 200 m or less in depth, i.e., along the Koryak-Kamchatka coast, in the central sector, and in southern Bristol Bay. A high proportion of those in Bristol Bay appeared to be immature and nonbreeding animals, with which were mixed a few harbor seals.

Pinnipeds were scarce to absent in the ice over most of the eastern Bering Sea shelf, north of lat. 60°N, as noted in previous surveys by Kenyon (footnotes 5, 6). That region, which comprises most of the inner shelf oceanographic domain, appears to be shunned in part because of its dense, heavy ice cover (McNutt 1981); it may be little used also because of poor secondary production of zooplankton, ichthyoplankton, and benthos on which forage fishes and the pinnipeds themselves might feed (Alton 1974; Motoda and Minoda 1974; Waldron 1981).

¹²Burns, J. J., L. H. Shapiro, and F. H. Fay. 1980. The relationships of marine mammal distributions, densities, and activities to sea ice conditions. Final report, R. U. 248/249, 172 p. Outer Continental Shelf Environmental Assessment Program, NOAA Environ. Res. Lab., Boulder, Colo.

¹³Braham, H. W., R. D. Everitt, B. D. Krogman, D. J. Rugh, and D. E. Withrow. 1977. Marine mammals of the Bering Sea: Preliminary analysis of distribution and abundance, 1975-76. Processed rep., 90 p. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, Seattle, WA 98115.

¹⁴F. H. Fay, Associate Professor, Institute of Marine Science, University of Alaska, Fairbanks, AK 99701, pers. commun. April 1981.

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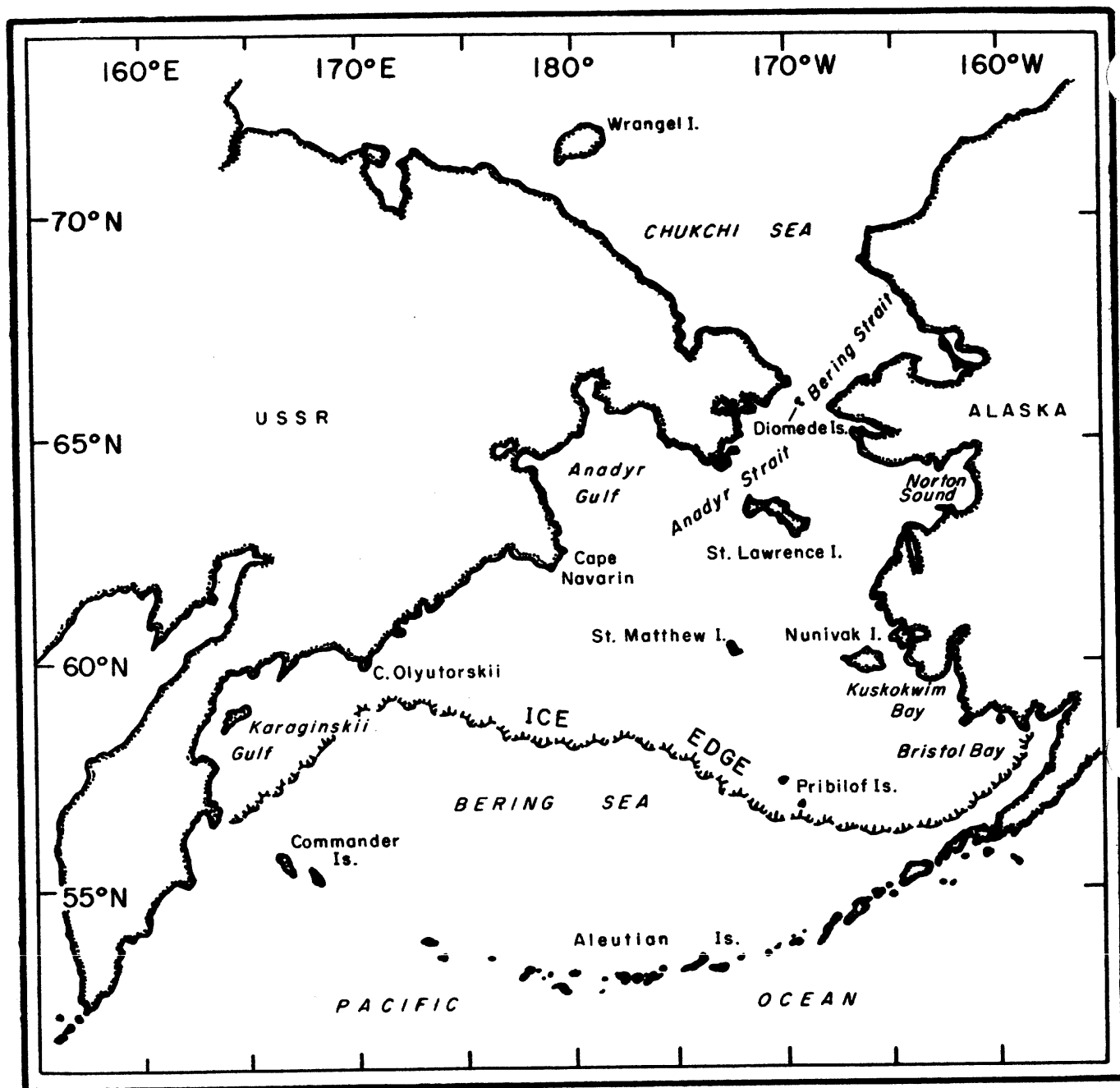


Figure 1.— Study area in which cooperative Soviet-American aerial surveys were conducted. Ice edge is approximate maximum in Bering Sea in April 1976.

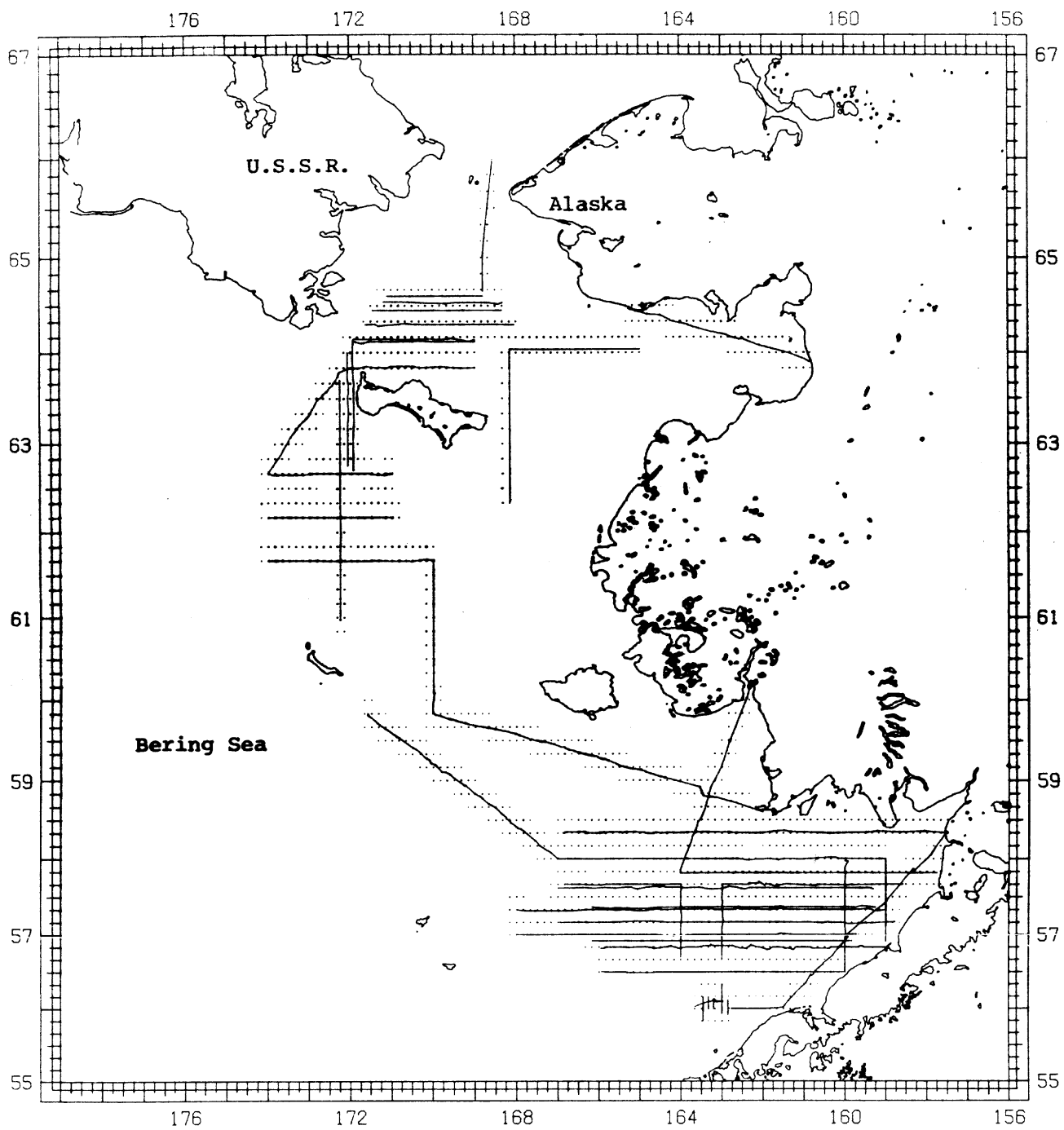


Figure 2.— Computer plot of aerial survey strips flown over eastern Bering Sea by NMFS scientists in April 1976. Dots depict corners of 10×10 minute latitude by longitude cells which were overflown by the aircraft.

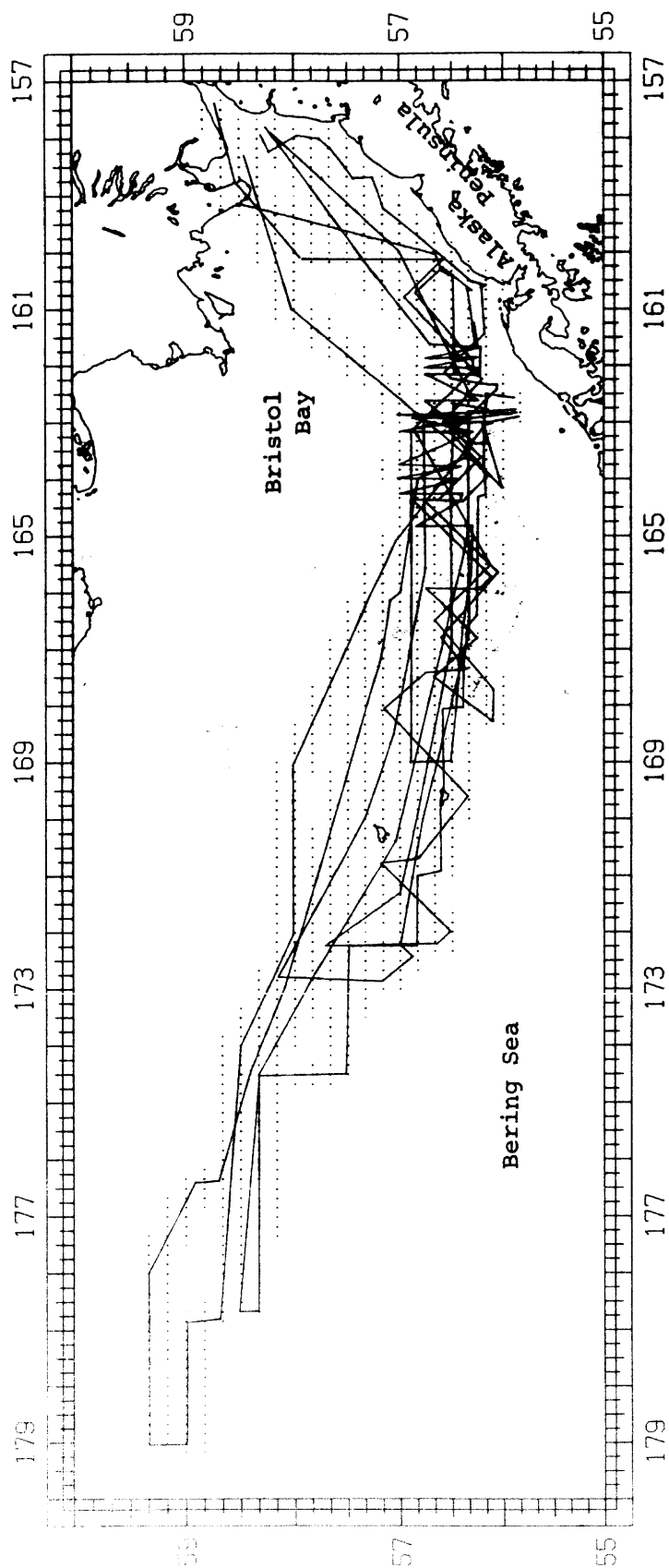


Figure 3.—Computer plot of aerial survey strips flown in southeastern Bering Sea by ADF&G scientists in April 1976. Dots depict corners of 10×10 minute latitude by longitude cells which were overflowed by the aircraft. The southern limit of surveys marks the southern edge of the pack ice; the northern limit of surveys approximates the inner margin of the ice front.

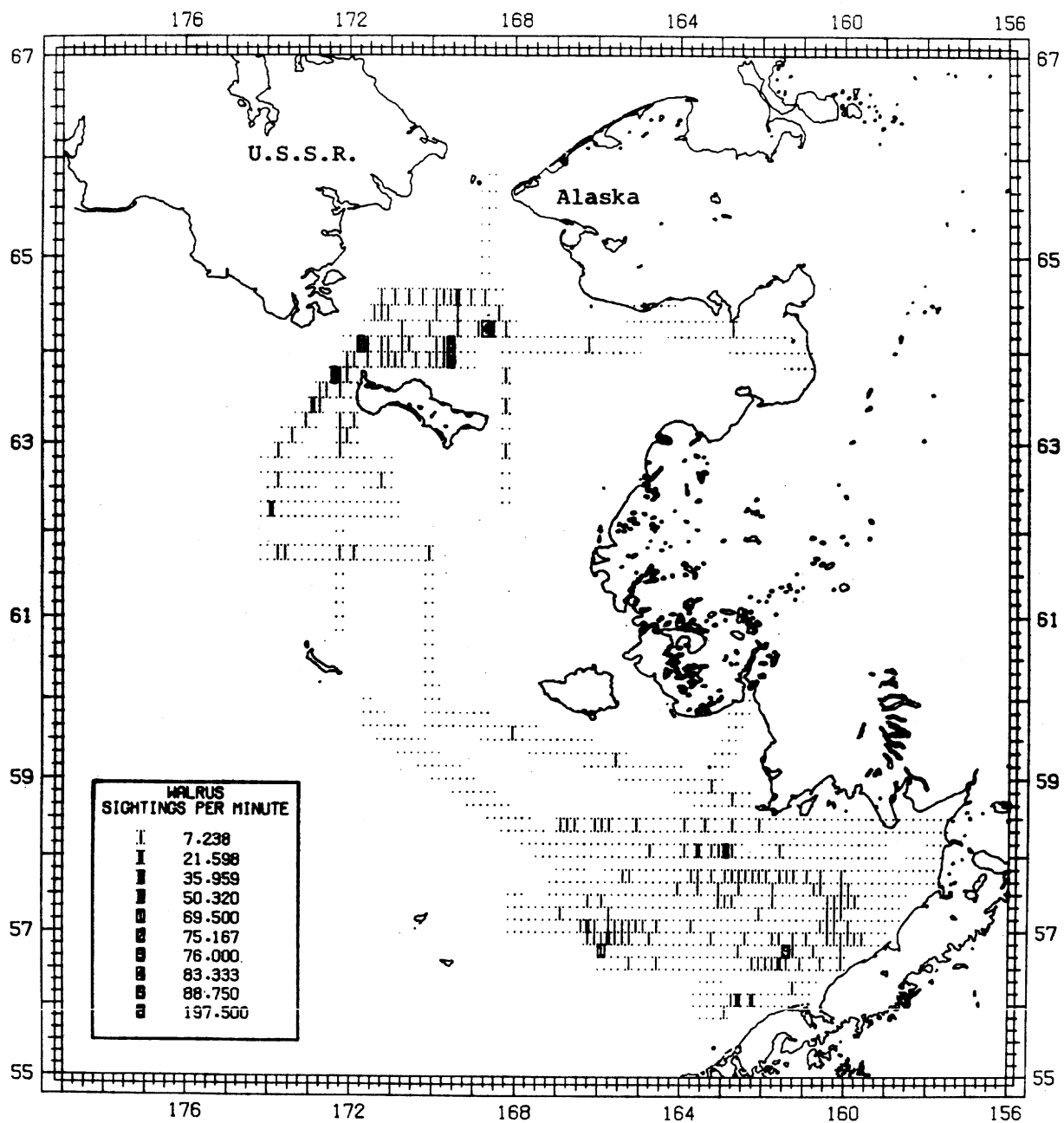


Figure 4.—Computer plots of walrus density from NMFS aerial surveys 6-23 April 1976.

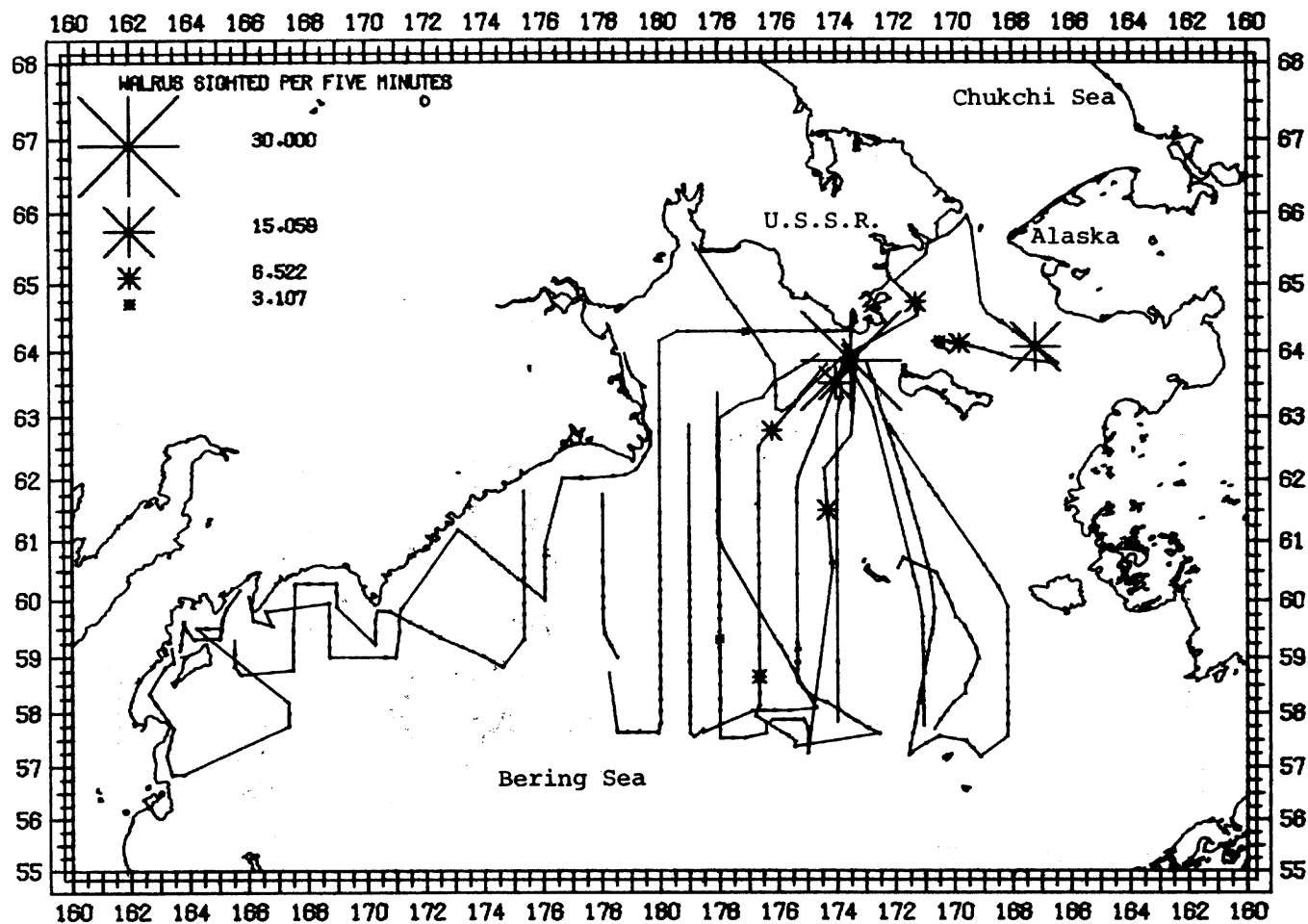


Figure 5.—Computer plots of walrus density in relation to aerial survey strips from TINRO aerial surveys, 12-26 April 1976. Star symbols are centered on positions where walrus were observed.

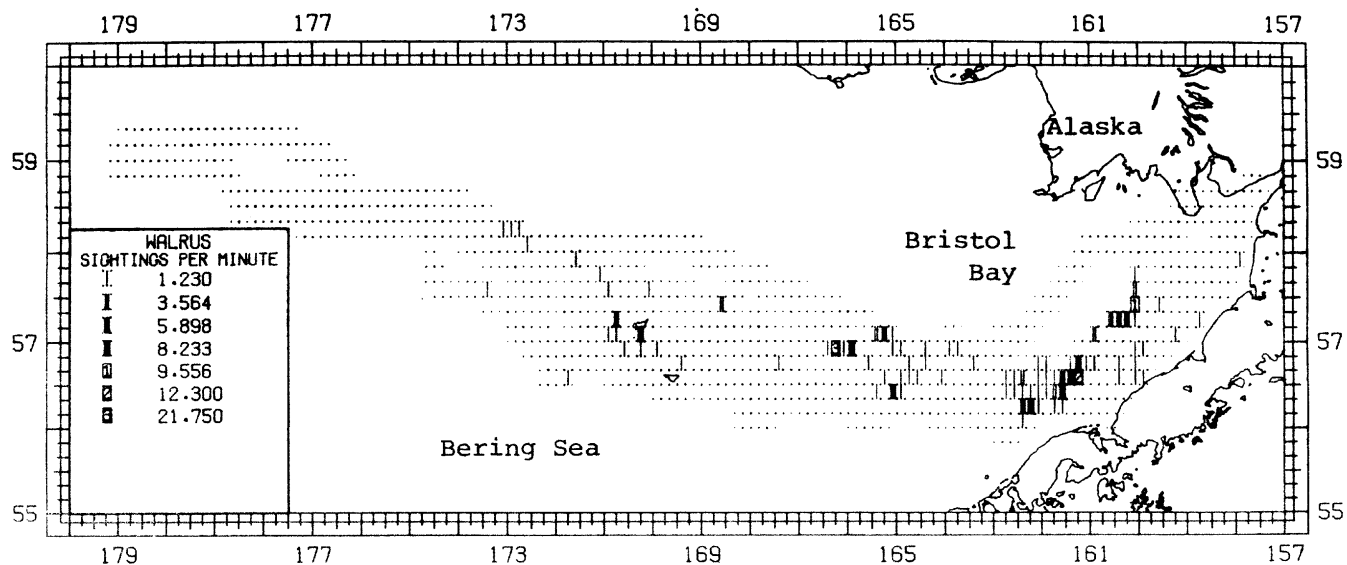


Figure 6.—Computer plots of walrus density from ADF&G aerial surveys, 8-23 April 1976.

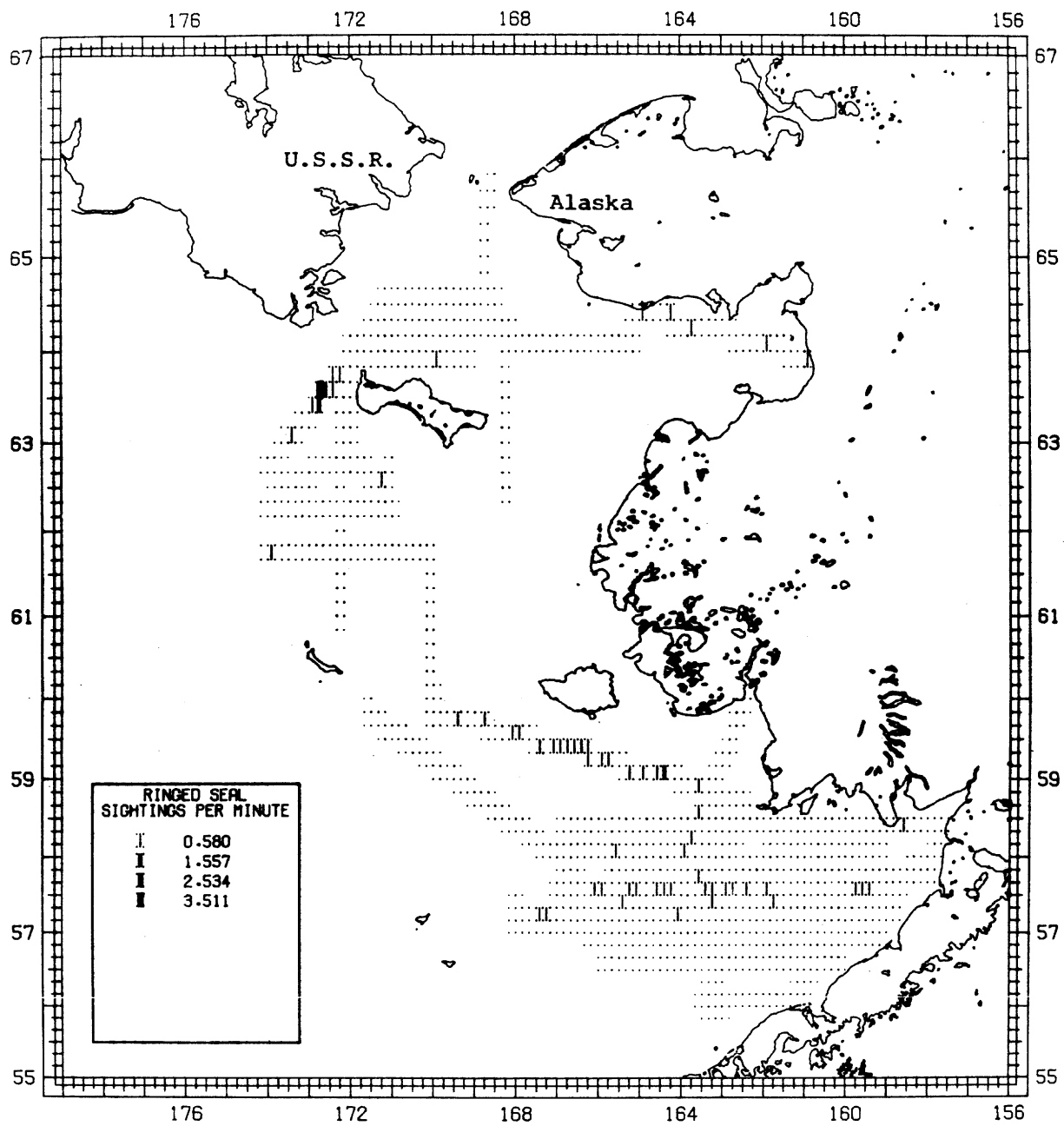


Figure 7.— Computer plots of ringed seal density from NMFS aerial surveys, 6-23 April 1976.

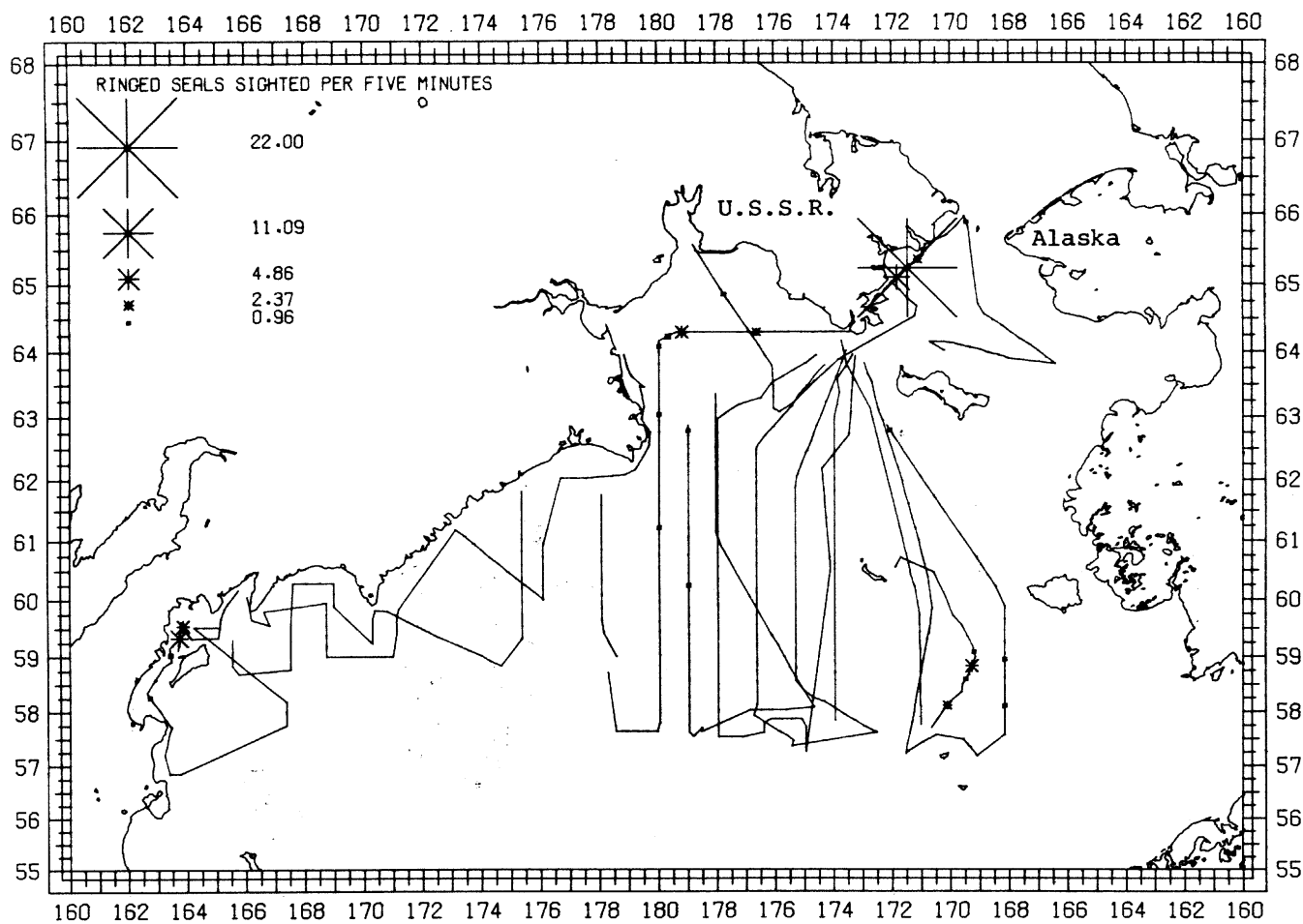


Figure 8.—Computer plot of ringed seal density from TINRO aerial surveys, 12-26 April 1976.

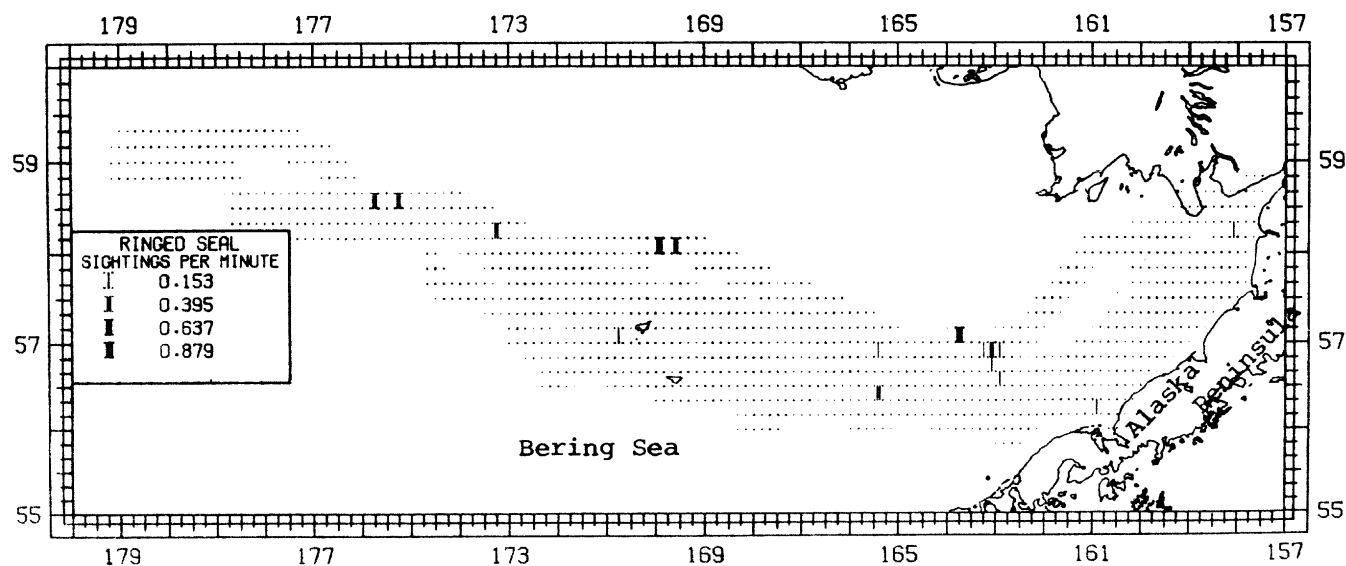


Figure 9.—Computer plot of ringed seal density from ADF&G aerial surveys, 8-23 April 1976.

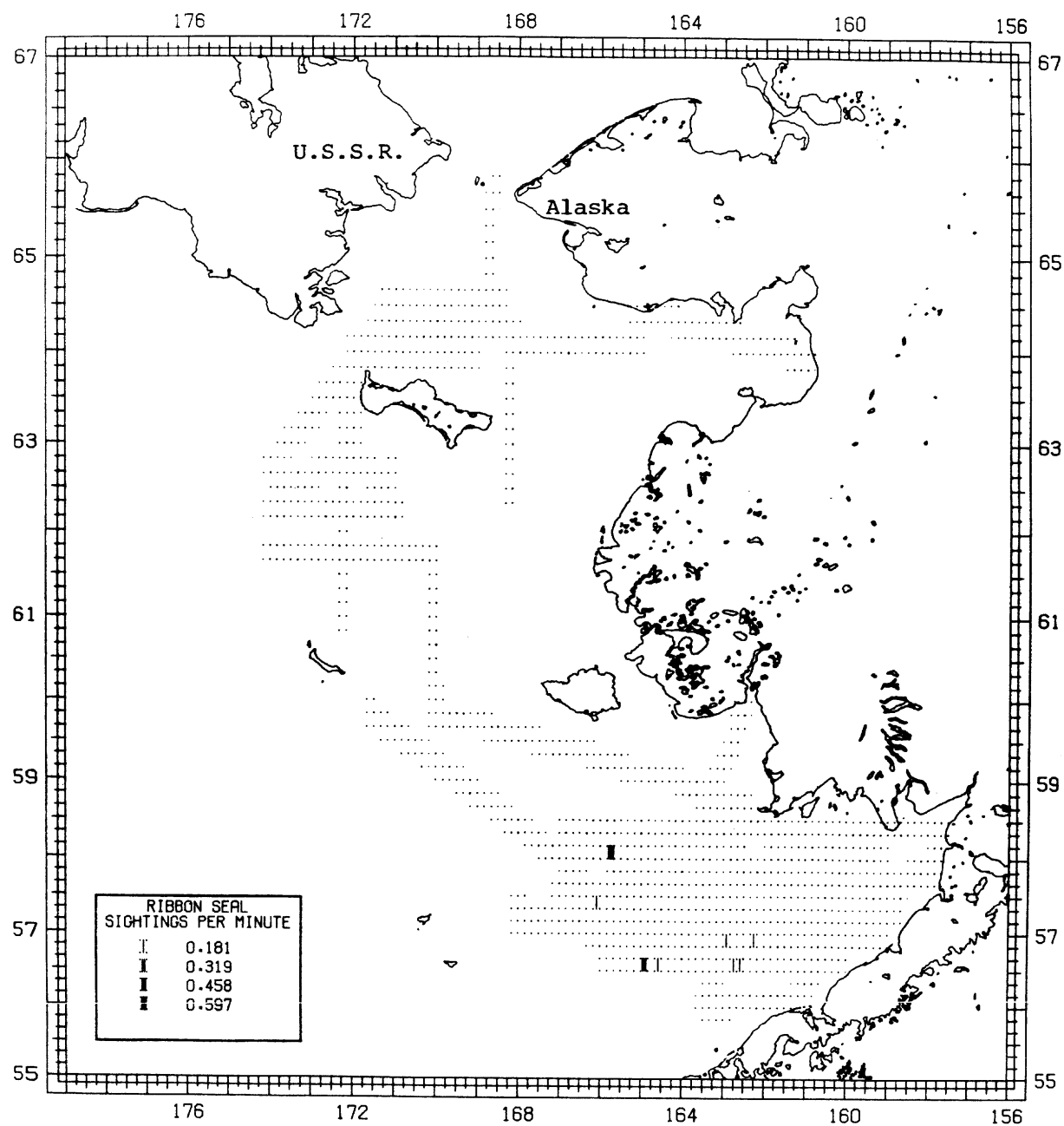


Figure 10.—Computer plot of ribbon seal density from NMFS aerial surveys, 6-23 April 1976.

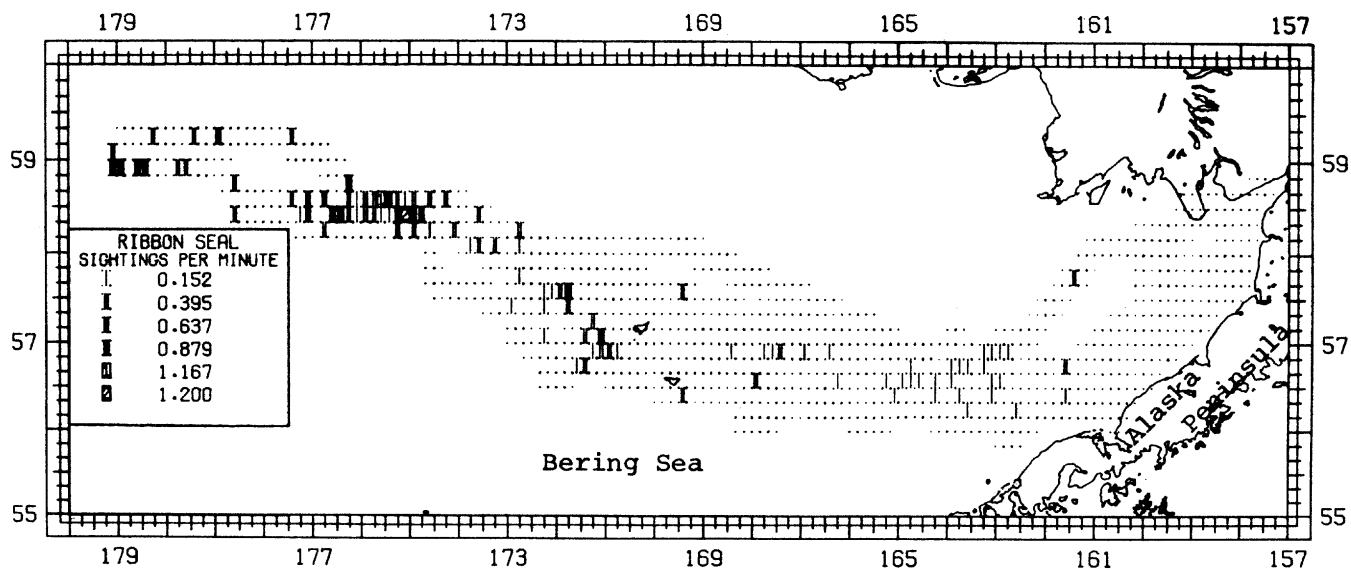


Figure 11.—Computer plot of ribbon seal density from ADF&G aerial surveys, 8-23 April 1976.

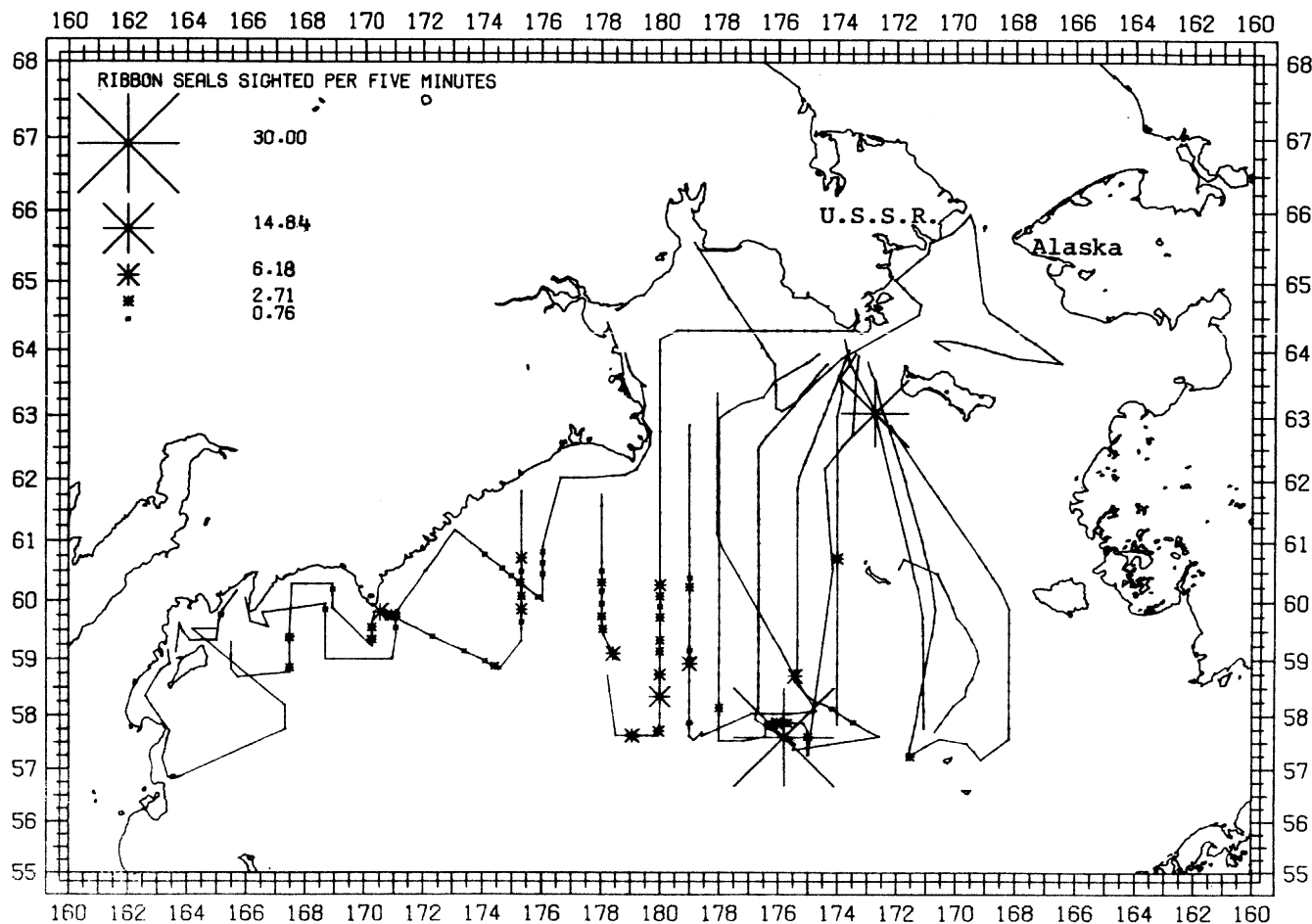


Figure 12.—Computer plot of ribbon seal density from TINRO aerial surveys, 12-26 April 1976.

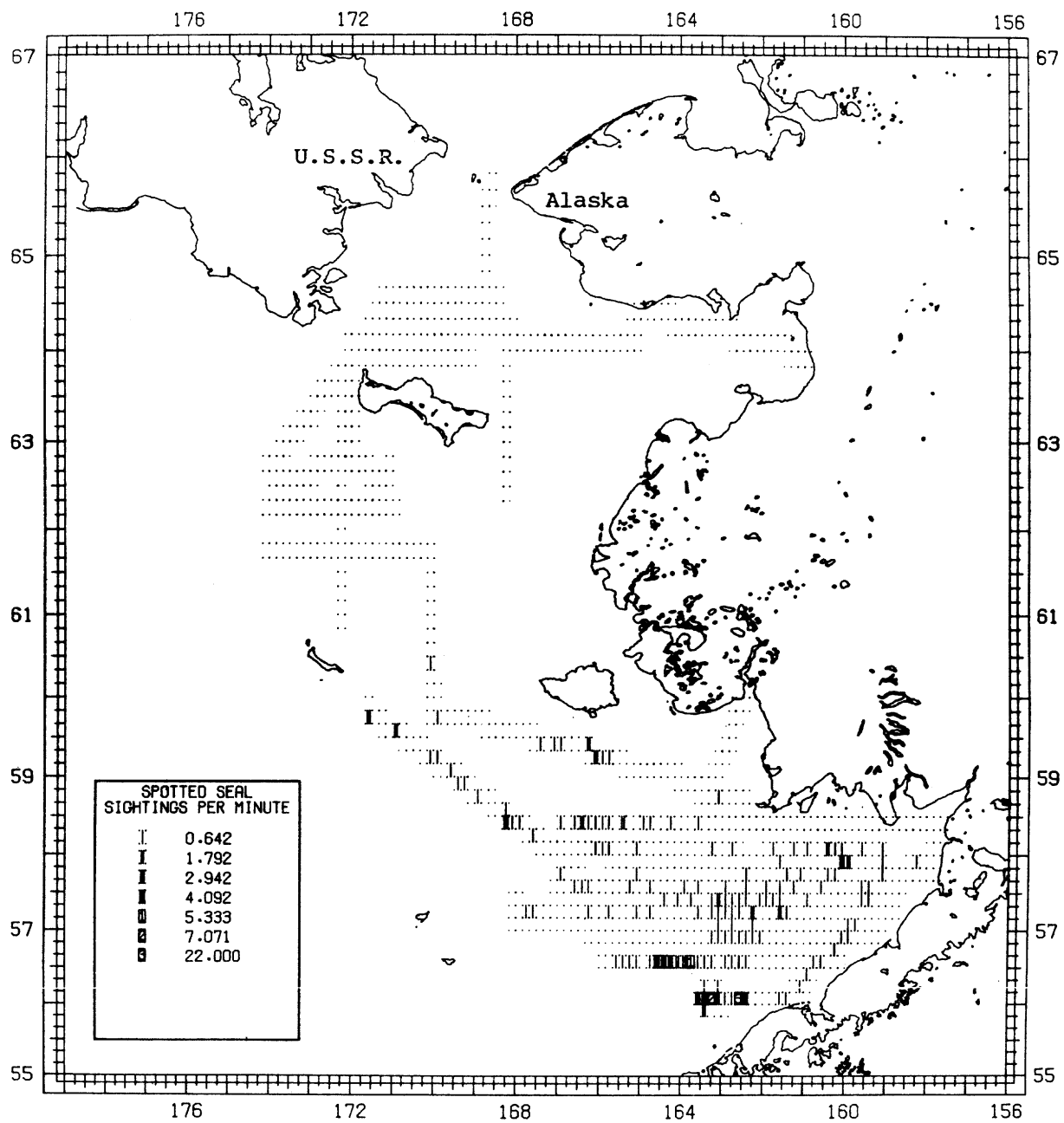


Figure 13.—Computer plot of spotted seal density from NMFS aerial surveys, 6-23 April 1976.

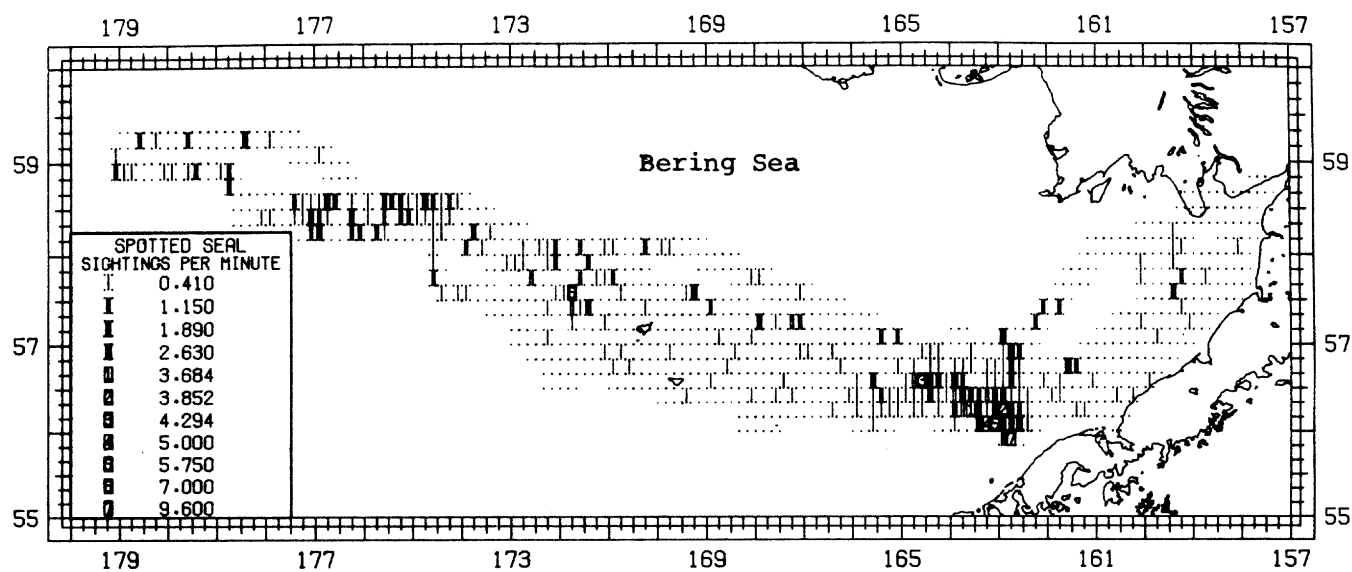


Figure 14.—Computer plot of spotted seal density from ADF&G aerial surveys, 8-23 April 1976.

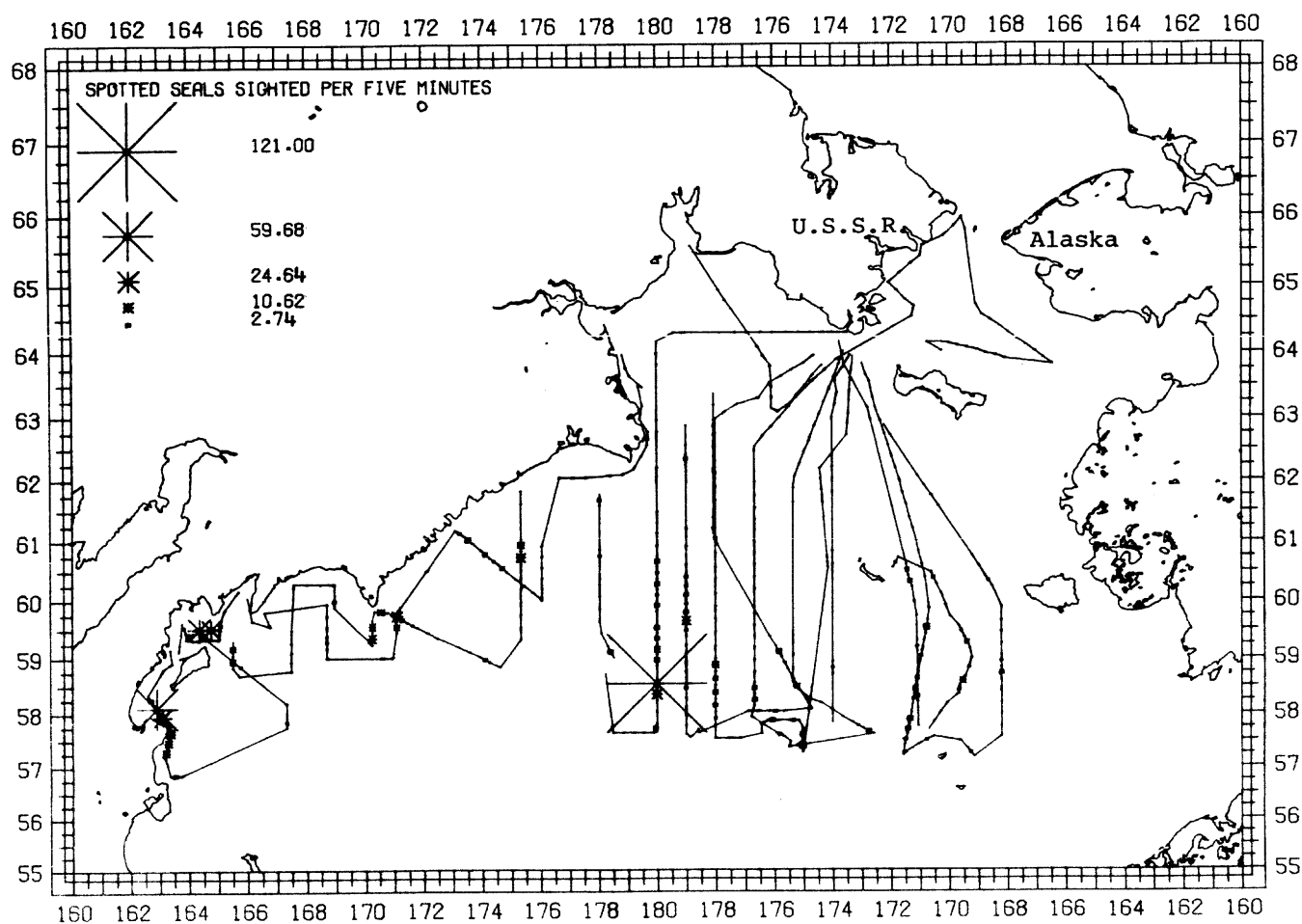


Figure 15.—Computer plot of spotted seal density from TINRO aerial surveys, 12-26 April 1976.

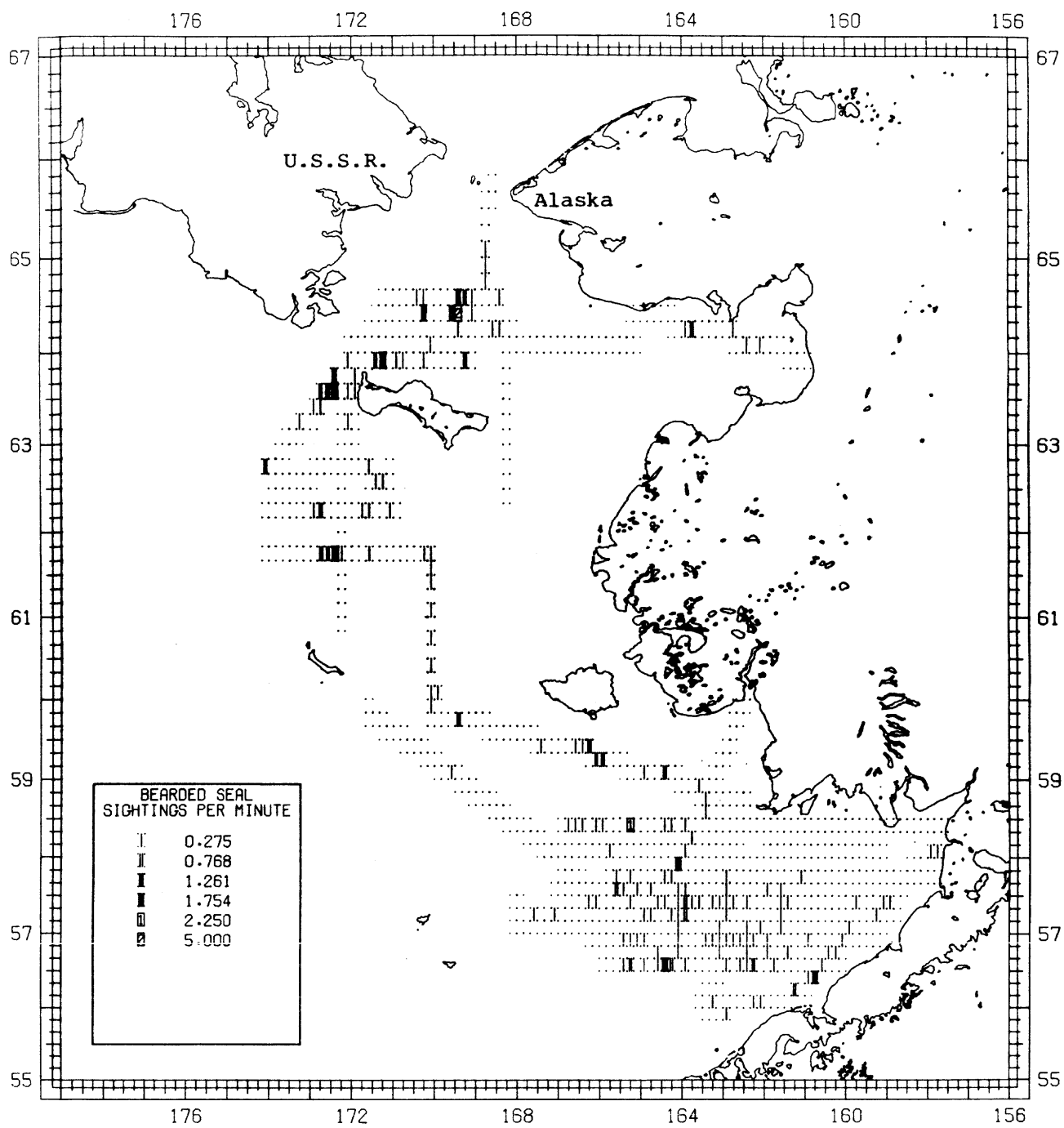


Figure 16.— Computer plot of bearded seal density from NMFS aerial surveys, 6-23 April 1976.

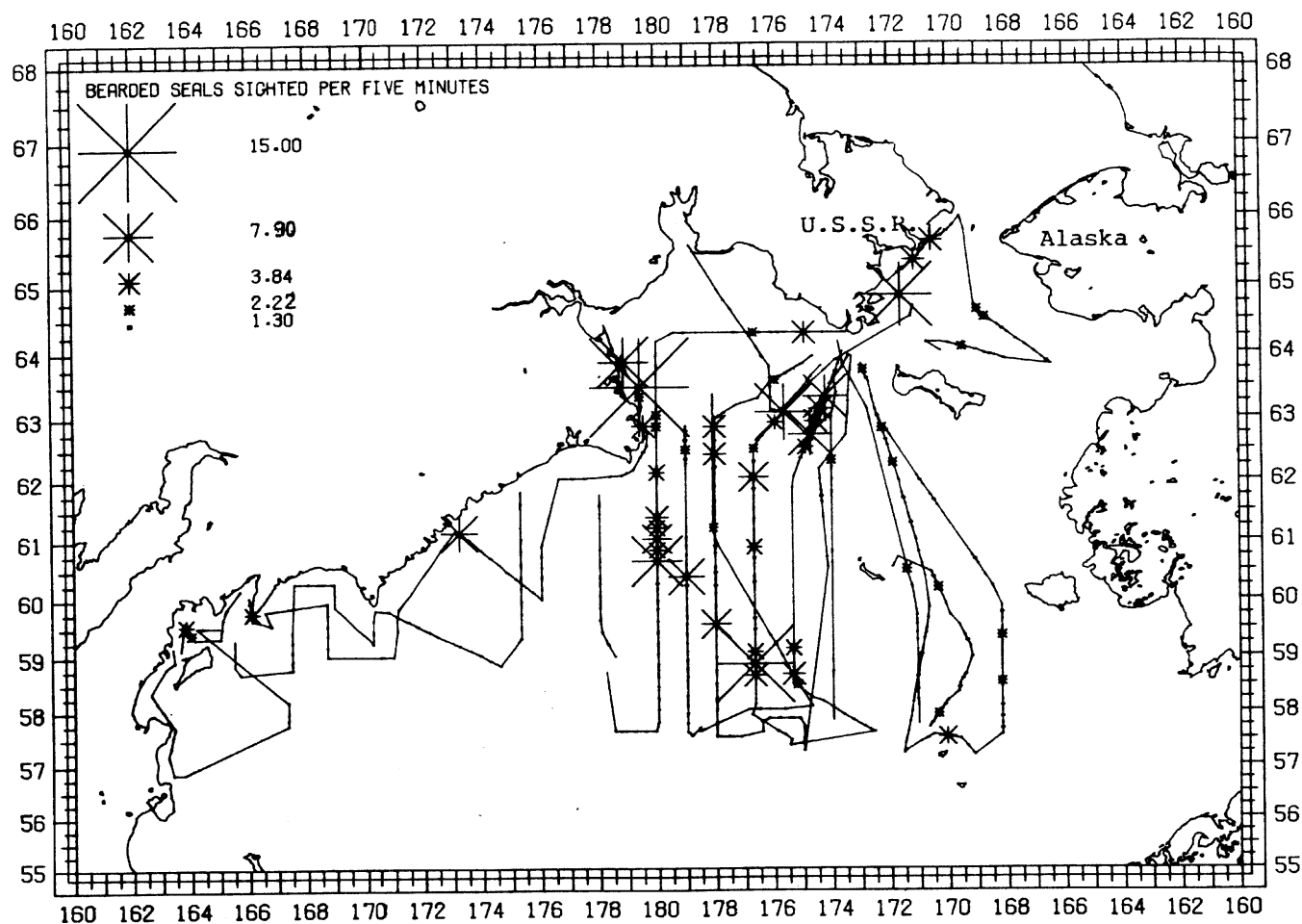


Figure 17.—Computer plot of bearded seal density from TINRO aerial surveys, 12-26 April 1976.

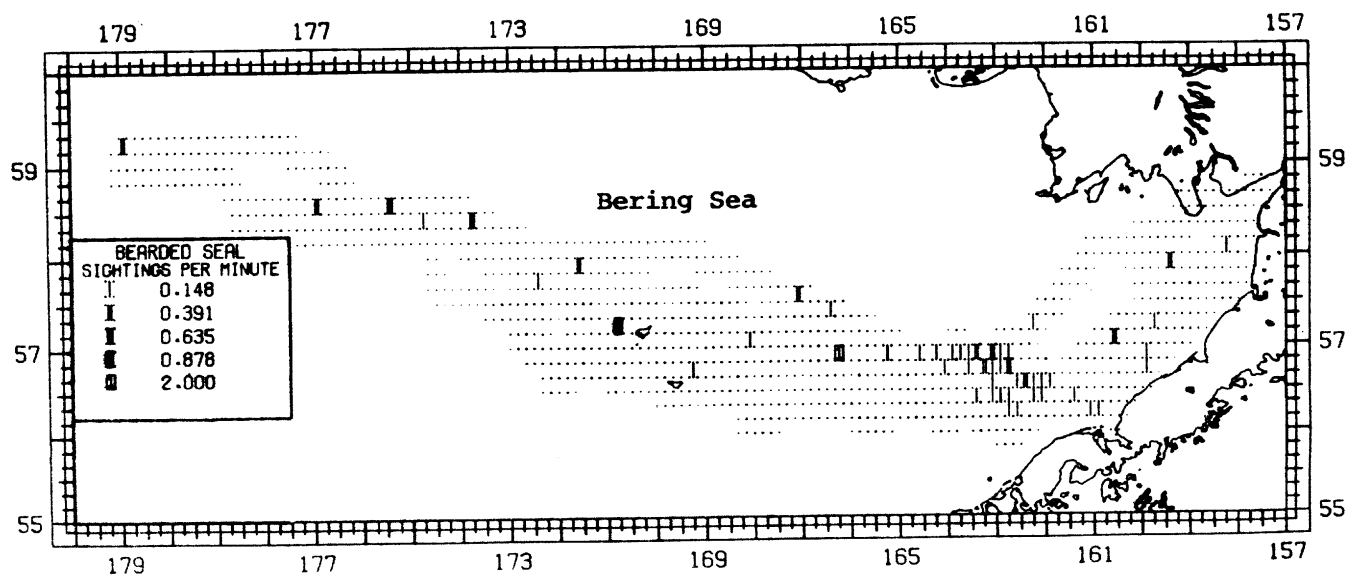


Figure 18.—Computer plot of bearded seal density from ADF&G aerial surveys, 8-23 April 1976.

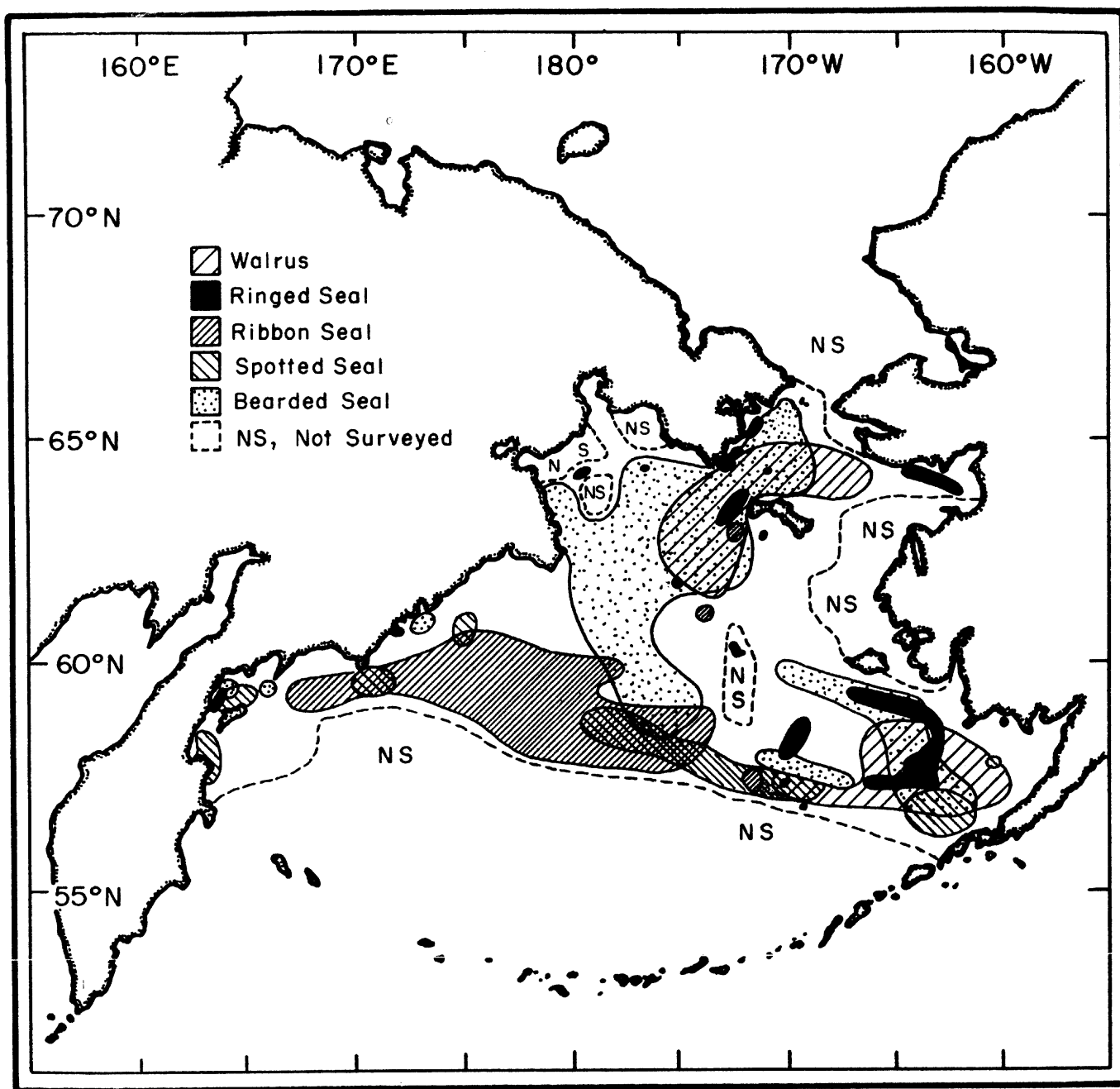


Figure 19.—Centers of abundance of ice-associated pinnipeds in the Bering Sea pack ice, based on numbers sighted per minute during NMFS, ADF&G, and TINRO aerial surveys, 6-26 April 1976. Areas indicated for walrus and spotted seal include only those where at least 2/min were sighted, and for ringed, ribbon, and bearded seal, at least 0.5/min.