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Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

Volume 31 May 1985

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National Oceanic and Atmospheric Administration
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OUTER CONTINENTAL SHELF
ENVIRONMENTAL ASSESSMENT PROGRAM

FINAL REPORTS OF PRINCIPAL INVESTIGATORS

VOLUME 31

MAY 1985

U.S. DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
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OFFICE OF OCEANOGRAPHY AND MARINE ASSESSMENT
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Outer Continental Shelf Environmental Assessment Program

Final Reports of Principal Investigators

VOLUME 31 MAY 1985

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NOTE: The "Main Body" of this report was published in Volume 11 (1981) of this series, pages 175-487.

ECOLOGICAL STUDIES IN THE BERING STRAIT REGION,
APPENDICES I-X

by

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Final Report
Outer Continental Shelf Environmental Assessment Program
Research Unit 237

1982

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APPENDIX I.
GEOLOGICAL SETTING

(Precis of C. H. Nelson, D. M. Hopkins, and D. W. Scholl 1974).
With Comments on Landforms and the Implications for
Seabirds and Waterfowl.

A. Geological History and Topography

The Bering Strait Region is a geographical area of the Continental Shelf bordered on the north and south by transcurrent faults. These transcurrent faults reflect the release of energy associated with stresses of movements of crustal plates. The faults seem to have played important roles in the formation and destruction of intercontinental land connections which make this region important biologically.

Major seabird breeding sites are associated with these transcurrent faults at the edges of the Bering Strait Region. One set of faults runs along the northern border of the Gulf of Anadyr and along Saint Lawrence Island. Another runs from Golovin north into the center of the Seward Peninsula and westward to the area around King Island. Another parallels the narrow part of the Bering Strait and runs along the north shore of the Chukotski Peninsula. Another runs northwestward from Cape Thompson/Cape Lisburne (the Lisburne Peninsula).

The field of faults runs along a flex in the continental structure which is concave toward the Arctic Ocean. Reverse flexes, concave to the Pacific Ocean, occur on both ends of the flex, one in Siberia and one in Alaska. These flexes seem to result from bending in Siberia relative to North America as a consequence of rifting in the Arctic and Atlantic Oceans. Another consequence of this bending may have been a shift of the subduction zone from the continental margin in the central Bering Sea to the Aleutian Trench.

This evidently happened at the beginning of the Cenozoic, when Eastern Siberia and the northwest part of North America began to rub against the Pacific Plate. The Aleutian Basin, south of the Continental Shelf and north of the Aleutian Islands, is a trace of the abyssal sea floor that existed prior to the meeting of the Pacific Plate with the North American/Eastern Siberian Plate.

The fundamental processes of metamorphosis and mineralization associated with plate tectonics have been followed by glacial and subaerial weathering, erosion, and shoreline processes which changed with oscillations in sea level. These have combined to produce the deposits of heavy metals for which the region is well known. Placer and mother-lode mines for tin, gold, mercury, and platinum occur in the Seward Peninsula. Mercury, chromium, and copper are found in beaches on the south shore of the Seward Peninsula in concentrations high enough to be toxic, but are not high enough for present techniques of extraction to be economically worthwhile.

The location of gold placers at Daniels Creek next to the seabird cliffs at Bluff symbolizes the impact of special geological events on biology and economics, hence contemporary problems. On the one hand, mineralization followed by frost-riving soil creep and debris transport in spring freshets has deposited gold-bearing gravels in highly economical concentrations; these gravels are associated with Pleistocene beach levels. The nearly vertical sea cliffs on which the seabirds nest were produced by metamorphosis of sedimentary rocks, frost riving and plucking, in combination with undermining by the sea and removal of debris which collapses from the rock faces. Outcrops of similar slightly metamorphosed rocks occur in the friable cliffs at Cape Denbigh. Cliffs made of rocks of several stages along the spectrum of metamorphosis provide nesting sites for seabirds at Cape Lisburne and Cape Thompson.

Vulcanism also results from the crustal stresses which produce metamorphosis and transcurrent faults. Vulcanism is widespread in the Bering Strait and has been important in producing islands and cliffs for the major seabird cities.

Little Diomede, King Island, and Saint Lawrence Island were produced by volcanic activity. For example, the sea cliffs made of broken lava which flowed north from the mountains behind Savoonga provide sites for the thousands of kittiwakes, murres, and cormorants which nest there. The same structure supplied nesting cliffs on tiny Egg Island in southeastern Norton Sound.

Frost riving, active in the brittle volcanic material, is the source of frost-moved rubbles which characterize the mountain slopes of many Alaskan mountains. Puffins and auklets nest in rubble on the tongues of lava protruding east and west of Savoonga, on Sevuokok Mountain near Gambel, and on the upper slopes of the mountains between Bunnell Capes and Southwest Capes on Saint Lawrence Island. The rubble slopes on the top of King Island and on Little Diomede provide miles of tunnels and caverns where auklets nest. Although similar rubbles are found on the west side of Sledge Island and on Besboro Island, a trivial number of nesting auklets or none occur in the low saline waters of Norton Sound.

Mountain glaciers occupied the higher places along the Siberian and Alaskan Peninsulas during the Pleistocene, but lack of rain and snowfall kept interior Alaska and west coastal Alaska free of glaciers. During most of the Pleistocene, the outlet of Alaska's major river, the Yukon, lay north of Saint Lawrence Island and emptied into the Chirikov Basin. In the most recent Pleistocene, it emptied south of Saint Lawrence Island over the edge of the Continental Shelf through one of the deepest submarine canyons known. Today it empties into the southeastern corner of Norton Sound and dictates the characteristics of the Alaskan Coastal Water which occupies Norton Sound and flows northward along the Alaskan shore through the Bering Strait.

It would be an understatement to suggest that deflection of this river water to flow southwest over the Continental Shelf into the deep Bering Sea between Saint Lawrence and Saint Matthew Islands would mean drastic changes in climate and the nature of all water masses in the Bering Strait Region. The lowering of sea level which was also associated with glacial advances and resulted in the Bering land bridge would cut off completely the flow of Bering Sea water which now is a predominant influence on the water, flora, and fauna as far north as Point Barrow (see next section).

The intense frost action associated with periglacial climate has sharpened peaks, riven blocks off bedrock, and moved large volumes of mantle to form convex slopes. The riving of massive blocks and their breaking or reduction in size by frost has continued. Movement of rubble is kept active by "over-steepening" at the foot of slopes where storm surges and movements of sea ice remove stone blocks from the foot of cliffs.

The frost-riving, soil creep, and special pattern of river discharge in which spring freshets account for the majority of stream water flow are responsible for the rolling landscape, convex hill slopes, broad depositional slopes, and narrow debris-clogged valleys. The formation of gold placers is associated with frost-reduced sediments and periodic torrential river flow. River-run salmon are also characteristic of regions where large spring freshets contribute readily identifiable water masses into coastal shallows and make it easy for the fish to recognize their native stream. The large volume of sediments produced by frost riving and creep carried to the sea on freshets have produced a virtually uninterrupted beach extending from the Alaskan Peninsula to beyond the MacKenzie River.

The lagoons behind these beaches are important feeding and resting sites for gulls, terns, waterfowl, and shorebirds on migration and on breeding grounds. The productivity of these lagoons is very high and as a consequence the lagoons not only support the local waterfowl but also contribute nutrients to the shallow Alaskan Coastal Waters (Hood and Reeburgh 1974; Johnson 1956).

On the convex hillsides and thaw sinks produced under the regimen of frost action are many small ponds and large areas of marshy and boggy ground on the uplands. These are used as breeding grounds by waterfowl and shorebirds.

The coastal landscape provides redundancy of lagoons, wetlands, lakes, and marshes which combine to offer exceptionally favorable feeding and breeding habitat for waterfowl and shorebirds.

B. Bathymetry (see Main Body, Figure 10, p. 212)

The Bering Sea Basin is divisible into two major parts. The first is the deep basin north of the Aleutian Islands which is divided into an eastern and western part by Browers Bank. The second is the Alaskan-Siberian

Continental Shelf which extends northwest from Bristol Bay and the Pribilof Islands to Cape Navarin and north from south of Saint Matthew Island through the Bering Strait to the edge of the basin of the Arctic Ocean.

North of Nunivak Island and Saint Matthew Island the shelf water is relatively shallow, under 40 fathoms. Deep water marks areas of scouring by currents on the east and west ends of Saint Lawrence Island, 20-30 fathoms. The Alaskan Coastal Waters are shallower, under 20 fathoms, and under 10 fathoms in most of Norton Sound except for a deeper channel from Cape Nome to Bluff. The water is especially shallow off the Yukon Delta and in eastern Norton Sound and often takes on the brownish color of the muddy bottom.

Most of the Chirikov Basin is 20-25 fathoms deep, though within 20 miles of the Alaskan and Siberian shores it is under 20 fathoms. Thus the bottom topography on the Alaskan shore forms a curve at 10 fathoms, sweeping north from off Cape Romanzoff past the entrance to Norton Sound and northwest to the Bering Strait. Depths reach 30 fathoms in the east channel of the Bering Strait. Another sweeping curve at a depth of about 15 fathoms crosses the mouth of Kotzebue Sound, first northeast toward Kivalina and then northwest toward Point Hope. Depths are less than 10 fathoms in Kotzebue Sound.

The main body of the Chukchi Sea is between 20 and 30 fathoms deep. North of the Lisburne Peninsula water 10-20 fathoms deep is found towards Point Lay and Icy Cape.

C. Bottom Topography and Sediments. (Precis of: D.M. Hopkins, C.H. Nelson, R.B. Perry, and T.R. Alpha, 1976; and of D.A. McManus, V. Kolla, D.M. Hopkins, and C.H. Nelson, 1977).

The southeastern part of the Norton Basin is a shallow plain; the northwestern region is undulating and hummocky, and is more complex in the nearshore zone. Many relief features of the present sea bottom were formed by glacial, fluvial, and littoral (erosional and depositional) processes during Pleistocene low-sea-level episodes, but they have been modified by submarine erosion and deposition of the past few thousand years.

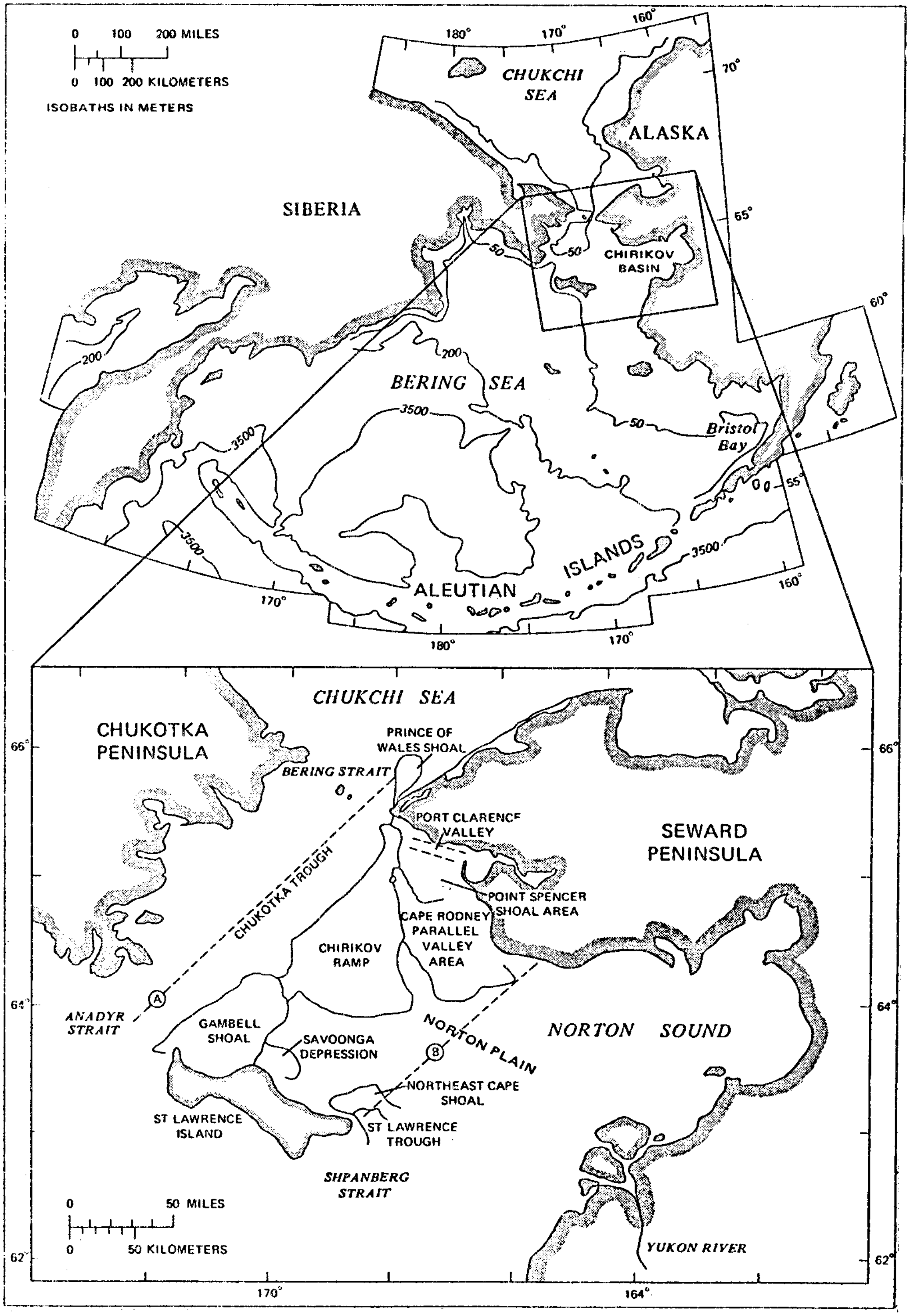
In the east, the monotonously flat Norton Plain has relief of about 2 meters, over distances of 30 kilometers. On the northwest, this plain grades into the Chirikov Ramp extending south and southwest from King Island. The slope of the Chirikov Ramp is steeper, twice that of the Norton Plain, and slopes to the west and northwest. Shallow, branching subparallel swales of 4 to 5 meters relief mark the slope toward the deeper water of the Chukotka Trough to the west (Figure 1).

The Chukotka Trough lies along the western edge of the region, against the Siberian shore. It is from 40 to 60 meters in depth; the bottom consists of hillocks, swales and closed depressions of 3 to 6 meters relief, for which there seems to be no coherent drainage pattern. The Trough ends on the north in a 10 meter high scarp at the southern entrance to the Bering Strait.

Distinct sea valleys mark the Bering and Anadyr Straits, and a less well-marked sea valley marks Shpanberg Strait. Shoal water marks the northern ends of these sea valleys: the Gambel Shoal is coarser material northeast of the Anadyr Strait, the Wales Shoal north of the Bering Strait, and the Northeast Cape Shoal at the northern end of Saint Lawrence Trough.

The King Island Valley, an almost linear valley 70 kilometers in length, extends south-southeast from King Island. It is 2 to 3 kilometers broad and 5 to 10 meters deep, and separates the Chirikov Ramp from the Cape Rodney Parallel Valley area which lies between Sledge Island and King Island. The bottom of the Parallel Valley area consists of broad, low ridges and clearly

Figure 1. From: McManus, Kolla, Hopkins and Nelson, 1977 (Figure 1). Index map of continental shelf in northern Bering Sea showing major physiographic units and sources. Sources include: U.S. Defense Mapping Agency Hydrographic Center charts, National Ocean Survey, Creager and McManus (1967), and McManus, Venkatarathem, Hopkins, and Nelson (1974).



marked shallow valleys of 5 meters relief with a northwest sweeping curve. Shoal areas consisting of constructional ridges 5 to 20 meters high, extend southwest and northwest of Point Spencer at the northern end of the Parallel Valley system. Port Clarence Valley, 4 to 5 kilometers broad and 4 meters deep, runs between the shoals and the abrupt scarp of the York Mountains.

The following is taken from the Abstract of "Distribution of bottom sediments on the continental shelf, northern Bering Sea", by McManus, Kolla, Hopkins and Nelson (1977). (See also, Figure 2.)

> Most of the sediment contributed to the northern Bering Sea today (modern sediment) is associated with the Yukon River runoff and the high-speed currents (30-40 cm/sec near the bottom) within the Alaskan Coastal Water, which sets northward along the coast through the Bering Strait into the Chukchi Sea. Most sediment is silt sized but includes some very fine grained sand and clay-sized material. The very fine sand extends northward across the mouth of Norton Sound, where it mixes on the west with relict Yukon silt that covers southern Norton Sound.
>
> Much of the Yukon silt enters Norton Sound, but there is only a thin accumulation there, except near the delta. The silt issues from the sound along the north side, where a silt deposit is in presumed dynamic equilibrium, thereby marking the dispersal path through a depression into the coastal current. The modern silt associated with the coastal current is considered a dynamic component of the bottom sediment, which otherwise consists of relict sand and gravel. The net transport of the silt is through the Bering Strait and into the Chukchi Sea.
>
> Impressed on the steady northward-setting current are irregular large-velocity fluctuations produced by tidal currents and partly by the wind regime. For the area as a whole, tidal currents and wind drift are believed to be more significant than wave drift or estuarine-type density circulation.
>
> Where the coastal current is strongest, the sediment is a relict or residual lag sand and gravel derived from glacial material or from metamorphic bedrock of Seward Peninsula. Under the slower Modified Shelf Water offshore of the coastal water, the bottom sediment also is relict Yukon sand, in part derived from glacial moraines. Modern sediments do not accumulate beneath the Modified Shelf Water, as they do beneath the coastal water.
>
> Northern Bering Sea was subaerially exposed during the period of eustatically lowered sea level (i.e. responding to the weight of continental ice) that coincided with the last glaciation. However, the surface sediments provide no indication that the Yukon River has ever drained northward into the Arctic Ocean. Until relatively recent time, the Yukon drained southward into southern Bering Sea. The river

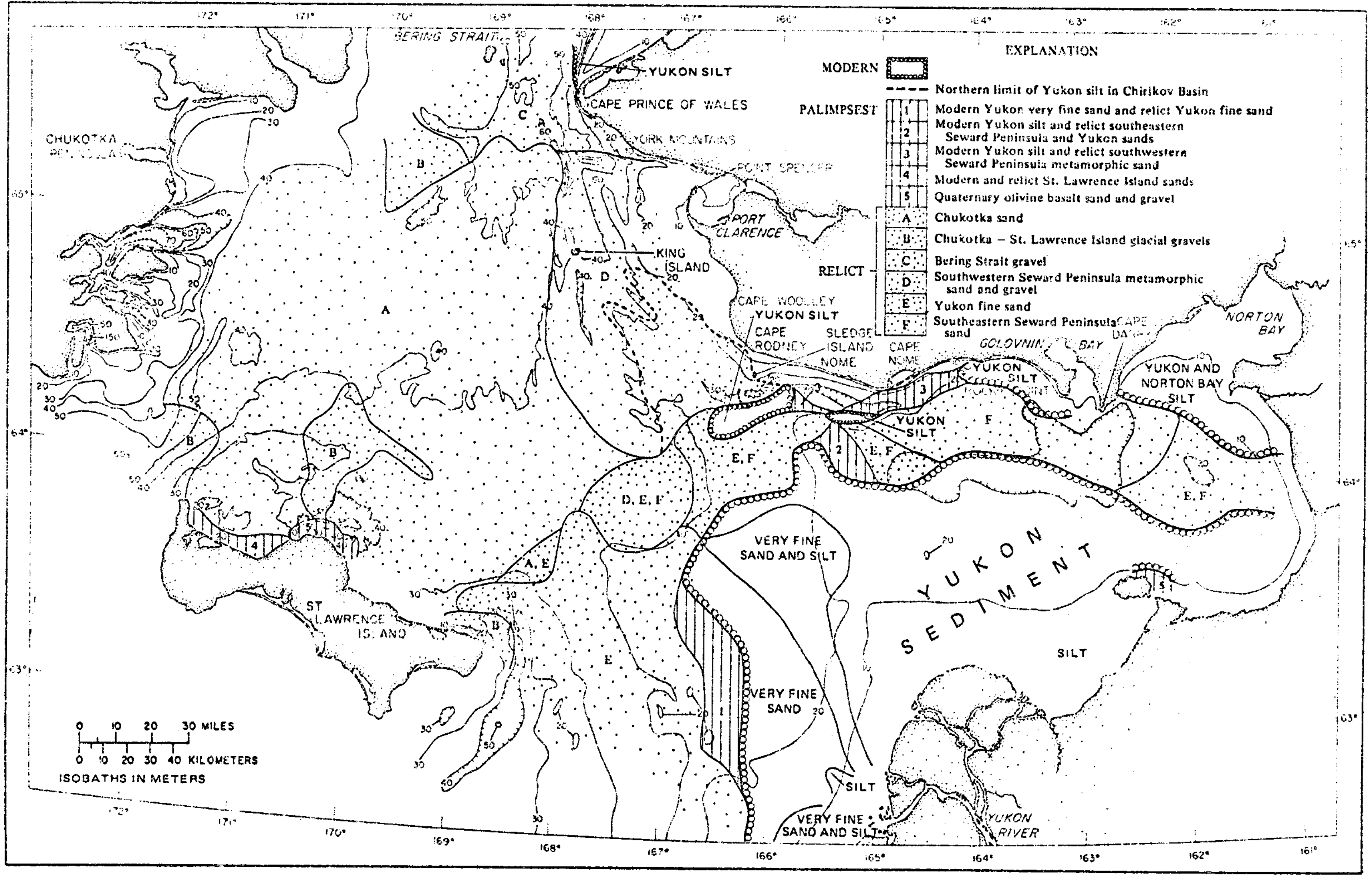


Figure 2. Bottom-sediment distribution. Relict sediments may include residual material. From McManus, Kolla, Hopkins and Nelson 1977, Figure 15; source of data is McManus, Venkatarathnam, Hopkins, and Nelson (1974).

mouth has been in its present northern position for only a geologically brief period.

Seaward size grading in relict sands is ascribed to the present day strong current paralleling the isobaths.

This geological information has the following implications for the biological systems. The active deposition of fine-grained materials in the southern part of Norton Sound north of the mouth of the Yukon, establishes a set of conditions favorable for the abundant growth of detritus-based benthic communities. Toward the east, the waters, and hence the sediments, are disturbed little by currents. The sediments tend to be softer and thus, are more suitable habitat for different species of benthic animals than the more active sediments to the west. Those to the west are disturbed and redeposited by storm surges of the northward setting current across the mouth of Norton Sound. Other parts of the Norton Basin, such as the Chirikov Ramp and the western part of the Norton Plain, and between the Savoonga Depression and the Northeast Cape Shoal, are regions of slower currents and less disturbed sediments. These also are suitable for a rich and abundant benthic fauna which make the areas attractive to Walrus, Bearded Seals and Gray Whales.

The greater relief of the Chukotka Trough and of the Cape Rodney Parallel Valley Area reflects greater turbulence, and the coarser bottom sediments in these places indicate the retention of materials in the water column. This effect is especially marked in the Anadyr Strait and the Bering Strait where the northward setting water is forced over a sill and confined between Little Diomede and Cape Wales.

Shallower water northeast of Gambel on Saint Lawrence Island, east and southeast of King Island, over the shoals off Point Spencer, and over the Wales shoal, seem to have characteristics attractive to some seabirds. These conditions and their effects on seabirds are discussed in later sections of these appendices.

APPENDIX II.
OCEANOGRAPHY: ORIGINS, CHARACTERISTICS, AND MOVEMENTS OF WATER MASSES OF THE NORTHERN BERING SEA AND BERING STRAIT

(Precis of Fleming and Heggarty 1966; Coachman, Aagaard, and Tripp 1975)

The synthetic process now underway in the Bering Sea Review will make available the large amount of information gathered under the National Oceanic and Atmospheric Administration's Outer Continental Shelf Environmental Assessment Program (OCSEAP). Little of that material has so far been available in a form useful in preparing a comprehensive oceanographic picture of the northern Bering Sea and Bering Strait. Consequently, most of this survey is based on studies made before the OCSEA Program and summarized in "The Oceanography of the Bering Sea" (Hood and Kelley, eds., 1974) (especially Chapter 3, "Circulation, transport and water exchange in the western Bering Sea" by Hughes, Coachman and Aagaard); in "The Physical Oceanography of the Bering Strait Region" (Coachman, Aagaard, and Tripp 1975); and in "Environment of the Cape Thompson Region, Alaska" (Wilimovsky and Wolfe, eds., 1966).

Studies of physical and chemical oceanography of the Bering Sea have been made primarily south of a line from Cape Navarin, Siberia, to Nunivak Island, Alaska; that is, in Bristol Bay, the Aleutian Islands, and the Bering Sea gyre (Hood and Kelley, eds., 1974). Some data on water masses and currents in the Bering Strait and Chukchi Sea are published in Wilimovsky and Wolfe (1966) and in Coachman, Aagaard, and Tripp (1975).

Hughes et al. (1974) summarized the water masses as follows. First, North Pacific water flows through deep passes between the Aleutian Islands into the deep basin between the Aleutians and the Continental Shelf. Some of this water of deep origin flows up over the edge of the Continental Shelf and continues northward around both ends of Saint Lawrence Island and into the Chirikov Basin. This water moves on through the Bering Strait and the Chukchi Sea, penetrating the waters as far north and west as Herald Shoal. Deep water from the Arctic Ocean, which is considered a part of the North Atlantic water mass, moves along the bottom of Barrow Canyon and Herald Canyon, but does not contribute to the water of the Chukchi Sea south of Icy Cape.

A second source of water on the Continental Shelf is the outflow of the major Alaskan rivers north of Bristol Bay. These warm waters of low salinity renewed each year by spring freshets dominate the shallow waters within 25 miles of the Alaska coast.

The interactions between river water, river-borne materials, the shallow waters of the Continental Shelf, and the waters rising over the shelf out of the ocean depths provide the physical and chemical background setting for the biological processes we are studying in the Bering Strait Region.

A. Major Water Masses

Coachman, Aagaard, and Tripp (1975) described the water masses in the northern Bering Sea, arguing for the existence of three main water masses: Bering Shelf, Alaskan Coastal, and Anadyr (see Main Body, Figure 10).

The first, Bering Shelf Water, occupies the middle of the shelf. It is made up of saline Bering Sea water which is reported to be mixed with cold "resident" (overwintered) shelf water and melting sea ice in the region south of Saint Lawrence Island. The result is a water mass of moderate temperature ($2-6^o$) and moderate salinity (32.4-32.8 o/oo). It is assumed that this water becomes uniform from top to bottom as a consequence of circulation under the ice in winter.

The second, Alaskan Coastal Water, is separated sharply from the shelf water on the east. This water, warmer (6-10°) and of markedly lower salinity (30-31 o/oo), is identified north of Nunivak Island and is formed of water which persisted through the previous winter (salinity 32 o/oo), and dominated by outflow of fresh water from interior Alaska via the Kuskokwim, Yukon, Kobuk, and Noatak Rivers. River plumes are clearly delineated by high measurements of $P\text{-}CO_2$ (Hood and Reeburgh 1974); high levels of carbon dioxide are characteristic of the waters between the Kuskokwim River and the Seward Peninsula. This coastal water is virtually the only water in Norton Sound and inner Kotzebue Sound, inside of Cape Espenberg and Kruzenstern. The water in eastern Norton Sound apparently forms a largely independent gyre partially isolated from the other water masses. Kotzebue Sound resembles Norton Sound (see Main Body, Figures 29 and 30, pages 385 and 386) in having a circulation of low saline water largely isolated from the major northward flow. Kotzebue Sound also contains cold remnants of ice-melt water along the bottom.

During the summer the more or less isolated bodies of low saline water in inner Norton Sound, Kotzebue Sound, and northeast of Cape Lisburne usually become quite warm. Their low salinities and warmth have important effects on the biology of these subregions: The copepod faunas differ fundamentally from those of the cold saline waters to the west (see Main Body, Figure 11, page 216); Saffron Cod replaces Arctic Cod, and Sand Lance is seasonally very abundant.

The third water mass, Anadyr Water, occurs against the Siberian shore. It flows out of the basin in the Gulf of Anadyr northward past the western end of Saint Lawrence Island into the deep waters of the western Chirikov

Basin. The water is cold (1-2°C), highly saline (32.8-33.2 o/oo), of low partial pressure of CO_2, and is rich in nitrates. This western area has high primary productivity, 600 mg $C/m^2/day$. The use of nutrients is balanced by an increased contribution of nitrate and CO_2 from deep source water.

There appears to be a difference of technical opinion as to the origin or formation of the Anadyr Water. Coachman, Aagaard, and Tripp (1975) suggest that it rises out of the Bering Sea Deep over the shelf edge near Cape Navarin and; steered by the bottom topography, circulates around the inner part of the Anadyr Gulf without extensive mixing with the cold water which occupies the bottom of the center of the Gulf. They suggest that this water is cooled in transit and that within 25 km of shore it shows influence of outflow of Siberian rivers. In contrast, Fleming and Heggarty (1966) suggested that this water is a product of upwelling all along the Siberian shore, as the northward moving water diverges to the northeast in response to Coriolis effects. The difference may be resolved by establishing the source and life histories of the food organisms preyed upon by the auklets in the Chirikov Basin.

Coachman, Aagaard, and Tripp suggested that Norton Sound is an important source of the Alaskan Coastal Water which is still identifiable north of Bering Strait in the southeastern Chukchi Sea: it can be identified as far north as Herald Shoal and occasionally in lenses moving east of Point Barrow. In discussions of the water masses of the region these authors emphasized the lack of vertical mixing between surface waters and deeper, colder, more saline waters; hence the stability of the water mass. This segregation of water masses by steep pycnoclines at depths should prevent rise of nutrients into the euphotic zone. Therefore, detailed examination of water masses studied by Coachman, Aagaard, and Tripp seems to help little in understanding this aspect of productivity and biological structures of the region.

B. Currents

It was formerly believed that during the winter water was stationary or flowed south through the Bering Strait and that northward flow was a phenomenon of the summer months. Coachman, Aagaard, and Tripp (1975) concluded that flow is northward all year and that the flow is driven by barometric pressures. Reversed flows, they believe, are temporary phenomena reflecting local winds. They observed that high barometric pressures in Nome and lows in northeast Siberia are associated with days of north winds. These winds reduce flow through the strait and lower the water level in Norton Sound. Low pressures in Norton Sound accompany southeast winds and increase the velocity of flow through the Bering Strait (see Figure 3).

Chirikov Basin: The northward flow of water across the Continental Shelf accelerates where it is confined at the east and west ends of Saint Lawrence Island. Then this Bering Shelf Water veers east in response to Coriolis effects,and restricts the Alaska Coastal Waters to within about 25 km of the Alaskan Coast. The Anadyr Water intrudes to the eastward towards King Island. Being confined, the water in the east part of the Chirikov Basin accelerates between Cape Rodney and Wales because of Bernoulli's Principle. As in river systems, when this water accelerates, it picks up and carries sand and moves gravel. When flow decelerates it drops its load.

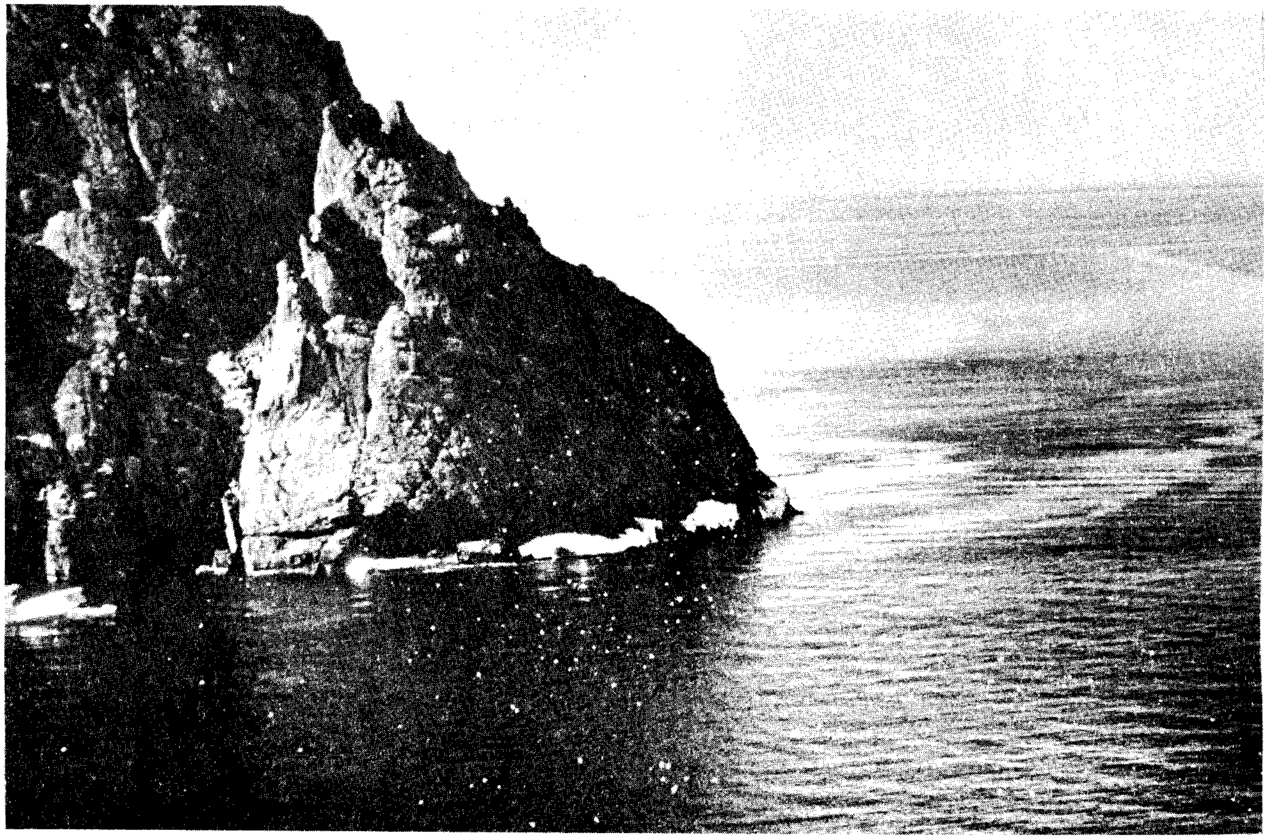


Figure 3. Photo of Little Diomede Island - flow of water through the Bering Strait. Streaks of smooth water mark the northward flow of water out of the Chirikov Basin past the southeast corner of Little Diomede Island.

This acceleration past barriers followed by slowing beyond them has produced gravel and sand spits on the north end of Sledge Island (Figure 4), at Cape Spencer, and the shoal which extends 75 km north of Cape Prince of Wales. Slowing of Anadyr current after the flow through Anadyr Strait has produced the gravel spit northeast of Gambel.

Southern Chukchi Sea: Most of the flow of water through the Bering Strait is in the channel east of Little Diomede at a velocity of about 3 knots (150 cm/sec) near Wales spit; water flows at half that speed at 10 m depth and near Little Diomede, and slower still at 1/3 knot (20 cm/sec) west of Big Diomede (Ratmanova). Water moving north veers east again off Shishmaref and circles through the deeper outer parts of Kotzebue Sound. The water slows after confinement and acceleration in the northern Chirikov Basin and Bering Strait. As the water slows deposition has produced Wales shoal and the long beaches from Wales to Cape Espenberg. A large part of these sediments may have come indirectly from the Yukon and Anadyr Rivers.

The saline water under the Alaskan Coastal Water and the mass of the Bering Shelf Water are steered north and northwest along the eastern edge of the Chirikov Basin by the form and the bottom contours at roughly 20 meters of depth (10 fathoms) (see Main Body, Figures 9 and 10, pages 212 and 213). The Alaskan Coastal Water turns north and northwest off Kivalina steered by the shape of the bottom. It accelerates as it turns northwest and is confined between the land (Kivalina-Cape Thompson) and the main water mass. It slows again as it passes the headland and deposits the spit at Point Hope. The main mass of Bering Shelf-Anadyr Water is shown by Landsat photos to form a counter-clockwise eddy west of Point Hope.

In the southeastern Chukchi Sea, the Alaskan Coastal Water is distinguishable from the western waters. The western waters do not seem

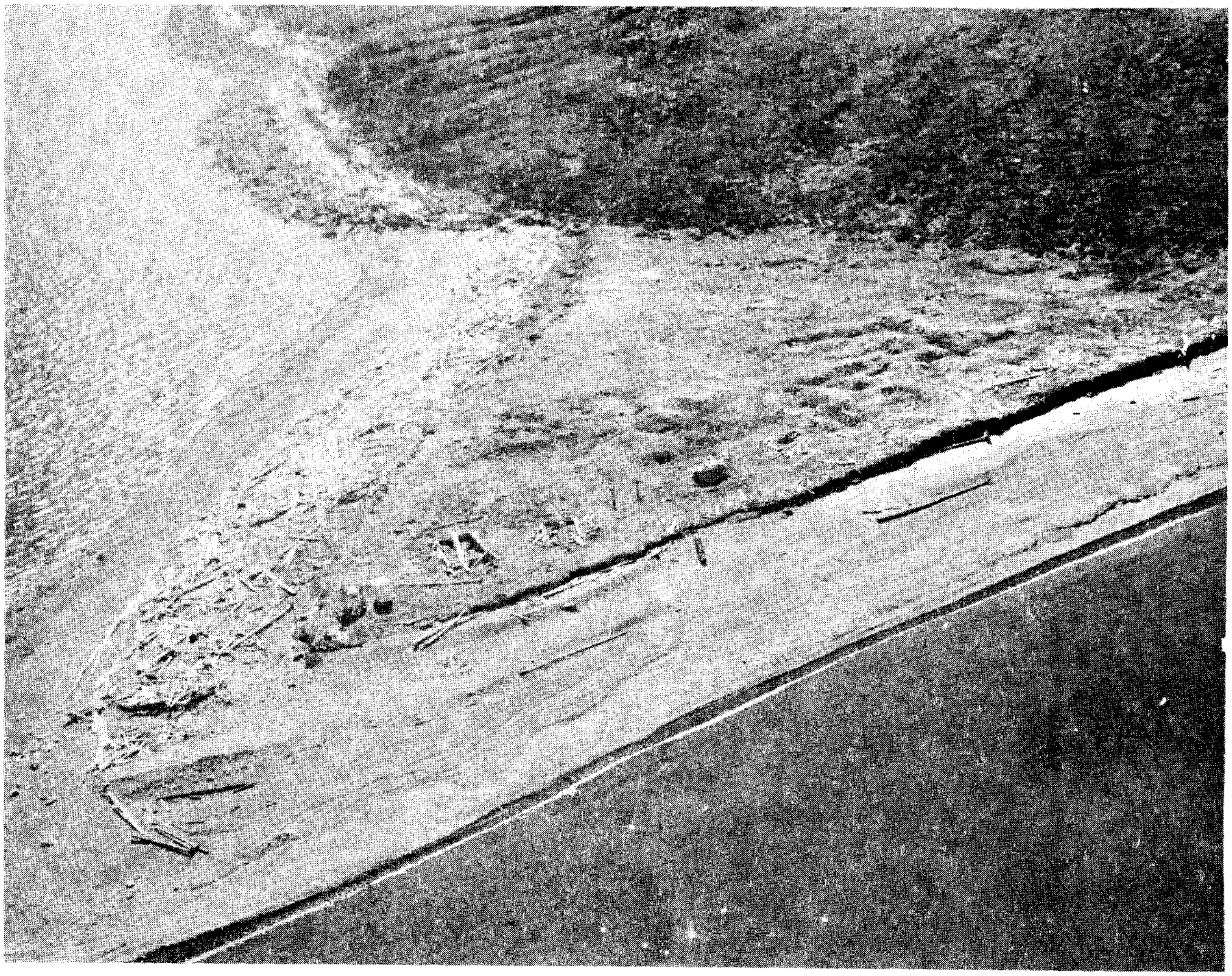


Figure 4. Gravel spit, driftwood and house pits on the north end of Sledge Island.
This photo, taken by J. Bartonek, shows sediments collected on a spit, windrows of driftwood, and pits which mark the site of a former Eskimo village. All of these are indications of the extreme strong currents and eddies.

to be separable into Bering Shelf Water and Anadyr Water as described for the Chirikov Basin. It may be that the distinctions are clouded by vertical and horizontal mixing while passing through the strait. A cold current moves southeastward along the north coast of Siberia, but this flow seldom if ever penetrates as far as Cape Dezhneva and does not contribute an important amount of water to the southern or eastern Chukchi Sea.

Off Point Hope the Alaskan Coastal Water turns north and divides into two streams; one moves northwest (apparently north of the westward curl of Bering Shelf-Anadyr Water) to pass south of Herald Shoal. The other veers northeast past Point Lay and Icy Cape. A clockwise eddy forms between Cape Lisburne and Point Lay.

C. Tidal Effects

Tidal currents and eddies modify the general pattern of movement. The schedule of tides is complicated by the fact that tides run once a day in Norton Sound and twice a day on the Siberian shore. At Nome the tides run twice a day for a few days after the moon passes the equator, but become daily when the moon has maximum declination. The tides in the Chukchi Sea are traditionally considered to be in response to progressive waves coming from the deep arctic basin. The tides on the Alaskan and western Canadian Arctic shores are a mixture of daily and twice daily periods.

Measurements of current flow record passage of strong eddies along the main flow; these may reverse temporarily the direction of tidal flow. Although much stronger than tidal currents, they run for shorter periods of time. Some have an average period of about two days, and suggest responses to the several-day patterns of atmospheric movement characteristic of the Bering Strait region.

During the years we were in the area, the sea ice moved north primarily east of King Island (Ukivok) and after the sea ice had disappeared we often saw an area of rough water between King Island and Sledge Island. It seems reasonable to think that this turbulence is the "middle water" which the King Islanders or Diomeders say often forces them to turn back on their trips to and from the mainland. They say they have no way of predicting when or how bad this rough water will be, no matter how calm the water may be around the island or the mainland. One might expect this sort of turbulence to result where two rather well-defined water masses sheer against each other or where tidal currents and main flow converge or conflict on the margins of eddies.

APPENDIX III.
PRODUCTIVITY

A. Sources

Productivity is said to be high in areas where resources are concentrated, such as nutrients for phytoplankton or vulnerable prey for animals. It is necessary that resources be available to the organisms, i.e., in the euphotic zone or available to stereotyped feeding techniques.

In most cases productive areas are regions of upwelling. Water comes up from below; it is cold, saline, and contains nitrates, phosphates, and carbon dioxide, as well as organisms carried up from the deep.

Areas of upwellings include a) regions where flow of water along the bottom meets an obstacle and moves up, e.g. at the edge of a continental shelf; b) where, as a result of winds, Coriolis effects or inertia, surface water moves away and is replaced from below (called a divergence); c) where two currents sheer against one another or one current pushes against a stationary body of water, as at the mouth of a river. In these circumstances resources may be concentrated in lenses of vertical circulation (called convergences or fronts). d) In northern seas there is a peculiar circumstance--the special phenomena at the edge of melting sea ice.

Highly productive upwelling areas have been reported in the central and southern Bering Sea in a) the upwelled water north of the Aleutian Passes, b) the water flowing up the Continental Slope around the Pribilof Islands and along the shelf break to the northwest, and c) along the southwest-northeast trending zone off the coast of Kamchatka.

The high mineral content of the low saline Alaska Coastal Water does not seem to stimulate levels of primary productivity as high as those in the Frazer River Plume, or as high as those along the slope of the Continental Shelf and along the coast of Siberia. Cold waters rich in nutrients have been reported in the western Chirikov Basin; Fleming and Heggarty suggested these waters result from divergence of water away from the Siberian Coast as the northward-flowing water moves eastward in response to Coriolis forces.

Turbulence in response to the confinement of water flowing through narrow straits is responsible for upwelling west and east of Saint Lawrence Island. This effect may be the major source of nutrients for the unusually productive area of the Bering Strait itself.

Moderate levels of productivity have been reported on the edges of the Bering Shelf Water in the southern Chukchi Sea west of Point Hope.

River plumes provide fronts or convergences at their seaward edge. Food tends to concentrate there and attracts waterfowl in spring and kittiwakes, murres, and puffins at the mouth of Golovin Lagoon in summer. The outlets of the large coastal lagoons provide food both at convergences and in the shallow estuaries. For these reasons outlets of lagoons and river estauries are gathering places for fish, gulls, and terns, seals, bears, and people.

Long lines of "slicks" paralleling the direction of the wind and of tidal currents occur in Norton Sound (Figure 5) and from King Island to and through the Bering Strait. Flotsam collects along these slicks and kittiwakes, Aleutian Terns, phalaropes, and at times murres and puffins congregate along the lines.

Figure 5. Streaks from flow of water in northern Norton Sound. Streaks of smooth water mark the flow of water westward from Cape Darby past Cape Nome. This photo was taken looking from Cape Nome to Rocky Point over the deeper water valley where stronger westward currents and fine sediments reflecting contemporary deposition. (Drury photo).

B. Productivity at the Ice-Edge

The edge of the melting sea ice in spring is very important in the lives of seabirds and sea mammals at a critical time when these animals are feeding actively in preparation for the exertion of reproduction.

The high productivity with the edge of the ice has been described by McRoy and Goering (1974), Alexander (1974), and Divoky (1978) as associated with differential temperature changes during the thaw. These appear to release minerals and allow a bloom of, primarily, benthic algae to thrive on the underside of the ice. Amphipods, copepods, and fish such as Boreogadus crop these algae. The most evident effect is an association of seabirds with the windrows of pan ice during break-up (Divoky 1978).

During break-up of the sea ice in spring, fields of ice pans collect along the western edge of the Alaskan Coastal Water and follow the border northwestward toward the Bering Strait. Auklets occur further east in the Chirikov Basin around drift ice. Murres and gulls occur in numbers larger in areas of drift ice than on open water. The ice is also used by sea mammals: Ringed, Common, and Bearded Seals, and Walrus.

During summer the seabirds gather in the western parts of the Bering Shelf Water west of King Island and around the western end of Saint Lawrence Island.

Similar effects have been reported along the fronts between Alaskan Coastal Water and Bering Shelf Water southwest of the Lisburne Peninsula.

C. Location of Primary Productivity and Phytoplankton Biomass

Almost all information available on phytoplankton flora in the Bering Sea applies to the region south of Saint Lawrence Island. A couple of stations have been occupied at the mouth of Norton Sound and in the area between King Island and the Bering Strait. One well-analyzed set of samples was taken in the Bering Strait and there is a small set of general plankton samples from the southeastern Chukchi Sea. Studies of the phytoplankton include some measurements of biomass; but we have not found any studies in which the flora, biomass, and primary productivity have been correlated. Consequently, these comments are interpretations and extrapolations from findings in neighboring areas in the southern part of the Bering Sea.

In general, high standing crop, measured as biomass in cells per cubic meter, is associated with high rate of productivity, measured in milligrams of carbon produced per square meter of water per day. However, exceptions are reported: east of Bower's Bank standing crop is low and productivity high; south of Nunivak Island standing crop is high yet productivity low (Hood & Kelley, 1974).

Karohji (1958) reported high biomass of phytoplankton on the Continental Shelf between Nunivak and north of Saint Lawrence Island (6,800,000 cells per cubic meter) and in the area at the northern part of the Bering Sea Deep and western edge of the shelf off Cape Navarin (8,900,000 cells per cubic meter). In this northern part of the Bering Sea and off the coast of Kamchatka, primary productivity has been measured at 350 mg C/m^2/day. In the mouth of Norton Sound high standing crop has been reported (English 1966), but productivity data are not available. Very high standing crop and very high primary productivity occur in the Bering Strait itself. McRoy *et al.* (1972) determined that plant plankton fix 1,000 milligrams of carbon per square meter of water per day. This amount of carbon makes this area one of the most productive in the world, even though it falls at the low end of the measure of productivity of the world's better-known upwelling systems.

Phytoplankton biomass is strongly affected by grazing of herbivorous copepods. It is reported that high densities of zooplankton occur along most of the shelf edge south of the Pribilof Islands, and that these are associated with low densities of phytoplankton, as if growth of zooplankton was at the expense of the phytoplankton. Zooplankton feeding reduces their own food; thus, if growth and reproduction of phytoplankton is slow, the zooplankton biomass is limited by food shortage.

Off the coast of Siberia between Cape Navarin and Cape Olyutorskii, primary productivity is high enough to maintain large biomasses of both phytoplankton and zooplankton.

In addition to the effects of herbivores grazing on phytoplankton, we can expect marked differences between years in the growth and reproduction of phytoplankton. English (1966) reported a reversal of relative numbers of zooplankton to phytoplankton between two years in the area of Chirikov Basin and the southern Chukchi Sea.

APPENDIX IV.
TROPHIC LEVELS

A. Distribution of Fauna and Flora

Karohji (1958) suggests that the diatom flora of the Continental Shelf is generally similar, and contrasts it with that of the Deep Bering Sea Basin and that of the northern North Pacific. Motoda and Minoda (1974) indicate that a plankton flora typical of the Continental Shelf occurs in the mouth of Bristol Bay and across the Continental Shelf from Nunivak Island to the area east of Cape Navarin. We presume that this flora is what is carried north through the Bering Strait Region. It is not clear whether Bristol Bay, Norton Sound and Kotzebue Sound have a flora separate from the flora of the more saline waters to the west.

In the Alaskan Coastal Waters, neritic forms are more abundant at the surface, but cold-water forms (e.g. _Coscinodiscus curvatulus_ and _Fragilaria oceania_ which are also reported to be active under the sea ice) appear at greater depths. The two groups can exist together on the Bering Shelf because none of the water is deeper than the 100 m reported to be the lower average limit for diatoms in the euphotic zone in summer.

The flora of the Alaskan Coastal Waters is dominated by _Nitzschia seriata_ and _Chaetoceros_ (Section Hyalochaete) -- especially _Chaetoceros debilis_. Dinoflagellates such as _Ceratium longipes_ and _C. lineatum_ and _Peridinium_ spp., are reported to be major constituents between Nunivak Island and Norton Sound and also in coastal water in the Gulf of Anadyr.

Karohji reports that the flora of the area east of Cape Navarin, which he calls the Northern Bering Sea, is also dominated by neritic diatoms, e.g. _Nitzschia seriata_ and _Chaetoceros_ (Section Hyalochaete), especially _Chaetoceros furcellatus_. In accordance with this, the diatoms in the water flowing through the Strait of Anadyr should be primarily neritic. Influence of flora from the Bering Sea Basin is indicated by the presence of Thalassiothrix longissima, Denticula seminae, Chaetoceros (Section Phaeoceros) -- especially Chaetoceros atlanticus and C. convolutus, and Coscinodiscus oculus f. iridis. Brief reference to the occurrence of blooms of Chaetoceros, Coscinodiscus and Thalassiosira in the Bering Strait Region (English, 1966) suggests that some of the flora of the Bering Sea Basin is included and thrives in the Bering Shelf Water flowing north.

B. The Detritus-based System in Norton Sound

Few phytoplankton data have been collected in either the Saint Lawrence Island waters or Norton Sound. Although it is not known when the peak of the phytoplankton bloom occurs, it is suspected to be in late May or early June. Although primary producers must be active in the water column within Norton Sound, the short period available for primary production, the warmer, less dense water that will not "float" the larger Copepods, and the heavy suspended load of sediments in the water in the southern portion of Norton Sound seem to reduce the importance of production in the water column.

Geological observations of the behavior of sediments in the Yukon River's plume, and observations on the distribution of epifauna and selected infauna (animals living on or in the bottom sediments) taken by trawl, as well as the food of bottom-feeding Starry Flounders (Platichthys stellatus), strongly suggest that Norton Sound is a depositing system with its component benthic species dependent on an annual and substantial flow of carbon from the Yukon River, the many rivers within Norton Sound, seagrass (Zostera) beds and intertidal algae.

The detrital input and associated sediment delivered to the Norton Sound benthos from adjacent river systems are associated with rich microbial components. These microbial components represent an important source of primary productivity available to the benthic systems. It is to be expected that deposition of sediments and detrital materials, together with their associated bacterial flora, result in the establishment of deposit and detrital-feeding species because water circulation within the eastern portion of Norton Sound is sluggish. The western or outer portion of Norton Sound is also an important depositing environment, but the sediments there are resuspended and redistributed by greater movement of overlying water than found in the inner sound. This is consistent with the presence of deposit-feeding organisms characteristic of unstable depositing sediments, e.g. sand dollars (Echinarachnius), the clam Yoldia, and the polychaete worm Pectinaria (Feder and Jewett 1978).

The ideas and data which follow in the discussion of detrital systems were presented by H. Feder to the Norton Sound Synthesis Meeting in 1980. (See also Feder and Jewett, 1978).

The presence of the omnivorous sea urchin, Strongylocentrotus droebachiensis, is an indicator of a detritus-based fauna taking advantage of plant material raining from local rivers. Many of the other species present are predatory on deposit-feeding infauna. King Crabs (Paralithodes camtschatica) presumably take deposit feeders such as the clam Yoldia sp., Polychaetes Pectinaria and Cistenides, and the Brittle Star Diamphiodia. Sea stars such as Leptasterias, Evasterias and Lethasterias also utilize many deposit-feeding as well as some suspension-feeding infaunal species of quasi-turbulent areas, e.g. Cockles Serripes and Clinocardium and the sand dollar Echinarachnius. Hermit crabs (Pagurus trigonocheirus and P. capilatus) and the shrimp (Argis lar) are presumed to feed on deposit-feeders. The large snails *Neptunia heros*, *N. ventricosa* and probably *Beringius beringi*, are predators on deposit-feeding infaunal species such as the clam *Yoldia*, and the Polychaetes *Cistenides* and *Pectinaria*.

Commercial King Crab fishing in Norton Sound has been underway since 1977. The area of most intense fishing and, consequently, the highest landings is the northern portion of the Sound, particularly the region between Cape Rodney and Rocky Point, extending south to Latitude 63° North. This is an area where geologists have found contemporary active deposition of fine-grained sediments, oceanographers have found a fairly strong westward current, and microbial biologists found the highest rates of nitrogen fixation (characteristically found with a high C:N ratio in detrital particles) for the Sound. This region, extending to about 25 km south of Cape Nome, is also where many other epifaunal species occur in highest biomass, e.g. four species of sea stars, sea urchins, Red King Crab, Hyas Crab, two Hermit Crabs, Argis shrimp, and two species of snails.

C. Zooplankton

Reports on zooplankton have been divided into studies on small, herbivorous Copepods and larger crustaceans (Euphausiids, Decapods, and Amphipods). The Bering Sea has a rich and diverse fauna of Copepods. These are the primary herbivores on the phytoplankton and form the base of the food webs of larger organisms.

Copepods show a general segregation into a fauna of the Bering Sea Deep which contributes to the fauna of the shelf waters, and a fauna of the low saline Alaska Coastal Waters between Nunivak Island and Norton
(see Table 1)
Sound /. Copepods of the deep Bering Sea are found around Saint Lawrence

Table 1.

Groups of Copepod Species

Neritic Water	Central Bering Sea	Circumpolar
Acartia clausi	Calanus cristatus	Calanus finmarchicus
Acartia longiremis	Calanus tonsus	(= C. glacialis)
Centropages mcmurrichi	(= C. plumchrus)	Calanus hyperboreus
Epilabidocera amphitrites	Metridia lucens	Metridia longa
Eurytemora herdmani	Oithona similis	Microcalanus pygmaeus
Tortanus discaudatus	Oncaea borealis	Oithona similis
	Pseudocalanus minutus	Pseudocalanus minutus

Island but they are replaced by the copepod species of northern affinities which can reproduce in saline cold water north of Saint Lawrence Island as the waters move north into the Chukchi Sea.

1. Copepods of the Alaskan Coastal Water

Copepods characteristic of the low saline water of the shallow eastern Bering Sea occur well north of the Bering Strait on the Alaskan side. These include *Acartia clausi*, *Centropages mcmurrichi*, *Epilabidocera amphitrites*, *Eurytemora herdmani*, *E. transversalis*, and *Tortanus discaudatus*, and the cladoceran *Evadne normandi*. Neimark's studies (1979) show that the trend toward a specialized copepod fauna in neritic waters is exaggerated in inner Norton Sound; see Table 2 and Figure 6.

2. Some Observations on Transfer of Energy to Higher Trophic Levels

a. In Norton Sound:

The study by Neimark, Cooney and Geist (1979) of feeding behavior of coastal fish in Norton Sound establishes some of the major links between lower trophic levels, the herbivorous and carnivorous invertebrates, and the "bait" fish upon which seabirds depend. The authors make several points worth repeating. The species of fish they studied were primarily "generalists," a series of adaptations which allows species to feed on whatever food is available and thus to compensate for wide changes in their prey as a consequence of changes in temperature, salinity and currents. At the same time the species of fish showed selectivity even among the most abundant prey items.

The authors examined the foreguts of the most numerous fish, Saffron Cod and Rainbow Smelt caught in floating and sinking gill nets. They compared the contents with contents of net hauls for plankton. The most abundant zooplankters were copepods *Acartia* and *Eurytemora* and the cladocerans *Podon* and *Evadne* (see illustrations, Figure 7.)

Table 2 . Occurrence of zooplankton taxa in the Norton Sound coastal samples, July - August, 1976. Table 3 in Neimark, 1979: Zooplankton ecology in Norton Sound, Alaska.

	Mean Numerical Abundance[1]	Dominance	Frequency of Occurrence[2]
Taxonomic Category	No./m^3	% Abundance	%
Acartia clausi	1601	61	100
Podon sp.	508	19	89
Evadne sp.	339	13	86
Pseudocalanus spp.	32	1	44
Centropages abdominalis	28	1	61
Gastropod veligers	28	1	31
Bivalve veligers	25	1	33
Eurytemora pacifica	14	1	69
Eurytemora herdmani	14	1	39
Acartia bifilosa	7	<1	14
Crangonidae zoea	3	<1	81
Cirripedia	3	<1	28
Tortanus discaudatus	2	<1	25
Obelia longissima	2	<1	8
Acartia longiremis	1	<1	8
Spionidae	1	<1	8
Obelia sp.	P	<1	17
Copepod nauplii	P	<1	6
Teleost eggs	P	<1	8
Cyanea capillata	P	<1	39
Clupea harengus	T	<1	47
Insects (unidentified)	T	<1	6
Pleuronectidae	T	<1	14
Stichaeidae	T	<1	6
Diptera	T	<1	25
Autolytus sp.	T	<1	22
Platichthys stellatus	T	<1	8
Sagitta sp.	T	<1	17
Lamprops sp.	T	<1	14
Ammodytes hexapterus	T	<1	6

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[1] Present (P) implies less than one individual per cubic meter, while trace (T) means less than one individual per 10 cubic meters.

[2] Taxa which occurred in only 1 of the 36 processed samples were not included in this table.

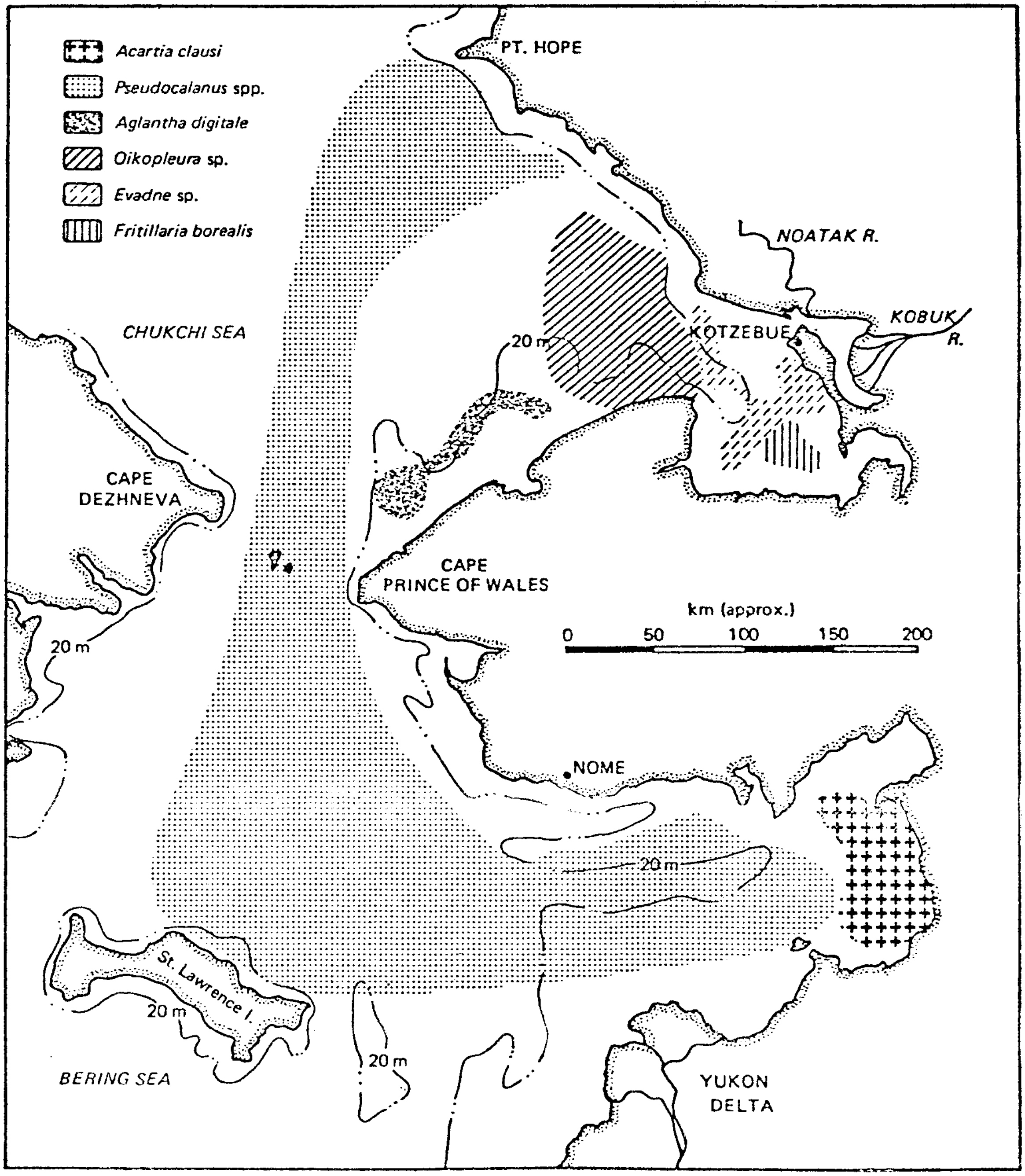

Figure 6 . Summer distributions of the numerically dominant zooplankton species in regions of the Bering and Chukchi Seas, 1976. Figure 14, in Neimark, 1979: Zooplankton ecology of Norton Sound, Alaska. Refer to Figure 15 in Neimark, 1979, for station locations.

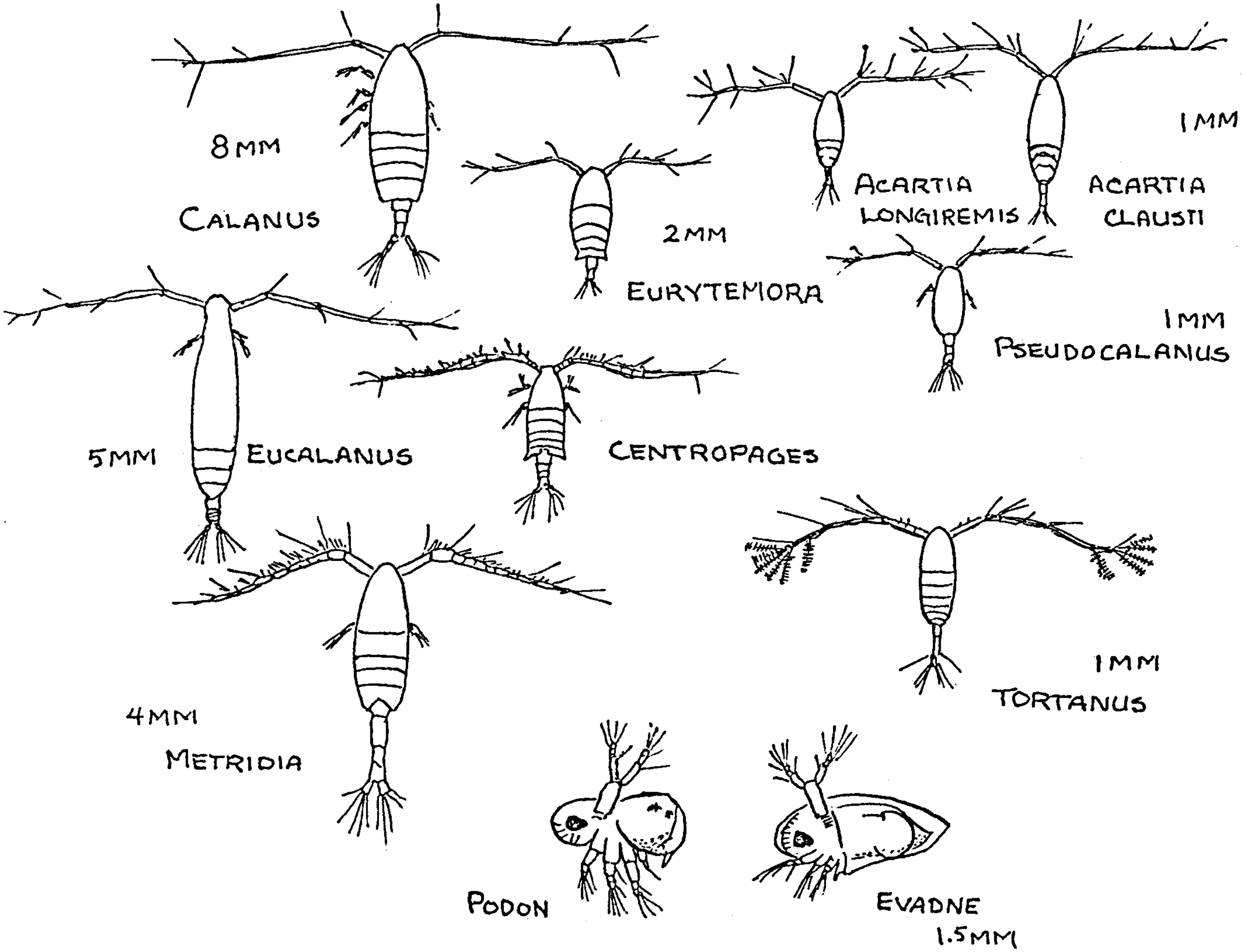

Figure 7. Zooplankton of the marine community of the Bering Strait Region. (drawing W. Drury)

The fish are not feeding simply on whatever is available. The copepod Acartia and the cladoceran Evadne are less abundantly represented in fish foreguts than in net samples from the same area. At the same time Eurytemora was more heavily represented in stomachs than in the net hauls, as were bottom living harpacticoid copepods, bivalve zoea and crangonid zoea. It was apparently more efficient to consume larger benthic forms than the small planktonic crustacea. Furthermore the benthic food sources seem to be more dependable.

b. The mouth of Norton Sound:

In deeper, cooler and more saline waters to the west, benthic food sources are less important. The warm water Acartia clausi decreases and carnivorous copepods become dominant, replacing the smaller, herbivorous copepods. The larger copepods Pseudocalanus sp. and two species of Calanus, including C. finmarchiais, were the dominant zooplankters.

Larger planktonic forms become the food base for fishes feeding pelagically. For instance, Euphausia pacifica which may feed on phytoplankton along the coast in Bristol Bay, seems to feed on microzooplankton offshore where phytoplankton is too small. In addition the offshore, predatory chaetognath, Sagitta (Arrow-worm), may become an important link. It has been suggested that Sagitta may convert the unavailable small food items into a resource useable by the bait fish offshore all summer by feeding on microzooplankton, herbivorous copepods swept out from coastal zones, on previous "pulses" of production from southern Bering Sea, and bathypelagic (deep water) copepods swept up over the shelf edge in spring. The capriciousness of this sort of a link can affect the whole complexion of the food resource of the small pelagic fish in the Norton Basin area.

3. Copepods of the Bering Shelf and the Saint Lawrence Island Waters

North of a line from Nunivak Island to the Anadyr Basin a more northern copepod (Table 1) fauna replaces the fauna coming out of the deep Bering Sea. Copepods of the southern Bering Sea fauna (*Calanus tonsus*, *C. cristatus*, *Eucalanus bungii* and *Metridia lucens*) are carried north and occur together with abundant wide-ranging northern or subarctic forms (e.g. *Calanus finmarchicus*, *Calanus marshallae*, *C. hyperboreus*, and *Metridia longa*) in the St. Lawrence Island waters. The larger copepods graze on large-celled diatoms (e.g. *Cosinodiscus* and *Thallasosira*) in the cold, saline hence more buoyant water. The mixture makes up the bulk of the copepod fauna of the shallow water from the edge of the Continental Shelf to Point Barrow. The presence of the Bering Sea elements confirms the central role of northward flow of water in the marine biology of this area. The northern fauna, primarily *C. finmarchicus*, replaces the southern fauna because it reproduces in the northern waters.

The Calanoid copepods from the central Bering Sea breed in deep, cold water at depths of 100-200 m, and retreat to deep water as the surface waters warm in their southern range. These animals are carried north into waters where they cannot breed and thus are progressively replaced in the copepod fauna north of Saint Lawrence Island and are nearly absent north of the Bering Strait; however, the immature copepods feed, grow, and fatten up to Copepodite Stage V, and because these forms are larger than many of the other adult copepods they are used as food (*Calanus cristatus* and *Eucalanus b. bungii)* by Least Auklets near Gambel (Bédard 1969). The copepods seem to be fed upon also by Chaetognaths, Euphausiids and Hyperiid Amphipods.

Calanus cristatus spawns in deep water in mid-winter (December to February). Its copepodite stages are carried into the southern part of the

Bering Strait Region around the time of ice break-up. Occasionally they come to the surface in compact swarms. Calanus finmarchicus spawns from the surface to a depth of 200 m, and starts to spawn at the beginning of the phytoplankton bloom. The nauplii larvae increase in number to a maximum in mid-June. Because they disappear during June-July, the annual productivity of this species, which is one of the largest and most numerous, does not become available until the fat, almost full-grown Copepodite Stage V reappears at the surface in early August-September.

Although these are forms of relatively deep water, the shallowness (25-30 fathoms) of the water in the Bering Strait Region allows seabirds to feed throughout the water column; as these forms are carried north they are made available as food. Furthermore, Bogarov (1946) reported that at latitudes where there are 24 hours of daylight, such as in the Barent's Sea, copepods do not perform their usual vertical diurnal migrations which take them deeper during the day. Thus, the copepods are vulnerable and available as food organisms, both for Least Auklets and for other crustacea and small fish.

4. Amphipods and Euphausiids

North of the Bering Sea Basin the Hyperiid Amphipod Parathemisto pacifica is progressively replaced by P. libellula, and the Euphausiids Thysaneossa longipes and T. inermis are replaced by T. raschii.

a. The Euphausiids T. inermis and T. raschii are rapid-swimming mid-water to bottom forms which perform diurnal movements in deep water. T. inermis is considered to belong to a fauna of the continental slope southeast of the Kamchatka Peninsula. It is carried north over the edge of the Continental Shelf, and although equally numerous with T. raschii around Saint Lawrence Island (Bédard 1969), it drops out further north and is almost absent north of the Bering Strait. Its presence among the crustaceans in the waters northwest of Saint Lawrence Island and into the southern Chukchi Sea is further evidence of the northward flow of water.

Apparently T. raschii rises to the surface to spawn in the Anadyr Basin soon after the ice leaves. Young forms appear in the diet of Crested Auklets in June, and adolescent and younger forms are found at or near the surface to a depth of 50 m until September. These Euphausiids apparently may spawn first in their third year in cold years. Their appearance at the surface of the water in the Bering Strait Region does not seem to be related to vertical migration.

Euphausiids are filter feeders and one presumes feed on diatoms; animal remains have been found in their stomachs and studies under laboratory conditions suggest that individuals prefer food particles of large sizes. (One would expect that they would not avoid fat Copepodite V stages.)

b. Amphipods carry their young in brood pouches until the young reach a length of 2-3 mm and are released. Amphipods are active under the winter ice in the Beaufort Sea. Young of a length of 3-5 mm are found in the diet of Least Auklets in May, June, and July, as if released in the spring at about the time of ice break-up. It may be that the young are released so as to take advantage of the bloom of food which begins at the edge of the ice. Little is known about swarming or changes in distribution in the water column; they do not show peaks of abundance in the summer. Their numbers and biology seem to be related closely with events taking place under the ice.

It is known that large individuals, up to 50 mm, are predaceous on smaller copepods. They have large compound eyes and legs efficient for catching. They may be serving as an important step in transfer of energy and food from the small filter feeders to the active vertebrates.

Use of larger zooplankton as food:

The common Hyperiid Amphipod Parathemisto libellula is of lesser importance in the diet of auklets around Saint Lawrence Island, but it is very important in the diet of kittiwakes and Thick-billed Murres in other parts of the Bering Sea and Gulf of Alaska.

A variety of genera of Gammarid Amphipods are epifaunal and infaunal members of the benthic community. The sandy bottom characteristic of the Anadyr Strait and the Bering Strait Region is suitable for extensive benthic communities which include the benthic amphipods. These would seem to supply an important source of food to larger animals, from waterfowl in shallow water to Gray Whales around Saint Lawrence Island and on the Chirikov Ramp south and southwest of King Island. Their importance is still not known or documented.

5. Some Observations on Transfer of Energy to Higher Levels in the Saint Lawrence Island Waters and the Bering Strait:

Benthic invertebrates are available in the western waters. Seabirds apparently depend on benthic gammarids and mysidea when they first come back in spring. Gammarids and Polychaete worms are known to be important resources for marine waterfowl and are presumed to be important for demersal flatfish, arctic cod, Bearded Seals, and Gray Whales which are benthic feeders in the areas of deeper sediments around Saint Lawrence Island along the Chirikov Ramp and in the southern Chukchi Sea. The Lamellibranch molluscs of these same sediments provide the bases for the large Walrus populations.

In addition to the benthic systems, these denser western waters support a rich pelagic system. Bédard (1969) described the "ever-dominant copepods Pseudocalanus, Metridia and the copepod and barnacle nanplii, all of which are so tiny that they would require special filtering apparatus to be fed upon."

Johnson (1953) described the large populations of larvae of a number of benthic invertebrates which floated in the waters of the Norton Basin in late spring and summer. Most numerous were Echinoid larvae. Echinopleuteus and Bipinnarian larvae of Sea Stars were especially abundant in the warmer Alaskan Coastal waters; but Ophiopleuteus larvae of Brittle Stars were widely distributed to the west. Larvae of Lamellibranchs were numerous from Nome to Siberia. Barnacle larvae were widespread and well represented. The Chaetognath *Sagitta* was abundant all across the region. The appendicularian Oikopleura was numerous in oceanic waters and was replaced in Alaskan Coastal Waters by Fritilaria.

These small zooplankton are the basis of energy transfer from phytoplankton to vertebrates, the larger copepods *Calanus* and *Pseudocalanus* being carnivorous on forms such as these and the smaller copepods. The Euphausiids *Thysanoessa* feed on copepods and, one presumes these larvae to some extent, while the larger *Parathemisto* are general carnivores.

Bédard reported that the seabirds shift their diet from benthic forms to large calanoid copepods and Euphausiids as soon as these appear in spring. He described the diet of auklets in the Anadyr Strait according to observations 1964-1966. Searing (1977) made some additional comments based on his observations at Kongok Bay in 1976.

Upon arrival in June, Least Auklets depended heavily on epibenthic Gammarids, Mysids, young stages of the Hyperiid Amphipod *Parathemisto*, *Calanus finmarchicus*, and some of the southern Bering Sea forms: *Calanus* (*Neocalanus*) *cristatus* and *Eucalanus bungii*. During the egg-laying period they fed on Caridean Decapod larvae, Gammarids, young stages of *Parathemisto*, and some *Calanus finmarchicus*. They brought almost exclusively *Calanus finmarchicus* to their young (some *C. cristatus*, young Euphausiids (*Thysanoessa*) and *Parathemisto* were also brought).

Crested Auklets depended on epibenthic Mysids and Gammarids on arrival in spring. The auklets shifted to Euphausiids as soon as these appeared, though they took *Calanus finmarchicus*, *Parathemisto* and Carideans as alternatives. Bédard found that when they were feeding young, they brought almost exclusively *Thysanoessa* (both *T. inermis* and *T. raschii*). In 1976, Searing found Least Auklets and Crested Auklets feeding on *Calanus* (*Neocalanus*) *plumchrus* at Owalit Mountain/Kungok Bay, west of the Southwest Capes. His findings differ sharply with Bédard's of 1964-1966. Bedard worked at Gambel, at the exit of the Anadyr Strait, while Searing worked at the southern entrance. Searing suggested that the differences might reflect: 1) differences between the years; 2) differences between the two places; 3) confusion in taxonomy (i.e., someone misidentifying copepods).

Parakeet Auklets, on arrival, fed on Gammarids. In July, they fed on Mysids, *Calanus cristatus*, and some *Thysanoessa*, and during egg-laying period, on *Parathemisto*. In addition to the crustacea, they took Cephalopods, Pteropods (*Clione*), and fish larvae (especially Cottids, *Ammodytes*, and flatfish), and Polychaete worms (see Figure 8, from Ainley and Sanger, 1979).

6. Gradients in the Occurrence of Larger Zooplankton Towards the North

Bédard (1969) found that the auklets in the Saint Lawrence Island waters fed on approximately equal numbers of *Thysanoessa inermis* (the

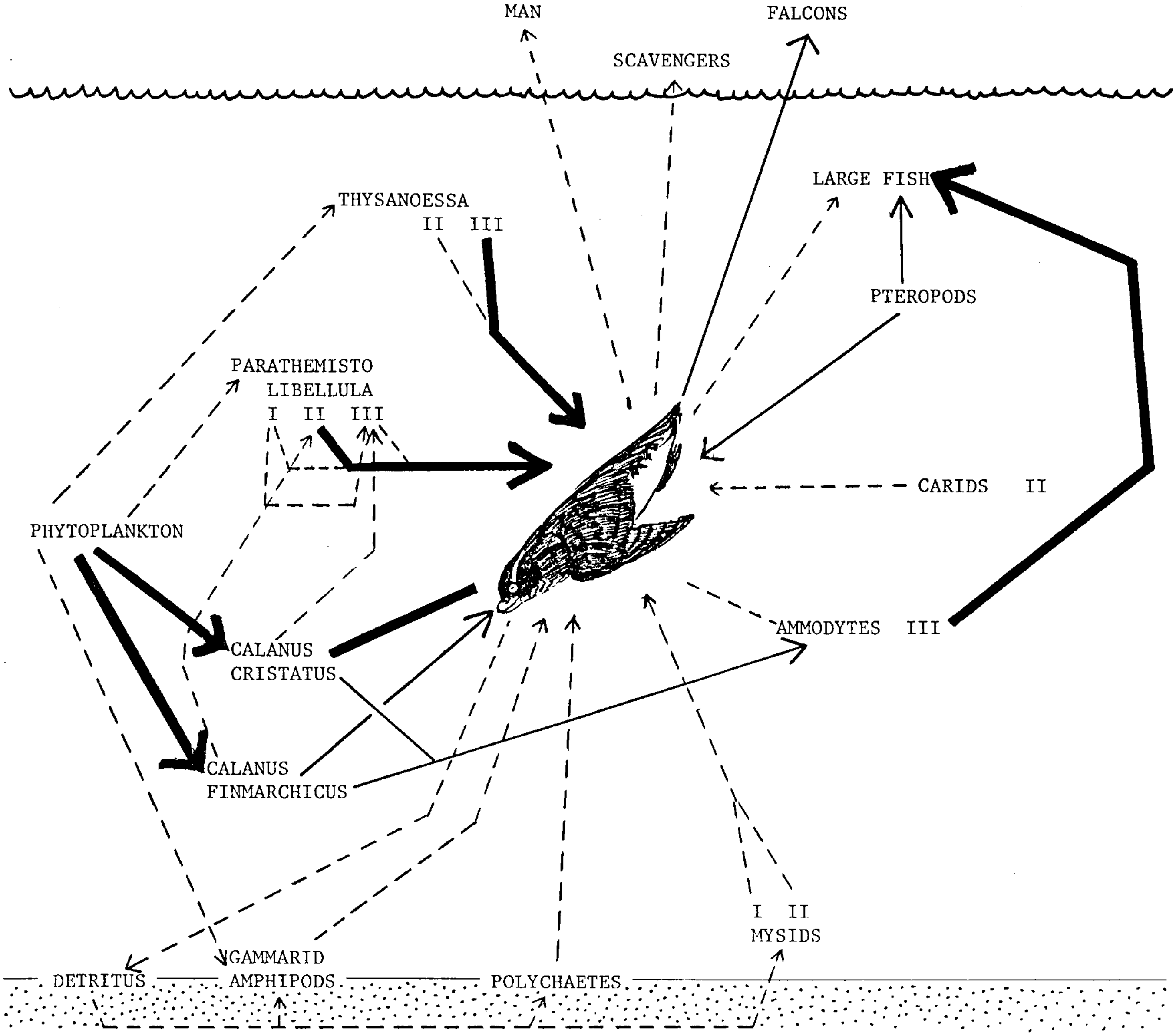

Figure 8. Schematic food web of the Parakeet Auklet in the eastern Bering Sea. From Ainley and Sanger (1979): figure 2 (based on Bédard 1969 and Dunbar 1946). Arrow sizes indicate relative importance of prey and Roman numerals refer to prey sizes.

southern element). Bédard found Amphipods taken by the auklets were primarily Parathemisto libellula; Parathemisto pacifica occurred only in small numbers. English's reports (1966) from the southern Chukchi Sea indicate that T. inermis drop out of the marine system, and it appears that in the Bering Strait Region, P. libellula and Thysanoessa raschii make up the majority of the food supply of the predators on larger zooplankton (e.g. Crested Auklet, Parakeet Auklet, Pigeon Guillemot, Kittlitz's Murrelet, Thick-billed Murre, and Black-legged Kittiwake). One presumes that a number of bottom and mid-water fish also depend on them.

It is interesting to see that according to these notes on foods, the Crested Auklets at Kungok Bay, southwestern Saint Lawrence Island in 1976, were feeding on the smaller Calanoids and caught few Thysanoessa. Thus, they would appear to be vulnerable to shortages of the preferred food, while Least and Parakeet Auklets would be much less affected by failure of the Euphausiids. Crested Auklets are reported to be subject to large changes in their populations sizes in the Aleutian Islands; this would be consistent with a variable food supply. Also, Least Auklets, depending on smaller prey, have a more diverse and abundant food base (Schoener 1965). The effects of the decrease in numbers of Euphausiids as compared to Calanoid copepods, and/or the increase in unreliability of the resource, may be responsible for the increase in relative numbers of Least Auklets as compared to Crested Auklets in the Bering Strait.

It will be important to understand further why all three auklet populations decrease so sharply north of Little Diomede Island (see Appendix V, and main body, Section IV). This is the case, despite the presence further north (north of Cape Lisburne) of appropriate food organisms (such as *Calanus cristatus*, *C. finmarchicus*, *Eucalanus bungii*, *Neo Mysis*, *Parathemisto libellula*, gammarids, *Thysanoessa inermis*, *T. raschii* and *Pandalus goniurus*), according to a report on mid-water trawls in this region (Wing and Barr, 1977). Benthic feeding organisms, e.g. Bearded Seals, Walrus and Gray Whales, feed extensively in the southern Chukchi Sea, so there must be some important changes in conditions in the mid-water and surface water.

D. Fish

1. Methods and Overview:

Wolotira (1977) and Barton (1978) surveyed ground fish (demersal) and mid-water and surface fish (pelagic) of the Bering Strait Region. They were interested in the commercially valuable fish and the gear they used (otter trawls, mid-water gill nets, and beach seines) was designed to assess fish stocks available for human exploitation. Their samples probably do not measure the abundance and distribution of fish available to seabirds.

Their results suggest that the fish fauna of the Alaskan Coastal Waters is demonstrably different from that of the Bering Shelf Waters. Samples were not taken far enough west to sample Anadyr Water representatively.

The following fish were most abundant in areas within Alaskan Coastal Waters: Pacific Herring, Sand Lance, Saffron Cod, Arctic Cod, and several flatfish: Starry Flounder, Alaska Plaice, Yellowfin Sole, and Longhead Dab. The following were more abundant in Bering Shelf Water: Snailfish, Walleye Pollock, Capelin, Bering Flounder, and Shorthorn Sculpin. It is not clear whether the differences reflect depths to the bottom, the nature of the bottom sediments or the water column.

Although both Saffron Cod and Arctic Cod were more numerous in neritic waters than offshore, Saffron Cod is much more numerous than Arctic Cod in the warmer waters of Norton Sound (Table 3). This conforms to our observations of the frequency of Saffron Cod in stomachs of Common Murres shot near Bluff and the frequency of both Arctic Cod and Saffron Cod in stomachs of murres shot near Cape Thonpson (Swartz 1966).

Pacific Herring was abundant enough in Norton Sound during the years 1968, 1969, 1971, and 1974, to support an important Japanese gill net fishery. The fish were scarce in 1976 and subsequent years, and were seldom seen in the diet of the seabirds at Bluff. One wonders whether herring might appear more frequently in the diet of seabirds of Norton Sound when the herring populations are large.

Capelin occurred in the fisheries samples at the mouth of Norton Sound and this fish, which is of great importance to seabirds in the Gulf of Alaska and North Atlantic, appeared in small numbers in our few samples from Sledge Island. They are absent from our samples from Bluff.

2. Some Relevant Data from Fisheries Surveys

In the following section we include a precis of data reported by fisheries studies. These show the distribution and relative abundance of the most numerous fish in the Norton Basin according to the techniques of sampling used in the studies. This is one measure of abundance, but it is not clear how reliable it is for assessing the food available to seabirds.

It is clear from our studies that while the absolute abundance of the species as indicated by the fisheries sample sets a lower limit of use, the birds are selecting fish with little relation to the absolute abundance alone. Most abundant species are not used and the most frequently used fish are not outstandingly abundant.

a. Relative abundance of the twenty most abundant fish in the Bering Strait Region:

The following table and charts are taken from Wolotira, 1977. The data were collected using a "demersal trawl" (otter trawl or drag) towed at 3.5 knots for an average distance of 1.65 nautical miles. Data were also collected using a "pelagic trawl" (mid-water trawl) towed at 4.5 knots.

Rank order of abundance indicates which species are most abundant. Comparison among the tables shows how the relative abundance changes between the regions of the study: a) the Southeast Chukchi Sea; b) Kotzebue Sound; c) Chirikov Basin, north of Saint Lawrence Island; and d) Norton Sound. Note that these are fish which occur in the middle of the water column or on the bottom. One would not expect Sand Lance to be well represented, both because of the places fished and because of the size of mesh used.

Although a few species are represented abundantly in all samples, they exchange positions of predominance. Note that a few species are really abundant, several are moderately abundant, and many are infrequent. This is the phenomenon of exponential decrease in relative abundance of species reported first for plants (Gleason 1920), but observable in most faunas as well as floras (Preston 1948).

The size of samples taken in the several areas differs, but because we have presented the proportion of the fish catch per unit effort the data are comparable.

Table 3 . Relative abundance of the twenty most abundant fish in the Bering Strait Region, from Wolotira (1977), Tables VIII-15-18, pages 109-112; fisheries data collected on vessel Miller Freeman.

Rank order of abundance of the 20 most abundant fish taxa in
a) the southeastern Chukchi Sea (subarea 1, BLM/OCS survey, 1976);
b) Kotzebue Sound (subarea 2, BLM/OCS survey, 1976);
c) the northern Bering Sea, north of St. Lawrence Island (subarea 3, BLM/OCS survey, 1976);
d) Norton Sound (subarea 4, BLM/OCS survey 1976).

a) southeast Chukchi Sea

Rank	Taxon	Proportion of fish CPUE[1]
1	Starry flounder	0.205
2	Pacific halibut[2]	0.118
3	Saffron cod	0.114
4	Pacific herring	0.096
5	Arctic cod	0.076
6	Shorthorn sculpin	0.067
7	Alaska plaice	0.058
8	Unidentified snailfish	0.050
9	Toothed smelt	0.037
10	Polar eelpout	0.031
11	Walleye pollock	0.030
12	Bering flounder	0.027
13	Arctic staghorn sculpin	0.021
14	Yellowfin sole	0.013
15	Sturgeon poacher	0.012
16	Capelin	0.012
17	Antlered sculpin	0.008
18	Wattled eelpout	0.007
19	Belligerent sculpin	0.005
20	Slender eelblenny	0.004

b) Kotzebue Sound

Rank	Taxon	Proportion of fish CPUE[1]
1	Pacific herring	0.404
2	Saffron cod	0.235
3	Toothed smelt	0.184
4	Alaska plaice	0.037
5	Starry flounder	0.028
6	Yellowfin sole	0.023
7	Arctic cod	0.021
8	Polar eelpout	0.010
9	Arctic staghorn sculpin	0.009
10	Antlered sculpin	0.008
11	Bering flounder	0.008
12	Wattled eelpout	0.006
13	Slender eelblenny	0.006
14	Shorthorn sculpin	0.004
15	Longhead dab	0.004
16	Unidentified snailfish	0.002
17	Ribbed sculpin	0.002
18	Sturgeon poacher	0.002
19	Capelin	0.001
20	Belligerent sculpin	0.001

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[1] Proportion of catch per unit effort, total fish only. Fish CPUE = 2.70 kg/km trawled.

[2] Total catch for this species = 1 large fish (44.2 kg).

[3] Proportion of catch per unit effort, total fish only. Fish CPUE = 5.44 kg/km trawled.

Table 3 , continued.

c) northern Bering Sea, north of St. Lawrence Island

Rank	Taxon	Proportion of fish CPUE[4]
1	Saffron cod	0.433
2	Shorthorn sculpin	0.205
3	Starry flounder	0.071
4	Toothed smelt	0.056
5	Pacific herring	0.027
6	Alaska plaice	0.026
7	Arctic staghorn sculpin	0.024
8	Arctic cod	0.024
9	Plain sculpin	0.022
10	Polar eelpout	0.020
11	Yellowfin sole	0.014
12	Unidentified snailfish	0.013
13	Belligerent sculpin	0.010
14	King salmon	0.007
15	Capelin	0.006
16	Antlered sculpin	0.006
17	Walleye pollock	0.005
18	Bering wolffish	0.005
19	Sturgeon poacher	0.004
20	Longhead dab	0.004

d) Norton Sound

Rank	Taxon	Proportion of Fish CPUE[5]
1	Saffron cod	0.604
2	Starry flounder	0.168
3	Yellowfin sole	0.053
4	Alaska plaice	0.032
5	Plain sculpin	0.026
6	Toothed smelt	0.018
7	Arctic cod	0.016
8	Shorthorn sculpin	0.015
9	Pacific herring	0.009
10	Arctic staghorn sculpin	0.008
11	Fourhorn sculpin	0.007
12	Antlered sculpin	0.007
13	Polar eelpout	0.006
14	Longhead dab	0.006
15	Slender eelblenny	0.005
16	Sturgeon poacher	0.003
17	Wattled eelpout	0.003
18	Arctic flounder	0.003
19	Belligerent sculpin	0.003
20	*Lumpenus mackayi*	0.003

[4] Proportion of catch per unit effort, total fish only. Fish CPUE = 5.97 kg/km trawled.

[5] Proportion of catch per unit effort, total fish only. Fish CPUE = 10.87 kg/km trawled.

b. Distribution of some of the more abundant fish in the Bering Strait Region

The following charts are from Wolotira et al. (1977), and indicate where some common fish were caught by otter trawls and mid-water trawls. They also indicate, by the density of the hatching, the places where the fish were most abundant by weight. Examination of these charts suggests some of the lower limits of use set by absolute occurrence of the fish species. For example: a) Capelin occur in the Chirikov Basin, but are very scarce in Norton Sound; one would not expect Capelin to be used extensively in Norton Sound, but they might be used at Sledge Island; b) Saffron Cod are more abundant in Norton Sound than in Kotzebue Sound and Arctic Cod become more abundant in the cold water southwest of Cape Thompson. One would expect murres feeding at Bluff to catch more Saffron Cod and those feeding west from Cape Thompson to catch more Arctic Cod. Note that the studies made in 1959 did not include samples in Norton Sound. c) Pricklebacks are indeed widespread but are nowhere abundant. Therefore, there must be special reasons why Pricklebacks constitute such a high proportion of the fish brought to the cliffs by seabirds. One presumes that the reason is that Pricklebacks are the most desirable in terms of bringing as large a fish as possible, of the most efficient shape.

3. Fisheries Resources Dependent on the Detrital System

a. Demersal fish:

Despite the apparent abundance of benthos, demersal fish (bottom living or ground fish) are relatively small and sparce in the Norton Basin. It has been suggested that coldness of the water is responsible for there not being any significant stocks of commercial fish. The dominant species of demersal fish are Saffron Cod ane Starry Flounder and Yellowfin Sole

Table 4

Relative Abundance of Inshore Pelagic Fish in Inner Norton Sound

In percent composition of the catch made by beach seines
and floating and sinking gillnets - after Barton, 1978

GOLOVIN BAY		
Sand Lance	81%	
Pink Salmon	6%	(6% juv.)
Chum Salmon	2%	(2% juv.)
Boreal Smelt	2%	
Saffron Cod	2%	
Pond Smelt	2%	
Least Cisco	2%	
Humpback Whitefish	1%	

CAPE DENBIGH TO STEBBINS	
Boreal Smelt	37%
Saffron Cod	17%
Sand Lance	9%
Pacific Herring	7%
Bering Cisco	4%
Starry Flounder	4%
Arctic Flounder	4%
Arctic Char	3%
Bering Poacher	3%
Pink Salmon	3%
Pricklebacks	2%
Least Cisco	2%
Pond Smelt	1%

Frequency of occurrence is the percent of the stations at which each species was found.
Relative abundance is the percent of the total finfish captured represented by the total of individuals in the species.
Gill nets were set for 8-10 hours. They were 640 meters long and made up of 7 shackles or shots.

These data were collected in ways suitable for investigating the fishes at the surface where kittiwakes and puffins fish, and indicate the relative abundance of some common fish. The results, from Barton (1978), are consistent with the results obtained by Wolotira for bottom fish, namely that the birds are selecting their prey, not necessarily catching the most abundant species.

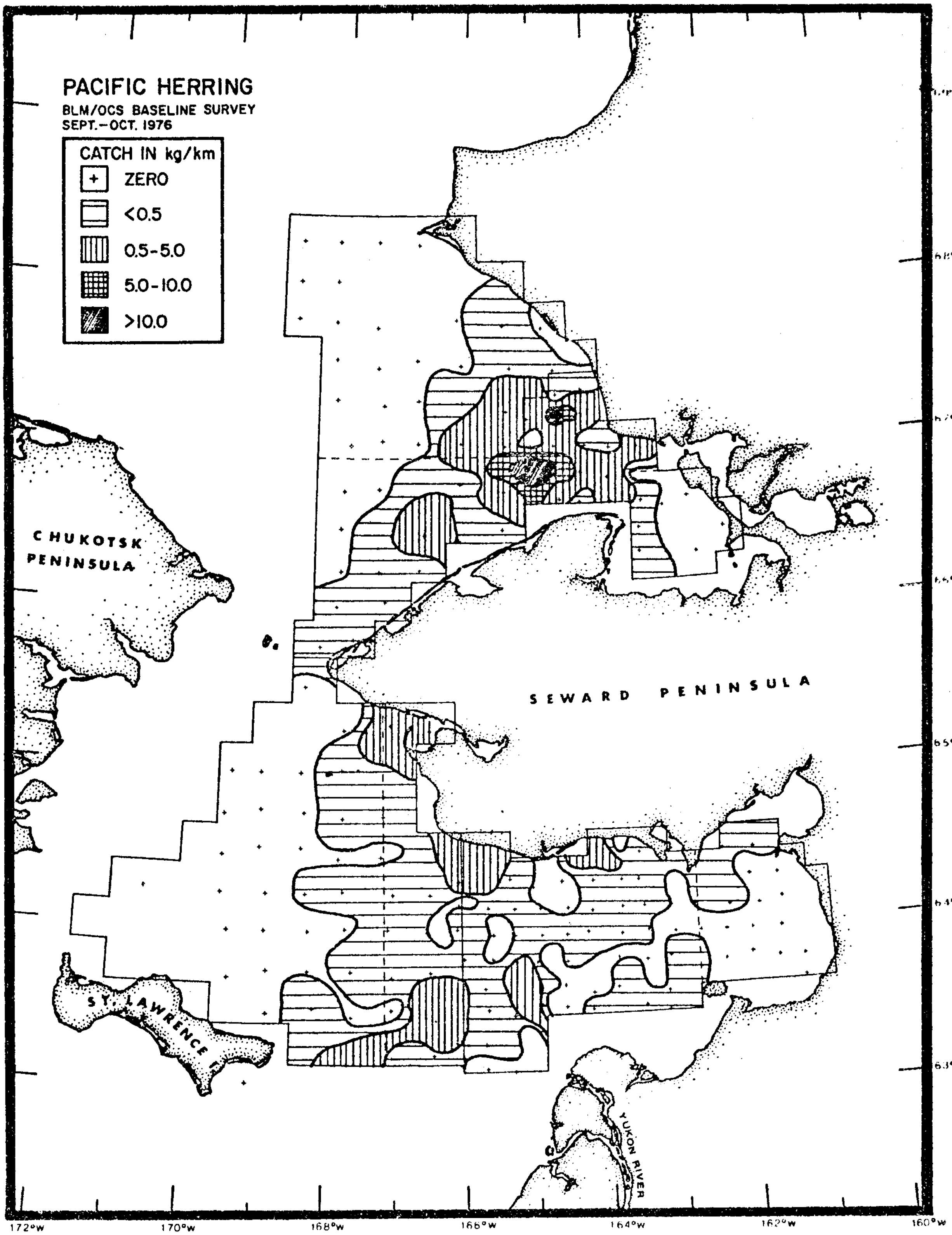


Figure 9 . Distribution and relative abundance by weight of Pacific Herring in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira *et al.*, 1977, Figure VIII-59, page 152.

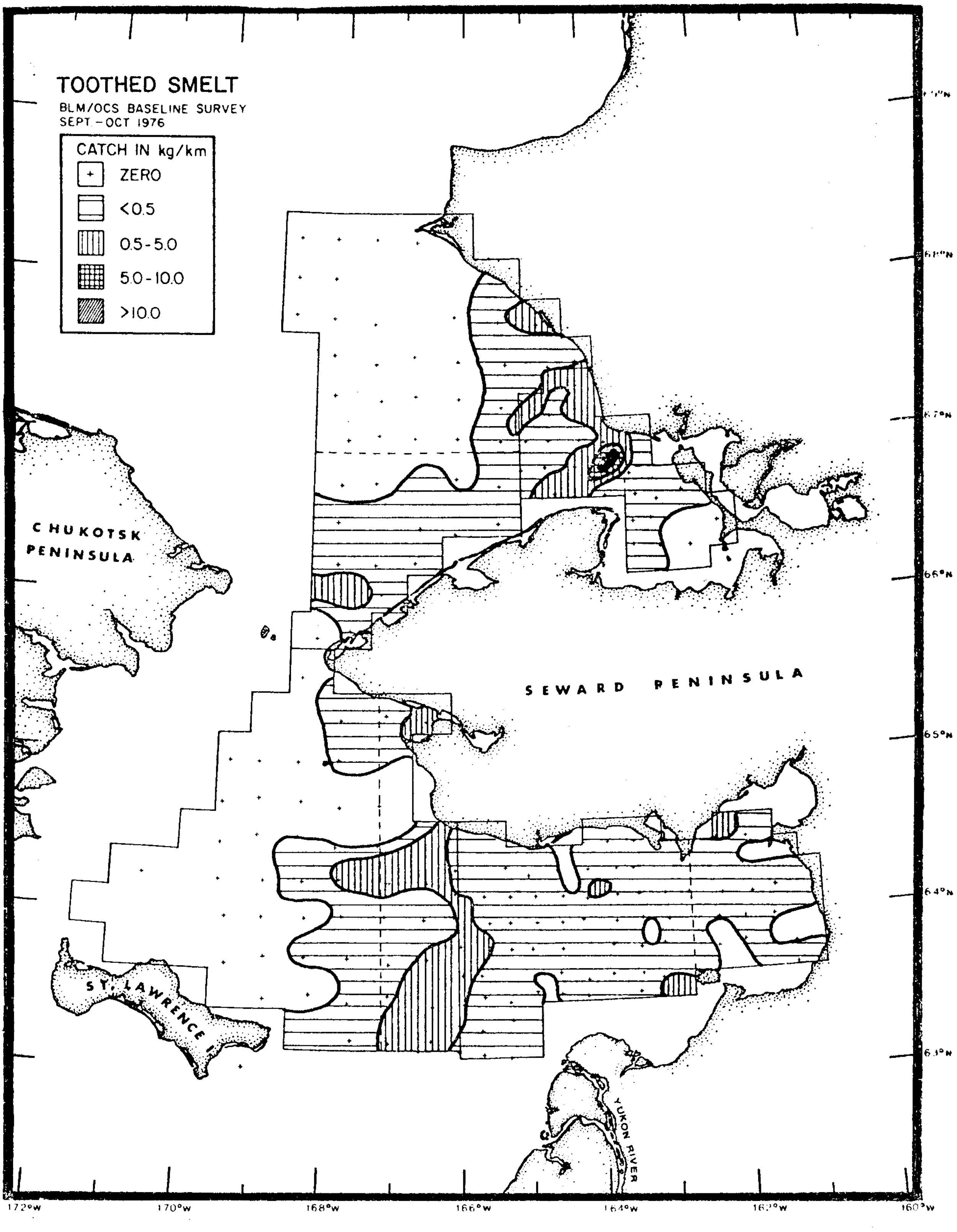


Figure 10 . Distribution and relative abundance by weight of Toothed Smelt in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira et al., 1977, Figure VIII-65, page 163.

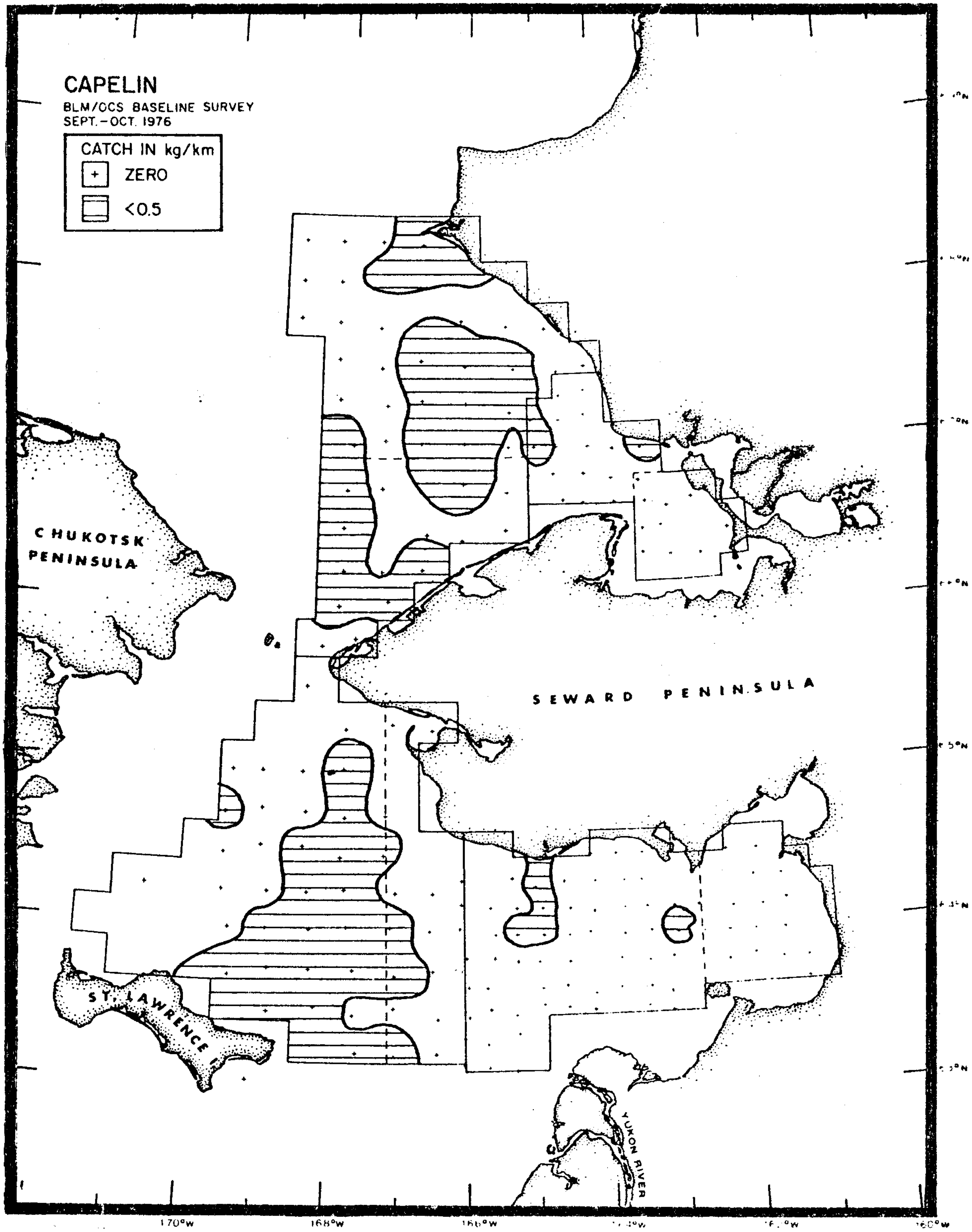


Figure 11. Distribution and relative abundance by weight of Capelin in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira <u>et al</u>., 1977, Figure VIII-96, page 215.

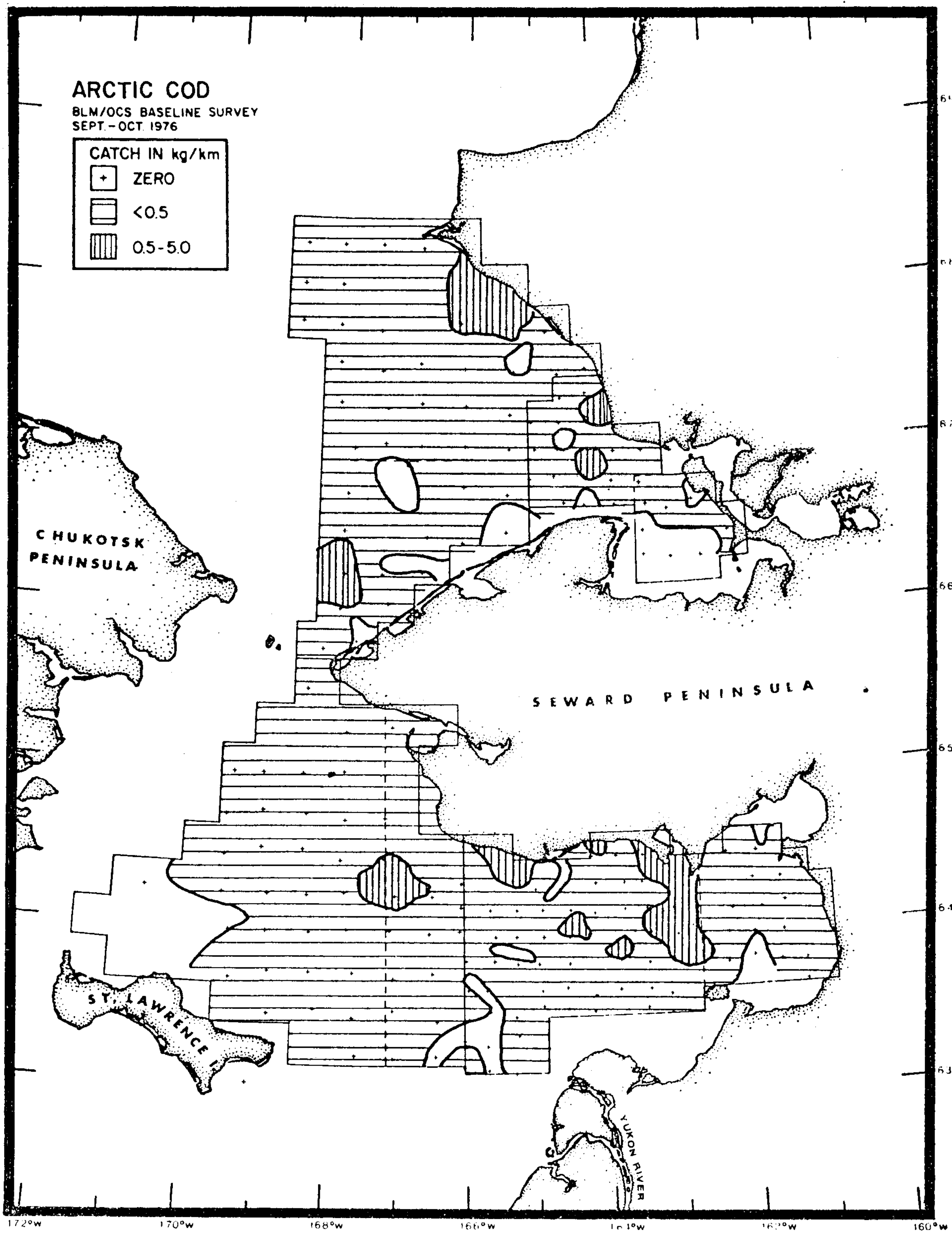


Figure 12 . Distribution and relative abundance by weight of Arctic Cod in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira *et al*., 1977, Figure VIII-83, page 195.

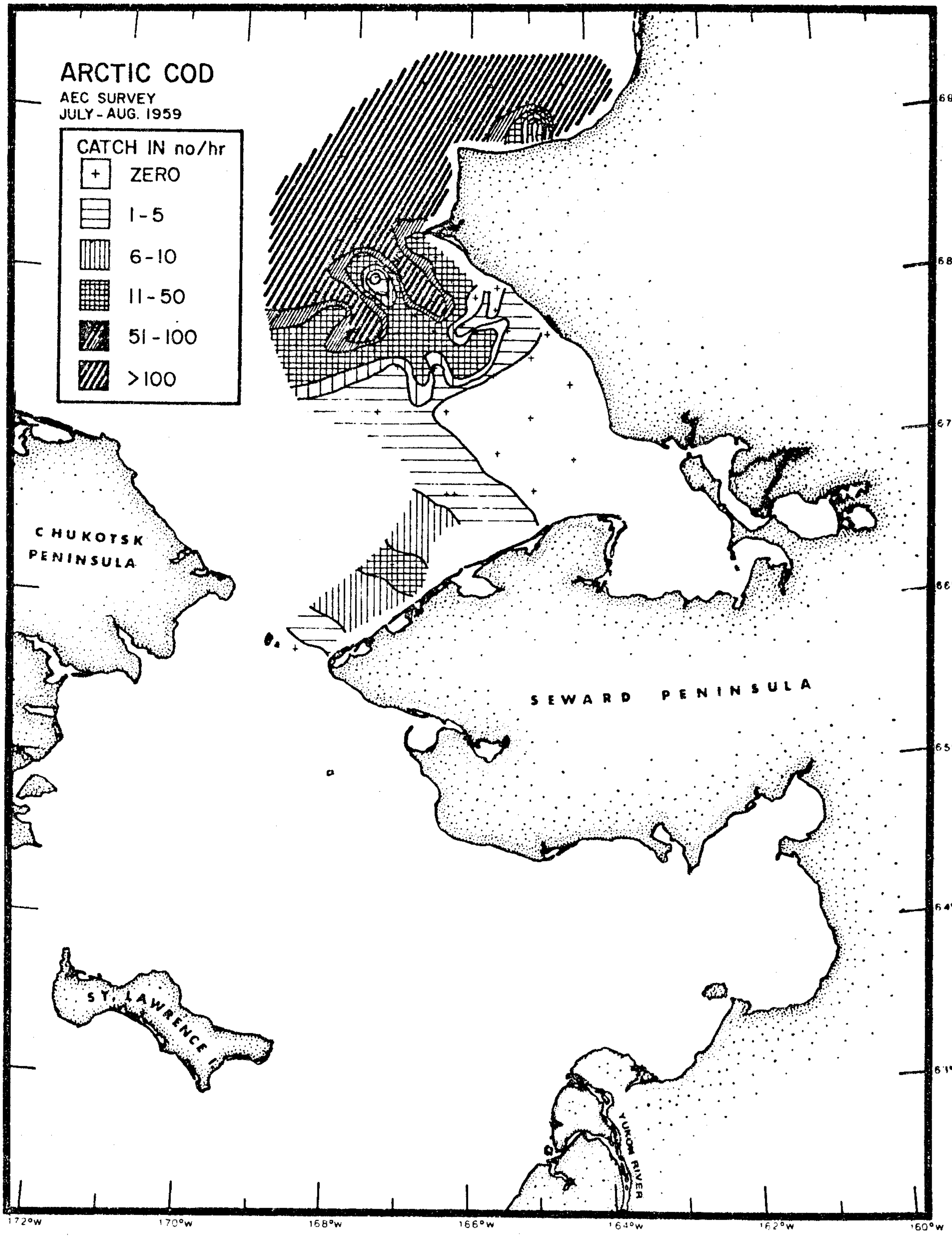


Figure 13. Distribution and relative abundance by numbers of Arctic Cod in the southeastern Chukchi Sea during 1959; from Wolotira et al., 1977, Figure IX-1, page 273.

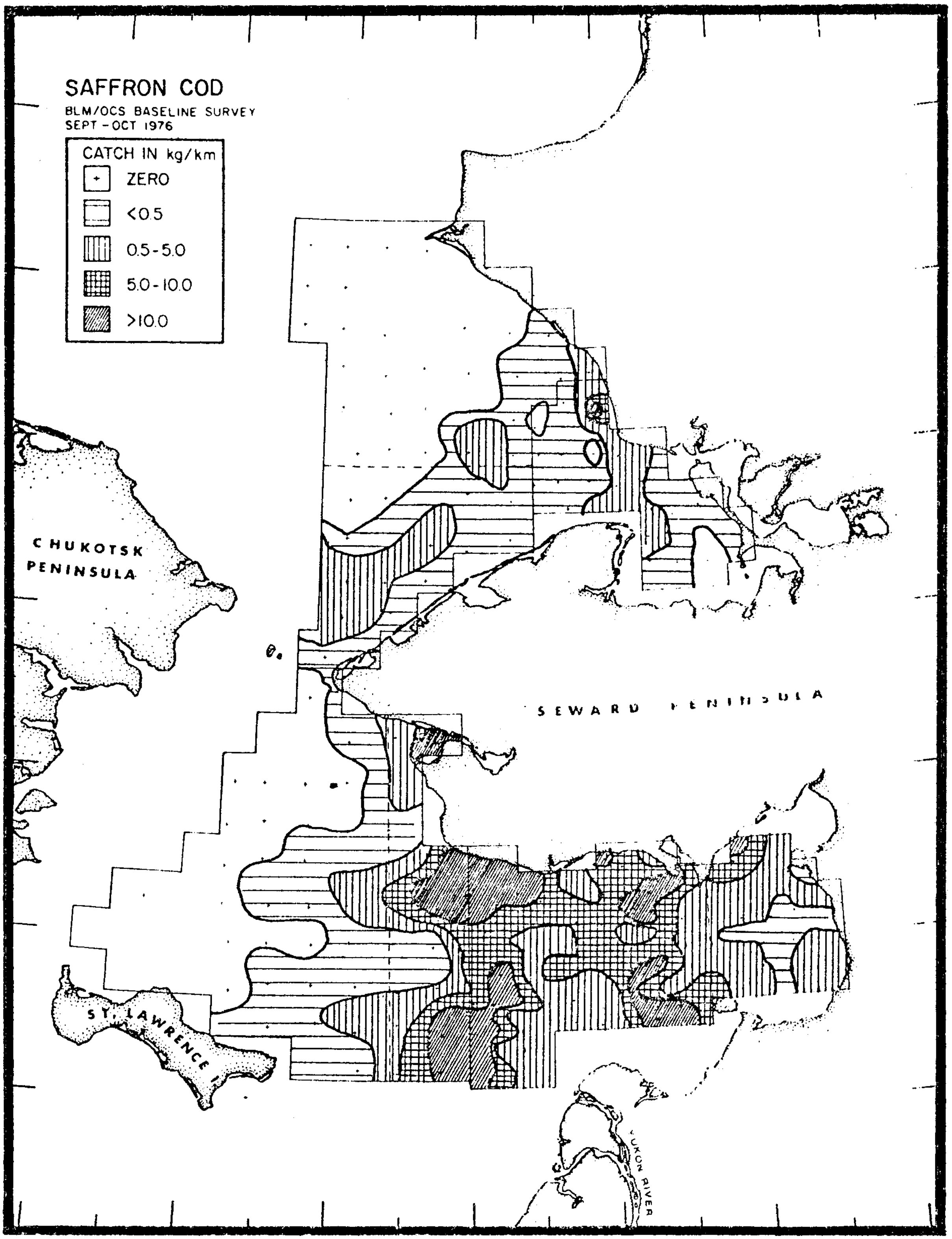


Figure 14. Distribution and relative abundance by weight of Saffron Cod in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira et al., 1977, Figure VIII-45, page 127.

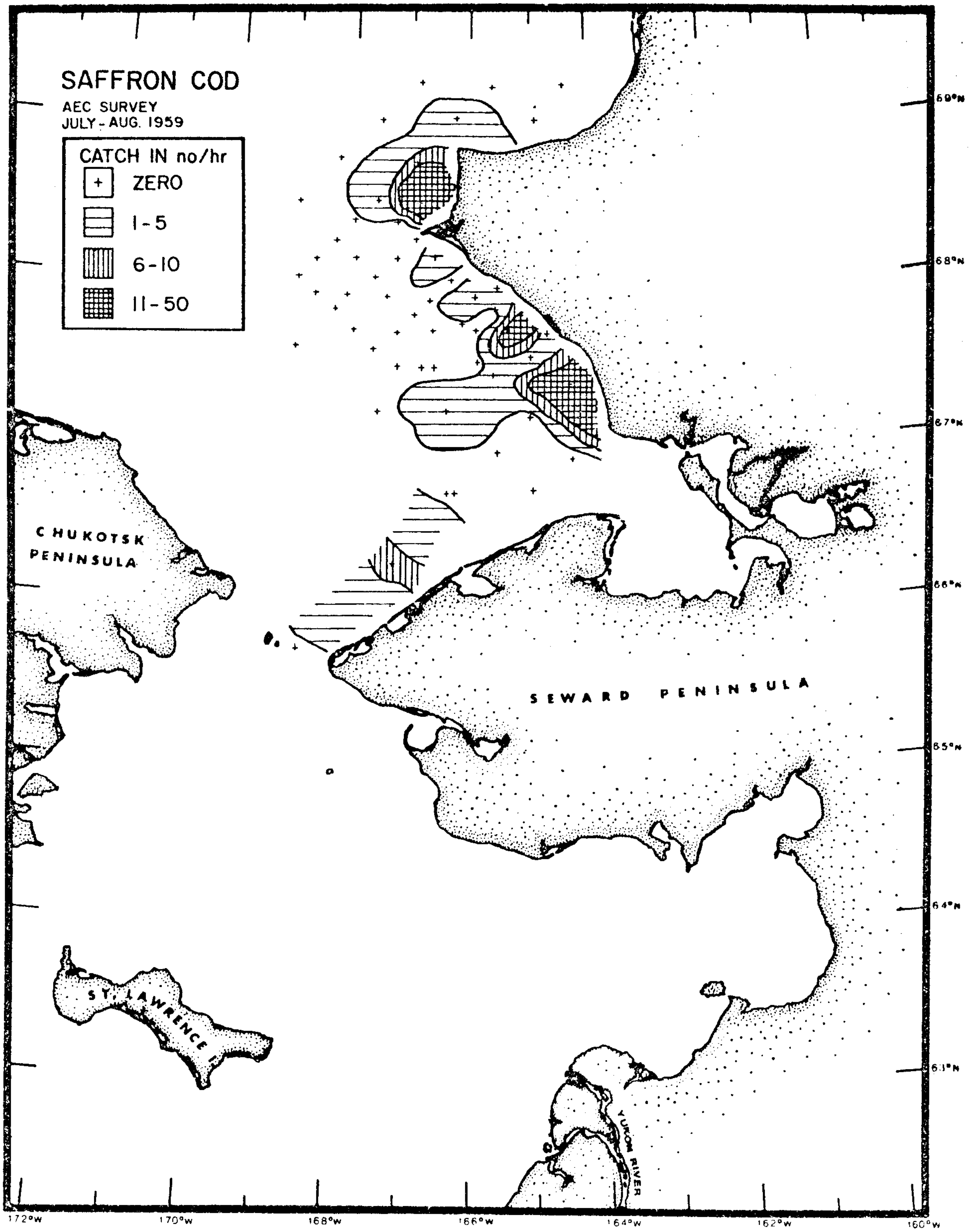


Figure 15 . Distribution and relative abundance by numbers of Saffron Cod in the southeastern Chukchi Sea during 1959; from Wolotira et al., 1977, Figure IX-7, page 280.

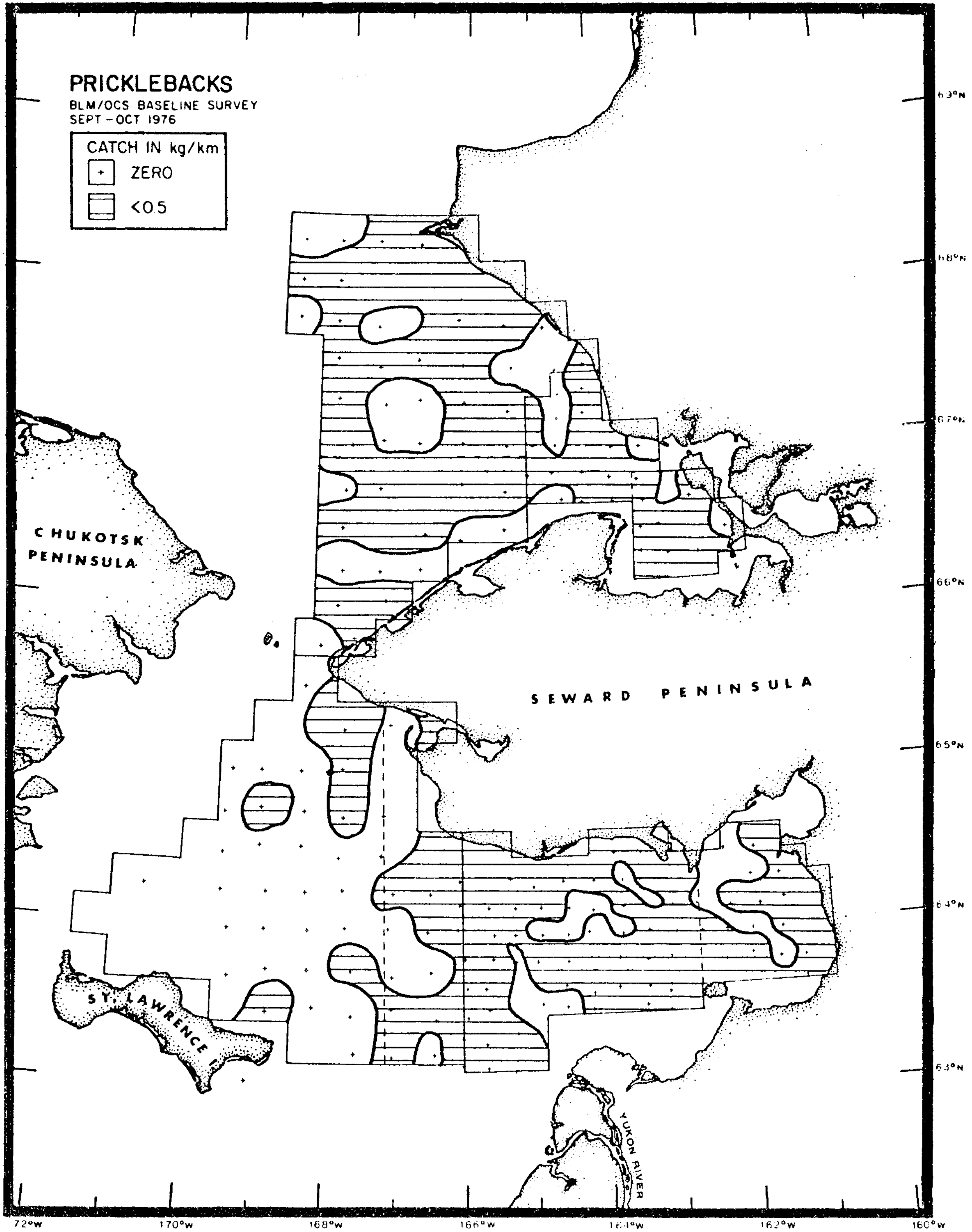


Figure 16. Distribution and relative abundance of Pricklebacks in Norton Sound, the southeastern Chukchi Sea and adjacent waters (BLM/OCS survey, 1976); from Wolotira et al., 1977, Figure VIII-23, page 87.

(Limanda aspera). Cod usually move inshore in the fall and during the winter Arctic Cod or Blue Cod (Boreogadus saida), as well as Saffron or Tom Cod, become available to fishermen. Cod usually move offshore in spring when many flatfish such as Yellowfin Sole move inshore. During the summer most demersal fish are present in highest densities in outer Norton Sound west of a line from Stewart Island to Cape Darby. Beyond the front at the mouth of Norton Sound, the border between the Alaskan Coastal Water and shelf water, the waters are of low importance for commercial demersal fish.

Spawning of Yellowfin Sole is thought to be in late spring; the eggs are pelagic (float). During the 1976 survey of demersal fish a very large proportion of the young were found in mid- and inner Norton Sound, and no young Starry Flounder (less than five and six years old) were found.

Although Pacific Sandlance is considered a demersal fish by fisheries biologists, the species is a major item in the diet of surface feeding seabirds. According to the behavior of these seabirds and the schedule of appearance of Sand Lance as food, the fish move on shore in late July and move progressively eastward with the season. Sand Lance is especially abundant according to fisheries surveys near Port Clarence/Grantley Harbor, off Bluff, and at Golovin.

b. Pelagic fish:

All of the dominant pelagic fish are abundant and well enough dispersed to be used for subsistence and to be important elements in the diets of marine mammals. The dominant pelagic fishes include four species of Salmon Oncorhynchus (primarily Chum and Pink; some Coho, and rarely

King), Pacific Herring *Clupea harengus pallasi*, Toothed or Rainbow Smelt, *Osmerus eperlanus* (*mordax*) and Capelin *Mallotus villosus*. All are schooling species with clumped distributions, primarily in eastern Norton Sound. Although much information is available on their general biology, little information is available on them for Norton Sound.

In the winter Salmon probably occur offshore, south of this region. Adults and juveniles are found in the nearshore zone of Norton Sound throughout the ice-free season. Adults appear in January, and juveniles are found in the lower reaches of all rivers during late spring and summer.

Norton Sound apparently supports large numbers of the immature fish of many northern Bering Sea species. Some forms such as Arctic Cod spawn under the ice and their eggs develop slowly. Others such as Herring, Capelin, Smelt and Saffron Cod make heavy use of embayments, estuaries and lagoons for spawning and growth of early stages. For all of these the shallow, low-saline waters of inner Norton Sound and the coastal lagoons may be important links in their life histories.

E. Marine Birds

1. As one goes east from Cape Nome Common Murres, Black-legged Kittiwakes, Pelagic Cormorants, and Horned Puffins make up the seabird populations. Gull, Cormorant, and Puffin nesting aggregations are smaller and scattered along the coast on small headlands. Instead of nesting in isolated pairs, Arctic Terns gather into large colonies. Aleutian Terns are present as well. Chum and Pink Salmon run the rivers in early summer and as a consequence Glaucous Gulls gather along the rivers and shorelines in mid- and late summer. Most waterfowl migration consists of geese and freshwater ducks. Whistling Swans, Canada Geese, Pintail, Baldpate, and Greater Scaup

are numerous in the lower reaches of rivers that flow into salt marshes or send out distributaries onto broad mudflats. These waterfowl congregate in late July and large numbers persist into late September (see Main Body, Section VII on Coastal Habitats). On the uplands, the tundra vegetation is wetter and taller as more shrubs, including blueberries, grow; east of Golovin, White Spruce grows.

In Norton Sound and the rest of the Alaskan Coastal Water, the predominance of fish-eating seabirds and virtual absence of crustacean eaters (with the exception of small numbers of Parakeet Auklets which have a diverse diet) would appear to be related to available food. Norton Sound is a detrital system. Lack of larger copepods may be a reflection of less dense water and a lack of suitable floating green plants for them, and hence, Euphausiids, and Amphipods are absent as well. Some planktonic and benthic crustacean food (small copepods, Cladocerans and detritus-feeding mysids) must be available to small "silver fish." The small fishes, Herring, Rainbow Smelt, Salmon smolt, Saffron Cod, and especially Sand Lance, provide food for the Common Murres, Horned Puffins, and Kittiwakes.

2. As one goes west from Cape Nome along the southern shore of the Seward Peninsula, migratory seafowl (King Eiders, Oldsquaws, and Black Scoters) are numerous in spring. Auklets become conspicuous elements of the seabird fauna west of Sledge Island and Thick-billed Murres are a major percentage of the murre population. On land beyond Cape Woolley, tundra vegetation becomes progressively lower and more scattered and the waterfowl of fresh water and lowland tundra become progressively sparser.

Long sandy barrier beaches cut off productive lagoon systems beyond Cape Prince of Wales along the northwest shore of the Seward Peninsula and the shore between Kotzebue and the Lisburne Peninsula. The inlets are sites of nesting Arctic Terns and small groups of Glaucous Gulls and Mew Gulls, and near Shishmaref, Sabine's Gulls. The lagoon margins provide nesting sites and molting grounds for loons and waterfowl. The sand dune hollows provide nesting grounds for shorebirds (sandpipers, curlews, phalaropes) and waterfowl. Formerly, nesting geese were abundant in some places. The few seacliffs in southern Kotzebue Sound are sites of small cities of murres and kittiwakes, and the till-covered islands south of Kotzebue support large nesting populations of Horned Puffins.

Most of the lowlands are vegetated with bushy wet tundra vegetation. The vegetation of the uplands is sparser; low places are grassy and sedgy. The uplands of all of northwest Alaska are nesting grounds for shorebirds (godwits, turnstones, surfbirds, plovers).

Almost all of the nesting birds from the uplands, lowlands, and marshes (loons, ducks, geese, swans, sandpipers, plovers, phalaropes, gulls, terns, and cranes) gather on and around the coastal lagoons at some part of their annual cycle, making use of some part of the high biological productivity.

At the northern limit of the Bering Strait Region the cliffs of the Lisburne Peninsula supply breeding sites for seabirds. Some use the productive waters along the convergence of the Bering Shelf Water and Alaskan Coastal Water off Cape Thompson, where Arctic Cod is abundant. Others depend on Sand Lance, which seems to be associated with Alaskan Coastal Water southeast of Cape Thompson and northeast of Cape Lisburne toward Point Lay.

The multitudes of seabirds associated with these cliffs suggest that the waters further northeast along the Arctic lowland would support abundant seabirds if there were cliffs for them to breed on.

F. Marine Mammals

Marine mammals are relatively inconspicuous in Norton Sound, other than small seals and Walrus that drift past on the outer edge of the drift ice in spring. Spotted Seals spend the summer in eastern Norton Sound. The other seals leave. The shoals of Sand Lance do not seem adequate or dependable enough to attract significant numbers of marine mammals into the waters east of Sledge Island. Norton Sound, however, is the range of one of Alaska's major herds of Beluga Whales. Their presence may be associated with the large area of open water, polynya, that is reported to exist off the Yukon Delta in winter. Occasionally porpoises and rarely Minke Whales appear.

The region of the Saint Lawrence Island Waters, Chirikov Basin, Bering Strait, and southern Chukchi Sea is the site of spring gatherings of 120,000 Walrus and summer gatherings of some 15,000 Gray Whales. According to Braham (1978) the two species, Walrus and Gray Whale, combine to form biomass in the order of trillions (10^{12}) of kilograms. The area to the west is the range of formerly large numbers of Bowhead Whales , Finback and Minke Whales. These surface feeding whales are now seldom seen. At present only the benthic-feeding Walrus and Gray Whales are conspicuous. Herds of Walrus feed in the areas south and north of Saint Lawrence Island where eddies allow collection of sediments and benthic invertebrates. They float north through the Bering Strait on drift ice and spend the summer feeding on the benthos in the southern Chukchi Sea. Bearded, Ringed, and Spotted (Common) Seals, which feed primarily on fish and crustacea near the bottom, are numerous and conspicuous on the spring ice. One wonders whether the decrease in plankton-feeding Bowhead and Finback Whales has had an effect on the crustacean food available to auklets.

The Strait appears to form the southern limit of the Polar Bear's winter distribution.

Johnson, Fiscus, Ostenson, and Barbour (1966) indicate that the ice southeast of Point Hope is especially favorable for Bearded and Ringed Seals. This area is along the edge of the Alaskan Coastal Water where it sheers against the Bering Shelf Water.

The movement of Bowhead Whales past Point Hope in April and May is now an event of international importance. Bowhead Whales are reported from the Siberian side of the Chukchi Sea only in October, but a large herd of Gray Whales is known to summer there.

G. Human Settlements

In the southeastern part of the region the Eskimos of the Yukon Delta area speak Yupik. Traditionally, they are river people and depend on river runs of salmon for food for themselves and their dogs, and on waterfowl, caribou, and to some extent small seals for food and clothes.

When first visited by Zagoskin, innermost Norton Sound from Unalakleet to Koyuk was an area of interchange between northern Eskimos, southern Eskimos and Indians from inland. People from the Yukon River came overland to Unalakleet for trading and there, as in the lower Kuskokwim River, tolerant interactions occurred between Athapascan Indians and Eskimos. People from the Noatak and what is now Kotzebue came down the river drainage system behind Buckland to Koyuk. So, Athapascans, Yupik speakers, and Inupiat speakers met and to some extent exchanged goods and ideas.

Inupiat is the primary language at Koyuk and west along the south shore of the Seward Peninsula; but Yupik influence is evident in many ways, such as the barabaras (sod houses) and intermarriage with people from the delta.

At Cape Nome there was a large prehistoric village that made significant use of whales. West of Cape Nome the Inupiat people traditionally depended primarily on hunting sea mammals and seabirds for food and clothes. Smaller seals, Spotted and Ringed, are common and the larger Bearded Seal and especially Walrus were items of major social and economic importance. The people at Ayak (Sledge Island), Ukivok (King Island), and Ignalook (Little Diomede), and presumably those at Big Diomede and Wales, developed a culture which depended primarily on hunting sea mammals by travelling across the sea ice that was drifting around in the Saint Lawrence Island waters. Their ability to travel and to survive in this most inhospitable of environments was a peak of ecological adaptation. Few, if any, now practice the old way of life. Although many hunt out on the ice, they are now heavily dependent on white man's technology even for this.

Traditional settlements in this western part of the area consisted of a number of relatively large (100-125 people) settlements and many small mobile groups of single or several families. Whaling, primarily for the Bowhead, was important at western Saint Lawrence Island and at Point Hope, and a complex social structure emerged, responding to the opportunities provided by this special food supply. Although traditionalists suggest that whaling was pursued for thousands of years in this region, other analysis indicates that whaling is relatively recent. It seems to have appeared about 1000 years ago, when the technology of tying strings of sealskin bladders on long thongs to the harpoon strings diffused into the region from Japan. According to Ray (1976), whaling was relatively unimportant in the settlements within the narrow Bering Strait; that is, King Island, the Diomede Islands, and Wales. The people of King Island reportedly left the island in the summer, dispersing to use resources on the western coast of the Seward Peninsula. The fact that the main Eskimo settlement in Grantly Harbor was traditionally at the mouth of the Tuksuk Channel rather than at the present site of Teller may have been a result of accommodation between the local people and the depredations of summer travelers from King Island.

Although whaling was pursued by the Eskimos at both limits of this area, Saint Lawrence Island and Point Hope, the language groups of the two are different. The people of Point Hope, Kotzebue Sound, the Diomede Islands, Wales, King Island, and the coast of the Seward Peninsula as far as Koyuk and Unalakleet speak Inupiat, the language of the Eskimo of the Arctic Coast of North America. The people of Saint Lawrence Island, however, speak a Siberian form of Yupik. It seems probable that this separation depends on relatively recent tribal movements, i.e., the western end of Saint Lawrence is within sight of Eastern Siberia and is quite remote from the Seward Peninsula and associated islands. It would seem contrived to argue that the separation reflected some important ecological barrier.

The settlements at Wales were, one presumes, dependent on sea mammals and waterfowl. It is not clear whether they were able to make an accommodation with the people of Little Diomede to crop the island's seabirds, but it is unlikely. Early reports indicate that the Eskimos of Wales led a marginal existence.

The entrances to the large lagoons on the northwest shore of the Seward Peninsula such as Shishmaref are traditional village sites. Part of the resources formerly at Shishmaref was a breeding population of geese, now exterminated.

The deltas of the Noatak and Kobuk Rivers resemble the Yukon Delta, and supplied fish and waterfowl resources for the people of the broad lowlands. The people of these rivers had access to caribou and sheep from the hills. Diverse resources from the sea and uplands were apparently available to the people from Sheshalik, Kivalina, and Point Hope.

The people at Point Hope (Tigara) were close to natural polynya, to ice productive for seal hunting, to the seabirds at Cape Thompson (Eesook and Imnikpuk), and to Bowhead and Beluga Whales migrating along leads in the spring.

A former community at Wevak, now destroyed, was probably associated with the bird cliffs at what is now called Cape Lisburne. As Tuck (1960) pointed out, natives consistently have abandoned summer villages at the foot of bird cliffs as one of the first effects of rising standards of living.

APPENDIX V.
DISTRIBUTION OF BIRDS AT SEA

A. Introduction

The patterns of distribution of birds at sea provide good indicators of the important features of their worlds. Seabirds' lives are determined by conditions at sea and the biological characteristics controlled by water masses. They come to land only to breed.

Our data were collected in the course of survey flights over the Saint Lawrence Island waters, Norton Sound, the Bering Strait, and the eastern Chukchi Sea north to Point Lay. The tracklines of our survey flights are shown in the figures in Section D in this appendix. We planned our flights so that each line had a fixed starting point and ending point identifiable by topography, e.g., from Sledge Island to King Island, from King Island to Wales Mountain, from King Island to Savoonga on Saint Lawrence Island, or from the Northeast Cape of Saint Lawrence Island to Sledge Island (Figure A; see also Figures B and C). We surveyed these routes twice in 1977 and three times in 1978.

At 120 knots the plane moved about 10 nautical miles (10 minutes of latitude) in a 5-minute period. Using the 30° angle of observation--60° below the horizontal--the observers on the two sides of the plane flying at about 120 feet altitude have surveyed about 1 square kilometer of water surface. These averages are affected by head winds or tail winds, but we can compensate for these effects because we know precisely where each survey trackline started, where it stopped, and how long it took to fly that leg. The details of our techniques are explained below.

B. Methods

1. Surveys

a) Vehicles. The obvious vehicles for surveying the northern Bering Sea looking for seabirds are ship and aircraft. Each has its advantages, but clearly aircraft was preferable for the work we did. Aircraft allows for rapid coverage of a large area of ocean in order to find where birds occur and the patterns in which they occur, i.e., whether dispersed or clumped. Compared to an airplane, any ship will be very slow, and thus is less suitable for locating the general pattern of birds at sea. Once we know where the birds gather we can then ask questions which might be answered by detailed work such as from shipboard. Ships are well suited for close observations of behavior of birds on the surface, such as feeding behavior, and are the best platforms for shooting birds to collect stomachs. Work aboard ship complements the work that can be done from aircraft.

b) Types of Aircraft. For prolonged flights over the ocean it is necessary to have a twin-engine plane; for making transects it is important to have clear visibility from the passenger seats as well as co-pilot seat. With two observers, duplicate information can be obtained from the observers on each side of the aircraft. In 1976, we used a deHaviland "Islander" operated by Munz Northern Airlines out of Nome. This plane provided excellent visibility from the co-pilot's seat, but poor visibility from the passenger seats.

We tried the Cessna 336 in 1976, using a plane flown by Nome Flying Service, and it proved to be very satisfactory. Though we had made arrangements to use this aircraft in 1977, when we arrived in Nome we learned that the plane had been sold. We then made arrangements through Donald Olson of Golovin to charter a 336 from Arctic Aviation of Kenai during June and August of 1977. The plane was based in Kenai and we paid for 10 hours of "deadhead time" for each set of survey tracklines. Although we were given an excellent price, the lost time and the inconvenience led us to make special arrangements in 1978 with Donald Olson. This arrangement proved to be excellent.

c) Limitations of survey by aircraft. The most serious limitations set on aircraft surveys are 1) that U.S. aircraft are excluded from the western half of the area which we would like to study; and 2) that navigation in aircraft is much less precise than on shipboard. Additional limitations include 3) that it is difficult to maintain consistency of transect width as the plane's altitude changes; and 4) that identification of some species is often difficult. Some of these limitations are only apparent, or can be overcome. One must judge how fine-grained is the distribution of birds at sea before one judges whether the navigation of the aircraft must be precise. The precision of detail one is trying to distinguish should dictate how precisely the width of the transect and the altitude of the aircraft must be maintained. We are convinced that by using aircraft we collected much more data than we could have from shipboard and that the data are precise and rigorous enough to satisfy our objectives. Moreover, expenses would increase several fold if we were to try to improve the rigor. Thus, it makes neither scientific nor economic sense to collect data of any greater precision.

Our tracklines were, as we said, "anchored" on an identifiable "point of departure" for our "ded"/(deduced) reckoning. We planned the grid so that as few lines as possible depended on extrapolated positions. Actual tracks over the water could be deduced from points of departure and arrival, elapsed times, and hence calculated rates of progress.

Inconsistency results from the effects of wind drift and anomalies of the compass headings of our plane. Not only are the magnetic courses in this part of the world evidently approximate, but the deviation or declination of the plane's compass was different on different headings. We anticipated most of this difficulty by setting a gyro compass at departure from the airfield. We are confident that we have removed errors to the level of "significant figures."

2. Techniques

a) Instructions for shipboard transects have been provided 1) for use by the British Royal Navy; 2) by Germaine and Brown for use in PIROP in western Atlantic water; 3) for use in the "Pacific Ocean Survey," and in Antarctic studies (Cline et al. 1969); and 4) for use on "ships of opportunity" during OCSEAP by Coulter, Heineman, and Wiens and by Lensink's group of the U.S. Fish and Wildlife Service. Many people have discussed the advantages and disadvantages of these systems. All use standard periods of watch, areas surveyed, and distances to which birds are counted.

For our shipboard watch we used 10-minute periods, an arc of 90° on one side from directly ahead of the ship, and tried to identify in our counts those birds which were within 200 meters of the ship. We reviewed our technique with Juan Guzman of the University of Calgary who was on Surveyor when we did our transect work from shipboard. It is important to recognize that visual acuity varies greatly. The acuity of one of our observers was much less than that of the other observer. Attention span also varied.

b) On aerial transects we used techniques described by Craig Harrison of the Coastal Ecosystems group of U.S. Fish and Wildlife Service. We counted the birds seen within a swath from approximately under the aircraft out to 60° from vertical; we marked this point on the strut of the "336." We kept records for five-minute periods (Harrison and others used two-minute periods) determined by a standard kitchen timer which rang a bell. This timing mechanism was accurate within 10 to 20 seconds.

In some places we also recorded birds seen "outside" the survey line, but we did not emphasize this effort because our attention was distracted from the important area by looking "outside." Lapses in attention may be the most serious cause of failures in precision and consistency. The Fish and Wildlife Service group had a "spare" observer to spell the other two.

Maintaining altitude was difficult. Altitude often varied between 90 feet and 140 feet and seldom went below 60 or above 160 feet. These failures of consistency have their toll, but again we do not think that they affect the conclusions we have drawn.

Indefiniteness in altitude affects size of the transect sample and our identifications. They affect comparing four murres with six murres, but not comparing two with ten, twenty, or fifty. Birds dive ahead of the aircraft if it flies too low and if the aircraft is too high Crested Auklets begin to resemble Least Auklets, and Parakeet Auklets can be confused with murres. Several observers did not separate species of auklets for that reason. The categories which we considered important were: murres, auklets, ducks, puffins, Glaucous Gulls, kittiwakes, jaegers. There is no confusion among these in our data.

Of more serious concern is the effect of glare from the sun on one side of the airplane which may seriously affect those counts. It is also important that birds become highly visible when the sea is glassy calm in contrast to when the surface is ruffled, marked with white caps, or boiling in current rips. In our experience, however, our observations made in the most unfavorable conditions conform to the pattern of those made when the situation is ideal, with the sea flat and the sky overcast.

C. Results

In the following paragraphs we point out and comment on some regularities in the distribution of seabirds in Norton Sound, the Saint Lawrence Island Waters (primarily the Chirikov Basin) and the southeastern Chukchi Sea. It must be realized that these statements are based on a few, superficial surveys of the area. We believe, however, that the correlations offered by these results are sufficiently sensible and important to justify organizing a systematic grid to be run regularly to establish the validity of what we suggest. We believe they are important because the correlations are with clear elements of the physical features of the area and with the biological structure of the systems. In this way the seabirds are acting as readily observed indicators of subsets of the biological and physical oceanography of the Norton Basin.

1. Areas of Concentration of Seabirds

As we have said before, seabirds were numerous west and north of King Island rather than to the east (see also Shuntov 1961).

a. There is an oval area in which one can expect to see 10 to 50 birds per square kilometer. This area extends 100 km to the south of King Island, west to the International Date Line and beyond, almost 25 km east of King Island, and north to the Bering Strait. Inside that area there is a smaller area, perhaps 75 km from King Island to the south, in which one can expect to see densities of up to 100 birds per square kilometer.

b. An area of very high density of seabirds, occasionally over 300 birds per square kilometer, is found south, southwest, and west of the western end of Saint Lawrence Island, extending out as far as the edge of the air space in which we are allowed to fly. This concentration, 50-100 birds per square kilometer, extends 50 kilometers north of Gambel. A zone of lesser density, 10-50 birds per square kilometer, extends out 90 kilometers northeast from Gambel and 50 kilometers north from Savoonga.

c. Another area of high density, up to 200 birds per square kilometer, is found from a point 25 kilometers south of Fairway Rock to 25 kilometers north of Little Diomede. Occasionally an area less dense, 10-50 birds per square kilometer, associated with drifting ice, extends another 50 kilometers to the north of Little Diomede Island. Ordinarily, the density drops off sharply at 20-30 kilometers north of the island.

d. The mixing zone where the eastern edge of the Bering Shelf Water meets Alaskan Coastal Water, lies along a line from Northeast Cape on Saint Lawrence Island to a point about 30 kilometers east of King Island. According to our observations, drifting ice moving north concentrates along this convergence and feeding seabirds (including crustacean feeders) and migrating waterfowl follow the line of pack ice. Another area of sea ice exists north of Saint Lawrence Island where shelf ice persists after most of the Chirikov Basin has thawed. This seems to be related to the relative stability of shelf water in the lee of the island.

Our observations indicate that the distribution of birds closely corresponds to the distribution of sea ice in spring and of the cold, saline water in summer (see figures that follow in this appendix).

The relation of the observed distribution of seabirds to the findings of fisheries biologists is obscure. In fact, the most complete report available to us, that by Wolotira _et al_. 1977, shows that the commercially valuable bottom fish are concentrated in the warmer shallower water in Norton Sound and are relatively less abundant in the deeper, colder western waters. Among the seabirds, the fish-eating species are evenly distributed from east to west across the region and the plankton feeders are more abundant to the west. Thus, these findings do not correlate with any of ours.

2. _Changes in the Distribution of Birds at Sea Through the Summer Season_

These comments apply to our aerial observations over Norton Sound and the Chirikov Basin. We did not run systematic surveys of the southeastern Chukchi Sea.

a. _In June_, most of the seabirds occur further east than they do later in the season. This may be related to the concentration of drifting ice. In the years when we flew, ice was east of King Island. We found an aggregation of all three species of auklets along drift ice right in Norton Sound on June 4, 1976. When the ice is moving through, auklets occur northeast of Savoonga, southeast and east of King Island. When drift ice was present in the eastern Chirikov Basin there were proportionately fewer auklets west of King Island (except for dense flocks of courting birds close to the island), and in the Saint Lawrence Island area where there was little drift ice. We do not know whether the main ice occurs sporadically west of King Island and what the distribution of birds would be in that case.

We saw more murres at sea in June than we saw later; many of these were in a cresent pattern from south and southeast to east of King Island. Murres were widely dispersed in June, while later on they gathered on a few seemingly preferred fishing grounds. This may be related to their feeding early in the season on crustacea or Arctic Cod associated with the ice, and later at concentrations of fish.

Waterfowl (Oldsquaw and Common Eiders, King Eiders and Black Scoters) were seen flying along the edges of the drifting ice and in flocks in large leads in the drift ice. Migrating flocks of Black Scoters seemed to follow the edges of the windrows of drift ice as "leading lines", that is, as if they used the edges as a geographic feature to guide their migration.

b. In July, we saw virtually no birds feeding between Sledge Island and the Northeast Cape of Saint Lawrence Island.

Some murres and a few auklets feed in the area which lies half to two-thirds of the way between Sledge Island and King Island. Our few data suggest that when the Gray Whales are present in July they occupy the southwest quadrant, and murres feed in an area to the southeast of King Island and in another area to the northwest of the island. Murres also feed in large numbers southwest, west, and north of Gambel, and in an area from 20 miles south of Fairway Rock to 10 miles north of Little Diomede. In this northern area we have found the clearest evidence of murres selecting one body of water to the exclusion of others. When we passed over a "front" marked by a slick and sometimes by spindrift from one water mass into a water mass of different color, we occasionally passed from "many murres" to "none," or vice versa.

In July, auklets were found in large numbers from Gambel to southwest of King Island, in lesser numbers west and northwest of King Island, and in very large numbers between Fairway Rock and the Diomedes and a short distance to the north. At this season, we saw few auklets between King Island and Savoonga.

In July, the "balls" of Sand Lance arrived in the Alaskan Coastal Water off the Seward Peninsula, apparently moving into Norton Sound from the west; feeding melées of kittiwakes, puffins, and a few murres, associated with these dense schools, occurred first off Sledge Island and later in the season off Safety Lagoon and southeast of the Cliffs at Bluff.

c. In August, murres persisted in the feeding grounds southeast of King Island and occurred all along the track from King Island to Gambel and beyond into the Anadyr Strait. Murres also occurred north of King Island and in the "front" waters near the Bering Strait. Moderate numbers of auklets occurred from north of King Island along a line to the southwest toward Gambel, the numbers becoming heavy within 40 miles of Saint Lawrence Island and near the Diomede Islands. Both murres and auklets were numerous in the Anadyr Strait west of Gambel and to the southwest of Bunnell Cape on Saint Lawrence Island.

Large, dense flocks of auklets flying southwest were seen from Gambel on Saint Lawrence Island during all summer months. This suggests that birds from the nesting grounds near Gambel or Savoonga may commute to feeding grounds in the Anadyr Strait, or that auklets from Owalit Mountain and Bunnell Cape commute to feeding grounds north of Gambel.

We noticed that when fog patches lie close to the nesting areas, large numbers of all species are found close, within 5 nautical miles of the cliffs, and many fewer beyond.

The waters of Norton Sound were virtually empty of birds in August beyond 20 miles from the Cliffs at Bluff, although there were small feeding aggregations off the mouth of Golovin Bay.

Shearwaters moved into the Chirikov Basin in mid-August and September (Divoky *et al*. 1977, 1978) and concentrated between King Island and the western part of Saint Lawrence Island, although some flocks were also seen south of Sledge Island and north of King Island. Divoky *et al*. reported large numbers of shearwaters in the Bering Strait and southernmost Chukchi Sea in September.

3. *Patterns of Distributions of Individual Species*

Each species has a characteristic pattern of distribution which, one presumes, reflects the "foraging tactics" of that species.

Auklets tend to feed in flocks, *murres* are more dispersed (see "6. An Example..."; *kittiwakes* are widely distributed in small numbers, and they have a specialty: they feed in the debris brought to the surface by feeding Gray Whales, as do, to a lesser extent, puffins, murres, and Glaucous Gulls. Auklets and Thick-billed Murres occur in much larger numbers in the Chirikov Basin than in Norton Sound; their numbers apparently increase even further as one goes into western Saint Lawrence Island waters and in the Bering Strait.

Pelagic Cormorants are seldom seen more than 5 nautical miles from a nesting or loafing rock. When occasionally they have been seen further off, they were associated with or perched on ice pans.

Glaucous Gulls are found scattered along the sand beaches. They also occur in flocks around the seabird cities, at inlets to lagoons, and at the mouths of rivers. They have breeding territories at bird cliffs and on islands in tundra lakes. They are seldom seen over the open sea and if so, they are associated with the smudges made by Gray Whales or with seals on ice pans.

Where herds of Walrus are hauled out on ice pans in June there are congregations of immature and adult Glaucous Gulls. They also congregate at carcasses of Walrus, whether floating, butchered on ice pans, or stranded on the beaches.

Black-legged Kittiwakes are seen close (within 20 miles) to nesting areas and beyond that are very sparse and highly clumped. They occur consistently over debris brought up by Gray Whales. We have seen them in feeding melées east and southeast of King Island, between Cape Spencer and York Mountains, east of Little Diomede Island, and between Sledge Island and the mouth of Golovin Bay. When the pack ice is drifting northward east of King Island, kittiwakes occur in groups in the same areas as murres; that is, along the edges of the ice or clumped here and there where pans of ice are widely scattered. Kittiwakes also occur in large and dense flocks on freshwater ponds near the coast and at the mouths of rivers. Gould's data for September 1975, west and northwest of King Island, indicate a lack of kittiwakes and reflects the small numbers of kittiwakes nesting on King Island. In September 1976, Divoky et al. (1978) found kittiwakes scattered near the large kittiwake city at Little Diomede Island.

Pomarine Jaegers are seen far at sea in small numbers. They are usually seen near drifting ice and especially near pods of marine mammals. They occur with Glaucous Gulls where Walrus have been butchered.

Thick-billed Murres and Common Murres occur in a half-moon shaped pattern extending east to south about half way between Sledge Island and King Island. They aggregate along the edges of windrows of ice pans in June and occur with the ice further east at that time than they do later in the year. At the edges of bands of ice pans west of Sledge in June, there is a concentration of murres where ice pans are scattered; where ice cover is more than 60% , the number of murres is much smaller.

They occur, scattered widely, distributed at sea in loose aggregations, between King Island and Savoonga or Gambel. Murres are less numerous in the area to the southwest of King Island where Gray Whales are most numerous. Murres are numerous south and west of Sledge Island and in the area west, northwest, and north of King Island. Murres occasionally occur in moderately dense groups between King Island and Wales and between Fairway Rock and Little Diomede. They gather in certain water masses east of Little Diomede. They are numerous within 30 miles of the seabird cliffs around Savoonga and the Southwest Capes on Saint Lawrence Island, and within 10 miles of Cape Thompson and Cape Lisburne. Murres are scattered out to about 25 miles south of the cliffs at Bluff and gather near the mouth of Golovin Bay, and to a lesser extent between Topkok and Safety Lagoon.

When the light was good, we tried to separate those murres which appeared to be brown (presumed to be Common Murres) from those appearing to be black (reportedly Thick-billed Murres). These observations suggest that Thick-billed Murres occur further offshore than Common Murres, but we need many more observations. We are not convinced that this distinction is dependable because some Thick-billed Murres appear to have brown heads and because, in the diffuse light, most murres look intermediate between black and brown. It would be desirable, however, to make counts of "black" and "brown" murres at several times of year to establish the geographical segregation of the two species at sea.

Pigeon Guillemots have been seen close to the rubble slopes where they nest and occasionally have been reported tens of miles at sea. It is hard to assess the possibility of misidentification of those seen at sea because they have been reported by relatively inexperienced observers. Some plumages of Steller's Eiders resemble a Pigeon Guillemot in flight and these small eiders are seen occasionally far at sea.

Kittlitz's Murrelet deserves special attention because the species is rare and widely scattered. Individuals have been seen from about 10 miles south of Sledge Island through an arc to the southwest and west to a point 10-15 miles west of Cape Woolley, and also northeast of Cape Lisburne and southwest of Cape York.

Auklets are easily recognizable as such, but distinguishing among the species is often difficult. Usually separating Crested Auklets from Least Auklets is straightforward unless the altitude of the aircraft is varying. Least Auklets are recognized by small size, pale belly, and buzzy flight. Crested Auklets have a somewhat clearer separation of the wingbeats, are larger, and have dark bellies. Parakeet Auklets are clearly distinguishable when one gets a good look. They have longer wings than the other auklets and show a lot of white flank feathers as they take off. They appear blacker than the other auklets and have a white belly.

Although auklets occur further east during June when ice pans are drifting north, their primary feeding grounds are west of a line extending north from Savoonga through King Island. In this area of ocean, restriction by the International Date Line becomes significant. In June, auklets have been seen in moderate numbers half way between King Island and Cape Rodney on the Seward Peninsula in calm water surrounded by ice pans. They were also seen between Savoonga and Sledge Island in June when the ice had recently moved through. They are often seen together with feeding murres in June, two-thirds of the way from Sledge to King Island. The largest numbers of auklets unquestionably occur a) southwest, west, and northwest of Saint Lawrence Island, and b) in extraordinary concentrations in the Bering Strait. In June and occasionally later, dense active rafts of (most often) 50, up to 100, 500, or 800 Crested Auklets are found within 10 miles of the major rubble slopes where they breed. In July and August, auklets are found along the edge of the international border. Our experience is that they continue to be numerous when one drifts too far west and crosses the International Date Line.

Our data suggest little regarding segregation of the feeding waters of the three species of auklets. Our impression is that Crested Auklets may forage farther to the east and southeast than Least Auklets, whose numbers are conspicuously high near Saint Lawrence Island and in the Bering Strait. According to our results, Parakeet Auklets occur mostly south, and perhaps to the southeast, of King Island. However, Parakeet Auklets are sparse and occur with other auklets; so the problem of attention arises in assigning a distribution to this relatively infrequent species, i.e., "not looking for" Parakeet Auklets and "looking for" Parakeet Auklets once one has been noticed. Both of these human weaknesses will bias reports of distribution of Parakeet Auklets to be clumped. Parakeet Auklets, which feed on a broader spectrum of crustacea than do other auklets, occur in Norton Sound in small numbers.

Horned Puffin may be the one species of seabirds in our region for which one can refer to "feeding radii." They appear to stay closer to the bird cliffs than do murres or kittiwakes. Moderate numbers are observed within 10 miles of nesting areas. Then there is usually a ring of area in which there are few birds; beyond that area, they are seen in small numbers out to 35 nautical miles. The small numbers seen at longer distances from nests may erroneously suggest "over dispersal" simply because of the exponentially larger area of water at greater distance. Puffins rush to gather at kittiwake feeding melées and are seen at smudges raised by Grey Whales.

Tufted Puffins' distribution resembles that of Horned Puffins, and Tufted Puffins occur at greater distances from breeding grounds than do Horned Puffins. We have seen larger numbers of Tufted Puffins at sea than we would have anticipated according to the numbers among nesting birds. We saw Tufted Puffins in larger numbers than expected southwest of Sledge Island and southeast of King Island; we don't know why.

4. Relation of the Distribution of Seabirds to Bottom Topography

The ten-fathom curve has been shown on some of the maps that follow the text in this Appendix. The distribution of sightings suggest that some correlations exist between the distribution of seabirds and the nature of the bottom.

Black-legged Kittiwakes seem to prefer the edges between shallower and deeper water and to search the Chirikov Ramp, presumable looking for the Gray Whales which congregate there.

Murres occur over shallower water and appear to search the waters over the Cape Rodney Parallel Valleys, Gambel Shoal, and, perhaps, the Wales Shoal. Our sightings seem to fall primarily in water less than 20 meters. In the southeastern Chukchi Sea, they appear to feed on the edge of the deeper water, which is the edge of the Alaskan Coastal Water southwest of Cape Thompson. They feed in the gyre northeast of Cape Lisburne in larger numbers than in the water flowing north past the cliffs. They were numerous all through the Anadyr Strait and some kilometers north of Gambel. It appears that murres prefer bottom of uneven topography, with coarser sediments and some rocks. They were seen less often than expected over the benthic-rich sediments of the Chirikov Ramp.

Horned and Tufted Puffins were seen over shallower water.

Crested and Least Auklets were seen primarily over the Chukotka Trough, the Anadyr Sea Valley, and the Bering Strait Sea Valley. It may be that the birds are in these waters because of more turbulence, higher salinity (both of which contribute to higher productivity of large Copepods) or to greater depth of the water, i.e., over thirty meters.

5. Summary of Distributions

The major correlation is with the two main bodies of water. The widespread circumboreal species of seabirds are about equally distributed across the two. Auklets and Thick-billed Murres are virtually restricted to the western part of the more saline and colder waters. This correlation seems to reflect whether the systems are detrital or pelagic, that is, whether most of the productivity cycles through benthos because organic matter settles out of the water column or whether enough organic productivity is cropped by large copepods while still in the euphotic zone to support crustacean-feeding vertebrates.

Further correlations exist: 1) between distributions and depth of water, whether greater than or less than 10 fathoms (20 meters); 2) between distributions and whether the bottom is covered with deep, soft sediments or is rocky; 3) between distributions and the turbulence of the water; and 4) between seabird distributions and the distribution of ice floes along the western edge of the Alaskan Coastal Water and the movement of this ice northward along the front of the coastal water with the Bering Shelf Water.

6. An Example of Data Transcribed

The data displayed in Table V.1, are directly transcribed from the tape recorder as recorded during a transect southwest from Owalit Mount on Saint Lawrence Island, then northeast up to Anadyr Strait towards Gambel on August 17, 1978. These data correspond to Figures I.B.2g, I.B.4d, and I.B.5d. The columns in Table V.1 should be read from the top down: this vertical movement indicates the passage of time. Times are shown on the right hand side of the column and are given on 24-hour clock set to Bering Sea Time: i.e., minus 11 hours Greenwich Mean Time.

The point is to show that the distribution of murres is relatively uniform. That of the auklets is patchy and the birds tend to be clumped in flocks, often dense ones. This transect records one of the densest concentrations of birds we found.

Table V.1 Data transcribed as recorded during a transect southwest from Owalit Mountain, Saint Lawrence Island, then northeast up the Anadyr Strait towards Gambel, August 17, 1978, starting at 1330 hours.

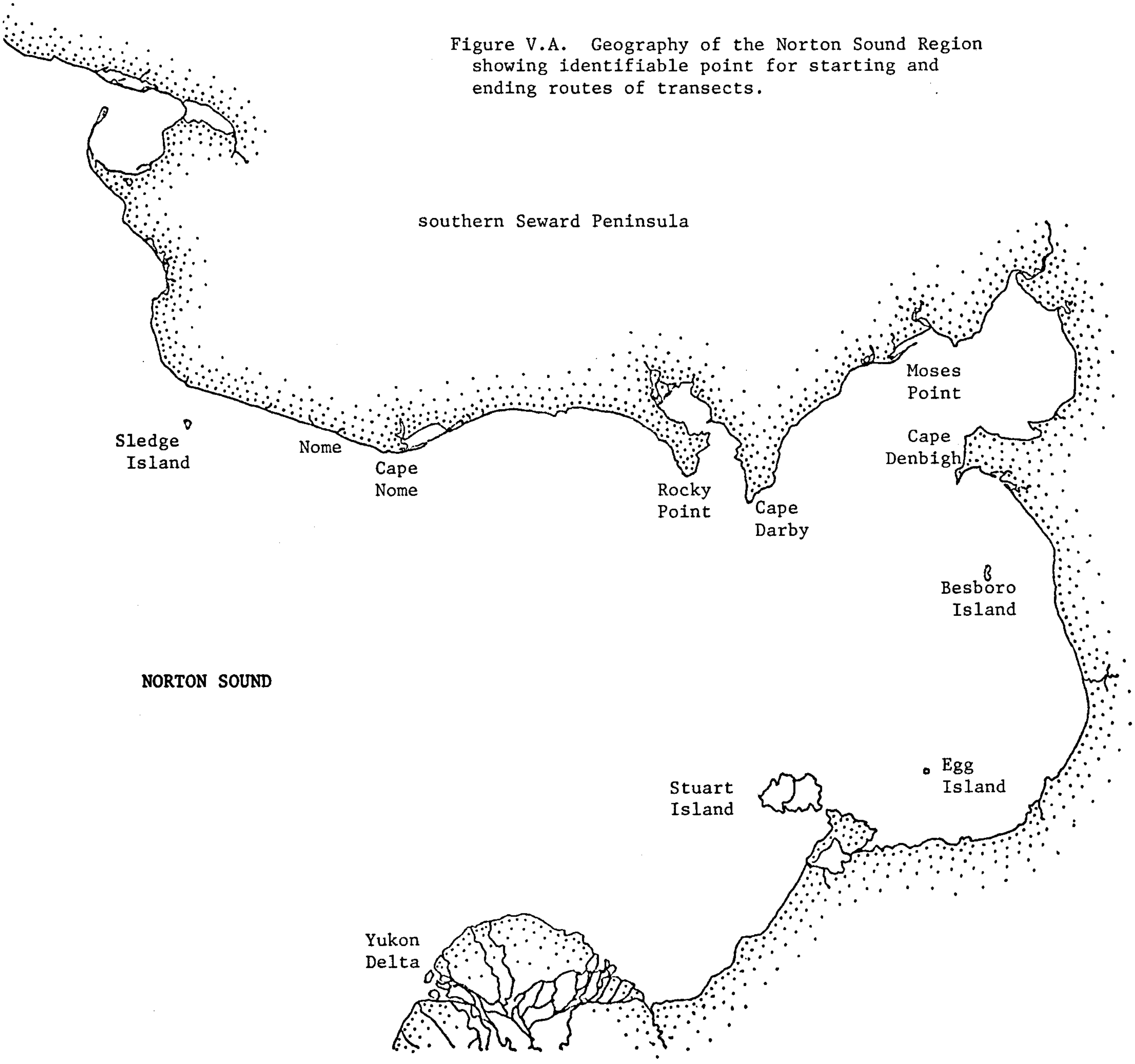
Murres	Crested Auklets	Least Auklets	Time
			1330
1			
3			
2		10	
1			
1	3		
		8	
	2		
1			
1			
5		60	
	4		
	1		
	3		
	15		
	20		
		40	
	8		
1	3		
1		1	
		2	
1		20	
1			
1			
1			
1	1		
	4		
	1		
	1	75	
		1	
	4		
3	4		
	1		
	8		
	1		
1	4	30	
2		3	
	4	15	
		2	
2	1	3	
1	1	5	
	2		
1	4		
		2	
		15	
		35	
		12	
		8	
		40	
		5	1335
		6	
		15	
		4	
		30	
1		10	
1		8	
	1		
	4		
	3		
1	3	3	
1	2	5	
		3	
		15	
		2	
		8	
1		7	
	1	5	
		2	
		2	
		1	
		1	
1	1	25	
1	2		
1		5	
	2	1	
	1		
1	1		
	2		
1			
1	1	1	
	4		
	1		
1			
1			
1			
2	1		
	2	1	
1			
1			
2			
2			
1			1340
1	12		
	1		
	1		
1	1		
	12		
1	20		

Table V.1 -continued. Data Transcribed from Transect.

Murres	Crested Auklets	Least Auklets	Time
1		5	
		8	
	6	15	
		5	
	8	25	
		2	
		1	
		2	
		3	
		2	
		11	
	1		1345 Turn to north-east course
	5		
	2		
1			
1			
1			
	1		
	1		
	8		
1			
1			
1			
	2		
1	1		
2			1350
4			
1	2	1	
1	1		
1			
1	2	1	
3			
1			
1			
2			
	4	15	
		2	
2	2	7	
	1		
1			
2			
1	2	12	
2	1	1	
1	1		
1	1		
	2		1355
	1	8	
1	4		
		1	
1	1	1	
	1		
	1		

Murres	Crested Auklets	Least Auklets	Time
1	1	1	
	2		
	4	8	
	2	2	
	2	15	
	1	2	
	1		
	2		
	8		1400 Turn to course parallel to the shore
	25		
	70		
	20		
4	30		
	30		
	20		
	2		
	1		
	15		
	4		
	50		
	3		
	1		
	1		
	1	15	
	1		
	12		
	2		
	15		
	1		
	6		
	3		
	2		
	2		
	1		
	4		
	1		
	1		
1		1	1405
	1		
2	1		

Figure V.A. Geography of the Norton Sound Region showing identifiable point for starting and ending routes of transects.



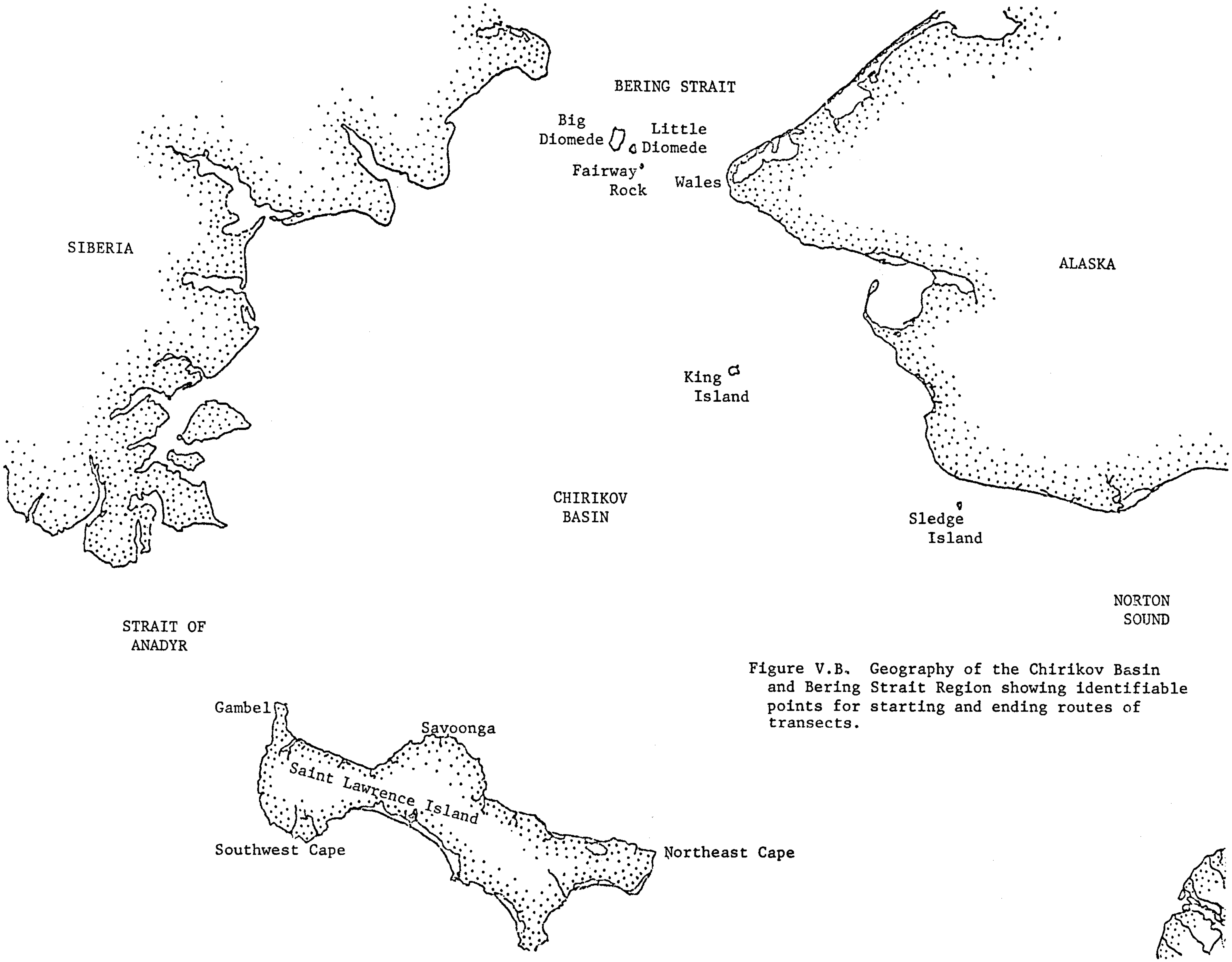


Figure V.B. Geography of the Chirikov Basin and Bering Strait Region showing identifiable points for starting and ending routes of transects.

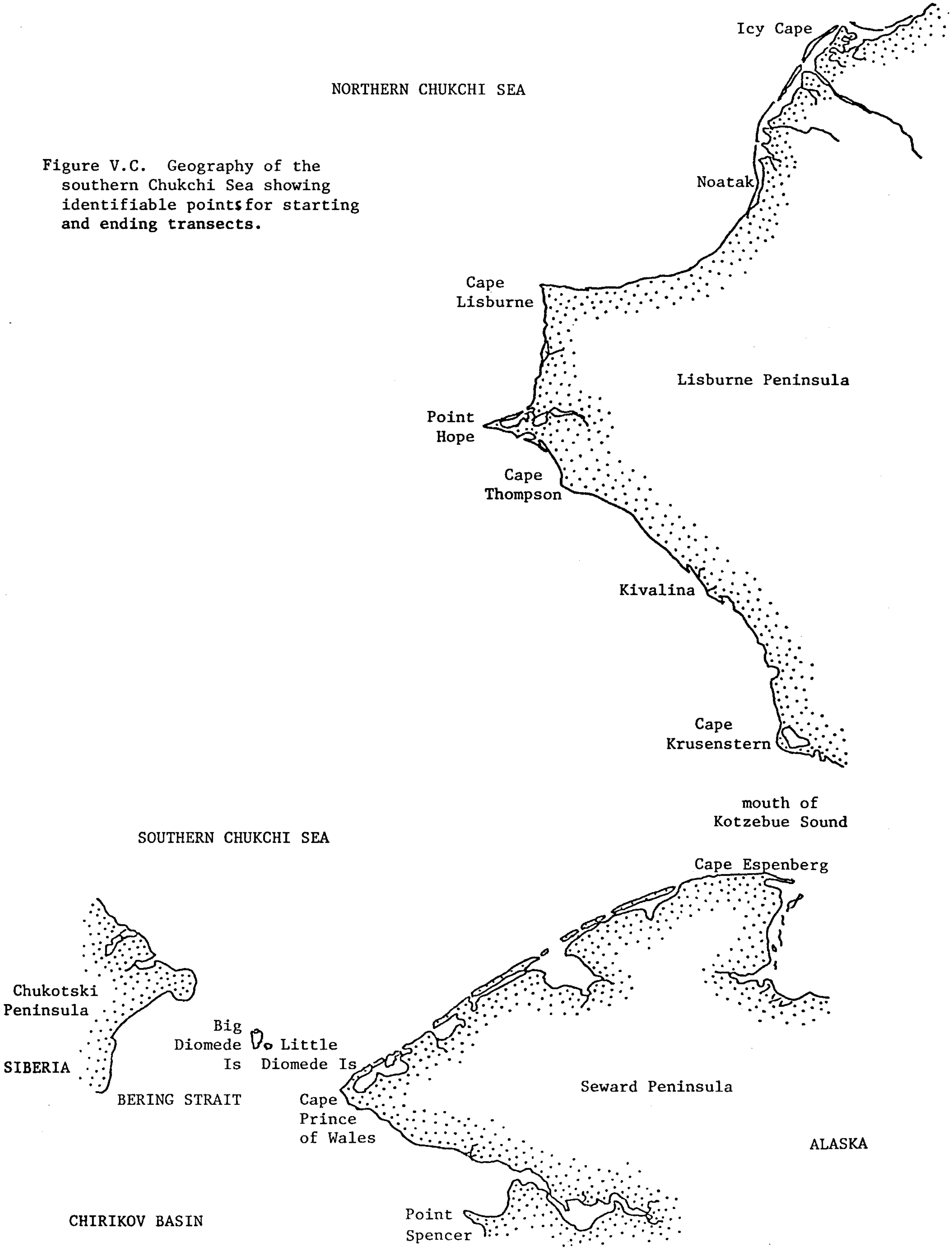


Figure V.C. Geography of the southern Chukchi Sea showing identifiable points for starting and ending transects.

D. Maps of the Distribution of Birds at Sea

The following collection of maps illustrates the distribution of birds at sea, both early in the season in the presence of ice and later on in July, August, September and October. Transects have been charted for observations of murres, auklets (all inclusive, i.e., unidentified + Least + Crested + Parakeet), Least Auklets, Crested Auklets, Parakeet Auklets, Horned Puffins, Tufted Puffins, Glaucous Gulls, and Black-legged Kittiwakes.

We include general representations of the distribution of sea ice in the month of June based on data from flights during only two springs (Drury *et al.*, in 1977 and 1978). Also included are maps showing very general densities of ice along the routes of transects.

The data on the distribution of birds at sea used in the maps come from transects conducted by Drury *et al.*, in 1976, 1977 and 1978, and Harrison in 1976 (1977); and surface transects (shipboard surveys) conducted by Drury *et al.*, in 1976, Gould *et al.*, in 1976, and Divoky *et al.*,in 1975, 1976 and 1978 (1978, 1979).

The maps are divided into two groups: data from aerial surveys and from surface surveys. Within each group maps are segregated by region: Norton Sound, Chirikov Basin, northern Bering Sea including both Norton Sound and the Chirikov Basin, the southern Chukchi Sea, and the northern Chukchi Sea. Maps of transects run in the same region are further segregated by species and then month. An annotated list of the maps, in outline form with page numbers precedes the maps, on pages 103 to 110; the figure number on each map corresponds to its outline number (e.g., the distribution of Least Auklets along aerial transect lines run over the Chirikov Basin in August is shown in Figure I.B.4e).

Figures I.A.1a through II.D.8b. The Distribution of Birds at Sea.

Below is a list of the figures which follow, as described in the preceding pages. These figures extend from page 111 to page 314.

*Asterisks before a figure listed below indicate that the data presented in that figure was obtained when sea ice was present.

page

B. Chirikov Basin - maps from Drury _et_ _al_.

C. The Bering Sea, including Norton Sound and the Chirikov Basin - maps from Harrison (1977)

page

4. Least Auklets

5. Crested Auklets

6. Parakeet Auklets

7. Horned Puffins

8. Tufted Puffins

9. Glaucous Gulls

A. Norton Sound - maps from Drury et al.

B. Chirikov Basin - maps from Drury et al., Gould et al., and Gould et al.

C. Southern Chukchi Sea - maps from Divoky *et al*

D. Northern Chukchi Sea - maps from Divoky *et al*.

NOTE

We feel that it is important to remind the reader of some obvious things: the area of a ring between 10 and 20 km from a seabird city is much smaller than the area of a ring between 50 and 60 km. This has an important effect on the "density" of birds seen at sea. For example, if 15,000 murres leave King Island in all directions and 1500 settle on each ring that is 10 km across, i.e., 1500 at 1-10 km, 1500 at 20-30 km, etc., then the number seen by aerial transects will be as follows:

0-10	4.7
10-20	1.6
20-30	1.0
30-40	0.7
40-50	0.5
50-60	0.4

I. AERIAL TRANSECTS

A. Norton Sound

B. Chirikov Basin

C. Bering Sea, including Norton Sound and the Chirikov Basin

D. Southern Chukchi Sea

The 40-fathom depth is outlined on the maps of the Chirikov Basin.

Figure I.A.1a
Representation of ice coverage along route of surveys run on June 4, 1976 (Drury et al.).

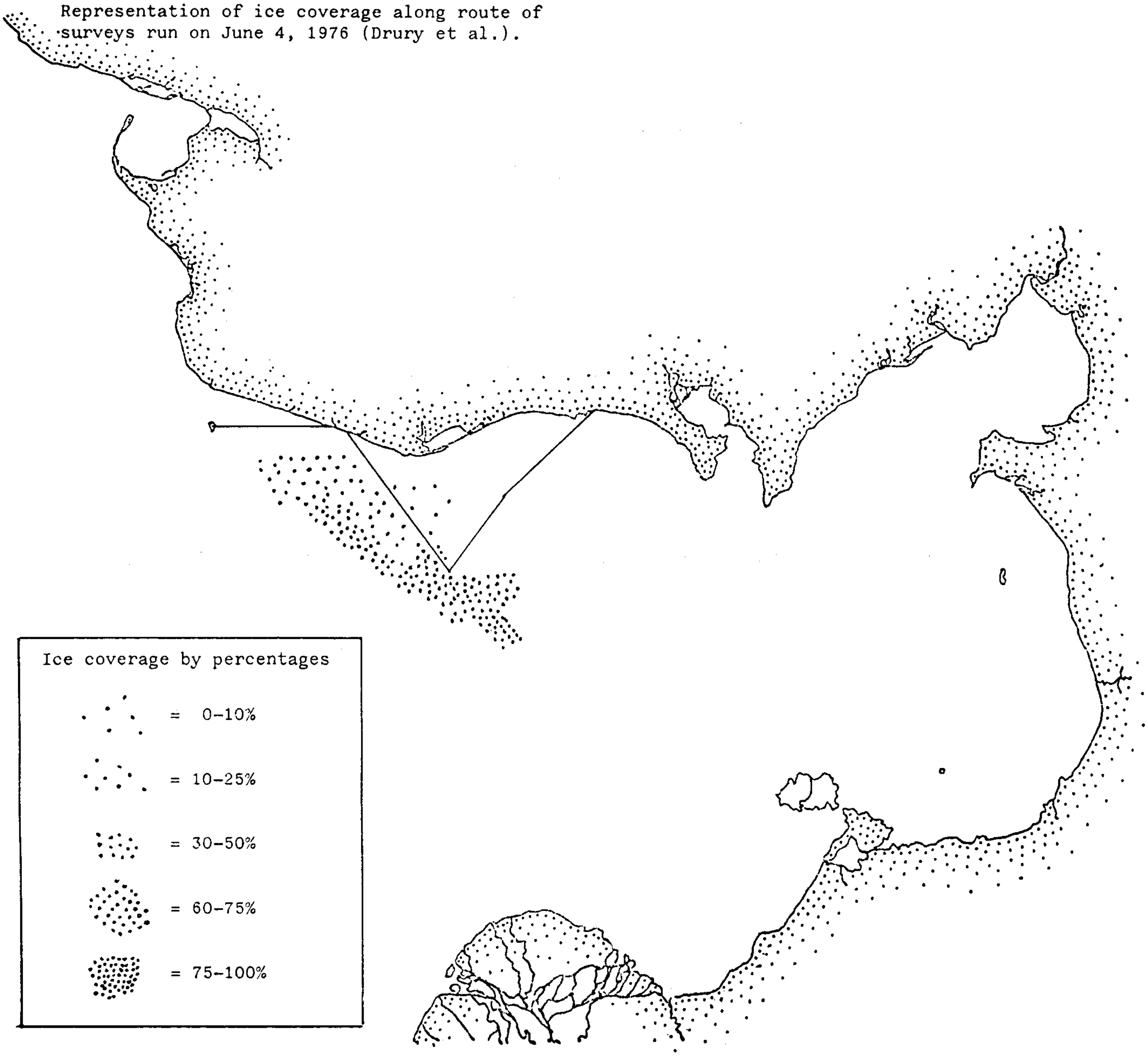


Figure I.A.1b
Representation of ice coverage along route of surveys run on June 7, 1978 (Drury et al.).

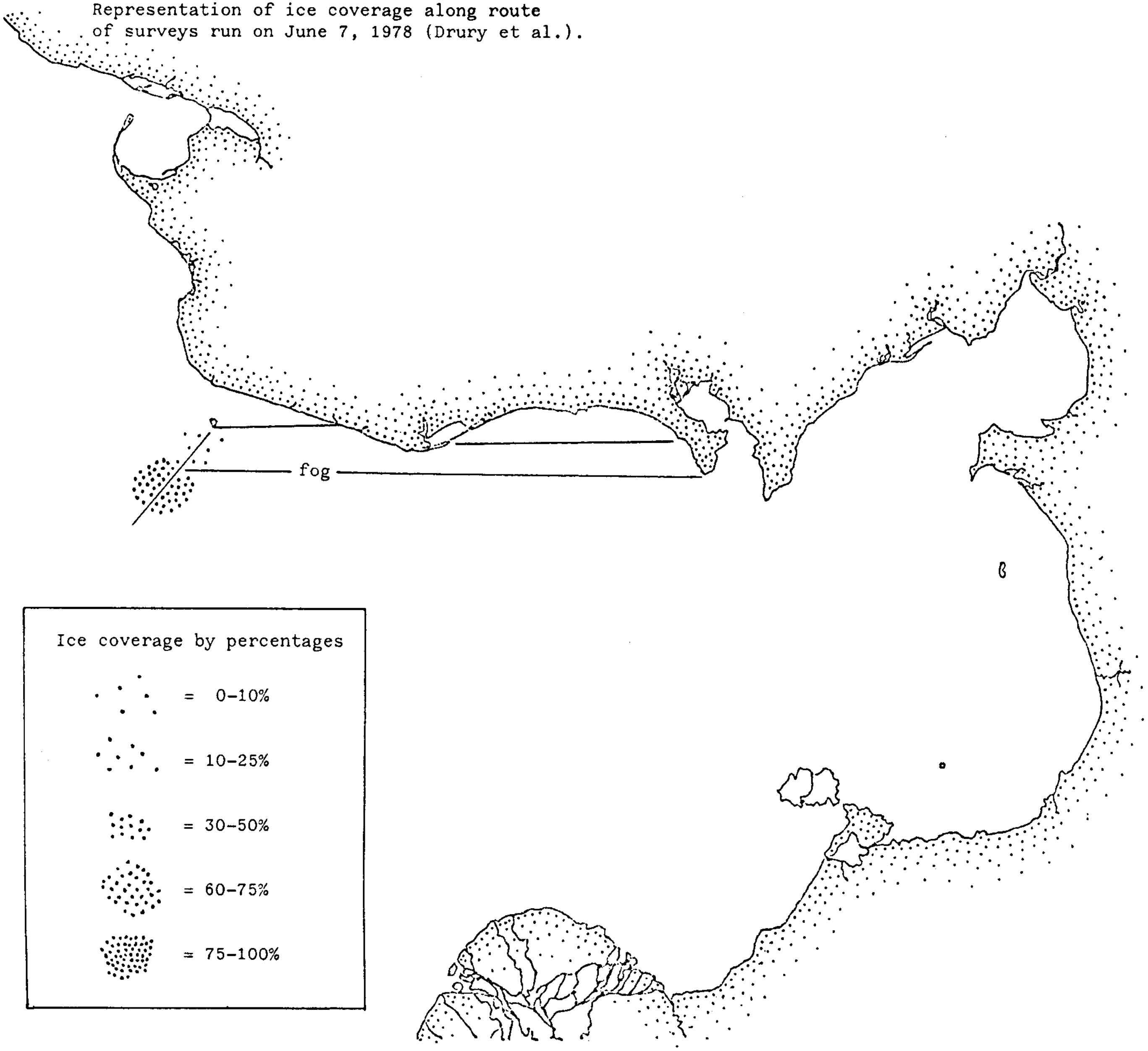
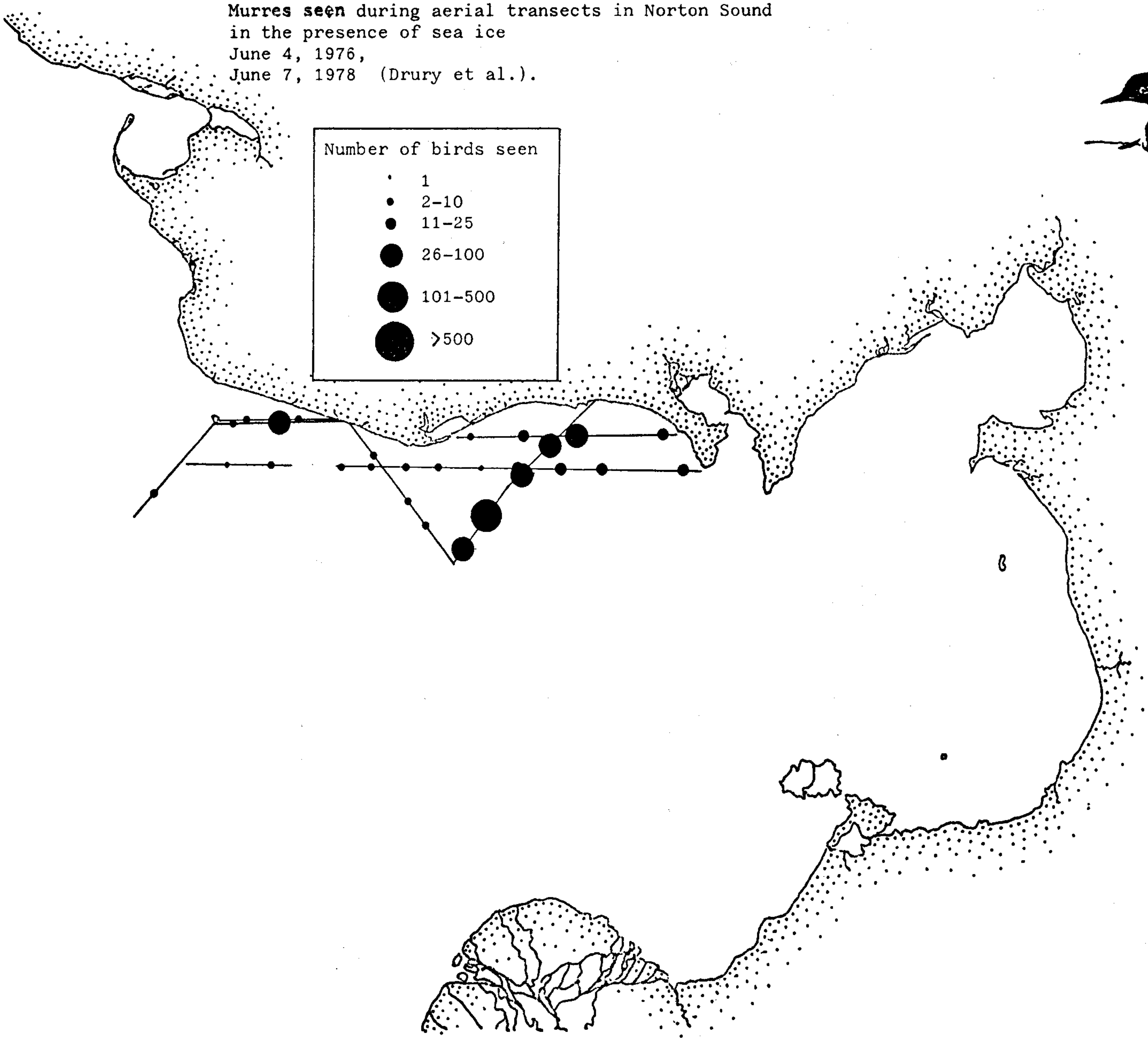


Figure I.A.2a
Murres seen during aerial transects in Norton Sound in the presence of sea ice
June 4, 1976,
June 7, 1978 (Drury et al.).



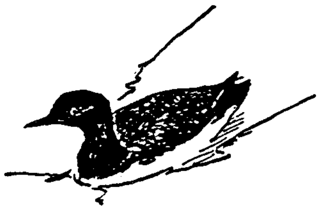
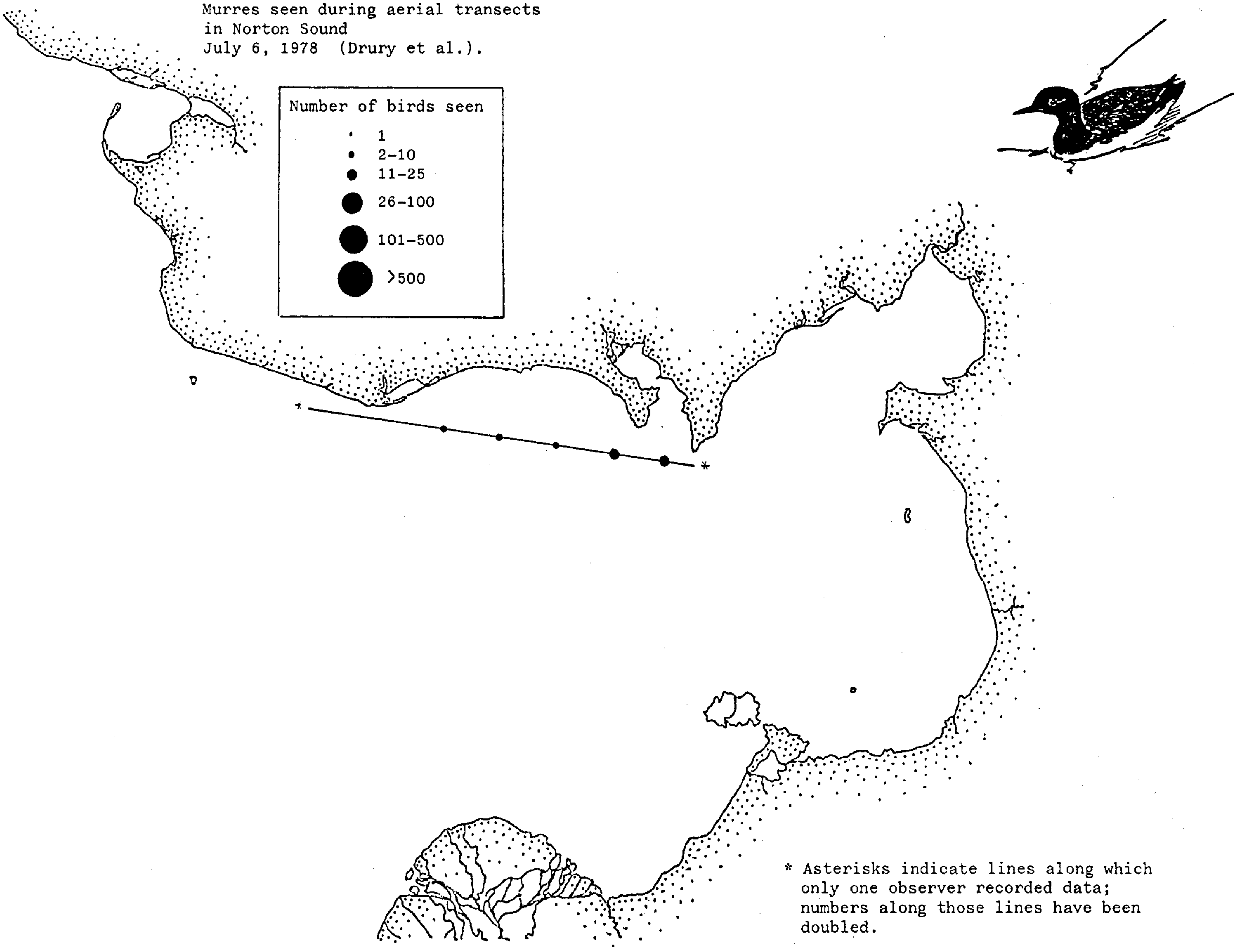
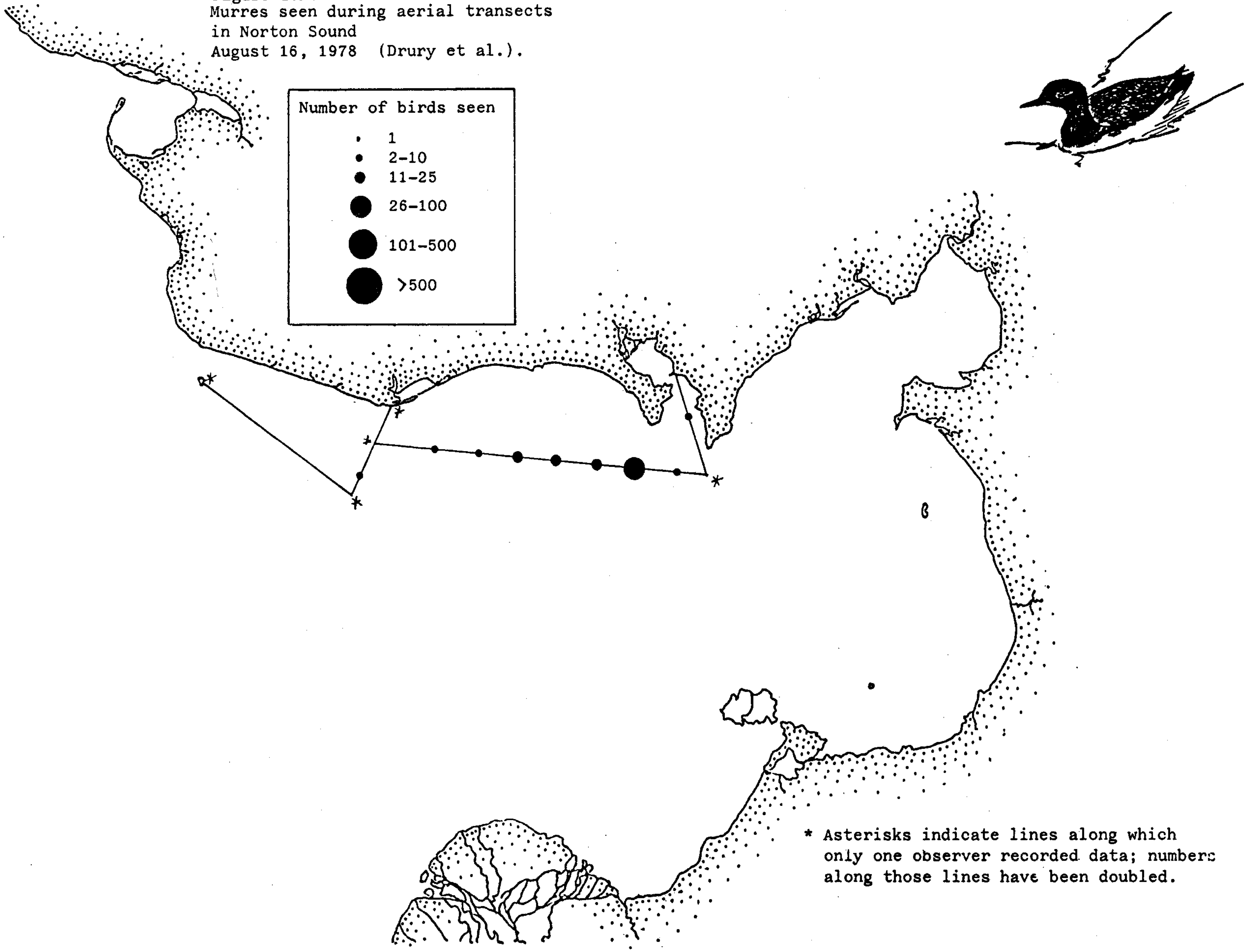


Figure I.A.2b
Murres seen during aerial transects
in Norton Sound
July 6, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.A.2c
Murres seen during aerial transects in Norton Sound
August 16, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.A.3a
All Auklets (Least + Crested + Parakeet + Unidentified)
seen during aerial transects in Norton Sound in the presence of sea ice
June 4, 1976,
June 7, 1978 (Drury et al.).

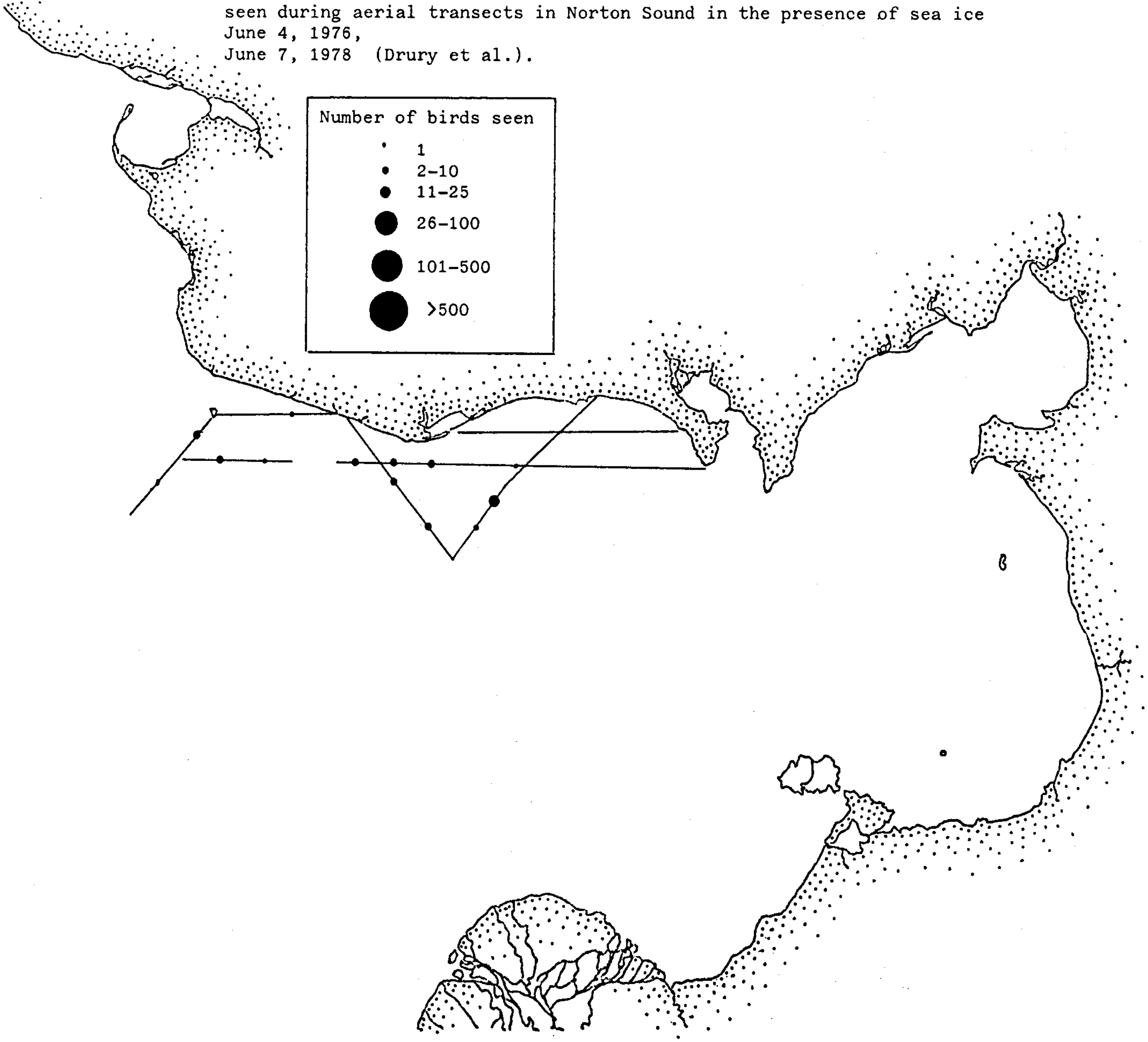


Figure I.A.3b
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in Norton Sound July 6, 1978 (Drury et al.).

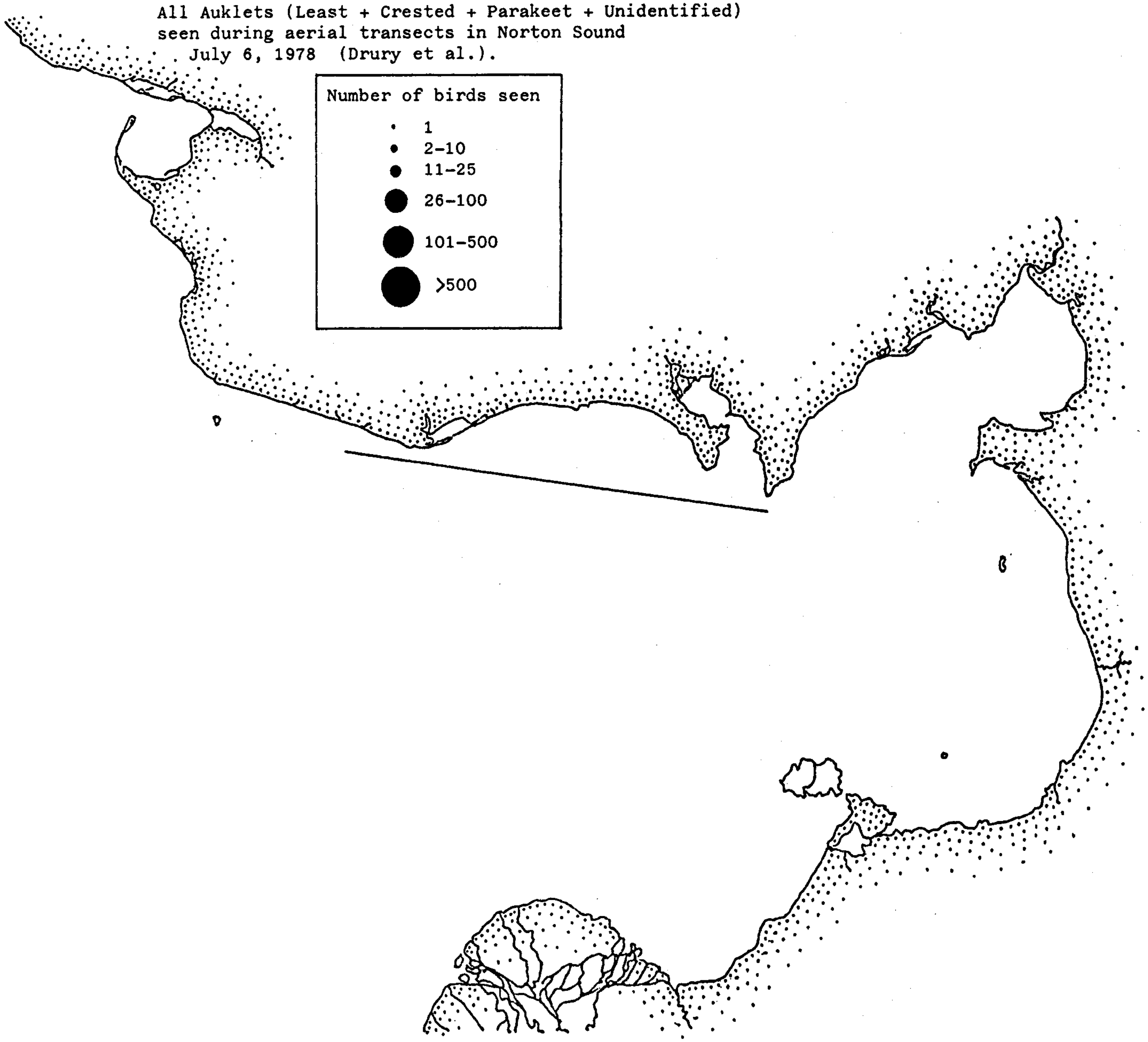


Figure I.A.3c
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in Norton Sound August 16, 1978 (Drury et al.).

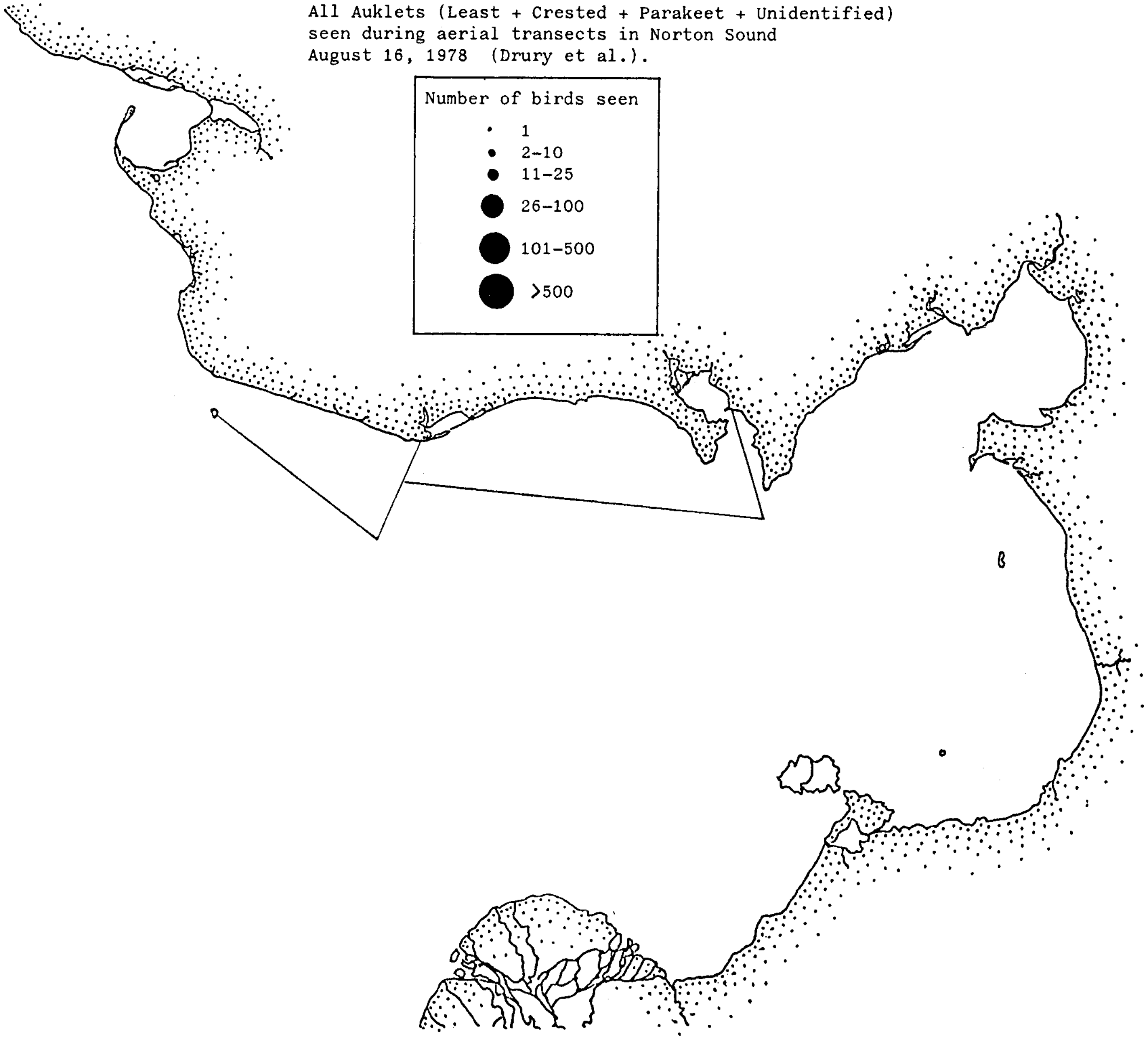


Figure I.A.4
Least Auklets seen during aerial transects
in Norton Sound in the presence of sea ice

June 7, 1978 (Drury et al.).

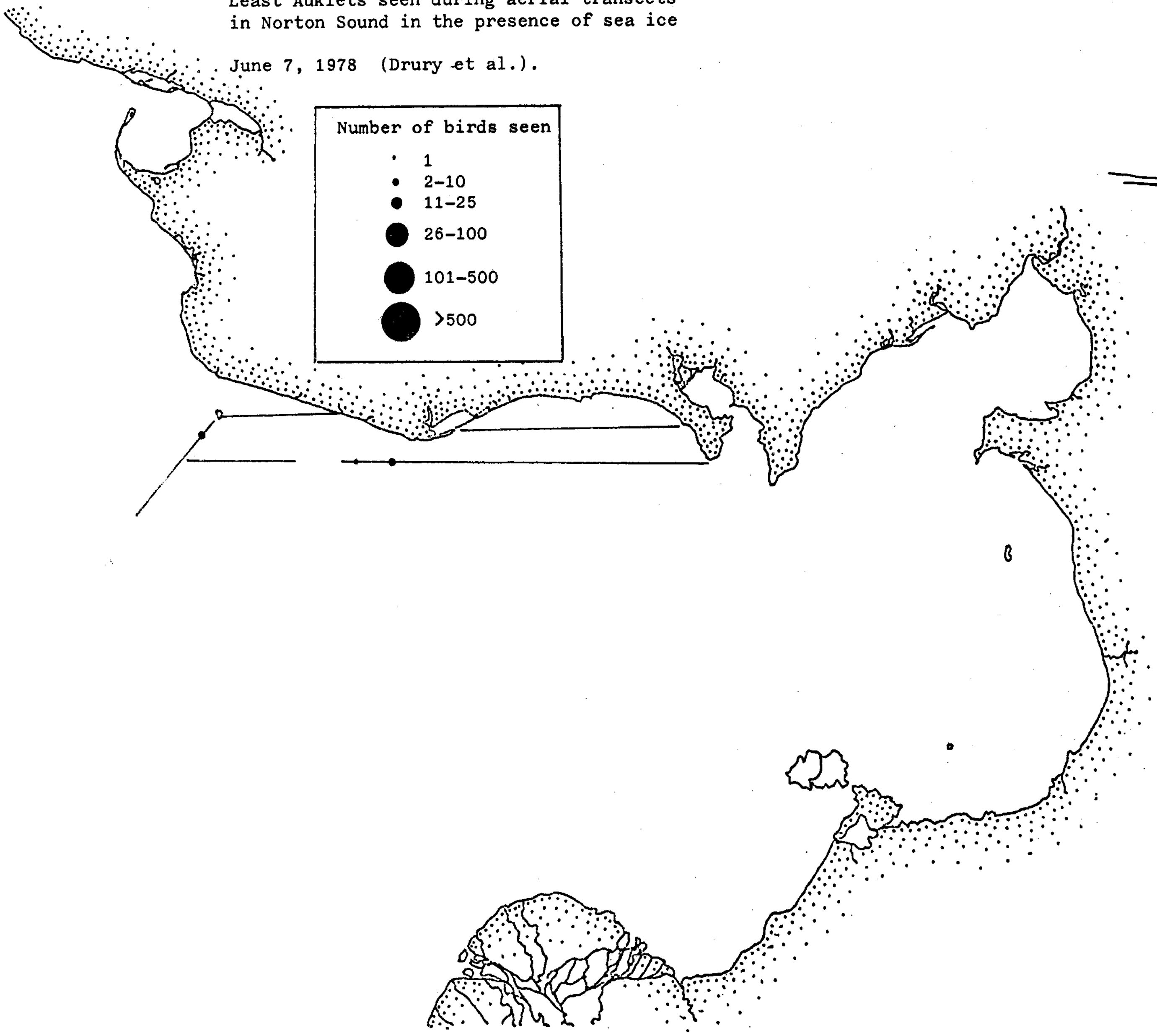
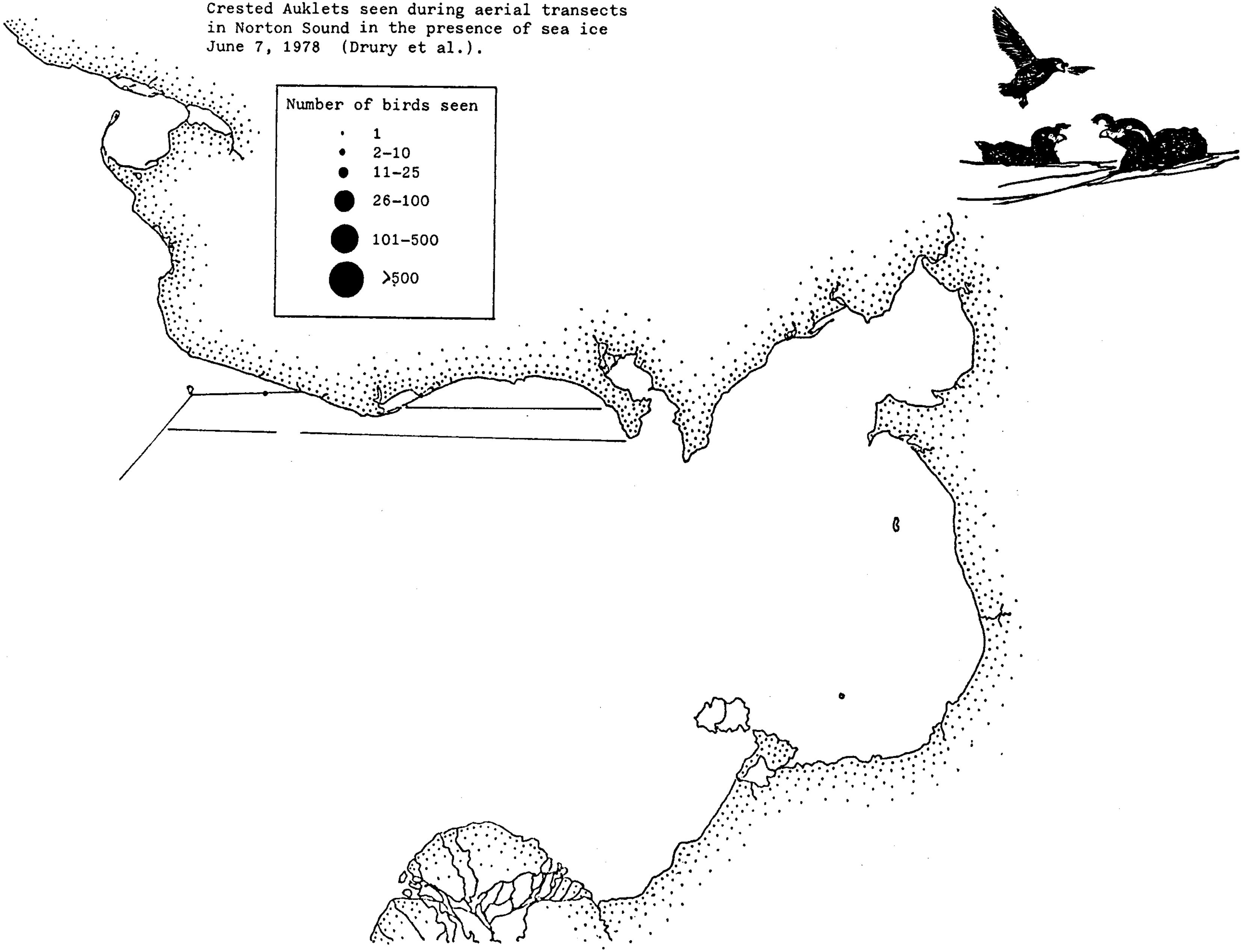


Figure I.A.5
Crested Auklets seen during aerial transects
in Norton Sound in the presence of sea ice
June 7, 1978 (Drury et al.).



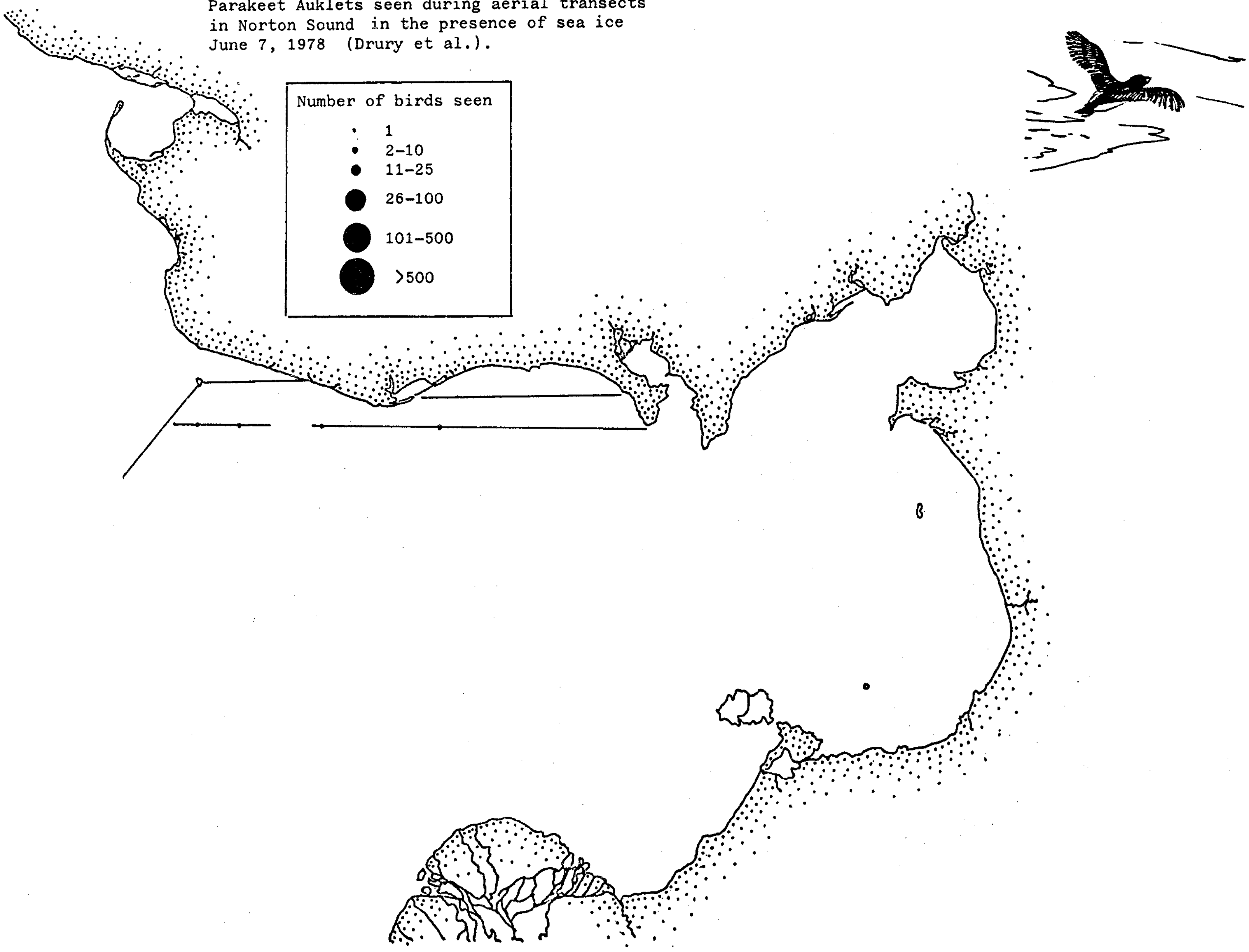


Figure I.A.6
Parakeet Auklets seen during aerial transects in Norton Sound in the presence of sea ice June 7, 1978 (Drury et al.).

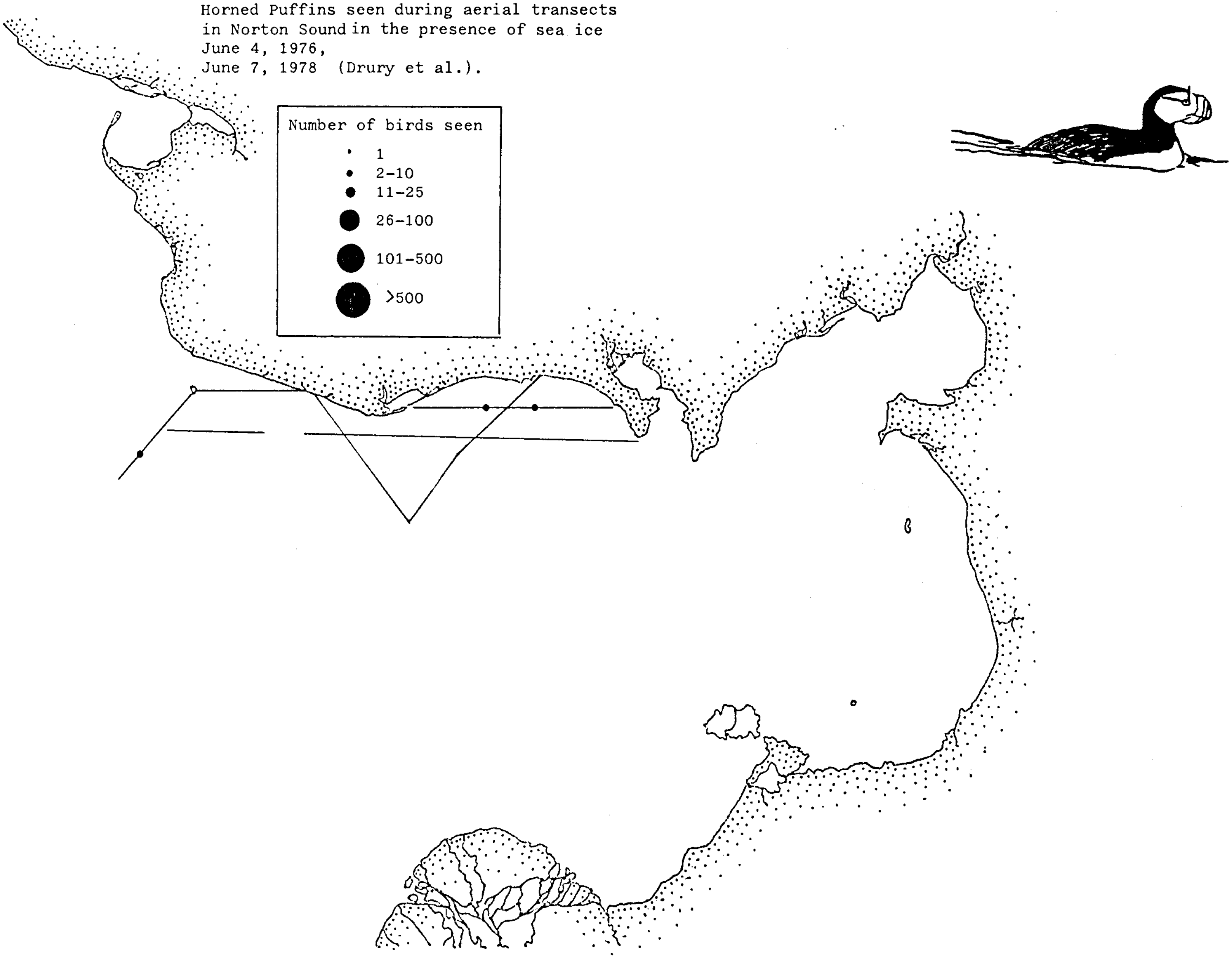
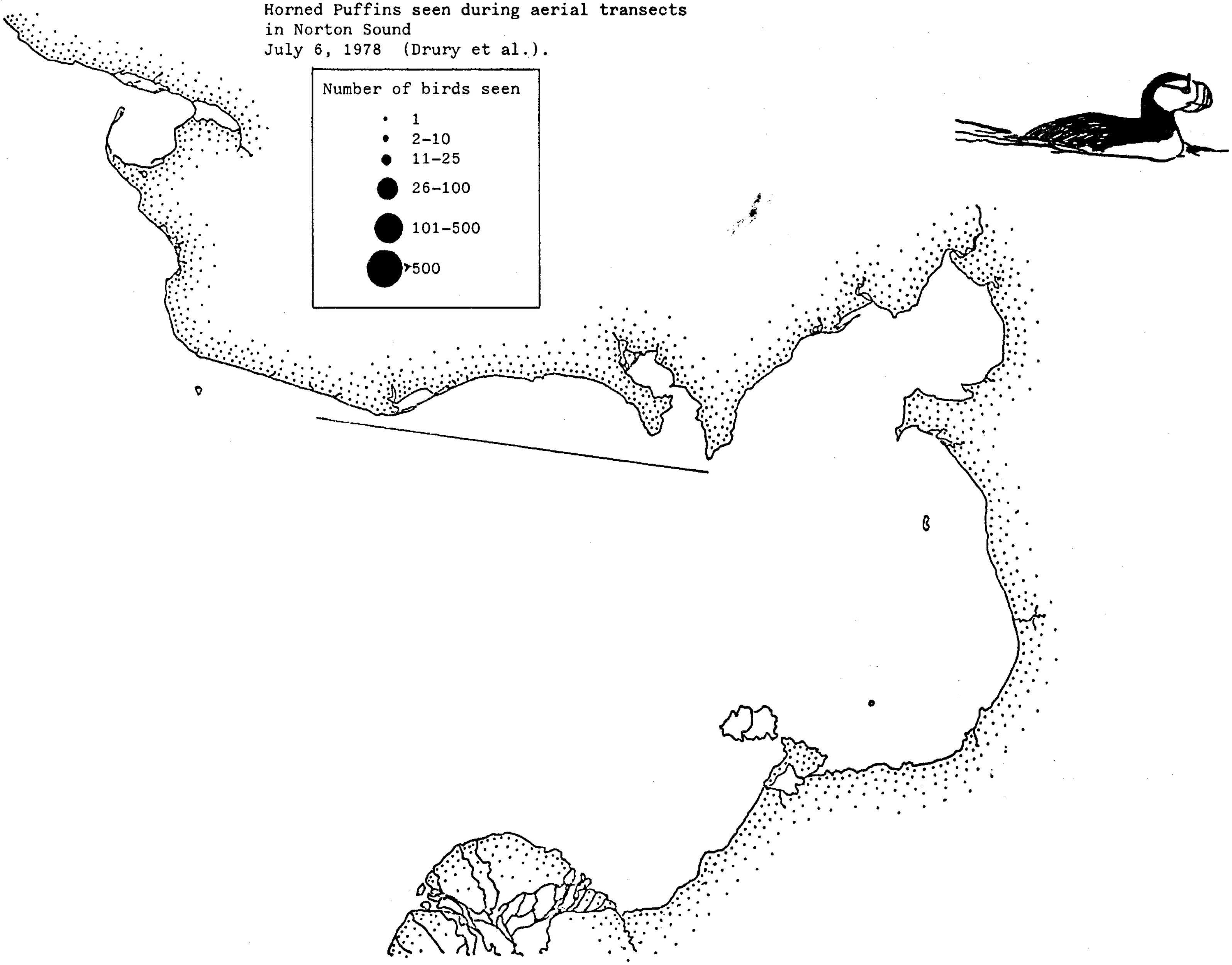


Figure I.A.7a
Horned Puffins seen during aerial transects
in Norton Sound in the presence of sea ice
June 4, 1976,
June 7, 1978 (Drury et al.).

Figure I.A.7b
Horned Puffins seen during aerial transects
in Norton Sound
July 6, 1978 (Drury et al.).



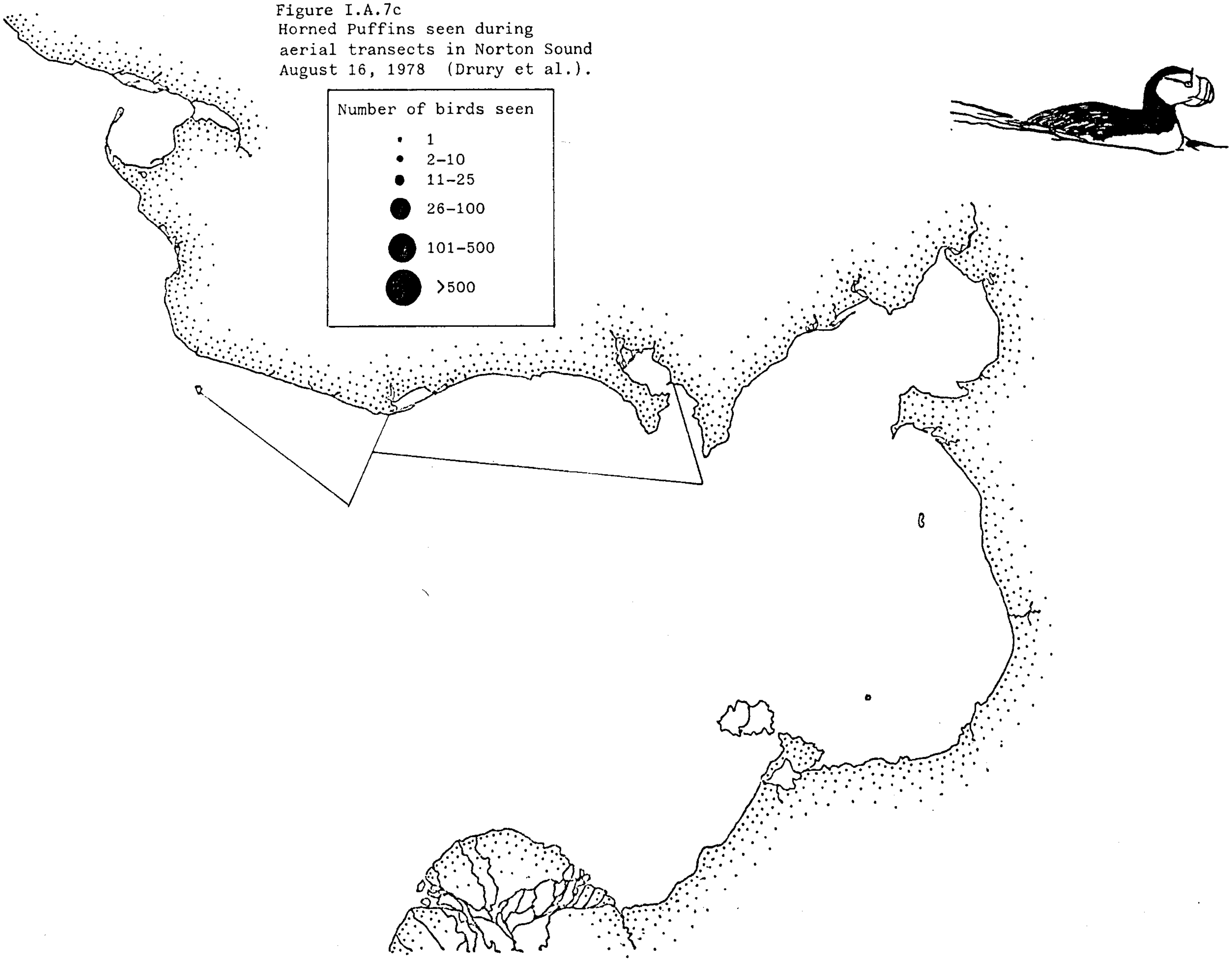


Figure I.A.7c
Horned Puffins seen during
aerial transects in Norton Sound
August 16, 1978 (Drury et al.).

Figure I.A.8a
Tufted Puffins seen during aerial transects in Norton Sound in the presence of sea ice
June 4, 1976,
June 7, 1978 (Drury et al.).

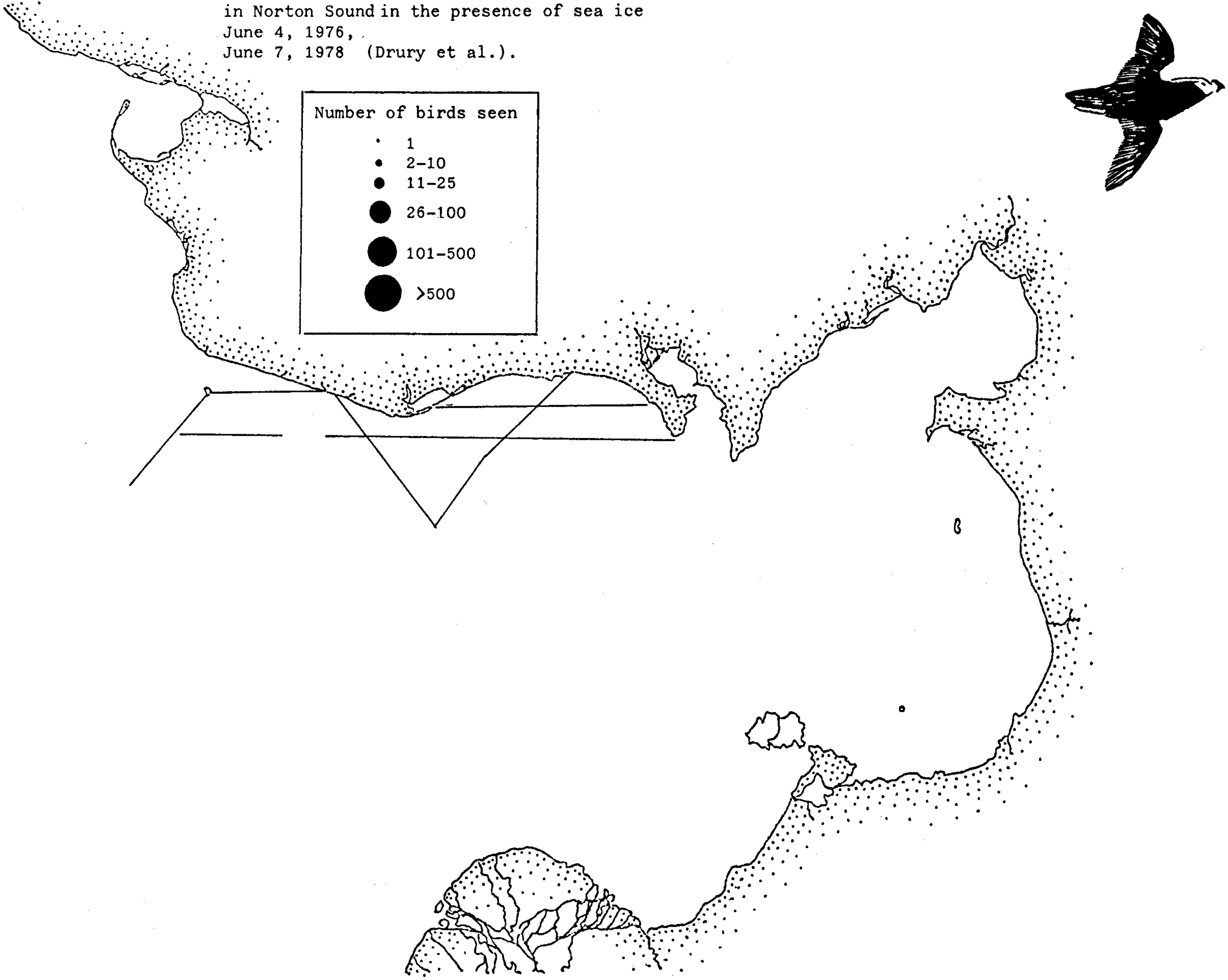


Figure I.A.8b
Tufted Puffins seen during
aerial transects in Norton Sound
July 6, 1978 (Drury et al.).

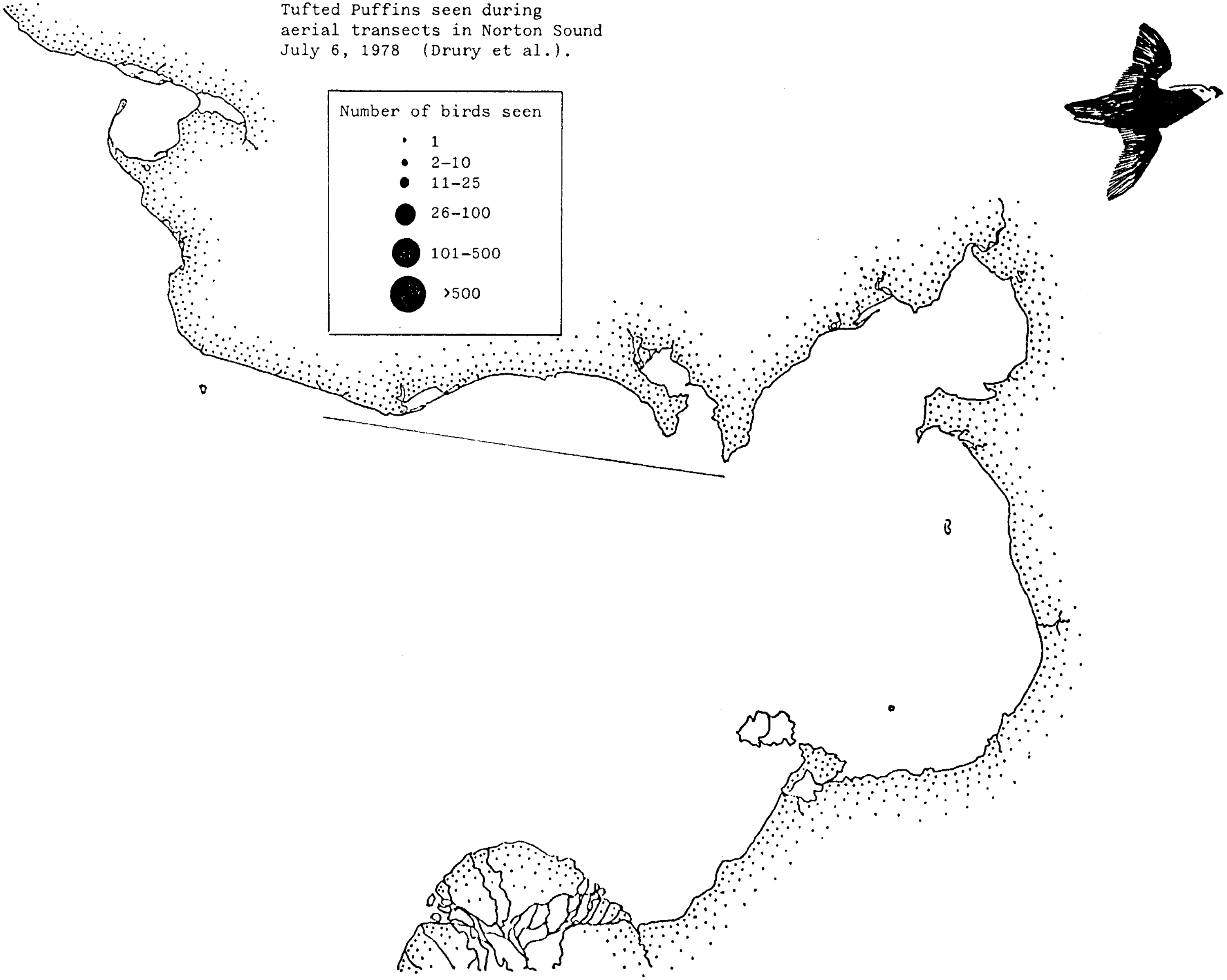
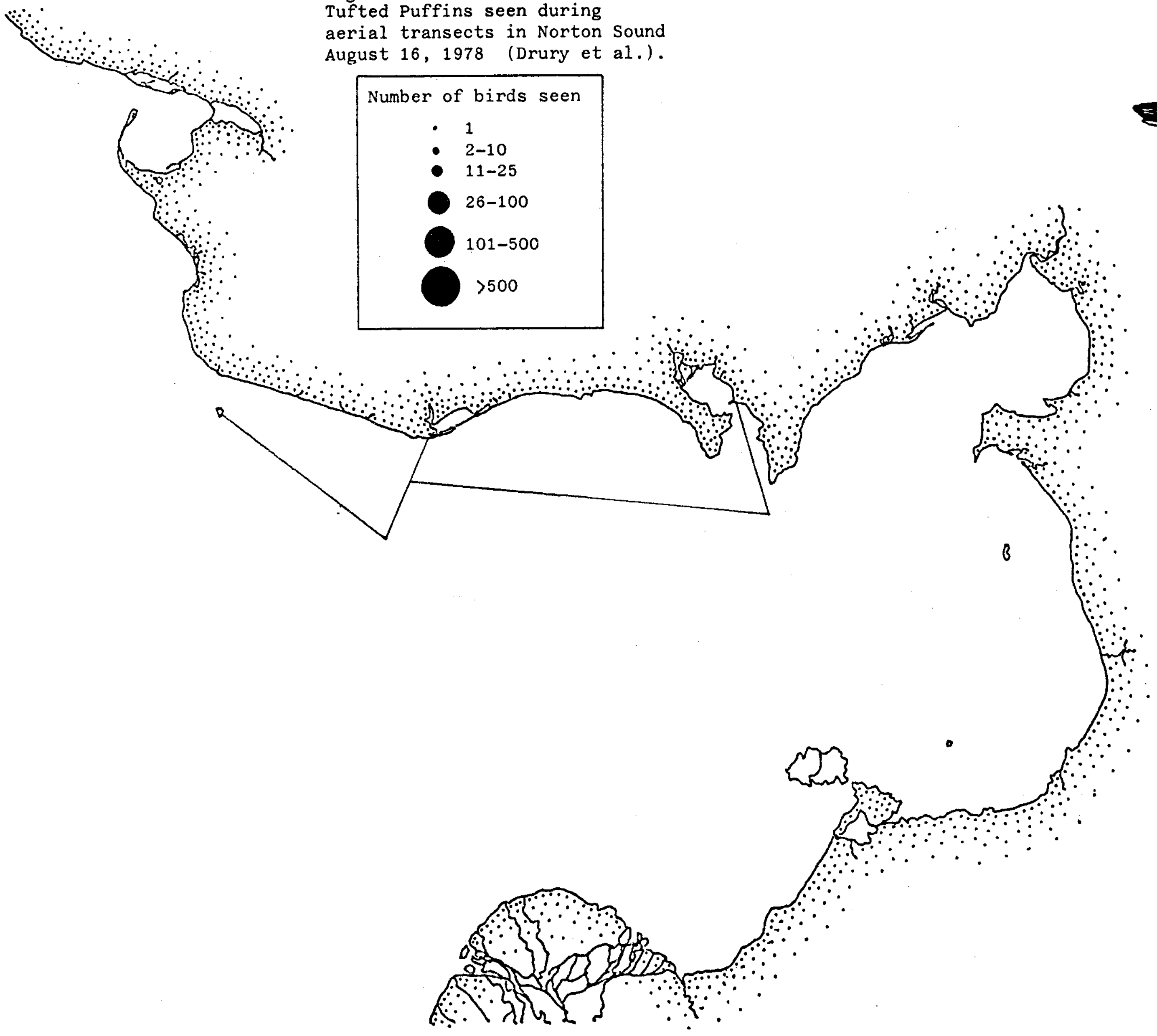


Figure I.A.8c
Tufted Puffins seen during
aerial transects in Norton Sound
August 16, 1978 (Drury et al.).



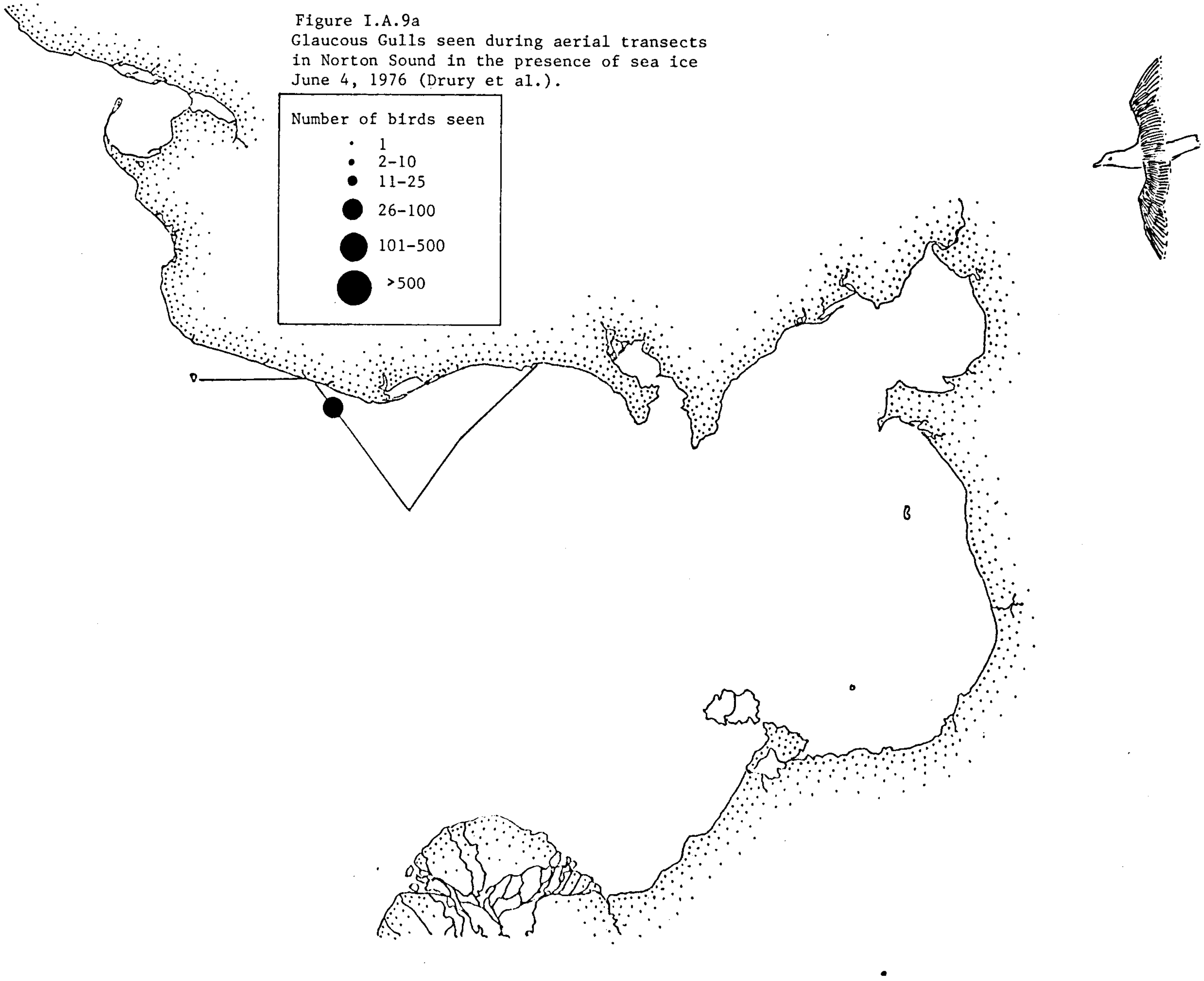


Figure I.A.9a
Glaucous Gulls seen during aerial transects in Norton Sound in the presence of sea ice June 4, 1976 (Drury et al.).

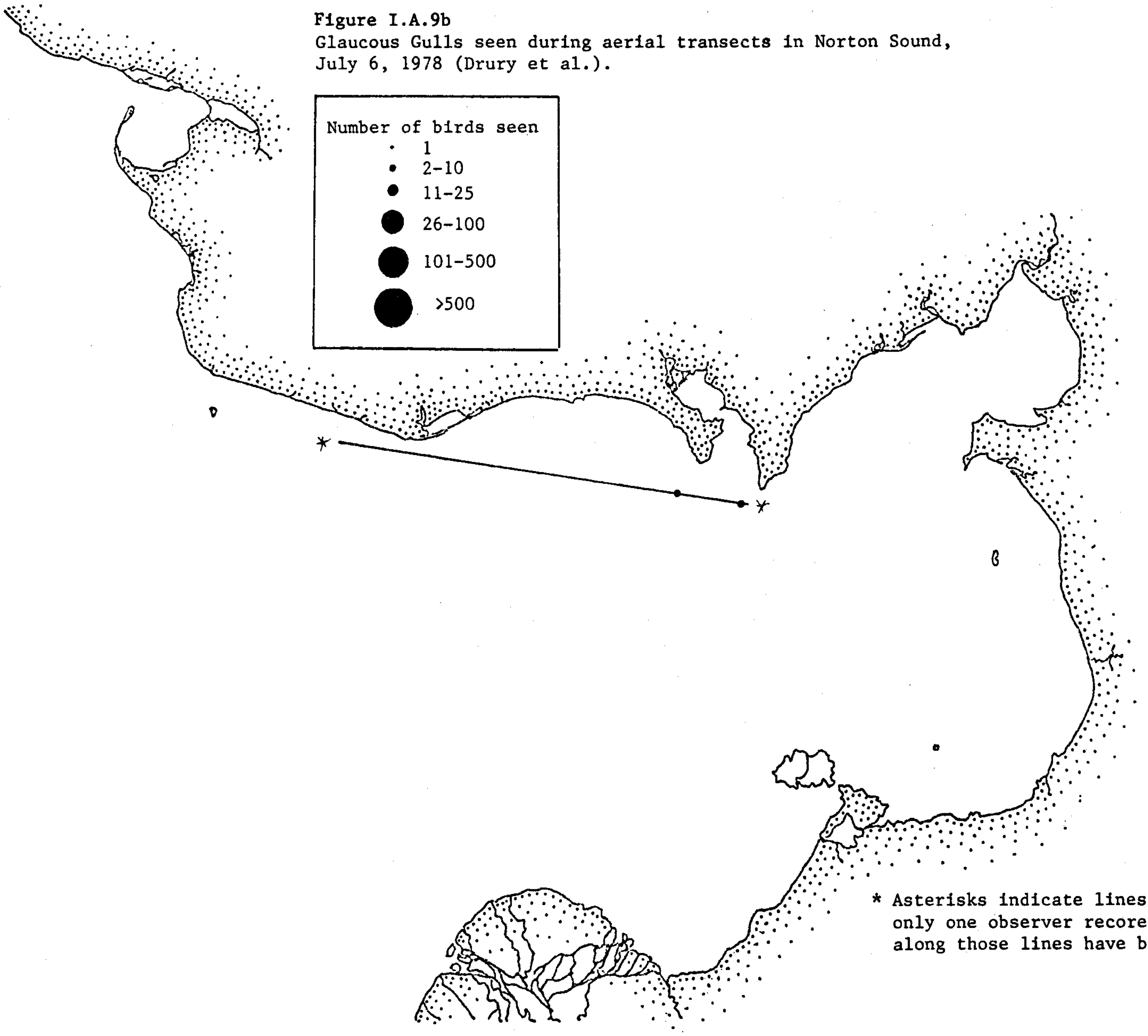


Figure I.A.9b
Glaucous Gulls seen during aerial transects in Norton Sound, July 6, 1978 (Drury et al.).

* Asterisks indicate lines along which only one observer recorede data; numbers along those lines have been doubled.

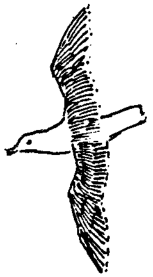
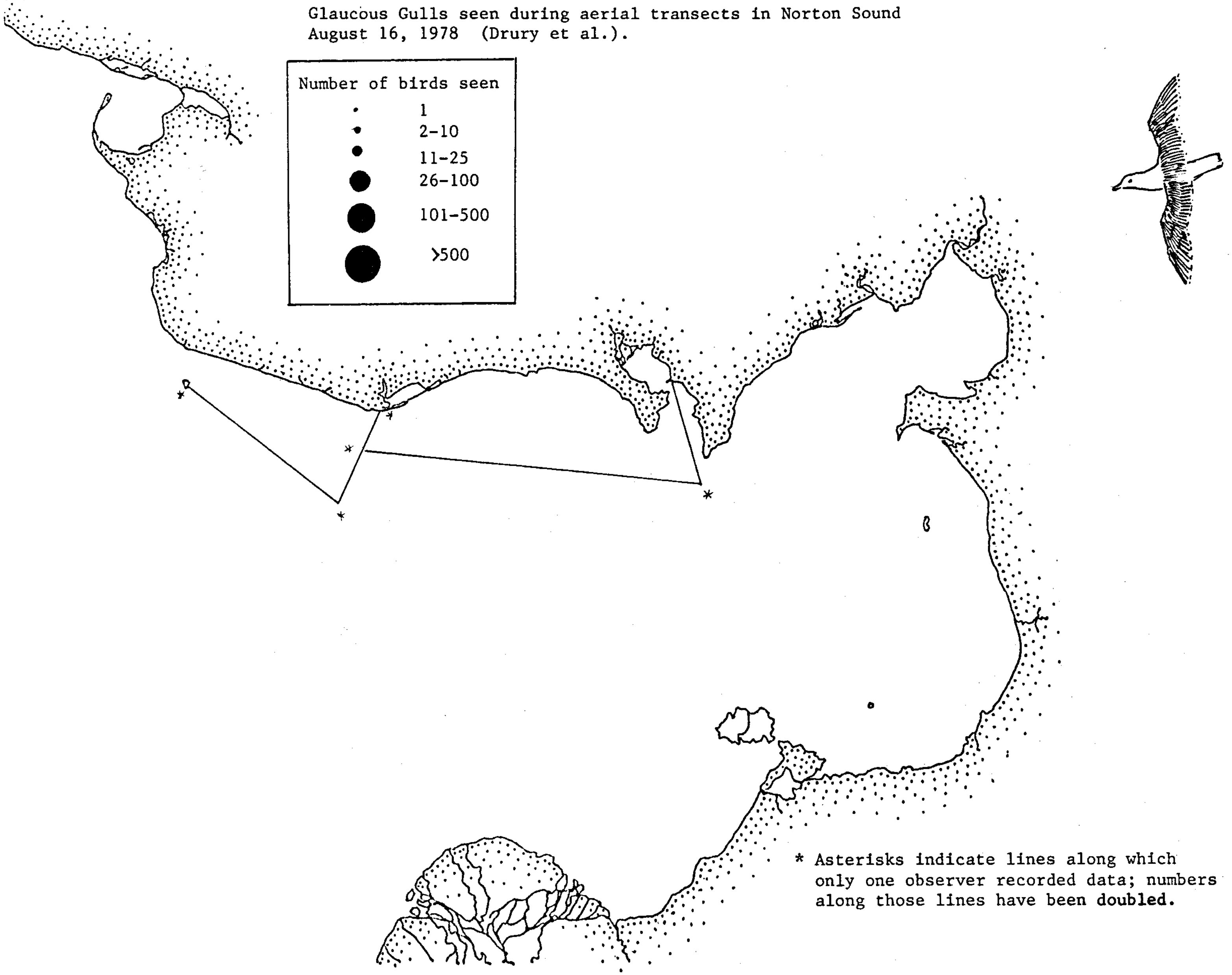


Figure I.A.9c

Glaucous Gulls seen during aerial transects in Norton Sound August 16, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been **doubled.**

Figure I.A.10a

Black-legged Kittiwakes seen during
aerial transects in Norton Sound in the presence of sea ice
June 4, 1976,
June 7, 1978 (Drury et al.).

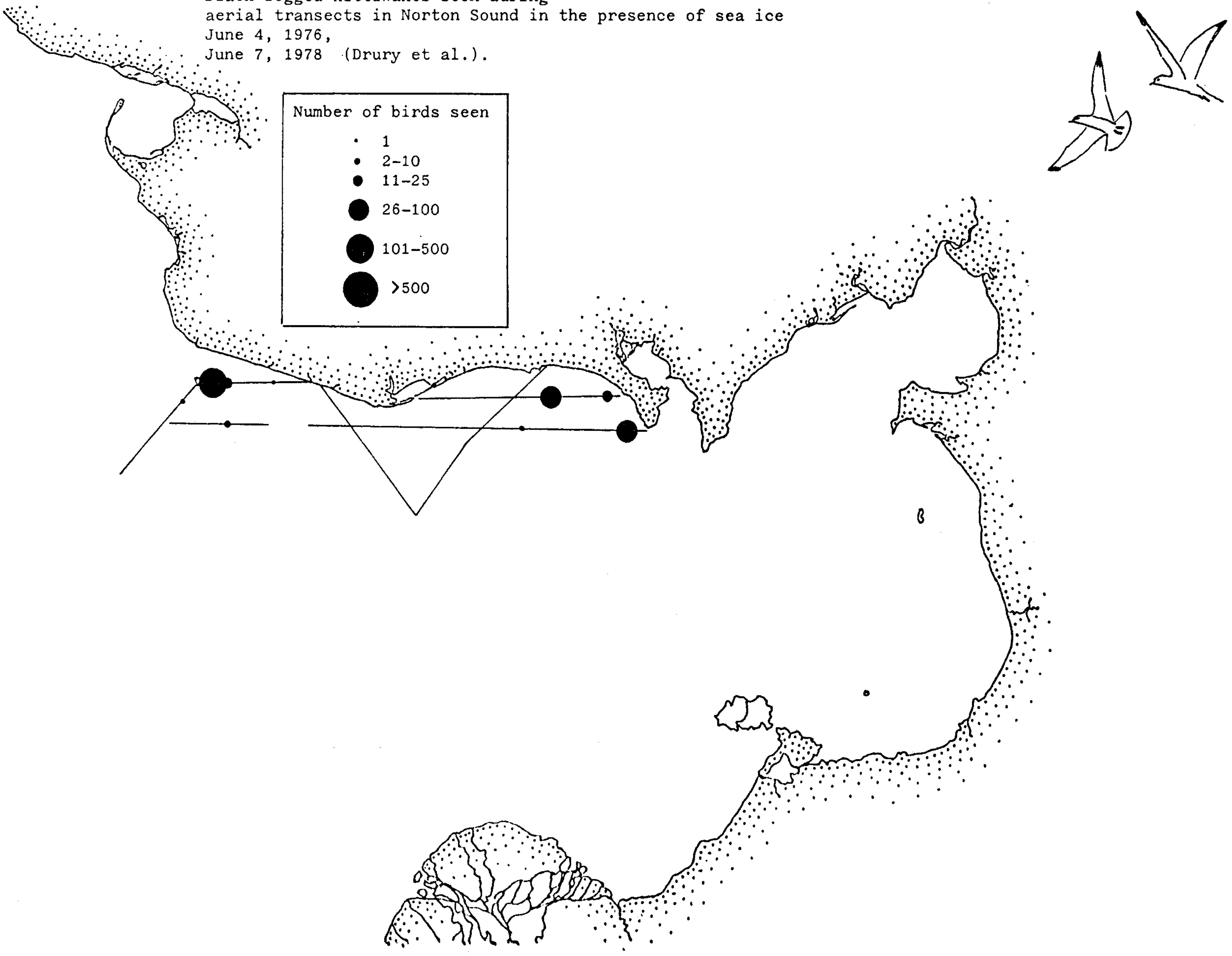
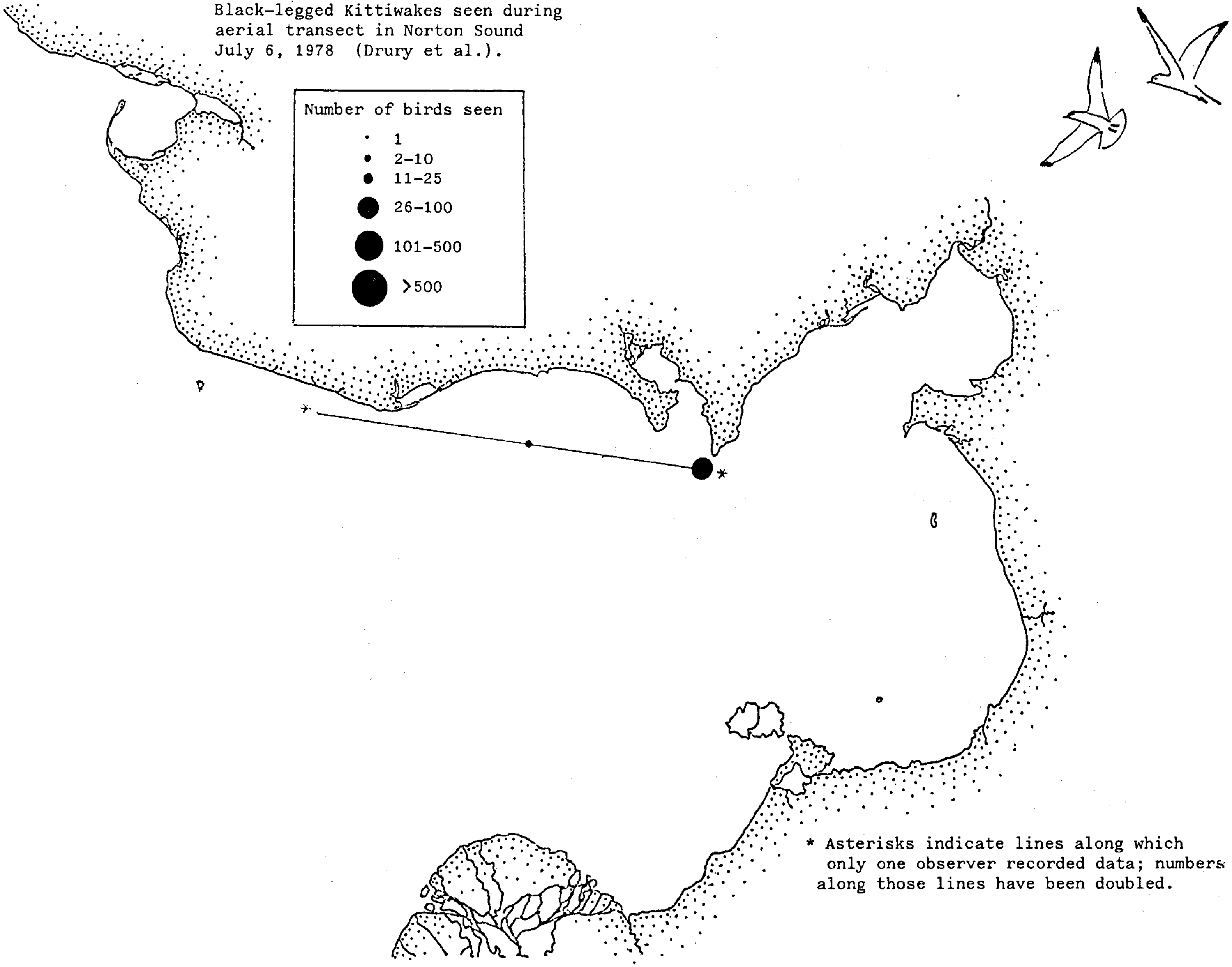
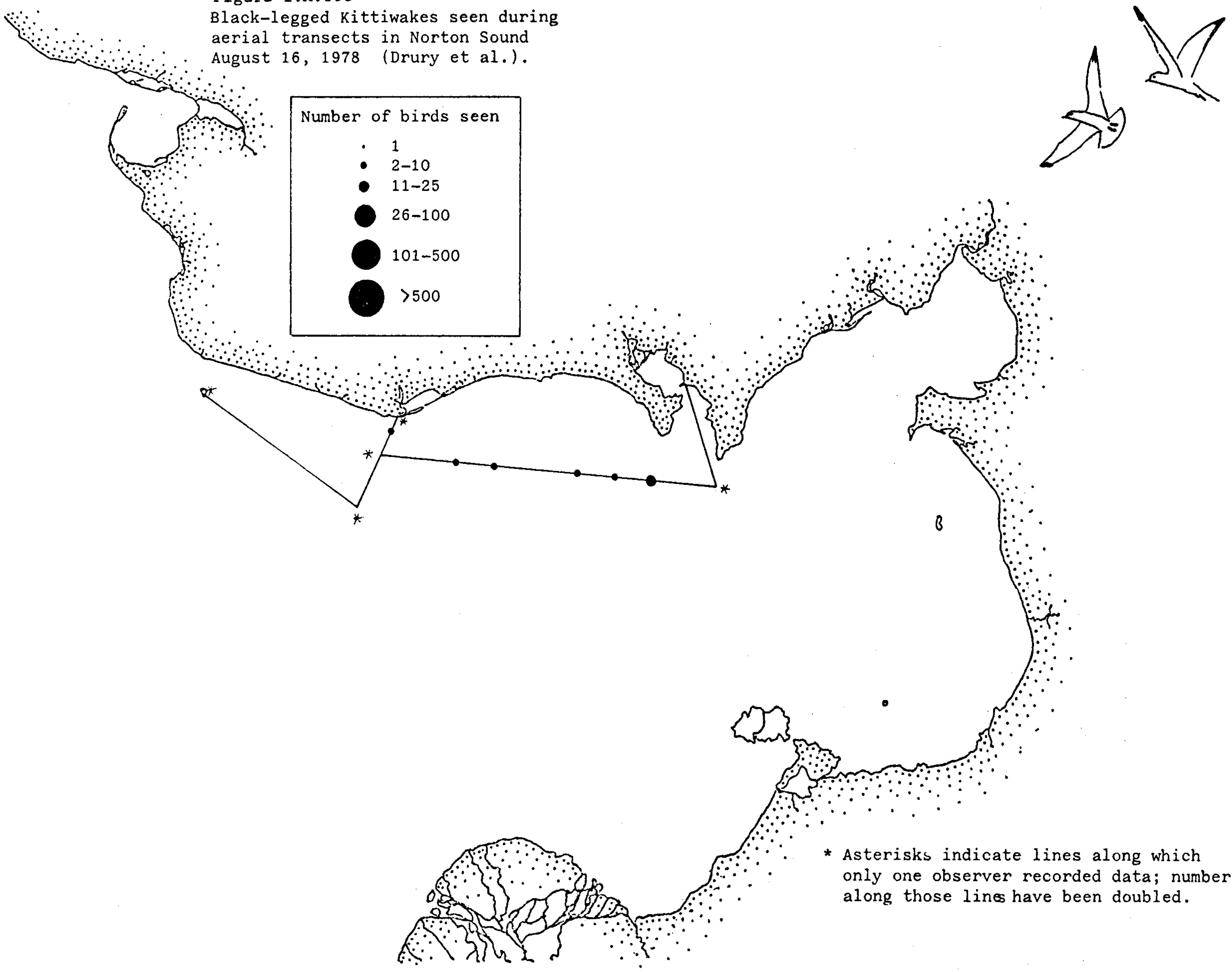


Figure I.A.10b
Black-legged Kittiwakes seen during aerial transect in Norton Sound July 6, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.A.10c
Black-legged Kittiwakes seen during aerial transects in Norton Sound August 16, 1978 (Drury et al.).



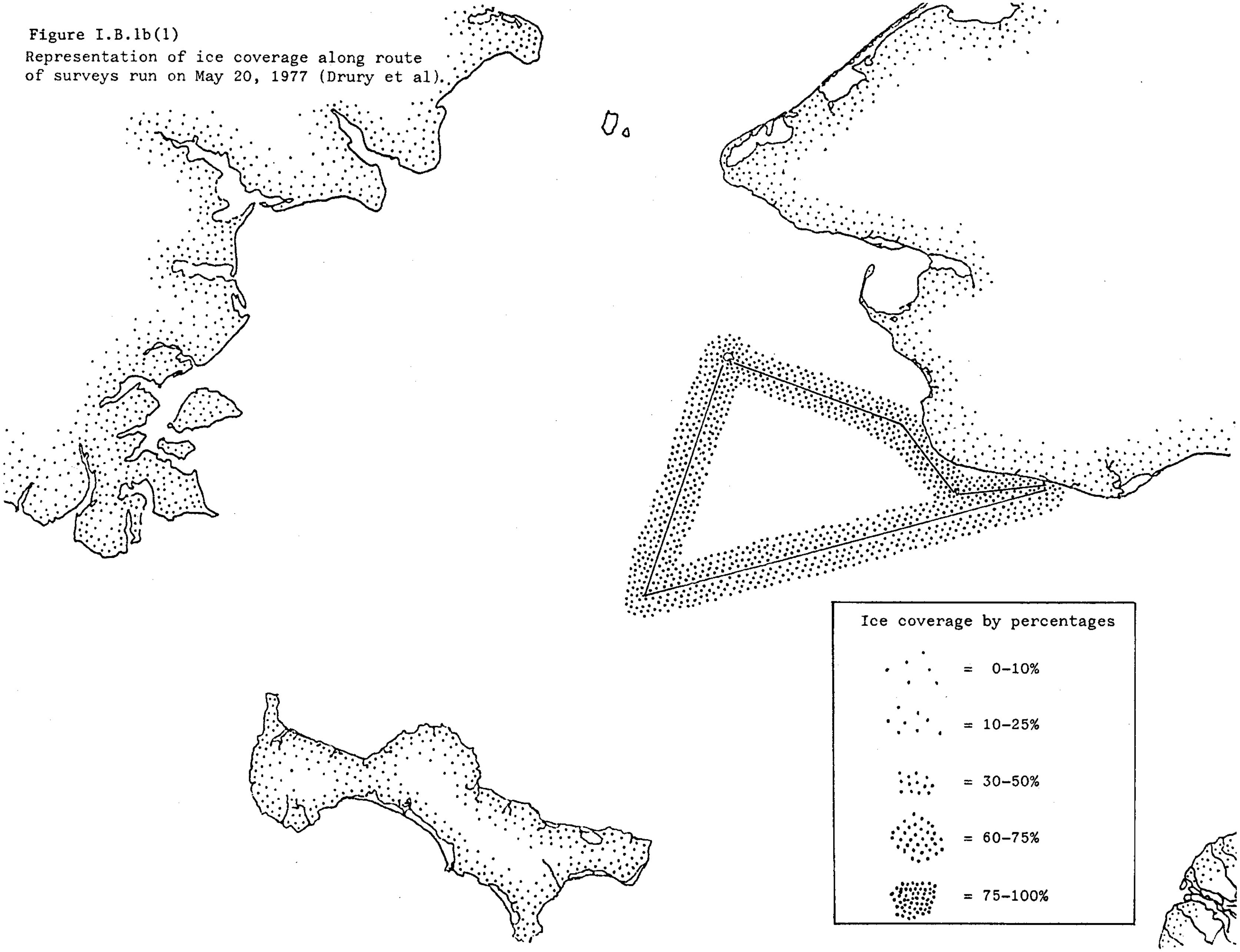
* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.B.1a(1)
General representation of the distribution of ice in the northeastern Bering Sea in early June.

Figure I.B.1a(2)
General representation of the distribution of ice in the northeastern Bering Sea in mid-June.

Figure I.B.1a(3)
General representation of the distribtution of ice in the northeastern Bering Sea in late June.

Figure I.B.1b(1)
Representation of ice coverage along route of surveys run on May 20, 1977 (Drury et al).



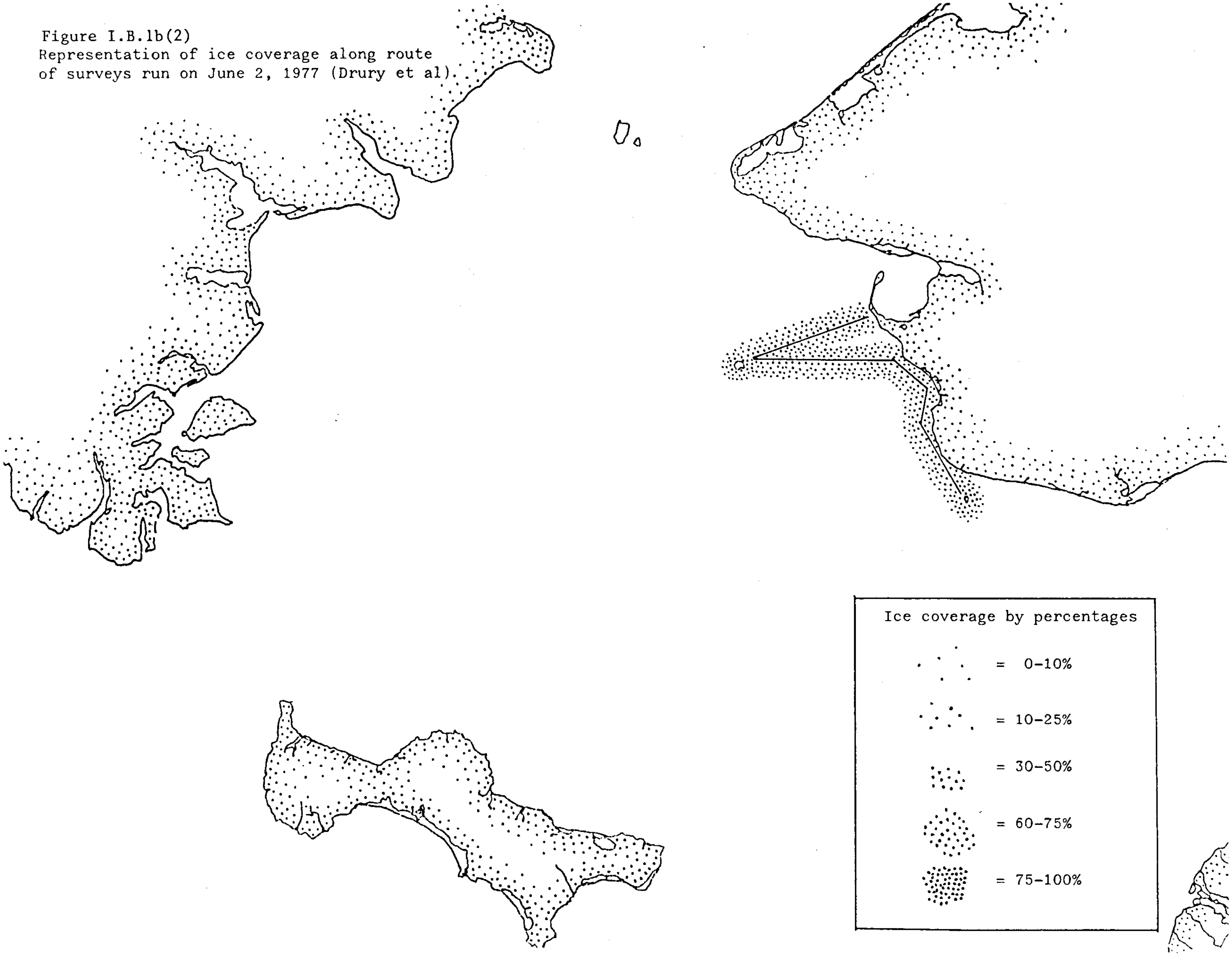


Figure I.B.1b(2)
Representation of ice coverage along route of surveys run on June 2, 1977 (Drury et al).

Figure I.B.1b(3)
Representation of ice coverage along route of surveys run on June 8, 9, 12, 1978 (Drury et al.).

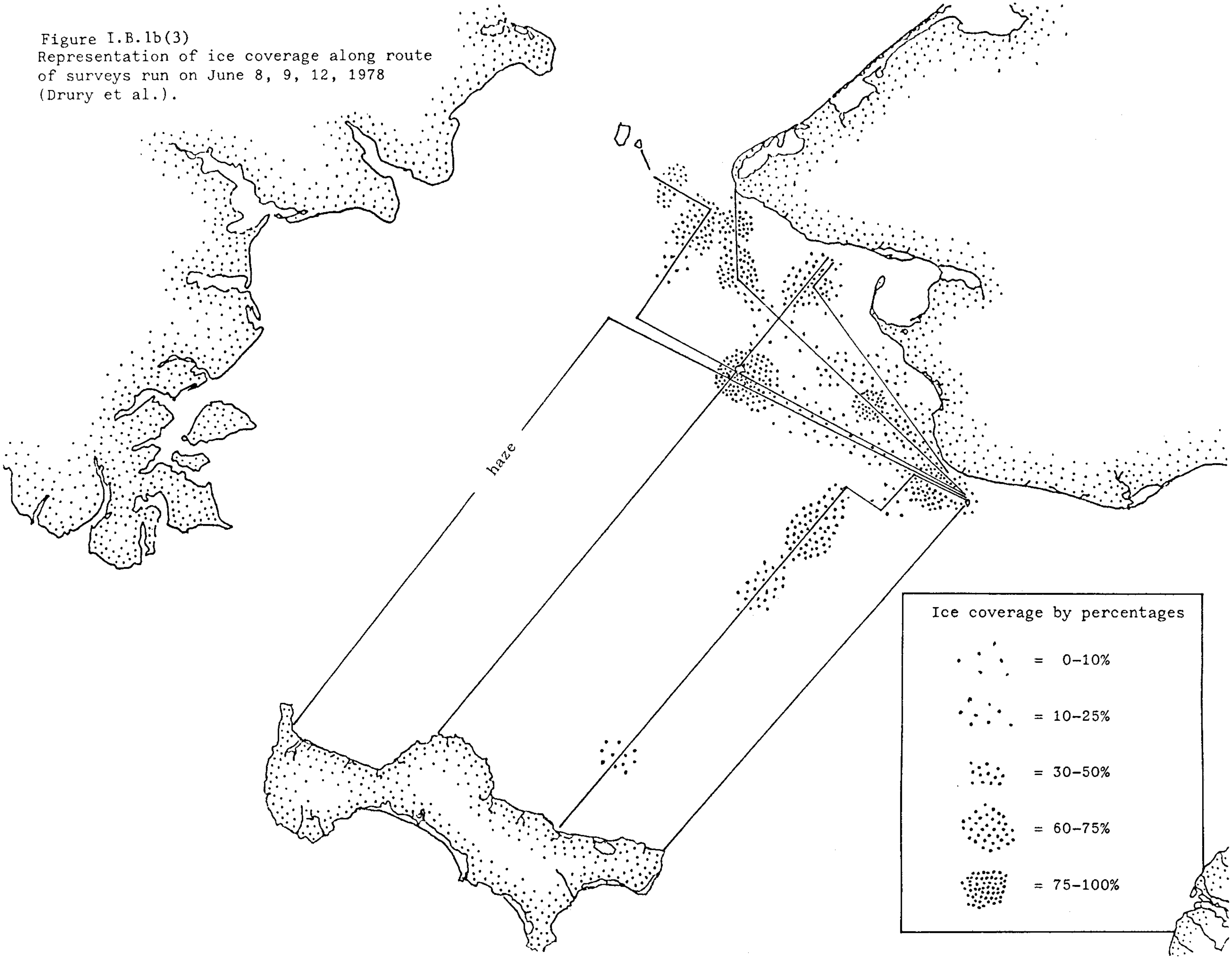


Figure I.B.1b(4)
Representation of ice coverage along route of surveys run on June 22, 23, 24, 1977 (Drury et al.).

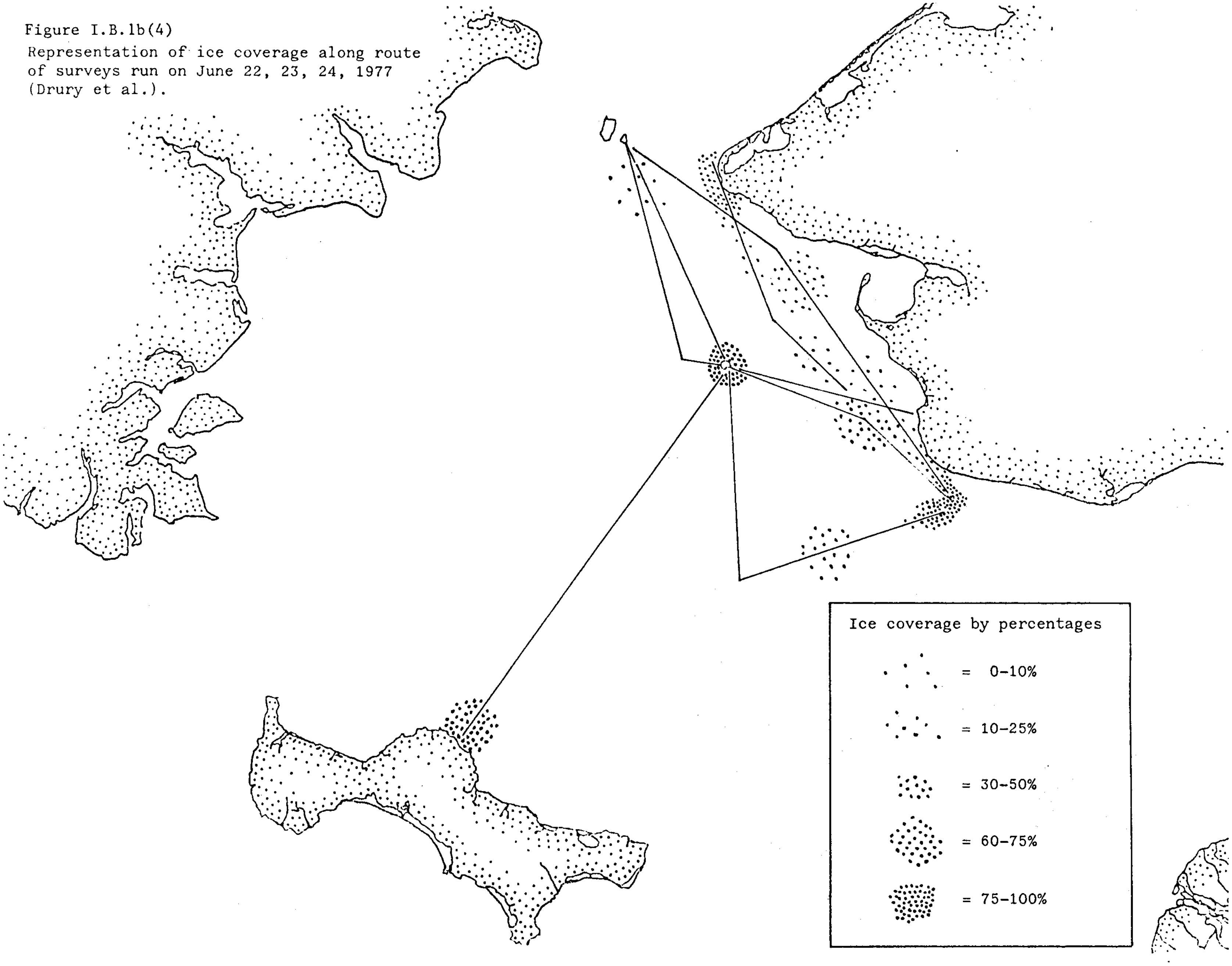


Figure I.B.2a
Murres seen during aerial transects in the presence of sea ice on May 20, 1977 (Drury et al.).

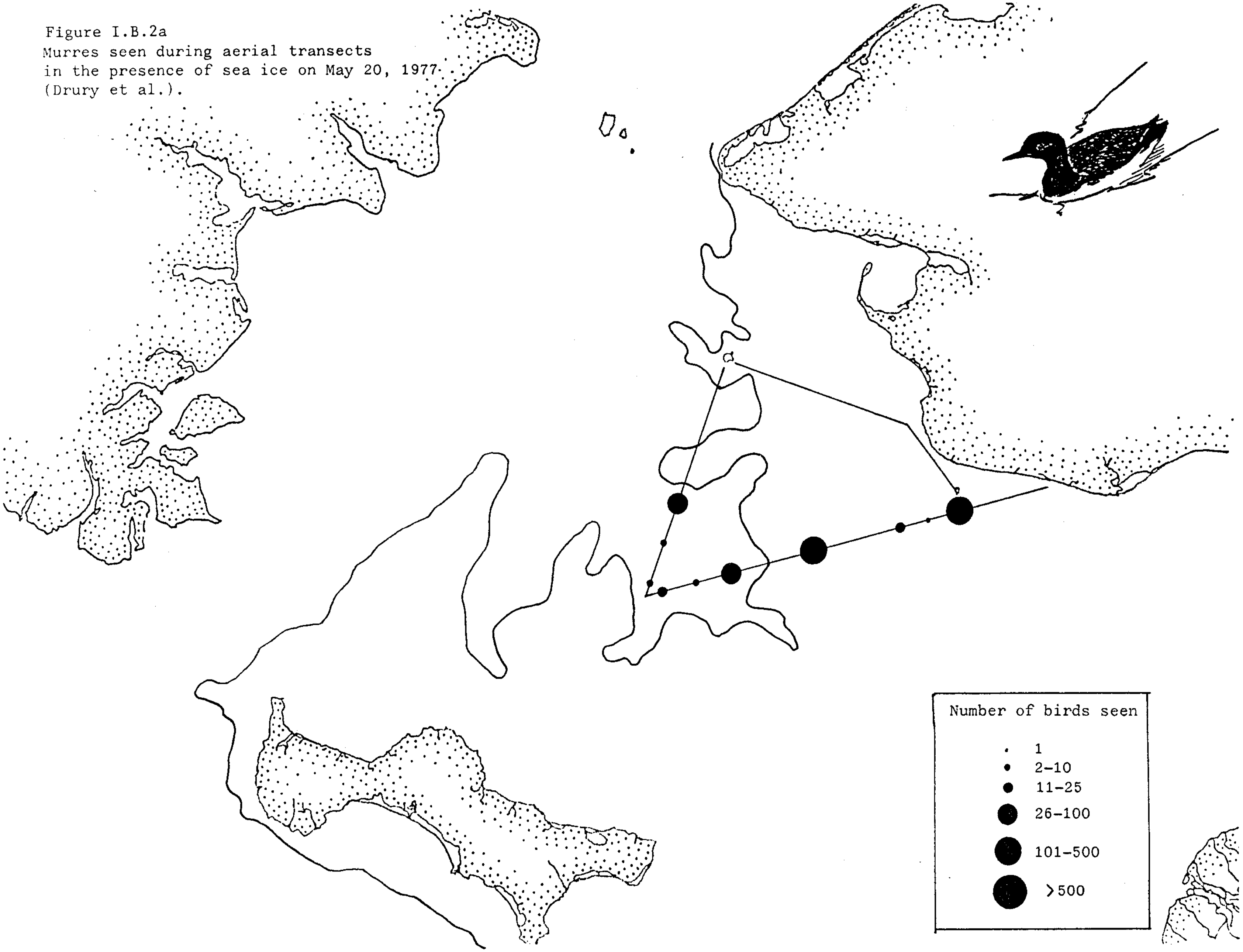


Figure I.B.2b
Murres seen during aerial transects in the presence of sea ice on June 2, 1977 (Drury et al.).

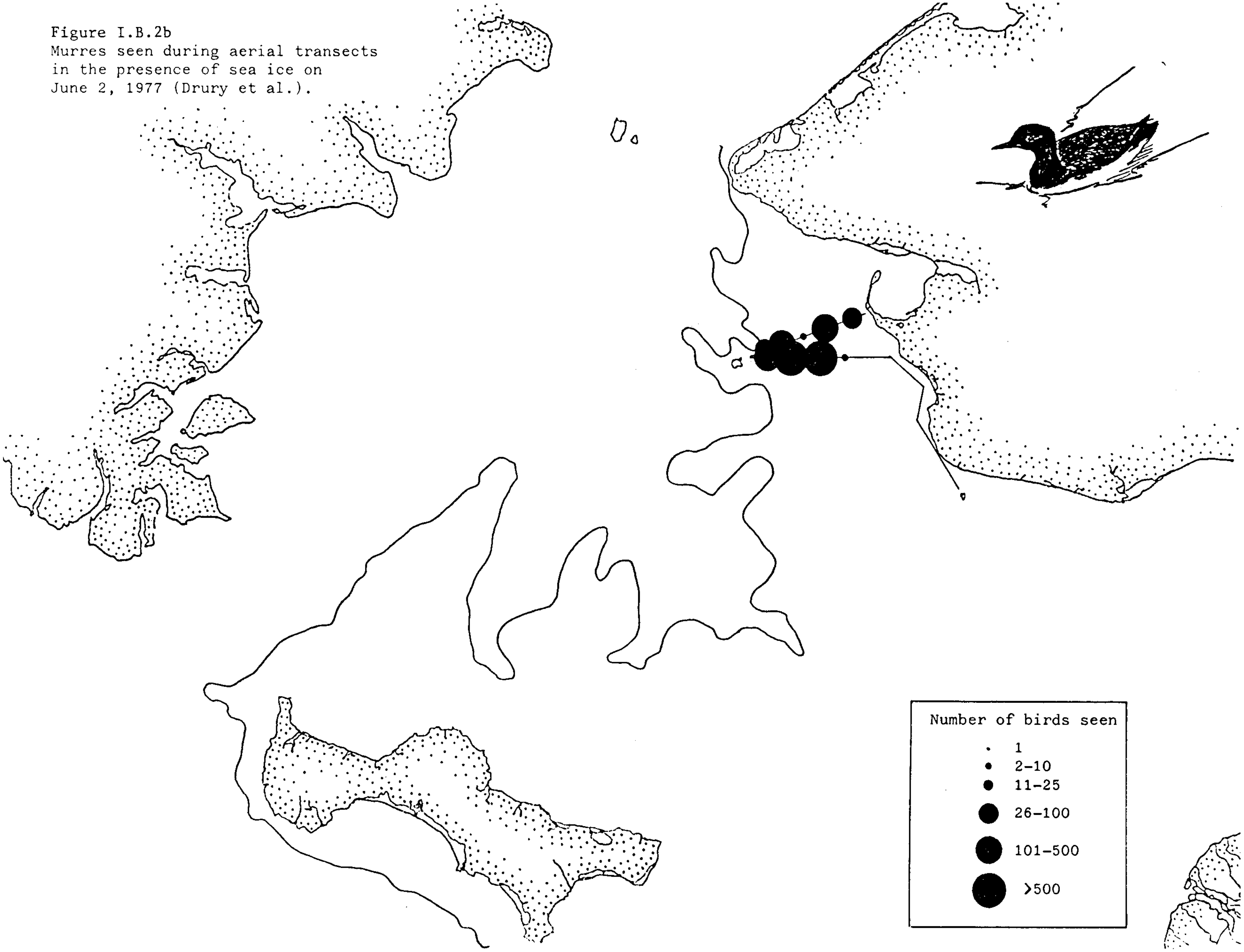


Figure I.B.2c
Murres seen during aerial transects in the presence of sea ice on June 4, 1976 (Drury et al.).

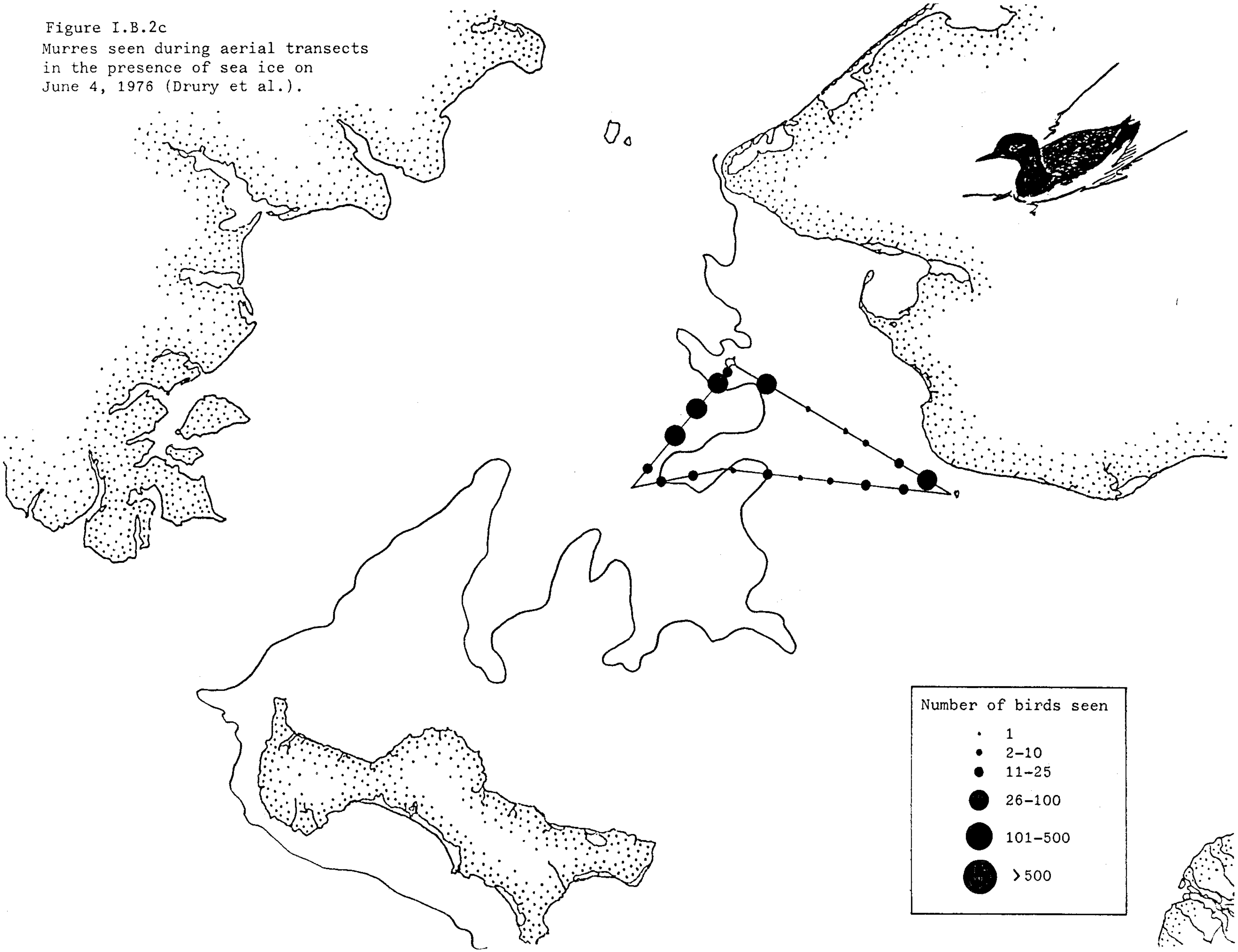
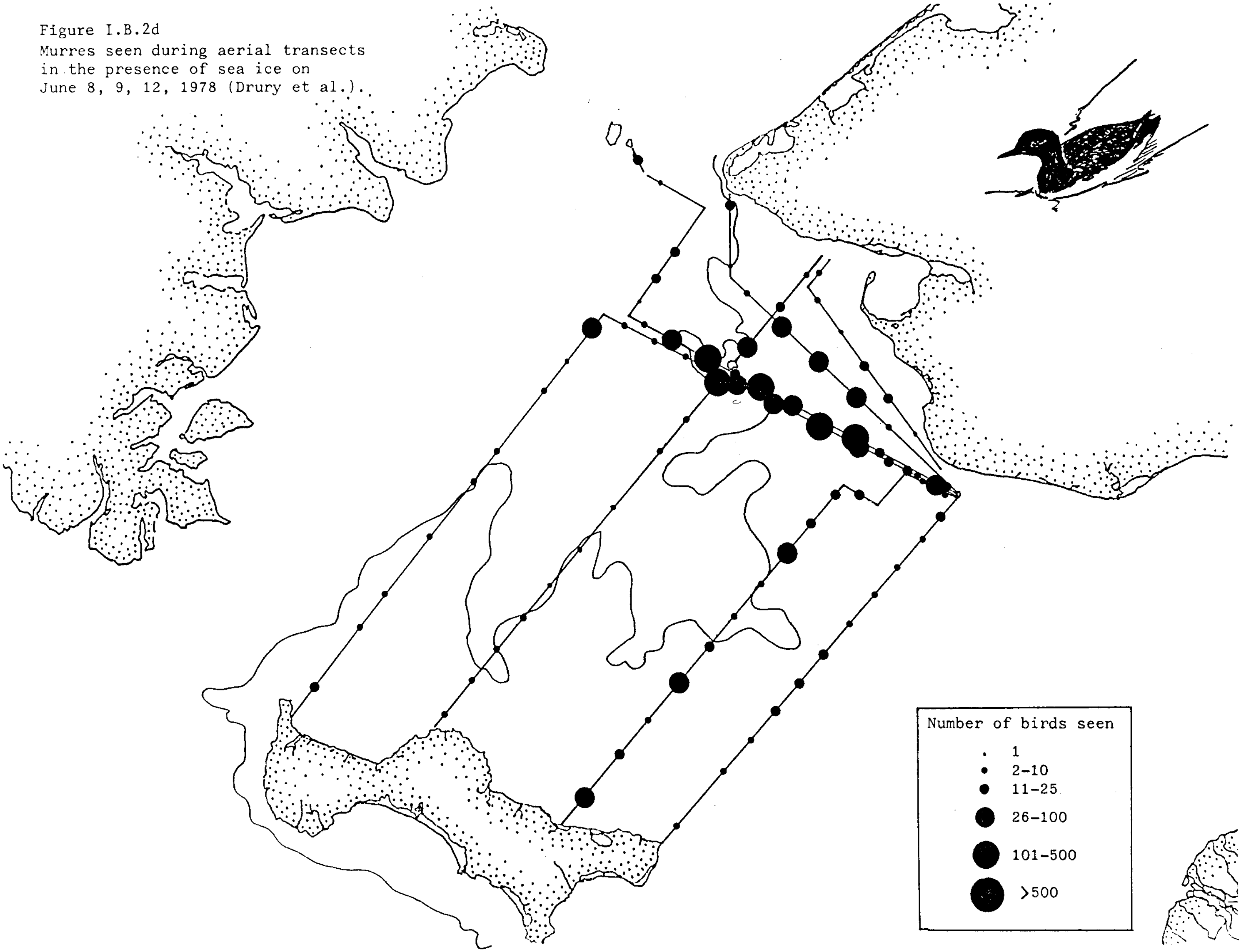


Figure I.B.2d
Murres seen during aerial transects
in the presence of sea ice on
June 8, 9, 12, 1978 (Drury et al.).



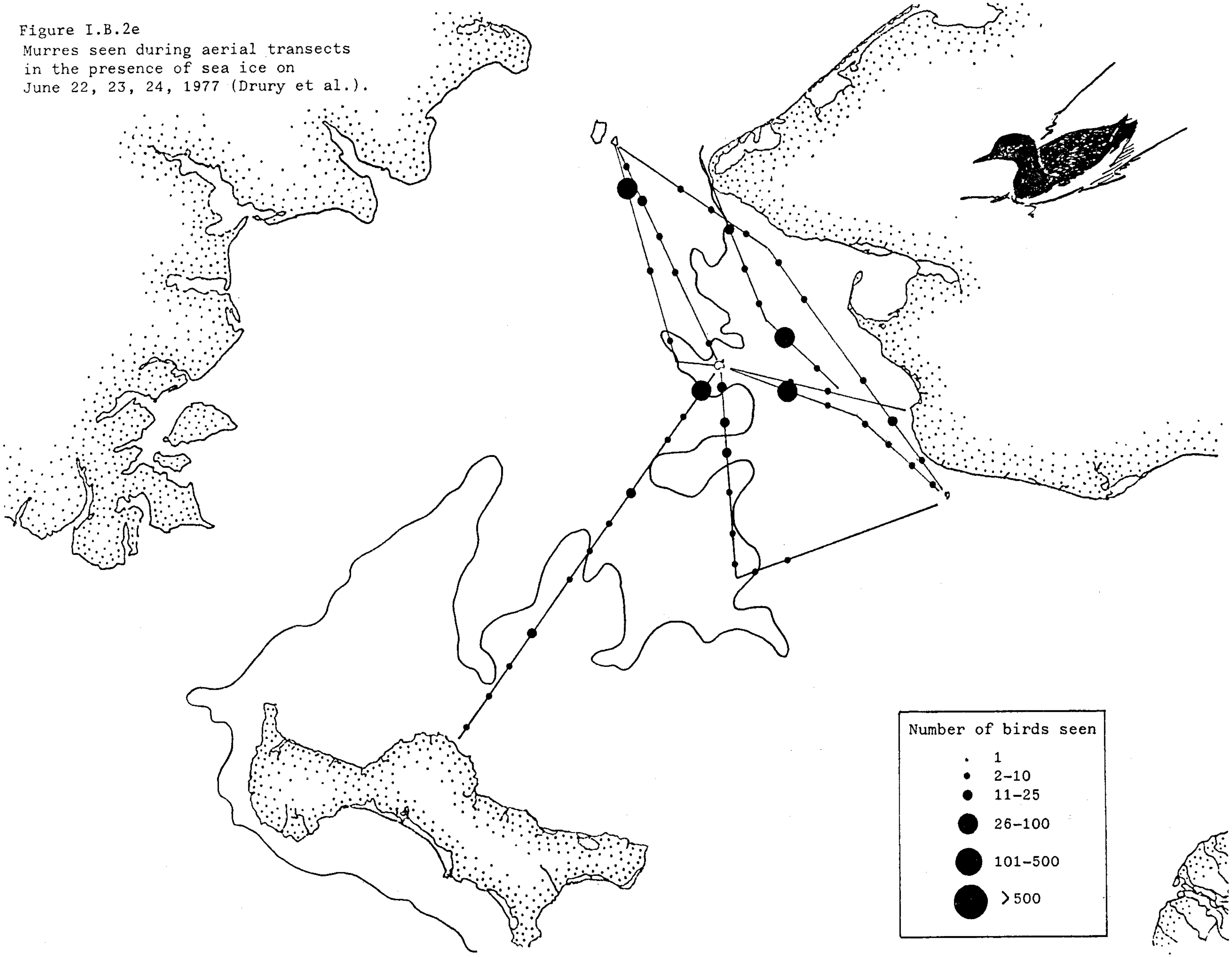


Figure I.B.2e
Murres seen during aerial transects in the presence of sea ice on June 22, 23, 24, 1977 (Drury et al.).

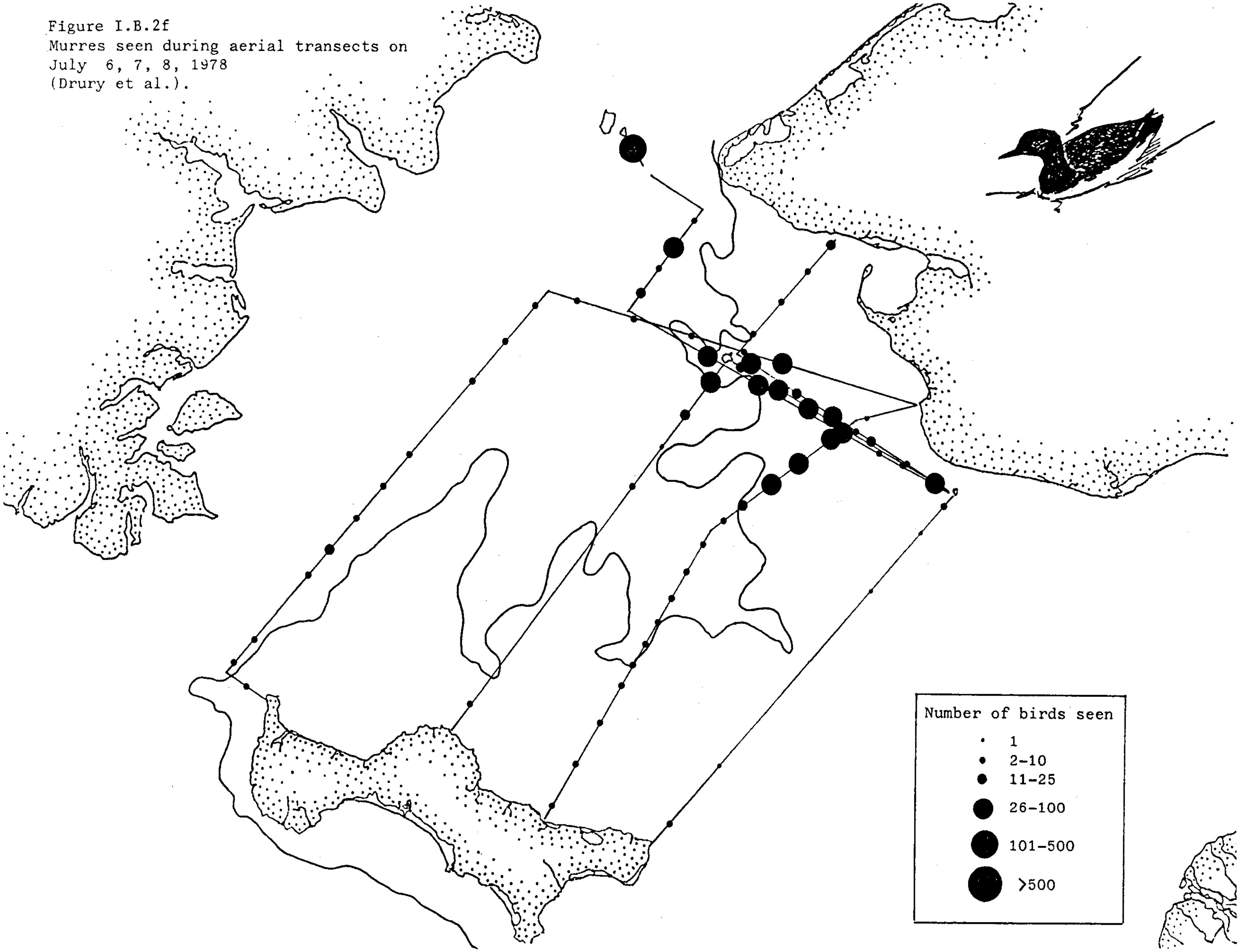


Figure I.B.2f
Murres seen during aerial transects on
July 6, 7, 8, 1978
(Drury et al.).

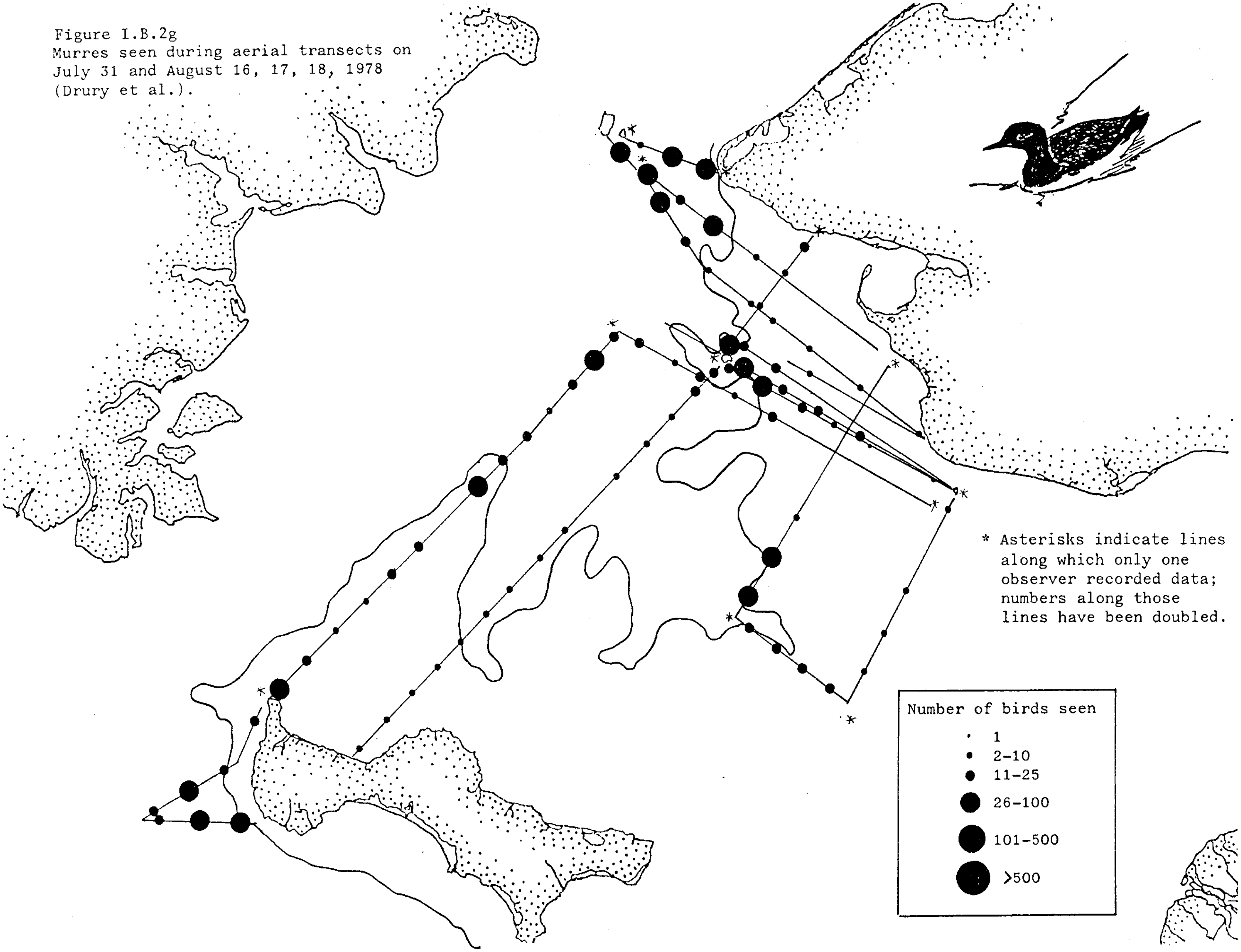


Figure I.B.2g
Murres seen during aerial transects on July 31 and August 16, 17, 18, 1978 (Drury et al.).

Figure I.B.2h
Murres seen during aerial transects on
August 21 and 22, 1977
(Drury et al.).

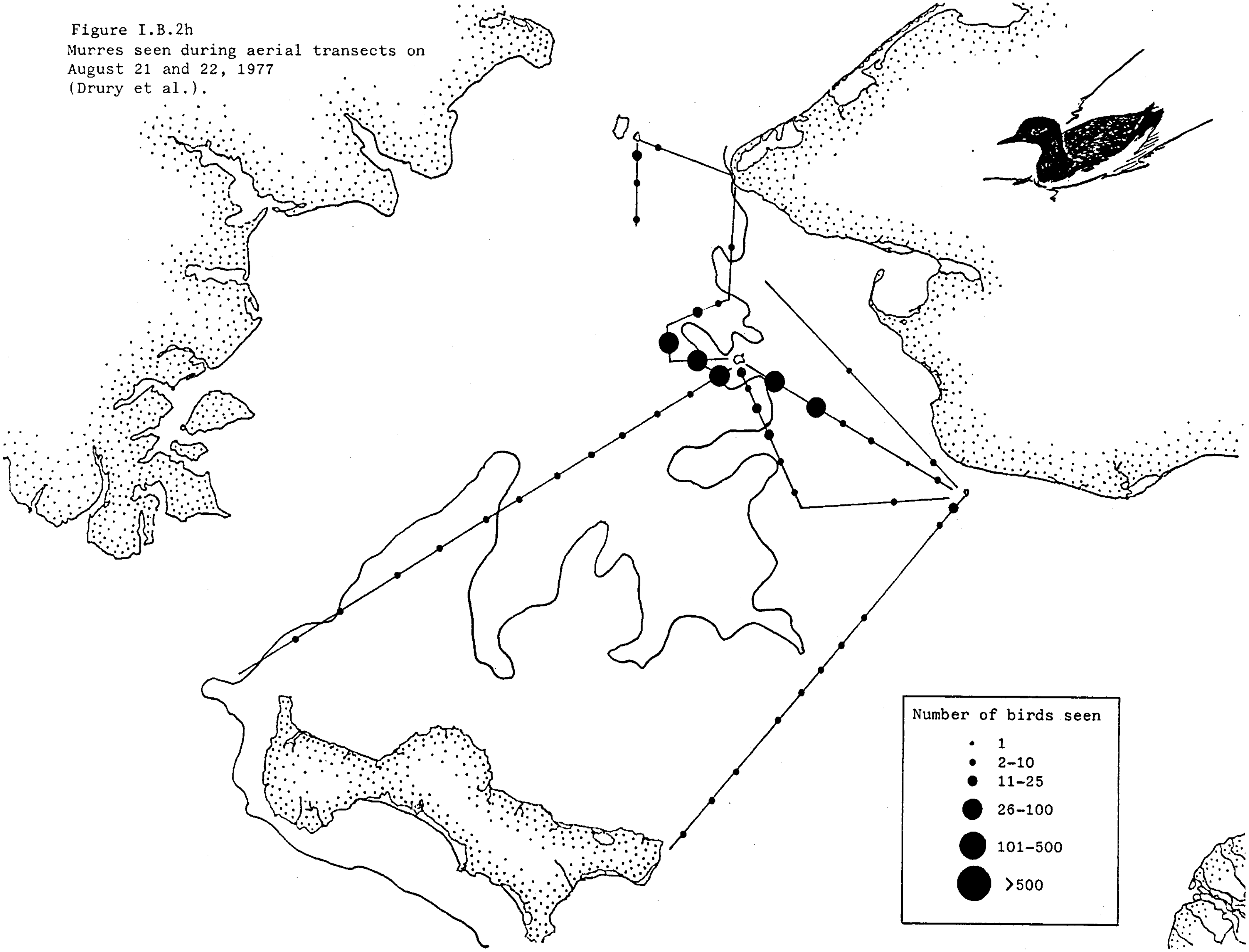


Figure I.B.3a
All Auklets (Least + Crested + Parakeet + Unidentified) seen in the presence of sea ice on May 20, 1977 (Drury et al.).

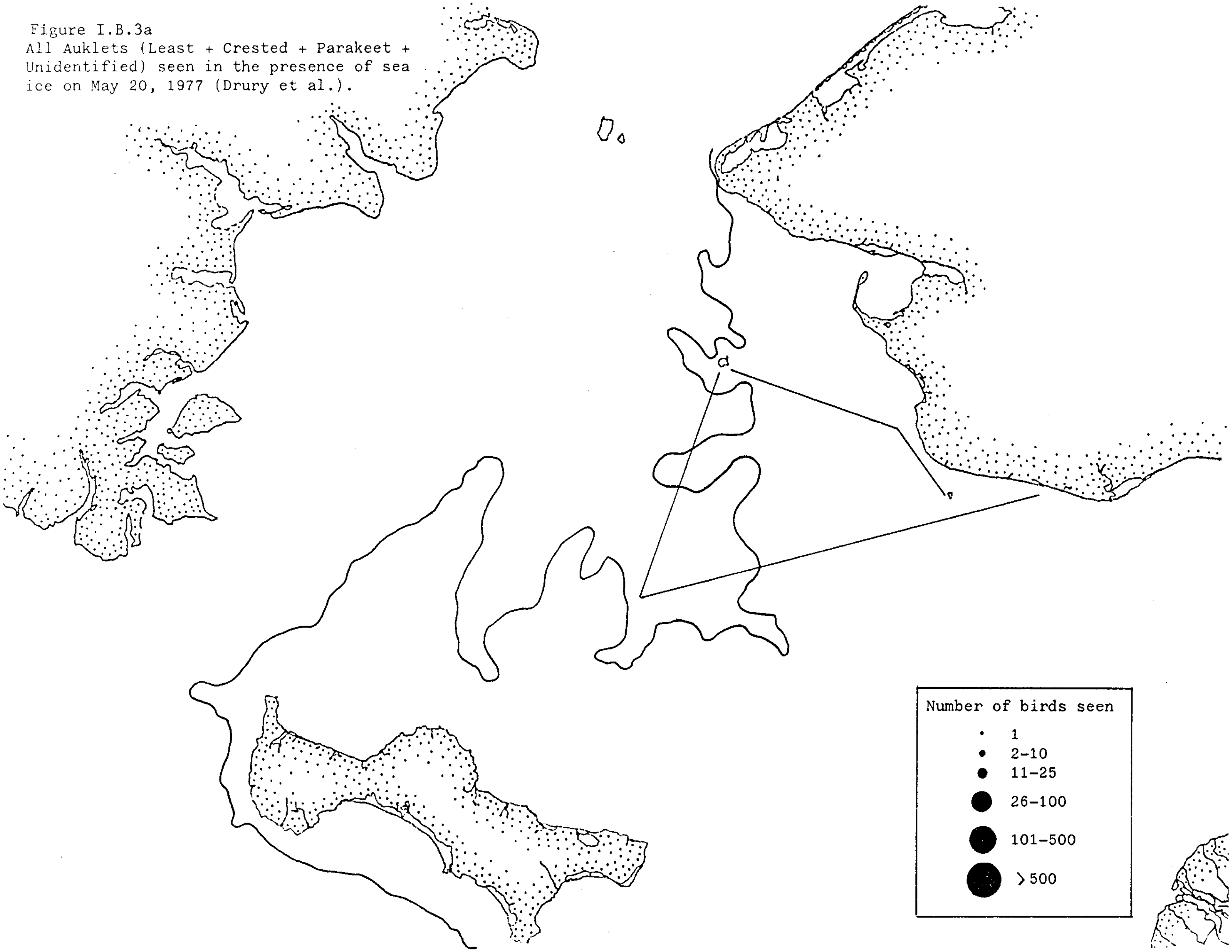


Figure I.B.3b
All Auklets (Least + Crested + Parakeet + Unidentified) seen in the presence of sea ice on June 2, 1977 (Drury et al.).

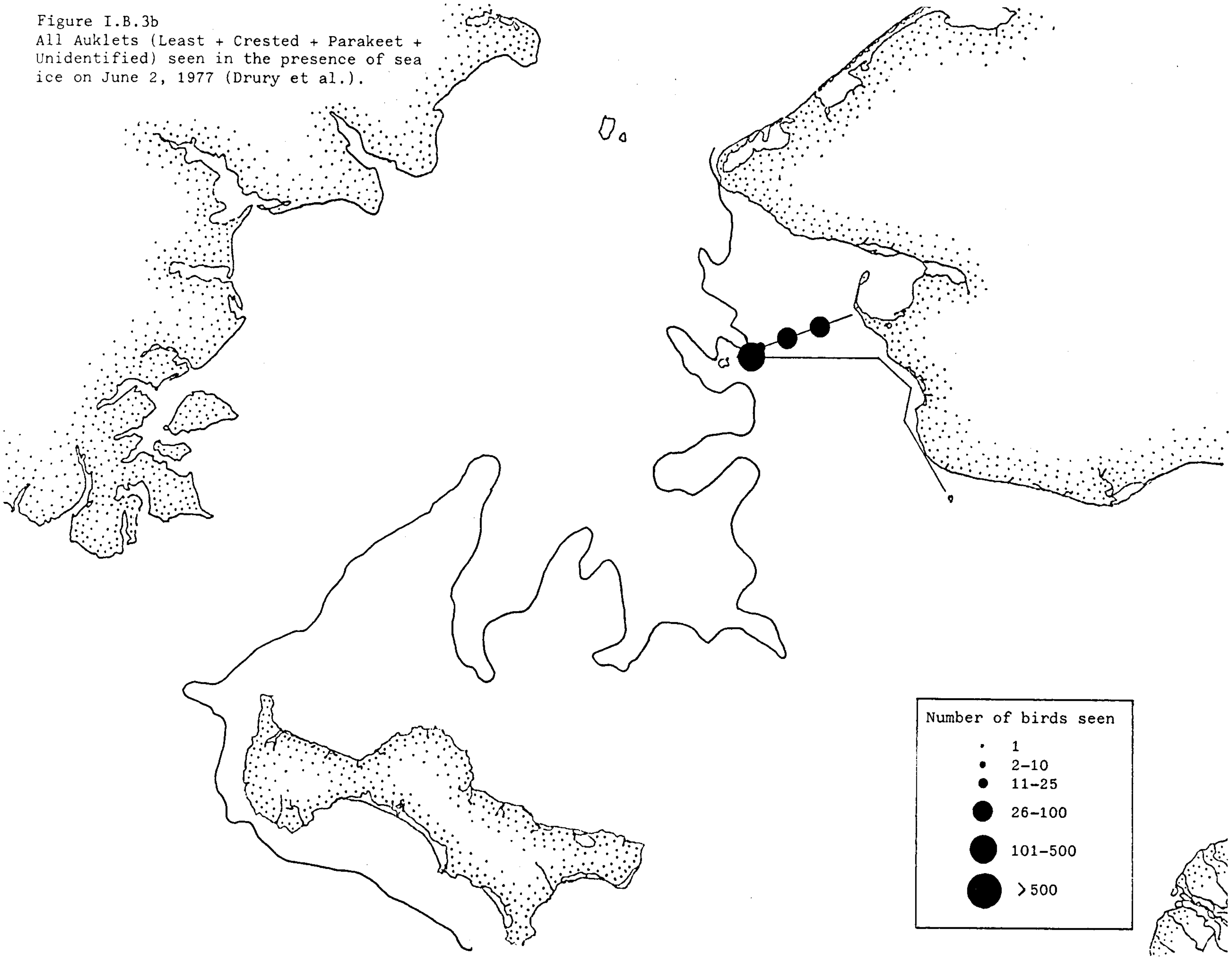


Figure I.B.3c
All Auklets (Least + Crested + Parakeet + Unidentified) seen in the presence of sea ice on June 4, 1976 (Drury et al.).

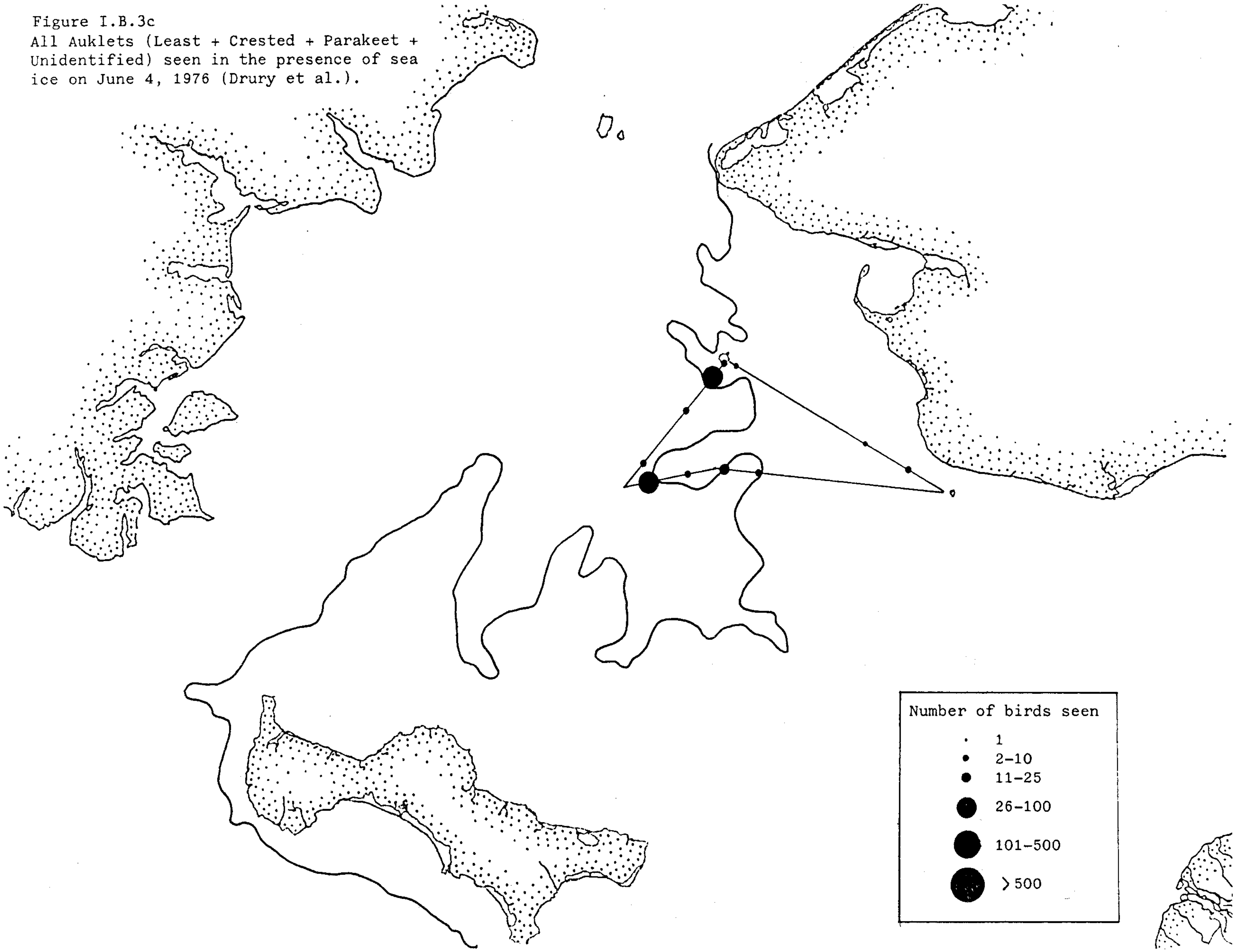


Figure I.B.3d
All Auklets (Least + Crested + Parakeet + Unidentified) seen in the presence of sea ice on June 8, 9, 12, 1978 (Drury et al.).

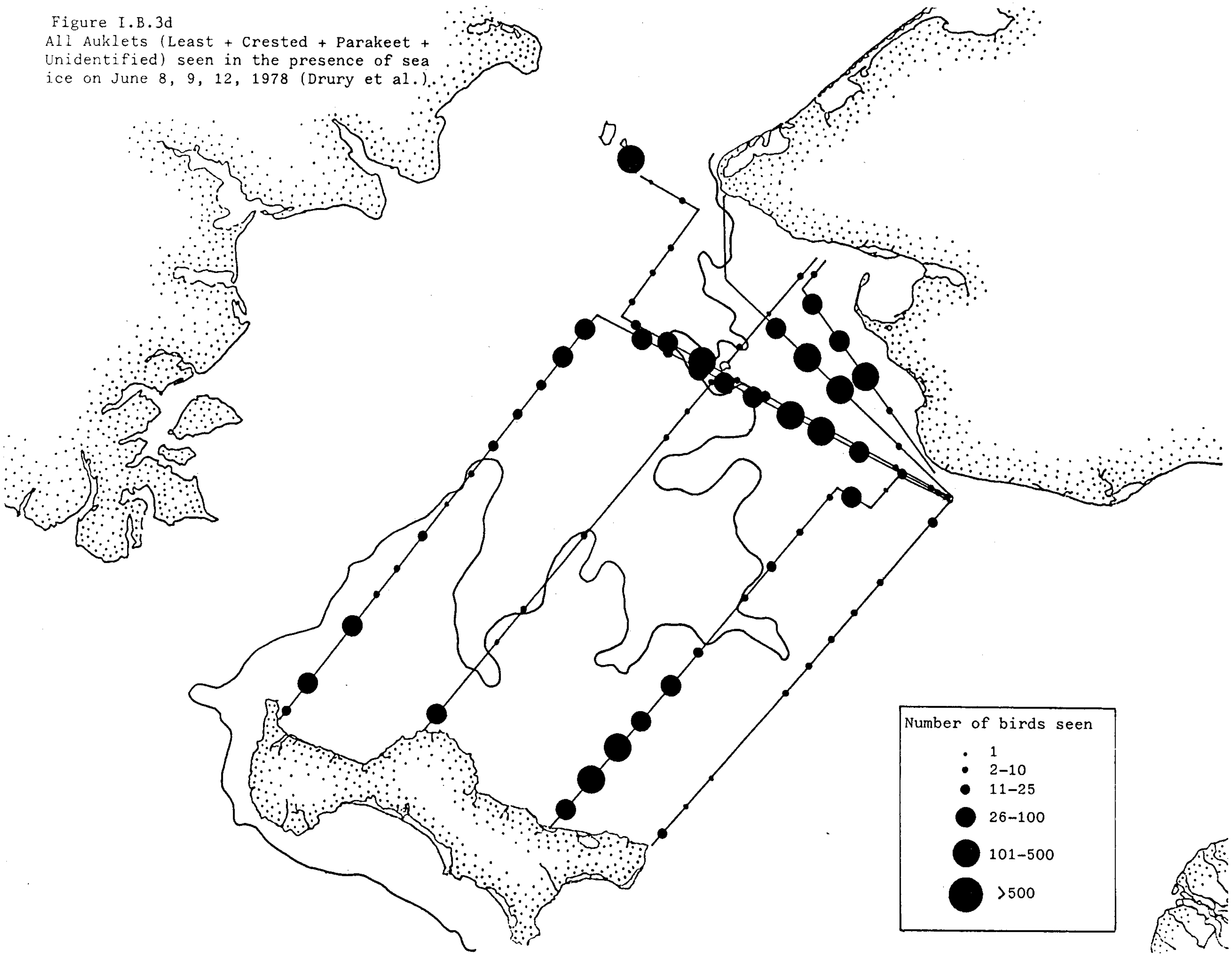


Figure I.B.3e
All Auklets (Least + Crested + Parakeet + Unidentified) seen in the presence of sea ice on June 22, 23, 24, 1977 (Drury et al.)

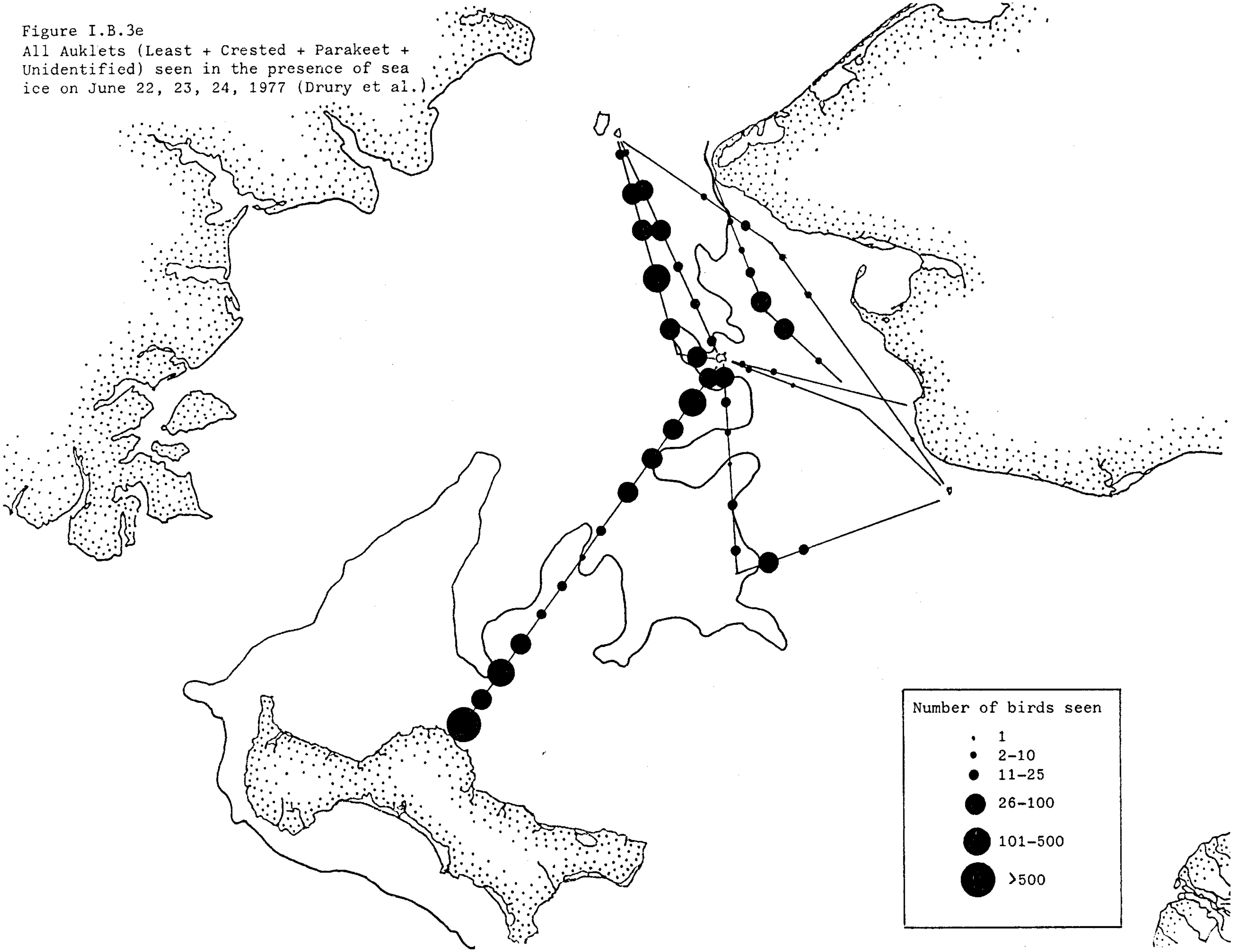


Figure I.B.3f
All Auklets (Least + Crested +
Parakeet + Unidentified) seen on
July 6, 7, 8, 1978
(Drury et al.).

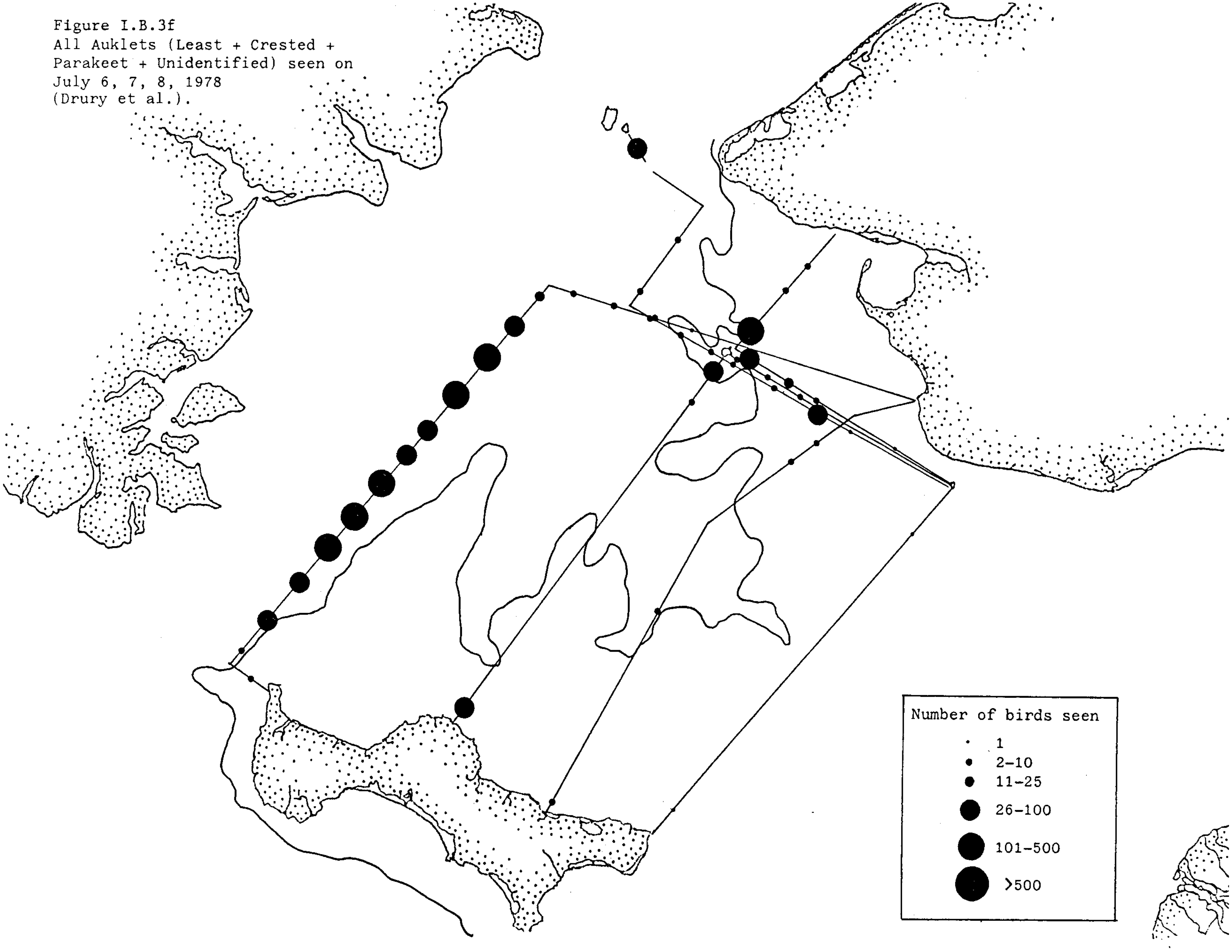
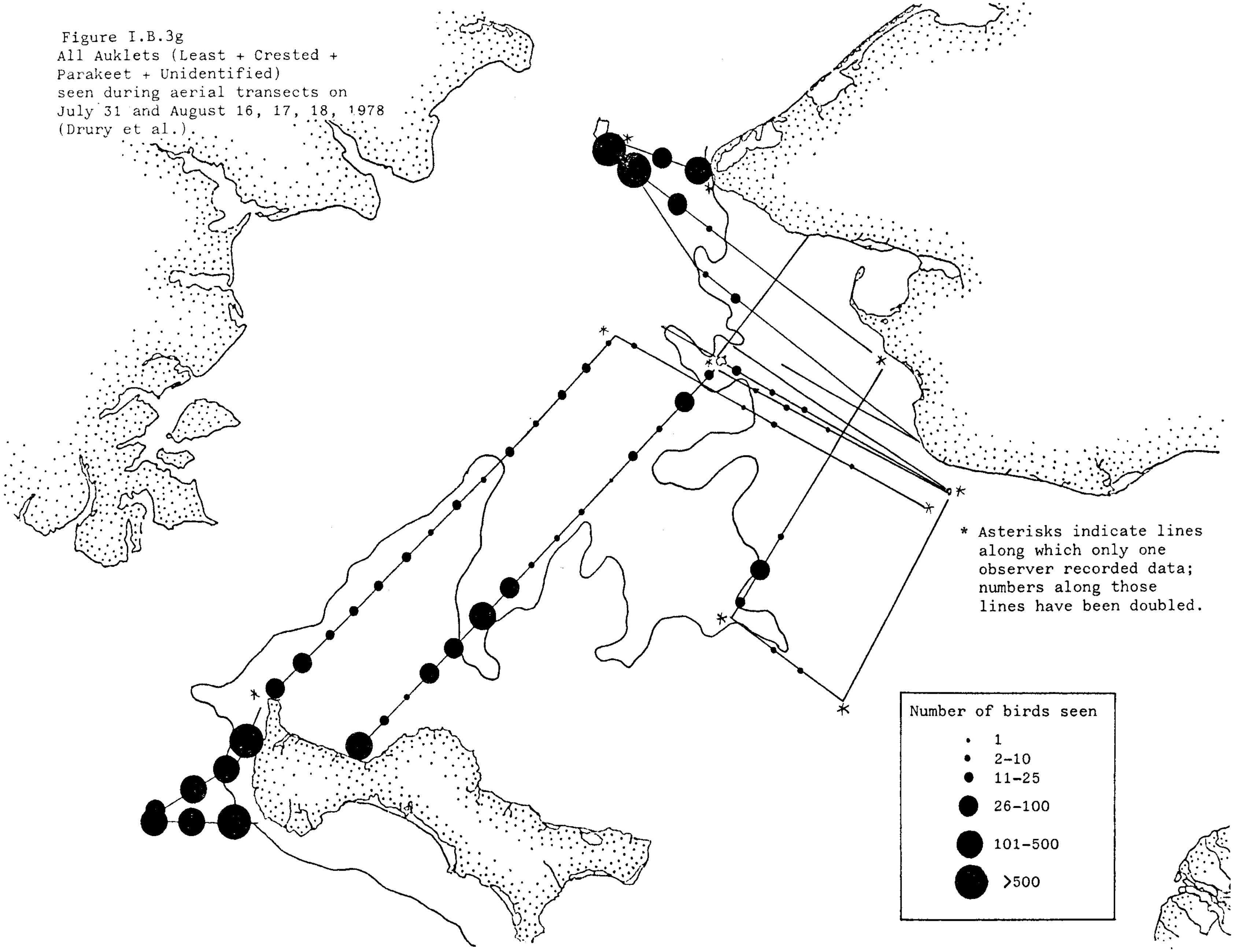


Figure I.B.3g
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects on July 31 and August 16, 17, 18, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.B.3h
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects on August 21, 22, 1977 (Drury et al.).

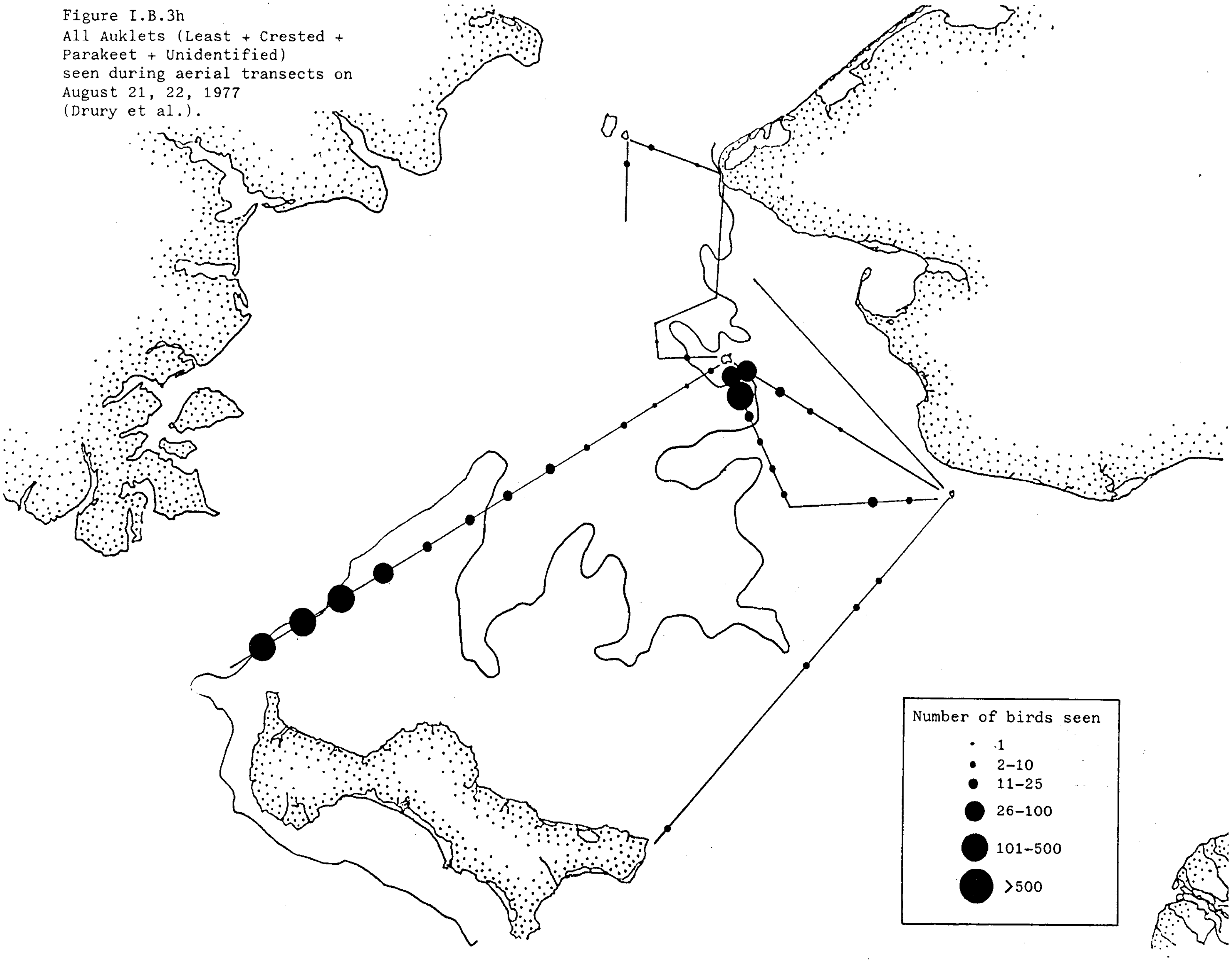


Figure I.B.4a
Least Auklets seen during aerial transects in the presence of sea ice on June 8, 9, 12, 1978 (Drury et al.).

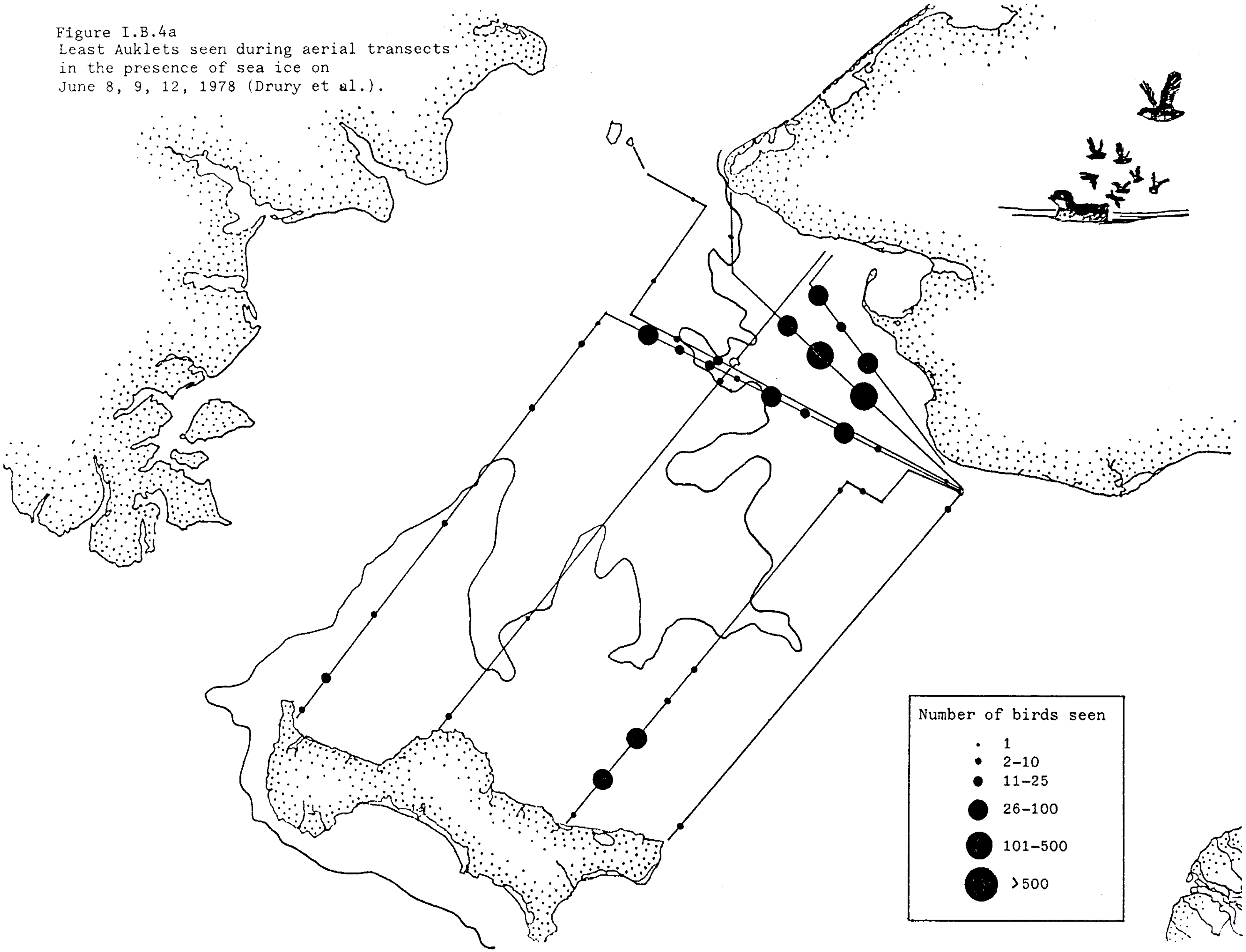


Figure I.B.4b
Least Auklets seen during aerial transects in the presence of sea ice on June 22, 23, 24, 1977 (Drury et al.).

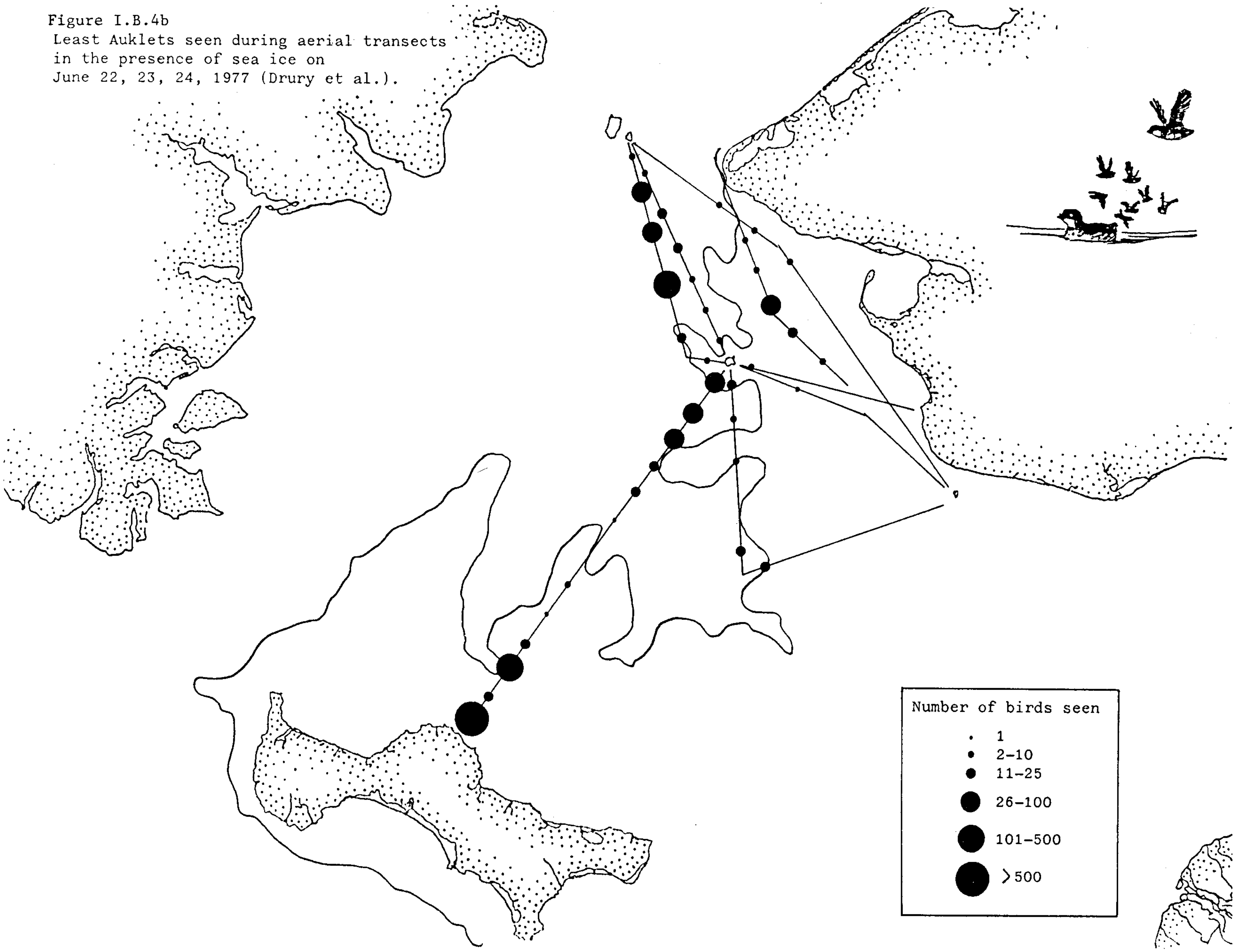
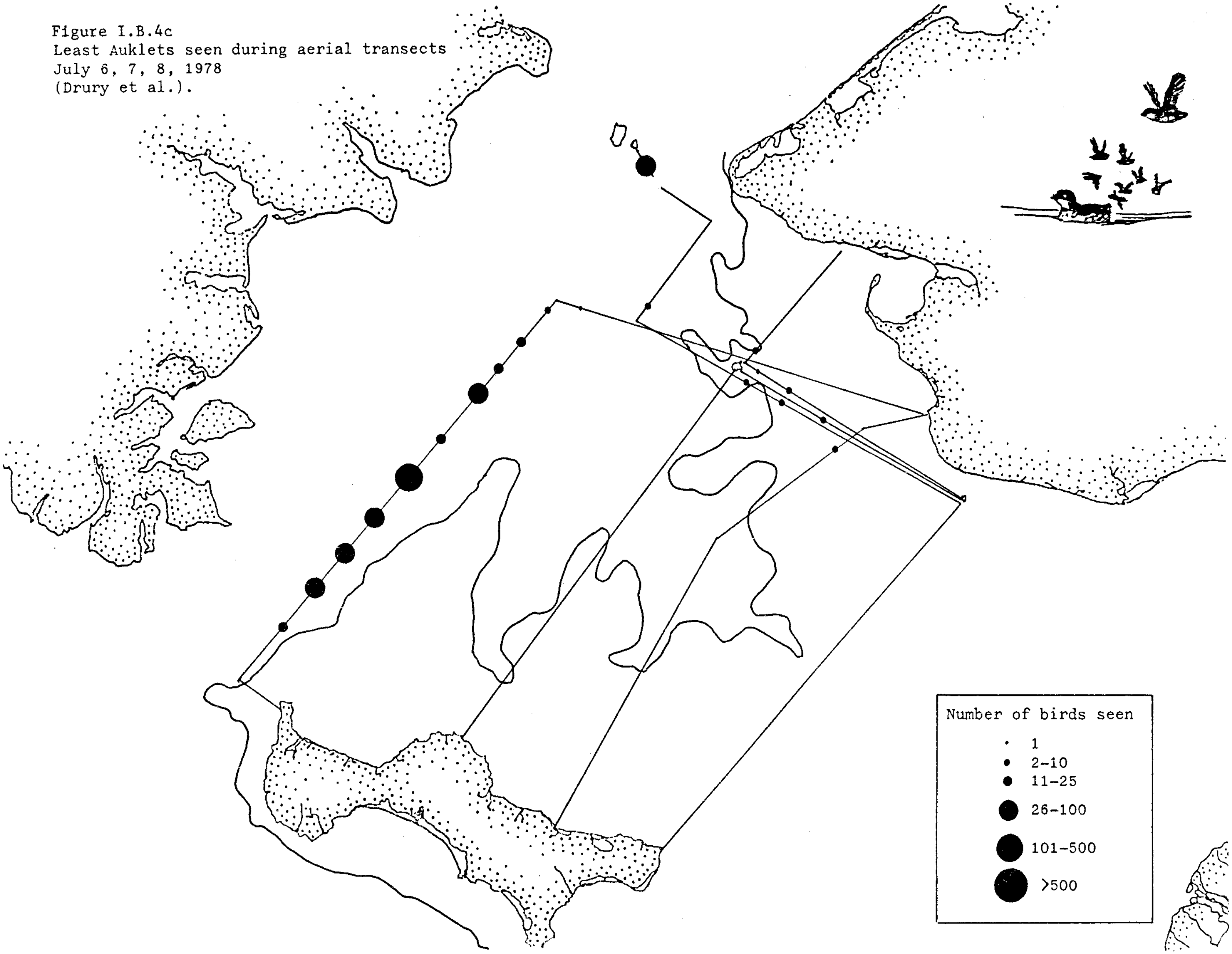


Figure I.B.4c
Least Auklets seen during aerial transects
July 6, 7, 8, 1978
(Drury et al.).



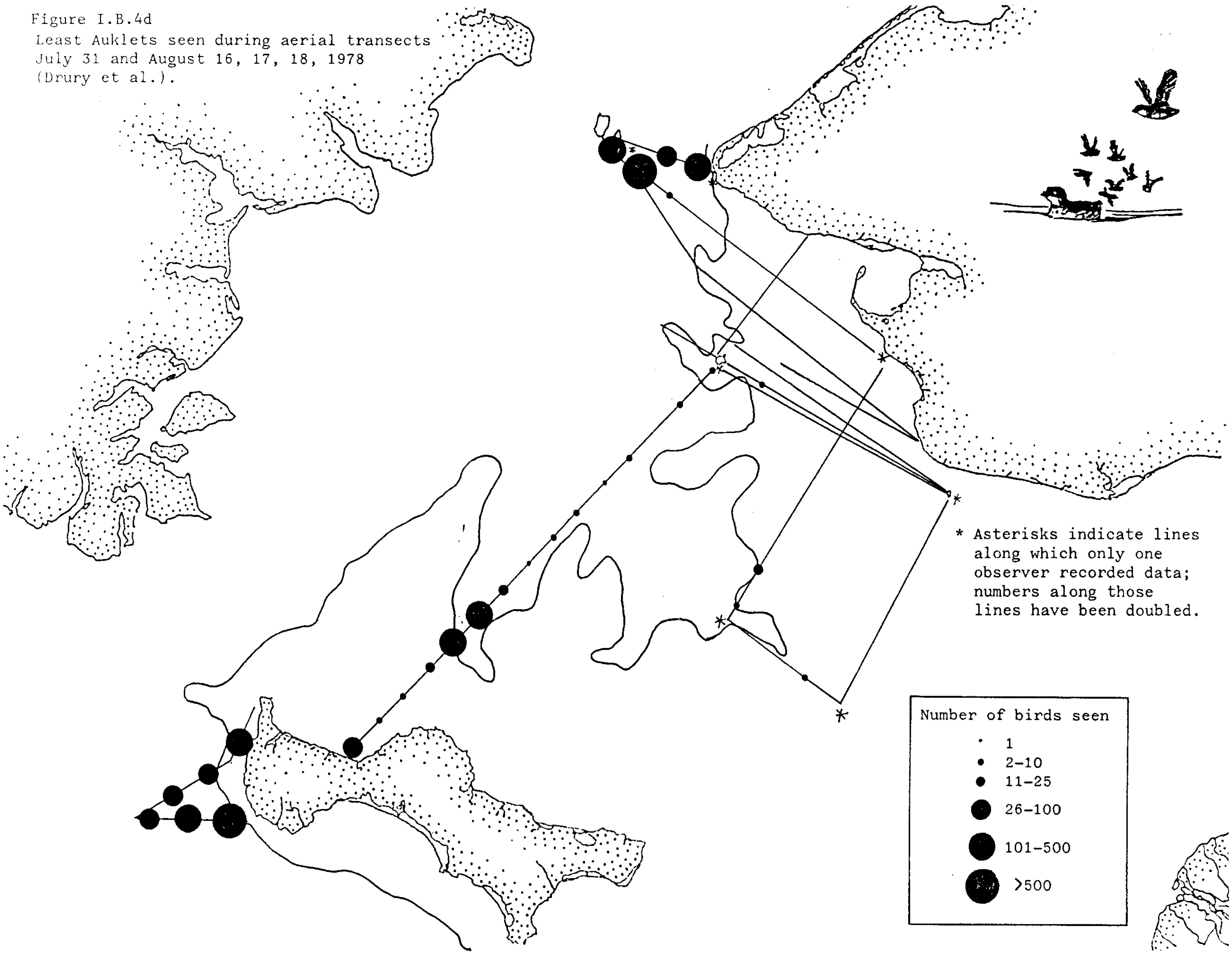


Figure I.B.4d
Least Auklets seen during aerial transects
July 31 and August 16, 17, 18, 1978
(Drury et al.).

* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.B.4e
Least Auklets seen during aerial transects
August 21, 22, 1977
(Drury et al.).

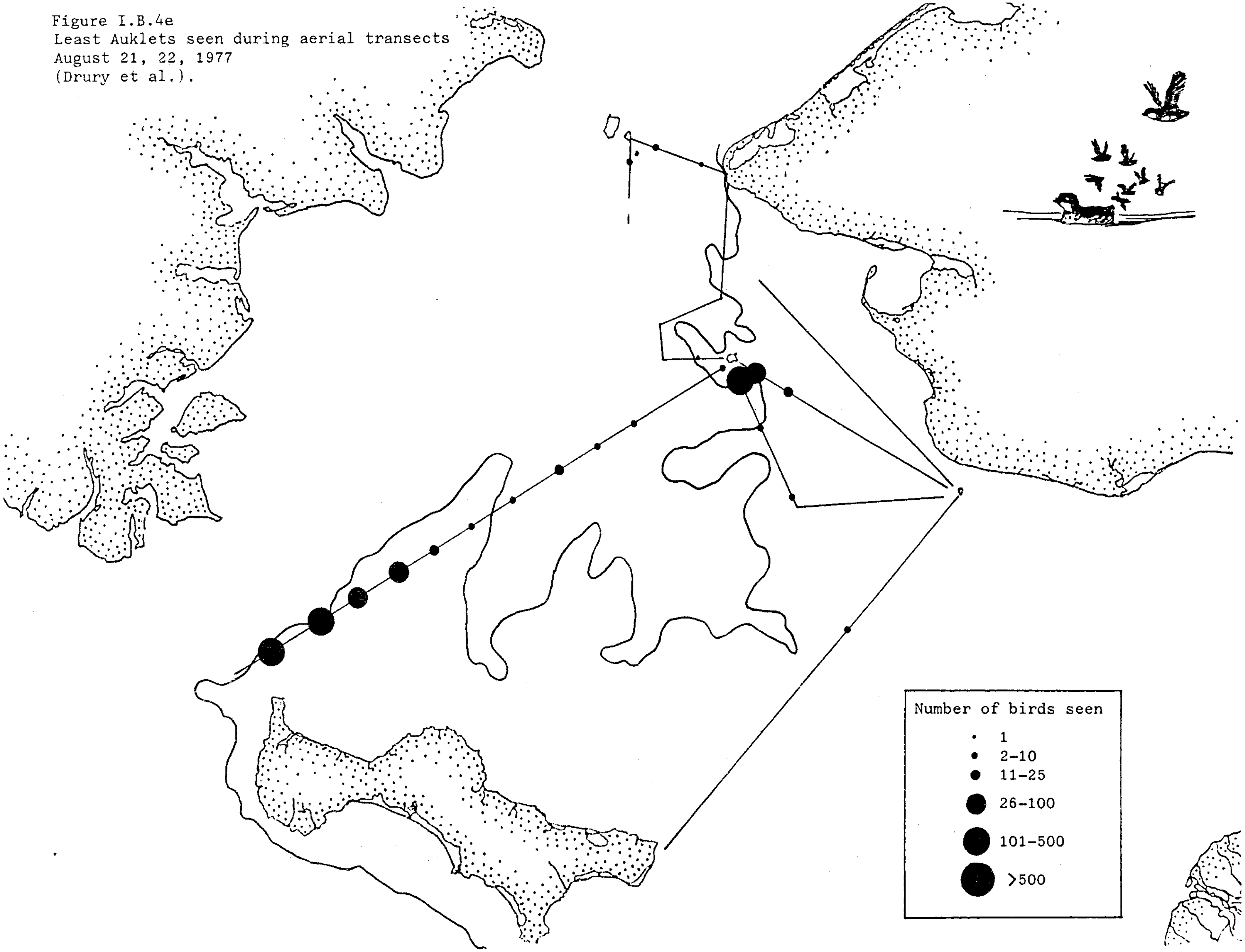


Figure I.B.5a
Crested Auklets seen during aerial transects in the presence of sea ice on June 8, 9, 12, 1978 (Drury et al.).

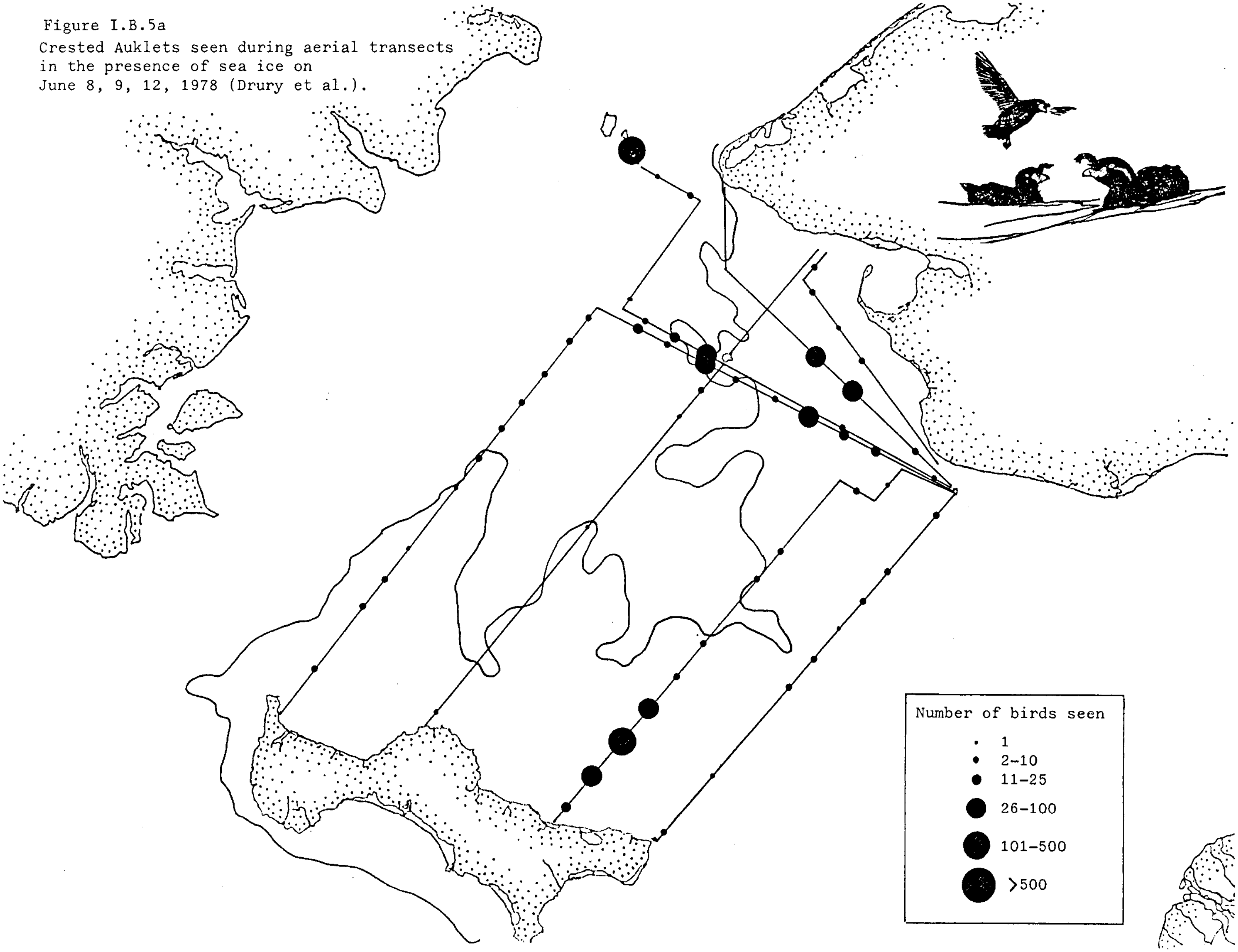


Figure I.B.5b
Crested Auklets seen during aerial transects in the presence of sea ice on June 22, 23, 24, 1977 (Drury et al.).

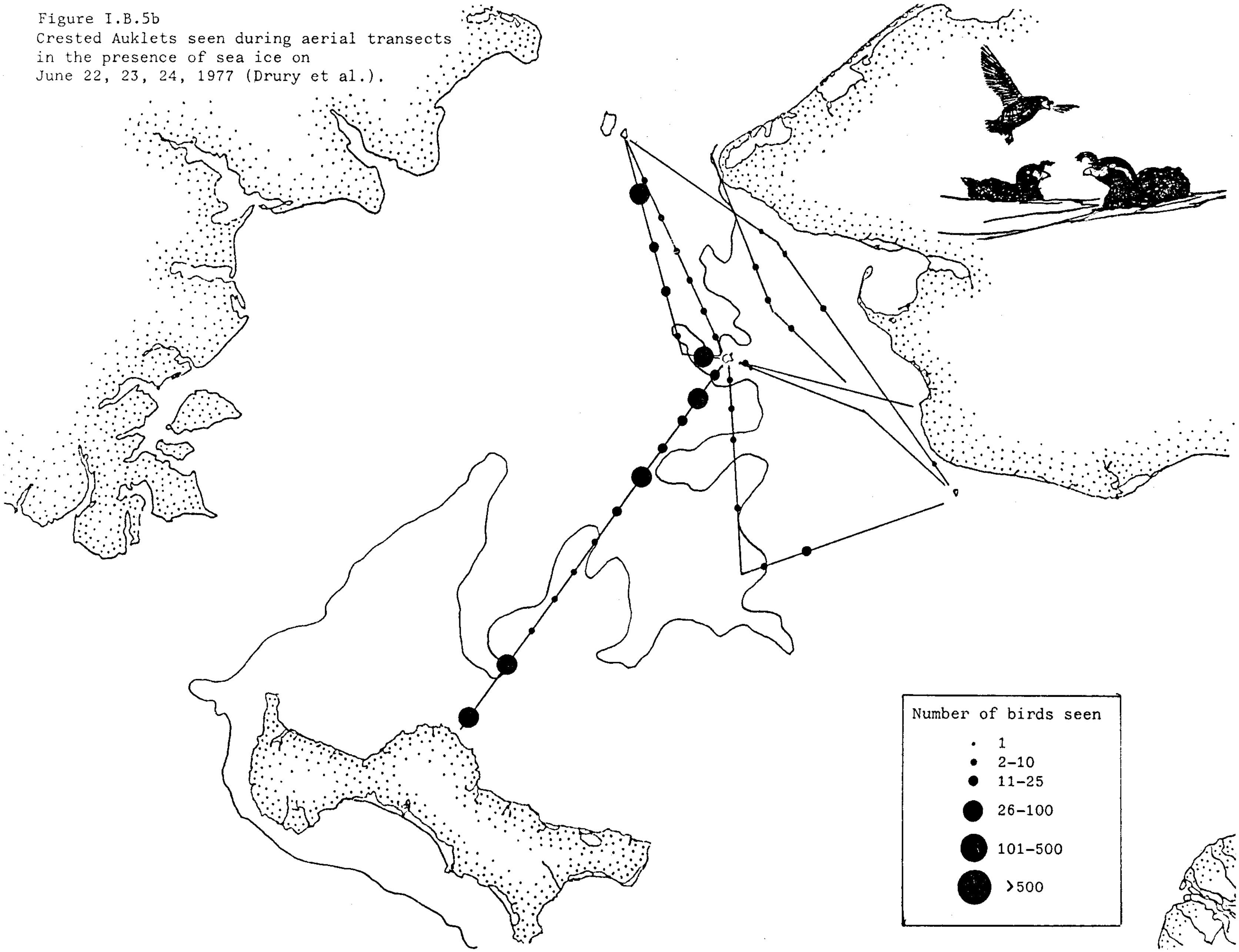


Figure I.B.5c
Crested Auklets seen during aerial transects
July 6, 7, 8, 1978
(Drury et al.).

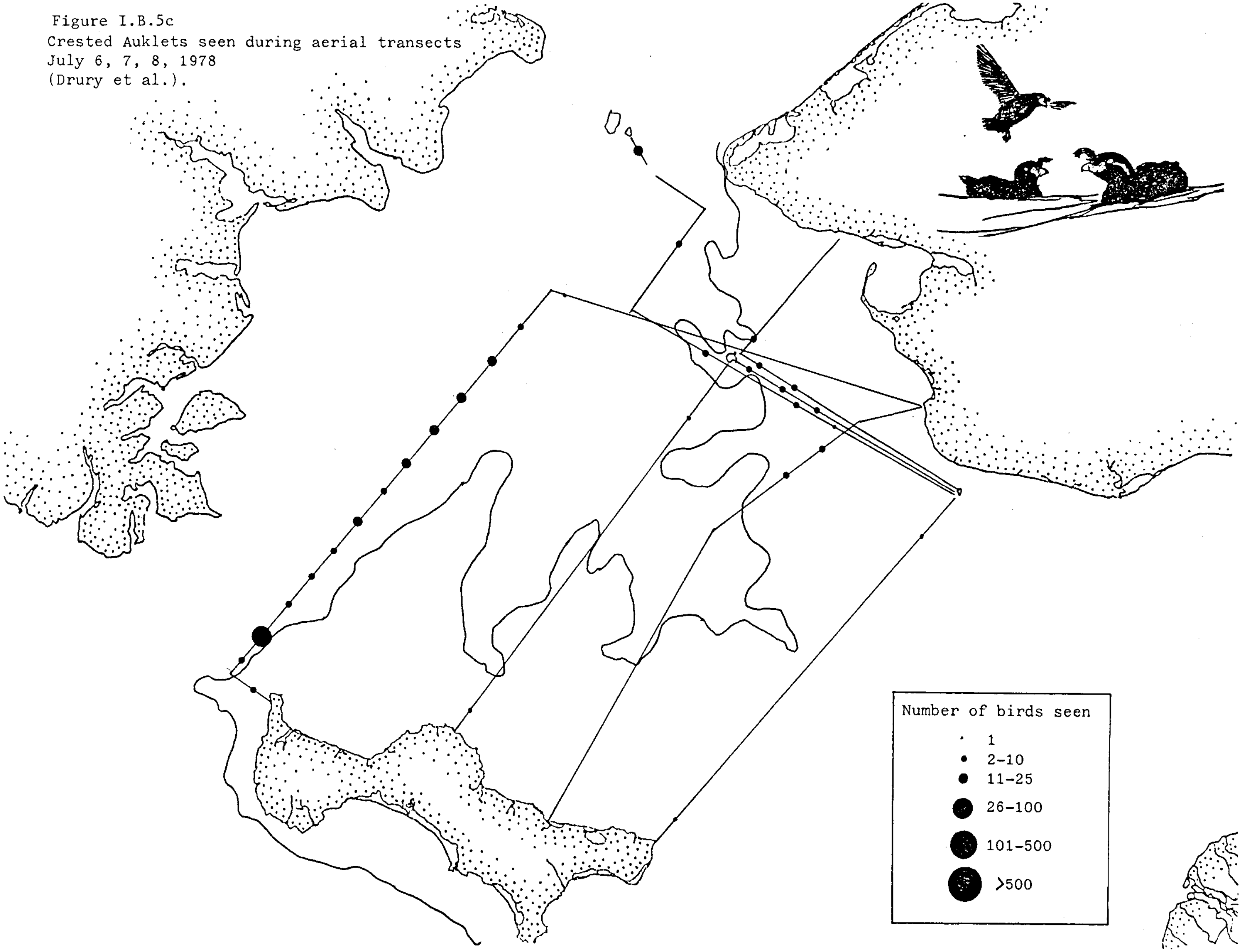
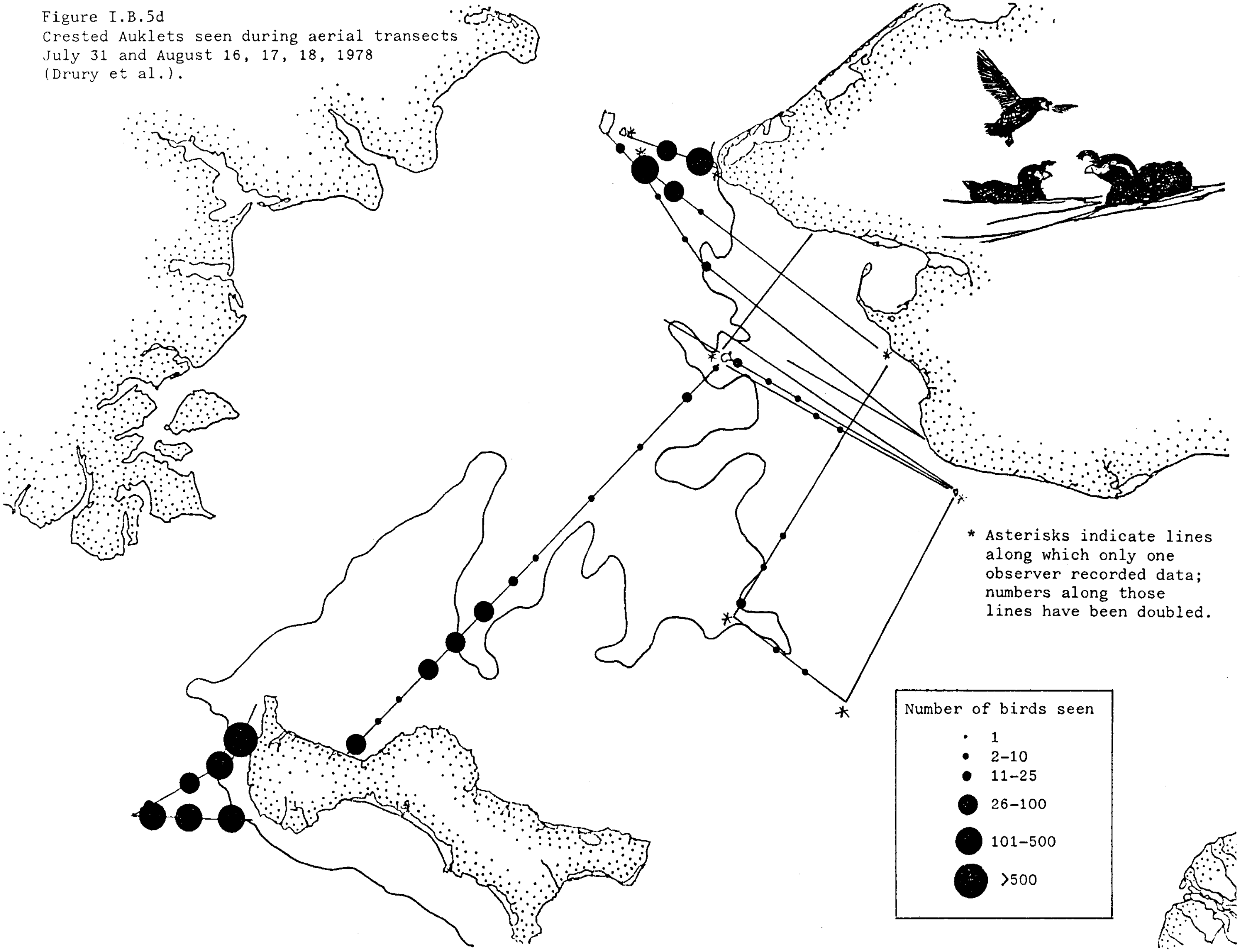


Figure I.B.5d
Crested Auklets seen during aerial transects
July 31 and August 16, 17, 18, 1978
(Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.B.5e
Crested Auklets seen during aerial transects
August 21, 22, 1977
(Drury et al.).

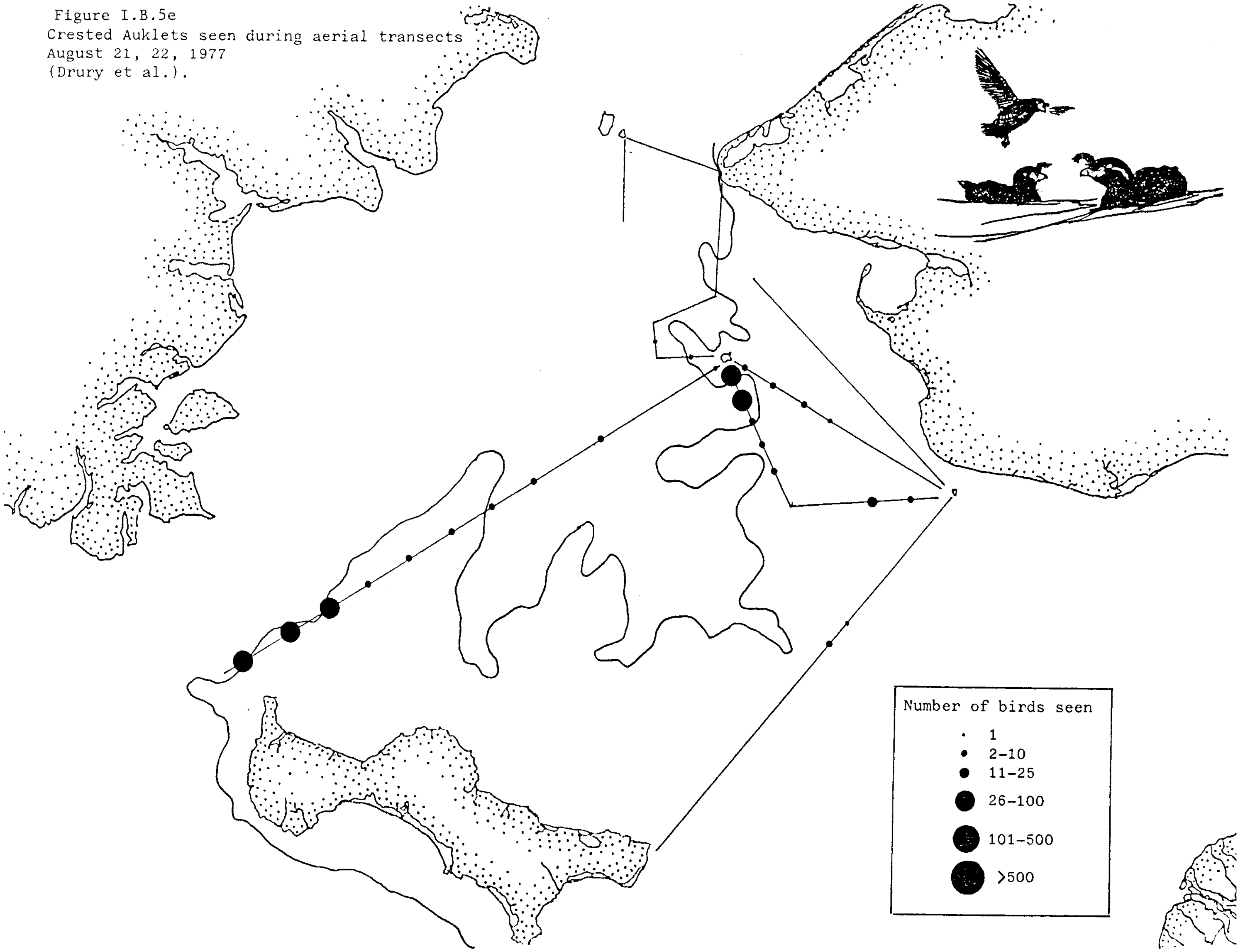


Figure I.B.6a
Parakeet Auklets seen during aerial transects in the presence of sea ice on June 8, 9, 12, 1978, and June 22, 23, 24, 1977 (Drury et al.).

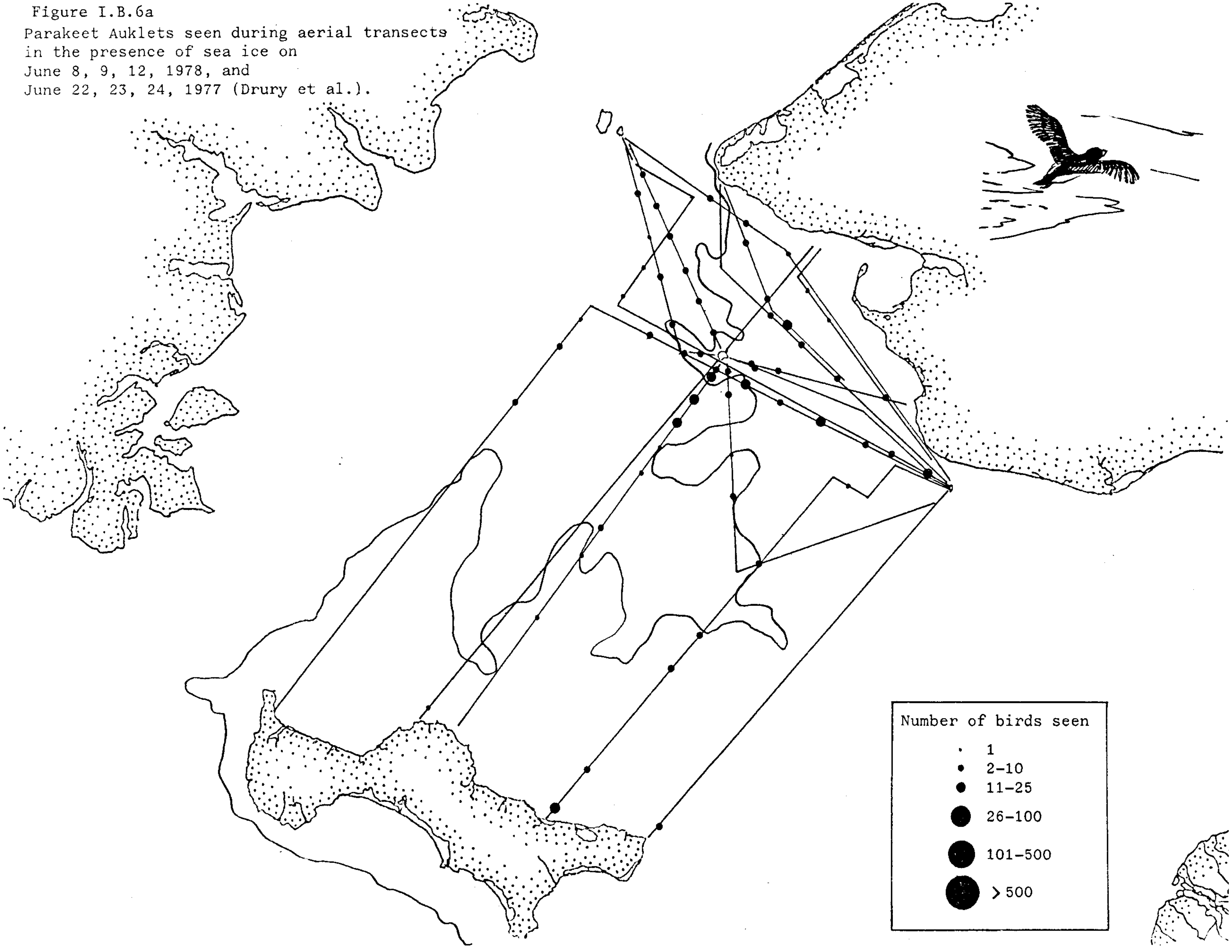


Figure I.B.6b
Parakeet Auklets seen during aerial transects
July 6, 7, 8, 1978
(Drury et al.).

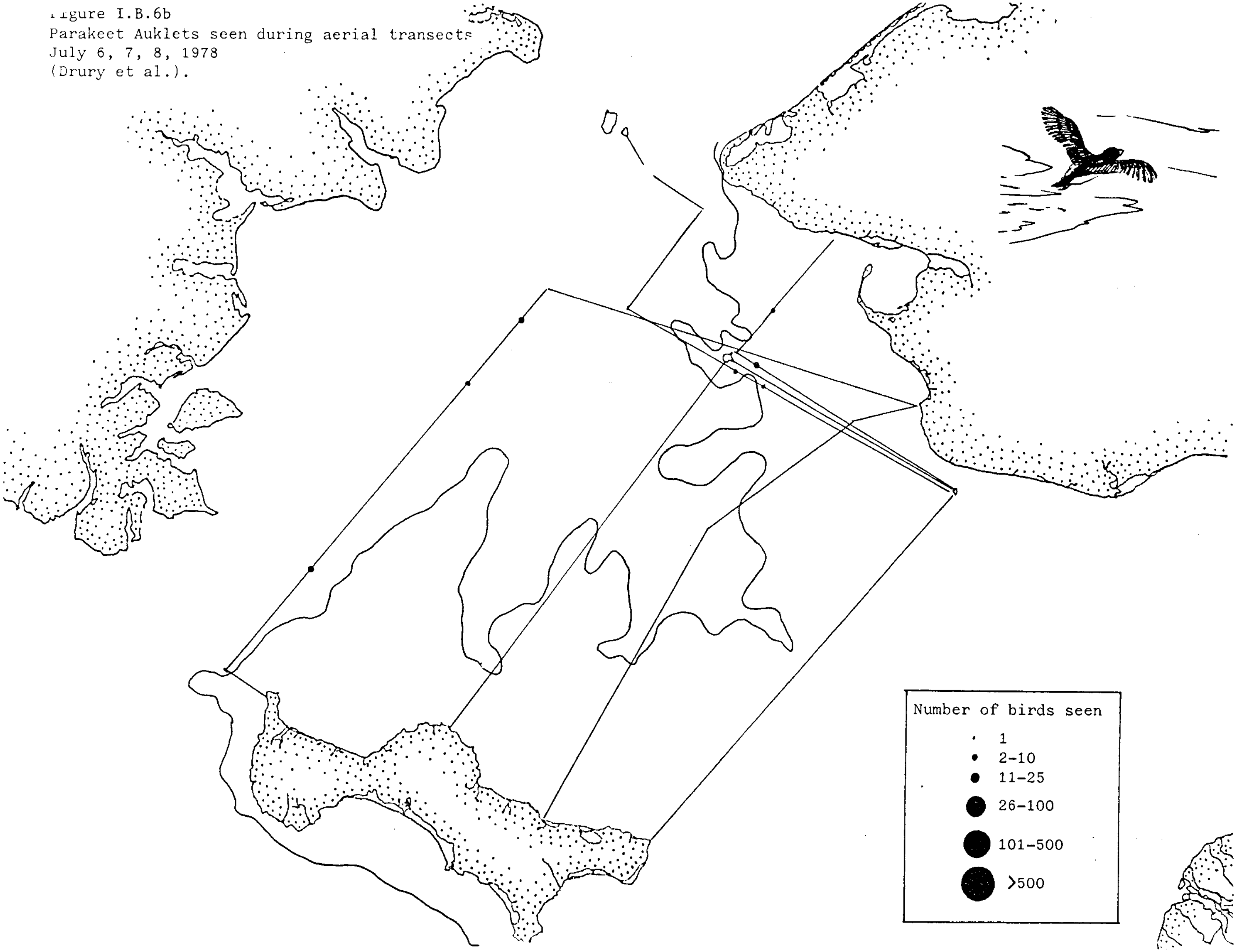
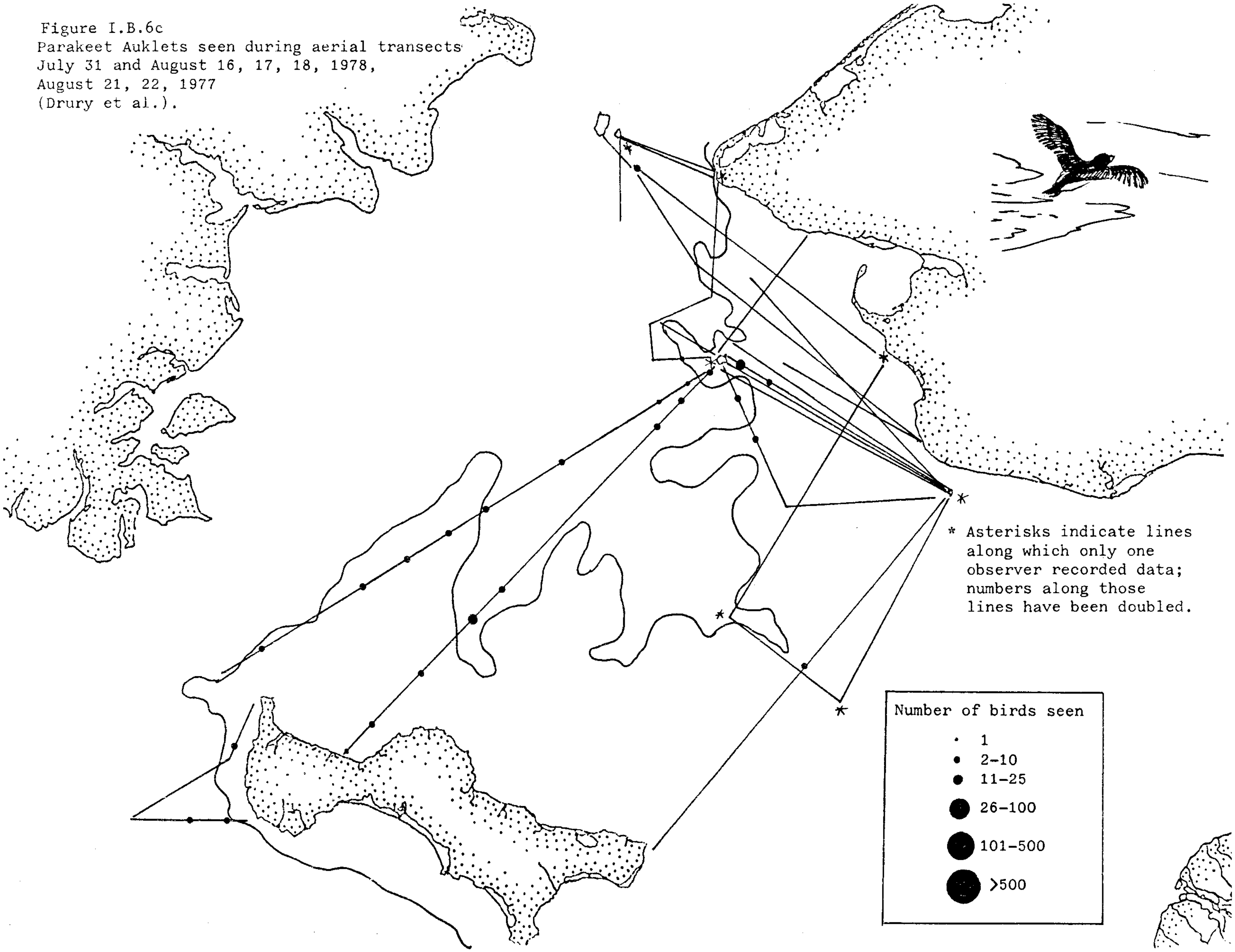
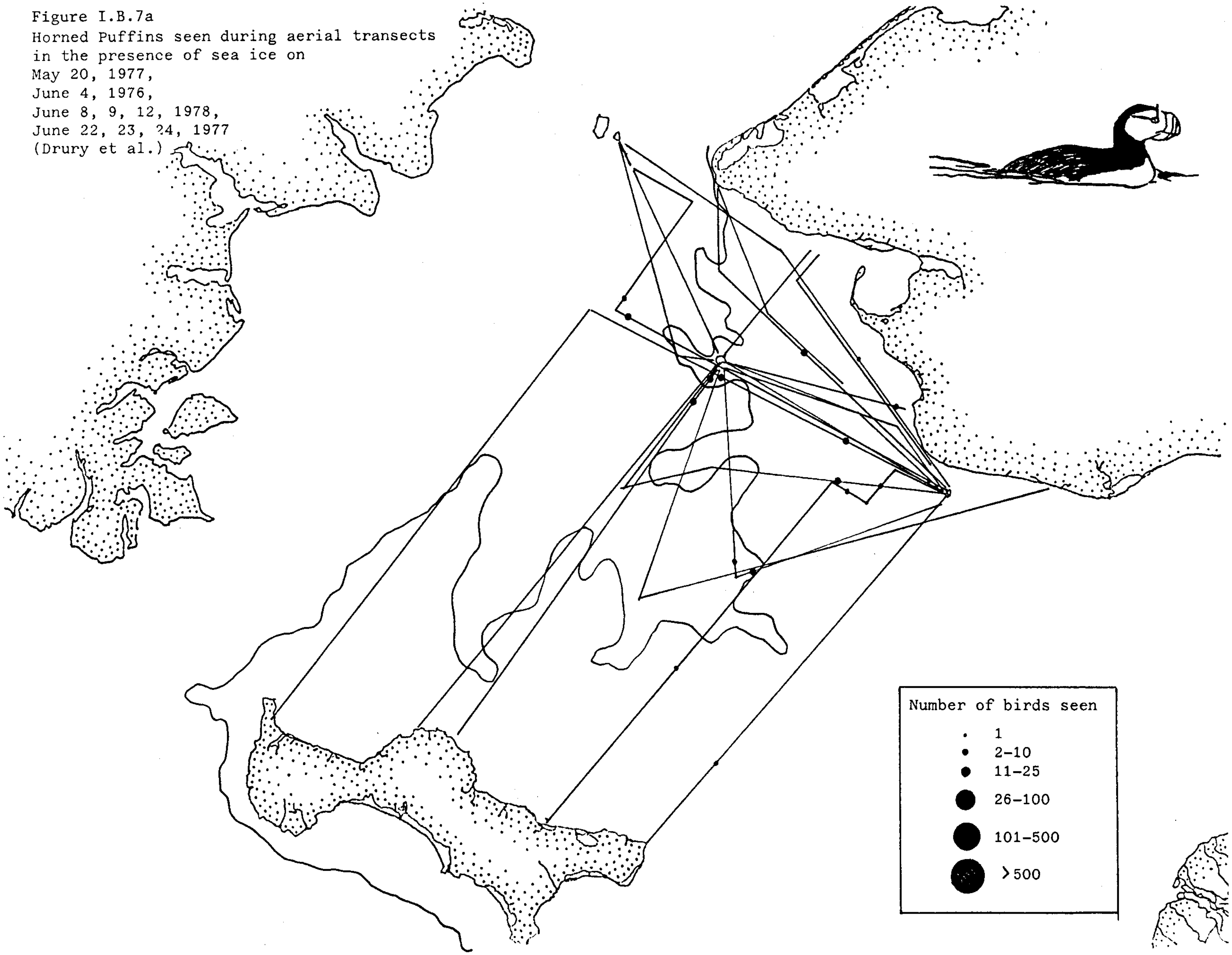


Figure I.B.6c
Parakeet Auklets seen during aerial transects
July 31 and August 16, 17, 18, 1978,
August 21, 22, 1977
(Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.B.7a
Horned Puffins seen during aerial transects
in the presence of sea ice on
May 20, 1977,
June 4, 1976,
June 8, 9, 12, 1978,
June 22, 23, 24, 1977
(Drury et al.)



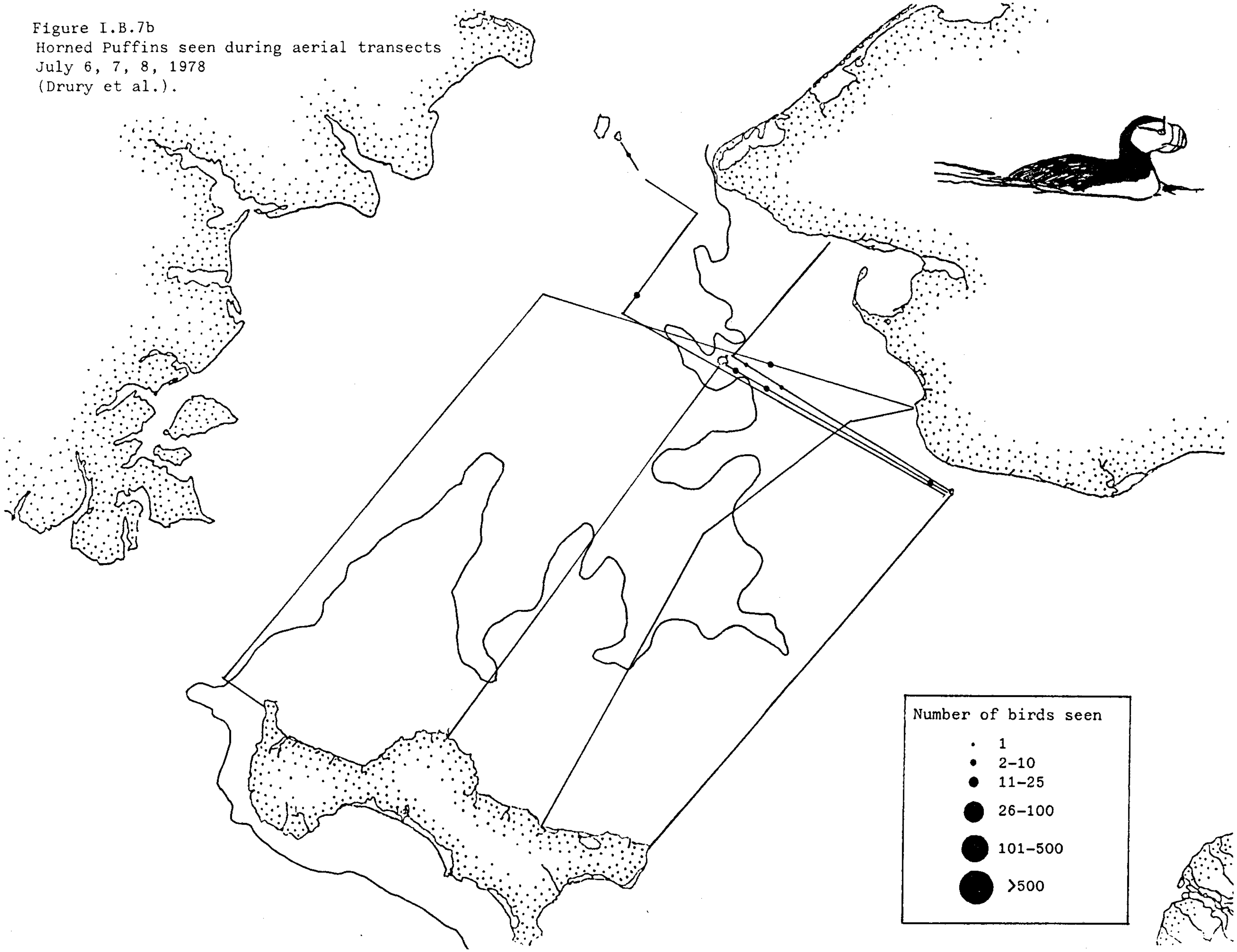
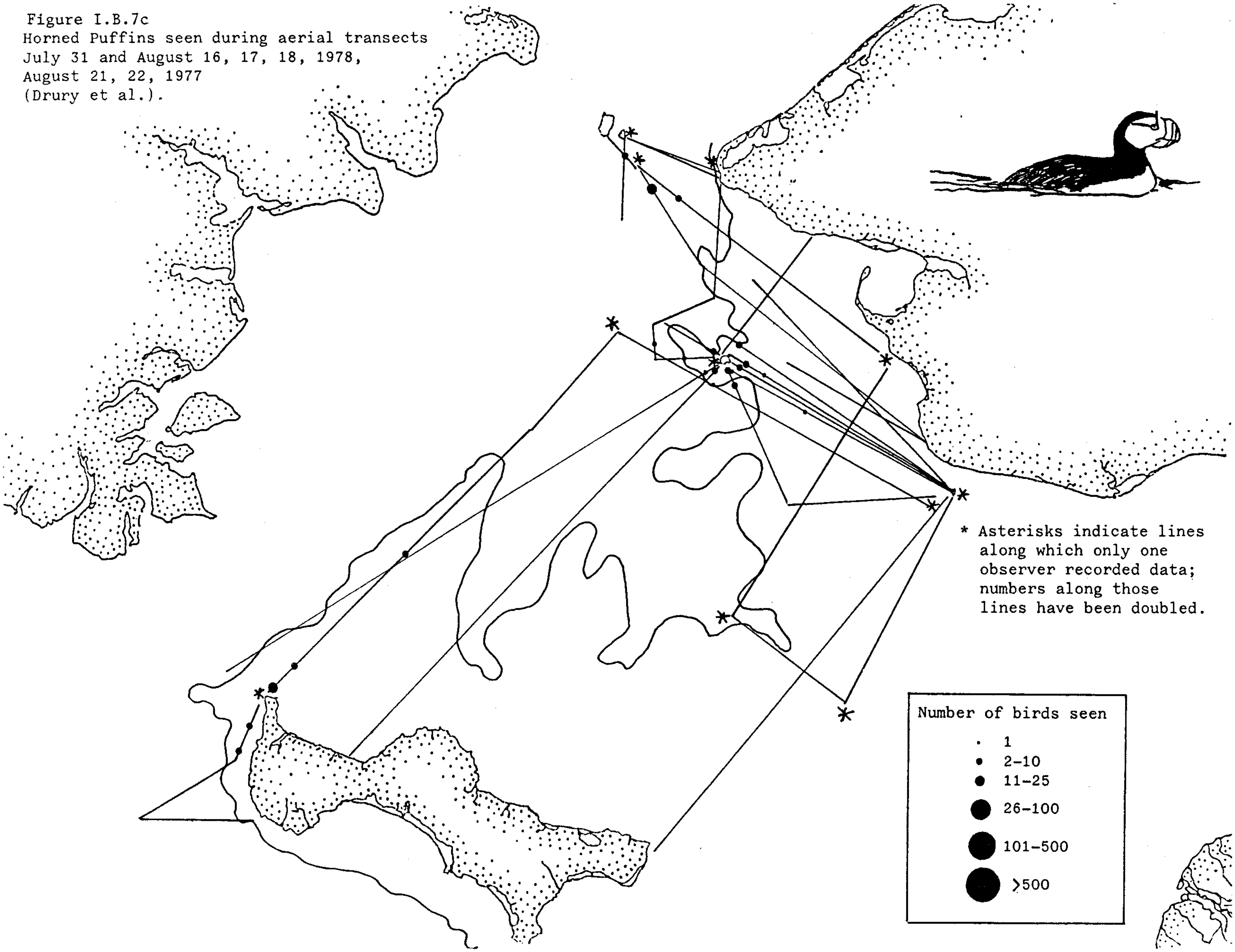


Figure I.B.7b
Horned Puffins seen during aerial transects
July 6, 7, 8, 1978
(Drury et al.).

Figure I.B.7c
Horned Puffins seen during aerial transects
July 31 and August 16, 17, 18, 1978,
August 21, 22, 1977
(Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

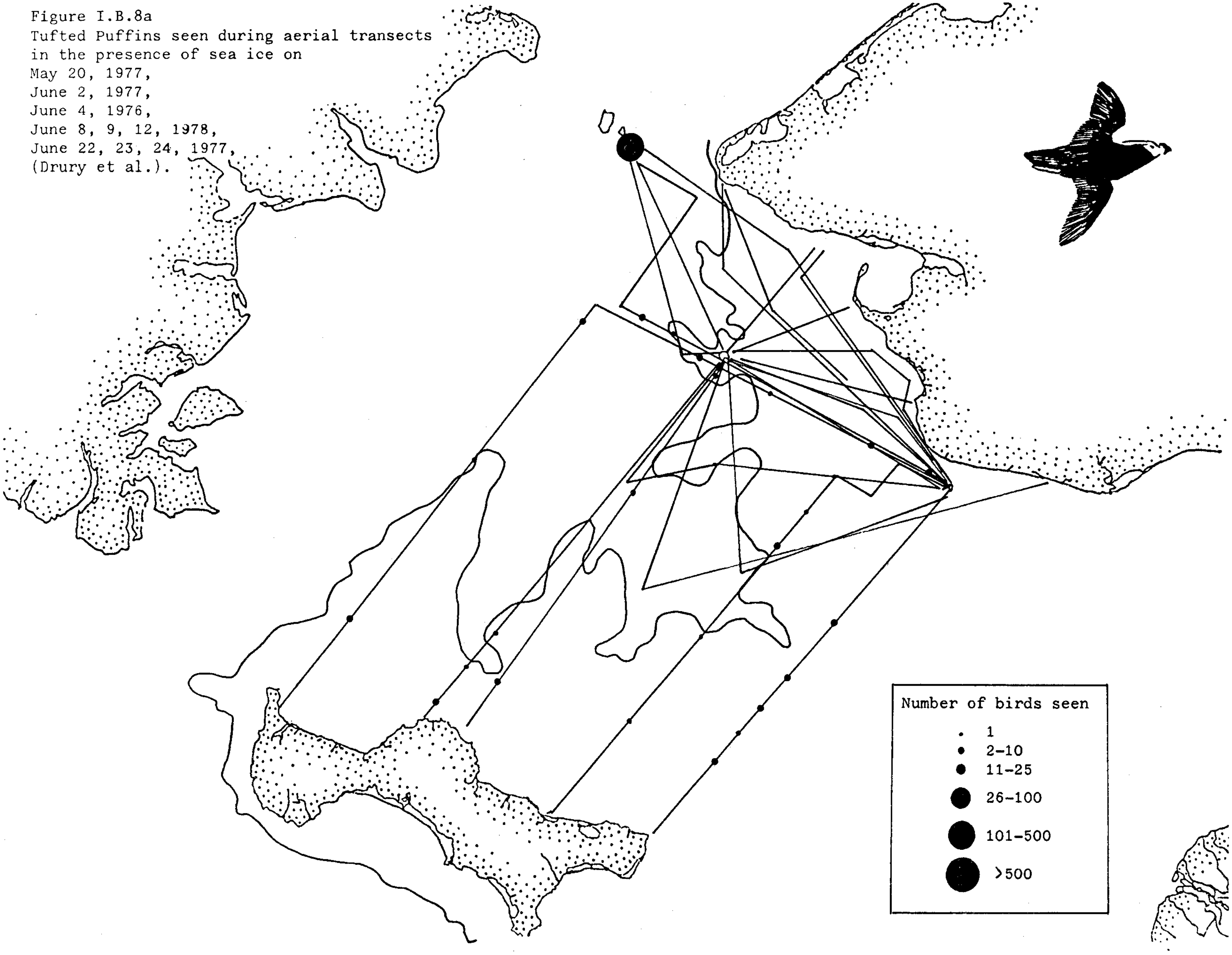


Figure I.B.8a
Tufted Puffins seen during aerial transects
in the presence of sea ice on
May 20, 1977,
June 2, 1977,
June 4, 1976,
June 8, 9, 12, 1978,
June 22, 23, 24, 1977,
(Drury et al.).

Figure I.B.8b
Tufted Puffins seen during aerial transects
July 6, 7, 8, 1978
(Drury et al.).

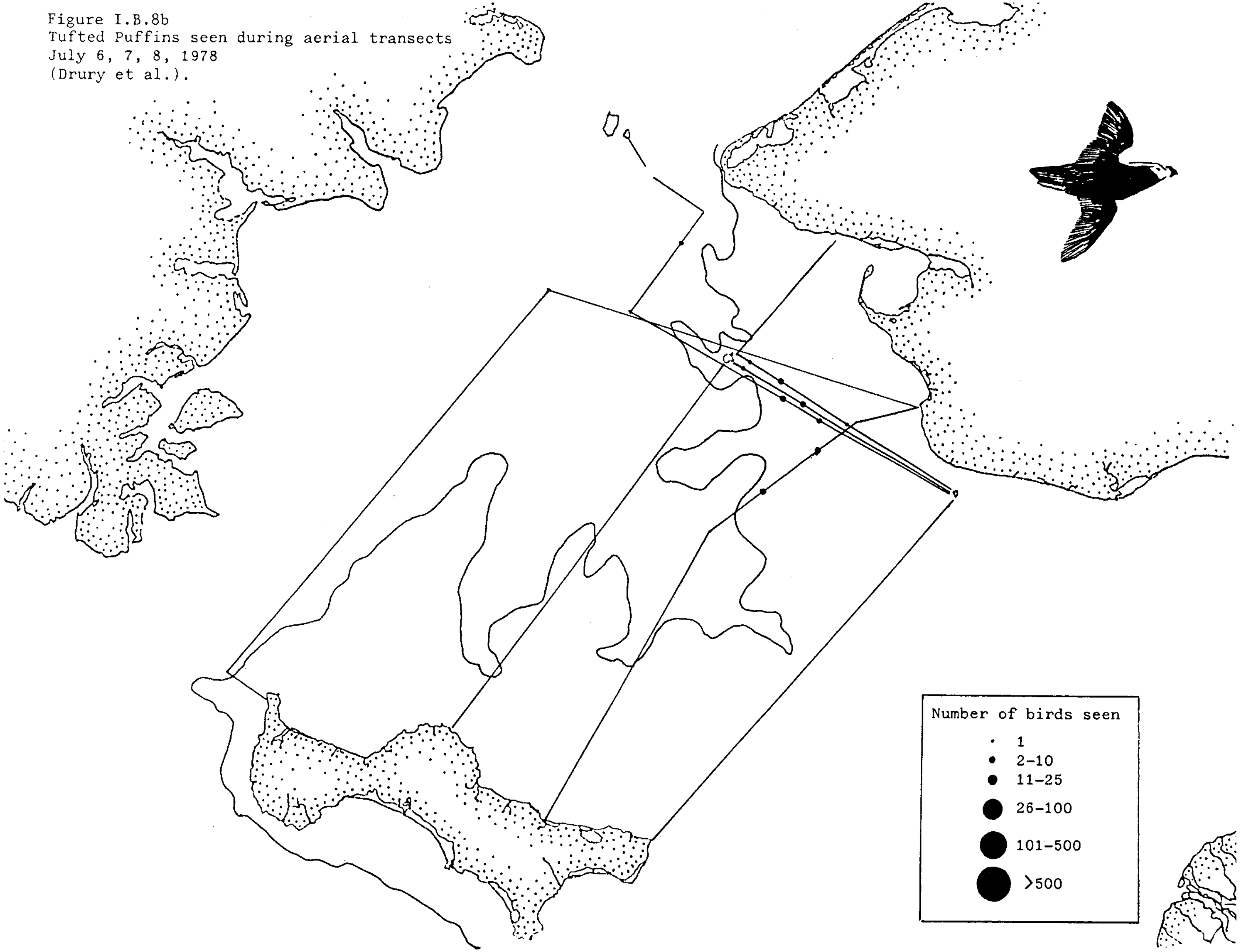


Figure I.B.8c
Tufted Puffins seen during aerial transects July 31 and August 16, 17, 18, 1978, August 21, 22, 1977 (Drury et al.).

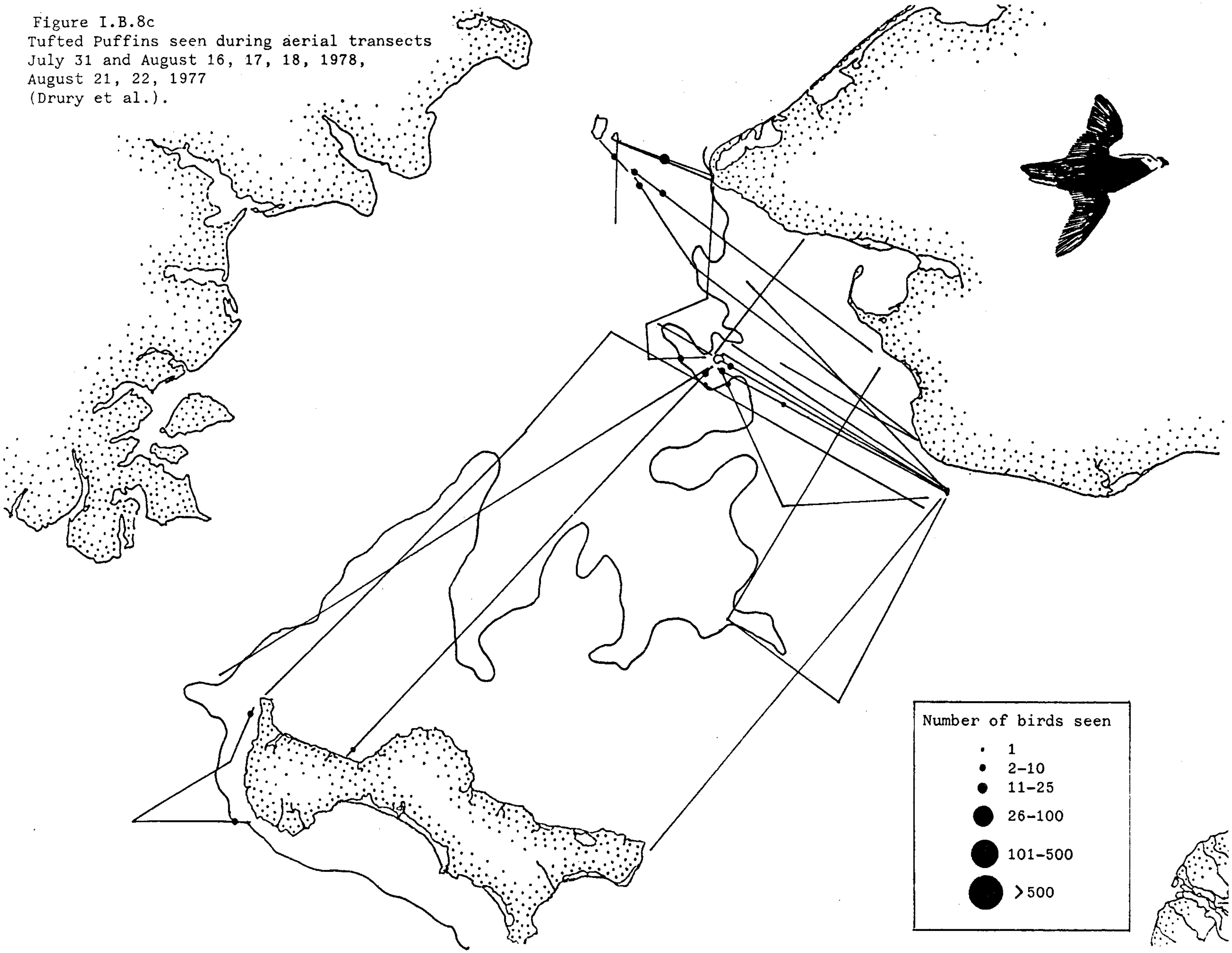


Figure I.B.9a

Glaucous Gulls seen during aerial transects in the presence of sea ice on
May 20, 1977,
June 2, 1977,
June 4, 1976,
June 8, 9 & 12, 1978,
June 22, 23 & 24, 1977
(Drury et al.).

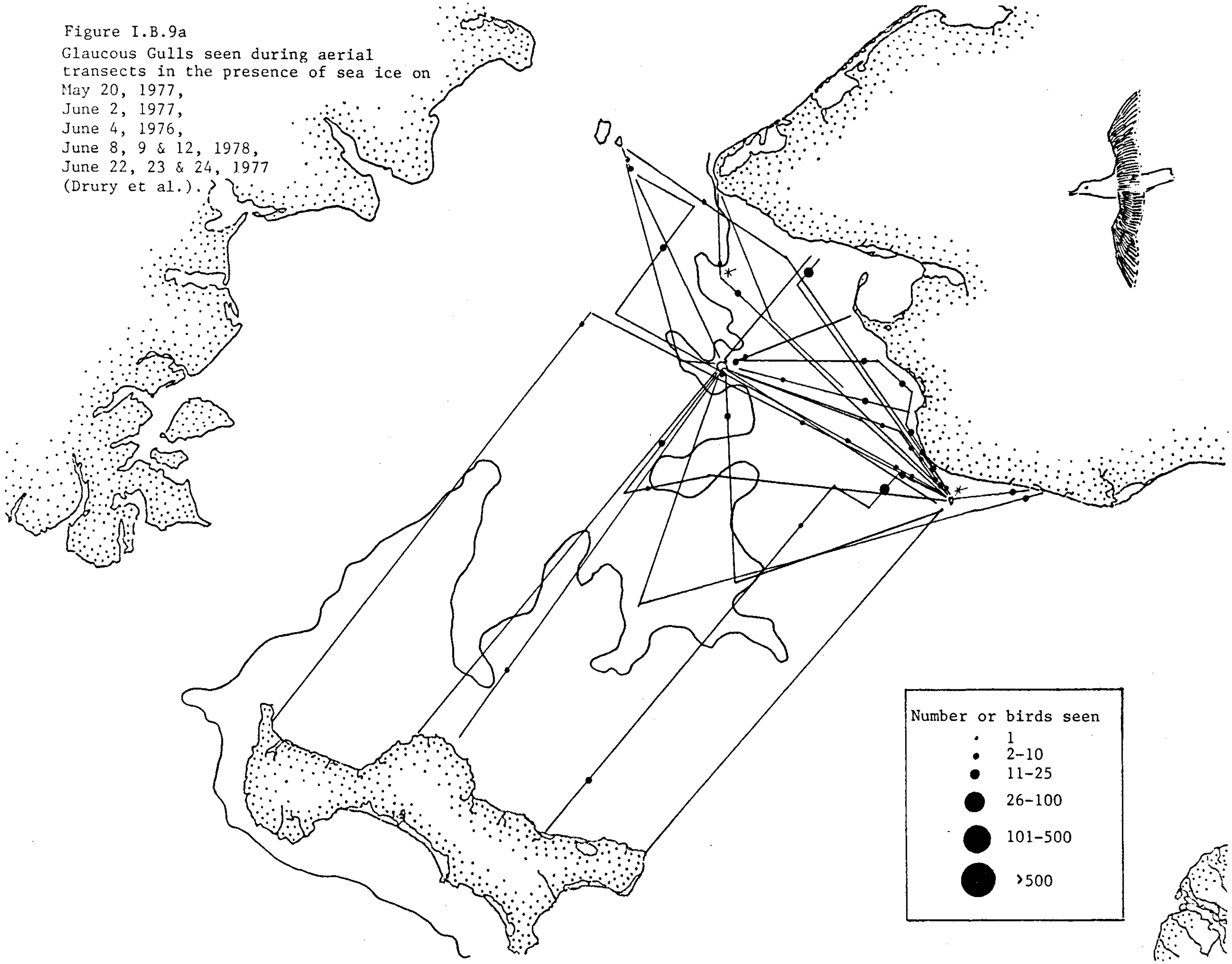


Figure I.B.9b
Glaucous Gulls seen during
aerial transects on
July 6, 7 & 8, 1978
(Drury et al.).

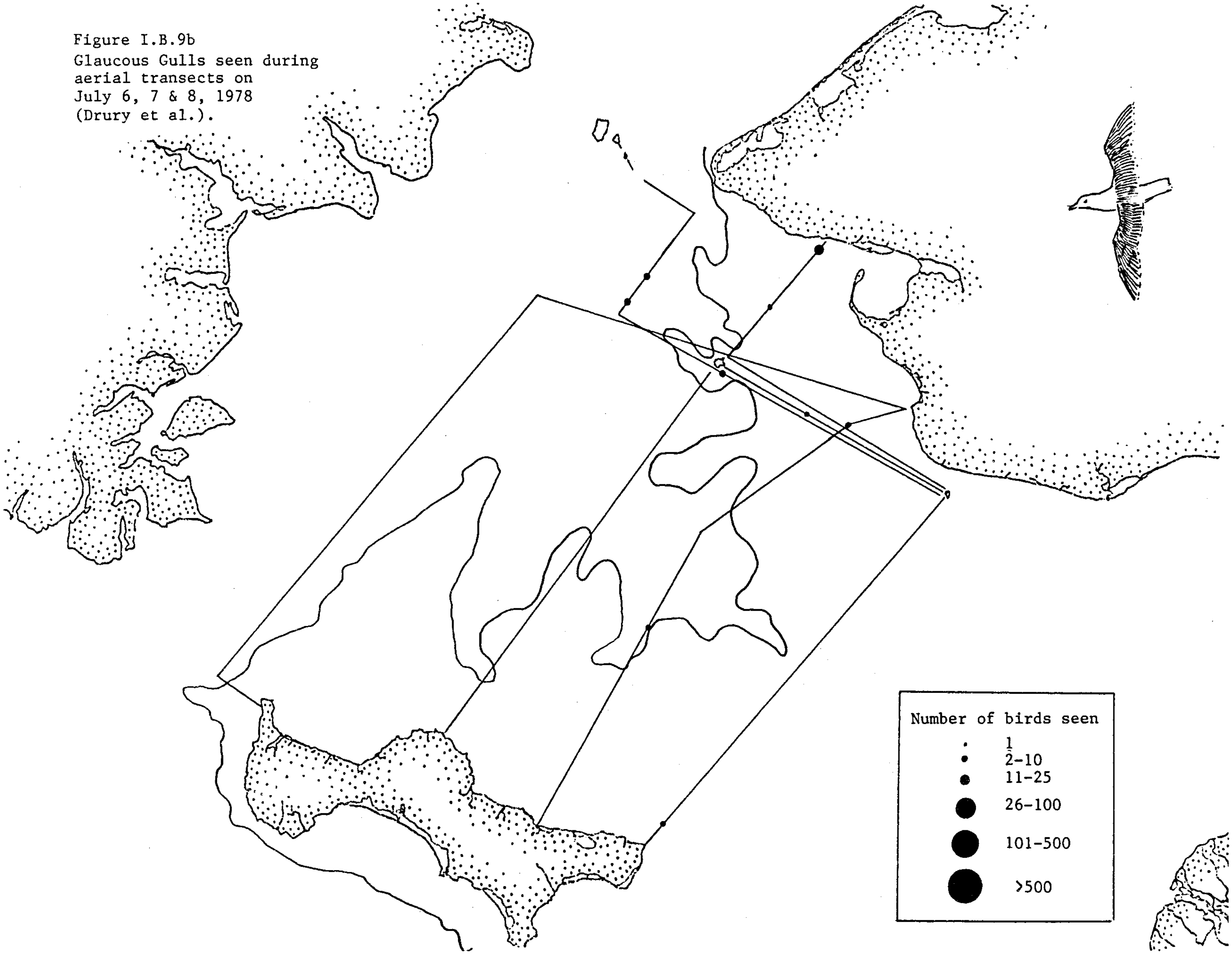
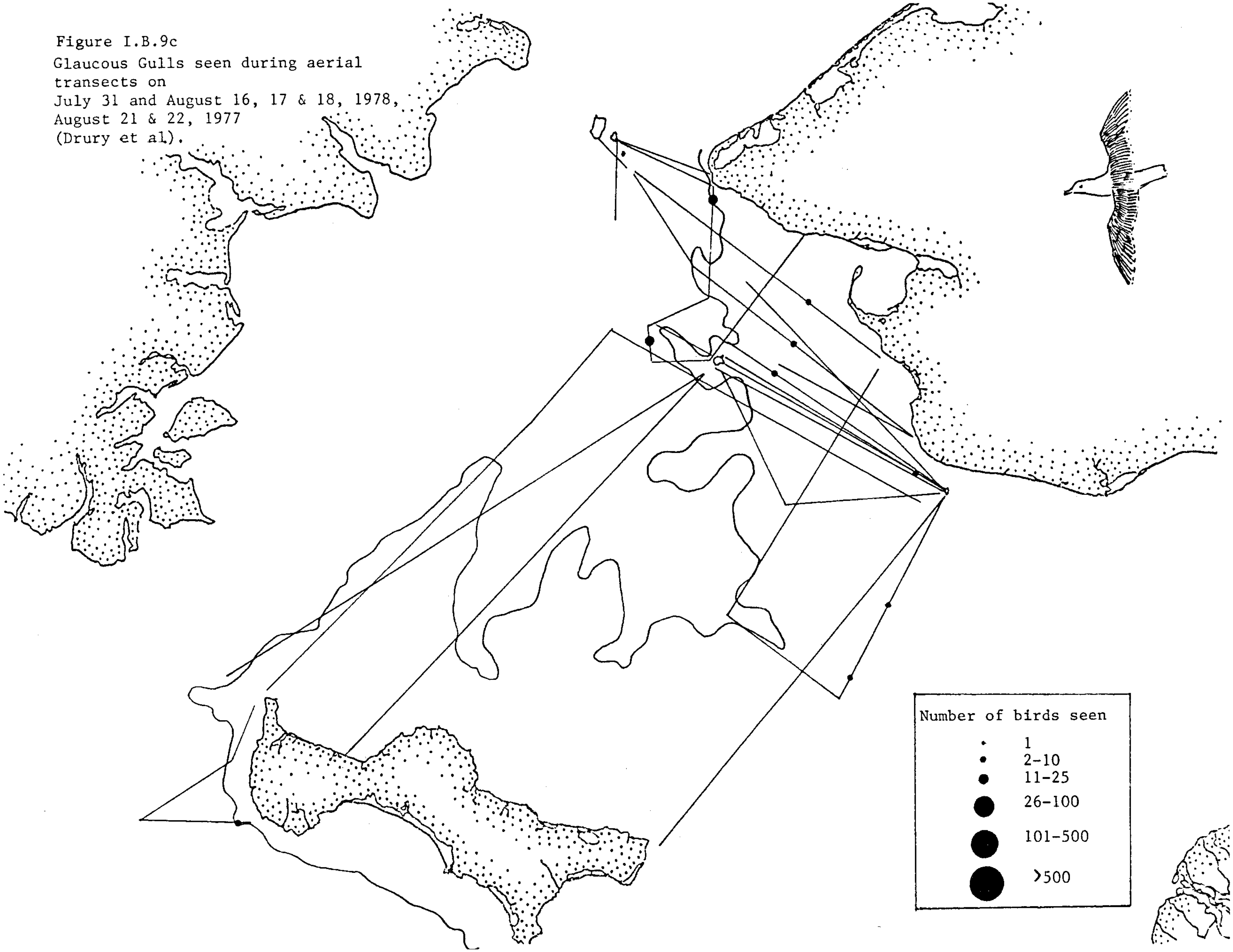


Figure I.B.9c

Glaucous Gulls seen during aerial transects on July 31 and August 16, 17 & 18, 1978, August 21 & 22, 1977 (Drury et al).



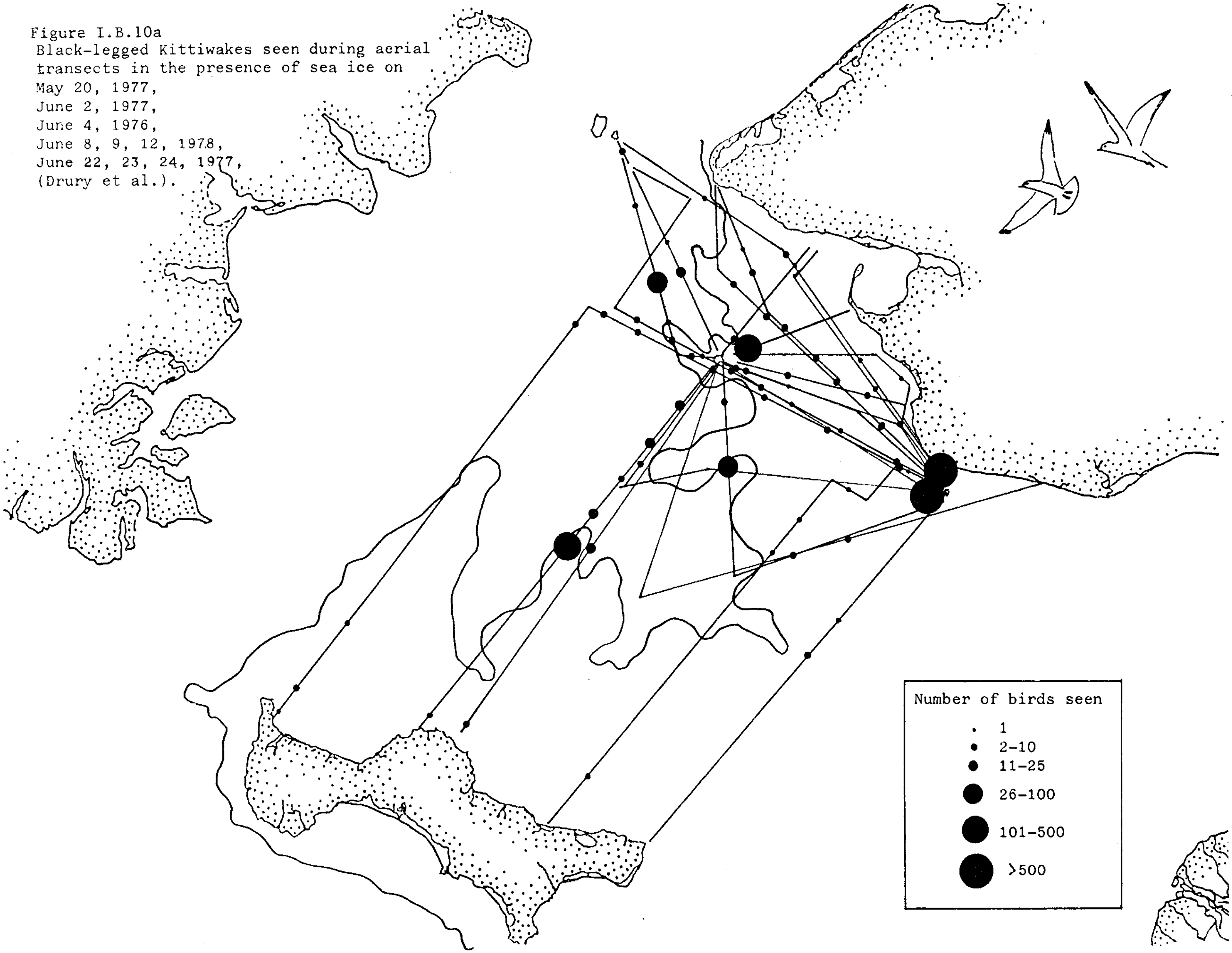


Figure I.B.10a
Black-legged Kittiwakes seen during aerial transects in the presence of sea ice on
May 20, 1977,
June 2, 1977,
June 4, 1976,
June 8, 9, 12, 1978,
June 22, 23, 24, 1977,
(Drury et al.).

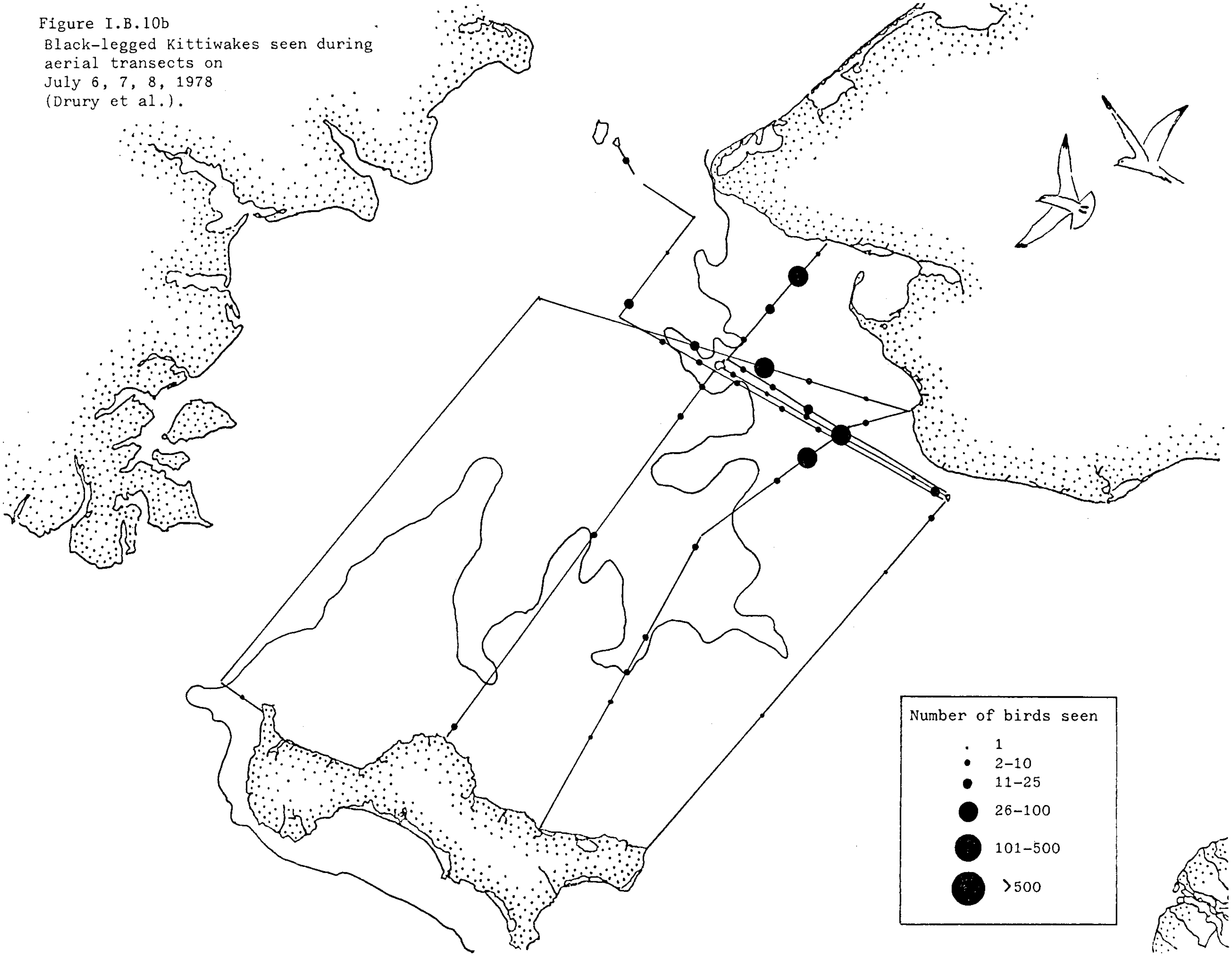
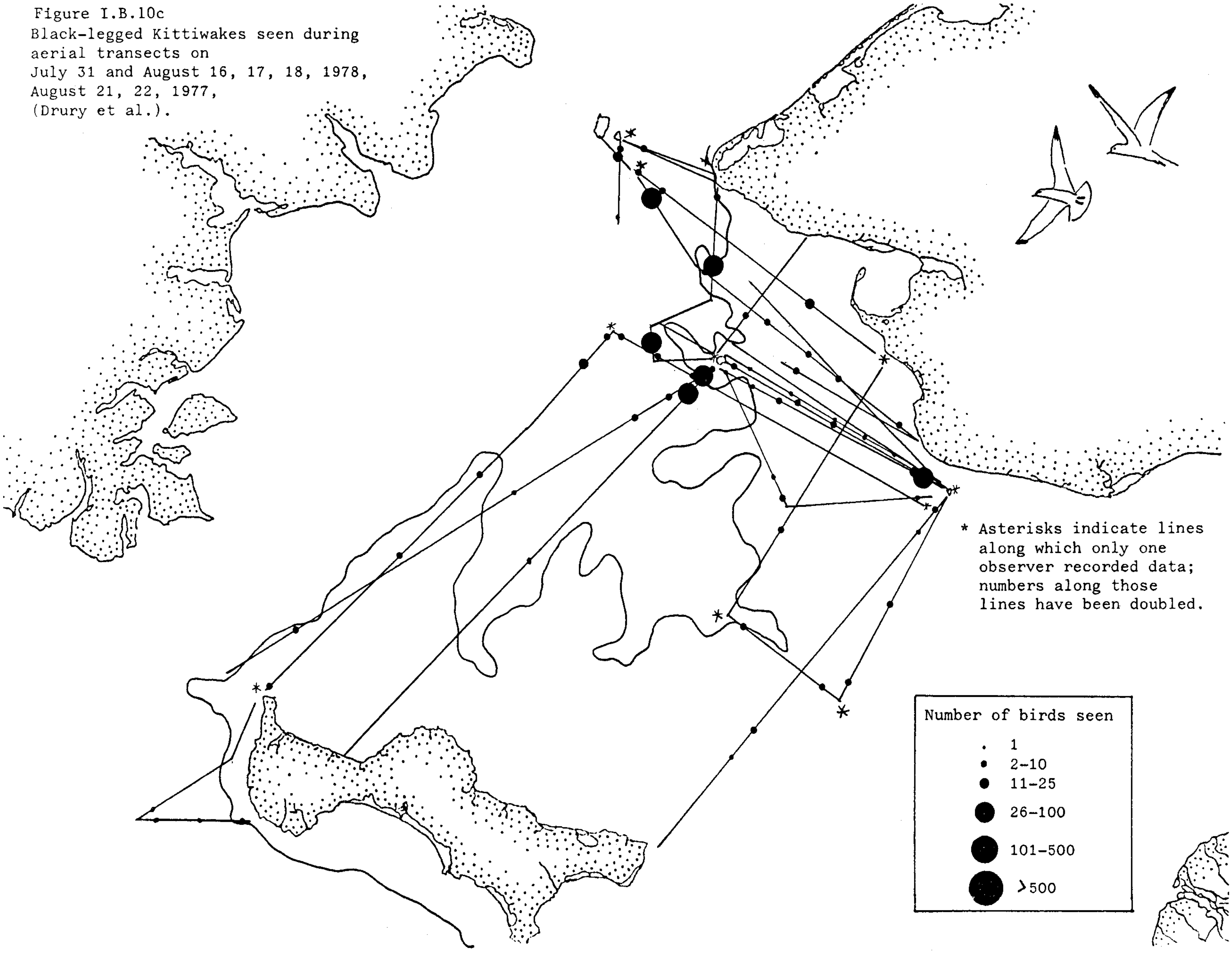


Figure I.B.10b
Black-legged Kittiwakes seen during aerial transects on July 6, 7, 8, 1978 (Drury et al.).

Figure I.B.10c
Black-legged Kittiwakes seen during aerial transects on July 31 and August 16, 17, 18, 1978, August 21, 22, 1977, (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.C.1a Distribution and abundance of murres in the Bering Sea in June 1976. Aerial surveys, USFWS; Figure 148, page 265, in Harrison 1977.

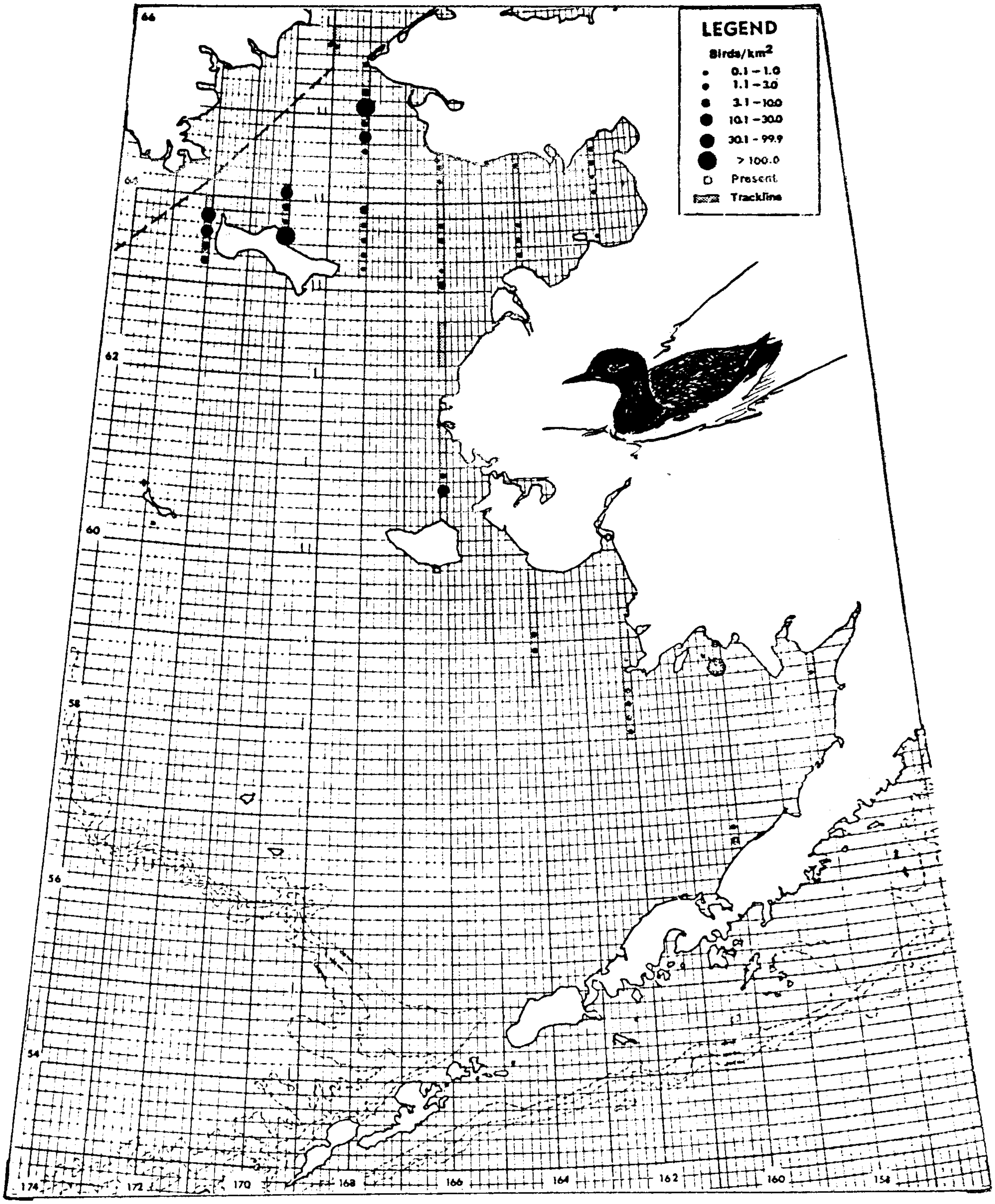


Figure I.C.1b Distribution and abundance of murres in the Bering Sea in August 1976. Aerial surveys, USFWS: Figure 150, page 267, in Harrison 1977.

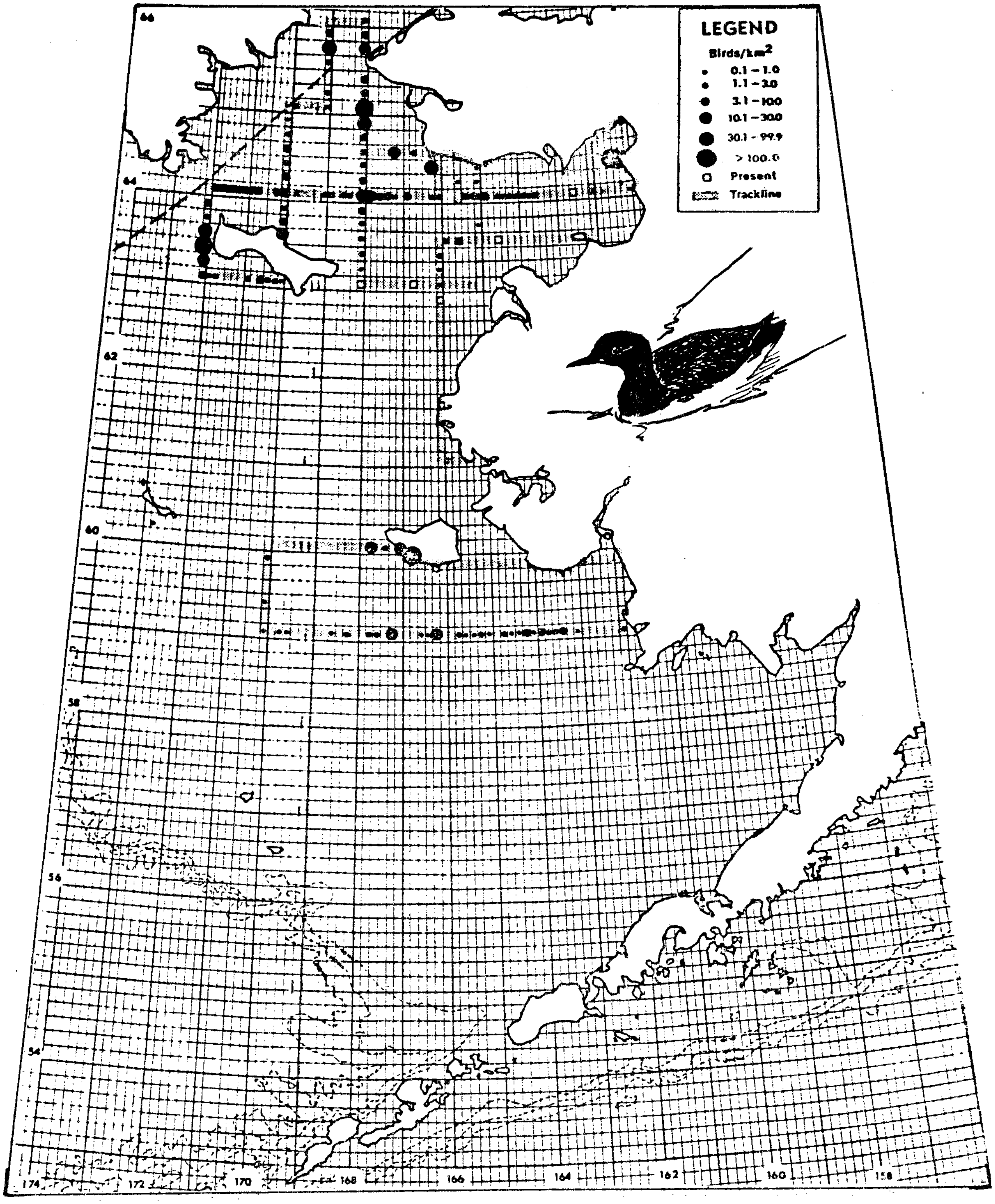


Figure I.C.1c Distribution and abundance of murres in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 151, page 268, in Harrison 1977.

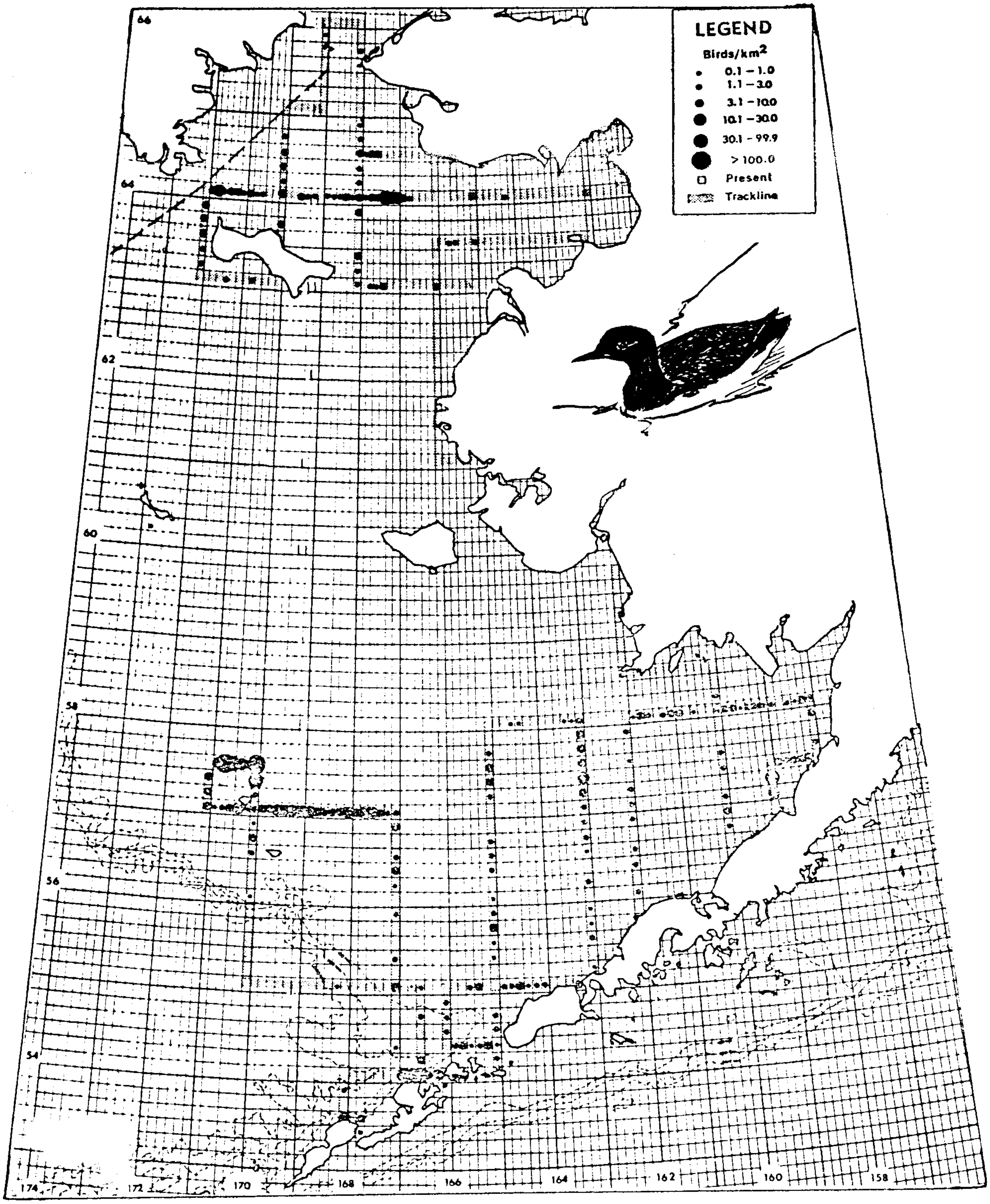


Figure I.C.2a Distribution and abundance on Least Auklets in the Bering Sea in August 1976: no Least Auklets were observed in March, June, or July 1976. Aerial surveys, USFWS: Figure 160, page 277, in Harrison 1977.

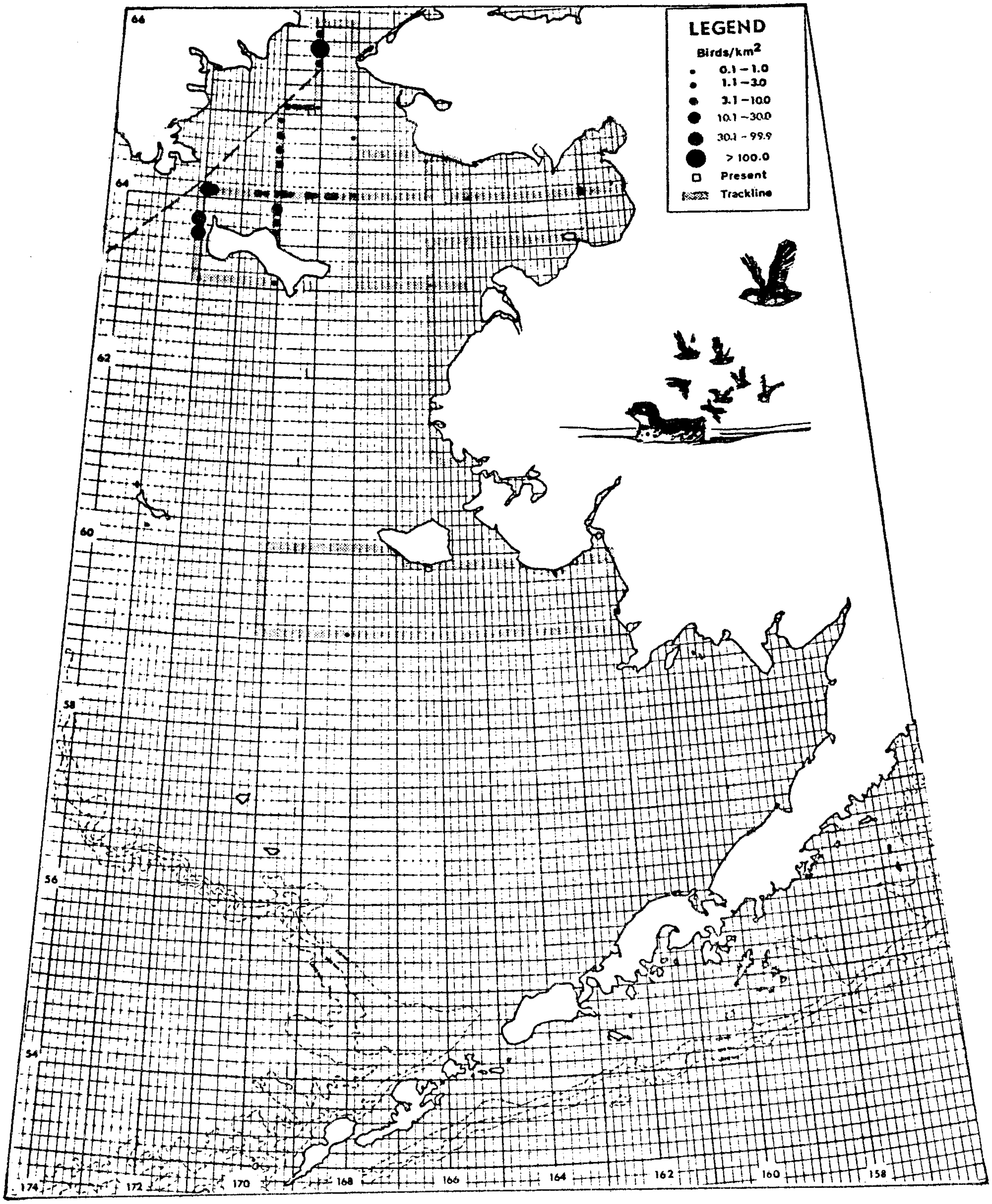


Figure I.C.2b Distribution and abundance of Least Auklets in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 161, page 278, in Harrison 1977.

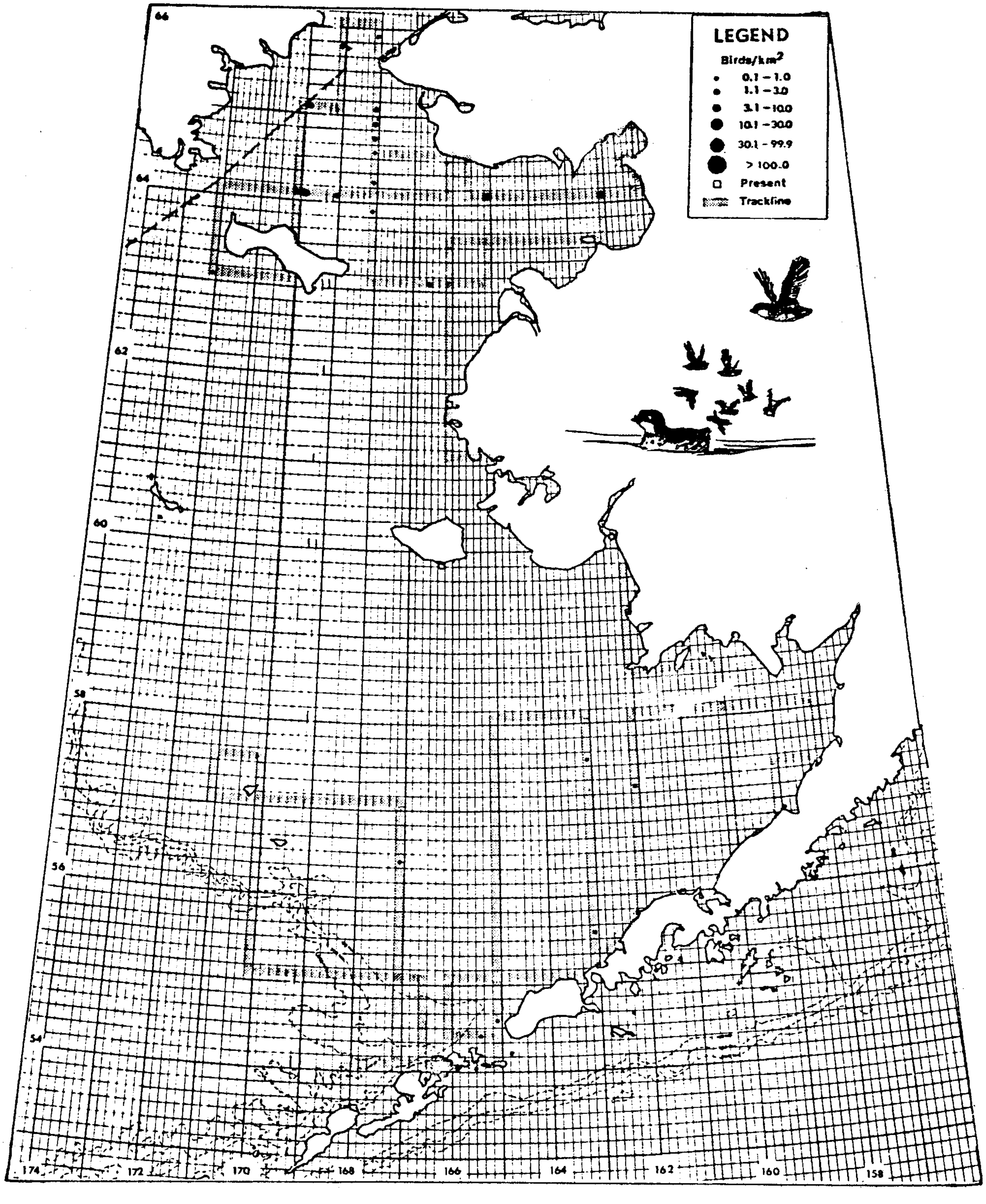


Figure I.C.3a Distribution and abundance of Crested Auklets in the Bering Sea in August 1976: no Crested Auklets were identified in June or July 1976. Aerial surveys, USFWS: Figure 157, page 274, in Harrison 1977.

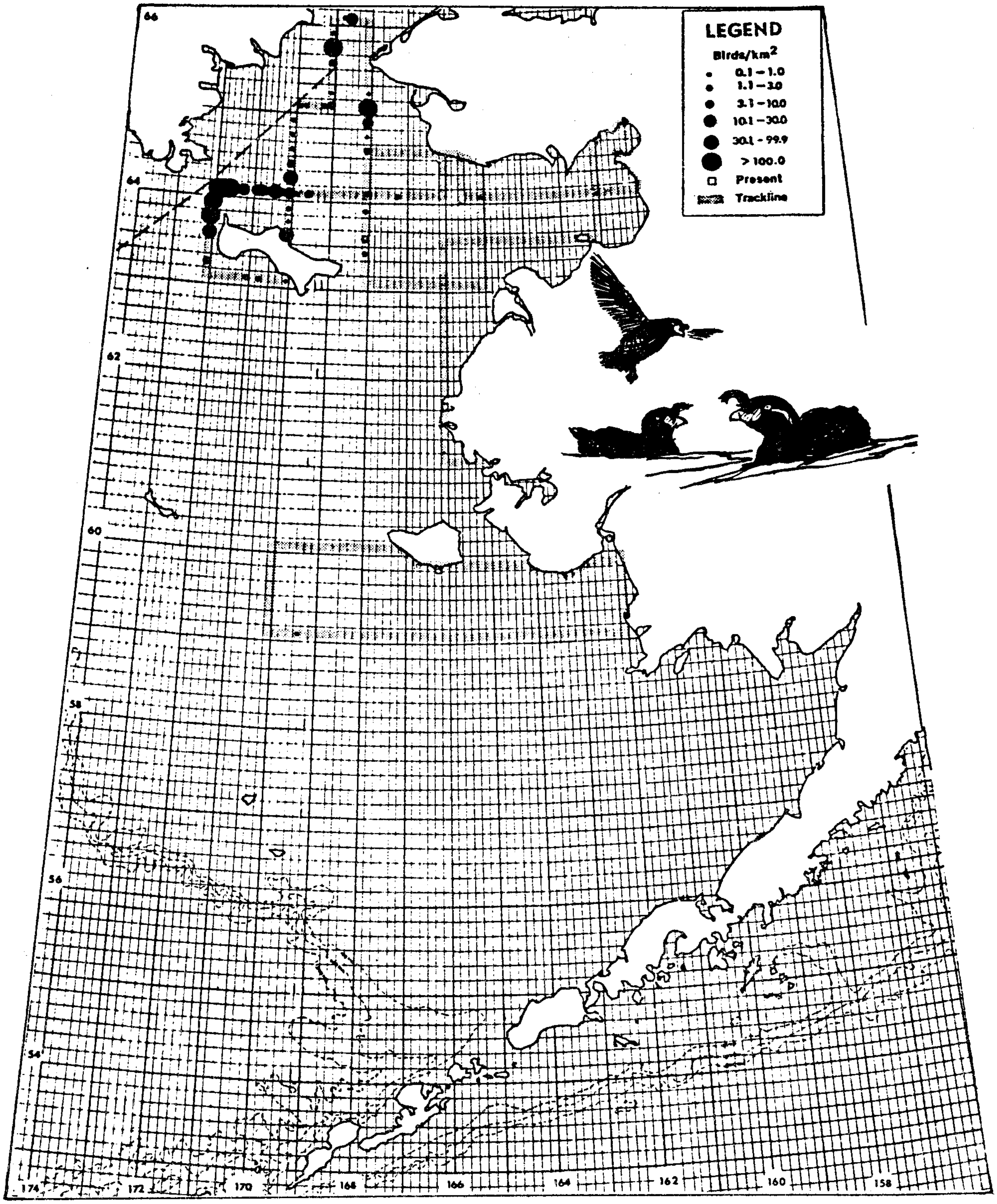


Figure I.C.3b Distribution and abundance of Crested Auklets in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 158, page 275, in Harrison 1977.

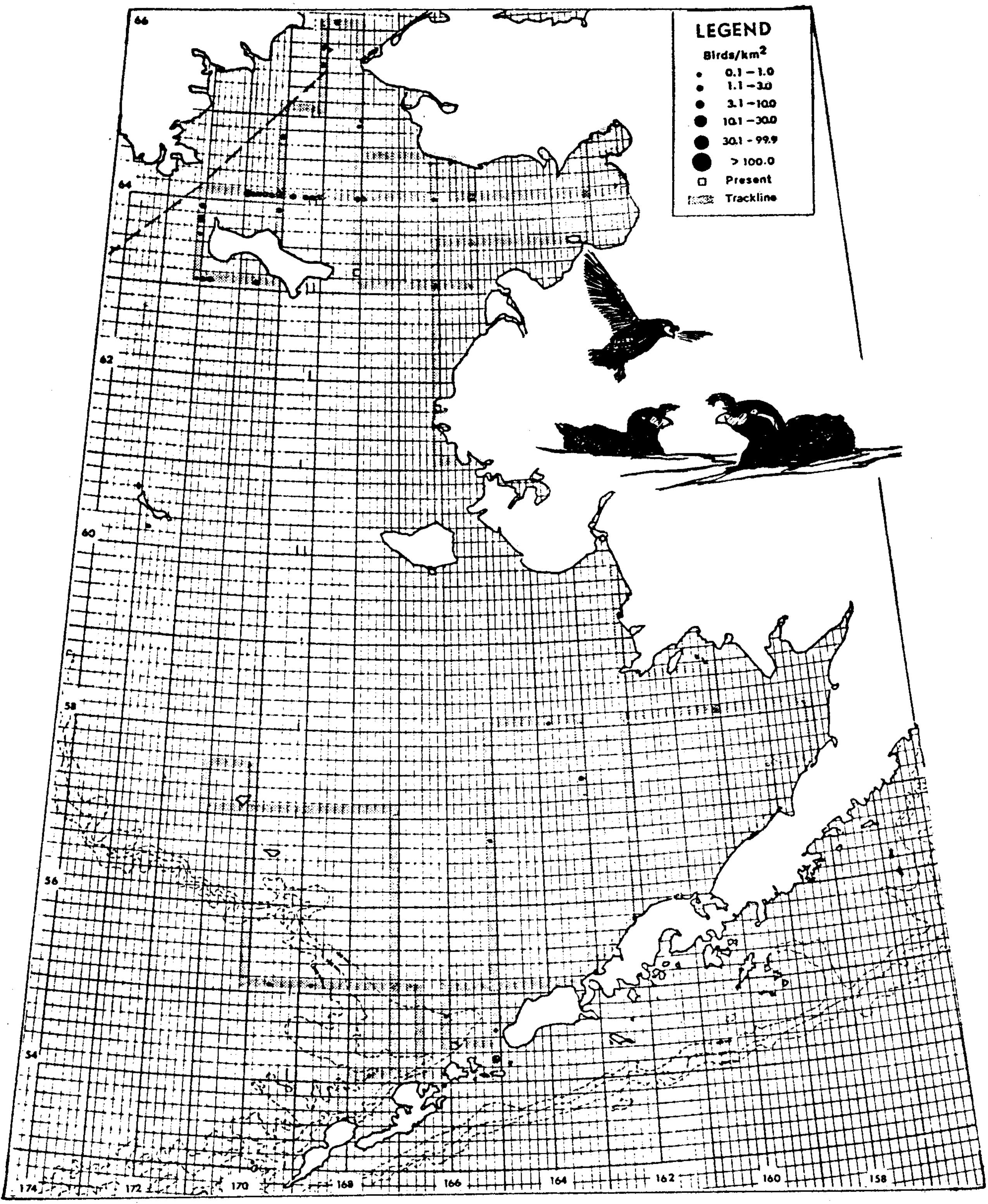


Figure I.C.4a Distribution and abundance of Parakeet Auklets in the Bering Sea in August 1976: no Parakeet Auklets were identified in March, June or July, 1976. Aerial surveys, USFWS: Figure 153, page 270, in Harrison 1977.

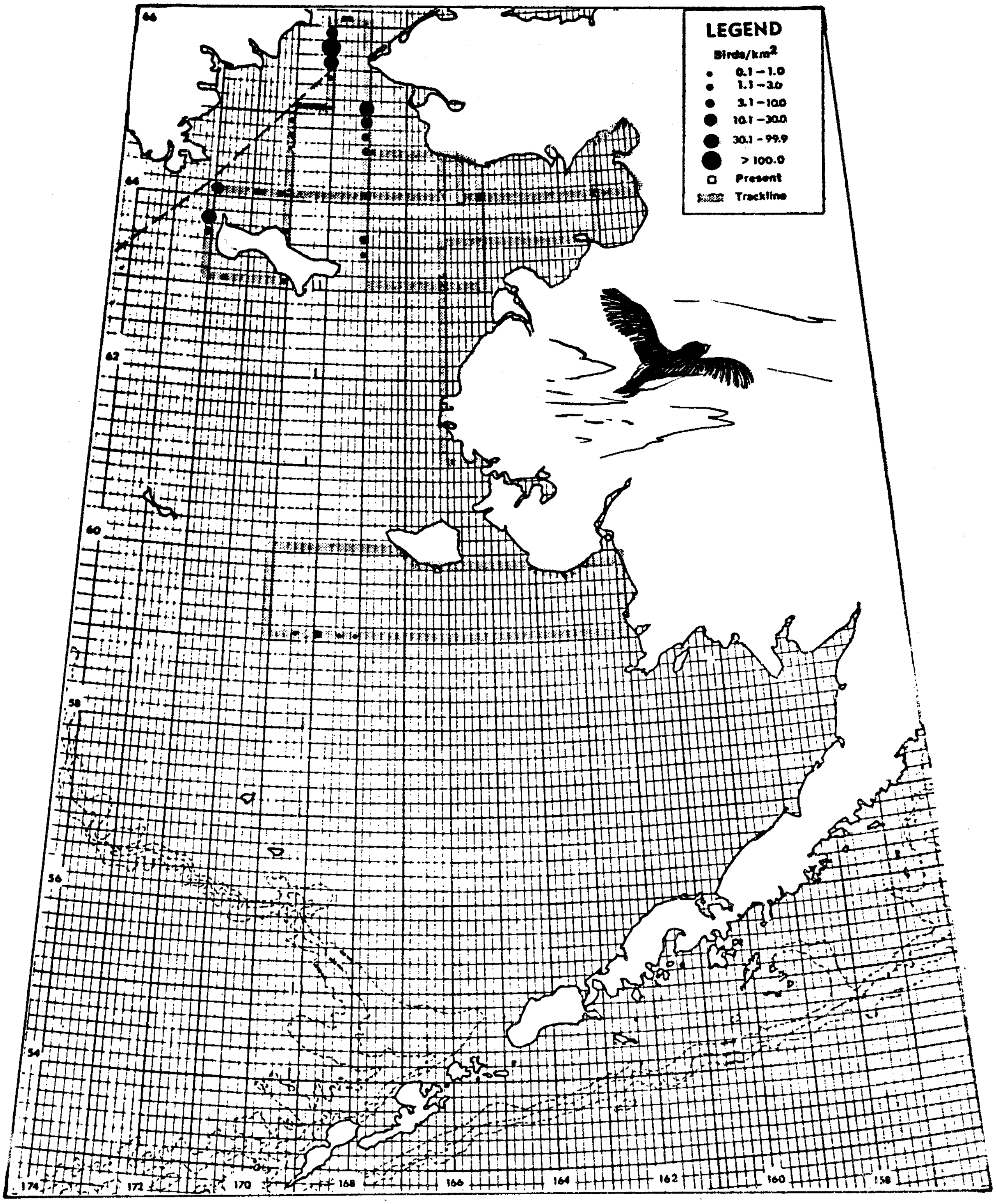


Figure I.C.4b Distribution and abundance of Parakeet Auklets in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 154, page 271, in Harrison 1977.

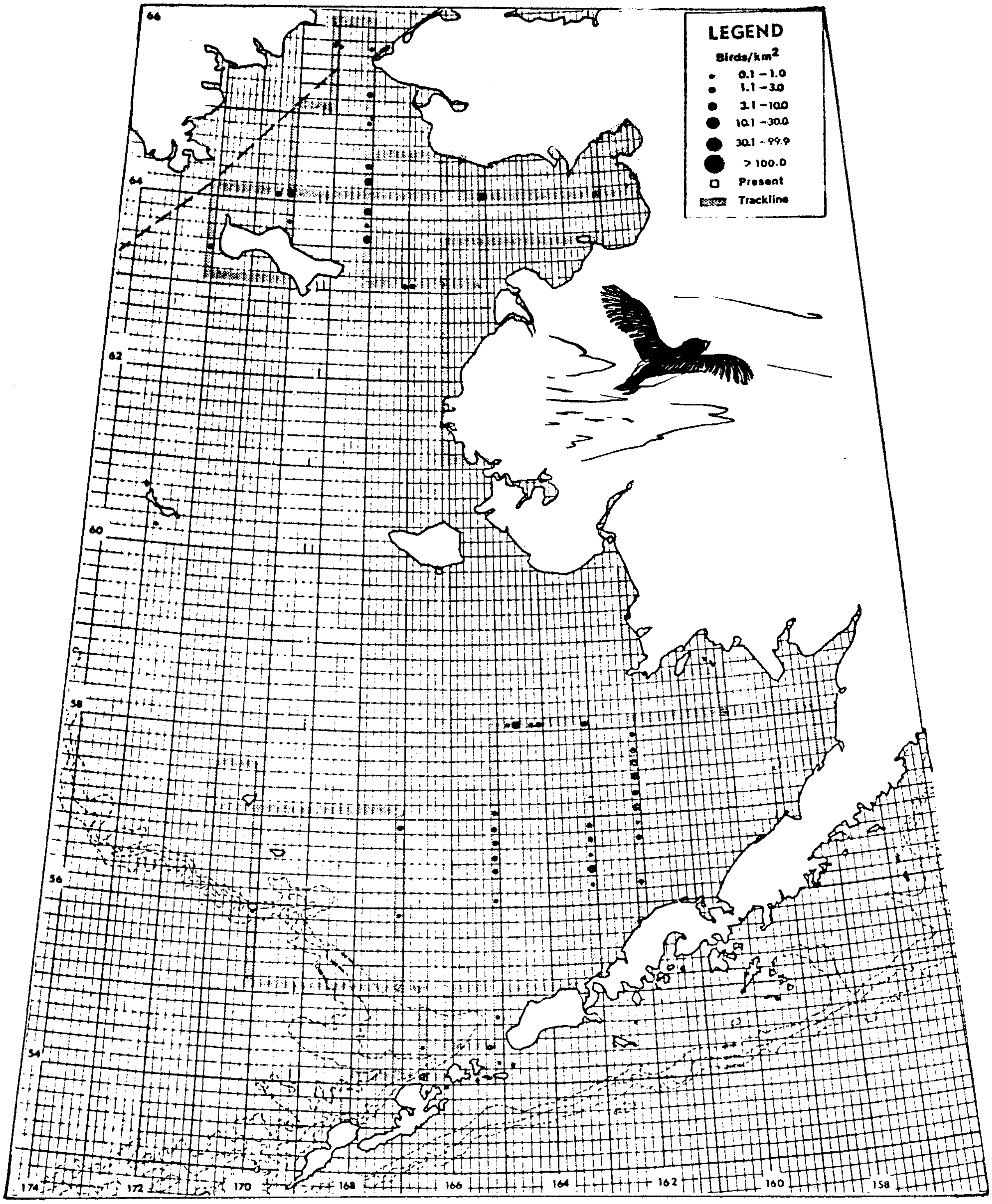


Figure I.C.5a Distribution and abundance of Horned Puffins in the Bering Sea in June 1976. Aerial surveys, USFWS: Figure 168, page 285, in Harrison 1977.

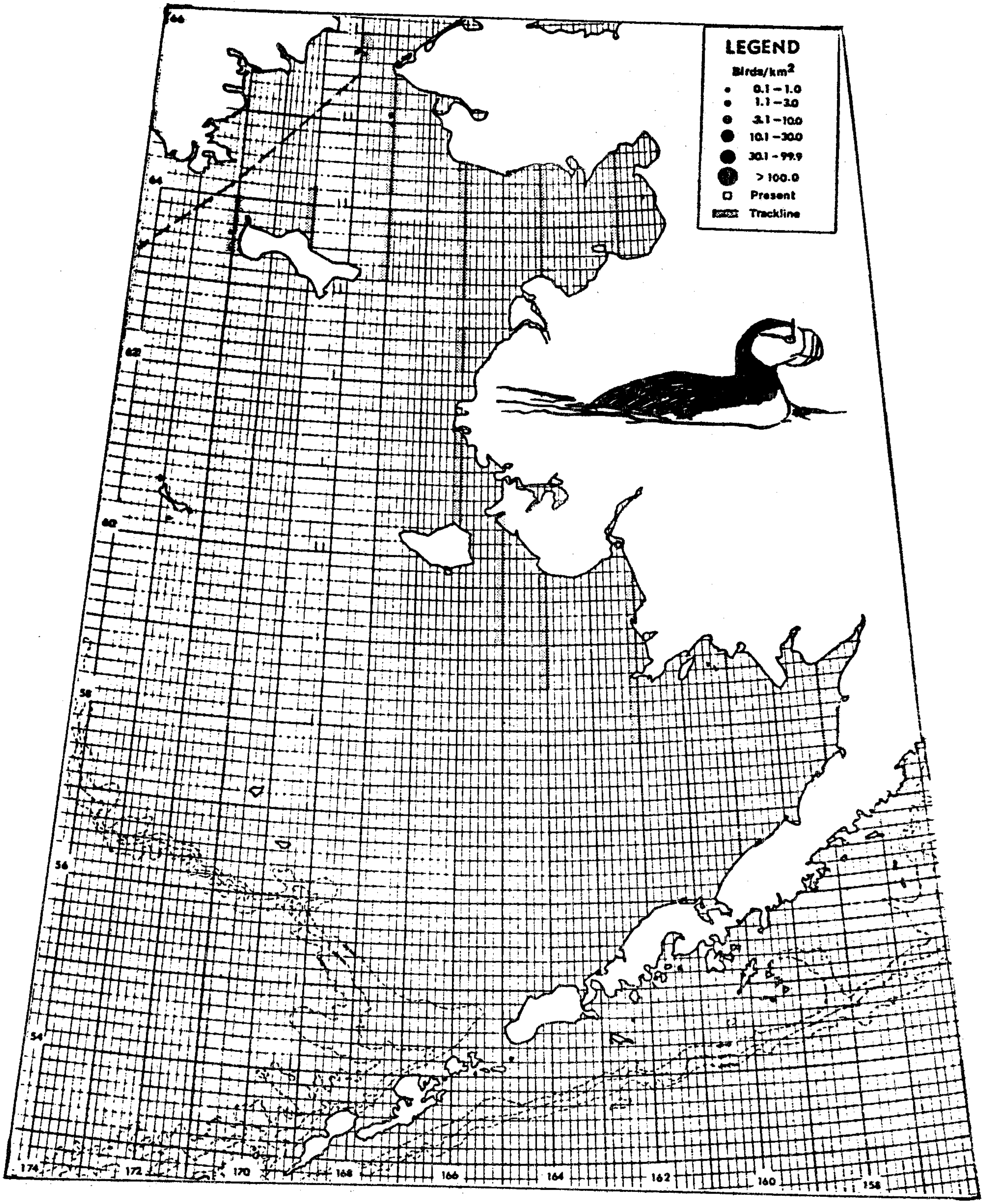


Figure I.C.5b Distribution and abundance of Horned Puffins in the Bering Sea in August 1976. Aerial surveys, USFWS: Figure 170, page 287, in Harrison 1977.

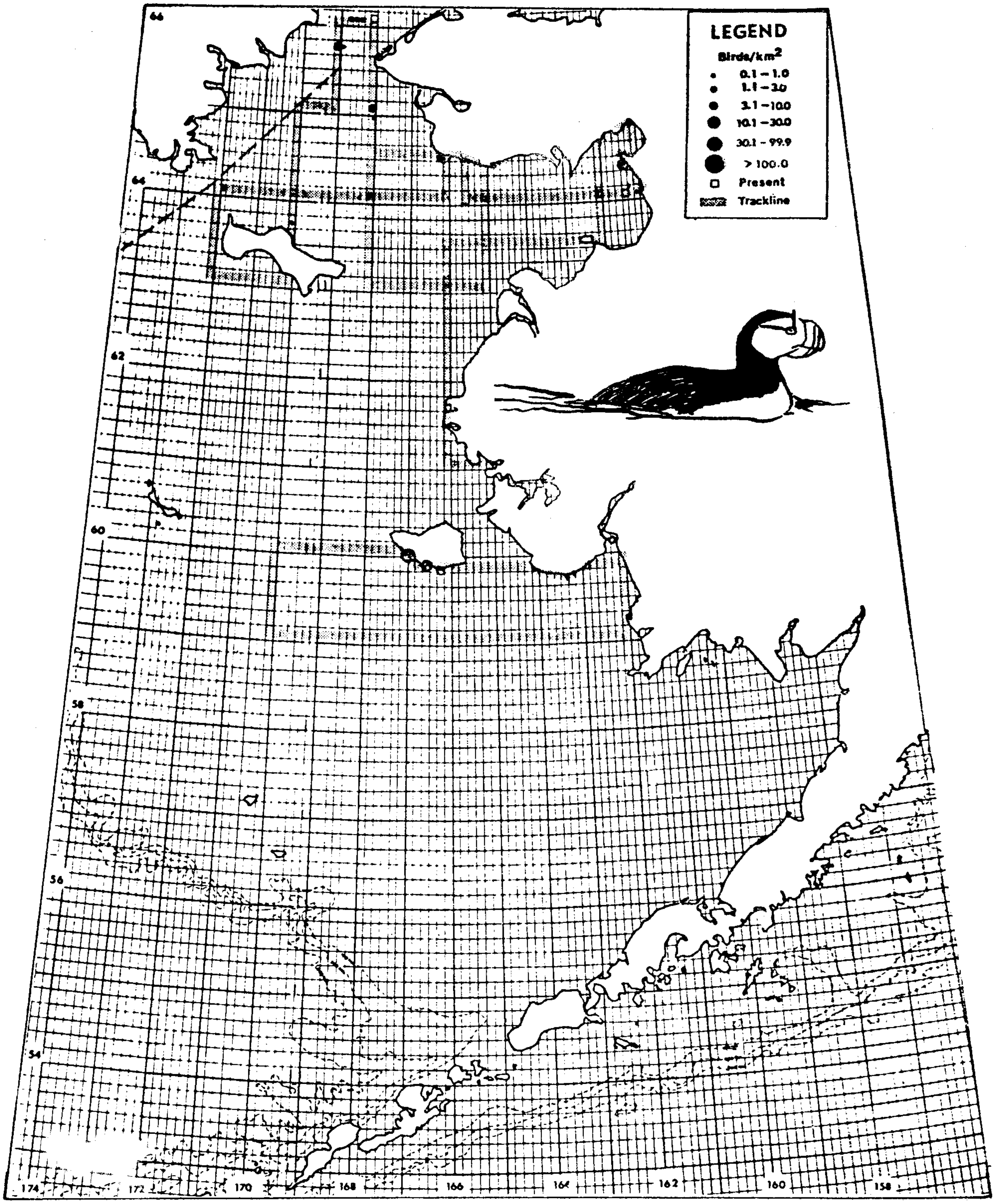


Figure I.C.5c Distribution and abundance of Horned Puffins in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 171, page 288, in Harrison 1977.

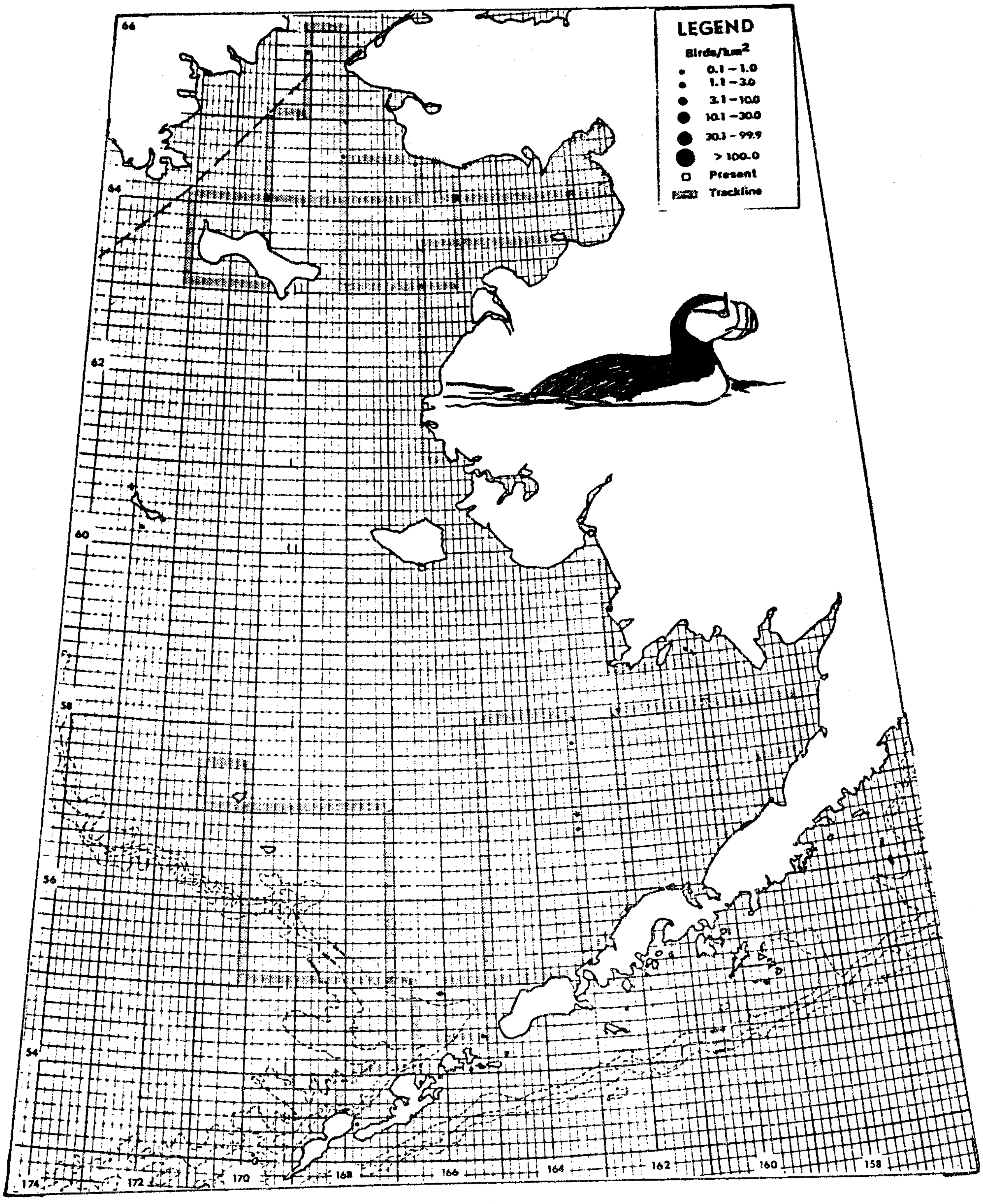


Figure I.C.6a Distribution and abundance of Tufted Puffins in the Bering Sea in June 1976: no Tufted Puffins were observed in February or March 1976. Aerial surveys, USFWS: Figure 163, page 280, in Harrison 1977.

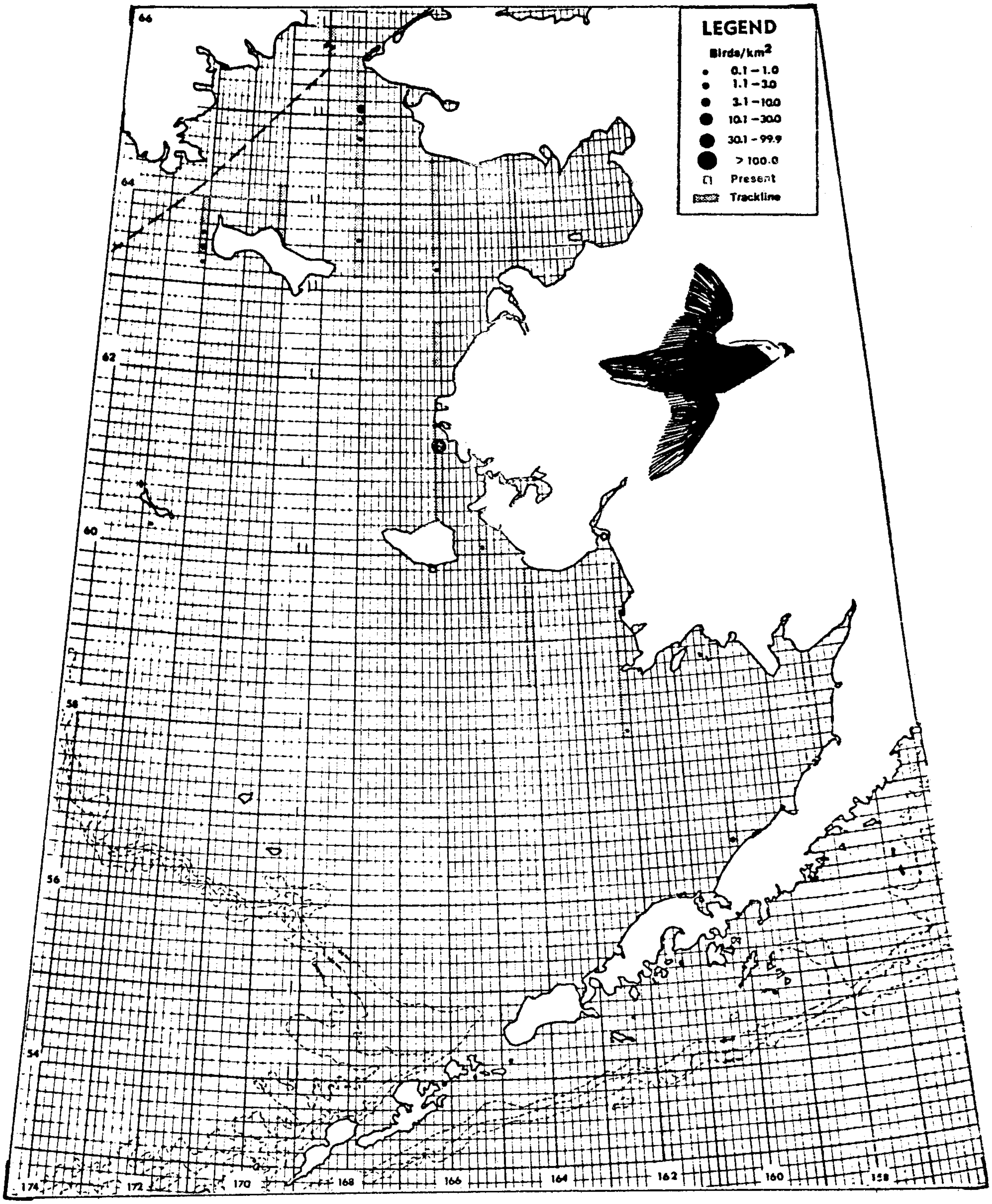


Figure I.C.6b Distribution and abundance of Tufted Puffins in the Bering Sea in August 1976. Aerial surveys, USFWS: Figure 165, page 282, in Harrison 1977.

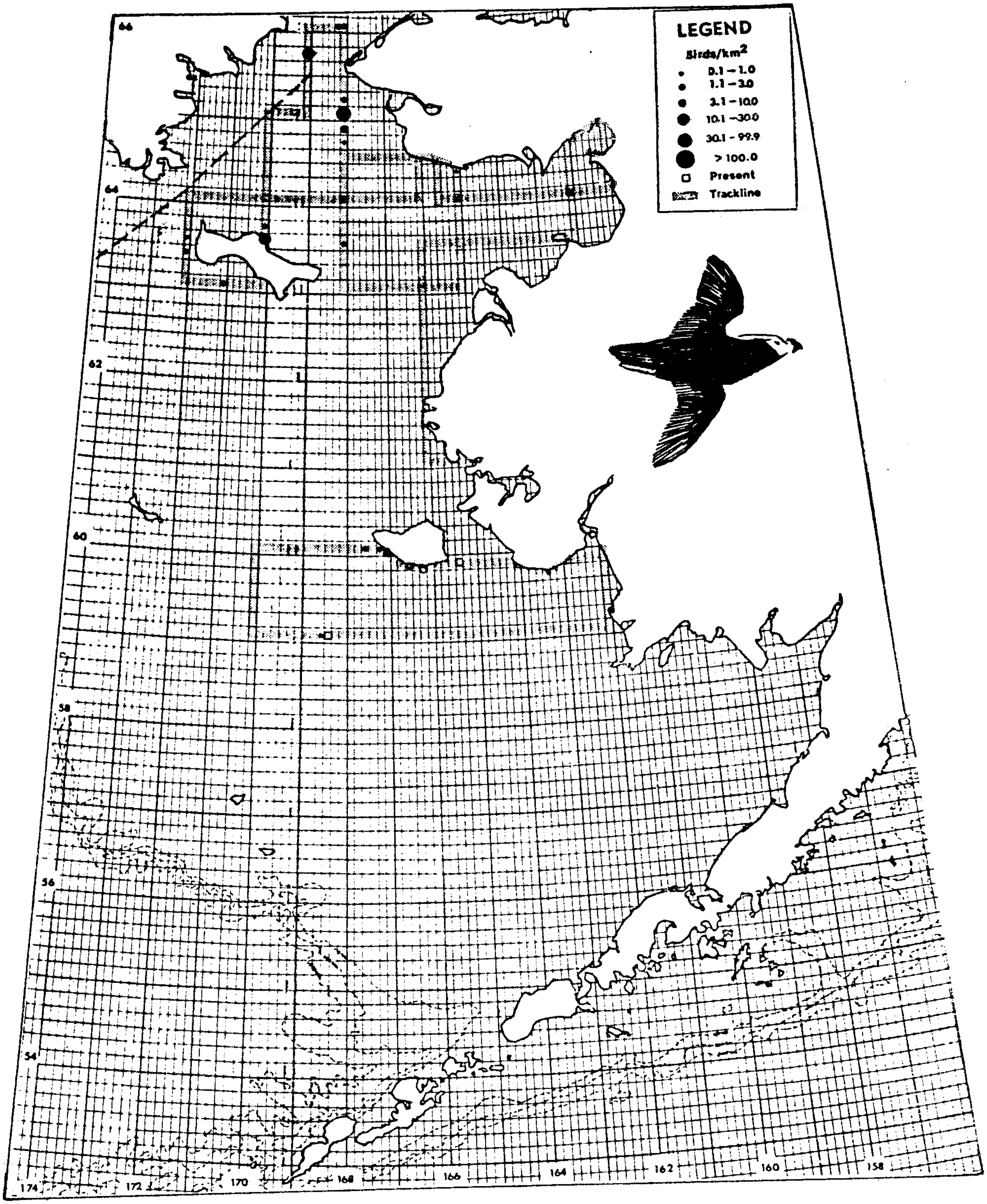


Figure I.C.6c Distribution and abundance of Tufted Puffins in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 166, page 283, in Harrison 1977.

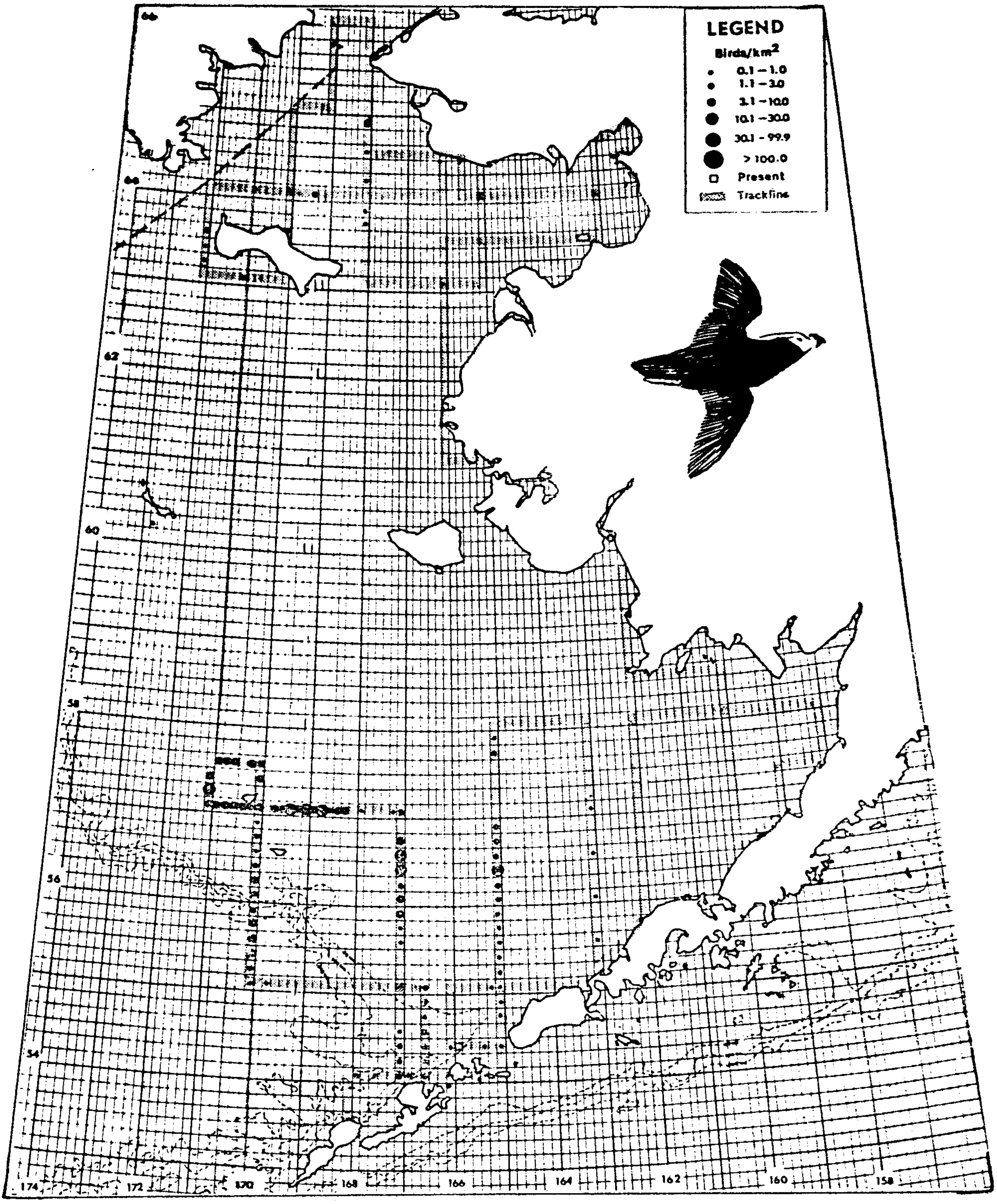


Figure I.C.7a Distribution and abundance of Glaucous Gulls in the Bering Sea in June 1976. Aerial surveys, USFWS: Figure 111, page 228, in Harrison 1977.

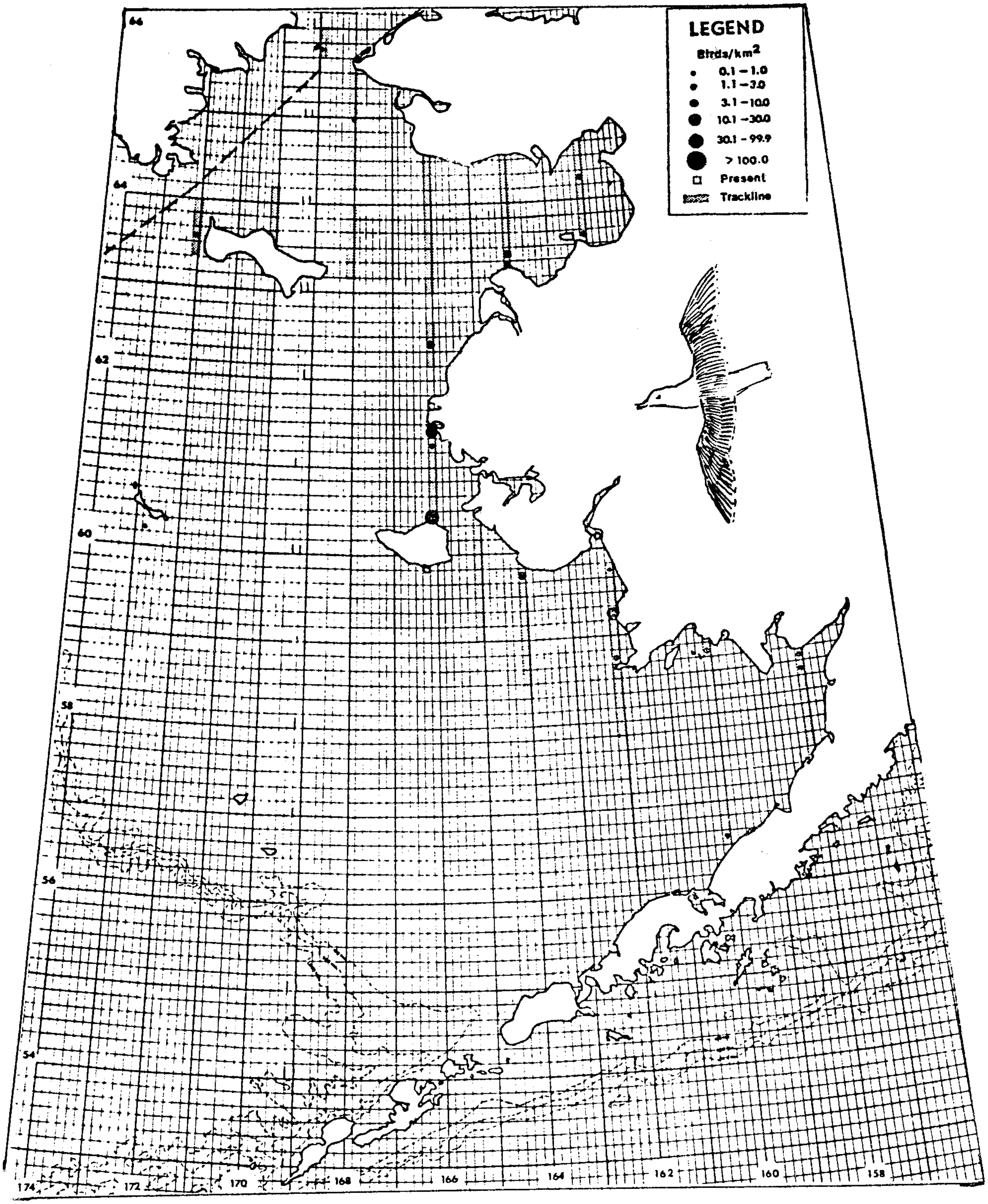


Figure I.C.7b Distribution and abundance of Glaucous Gulls in the Bering Sea in August 1976: no Glaucous Gulls were observed in July 1976. Aerial surveys, USFWS: Figure 112, page 229, in Harrison 1977.

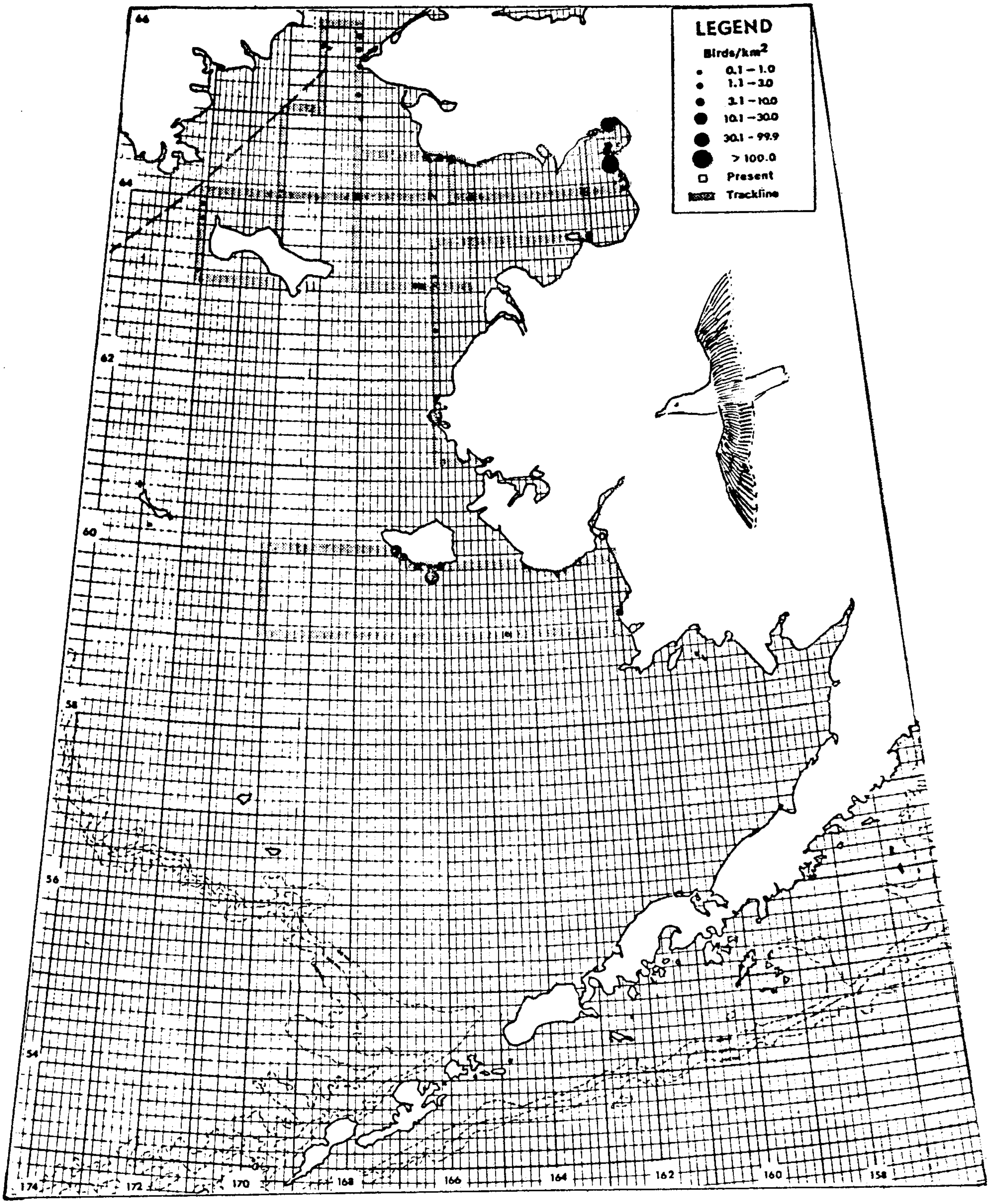


Figure I.C.7c Distribution and abundance of Glaucous Gulls in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 113, page 230, in Harrison 1977.

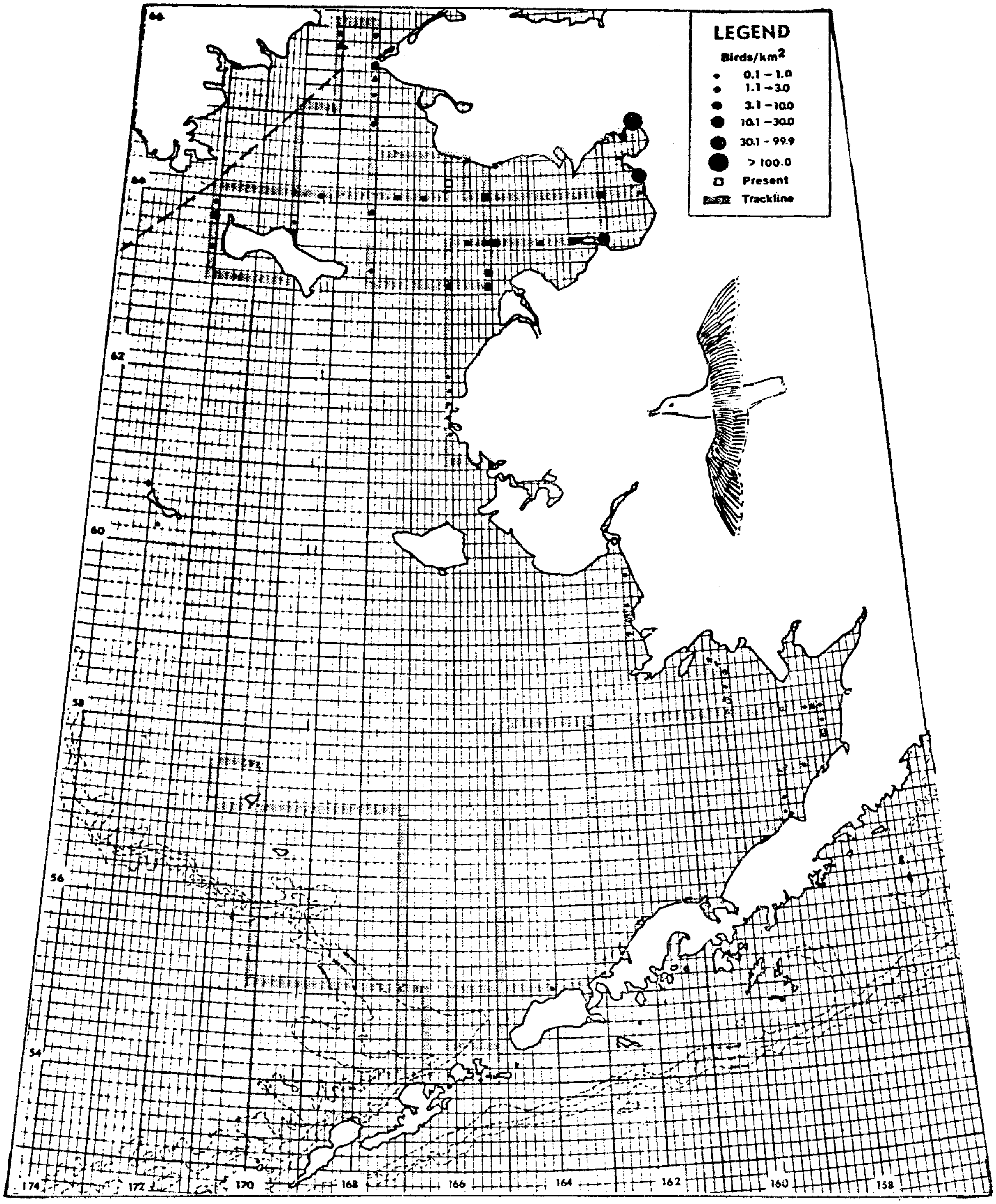


Figure I.C.8a Distribution and abundance of Black-legged Kittiwakes in the Bering Sea in June 1976. Aerial surveys, USFWS: Figure 126, page 243, in Harrison 1977.

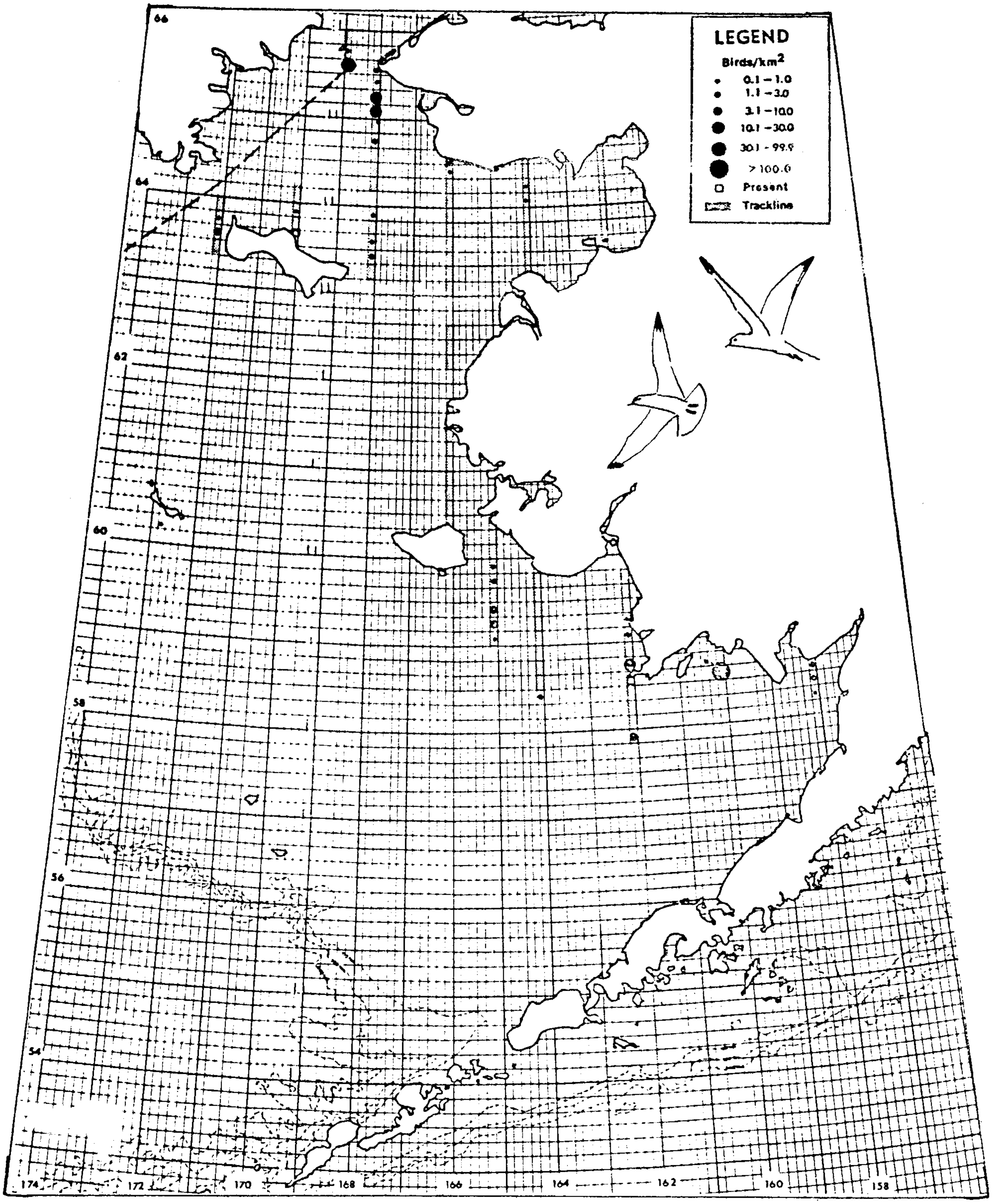
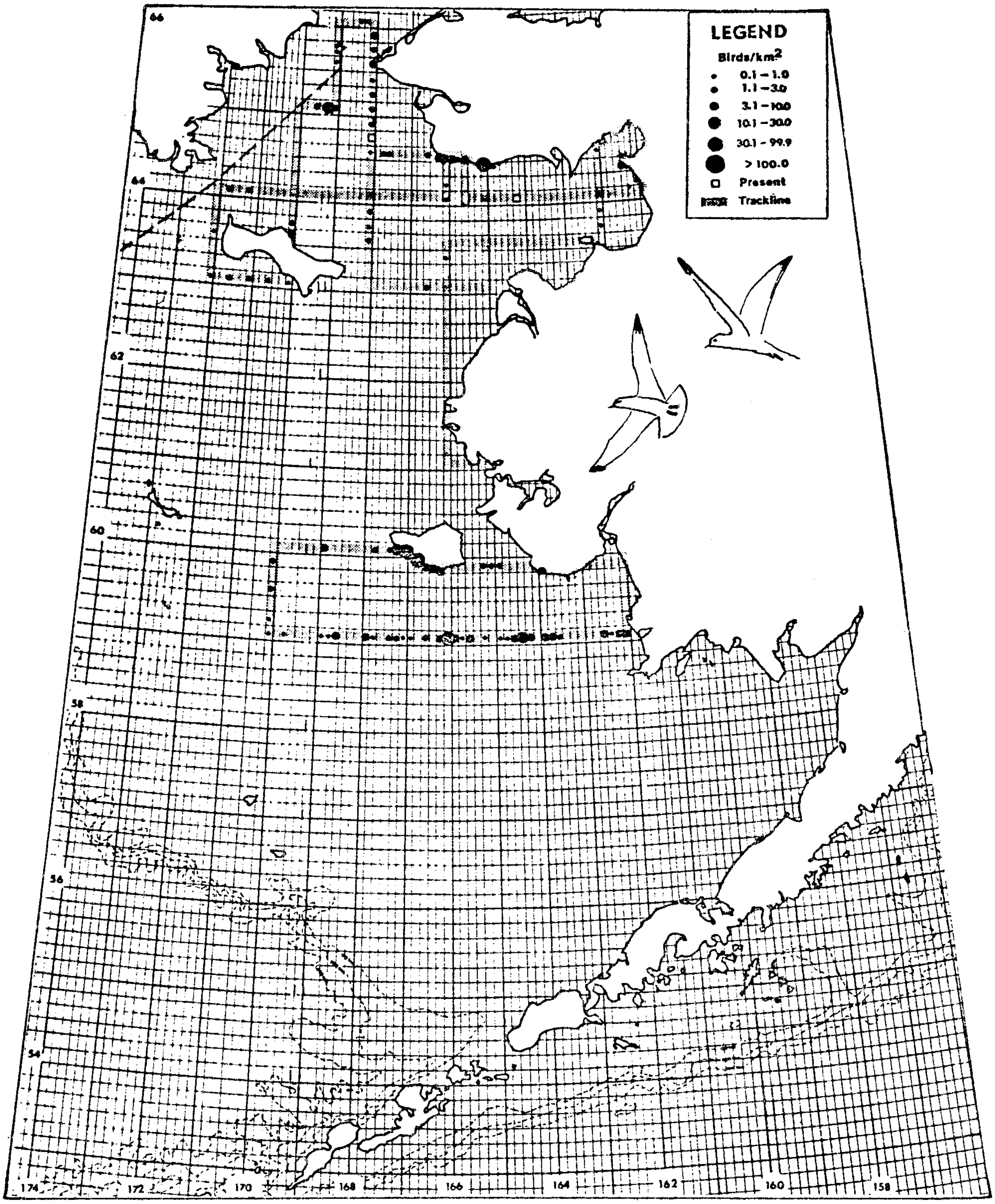


Figure I.C.8b Distribution and abundance of Black-legged Kittiwakes in the Bering Sea in August 1976. Aerial surveys, USFWS: Figure 128, page 245, in Harrison 1977.



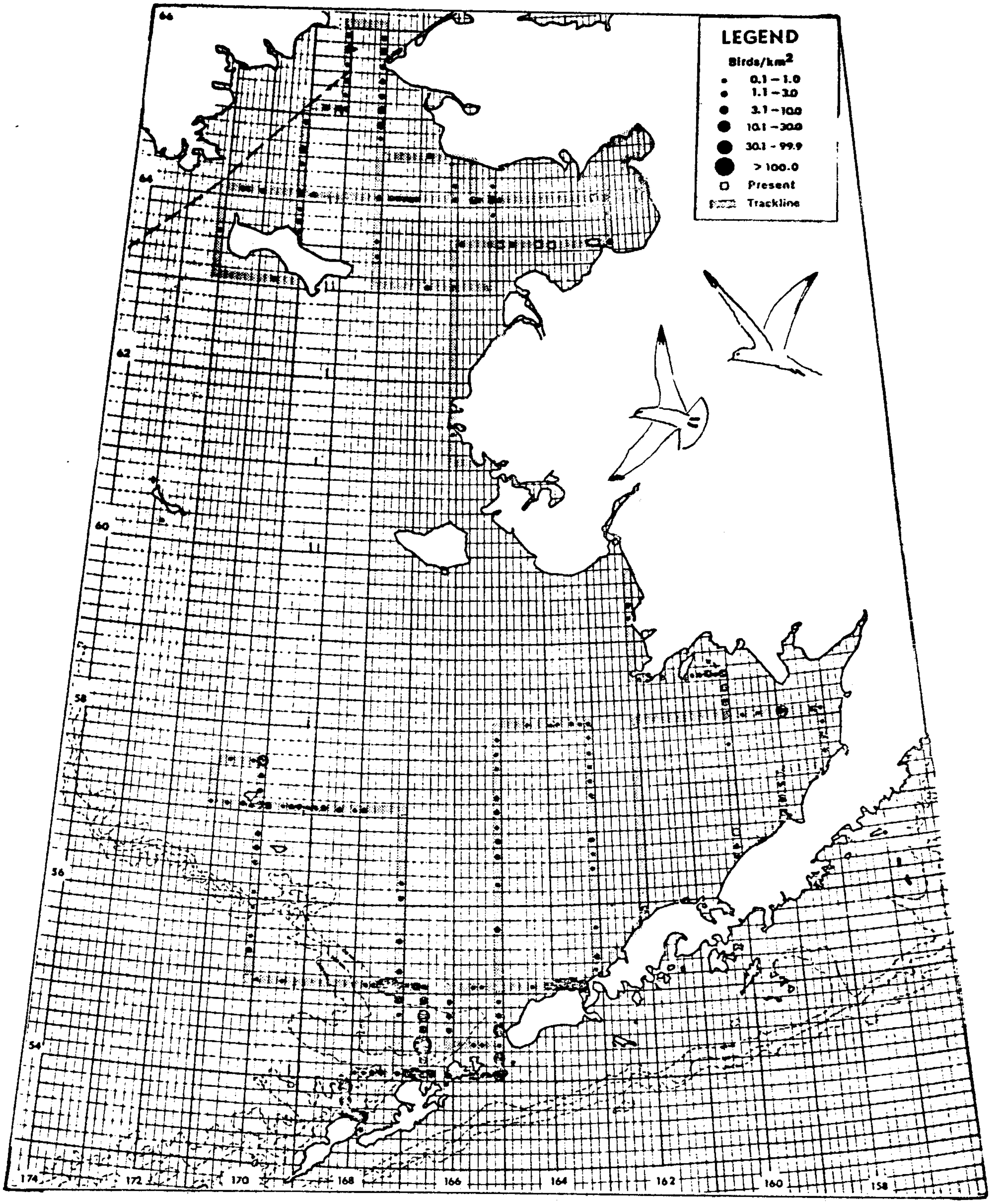


Figure I.C.8c Distribution and abundance of Black-legged Kittiwakes in the Bering Sea in October 1976. Aerial surveys, USFWS: Figure 129, page 246, in Harrison 1977.

Figure I.D.1a
Representation of ice coverage along route of surveys run on June 9, 1978 (Drury et al.).

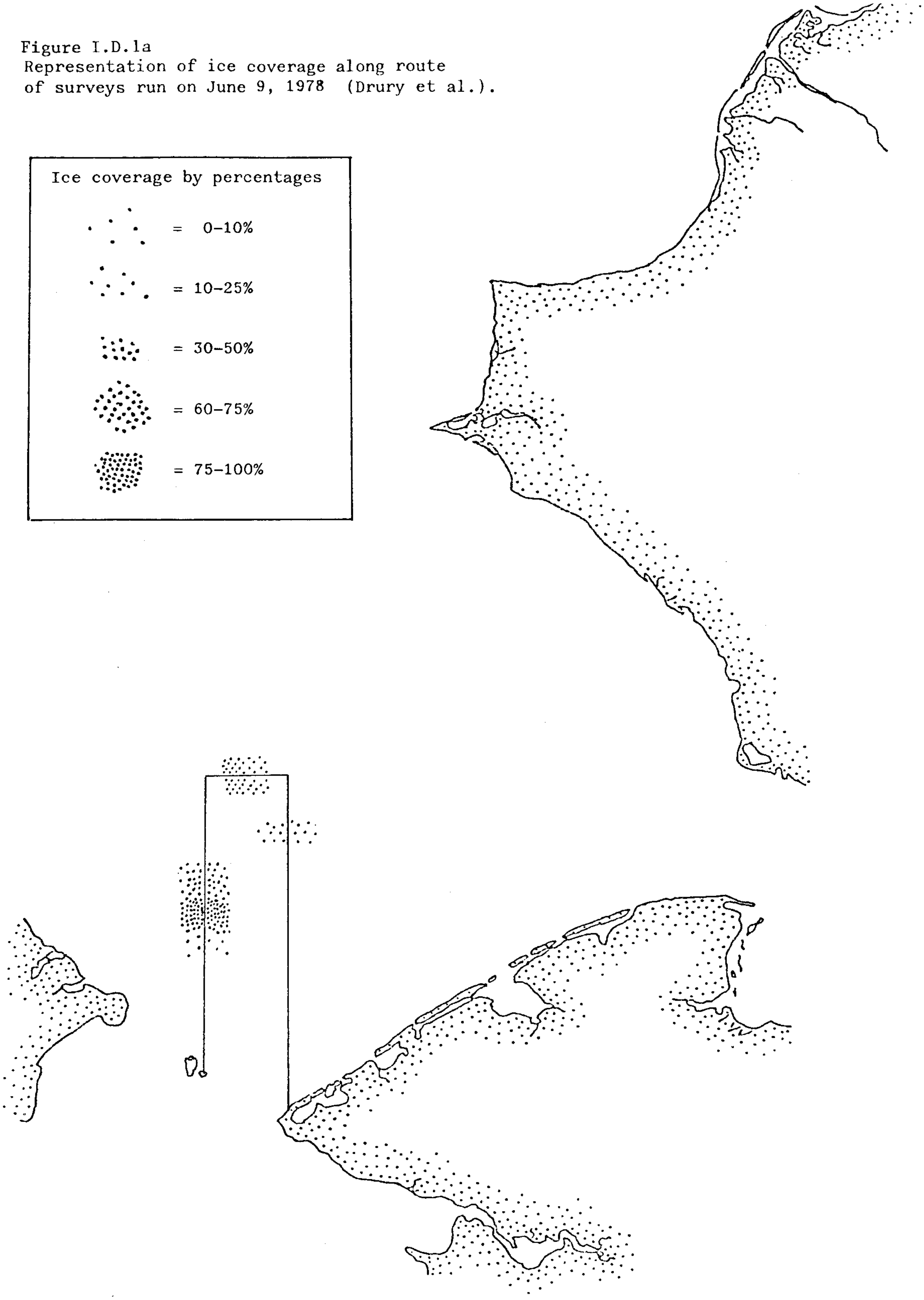
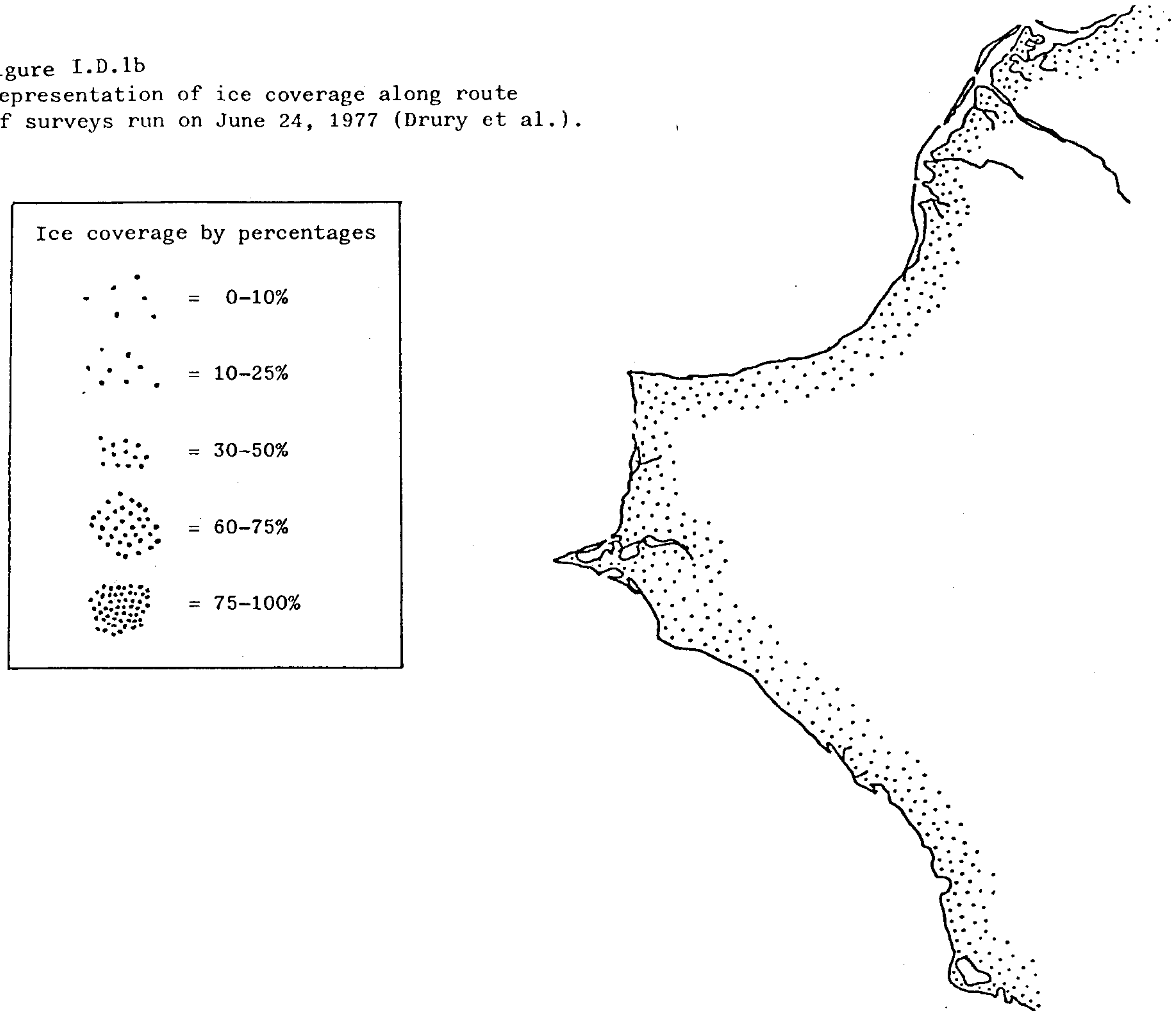


Figure I.D.1b
Representation of ice coverage along route of surveys run on June 24, 1977 (Drury et al.).



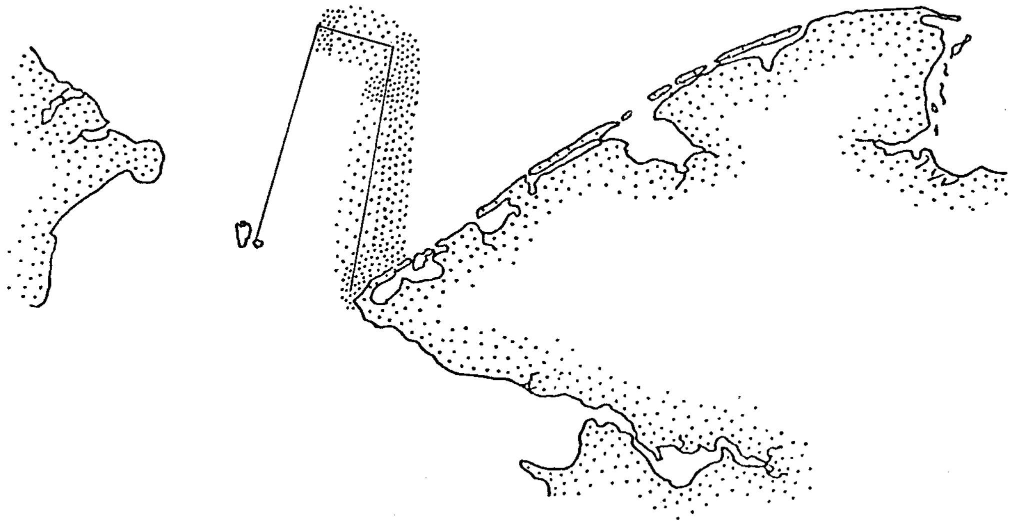


Figure I.D.2a
Murres seen during aerial transects
in the Chukchi Sea in the presence
of sea ice on
June 9, 1978 (Drury et al.).

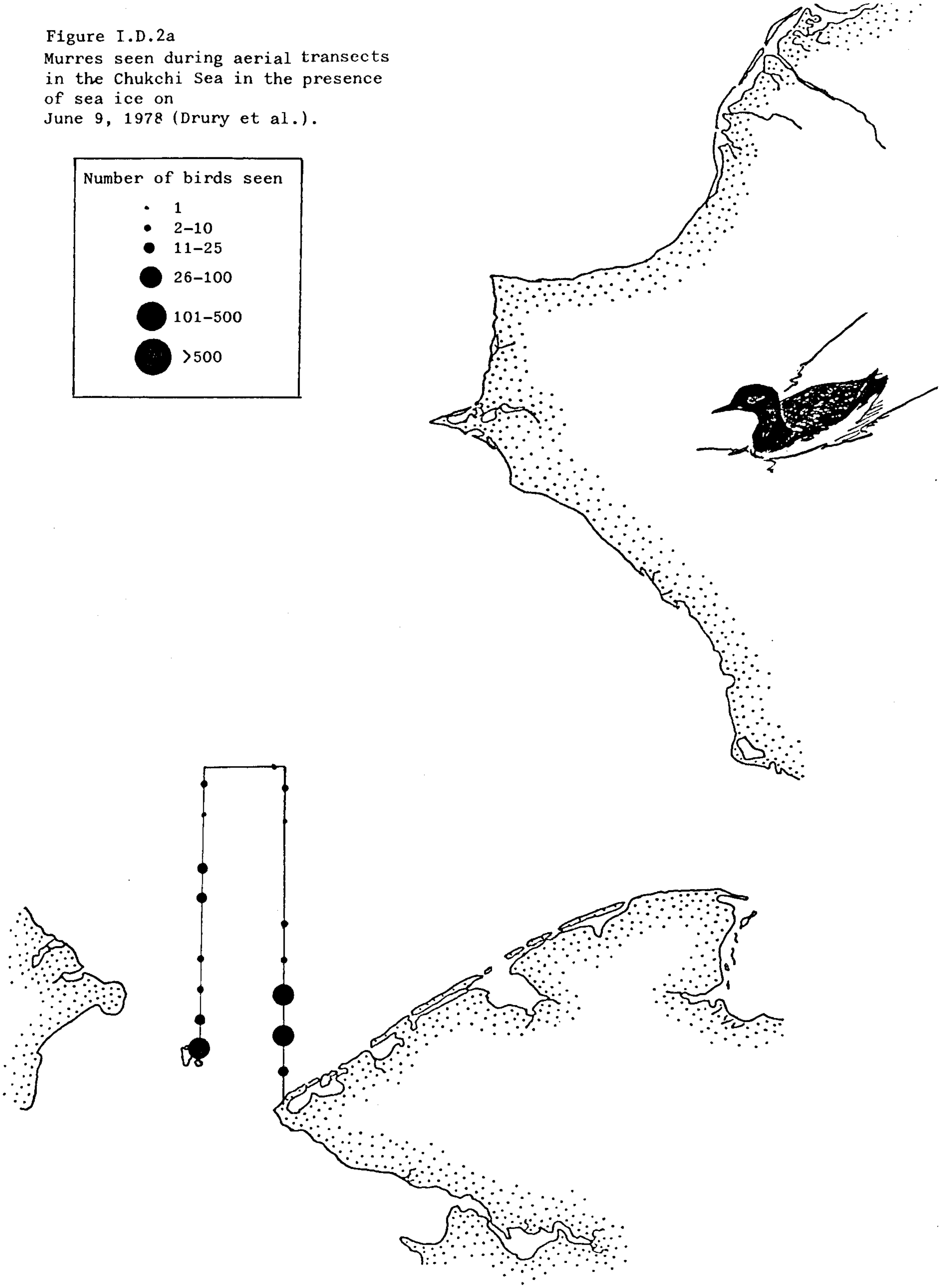


Figure I.D.2b

Murres seen during aerial transects
in the Chukchi Sea in the presence of sea ice
June 24, 1977 (Drury et al.).

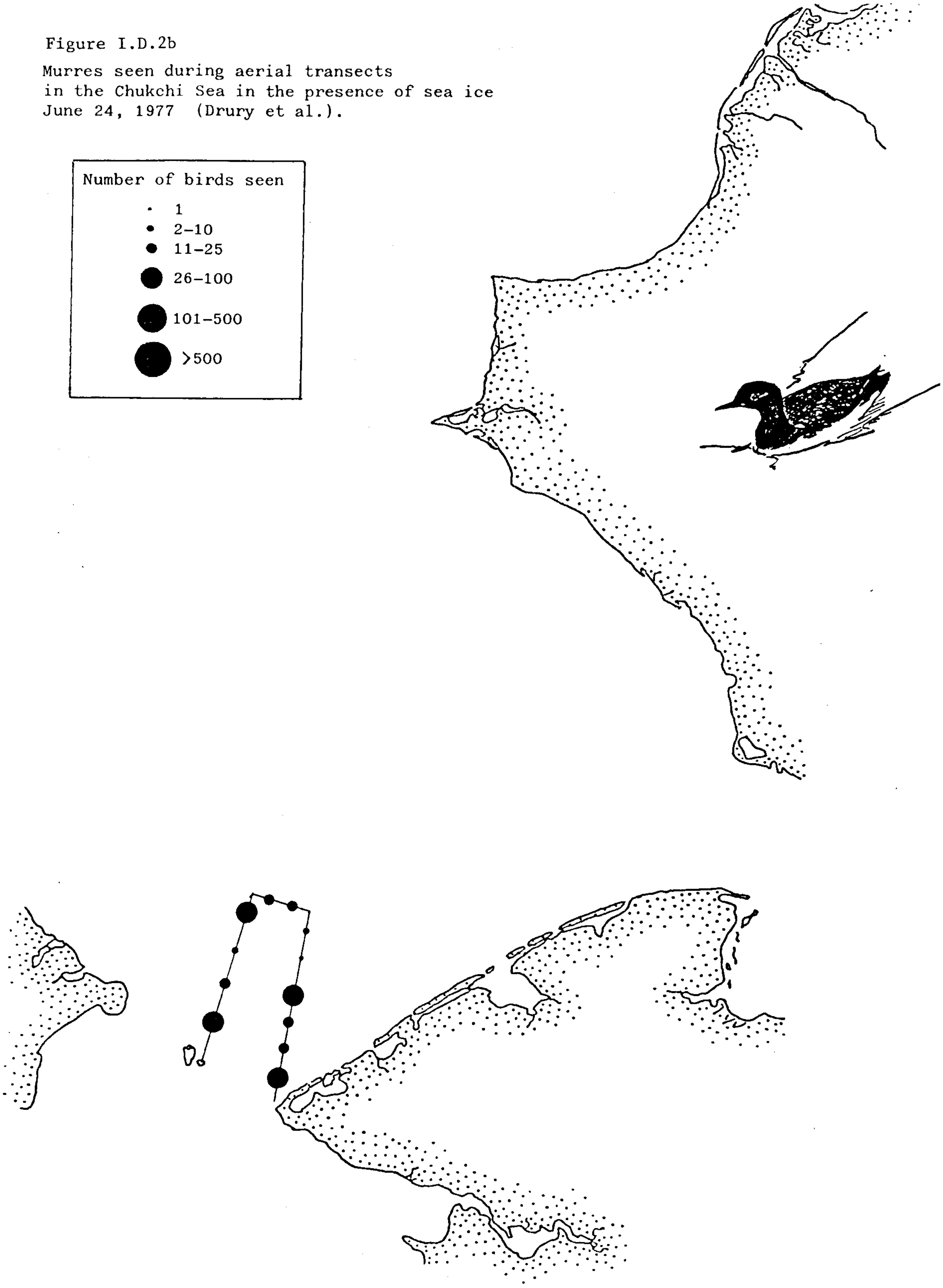


Figure I.D.2c Distribution and abundance of murres in the Chukchi Sea in June 1976. Aerial surveys, USFWS: Figure 51, page 167, in Harrison 1977.

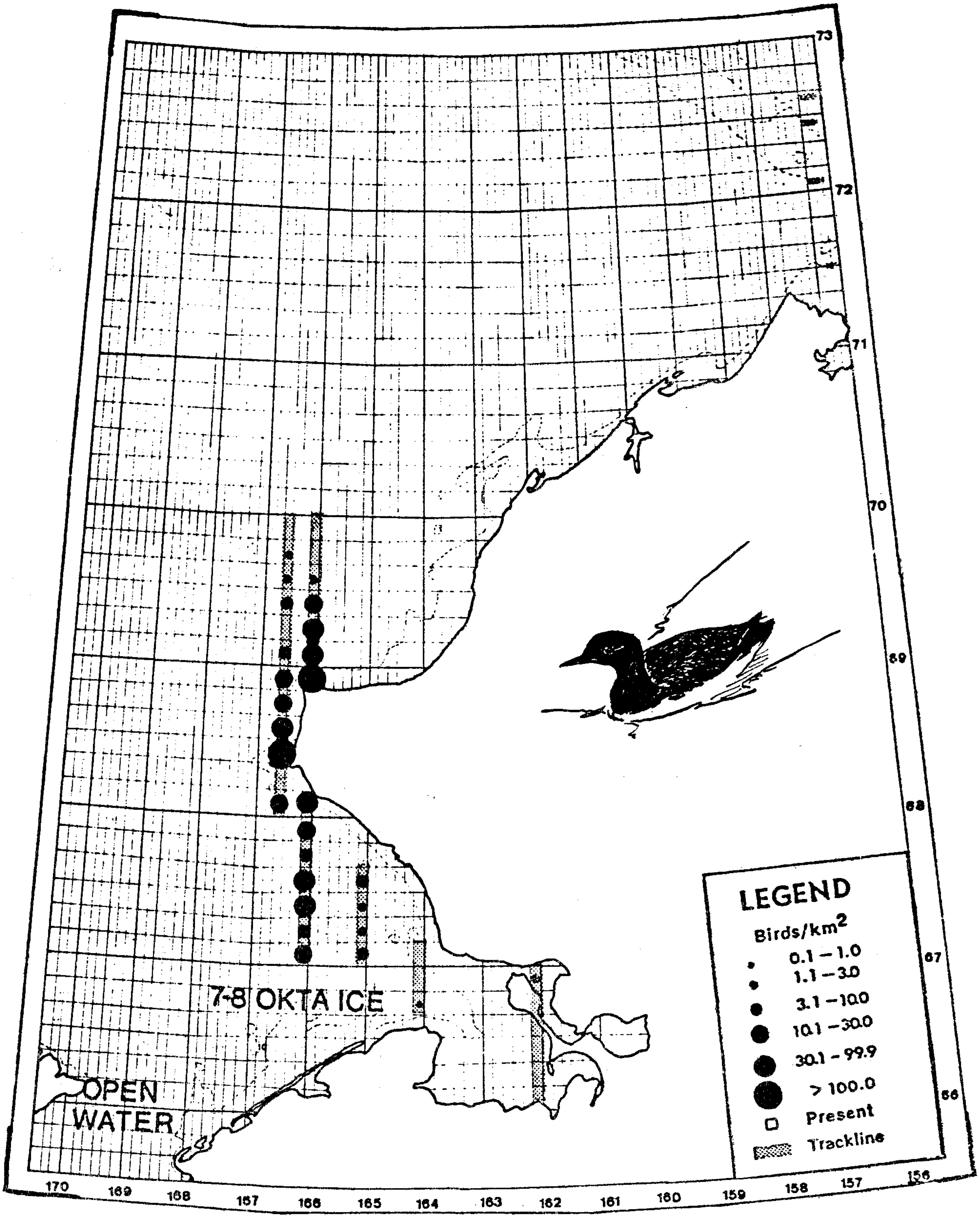


Figure I.D.2d
Murres seen during aerial transects
in the Chukchi Sea
July 7, 1978 (Drury et al.).

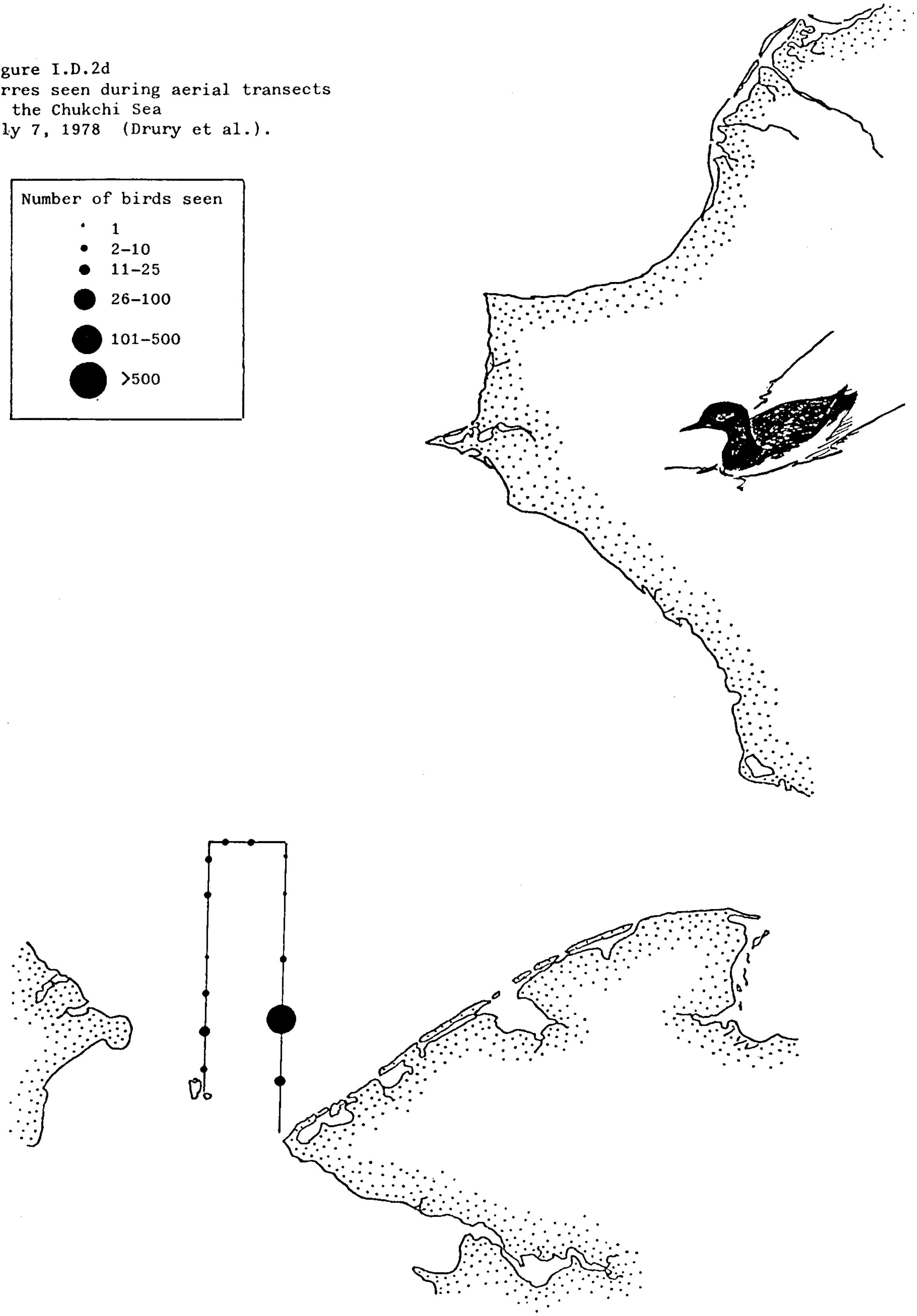
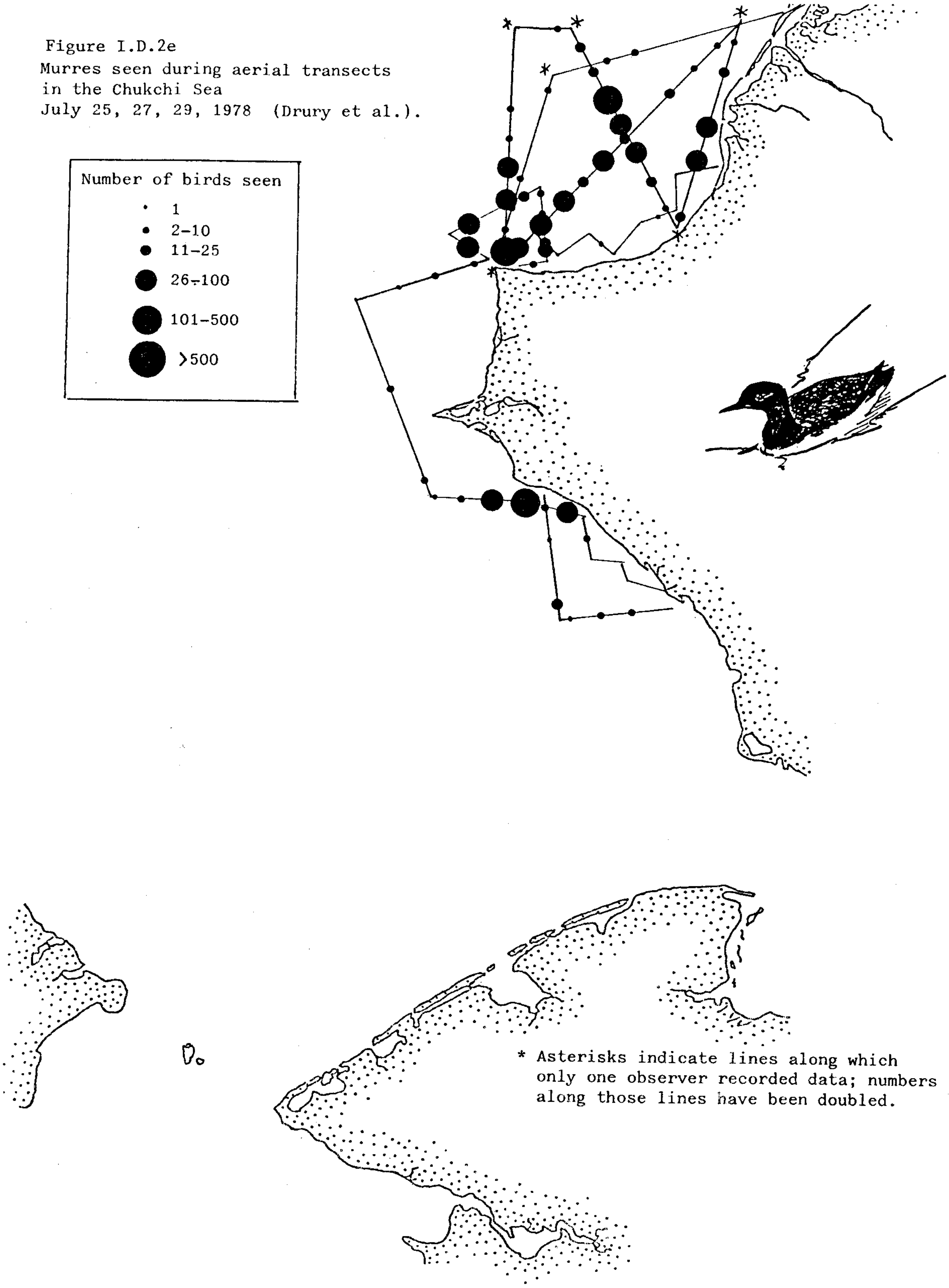
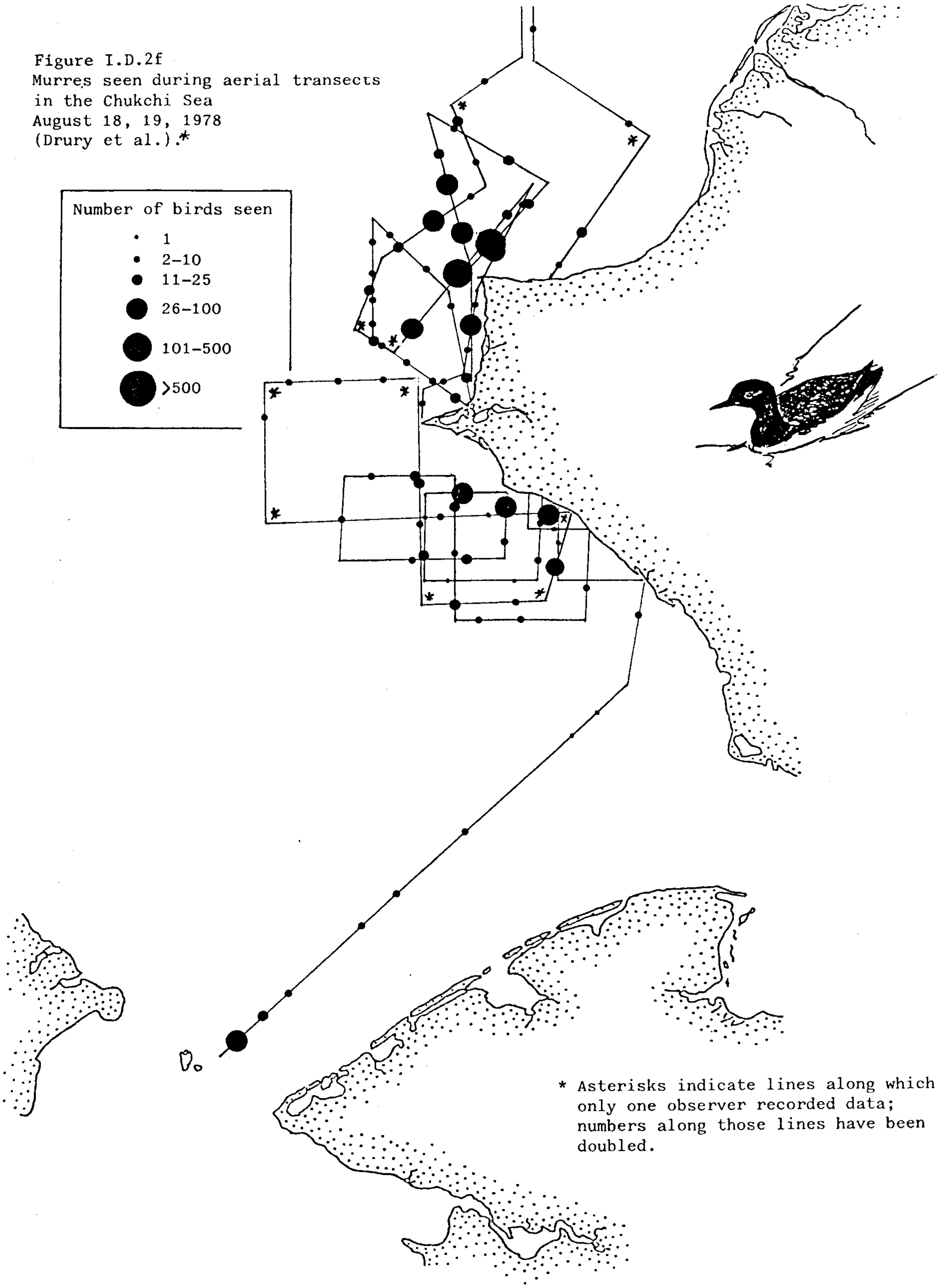


Figure I.D.2e
Murres seen during aerial transects
in the Chukchi Sea
July 25, 27, 29, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.2f
Murres seen during aerial transects
in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.2g Distribution and abundance of murres in the Chukchi Sea in August 1976. Aerial surveys, USFWS: Figure 52, page 168, in Harrison 1977.

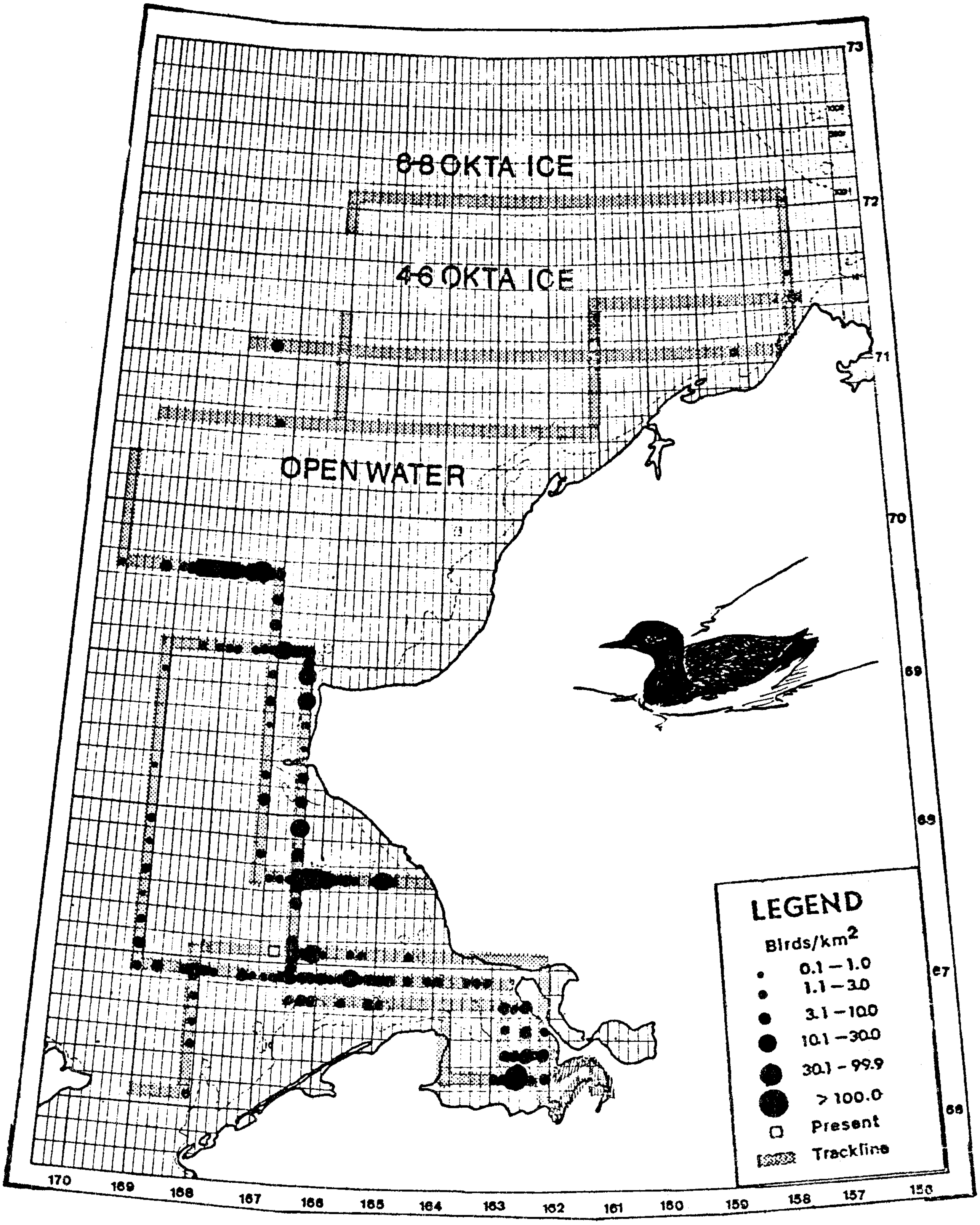


Figure I.D.2h Distribution and abundance of murres in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 53, page 169, in Harrison 1977.

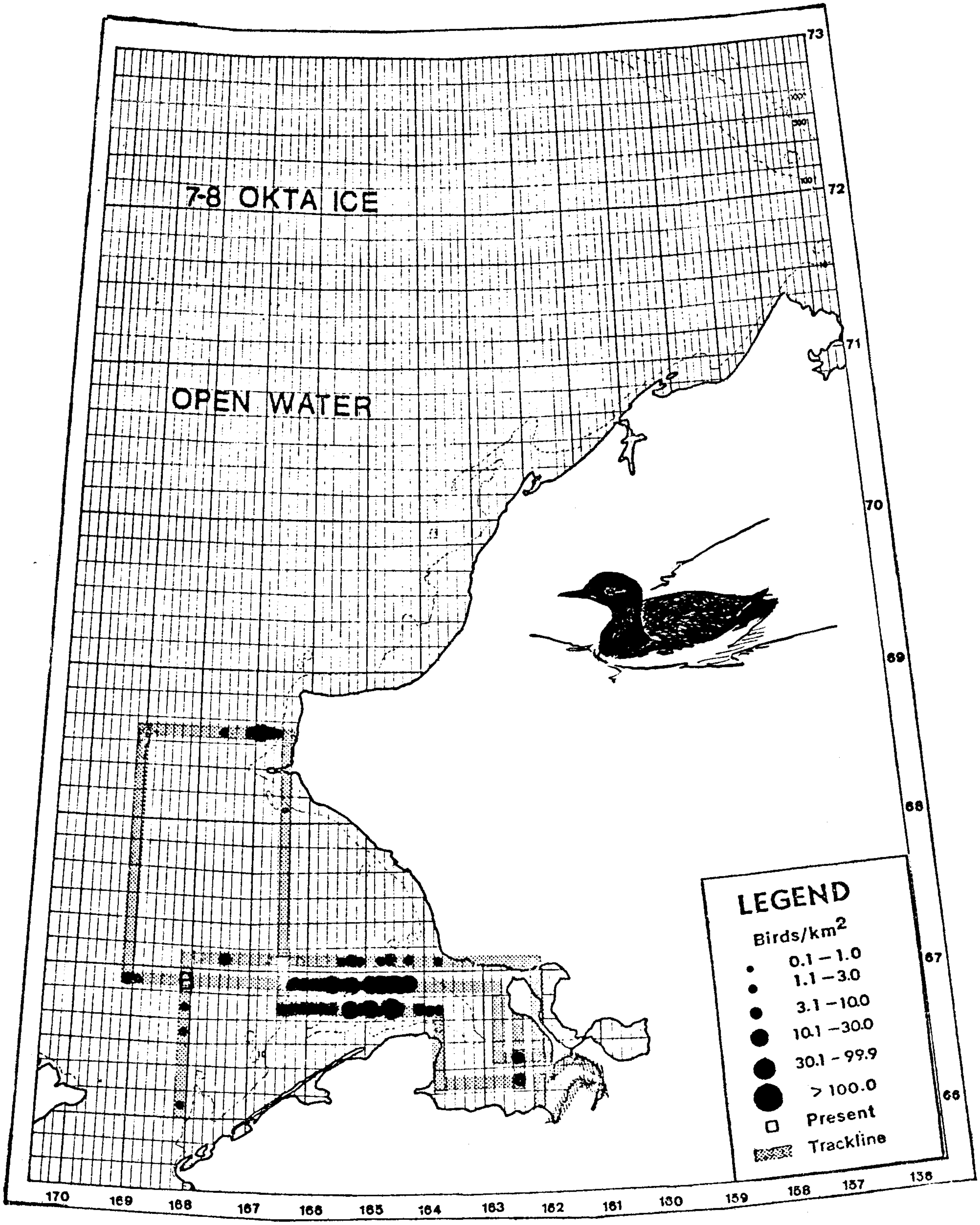


Figure I.D.3a
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in the Chukchi Sea in the presence of sea ice on June 9, 1978 (Drury et al.).

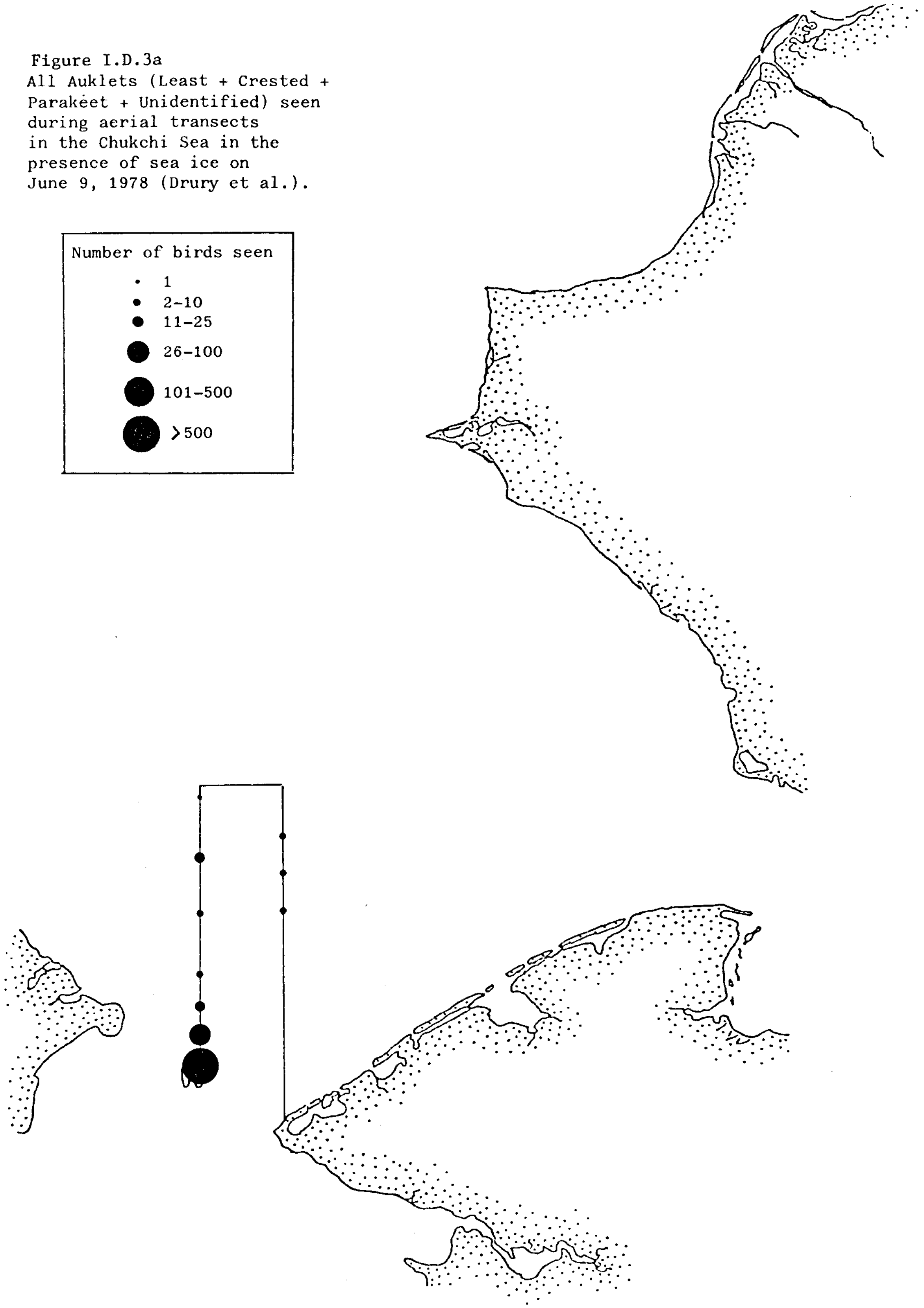


Figure I.D.3b
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

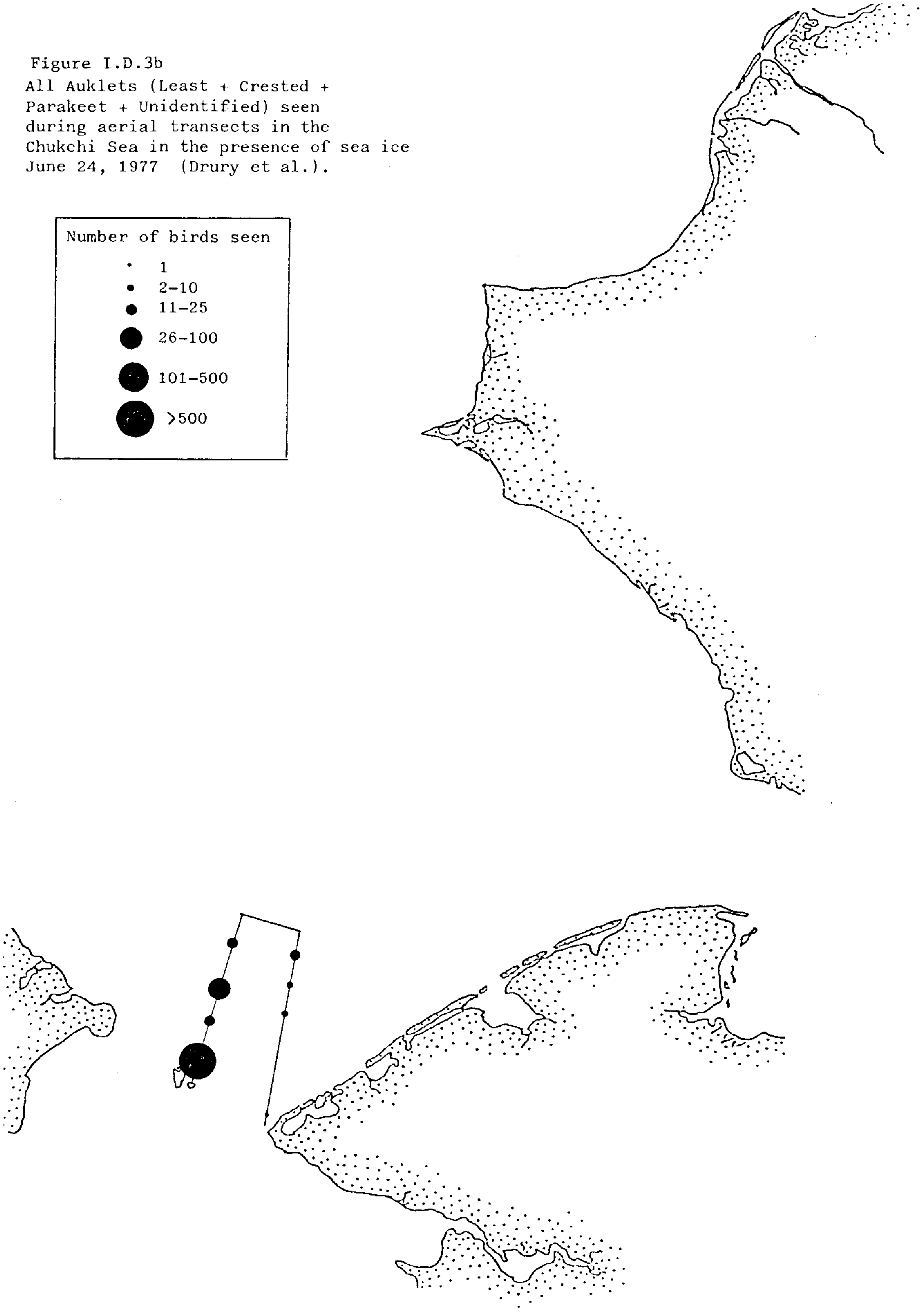


Figure I.D.3c
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in the Chukchi Sea
July 7, 1978 (Drury et al.).

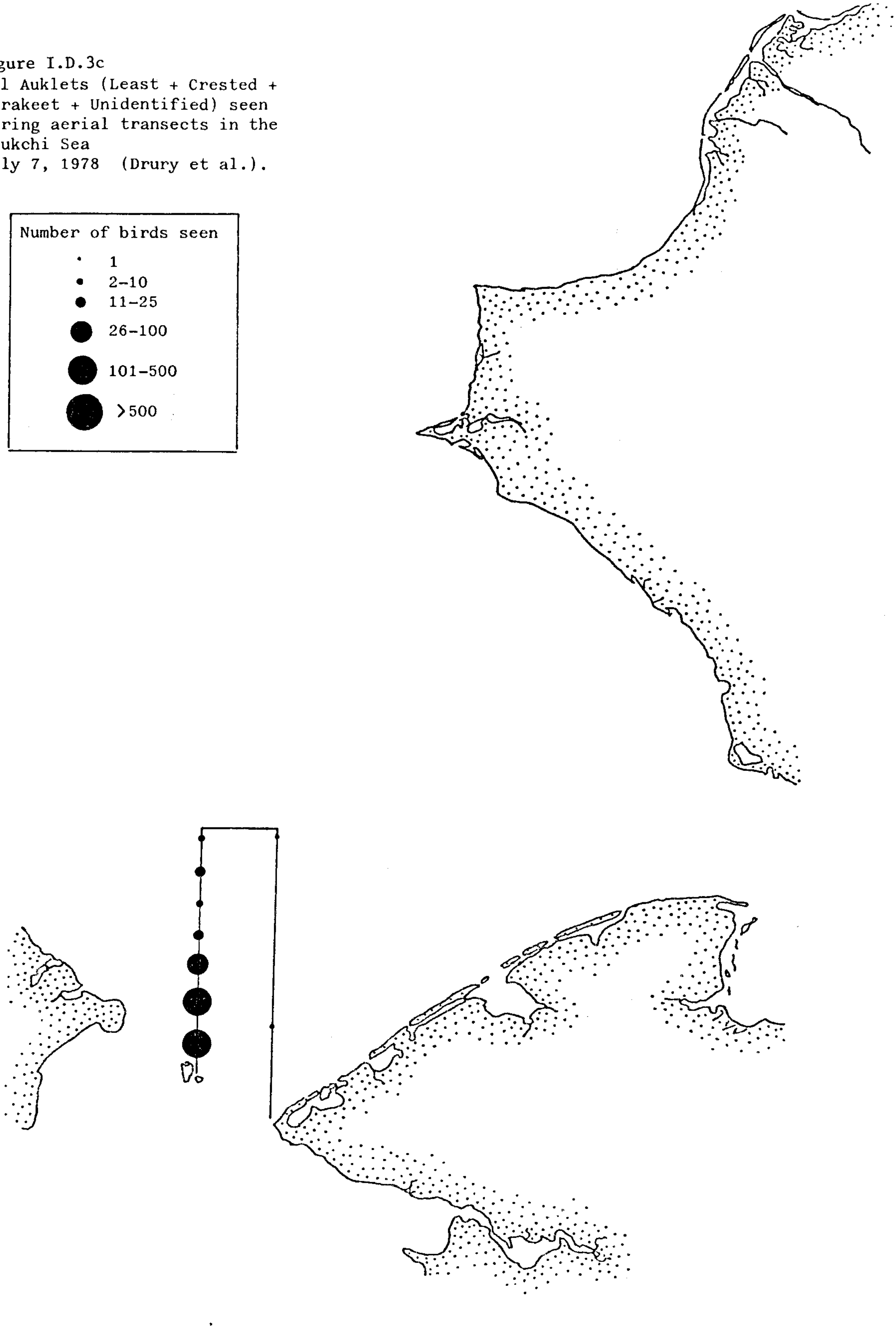
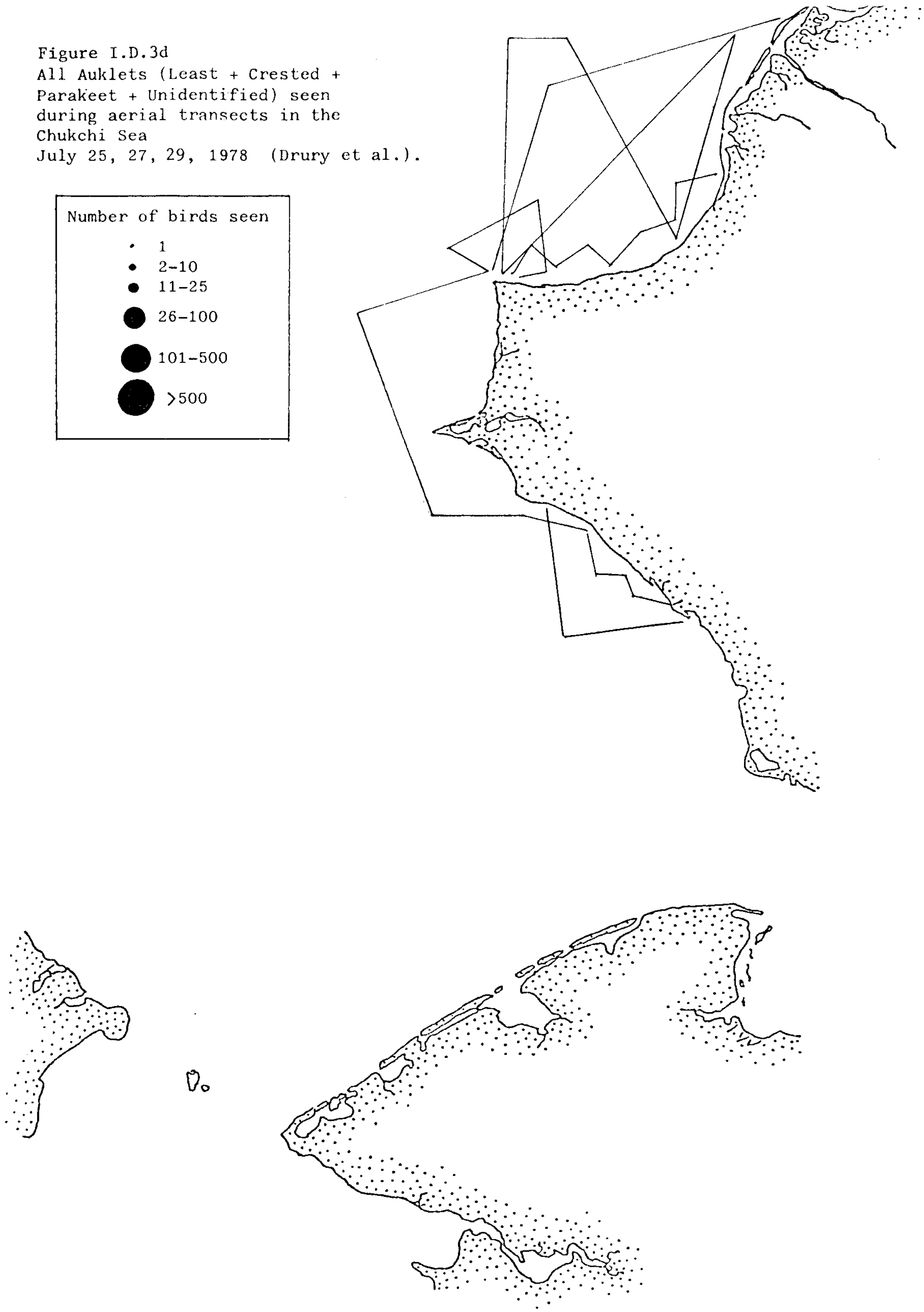


Figure I.D.3d
All Auklets (Least + Crested + Parakeet + Unidentified) seen during aerial transects in the Chukchi Sea
July 25, 27, 29, 1978 (Drury et al.).



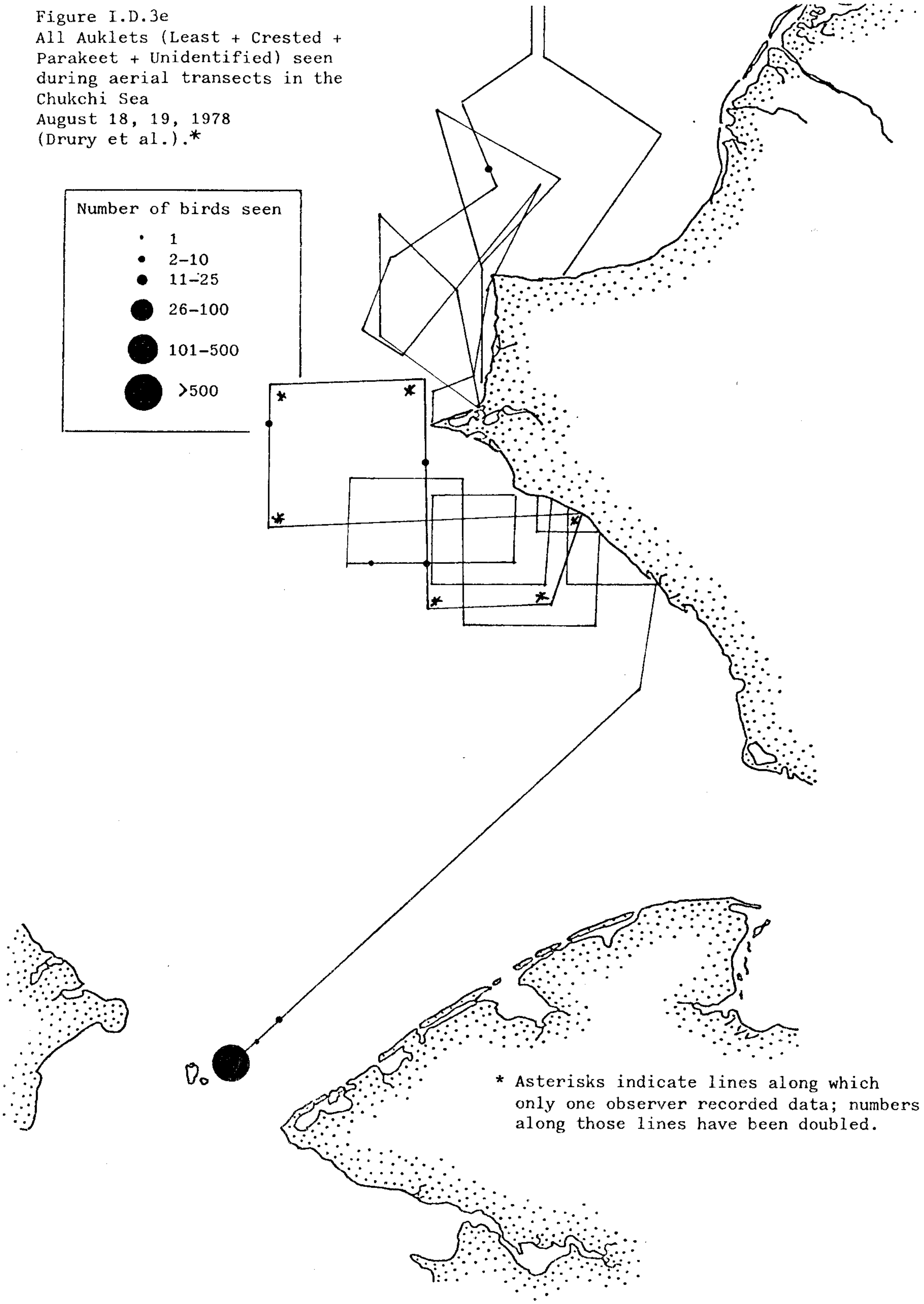


Figure I.D.3e
All Auklets (Least + Crested +
Parakeet + Unidentified) seen
during aerial transects in the
Chukchi Sea
August 18, 19, 1978
(Drury et al.).*

* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.4a

Least Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

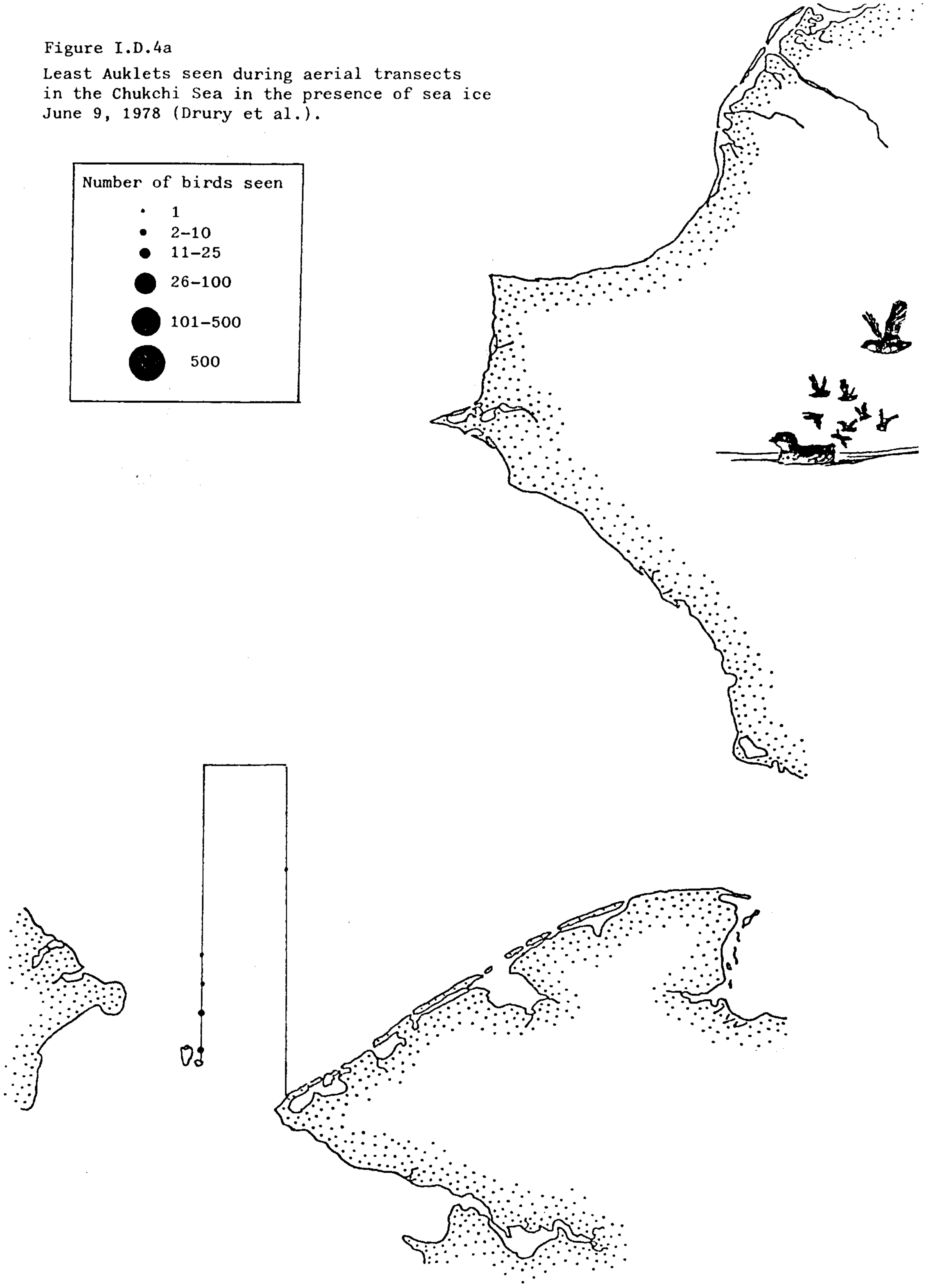


Figure I.D.4b
Least Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

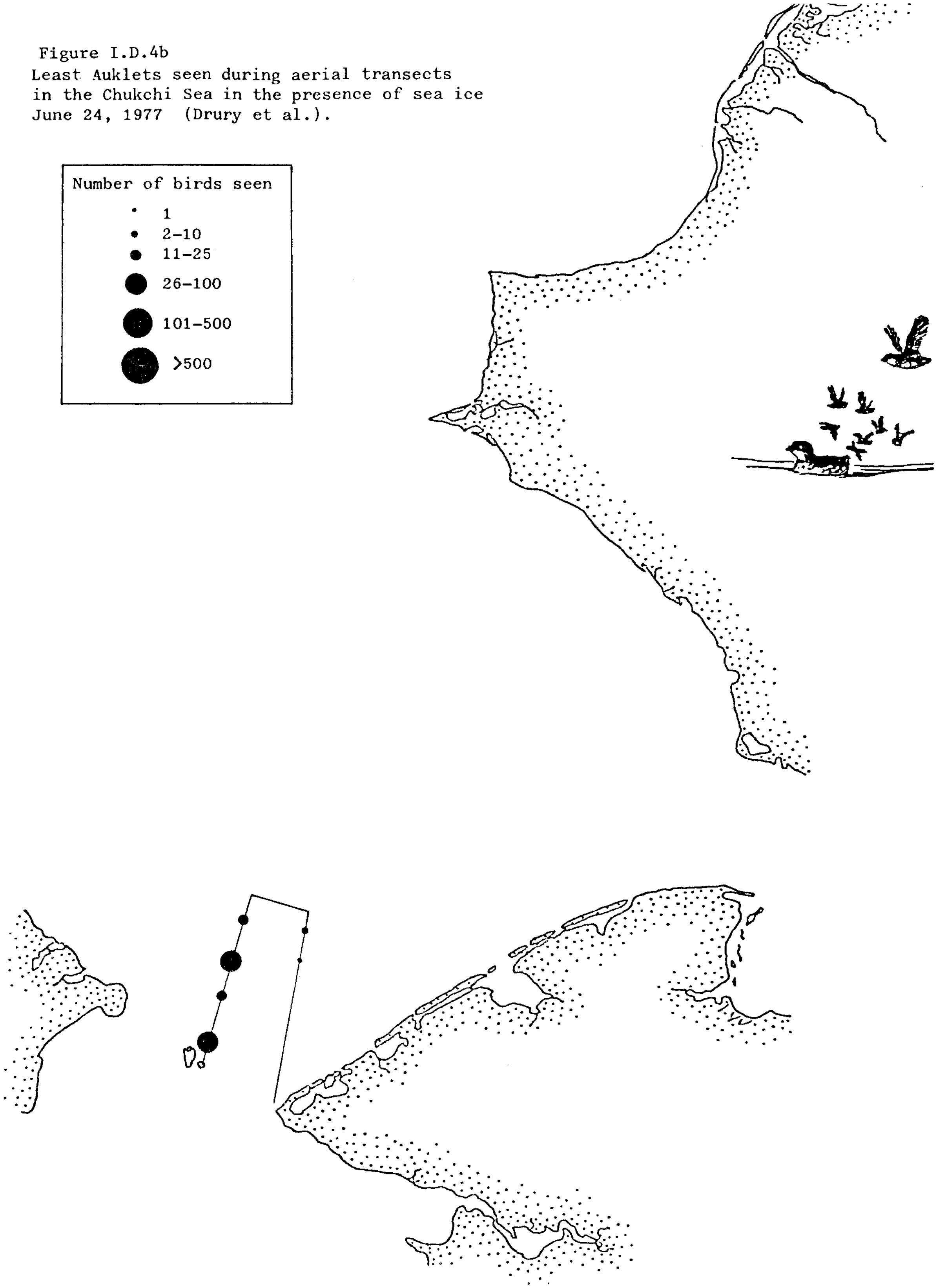


Figure I.D.4c
Least Auklets seen during
aerial transects in the Chukchi Sea
July 7, 1978 (Drury et al.).

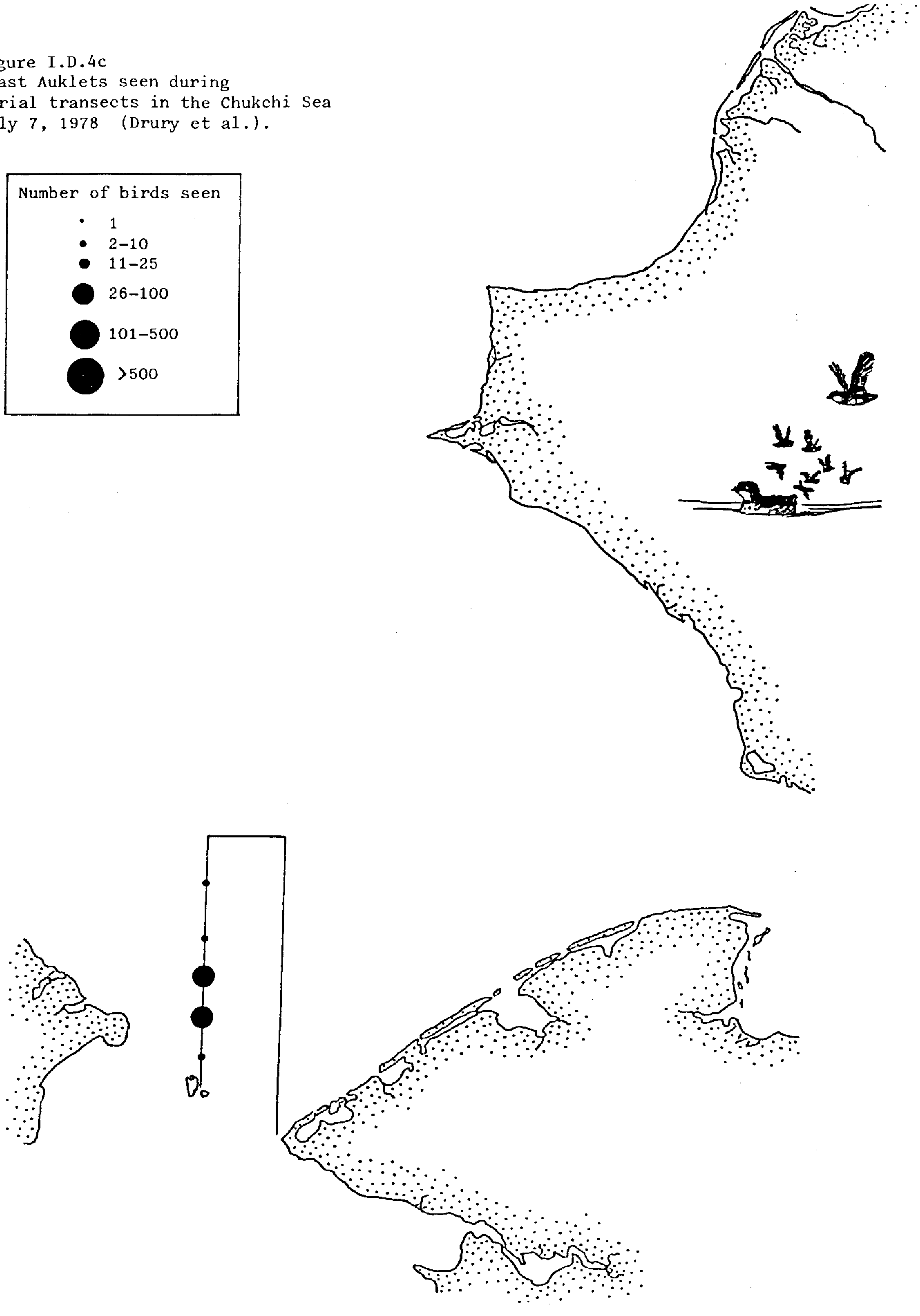
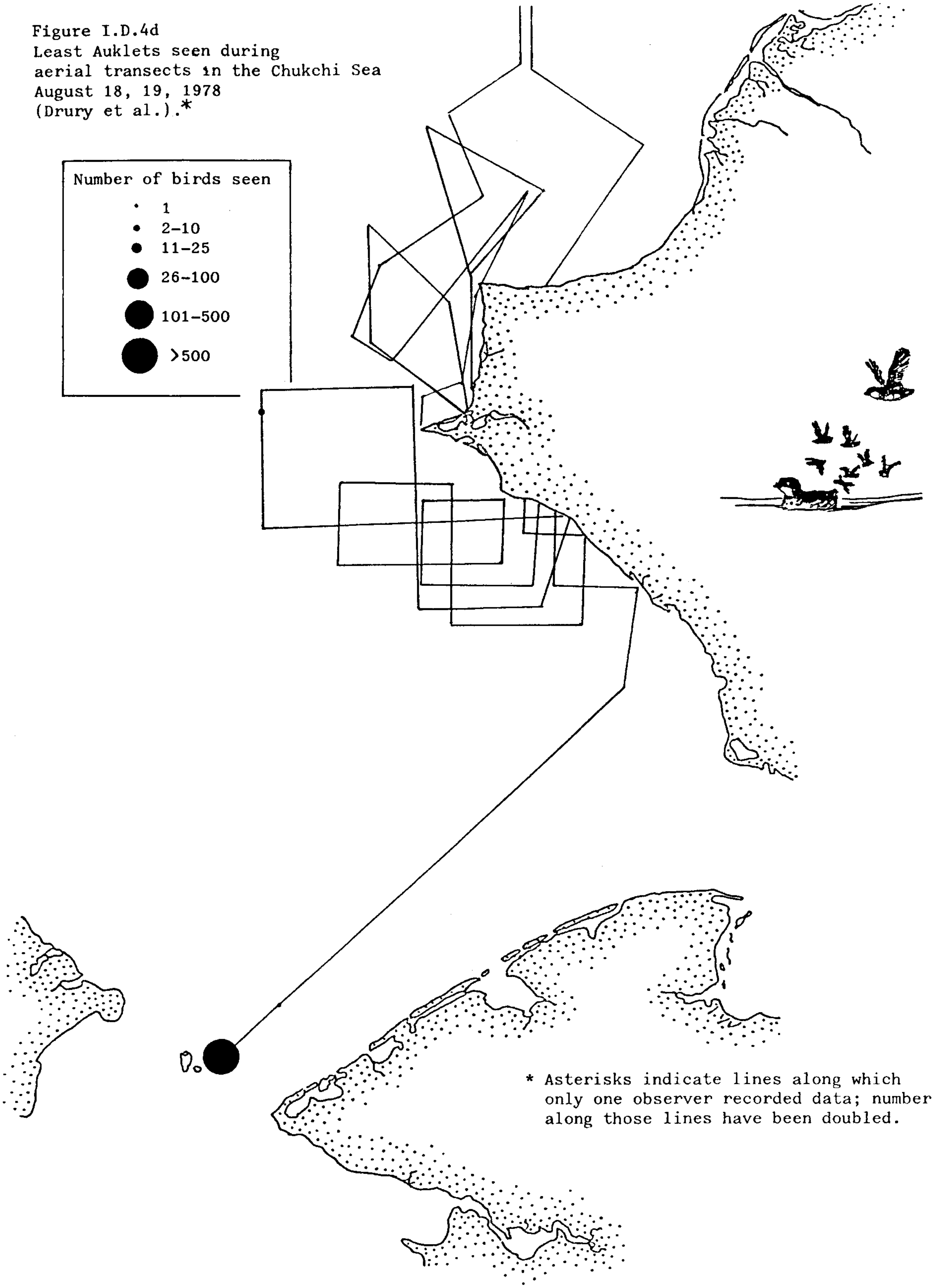


Figure I.D.4d
Least Auklets seen during
aerial transects in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.4e Distribution and abundance of Least Auklets in the Chukchi Sea in August 1976: no Least Auklets were identified in June 1976. Aerial surveys, USFWS: Figure 62, page 178, in Harrison 1977.

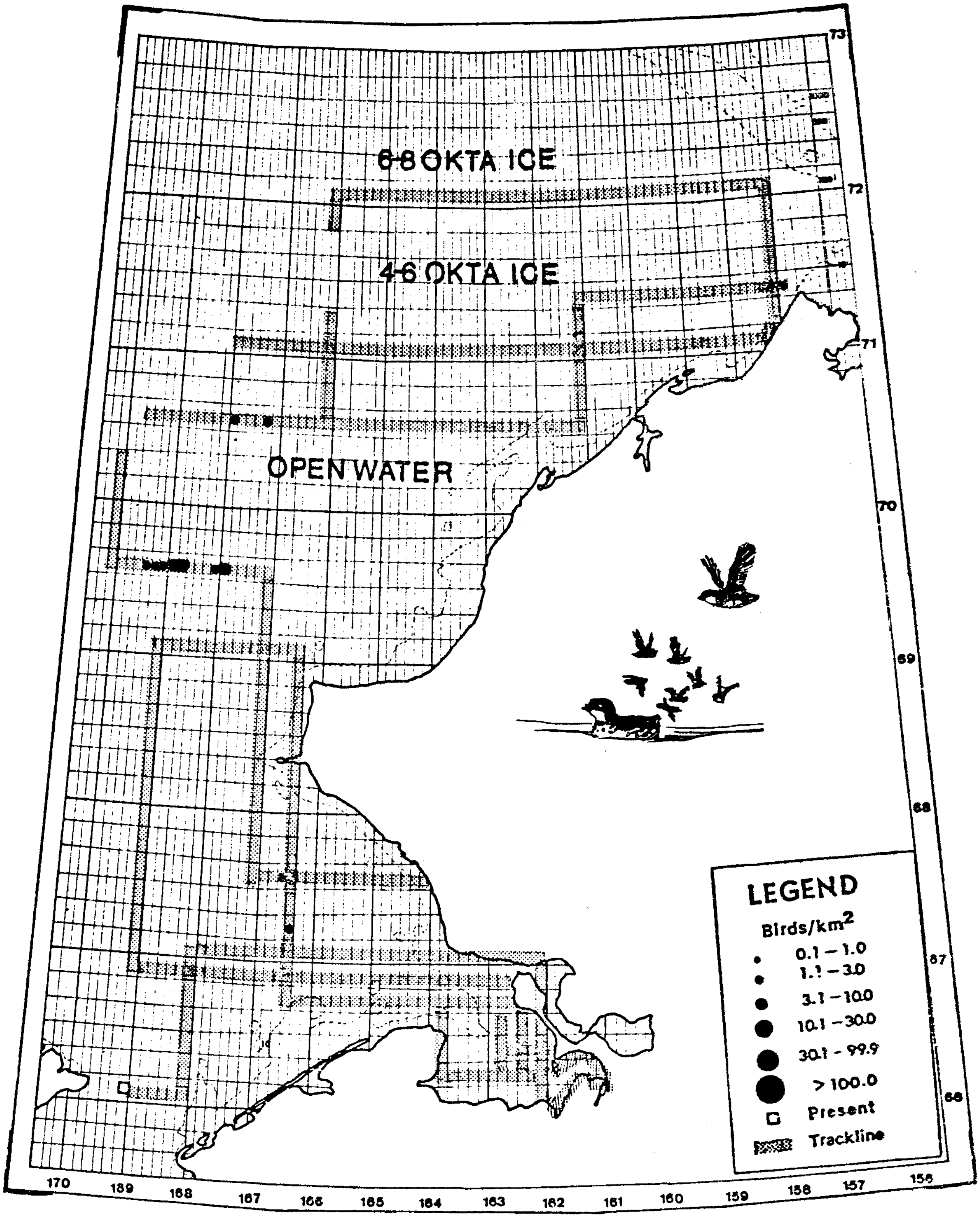


Figure I.D.4f Distribution and abundance of Least Auklets in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 63, page 179, in Harrison 1977.

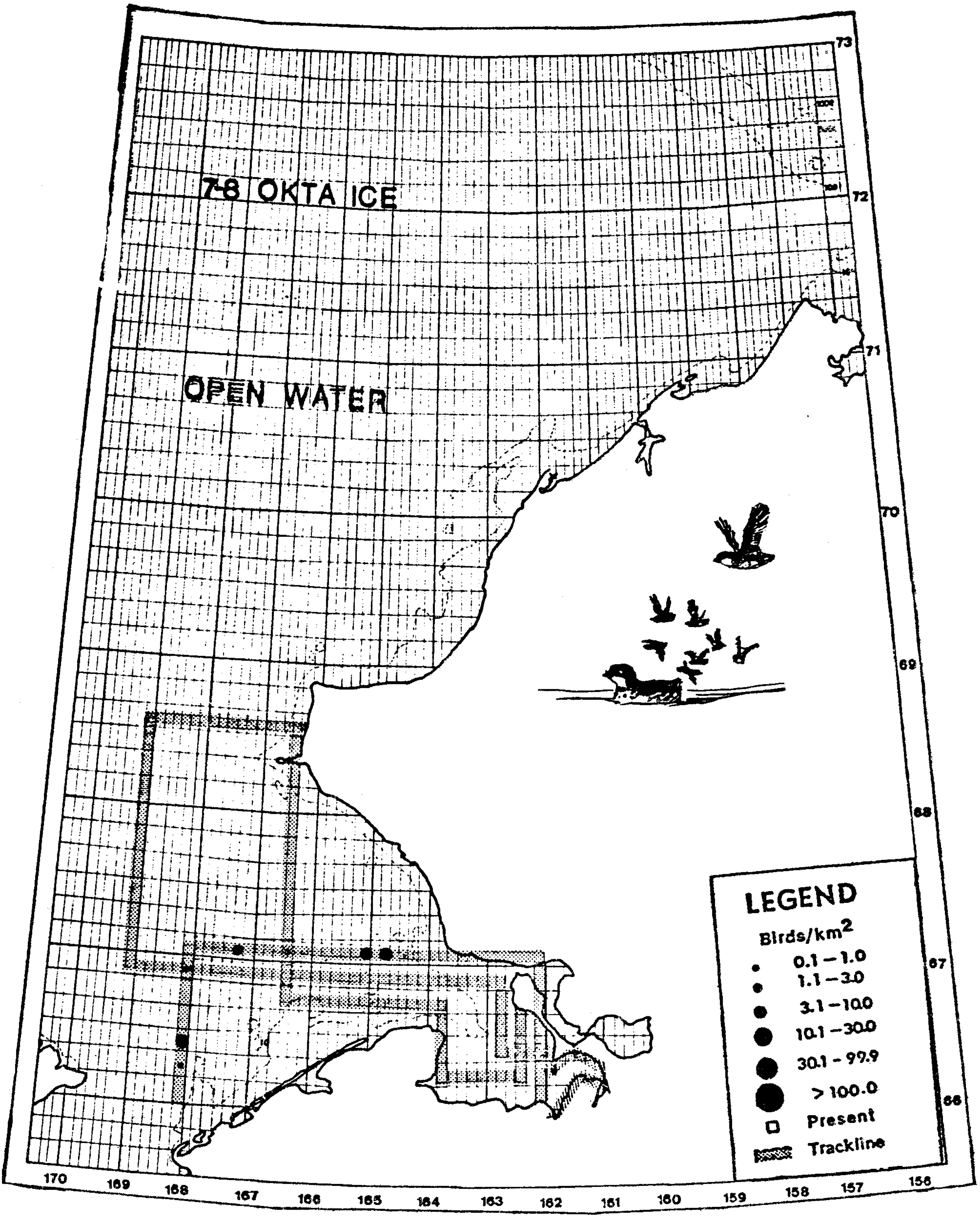


Figure I.D.5a
Crested Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

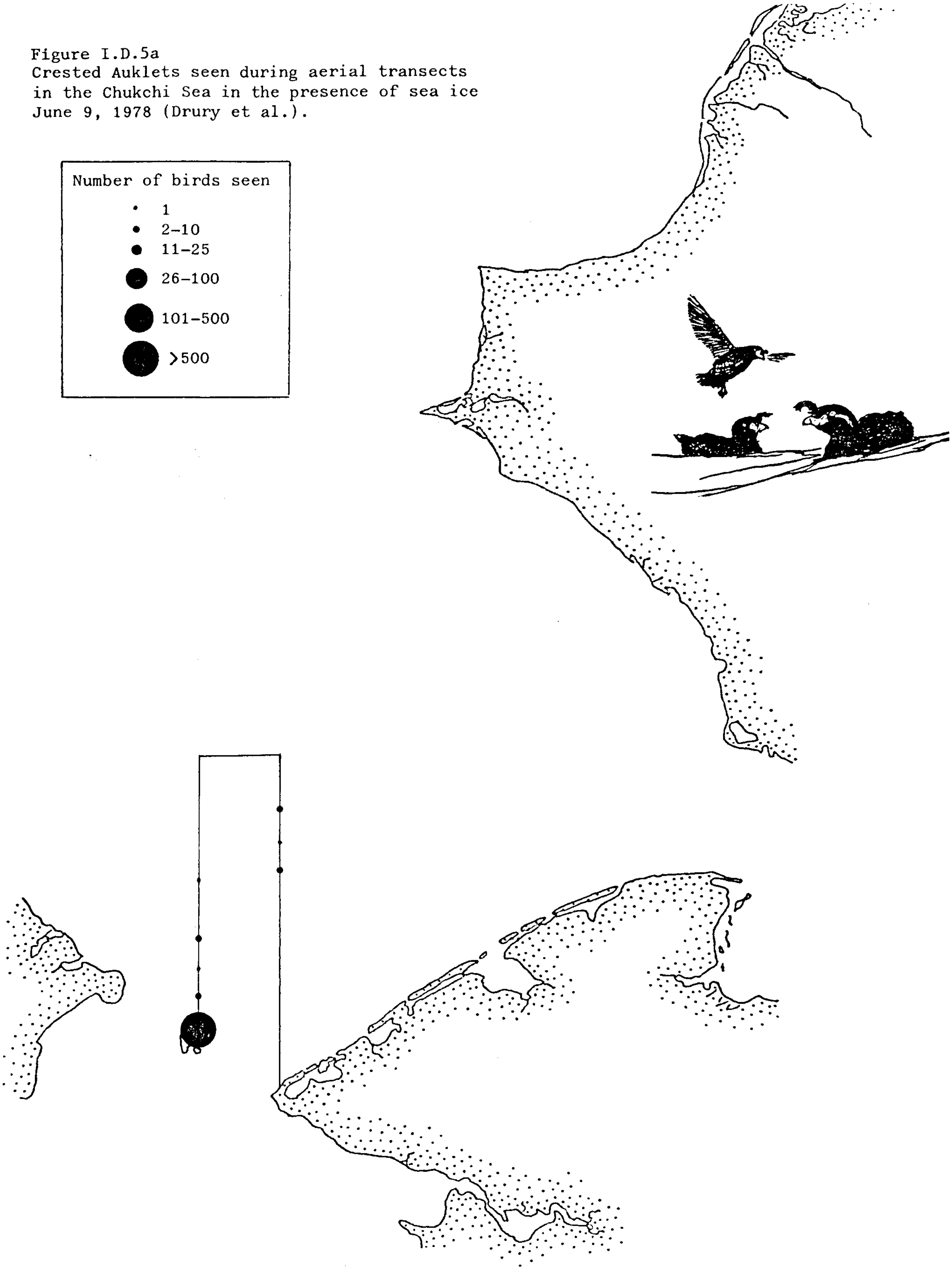


Figure I.D.5b
Crested Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

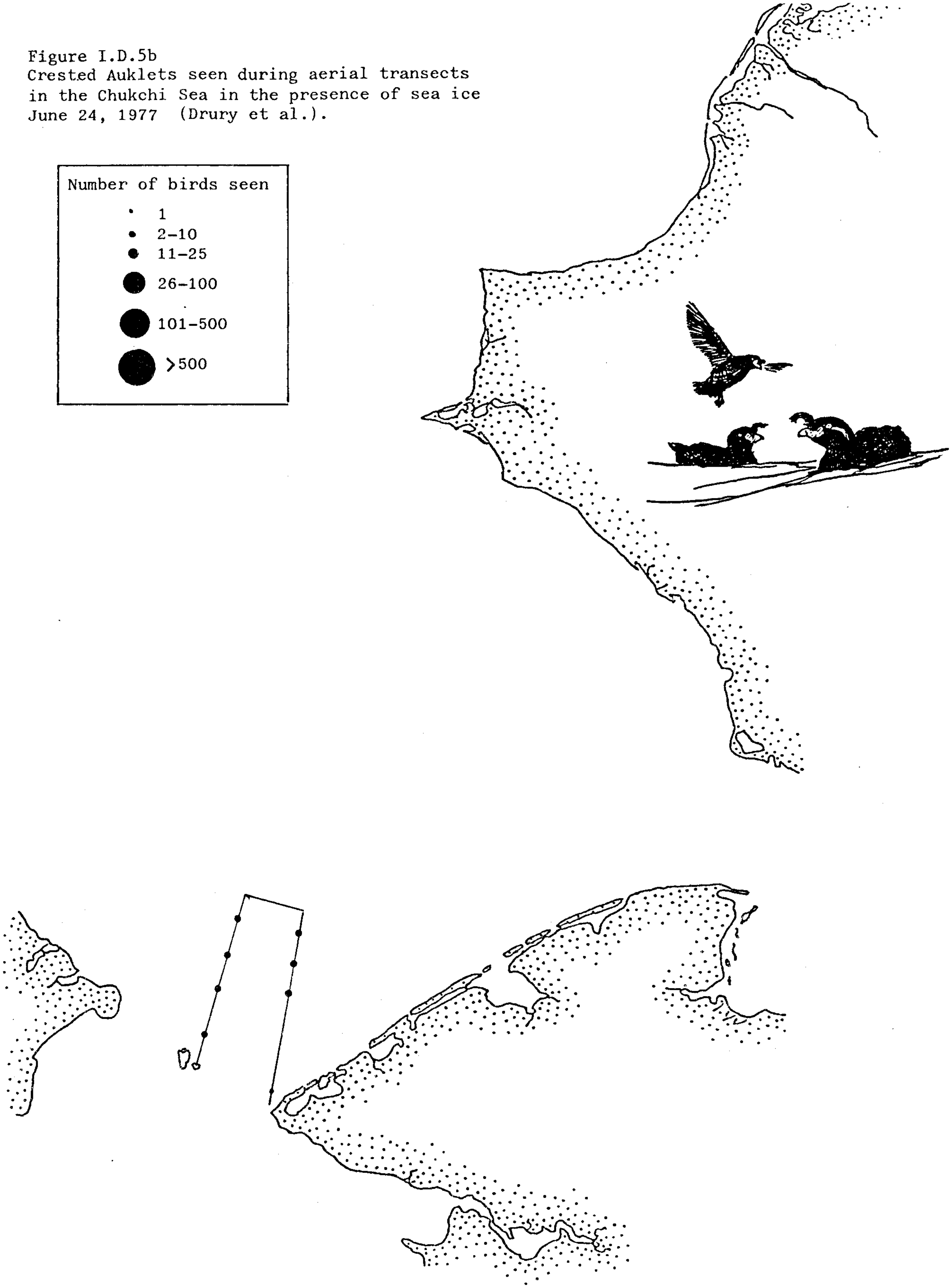
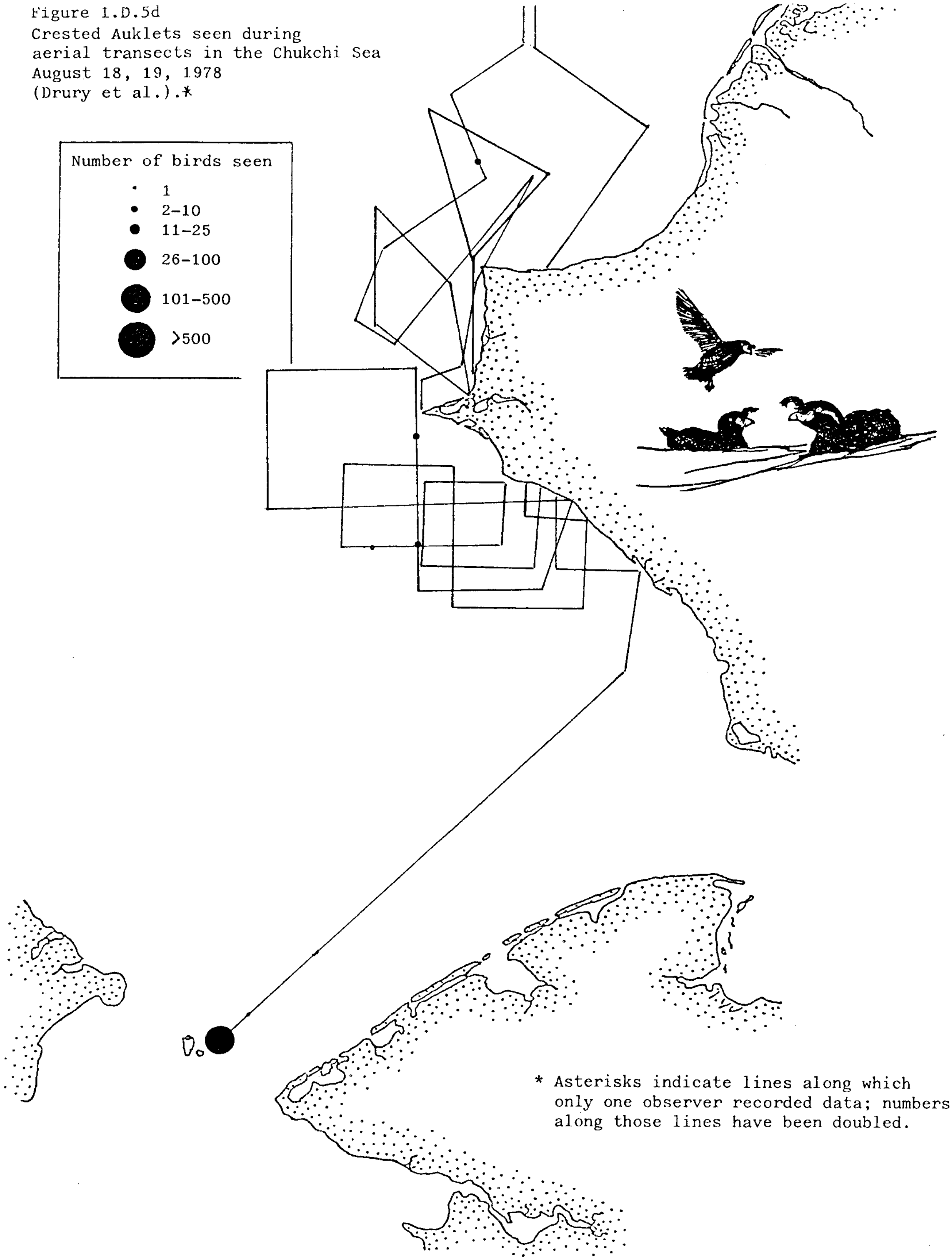


Figure I.D.5c
Crested Auklets seen during
aerial transects in the Chukchi Sea
July 7, 1978 (Drury et al.).

Figure I.D.5d
Crested Auklets seen during
aerial transects in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

igure I.D.5e Distribution and abundance of Crested Auklets in the Chukchi Sea in August 1976: no Crested Auklets were identified in June 1976. Aerial surveys, USFWS: Figure 60, page 176, in Harrison 1977.

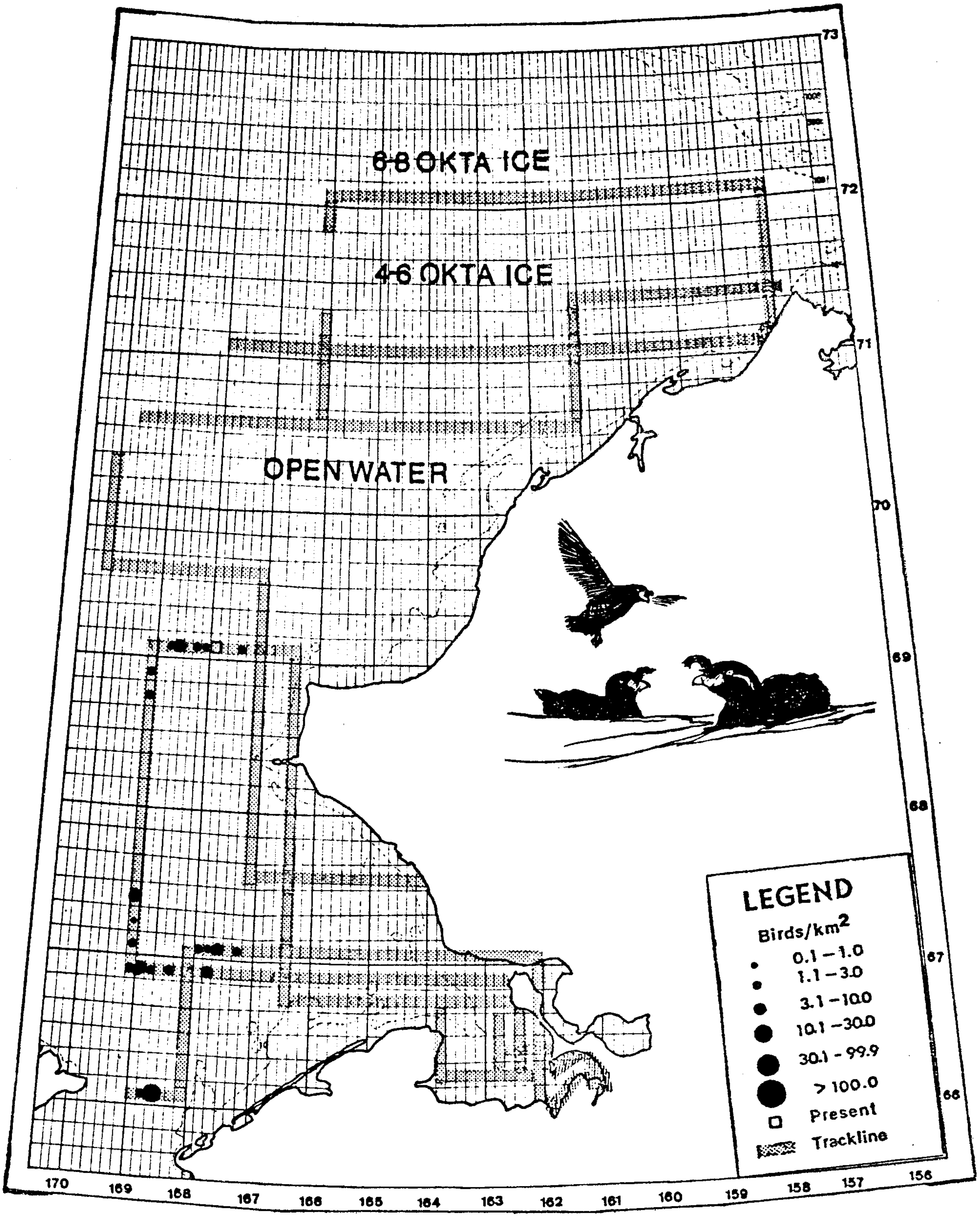


Figure I.D.5f Distribution and abundance of Crested Auklets in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 61, page 177, in Harrison 1977.

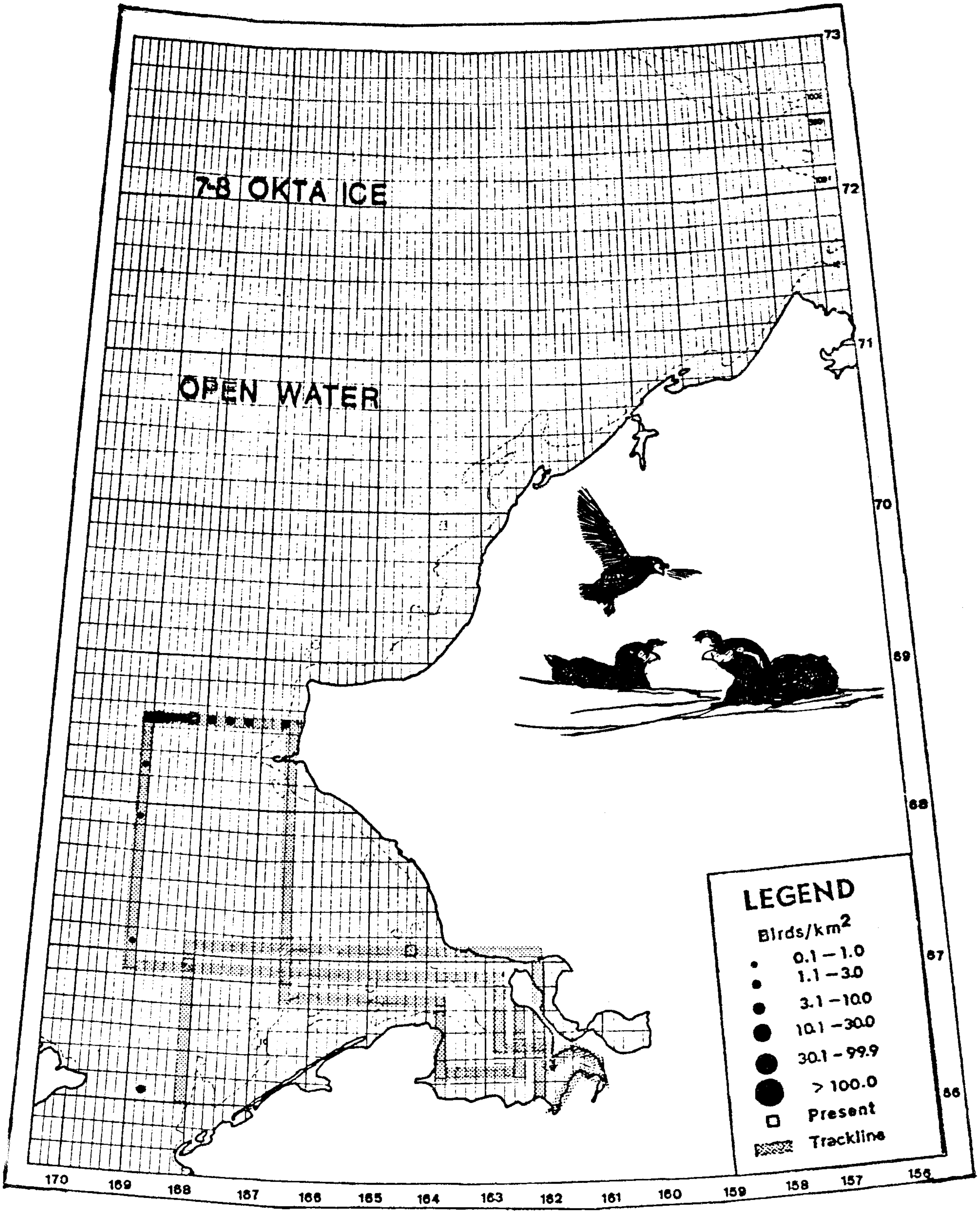


Figure I.D.6a
Parakeet Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

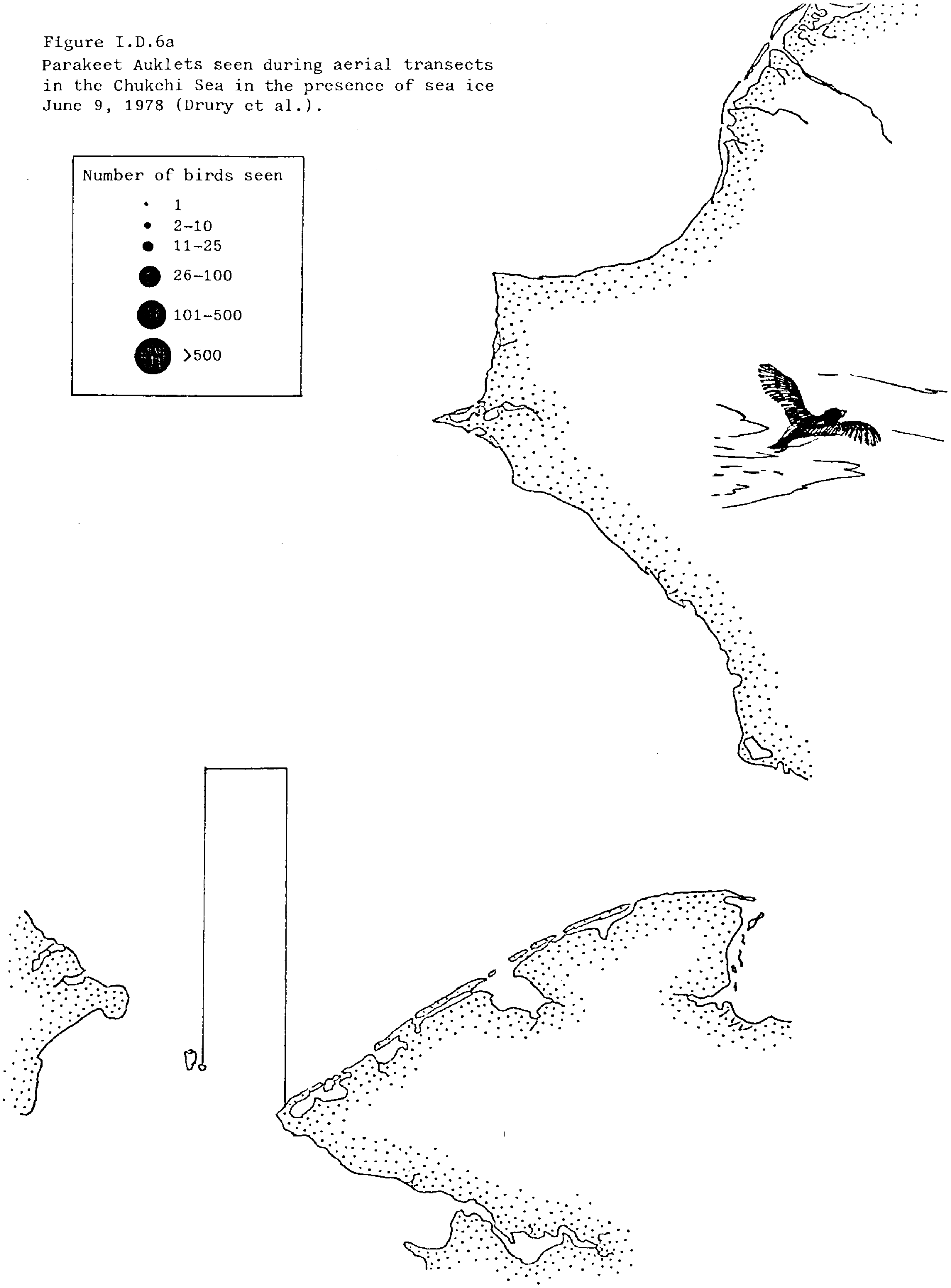
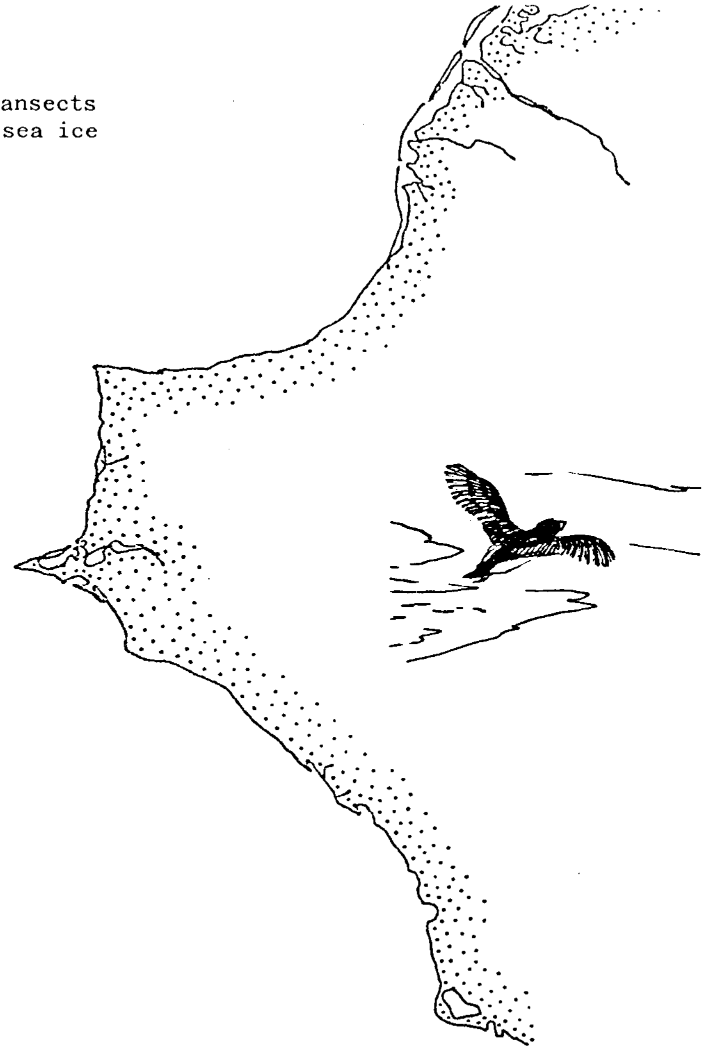


Figure I.D.6b
Parakeet Auklets seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

Number of birds seen	
·	1
•	2-10
●	11-25
●	26-100
●	101-500
●	>500



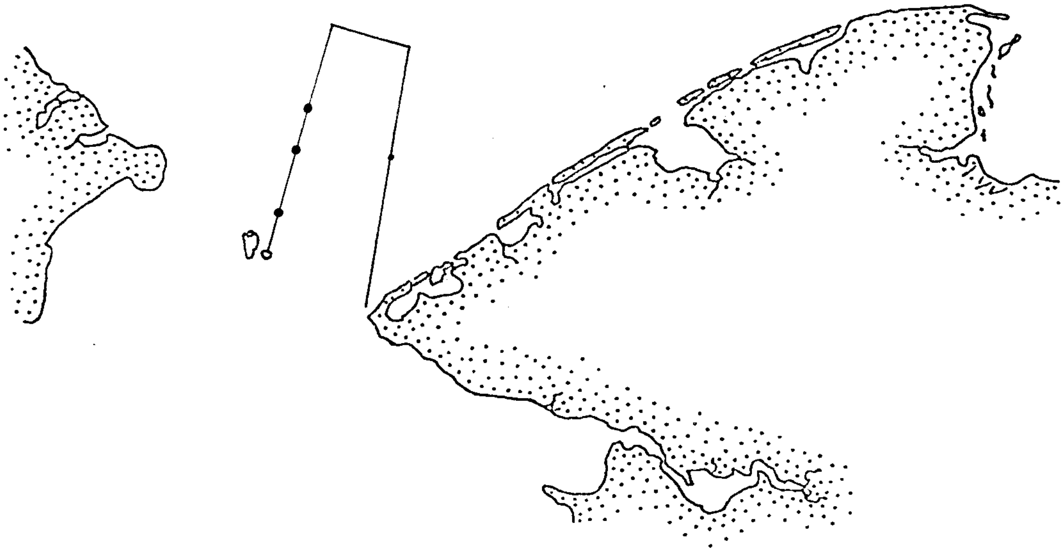


Figure I.D.6c
Parakeet Auklets seen during aerial transects in the Chukchi Sea July 7, 1978 (Drury et al.).

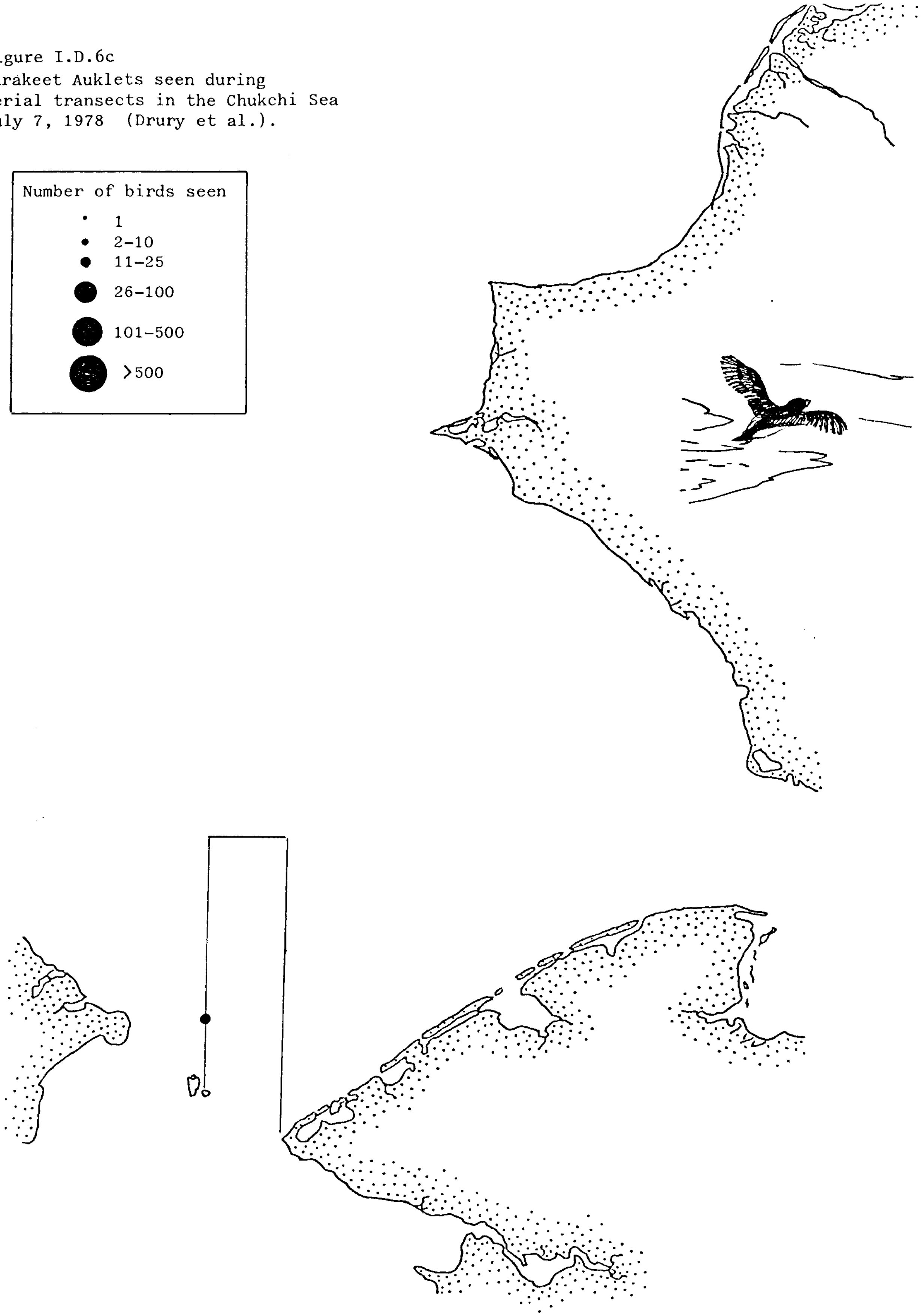
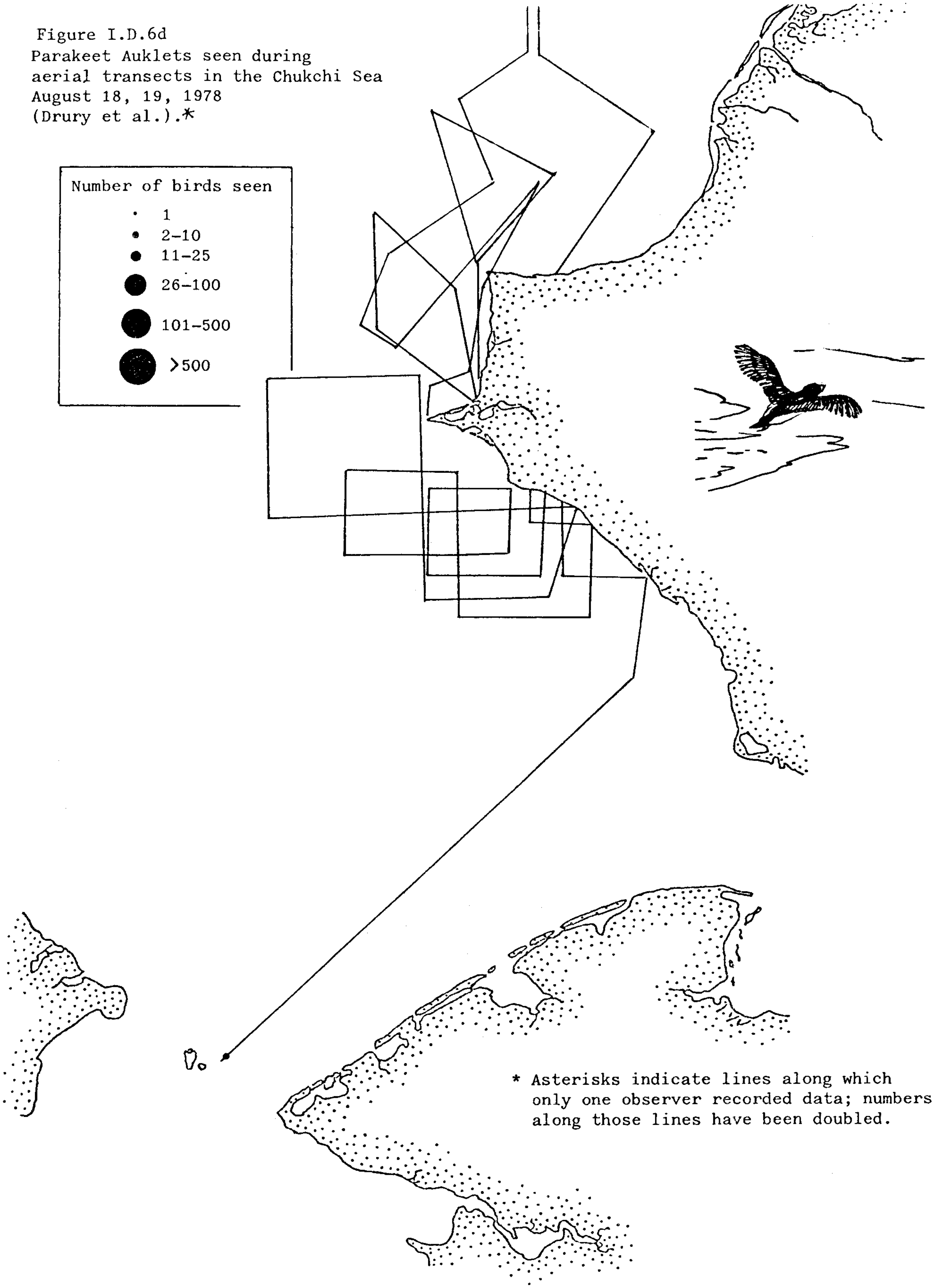


Figure I.D.6d
Parakeet Auklets seen during
aerial transects in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.6e Distribution and abundance of Parakeet Auklets in the Chukchi Sea in August 1976: no Parakeet Auklets were identified in June 1976. Aerial surveys, USFWS: Figure 58, page 174, in Harrison 1977.

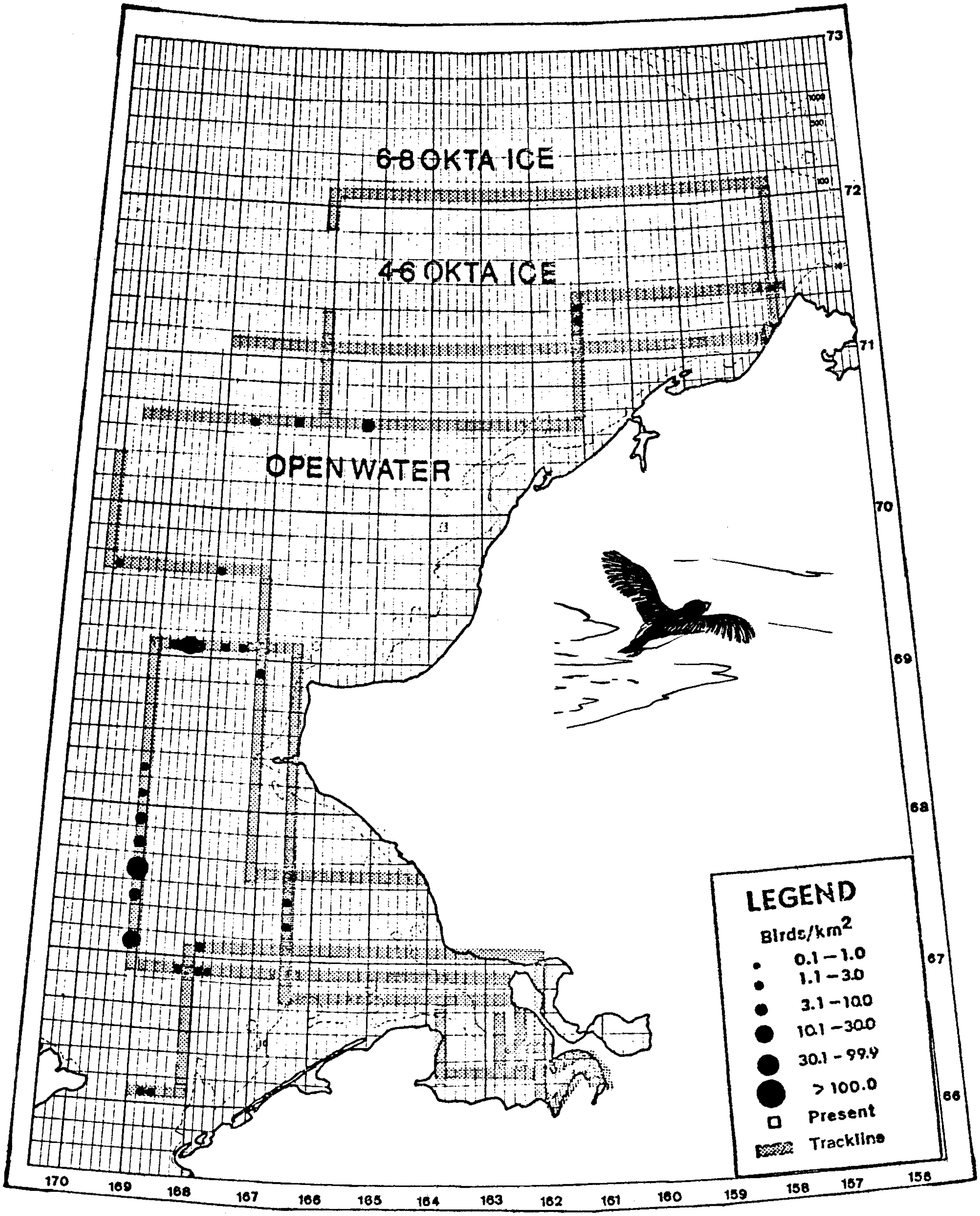


Figure I.D.6f Distribution and abundance of Parakeet Auklets in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 59, page 175, in Harrison 1977.

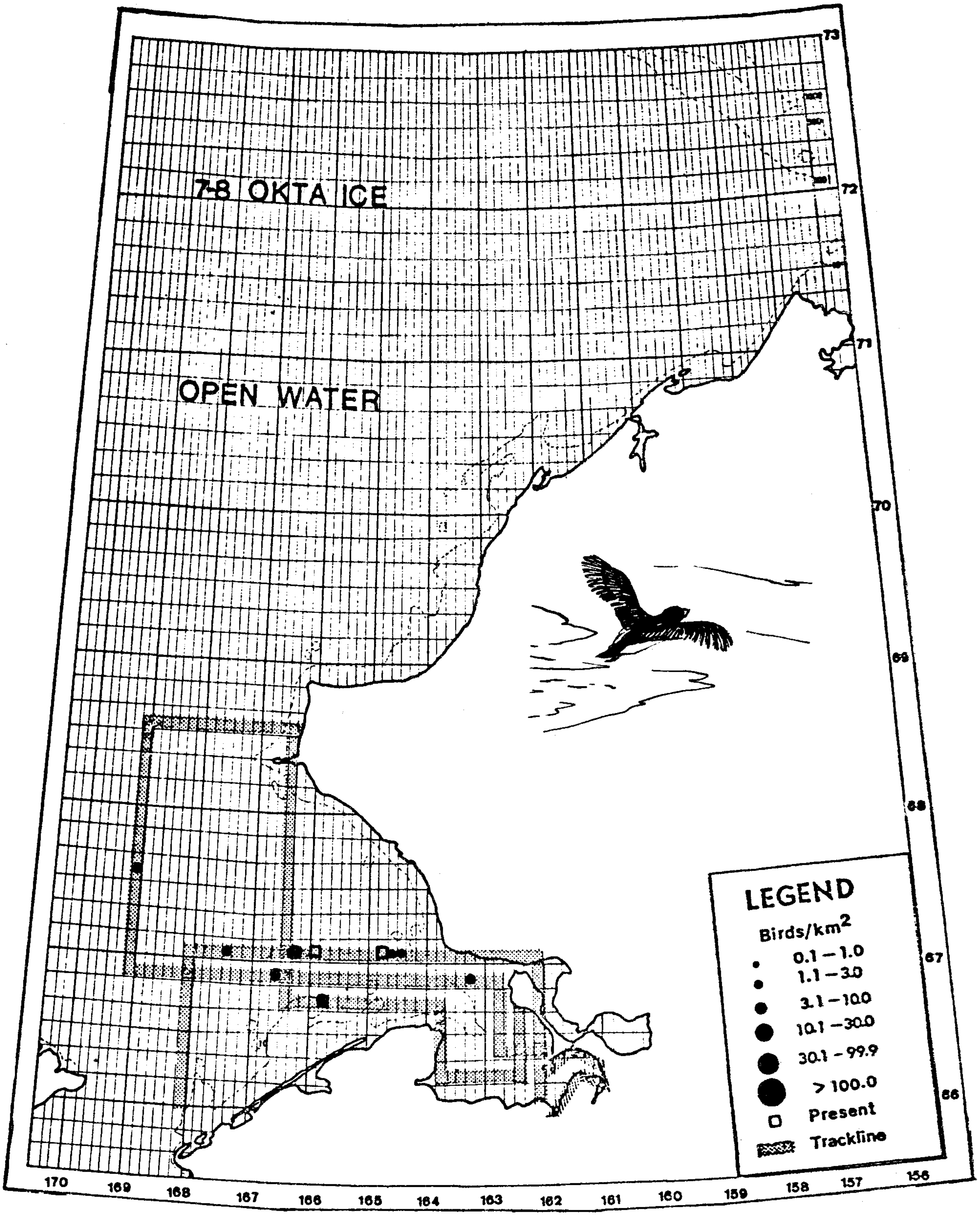


Figure I.D.7a
Horned Puffins seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

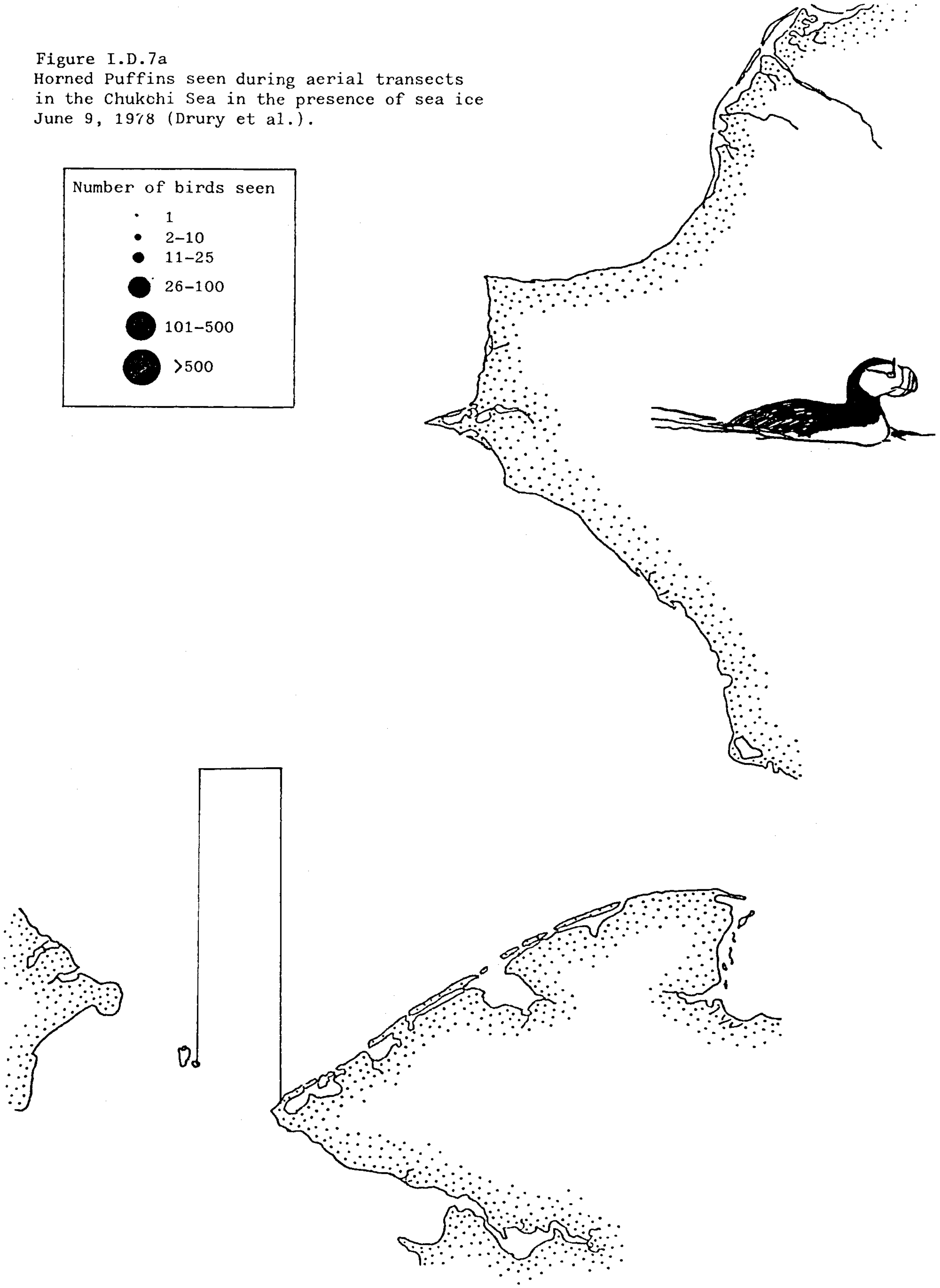
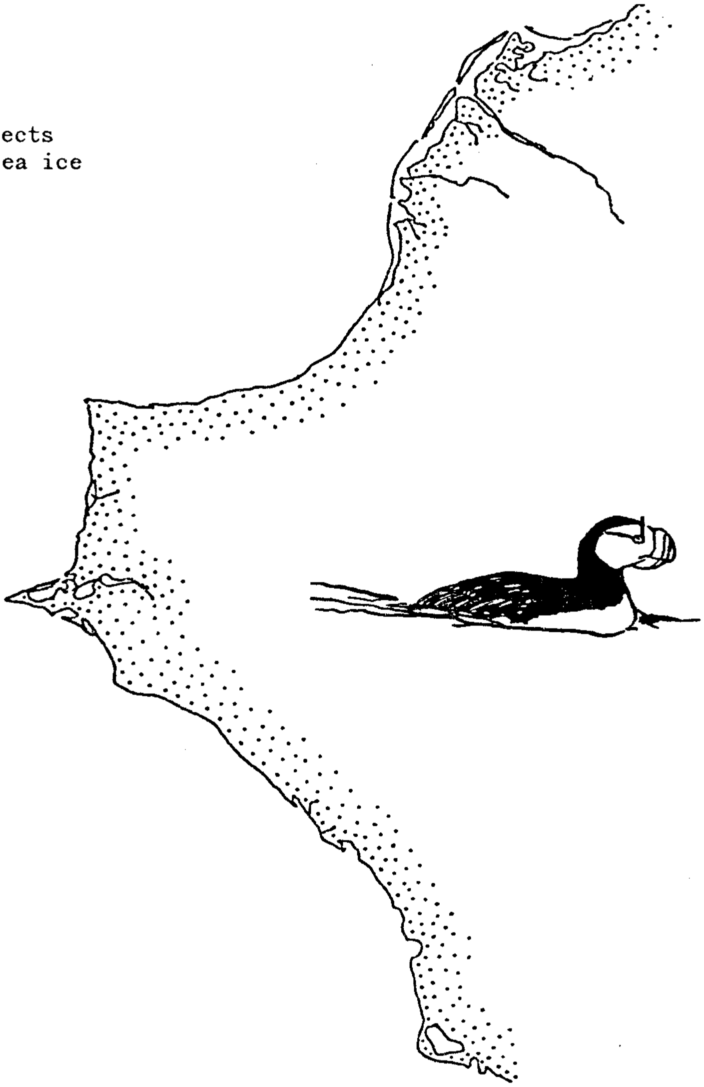


Figure I.D.7b
Horned Puffins seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

Number of birds seen

•	1
•	2-10
●	11-25
●	26-100
●	101-500
●	>500



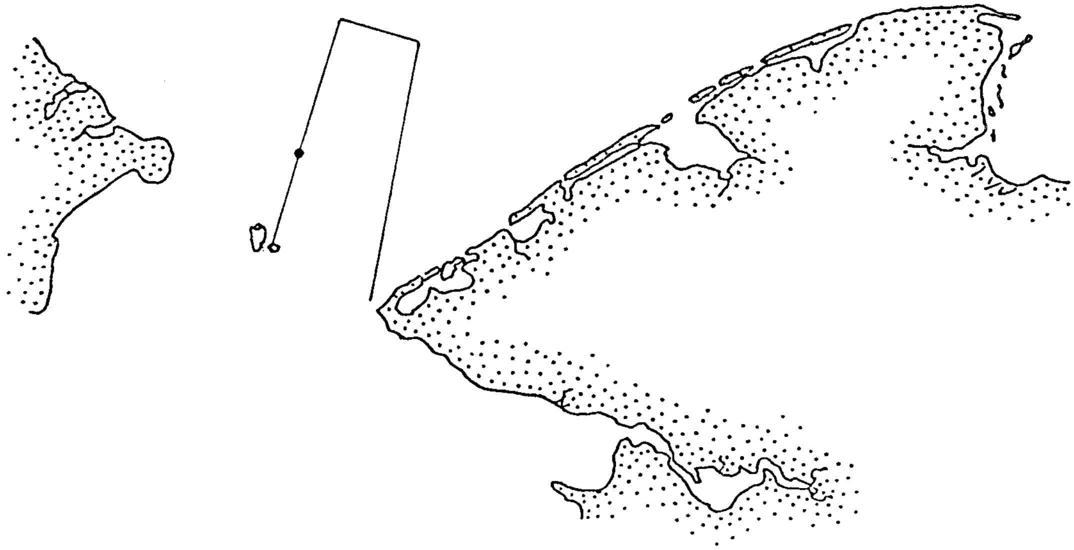


Figure I.D.7c
Horned Puffins seen during
aerial transects in the Chukchi Sea
July 7, 1978 (Drury et al.).

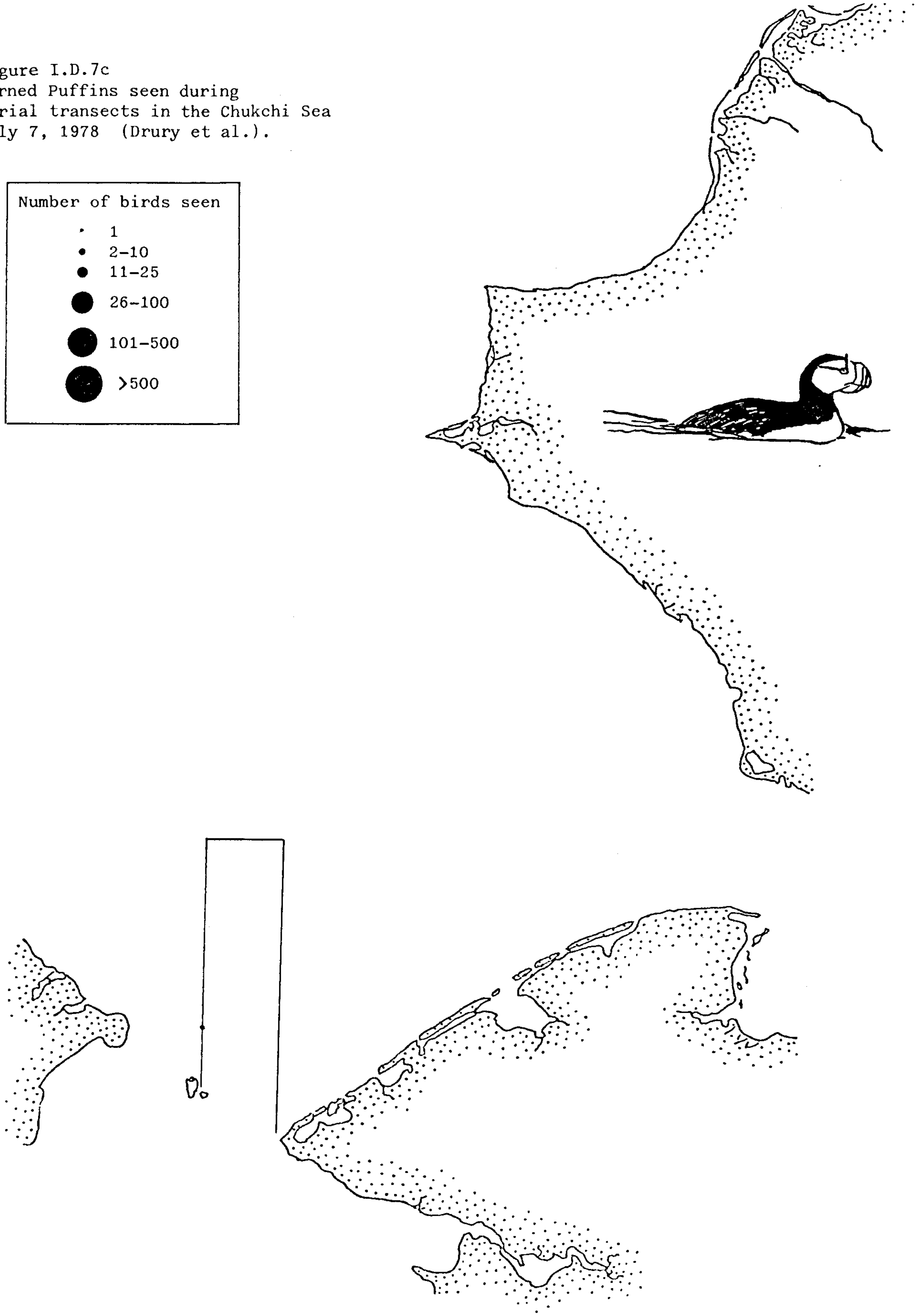
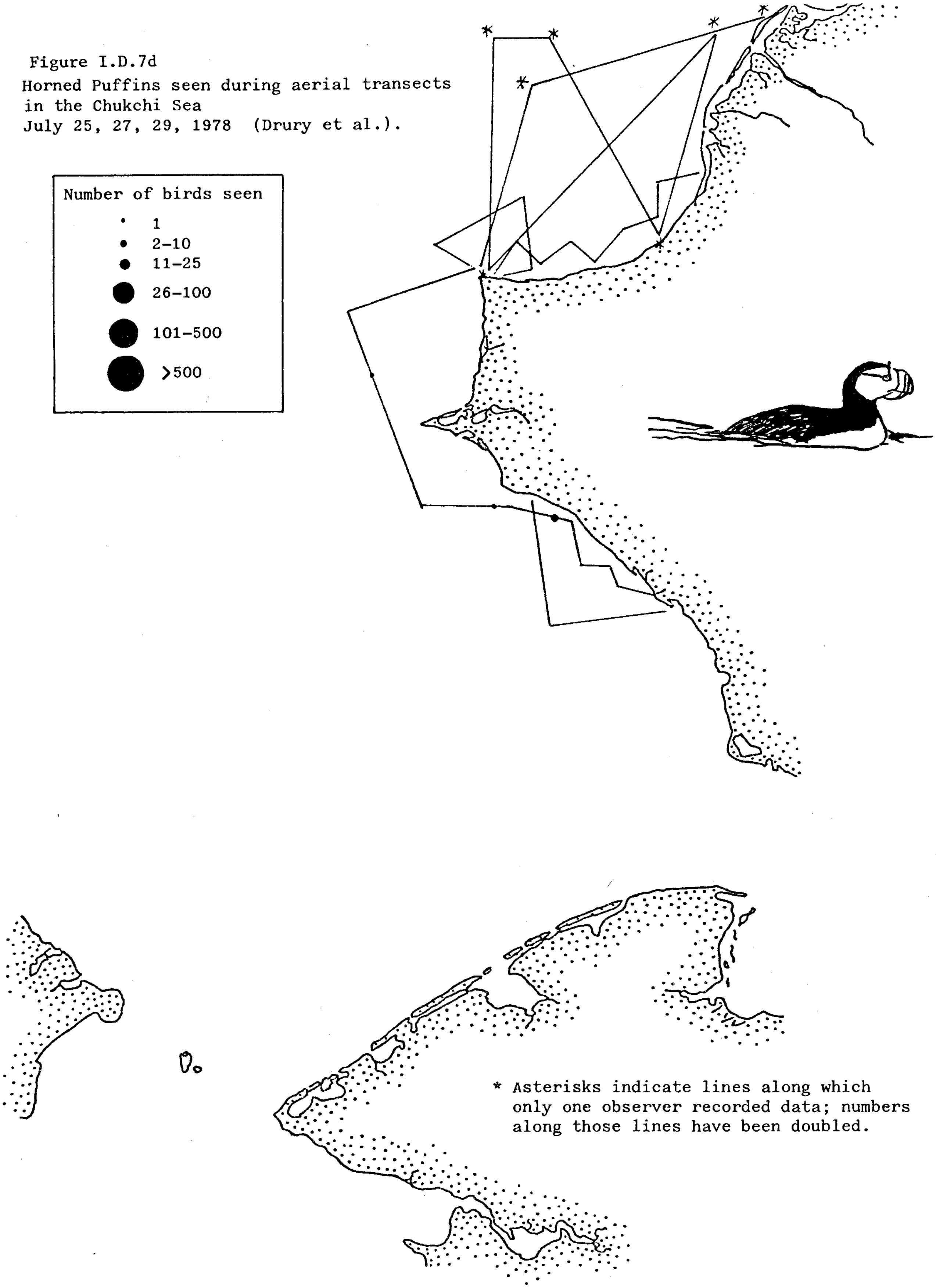
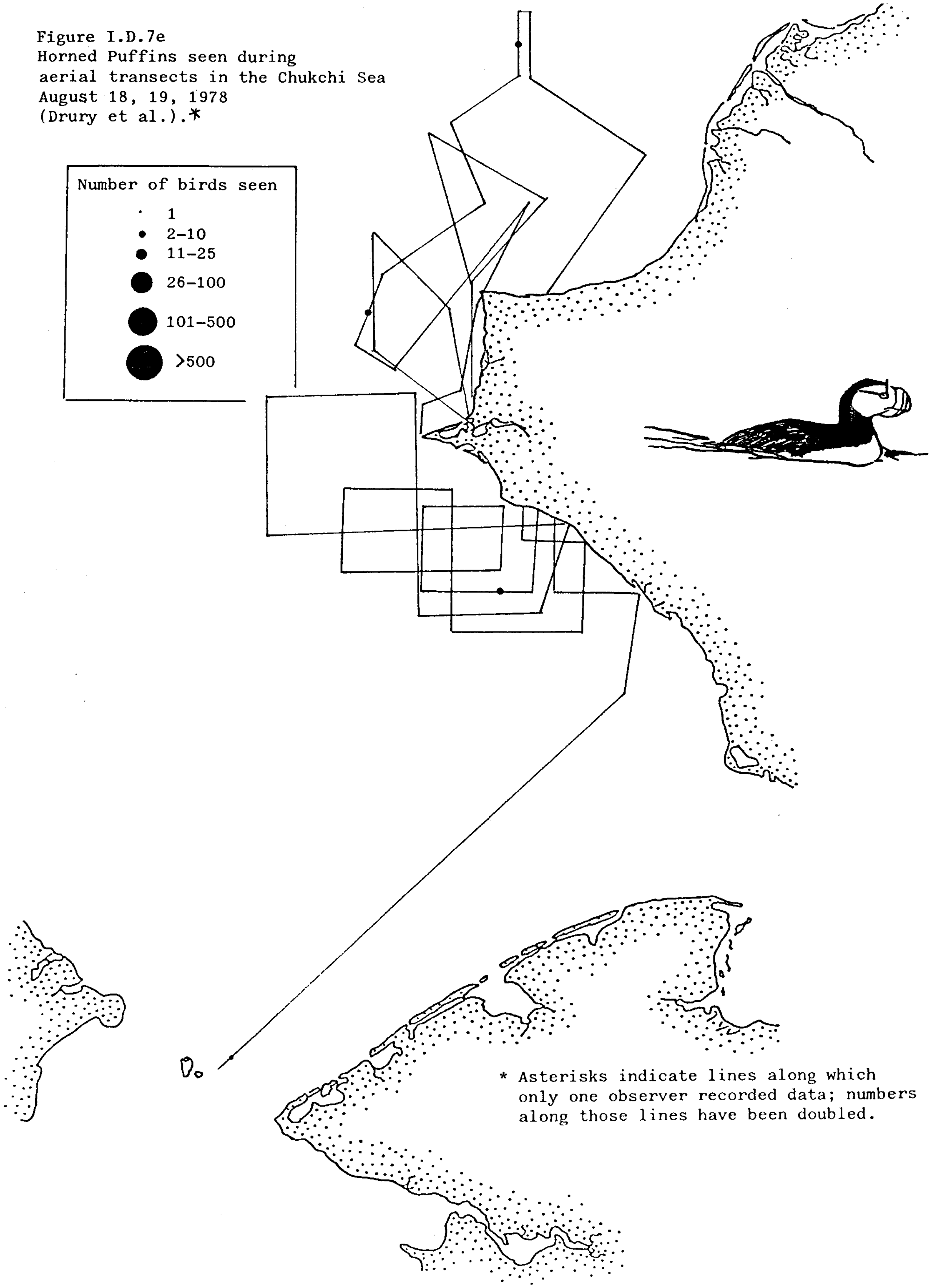


Figure I.D.7d
Horned Puffins seen during aerial transects in the Chukchi Sea
July 25, 27, 29, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.7e
Horned Puffins seen during
aerial transects in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.7f Distribution and abundance of Horned Puffins in the Chukchi Sea in August 1976: no Horned Puffins were observed in June 1976. Aerial surveys, USFWS: Figure 64, page 180, in Harrison 1977.

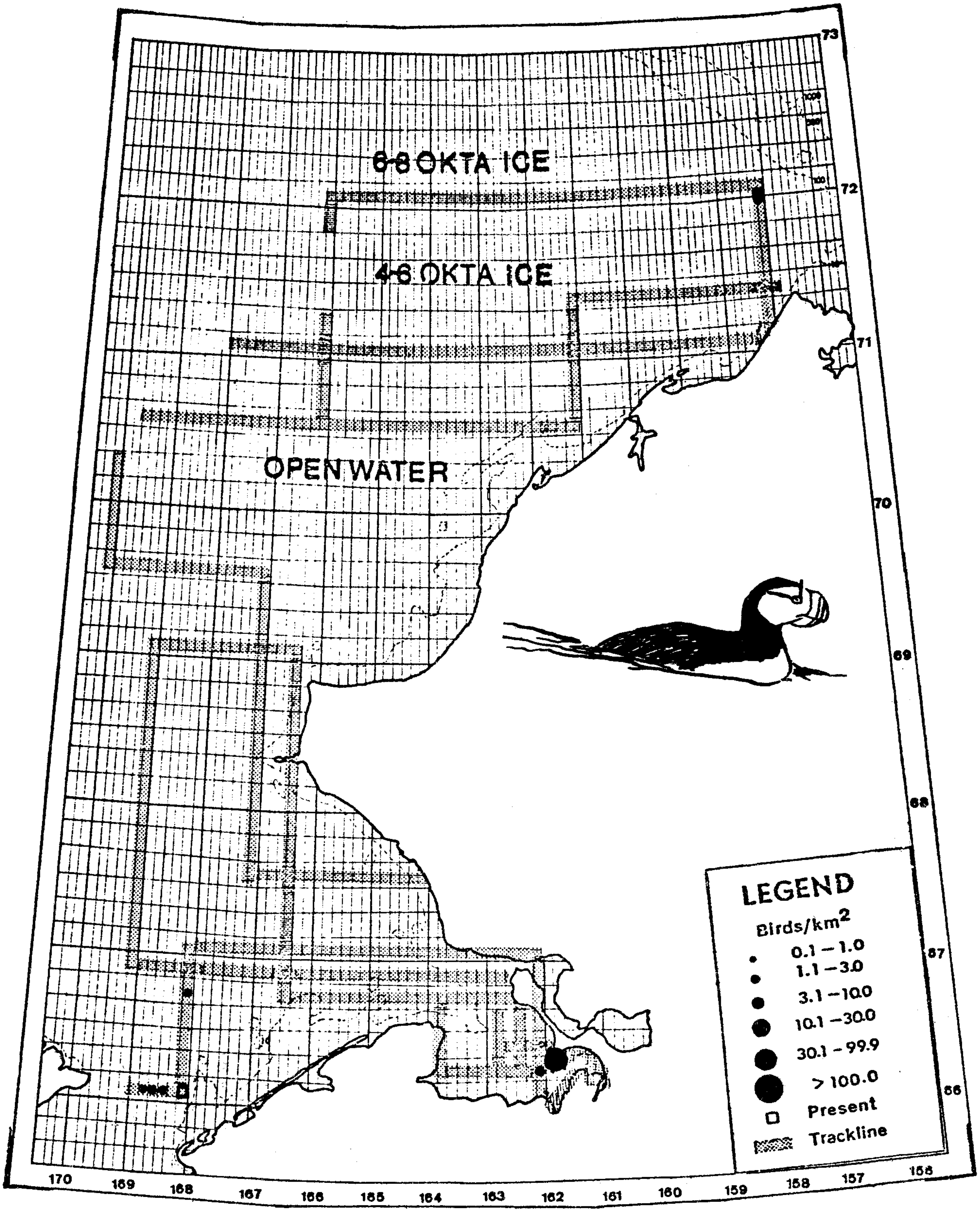


Figure I.D.7g Distribution and abundance of Horned Puffins in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 65, page 181, in Harrison 1977.

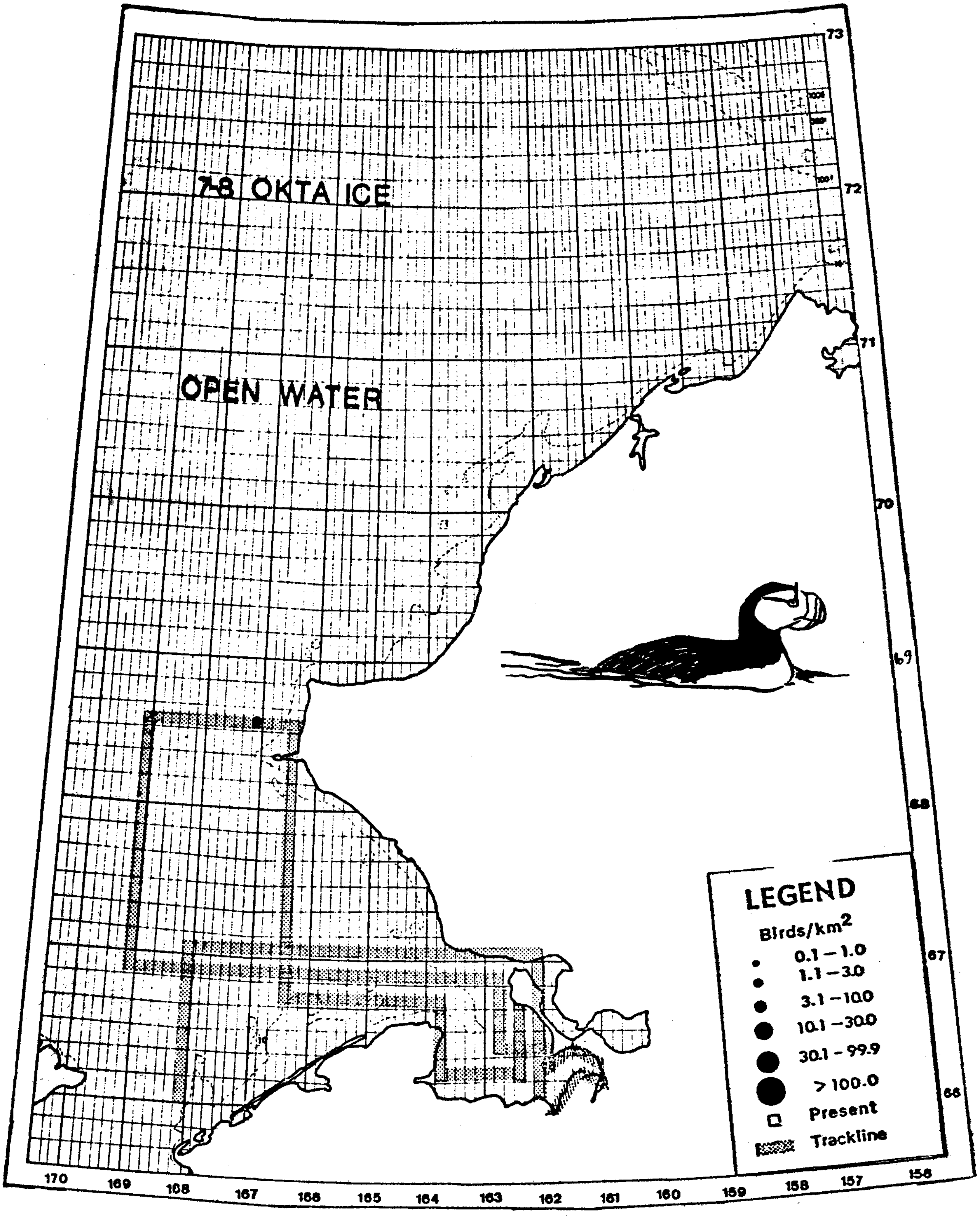


Figure I.D.8a
Tufted Puffins seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

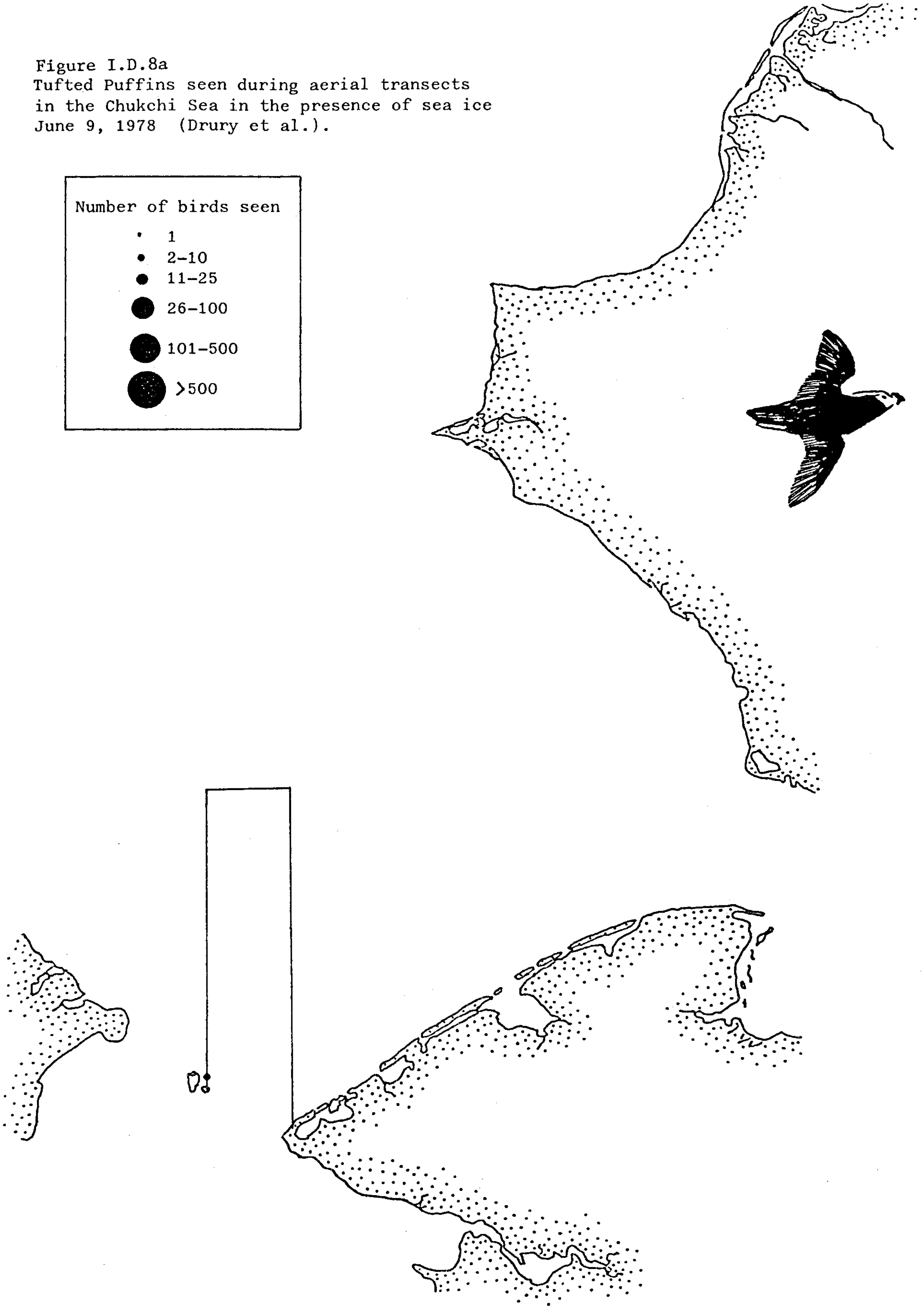
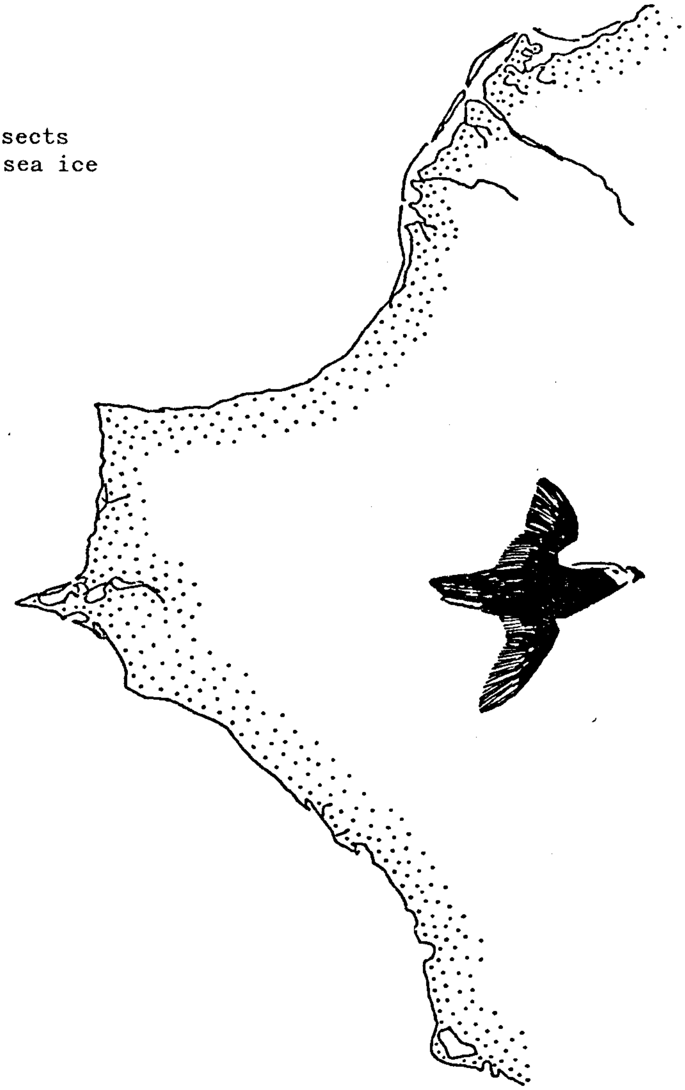


Figure I.D.8b
Tufted Puffins seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

Number of birds seen

•	1
•	2-10
●	11-25
●	26-100
●	101-500
●	>500



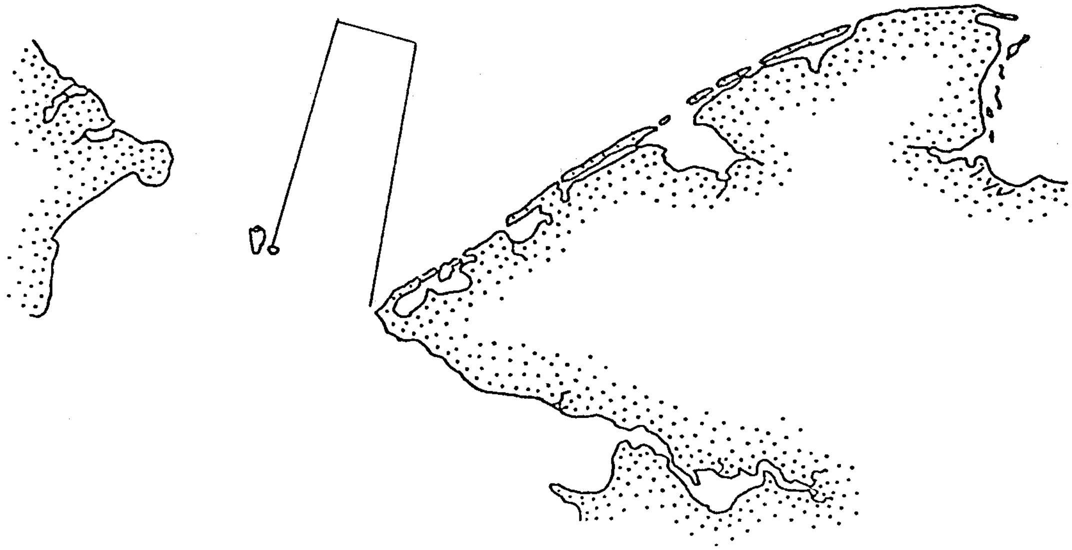


Figure I.D.8c
Tufted Puffins seen during aerial transects
in the Chukchi Sea
July 7, 1978 (Drury et al.).

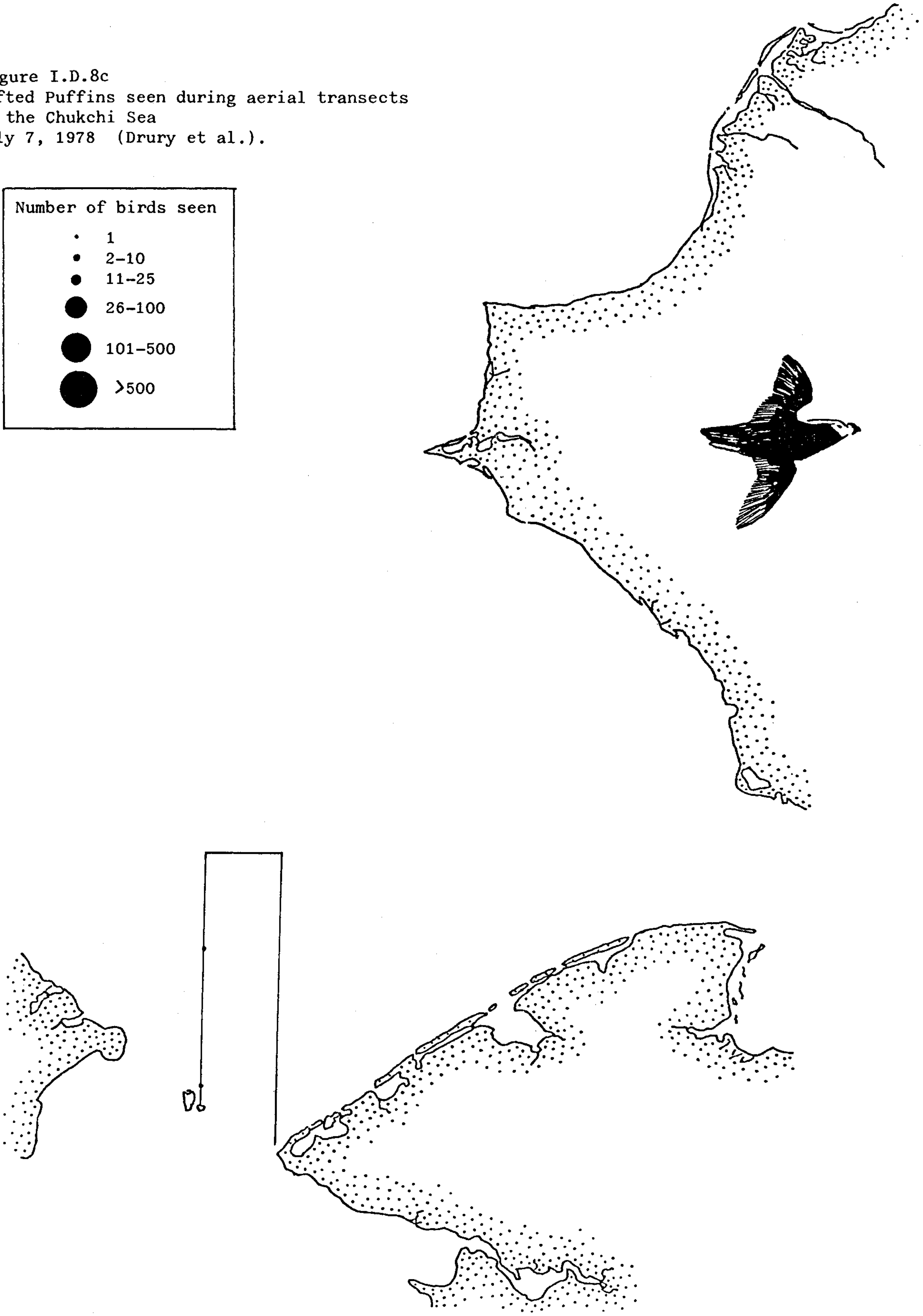
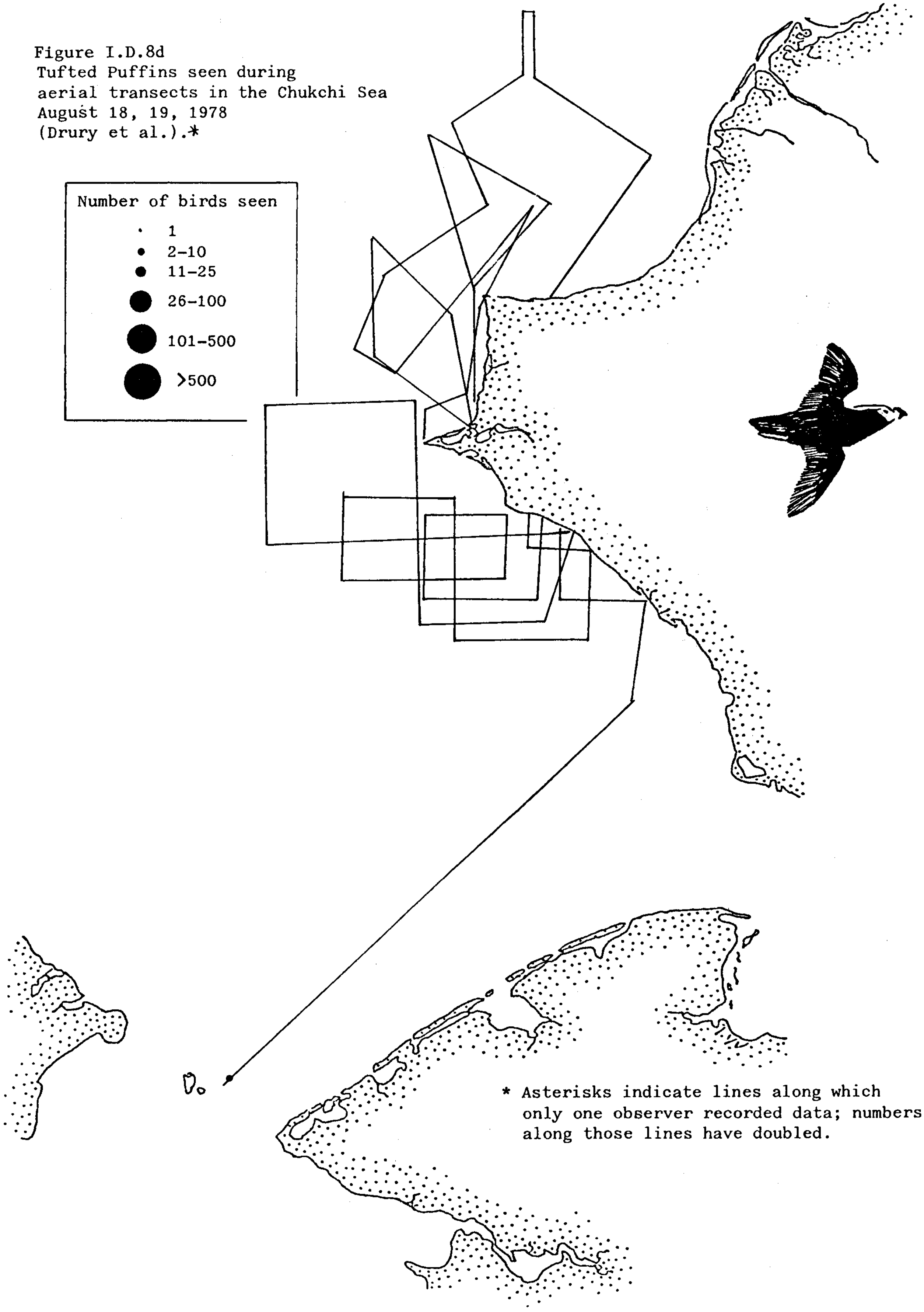


Figure I.D.8d
Tufted Puffins seen during
aerial transects in the Chukchi Sea
August 18, 19, 1978
(Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have doubled.

Figure I.D.8e Distribution and abundance of Tufted Puffins in the Chukchi Sea in August 1976: no Tufted Puffins were observed in June or October 1976. Aerial surveys, USFWS: Figure 66, page 182, in Harrison 1977.

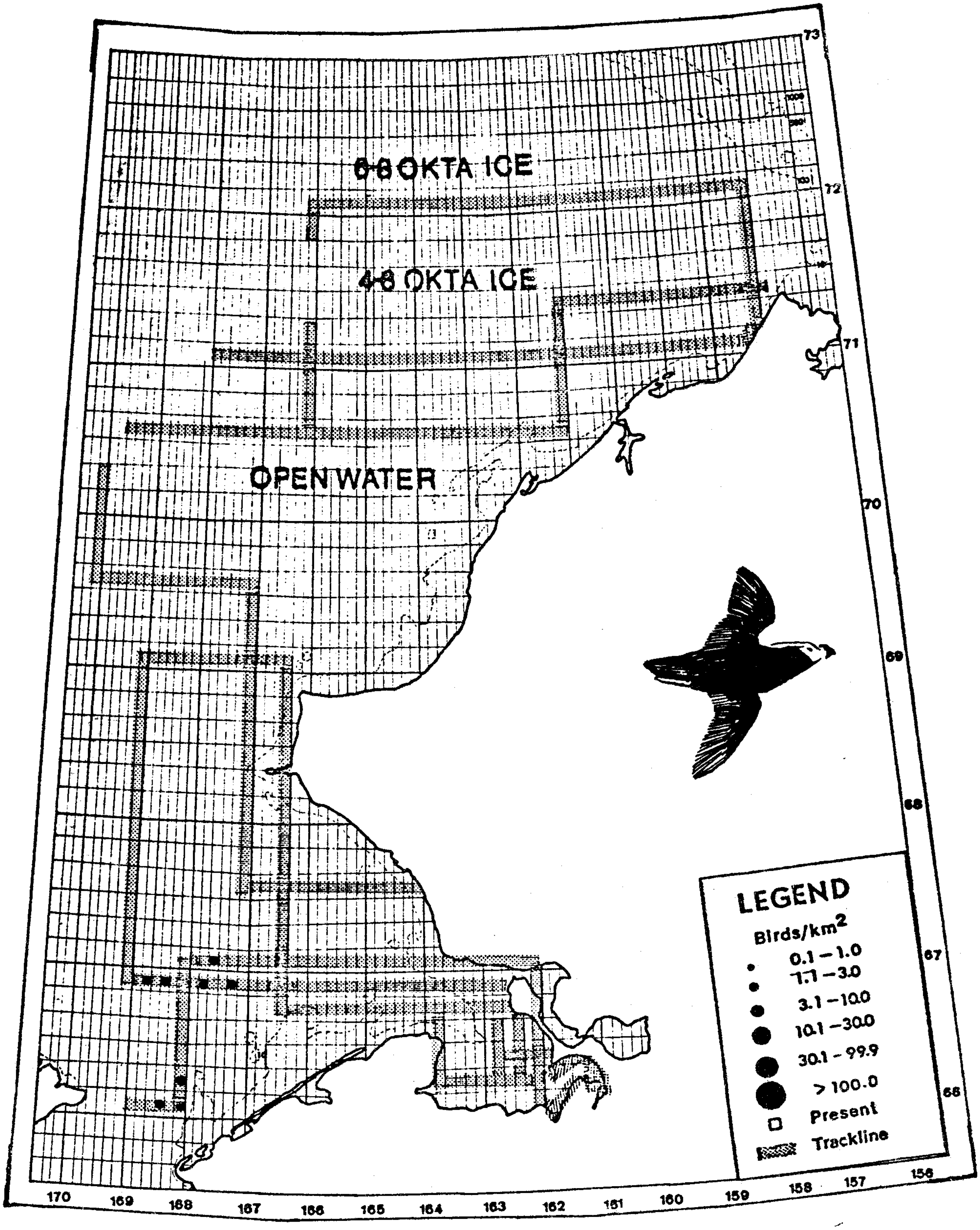
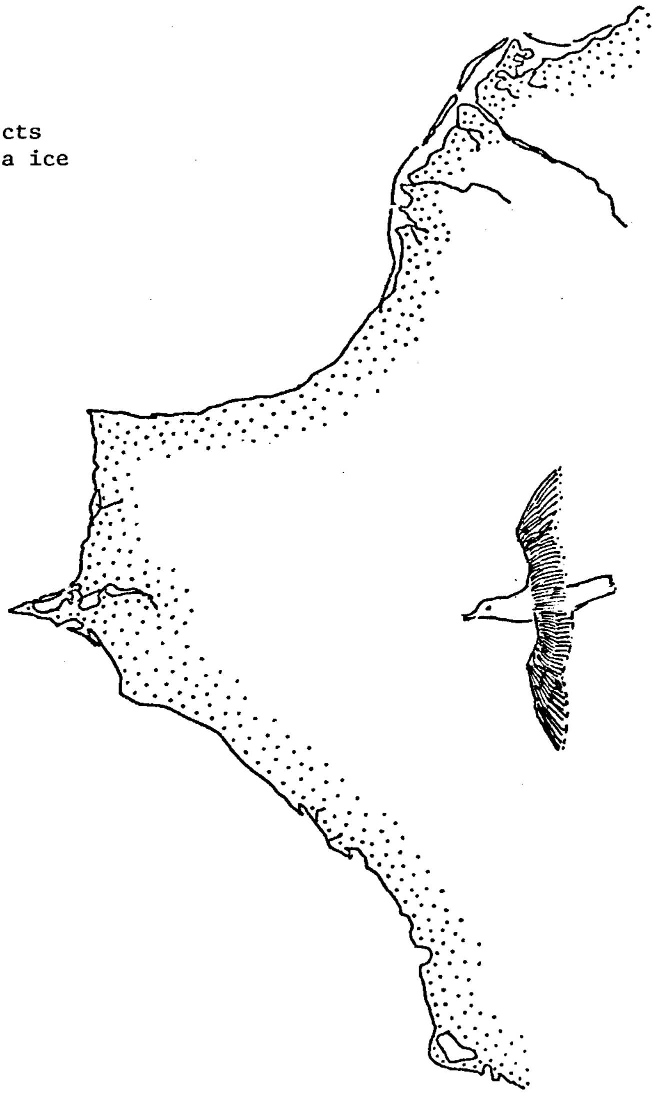


Figure I.D.9a

Glaucous Gulls seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

Number of birds seen

- • 1
- • 2-10
- ● 11-25
- ● 26-100
- ● 101-500
- ● >500



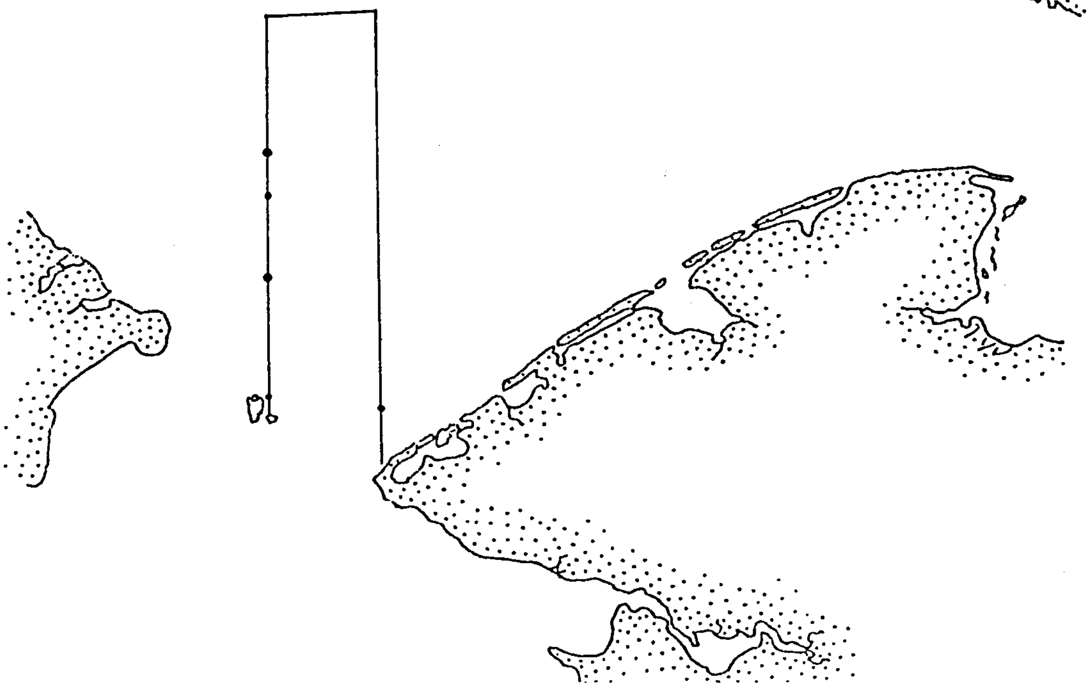


Figure I.D.9b
Glaucous Gulls seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

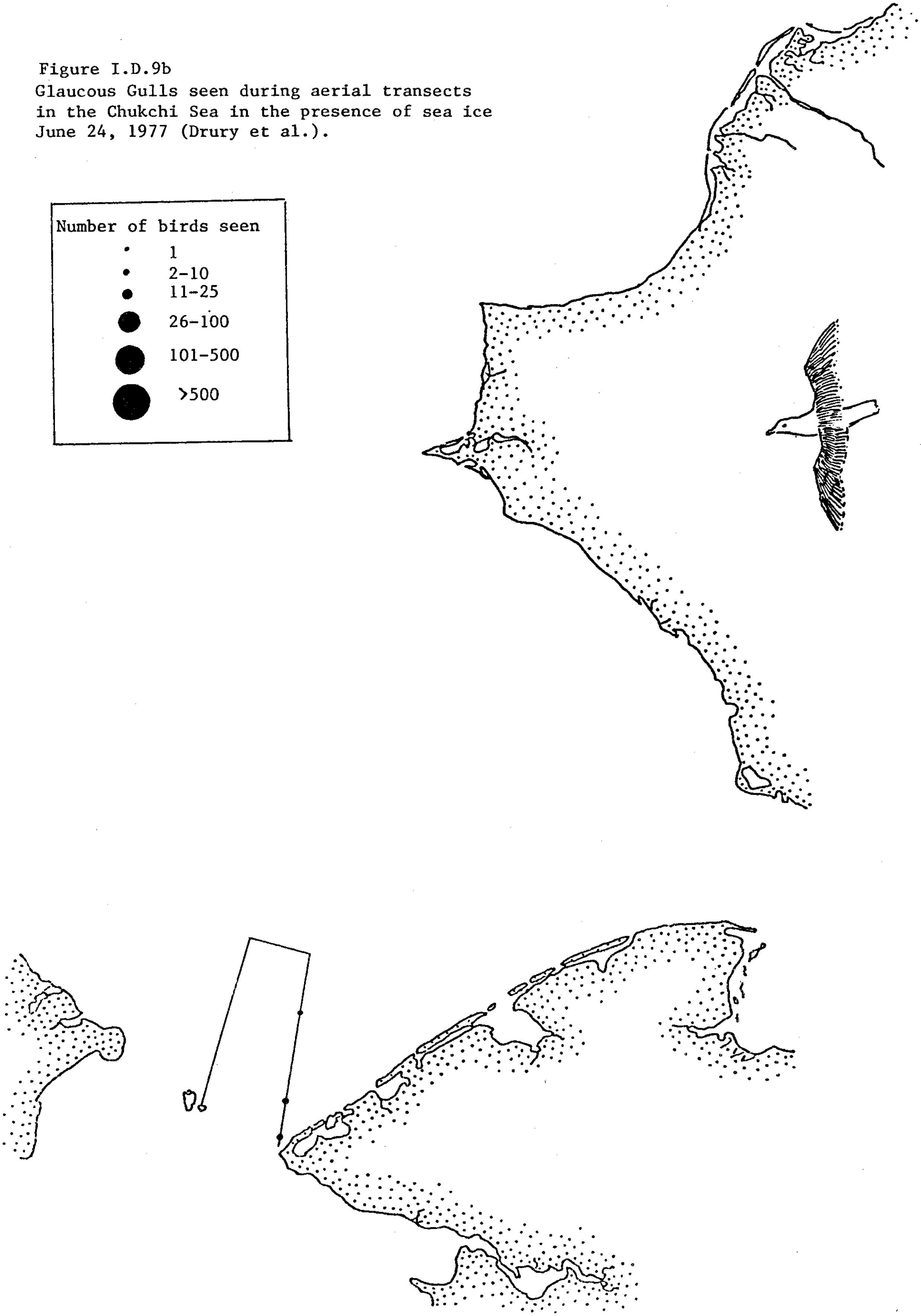


Figure I.D.9c Distribution and abundance of Glaucous Gulls in the Chukchi Sea in June 1976. Aerial surveys, USFWS: Figure 40, page 156, in Harrison 1977.

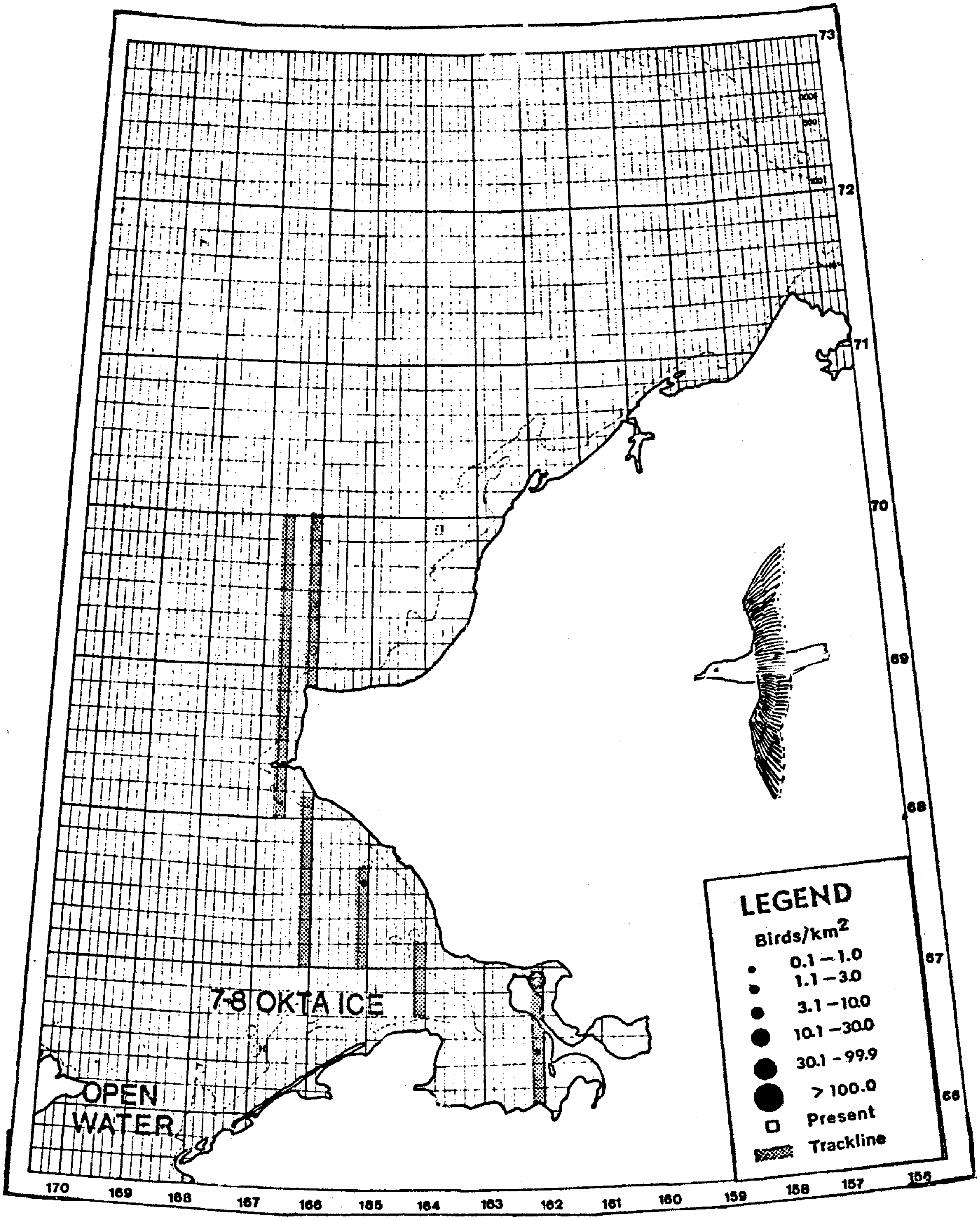


Figure I.D.9d
Glaucous Gulls seen during aerial transects
in the Chukchi Sea
July 7, 1978 (Drury et al.).

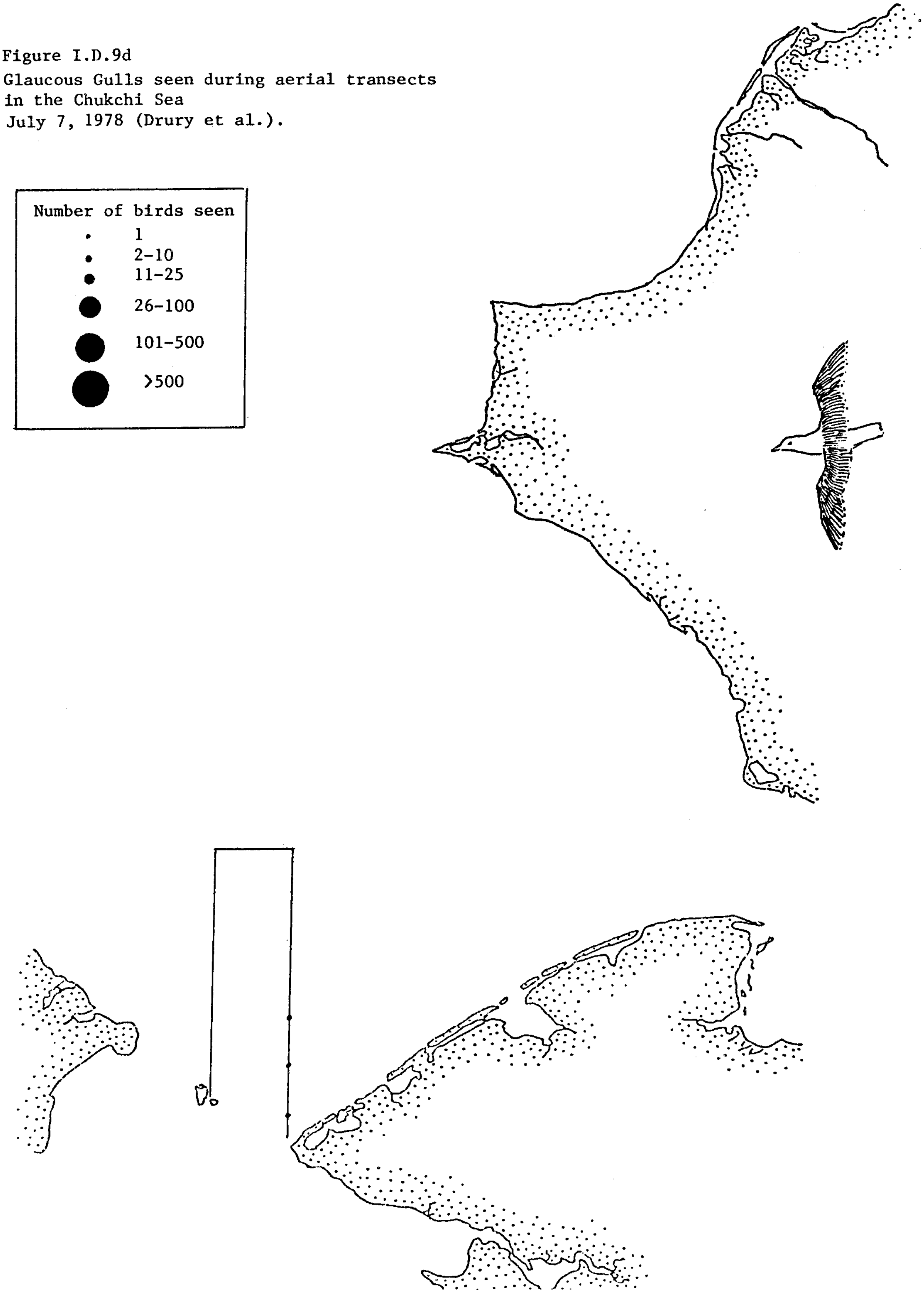
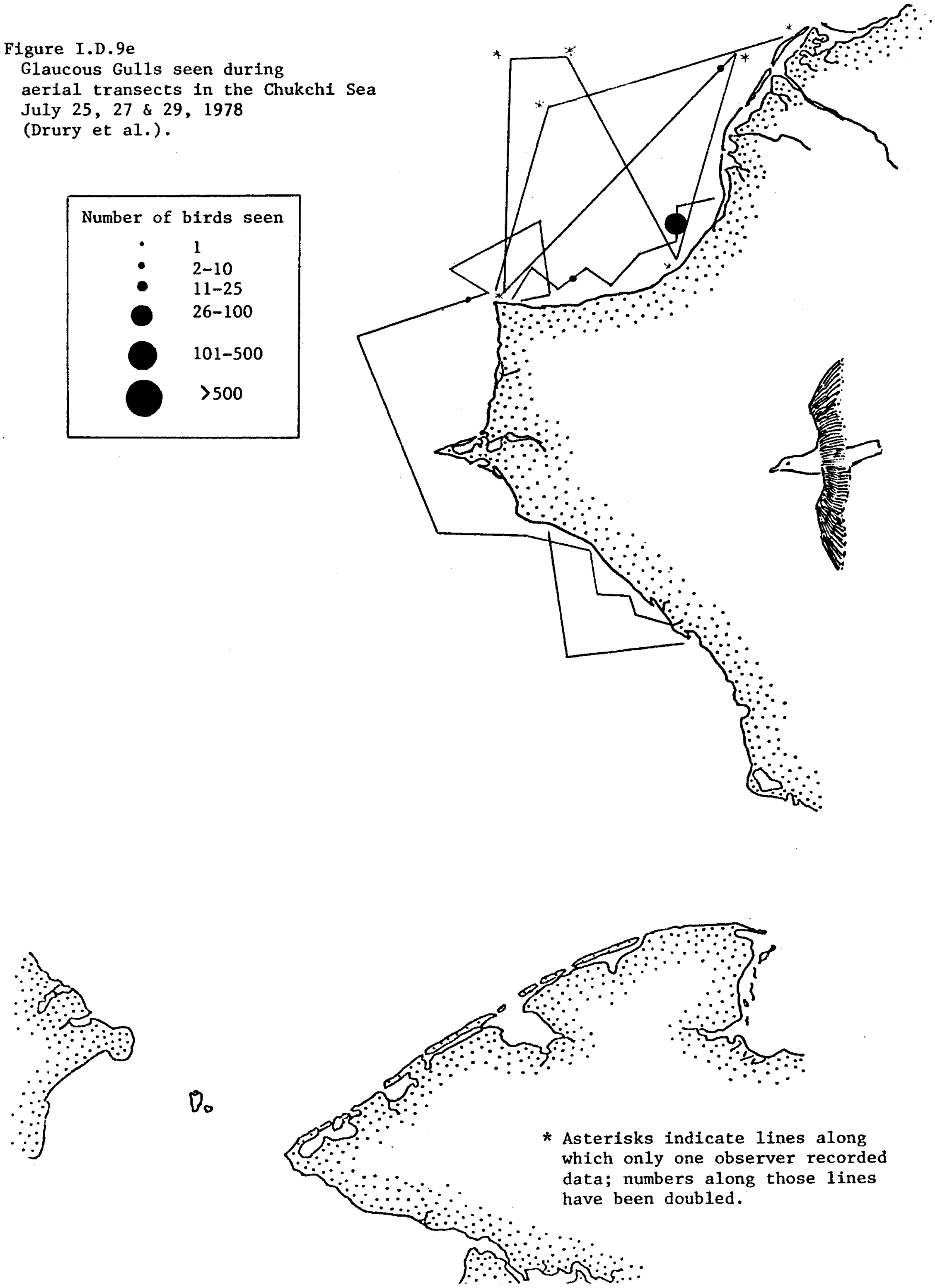
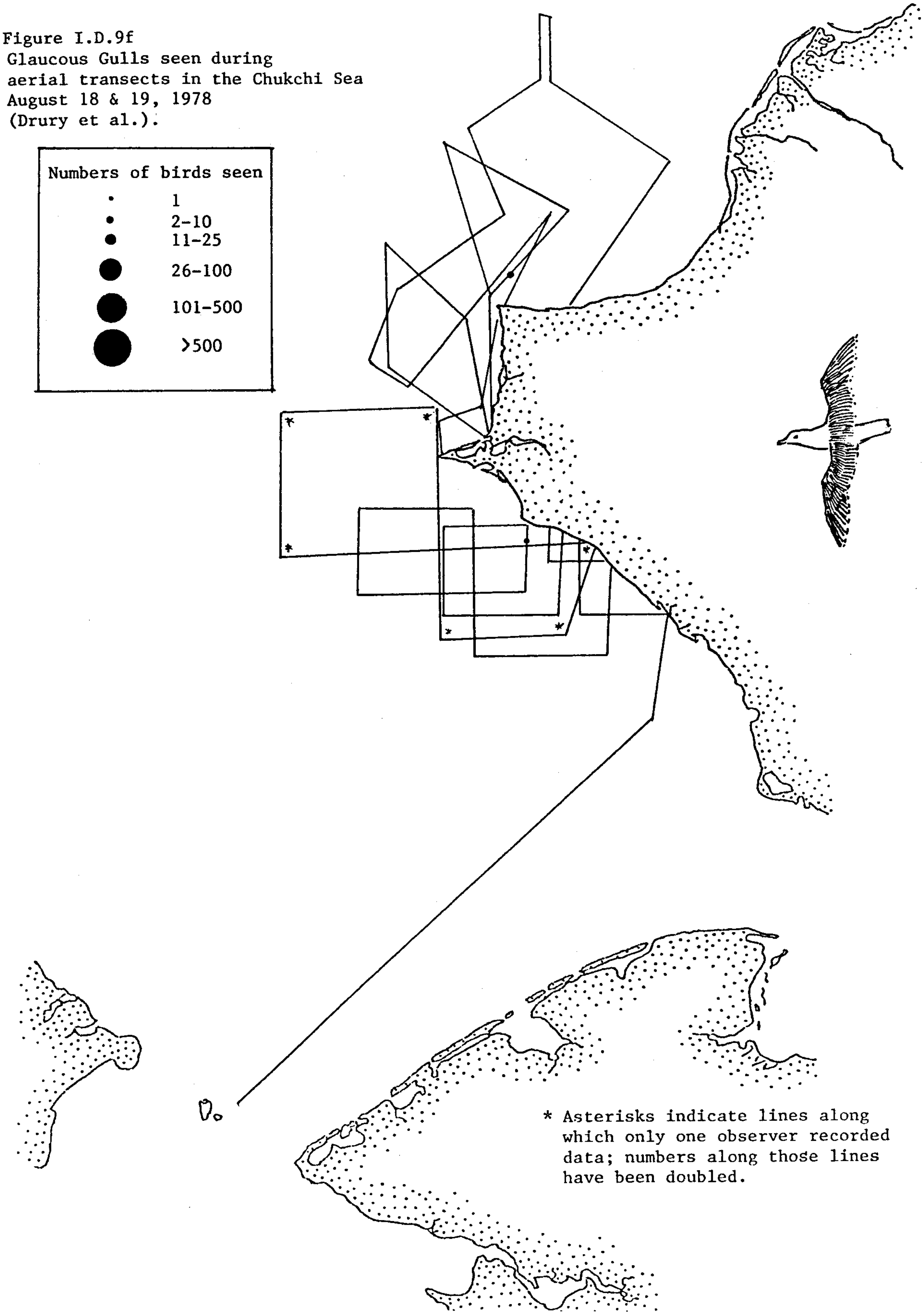


Figure I.D.9e
Glaucous Gulls seen during
aerial transects in the Chukchi Sea
July 25, 27 & 29, 1978
(Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.9f
Glaucous Gulls seen during
aerial transects in the Chukchi Sea
August 18 & 19, 1978
(Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.9g Distribution and abundance of Glaucous Gulls in the Chukchi Sea in August 1976. Aerial surveys, USFWS: Figure 41, page 157, in Harrison 1977.

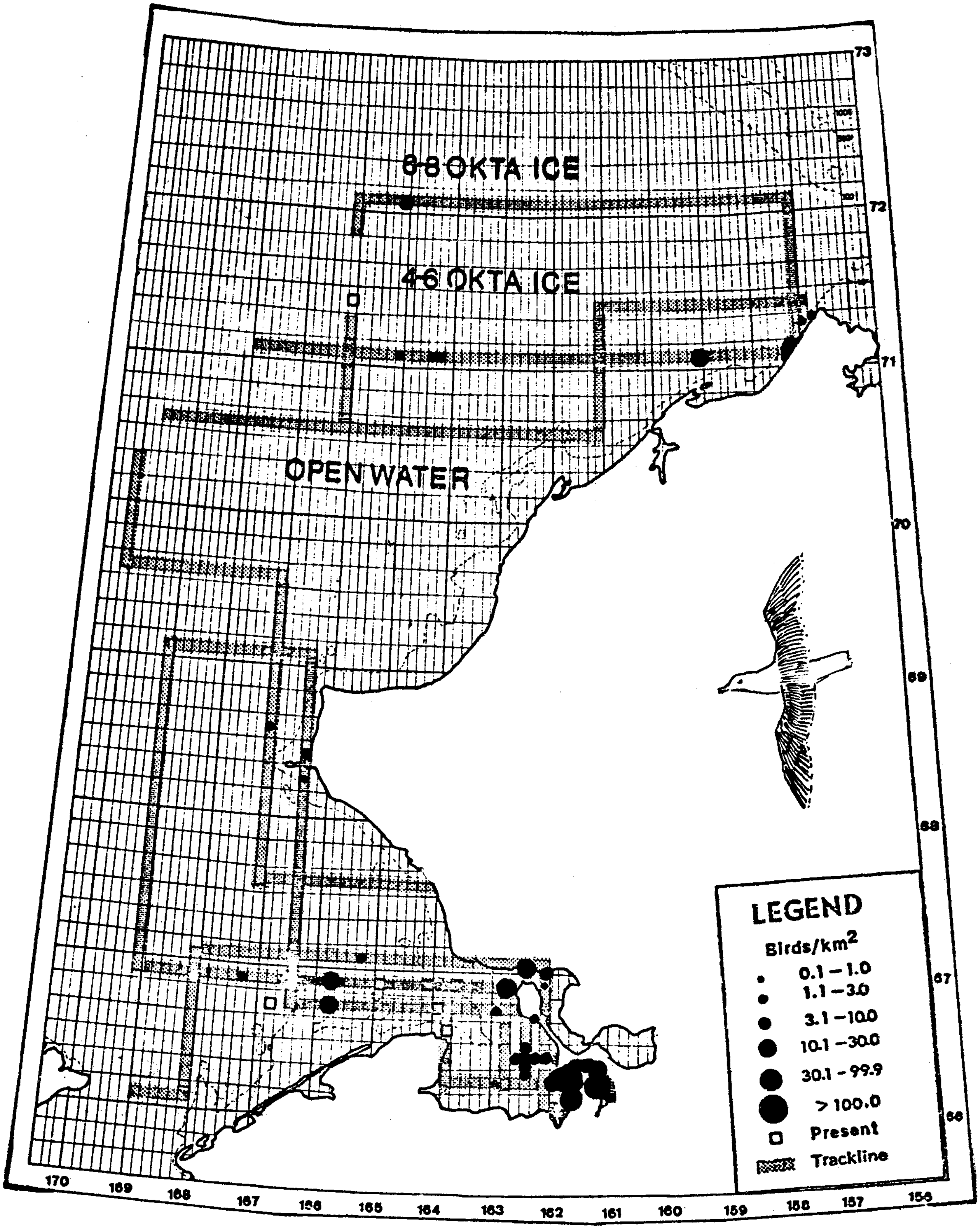


Figure I.D.9h Distribution and abundance of Glaucous Gulls in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 42, page 158, in Harrison 1977.

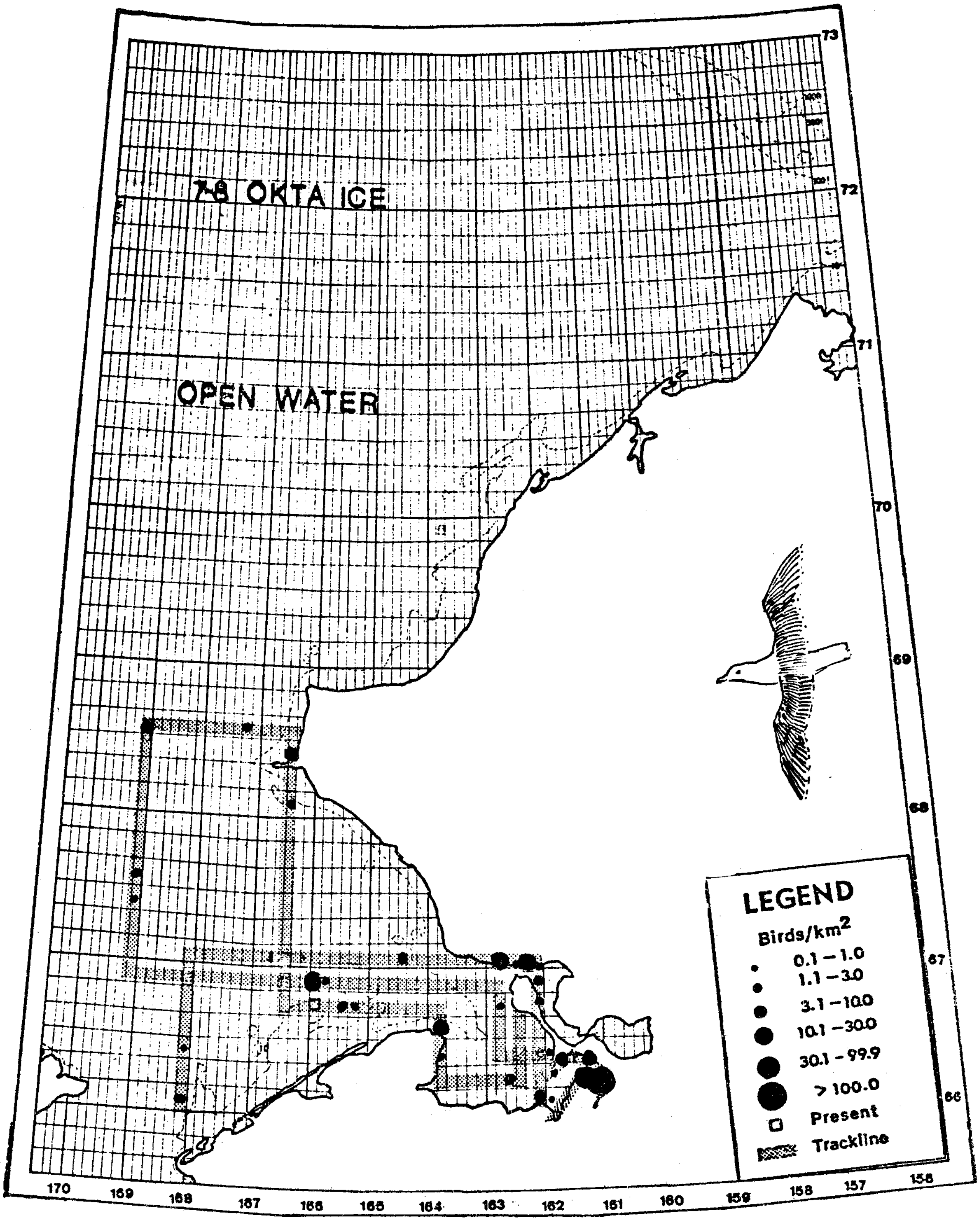


Figure I.D.10a
Black-legged Kittiwakes seen during aerial transects in the Chukchi Sea in the presence of sea ice June 9, 1978 (Drury et al.).

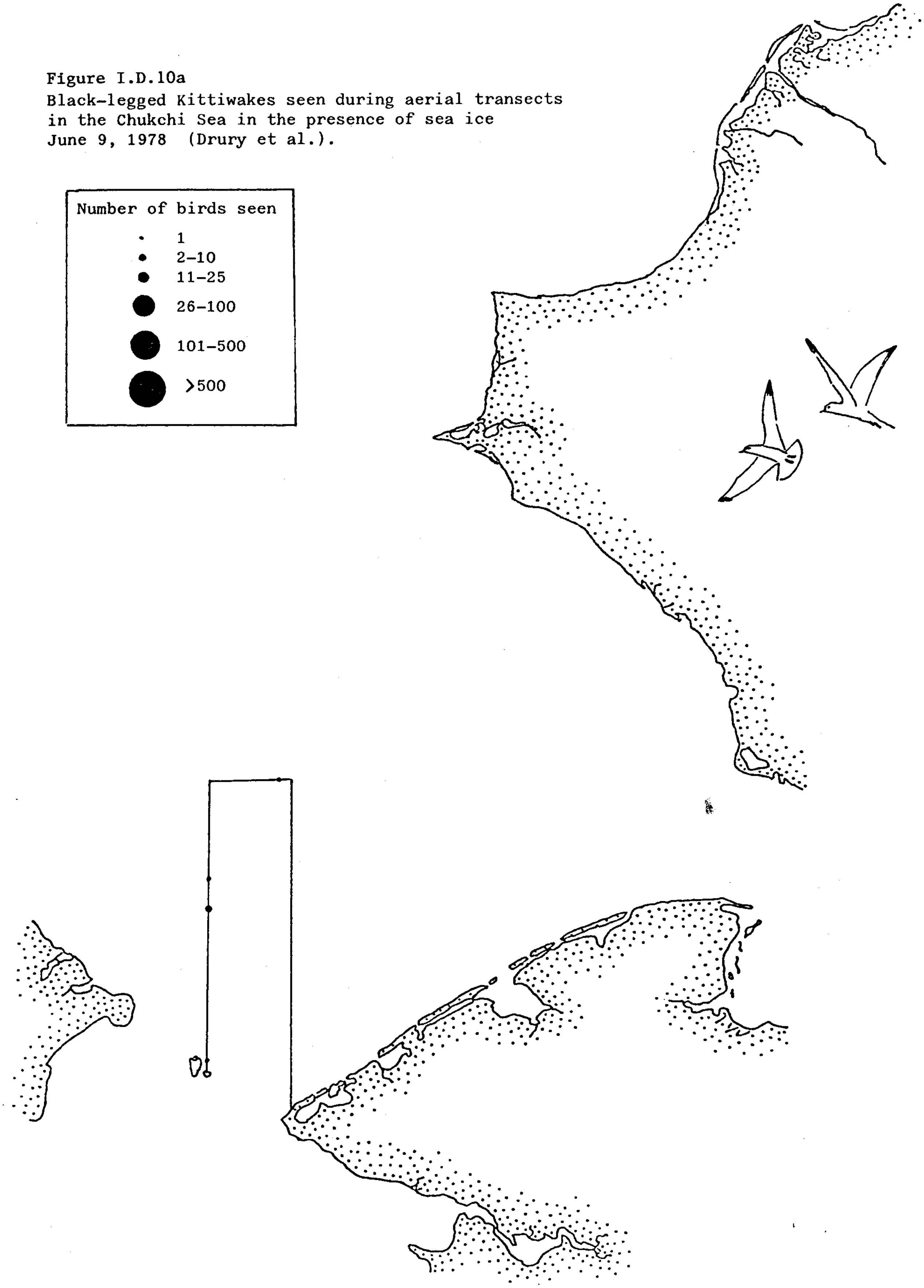


Figure I.D.10b
Black-legged Kittiwakes seen during aerial transects in the Chukchi Sea in the presence of sea ice June 24, 1977 (Drury et al.).

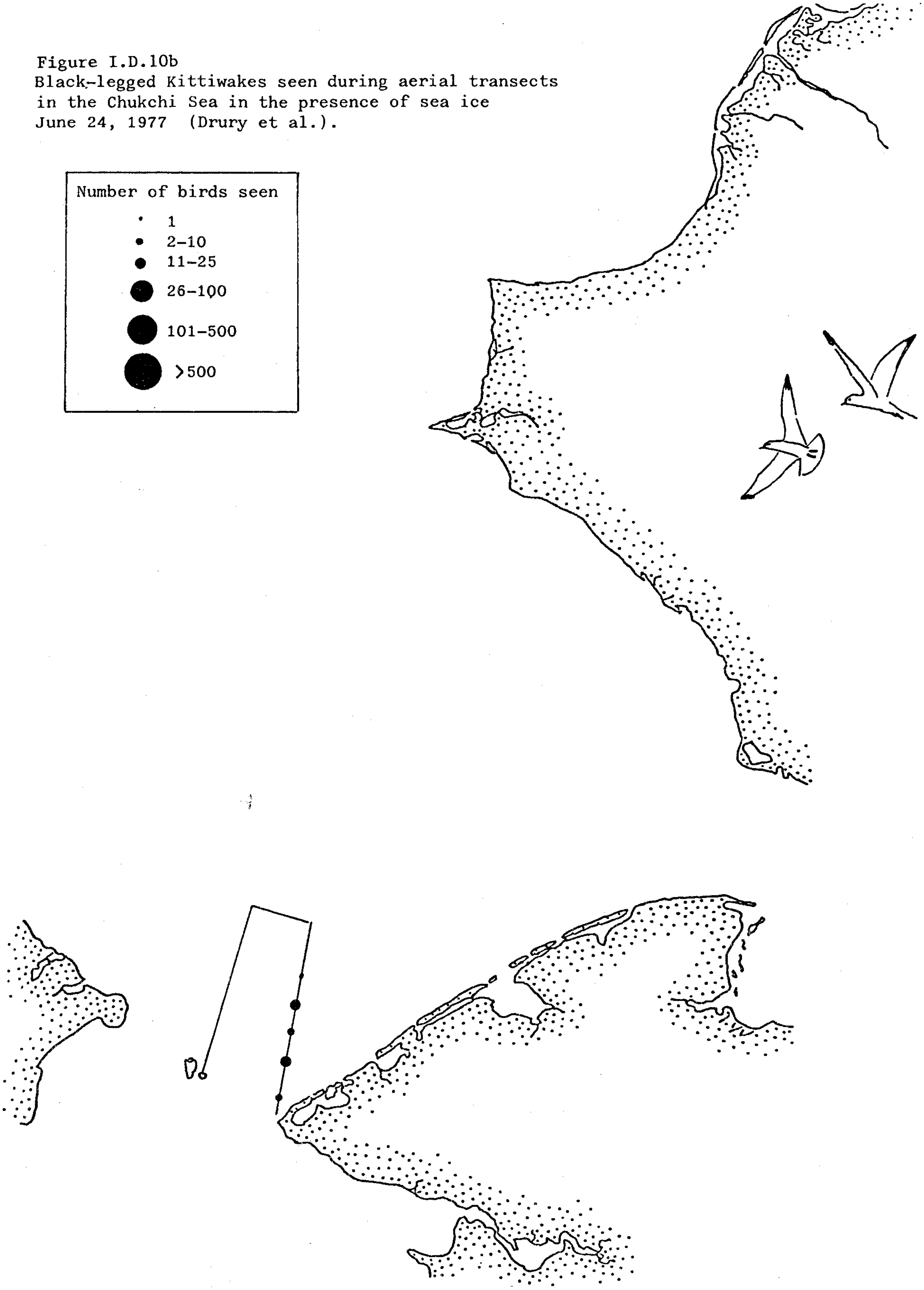


Figure I.D.10c Distribution and abundance of Black-legged Kittiwakes in the Chukchi Sea in June 1976. Aerial surveys, USFWS: Figure 43, page 159, in Harrison 1977.

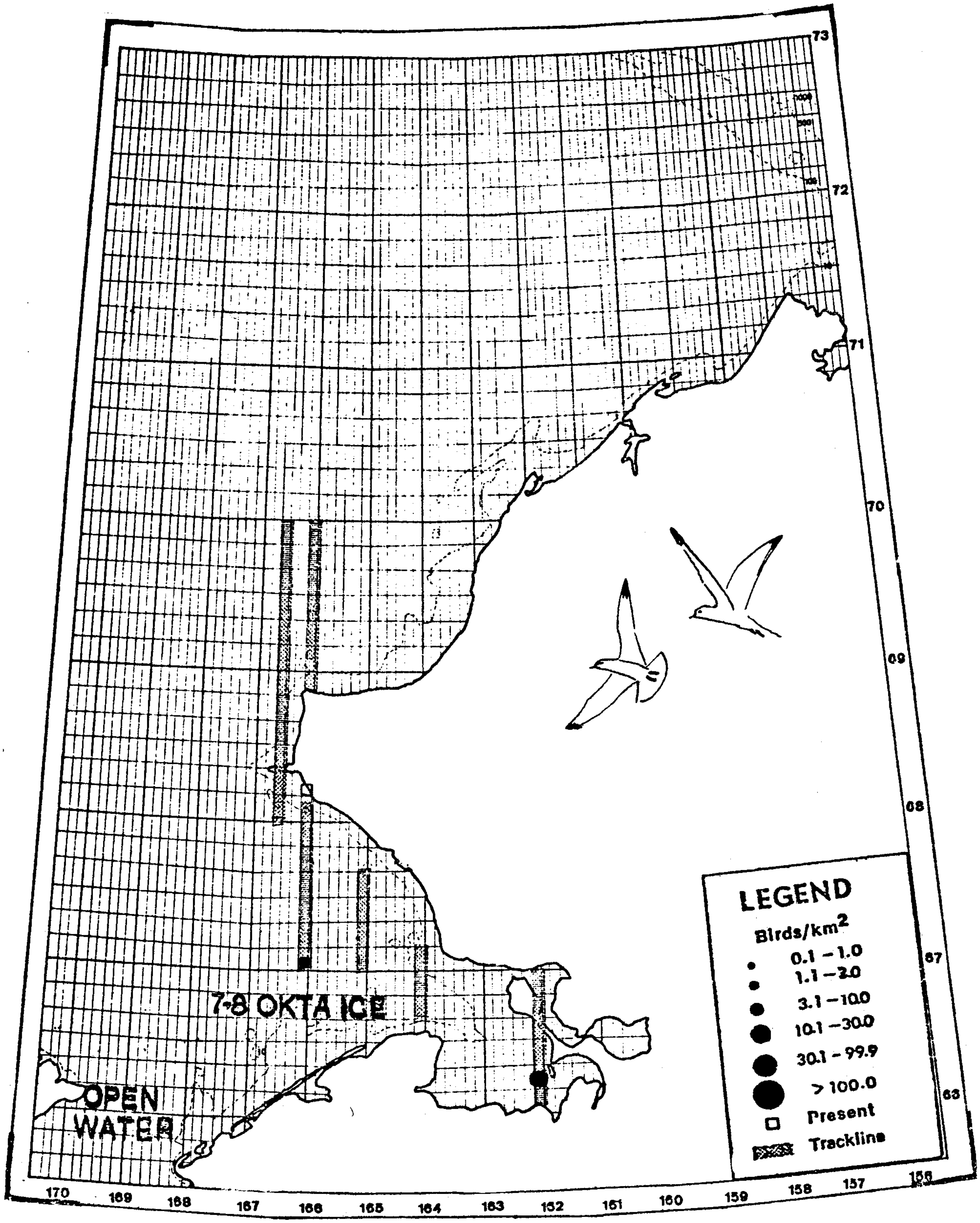


Figure I.D.10d
Black-legged Kittiwakes seen during aerial transects in the Chukchi Sea July 7, 1978 (Drury et al.).

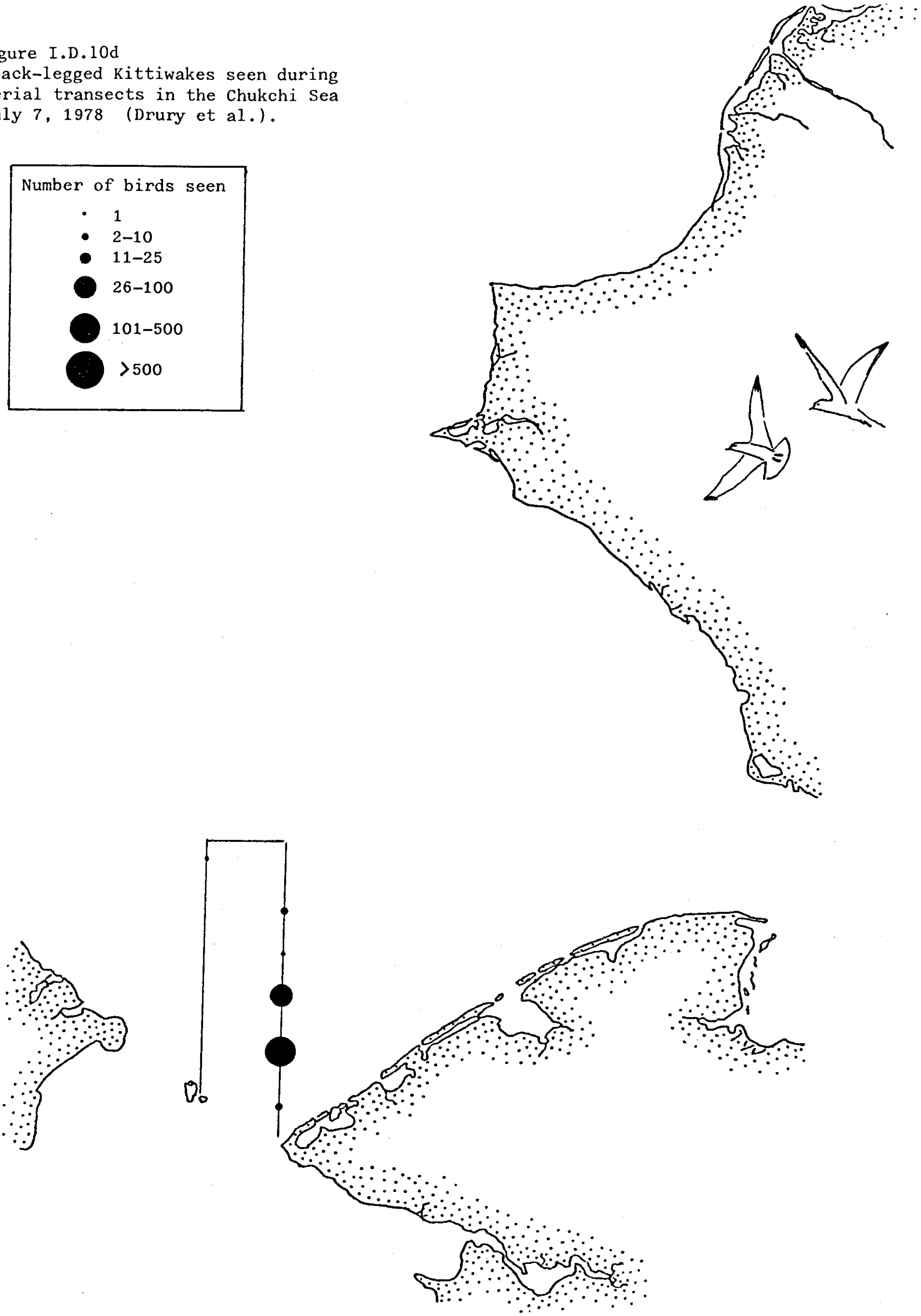
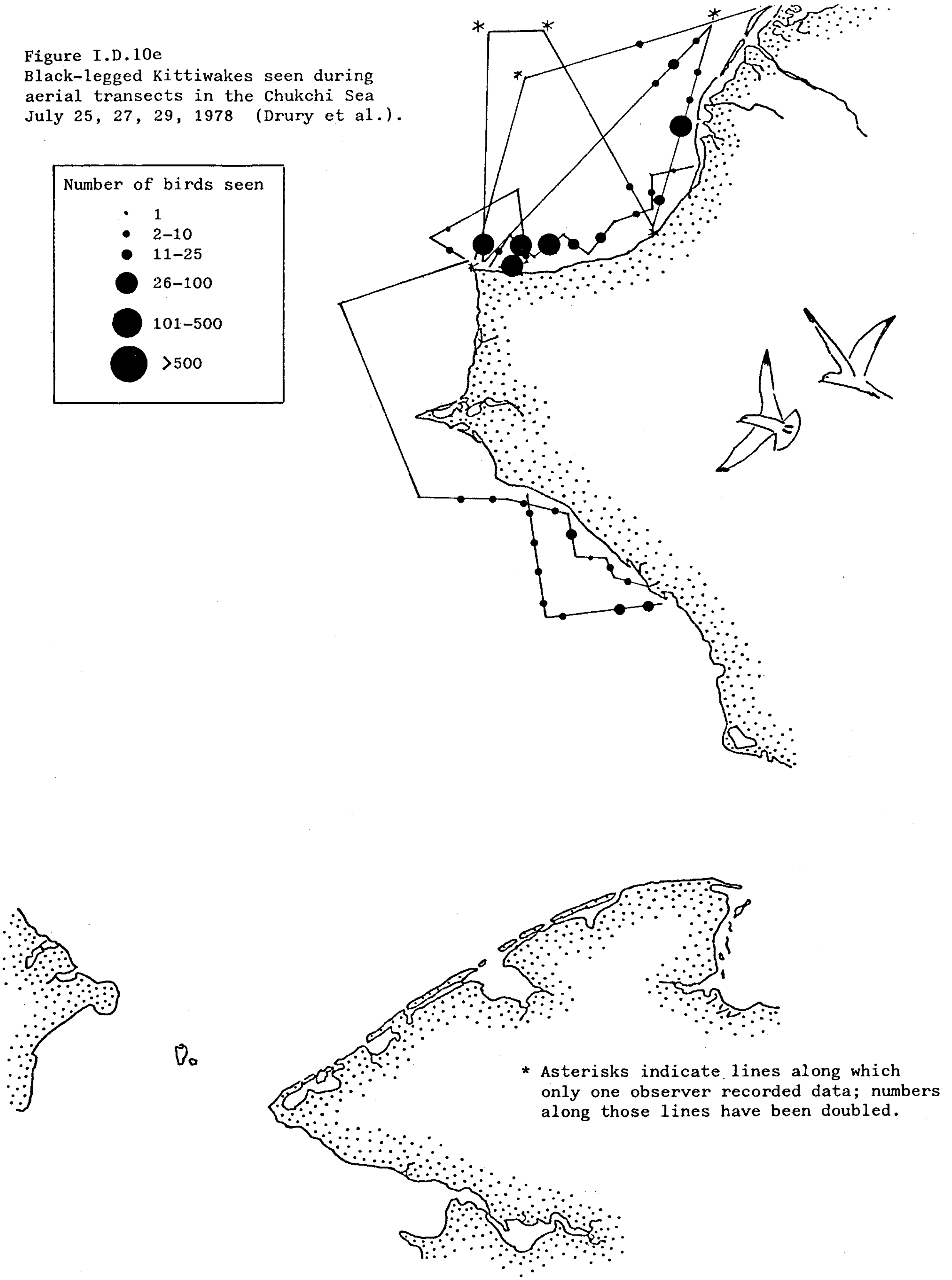
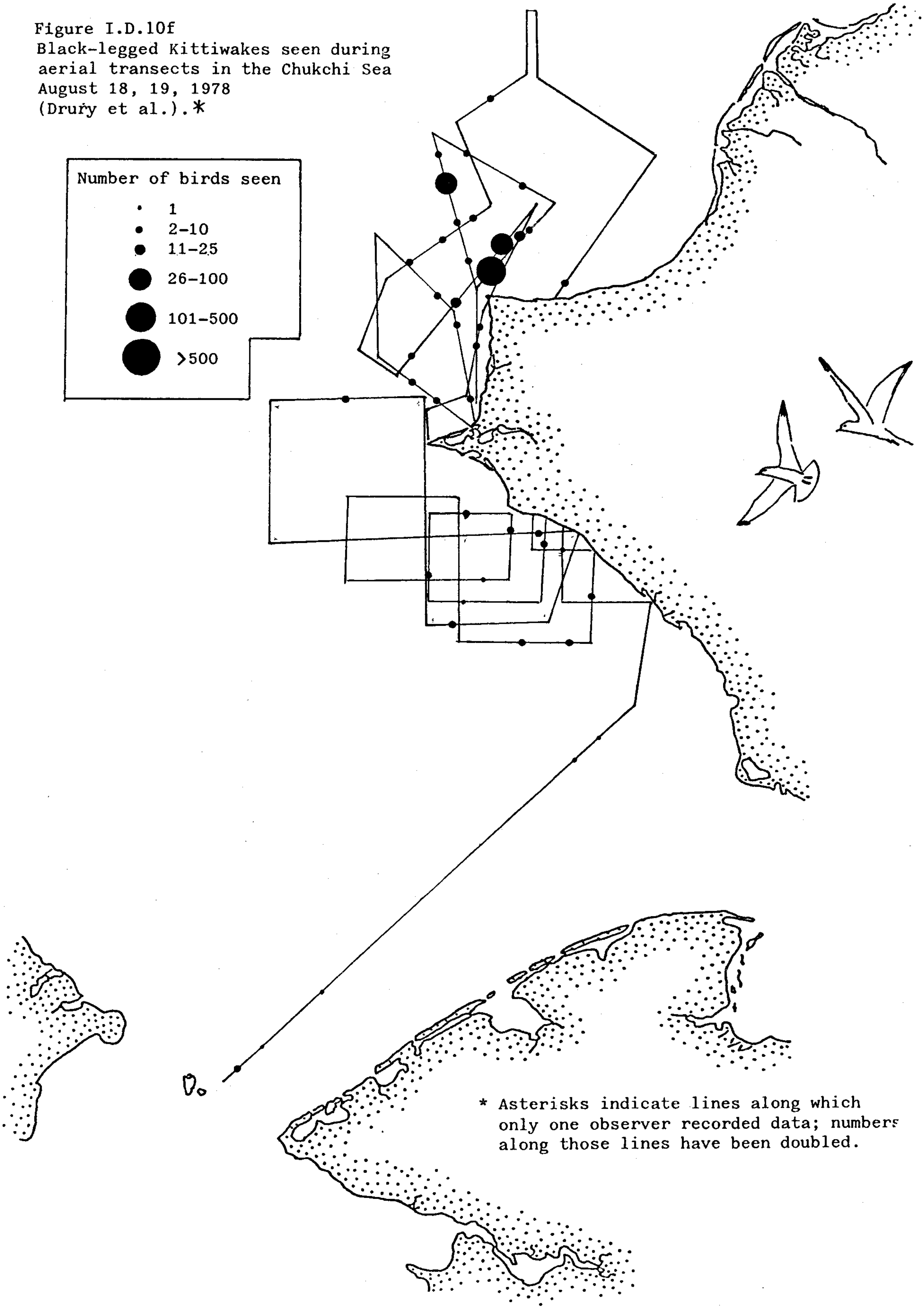


Figure I.D.10e
Black-legged Kittiwakes seen during aerial transects in the Chukchi Sea July 25, 27, 29, 1978 (Drury et al.).



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.10f
Black-legged Kittiwakes seen during aerial transects in the Chukchi Sea August 18, 19, 1978 (Drury et al.).*



* Asterisks indicate lines along which only one observer recorded data; numbers along those lines have been doubled.

Figure I.D.10g Distribution and abundance of Black-legged Kittiwakes in the Chukchi Sea in August 1976. Aerial surveys, USFWS: Figure 44, page 160, in Harrison 1977.

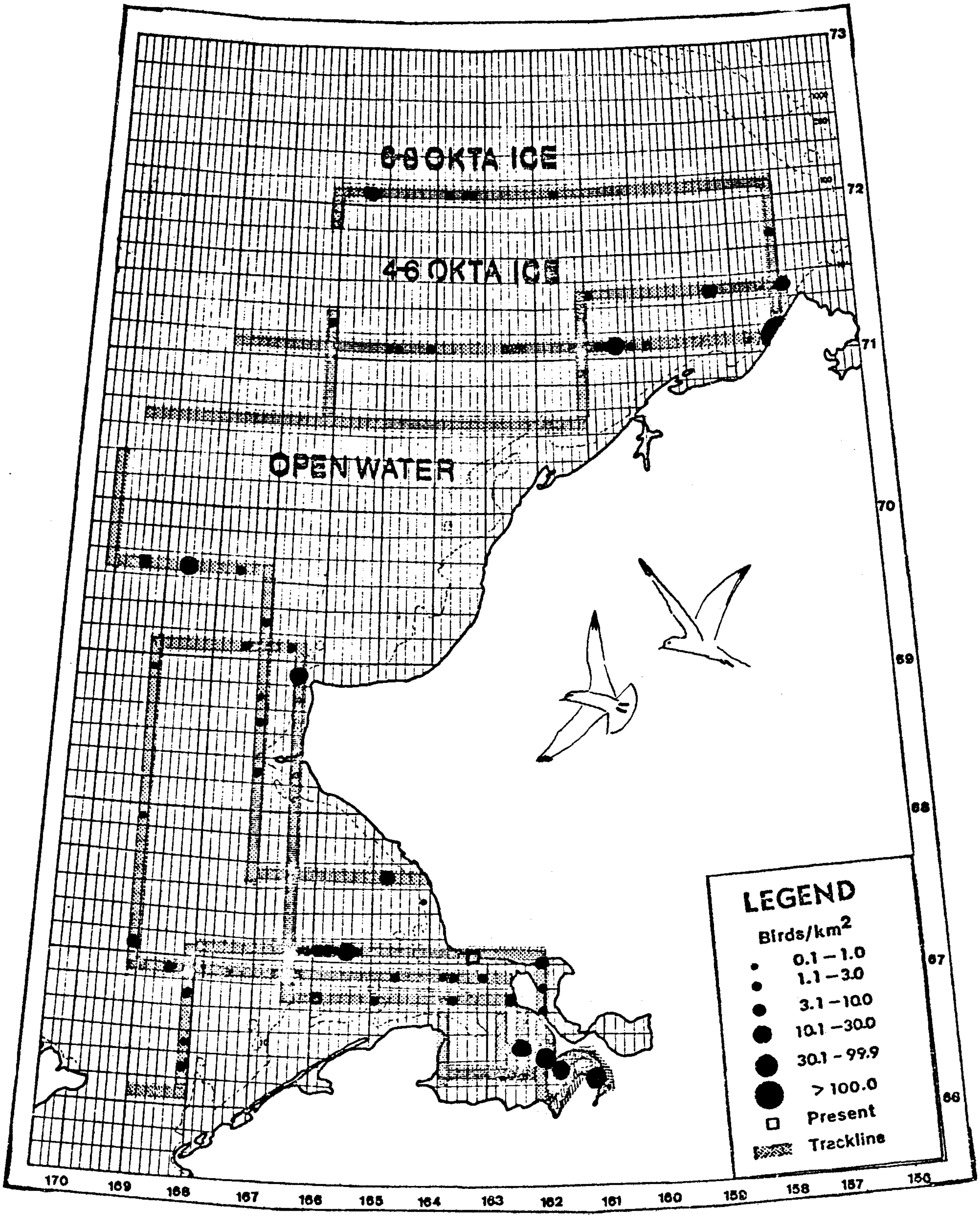
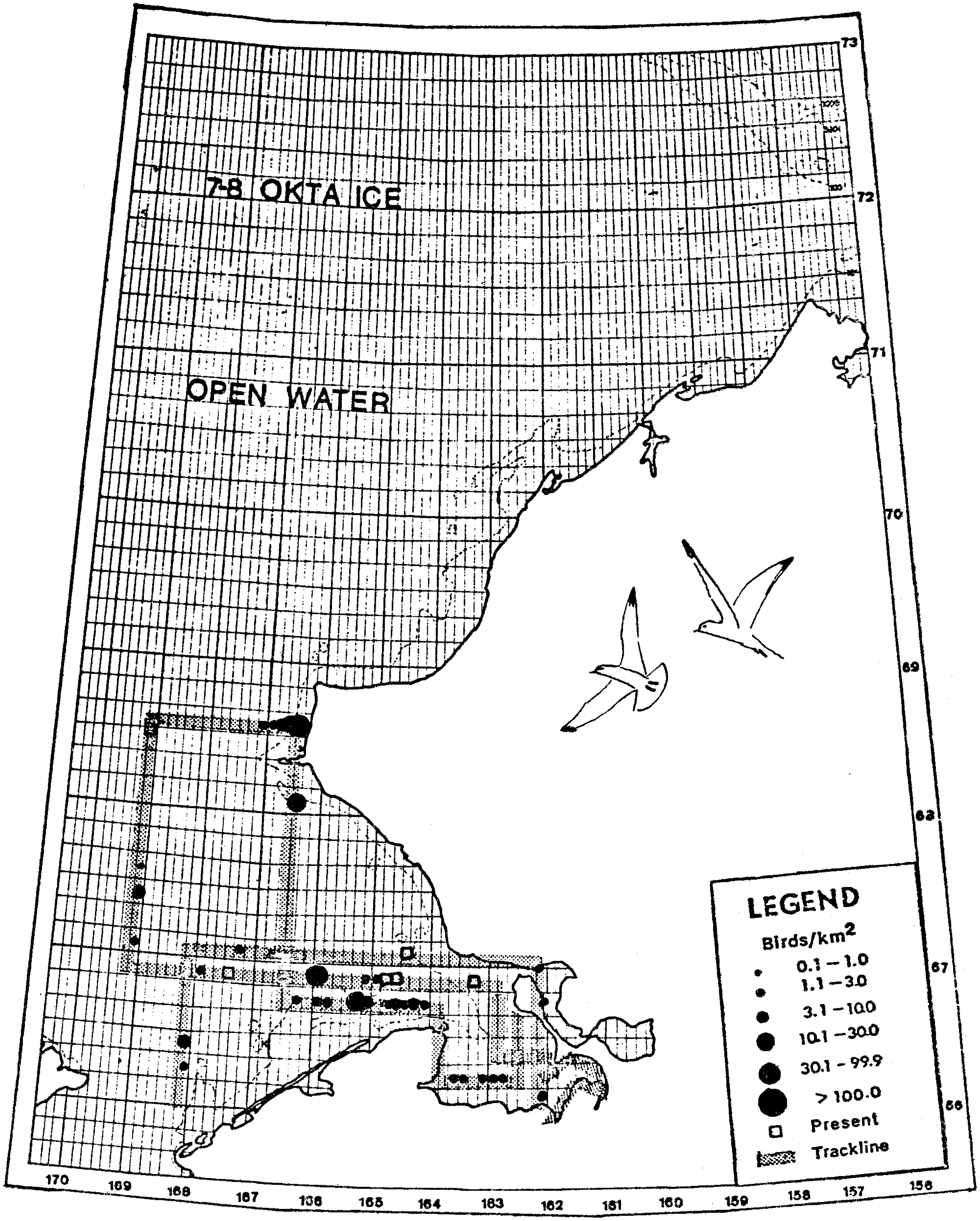


Figure I.D.10h Distribution and abundance of Black-legged Kittiwakes in the Chukchi Sea in October 1976. Aerial surveys, USFWS: Figure 45, page 161, in Harrison 1977.



II. SURFACE TRANSECTS (shipboard surveys)

- A. Norton Sound
- B. Chirikov Basin
- C. Southern Chukchi Sea
- D. Northern Chukchi Sea

The 40-fathom depth is outlined on the maps of the Chirikov Basin.

Figure II.A.1
Murres seen during surface transects in Norton Sound aboard Surveyor August 5-13, 1976 (Drury et al.).

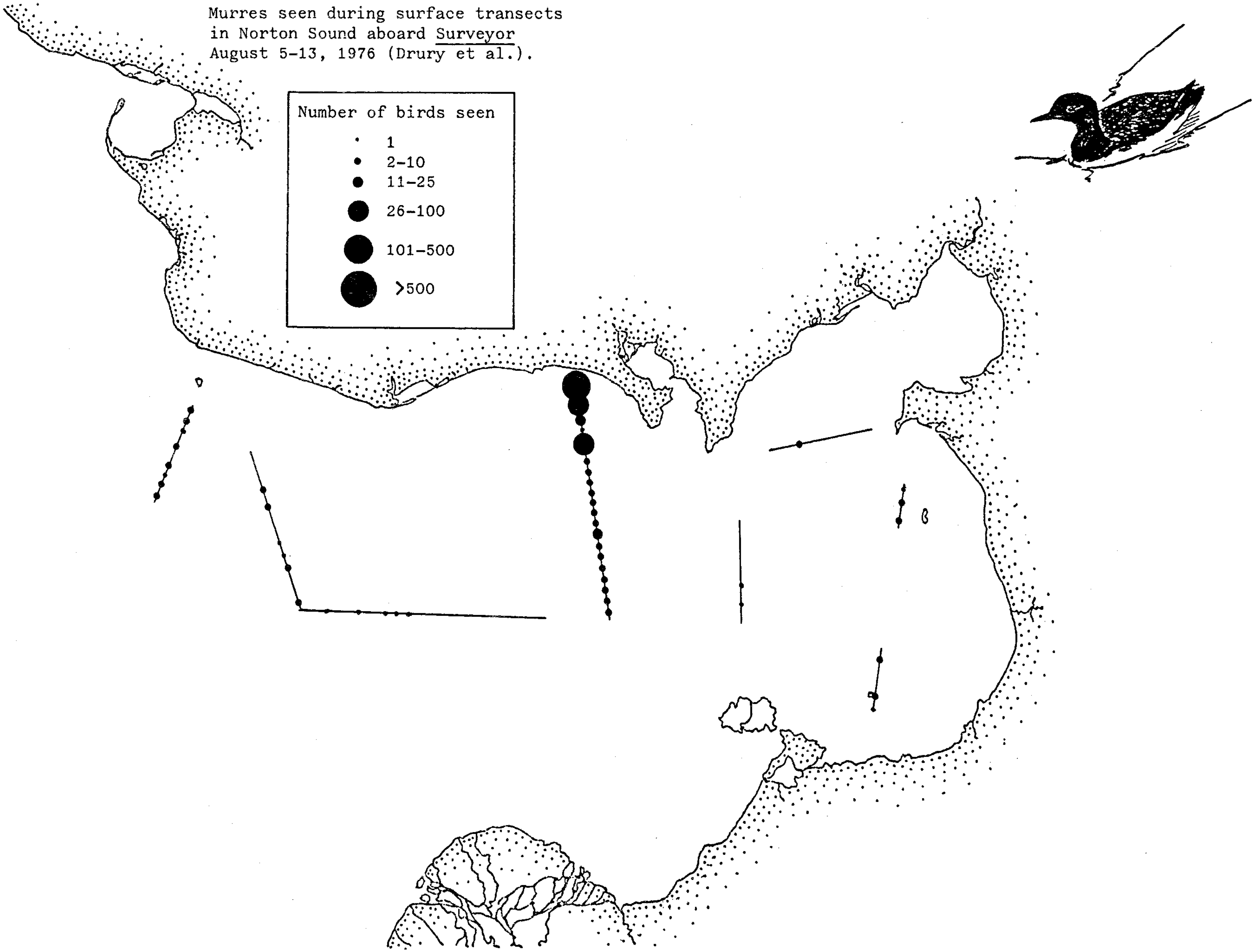


Figure II.A.2
All Auklets (Least + Crested + Parakeet + Unidentified) seen during surface transects in Norton Sound aboard <u>Surveyor</u>, August 5-13, 1976 (Drury et al.).

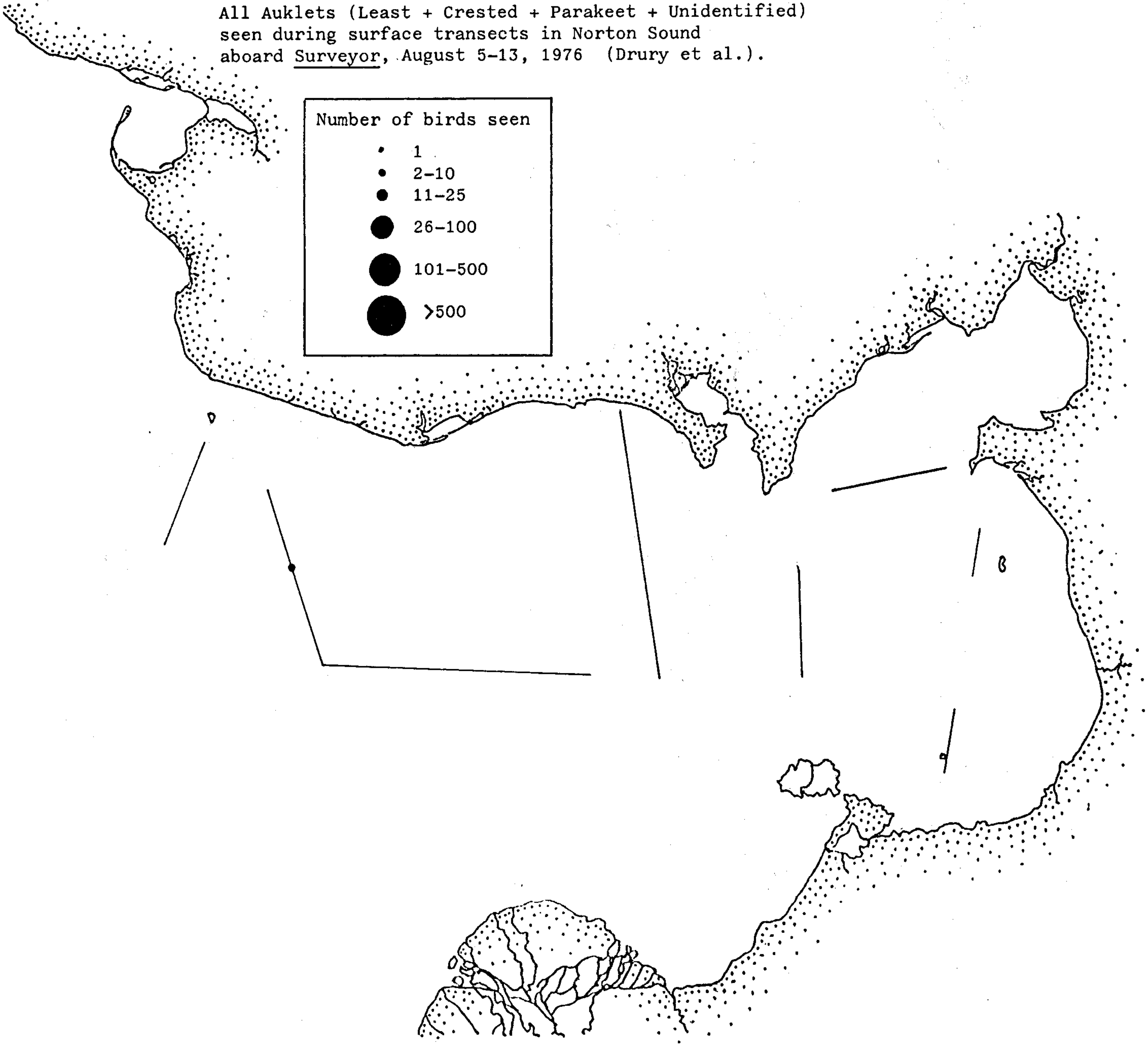


Figure II.A.3
Horned Puffins seen during surface transects in Norton Sound aboard Surveyor August 5-13, 1976 (Drury et al.).

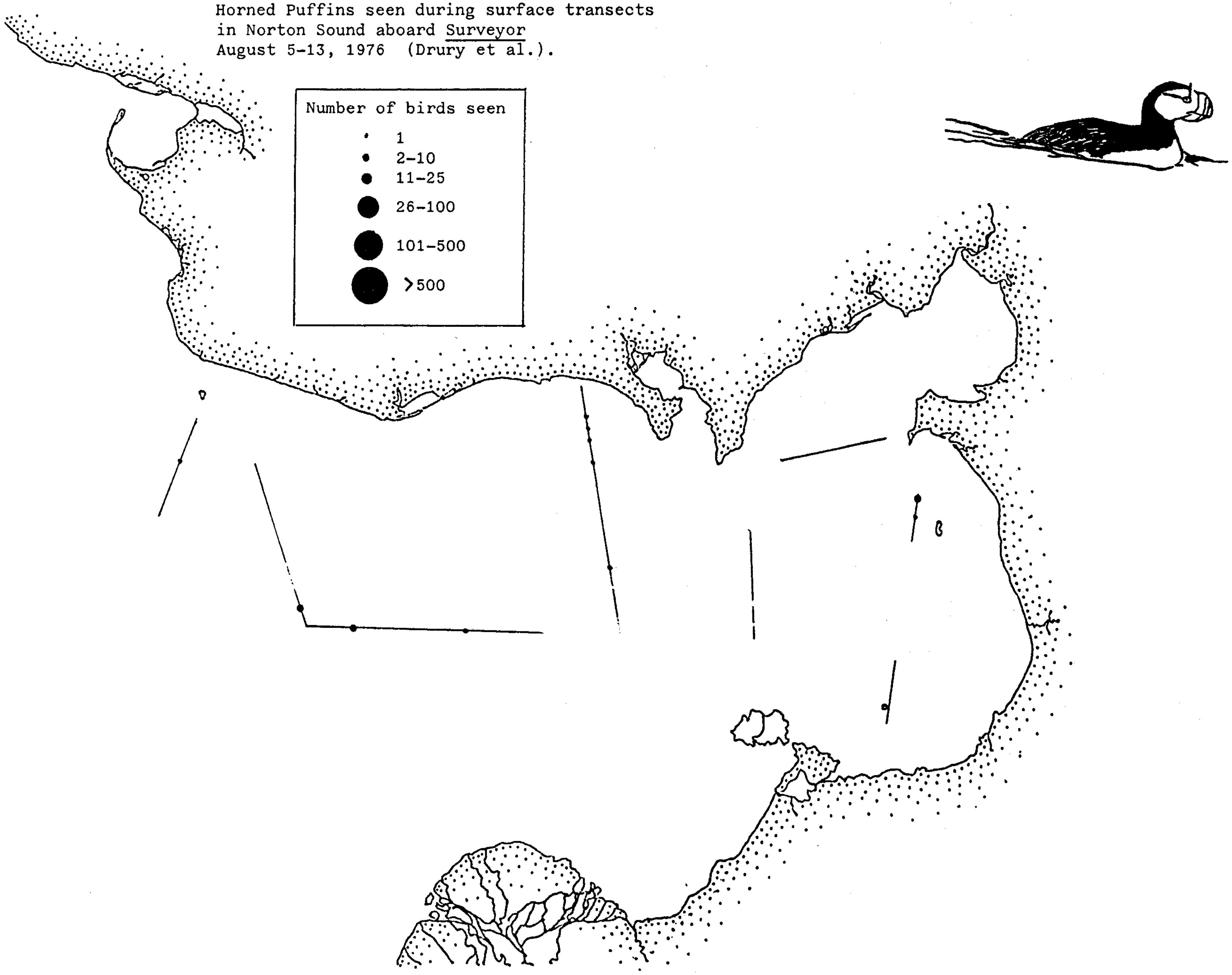


Figure II.A.4

Black-legged Kittiwakes seen during
surface transects in Norton Sound aboard *Surveyor*
August 5-13, 1976 (Drury et al.).

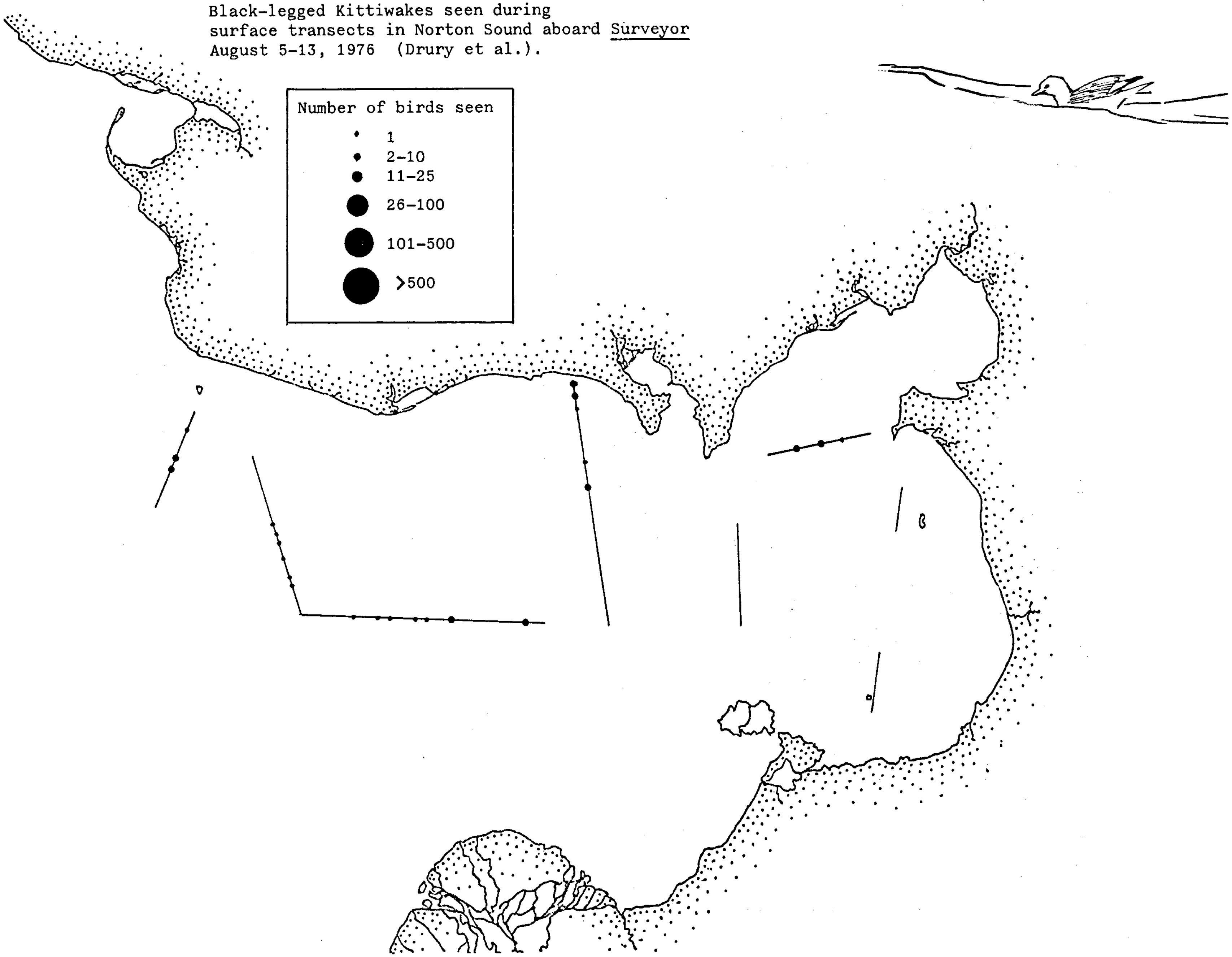


Figure II.B.1 Cruise track during periods of observation in the northern Bering Sea, from May 27 to June 10, 1978. Figure 98, page 229, in Divoky et al., 1979.

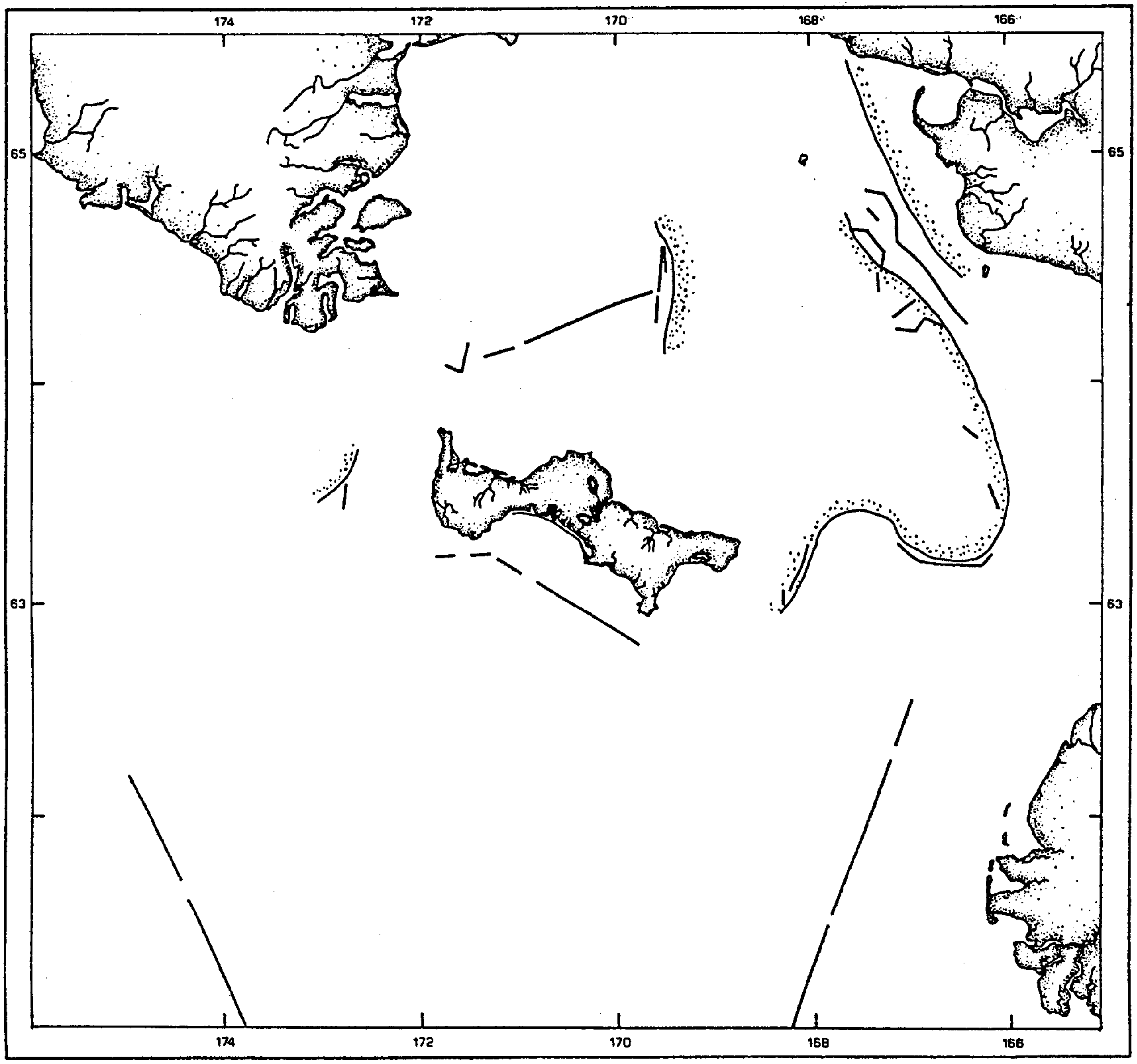


Figure II.B.2a Distribution and abundance of murres in the northern Bering Sea, May 27 to June 10, 1978. Figure 107, page 238, in Divoky et al., 1979.

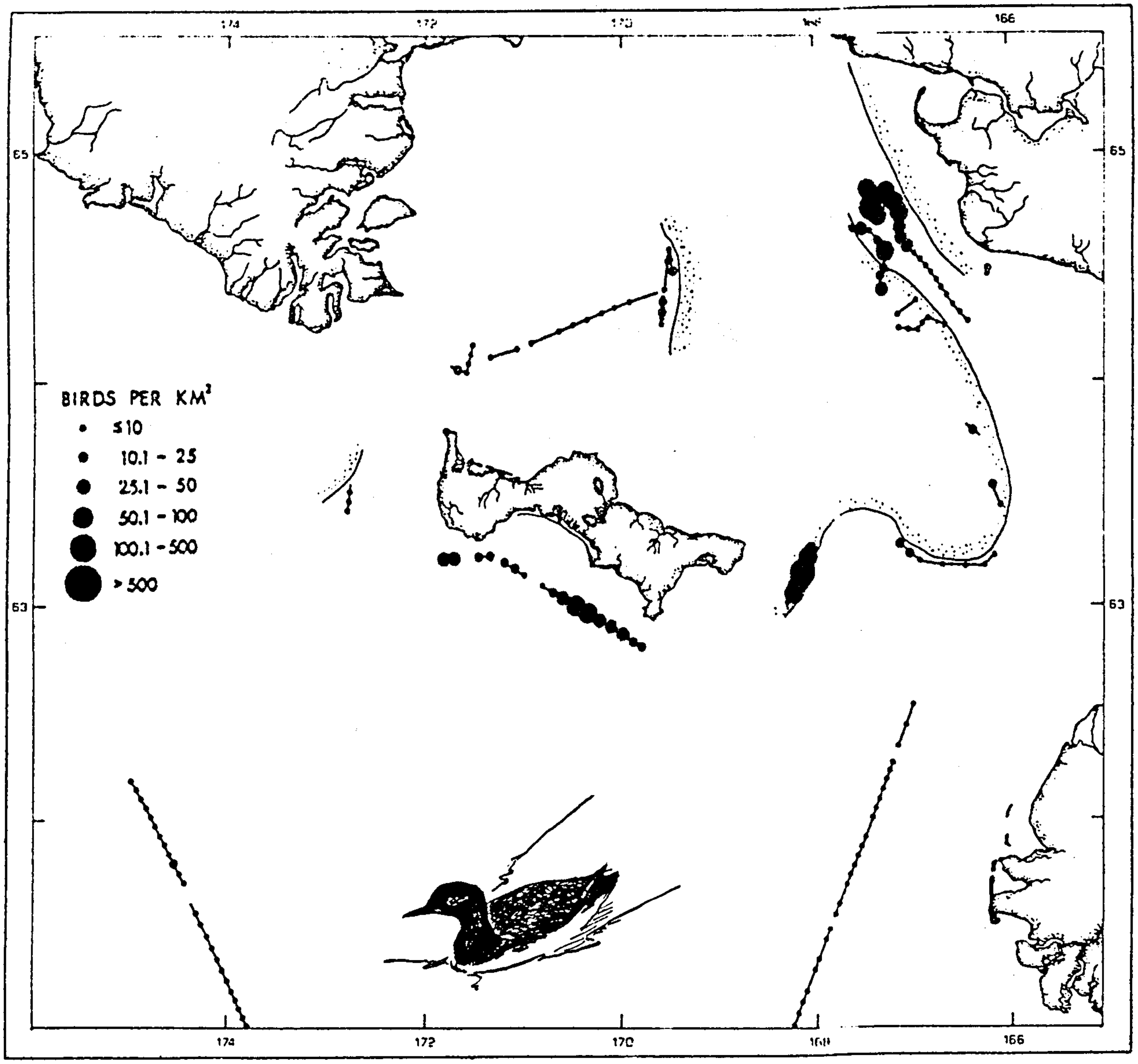


Figure II.B.2b
Murres seen during surface transects aboard Surveyor
August 5-13, 1976 (Drury et al.),
September 7, 8, 1976 (Gould et al.).

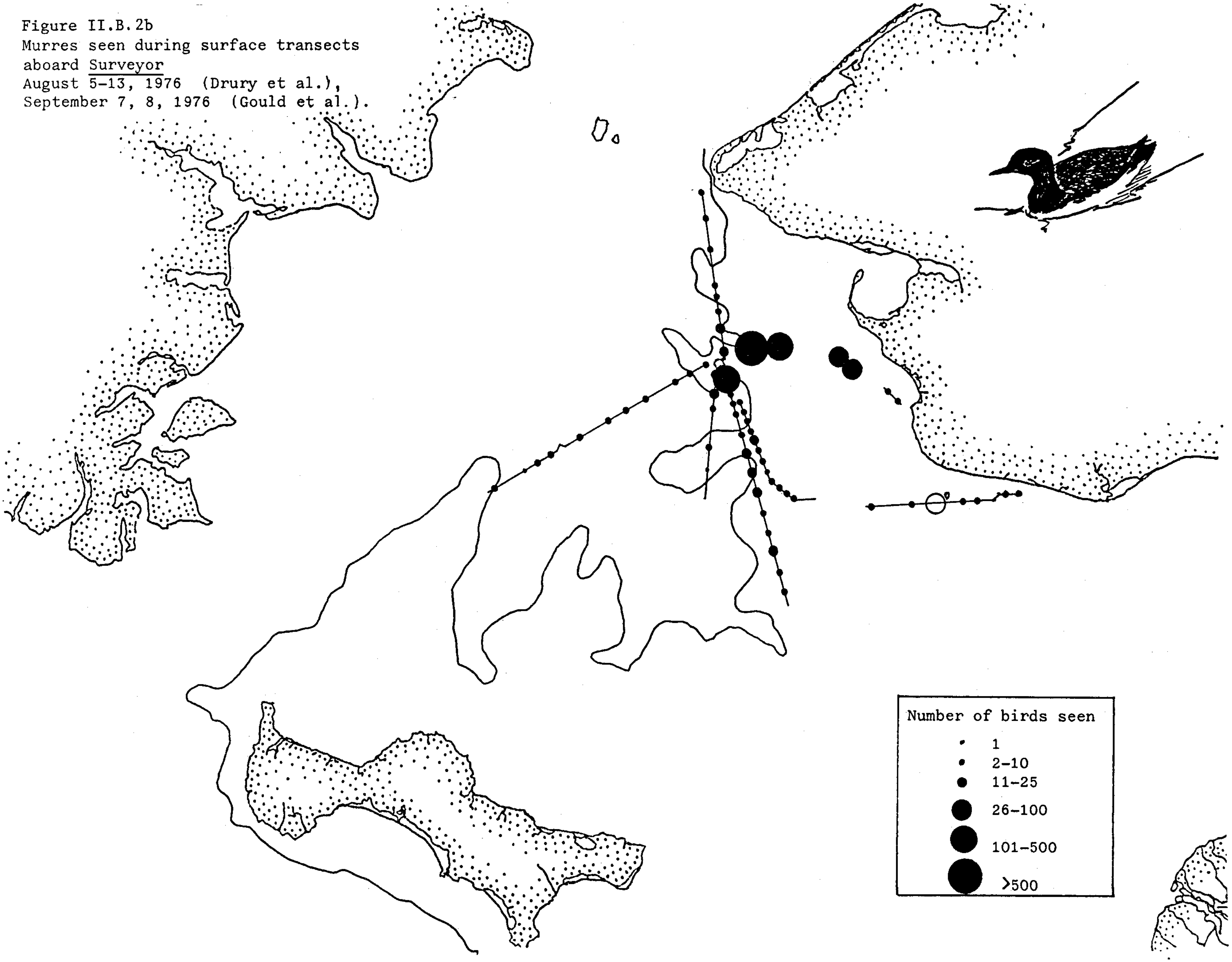


Figure II.B.3
All Auklets (Least + Crested + Parakeet + Unidentified) seen during surface transects aboard <u>Surveyor</u> August 5-13, 1976 (Drury et al.), September 7, 8, 1976 (Gould et al.).

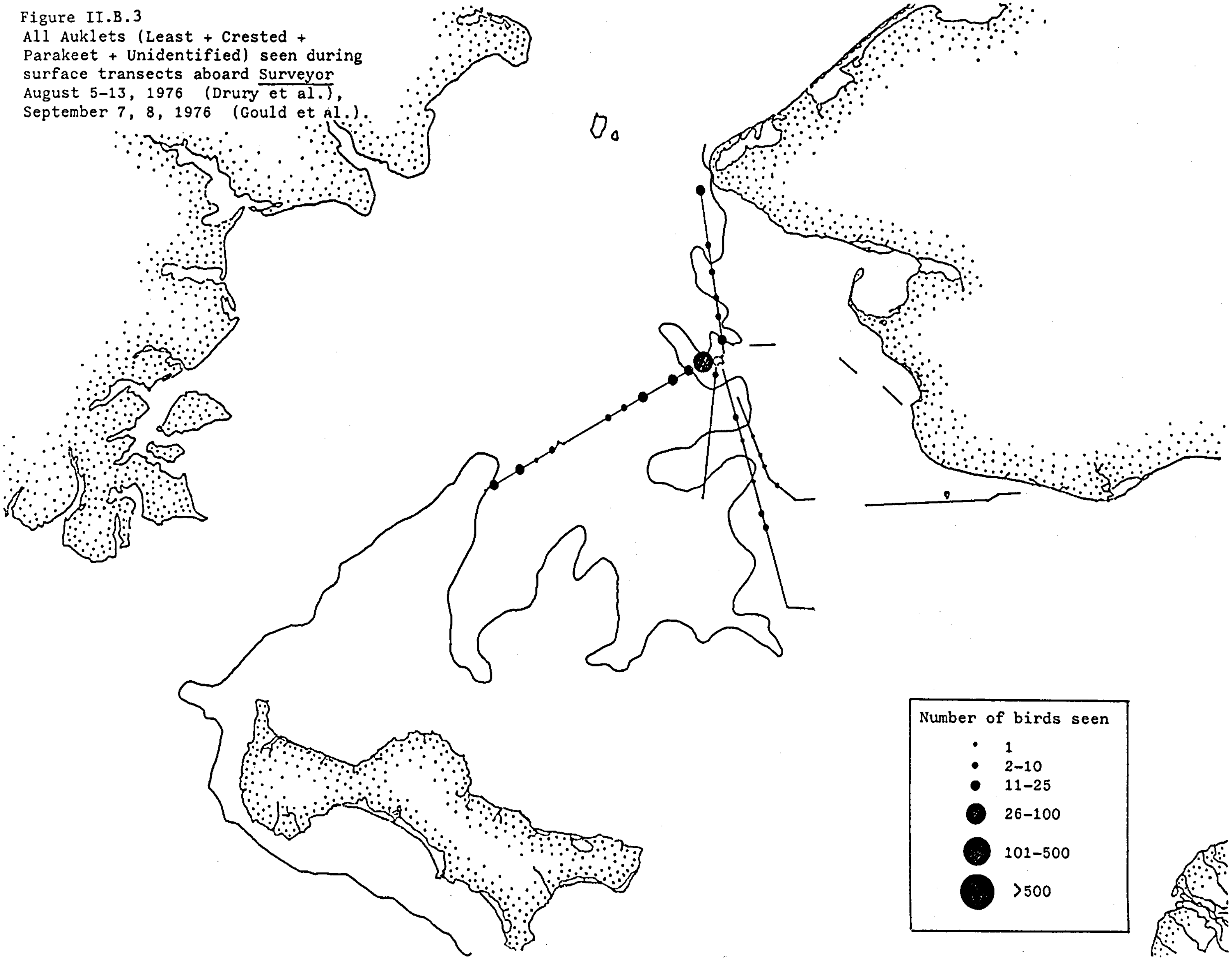


Figure II.B.4a Distribution and abundance of Least Auklets in the northern Bering Sea, May 27 to June 10, 1978. Figure 110, page 241 in Divoky et al., 1979.

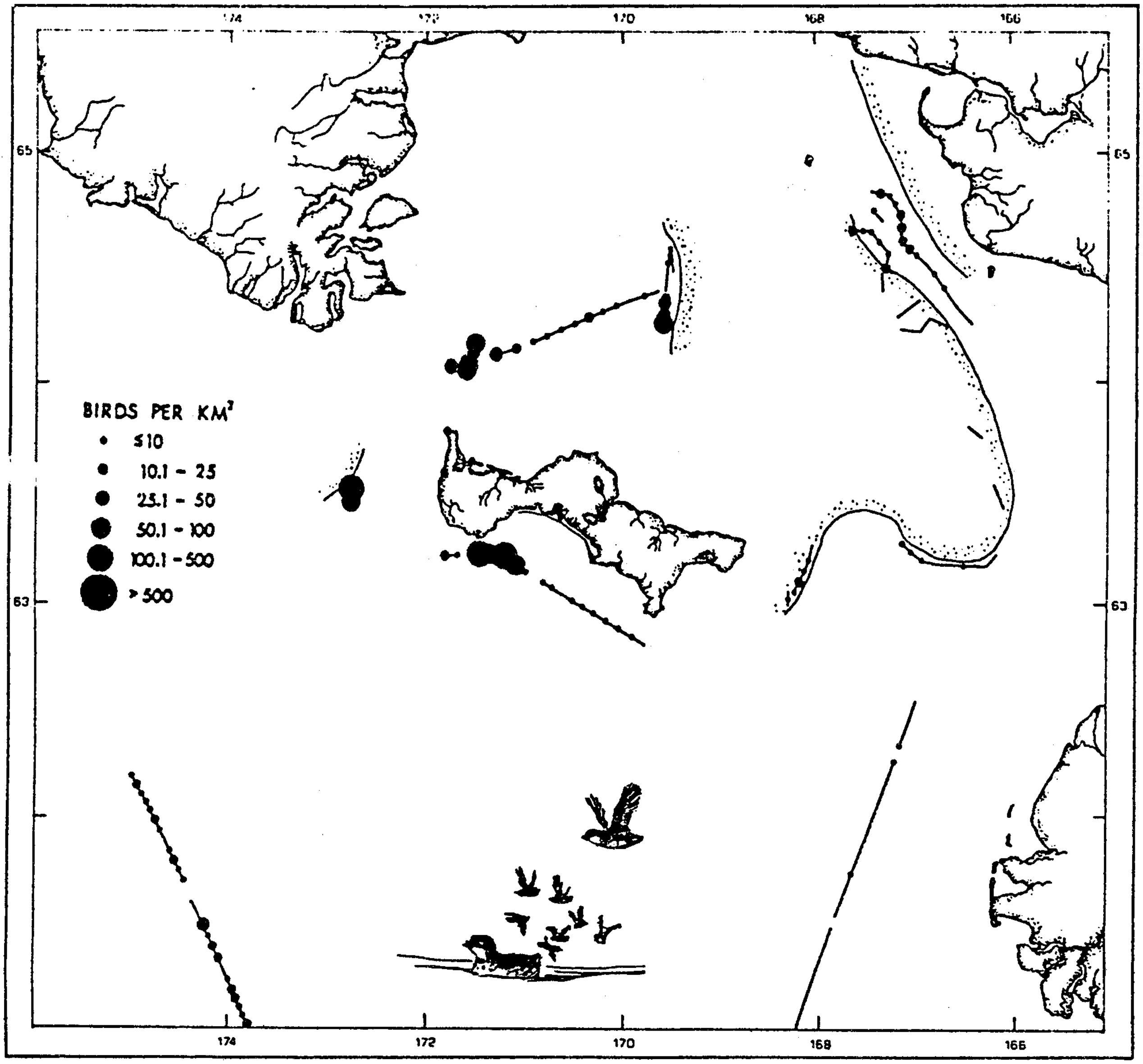


Figure II.B.4b
Least Auklets seen during surface transects aboard Surveyor
September 7, 8, 1976 (Gould et al.).

Figure II.B.5
Crested Auklets seen during
surface transects aboard Surveyor
September 7, 8, 1976 (Gould et al.).

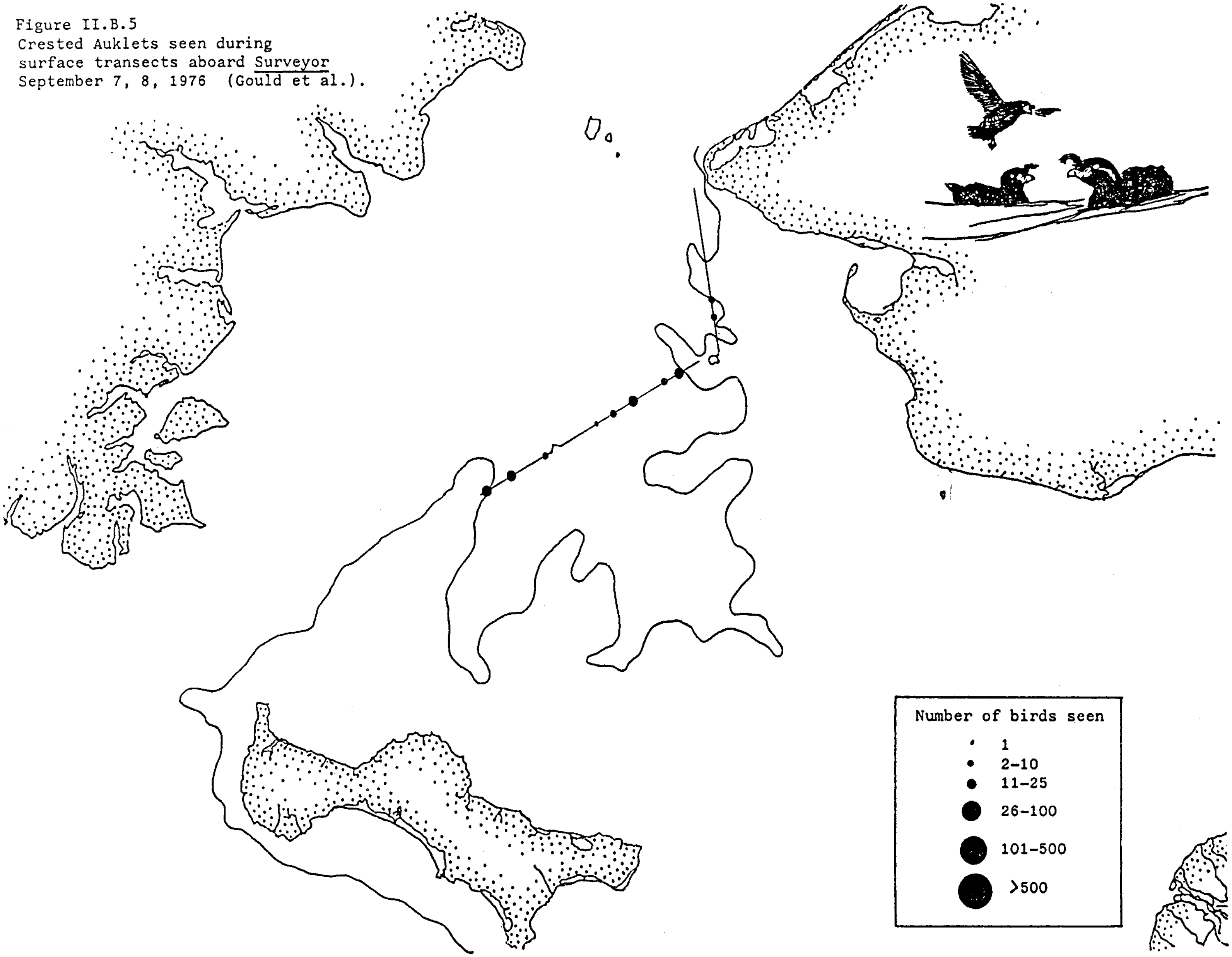
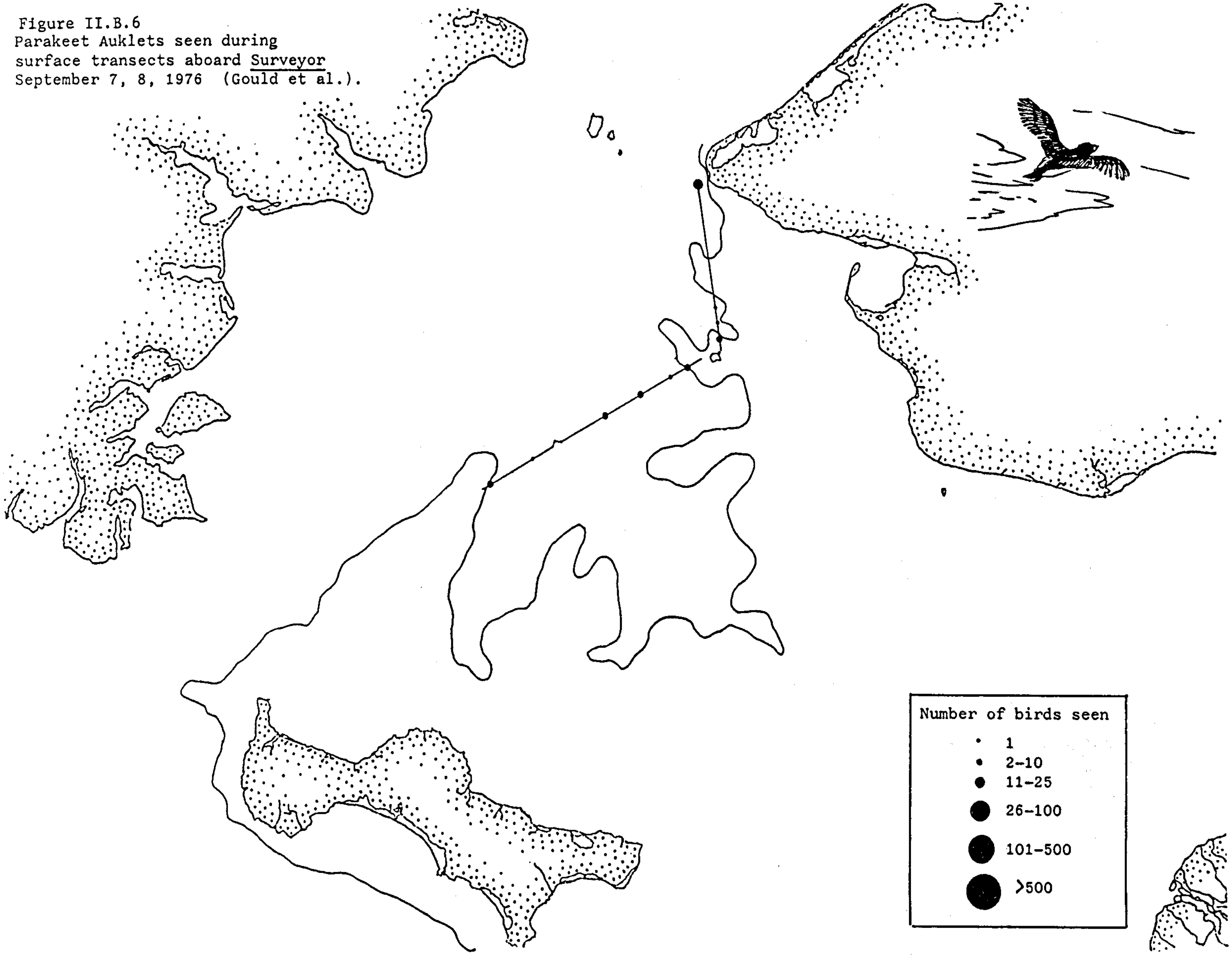


Figure II.B.6
Parakeet Auklets seen during
surface transects aboard Surveyor
September 7, 8, 1976 (Gould et al.).



igure II.B.7
orned Puffins seen during
urface transects aboard Surveyor
ugust 5-13, 1976 (Drury et al.),
eptember 7, 8, 1976 (Gould et al.).

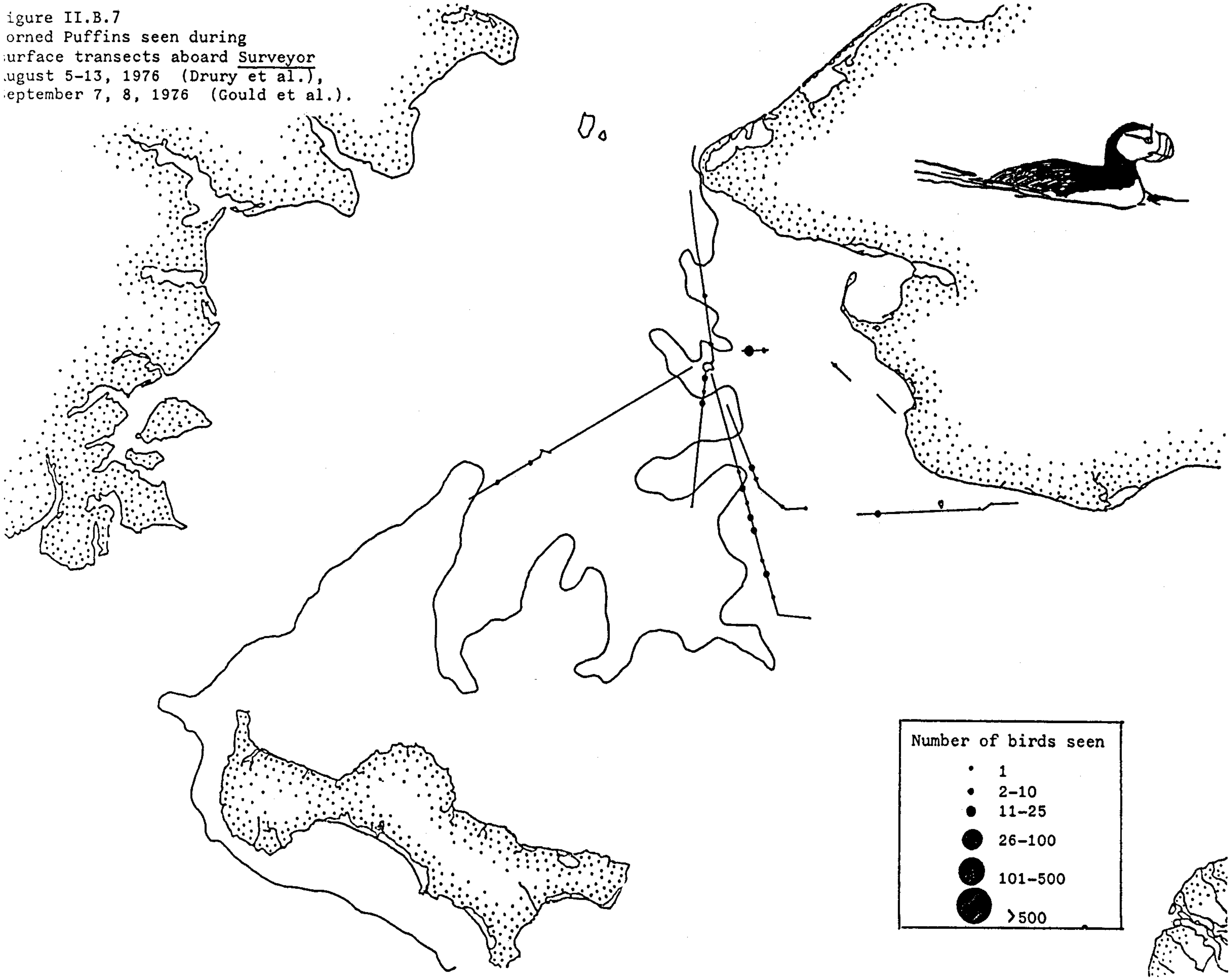


Figure II.B.8
Tufted Puffins seen during surface transects aboard <u>Surveyor</u> September 7, 8, 1976 (Gould et al.).

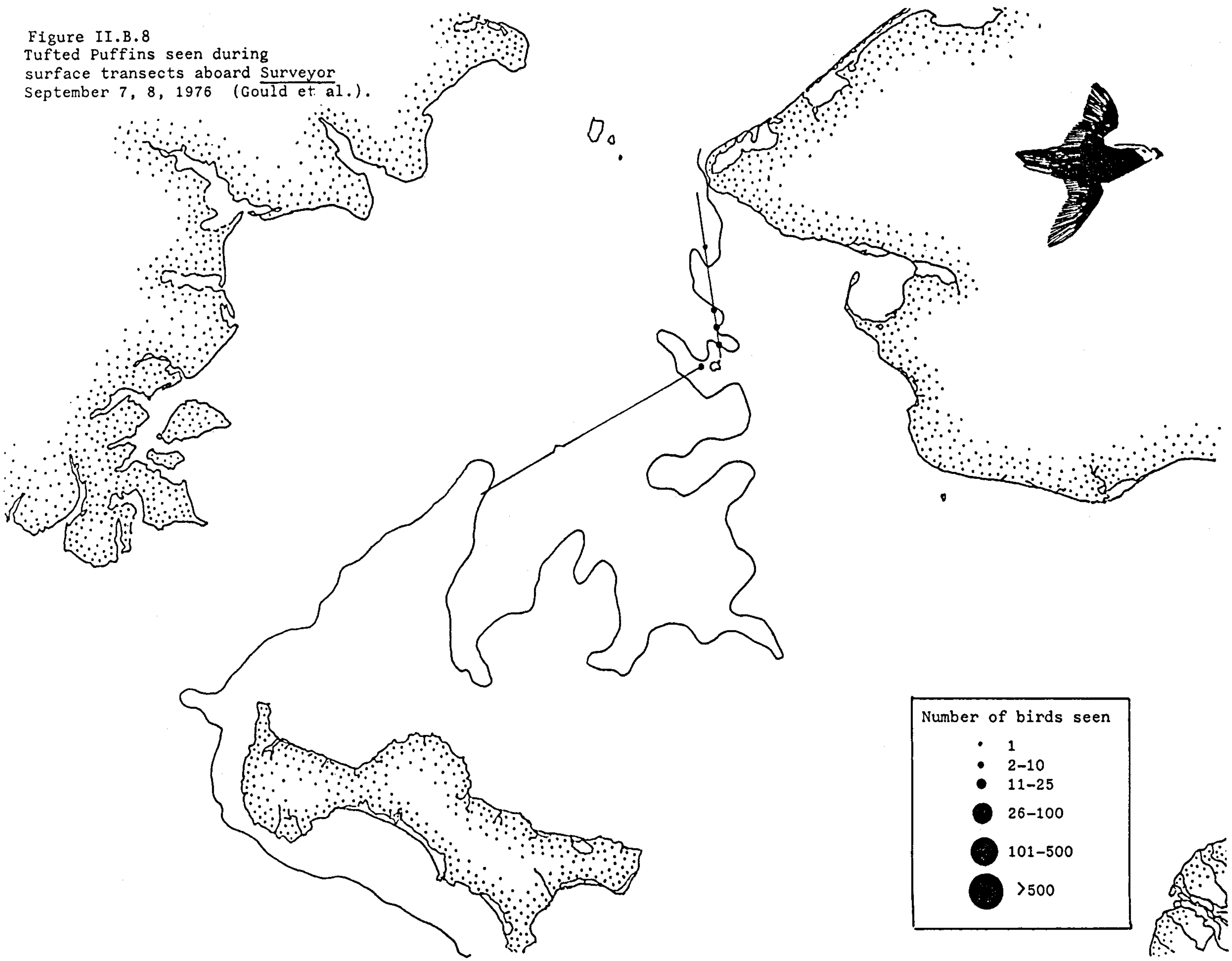


Figure II.B.9

Glaucous Gulls seen during surface transects aboard *Surveyor* September 7 & 8, 1976 (Gould et al.).

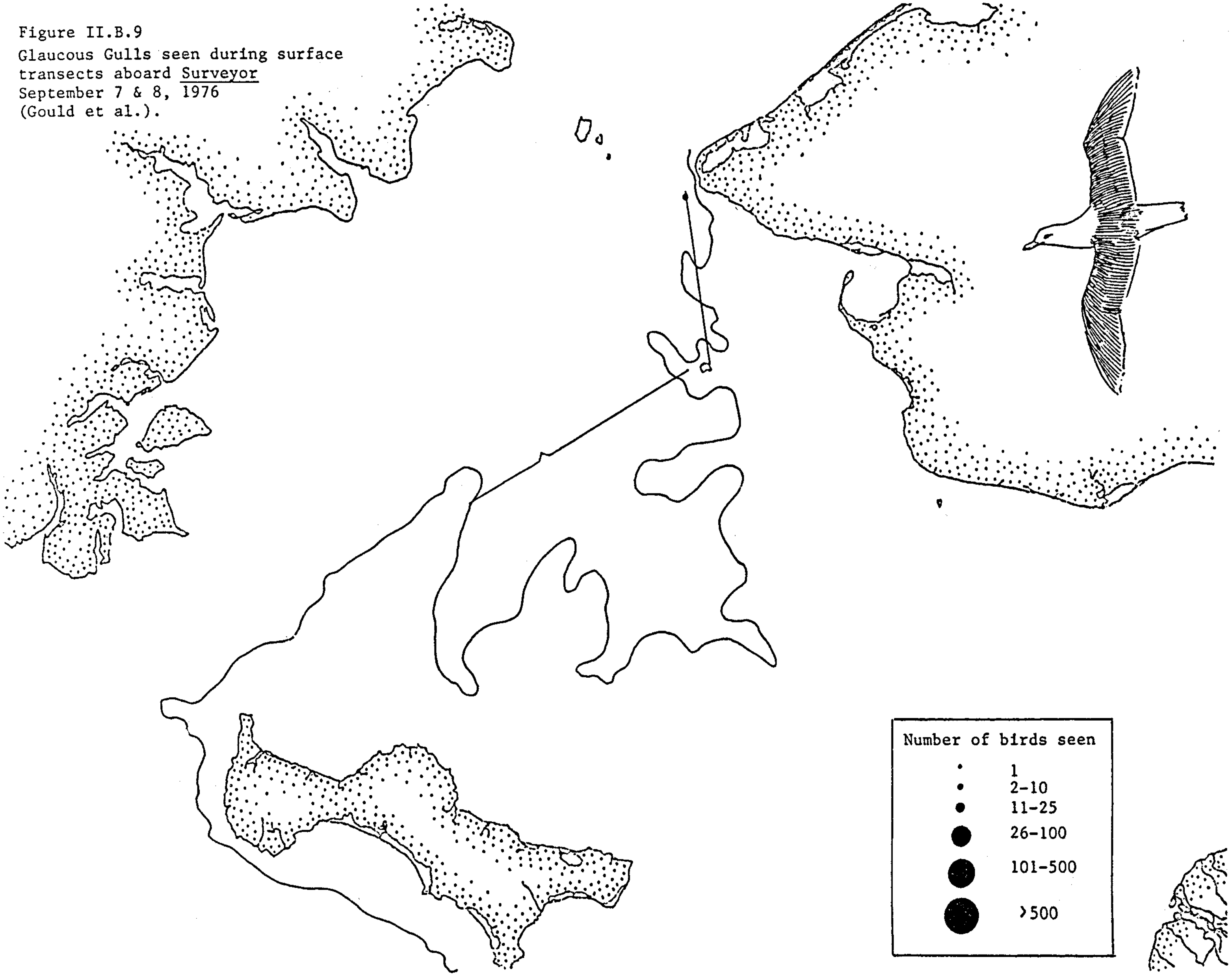


Figure II.B.10a Distribution and abundance of Black-legged Kittiwakes in the northern Bering Sea, May 27 to June 10, 1978. Figure 104, pate 235, in Divoky et al., 1979.

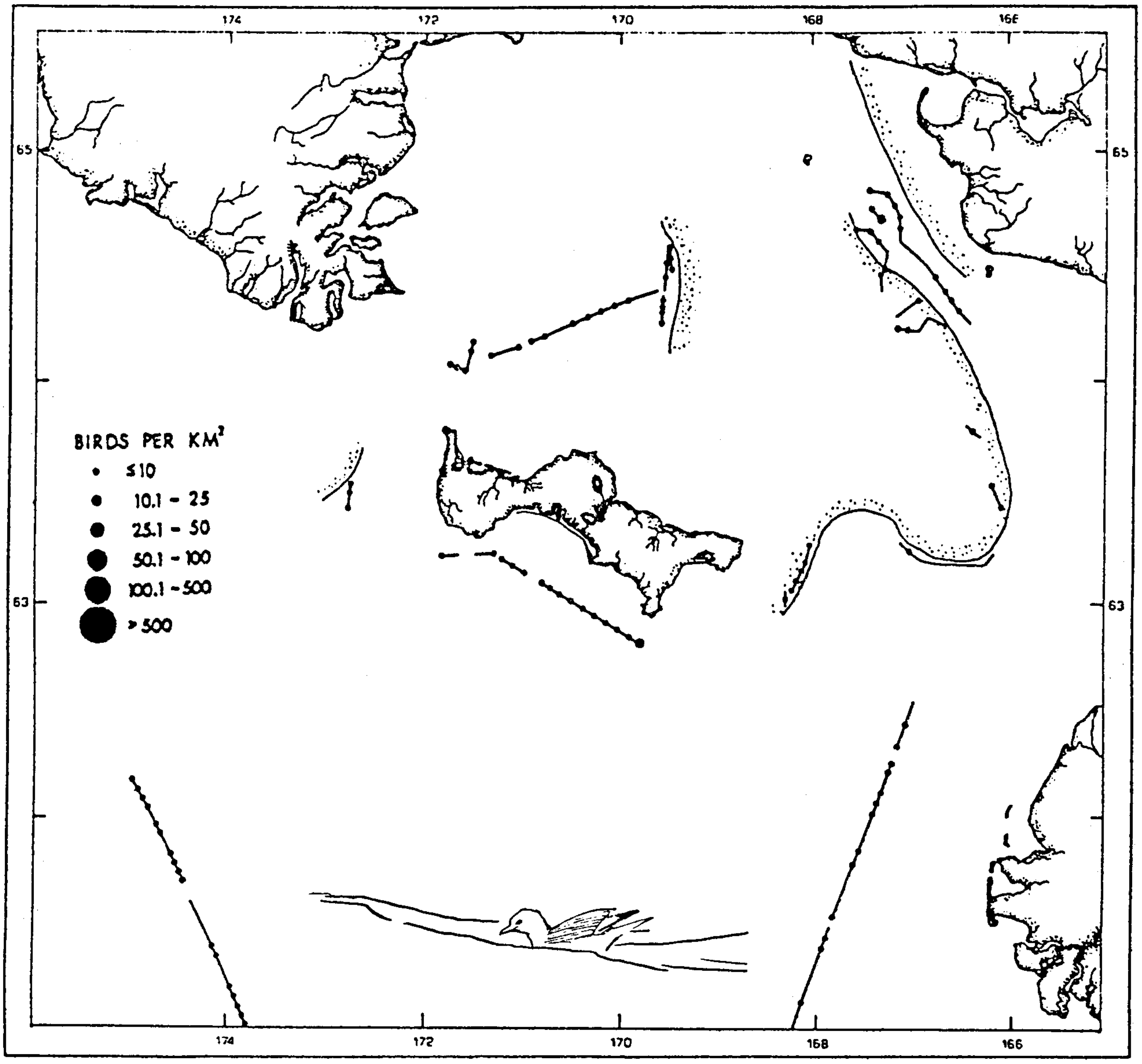


Figure II.B.10b
Black-legged Kittiwakes seen during surface transects aboard Surveyor August 5-13, 1976 (Drury et al.), September 7, 8, 1976 (Gould et al.).

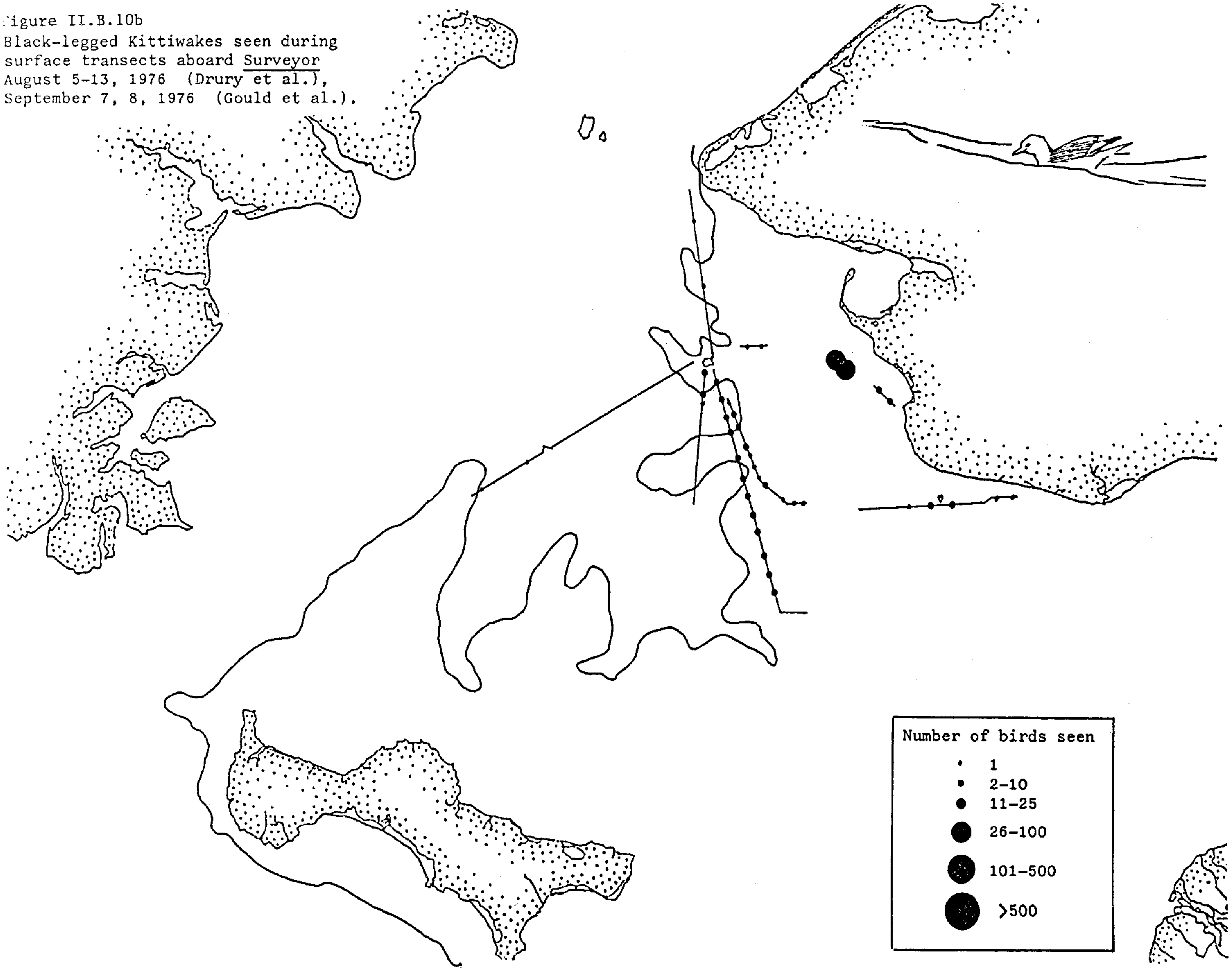


Figure II.C.1a Distribution and abundance of all murres in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 56, page 189, in Divoky et al., 1979.

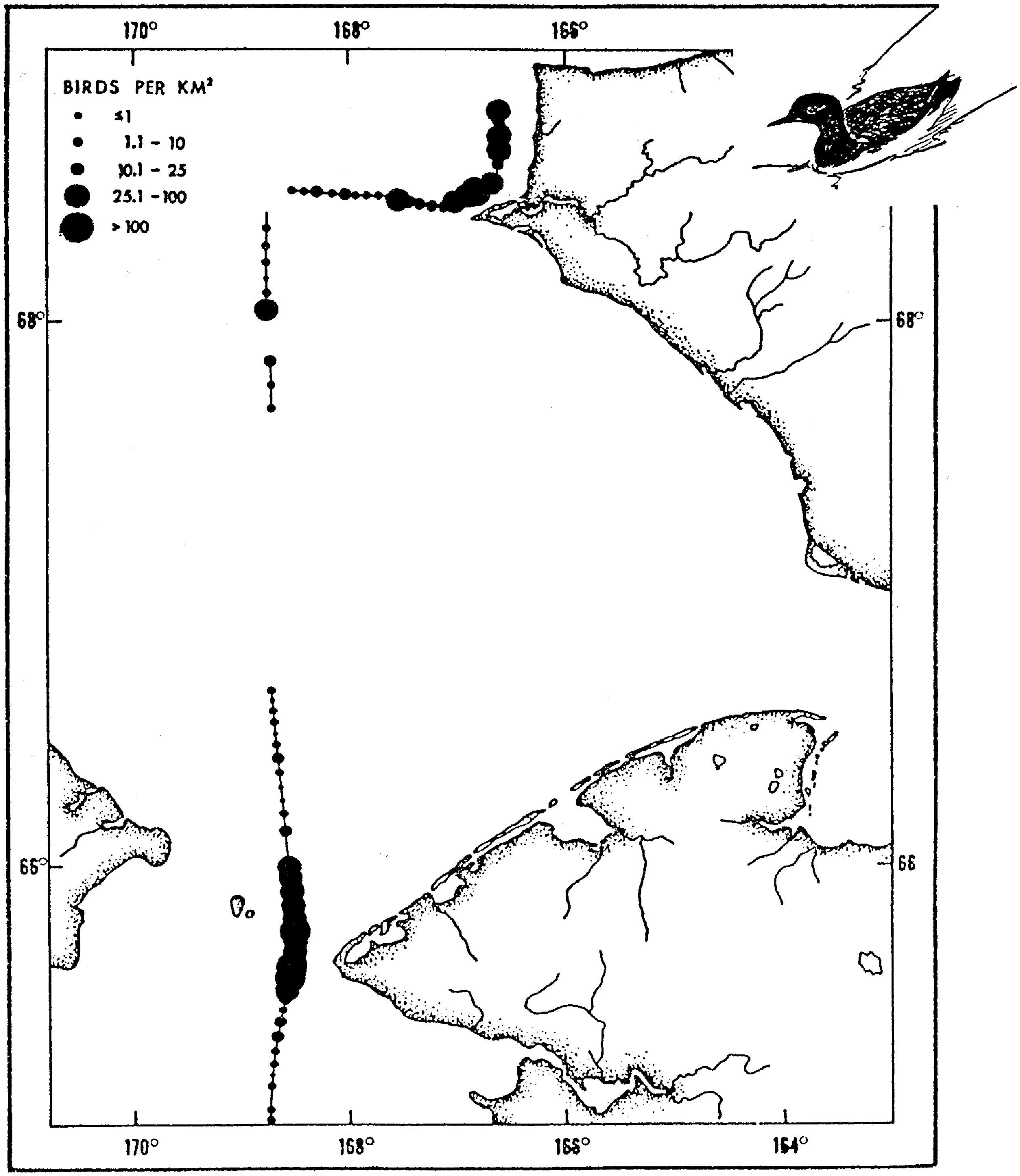


Figure II.C.1b. Distribution and abundance of murres in the Bering Strait and southern Chukchi Sea, September 15-20, & 22, 1976. Figure 172, page 199, in Divoky et al., 1978.

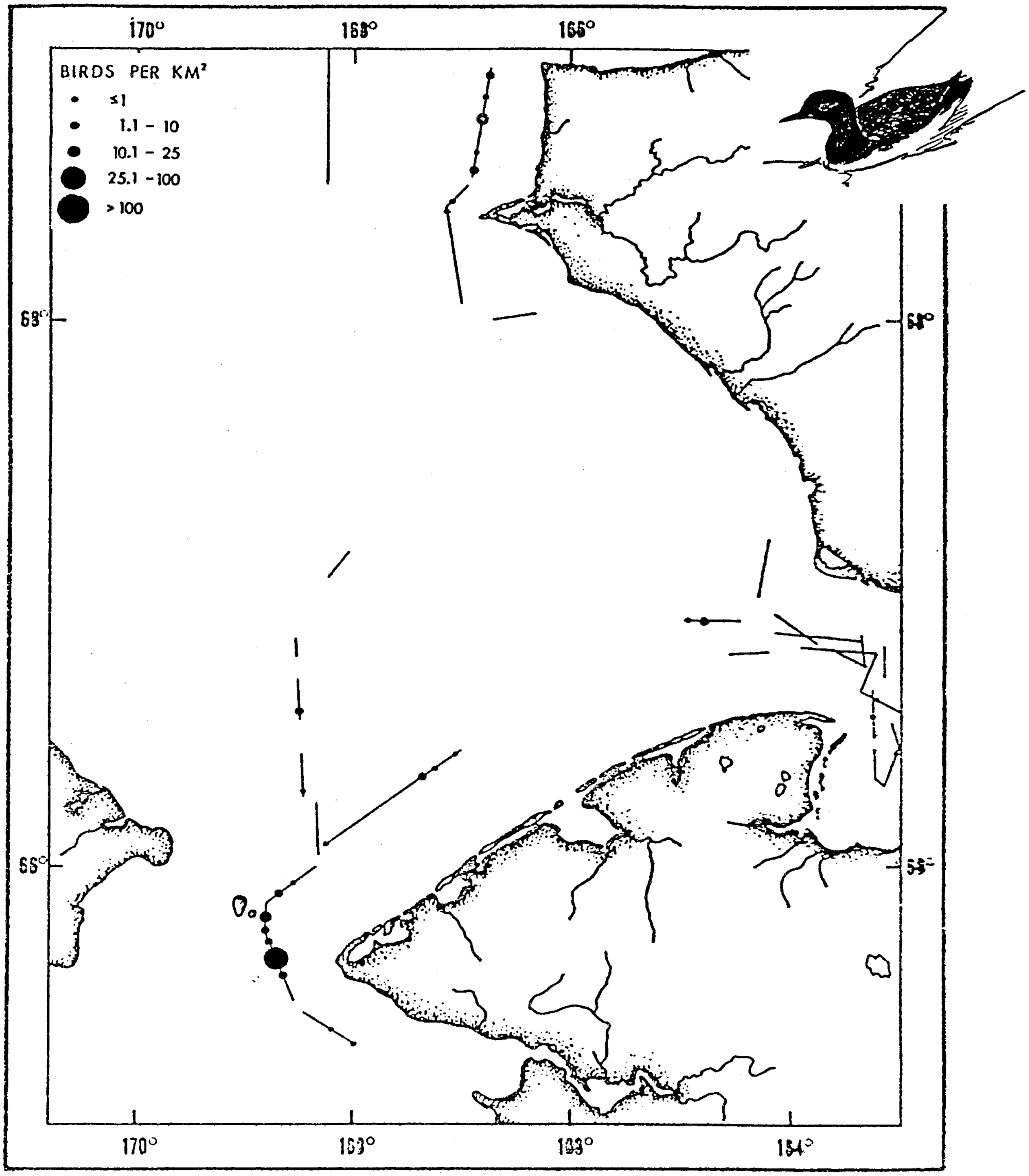


Figure II.C.1c Distribution and abundance of murres in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 79, page 211, in Divoky et al., 1979.

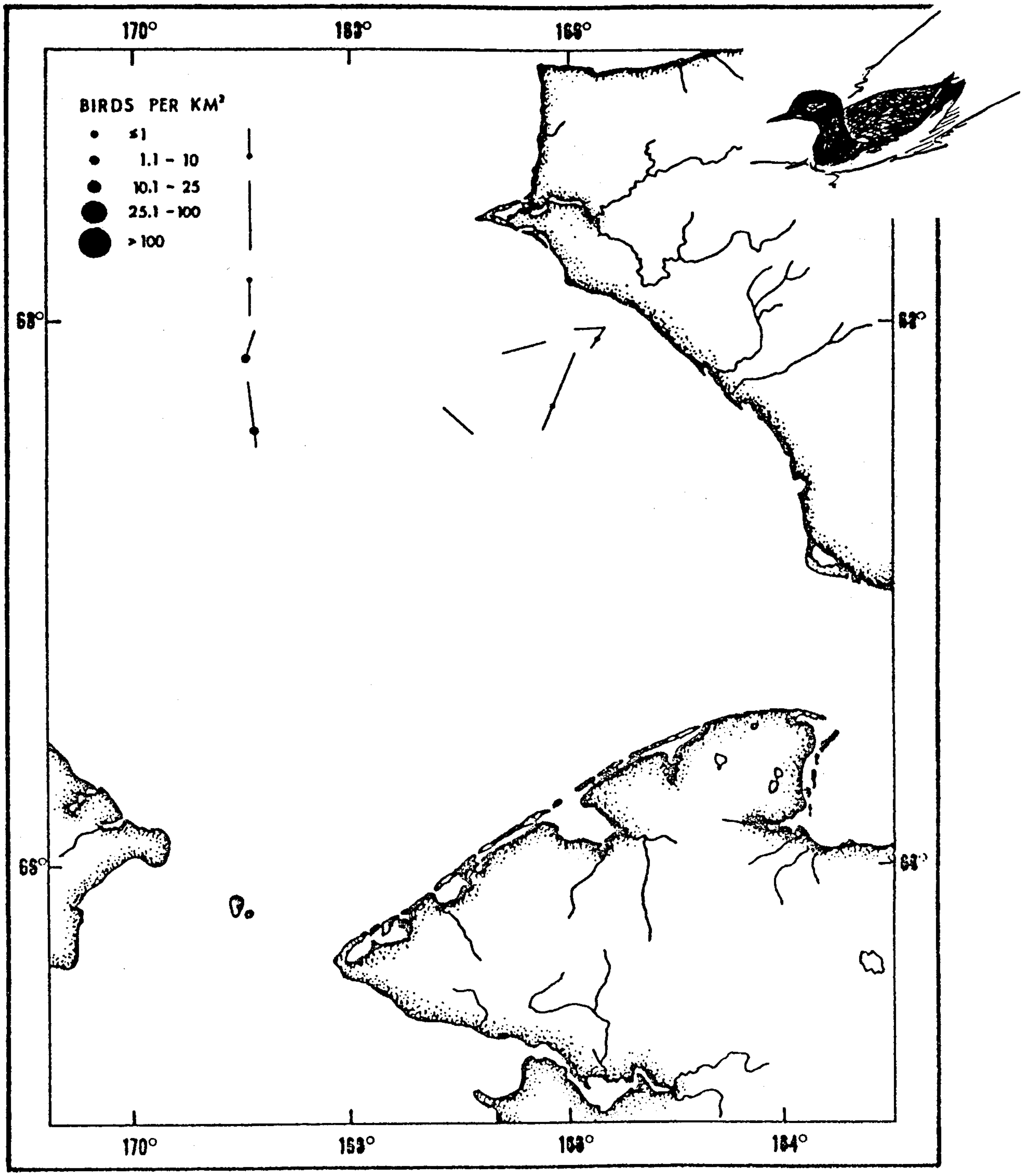


Figure II.C.2 Distribution and abundance of Common Murres in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 52, page 185, in Divoky et al., 1979.

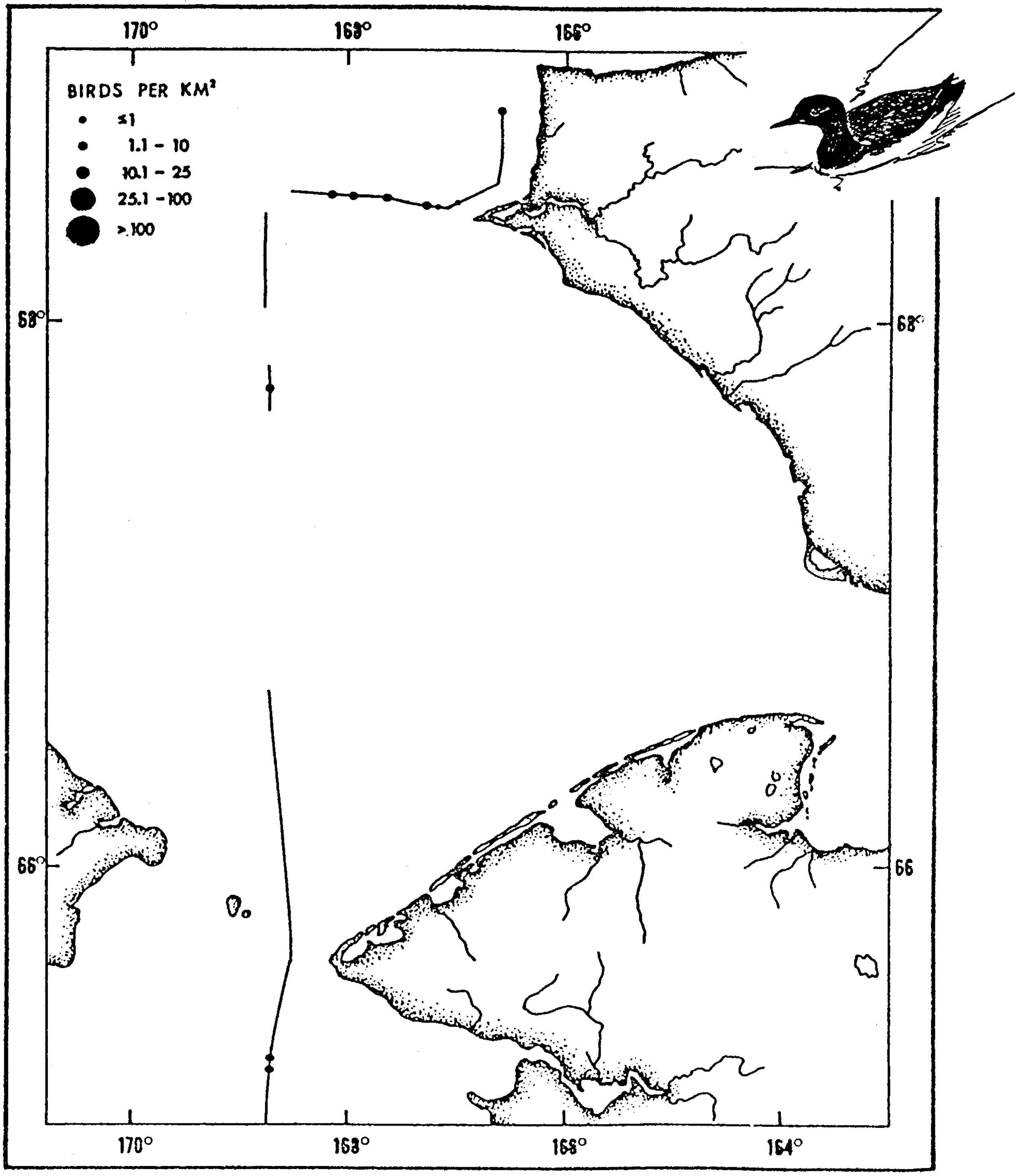


Figure II.C.3 Distribution and abundance of Thick-billed Murres in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 54, page 187, in Divoky et al., 1979.

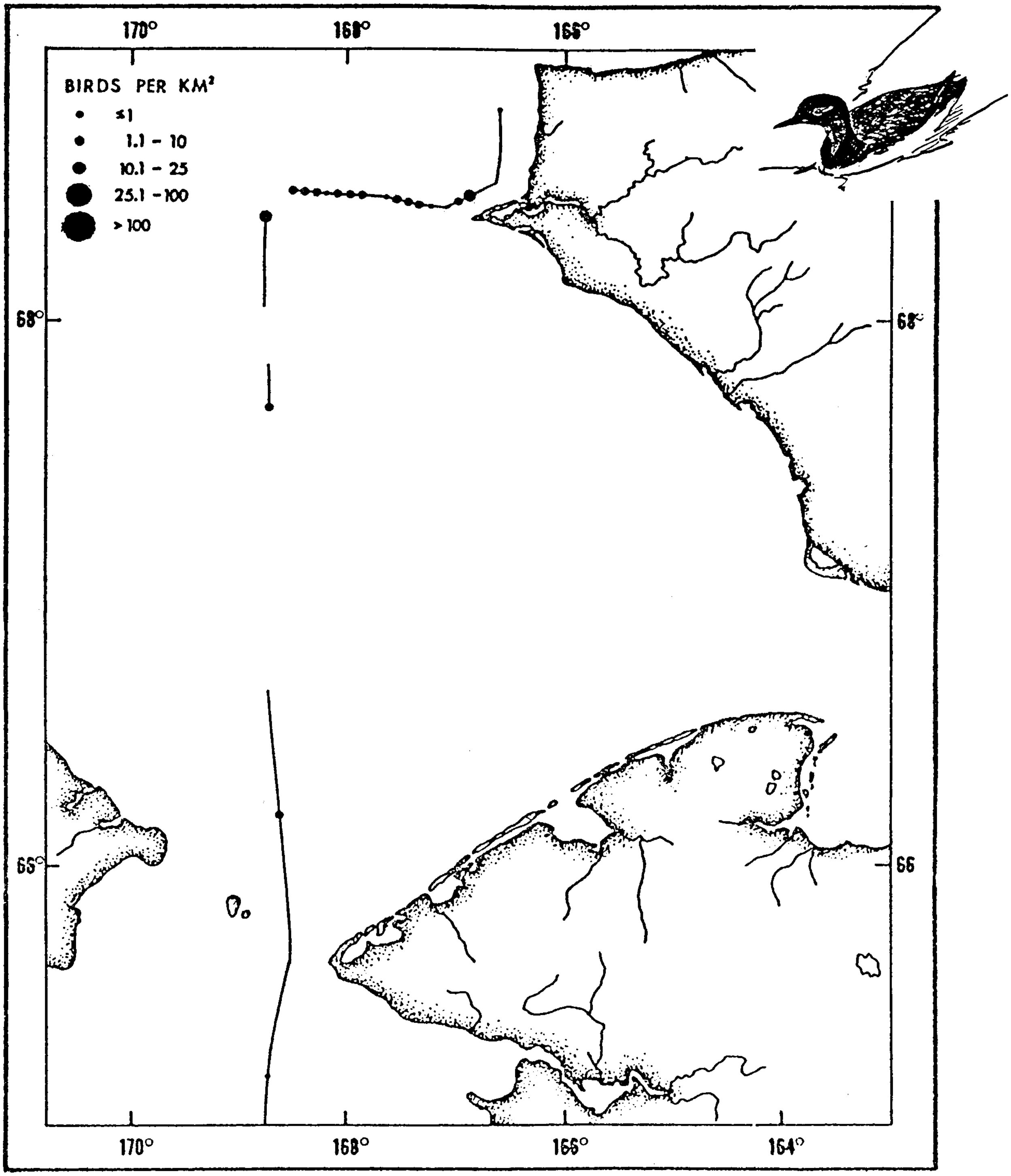


Figure II.C.4a Distribution and abundance of Least Auklets in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 61, page 193, in Divoky et al., 1979.

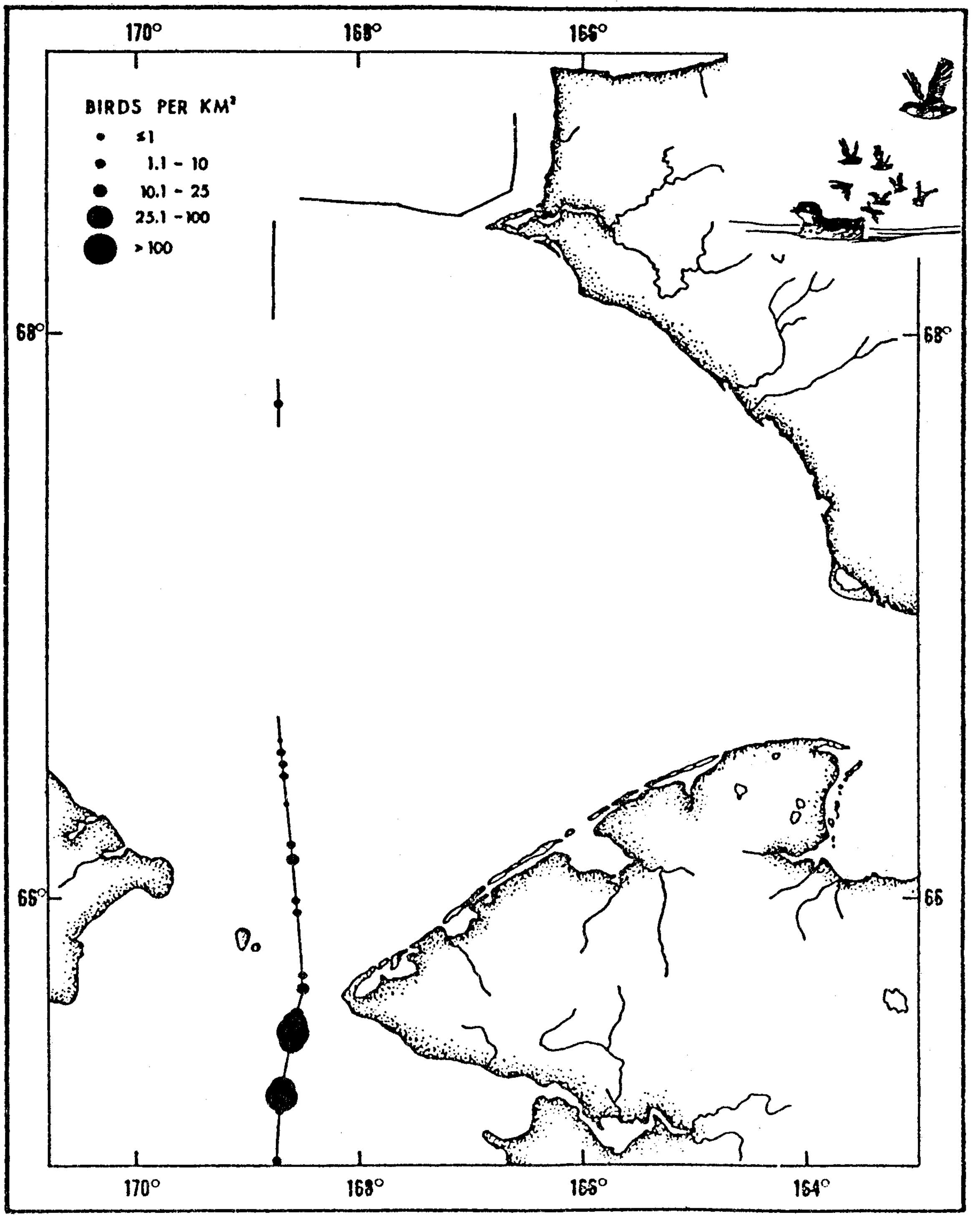


Figure II.C.4b Distribution and abundance of Least Auklets in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 83, page 214, in Divoky et al., 1979.

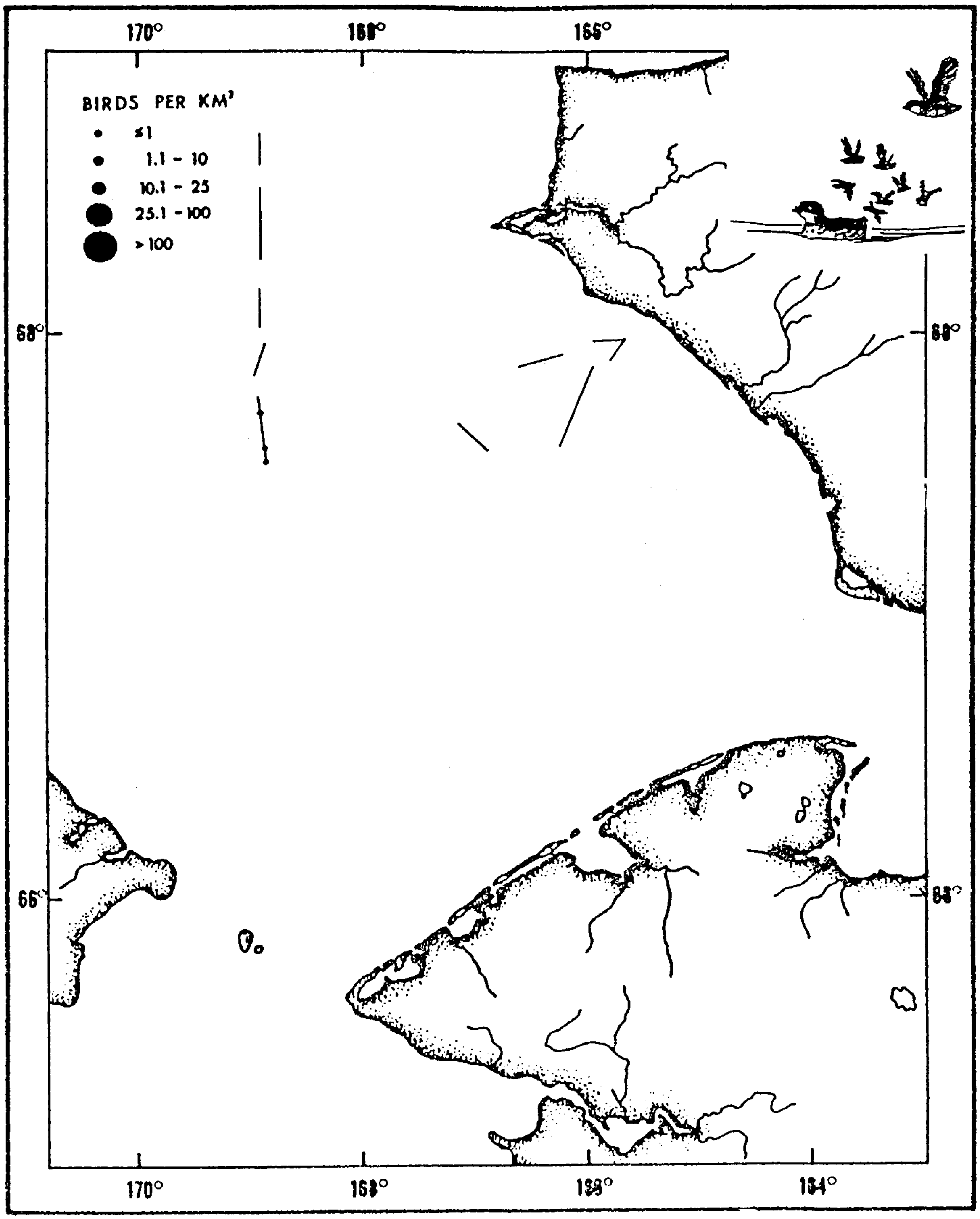


Figure II.C.5a Distribution and abundance of Crested Auklets in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 60, page 192, in Divoky et al., 1979.

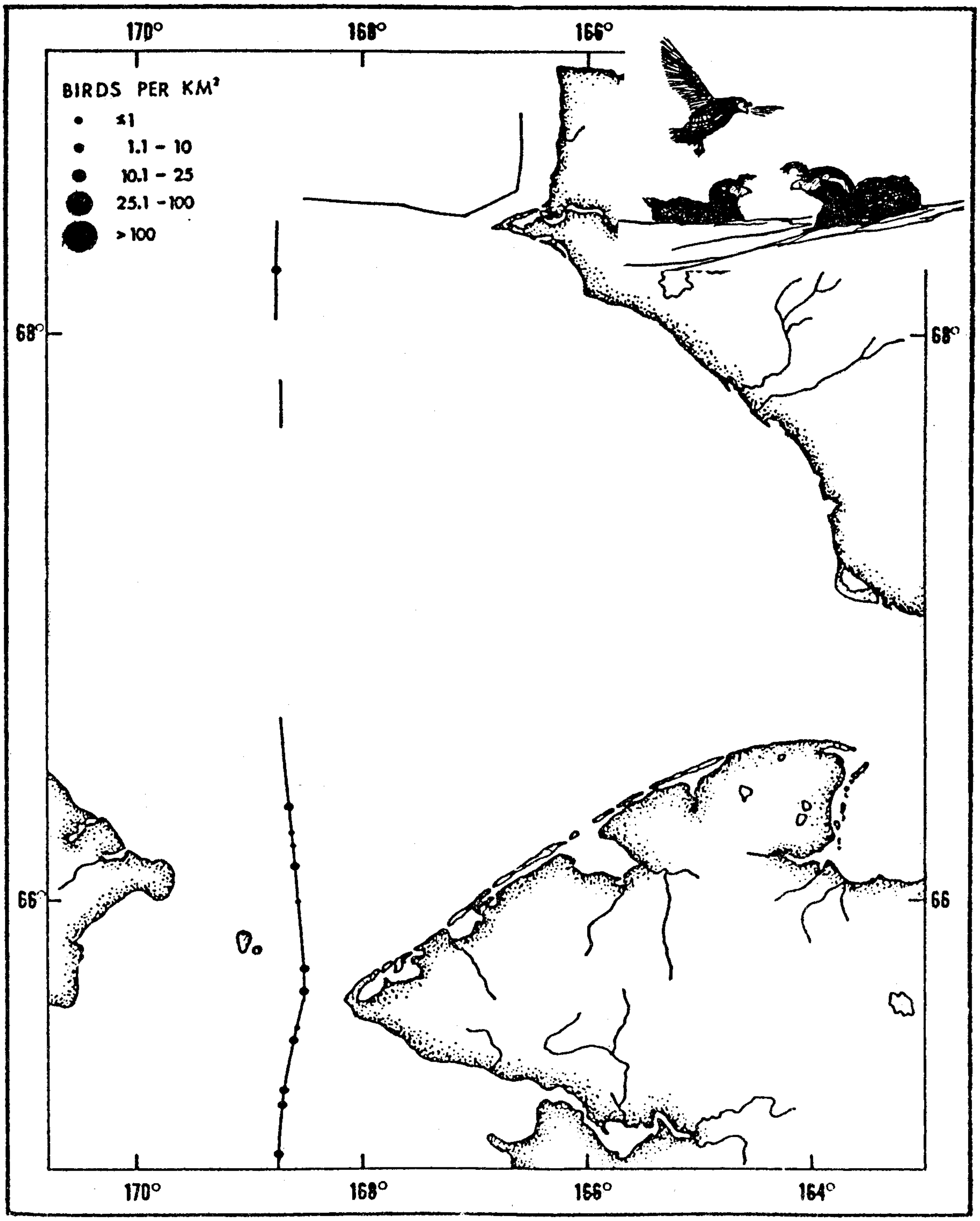


Figure II.C.5b Distribution and abundance of Crested Auklets in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 82, page 213, in Divoky et al., 1979.

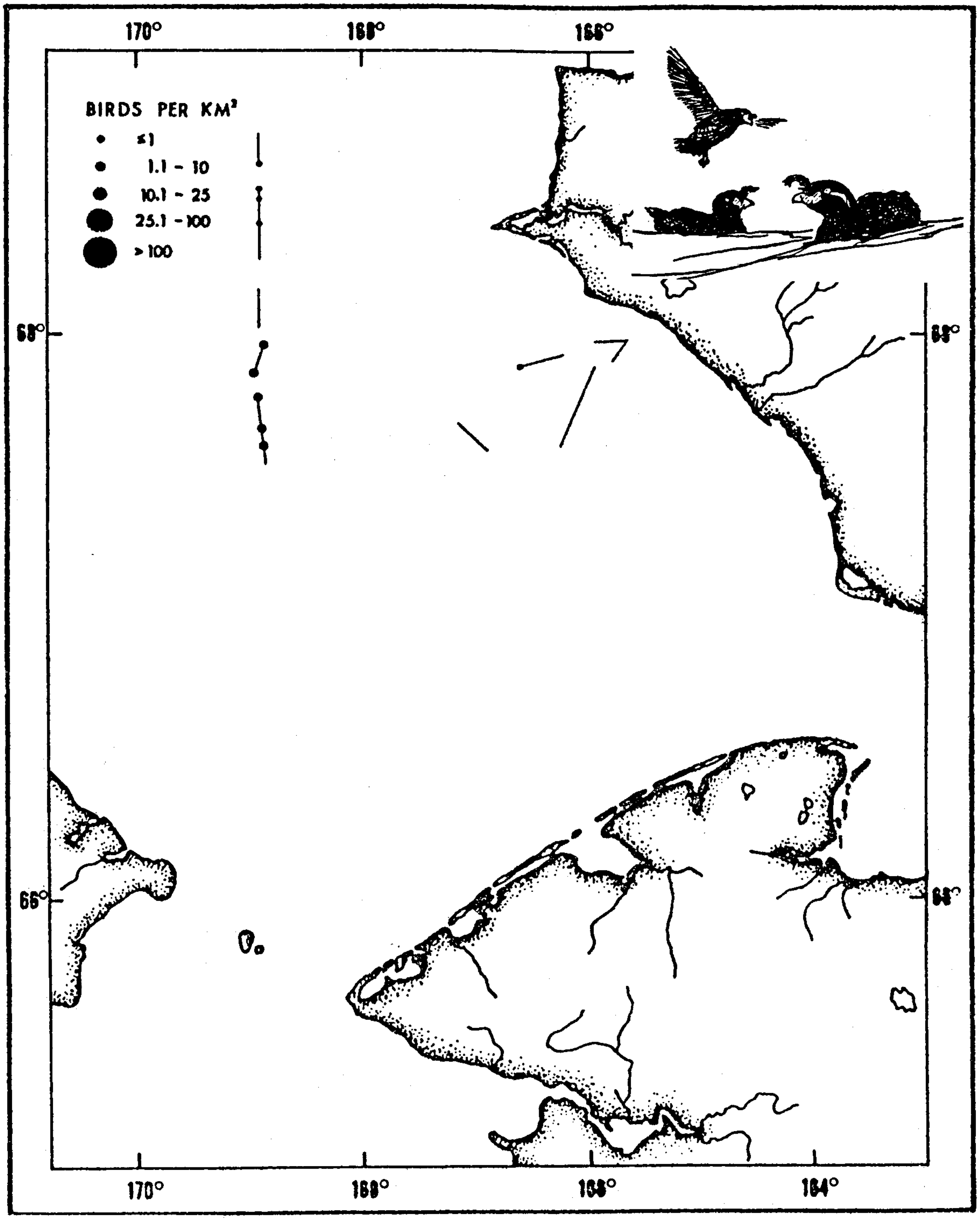


Figure II.C.6a Distribution and abundance of Parakeet Auklets in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 59, page 191, in Divoky et al., 1979.

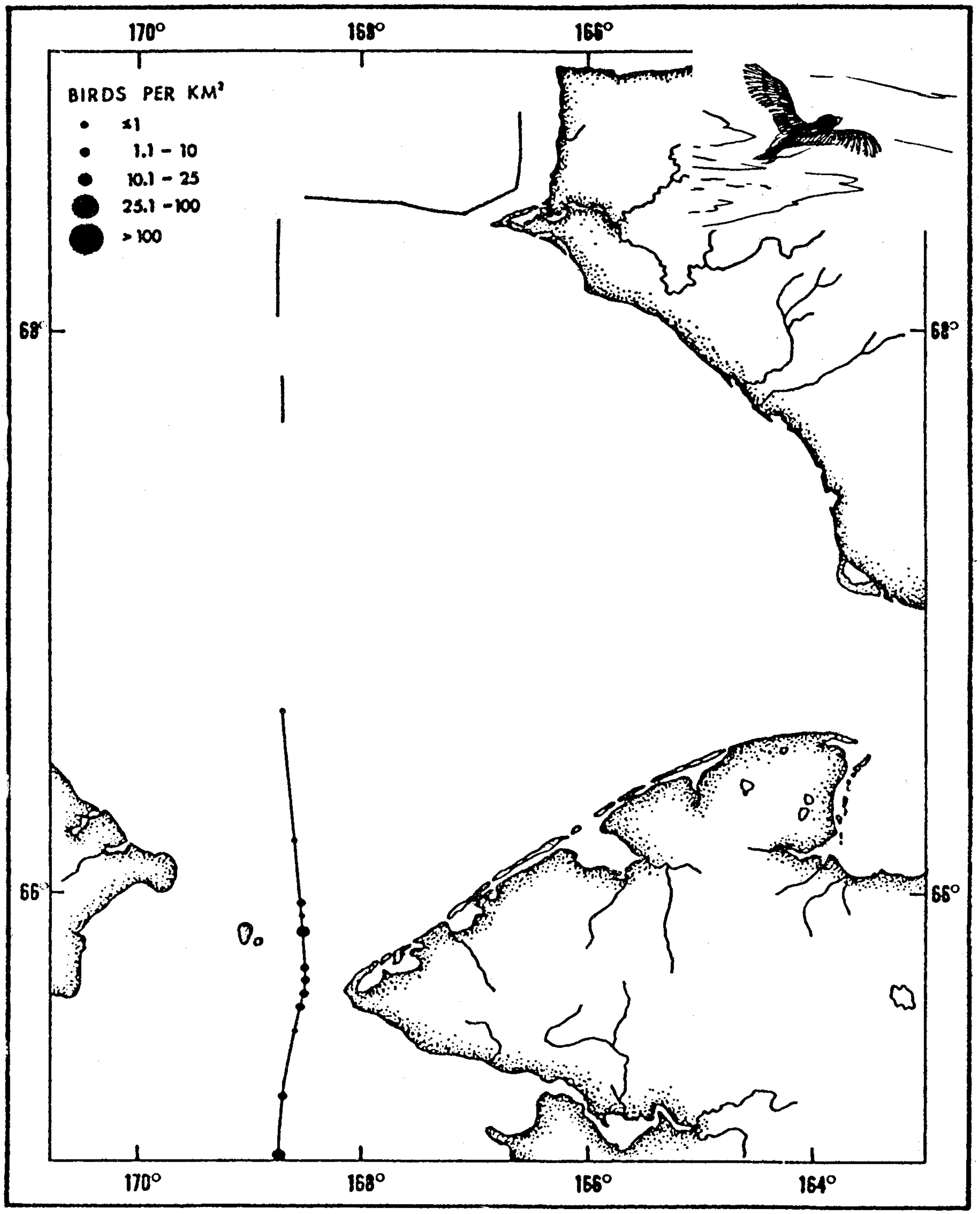


Figure II.C.6b Distribution and abundance of Parakeet Auklets in the Bering Strait and southern Chukchi Sea, September 15-20, & 22, 1976. Figure 174, page 201, in Divoky et al., 1978.

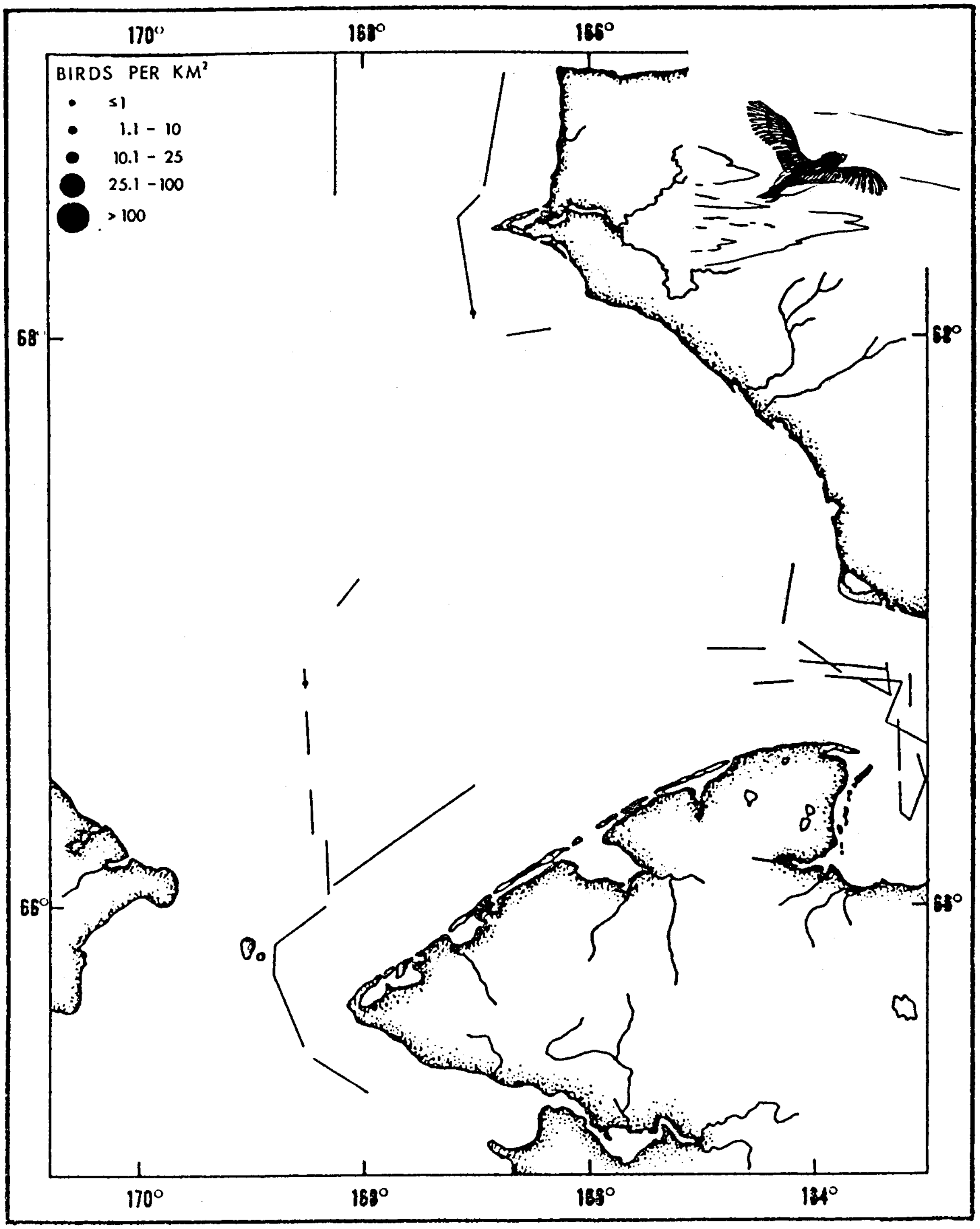


Figure II.C.6c Distribution and abundance of Parakeet Auklets in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 81, page 212, in Divoky et al., 1979.

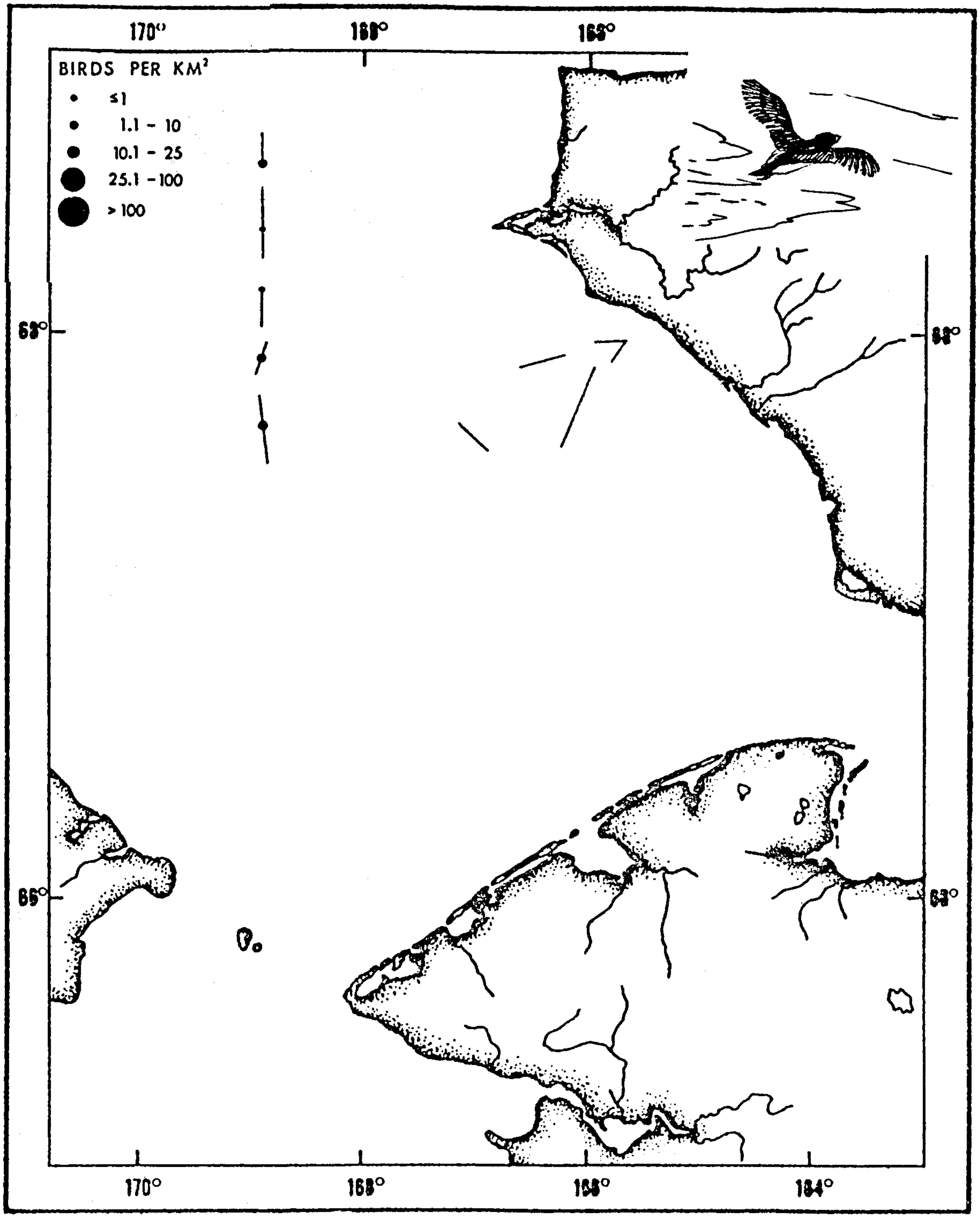


Figure II.C.7a Distribution and abundance of Horned Puffins in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 63, page 195, in Divoky et al., 1979.

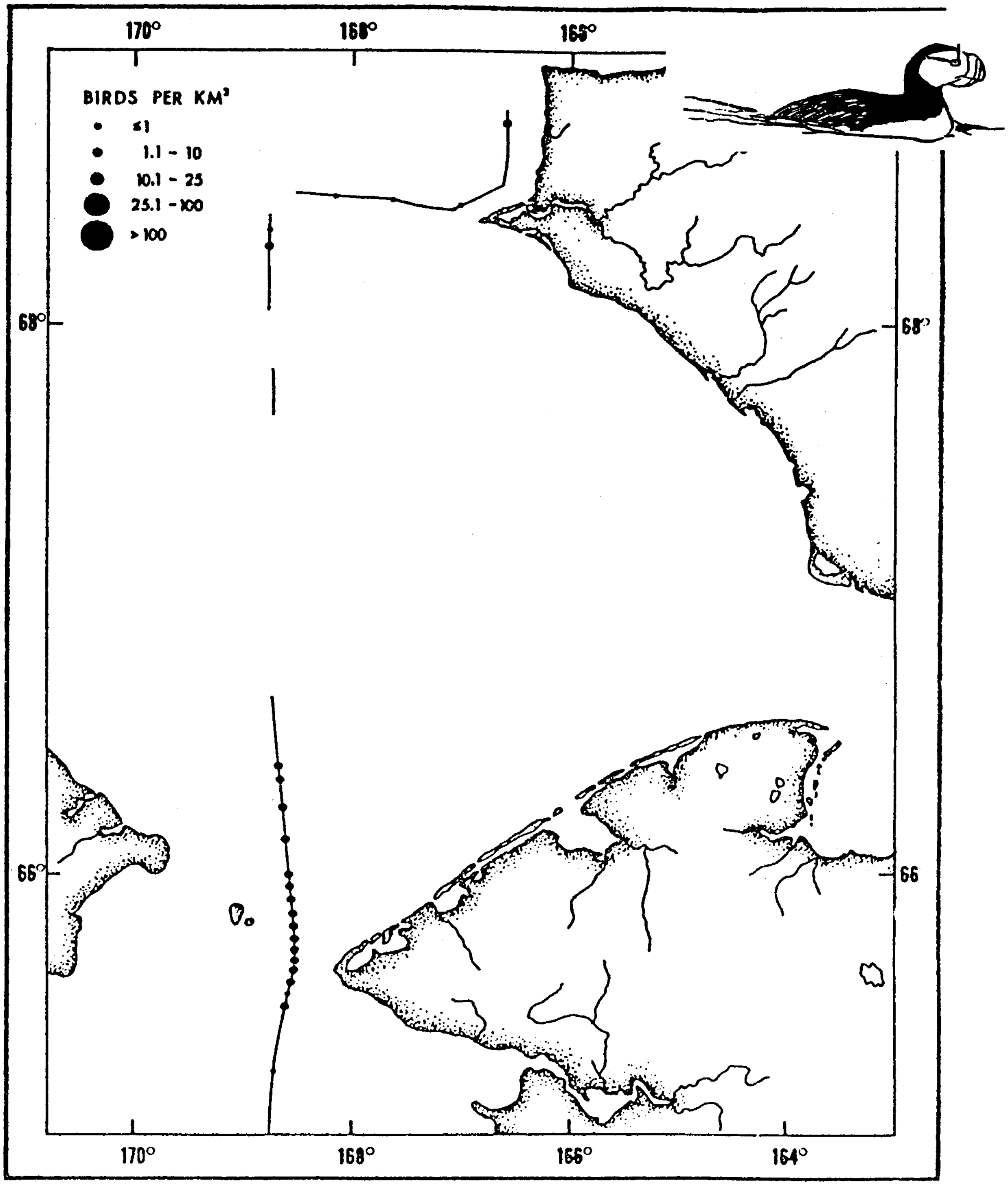
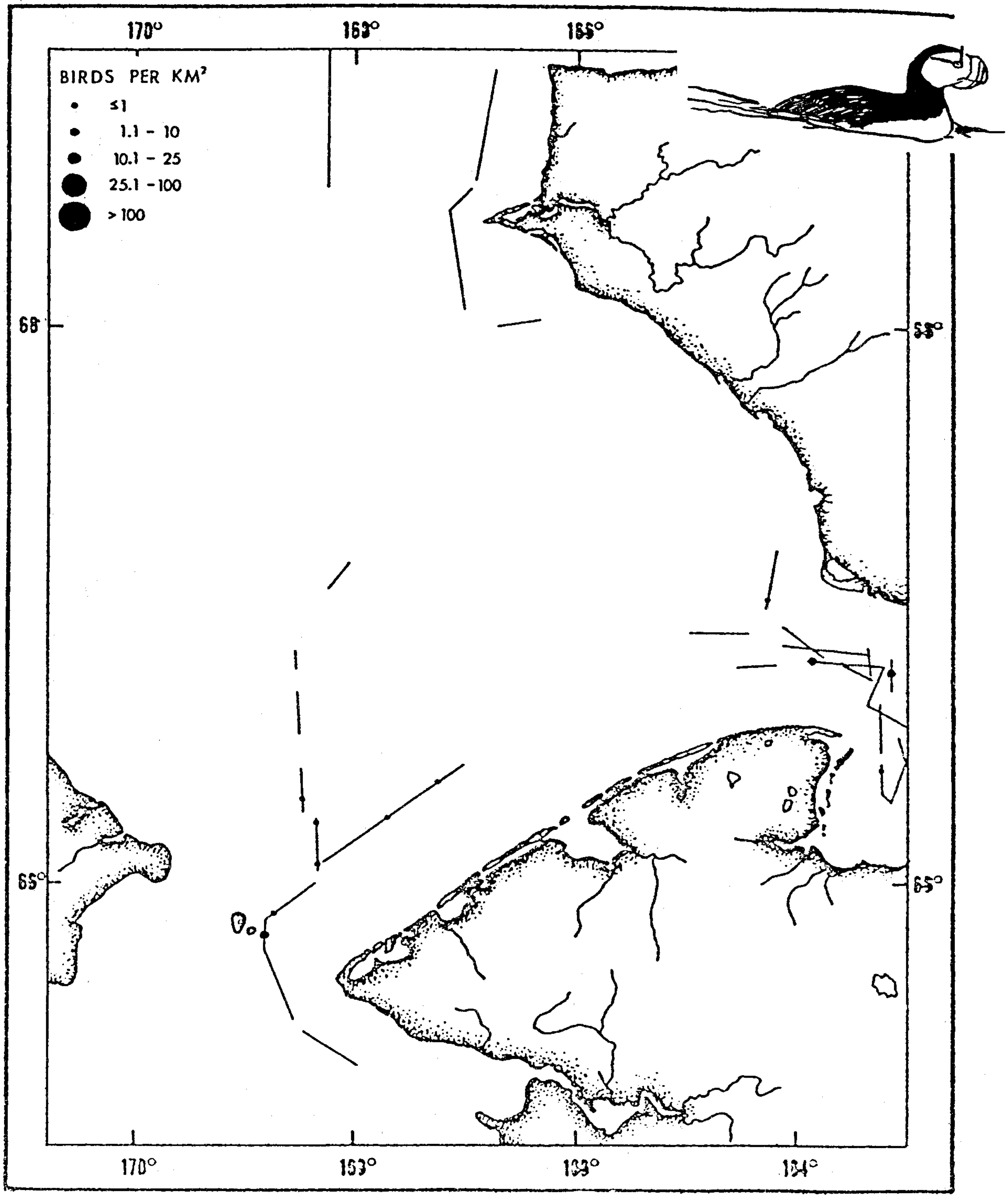


Figure II.C.7b Distribution and abundance of Horned Puffins in the Bering Strait and southern Chukchi Sea, September 15-20, &22, 1976. Figure 178, page 205, in Divoky et al., 1978.



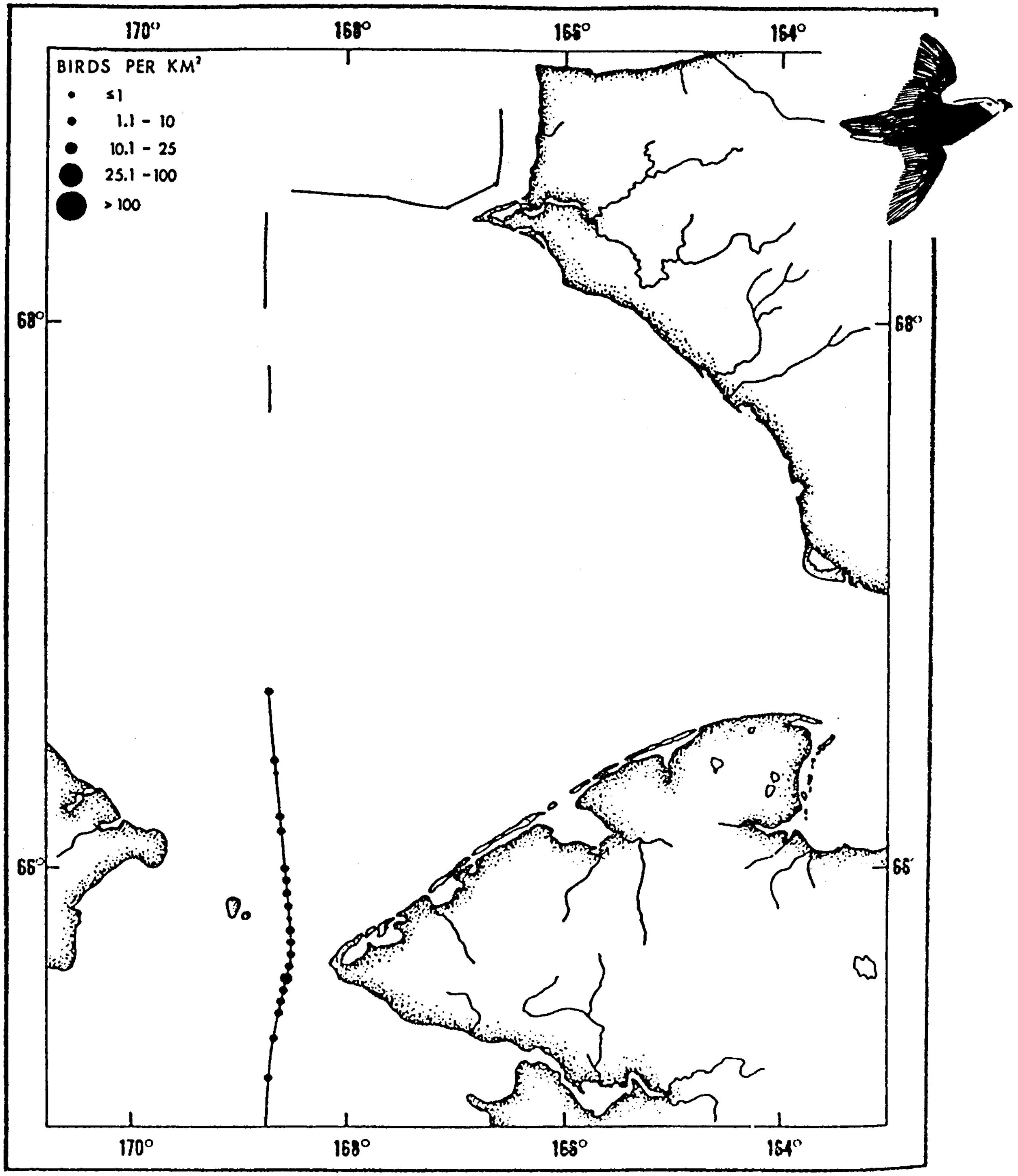


Figure II.C.8a Distribution and abundance of Tufted Puffins in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 65, page 197, in Divoky et al., 1979.

Figure II.C.8b Distribution and abundance of Tufted Puffins in the Bering Strait and southern Chukchi Sea, September 15-20, &22, 1976. Figure 179, pate 206, in Divoky et al., 1978.

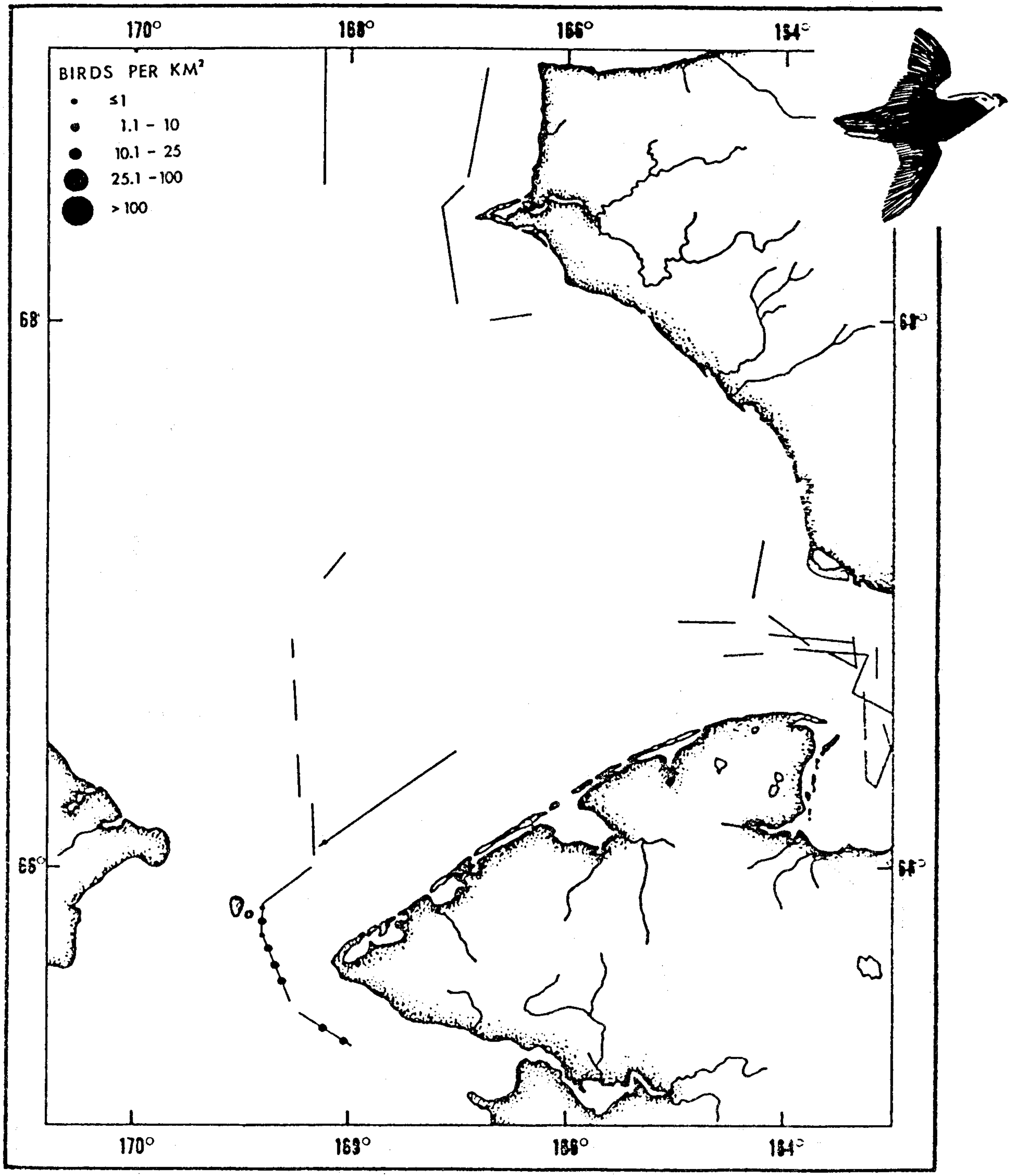


Figure II.C.9a Distribution and abundance of Glaucous Gulls in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 46, page 180, in Divoky et al., 1979.

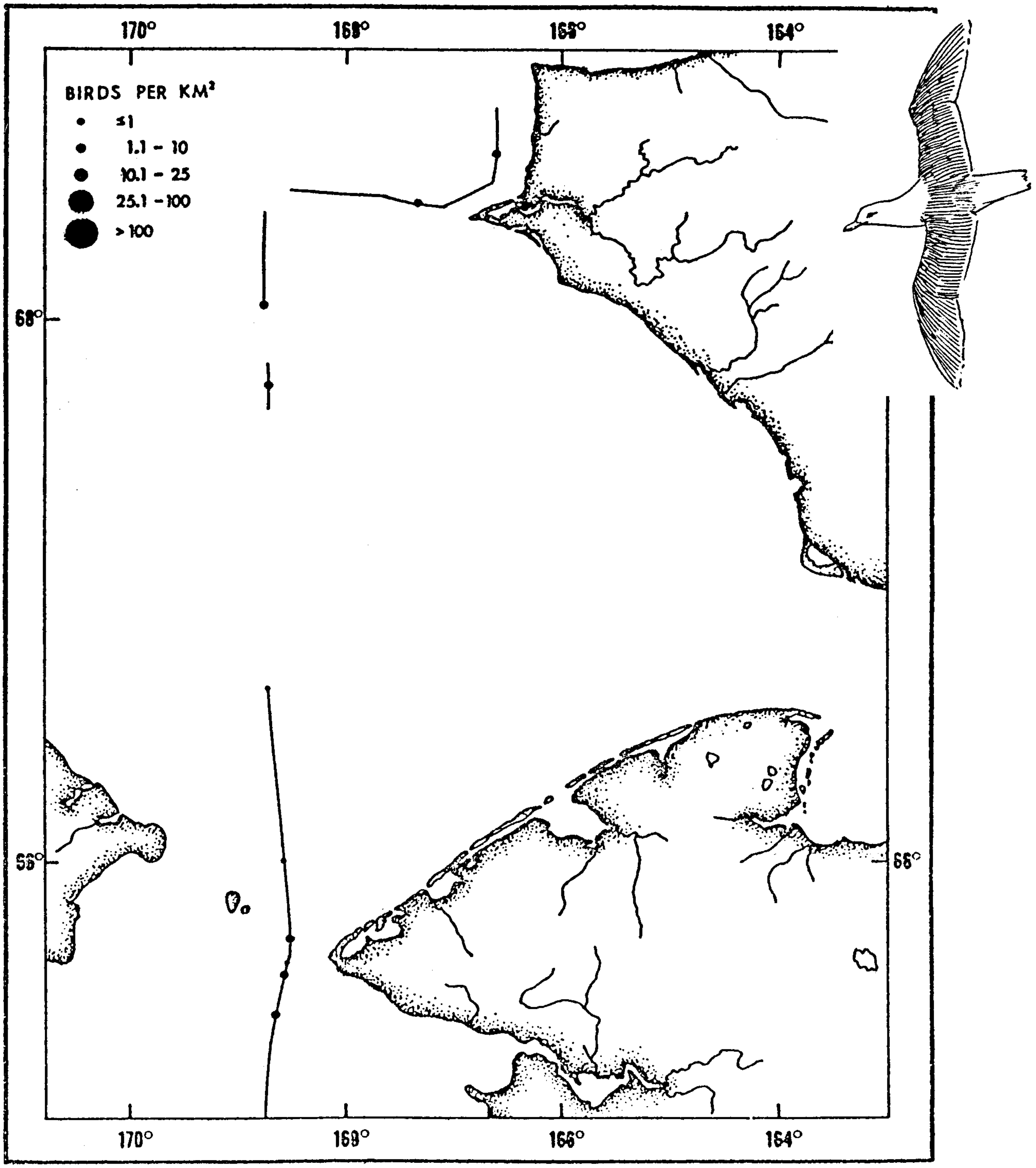


Figure II.C.9b Distribution and abundance of Glaucous Gulls in the Bering Strait and southern Chukchi Sea, September 15-20, & 22, 1976. Figure 168, page 195, in Divoky et al., 1978.

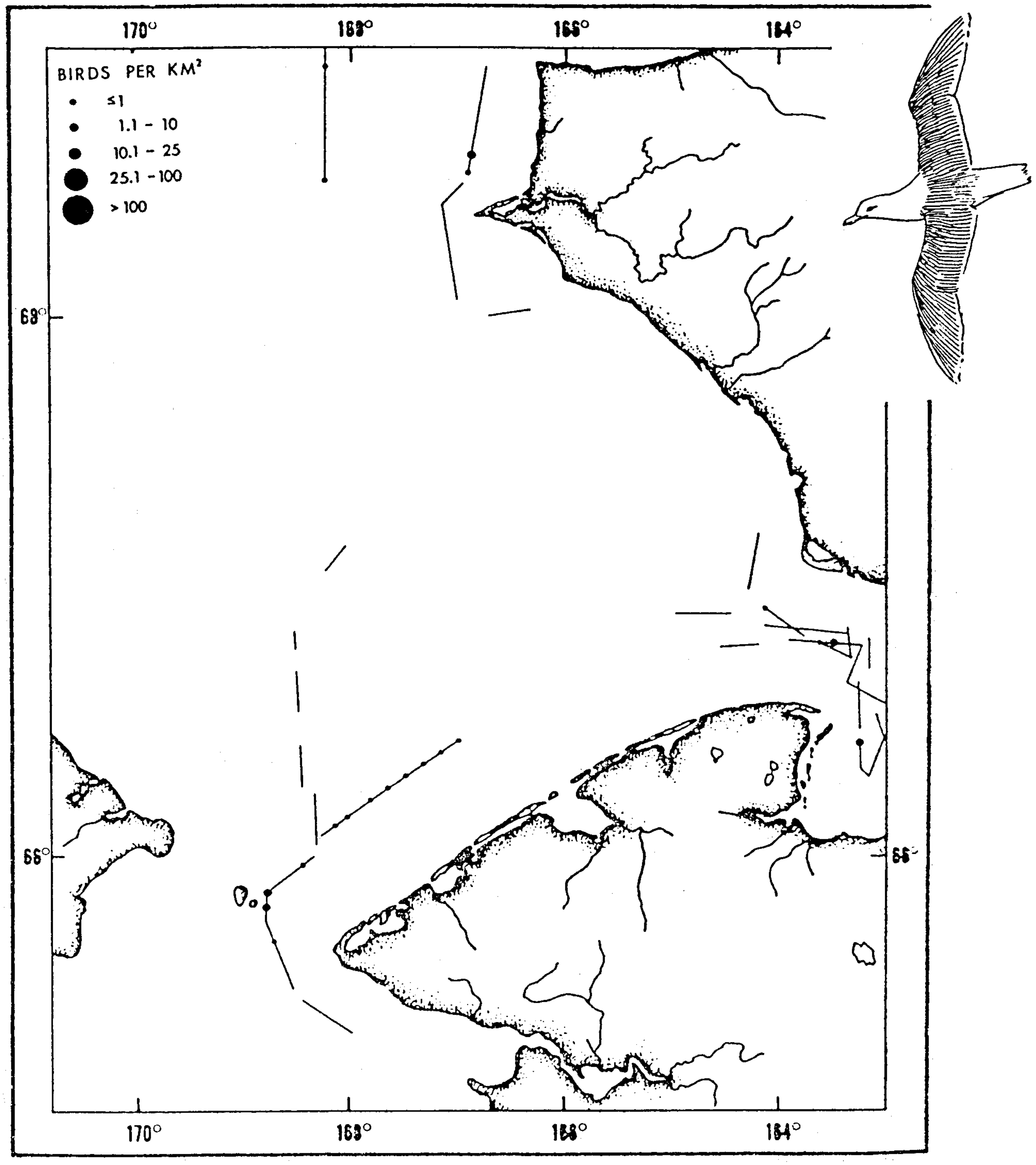


Figure II.C.9c Distribution and abundance of Glaucous Gulls in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 76, page 208, in Divoky et al., 1979.

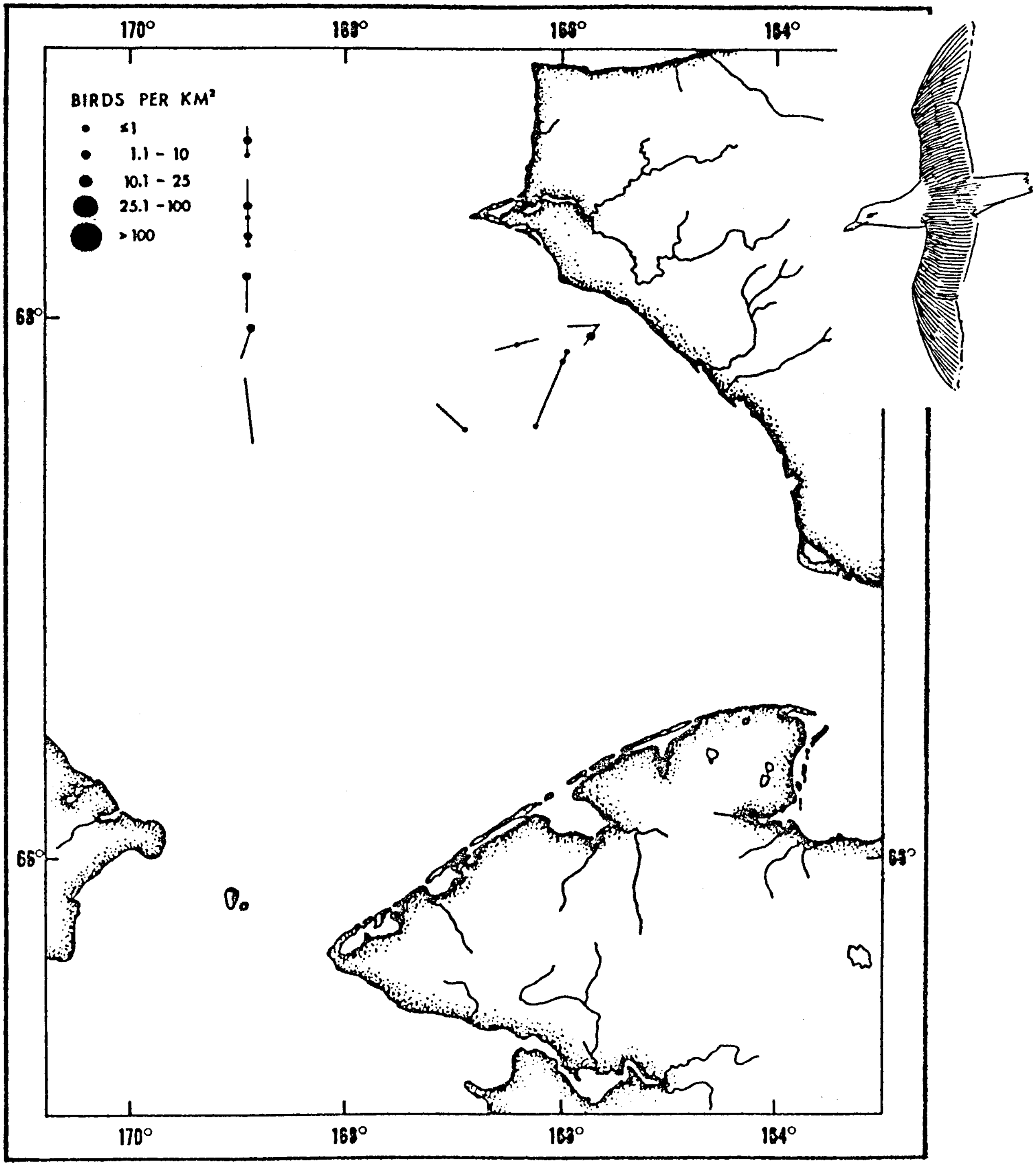


Figure II.C.10a Distribution and abundance of Black-legged Kittiwakes in the Bering Strait and southern Chukchi Sea, July 31 - August 1, 1975. Figure 48, page 182, in Divoky et al., 1979.

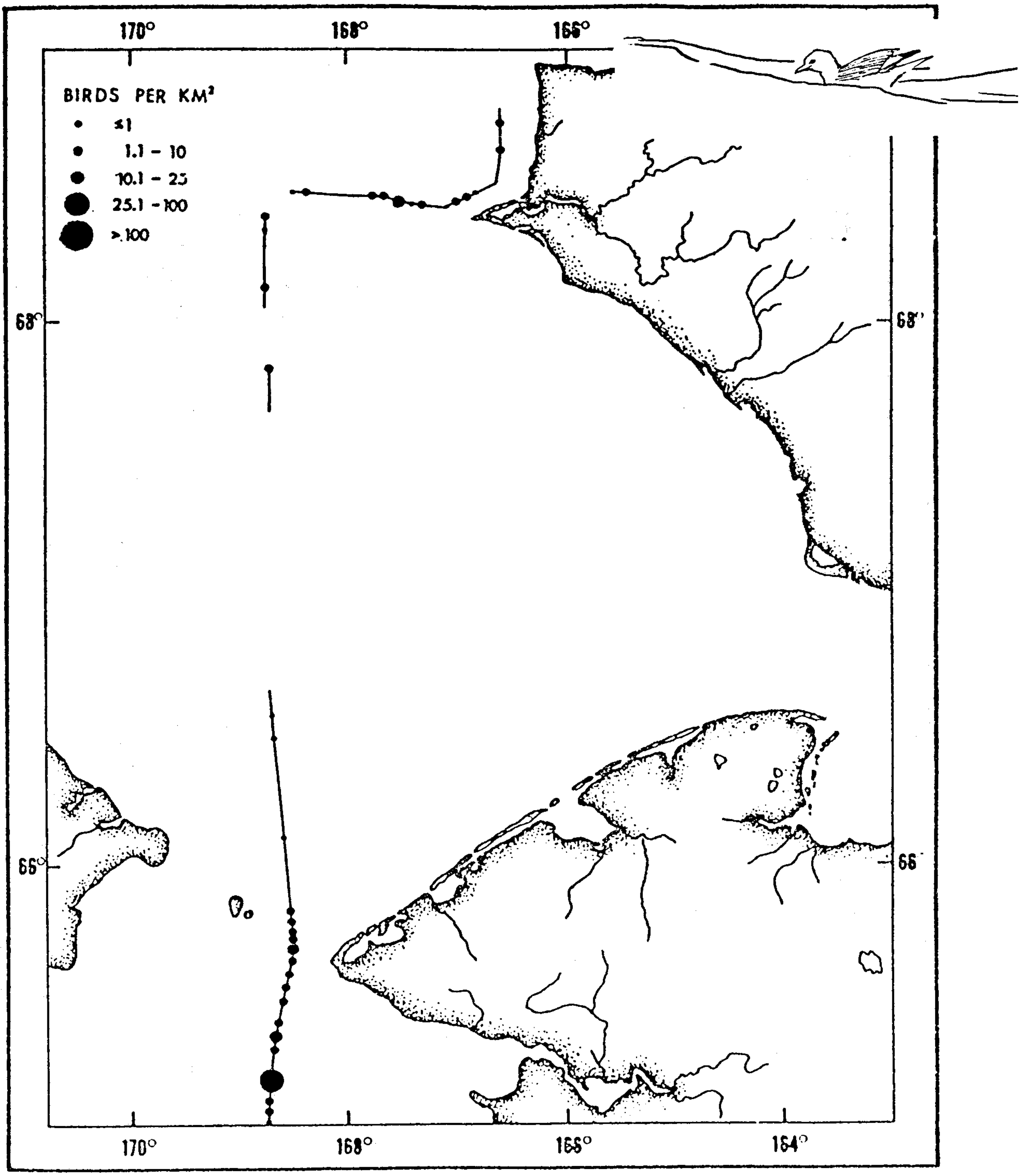


Figure II.C.10b Distribution and abundance of Black-legged Kittiwakes in the Bering Strait and southern Chukchi Sea, September 15-20, & 22, 1976. Figure 170, page 197, in Divoky et al, 1978.

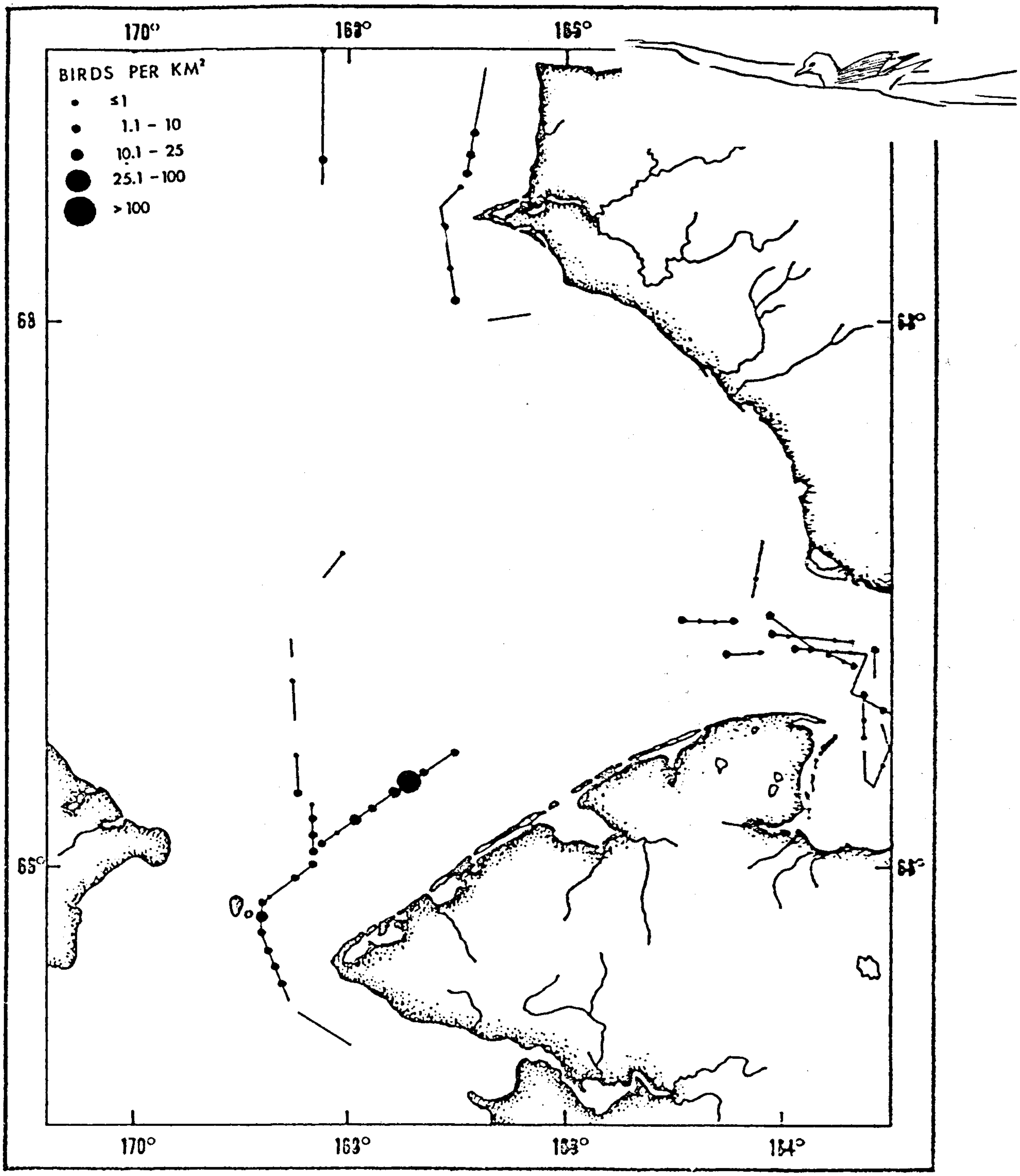


Figure II.C.10c Distribution and abundance of Black-legged Kittiwakes in the Bering Strait and southern Chukchi Sea, September 28-29, 1976. Figure 77, page 209, in Divoky et al., 1979.

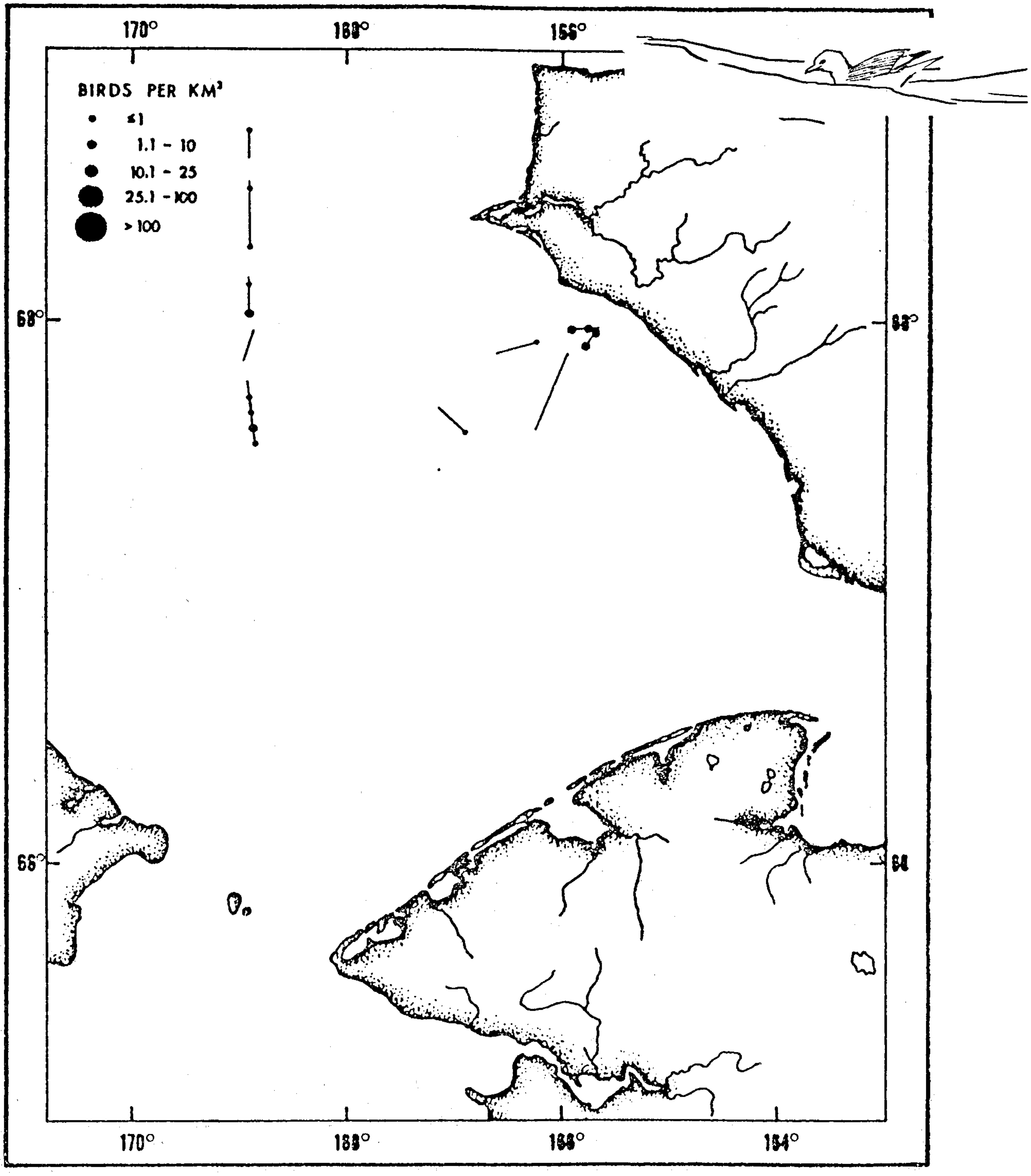


Figure II.D.1 . Distribution and abundance of murres in the northern Chukchi Sea, September 20-22, 1976. Figure 173, page 200, in Divoky et al., 1978.

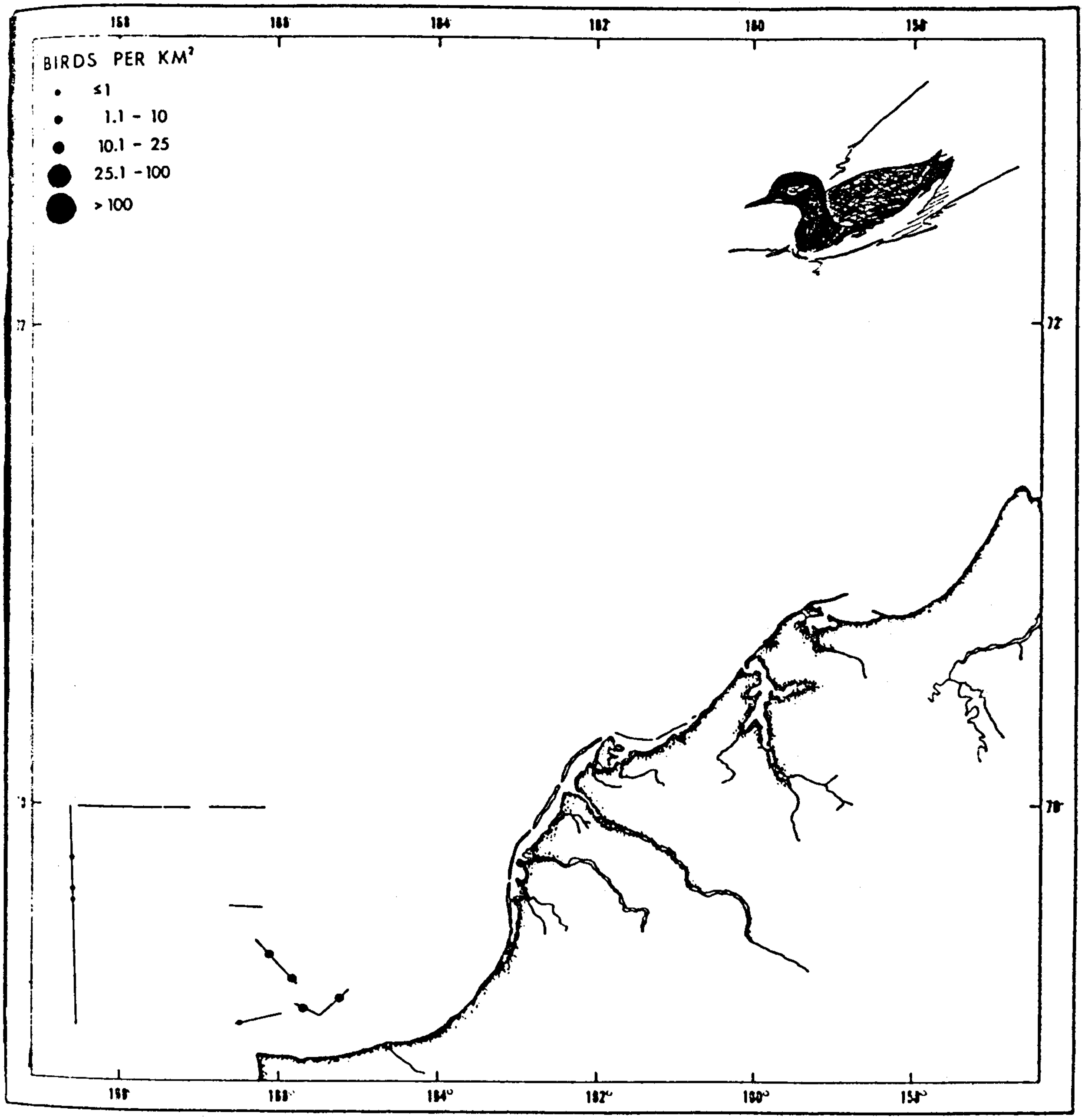


Figure II.D.2 Distribution and abundance of Common Murres in the northern Chukchi Sea, August 2-25, 1975.
Figure 51, page 184, in Divoky et al., 1979.

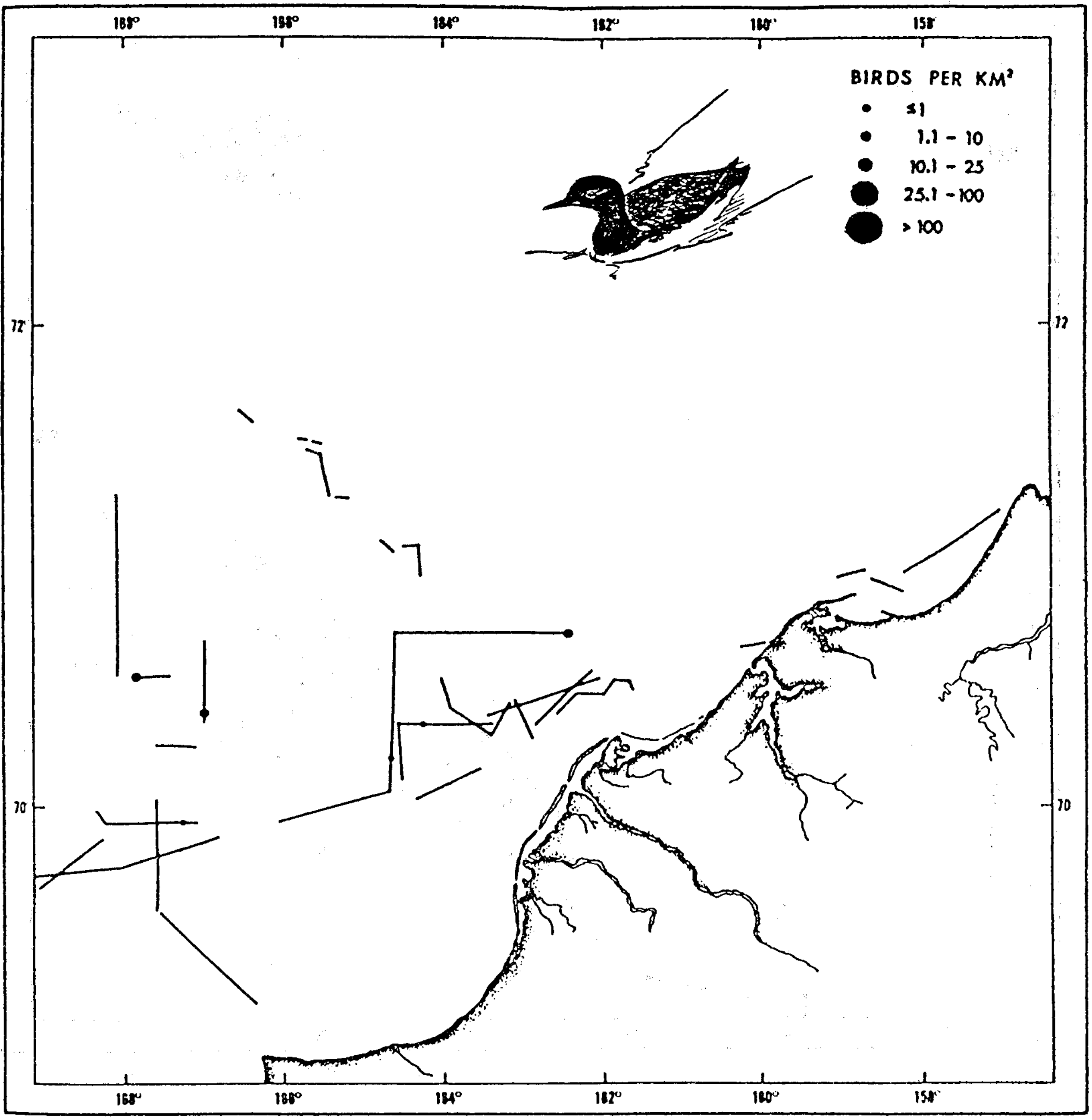


Figure II.D.3 Distribution and abundance of Thick-billed Murres in the northern Chukchi Sea, August 2-25, 1975.
Figure 53, page 186, in Divoky et al., 1979.

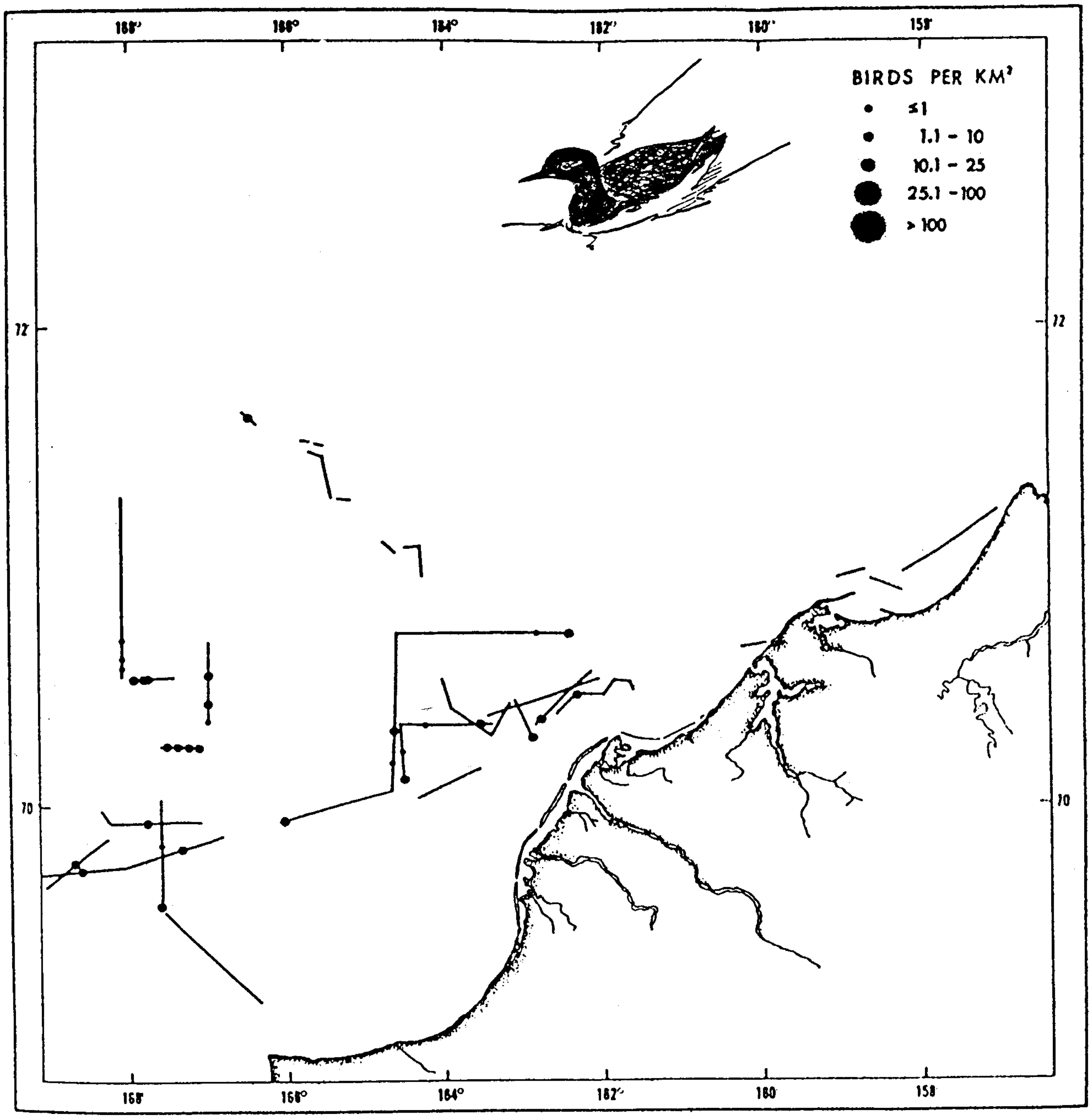


Figure II.D.4 Distribution and abundance of Parakeet Auklets in the northern Chukchi Sea, September 20-22, 1976. Figure 175, page 202, in Divoky et al., 1978.

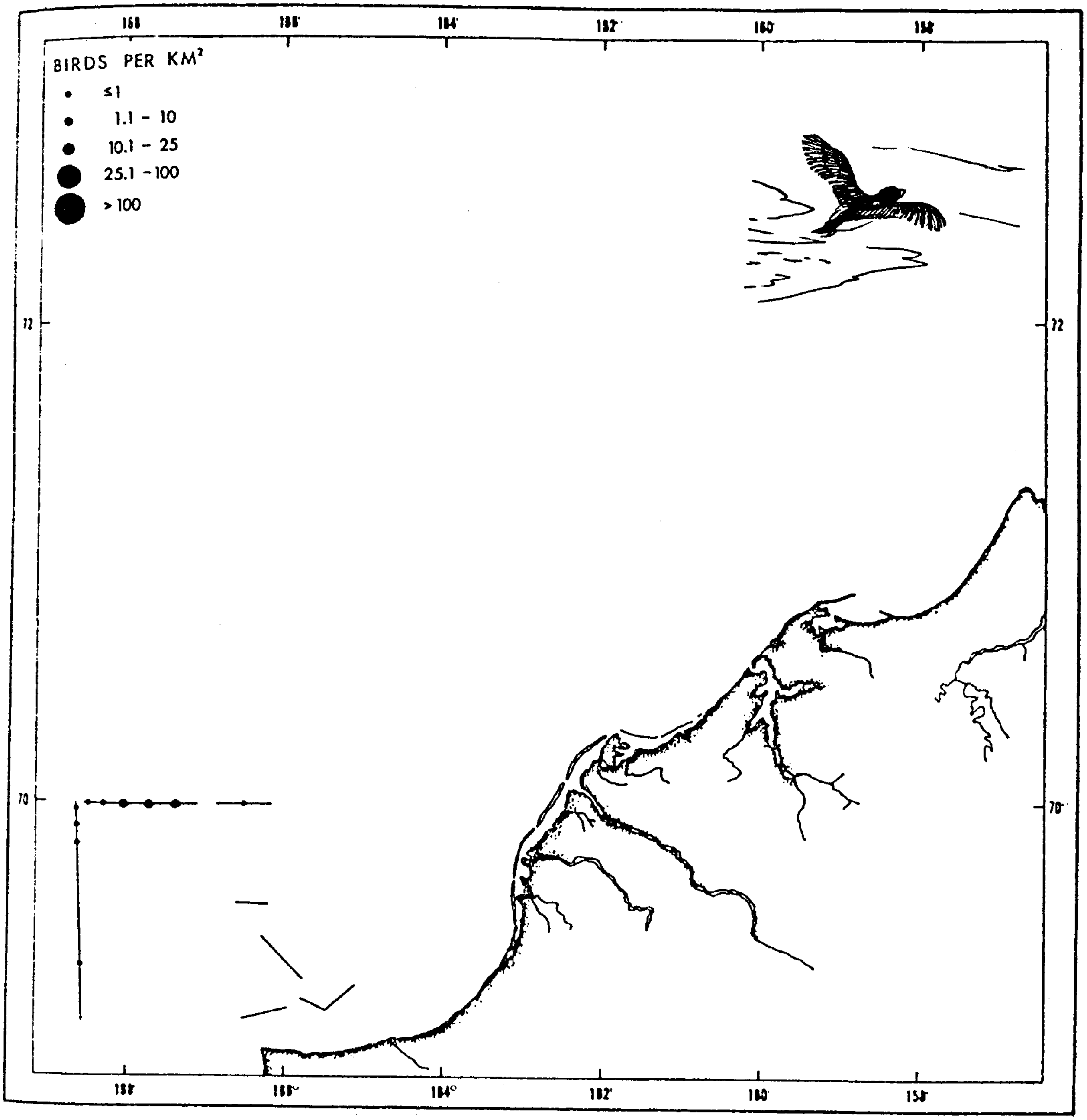


Figure II.D.5 Distribution and abundance of Horned Puffins in the northern Chukchi Sea, August 2-25, 1975.
Figure 62, page 194, in Divoky et al., 1979.

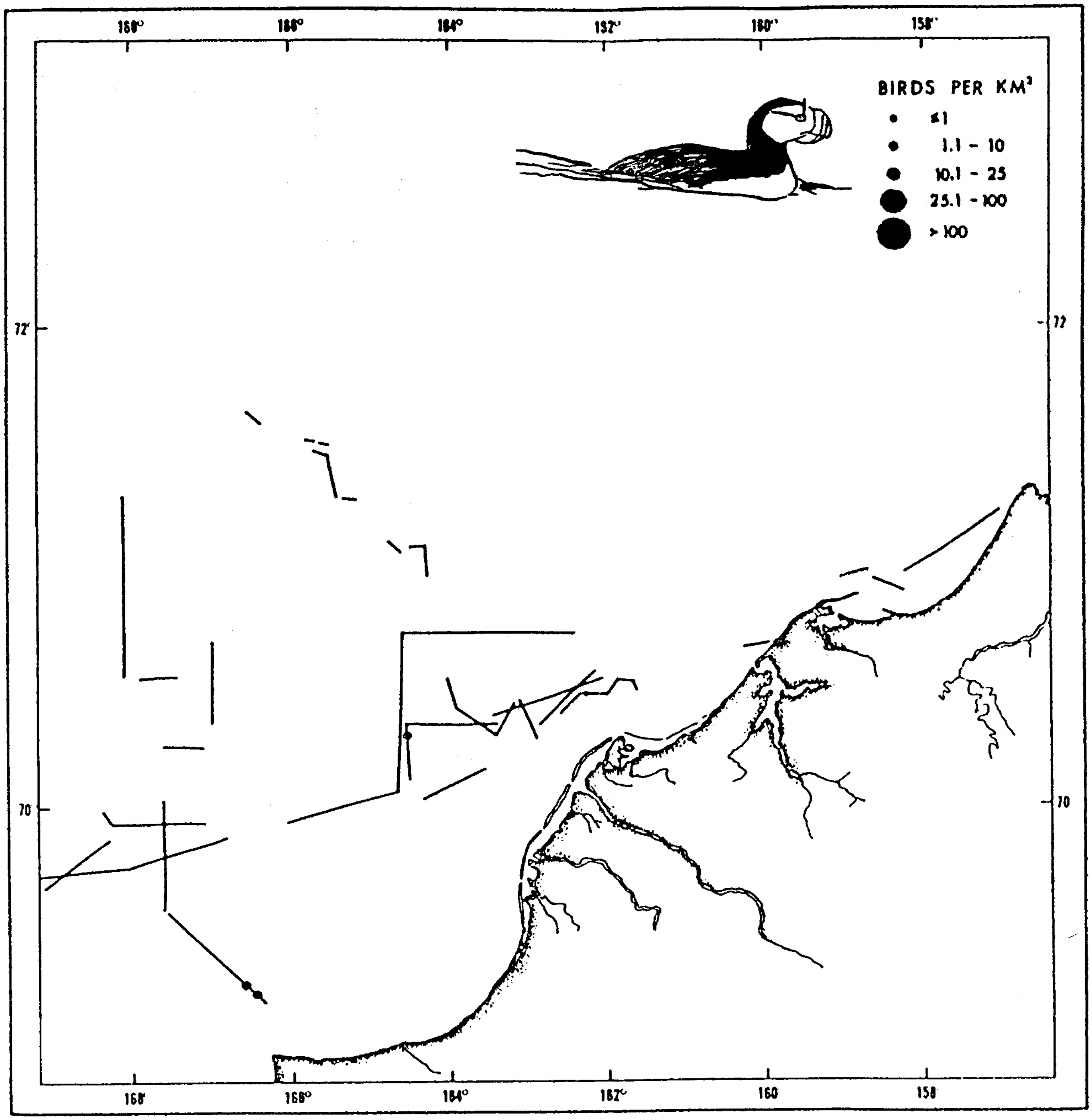


Figure II.D.6 Distribution and abundance of Tufted Puffins in the northern Chukchi Sea, August 2 -25, 1975.
Figure 64, page 196, in Divoky et al., 1979.

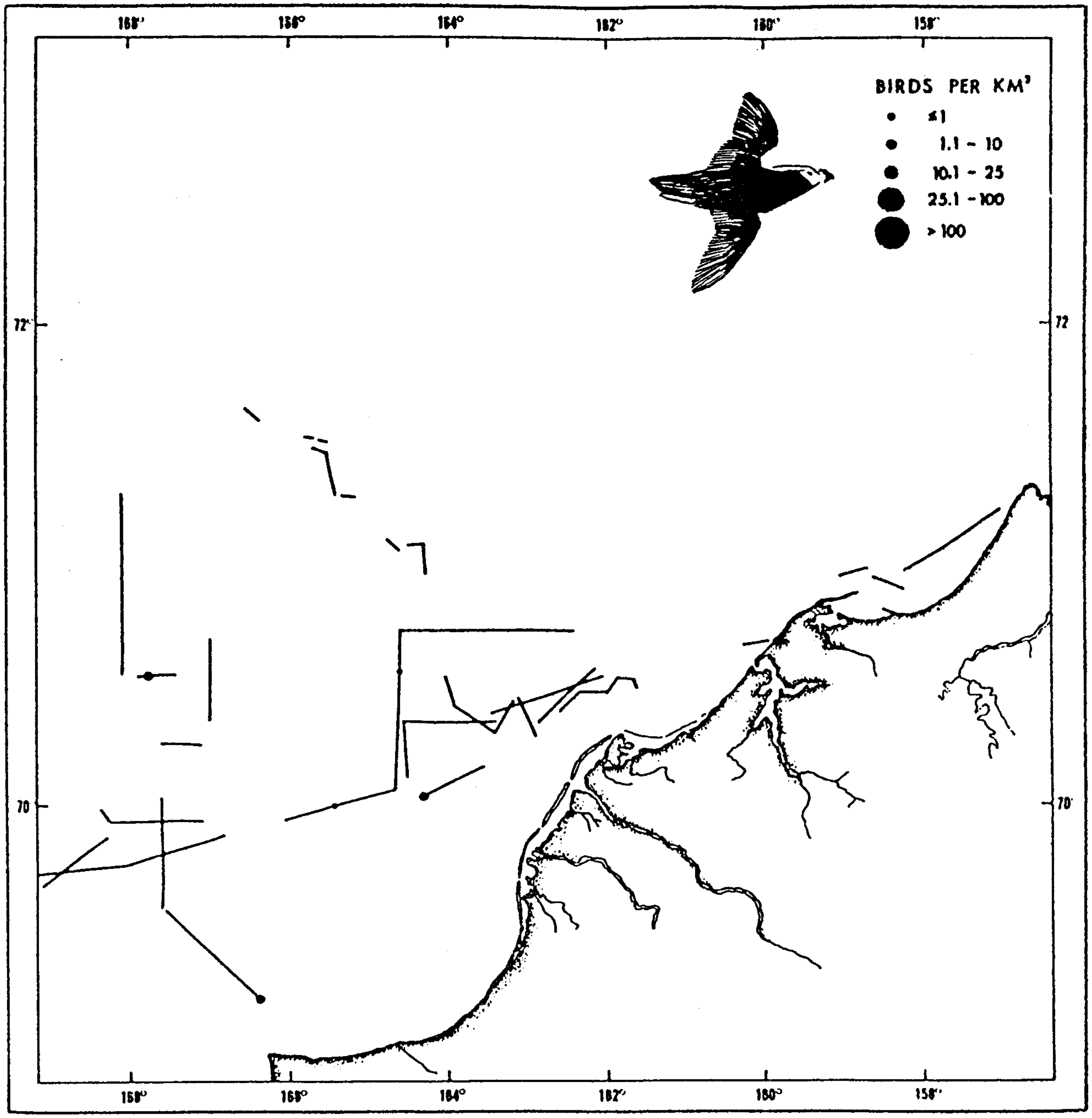


Figure II.D.7a Distribution and abundance of Glaucous Gulls in the northern Chukchi Sea, August 2-25, 1975. Figure 45, page 179, in Divoky et al., 1979.

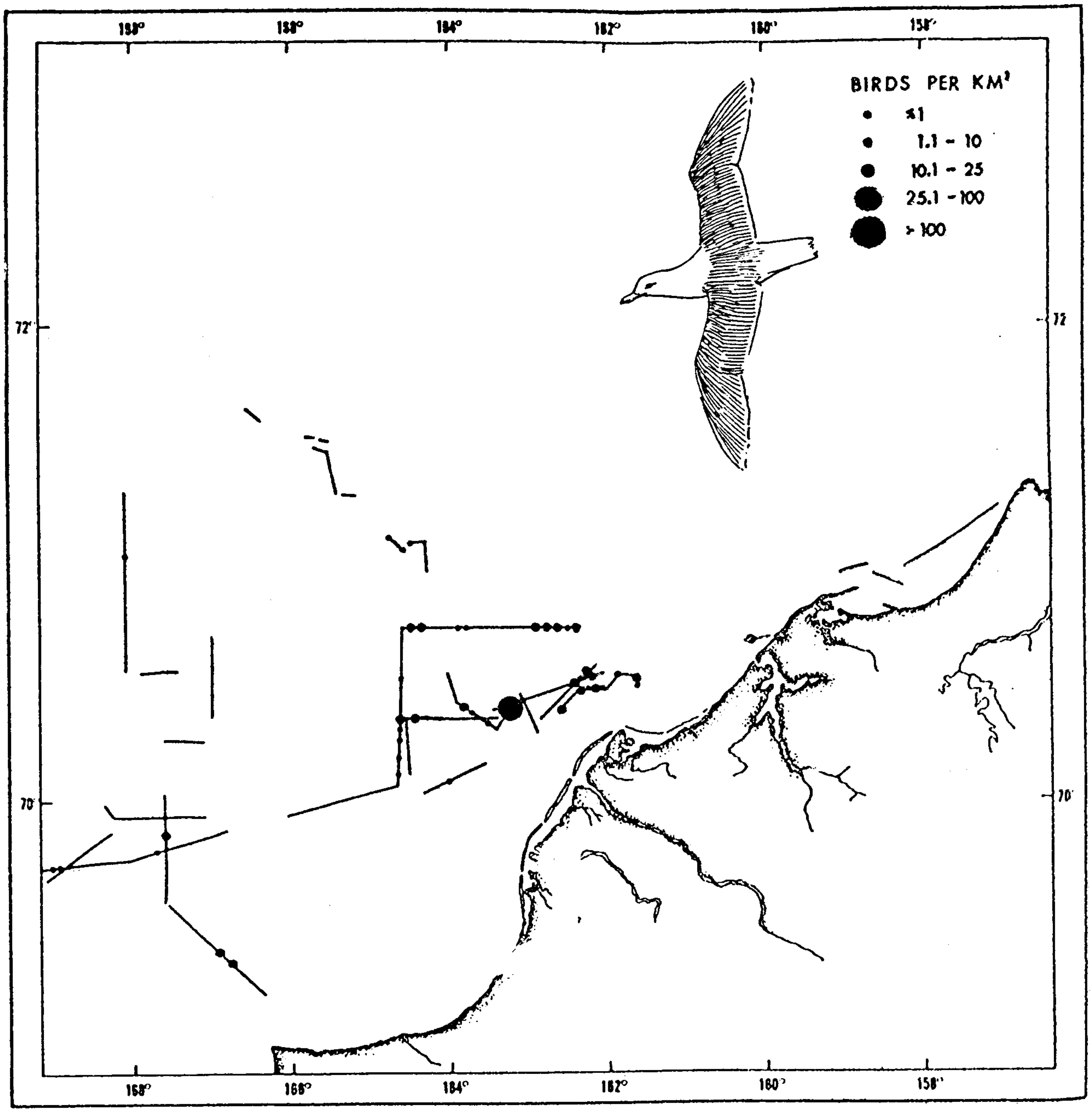


Figure II.D.7b Distribution and abuncance of Glaucous Gulls in the northern Chukchi Sea, September 20-22, 1976. Figure 169, page 196, in Divoky et al., 1978.

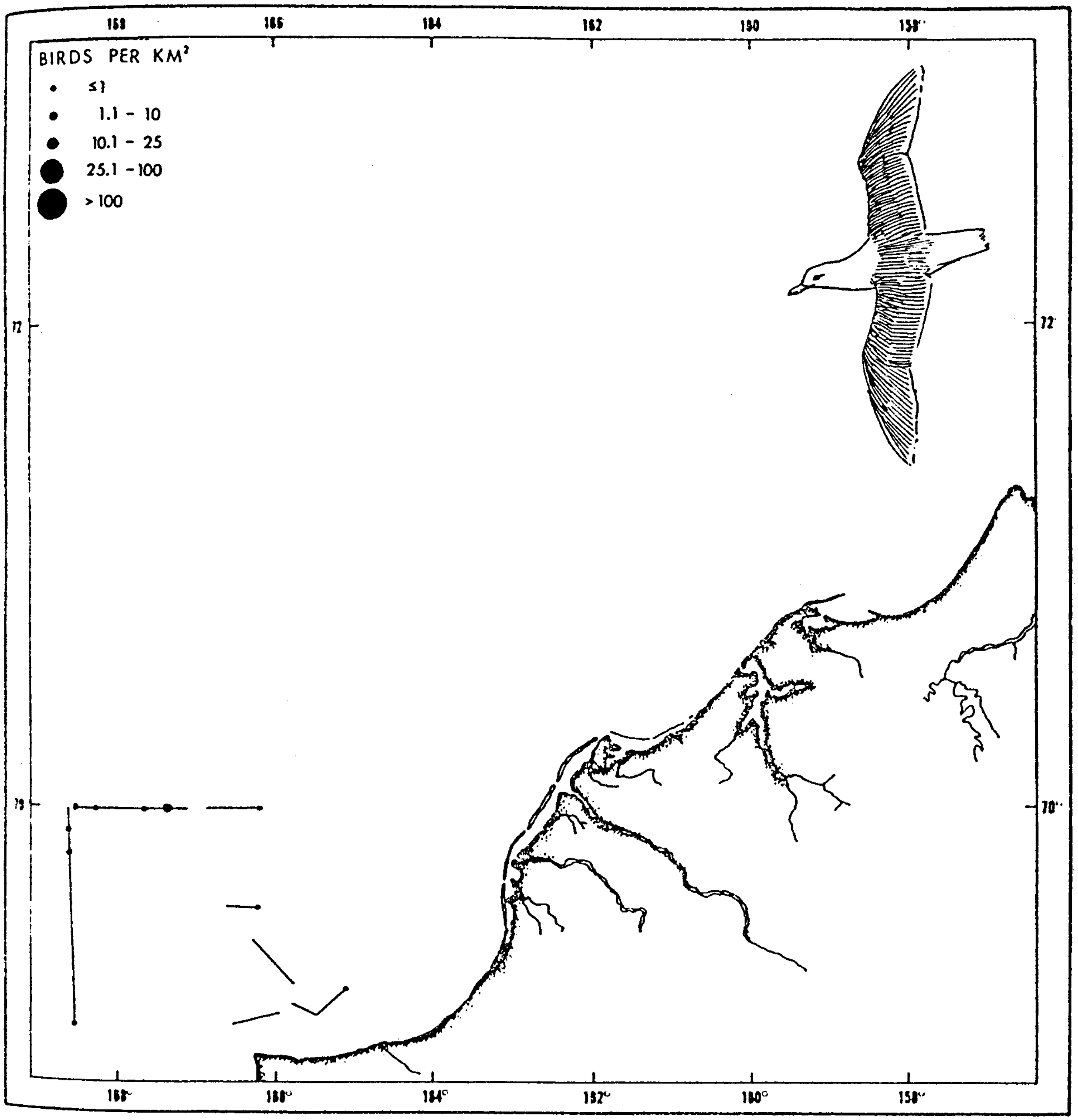


Figure II.D.8a Distribution and abundance of Black-legged Kittiwakes in the northern Chukchi Sea, August 2-25, 1975. Figure 47, page 181, in Divoky et al., 1979.

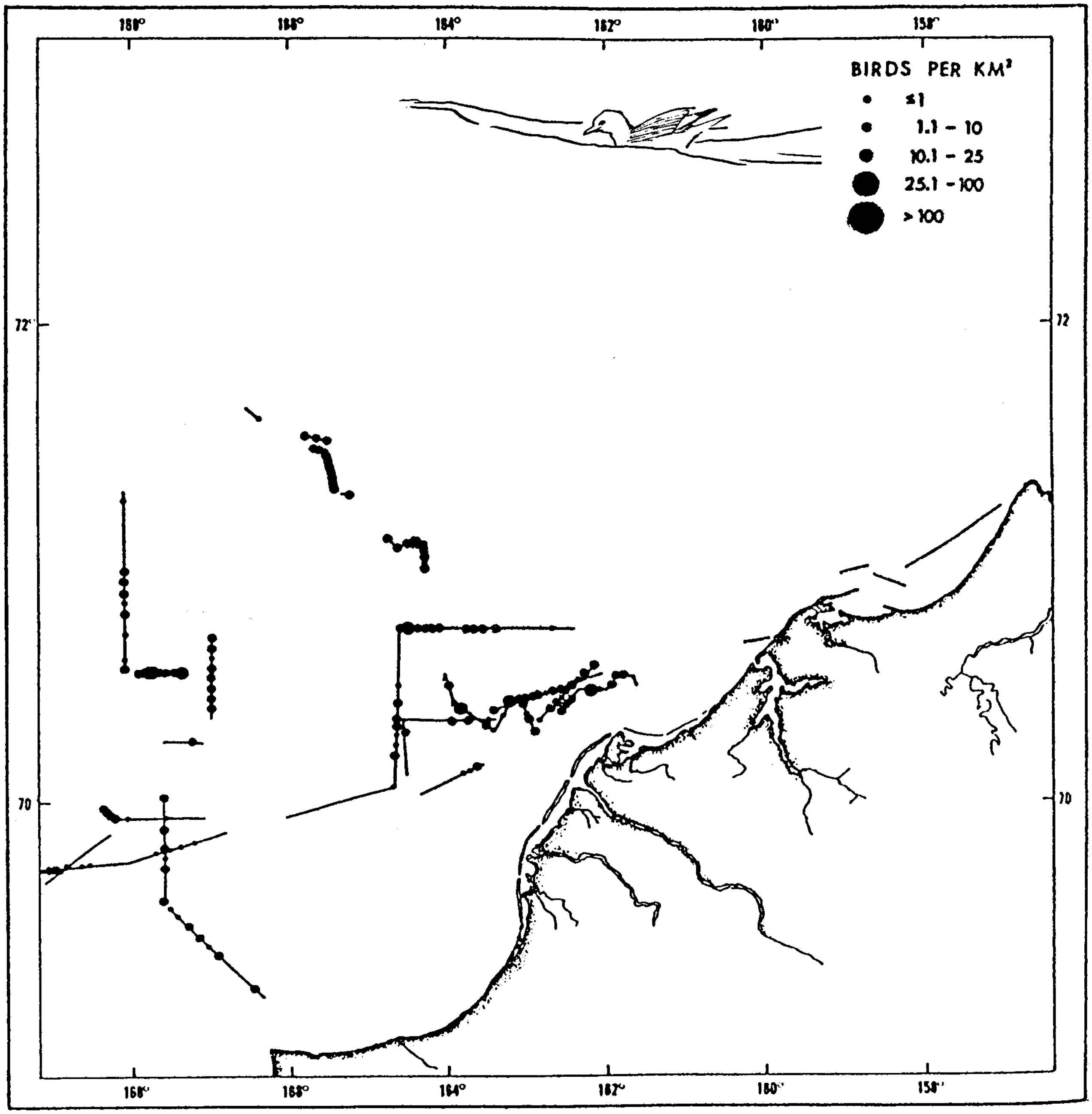
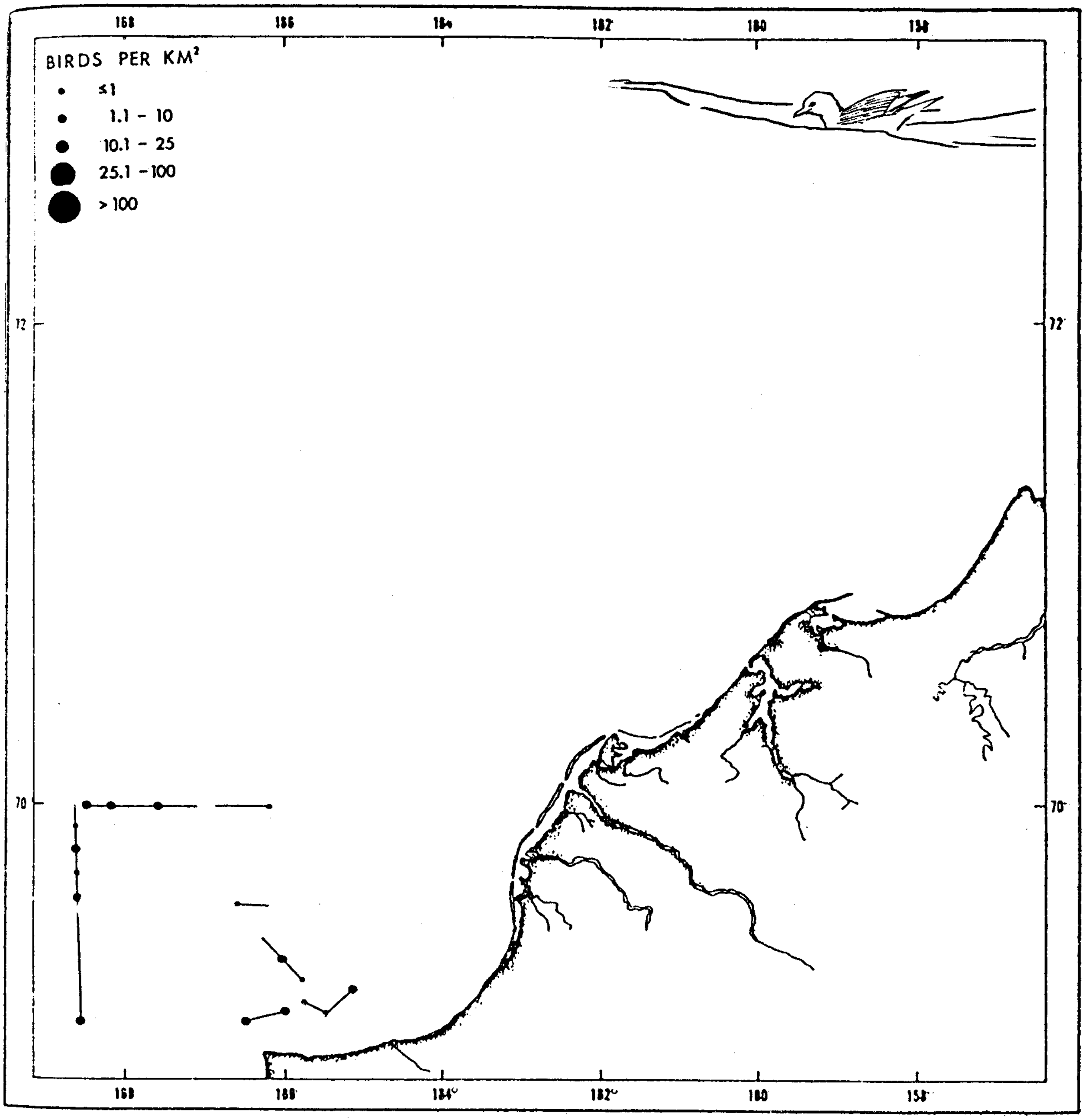


Figure II.D.8b Distribution and abundance of Black-legged Kittiwakes in the northern Chukchi Sea, September 20-22, 1976. Figure 171, page 198, in Divoky et al., 1978.



APPENDIX VI.

MAJOR PLAYERS: SPECIES ACCOUNTS OF THE FISH AND SEABIRDS THAT PLAY MAJOR ROLES IN THE MARINE ECOSYSTEM OF THE BERING STRAIT REGION

A. ARCTIC COD OR TOMCOD

The common names Arctic Cod and Tomcod refer to more than one species of small codfish. In northwest Alaska three fish are included in this group: *Arctogadus*, *Boreogadus* and *Eleginus*. *Boreogadus saida* occurs in cold waters at the edge of the ice all across Siberia and Canada, and deserves the widespread common name of Arctic Cod. *Arctogadus glacialis* is a fish of even colder water north of our region and deserves the name Polar Cod. *Eleginus gracilis* or Saffron Cod is a fish of warmer water than *Boreogadus*, and its distribution is limited to the Bering Sea Region.

In Norton Sound *Boreogadus* is often called Blue Cod while *Eleginus* is called Tomcod.

Arctic Cod (Figure 1) is abundant in the colder waters of the Bering Strait Region and the Chukchi Sea west of Point Hope. Saffron Cod is the primary species in the Alaskan Coastal Waters of Kotzebue Sound and Norton Sound. While all three species thrive in brackish water, Polar Cod and Saffron Cod are confined to low saline or shallow coastal waters, lagoons or the lower reaches of rivers. Arctic Cod occurs both in coastal and in offshore waters off northwestern Siberia in the Kara Sea, Barents Sea and off Spitzbergen. It is believed that the fish that appear in deep waters there were carried passively by drifting under pans of ice.

The biology of Arctic Cod is much better known than the other species. The cold water of the Bering Sea is well known as one of the spawning grounds of this fish (Zenkevich 1963). The species usually spawns in

January and February under the edge of the ice, in water between 0°C and 1.8°C. Eggs are large for codfish eggs, larger than those of the Atlantic Cod (Gadus morrhua) which as an adult is much larger than Arctic Cod. The large size is associated with a long period spent by the embryo in brackish water. Unlike the eggs of other cod fish, they have little pigment as they are sheltered from the sun by ice. Larvae appear in May and June in eggs developing in water at 2-5°C, and grow at the edge of the ice in temperatures of 5-7°C. Their rapid growth in June and July benefits from the spring bloom of algae and zooplankton. Juvenile fish appear in August. These events suggest that the growth of the younger stages is adjusted to take advantage of the highly productive water under the spring ice.

Lagoons behind the barrier islands along the Beaufort Sea coast supply nursery grounds where food is abundant and predation is light. Some Arctic Cod spend the summer in Simpson Lagoon, where they presumably are feeding primarily on the detritus feeding Gammarid Amphipods, as are waterfowl. Ponomarenko (1968) reported that as the larvae and fry grow, they feed on Copepod eggs, then nauplii larvae, and then Copepodite stages. Andriyashev (1954) reported that Arctic Cod mature in four years at a length of about 190 mm. Maximum size is 320 mm (Quast, 1974).

Saffron Cod spawn in fall-winter in shallow, near-shore waters with sandy bottom. Their eggs sink to the bottom (demersal).

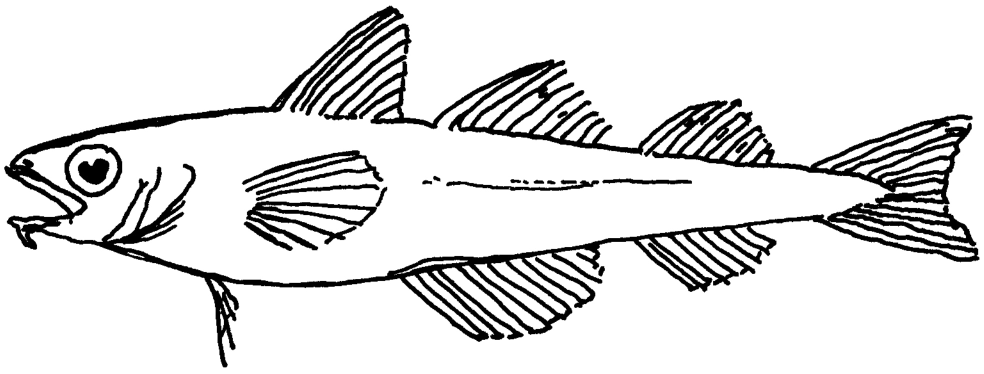
In Lancaster Sound, in the Canadian Eastern Arctic, Arctic Cod concentrate at the edge of fast ice in coastal waters in the summer, especially at the ice/water interface. Major concentrations occurred most often in estuarine habitats: in waters with landfast ice, in bays, or where streams or rivers flowed into the sea (Nettleship and Gaston, 1978).

Sea ice supports an in-ice algal bloom, and multi-year ice is known to support an under-ice fauna of zooplankton and Arctic Cod. The underside of multi-year ice has extensive and numerous keels and pockets which create a large surface. Amphipods concentrate on the underside, presumably to feed on the plankton blooms (Mohr and Geiger, 1968; MacGinitie, 1955), but they are known to be active under the sea ice all winter along the Beaufort Sea coast. The underside of multi-year ice is thus similar to a reef in that it has a fish and invertebrate population (Divoky, 1978). Gammarid Amphipods, *Apherusa* and *Onisimus*, have been reported from under the ice along the north shore of Alaska.

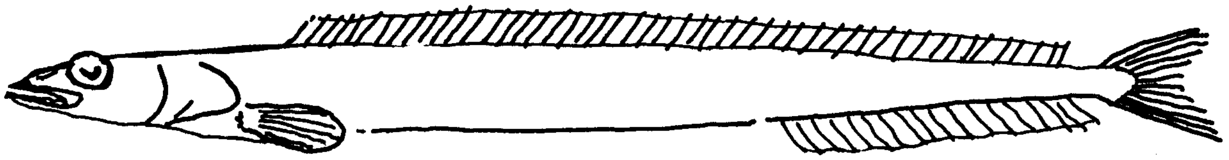
Hognestad (1968) reported that in the East Barents Sea in September Arctic Cod fed primarily on *Calanus finnmarchicus*, Hyperiid Amphipods and Appendicularians (tadpole-like Tunicates). Frost (1978) reported that in the Beaufort Sea they were feeding on copepods, *Calanus glacialis* (*finmarchicus*), *Calanus hyperboreus*, *Euchaeta glacialis* and the Hyperiid Amphipod *Parathemisto libellula*.

Small cod are fed upon by many species of fish: char, Saffron Cod, flounders, and sculpins, and larger individuals are fed on by Common Seals, Ringed Seals, Harp Seals, Walrus, Belugas, sea gulls, skuas, murres, puffins and Black Guillemots. Arctic Cod are important in the diet of Eskimos in several parts of the Beaufort Sea, the Arctic Coast and in Hudson's Bay.

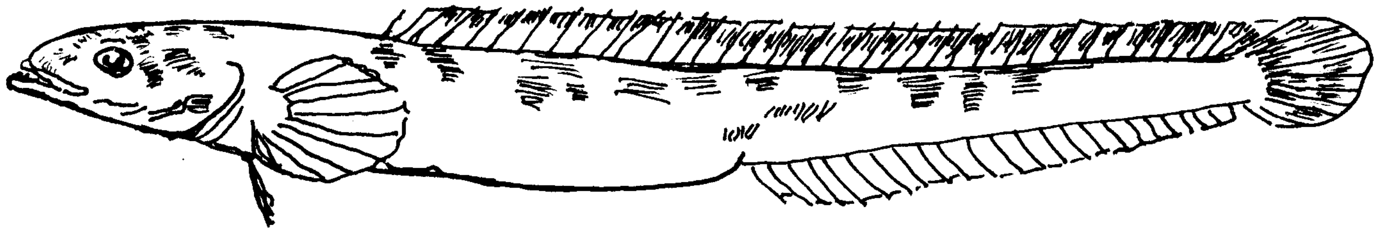
Quast (1974) suggested that Arctic Cod in the southeastern Chukchi Sea moved down in the water column as an adaptation to avoid intense predation from murres. His studies showed that there was a constant pattern of increasing density of cod with depth despite changes in



BOREOGADUS SAIDA TO 25 CM



AMMODYTES HEXAPTERUS TO 20 CM



LUMPENUS FABRICII TO 25 CM

Figure 1. Arctic Cod, Sand Lance and Prickleback.

salinity and the effects of upwelling and downwelling associated with turbulence. He suggested that remaining in murky depths increases protection from murres, yet allows the fish to move up and to see their prey against the light above.

Wolotira (1977) found that Arctic Cod associated with colder waters in the Saint Lawrence Island waters and off Point Hope. They found more Saffron Cod in the warmer waters of both Kotzebue Sound and Norton Sound.

Quast (1974) found Arctic Cod to be ten times more abundant than Sand Lance in the cold water off Point Hope in September. Barton (1978) reported that Sand Lance was, by contrast, three times more abundant than Pink Salmon, Chum Salmon, and Saffron Cod in Golovin Bay. Saffron Cod was the fish caught most frequently in beach-seines and gillnets along the shores of eastern Norton Sound.

B. SAND LANCE

In the Atlantic, Sand Launce, Launce, or Sand Eel.
In Scandinavia, Sil as in Silgrissla - Black Guillemot.

Sand Lance are small fish found throughout the oceans of the world, and their populations supply an important food resource for predatory fish (cod, salmon, halibut), mammals (Fur Seals, Common Seals) and seabirds. Their habits of burrowing into the sand and of forming great shoals may be adaptations to escape predation.

In life Sand Lance have intensely blue, irridescent backs, shiny silvery sides and conspicuous eyes. The color soon fades after death to olive or tan. Ammodytes hexapterus are very slender fish that usually grow to about 10 cm (Figure 1), but individuals reach 15 or 17 cm.

Although A. hexapterus is not known to spawn in our region, A. tobyanus has been reported by Andriyashev (1954) to spawn in relatively shallow water under the ice on sandy bottom in late winter. This agrees with reports that they spawn in winter at 10 fathoms in the southern North Sea. The eggs sink and stick to grains of sand. The eggs hatch from January to March, and in the next months the larvae are dispersed widely by currents and winds, even over deep water. It is not known where they spawn in the northern Bering Sea. Wolotira (1980) suggests that spawning occurs nearshore in spring because adults are found there, and recently hatched larvae have been found in June and July by Barton. In the southeastern Bering Sea they spawn near Cape Newenham. Larvae are present at the start of the spring phytoplankton bloom. The young are 20-30 mm long by June in southern Alaska. By August they have drifted as far north as 60°N. Abundance in the northern parts of the range is progressively later. The fish are up to 80 mm long by late September.

In most parts of their range, Sand Lance spend the winter in deeper water and come inshore in spring. The little ones assemble offshore in July and August and move inshore in great shoals. Most adults are found primarily in water shallower than 25 fathoms close to land, but it is not known whether this is a spilling over of some population elements or whether the majority leave deep water. Neither temperature or salinity are thought to be critical. Their arrival from offshore appears to coincide with the appearance of larval fish and crustacea.

In July and August, dense shoals of Sand Lance move into the shallow water of eastern Norton Sound. At approximately the same time, they appear in the shallow water off Kivalina and in the gyre east of Cape

Lisburne, and become the major food for the seabirds in both areas. In ball-like and snake-like schools they move along the sandy barrier beaches a few tens of yards or a few miles offshore. The flickering white wings of feeding kittiwakes accompany the shoals all summer.

Most growth is in spring and during the first two years. Growth is slowed in winter, and by the end of the second summer the young are about 130 mm long, by which time they are ready to spawn. Older stages and larger fish are much less numerous, but in extreme cases they survive up to five years and reach 170 mm. Older fish seem to restrict their activities to shallow sandy bottoms. Although one-year-old fish spawn, most of the eggs are contributed by the two- and three-year age classes.

Sand Lance is an important element in the marine communities in the Bering Strait Region, and plays a role similar to those played by Herring and Capelin in other parts of the ranges of the circumboreal seabirds. In September in the southeastern Chukchi Sea, Quast (1974) found Sand Lance were second in abundance after Arctic Cod in his trawls. In Norton Sound they are abundant and of great importance to predaceous vertebrates. They made up about 80% of Barton's catch in Golovin Bay (Barton 1978). They made up 9% of the catch between Cape Denbigh and Stebbins in southeastern Norton Sound.

In Scandinavia, Sand Lance feed on Copepods and fish fry, including their own; off Japan they feed on Copepods, Chaetognaths and fish larvae; in the North Sea they feed on Amphipods and Annelid worms.

In the Atlantic Ocean they are fed on heavily by Herring, cod, Hake, Haddock, Halibut and Ling Cod. In the Pacific they are fed on by Silver Salmon, Sockeye Salmon, Chinook Salmon and Coho Salmon, Fin Whales Minke Whales, Harbor Porpoises, Fur Seals and Bearded Seals. In Norton Sound they are eaten by murres, Horned Puffins, Tufted Puffins and Black-legged Kittiwakes. We have watched Minke Whales rush toward feeding melees, and as their wake passed right through the feeding birds, the flock dispersed. We have also seen Spotted Seals and Harbor (Common) Porpoises associated with school of Sand Lance.

In our experience, feeding flocks of kittiwakes are indicators of the locations and movements of Sand Lance in Norton Sound. Although we could not get far offshore our impression was that feeding flocks were concentrated in shallow water ½ to 3 miles from shore. In 1975, in mid-July, we saw four feeding melees off Sledge Island; in mid-August, 4-6 melees were to be seen on relatively calm days in the shallow water within a few miles of the barrier beach at Safety Lagoon. In mid-September on calm days, 4-8 feeding melees could be seen within three miles of shore from east of Square Rock to Topkok Head. In early September, the shoals of fish were close to Bluff. On still days we could see two to eight melees at once looking to the west from the high Bluff. In 1977, a year of poor reproductive performance among kittiwakes, the appearance of Sand Lance in the diet of nestling kittiwakes coincided with the shift in feeding behavior of adults from pecking at the surface to making shallow dives. This shift began in the first week of August at Bluff. In the second week of August we saw frequent melees of 100-500 birds making shallow and deep dives. In the second and third weeks massive schools were visible from the cliffs.

In this period when food given to chicks by adult kittiwakes was identifiable, it consisted of small Sand Lance (Ammodytes). We saw groups of diving kittiwakes mixed with puffins and murres on 5 August. On 13 August there were large melees visible "everywhere". This period of abundant food reached its peak between 21 and 24 August, when schools of Ammodytes of 10 m^2 or greater in surface size were swimming within a quarter of a mile of the cliffs, and some along the base of the cliffs. Murres and puffins attacked these schools from underneath, which may have driven some of the fish close to the surface, as the kittiwakes frequently caught more than one fish in single shallow stabs. These Ammodytes were mostly one and one half inches long. In the fourth week the melees continued but became smaller, fewer and more dispersed. In the first week of September one melee of 75 kittiwakes was seen making deep dives.

In 1978, a year of outstanding reproductive success among kittiwakes at Bluff, kittiwake feeding melees were most obvious during July and early August. Observations are summarized in Tables 1a & 1b, and indicate the daily frequency of feeding melees and the species involved. These gatherings were seen as close as one and one-half miles and as far off shore as we could see. They were usually seen between Bluff and Square Rock.

From 9-12 August, Edward Murphy collected murres and kittiwakes for their stomach contents. Although the data are not yet analyzed, it was obvious that over 90% of the kittiwakes' diet consisted of 1½ - 2 inch long Sand Lance (Ammodytes). This is consistent with what we have found over four years, in the regurgitations of chicks. Sand Lance appear to play a critical role in the reproductive success of Black-legged Kittiwakes at Bluff.

Murres, while eating Sand Lance themselves, apparently concentrated on Prickleback (Lumpenus) as the food they brought to their mate or young.

It is important to learn more about the biology of this species, its comings and goings, the timing of its movements, and the causes of reproductive success and failure.

Table 1a.
Summary of Black-legged Kittiwake feeding behavior observed near Bluff Cliffs during the summer of 1977.

Month	First Week	Second Week	Third Week	Fourth Week
JUNE		Infreq. in groups of 50-100, with Glaucous Gulls, taking 2-8 inch fish, some <u>Eleginus</u>. Dive from air.	Infreq. in mixed groups. Dive from air.	Groups of 100-300 feed on surface or make shallow dunks - food too small to see (small crustacea?).
JULY	One melee of 400 birds with Glaucous Gulls, taking 4 inch fish.	Groups of 100-200 feed using shallow dabs at surface.	Continued infrequent melees taking indiscernible food by shallow dabs.	
AUGUST	Chicks fed <u>Ammodytes</u>. Group of 100 adults seen making shallow dives.	Frequent melees of 100-500 birds making shallow and deep dives. Schools of <u>Ammodytes</u> apparently moving into vicinity.	Massive schools of <u>Ammodytes</u> visible close to cliffs. Schools often close to surface allowing kittiwakes to catch multiple fish at surface. Frequent simultaneous melees of 100 birds each along entire length of cliffs.	Melees over <u>Ammodytes</u> schools continue, become smaller, fewer, and more dispersed.
SEPT	One melee of 75 kittiwakes making deep dives.			

Table 1b. Feeding frenzies or melees seen in the area of Bluff Cliffs and Square Rock, 1978.

	FIRST WEEK	SECOND WEEK	THIRD WEEK	FOURTH WEEK
MAY				30 May: kittiwakes take no notice of 6-8" fish in cove below Stake 15.
JUNE		12 June: at night, several groups, not melees, feeding close to shore in breakers east of Square Rock.		
JULY	One to two melees seen almost daily, west of Bluff and southeast of Square Rock; up to 150 kittiwakes.	Many small melees off Taylor Lagoon. 8 July: 1-5 groups scattered periodically.	15 July: 1 melee off Bluff. 17 July: 4 melees between Bluff and Square Rock.	22 July: melee of 100 kittiwakes near east end of Bluff; one at Tonok; another at Tonok of 100 kittiwakes, 25 cormorants, 20 puffins, 30 murres, 15 gulls; two melees off Tonok beach of more than 75 kittiwakes each; one off Koyana Cove of 75-100 kittiwakes. 23 July: one of 200 kittiwakes, 30 gulls, 5 Horned Puffins, 5 murres, 5 cormorants.
AUGUST	Frequency of melees on the increase; kittiwake chicks regurgitating Sand Lance during weighing.	8 August: one melee off Koyana Cove early a.m.; another 150 yards off Farland Point at Bluff of 40 kittiwakes, 5 Horned Puffins. 14 August: late a.m. off Koyana Cove - one of 150 kittiwakes, 12-25 murres; one of 50 kittiwakes, some murres; one two miles east of Square Rock of 150-200 kittiwakes. 13 August: 3 melees Bluff area.		

C. PRICKLEBACK OR SLENDER EELBLENNY - Lumpenus fabricii.

(Fig. 1)

This long, slender fish/is the major food item brought to the cliffs by courting murres and those that are feeding young. We have observations of this at Sledge Island and at Bluff. The length of this fish and the characteristic opacity which suggests the plastic chord used for a tourniquet, make it easily identified. Lumpenus fabricii is the northern representative of a widespread boreal genus.

Barton and Wolotira found this fish to be widespread though small in number in their nets and tows. Lumpenus appear to live on rocky bottoms in shoal water a fathom or more below low tide but not next to the beach. They haunt sheltered places; related species are reported to dig burrows. The skin divers surveying subtidal communities around the shores of Norton Sound in 1976, reported seeing Pricklebacks frequently.

Adult Lumpenus spawn in fall and winter, laying clusters of eggs on the bottom. In some species spawning is in shallow water. Eggs hatch with the spring plankton bloom and larvae may be abundant at the surface. Food of larvae is largely copepods. The larvae of the closely related Lumpenus sagitta remain pelagic for 2-3 months by which time they grow to 40-45 mm. At that point they settle to the bottom. Their food is indicated by the observation that larger individuals can be caught on hooks using marine worms as bait.

A closely related species in the north Atlantic has been found in the stomachs of Cod (Gadus morhua), Halibut (Hippoglossus hippoglossus) and Pollack (Pollachius virens).

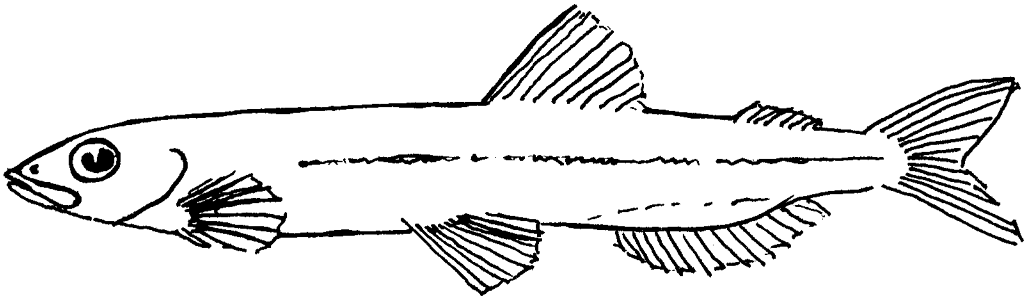
This information was gathered from Hart (1973), Leim and Scott (1966), Bigelow and Schroeder (1953), and a letter from J. E. Blackburn of Alaska Department of Fish and Game.

D. CAPELIN (Mallotus villosus), SMELT (Osmerus eperlanus - mordax), HERRING (Clupea harengus pallasi) AND SALMON (Pink -Oncorhynchus gorbuscha- and Chum/Dog -O. keta). See Figure 2.

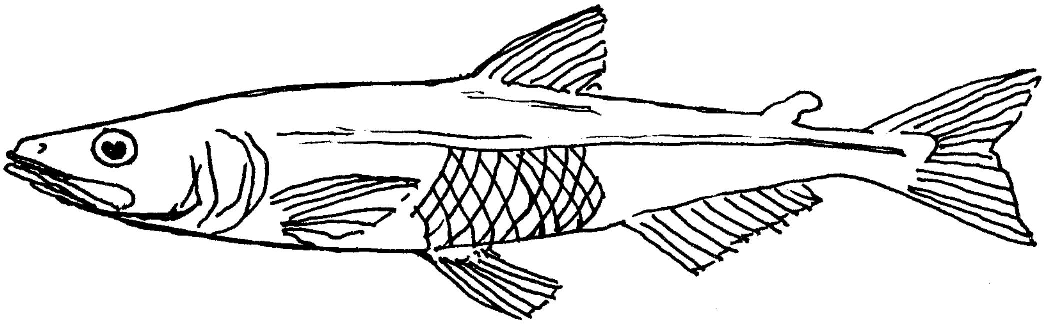
These are all fish which are important foods for seabirds such as murres, puffins and kittiwakes. Capelin, Smelt and Herring are especially important as foods in other parts of the ranges of the circumboreal species. All are small, slender, silver fish which come into shallow water to spawn, a habit which apparently makes them vulnerable to predation by seabirds when the birds are at their nesting cliffs.

The information available for Norton Sound suggests that Herring spawn on and around objects including grass and seaweed in shallow water around the southeast and east shores of the Sound. Smelt reportedly spawn in fresher estaurine water, perhaps in Golovin Bay. Capelin are reported to spawn in coarse sand and pebbly beaches, such as the beaches along the south shore of the Seward Peninsula. Salmon spawn in shallow places in the rivers.

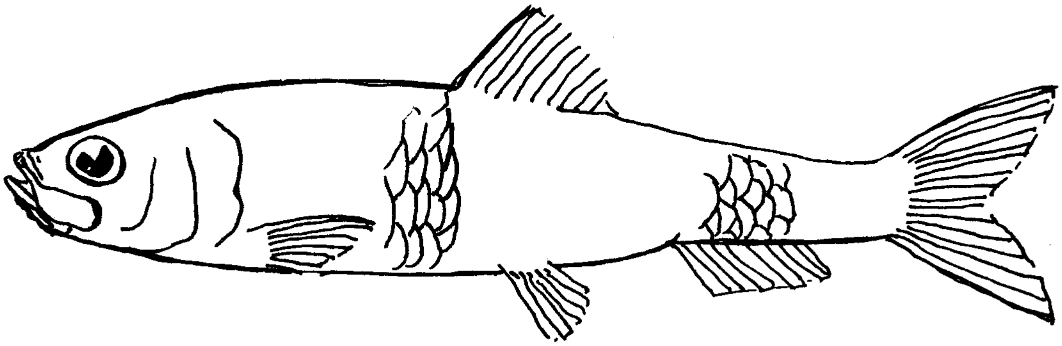
In the following paragraphs we offer some speculations as to why these fish, which are of the right size, shape, and behavior to provide the proper search image as prey, are "under-used". Understanding why they are not used is as useful in comprehending the structure of marine bird communities as it is to understand why others are used. For example, Lumpenus fabricii is over-used. According to all assessments of the fisheries stocks this is an obscure bottom fish.



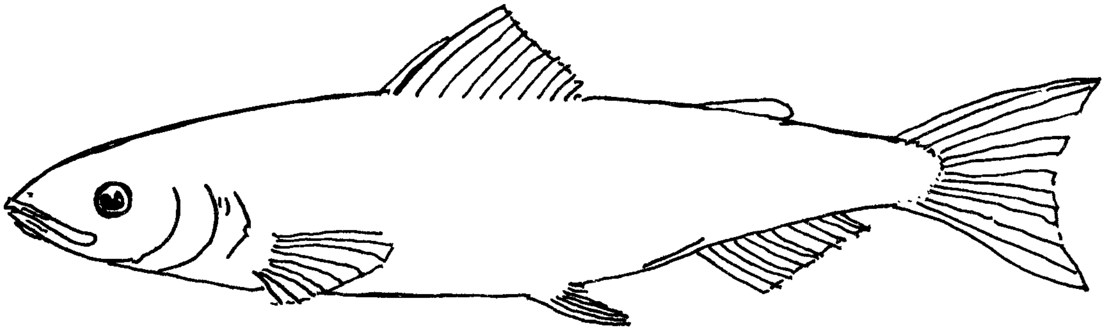
MALLOTUS VILLOSUS TO 20 CM



OSMERUS MORDAX TO 20 CM



CLUPEA HARENGUS TO 25 CM



ONCORHYNCHUS KETA TO 100 CM

Figure 2. Capelin, Smelt, Herring and Salmon.

There are reports of large numbers of Capelin in Norton Sound at the turn of the century, but Capelin are reportedly fish of colder more saline water than Norton Sound. Their presence off Cape Navarin and in the Anadyr Strait is consistent with this preference for cold saline water. Eskimos at Golovin call Capelin "Candlefish" which suggests their being numerous enough in the past to be used. Adults and eggs have been found during ice break-up in nearshore waters of relatively high salinity. The eggs remain buried in the intertidal zone for two weeks or more. It was expected that they would be present along the beaches at Bluff in the mid-1970's, and biologists from Alaska Department of Fisheries suggested that the loose shoals we saw in the breakers and close along the beach near Bluff in July 1975 might be Capelin. Our finding some Capelin dropped on the ledges at Sledge Island suggests that the birds do use some Capelin and that their presence can be detected. So we conclude that, at present, Capelin (which are an important resource for seabirds elsewhere) occur in the colder, saline waters to the southwest and are not available to the birds we studied in inner Norton Sound. Further studies at Sledge Island, King Island and Little Diomede should clarify this; it will be interesting to see whether Capelin are included in the diets of the birds on Saint Lawrence Island.

Smelt are recorded in large numbers in gill nets and beach seines in Port Clarence/Grantly Harbor and in Golovin Bay (Barton 1978), but they are scarce in the main part of Norton Sound. Local residents report major spawning in the fall. They spawn in freshwater streams and estuarine areas of low salinity. The eggs cling to rocks and aquatic plants. We found no Smelt in our samples from the ledges and we saw no murres or kittiwakes feeding inside the mouth of Golovin Bay. We saw Glaucous Gulls and Red-breasted

Mergansers feeding inside and it will be interesting to establish whether these species feed on Smelt. The absence of Smelt may reflect their arrival late in the season and in essentially "inland", brackish waters which are not regularly productive enough to attract the seabirds from Bluff.

Barton (1978) found large numbers of Pink and Chum Salmon smolt in Golovin Bay. In the winter salmon probably occur offshore, south of this region. Adults and juveniles are found close to shore in Norton Sound throughout the ice-free season. Adults appear as early as January and juveniles are found in the lower parts of all the rivers during late spring and summer. The birds brought some salmon to the cliffs at Bluff in late June and early July, a time when they also brought in a few Herring (according to our observations of birds at the ledges). But these fish made up a small part of the total of fish brought in. It may be that salmon stay in brackish water, like Smelt. Hence, Barton caught them as they entered or left the rivers. Those that go to sea may "keep going" through Norton Sound and thus provide only a small resource because they spend little time in transit.

Herring supported fisheries at Golovin and in Grantly Harbor during the Gold Rush Years and again in the late 1960's. Poor success at spawning deflated this fishery. Information from commercial and subsistence catch of Herring in Norton Sound suggests that they move inshore in mid- or late June and spawn in the inner sound. They spawn in subtidal regions among patches of Bladder Wrack (*Fucus*) and Eelgrass (*Zostera*). The eggs are adhesive, and hatch in about three weeks. Herring have been reported to spawn at high density at Bluff, from Cape Darby to Moses Point, Norton Bay, from Cape Denbigh to Arctic Hills and east of Saint Michael. Herring start to move offshore during August-September and over-wintering schools appear north of the Pribilof Islands in October.

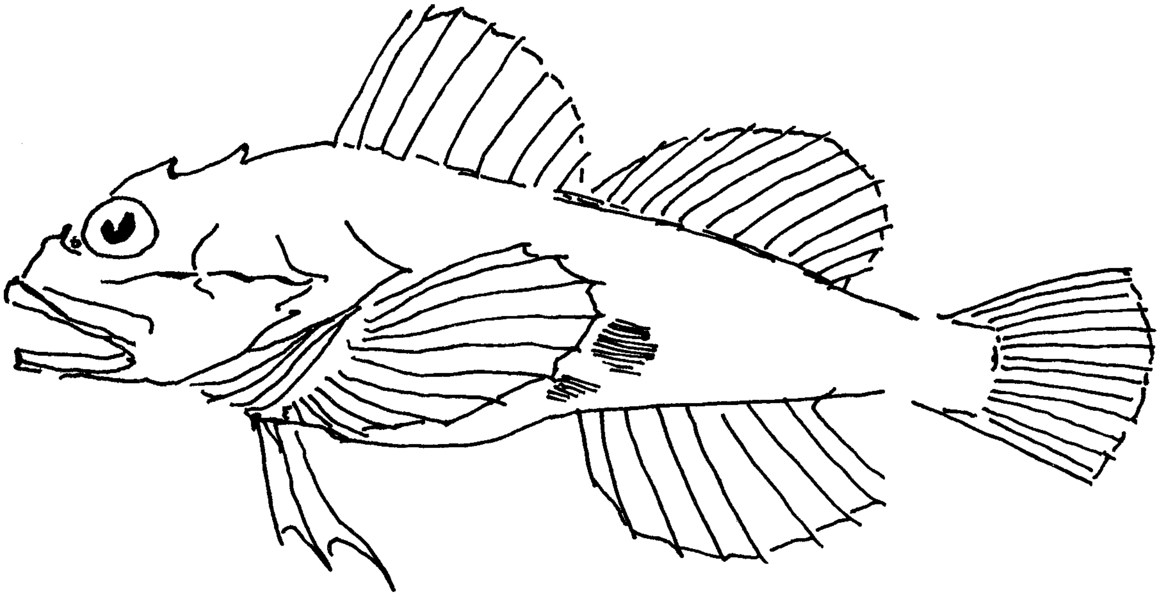
Our finding almost no Herring in the samples at the cliffs and in stomachs suggests either that the stocks were low or the seabirds preferred other fish. Herring are used widely and intensively by seabirds in other places. Kittiwakes, terns and puffins take first-year fish; murres take second-year fish. It would be useful to confirm whether availability or preference, or both, are involved by investigating the subject when there is a boom in Herring.

E. SCULPINS - Cottidae

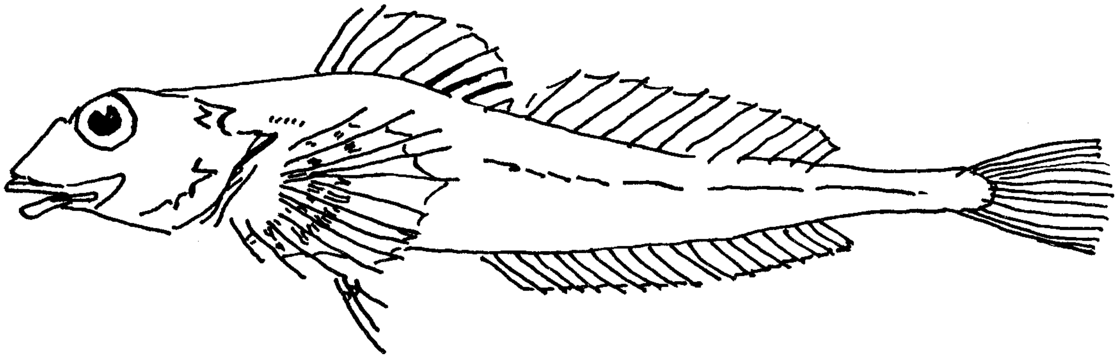
This is a homogeneous group which is represented by an unusually large number of species in the Bering Sea. The group is characterized by spiny heads, large eyes, wide gill openings, spiny pre-opercular bones, broad mouths, slender bodies, two dorsal fins (one spiny and one soft-rayed), large fan-like pectoral fins, ventral fins reduced to three long rays, and small caudal fins (Figure 3). The defense behavior characteristic of the group is flattening the head and spreading the gill-covers and bat wing-like pectorals. When the fish dart ahead, the pectorals are folded against the body. Otherwise, sculpins are generally sluggish fish.

Sculpins are bottom fish, found primarily in shallow, though not shoal, water. Color varies with their habitat; they are brownish or reddish with black, orange, yellow or white splotches, which suggests that they lie in hiding.

Most sculpins are short in length, though some reach three feet. Shorthorn Sculpins (Myoxocephalus scorpius) over 50 centimeters (cm) in length are rare. Ribbed Sculpin (Triglops pingeli) is usually less than 15 cm. Arctic Staghorn Sculpin (Gymnocanthus tricuspis) reaches 25 cm. Twohorn Sculpin



MYOXOCEPHALUS SCORPIUS TO 50 CM



TRIGLOPS PINGELI TO 15 CM

Figure 3. Sculpins.

(Icelus bicornis) usually grows to 10 cm, and is found near ledges, under weeds along more or less smooth bottom in water less than 10 fathoms (20m).

Most sculpins spawn in winter, November-February. In the case of the Shorthorn Sculpin, the fish gather in schools on sandy or weedy bottom, with females greatly outnumbering males. This and the fact that males are more brightly colored suggest that there is competition for status.

Among arctic members of the genera Artediellus (Hookear Sculpin), Gymnocanthus and Icelus, the males have a long anal papilla through which both urinary and sperm ducts pass. It is thought that this serves as a copulatory organ, that fertilization takes place within the female and that she lays the eggs soon after fertilization.

The eggs of the Shorthorn Sculpin sink and stick together in a spongy mass on sandy bottom, crevices or rock pools. The male may guard eggs, and may clasp them in his pectoral fins. Eggs have been found as late as May. Larvae hatch at about 7-8 mm long, and soon rise to the surface where they drift until they are 20-25 mm long. In European waters in July, the young fish may reach 38 mm in length, while in the Gulf of Maine in September, they may be 60-80 mm.

F. PELAGIC CORMORANT (Phalacrocorax pelagicus pelagicus)

1. Description of Species

Cormorants inhabit all continents, but only one species is found in the northern Bering Sea. Pelagic Cormorants feed in shallow water and generally do not travel far from their nesting cliffs. They nest in a large number of small colonies on vertical rock faces and seldom more than 100 birds are together.

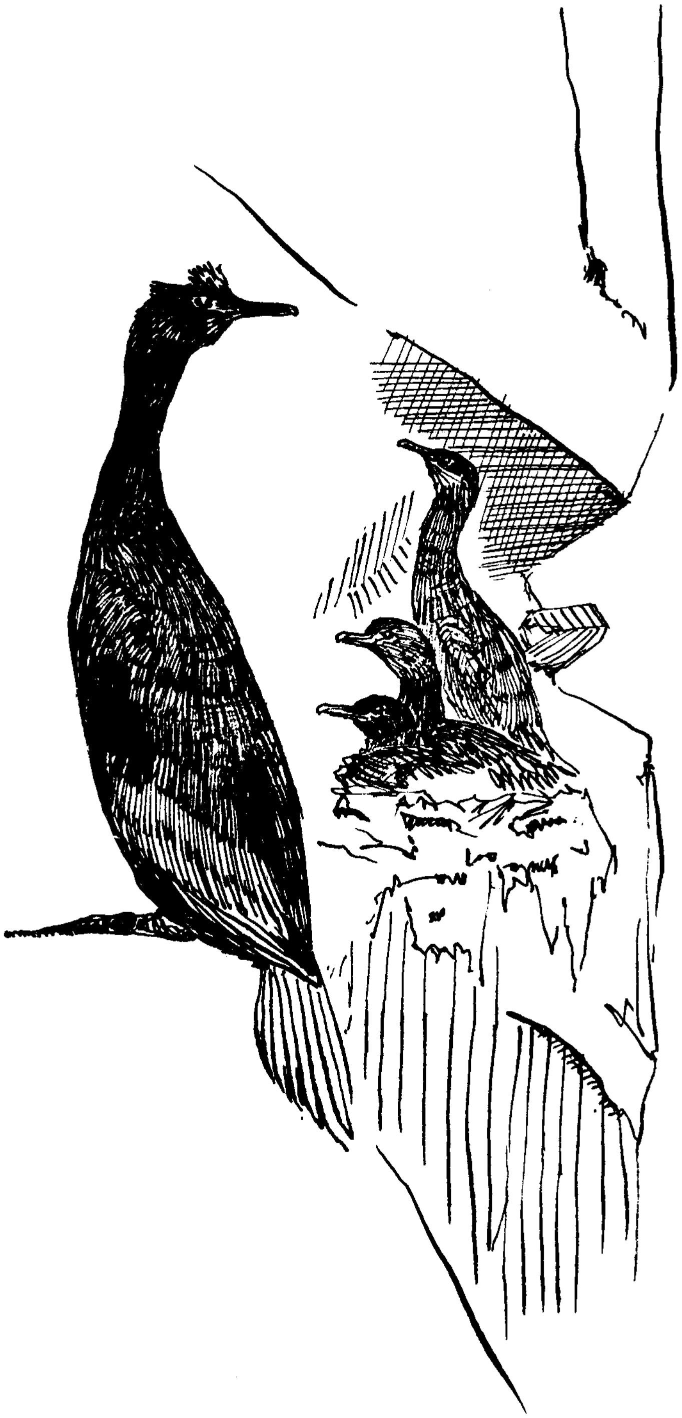
Two subspecies of Pelagic Commorant have been recognized as breeding in North America; only Phalacrocorax pelagicus pelagicus breeds in Alaska, northeastern Asia, and throughout British Columbia, while P. p. resplendens breeds only as far north as extreme southern British Columbia (Dick, in press). Among Pelagic Cormorants of the northern Bering Sea, females do not show the white flank spots referred to in many field guides as diagnostic of the species.

In the southern Bering Sea there are three additional species of cormorant: Red-faced (Phalacrocorax urile), Brandt's (P. penicillatus) and Double-crested (P. auritus). A flightless endemic species, now extinct, occupied the Commander Islands. In the North Atlantic there are three species. The largest number of species occurring together is found in the South American-Australian region.

These birds have two highly specialized features. First, their eyes can focus through a wide range of diopters and this allows them to focus sharply under water or in air. Second, they intentionally soak their wing feathers when they are feeding. This presumably gives them a barely positive buoyancy, and thus is energy saving. It also means that cormorants characteristically stand holding their wings out to dry them.

They keep their wings folded when swimming under water and use their feet, which have four toes supporting the webbing, for propulsion. Most diving birds have webbing between only three toes; auks, murres and some diving ducks use their wings (with primaries closed) to "fly" under water.

Cormorants feed on a variety of bottom fish, from small cod, sculpins and flounder, to 12-18 inch-long wolffish. They fish close to shore and often join feeding assemblages of other seabirds at temporary or local concentrations of food.



Pelagic Cormorants

Cormorants gather in small flocks on the sea ice moving north across the Chirikov Basin. These are probably subadults because the breeding cliffs have long since been occupied by nesting adults, at the season when these birds are seen perched on the hillocks of ice.

Migrating Pelagic Cormorants are seen moving north along the coast of the southern Bering Sea from mid-April to early May. The breeding adults establish territories and build their nests earlier than their fellow cliff-dwellers, the kittiwakes and murres. By the time the kittiwakes take up residence and begin gathering nesting materials, the Pelagic Cormorants have already begun to lay their eggs (Dick in press).

Cormorants are the last birds to leave the bird cliffs in fall (Martin Olson pers. comm.)

There is no conclusive evidence as to where this species winters.

2. Value of Cormorants in OCS Studies

Localized effects of contamination or disturbance will be found in segments of the widely dispersed cormorant populations. Because they feed along the bottom, cormorants will be vulnerable to the effects of oil or other contaminants both floating on the surface and along the bottom. Thus they serve as indicators of the direct, local effects of spilled contaminants. Because cormorants forage at short range in nearshore waters, starvation of chicks can be used to indicate local shortages of food.

G. GLAUCOUS GULL (Larus hyperboreus)

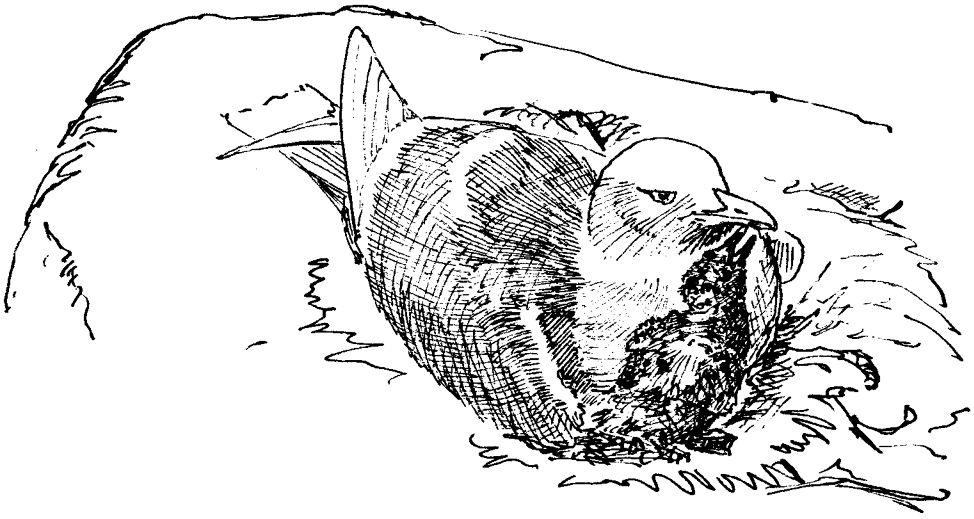
1. Description of Species

The "large gull" species of northwest and arctic Alaska is the Glaucous Gull. Although their wing tips are all white (most Larus gulls have some black pattern on the wing tips), Glaucous Gulls in the northern Bering Sea closely resemble Herring Gulls (Larus argentatus). In the region between the mouths of the Yukon and Kuskokwim Rivers they are reported to interbreed with Glaucous-winged Gulls, a subspecies of Herring Gull. Glaucous Gulls also interbreed with Herring Gulls where they meet in southeastern Iceland.

Glaucous Gulls live all along the sandy and rocky shores of northwest Alaska. They nest in a variety of circumstances: a) as single pairs on tundra ponds near the coast or far inland, b) as colonies of a few pairs to over 100 pairs on islands in large lowland lakes near the sea, c) as individual pairs or groups of up to 50 pairs spaced along the cliff tops of major seabird nesting cities, and d) in loose gulleries of a few to a few dozen pairs on smaller cliffs such as those where Pelagic Cormorants and Horned Puffins nest.

Glaucous Gulls sometimes select the tops of rock stacks to nest, and exclude from their territories large numbers of Common Murres, which otherwise would crowd densely on these places (Tuck, 1960; Birkhead 1978) (Appndx VIII, Figs. 5a & 5b). In this way, Glaucous Gulls exclude Common Murres from one of their preferred and most productive habitats.

Small numbers ride the ice north through the Bering Strait with herds of Walrus. Occasionally, they are seen feeding around Gray Whales (Harrison 1979). They have been reported around fishing boats along the Continental Shelf. Once the ice has left Norton Sound and Chirikov Basin they are seldom seen very far from shore.



Glaucous Gull on Nest with Chick

These gulls feed on a wide variety of foods, including virtually anything they find along the seashore, rivers, lakes or wet tundra: sick and young birds and small mammals, spawning and schooling fish, and eggs and young of seabirds and waterfowl. They gather in flocks at the mouths of rivers and inlets at the mouths of lagoons. In August and September, they feed on blueberries. They follow salmon upstream to spawning beds far inland at the headwaters of the river and gather in large flocks when the fish die after spawning. Individuals or pairs are often seen defending a Walrus carcass washed up on the beach; in many cases, flocks gather at carcasses torn apart by Brown Bears (Ursus arctos). Glaucous Gulls are not very effective predators on the eggs of kittiwakes and murres at Bluff; but the resident pairs catch many murre chicks (though a small percentage of the total) as the chicks jump from the ledges from mid-August into September. Resident gulls exclude most other gulls from their feeding territories and as a consequence limit the number of young taken.

Glaucous Gulls also gather at fishcamps along the beaches and up rivers. They congregate at dumps near small villages, towns, and at the larger settlements, such as Kotzebue, Nome, Unalakleet, and Savoonga.

Gulls are abundant along the shores of Norton Sound, the Bering Strait, Kotzebue Sound, and the Lisburne Peninsula. A lot of adults seem to be non-breeders. These and the large numbers of birds in immature plumage both at sea (reported by observers of the Fish and Wildlife Service and by Divoky), and alongshore suggest that Glaucous Gulls in the northern Bering/southern Chukchi areas may be beginning or are already embarked upon a population boom, similar to that enjoyed by Herring Gulls in the North Atlantic.

2. Age Structure of Glaucous Gull Population in Northwest Alaska

Glaucous Gulls have four readily recognizable plumage/age categories. To simplify the task of assigning age groups, we used only three categories: birds of the year (fledged chicks), subadults, and adults. The category of subadults includes birds that are both one and two years old with plumage intermediate between the uniformly tan birds of the year and the uniformly gray and white adults.

Subadult Glaucous Gulls move gradually into the northern part of the breeding range during the course of the summer and tend to be in small flocks near inlets or villages. Young of the year begin to fledge in mid-August.

Surveys of Gulls along the Coast

A survey made in late July will show most of the subadults, without the practical difficulty introduced by trying to estimate numbers of three different age groups at the same time. We made censuses by flying along the beach at about 100 feet altitude, entering data on a small tape recorder. We estimated the total numbers of each flock and counted the numbers of subadults and chicks.

Each year of our study we surveyed the coast of the Seward Peninsula from Cape Spencer to Unalakleet and Tolstoi Point; the survey made in 1978 includes the beach from Wainwright to Tolstoi Point.

	1975	1976	1977	1978
adults	392 (71%)	1385 (65%)	2420 (88%)	3652 (70%)
subadults	83 (15%)	440 (21%)	196 (07%)	1211 (23%)
chicks	79 (14%)	300 (14%)	130 (05%)	329 (06%)

There are a number of limitations to these data - because we were learning and made several mistakes and because counting Glaucous Gulls was not the primary focus of several of our aerial exercises. At the end of the flights in 1975, we learned that one of the observers omitted all flocks of gulls which were too large to count, i.e., that would require estimation. Because very small and very large groups are biased toward adults, we had to discard those data, and as a consequence the sample for 1975 is small. In 1977, the observers did not distinguish age types between Koyuk and Unalakleet, an area in which a major portion of the subadults occurs. In 1978, there seemed to be an unusually large concentration of adults and subadults around Nome, and our counts were made in mid-August which was before the bulk of chicks had moved out onto the beaches. Thus, we are not confident that the low numbers of chicks in 1978 reflect reproductive failure for that year.

In the course of the 1978 surveys the number of subadults was small in the north, increasing as we came south, reaching a maximum near Nome and Unalakleet where the flocks contained 50% or more subadults. There were also differences in the percentages of fledged chicks along the coast. The percentages were low between Cape Thompson and Cape Krusenstern, very high in the south end of Kotzebue Sound, and high between Cape Nome and Cape Darby. Because the flights were made before the peak of fledging, the differences may not mean anything; however, it could be that the production of chicks is higher in those areas where food is made available by settlements and salmon runs. In 1978, there were especially good salmon runs on the south shore of the Seward Peninsula, and reportedly up on the Noatak River (which we did not survey).

The numbers of gulls and the relative number of subadults increases at inlets to lagoons and near villages or fish-camps (oddly, the increase in numbers consistently seemed to be on the southern sides of both).

The number of subadults varies between the years. This may reflect the lack of attachment to site among subadults, a characteristic which allows them to gather where fishing is good. Subadults tended to occur as small groups, of 15 to 20, rather than as singles or as members of the very large flocks, 100-300. Most Walrus carcasses either had one adult territorial gull which gave a "long call" as we flew over, or had several adult gulls and a few subadults (2 or 3 subadults in a flock of 6 to 10).

If we tally up all the adults on the Seward Peninsula coast for all four years of survey and do the same for other age groups, and compare the resulting percentages with those recorded in Massachusetts and on the entire East Coast between the Maritime Provinces and Mexico in a winter sample taken in 1965 (Kadlec and Drury, 1968), we get:

	Seward Peninsula	Massachusetts	East Coast
adults	7849 (74%)	80,223 (70%)	426,000 (68%)
subadults	1930 (18%)	18,377 (16%)	105,000 (18%)
chicks	838 (08%)	15,391 (14%)	91,000 (15%)

The sample sizes are different, though the coastline of the Seward Peninsula is much longer than that of Massachusetts.

It is worth noting the similarity of the percentages of subadults. The percentage of subadults is a good indicator of whether a gull population is increasing or decreasing, as it integrates reproductive success and survival/mortality of the immature years.

It appears that the proportion of birds of the year (chicks) to subadults and adults was low on the Seward Peninsula in 1977 and 1978. The counts of chicks, subadults and adults in 1975 and 1976, are similar to those on the East Coast. This shift may be due to the reduction of available food supply as Walrus carcasses. Until about 1976, the heavy kill of Walrus for ivory produced a subsidy to the gulls in the form of rotting carcasses which littered the beach between Cape Espenberg and Norton Sound. In 1977, the natives began slitting the bellies of the Walrus from which they took the ivory but not meat. This was to avoid the "unfavorable publicity" of the rotting carcasses coming up on the beaches. The change in the behavior of hunters has greatly reduced the number of carcasses available and therefore may have secondary effects on the population of gulls.

Patten (pers. comm.) has estimated that a proportion of 4-5% juveniles in a total population would typify a stabilized structure. We need to know the survival rate of Alaskan adults to predict with any confidence. Nevertheless, the 8% of first year birds and especially the 18% of subadults leads us to anticipate an increase in the population size of gulls in northwestern Alaska. We presume that this increase will be compounded by the secondary effects of petroleum development in northwest Alaska.

H. BLACK-LEGGED KITTIWAKE (Rissa tridactyla)

1. General Description and Remarks

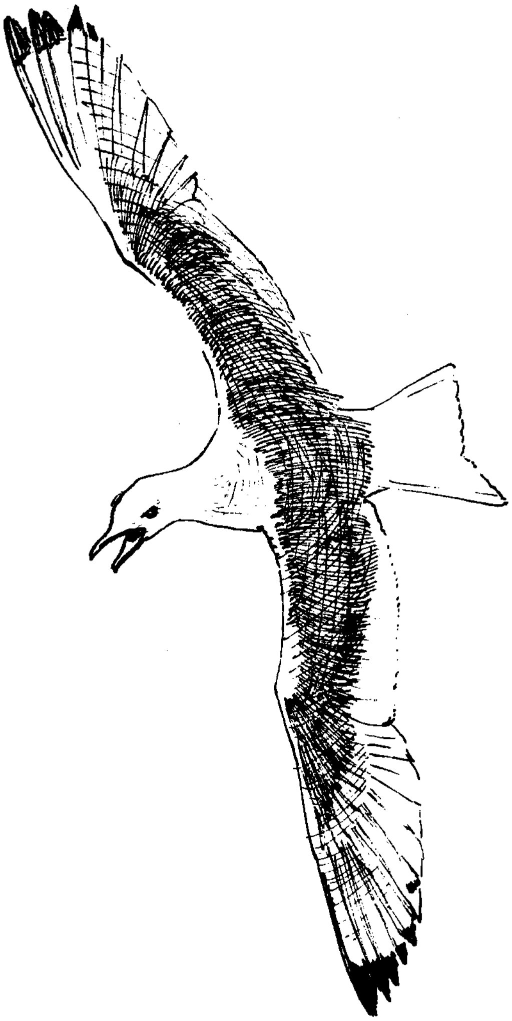
Kittiwakes are a conspicuous element of sea-bird cities, although they make up a small proportion of the total numbers of inhabitants. Their numbers are eclipsed by large numbers of murres or auklets in the same cities in the Bering Sea. Yet, their adaptation to nesting on ledges along precipitous sea cliffs has allowed kittiwakes to become much more numerous than the gulls who nest on level ground. In the southern Bering Sea there is a second species, the Red-legged Kittiwake, which nests almost exclusively on the Pribilof Islands, although there are a few colonies along the Aleutian Islands.

Black-legged Kittiwakes have been studied in detail in the North Atlantic and along the northwest coast of Siberia.

Except for the flocks which accompany commercial fishing boats they are not conspicuous around humans. Kittiwakes leave shallow water in autumn and spend their non-breeding season on offshore banks or along the edges of the Continental Shelf.

Kittiwakes feed on small bits of food which they take from the surface of the sea: small fish, invertebrates, and offal which they pick from the surface or close under the surface. Thus, variations in conditions of the sea change the availability of their food supply. In the Bering Strait Region early in the breeding season, they can be seen pecking tiny food objects; they feed and flock around floes of ice during break-up, apparently feeding on small fish and invertebrates which accompany the ice.

During the years of our study, the success of kittiwake reproduction was determined by activities of the birds during and immediately following



Black-legged Kittiwake in flight

the laying of eggs. We observed that periodic absence of birds from the cliffs, presumably looking for food, was associated with small clutches and failure of many pairs (Figure 5).

Feeding melées of kittiwakes gather over shoals of Sand Lance, which come into the range of their breeding cliffs. The melées become conspicuous in July and August and seem to attract several other seabird species. The gulls dissipate as the fish sound. Abundance of Sand Lance has had a strong effect on the success of breeding kittiwakes at Bluff Cliffs, Sledge Island, Cape Thompson and Cape Lisburne. Kittiwakes also seek food far from their colonies, and are often seen feeding in the mud which Gray Whales bring to the surface.

2. Characteristics of Kittiwake Breeding in the Bering Strait Region

Our observations of the breeding success of Black-legged Kittiwakes at Bluff Cliffs over a four-year period (1975-1978), have been supplemented by those of E.C. Murphy there in 1979, and by those at other colonies in the southern Bering and southern Chukchi Seas. These observations have led us to a number of conclusions about the characteristics of kittiwake breeding.

a. Trends in Reproductive Success

Reproductive success of kittiwakes in northwest Alaska is characterized by years of very low success ("bust" or "bad" years) or those of extremely high success ("boom" or "good" years in which one or two chicks are produced per breeding pair).

While assessment of whether a season was a "boom" or a "bust" is relatively straightforward, determination of the cause(s) of failure may be difficult. Among the several factors which contribute to the success of a season, the most critical may be the timing of the break-up of sea ice and the weather in late May and

Figure 5. Nest of Black-legged Kittiwake with chick, age 3a.

June. Both of these affect access to the breeding cliffs, availability of foods, and accessibility of nest materials. The availability of food items is related to and dependent on a series of events or conditions in the sea.

When the sea ice breaks up and moves out early, i.e. mid-May to early June, rather than mid-June or later, the birds have early access to their breeding sites and to food in leads in the ice. The early start gives them an advantage in an otherwise temporally constrained season. When spring runoff and spring rains have saturated the tundra and spring storms have torn Eel grass up from the sea bottom and windrows collect along the shore, kittiwakes can gather nest materials easily (Drury & Ramsdell 1979; Maunder & Threlfall 1972). In a year when food supplies are plentiful and available through the season kittiwakes do not travel great distances and can easily bring food to their mates and their chicks. Stormy weather, especially just after the eggs are laid, may be disastrous to the survival of chicks (Drury and Steele 1977, and Steele, unpubl. mans. 1977). Presumably, when weather is good and food supplies are abundant and nearby, the growth rates and fledging weights of chicks will be greater, and post-fledging success also enhanced.

b. Trends in Success at Bluff Cliffs

Coulson and White (1961) suggested that in any given year, the birds that lay the larger clutches are the older, more experienced birds. In a good year when many kittiwakes lay eggs, more inexperienced birds participate. It is probable that only the experienced breeders attempt to reproduce in a bad year.

At Bluff, reproductive success was extremely low in 1976, slightly higher in 1977, substantially higher in 1975, and very high in both 1978 and 1979. Indications of whether a year is good or bad are manifested by a number of characteristics which are obvious to the observer at the cliffs.

1) In good years, 1978 and 1979, the number of adults present was high and attendance was relatively constant through the season (see Main Body, Fig. 21, p. 347; and Table 2). In bad years the number of adults at the cliffs decreased near mid-season; the drop in number in 1976, as seen in Figure 21, is notably dramatic. Totals of birds counted at the cliffs varied by as much as 3000 birds in 1977, and by over 3000 in 1976. The highest number of birds were counted in 1979, a year of high success. The population at Bluff Cliffs in a good year is 6000-8000 kittiwakes as shown in Table 3 .

2) In good years, many nests were built (Table 4) early in the season and were maintained. In bad years few nests were built; most were poorly maintained and they deteriorated through the season as attendance diminished.

3) The peaks of laying and hatching occurred earlier in good years than in bad years (see Main Body: Table 18, p. 351; and Figure 22, p. 353), even though the first date at which eggs were seen each year did not vary importantly.

4) In a good year, 1978, when many nests were built, most received eggs (Table 6); in bad years, the peak of laying was later, fewer eggs were laid and fewer clutches were completed (Tables 5 and 6). In 1978, 26% more nests were built than in 1976, and 79% more were built than in 1977. A higher percentage of those nests built in 1978 received eggs than in previous years.

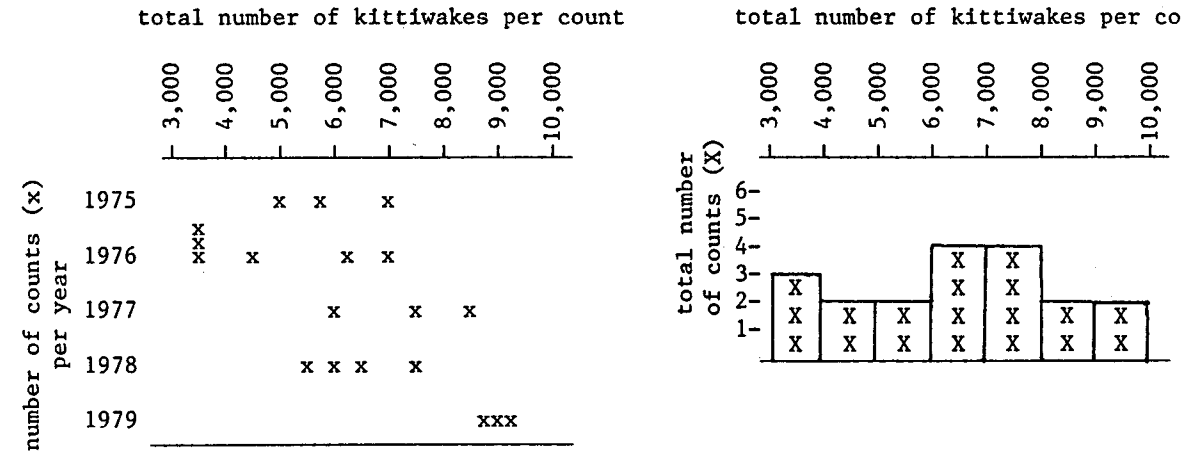
5) Clutch size was much larger in good years and smallest in bad years (Table 5). Clutches were fewest in number and smallest in size in 1977.

Table 2.
Numbers of Black-legged Kittiwakes counted at Bluff Cliffs, 1975-1979. Counts made from a boat passing slowly in front of the cliffs.

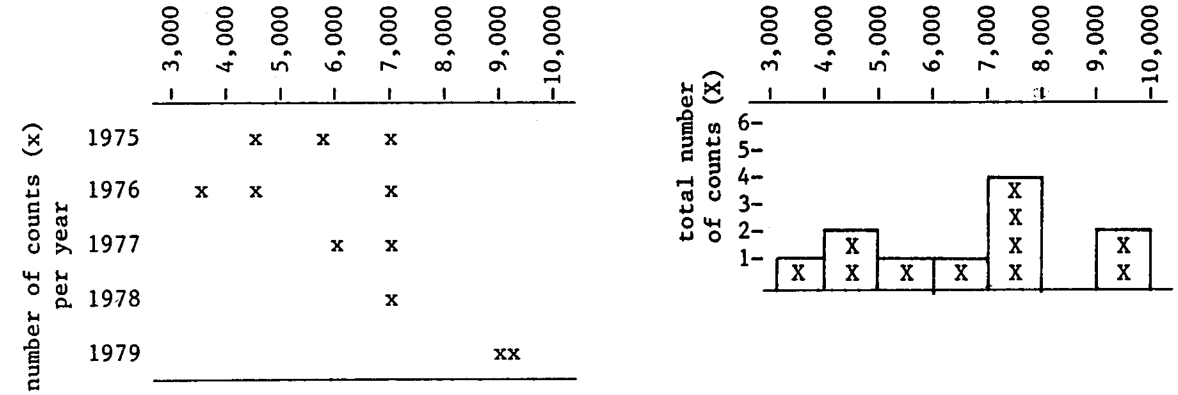
	1975	1976	1977	1978	1979
count (date)		3350 (16 Jun)			
	4985 (3 Jul)	6155 (30 Jun)		6040 (26 Jun)	
	7010 (4 Jul)	4616 (9 Jul)	6030 (7 Jul)		
		3520 (11 Jul)			
				7760 (18 Jul)	9225 (20 Jul)
	5795 (1 Aug)	7045 (26 Jul)	7386 (29 Jul)		9115 (31 Jul)
				6360 (9 Aug)	8720 (7 Aug)
		3690 (12 Aug)	8585 (19 Aug)	5825 (13 Aug)	

Table 3.
Distribution of counts of Black-legged Kittiwakes at Bluff Cliffs throughout the breeding season; data from 1975-1978 from Drury et al., 1979 from Murphy et al.

ALL COUNTS



COUNTS MADE BETWEEN JULY 1 AND AUGUST 1, 1975-1979



Number of counts in increments of five-hundred kittiwakes

3000-3500	3500-4000	4000-4500	4500-5000	5000-5500	5500-6000	6000-6500	6500-7000	7000-7500	7500-8000	8000-8500	8500-9000
0	1	0	2	0	1	1	0	3	1	0	2

Table 4.
Black-legged Kittiwake nests built relative to the number of sites monitored within areas of study geographically comparable from year to year, 1976-1979, at Stakes 8, 10, 13, and 14, Bluff Cliffs.

	1976			1977			1978			1979		
stake	no. of sites	no. of nests	ratio	no. of sites	no. of nests*	ratio	no. of sites	no. of nests	ratio	no. of sites	no. of nests	ratio
8	23	19	0.83	28	13	0.46	29	20	0.69	25	22	0.88
10	23	20	0.87	31	10	0.32	39	26	0.67	30	23	0.77
13	44	29	0.66	48	28	0.58	52	38	0.73	39	36	0.92
14	26	22	0.85	34	12	0.35	37	29	0.78	32	32	1.00
total	116	90		141	63		157	113		126	113	
ratio of total nests built to total sites monitored ± 95% confidence limits	0.78 ± 0.077 n = 116 st.dv. = 0.419			0.45 ± 0.082 n = 141 st.dv. = 0.499			0.72 ± 0.071 n = 157 st.dv. = 0.451			0.90 ± 0.054 n = 126 st.dv. = 0.305		

* In 1978, we used the following definition of nest (as agreed on by OCS researchers at the January 1977 meeting of the Pacific Seabird Group): " any mud platform showing evidence of activity in the current season". In 1977, our definition of nest was much narrower, and so even though fewer nests were built the number of sites assigned nest status is a conservative number.

Table 5.
Clutch sizes of Black-legged Kittiwakes at Bluff at areas of study geographically comparable from 1976-1978, at Stakes 8, 10, 13, and 14. In 1979, observations at study areas were undertaken too far into the incubation period for useable data on clutch size to be obtained.

stake	1976 no. of eggs	1976 no. of clutches	1976 clutch size	1977 no. of eggs	1977 no. of clutches	1977 clutch size	1978 no. of eggs	1978 no. of clutches	1978 clutch size
8	3	3	1.00	5	4	1.25	35	19	1.84
10	4	4	1.00	7	7	1.00	37	21	1.76
13	12	10	1.20	9	9	1.00	60	36	1.67
14	12	11	1.09	5	4	1.25	43	25	1.72
total	31	28		26	24		175	101	
mean clutch size ± 95% confidence limits	1.11 ± 0.122 n = 28 st.dv. = 0.315			1.08 ± 0.378 n = 24 st.dv. = 0.893			1.73 ± 0.088 n = 101 st.dv. = 0.445		

Table 6.
Egg-laying effort at study areas at Bluff Cliffs, 1975-1978. Data for 1976-1978 are from study areas geographically comparable among the three years.

year	no. of nests	no. of clutches	average clutch size (eggs/cl)	% nests empty	date 1st egg appeared at colony	date of peak of laying
1975	35*	24*	1.22	32%'	21 June	~6 July
1976	90	28	1.11	69%	21 June	5 July
1977	63	24	1.08	62%	20 June	7 July
1978	113	101	1.73	11%	18 June	24 June

* These data for 1975 are from Stake 3; data for 1976-1978 are from Stakes 8, 10, 13, & 14.

' This figure is derived from data from Stake 3, 4, and 10.

6) The ratio of chicks fledged to nests built was significantly higher in good years (Table 7). The next section discusses the process of estimating reproductive success by comparing the number of chicks produced to the number of breeding pairs.

Estimating Reproductive Success

To estimate reproductive success we used data gathered at study sites through the season. The data gave a ratio of chicks fledged to nests built (the building of a nest confirms the presence of a pair of adult kittiwakes) (Table 7). We also made a survey of the entire length of the cliffs for the number of nests and chicks counted on one day at or after the peak of hatching and before fledging (chick census). This also gave a ratio of chicks to nests (Table 8) (see Appendix IX , "Methods Used at Bluff"). The difference between the estimates of reproductive success from these two samples within one year was negligible as compared to the differences among the years. The data in Table 9 support the idea that a strategically-timed count can supply data adequate for determination of the level of reproductive success for that season. We are not interested in tenths of percentages so much as at which place on the boom/bust seesaw the kittiwakes sat on in any one year.

Because the differences between a good year and a bad year are so marked, a short-term study should produce the data necessary to assess reproductive success. Indications of the potential level of success will be seen early in the season by a) the number of nests built relative to the number of sites occupied and later by b) the number of chicks that survive their first week.

Table 8.
Comparison of the numbers of nests, chicks and broods counted during chick censuses at Bluff, conducted on one day of each brooding period in 1975, 1976, 1977 and 1978.

	1975		1976		1977		1978	
no. of nests	1500		1827		1547		2524	
no. of chicks	708		46		151		2412	
chicks/nest	0.47		0.03		0.10		0.96	
no. of broods	698		46		150		2156	
1 chick (%)	670	(97.2%)	46	(100%)	149	(99.3%)	1904	(88.0%)
2 chick (%)	19	(2.8%)	0		1	(0.7%)	248	(11.5%)
3 chick (%)	0		0		0		4	(0.2%)
no. of single chicks (% of total no. chx)	670	(94.6%)	46	(100%)	149	(98.7%)	1904	(78.9%)
no. of twins (% of total no. chx)	38	(5.4%)	0		2	(1.3%)	496	(20.6%)
no. of triplets (% of total no. of chx)	0		0		0		12	(0.5%)

Table 7.
Reproductive success in Black-legged Kittiwakes at Bluff Cliffs, as chicks fledged per nest built within areas of study geographically comparable from 1976-1979, at Stakes 8, 10, 13, and 14.

	1976			1977			1978			1979		
stake	no. of chicks	no. of nests	chicks per nest	no. of chicks	no. of nests	chicks per nest	no. of chicks	no. of nests	chicks per nest	no. of chicks	no. of nests	chicks per nest
8	0	19	0.00	0	13	0.00	18	20	0.90	21	22	0.96
10	0	20	0.00	1	10	0.10	19	26	0.73	24	23	1.04
13	0	29	0.00	3	28	0.11	36	38	0.95	37	36	1.03
14	3	22	0.14	0	12	0.00	21	29	0.72	34	32	1.06
total	3	90		4	63		94	113		116	113	
mean number of chicks fledged per nest built ± 95% confidence limits	0.03 ± 0.038 n = 90 st. dv. - 0.181			0.06 ± 0.060 n = 63 st.dv. = 0.246			0.83 ± 0.050 n = 113 st.dv. = 0.516			1.03 ± 0.120 n = 113 st.dv. = 0.646		

Table 9.
Comparison of (a) the estimates of reproductive success (chicks fledged per nest built) from data collected through the season, to (b) the estimates of reproductive success based on chick census data (chicks present late in the nestling period per nest visible), at Bluff Cliffs.

year	(a) reproductive success: chicks/nests at stakes	(b) chick census: chicks/nest on one day along entire cliff
1975	0.59	0.47
1976	0.03	0.03
1977	0.06	0.10
1978	0.83	0.96

The most effective time to estimate reproductive success is when kittiwake chicks are about age 3b/4 (that is, two to three weeks old [see Table 13 on page 49]) and big enough to be seen easily. Chick censuses conducted at this time, before fledging has begun, have provided data useful in estimating reproductive success by relating the number of chicks present to the number of nests (or the number of sites occupied by adults), as seen in Table 8. The number of nests built (which is used in estimates of success using data gathered at the stakes) may be difficult to count or estimate this late in the season, especially in bad years because nests built early in the season deteriorate. Regardless of this, occupied sites can be counted and used in comparing year to year differences in reproductive achievement; in bad years the ratio of chicks to nests or chicks to sites occupied will differ dramatically from those in good years.

Short-term surveys conducted mid-season also can yield data useful for estimating reproductive success, especially if conducted at or near the peak of hatching. At this time the number of eggs still unhatched is approximately equal to the number hatched. The resulting estimate of success (chicks per nest) may be slightly higher than the final tally of chicks fledged per nest built.

Table 10 compares the estimates of reproductive success (chicks fledged per nest built; last column) in geographically comparable study areas each year at Bluff, to the numbers of eggs and chicks present on days when (a) the number of eggs is greater than chicks (i.e., just before hatching has begun), (b) the number of eggs still unhatched is nearly equal to the number unhatched (i.e., at the peak of hatching), and (c) the number of chicks present in the nests is greater than the number of eggs still present. Of these three counts, the number of chicks per nest counted on one day at or near the peak of hatching for both good and bad years is the closest approximation of the number of chicks actually fledged (Tables 10 & 11). The number of eggs laid does not seem to be useful for

Table 10.
Comparison of estimates of reproductive success (chicks fledged per nest built) based on three counts conducted each year, 1975-1978, at study areas of Black-legged Kittiwakes, Bluff Cliffs.

year	nests	(date)	eggs	eggs/nests	(date)	eggs	eggs/nests	chicks	chicks/nest	(date)	eggs	eggs/nests	chicks	chicks/nest	total chicks fldgd	chicks fldgd/nest
1975	41				(8/5)	1	0.02	25	0.61	(8/16)	0	0	26	0.63	24	0.59
1976	90	(7/11)	14	0.16	(8/5)	3	0.03	2	0.02	(8/19)	1	0.01	3	0.03	3	0.03
1977	63	(7/9-10)	13	0.21	(8/5)	5	0.08	4	0.06	(8/17-21)	0	0	5	0.08	4	0.06
	110	(7/10)	30	0.27	(8/5)	10	0.09	14	0.13	(8/16-17)	4	0.04	13	0.12	13	0.12
1978	113	(6/25)	93	0.82	(7/20-22)	75	0.66	71	0.63	(7/31)	3	0.03	102	0.90	94	0.83
		count made when the number of eggs is greater than the number of chicks, i.e., just before onset of hatching			count made when the number of eggs unhatched is nearly equal to the the number hatched, i.e., at the peak of hatching [peak of hatching: 1975 30 July 1976 30 July - 4 Aug 1977 28 July - 12 Aug 1978 21 July].					count made when the number of chicks present in nests is greater than the number of eggs still unhatched						

Table 11.
Comparison of the number of chicks fledged with counts of chicks on particular days, at four study areas at Bluff Cliffs, 1976-1978. Chick counts on two different days are given for 1978; one was on about the same day as the 1976 and 1977 counts, and the other was conducted when the number of chicks hatched was roughly equal to the number of eggs still unhatched (i.e., at the peak of hatching).

year	stake	no. of nests	total no. of chicks fledged from stake	(date) and chicks seen on given day per nest built ch = chicks e = eggs n = nests	total no. of chicks fledged per nest built
1976	8	19	0	(8/5) = 0	0
	10	20	0	(8/5) = 0	0
	13	29	0	(8/5) = 0	0
	14	22	3	(8/5) [3ch + 2e] 3ch/22n = 0.14	0.14
	total	90	3	3ch/90n = 0.03	0.03
1977	8	13	0	(8/5) = 0	0
	10	10	1	(8/5) [4e] = 0	0.10
	13	28	3	(8/5) [3ch + 1e] 3ch/28n = 0.11	0.11
	14	12	0	(8/5) [1ch] 1ch/12n = 0.08	0.00
	total	63	4	4ch/63n = 0.06	0.06
1978	8	20	18	(7/22) [16ch + 13e] 16ch/20n = 0.80 (8/6) [20ch + 1e] 20ch/20n = 1.00	0.90
	10	26	19	(7/22) [18ch + 17e] 18ch/26n = 0.69 (8/6) [20ch] 20ch/26n = 0.77	0.73
	13	38	36	(7/20) [20ch + 27e] 20ch/38n = 0.53 (8/6) [37ch + 1e] 37ch/38n = 0.97	0.95
	14	29	21	(7/20) [17ch + 18e] 17ch/29n = 0.59 (8/6) [21ch + 2e] 21ch/29n = 0.72	0.72
	total	113	94	(7/20-22) 71ch/113n = 0.63 (8/6) 98ch/113n = 0.87	0.83

estimating reproductive success; but clutch size, date of the peak of laying and the proportion of nests receiving eggs do indicate the potential level of success. During incubation in a bad year better than half the nests were empty, and in a good year most nests contained eggs (Tables 6, 10 & 11).

The similarity of the number of chicks present at or shortly after the peak of hatching, to the number of chicks that fledged indicates: (i) the second half of the eggs that hatch tend to fail; (ii) when two-chick broods are more common (in good years), the second chick tends to fail; or (iii) few of the chicks that survive one week fail.

Growth of Kittiwake Chicks

The average daily increase in weight (grams per day) over an eighteen-day period was computed for each of 21 chicks in 1978, and 36 chicks in 1979, at each of three study areas at Bluff; the data are presented in Table 12. Both were good years; we do not have data from bad years. Chicks grew more rapidly in 1979 than in 1978, suggesting a more abundant and nearer food supply in 1979, because it is most unlikely that more experienced breeders were present that year only. The higher the weights of chicks at fledging the greater their chances of post-fledging survival.

Table 13 lists the characteristivs of kittiwake chicks we used to ascribe ages to the young in the nests.

c. Trends in Success Among Colonies

There is a temporal gradient in the beginning of the breeding season in the Bering Strait Region (Table 14); generally, kittiwakes begin breeding later in the north as might be expected in light of the progressively later break-up and northward movement of sea ice through the spring.

Table 15 compares the population sizes, breeding effort and success of Black-legged Kittiwakes at seabird cities around the Bering Strait Region.

Table 12.

Average Increases in Weight (gm gained per day) of Black-legged Kittiwake Chicks at 3 study areas at Bluff in 1978 and 1979.

Location	Average increase in weight: gm/day	
	1978	1979
Eagle Beach	15.5 ± 1.9 gm/day	24.8 ± 5.0 gm/day
Thumbstack	15.8 ± 3.0 gm/day	18.9 ± 2.8 gm/day
Castle Rock	15.5 ± 2.2 gm/day	18.6 ± 3.6 gm/day
Overall	15.26 ± 2.8 gm/day	(20.8)

Table 13.
Identifiable stages of kittiwake chick growth.

1a	Chick downy with buff brown to red tint; lies or crouches in nest; egg tooth on bill; head and body of similar size.
1b	Defecates over edge of nest.
2	Downy, but more uniformly gray; active - stands, walks in nest; loses egg tooth but bill tip is pale, body large relative to head.
3a	Downy, becoming feathered: black on elbows; silver back feathers emerge; dark pinfeathers visible on forearm.
3b	Mixed down and feathers; can first clearly see black tail feathers; pinfeathers have erupted into feathers on wing with dark feathers on forearm; down on collar; black ear patch and black smudge between eye and bill.
4a	Length of tail feathers is equalled by length of primaries; mostly feathered out; down still on back of head, flanks, rump; white visible at base of tail feathers.
4b	No down; flying.

Table 14.
Phenology of Black-legged Kittiwakes in the Bering Strait Region, Alaska.

	1959	1960	1961	1975	1976	1977	1978
first egg							
Cape Thompson	22 June	21 June	25 June		4 July	2 July*	
Cape Lisburne						1 July	
Little Diomede Is.						28 June	
King Is.					none seen		
Bluff Cliffs				21 June*	21 June	19-22 Jun	18 June
first hatch							
Cape Thompson	20 July	17 July	22 July		9 Aug	10 July*	
Cape Lisburne						10 July	
Little Diomede Is.						24 July	
King Is.					not obsrvd		
Bluff Cliffs				18 July*	19 July	17-20 Jul	10 July
first fledge							
Cape Thompson	30 Aug	20 Aug	27 Aug		not obsrvd	23 Aug	
Cape Lisburne						--	
Little Diomede Is.						not obsrvd	
King Is.					not obsvrd		
Bluff Cliffs				by 1 Sept	27 Aug		21 Aug

* Asterisks indicate dates which were calculated on the basis of a 27-day incubation period and a 44-day nestling period (Coulson & White, 1958; Drury et al., 1978).

Table 15. Measurements of Reproductive Effort and Success of Black-legged Kittiwakes in the northern Bering and southern Chukchi Seas.

	year	Cape Lisburne	Cape Thompson	Little Diomede Island	King Island	Sledge Island	Bluffs Cliffs	Square Rock	Cape Denbigh	Egg Island
pop. est.	1960		14,500							
	1961		14,800							
	1975					750-1250	7000-7200	800	500-700	200-300
	1976		10,500		3000-6000	1300	6000-7000	575	1800N+650S	525
	1977	15-25,000	10,200	17-20,000		800-1100	6000-8600	1210		
	1978	20,000				2500	6000-7800	1100-1500		
	1979						8700-9200			
no. of nests sampled	1975					125	226			
	1976	140			72	204	2244	121	765	92
		132					515			
	1977	144	238	149		122	705	138		
				116' & 46'		317	514 & 110			
	1978	151	220			56	2524 & 113			
% of nests w/eggs	1975					65%	68%			
	1976	22%					29%			
	1977	53%	56% - 72%		39% & 50%		38%	48%		
	1978		44%			91%	89%	82%		
ave. clutch size (brood-clutch size)	1960		1.92							
	1961		1.88							
	1975					1.53	1.22			
	1976		(1.00)				1.11			
	1977	1.11 & 1.16	1.15-1.20	1.27		1.53	1.08-1.16	1.26		
			(1.04)	1.17						
	1978	1.24				1.75	1.73	1.75		
		(1.19)	(1.08)							
incub. adults per nest counted	1976				0.01-0.28	0.04-0.15	0.16	0.08	0.27	0.38
chicks fldgd per nest built (or counted)	1975					0.51	0.42		0.50	
	1976	0.11	near 0		near 0	near 0	0.02	0.02		
		(8/27)*								
	1977	0.85**	0.56	0.34 &		0.05	0.10-0.12	0.23		
		1.14	0.64**	0.50		0.10	1.11			
		(8/26)*		(8/11)*			(8/9)*			
	1978	1.24					0.83 &	0.72		
		(7/25)*					(0.96)			

[See following page for explanation of superscripts: ' * **]

Explanation of superscripts in Table 15.

The second entries in some columns are data from stakes studied through the season as opposed to the other entries which represent data from all stakes, even those studied only occasionally through the season, or as opposed to counts made of entire colony.

The number of observations of nests where these two sets of data were obtained differed significantly; 20 observations of 116 nests, as opposed to 7 observations of 46 nests. This may account for the disparity in the estimates of clutch size and chicks per nests that follow.

* The asterisked numbers in the last section are the number of chicks and eggs found on the date indicated in parentheses, divided by the number of nests, at Cape Lisburne, Little Diomede Island, and Bluff Cliffs, in 1977.

** These data are the number of chicks fledged divided by the number of eggs laid.

Data for Table 15 are from the following sources: Swartz 1966; Springer, Roseneau & Johnson 1979; Drury 1976; Drury & Steele 1977; Biderman & Drury 1978, based on field notes of Steele, Steele & Watson summer 1977; Drury *et al*. 1978; Drury & Ramsdell 1979; Murphy field notes summer 1979.

Table 16.
Numbers of nests, eggs and chicks counted at Little Diomede Island in 1977, and at Bluff Cliffs in 1977 and 1978. Sample sizes are comparable between both places, and both years at Bluff.

		date	number of nests	number of eggs	number of chicks	$\frac{\text{chicks + eggs}}{\text{nests}}$
1977	Little Diomede Island	11 Aug	116	20	19	0.34
	Bluff Cliffs	5 Aug	110	10	14	0.23
1978	Bluff Cliffs	20-33 July	113	75	71	1.25

Table 16 Compares counts of eggs, chicks and nests made at Little Diomede Island in 1977, with counts made at Bluff Cliffs in 1977 and 1978 These data were included because of the comparable number of nests sampled. The disparity between the number of chicks and eggs counted in 1977 at both places and in 1978 at Bluff, is obvious and reflects the greater success of the 1978 season. In 1977, kittiwakes at Little Diomede seemed to reach an only marginally higher level of reproductive success than those at Bluff. Counts at both places were made at the peak of hatching, when the number of eggs unhatched was approximately equal to the number of chicks already hatched.

3. Feeding

In 1975, before Sand Lance arrived and feeding meleés were visible from Bluff, the major movement of kittiwakes away from and back to the cliffs was along the beaches. Most of the kittiwakes commuting away from the cliffs flew to the south and southwest. They flew steadily, close over the water, 1-2 meters or moderately high, 15-20 meters. When feeding, the birds hawked over the water dipping to the surface and often settled as if catching crustacea.

After the feeding melees began, many birds sat on the surface pecking, but the main meleé was made up of birds which hovered and dove like terns. The gulls went into the water with wings bent back as do Gannets. They dove out of sight and stayed down 1-3 seconds.

Our observations of birds which we judged to be commuting suggest that the kittiwakes from Bluff flew regularly as far as 50-75 miles to feed. In July many fed regularly on shoals just east of Safety Lagoon where we saw two melees during one trip.

Apparently, there was an important non-breeding population or breeding adults flew a long way for food, because when the feeding meleés were seen at Sledge Island in July, the number of kittiwakes around the nesting cliffs increased by 30-50%.

In August, the shoals evidently came closer to Bluff so that on 22 August we saw two feeding melées between Topkok and Bonanza River and four between Bonanza and the ferry crossing.

Our observations of feeding melées in 1977 are summarized in Tables 1a and 1b on pages 14a and 14b. Almost all of these feeding bouts occurred within a mile of the shore.

The food used in July was crustaceans, judging from the feeding behavior used; that is, predominantly swimming on the surface and pecking at or below the surface of the water.

Our watches indicated that rates of feeding varied widely during the season. On 29 July, concurrent with a 24-hour count, we observed a chick in a nest at study site 14 for about 45 minutes out of every hour. We did not see it fed once during the entire day, even though an adult was present most of the time, and there were several changes of adults. However, on 2 and 4 August, we observed three nests with chicks at study site 17, and saw them fed several times.

4. The Value of Kittiwakes in OCS Studies

The kittiwakes in the northern Bering Sea are perhaps the single species most useful for purposes of environmental assessment. They are convenient to study both the availability of prey and the mechanisms affecting reproductive success and failure. The fact that kittiwakes occupy discrete territories and built obvious nests makes them refreshingly easier to study than the crowded murres or those that disappear into burrows and rubble. They breed in large numbers which remain relatively constant through the breeding season.

Kittiwakes are probably insensitive to direct effects of spilled oil as they spend little time on the surface of the water. They are, however, sensitive to local changes in food supply; therefore, they may be most useful as indicators of changes in environmental conditions.

The following information (taken in part from Drury, Hunt and the Pacific Seabird Group, 1978) has been identified as important both for understanding the biology of Black-legged Kittiwakes and for using kittiwakes as tools in environmental assessment.

a. Reproductive Biology

i) There is a temporal gradient in the start of laying of eggs that varies from early in the Gulf of Alaska to late in the Bering Strait and Norton Sound. Apparently, there has been a historical change in phenology (breeding schedule) at Cape Thompson, where, in the late 1950s and early 1960s, egg-laying began earlier than during the present studies from 1975 to 1979.

ii) There are important and regular variations from one region to another in the percentage of nests in which eggs are laid and in the size of clutches; smaller clutches are laid and fewer nests receive eggs in the north (less than 25% in some years) than in the Gulf of Alaska. Again, historical informations suggests that in the 1950s on the Pribilof Islands, and in the 1960s at Cape Thompson, clutch size may have been larger than at present.

Black-legged Kittiwakes breeding in other parts of their circumpolar range, e.g. the northeast Atlantic Ocean where this species is reproducing well and the population is increasing, lay earlier and lay larger clutches than in Alaska. It is likely that timing of the start of clutches, clutch size and the percentage of nests receiving eggs all relate to the availability of food. This all suggests that presently the northern Bering Sea and Chukchi Sea kittiwake populations may be subject to some stress due to the timing of break-up of sea ice and the availability of food. Nevertheless, this northern region supports some large colonies of 20,000 to 35,000 birds.

iii) Important differences exist in the regularity of reproductive success in different geographic regions. From 1975 to 1977, these differences were usually expressed in the number of eggs hatching per nest, either because fewer eggs were laid or because eggs failed to hatch. Egg-loss, a major source of reproductive failure at least in the north, characteristically occurs in the first week after laying, as if the conditions depressing clutch size have a continuing influence on the intensity of the incubation drive. This is not always the case, however, as indicated by loss of chicks late in the season in an otherwise good year like 1979.

In some regions there are years of failure, and years of good success (high productivity) in which many pairs raise two chicks per nest. In other regions, reproductive performance is moderate every year and no parents have been able to raise twins (e.g. the Pribilof Islands).

iv) The reasons for reproductive failure have differed in different regions. In the north, particularly, lateness of ice break-up and absence of food have been suggested to be the primary influences, while in the Gulf of Alaska bird predators are reported to be the proximate causes of reproductive failure. In Prince William Sound predation by Bald Eagles and Common Ravens occurred into the early chick stages. Observations of birds on the nest suggest that lack of attentiveness and even absence from the nest during the early stages of incubation are responsible for the opportunities for predators to take eggs. This lack of concentration and the absences may reflect difficulty in finding food. Observations that certain individuals are present regularly and raise young during a general failure show that individual differences and capabilities are important.

b. Important and conspicuous regional variations in food used by kittiwakes

In the Gulf of Alaska, kittiwakes depend heavily on Capelin (Mallotus villosus), which is evidently a reliable resource. The use of Capelin is augmented by Sand Lance (Ammodytes hexapterus), which appear about the time kittiwake eggs hatch. In the southern Bering Sea, kittiwakes use a diverse food supply without depending heavily on any single species. In the northern Bering Sea and Chukchi Sea different colonies use different foods, but Capelin is unimportant. Arctic Cod (Boreogadus saida) is important in the Cape Thompson area. In the period of observation (1975 to 1978), Springer and Roseneau found that breeding success at the Cape Thompson and Cape Lisburne kittiwake cities depended to a great extent on the appearance of Sand Lance in the feeding range of the breeding birds.

Kittiwakes are evidently opportunists in their feeding. They will become specialists if suitable prey is available. Whether a colony has a consistent or a "boom/bust" economy seems to depend on the kinds and numbers of small fish and crustacea as well as the phenology of the organisms in the surrounding seas.

c. It is important for future monitoring of populations, measuring impact and predicting effects on populations, to know which colonies produce young at a rate higher than annual adult mortality, and whether the fledging weights of those young are high enough to ensure post-fledging survival so that they in effect export young. Any changes in these rates reflect environmental effects on these populations. It is also important to identify those colonies which do not produce enough young to maintain the population, i.e., those colonies which depend on immigration of young. This information is needed to determine what colonies are critical and at what rate a population might be able to increase.

I. OTHER GULLS

The gulls in the Bering Strait Region are mostly Glaucous Gulls and Black-legged Kittiwakes; but, several other species occur along the edges of the area. The Siberian subspecies of Herring Gull is seen commonly and evidently nests on Saint Lawrence Island. This species has a darker mantle than the local Glaucous Gulls and has black on the wing-tips. It nests on flat ground in most of its range. At Bluff, a Herring Gull paired with a Glaucous Gull, and they nested on a fan of debris below the main cliffs. The two species interbreed freely along the south shore of Iceland.

The Pacific Coast representative of the Herring Gull, the Glaucous-winged Gull (Larus glaucescens), reaches the southern margin of this region on the delta of the Kuskokwim River, and there interbreeds with Glaucous Gulls.

A number of subadult and a few adult Slaty-backed Gulls (Larus schistisagus) loaf among the gatherings of gulls where rivers enter lagoons, along the edge of the ice, and around carcasses or other offal on the coasts of Saint Lawrence Island, the Seward Peninsula, and occasionally farther north. The subadults resemble Herring Gulls or Glaucous Gulls but are larger and have coarser mottling in the subadult plumage. As adults they have black mantles.

Mew Gulls (Larus canus) nest in small numbers along rivers in northwestern Alaska and occur along most large rivers in this area. They make up part of the mixed gullery on the south-central shore of Saint Lawrence Island; elsewhere in this region they do not seem to nest in the company of Glaucous Gulls. Mew Gulls are a diminutive form of the familiar "seagull" and represent the circumboreal species group which includes Ring-billed Gulls (Larus delawarensis), perhaps Thayer's Gulls (*Larus thayeri*), and Iceland Gulls (*Larus leucopterus*). All of these are small and largely aerial feeders. The Mew Gulls have black wing tips with large white patches on the feather tips.

Three other smaller species occur regularly in this region: Ross's Gull (*Rhodostethia rosea*) and Ivory Gull (*Pagophila eburnea*) along the edge of the sea ice in winter, and Sabine's Gull (*Xema sabini*) nesting in small numbers north of Shishmaref on the northwest coast of the Seward Peninsula. All these gulls are small and tern-like in flight. Ross's Gull is white with grayish underwings and has a wedge-shaped tail. In adult plumage, the Ivory Gull is immaculately white. The Sabine's Gull has a black head in breeding plumage and a striking black and white pattern of triangles on the wings. Birds of these species spend much of their time flying, and feed by dipping food from the surface while in flight. Their flight is intermediate between that of the small gulls and terns.

J. TERNS

Two species of tern (*Sterna*) nest in the Bering Strait Region. Arctic Terns (*Sterna paradisaea*) have a wide range, all around the north, and occur in the Antarctic in a barely different form. Aleutian Terns (*Sterna aleutiea*) are endemic to the Bering Sea.

Arctic Terns nest in simple pairs or as a few together all along the Alaskan coast and Saint Lawrence Island, primarily at the mouths of rivers. We have seen two large terneries, one of about 50 pairs on the south shore of Saint Lawrence Island, and another of approximately 75 pairs near the mouth of Safety Lagoon. A few single pairs of Arctic Terns nest on gravel bars of the large rivers in the interior of the Seward Peninsula. Our reconnaissance of the beaches from Cape Prince of Wales to Wainwright in July and August suggested scattered nesting of Arctic Terns along the coast, and the presence of large terneries at Cape Kruzenstern and Cape Espenberg.

Henry Springer reports that 100 pairs of Aleutian Terns nest scattered across the islands in Safety Lagoon. Aleutian Terns also have been seen at Moses Point and nesting on islands in Brevig Lagoon. This species nests later than the Arctic Tern, and feeds several miles offshore; unlike Arctic Terns, the parents and young linger on the breeding grounds several weeks after the young fledge.

Arctic Terns fly tens of thousands of miles to winter in the Southern Hemisphere, while Aleutian Terns apparently spend the winter in the southern Bering Sea.

K. PIGEON GUILLEMOT (Cepphus columba)

The Pigeon Guillemot occurs along the Pacific coast of North America. The closely related Black Guillemot (Cepphus grylle) replaces the Pigeon Guillemot at and north of Cape Lisburne. It is a circumpolar species occuring across North America and the arctic coast of Siberia. Another closely related species replaces Pigeon Guillemots southwest of the Kamchatka Peninsula.

These birds are glossy black in the breeding season with white patches on their wings. Their feet and the lining of their mouths are bright red. In the winter they molt to a mostly white plumage speckled with black. Buillemots feed on small crustacea - Amphipods and Euphausiids, and slender fish such as Rock Eels and Pricklebacks.

Pigeon Guillemots nest under boulders at the foot of rocky cliffs near the sea. They occur in small numbers along the same shores where Pelagic Cormorants and puffins breed. The largest aggregation of Pigeon Guillemots in the northern Bering Sea breeds in the basaltic blocks spalled off the tongues of lava east and west of Savoonga on Saint Lawrence Island (see Appendix VIII, "Study Areas": Figure 18). Here, several hundred pairs breed. At most other bird cities there are a few or no more than several dozen pairs.

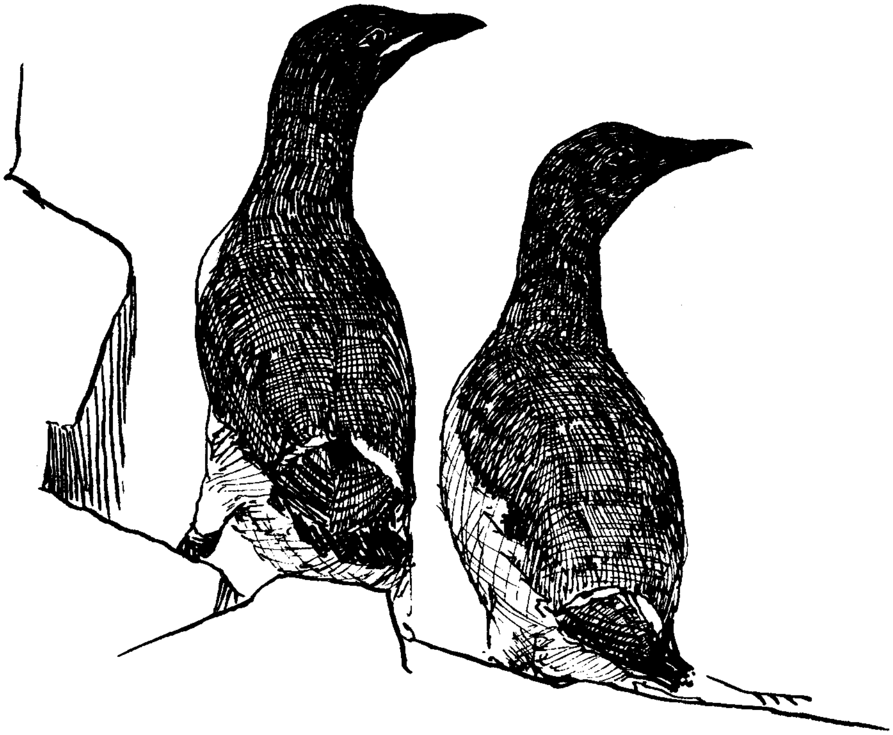
In England, the name "guillemot" is used for those species of *Uria* which are called murres in the United States and Canada.

L. MURRES Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*)

1. *Description of Species*

Two species of murre, Common and Thick-billed (Pallas' or Brunnich's), occur in Bering Strait Region and all around the arctic. The closely related Razor-billed Auk (*Alca torda*) occurs in the North Atlantic, as did the now extinct Great Auk (*Pinguinus impennis*). No other closely related species occur in the Pacific. In Great Britain murres are called guillemots.

Murres are the most widely distributed seabirds in the Bering Strait Region, and they make up the majority of seabirds except where Crested and Least Auklets nest. Murres are successful; they nest at high densities and they feed from the surface to the bottom of the water column in nearly all parts of the Continental Shelf. They breed as far north as there is open water in front of rocky vertical cliffs. They move south for the winter, either to the edge of the sea ice or to the banks along the edge of the Continental Shelf. Because they converge with human fishermen on good fishing grounds in the North Atlantic, North Pacific and southern Bering Sea, they are victims of gillnets set for salmon. It has been reported that hundreds of thousands of murres have been killed between Greenland and Newfoundland in the Atlantic and in the central Bering Sea as a consequence of tangles with gill nets (Ogi and Tsusita 1973).



Thick-billed Murre and Common Murre

Common and Thick-billed Murres occur together in the Atlantic and the Pacific. The Common Murre is predominantly a fish-eater and occurs in the Atlantic farther south than does the Thick-billed Murre. Thick-billed Murres feed on fish, but crustaceans make up as much as 40% of their diet. In the Bering Strait Region and in the southern Bering Sea, Common Murres occur, almost to the exclusion of Thick-billed Murres, in the shallow water of low salinity along the Alaskan coast. Thick-billed Murres are more numerous in the cold, saline waters to the west and north, e.g. the Pribilof Islands, Saint Lawrence Island, King Island, Little Diomede Island, Cape Thompson and Cape Lisburne.

Of the two species, the Common Murre, concentrating on a diet of fish, has a more slender bill. The Thick-billed Murre has a shorter, thicker bill (more like a "fly-catcher's"), with a silvery horizontal line at the corner of the gape (base of the bill). Both murres carry fish to the cliffs to offer to the females in courtship feeding; the white belly of a fish carried head into the gullet of the bird produces a white slash at the base of the bill (Figure 6). The white mark on the Thick-billed Murre's bill suggests such a belley of fish and may act as a stimulus during courtship.

Although both species will nest in dense aggregations on almost any surface where they can perch, where the two species occur together Common Murres prefer to nest in dense congregations on broad ledges (Figure 7) and on the tops of rocky islands called stacks. Thick-billed Murres nest on narrow ledges, often only one murre deep. There does not seem to be any evidence that the geographic distribution of the two species is influenced by the form of ledges available.

When murres come to their cliffs in late May in our region, after appearing off the cliffs on the water in the first open leads, they are very nervous. They spend short periods at the cliffs and easily become frightened;

Figure 6. Common Murre with fish. Note white belly of Lumpenus, which suggests the white spot along the gape of Thick-billed Murres.

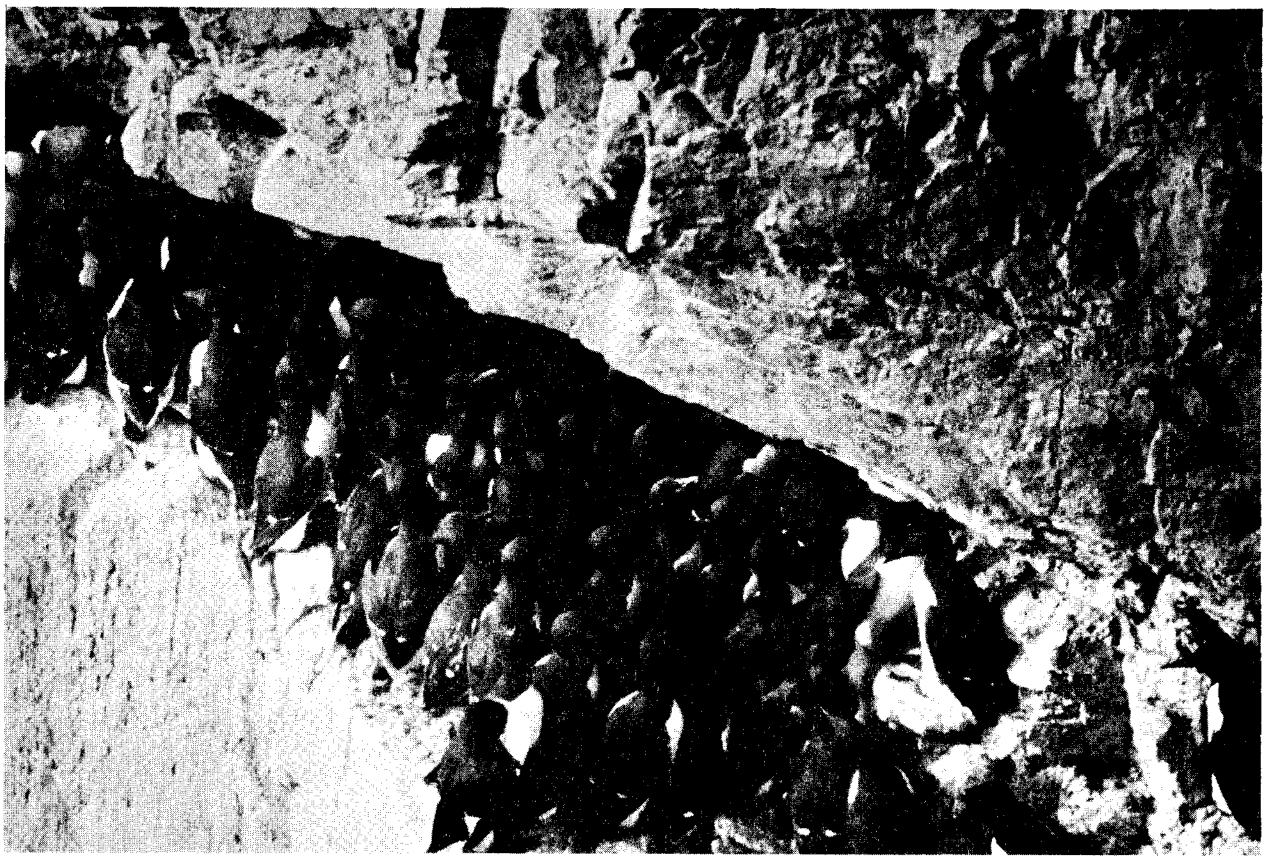


Figure 7. Shelf of Common Murres.

all will suddenly fly off. After a visit to the cliffs they may stay at sea for a day or two. Occasionally, what appears to be the entire breeding population will gather in broad, dispersed flocks in the smooth water in the leads near the breeding cliffs.

Neither species builds nests. The eggs of both species have an unusually steep conical shape. They roll in a narrow circle and this presumably, increases the odds that the egg will not roll off the ledge. Some murres lay their eggs on improbable places such as near vertical slopes, but many are able to hold their eggs between their belly and webbed feet and closely protect it against loss. The exchange of the egg when parents relieve each other during incubation is a complex, if not ludicrous performance which involves bowing, calling and pushing.

Murres feed many miles at sea and bring to the young one a single large fish: a large Sand Lance, Arctic or Saffron Cod, or more usually a Prickleback in our region. Bringing food thus is evidently an expensive exercise, and murres have an important adaptation to minimize the total energy cost during the breeding season. After 16-18 days on the ledge, the newly feathered chick leaps into the sea, often falling several hundred feet on buzzing stubs of tiny wings. One of the parents accompanies the leap of the successful chick, and the two swim off to sea, greatly shortening the distance to which the parents have to carry food.

2. The Biological Meaning of Changes in Numbers

The number of murres present at breeding colonies varies dramatically through the season (Table 17). We presume that daily and seasonal variations reflect a variety of levels of motivation toward breeding, though the details are obscure on first glance.

Table 17.
Numbers of Murres counted at Bluff Cliffs, 1975-1979.
Counts were made from a boat passing slowly in front of the cliffs. These counts include all murres, that is, murres flying and on the water, as well as those on the cliff, and correspond to Figure 20, **page 346, in the Main Body.**

	1975	1976	1977	1978	1979
count (date)		40,000 (30 May)	61,000 (21 May)	33,930 (27 May)	
		7,400 (16 Jun)		89,000 (28 May)	
				800 (31 May)	
	21,600 (3 Jul)	21,110 (30 Jun)	42,000 (28 Jun)	23,585 (26 Jun)	
	90,000 (4 Jul)	22,020 (9 Jul)	42,600 (7 Jul)		
		20,779 (11 Jul)			
		37,780 (13 Jul)		33,520 (18 Jul)	28,284 (20 Jul)
	69,900 (1 Aug)	45,200 (26 Jul)	42,250 (29 Jul)		43,275 (31 Jul)
		55,390 (12 Aug)		48,460 (9 Aug)	33,370 (7 Aug)
			36,100 (19 Aug)	32,080 (14 Aug)	
	6,565 (8 Sep)				

In this section we discuss in some detail what we have learned from counts and studies of Common Murres at Bluff Cliffs. We compare our interpretations with those of British and Scandinavian students working on the same species. (Parts of the following section are from "Coastal Surveys - Northeast and Northwest", Drury, in press).

Lloyd (1975) suggested that at least five counts be made at a nesting cliff in order to include expectable variation in the numbers of Razorbills, Common Murres, and Atlantic Puffins. The effects of the birds' comings and goings can be smoothed out by calculating means, which provide a sort of consistency; but it is necessary to understand the reasons for the changes if the consistency is to be valuable. One of the first things to learn is what different sub-populations of the birds are doing. Not all birds at nesting islands and cliffs are breeding; for example, we know the number of eggs produced is much smaller than half the maximum total number of birds present.

a. Estimating the proportion of breeding to non-breeding birds

We have made counts of Common Murres at the bird cliffs at Bluff that vary from 7,000 to 90,000 birds (see Main Body: Section V, "The Colony of Bluff", A, "Colony Numbers", pages 345-352; and Table 4 on page 287). We can show in this case that the actual "error" in each count is less than 10 percent; we can show that equally large changes in numbers may be recorded during a single 24-hour period. The birds really do come and go; one should be surprised if they did not.

We know that more birds are at the cliffs at certain times of year. Maximum numbers are often present during late May and June when birds first gather on the cliffs and on the water below the cliffs; however, minimum numbers may be present in the same period within a few days of a maximum count. Birkhead (1978) shows the same pattern among Common Murres at Skomer Island west of Wales. He recorded a tide of attendance running over several days when the birds first came. He also recorded a flux that runs its course during a 24-hour period. The tide may obscure the flux and the fluxes may be out of phase between two cliffs not very far apart, as is shown by our data from Bluff and from Square Rock in June of 1977 (Figure 8 , and also Figure 9, the results of 24-hour counts at Bluff in 1977 and in 1978).

Once eggs are laid a certain number of birds settle down and are present consistently. Additional birds come in during the day and leave late at night or early in the morning. The numbers reach a maximum late in evening. There is less coming and going during days of strong winds and choppy seas, as Birkhead (1976) reported, but if bad weather persists for several days the birds start to leave the cliffs anyway. After several days of storm an unusually large number of birds appear on the cliffs as soon as the sea calms.

The "extra" birds, those other than the "incubators", are of two sorts. One sort has relatively little attachment as is shown by their readily flying off when an observer or airplane is still at some distance. This number "flyers", has been larger during those years when reproductive success was low, e. g. 1976, than it was when reproductive success was moderate, 1975 and 1977, or when it was high, 1978 (see Main Body, Table 8, page 290). The second sort of "extra" birds, although they do not have eggs or chicks, are reluctant to fly. These two categories on average account for just under half of the birds on the cliffs at Bluff in the middle of a day during incubation in July and early August.

Figure 8. Twenty-four hour counts of murres at Stakes 14 & 15, Bluff, and at Square Rock, 1977.

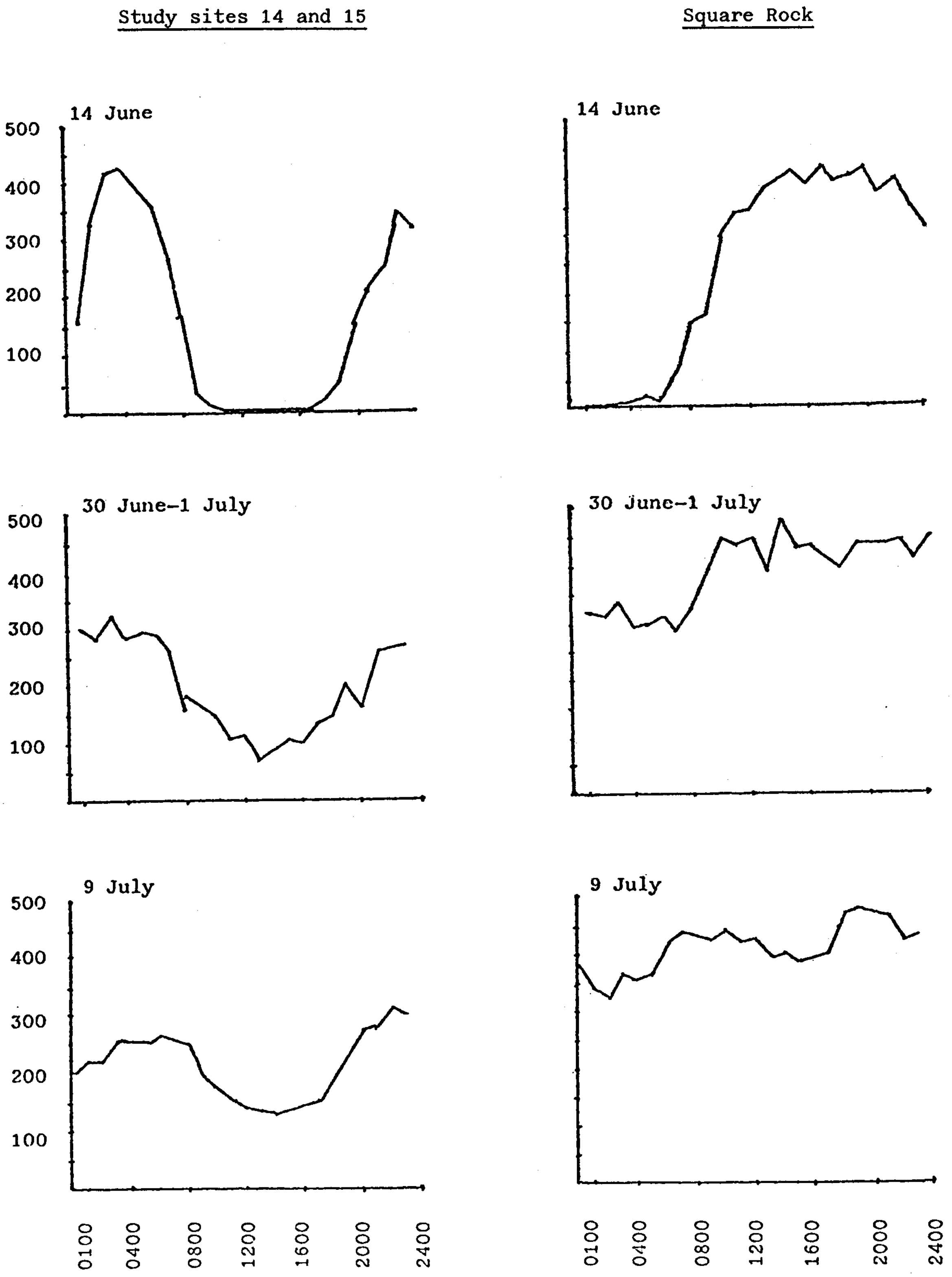


Figure 8 (continued). Twenty-four hour counts of murres, 1977.

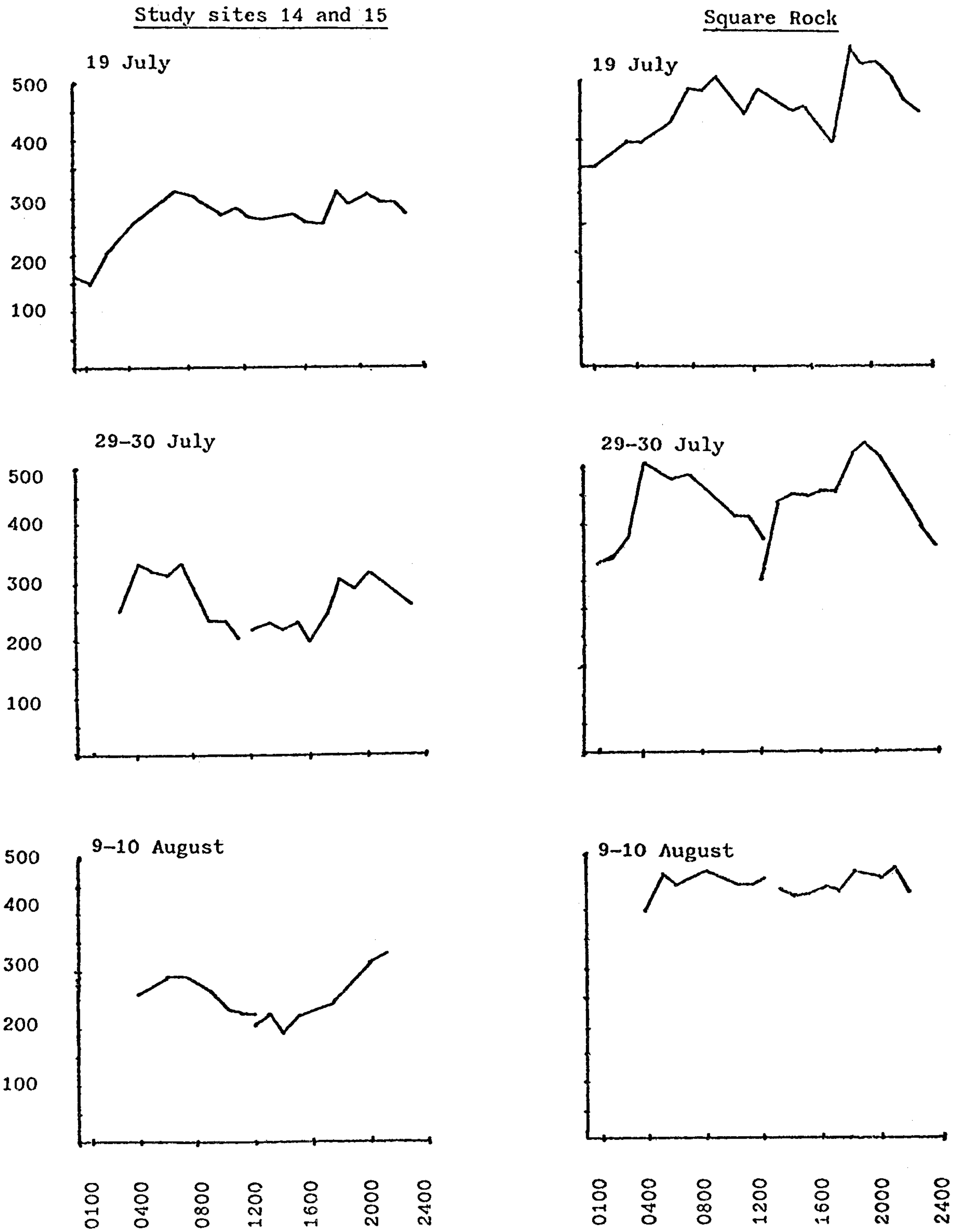
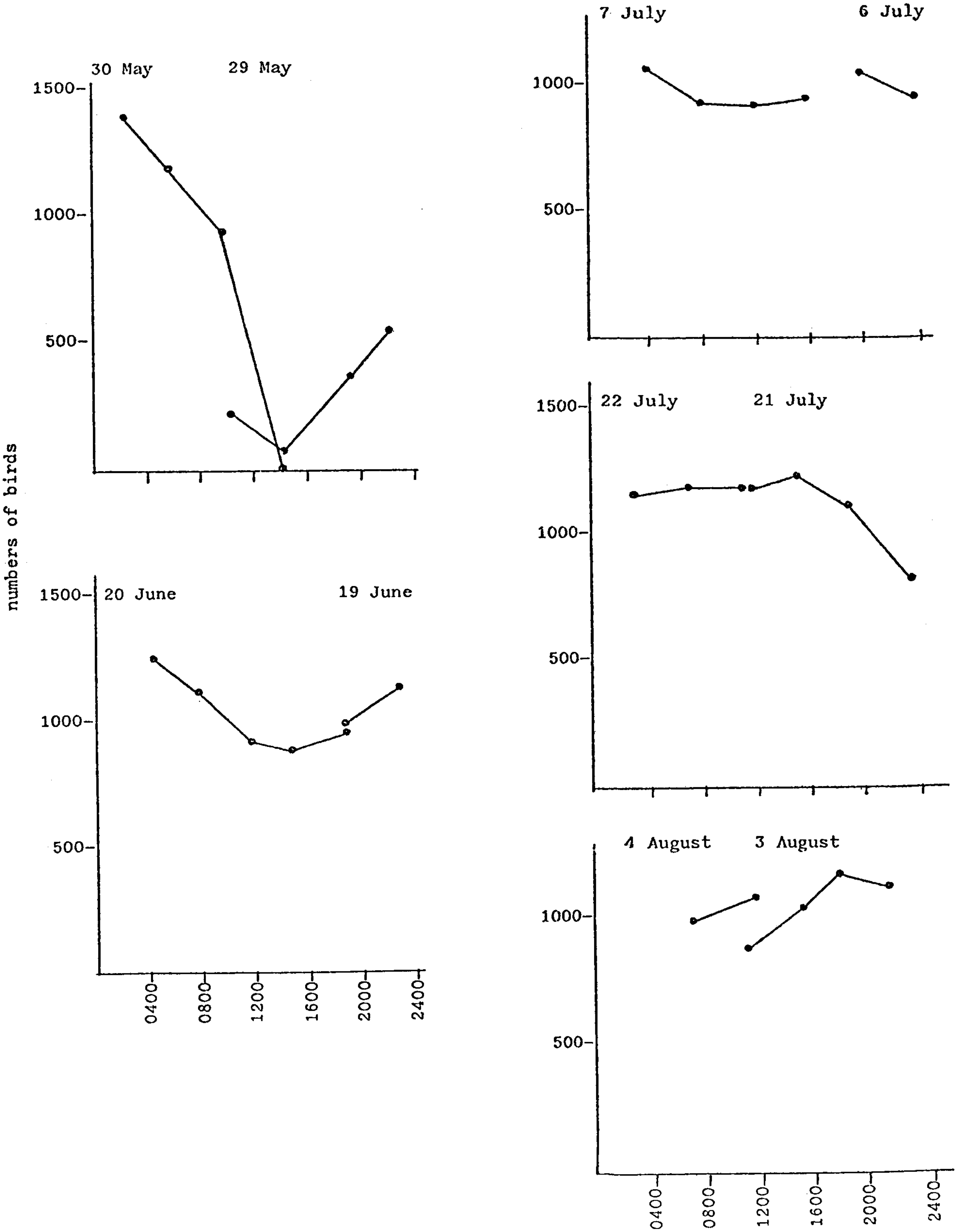


Figure 9. Twenty-four hour counts of murres, Stake 15, Bluff, 1978.



Chicks begin to fledge after the first week of August and, after that, birds leave the cliff in patches as the chicks jump. Some patches persist into September, around groups of unfledged chicks. These observations suggest that the presence of a chick attracts a number of adults to persist on the ledges close around the chick.

In the first half of August, there are at times large numbers of birds at the cliffs; apparently the additional birds are subadults visiting the ledges to prospect for nest sites. Occasionally, throughout the period of incubation, high counts occur; the reasons are not clear. It may be that non-breeders and failed-breeders return to the cliffs responding to their own motivation and to favorable conditions at sea. These waves may coincide and reinforce each other.

We need to relate the numbers which we count to the number of breeding pairs in order to know the productive elements of the population. We would like to have the sort of precise information which Dyck and Meltofte (1978) gathered at the Faroe Islands. They made a census of a cliff face called Høvdin (sic) on June 7, by watching through a telescope as Faeroese fowlers worked the entire face, and counting the eggs as the murres left with the progress of the eggers. Their overall percentage of eggs to birds was 51.1%; but using the size of the embryos, the authors calculated the proportion of eggs not yet laid and arrived at a figure of 67% for the number of pairs as a percent of total birds on the cliff. In 1978, we got the figure 0.56 in the course of a study of individual birds occupying mapped "breeding sites" (Table 18, and also, see Main Body, Table 19 on page 358). At each site we recorded whether an egg and/or chick appeared in the course of July and August by visiting the study area for several hours every other day and

Table 18.
Murre reproductive success at Stake 10, Bluff Cliffs, 1975-1979.
The size of the study area was expanded in 1977, as is evident from the increase in the average number of birds present from the 1975-76 data to the 1977-78 data.

						Reproductive Success	
year	average number of murres within year's study area	average number of sitters*	estimated number of breeding murres (ave no. x 0.6)	number of chicks hatched	number of chicks jumped	chicks jumped / sitters	chicks jumped / est. no. breeders
1975	72	--	43	--	13	--	0.30
1976	74	8	44	--	5	0.18	0.11
1977	154	53	92	68	59	0.38	0.64
1978	153	87*	92	89	79	0.52	0.87
1979	165	--	99	90	83+	--	0.84

* Average number of sitters is derived from the number of murres that appeared to be incubating an egg or chick, 1975-1977, and the number of murres assuming "incubating" or "brooding" postures at the moment the count was made in 1978 (the methods used in 1978 are described in Appendix IX, "Methods Used at Bluff"). Notice how closely the number of "sitters" in 1978 corresponds with the estimated number of breeding murres and the number of chicks hatched.

recording the actions of every bird. Southern, Carrick and Potter (1965) and Tuck (1960) used the figure of 0.6; this seems to be a good average figure to apply to averaged counts (described below) where detailed information is not available.

We soon noticed that some birds assumed characteristic postures and that many, although not all, of these were sheltering an egg or brooding a young one. The special postures (see Methods, Appendix IX) which murres assume when incubating an egg include facing the cliff face, lowering the breast, thus bending their back, and often raising their bill to rest it against the back wall of the ledge. The special posture of birds which are brooding young include lowering one wing and bending their back. Both "incubators" and "brooders" are often marked with excrement that has splattered on them during the hours they have held their posture.

Our observations of the locations of hundreds of murres over many hours have established that many murres "incubate" or "brood" over bare ledge, while many foster an egg or chick without assuming any recognizable posture. If, however, one can clear one's mind of this "bias introduced by reality" and simply count the total number of birds in an "incubating" or "brooding" posture, one can compare the results with the real numbers established by the laborious process of identifying individual eggs and chicks. We found very close correspondence over the several years of our study, whatever the cause. This technique, though perhaps anathema to a precise scientific mind, provides a way to get a quick estimate of the level of reproductive effort on any section of cliff. Our tests indicate that the difference between "incubators" and actual number of eggs or chicks is within the limits of variation in different parts of one set of cliffs.

b. Estimating the size of the breeding population

What figure should be used to multiply by 0.6 or 0.67 in order to arrive at a figure for "breeding birds"? For a single figure one might choose the average of counts made during the incubation period (see Drury and Ramsdell, 1979). It is important to identify the date and time at which counts were made and to associate the count with the stage in the daily cycle of coming and going at the cliff counted (see results and discussion of 24-hour counts in Drury *et al.*, 1978, and Drury and Ramsdell, 1979). One can minimize variation by counting at certain times of the day. In 1976, a poor year, we have seven counts which average 20,000. In 1977, a good year, we have three counts which average 36,200. In 1978, a good year, we have three counts which average 30,000. These counts, eliminating the poor year, give us a spread of 20,000 to 25,000 "breeding pairs" which is the same spread which we had arrived at in the course of detailed counts and corrections for the cliffs, face by face. If "flyers" are added (see Main Body, Tables 7 and 8 on page 290), the average of all birds in 1976 becomes 35,000; in 1978, the average becomes 32,500; and in 1977, the average becomes 42,000. Thus if one includes flyers, one decreases the differences between years.

The central breeding element varies much less than the maximum and minimum counts, and their numbers can be assessed in the northern Bering Sea by making five to ten counts in the middle of the day during mid and late July. The number which probably have eggs can be further assessed by counting 1) the "flyers" (birds which probably do not have eggs that year) as the census is made, and 2) the proportion of "incubators and brooders" to total adults from fixed study sites (see Appendix IX, "Methods Used at Bluff").

c. Discussion of variability in numbers among censuses

A fixed figure may be misleading in any of the numbers counted during the breeding season because variability is a norm, and this certainly applies to the numbers of birds estimated to be at the cliffs among years. One has to be careful about how one applies corrections, too. For example, the estimates of murres on the cliffs of Storra Karlsö in the Baltic in the 1950s, was 35,000 to 40,000; but Hedgren (1975) concluded that, because of differences in methods, his detailed estimate of 6,400 pairs (12,800 birds) should not be used to conclude a change in populations. Dyck and Meltofte (1975) considered their estimate of 9,650 pairs on one cliff in the Faeroes to correspond to an estimate of Nørrevang (1958) of 15,000 pairs; they supported their conclusion by quoting the field counts: 14,500 by Dyck and Meltofte, and 14,750 by Nørrevang.

Large changes in the size of murre populations have been reported during the last two decades. Some of these changes can be well documented, such as those on the cliffs in the Barents Sea, at the cliffs on the Faeroes, or in West Greenland. We probably should question some others, and until we know more about normal tides and surges in numbers, it will be hard to explain even these well-documented changes. Southern, Carrick and Potter (1965) suggested that flooding of some bird cliffs by newcomers who have moved over a substantial number of degrees of latitude might explain some changes. The decreases in the numbers of murres breeding on the cliffs in Greenland may be a response to heavy shooting pressure; but until the source is known for the murres responsible for the remarkable increase in numbers breeding on Funk Island, between Newfoundland and Greenland (20,000 in 1936, and 1,000,000 in 1958; Tuck, 1960), it will not be clear that the decrease in Greenland reflects mortality or reproductive failure or simply emigration (perhaps we can in good faith refer to the murre city on Funk Island as a colony).

There is other evidence to suggest that there may be large scale movements of these birds. Southern, Carrick and Potter (1965) studied several bird cliffs in northern Scotland, comparing counts of "bridled" individuals of Common Murres to non-bridled birds. The "bridled" form is limited to the Atlantic, is distinguishable by a white ring around the eye and a white line running from the ring back to the nape, and ranges from 1% of Common Murres in the south to over 50% in the north (Iceland and Bear Island).

At Hafnaberg (Iceland) at a cliff of 2,000 birds, bridled birds made up 28.8% in 1939, and 18.1% in 1949. At Saint Kilda at cliffs of 30,000 birds, bridled birds made up 16.5% in 1939, and 10.5% in 1948. At Hermaness in the Orkneys, bridled birds changed from 23.7% to 16.9% in the same years. During the subsequent decade, the changes were almost precisely reversed.

The speed of these changes is remarkable in a long-lived species (86-88% annual survival rate at the cliffs in northern Scotland), with a slow turnover of the population. If one suggests differential mortality or reproduction, the selection coefficients required are unrealistically large (0.5-0.7 , Southern, Carrick and Potter, 1965). These authors suggested movements of large numbers of birds over long distances, hence flooding of cliffs with newcomers.

We must consider the possibility of surges of large numbers of birds when we explain large changes in numbers of murres at some Alaskan cliffs, although estimates made in previous decades seem to be uniformly higher than those made during the 1970's.

Fay and Cade (1959) made general estimates of the numbers of birds on Saint Lawrence Island, and Kenyon and Brooks (1960) made estimates of the numbers of birds on Little Diomede Island in the 1950's. Staff of the U.S. Fish & Wildlife Service estimated numbers on many of the bird cliffs in the early 1970's. The authors of these estimates agree that we should not use the earlier estimates for detailed comparisons. Most estimates were made at a great distance and under circumstances which did not allow systematic treatment. The clearest explanation was offered by Kenyon (pers. comm.) who said that his lower estimates are the totals of his data, and the higher figures were numbers which he considered to be the upper limit possible. Our data from Little Diomede Island agree with his lower estimates (see Main Body, Figure 15, pages 298-299).

The circumstances are more complicated, however, in making comparisons between Swartz's estimates at Cape Thompson, 1959-1961, and those of Springer, Roseneau, and Murphy (1976, 1977, and 1978). The later authors have used Swartz's original notebooks to arrange to make counts at the same places and on the same dates as Swartz; they have found what seems to be a large decline in numbers. They are continuing the studies and will test stratified sets of samples both at Cape Thompson and at Bluff.

No matter how accurate each system of counting may be, the changes in numbers of birds at the cliffs which occur hour to hour, day to day, month to month, and the "surges" from year to year, make intermediate levels of precision misleading.

d. Variations in phenology

Table 19 presents the breeding phenology of murres at Cape Thompson (1959, 1960, 1961, 1976, 1977, 1978), Cape Lisburne (1976, 1977, 1978),

Table 19.
Phenology of murre breeding: dates first egg seen, first chick seen, and first sea-going jump.
"CM" refers to Common Murres, "TB" to Thick-billed Murres, and "B" to both.

year	location	1st egg seen		1st chick seen		1st jump	
1959	Cape Thompson	9 Jul	B	11 Aug	B	25 Aug	
1960	Cape Thompson	<27 Jun	B	30 Jul	CM	18 Aug	
				1 Aug	TB		
1961	Cape Thompson	23 Jun	CM	1 Aug	CM	19 Aug	
		24 Jun	TB	30 Jul	TB		
1975	Bluff Cliffs	<3 Jul		*23 Jul		' 10 Aug	
1976	Bluff Cliffs	21 Jun	CM	< 27 Jul		4 Sep	CM
		25 Jun	TB			18 Aug	TB
	King Island	2 Jul	CM	* 4 Aug	CM	*22 Aug	CM
		25 Jun	TB	*28 Aug	TB	*16 Aug	TB
	Cape Lisburne	* 6 Jun		* 9 Aug		27 Aug	
	Cape Thompson	4 Jul	TB	9 Aug	TB	>25 Aug	
1977	Bluff Cliffs	21 Jun		3 Aug	CM	20 Aug	B
	Little Diomede Island	<5 Jul	CM	>11 Aug		*>29 Aug	
		<3 Jul	TB				
	Cape Lisburne	24 Jun		* 2 Aug		20 Aug	
	Cape Thompson	25 Jun	TB	1 Aug	TB	23 Aug	
1978	Bluff Cliffs	12 Jun	CM	16 Jul	CM	31 Jul	CM
	Cape Lisburne	15 Jun		* 1 Aug		11 Aug	
	Cape Thompson	*23 Jun		*26 Jul		13 Aug	

' The date of first jump at Bluff in 1975 should not be compared to date of first jump in other years because in 1975, we spent many nights in early August looking for jumpers; in other years we did not expend as much effort looking as we did that first year, concentrating instead on peaks of jumping.

* Asterisks indicate dates were calculated on the basis on 33-day incubation period and 18-day nestling period, from available observed data (Tuck 1960, Drury et al., 1976-1979).

< Occurred earlier than date shown.

> Date was when observers left, not having yet seen a hatched, or jumped chick; so date shown is earlier than when first hatching or jumping probably occurred.

Data from: Swartz 1966; Springer, Roseneau & Johnson 1979; Drury 1976; Drury & Steele 1977; Biderman & Drury 1978, based on field notes of Steele, Steele & Watson 1977; Drury et al. 1978; Drury & Ramsdell 1979.

Little Diomede (1977), King Island (1976), and Bluff Cliffs (1975, 1976, 1977, 1978). A relative delay in the onset of breeding activities year to year at one location presumably reflects the environmental stresses to which the birds are subject. In many cases delays at the beginning are associated with poor reproductive success for that year.

3. The Value of Murres in OCS Studies

Murres are useful species to study for a number of reasons:

a. They occur in large numbers, are widespread, easily located and more conspicuous than the burrow and rubble nesting alcids.

b. Because as divers they spend a great deal of time on and under the surface of the water, murres, like other alcids, will be vulnerable to the direct effects of spilled oil and other contaminants.

c. i) Murres feed throughout the water column and so will indicate widespread effects on food chains.

   ii) The sensitivity of murres to changes in food supply will be reflected by changes in the attendance patterns of murres at the colony. We have documented the changes in numbers of murres at Bluff through the day and through the season. Food shortages will cause murres to forage widely and thus to be absent from the cliffs for longer periods. Food shortage and absence of adults are probably the causes of reduced reproductive performance.

Although the adults feed on a variety of fish including local cod and Sand Lance, the Prickleback or Eelblenny (Lumpenus) seems to be the preferred food item brought to the cliffs by Common Murres at Bluff to feed mates and chicks. Generally, Thick-billed Murres are better adapted to feeding on zooplankton and crustaceans than are Common Murres; they can shift between fish and zooplankton prey types. Should changes in sea conditions as a result of environmental perturbations cause shifts in the availability of food, the difference in feeding tactics may result in differential reproductive success between the two species. It would be important to demonstrate whether the reproductive performance of Thick-billed Murres suffers less from shortage of Sand Lance than does that of Common Murres at the bird cities in which both are numerous.

Changes in the distributions of murres at sea will be important indications of shifts in the availability of food resources. One of the first steps in such an exercise should be assessment of the segregation of feeding grounds at sea between "brown" murres (Common) and "black" murres (Thick-billed). This can be done, we are confident, from a small airplane flying at 75-100 feet, where conditions of light and sea conditions are favorable. Feeding ranges may vary widely year to year in response to these shifts of food. The distribution of Thick-billed Murres should correspond more closely to the distribution of zooplankton when contrasted with Common Murre distribution.

We have estimated the breeding population of Common Murres at Bluff Cliffs to be about 60% of the total population of murres occupying the cliff during the breeding season. Other researchers have arrived at similar ratios (Dyck and Meltofte, 1975 ; Southern, Carrick and Potter, 1965; Tuck, 1960). A change in the ratio of breeding to non-breeding birds should reflect changes in the population structure at the colony.

M. PUFFINS: Horned Puffin (Fratercula corniculata) and Tufted Puffin (Lunda cirrhata)

1. Description of Species

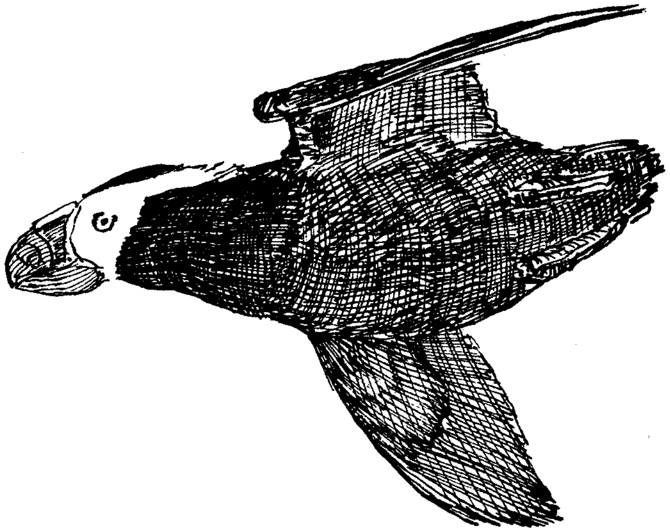
Horned Puffins are conspicuous among the seabirds of the Bering Strait. They nest in crevices and deep cracks on the faces of the cliffs, both in the major seabird cities, and on smaller rocky outcrops scattered along the shores of the region. In this they are like Pelagic Cormorants and Glaucous Gulls. Tufted Puffins also inhabit the region, but in small numbers. The two species will be treated together here.

They are members of a group represented further south by Rhinocerous Auklets (Cerorhinca monocerata), and in the Atlantic by Atlantic Puffins (Fratercula arctica). Both species occur in the Alaska Coastal Water as well as offshore.

Puffins are usually very numerous within their normal range. To the south in the Pacific, Tufted Puffins are more numerous than Horned Puffins.

In our region Horned Puffins nest primarily in crevices in the rocks. In most places outside of our region puffins prefer to nest in burrows excavated into turfy soil, and both Horned and Tufted will do so where they can. The presence of Arctic Foxes, which gain access to breeding islands over the sea ice, may suppress those elements of puffin populations which persist in excavating their own burrows in the northern part of the Bering Sea. On the top of Fairway Rock, where Arctic Foxes cannot reach, and on the islands in inner Kotzebue Sound, Tufted and Horned Puffins nest in burrows.

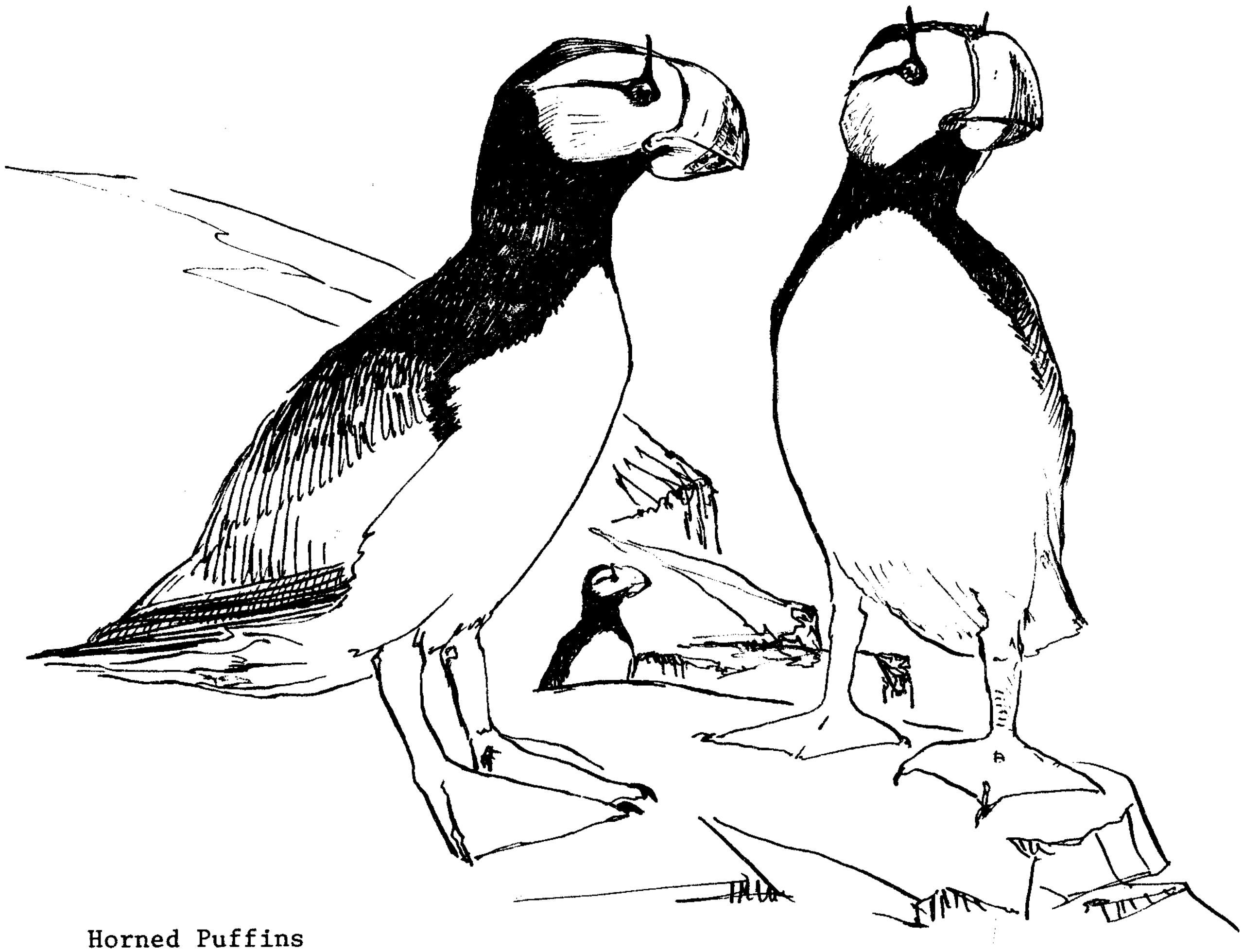
Puffins differ from other seabirds nesting on the faces of cliffs in that they have a long incubation period and the puffin chicks "loiter" in the well-protected burrows into September.



Tufted Puffin

Horned Puffins feed at "middle distances" offshore, i.e., up to 30 miles, but Tufted Puffins appear to feed at greater distances. Both species are attracted to the feeding melees of kittiwakes, apparently because they also feed on Sand Lance. The only food species we saw puffins bring to the cliffs at Bluff were Sand Lance (see Main Body, Figure 11, page 216). This seems to be the case at Cape Thompson also; however, Arctic Cod were also included in the diet at these cliffs in the Chukchi Sea.

During June, the puffin populations at the nesting cliffs are small and presumably include only breeding adults. In late July and August, a large influx occurs; in many cases up to ten times as many birds are loafing on the cliffs or flying along the cliff-tips. Other observers have reported this phenomenon among the puffins in northern regions. It may reflect intense competition for suitable burrows and a long individual life expectancy.



Horned Puffins

2. <u>Value of Puffins in OCS Studies</u>

Horned and Tufted Puffins nest in relatively small numbers in small colonies at dispersed locations. Any local effects of disturbance and contamination on some segments of the population can be contrasted with the unaffected segments. Puffins are extremely vulnerable to disturbance, particularly during the incubation stage of the reproductive cycle; apparently Tufted Puffins desert their burrows at the slightest provocation. Puffins are divers and therefore will be vulnerable to oil or other contaminants on the surface of the sea or dispersed through the water column, and thus will reflect the immediate and directs effects of local contaminants.

Figure 11. Horned Puffin with beakfull of Sand Lance.

N. PARAKEET AUKLETS (Cyclorrhynchus psittacula)

The life history and population dynamics of Parakeet Auklets are poorly understood because these birds disperse to breed and feed and are not numerous enough to attract attention among the hordes of other species. Parakeet Auklets are endemic to the Bering Sea; they nest in crevices and under rocks next to bedrock outcrops, and partially excavate burrows under rocks on vegetated rubble-covered slopes. Their geographical distribution is wider than Crested or Least Auklets, extends farther south into southeastern Alaska, and includes small numbers nesting in the shallow brackish waters of inner Norton Sound at Cape Denbigh, Egg Rock, Cape Darby and Bluff Cliffs. Their distribution and low numbers may be related to their varied diet which includes some benthic Amphipods and Mysids, as well as Euphausiids and fish. However, they apparently are not able to take advantage of the abundant benthos in Norton Sound, the Chirikov Basin and southern Chukchi Sea.

The scoop-like bill of Parakeet Auklets is conspicuously decorative, as it has become modified for sexual displays.

O. CRESTED AUKLETS (Aethia cristatella) and LEAST AUKLETS (Aethia pusilla)

1. Description of Species

Crested and Least Auklets are endemic to the Bering Sea and depend on dense populations of low level consumers. Least Auklets feed on Copepods, which are grazers at the first consumer level, and Crested Auklets feed primarily on Euphausiids and Hyperiids which are second level consumers. In the Atlantic, a single species of auk, the Dovekie (Alle alle), replaces the four species of auklets found in the Bering Sea in this niche.

They nest primarily in the underground tunnels , "catacombs", formed amidst the great rubble fields that result from frost riving and frost movement of blocks in the talus below cliffs of lava and basalt associated with volcanic activity all through this region. Although there are extensive rubble fields on Sledge Island and in eastern Norton Sound, such as at Besboro Island and in the bluffs between Cape Thompson and Cape Lisburne, auklets occur in numbers only in the vicinity of cold saline water in the western part of the Bering Strait Region, from Saint Lawrence Island to the Bering Strait.

Auklets appear in huge numbers at their nesting areas. The arrival of these flocks over the snow-covered islands in late May is an event which one will long remember, as the flocks which come together from the sea perform aerial manuevers.

Least Auklets become proportionately more numerous in the north while Cresteds are comparatively less frequent. This may reflect the distribution of their food. It has been suggested that the food of Least Auklets, primarily Copepods, is made up of two population sources. One is the southern Bering Sea (Calanus tonsus, C. cristatus, and Eucalanus bungii); these forms are carried north in the general shift of the water masses up over the shelf.

The northern element (*Calanus finmarchicus*, also called *C. glacialis*), replaces the southern forms because it reproduces in the northern waters while the southern forms do not. Bédard (1969) reported that Least Auklets at Gambel, Saint Lawrence Island in 1964-1966, were feeding primarily on *C. finmarchicus*. Searing (1977) found them to be feeding on *Neocalanus plumchrus* off Owalit Mountain in 1976 - a disaster year.

Bédard found that the primary foods of Crested Auklets at Saint Lawrence Island were the Euphausiids *Thysanoessa raschii* and *T. inermis*. These may be produced south of our area and may survive by feeding on the local production of *Calanus* Copepods. Apparently, *T. inermis* does not reproduce in the Chirikov Basin and the species is replaced as the water moves north to the Bering Strait where *T. raschii* and *Parathemisto libellula* are probably the staple foods.

It is very noticeable and deserves some explanation that the auklets of all kinds drop out of the marine system very sharply within 15 miles north of the Diomede Islands. Before these observations can be explained, it will be necessary to learn which species are nesting in what numbers on Big Diomede Island (Ratmanova); our brief, fog-shrouded and unplanned visit to that island indicated impressively high numbers of Crested Auklets, Pelagic Cormorants and Glaucous Gulls.

Auklets have broad bills adapted for catching the small food items upon which they depend. Their broad bills are, like their head plumages, modified for courtship and create bizarre effects in the appearances of Crested, Whiskered (*Aethia pygmaea*), and Parakeet Auklets.

2. Value of Auklets in OCS Studies

Auklets are conspicuous endemic components of the northern Bering Sea colonies. As zooplankton eaters their distribution at sea will be indicative of the distribution of zooplankton and water masses. Public interest in the auklet species is high. They deserve care in use as monitors; their population sizes are so large that even a small percentage error in population estimates means a difference of a large number of birds. Results of counts must be interpreted and calibrated carefully.

Auklets may serve an additional purpose in coming to understand the pelagic systems of the Saint Lawrence Island waters. By establishing which types of food organisms are preyed on by auklets, and by determining the source and life histories of these organisms in the Chirikov Basin, the difference in theories of the origin of Anadyr Water may be resolved. There are two schools of thought on the origin of Anadyr Water (described in the Main Body, Section II, "The Bering Sea and the Bering Strait Land Bridge", part B, "Water Masses, Currents and Productivity"; and Appendix II, "Oceanographic Setting"). Coachman, Aagaard and Tripp (1975) suggest that Anadyr Water comes over the shelf edge near Cape Navarin from the Bering Sea Deep, and circulates around the inner part of the Anadyr Gulf. Fleming and Heggarty (1966) suggest that Anadyr Water is the product of divergent upwelling all along the Siberian shore.

P. COMMENTS ON THE VALUE OF SEABIRDS IN OCS STUDIES

The variations in distribution of the breeding areas of each species suggest that disturbance will affect their populations differently. For the species whose breeding sites are dispersed, the birds at each breeding spot represent only a small percentage of the population. A disturbance at one of these sites will affect the population less than a disturbance at one of the big murre colonies. Disruption of breeding at Bluff would do serious damage to the Norton Sound murre and kittiwake populations.

The inter-colony differences in breeding biology suggest that work on the food resources available and the degree of genetic isolation among populations would be of interest. In terms of the protection of seabirds we want to know if some colonies were maintained, despite low productivity, by immigration from more productive colonies. If so, the productive colonies became more important in the total population of the region than their size would indicate. Disturbance of these colonies could weaken many seabird populations of the region. We have no data on exchange between colonies.

Studies of the distribution of birds at sea should be used to guide scientists to promising areas for oceanographic studies. Water masses and characteristics of the bottom topography in the Northern Bering Sea seem to be fundamental units of oceanic habitat. Seabirds can be useful as indicators of these water masses and bottom conditions. Large seabird colonies are situated in the proximity of strong oceanic currents where food resources are renewed continually. Shifts in the distribution of birds at sea may help us learn what is going on in the water masses.

Q. List of Bird Species Seen on the Seward Peninsula and in Norton Sound

As indicated in the introductory chapter, the Bering Sea region has a remarkably diverse fauna and flora. The reasons are a complex of geographic circumstances, historical and structural. Among marine birds the dominant element is Arctic Circumpolar. Birds seen on the Seward Peninsula are listed below, based on Brina Kessel's collection of sightings. Asterisks (*) indicate species of Siberian origin.

Common Loon (Gavia immer)
Yellow-billed Loon (Gavia adamsii)
Arctic Loon (Gavia arctica)
Red-throated Loon (Gavia stellata)
Red-necked Grebe (Podiceps grisegena)
Horned Grebe (Podiceps auritus)
Northern Fulmar (Fulmarus glacialis)
Short-tailed Shearwater (Puffinus tenuirostris)
Fork-tailed Storm-Petrel (Oceanodroma furcata)
Pelagic Cormorant (Phalacrocorax pelagicus)
Whistling Swan (Olor columbianus)
Canada Goose (Branta canadensis)
Black Brant (Branta bernicla)
Emperor Goose (Philacte canagica)
*Bean Goose (Anser fabalis)
White-fronted Goose (Anser albifrons)
Snow Goose (Chen caerulescens)
Mallard (Anas platyrhynchos)
Pintail (Anas acuta)
Green-winged Teal (Anas crecca)
*Baikal Teal (Anas formosa)
*European Widgeon (Anas penelope)
American Widgeon (Anas americana)
Northern Shoveler (Anas clypeata)
Canvasback (Aythya valisineria)
Greater Scaup (Aythya marila)
Lesser Scaup (Aythya fuligula)
Common Goldeneye (Bucephala clangula)
Bufflehead (Bucephala albeola)
Oldsquaw (Clangula hyemalis)
Harlequin Duck (Histrionicus histrionicus)
Steller's Eider (Polysticta stelleri)
Common Eider (Somateria mollissima)
King Eider (Somateria spectabilis)
Spectacled Eider (Somateria fischeri)
White-winged Scoter (Melanitta deglandi)
Surf Scoter (Melanitta perspicillata)
Black Scoter (Melanitta nigra)
Red-breasted Merganser (Mergus serrator)
Goshawk (Accipiter gentilis)
Rough-legged Hawk (Buteo lagopus)
Golden Eagle (Aquila chrysaetos)
Bald Eagle (Haliaeetus leucocephalus)

Marsh Hawk (Circus cyaneus)
Osprey (Pandion haliaetus)
Gyrfalcon (Falco rusticolus)
Peregrine Falcon (Falco peregrinus)
American Kestrel (Falco sparverius)
Spruce Grouse (Canachites canadensis)
Willow Ptarmigan (Lagopus lagopus)
Rock Ptarmigan (Lagopus mutus)
Sandhill Crane (Grus canadensis)
Semipalmated Plover (Charadrius semipalmatus)
*Mongolian Plover (Charadrius mongolus)
*Dotterel (Eudromias morinellus)
American Golden Plover (Pluvialis dominica)
Black-bellied Plover (Pluvialis squatarola)
Ruddy Turnstone (Arenaria interpres)
Black Turnstone (Arenaria melanocephala)
Surfbird (Aphriza virgata)
Semipalmated Sandpiper (Calidris pusilla)
Western Sandpiper (Calidris mauri)
*Rufous-necked Sandpiper (Calidris ruficollis)
Least Sandpiper (Calidris minutilla)
Baird's Sandpiper (Calidris bairdii)
Pectoral Sandpiper (Calidris melanotos)
*Sharp-tailed Sandpiper (Calidris acuminata)
Rock Sandpiper (Calidris ptilocnemis)
Dunlin (Calidris alpina)
Red Knot (Calidris canutus)
*Great Knot (Calidris tenuirostris)
Sanderling (Calidris alba)
*Ruff (Philomachus pugnax)
Buff-breasted Sandpiper (Tryngites subruficollis)
Long-billed Dowitcher (Limnodromus scolopaceus)
Stilt Sandpiper (Micropalama himantopus)
Greater Yellowlegs (Tringa melanoleuca)
Lesser Yellowlegs (Tringa flavipes)
Solitary Sandpiper (Tringa solitaria)
*Wood Sandpiper (Tringa glareola)
Wandering Tattler (Heteroscelus incanus)
Spotted Sandpiper (Actitis macularia)
*Bar-tailed Godwit (Limosa lapponica)
Hudsonian Godwit (Limosa haemastica)
Whimbrel (Numenius phaeopus)
Bristle-thighed Curlew (Numenius tahitiensis)
Common Snipe (Gallinago gallinago)
Red Phalarope (Phalaropus fulicarius)
Northern Phalarope (Phalaropus lobatus)
Pomarine Jaeger (Stercorarius pomarinus)
Parasitic Jaeger (Stercorarius parasiticus)
Long-tailed Jaeger (Stercorarius longicaudus)
Glaucous Gull (Larus hyperboreus)
Glaucous-winged Gull (Larus glaucescens)
*Slaty-backed Gull (Larus schistisagus)
Herring Gull (Larus argentatus)

Mew Gull (Larus canus)
Bonaparte's Gull (Larus philadelphia)
Ivory Gull (Pagophila eburnea)
Black-legged Kittiwake (Rissa tridactyla)
*Ross' Gull (Rhodostethia rosea)
Sabine's Gull (Xema sabini)
Arctic Tern (Sterna paradisaea)
Aleutian Tern (Sterna aleutica)
Common Murre (Uria aalge)
Thick-billed Murre (Uria lomvia)
Black Guillemot (Cepphus grylle)
Pigeon Guillemot (Cepphus columba)
Kittlitz's Murrelet (Brachyramphus brevirostris)
Parakeet Auklet (Cyclorrynchus psittacula)
Crested Auklet (Aethia cristatella)
Least Auklet (Aethia pusilla)
Horned Puffin (Fratercula corniculata)
Tufted Puffin (Lunda cirrhata)
Band-tailed Pigeon (Columba fasciata)
*Oriental Cuckoo (Cuculus saturatus)
Great Horned Owl (Bubo virginianus)
Snowy Owl (Nyctea scandiaca)
Hawk Owl (Surnia ulula)
Short-eared Owl (Asio flammeus)
Boreal Owl (Aegolius funereus)
*Wryneck (Jynx torquilla)
Common Flicker (Colaptes auratus)
Downy Woodpecker (Picoides pubescens)
Say's Phoebe (Sayornis saya)
Alder Flycatcher (Empidonax alnorum)
Western Wood Pewee (Contopus sordidulus)
Horned Lark (Eremophila alpestris)
Violet-green Swallow (Tachycineta thalassina)
Tree Swallow (Iridoprocne bicolor)
Bank Swallow (Riparia riparia)
House Martin (Delichon urbica)
Barn Swallow (Hirundo rustica)
Cliff Swallow (Petrochelidon pyrrhonota)
Purple Martin (Progne subis)
Gray Jay (Perisoreus canadensis)
Common Raven (Corvus corax)
Black-capped Chickadee (Parus atricapillus)
*Gray-headed Chickadee (Parus cinctus)
Boreal Chickadee (Parus hudsonicus)
Dipper (Cinclus mexicanus)
American Robin (Turdus migratorius)
Varied Thrush (Ixoreus naevius)
Gray-cheeked Thrush (Catharus minimus)
*Wheatear (Oenanthe oenanthe)
*Bluethroat (Luscinia svecica)
*Arctic Warbler (Phylloscopus borealis)
Ruby-crowned Kinglet (Regulus calendula)
*White Wagtail (Motacilla cinerea)

*Yellow Wagtail (Motacilla flava)
Water Pipit (Anthus spinoletta)
*Red-throated Pipit (Anthus cervinus)
*Indian Tree Pipit (Anthus hodgsoni)
Bohemian Waxwing (Bombycilla garrulus)
Northern Shrike (Lanius excubitor)
Orange-crowned Warbler (Vermivora celata)
Yellow Warbler (Dendroica petechia)
Yellow-rumped Warbler (Dendroica coronata)
Blackpoll Warbler (Dendroica striata)
Northern Waterthrush (Seiurus noveboracensis)
Wilson's Warbler (Wilsonia pusilla)
Red-winged Blackbird (Aeglaius phoeniceus)
Rusty Blackbird (Euphagus carolinus)
Pine Grosbeak (Pinicola enucleator)
Gray-crowned Rosy Finch (Leucosticte tephrocotis)
Hoary Redpoll (Carduelis hornemanni)
Common Redpoll (Carduelis flammea)
White-winged Crossbill (Loxia leucoptera)
Savannah Sparrow (Passerculus sandwichensis)
Dark-eyed Junco (Junco hyemalis)
Tree Sparrow (Spizella arborea)
White-crowned Sparrow (Zonotrichia leucophrys)
Golden-crowned Sparrow (Zonotrichia atricapilla)
Fox Sparrow (Passerella iliaca)
Lincoln's Sparrow (Melospiza lincolnii)
Lapland Longspur (Calcarius lapponicus)
Snow Bunting (Plectrophenax nivalis)
McKay's Bunting (Plectrophenax hyperboreus)

APPENDIX VII.
NUMBERS OF SEABIRDS AT THE CLIFFS

The following numbers are the best estimates and counts which we have found. Those marked with an asterisk have been taken from other reports, primarily those of Springer and Roseneau, Research Unit #460, and Sowles, Hatch and Lensink's Catalogue of Seabird Colonies (1978). The numbers made from the sea are counts made from small boats passing in front of the cliffs. Estimates made from the air are made from a small plane flying about 300 yards off the cliff face. The estimates we made of auklets were made by walking the perimeter of King Island and Little Diomede Island while the auklets were milling overhead in the evening shortly after they first returned to the islands.

PELAGIC CORMORANT

	Birds	Nests	Birds Estimates: air
Corwin Creek	35-45 * pairs		
Noyalik Peak	10 * "		
Cape Lisburne	80-85 * "		
Cape Lewis	60 * "		
Cape Dyer	25 * "		
Kilikralik Point	50 * "		
Cape Thompson	45 * "		
Choris Peninsula	5 * "		
Puffin Island	5 * "		
Chamisso Island	5 * "		
Cape Deceit 1	20		
Cape Deceit 2	20		
Little Diomede Island	100-160		
Fairway Rock	25	8	
Cape York-Tin City	120-180	20-60	
Cape Riley	100		
King Island	140	65	
Sledge Island	280-500	80-150	60-80
Topkok Head	230-385	84-165	75-140
Topkok East	35-60	8-15	
Bluff Cliffs	60-170	25-70	20-70
Square Rock	15	2-4	
Little Rocky Point	7		
Rocky Point	415-900	165-210	250
Cape Darby	325-450	100	
Cape Denbigh, North			50-75
Cape Denbigh, South			30-75
Egavik			5-10
Besboro Island		est. 50	50-90
Tolstoi Point			60
Black Point			20-25
Egg Island	1	1	
Stewart Island		1	1
East of Savoonga			40-80
Stolbi Rocks			35
West of Savoonga			20
Sevuokuk Mountain			2
Owalit Mountain			75-200
Snow banks nr. Owalit			165
Ivekan-Poovookpuk			100
Iwoonut to Southwest Cape			255
Singikpak Point			100-730

GLAUCOUS GULL

	Birds: surface	Nests	Pairs: surface	Birds: air est.
Sapunuk Ridge			40*	
Cape Lisburne			50*	
Noyalik Peak			15*	
Cape Lewis			50*	
Cape Dyer			50*	
Kilikralik			30*	
Cape Thompson			300*	1150
Kasik Lagoon			30*	
Cape Kruzenstern			40*	
Choris Peninsula			90*	
Puffin Island			75*	
Chamisso Island			80*	
Ninemile Point			80*	
Island so of Espenb.				450
Arctic Lagoon				10
Little Diomede			135	
Fairway Rock			30-50	100-150
Tin City-Cape York				35-50
Point Spencer		30		70
Cape Douglas		15		35-75
King Island	110-130	45		
Sledge Island	5-45	4	6	
Is. entr. to Safety L.	60			
Sunset-Sunrise		30		20-65
Topkok Head	22-300	21-36		30-120
Topkok East	35	2	2-10	
Bluff Cliffs	75-200	12-30	15-35	30
Square Rock	15-50	8-14	5-15	4-10
Rocky Point	100-1550		20	20-75
Little Rocky Point	100-450		8	
Cape Darby	290		50	
Cape Denbigh			25	
Egavik				5
Besboro Island				15-25 pairs
Tolstoi Point				10 "
Black Cove				3 "
Klikitarik				5 "
Whale and Beulah Is.				5 "
Egg Island				5 "
Stewart Island	100			"
Cliffs east of Savoonga (Singikpo & Myaughee)				35-45 pairs
Stolbi Rocks				6 "
Savoonga				15 "
W. of Savoonga-Kineeghit Pt.				50 "
Sevuokuk Mountain				5 "
Owalit Mountain				25-30 "
Ivekan-Poovookpuk				40 "
Iwoonut-Singikpak				190 "
Siknik Cape				125 "

BLACK-LEGGED KITTIWAKE

	Birds: surface		Birds: air est.
Cape Lisburne	15000-25000 *		
Cape Lewis	3000 *		
Cape Thompson	10500 *		
Sullivan Bluffs			550
Toawlaic Point			300
Cape Deceit			600
Little Diomede Island	17000-20000		12000-17500
Fairway Rock	650-750		
King Island	2300-3100		3000-6000
Sledge Island	750-2500		400-620
Bluff Cliffs	4000-8500		3000-3500
Square Rock	800-1200		
Cape Denbigh North	1200		1300-1500
Cape Denbigh South	650		600-800
Egg Island	500		650
East of Savoonga	49,000		4500
West of Savoonga			8500-12500
Owalit Mtn.	2000		
Ivekan-Poovookpuk			8000
Iwoonut-Southwest Cape			5000

ARCTIC TERN

	Pairs: Surface		Pairs: Air
S-W of Kivalina	30 *		
N-W of Cp. Kruzenstern	30 *		
Cape Kruzenstern 1	40 *		
Cape Kruzenstern 2	100 *		
North of Sheshalik	30 *		
Elephant Point	20 *		
Cape Espenberg 1			65
Cape Espenberg 2			15
So. of Cp. Espenberg			20
W of 'Espenberg'			20
N-E of Shishmaref 1			15
N-E of Shishmaref 2			6
S-W of Sarichef			15
Arctic Lagoon			6
Belmont Point, Nome	20		
Mouth of Eldorado R.			10
Safety Lagoon	100		
Moses Point	40*		
Caches,Moses Point			25
Inglutalik River			40
Unalakleet River			25
Black Cove Island			8
Pingootikook Bay	St.Lawrence Island		100

BLACK GUILLEMOT AND PIGEON GUILLEMOT

	Black Guillemot		Pigeon Guillemot	
	Birds: surface		Birds: surface	Birds: air
Cape Lisburne	215*		2*	
Cape Lewis	24*			
Sapunuk Ridge	9*			
South of Niak Creek	14*			
Cape Thompson	10*		5*	
Little Diomede Island			200-275	
Fairway Rock			85	
King Island			700-950	
Cape Riley			5	
Sledge Island	1		8-10	
Topkok Head			15	
Bluff Cliffs			4	
Rocky Point			3	
East of Savoonga			1010*	1500
West of Savoonga				600
Sevuokuk Mountain				1700
Owalit Mountain				150
Ivekan-Poovookpuk				100
Iwoonut-Singikpak				100

MURRE (COMBINING THICK-BILLED AND COMMON)

	Birds: surface	%C/%T-b	Birds: air
Cape Lisburne	160000-200000*		190000-220000
Noyalik Peak	20*		
Cape Lewis	25000-30000*		45000-55000
Cape Thompson	140000-185000*	65/35	175000-230000
Sullivan Bluffs			700
Toawlaic Point			1300
Cape Deceit			1300
Little Diomede Island	45000-50000	65/35	40000-45000
Fairway Rock	15000		15000-20000
King Island	75000-90000	50/50	60000-85000
Sledge Island	2500-6500	85/15	1200-4500
Bluff Cliffs	30000-55000	99/01	25000-35000
Square Rock	4000-6000	99/01	
Cape Denbigh North	5900	99/01	7000-8500
Cape Denbigh South	4300	99/01	6000-9500
Egg Island	2000	99/01	1200-2000
East of Savoonga	106000*		30000
West of Savoonga			35000-65000
Owalit Mountain	23000-27000	50/50	23000-28000
Ivekan-Poovookpuk			55000-70000
Iwoonut-Southwest Capes			35000-40000
Stolbi Rocks			6500

AUKLETS

	Least Auklet		Crested Auklet	Parakeet Auklet
	Birds: surface		Birds: surface	Birds: surface
Little Diomede Island	600000		80000-120000	10000
Fairway Rock	15000		10000	500
King Island	75000-85000		30000-40000	35000-50000
Sledge Island				85-165
Bluff Cliffs				35-75
Cape Denbigh South				5
Egg Island				5
Saint Lawrence Island, after Bedard & Searing				
Singikpo and Myaughee	450000-475000 *		220000 *	10000 @
Savoonga	50000 *		35000 *	1000 @
Kineeghit Point	15000 *		8000 *	4000 @
Sevuokuk Mountain	100000 *		70000 *	2000 *
Owalit-Kungok Basin	350000 *		175000 *	1500 @
Ivekan Mountain	100000 *		60000 *	10000 @
Iwoonut-Singikpak				1500 @
Bluff, Singikpo, Myaughee counts by F.H. Fay			2700000 *	50 *

@ estimated according to the area of suitable nesting terrain as compared to that on Sevuokuk Mountain surveyed by Bedard. Estimates made from the air by W.D.

HORNED PUFFIN

	Birds: surface		Birds: air	July-Aug. Max.
Cape Lisburne	1450*			
Cape Lewis	185-300*			
Cape Dyer	25*			
Cape Thompson	1500-1600*			
Choris Peninsula	230*			
Puffin Island	10000*			
Chamisso Island	4500*			
Cape Deceit			50	
Little Diomede Island	5000-8500		5000-7000	15000
Fairway Rock	75			3000 (air)
Cape York-Tin City			25	
Cape Riley			100	
King Island	800-3000		3150-5650	6000-17000
Sledge Island	55-160			
Topkok Head	50-70			230-310
Topkok East	35			
Bluff Cliffs	500-800			3000
Square Rock	70-100			400
Little Rocky Point	10			
Rocky Point	130-210			
Cape Darby West	100			
Cape Darby East	475			
Cape Denbigh North			40-55	200
Cape Denbigh South			35	
Besboro Island			150-250	
Egavik			10-15	
Tolstoi Point			15-20	
Black Cove Island			100	
Egg Island			150	
Whale and Beulah Is.			10-150	
N-W Stewart Island			185	
East of Savoonga	750*			4000 (air)
West of Savoonga				2500 (air)
Sevuokuk Mountain			250	1500 (air)
Owalit Mountain			600-850	
Ivekan-Poovookpuk			1700	
Iwoonut-Singikpak			2900	

TUFTED PUFFIN

	Birds: surface		Birds: air	July-August Max.
Corwin Creek	3*			
Cape Lisburne	20*			
Cape Lewis	1-4*			
Cape Dyer	4*			
Cape Thompson	30-40*			
Choris Peninsula	4*			
Puffin Island	10*			
Chamisso Island	10*			
Little Diomede Island	500-675			
Fairway Rock	300			800 (air)
King Island	250-1250			3150-5650
Sledge Island	3-15			
Topkok Head	10-35			
Bluff Cliffs	10			
Square Rock	1-6			
Rocky Point	6			
Cape Darby West	1			
Cape Darby East	475			
Cape Denbigh North			3	
Black Cove Island			2	
Egg Island			25	
Whale and Beulah Is.			5-10	
N-W Stewart Island			15	
East of Savoonga				350 (air)
West of Savoonga				500 (air)
Sevuokuk Mountain			50	500 (air)
Owalit Mountain			750	
Iwoonut-Singikpak			200	

APPENDIX VIII.
STUDY AREAS

Study areas for this project consisted of the coastal lagoons, wetlands and seabird cities on cliffs in Norton Sound and the Bering Strait Region. Intensive studies were conducted at Bluff Cliffs and Square Rock each year from 1975 to 1978, and short-term studies were conducted at Bluff in 1979 and 1980. Short-term surveys were made each year at Sledge Island, Topkok Head and Rocky Point, and at King Island in 1976, and Little Diomede Island in 1977. Aerial surveys were made from Stuart Island in southeastern Norton Sound west over the Chirikov Basin to Saint Lawrence Island, north beyond the Bering Strait and along the eastern shore of the Chukchi Sea to Wainwright; (data collected during aerial and shipboard surveys were presented in Appendix V, "Distribution of Birds at Sea"). Table 1 presents the locations of these studies (see also the Main Body of the Final Report, Section IV., "Distribution and Abundance of Seabirds During the Breeding Season", sections B and C; and Section VII, "Coastal Habitats of the Bering Strait Region", for descriptions of these study areas).

Descriptions of Colonies

A. Bluff

The Cliffs at Bluff are approximately 55 miles east of Nome on the mainland. They consist of vertical cliffs 100-200 feet in height, some of which extend up to 500 feet, with rounded hills at the top. The cliffs are approximately three miles long (Figures 1 and 2).

Bluff is accessible by small boat and airplane. An airstrip is located near the abandoned community and mine on Daniels Creek at the west end of the cliffs. Another, marginally useable, airstrip is located near the east end

Table 1.
Locations of Study Areas of Research Unit #237, #238, and #447.

	Location	Coordinates	
Intensive Studies	Bluff Cliffs and Square Rock	62 20'N	163 40-45'W
Short-term Surveys	Rocky Point	64 20'N	163 09'W
	Topkok Head	64 33'N	163 59'W
	Sledge Island	64 28'N	166 12-13'W
	King Island	64 58'N	168 04'W
	Little Diomede Island	65 45'N	168 55'W
	Fairway Rock	65 37'N	168 45'W
Aerial Transects	from Tolstoi Point south of Unalakleet --	63 30'N	161 00'W
	--to southwest of Saint Lawrence Island--	62 30'N	170 00'W
	--north to Wainwright	62 30'N	170 00'W
Waterfowl Surveys	from the Cape Denbigh and Shaktoolik region--	64 24'N 64 20'N	161 31'W 161 10'W
	--to Cape Spencer	65 00'N	166 50'W

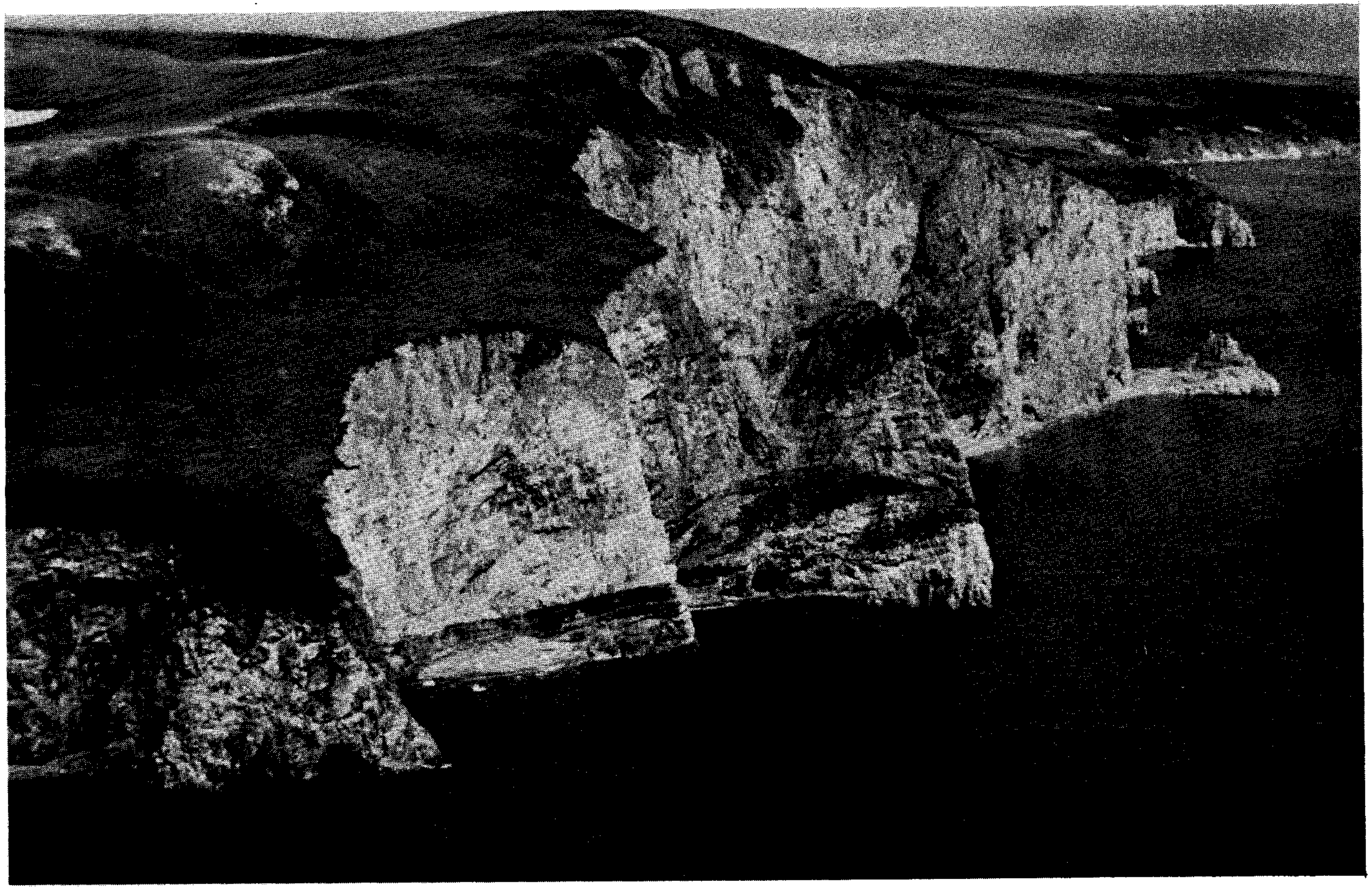


Figure 1.
The Cliffs at Bluff, showing the High Bluff from the west side of the cliffs, looking east toward Square Rock.

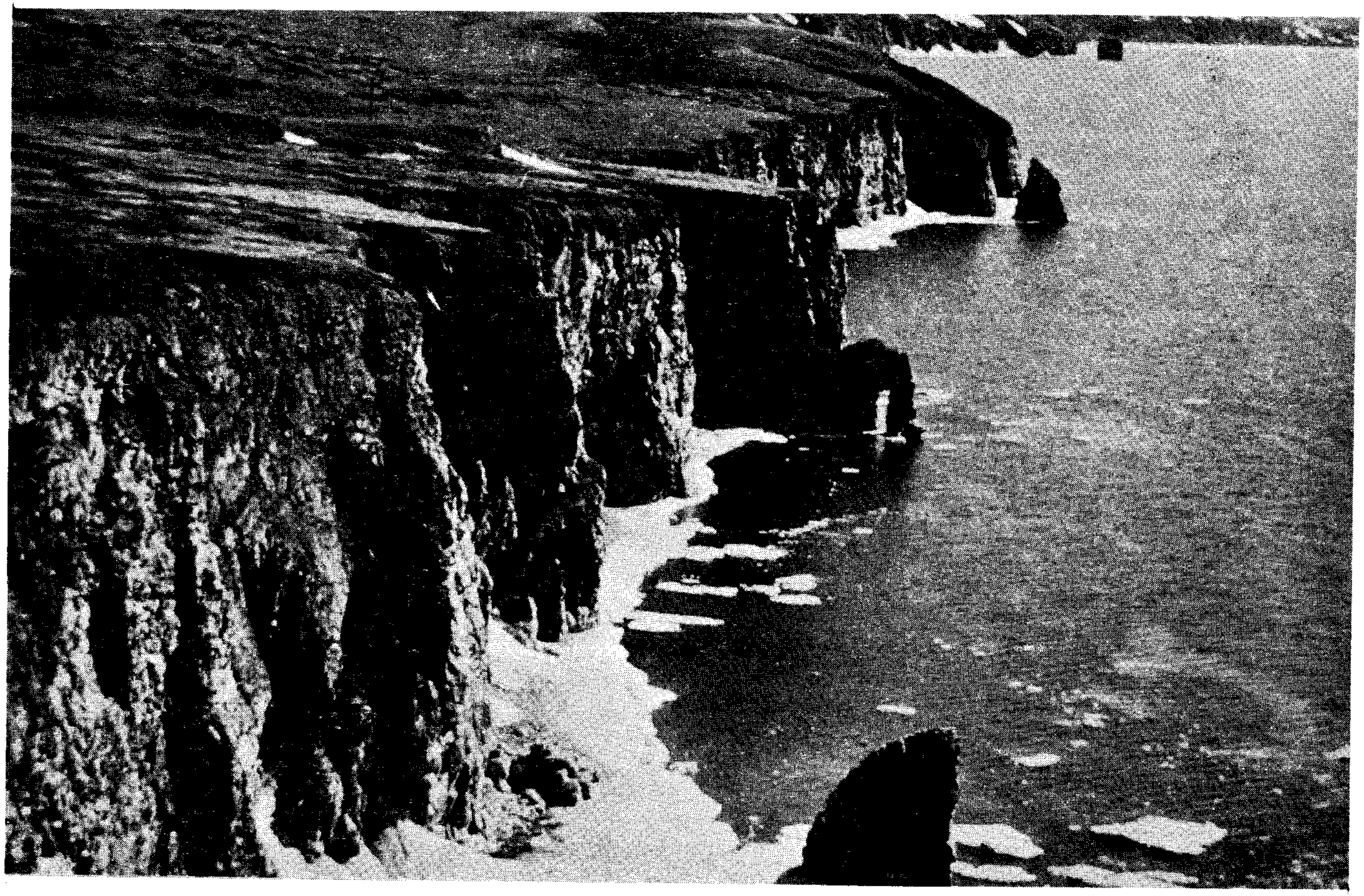


Figure 2.
The Cliffs at Bluff; view from below the High Bluff looking east. Square Rock is in the background on the upper right side of the photo. The Jackpole at Tucker Camp is in the upper left side of the photo.

behind Farland's cabins at Koyana Creek. Koyana Creek provides a good supply of drinking water.

Common Murres, Horned Puffins and Black-legged Kittiwakes nest along all the cliff faces from the western extremity of the cliffs to the stack with the rope offshore on the east. Further east murres, puffins and kittiwakes are scattered in patches.

The accessibility of the colony and vantage points which provide excellent views of sections of the cliff for study, as well as the presence of housing and water, make the Cliffs at Bluff an inexpensive and extremely comfortable place to conduct studies of the reproductive biology of the species present.

B. Square Rock

Square Rock is a separate colony 1.5 miles east of Koyana Creek, on the eastern end of the Cliffs at Bluff (Figures 2 and 3). Horned Puffins are relatively numerous along sections of cliffs of poorly consolidated sediments between the Rope Stack at Bluff and Square Rock. Murres and kittiwakes nest on the stack at Square Rock and on the adjacent mainland cliff (Figure 4). The occupied area on the mainland extends about 150 meters along the face. A mob of Common Murres gathers on top of Square Rock, leaving "sterilized" zones occupied by the territories of Glaucous Gulls (Figures 5a and b). Detailed descriptions of the locations of study sites at both Bluff and Square Rock are presented in Appendix IX, "Methods Used at Bluff".

C. Cape Denbigh

At Cape Denbigh the seabird cliffs are on the point which extends south from the main cape. The whole point, as seen from the west is shown in the top drawing of Figure 6. The cliffs are occupied in two portions. Within the northern section the murres and kittiwakes are crowded in two sections; the

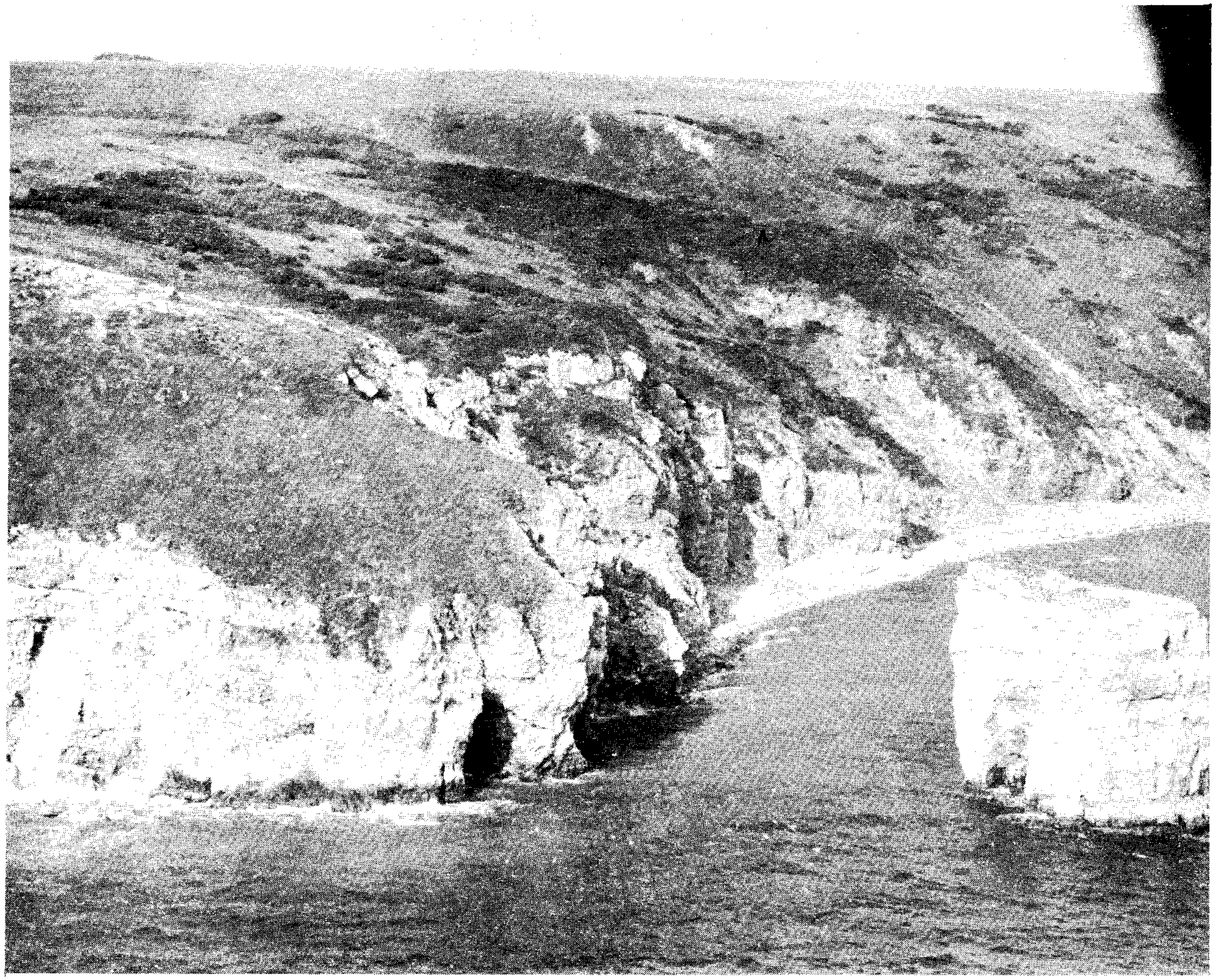
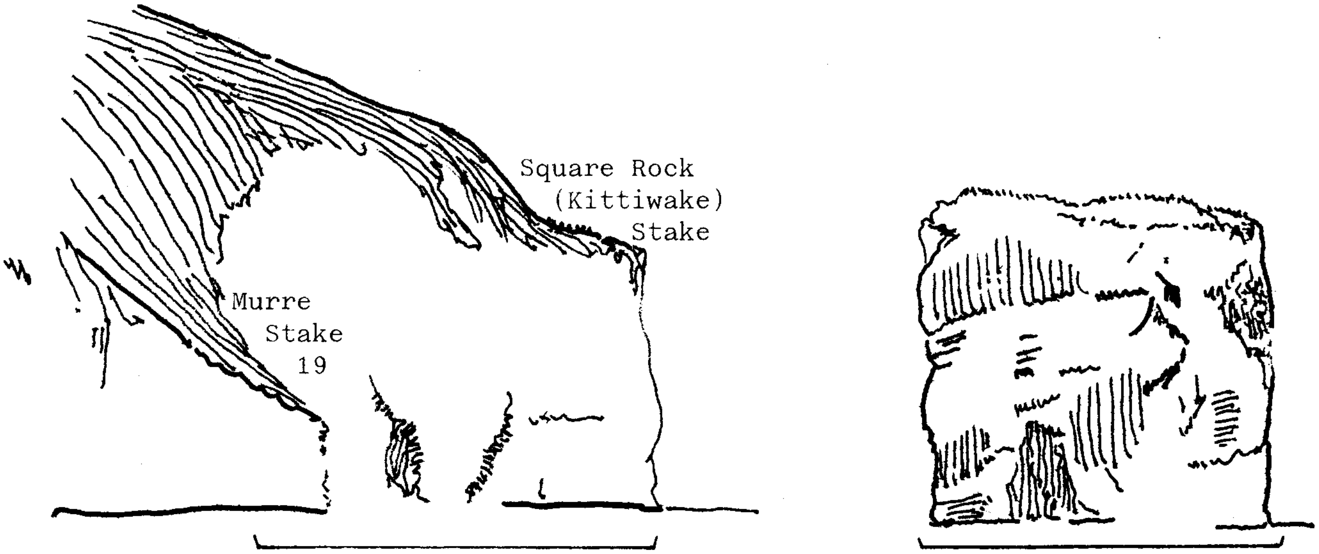


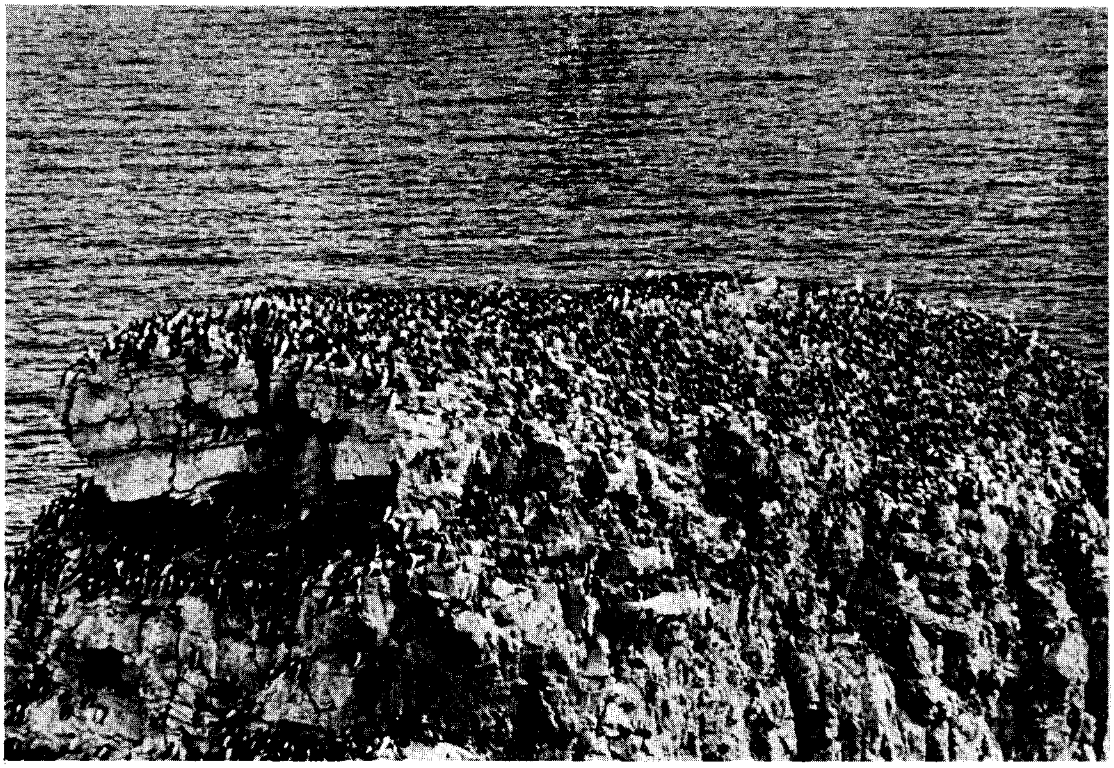
Figure 3.
Square Rock (right side of the photo) and adjacent mainland cliffs which are also occupied by seabirds. Bartonek photo, 1973.



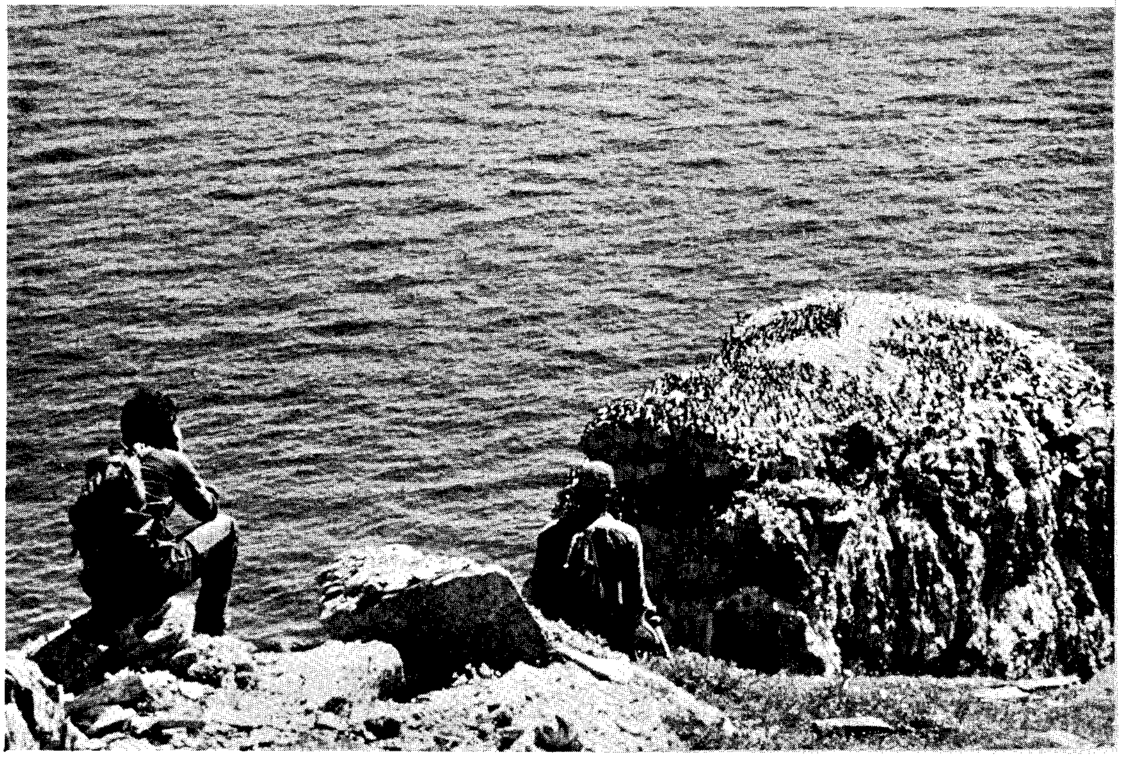
mainland bird cliffs

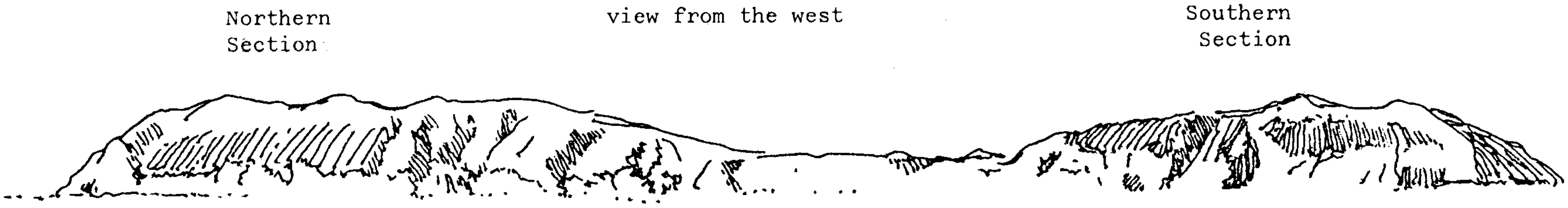
Square Rock

Figure 4. Square Rock and adjacent mainland cliffs. The kittiwake stake on the mainland is for study of kittiwakes on Square Rock; Stake 19 is used to study murres and kittiwakes on ledges below the kittiwake stake itself.

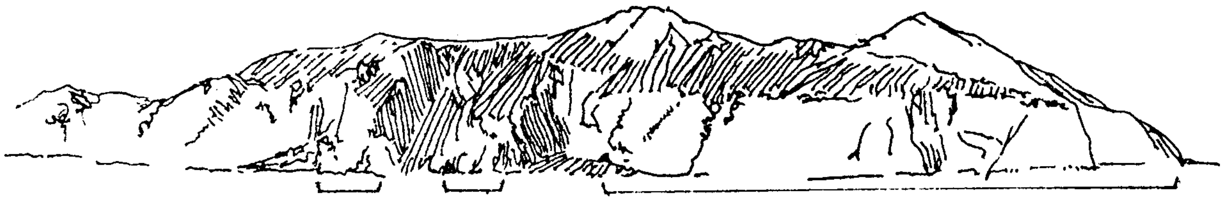


Figures 5a and 5b: the top of Square Rock as seen from the mainland.
a(upper photo): taken in 1976, this photo shows murres covering the top.
b(lower photo): taken in 1978, this photo shows the presence of Glaucous Gull territories, leaving "sterilized" zones empty of murres. These gulls are capable of out-competing murres for "preferred" nesting habitat (Tuck 1960), as shown in these two photos.





Northern Section



Southern Section

Figure 6. The seabird colony at Cape Denbigh. The brackets indicate the sections of the cliffs occupied by seabirds.

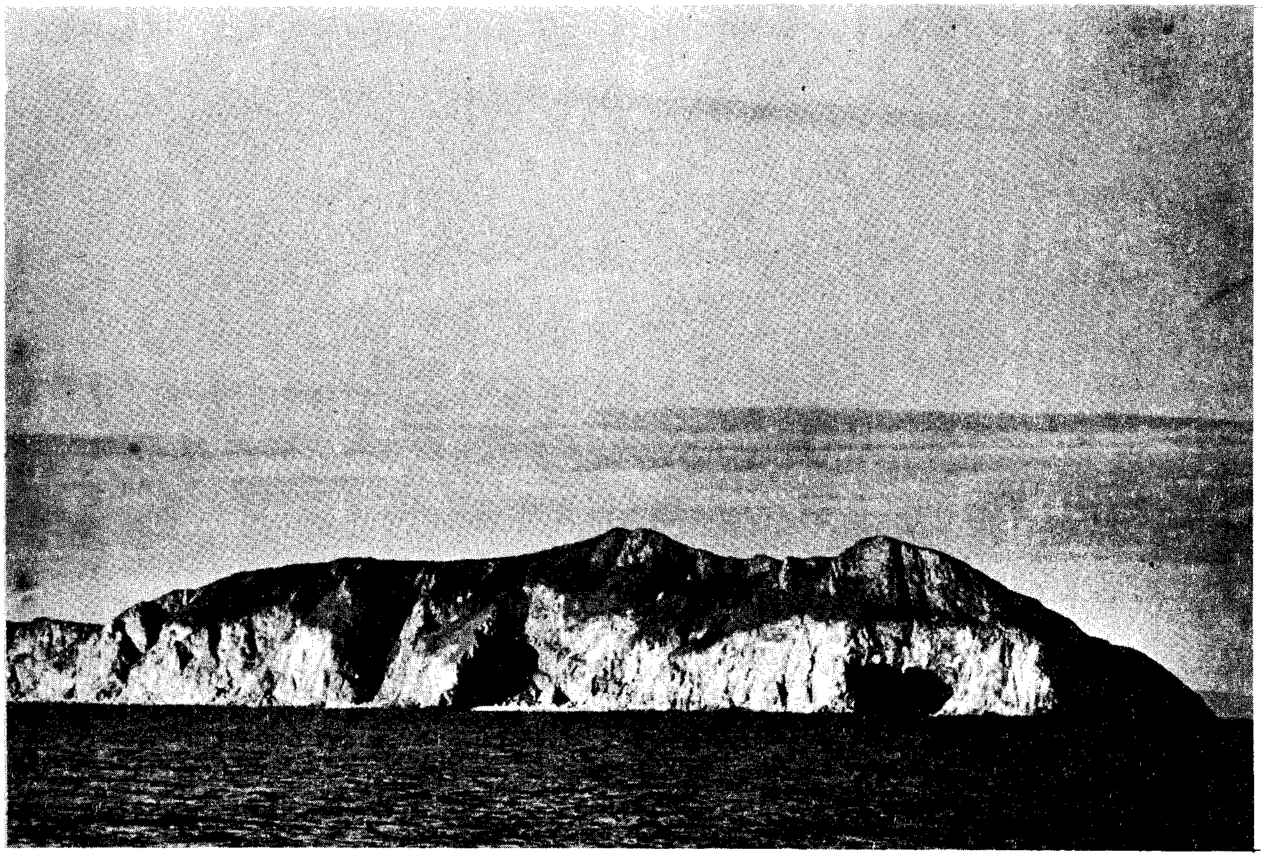


Figure 7.
Cape Denbigh in Norton Sound; the southern bird cliffs.

northern portion is shown in the middle sketch of Figure 6. There are additional small patches, sparsely occupied by murres, kittiwakes, and cormorants indicated in the drawings by the brackets. The nesting in the southern section (lower drawing and Figure 7) consists of a few dense patches separated by a beach. A large, long and 120-foot high section of cliff at the southernmost end is dense with murres and kittiwakes.

D. Egg Island

The cliffs on Egg Island are low (20-25 feet), and lie between a rubble depositional slope and the turf on top of the island. Figures 8(a) and 9 show a view of the cliffs as seen from the northwest and from the air. Figure 8(b), the lower drawing, shows the entire area occupied by murres and kittiwakes, as seen from just west of north. Most of the murres and nearly all the kittiwakes nest on the northwest corner on large outcrops under the place where the turf is lowest. Other murres nest further east in small patches. It appears that nearly all nesting ledges are accessible to egg-collecting. Horned Puffins are most numerous on the northwest, north and northeast sides of the island. We saw a few Parakeet Auklets near the edge of the nesting area.

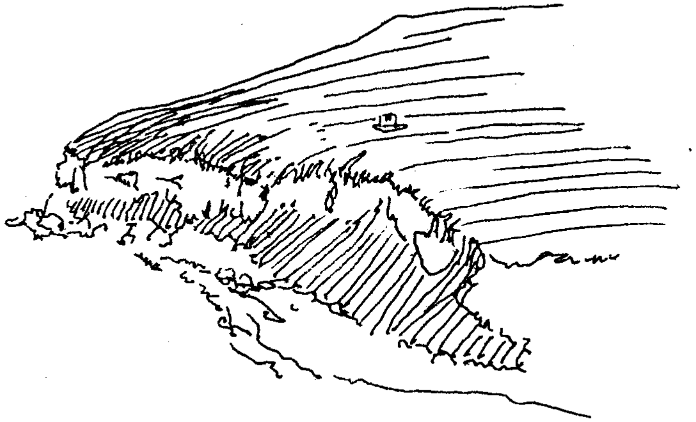
The southern part of the island is made up of blocks of columnar basalt. The same rock extends from Tolstoi Point to the east, and west to Stuart Island. The cracks in the basalt seem to be used as nesting crevices by Horned Puffins at several places.

E. Sledge Island

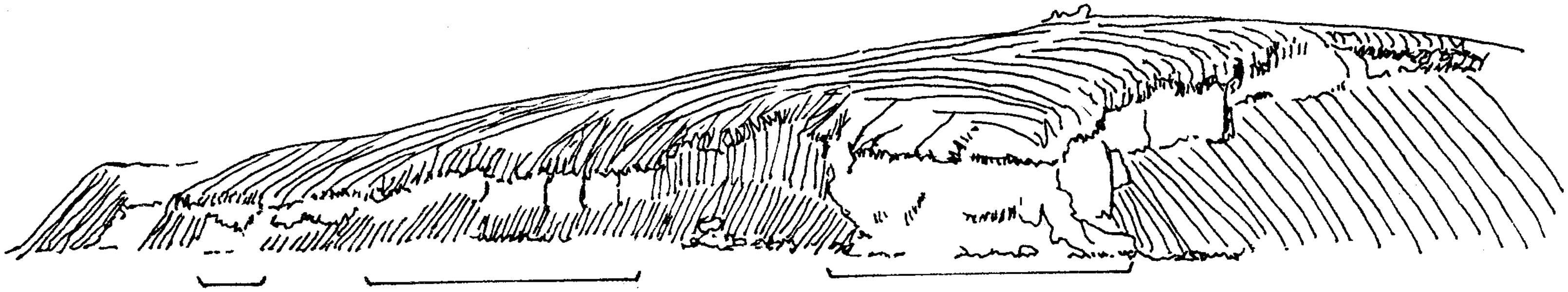
Sledge Island is located about 5 miles south of the Seward Peninsula, 25 miles west of Nome (Figure 10). It measures approximately 1 by 1.5 miles, and is about 700 feet high; the sides are steep with talus and grassy slopes

Figure 8. Egg Island.

The brackets in these two illustration indicate the locations of seabirds.



(a) Aerial view from the north.



(b) View from just west of north.

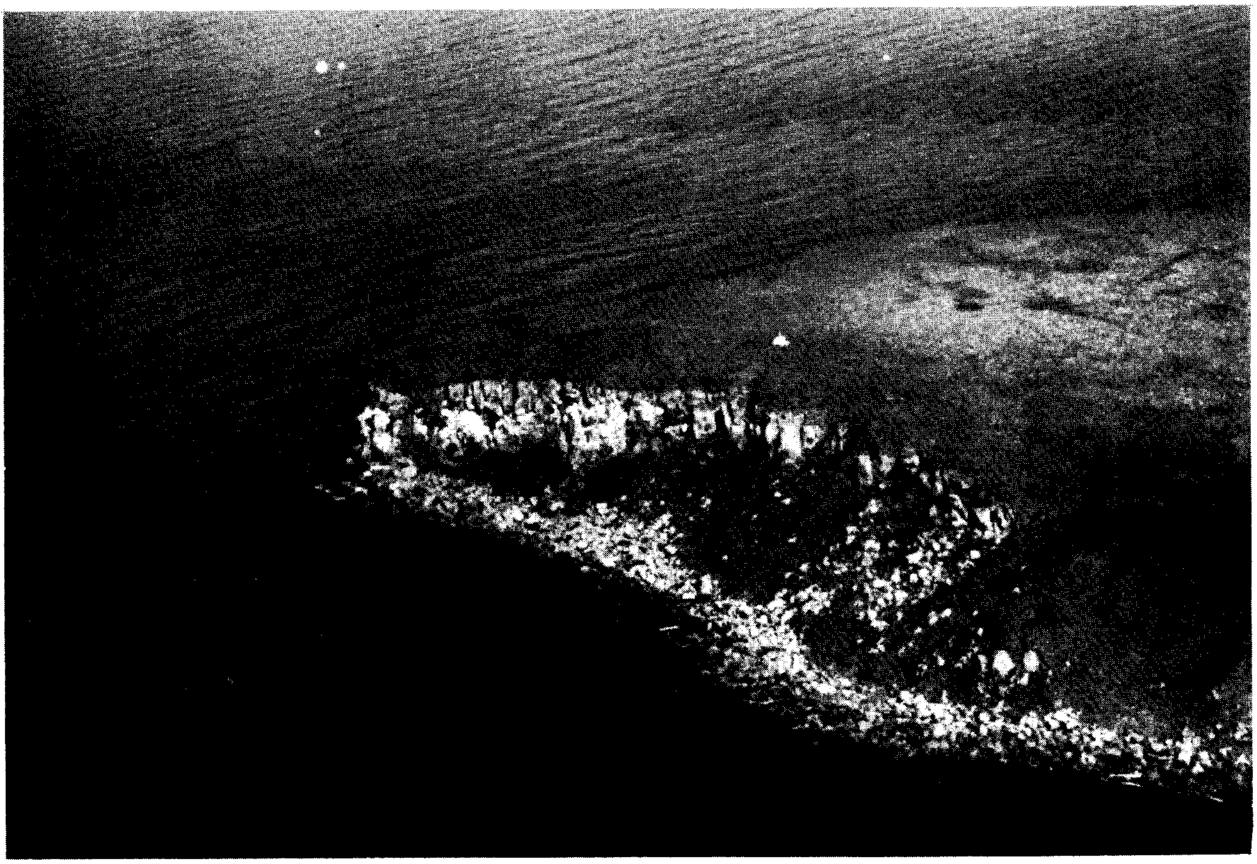


Figure 9.
Egg Island in Norton Sound; the northern tip with a small seabird city of Common Murres, Kittiwakes, and Horned Puffins.

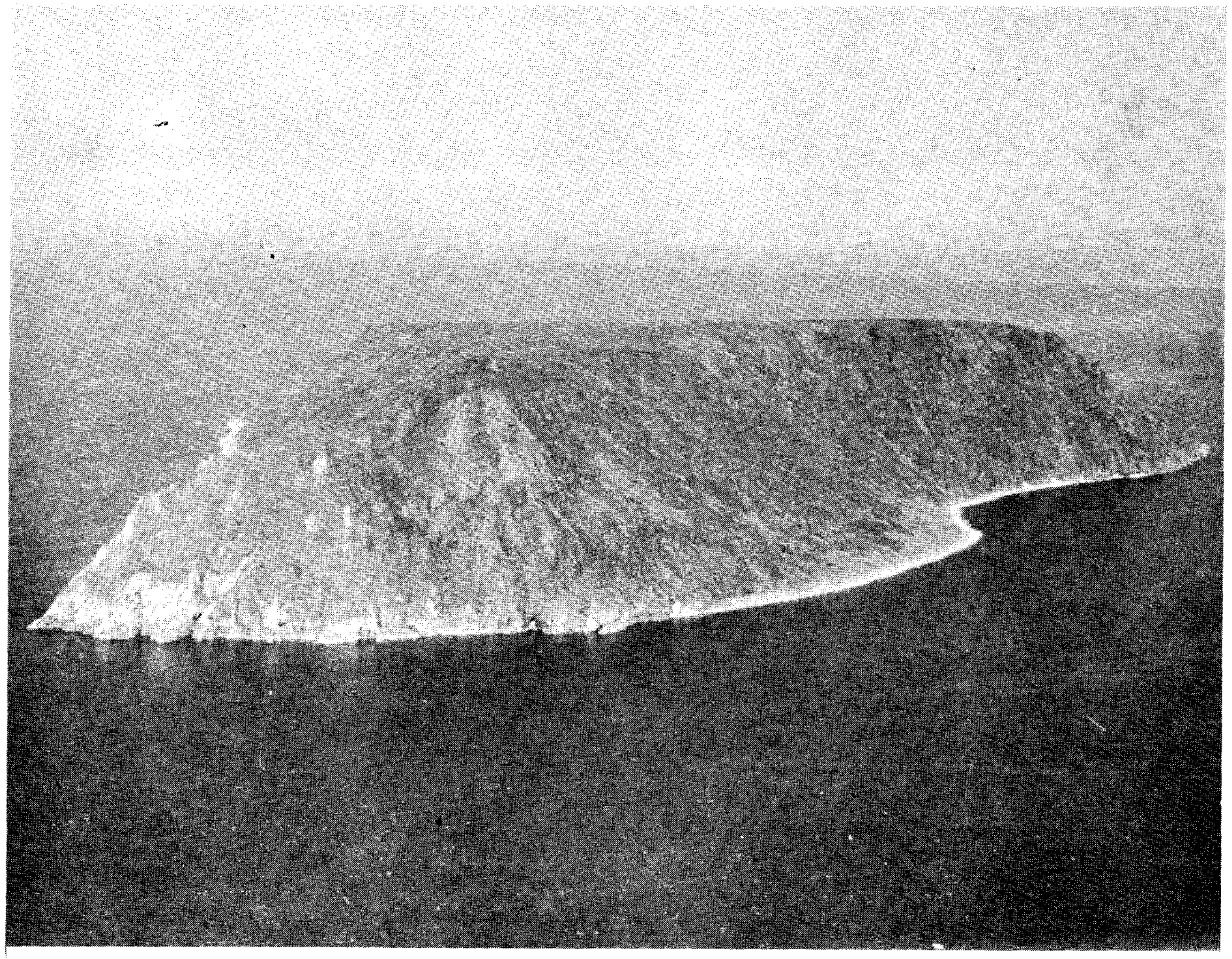


Figure 10.
Sledge Island, as seen from the southeast. Bartonek photo, 1973.

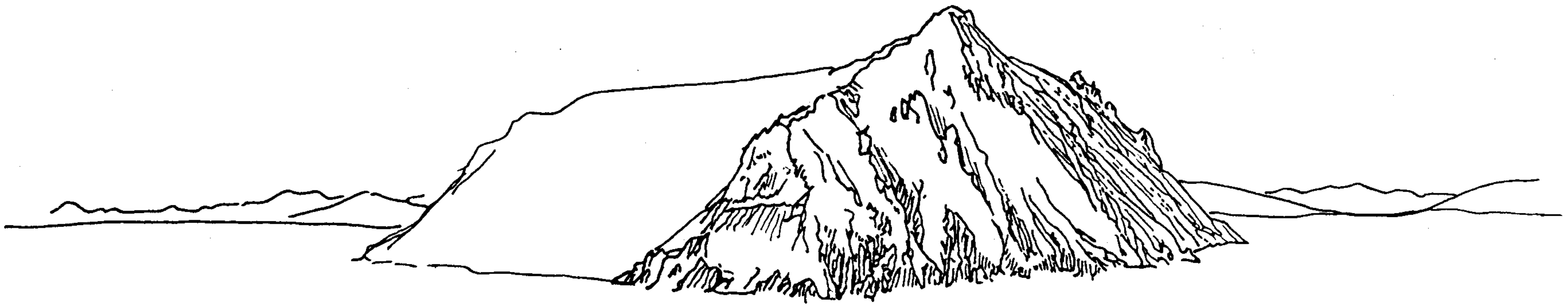


Figure 11 (a). Sledge Island as seen from the south at a distance of about 10 nautical miles.

Figure 11 (b). Location of Sledge Island.

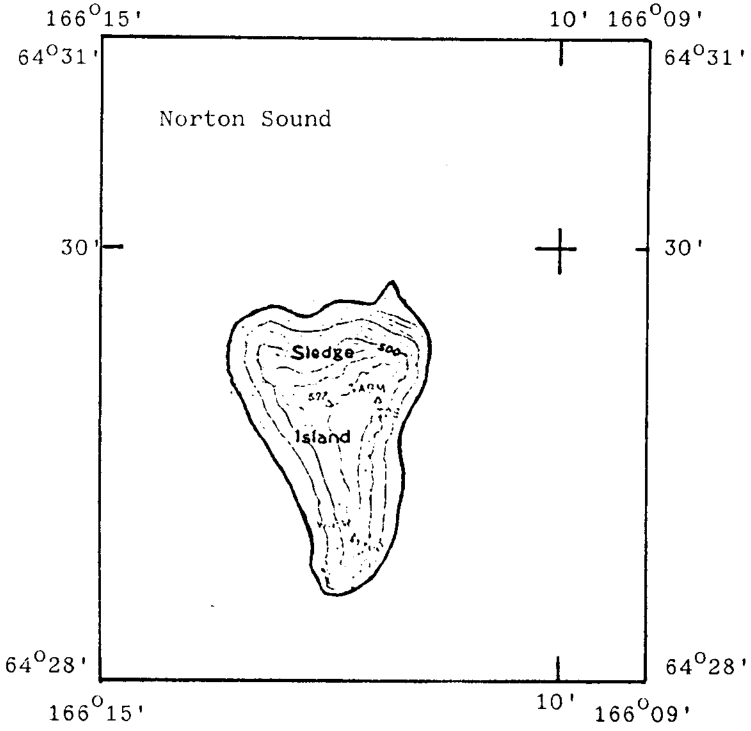
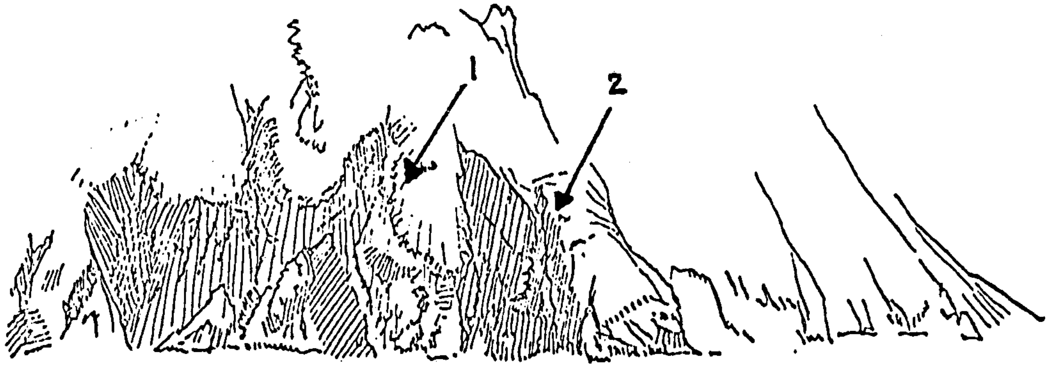


Figure 11 (c). The locations of two study sites on Sledge Island, which are marked by stakes, on the south end of the island.



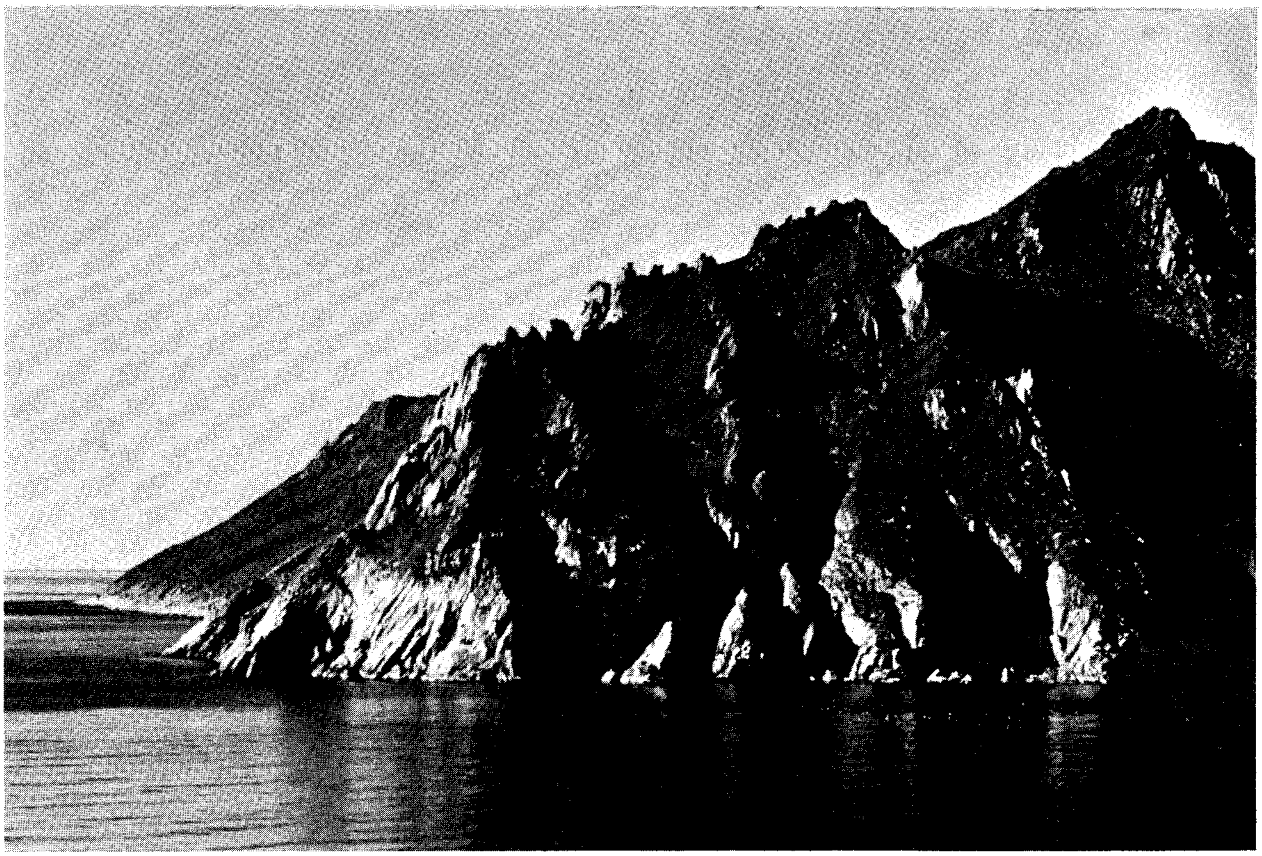


Figure 12.
Sledge Island; the cliffs at the south end where the nesting cliffs for murres, kittiwakes and cormorants are located.

and the top is flat and grassy. The illustration of the island in Figure 11, is a view from the south at a distance of about 10 nautical miles. The nesting cliffs for kittiwakes, murres and cormorants are on the south tip. Pelagic Cormorants nest on the south and northeast corners on low slopes as well as on rock stacks high on the slopes. There is a small group of Pelagic Cormorants, Horned Puffins and perhaps Parakeet Auklets nesting around some small rocky faces at the distant northeast corner on the east side. The arrows in Figure 11b show where study sites were set up.

Sledge Island is accessible by small boat from Nome. There is a good campsite on a gravel spit on the north end. Freshwater is available in small quantities.

F. Saint Lawrence Island

For description of St. Lawrence Island, please see the Main Body of this report; and Figures 13-21 herein.

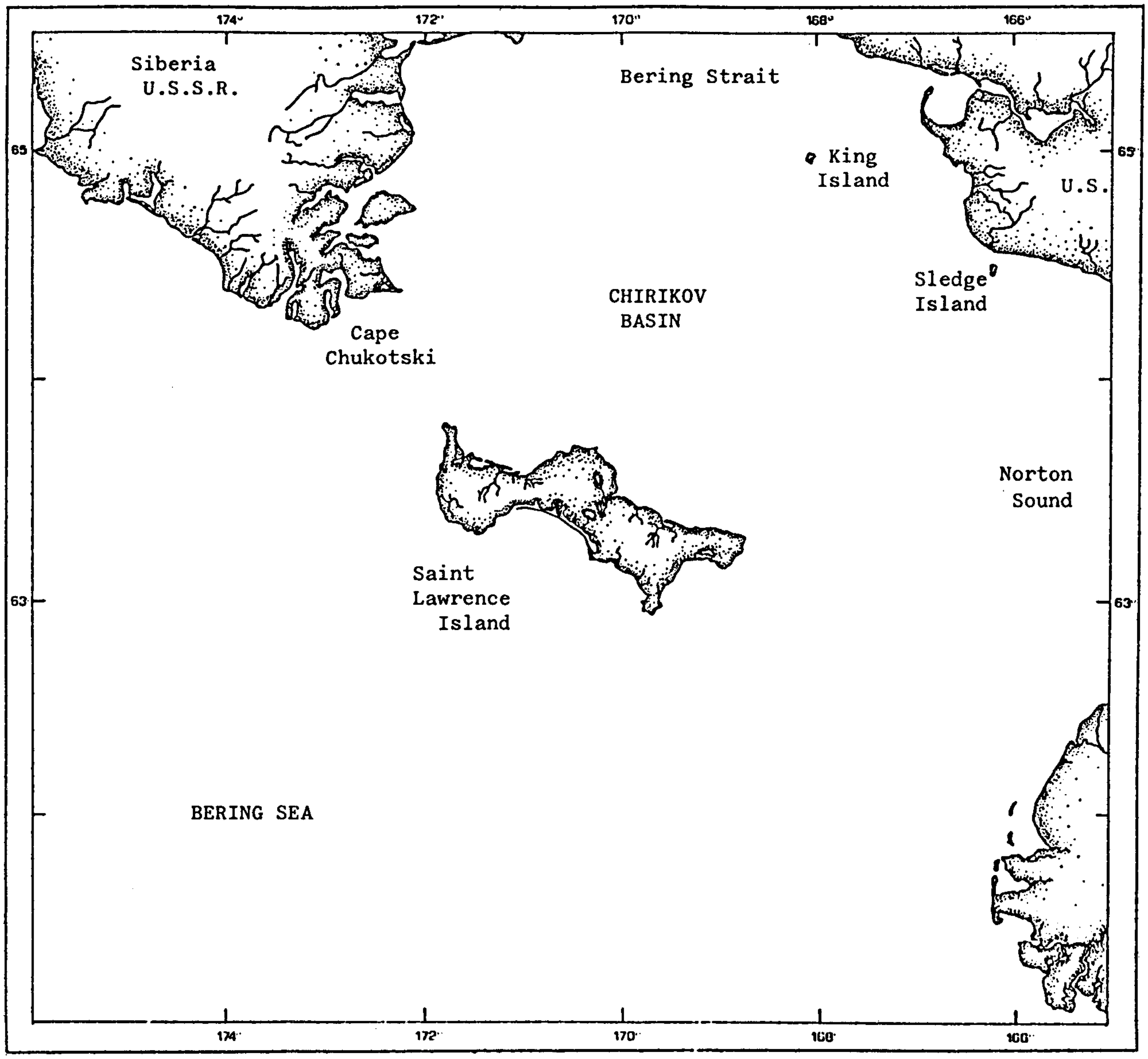
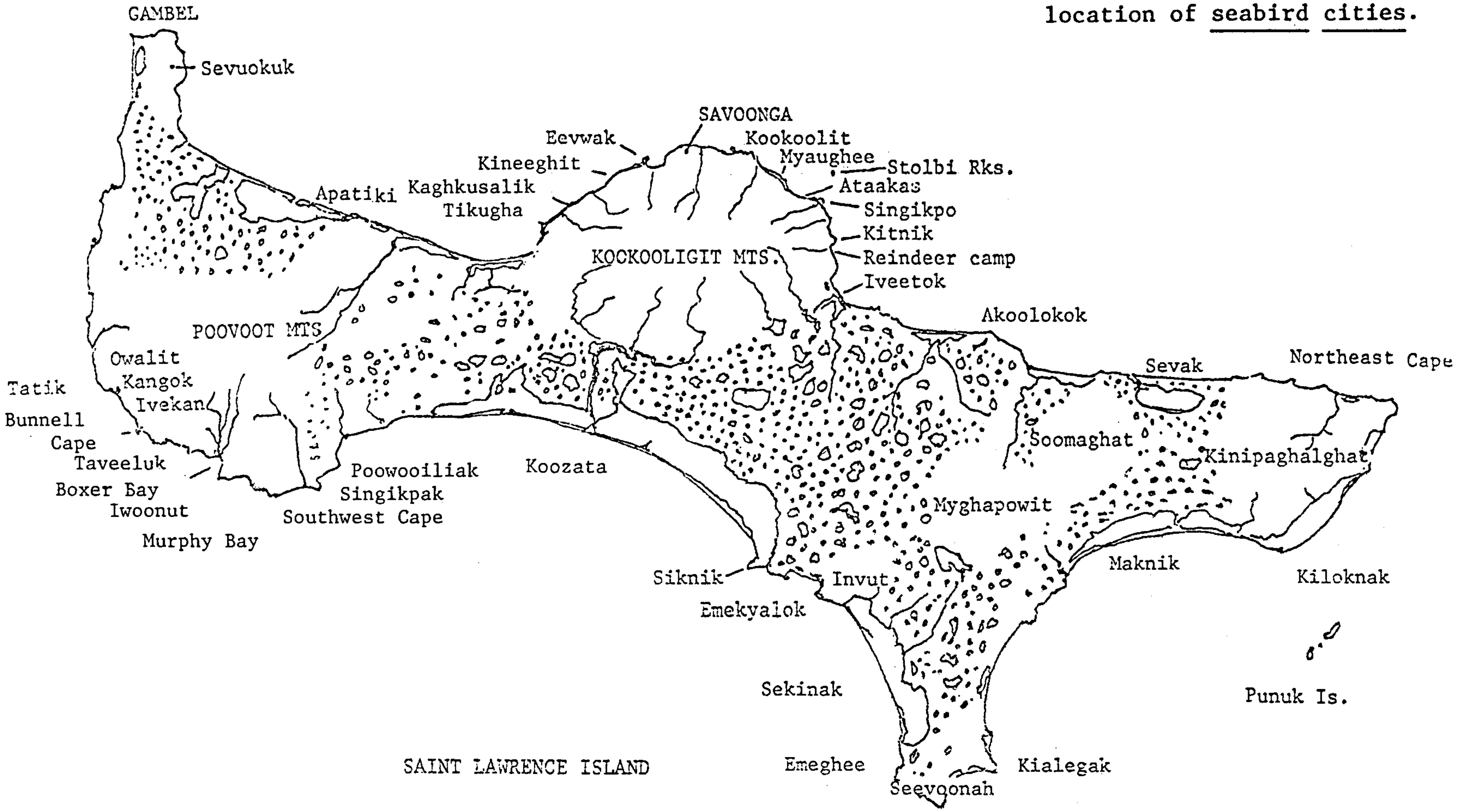


Figure 13. Context map showing locations of Saint Lawrence Island, Sledge Island and King Island.

Figure 14.
Saint Lawrence Island; place names referred to in the discussion of the location of <u>seabird</u> <u>cities</u>.



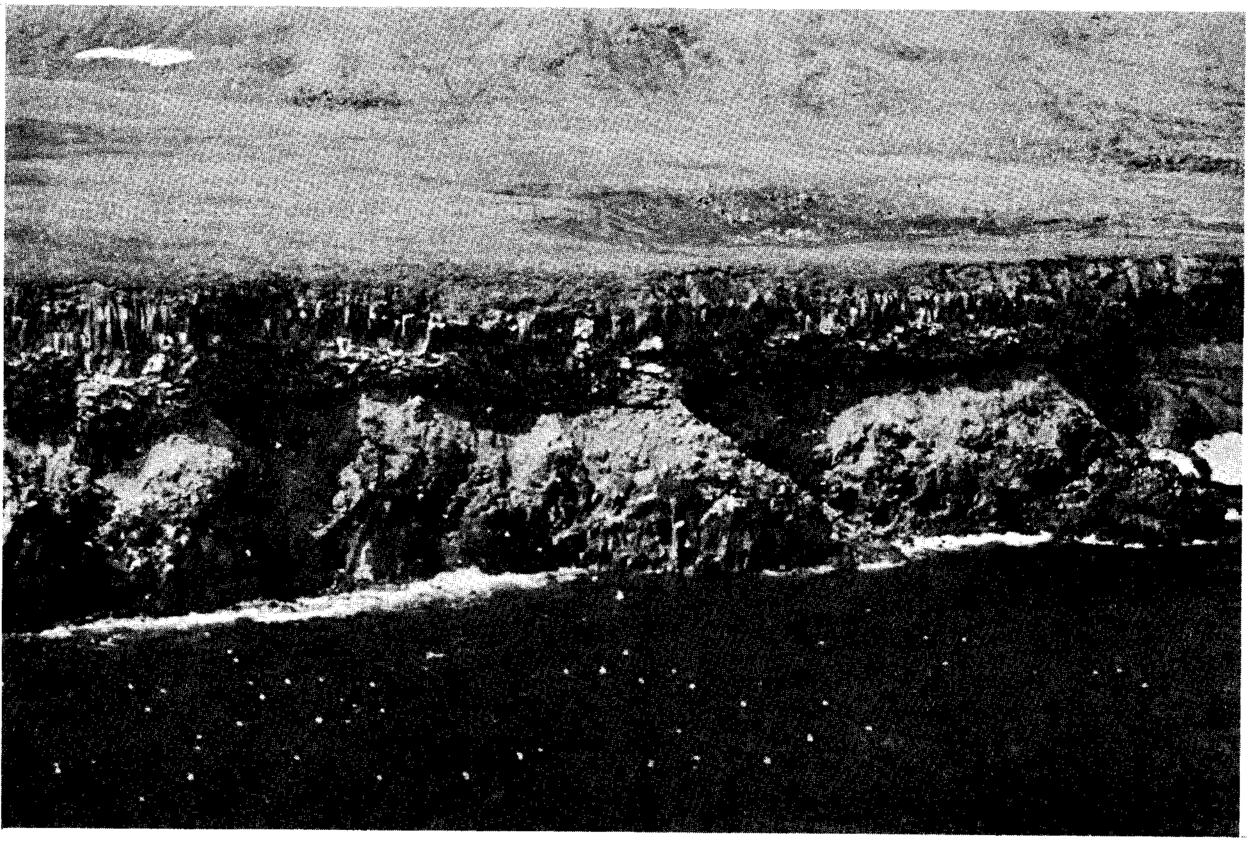


Figure 16.
Saint Lawrence Island; bird cliffs east of Savoonga.

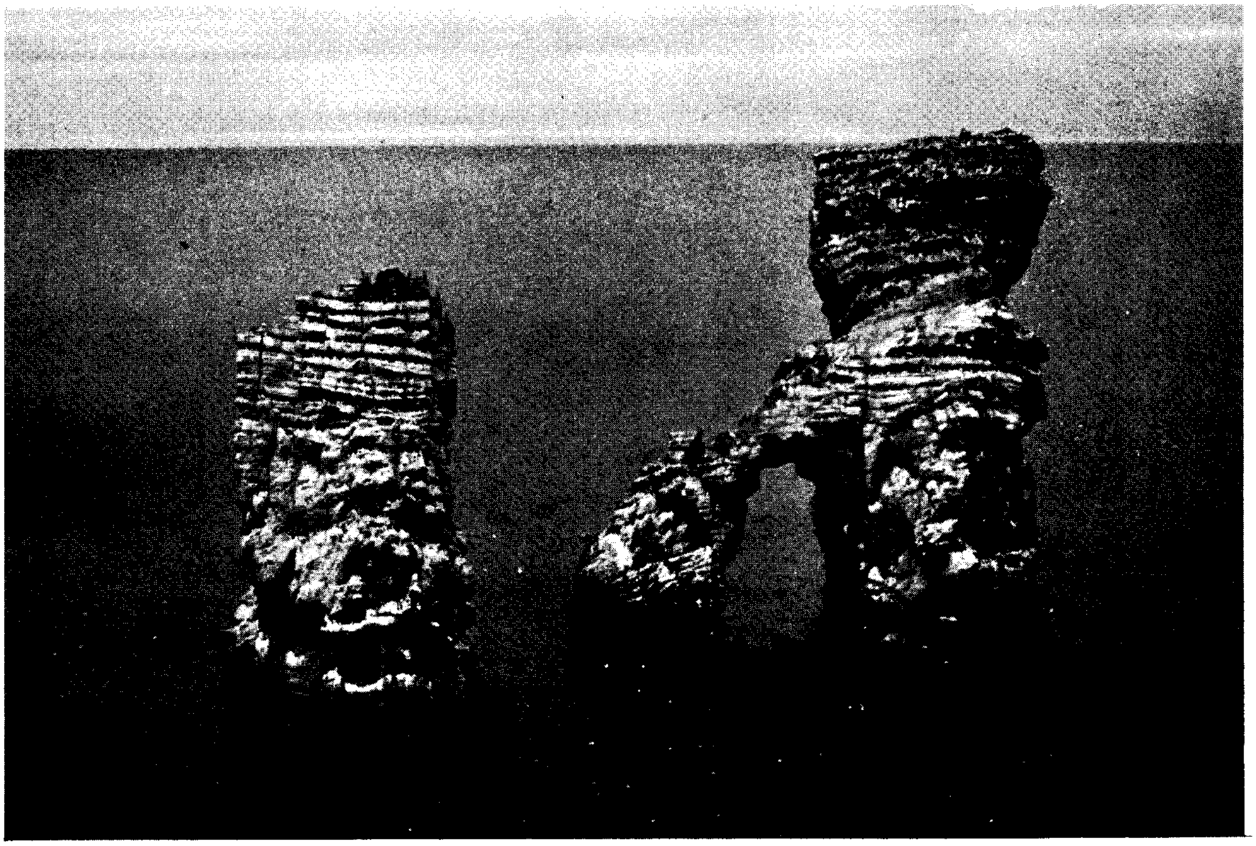


Figure 17.
Saint Lawrence Island; Stolbi Rocks, located east of Savoonga.

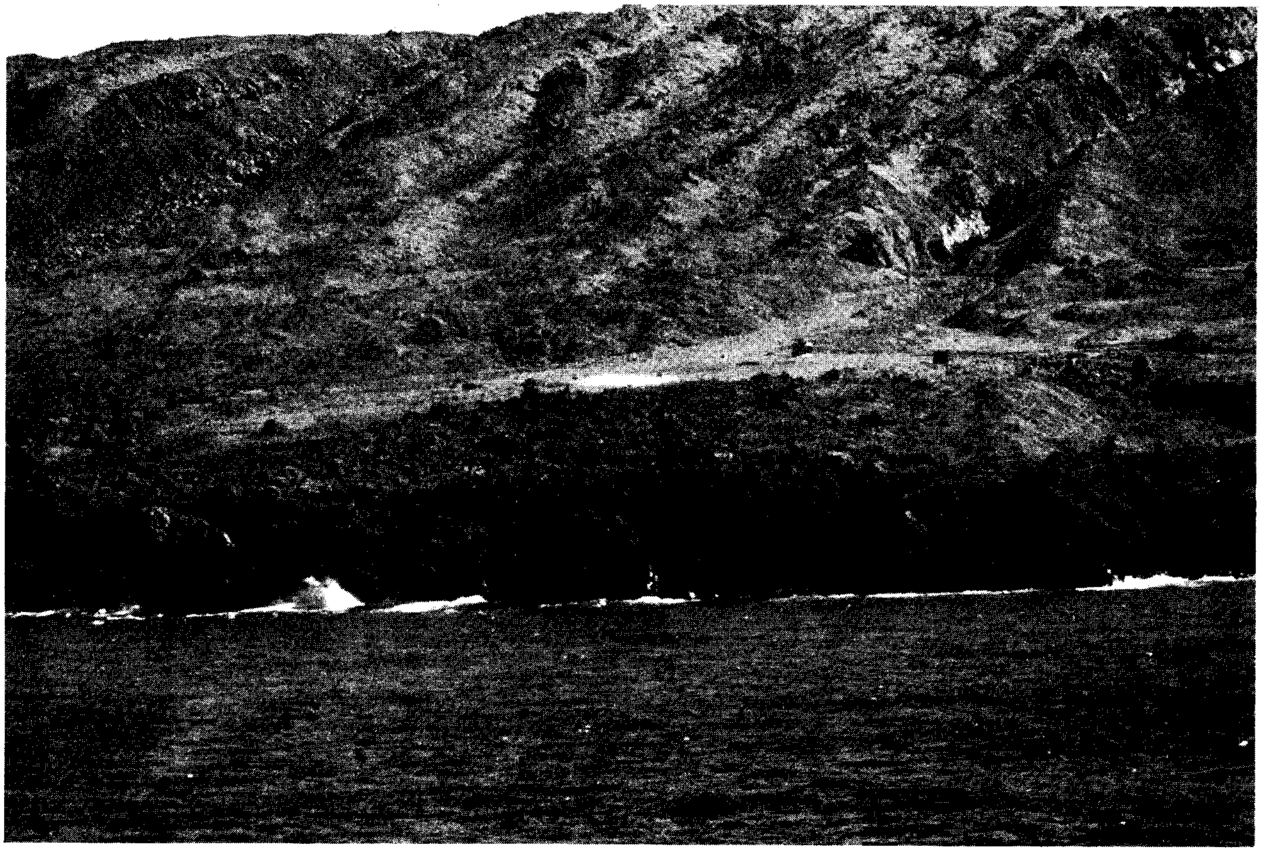


Figure 18.
Saint Lawrence Island; recent lava which separates Ataakas Camp from the cliffs at Reindeer Camp on the north shore of the island east of Savoonga.

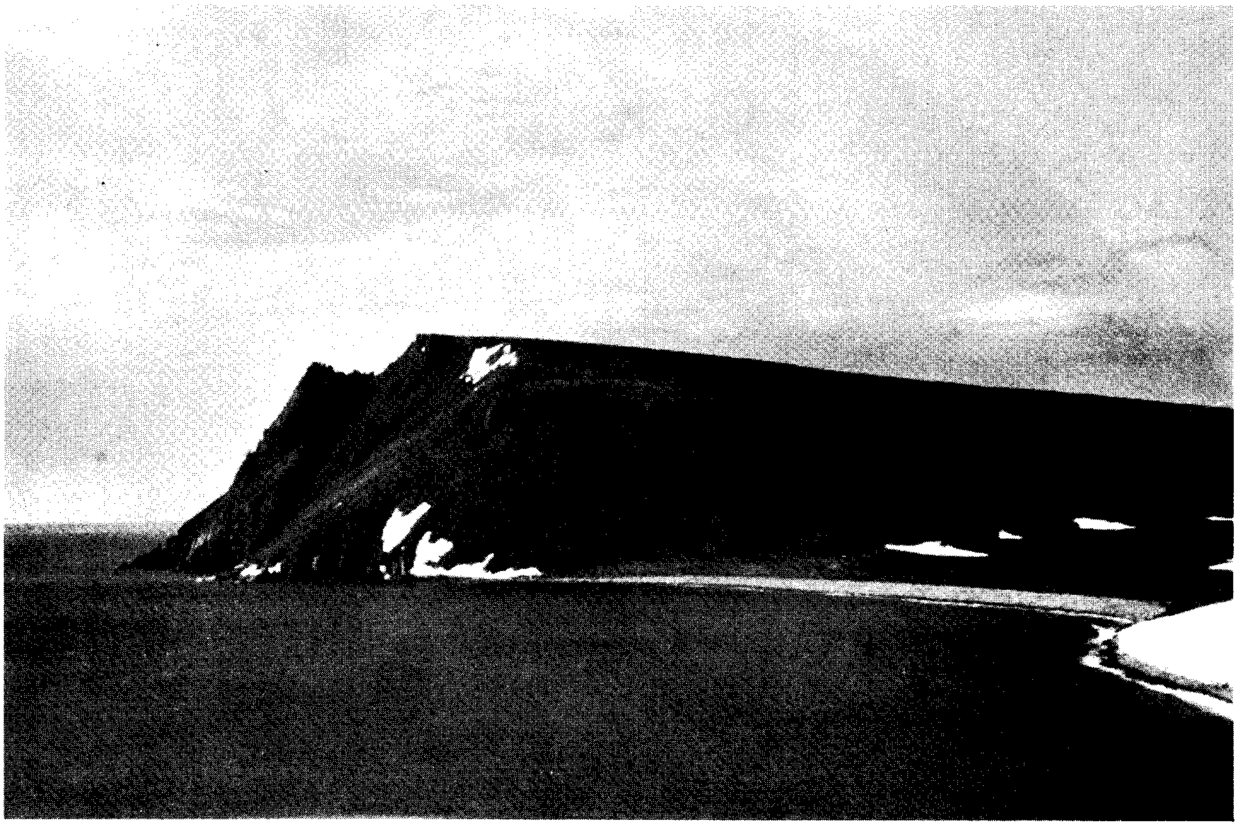


Figure 19.
Saint Lawrence Island; Sevuokok Mountain east of Gambel.

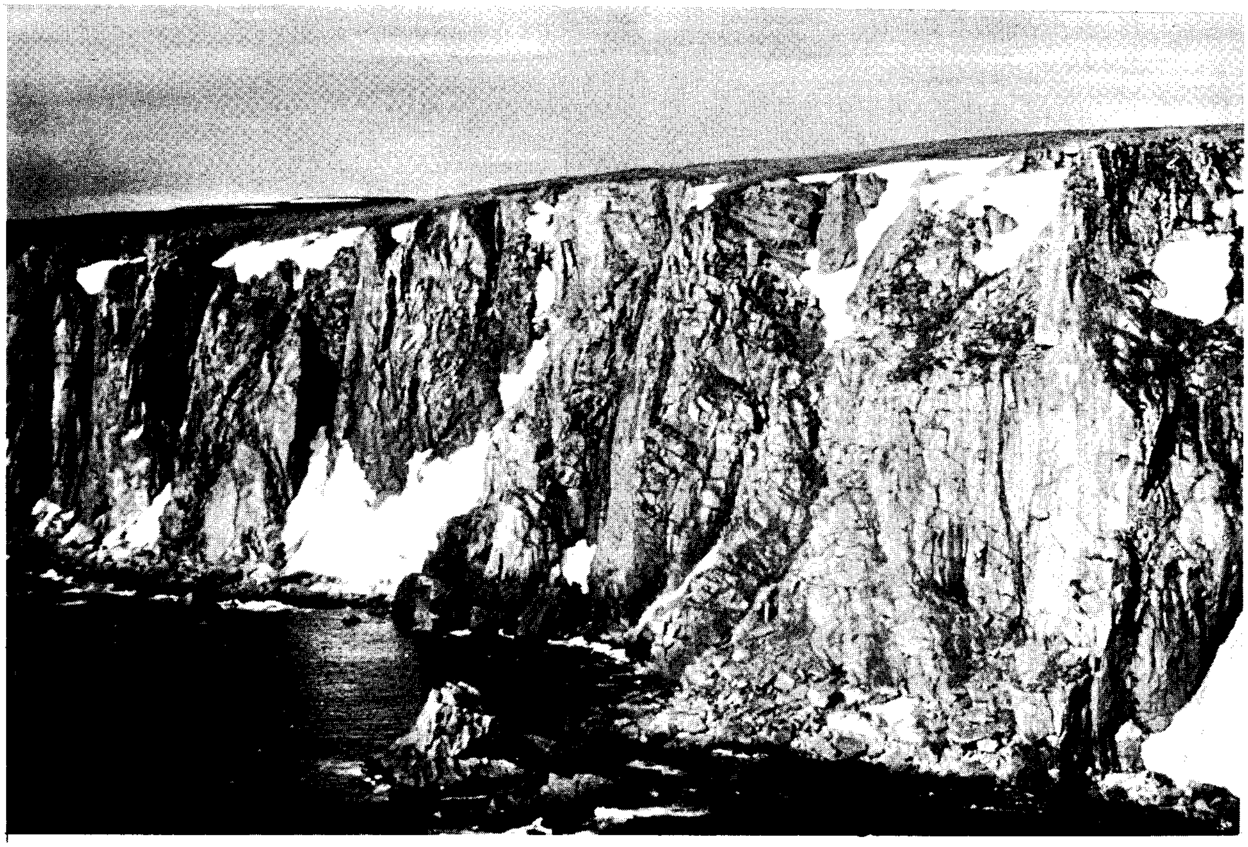


Figure 20.
Saint Lawrence Island; the cliffs east of Murphy Bay near Southwest Cape.

Figure 21.
Saint Lawrence Island; the cliffs of Ivekan Mountain west of Boxer Bay and east of Owalit Mountain on the southwest corner of the island.

G. King Island

and Fig. 23)

King Island (Figure 22/)lies in the Chirikov Basin, about forty nautical miles (75 km) south of Cape Prince of Wales, and about forty nautical miles west of the beaches at Cape Wooley. The water to the east is mostly less than 20 fathoms (40 meters), and that to the west is mostly deeper than 20 fathoms (to about 50 fathoms).

The island is 1200 feet (370 meters) high, largely granitic with bold outcrops forming arretes on the south and north sides, massive vertical slabs on the east side and "Stonehenge"-like monuments on the gently rolling uplands (Figures 24 and 25). Gullies extending down the sides of the island, at 40°-45° angles, and are heavily vegetated with grass (Calamagrostis).

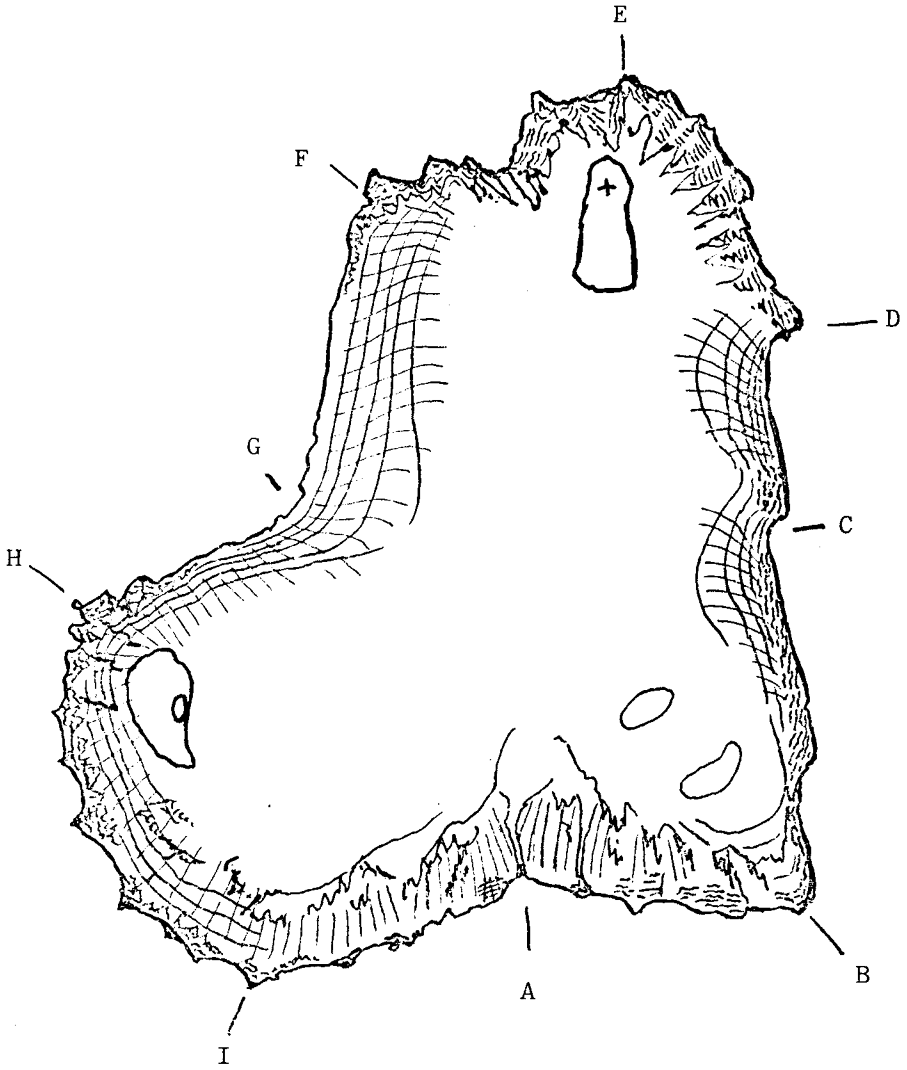
The village, Ukivok, abandoned for about fifteen years, lies on the shoulder of a fan of massive granite boulders (Figure 26, and "A" in Figure 22). The fan has been undermined by wave action during recent storms.

King Island, like Saint Lawrence Island and Little Diomede Island, is a nesting site for large numbers of Thick-billed Murres and three species of auklet; these four species are virtually absent from the seabird cities and waters in Norton Sound.

The north point of King Island, showing the bold outcrops of slabs of granite, is illustrated in Figures 27 and 28a. Tens of thousands of murres nest from near sea level to high on the cones near the sky line. Some kittiwakes nest within 50 feet of the water on the right side of the area shown and some others on the middle left.

The lower drawing in Figure 28 portrays King Island as seen from the southwest. The village is in the middle. Arrows and numbers represent the locations at which study sites were established. The "amphitheater behind the village" lies between the arrow numbered 5 and that numbered 2. In 1976,

Figure 22. King Island; drawing of aerial view showing important topographic points.



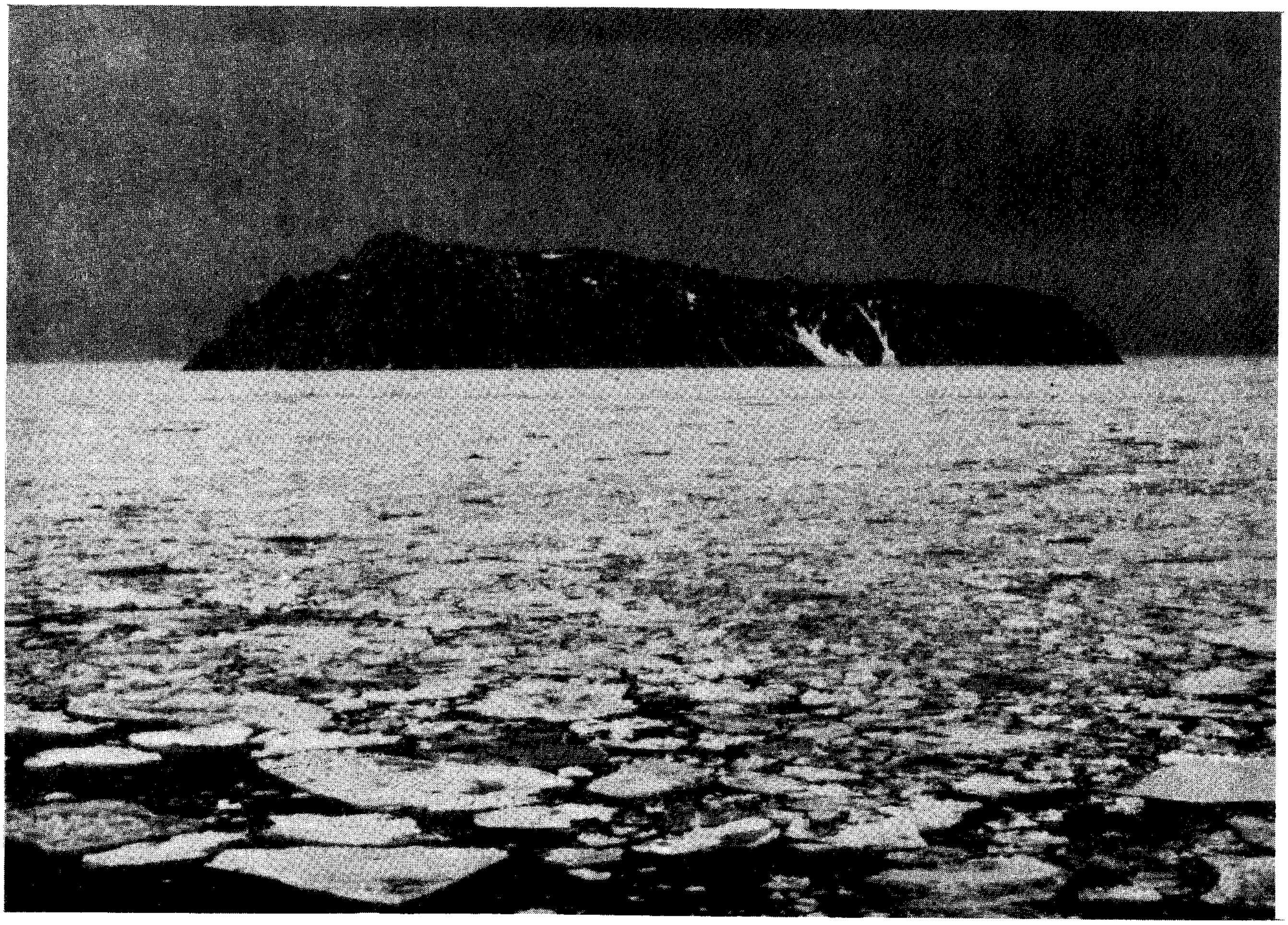


Figure 23.
King Island, as seen from the south.

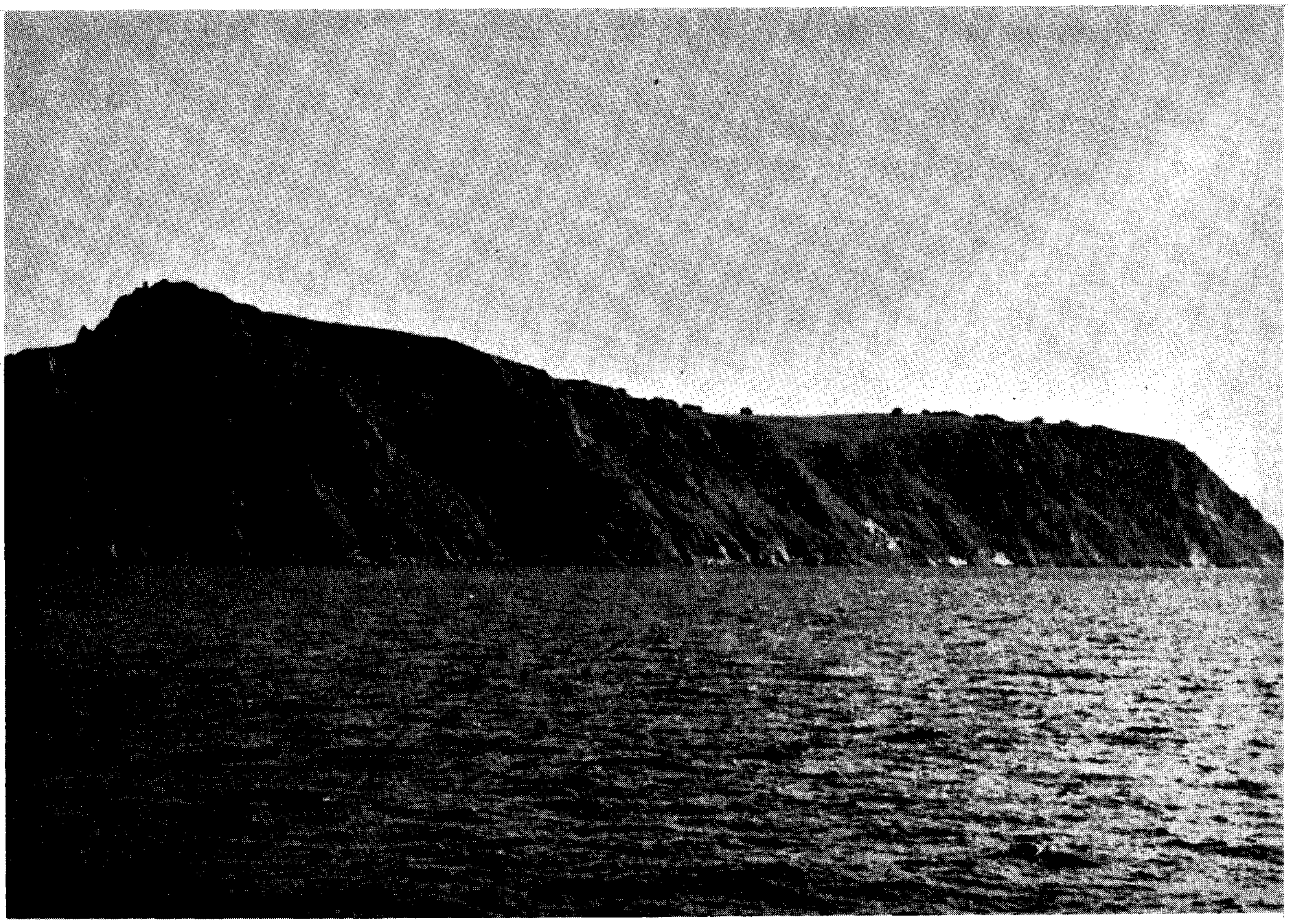


Figure 24.
King Island, as seen from the south, in summer.

Figure 25. King Island. View from the air, from the southwest. J. Bartonek, photo.

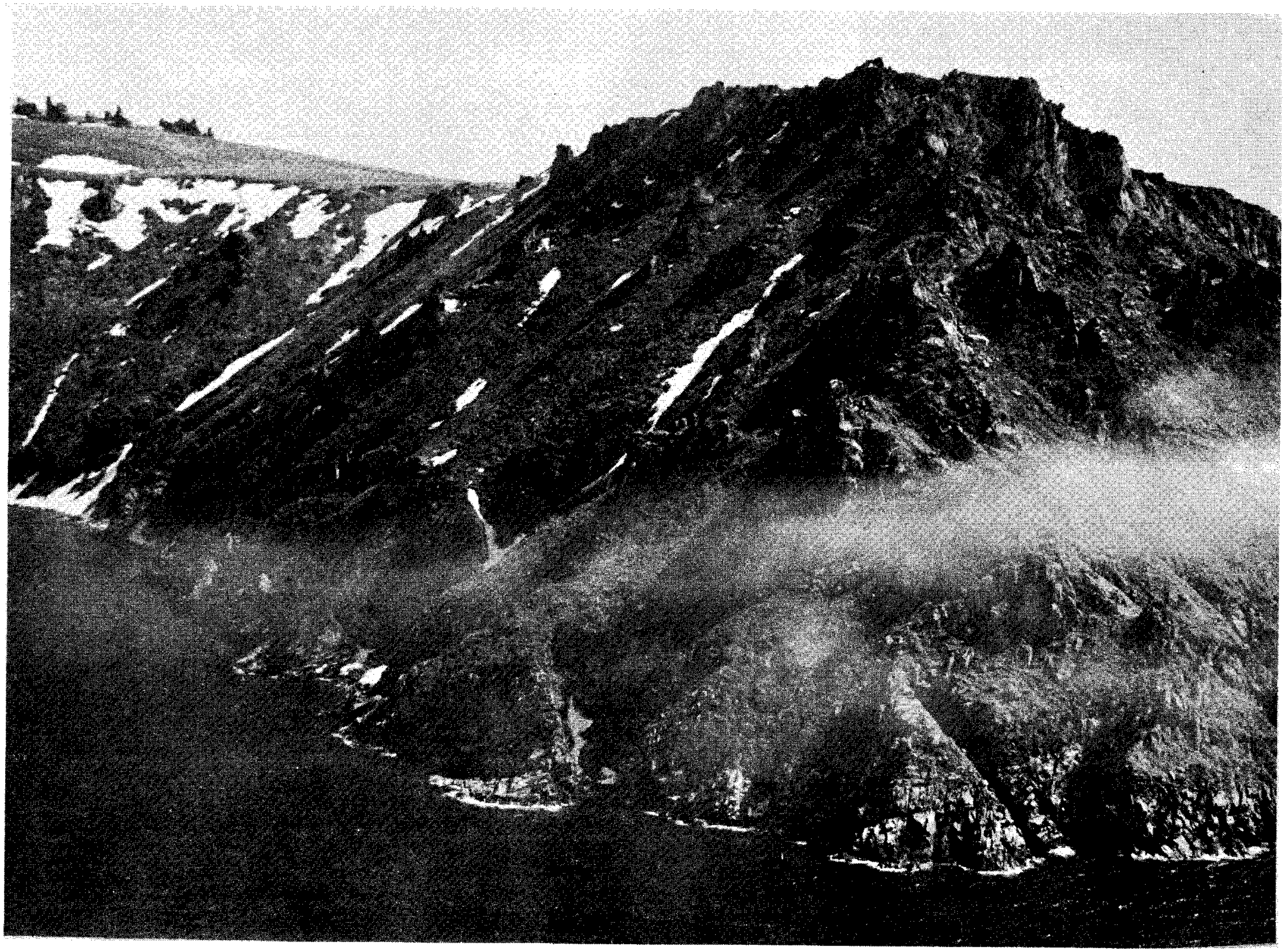


Figure 26.
The village of Ukivok on King Island.

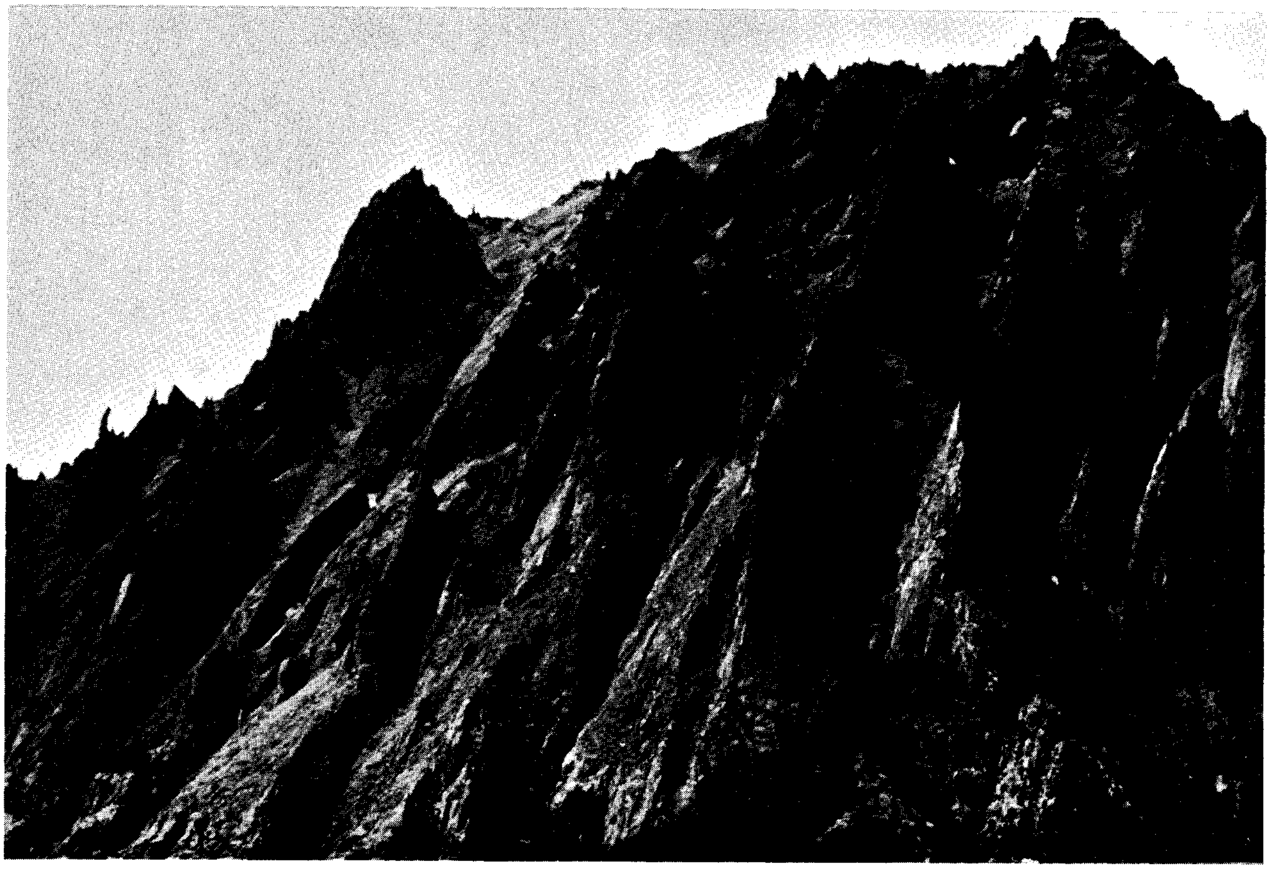


Figure 27.
The cliffs at the north corner of King Island.

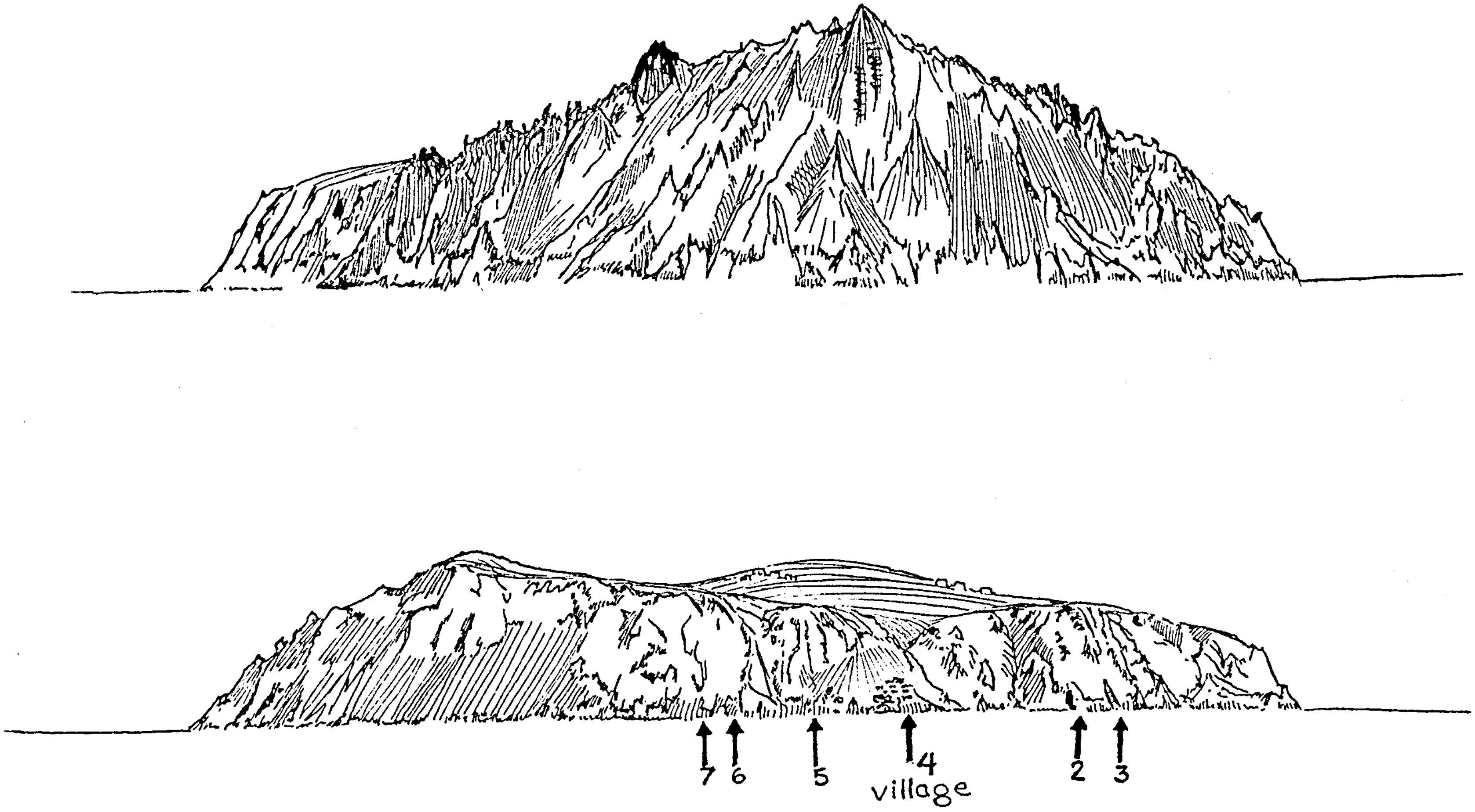


Figure 28. King Island. a: The upper drawing shows a view from the north of the north end of the island.

b: The lower drawing is a view from the southwest. The locations of study sites are indicated by the arrows, and the village of Ukivok lies in the middle.

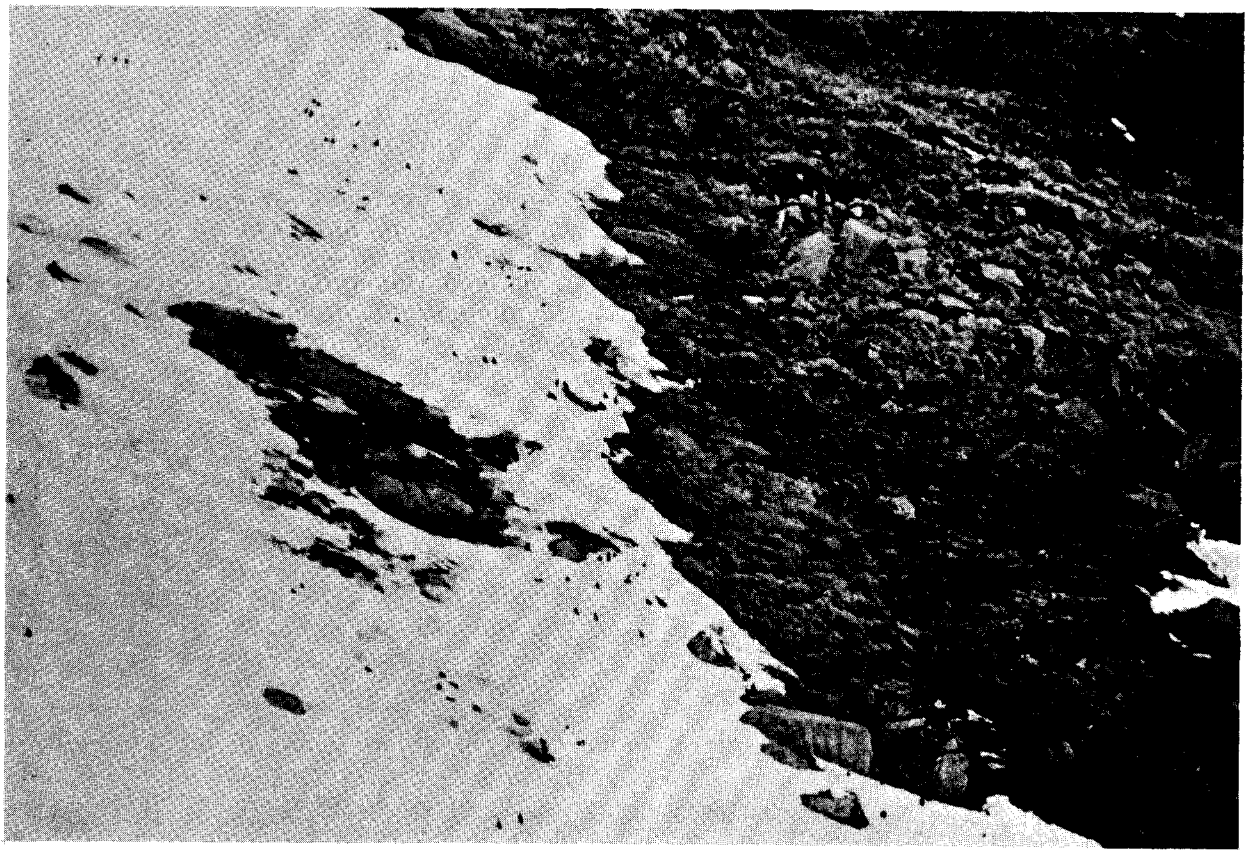


Figure 29.
King Island; the talus slope behind the village of Ukivok. The slope is blanketed with snow, yet the auklets can be seen on the snow above their burrows before the beginning of the breeding season.

there were a few murres nesting low on the wave-cut cliffs of this part of the island. Kittiwakes nested on wave-cut cliffs east of the village (Figure 22 , A-B), at several places on the southwest shore, and in an aggregation around the corner on the west side of the island (Figure 22 "H"). Horned Puffins nested in the grassy slopes between arrows 7 and 3, and in very large numbers on the grassy slopes on the southwest slopes (Figure 22 , "H-I"). Auklets nested in boulder fields on the slopes behind the village (Figure 29), and Parakeet Auklets nested in grassy slopes, especially on the southern and eastern sides of the island (Figure 22 , "C-D"). The greatest concentration of Crested and Least Auklets was among angular boulders on the highest, west side of the island.

H. Little Diomede Island

Little Diomede Island lies within the narrowest part of the Bering Strait, twenty nautical miles (37 km) west-northwest of Cape Prince of Wales, 2 nautical miles (3.7 km) east of Big Diomede Island (Figure 30), and twenty-three nautical miles (45.6 km) southeast of Cape Dezhneva, Siberia.

The island is characterized by steep sides sloping at 35° to 40° angles, a flat top about 400 meters above sea level, and a large drainage basin (area approximately 65,500 m^2) on the east side ("East Valley", Figure 31). The Eskimo village of Ignalook is at the base of a boulder fan on the northwest corner. A shallow bar extends toward Big Diomede from the town and the Eskimos say this goes most of the way to Big Diomede. The north-flowing current passing over this bar results in a rip or turbulence visible in almost any weather. It is a popular feeding area for kittiwakes.

The steep sides of the island (Figure 30) consist of a mixture of 1) rock faces, 2) vegetated slopes, and 3) talus of boulders. The major areas of talus are on the west side, 1,000 meters to the north and south of the village, and in the East Valley. The lower 30-50 meters on the sides consist of nearly vertical, wave-cut cliffs. These lower cliffs are nearly continuous around the island except for many small gullies and near Ignalook and the mouth of East Valley where the talus reaches the shore. The bedrock outcrops on the east side are more friable than the massive face on nearby Fairway Rock or the great slabs and arettes on King Island. On the north end of the island some of the vegetated slopes have poor drainage and are extremely wet. Near the southeastern corner there are large areas of bare soil. Otherwise the vegetated slopes are uniform.

The flat top of the island consists mainly of mat plants on large boulders. In general, the soil is too wet for burrow-nesting birds. Murres and kittiwakes nest mainly on the lower rock faces. Auklets nest under the boulders in the talus and puffins nest on the lower cliffs and higher bedrock outcrops. Traces of old trails were found on all parts of the island. A trail north from the town is still used and provided access to the cliffs where murres and kittiwakes nest.

I. Big Diomede Island

Big Diomede Island (Ratmanova, Siberia) appears to be generally similar to Little Diomede although much bigger, being 8.5 km from north to south (Figure 32). Clouds of auklets can be seen over the island, but Albert

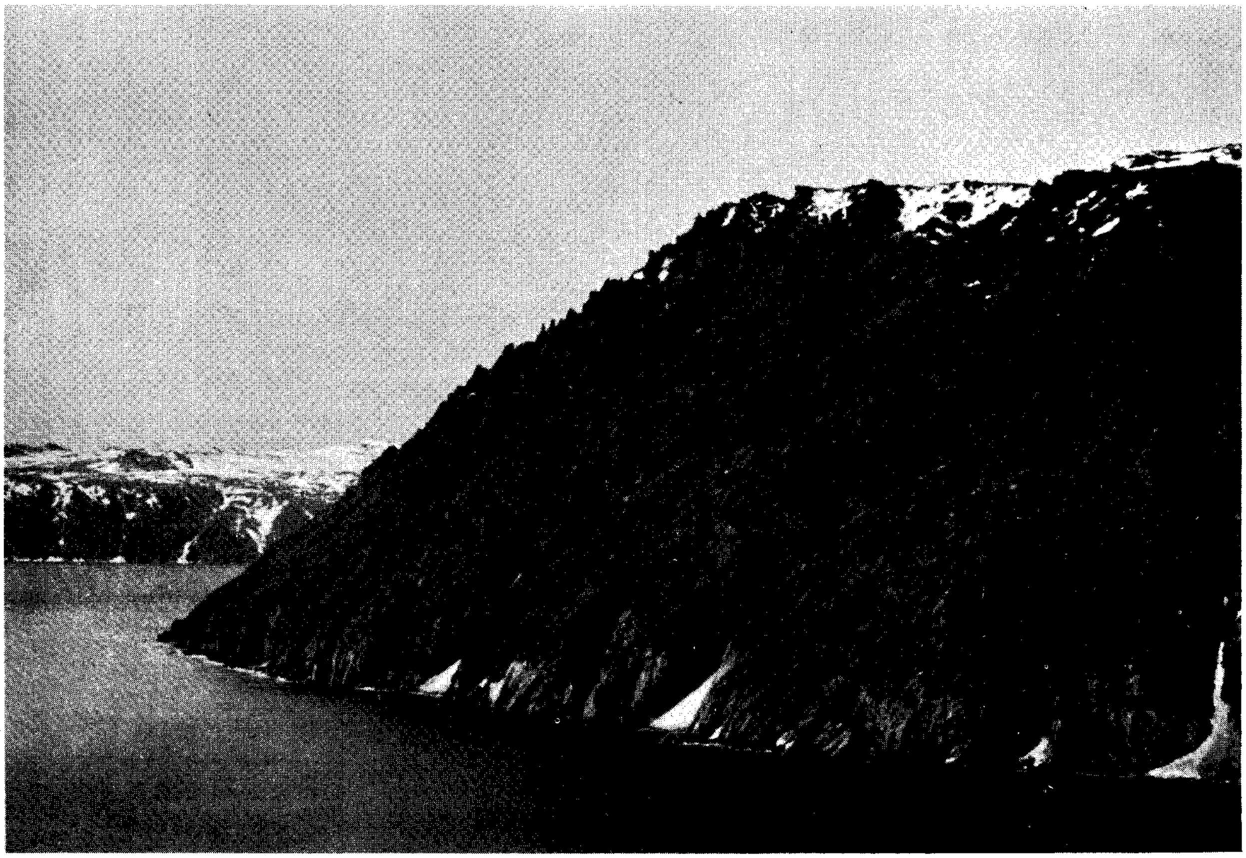
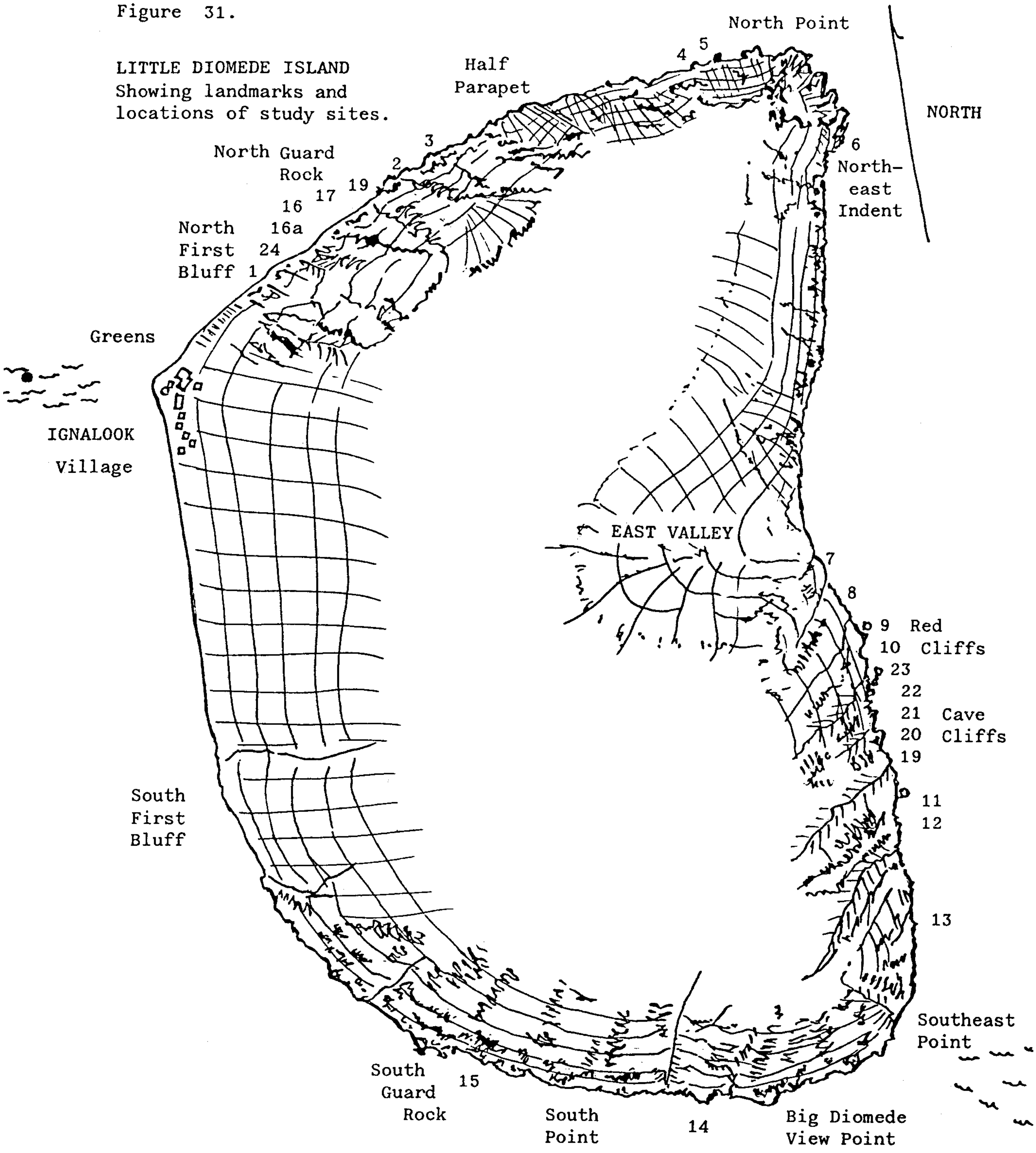


Figure 30.
Little Diomede Island; the southwest corner. Big Diomede Island is in the background on the left side of the photo.

Figure 31.

LITTLE DIOMEDE ISLAND
Showing landmarks and
locations of study sites.



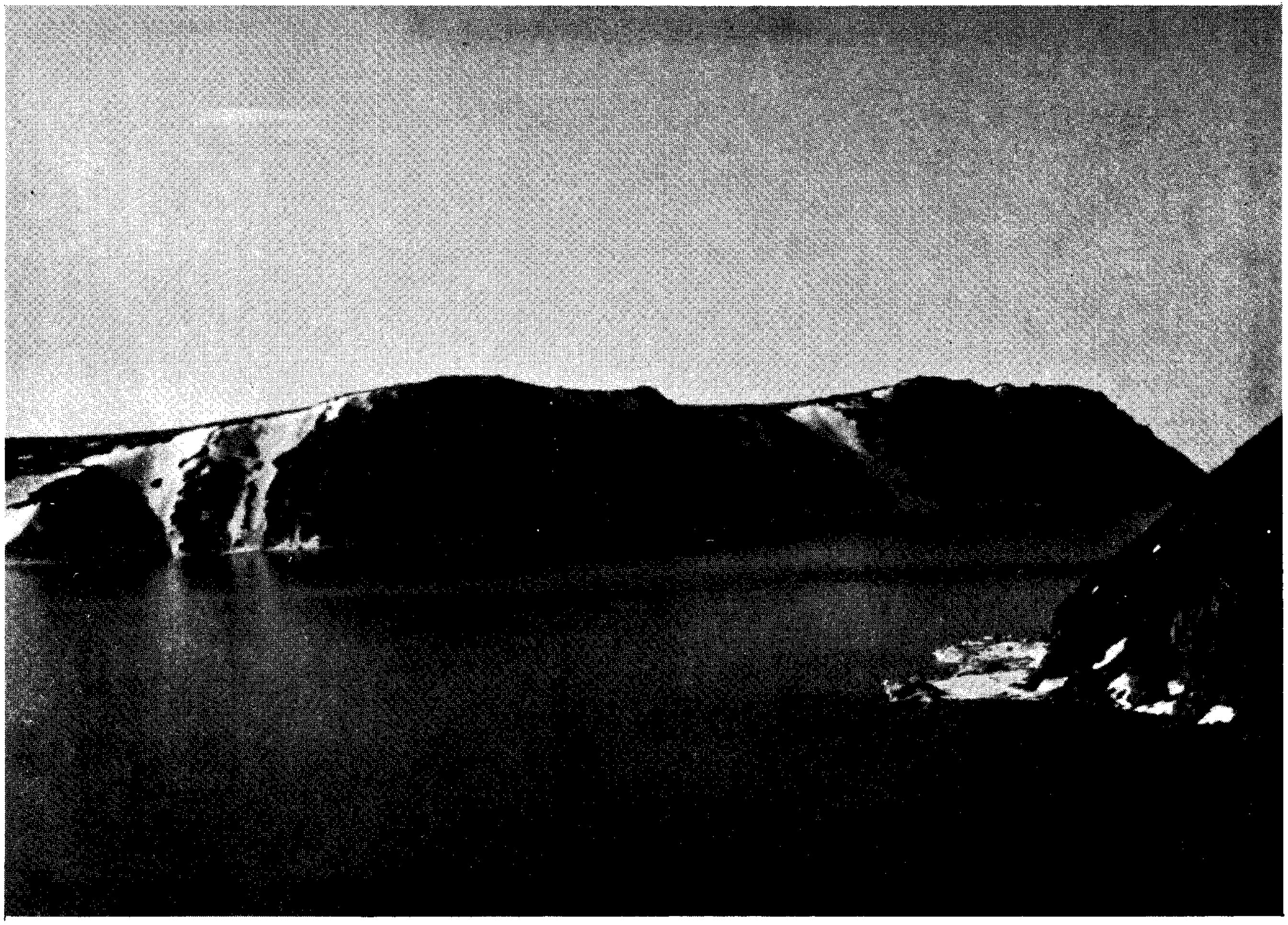


Figure 32.
Big Diomede Island with the southwest corner of Little Diomede Island in the foreground on the right side of the photo.

Ayahuk of Ignalook (Little Diomede) reported that there are significantly fewer Crested Auklets than on Little Diomede. The east side of the island (the only shoreline visible) is generally very steep and appears to have densities of nesting murres and kittiwakes similar to those on Little Diomede. A talus slope extends down to the water in the middle of the east shore of Big Diomede. The Eskimos say the slopes are gentle on the north and northwest coast.

J. Fairway Rock

Fairway Rock is a truncated cone, 534 feet (165 meters) high, 8 nautical miles (15 km) southeast of Little Diomede. The main tower is an outcrop of massive bedrock, apparently granite (Figure 33). The top and middle slopes are covered with thick grassy turf and the lower slopes are jumbles of boulders and rock faces. Populations of murres inhabit the rock faces while Least and Crested Auklets occupy burrows in the lower slopes. The grassy turf on the top appears from the air to have a dense population of Tufted Puffins and many Glaucous Gulls.

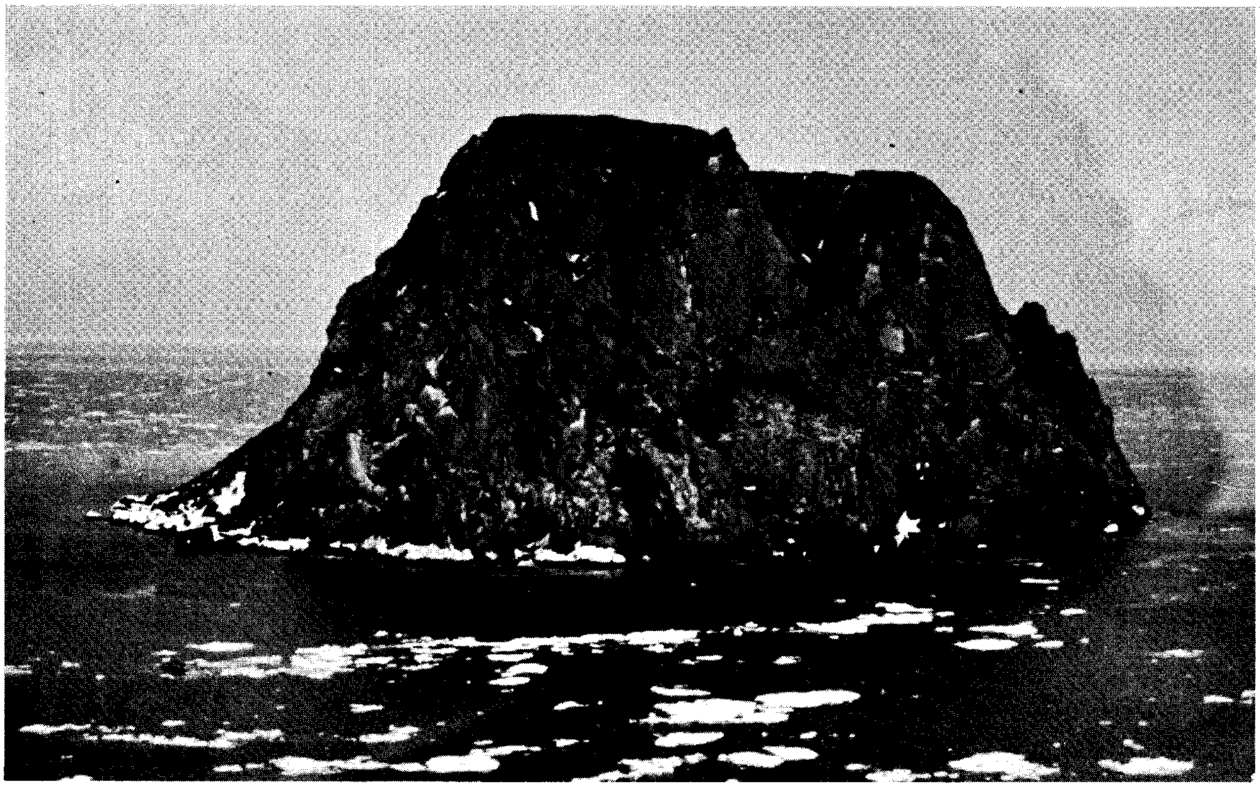


Figure 33.
Fairway Rock in June, as seen from the northwest.

APPENDIX IX.
METHODS USED AT SEABIRD CITIES

A. Bluff

Intensive studies of population sizes and reproductive efforts were conducted at Bluff by field parties of two to eight people, from May to late August or September, each year from 1975 to 1978. Short-term studies of one to three weeks' duration were conducted by Murphy (*et al*) under the aupices of this research unit in 1979 and 1980. Research activities included colony censuses, sample counts, twenty-four counts, and studies of reproductive success at the stakes; these are defined and described below. Illustrations and maps showing the locations of the study areas follow the text. Murphy used a copy of this appendix in draft form to conduct the short-term surveys in 1979 and 1980, in order to make the study areas geographically comparable.

1. Categories of Studies

a. Colony censuses were made from a small boat moving at 1-2 miles per hour, within 300 yards of the cliff. The purpose of these censuses was to count the birds at the colony.

The points which were used to separate subsections of the cliff for censusing are conspicuous and are indicated in Figures 1 and 3, by letters A through J. Each section between points was counted separately during censuses. From west to east, these are as follows:

A Metal barge at west end (Barge)

B Outside corner where cliff turns from facing southwest to facing south

C Low rock promontory shaped like an axe with grass on top (Axe)

D Promontory that looks like a castle (Castle)

C Axe
D Castle
E Thumbstack

F Arches
G Jackpole (mining camp)
H Rope Stack

I point with cavern
J Farland's Stack

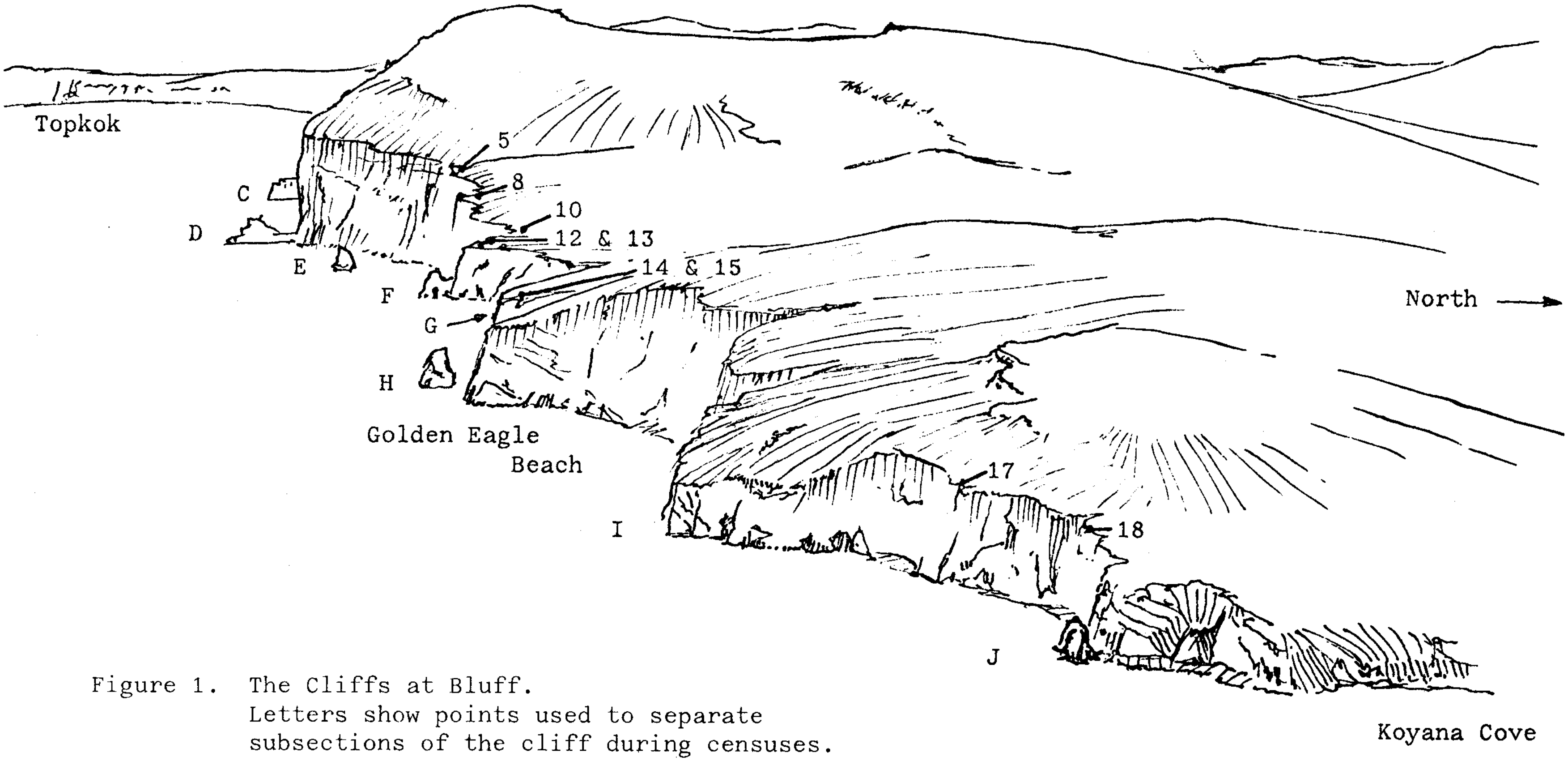


Figure 1. The Cliffs at Bluff.
Letters show points used to separate subsections of the cliff during censuses. Numbers indicate the locations of stakes from which study sites are viewed.

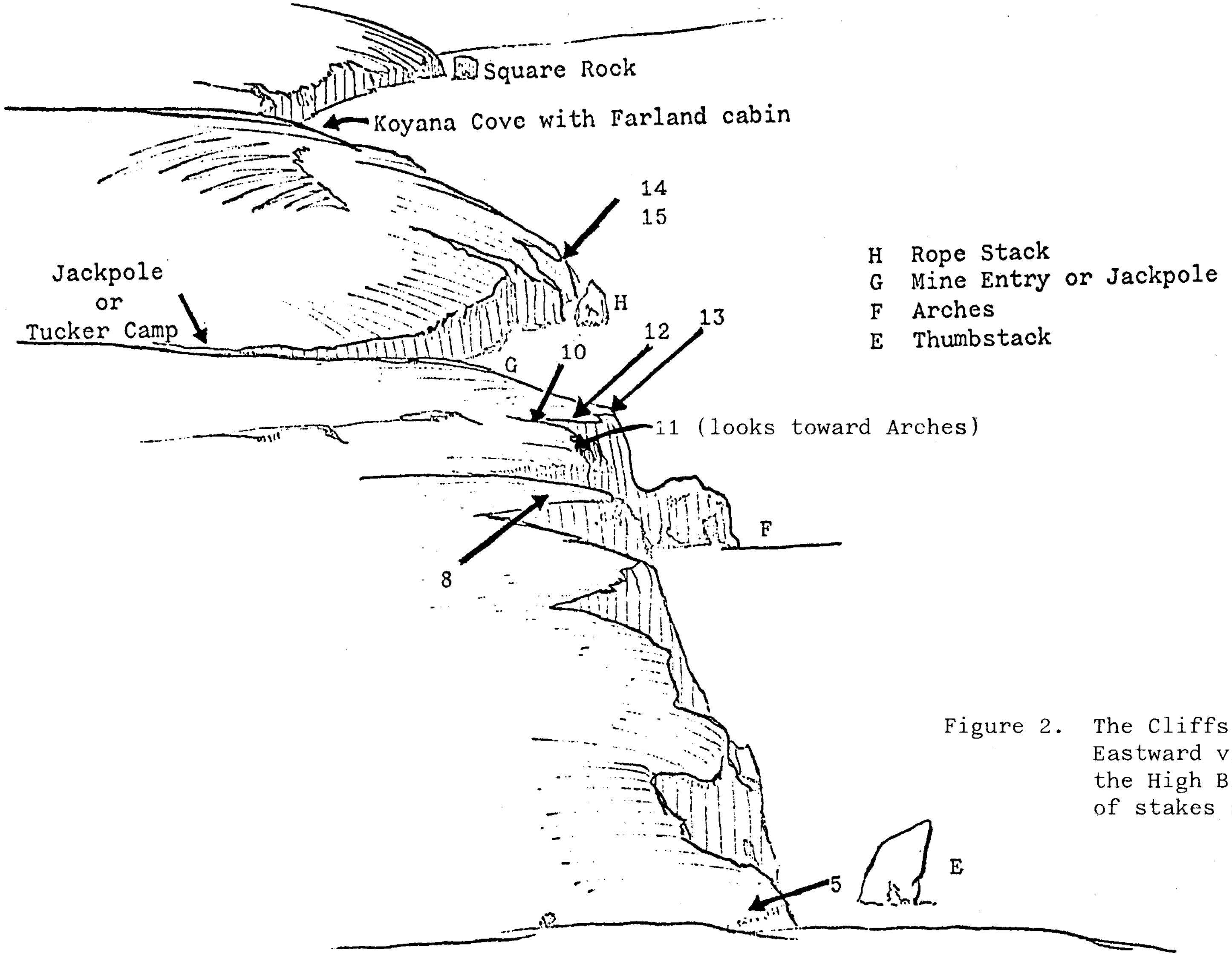


Figure 2. The Cliffs at Bluff. Eastward view from atop the High Bluff; numbers of stakes shown.

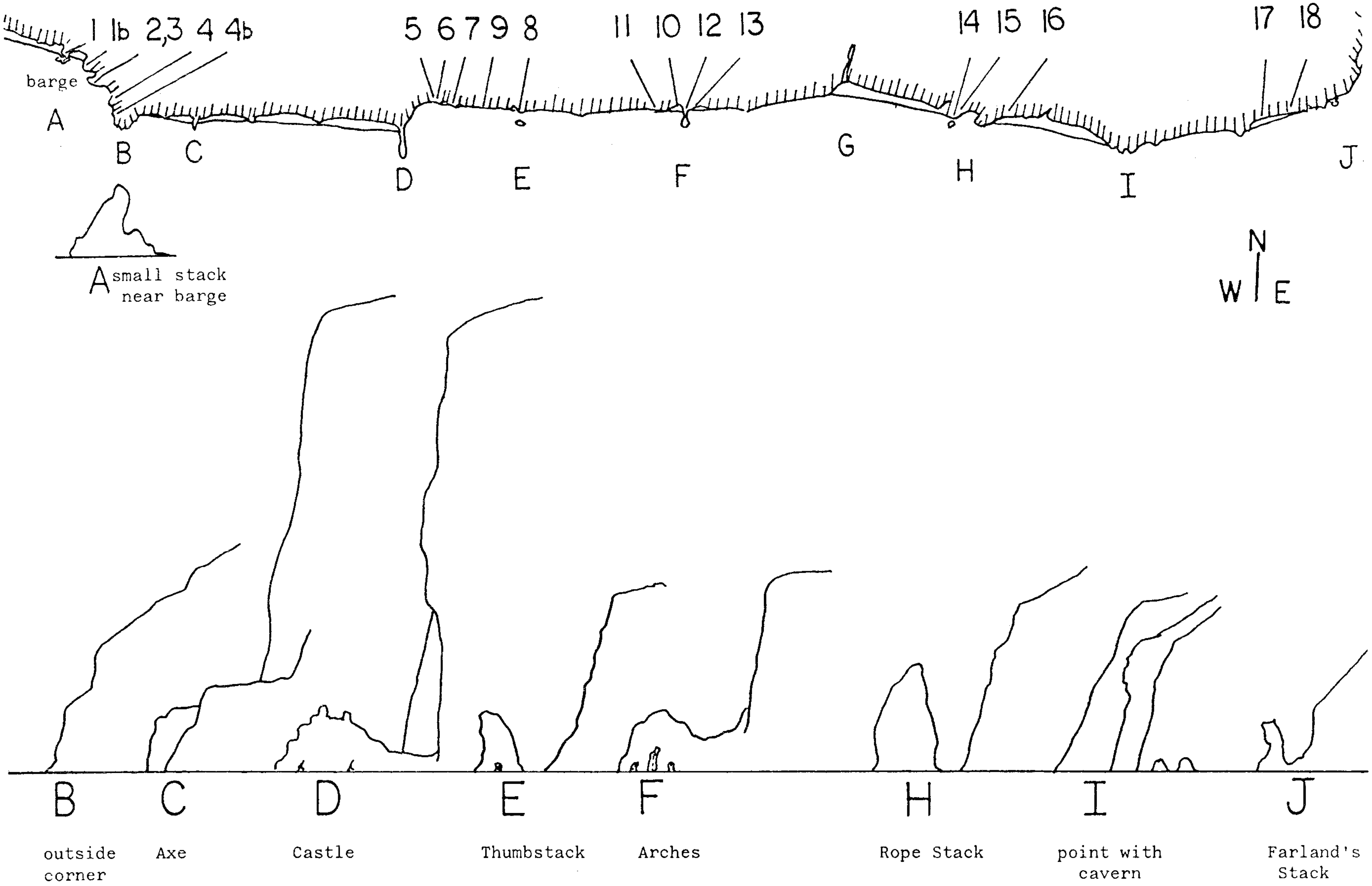


Figure 3. Conspicuous points along Bluff Cliffs used to separate cliff sections during colony censuses.

E Small rock stack shaped like a thumb (Thumbstack)

F Promontory with two natural arches under it (The Arches)

G Abandoned mining camp with a conspicuous "jack pole" and mine shafts in the cliff (Jackpole)

H Stack with a nylon rope on it used for egging (Rope Stack)

I Point with a tall, shallow cavern with a rounded roof

J Stack at east end (Farland's Stack)

We chose to census at the time of day when birds seemed most abundant (this shifted through the season). We often made more than one pass in front of the cliff. Because of wind direction we often started from the west end of the cliff; this meant we initially had to motor the length of the cliff at some distance out to sea so as to avoid disturbing the birds on the cliff.

If two people counted the same species, e.g. murres on the cliff, the highest number for each section was used in estimating population size because previous experience indicated that the higher number was more accurate. These counts were used in the diagrams of population fluctuations through the 1975-1978 seasons, and in estimates of reproductive effort and success for the entire colony.

b. Stakes were study sites located where especially good views of the cliff face were available, for the purposes of studying reproductive activities within fixed geographic areas of the cliff. These places were marked by a wooden stake driven into the ground. It is important to note that a stake marked the spot at the edge of the cliff where observers consistently sat and used telescopes, binoculars, and notebooks to make counts and record observations. Tables 1 and 2 (pages 476-480) list the types of data collected at each stake; the locations of the stakes can be seen in Figures 1-3, and in greater detail in Figures 4-53 (pages 481-528). Sample and twenty-four hour counts were made from stakes, as were studies of the reproductive success of murres and kittiwakes. In the case of kittiwakes, areas of cliff visible from the stake were mapped, and each spot where kittiwakes were perched within the map areas was numbered. Each murre stake included a mapped area divided into subsections defined by the details of topography of the cliff.

Eighteen study sites, each marked by a stake, were established in 1975. Stakes 1-4, nearest Daniels Creek, received major emphasis that year. We had to move from Daniels Creek to Koyana Creek on the opposite end of the bird cliffs in 1976. As a consequence, stakes 1-4 were largely abandoned except for the season of 1977.

c. Sample counts. Birds on four large sections of the cliff were counted from the clifftop several times through the summer for the purpose of monitoring changes in the numbers of birds at the cliffs through the season. The sections were chosen for an open view of a large densely occupied cliff face, for clear natural rock boundaries allowing easy identification of the area counted, and for spacing along the cliff. The sample-count areas were at Stakes 1, 3, 5, and 15. We made counts within 22-26 hours of when a colony census was made, so as to compare the seasonal and annual changes in numbers of the whole colony to changes in subsections of the colony.

d. Twenty-four hour counts were made of the cliff face at Stake 15 and at Square Rock to monitor changes in the numbers of birds at the cliff through the day, and to compare the changes among the days and between the two locations. These counts were made approximately every four hours for twenty-four hour periods staggered through the breeding season. The four-hour intervals between counts were timed so that counts fell before and after the period of relative darkness in the middle of the night.

2. The Studies

a. Reproductive schedule and success at kittiwake stakes. Map areas for the study of Black-legged Kittiwakes were identified on photographs of sections of the cliff. Studies were made at Stakes 8, 10, 13, 14, and 17. Individual sites within the mapped area were assigned a number for the season. Three types of attended sites were distinguished: (i) rock roost, where a bird was seen frequently; (ii) active non-nest, where a pair was seen during at least half of the visits to the stake, where new nest material was deposited but never became a nest; and (iii) nest, a substantial mud platform showing evidence of activity that season. During each stake visit, the status of the site and the numbers of adults, eggs and chicks at each occupied site were recorded. We have described the reproductive schedule based on our records of the appearance of eggs and chicks in nests in the five kittiwake map areas (see Main Body of Final Report, Section V, "The Colony of Bluff", and Appendix VI, "Major Players"). Reproductive success was determined by comparing the number of chicks produced with the number of nests built in the five map areas of the stakes.

In addition, a census of chicks along the entire cliff was undertaken during the advanced stages of the brooding period (mid-late August), when chicks in nests were large enough to be seen relatively easily. Counts were made of the numbers of nests, broods, and chicks in forty-two sections of cliff visible from the clifftop. A ratio of chicks per nest was calculated from these data and compared to reproductive success as recorded at the stakes.

b. Reproductive schedule and success at Common Murre stakes. Common Murre study areas were identified on photographs of cliff sections visible from Stakes 8, 10, 12 "inside", 12 "crack", 13, 14, and 15. Each map area was divided into subsections separated by obvious geographic features so as to include, on the average, six to eight birds. Visits to the stakes were made every two to three days, except at Stake 10 which was visited daily after hatching began. (See Appendix VI, "Major Players" for results of murre studies).

During each visit, the following data were collected for each subsection:

(1) The total number of adults in each subsection.

(2) A count was made of the number of "sitters"; these were adult murres assuming either incubating or brooding postures, described below. Assessment of whether or not a bird was a "sitter" was made only during the time it took to look briefly at each bird (five seconds or less). It should be noted that even though a bird might be assuming a "sitting" posture, it might not have an egg under it; likewise, not all eggs are covered by "sitters". We tried not to allow our knowledge of the presence or absence of an egg under a bird influence our decision of whether or not the bird was in the "sitter" posture when the sample was taken.

Among the "sitters" we recognized an "incubator" in those murres exhibiting any combination of the following characteristics:

- sitting on the ledge with "wrists" lowered close to the ledge
- edges of last secondary feathers partly spread and covering rump, but wrists not down or out
- breast pushed down, or belly flattened against the rock, breast feathers expanded, back stooped, sometimes with the neck bent back so that the bill is raised vertically and the throat is against cliff face
- guano on the back of a sitting bird
- body looks fat or inflated, but does not present characteristics associated with a "brooder" (described below)

As the breeding season progressed we defined "brooders" as separate from "incubators" as those with the following characteristics:

- assymetrical position of wings; one wrist up, one down, and the body rotated about an axis through the spinal column
- primaries on the ground and "wrist" held out away from body; a posture similar to this may be used by murres on hot days, and there may be a bias when the sun is strong; the posture of "sunning" murres has the two wings spread symmetrically.

Birds with strait spines, ventral surfaces that extend straight down to the feet, or that face the ocean were not considered to be in a posture of reproductive significance.

(3) Maps of each subsection in the map areas were drawn during each visit to a stake. Individual murres were represented by circles; each circle was given an "E" for the association of an egg with the bird, a "C" for chick, an "X" for nothing, or was left blank if we could not see under the bird. At Stake 10, each chick was identified by a letter on the map. In this study we concentrated on determining the number of chicks hatched, lost or fledged in each subsection, and spent little time on locating eggs. We had found in 1975 and 1976, that we spent a lot of time for few data in trying to locate eggs during incubation. We are more confident about the number of chicks produced than the estimated number of eggs hatched.

The number of chicks produced in each subsection at other stakes was calculated as the number of chicks "C" which appeared at one spot on the maps of the subsection for at least fourteen days. We assumed the average time a chick spends on the ledge to be eighteen days. As chicks may have been two to four days old before they were first seen, we calculated chick loss on the disappearance of chicks believed to be less than two weeks old. Chicks disappearing after having been seen on a ledge over a period of fourteen days or more were considered fledged.

The number of breeding pairs of murres was estimated by relating the average number of "sitters" to the average total number of adults at the stakes during the hatching period (a time of minimal fluctuations in the total number present). The number of chicks produced at each stake was then related to the estimated number of breeding pairs, resulting in a ratio of reproductive success, or the number of chicks produced per breeding pair.

c. Trophic studies: murres and kittiwakes. We entered remarks in field notebooks on feeding aggregations seen from land, and on fish brought to the cliffs. Stomach contents of murres and kittiwakes were collected from birds shot in August 1978.

d. Horned Puffin. We censused puffins along the coast between Topkok Head and Rocky Point periodically through each season; the results of these censuses are in annual reports. We made counts of puffins regularly for a month at Stake 18 in 1978 to determine seasonal and daily variations in attendance at the cliff. Unfortunately, the erratic attendance of this species requires that counts be conducted frequently through the day over a period of days; our sample counts were not done frequently enough to draw conclusions from the data. We obtained a little information on puffin reproduction gathered by peering into burrows visible from the top of the cliff.

e. Pelagic Cormorant and Glaucous Gull. We included Glaucous Gulls and Pelagic Cormorants in colony censuses through the season. Each season we located and monitored nests of both species, keeping track of the number of eggs laid, lost and hatched, and the number of chicks fledged. This work was not done as regularly or as carefully as the work on murres and kittiwakes.

f. Predators. An extensive study of predators was conducted in 1977. No special studies were made in 1975, 1976 and 1978, but notes on occurrence and reproductive success of Golden Eagles, falcons and Rough-legged Hawks were summarized. The species present included: Ravens, Glaucous Gulls, Foxes, Golden Eagles, Gyrfalcons, Peregrine Falcons, Rough-legged Hawks, Harriers, and Long-tailed Jaegers.

B. Square Rock

Counts of birds at Square Rock were made through the season and included birds on the water, on the sides and top of Square Rock itself, and on the adjacent mainland cliff. Studies of reproduction were made as at Bluff, by sitting on the mainland and peering down at the north side of Square Rock, and by sitting just west of Square Rock and looking at a section of mainland cliff and the west side of Square Rock (Stake 19). One murre and one kittiwake study area each were established, and count areas were outlined. Data were collected about every three days during 1976, 1977, and sporadically in 1978.

C. Topkok Head and Rocky Point

Visits were made to both Topkok and Rocky Point in August of 1976, 1977 and 1978. We counted the birds at Topkok in July, August and September 1975, on our commuting runs between Safety Lagoon and Bluff. Counts were made of all seabirds seen on these trips, and sample counts were made of nests and nest contents of Pelagic Cormorants and Glaucous Gulls, for estimates of reproductive success. Results appeared in annual reports. Our results are not very precise because we made single visits and different observers used different techniques. We suggest censuses be made more than once each season, weather permitting.

D. Sledge Island

Small parties went by boat to Sledge Island from Nome each year. Tents were set up behind a wind break on the gravel spit. Censuses of the seabirds were conducted, as well as visits to two study sites to sample reproductive success of Pelagic Cormorants and Black-legged Kittiwakes. A partial collection of the flora of the island was made.

Table 1. Data collected at each stake at Bluff Cliffs.

Stake Number	Murre Count	Kttwk Count	Puffin Count	Kttwk Map	Murre Map	Crmnt Nests	Gull Nests
1	X	X					X
1b					X		
2					X		
3	X	X		X			
4	X			X			X
4b				X			
5	X	X		X			X
8				X	X		
10				X	X		
11	X	X					
12 crack					X	X	
12 inside					X		
13				X	X	X	
14				X	X		X
15	X	X			X		
17				X			
18			X				X
Square Rock	X	X		X			X
19				X			

Table 2. Types of data collected at stakes at Bluff Cliffs, 1976-1978

SAMPLE COUNTS:	Species	Areas in which to count
Stake 1	i) murres	A) count upper crack B) above crack (upper) C) below crack
	ii) kittiwakes	A) above upper crack (upper) B) between cracks (middle) C) below lower crack (lower)
Stake 3 outer face	i) murres ii) kittiwakes/nests iii) cormorants/nests	Count entire outer face, all that is visible until view is obscured by inner face.
West of the Axe from above	i) murres ii) kittiwakes/nests	West toward the outer corner marked on drawing of High Bluff, view west to east).
Stake 5	i) murres ii) kittiwakes/nests	Count to the left of crack marked on photo, to vegetation.
Stake 11	i) murres ii) kittiwakes/nests	Two photos should be placed side by side, cliff on left, west side of arches on right to show entire face to be counted. Count is entire face from edge of Arches on right as far as vertical crack indicated in far left of cliff photo.
Stake 15	i) murres ii) kittiwakes/nests	Count entire far face to left as far as vegetation in cove.
Stake 18	i) Horned Puffins ii) Tufted Puffins iii) Parakeet Auklets	Count by standing at Stake; count cliffs to east, cliffs to west, birds flying and on water.
Square Rock	i) murres ii) kittiwakes/nests	Count on west side of Square Rock; area outlined on Stake 19 photo. Make count from mainland above Stake 19.
TWENTY-FOUR HOUR COUNTS:		
Stake 15	i) murres ii) kittiwakes/nests	Count entire far face to left as far as vegetation in cove.
Square Rock	i) murres ii) kittiwakes/nests	Count upper section of north side of Square Rock as seen from mainland stake. (see Figure 51, page 526.)

Table 2. (Continued)

BLACK-LEGGED KITTIWAKE STAKES: Locations of mapped areas for monitoring of individual sites on the cliff.

Regular:

Stake 8	Upper section of cliff on inside of the cove, mapped area outlined on photo.
Stake 10	Upper section of outer edge of cliff face adjacent to Arches west side.
Stake 13	East side of the Arches, mid-section of the inside arch, top of arch to sea level.
Stake 14	North side (inside) of Rope Stack; upper middle section, right of the rope.
Stake 17	Lower middle section of cliff section that faces east, characterized by a vertically flat rock face with "V" crack located in the middle of the kittiwake map area.
Square Rock	North side (inside) of Square Rock, one-third to half way up the side of the rock.

Occasional:

Stake 3	Inner face, low section outer edge. Detailed studies in 1975.
Stake 4	All sites to right of line drawn in photo. Detailed studies in 1975, 1977.
Stake 4b	Area is shown in two photos: 1) left side; all sites to right of crack, and 2) right side; all sites to left of another crack. Detailed studies in 1975, 1977.
Stake 5	To right of sample count area.
Stake 19	On mainland, located west of Square Rock; cliff faces west, observer looks east; area posed around outer crack.

CORMORANT NESTS: Studies made in 1977 and 1978.

Between Jackpole and Stake 13 are two stakes driven into the ground; two nests should be visible from each stake by looking west along cliff.
Two more nests are visible by walking out on point west of Stake 13 in line with Stake 12, with the Arches directly below; look east, back toward the cliff.

Table 2. (Continued)

COMMON MURRE STAKES:	Locations of mapped areas; each section divided into small mapped areas for study, divided according to geography.
Regular:	
Stake 8	Immediately left of kittiwake map area.
Stake 10	Long horizontal crack of murres, left of kittiwake map area, located on inner cliff face adjacent to west side of the Arches.
Stake 12 crack	A long horizontal crack high on cliff underneath Stake 10 viewing spot; crack is on cliff facing Stake 10 murre and kittiwakes areas.
Stake 12 inside	Lower and to the left of 12 crack.
Stake 13 east	Viewed from a spot east of Arches (stake in ground is not like other wooden stakes), along edge of cliff west of the Jackpole and 30-50 yards east of Stake 13 or the Arches.
Stake 14	On north side (inside) of Rope Stack, below kittiwake map area, mid-way up the stack.
Stake 15	On nearest cliff face, to the left of and adjacent to the Stake 14 viewing spot. Two photos are used; "upper" shows area 1, a shelf of murres; the other, "lower", is viewed by looking down from area 1.
Occasional:	
Stake 19	On mainland, looking east toward Square Rock in immediate background; murre areas located to left of kittiwake area.
THICK-BILLED MURRE:	
Stake 2	Area outlined at the top of the major horizontal crack.
Stake 15	Far face, outer section, low on cliff. Group of Thick-billed Murres mapped in 1977, indicated in photo titled "Stake 15 far face outer section TBM".

Table 2. (Continued)

PUFFIN BURROWS: Visible from top edge of the cliff.

East and West of Stake 19, 9 visible from cliff edge must be learned by experience).

East of Rope Stack; walk out on top of the east face at Stake 15 and look back, west, into the cove between Stake 15 near face and far face.

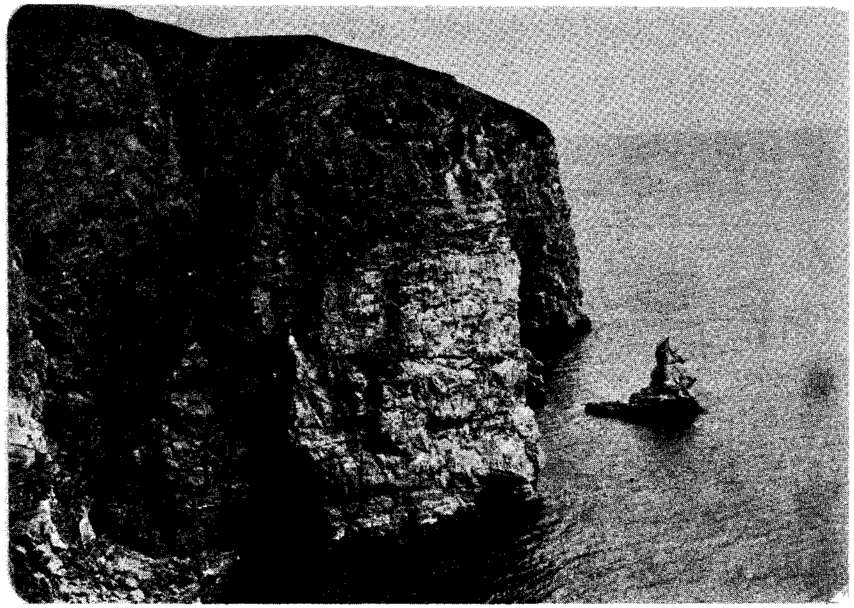
West of Stake 14 (Rope Stack); found three in 1978, between ravine next to Stake 14 and the Jackpole - precarious viewpoints...).

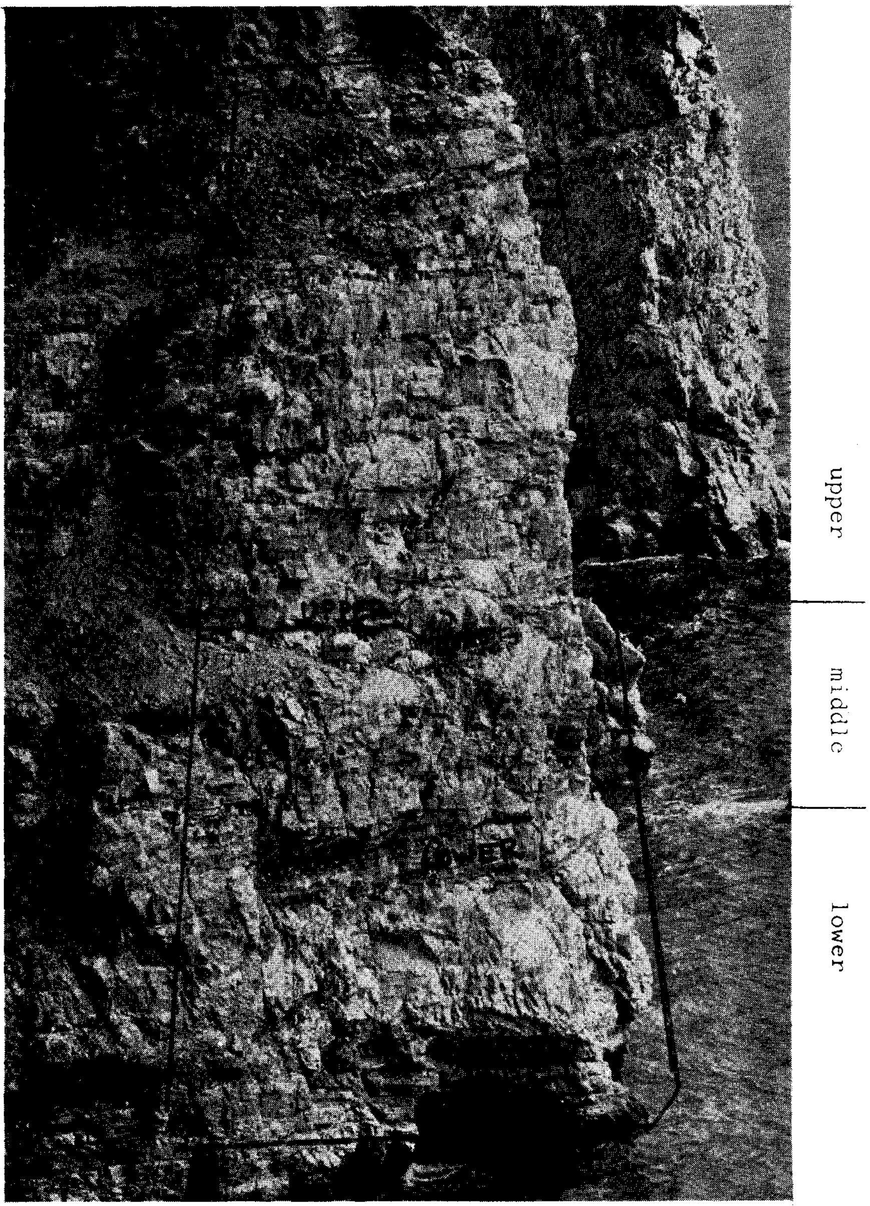
GLAUCOUS GULL NESTS:

1 on stack above the Barge below Stake 1.
1 or 2 across from Stake 4.
3 on the Castle.
2 or 3 below Stake 5.
1 on top of Rope Stack, seen from Stake 14.
1 on top of Farland's Stack, seen from just east of Stake 18.
8 on top of Square Rock.

Figure 4.
Stake 1; looking east. Sample counts. Murres: (a) count upper crack, (b) count above upper crack, and (c) count below crack. Kittiwakes: (a) count above upper crack, (b) count between upper and middle cracks, and (c) count below lower crack. Gulls: check nest on stack above the Barge below Stake 1.

Figure 5.
View of cliff section where Stake 1 is located.





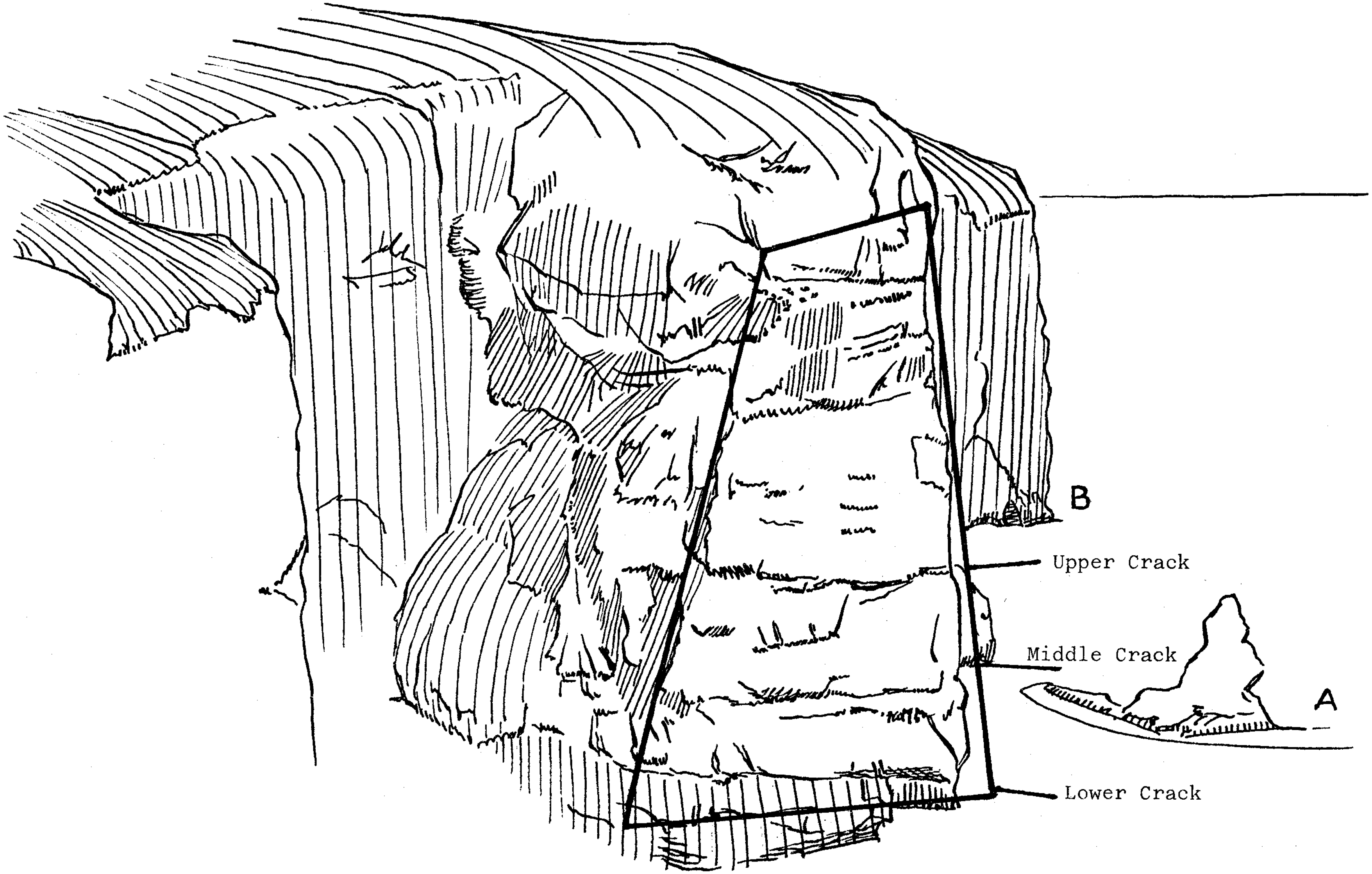


Figure 6. Drawing of Stake 1, showing location of Sample Count areas, and upper, middle and lower cracks.

Figure 7.
Stake 1B: section of cliff where murre map area occasionally studied (see Figure 8).

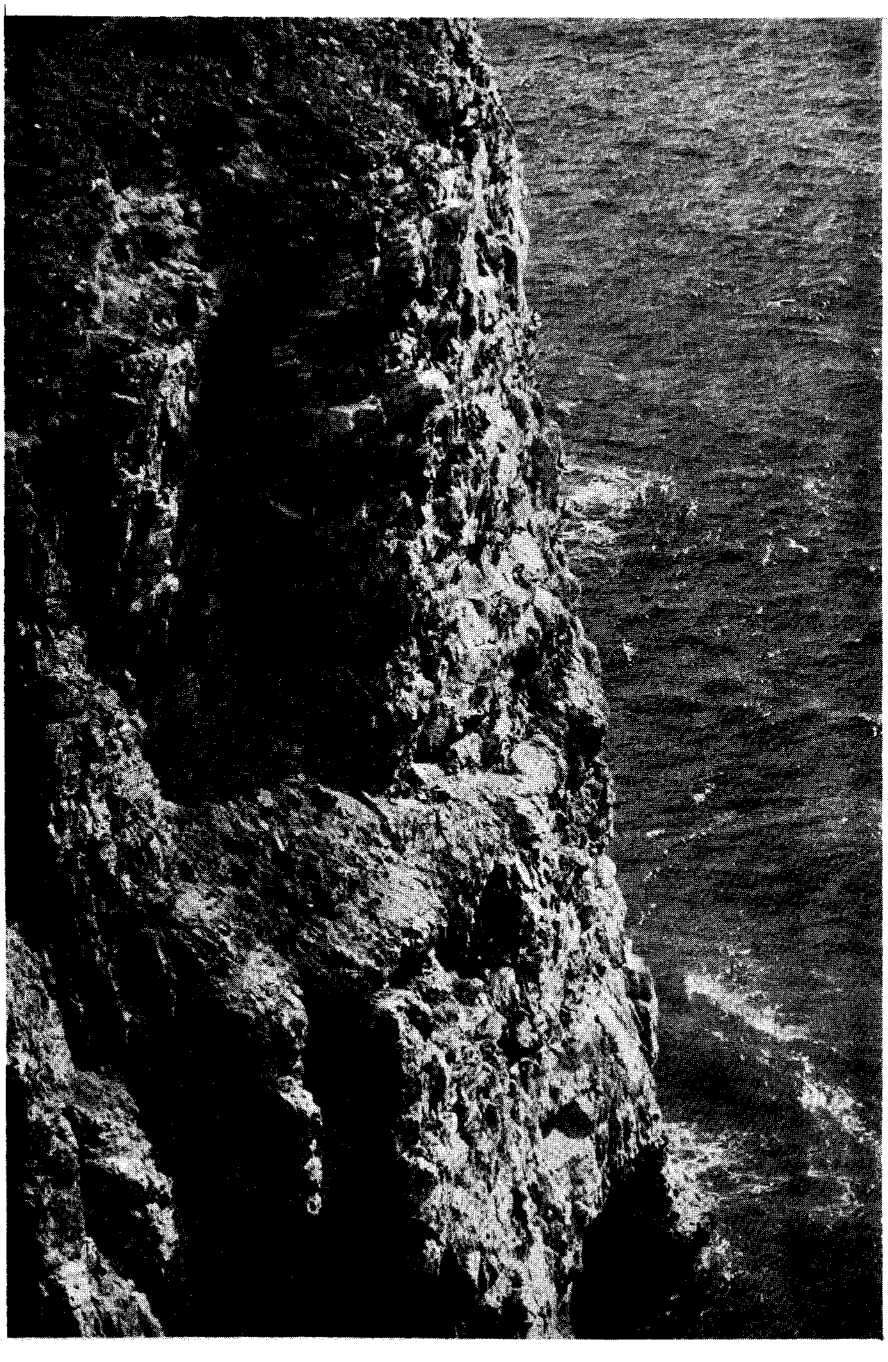


Figure 8.
Stake 1B: Murre map area: crescent, shelves and ledge; studied occasionally.

Figure 9.
Stake 2, looking west. Thick-billed Murre map area is outlined.

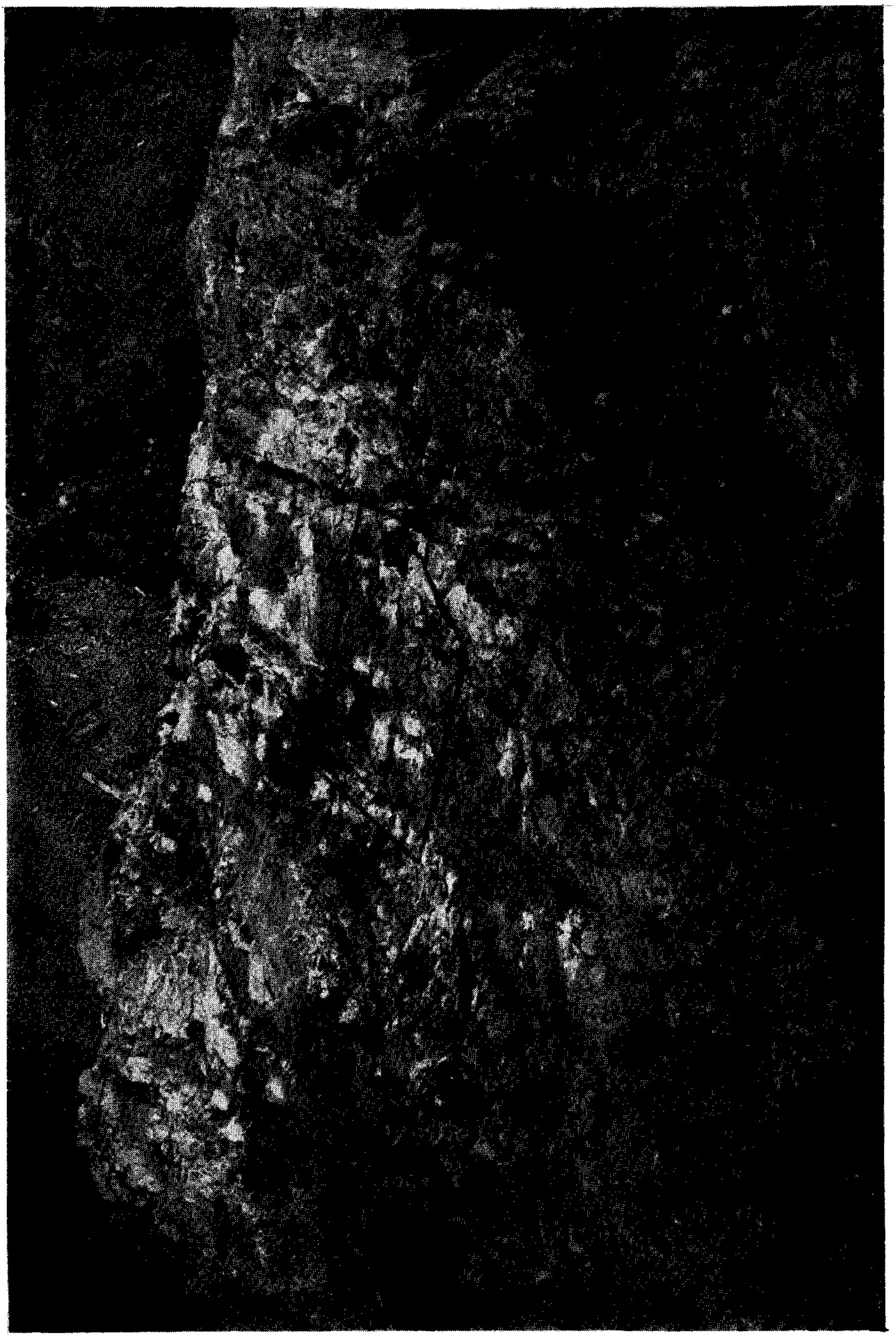


Figure 10.
Stake 3, looking east; shows outer face where sample counts are and inner face where kittiwake map area is located. Photo taken in 1975, before the face of the near cliff collapsed.

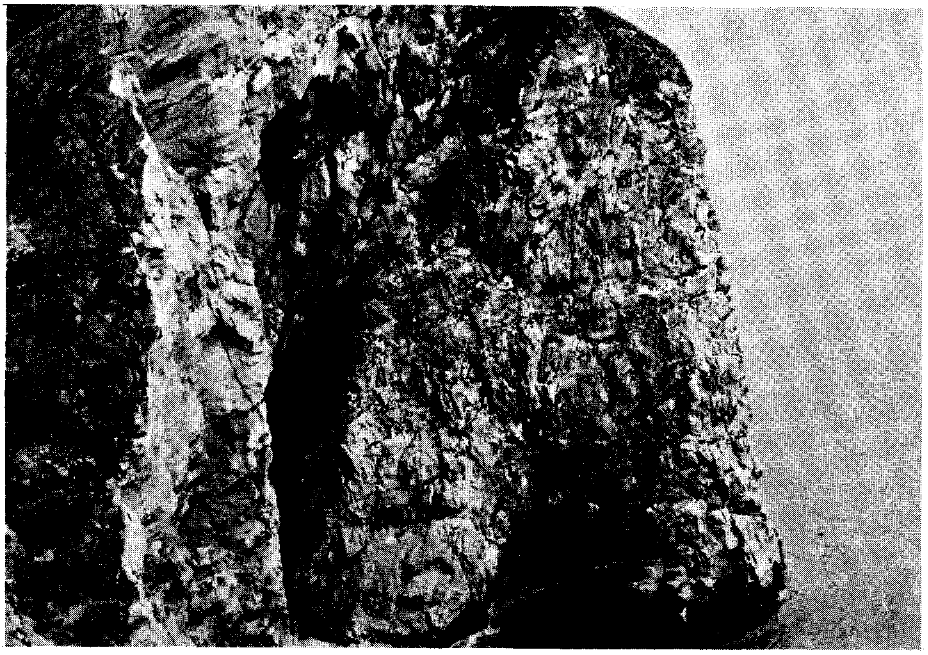


Figure 11.

Stake 3, looking east. Sample counts: count all murres, kittiwakes, kittiwake nests, cormorants and cormorant nests on the entire outer face, all that is visible until view is obscured by inner face.

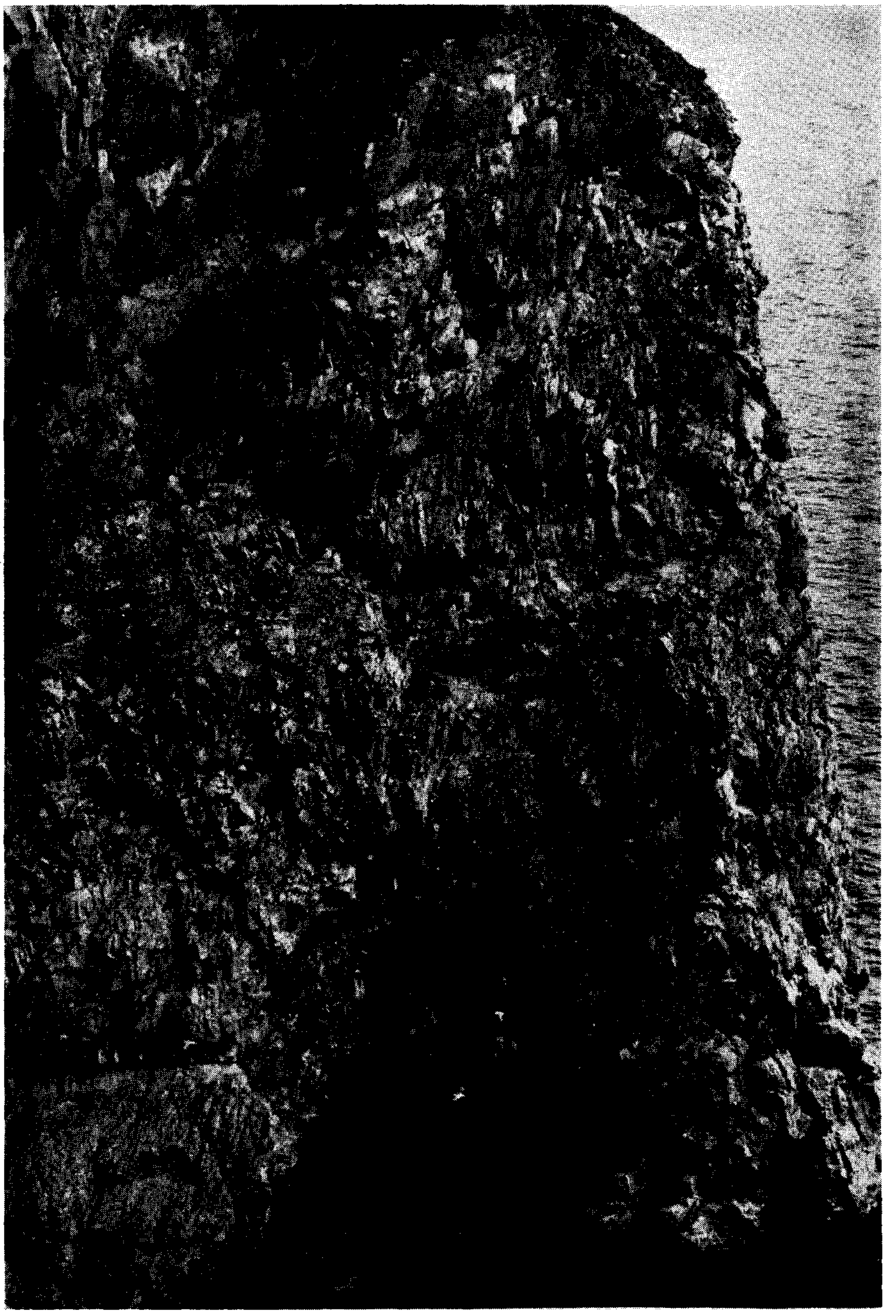


Figure 12.

Stake 3, looking east. Kittiwake Map Area: 1977: located on inner cliff face, low section, outer edge (studies occasionally through season). Studied in detail in 1975, before cliff face collapsed.

Figure 13.
Stake 3, as seen in 1975 and 1976, before the cliff face fell away as in the previous photo, Figure 12 , in 1977.

Figure 14.

Stake 4, looking down and west to opposite, far face.

Kittiwake Map Area: includes all occupied sites to the right of the line.

Glaucous Gulls: check 1 or 2 nests across from Stake 4, above and to the right of area shown on the photograph.

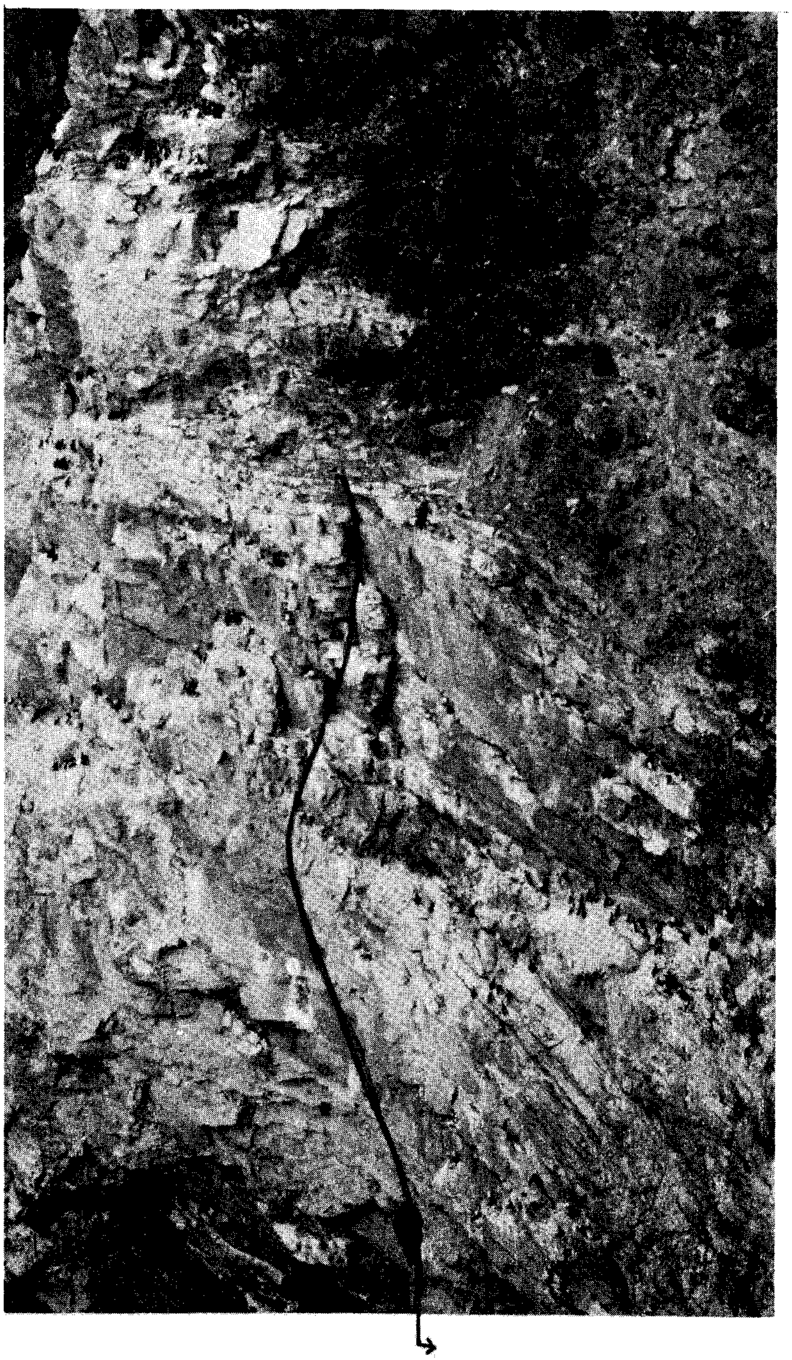


Figure 15.
Stake 4b, looking west and east.
Kittiwake Map Area: located between two cracks indicated below.

Figure 16.
View from above the Axe looking west toward "outer corner", or "B" (Figure 3).
Sample Count: count murres, kittiwakes, kittiwake nests on entire face [toward the outer corner].

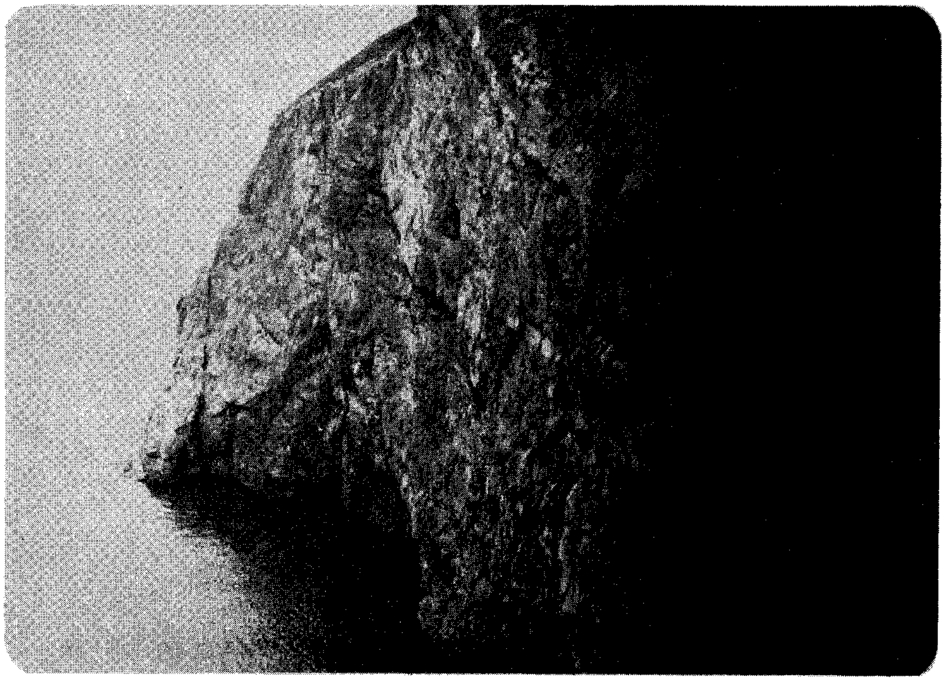
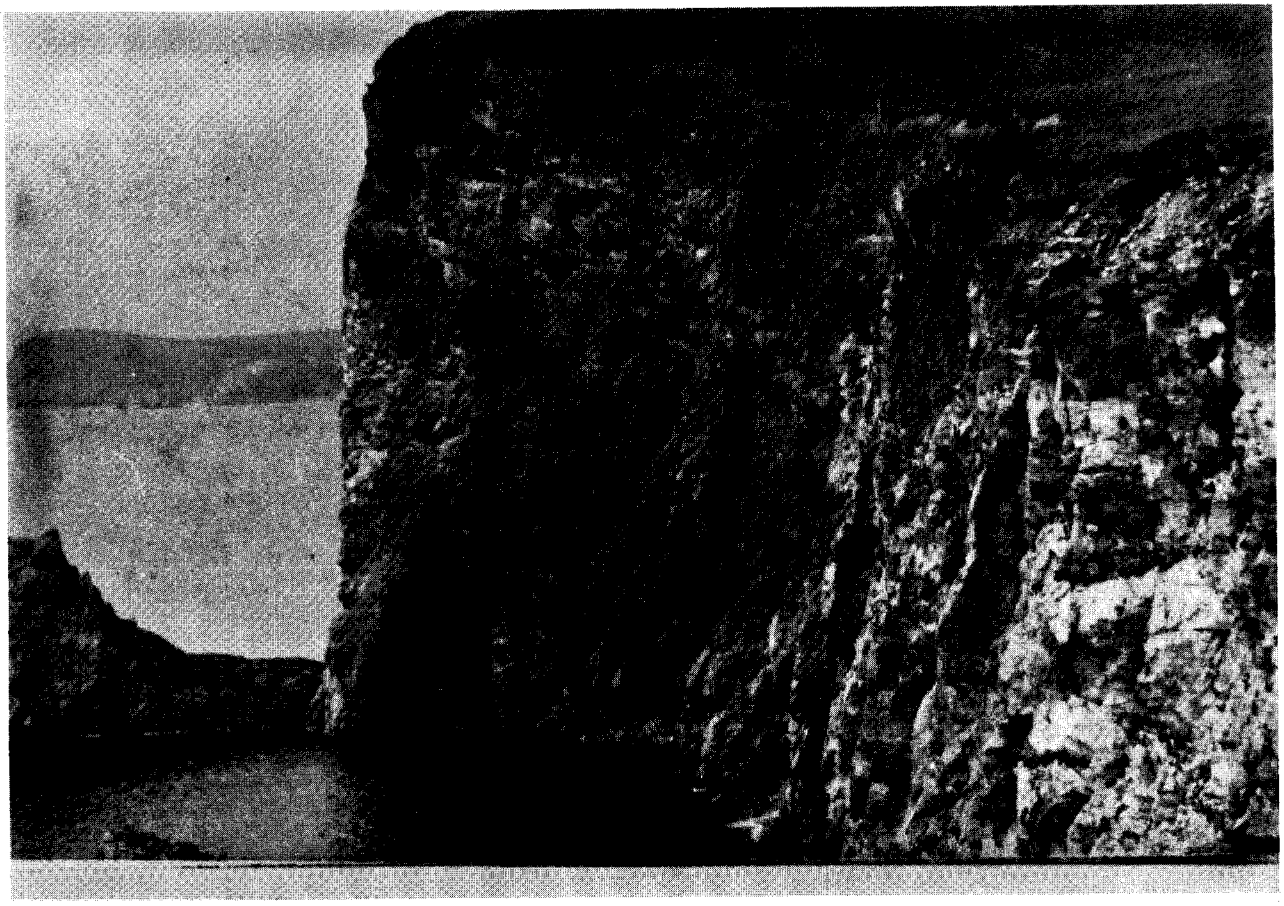


Figure 17.
View west from Stake 12, used here as a "context" photo. The Castle promontory is on the lower left, Topkok Head is in the distance on the left (above Castle), and Stake 10 can be seen in the upper right corner.

map area of Stake 5 below (see Figures 20 & 21)

stake of Stake 10



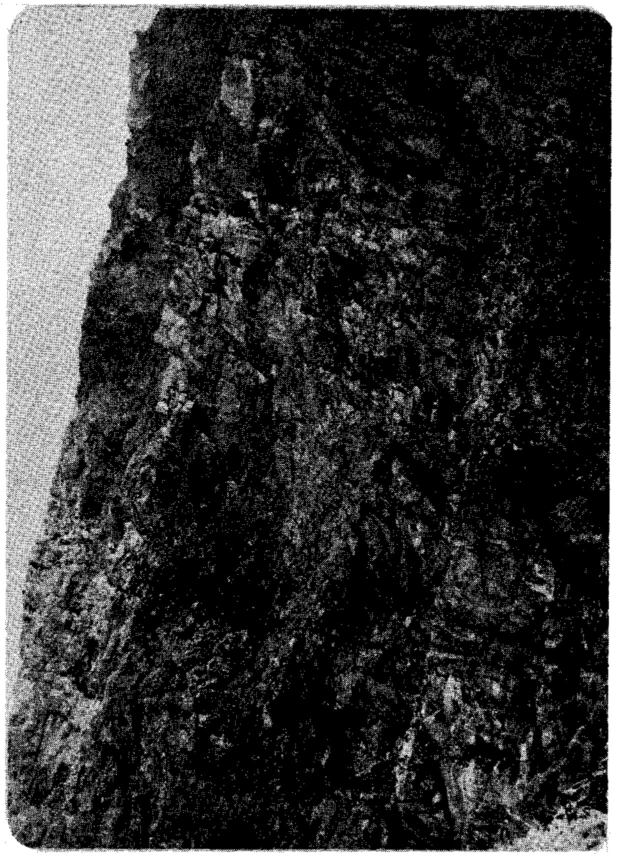
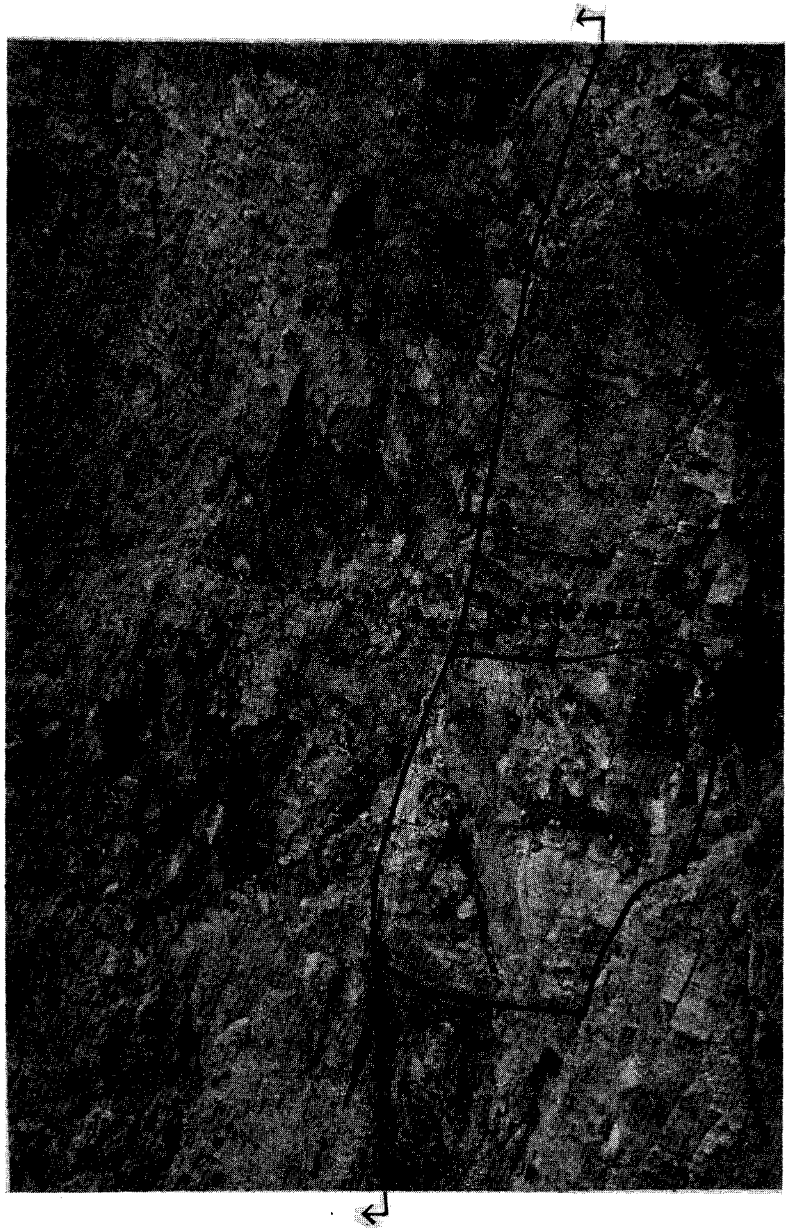


Figure 18. Stake 5 Sample Count Area.

Figure 19.
Stake 5, looking west toward Castle.
Sample Count: count murres, kittiwakes, and kittiwake nests to the left of the crack indicated. Kittiwake Map Area is outlined, to the right of the sample count area (see Figures 20 and 21).



count to the left of this crack
for sample count

Figure 20.
Stake 5; drawing of Sample Count area.
Kittiwake map area is located
to the right and below the
grassy area indicated here.

Figure 21.
Stake 5 Kittiwake Map Area; close-up photo.

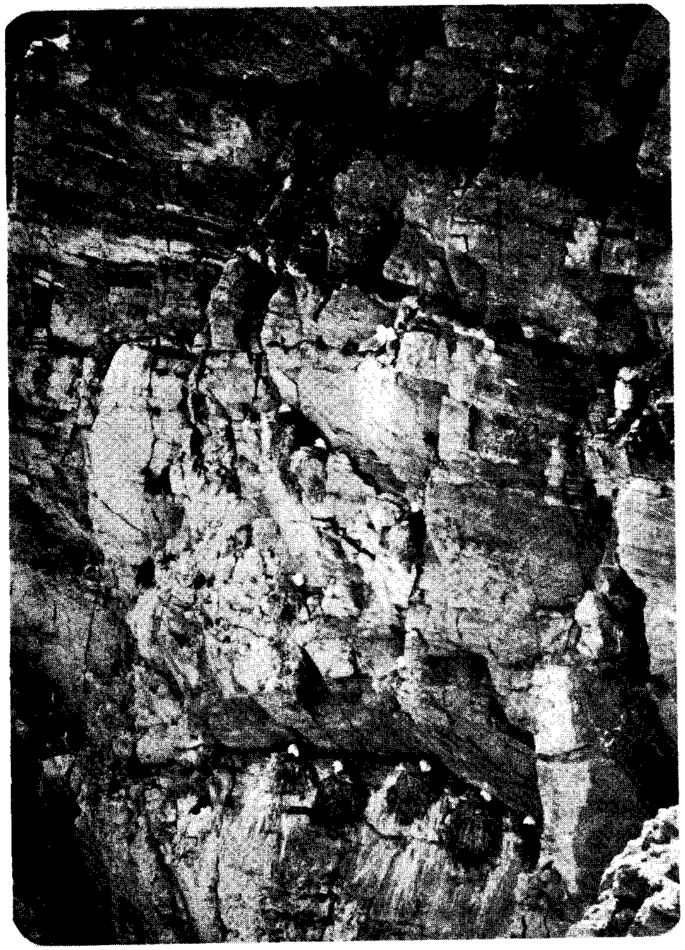


Figure 22.
Stake 8, looking west. Murre Map Area: on cliff face facing south (not east), map area is shown with subsections outlined. The kittiwake map area is to the right (see next figure).

Figure 23.

Stake 8, looking west. Kittiwake Map Area: map area is on cliff facing east, close to the inside of the cove and close to the top of the cliff. (Murre map area is to the left and below).

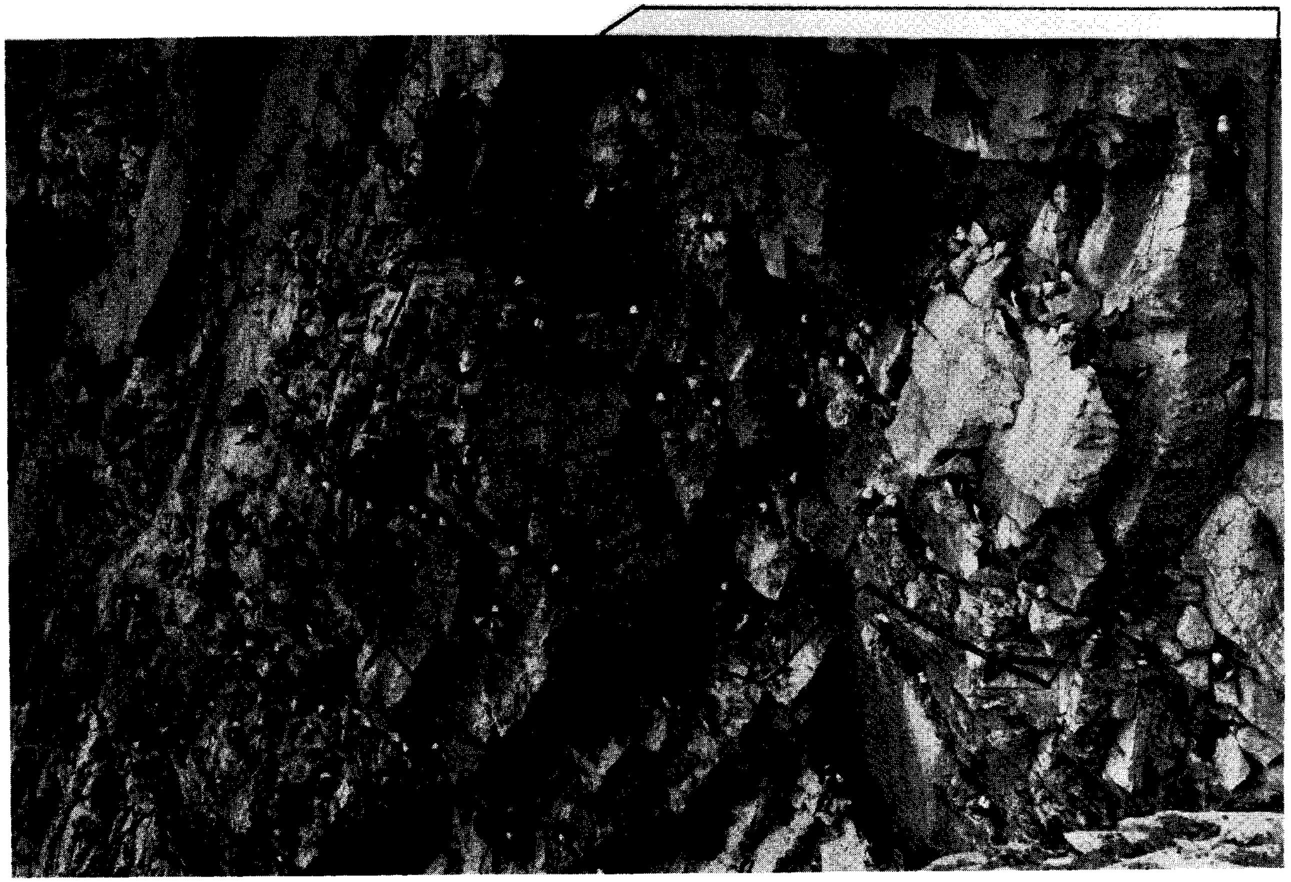


Figure 24.
View from Stake 9, used as a "context" photo here; arrows indicate the locations of Square Rock, Stake 14, the outer edge of the Rope Stack, the west side of the Arches, and Stake 10. View is looking east.

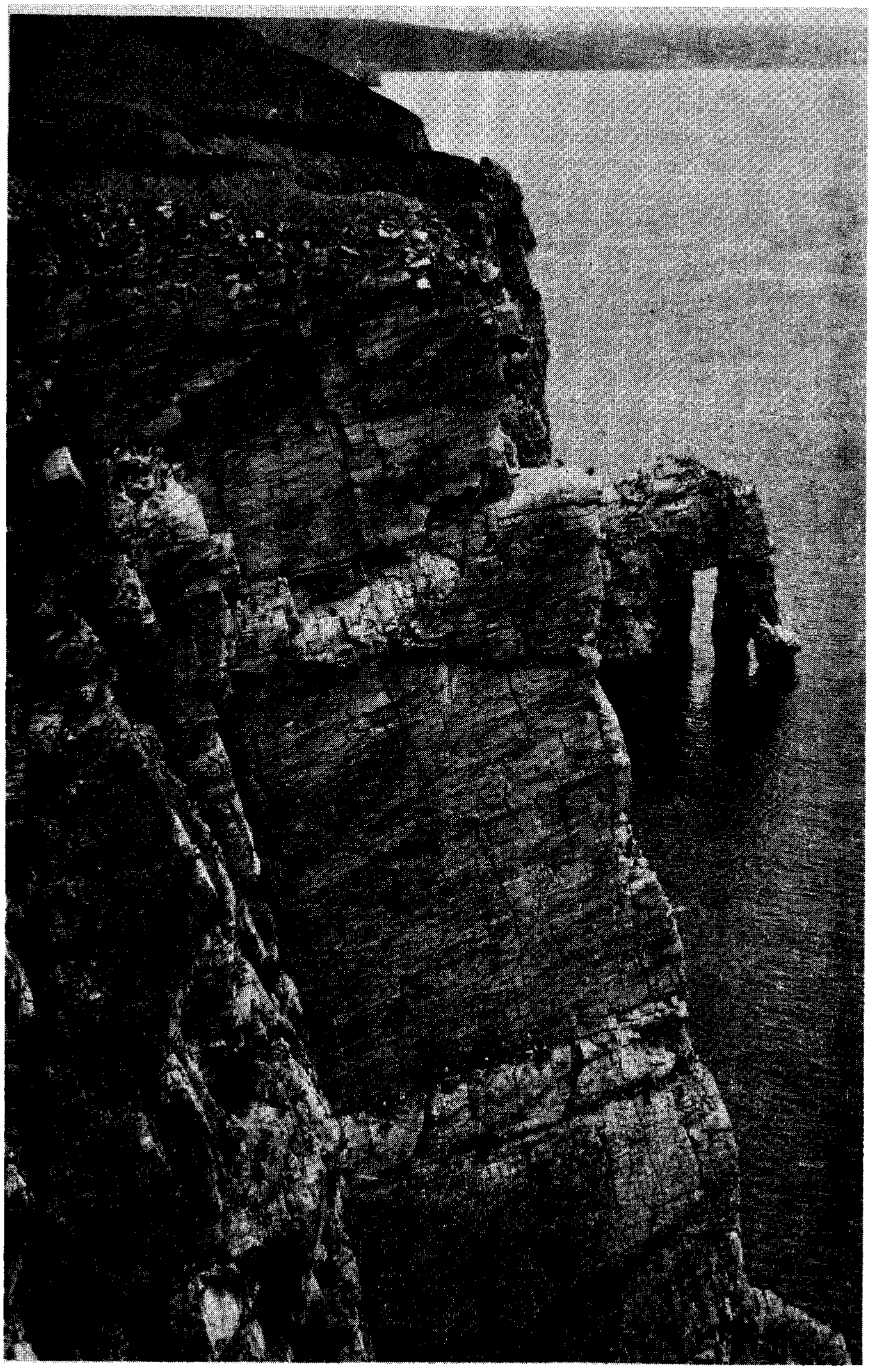


Figure 25.

Stake 10, looking east. Murre Map Area: long, horizontal crack of murres, located on the inner cliff face adjacent to the west side of the Arches, to the left of the kittiwake map area; also shown in Figures 26, 27, & 28.

Figure 26.
Stake 10, looking east. Murre Map Area close-up: subsections are outlined.

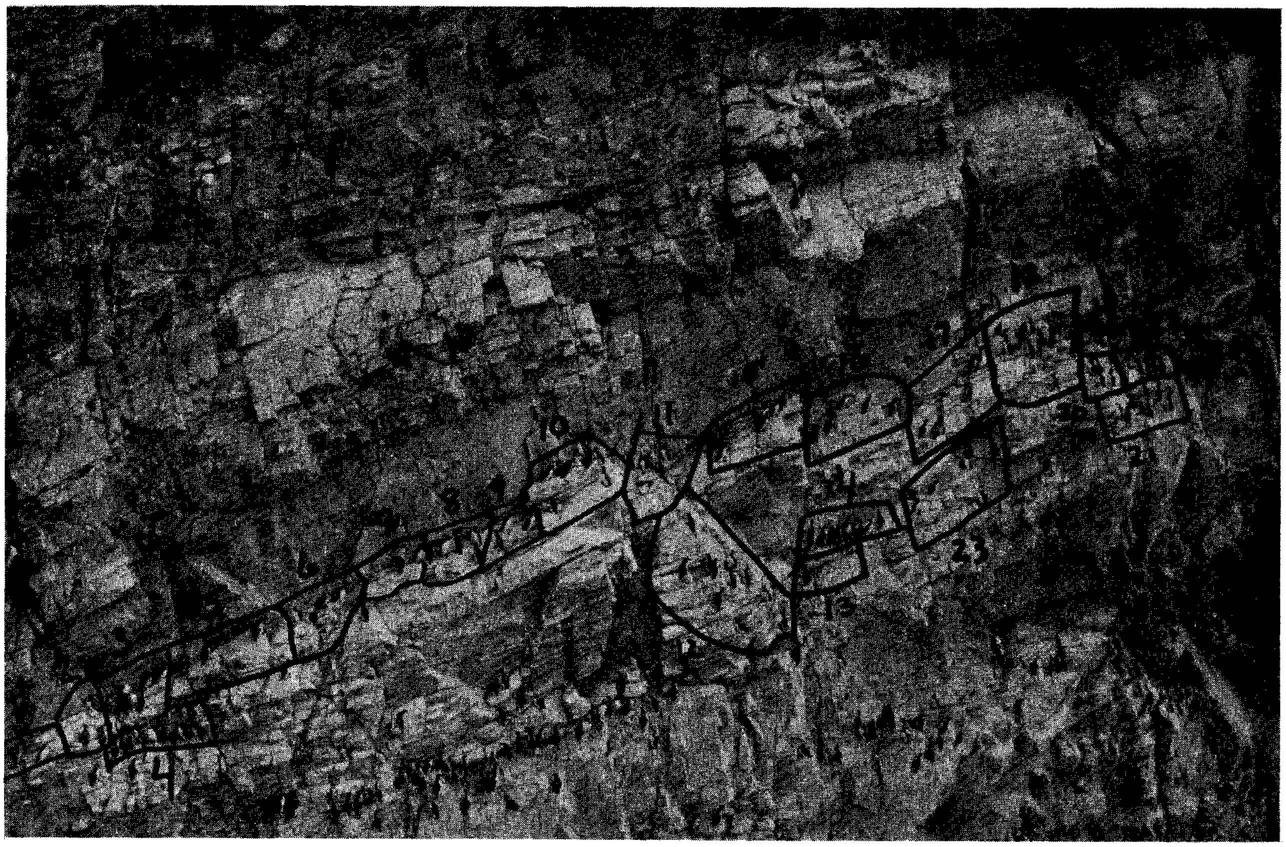
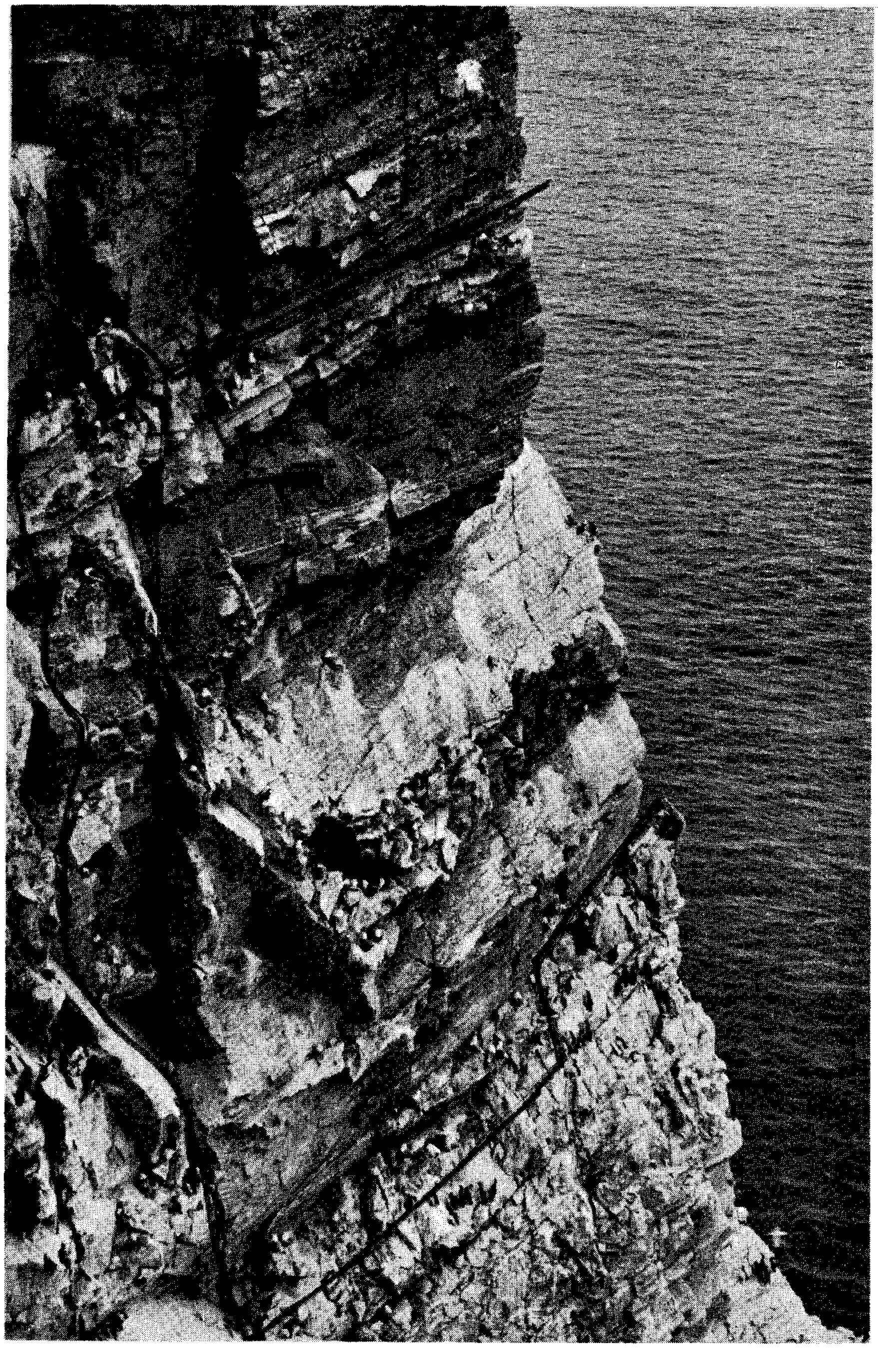


Figure 27.
An observer viewing the Stake 10 murre map area.
Photo shows how close one can sit to the edge of the cliff and how clearly one can see birds on the cliff faces in study areas.

Figure 28.
Stake 10, looking east on mainland cliff adjacent to the west side of the Arches. Kittiwake Map Area: located to the right of the murre map area, outlined in photo.



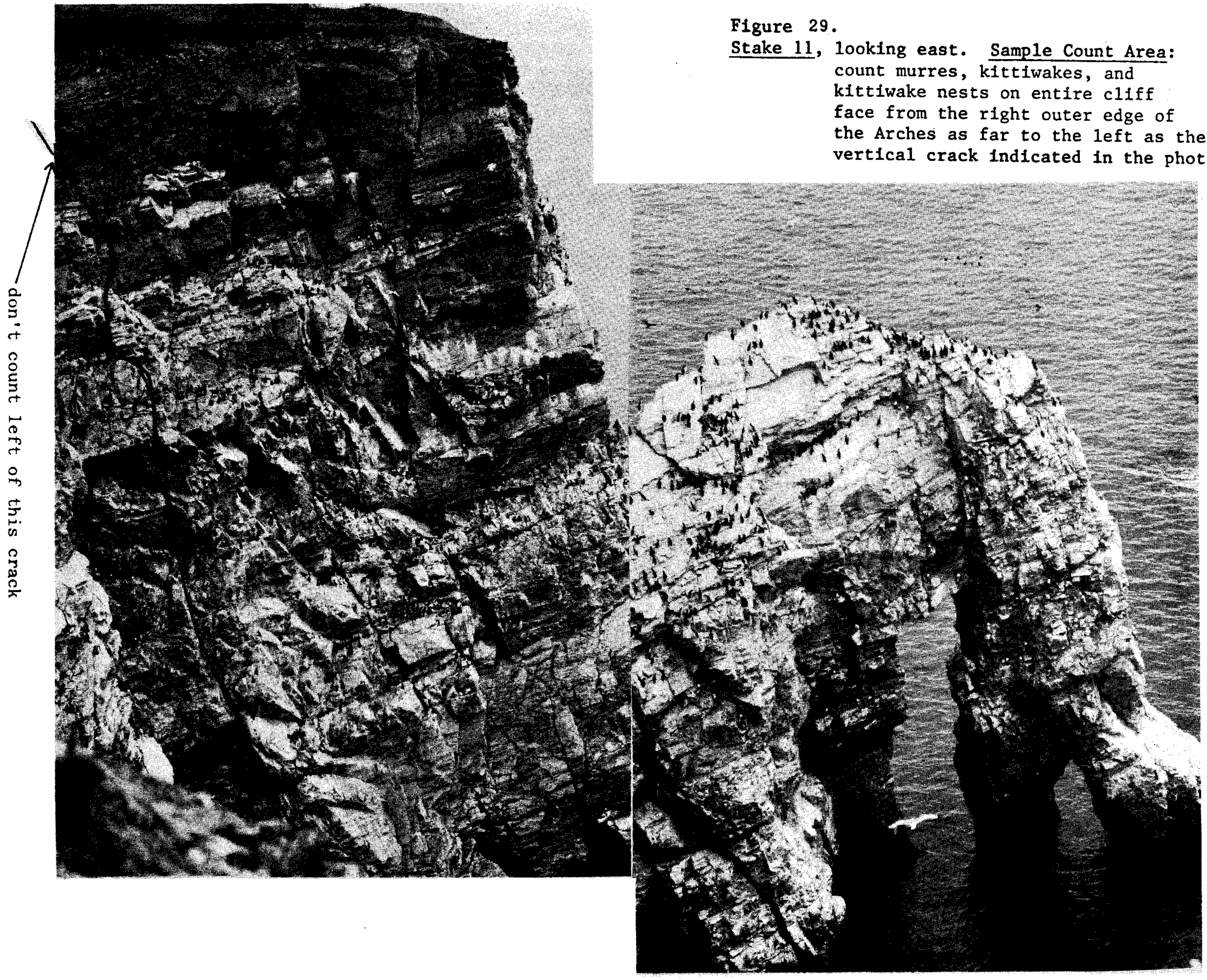


Figure 29.
Stake 11, looking east. Sample Count Area: count murres, kittiwakes, and kittiwake nests on entire cliff face from the right outer edge of the Arches as far to the left as the vertical crack indicated in the photo.

Figure 30.
Stake 11, diagram of sample count, showing divisions of cliff so that count may be conducted section by section.

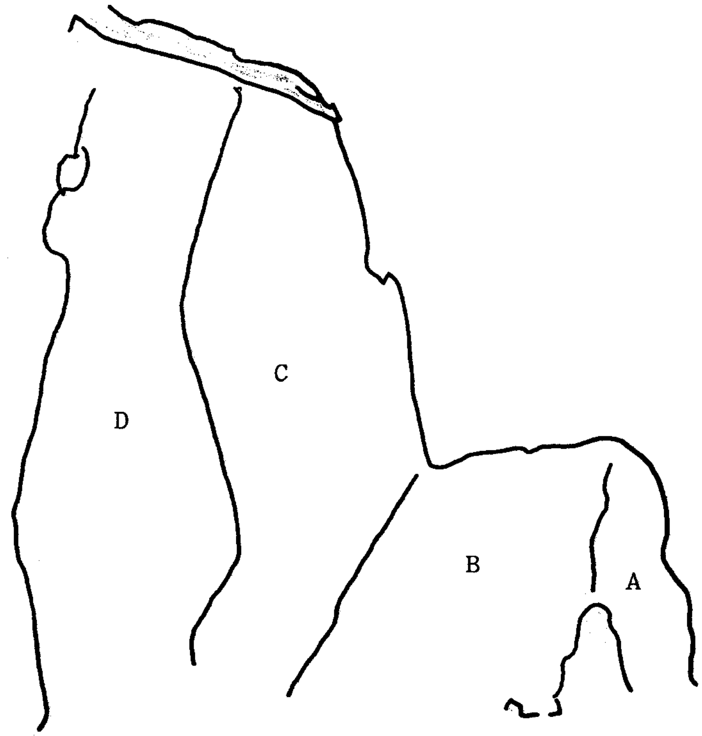


Figure 31.

Stake 12 "crack", looking west. Murre Map Area: a long, horizontal crack high on the cliff underneath the Stake 10 viewing spot; the crack is on the cliff face opposite the map areas of Stake 10.

[**grass at top of cliff**]

Figure 32.
Stake 12 "crack", looking west. Murre Map Area close-up: subsections of map area are outlined.

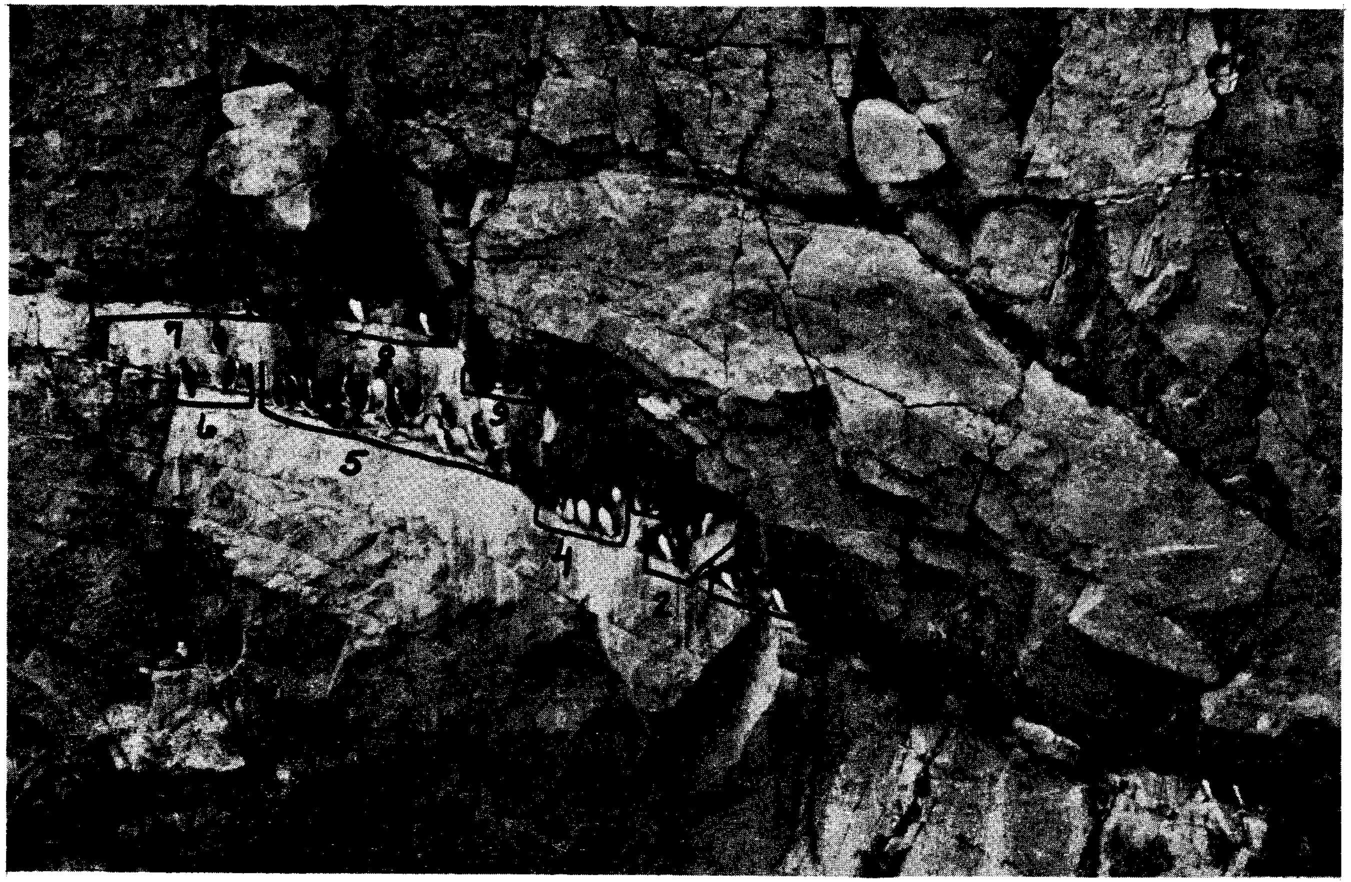


Figure 33.
<u>Stake 12 "inside"</u>, looking east to the left of Stake 12 "crack".
<u>Murre Map Area</u>: located to the left of the crack and lower on the cliff; subsections are outlined.

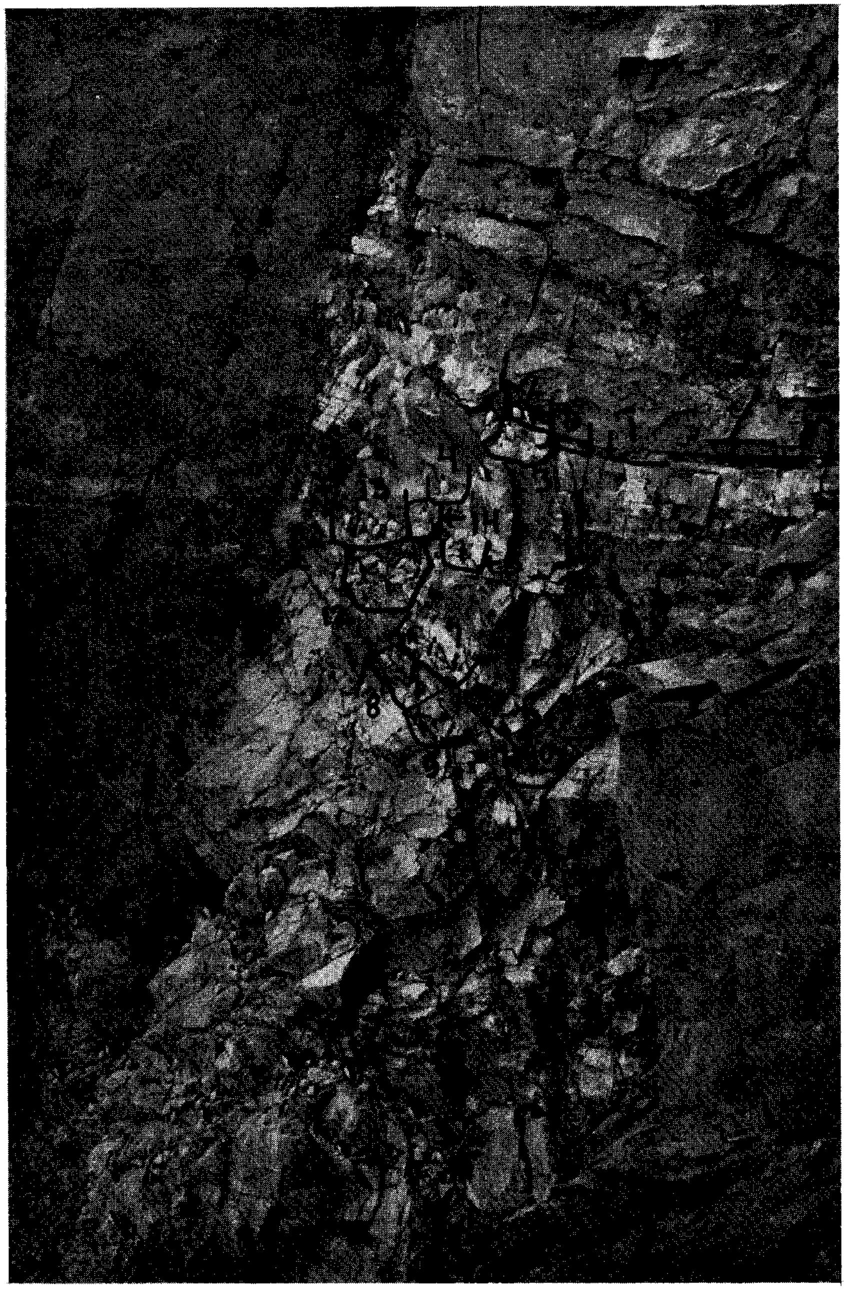


Figure 34.
Stake 13, looking west. Kittiwake Map Area: located on the east side of the Arches, map area is the entire mid-section of the inside Arch, from the top of the Arch to sea level. Stake 13 is driven into the ground just above and to the east of the Arches right at the edge of the cliff (be careful).

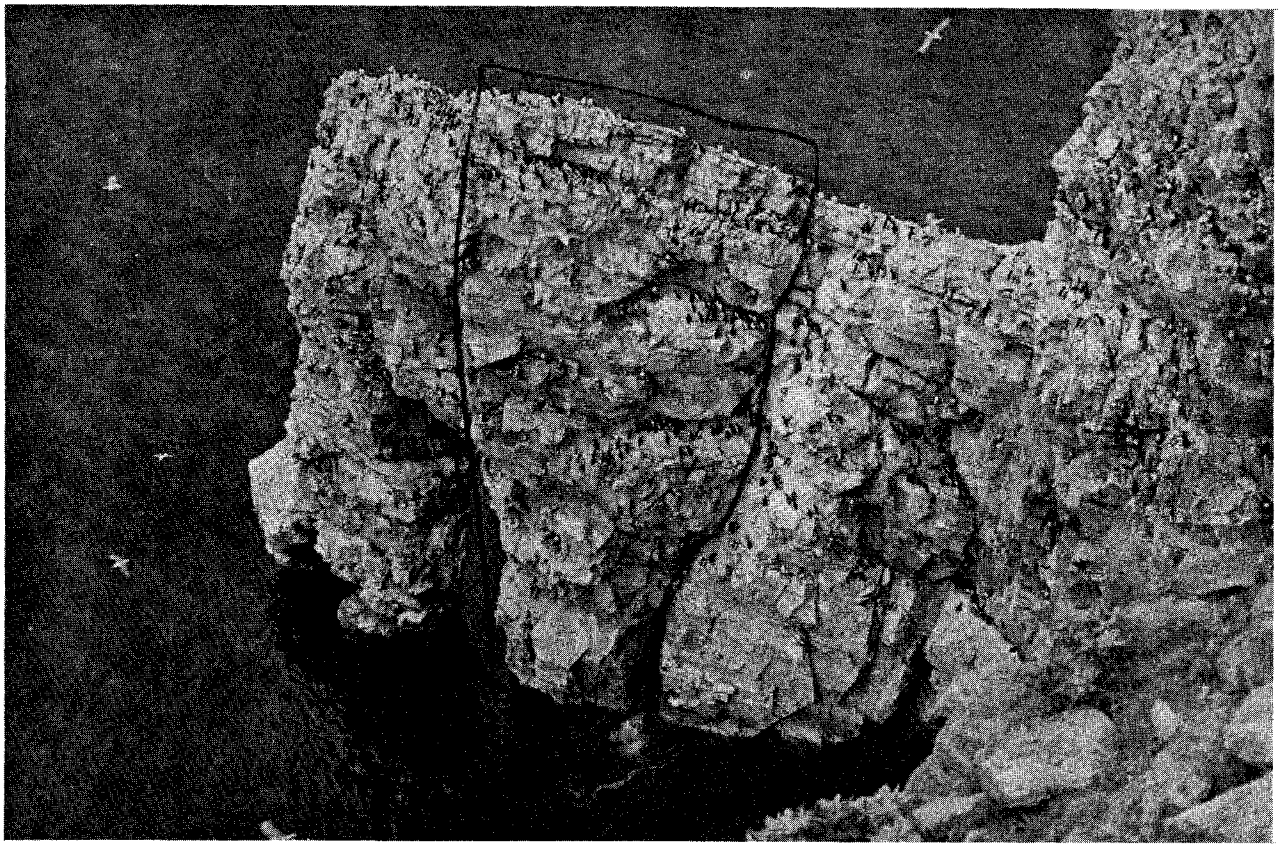


Figure 35.
Stake 13, looking west onto the east side of the Arches.
Kittiwake Map Area close-up.

Figure 36.
Stake 13 "east", looking west. Murre Map Area can be seen from a spot east of the Arches (there is a stake in the ground, 30-50 yards east of the Stake 13 kittiwake map area stake), along the edge of the cliff, west of the Jackpole.

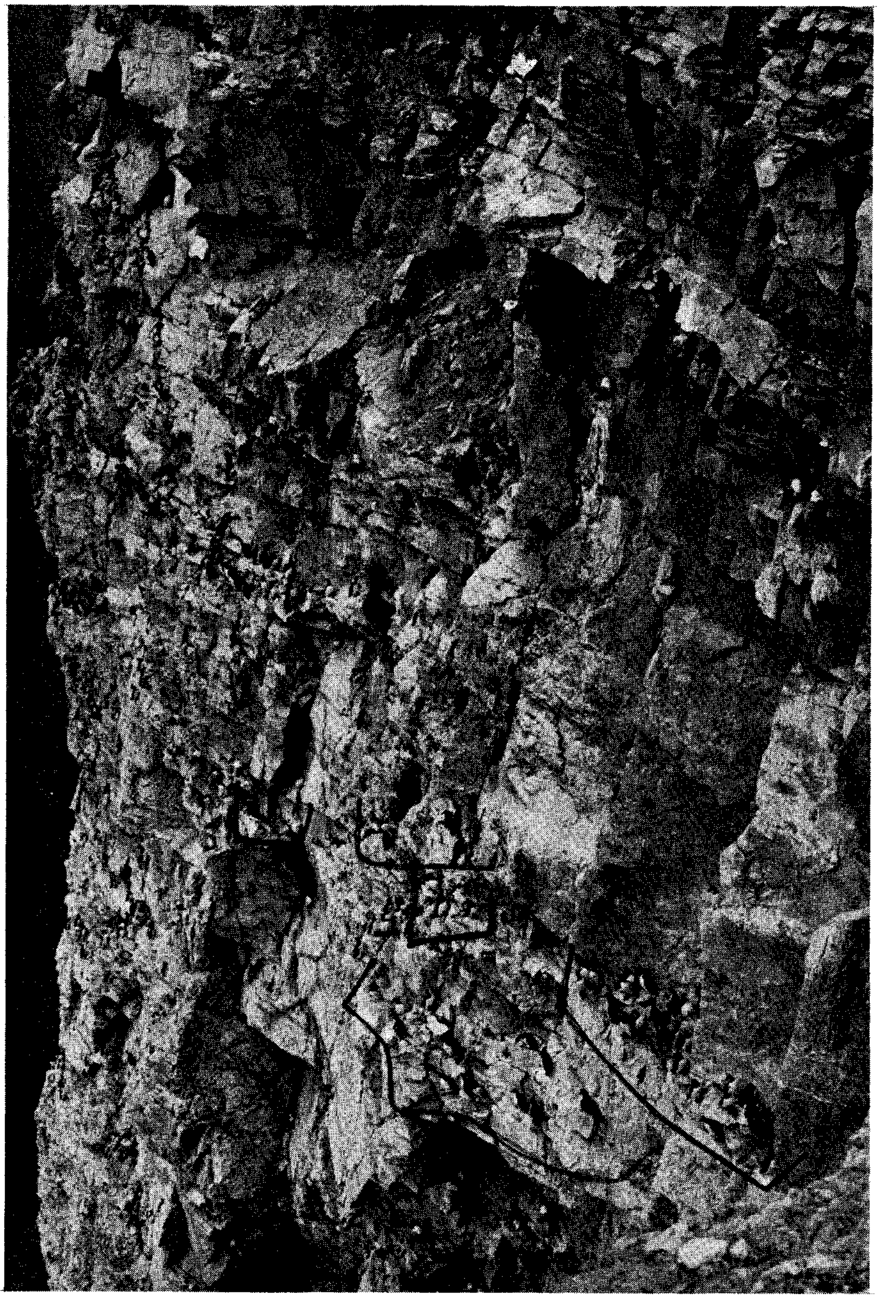


Figure 37.

<u>Stake 13 "east"</u>, looking west from spot east of the Arches.
<u>Murre Map Area</u> close-up, showing outlines
of subsections.

Figure 38.
<u>Stake 14</u>, looking south onto the north side of the Rope Stack. Both the kittiwake and murre map areas are outlined.

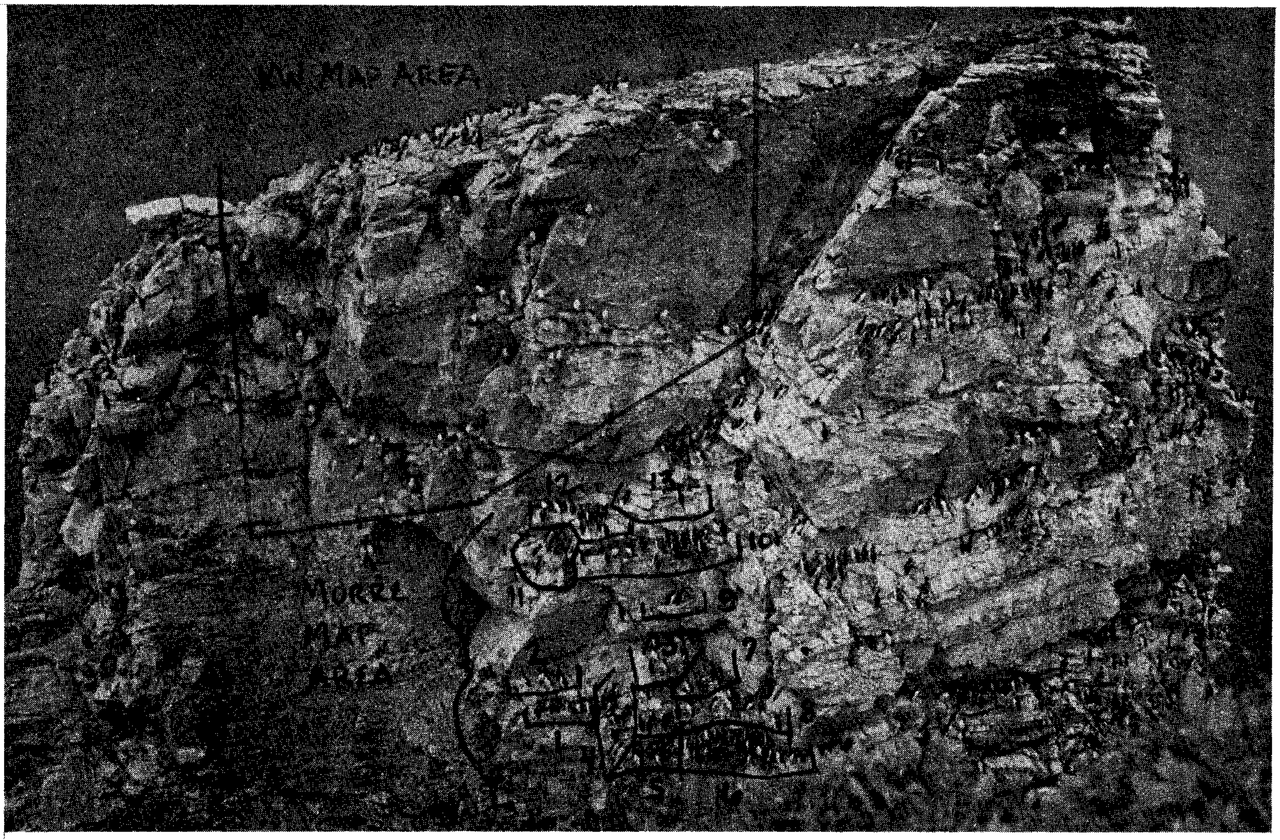


Figure 39.
Stake 14, north side of Rope Stack. Kittiwake Map Area: located on the upper mid-section, to the right of the rope indicated in the photo.

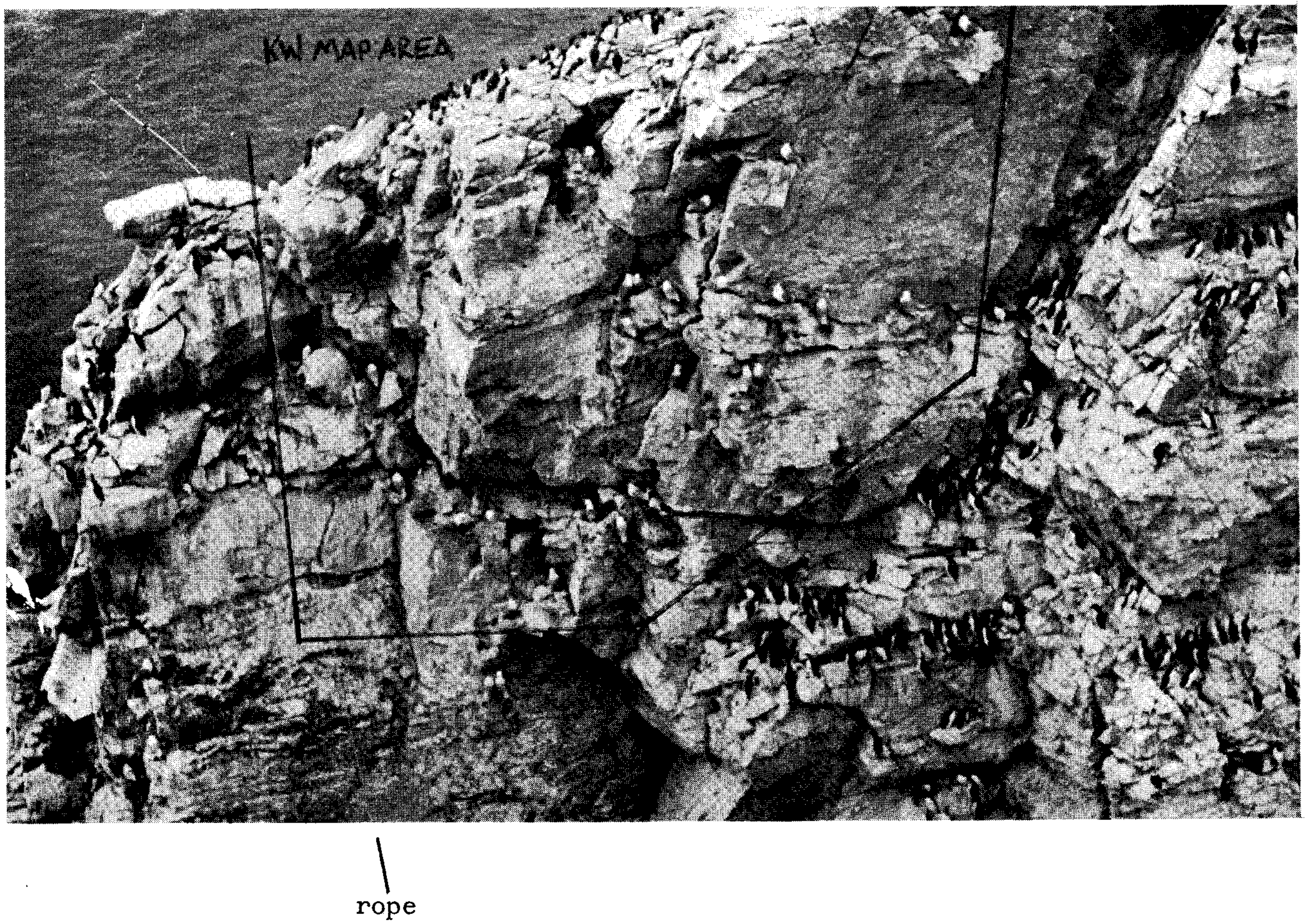


Figure 40.
Stake 14, north side of Rope Stack. Murre Map Area: located mid-way up the Rope Stack, below the kittiwake map area.

Figure 41.

Stake 15, far face. Sample Count and 24-Hour Count: count murres, kittiwakes, and kittiwake nests on entire far face to the left as far as the vegetation in the cove, from the top of the cliff to sea level.

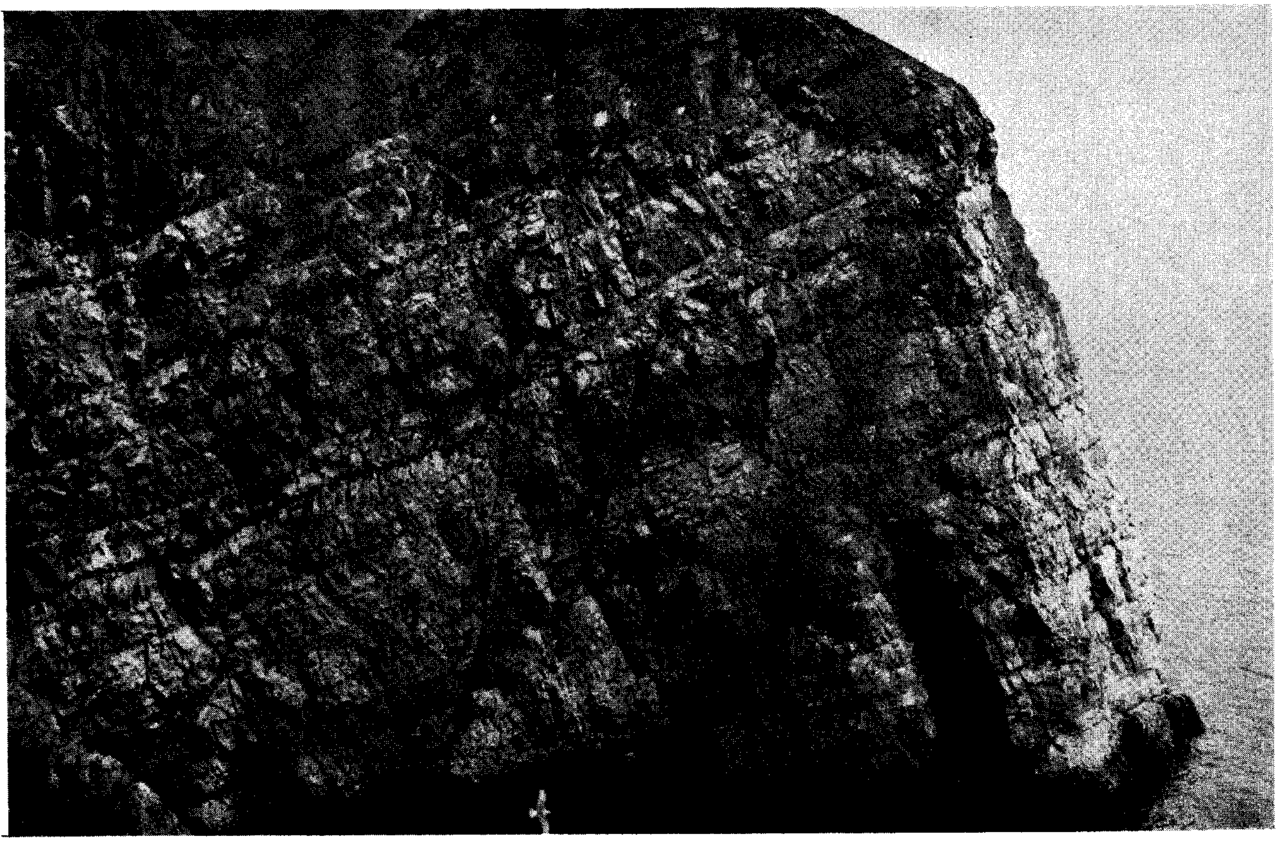


Figure 42.

<u>Stake 15, far face</u>. <u>Thick-billed Murre Map Area</u>: located on the outermost section of the far face, low on the cliff, outlined in the photo.

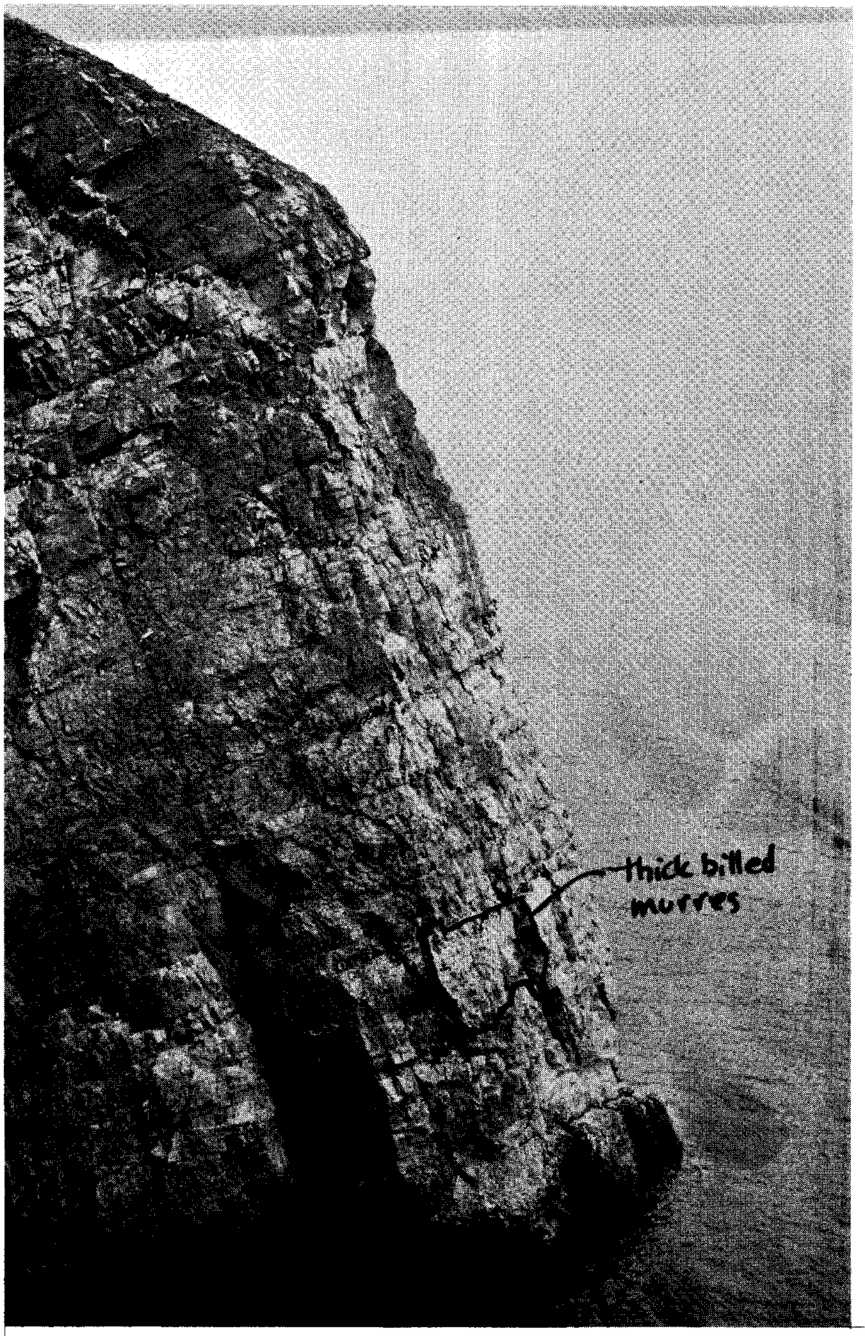


Figure 43.
Stake 15, near face. Common Murre Map Area: subsection "1" is shown; this shelf of murres is located near the top of the cliff, to the left and adjacent to the Stake 14 viewing spot, on the mainland north of the Rope Stack. The other subsections of the murre map area are located below subsection "1" and are shown in the next figure.

Figure 44.
Stake 15 near face. Murre Map Area, showing subsections "2" through "8", located below subsection "1".

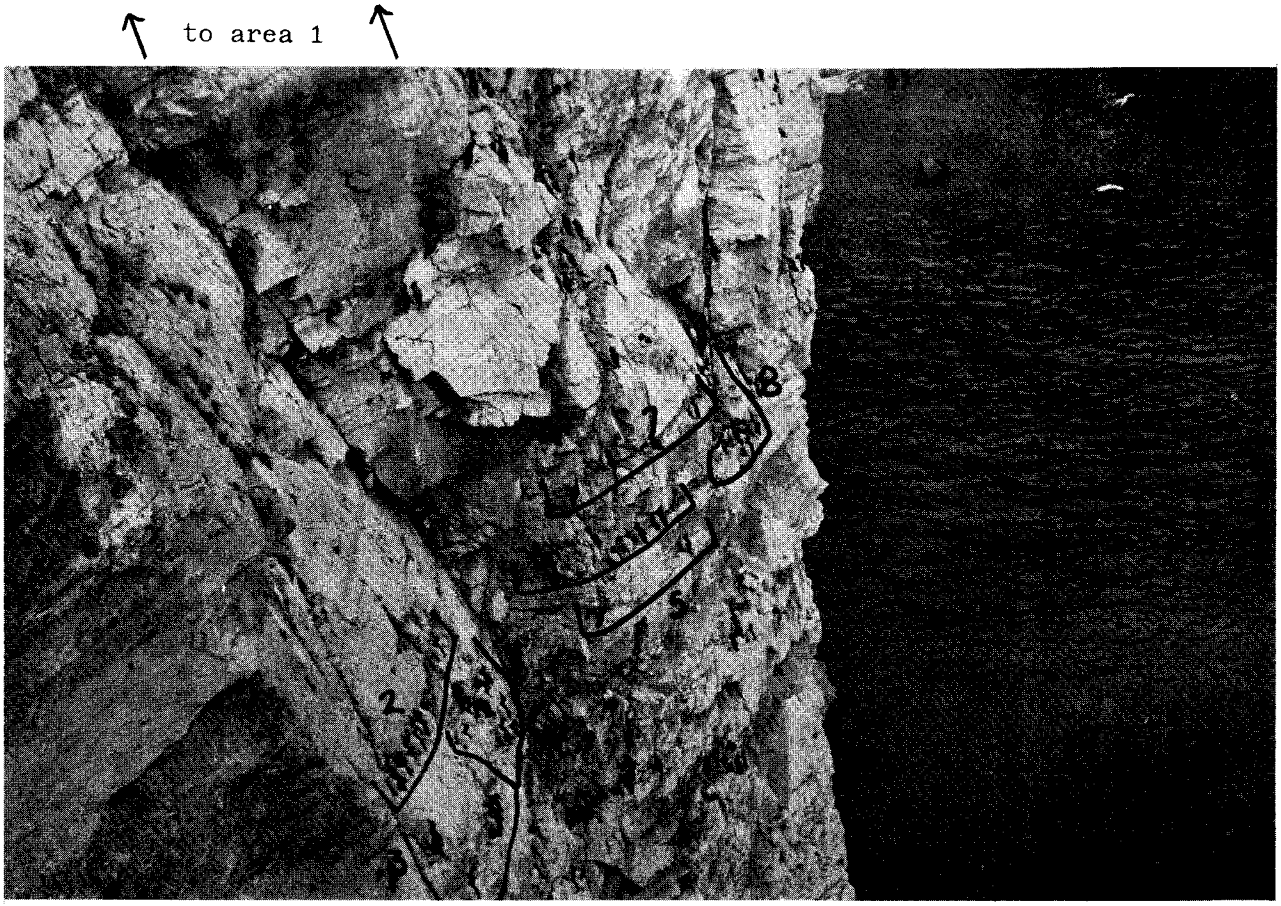


Figure 45.

Stake 17, looking west. Kittiwake Map Area: located on the lower mid-section of cliff section facing east, and characterized by a vertically flat rock face with a "V" crack located in the center of the map area (which is outlined).

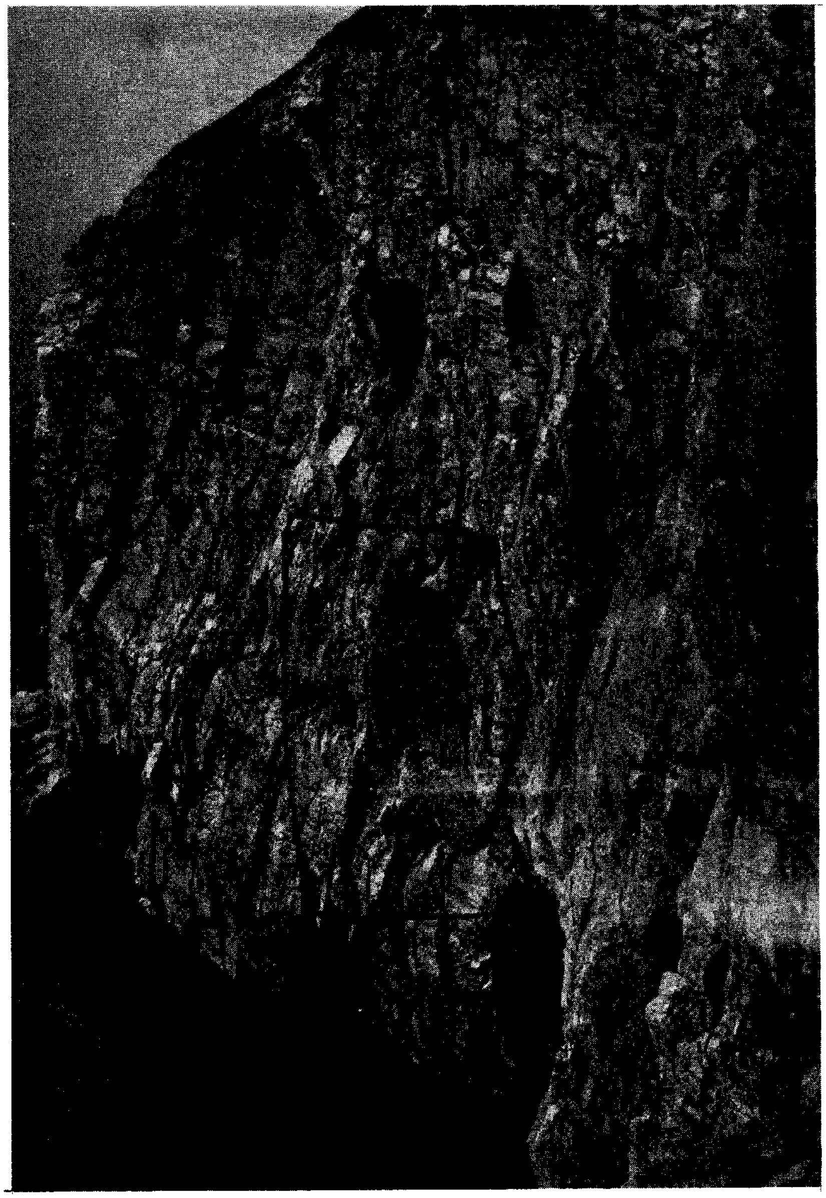


Figure 46.
<u>Stake 17</u>, looking west. <u>Kittiwake Map Area</u> close-up.

Figure 47
Places where counts are made of: (1) kittiwake nests
(2) nests with sitters; i.e., nests not seen into
(3) nests with chicks

Stake 1

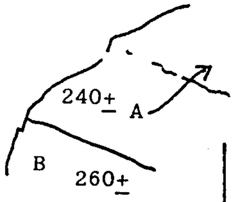
Stake 3 left near face [65±]
over arch on far face [40±]
outer face under arch [260±]

Stake 4 left of vertical crack
right of vertical crack

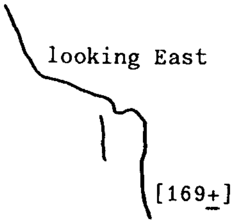
Stake 4b left [120±]
right [125±]

Above outer corner looking East
near face inside Axe [130±]
on Axe [325±]

Above ridge before Axe, looking West



looking East



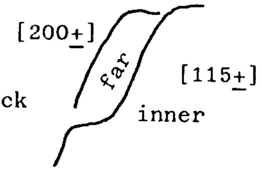
From East looking West onto east side of Axe [225±]

Stake 5 stake face looking West [45±]
face beyond [100±]

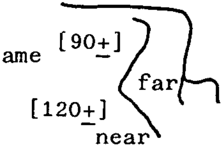
East side of Castle [230±]

Looking East from west side of Thumbstack [105±]

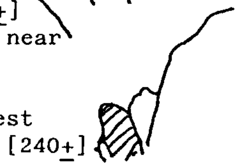
Stake 8 inside
middle face
east side of Thumbstack



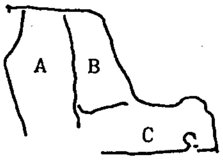
Looking East from same point



East of Stake 8 looking West



Stake 10



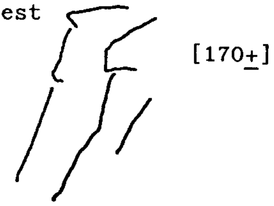
A [220±]
B [185±]
C [115±]

Stake 12 far face [115±]

Stake 13 on Arches [190±]
on face [165±]

Stake 15 looking East
to Jackpole
whole face

Outer point halfway to Jackpole from Stk 13
looking West



Last point West of Jackpole looking West

Figure 47 (cont'd).

Looking West near face just East of Jackpole

[30±]

Looking East, west side of Rope Stack

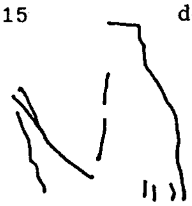
[155±]

West from Stake 14

[130±]

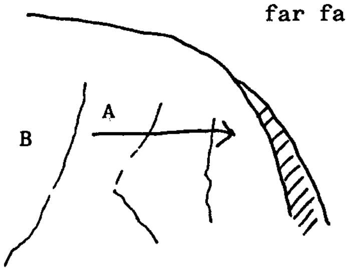
Stake 14 [47±]

Stake 15 down and east



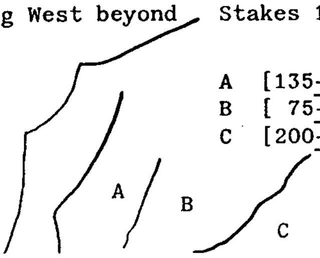
[80±]

far face East



A [75±]
B [150±]

Looking West beyond Stakes 14 & 15



A [135±]
B [75±]
C [200±]

West of deepest gully in Golden Eagle nest area

far [220±]
near [75±]

Over Eagle nest looking East

[150±]

Stake 17 [105±]

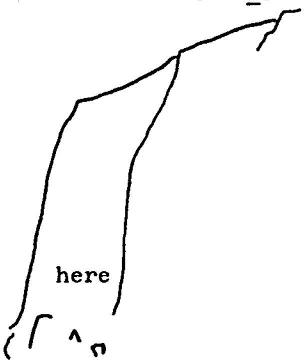


Figure 48.
View from Stake 19, showing the Stake 19 Murre Map Area, the Kittiwake Map Area, and the Square Rock Sample Count Area.
Stake 19 is located on the mainland west of Square Rock; the map area cliff faces west, the observer looks east with Square Rock in the background as in photo.

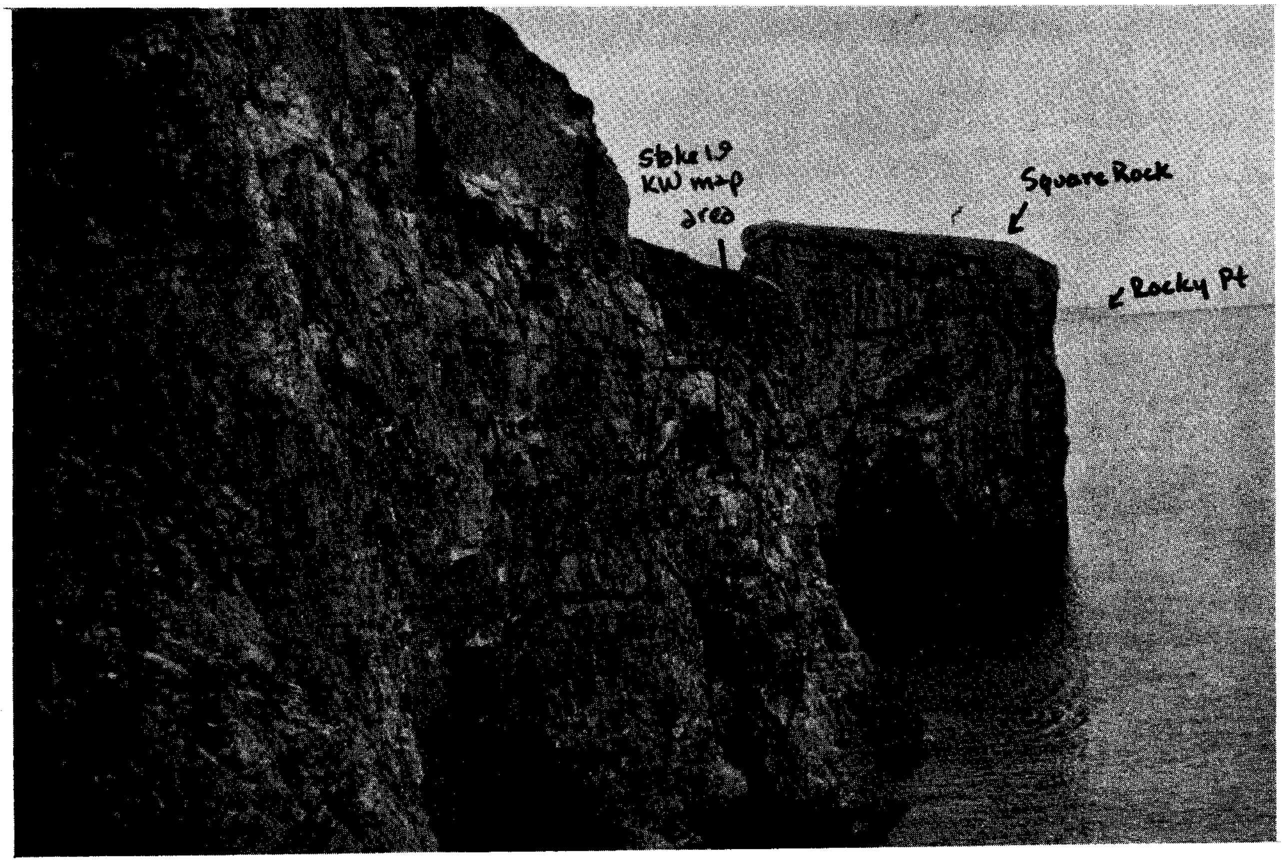
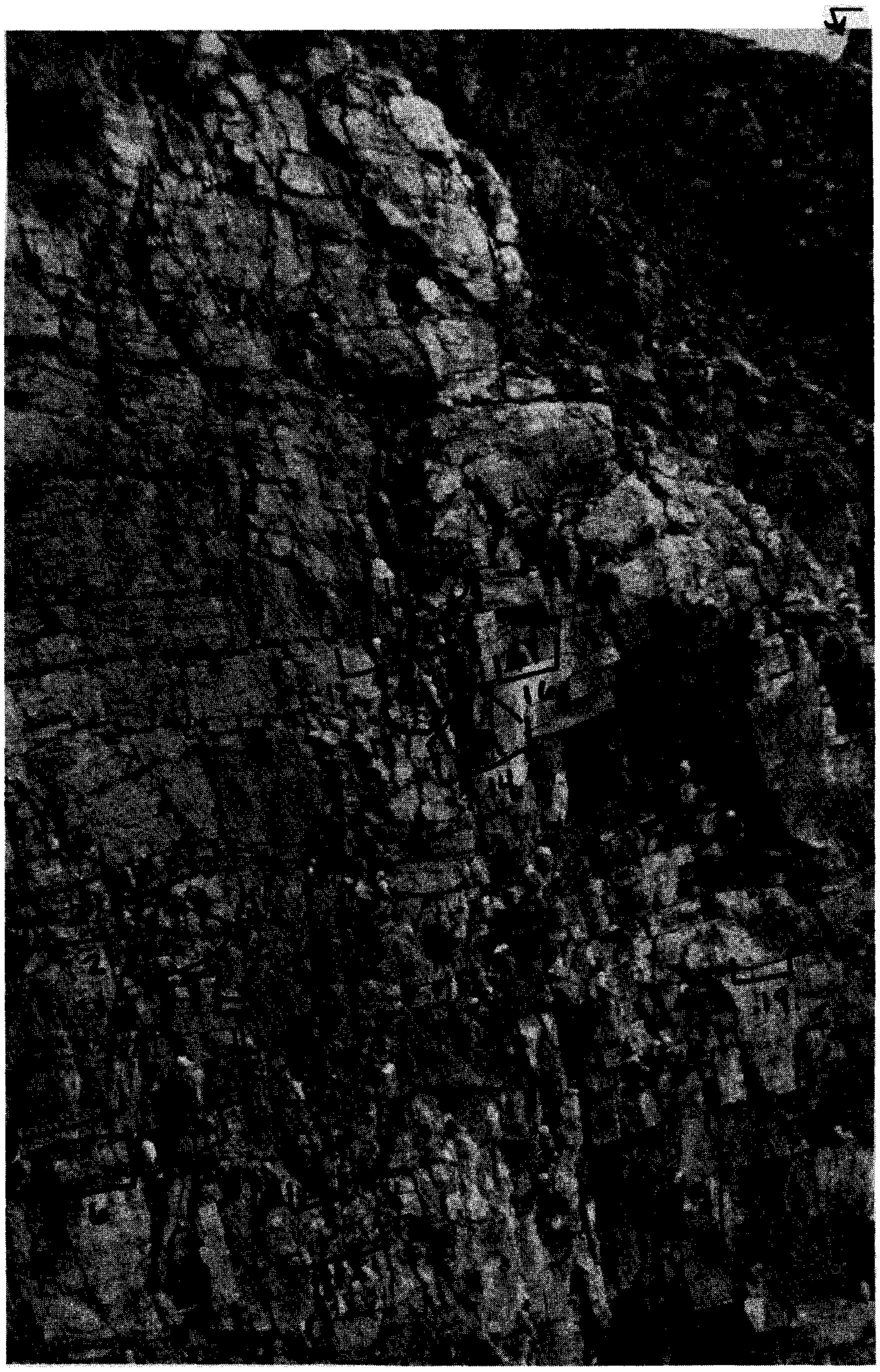


Figure 49.
Stake 19, looking east. Kittiwake Map Area close-up of area indicated in Figure 48.

Figure 50.
Stake 19, looking east. Murre Map Area close-up of area indicated in Figure 48.



(Square Rock in background)

Figure 51.

Square Rock Sample Count, conducted from the mainland above the Stake 19 map areas. The area of the count is outlined; count all murres, kittiwakes, and kittiwake nests. The top of the photo is the top of the area counted, i.e., birds on top of Square Rock were not counted in this sample.

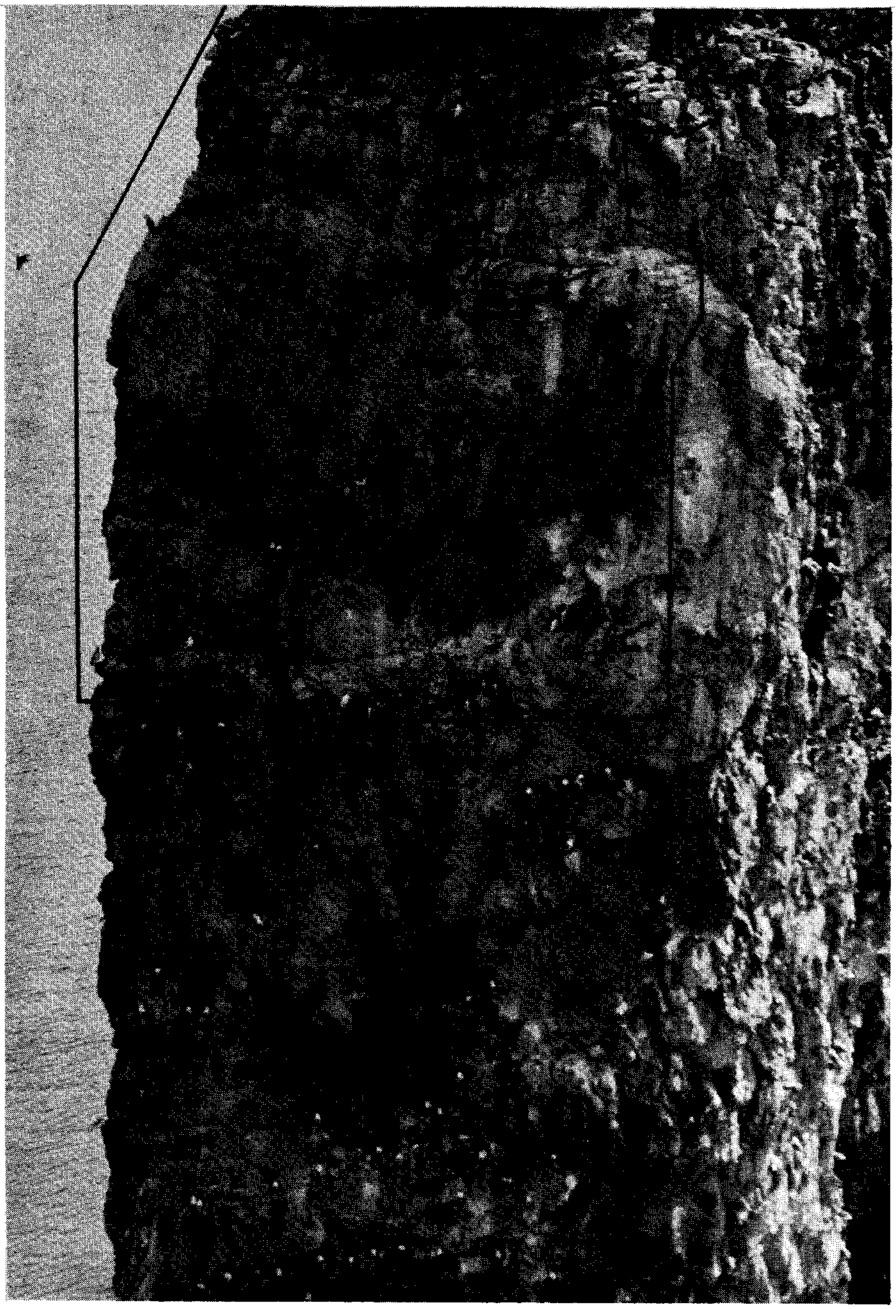


Figure 52.
Square Rock, looking from the mainland south onto the north side of the rock.
Kittiwake Map Area: located on the lower part of the rock, outlined in photo.

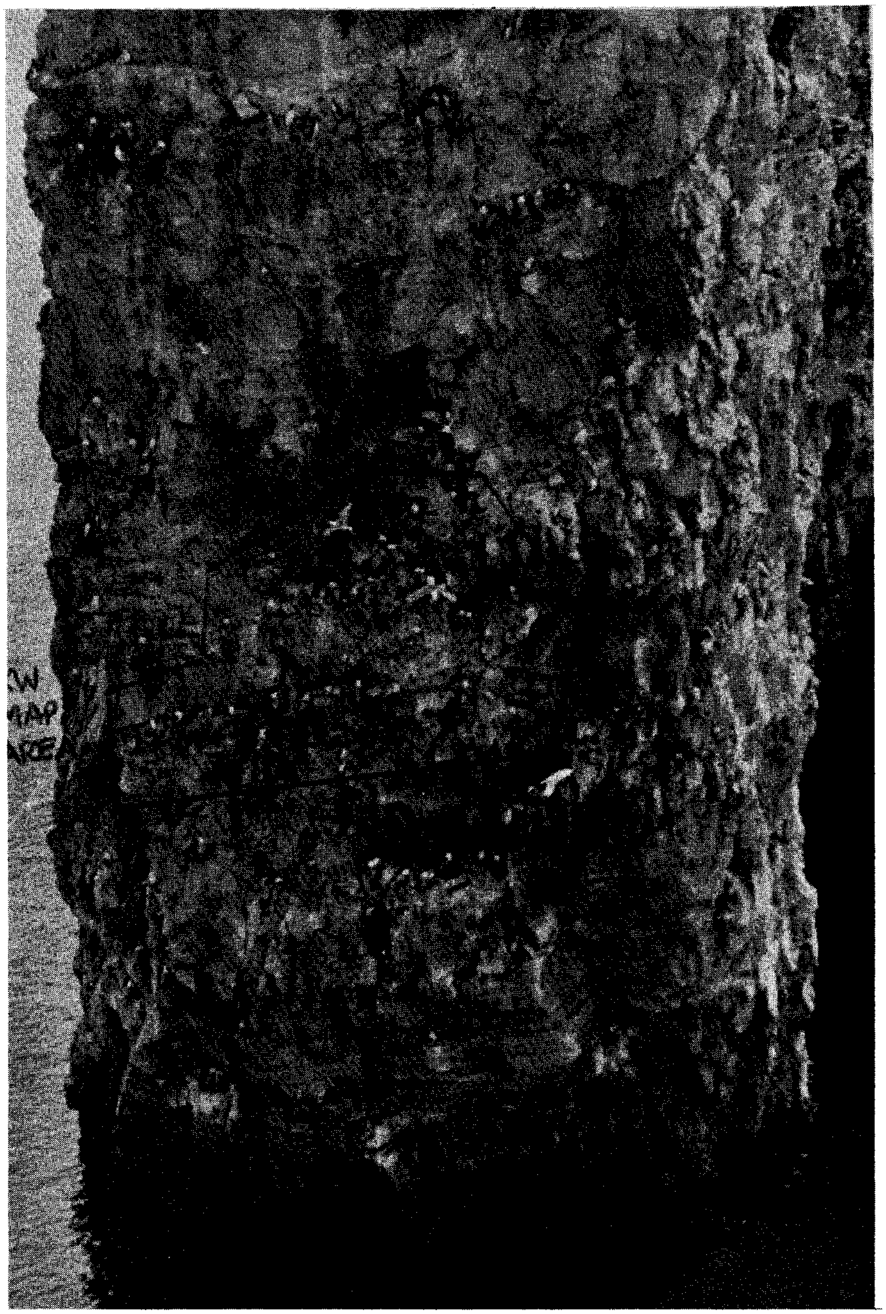


Figure 53.
Square Rock Kittiwake Map Area close-up.

APPENDIX X.
THEORETICAL FRAMEWORK UNDERLYING OUR STUDIES OF POPULATION AND COMMUNITY BIOLOGY OF SEABIRDS

A. Introduction

1. Statement of Purpose

We have been asked to bring together in one place our arguments for a Darwinian view of the functions of communities. The arguments will be familiar to many field ecologists studying vertebrates, and most field students of vertebrates think in Darwinian terms. However, the arguments against ecosystem development and for the primacy of selection of individuals do not appear to have been accepted by many physical and chemical oceanographers or students of trophic-dynamics and community function for the purpose of systems analysis and ecosystem modeling. There are, of course, important exceptions. We hope that by explaining the basic differences between our "probabilistic" view and what we have come to call the "deterministic" view of the functions of community, we can increase the number of people who really understand the theoretical foundation underlying the differences. Recently, some physical oceanographers have found that they can facilitate their research by cooperating with students of vertebrates, even some bird watchers, and we hope that we can abet that trend.

We apologize to those for whom these arguments will be "old hat"; but the ghosts of optimal ecosystem operation, maturity, stability, and efficiency are far from laid to rest. In part, the purpose of bringing these arguments together is to identify what most vertebrate ecologists accept as the tenets of community function and what leads the field biologists among the Principal Investigators of OCSEAP to oppose major aspects of policy in the program of research.

2. The Controversy

The controversy is between "deterministic" (closed system or developmental) and "probabilistic" (open system or kinetic) models of community biology. In this appendix we present and contrast the theoretical frameworks behind these two types of models, and present enough evidence in support of probabilistic models to make clear the basis from which we have conducted our studies of seabirds.

First, we delineate the differences between the assumptions inherent in the deterministic models and those in probabilistic models. We include an essay on "systems and environment" in which we review the history of theoretical ideas of landscape formation, plant ecology, and animal ecology, using developmental and kinetic models. Then we review our Darwinian approach to describing the behavior of populations in a section on phenomena observed in studies of Herring Gulls and apply this to the biology and population regulation of other birds and vertebrates. We believe the assumptions behind the developmental view are so deeply ingrained in people's minds that it is worth belaboring the differences.

We then review a theoretical contribution on seabird community biology (Cody 1973) in conjunction with some constructive criticism made by an experienced biologist (Bédard 1976). Lastly, we argue against assumptions made by OCSEAP about the couplings of natural systems and suggest the suitability of seabirds as indicators for monitoring impacts of some consequences of development on marine environments.

The term deterministic has been used to refer to systems for which a consistent condition of equilibrium can be predicted. The term implies the development of progressively more orderly interactions and interrelations among constituents within a consistent environment without influence from outside the system. Hence, the terms developmental and closed system apply to this way of thinking or paradigm (Kuhn 1970) because unidirectional progressive change with little or no influence from outside the system is implied.

The term probabilistic has been used to refer to systems for which many, often very different, steady states can be expected. The term implies response to events and forces from outside the system (hence open systems) and implies further that the system takes on new steady states in response to the rates, kinds, and amounts of influences from outside. Hence, the term open system or kinetic applies to this way of thinking, suggesting that there are many configurations of members or amounts and kinds of energy flows.

The terms "open systems" and "closed systems" were formulated by von Bertalanffy (1950, 1956) describing thermodynamic systems; therefore, the terms really should not be applied to the systems which we are considering. Yet, we can clarify our thinking by using the contrasts between these two extremes as an analogy. The differences refer to specific sets of assumptions, inherent in the writings of geomorphologists and plant and animal ecologists.

During the late 19th century, ideas of evolutionary development and evolution of societies were applied without considering the full meaning of Darwin's and Wallace's ideas of natural selection acting on individuals. The idea of evolution was applied to both the natural world and to human societies, and the processes of evolution were assumed to lead to improvement, hence, to the establishment of well-balanced systems in equilibrium with suitable environments; this was the balance of nature in its simplest terms.

Determinism was a popular view at the end of the 19th century. Climatic determinism was applied to vegetation and to human cultures. While determinism has been overtly rejected in many fields, the idea that systems evolve over time to improve the fit to the environment has persisted, as we discuss in section B.

As Harper (1977) put it:

> "A theory of natural selection that is based on the fitness of individuals leaves little room for the evolution of populations or species toward some optimum, such as better use of environmental resources, higher productivity per acre of land, more stable ecosystems, or even for the views that plants in some way become more efficient than their ancestors. Instead, both the study of evolutionary processes and of the natural behaviour of populations suggest that the principles of "beggar my neighbor" and "I'm all right Jack" dominate all and every aspect of evolution . . . Natural selection is about individuals and it would be surprising if the behaviour that favoured one individual against another was also the behaviour that maximized the performance of the population as a whole."

3. The Assumptions Behind the Models

The predictions of the models one prepares for systems are conditioned by the assumptions made about the long-term behavior of their environments. Further, the assumptions of some (e.g. deterministic) models limit the types of questions which can be asked within the framework of the model. This is not to say that the assumptions and the conclusions drawn from them are necessarily wrong, but rather that they preclude their own falsifications.

Below we present the basic assumptions characterizing a) deterministic or developmental models of community biology and b) probabilistic or kinetic models.

a. Developmental or deterministic models assume:

i) Natural selection acts on groups of organisms, in the forms of communities, species, or populations. Competition may be among individuals, but more importantly is manifest in competition among communities which coevolved and have continuity through time.

ii) Communities evolve along successional gradients toward optimal ecosystem functioning, culminating in a "climax" community characterized by maturity, stability, and equilibrium states among its members, hence independence of changes in its natural environment.

iii) Regional or topographic differences in communities can be related in a functional way to the age of the community (i.e., to the stage at which the community exists along the successional gradient) or to the maturity of the system.

iv) Stability of populations is evidence that a community is functioning at its optimal carrying capacity, having reached a steady state. Self-regulation of populations is implied, and self-regulation depends upon intrinsic feedback mechanisms such as density-dependent mortality (failure to breed or high mortality among young and adults). Self-regulation maintains stability by regulating animal numbers in ways that prevent over-exploitation of food supplies (Wynne-Edwards 1962) and extinction (Christian and Davis 1964).

v) A species whose numbers oscillate is somehow abnormal because its populations are not adjusted to local carrying capacity. Extinction results from such instability (Slobodkin 1961).

vi) Stability of a population or community indicates "health" of an ecosystem and changes in the "natural" constituents of a community constitute "damage" from which a community must recover.

vii) Systems function similarly over different parts of geographic ranges so that information gathered in one place will be directly applicable to other places.

b. <u>In contrast, probabilistic or kinetic models assume:</u>

i) Natural selection acts on individuals.

ii) Actions which favor individuals are selected for without regard for efficiency or functioning of community. Each community or group of individuals is in the process of change and so cooperative interactions are brief. Each individual is in competition to some degree with all other members of its population or community. The basic elements of a community or system are the primary producers and decomposers; additional members are opportunistic and temporary, depending upon the availability and accessibility of resources.

iii) Natural selection, acting in the orthodox way on individuals, can give rise to a population which adapts rapidly to "take advantage of" changing circumstances. As a consequence of repeated changes in environment, different types of behavior are favored in the same species at different times and places.

iv) The concept of carrying capacity is helpful only as a most general overview because the concept presupposes a stable environment. Environments are not stable or uniform and consequently significant variations in population size and density occur consistently in different parts of species' ranges. Fluctuations in populations are influenced by external forces indifferent to density. Regulatory mechanisms observed in one population or deduced in another may differ dramatically. Individuals survive and species escape extinction by the simple expedient of dispersing between partially isolated nuclei of population. These dispersive movements are indicative of unstable environments at the loci of population nuclei such that stability or steady state cannot be reached or maintained. The existence of two-way dispersive movements between population nuclei means that local extinction and resettlement do not disrupt genetic continuity or community function. Local extinctions may or may not be followed by replacement. Dispersion is one of the ways in which active vertebrates avoid being coupled to fluctuations in their resources.

v) Fluctuations in populations are "normal."
A species confined to one colony with little tendency to form new ones (i.e., natural selection has not favored individuals who "dispersed") will be in serious danger of extinction if, as is inevitable, the environment changes. This situation is likely to arise as a consequence of environmental stability, in contrast to the view that extinction results from instability.

vi) There may be no such thing as equilibrium to which a community tends to return after being disturbed or damaged.

vii) The study of the factors controlling population fluctuations helps one to learn about a population and the community in which it exists; one does not learn much by studying the population fluctuations as such. By understanding the strategies individuals use to cope with changes in their environments and the accidents and adaptations by which some individuals survive disasters, one can begin to relate information about groups which use similar strategies.

4. Historical Course of the Controversy

The controversy between "deterministic" and "probabilistic" models of community biology is an old one. Geologists were involved with it during the 1950s (Chorley 1962). There was a running debate among botanists from the 1920s through the 1950s. Among animal ecologists the topic remained undebated except for the dissent of Andrewartha, Birch, and others during the 1950s and 1960s, as during those years attention was devoted to theoretical ecology and modeling of ecosystems. The logical simplicity of density-dependent population control (Lack 1954 et seq.) made the deterministic models attractive to most ecologists, especially the theoretically inclined. This determinism was expressed most clearly in the papers by Wynne-Edwards (1959, 1962) (see next section) and grew into clearly formulated theory in the works of Margalef (1968) and Odum (1969): diversity, stability, productivity, and optimal functioning develop as the community matures.

It was stimulating to review these ideas in the 1960's when Crook (1962, 1963, 1965), Lack (1966), and Hamilton (1964) rebutted the arguments of group selection formulated by Wynne-Edwards, and when Murdoch (1966), then Ehrlich and Birch (1968) rebutted Hairston, Smith, and Slobodkin (1960). Yet the journal American Naturalist was rife with determinism, and virtually all participants in the symposium held at Brookhaven, New York, in 1968 implicitly or explicitly endorsed as common knowledge that there are functional interactions between diversity and stability. It was encouraging to see ecology texts of the 1970s (Krebbs 1972; Colinveaux 1973) which contrasted with the previous classic by Odum (1963) and with high school texts prepared by the American Institute of Biological Sciences at about the same time.

The differences in opinion among terrestrial ecologists had little influence on marine biologists with some exceptions; for example, Dunbar (1968) used the convenience of a deterministic model as the framework for his treatise on the "immaturity" of arctic marine systems. Further, the concepts of carrying capacity and hence maximum sustained yield had strong and unfortunate influence on the models and predictions prepared by fisheries biologists during this period.

5. "Type" vs. "Population" Thinking and the Rhetoric of Environmentalists

During the 1950s, as a reaction to what was called "type thinking," it became popular to refer to "population thinking." Type thinking considered an idealized "typical" individual as characteristic of a species (hence, non-conforming individuals were considered atypical varieties), as opposed to the considerations of "population thinking" which included all the variation found in a natural population, and recognized this variation as variation around an abstracted "average." Previously, many ecologists, consistent with their "type thinking," sought "typical" communities as the properly functioning ones, disregarding the non-conforming transitional aggregations which they regarded as atypical. This attitude was reinforced by the tendency of many ecologists to apply the concepts of population genetics in ways that implied that the population is the unit upon which natural selection acts, not the individual. That is, some ecologists thought a community was made up of organized components which have continuity through time, and thus they thought of a community as a unit of selection. Others thought of a species' population as a unit of selection; hence, one often heard talk of adaptations as being favorable for the species. By the end of the 1950s, these ideas had reached a culmination in the concept of "group selection," best verbalized by Wynne-Edwards (1959,1962) ; the members of a population had displays which measured the size of the population and then limited the number of individuals reproducing so as to avoid overcropping their resources. The ideas were also phrased by Slobodkin (1961) in the aphorism, "the prudent predator keeps its prey at maximum productivity."

At the heart of much of this school of thought lay the widely accepted theme of succession and climax, a series of concepts which matured with time to suggest that communities succeed each other along a gradient of increasing diversity, stability, organization, and hence integration of energy flow, until one community occupies the site because it makes most efficient use of the resources available. Implied, then, is competition among communities which have continuity through time.

One implication of the role of equilibrium was specifically stated during the 1940s and 1950s: if populations were inherently unstable they would inevitably and soon go extinct. The process of the random walk (Markhov process) was cited as a mathematical justification of the point. It seems that this idea grew out of thinking of a population as one whole closed system. The hazards of the random walk required that in order to survive very long populations should have internal mechanisms of density-dependent self-regulation. It is reasonable to offer the corollary to this that the security provided by density-dependent population regulation is increased by the presence of a net of additional species at equilibrium, hence a more stable community.

Most "environmentalist" rhetoric is phrased in terms of these concepts. Loss of species, especially loss of one of the "top consumers," or changes in the "natural" constituents of a community, has been viewed as damage which the processes of nature must repair if the local ecosystem is to regain "health." The natural processes by which the balance is restored are the processes of succession. Because stability is an important indicator of "health," changes in numbers are signs of damage which may have serious and deleterious effects unless promptly detected and reversed. Therefore, species whose numbers vary widely a) are not considered to be good indicators, or b) are indicators of successional, i.e., less-than-optimally adapted, communities.

We believe these concepts are based on faulty assumptions and intend to illuminate below the assumptions upon which we base our view of community function.

6. The Behavior of Populations: Stability and Variability

a. Density-dependent processes and the assumption of population stability: r, K, and carrying capacity.

The mechanism of feedback which provides stability was supplied in the form of density-dependent mortality (Nicholson 1933). The impact of this feedback was assumed to cause the inflection of the "sigmoid curve" and to regulate the density of populations "at equilibrium."

The basic element in this theoretical complex is the logistic curve for population growth and stabilization, formulated by Verhulst (1838), Lotka (1925), and Volterra (1926). Influenced by this formula, biologists have reasoned that by establishing the inherent rate of increase in a population ("r" or average natality relative to mortality) and by measuring the "carrying capacity of the environment" ("K" or the density of the population at saturation) one can predict a number of biological characteristics and processes: maximally productive population size, maximum rate of production of new individuals, hence maximum sustained yield. All of these are thought of as characteristic of a species. These assumptions have supplied the theoretical framework for much of applied biology, such as game management and fisheries practices.

Populations growing in relatively isolated situations have been observed to follow a sigmoid curve toward a steady state. We have data on the population growth of Herring Gulls on several Massachusetts breeding grounds which show short-period rapid increase followed by a long sequence of shallow oscillations (Drury and Nisbet 1972). But usually observations have been terminated at about the time the population passed through the point of inflection on the sigmoid curve.

The original concept of "r" was the inherent potential for population increase; "K" was a factor for the equilibrium level or carrying capacity of the environment, or the population level above which factors come into play which diminish population growth. MacArthur and Wilson (1967) expanded these traditional meanings to attractive alternatives which they associated with adaptations species have to ensure the survival of the species on islands. Little r species are those whose strategies of life involve rapid growth, early maturity, and production of a large number of young, all of which produce rapid population growth, hence instability. K species are those whose strategies involve slow growth to large size, delayed maturity, and production of few young, hence greater stability of population size.

The concept of carrying capacity embodies a number of defects. One is that the concept presupposes a stable environment. During the early decades of the 20th century most climatologists believed that a departure from the norms of a regional climate would set into motion processes which would return the climate to normal. During the last decades, however, climatologists and oceanographers have shown that environments are continuously in flux in space and time. A second defect in the concept of carrying capacity is that it requires that populations have "mechanisms" or "institutions" (Wynne-Edwards 1959) by which the population is kept stable at the carrying capacity; the growth potential of a population (positive and negative) is linked to the available resources by feedback mechanisms. A third defect is that the concept of carrying capacity cannot accommodate the common observation that significant variations in population size and density occur consistently in different parts of a species' range, an observation familiar to fisheries biologists. Another example is that nesting populations of Herring Gulls on some islands are very dense while others are very sparse. One might conclude that these different densities reflect differing carrying capacities. On many islands, however, densities vary within the island population by factors of 10. If that much local variation is explained by detailed local differences in carrying capacity, the concept has little value in understanding populations except in the abstract.

b. An attack on density-dependent mortality

Some theorists rejected the concept of carrying capacity as soon as it was formulated. Andrewartha and Birch (1954) predicted that fluctuations would be undamped or would be influenced primarily by forces other than by inherent population mechanisms, i.e., by external forces indifferent to density. Their supporting data were drawn from field studies of insects in arid climates and their ideas were generally ignored or rejected by ecologists studying "more developed and mature communities." Some of their ideas are directly relevant to seabirds: for example, the number of occupiable ledges on a seabird cliff are fixed and when they are full, no more birds can breed there regardless of the density of the population or amount of food available. For another example, some biological processes act in ways that reinforce fluctuations. In a seabird colony invaded by a predator, the smaller the prey population the larger the percentage of the population taken by each predator. The importance that predation has as a selecting factor is shown by the adaptations marine birds and waterfowl have made to avoid it. The fact that large colonies of seafowl are usually concentrated on isolated, predator-free islands is one obvious case (Lack 1966). Cliff nesting itself seems to be an adaptation of Kittiwakes for avoiding predation (Cullen 1957).

Marine birds are indeed vulnerable to predation when on land and to interference in their reproduction by harassment by other species. Nettleship (1972), studying the effects of Herring Gulls on Atlantic Puffins, showed that the effect of harassment and stealing of food from the parents was the reduction of the amount of food brought to the young and hence, the reduction of reproductive success. In those parts of the colony where gulls were numerous or where the puffins were at a disadvantage in escaping from gulls (i.e., on flat rather than steep slopes) the reproductive success of puffins was significantly lower than in areas away from the gulls. It has not been shown that these effects are density-dependent rather than periodic, disastrous events which result from the capricious appearances of a predator where waterbirds feed. As such, the interaction between terrestrial predators and their waterfowl prey are those of the wild oscillations of foxes and rabbits or of raptors and lemmings, which have been used as examples of unstable systems.

There are many observations of subtle adaptations by which some waterfowl counter predation, but it has not been shown that density-dependent mortality is relevant to selection in favor of these characteristics.

Barry (1967) described the density-avoiding adaptations of arctic-nesting geese to evade predation--specifically by foxes. Black Brant (_Branta nigricans_) nest on low coastal or delta islands and escape predation by remoteness. Snow Geese (_Chen caerulescens_) are colonial on large, flat areas, gaining protection in numbers. White-fronted Geese (_Anser albifrons_) are solitary nesters on inland swamps, as though "over-dispersed" among scrub willow.

Common Eiders (_Somateria mollissima_), Black Scoters (_Melanitta nigra_), Tufted Ducks (_Aythya fuligula_), and other ducks select gull colonies as nesting habitat. Although there is little doubt that the ducks choose gull colonies for nesting, there is some doubt as to the reasons. Finnish biologists (summarized by Bergman 1957; Hilden 1965) have concluded generally that gulls protect the duck nests from predation by Hooded Crows (Corvus corone).

Although their ideas are useful in understanding changes in population size of many species, primarily insect populations, the generality of Andrewartha and Birch's (1954) hypothesis is weakened because it conflicts with detailed studies of seabirds which show that in many cases local food resources do limit breeding success. This was shown by Ashmole (1963) for tropical terns and Hunt (1972) for some colonies of Herring Gulls on the New England coast.

Thus, as Andrewartha and others have pointed out, instances of density-dependent mortality are abundant. The question is whether a) density-dependent mortality is a necessary mechanism selected as one of the characteristics of a population so as to escape population oscillations, hence a sign of a healthy population, or b) a general statement of overall effects but not a mechanism or species characteristic, as Lack (1954, etc.) argued. We return to this in some detail in section C, in which we discuss specifically density phenomena in the population of Herring Gulls in New England.

7. The Darwinian Model to Which We Subscribe

a. Opportunism, probabilism, and the individual

Some important assumptions of the Darwinian view include: a) each community or group of individuals is in the process of change (individuals are coming and going) so that cooperative interactions are brief; b) each individual is to some degree in competition with all other members of its population and community; c) actions which favor individuals will be selected without regard for the efficiency or functioning of the community; d) local extinctions can be expected to be followed by replacement from overflow of flourishing populations; 4) while density-dependent mortality (which can include either failure to breed or high mortality among young and adults) is a logical necessity of the observation that populations do not vary over more than several orders of magnitude, this "process" is not a necessary "mechanism" developed by selection to account for the survival of the species.

The idea that displacement from an equilibrium stimulates the beginning of processes which tend to reestablish the equilibrium may be suitable for describing physical systems, but it is not appropriate for explaining biological systems. One cannot argue using logical symmetry that because high densities are associated with high mortality rates and inhibition of reproductive rates, mortality will be reduced or reproduction stimulated at low densities.

While there are keystone species whose presence affects the numbers of other species, the removal of a species from an open system can occur without "damage" to the system, though there may be change. The ecosystem operates as a functional unit with "whatever is present." For example, if wolves are removed from the boreal forest the world of Moose selects for different characteristics than fleetness, etc.; the change is not a disaster to the Moose. Similarly, in the case of many open systems interacting, stability of numbers of individuals of any species may be of little (or great) importance to the survival of that species, or to the survival of other species.

This is not to say that trends in diversity, stability, etc., do not exist. There are obviously places where primary productivity is higher than it is in other places, where there are more species, where food-webs are more complex, where some populations appear to vary little (segments of the communities are stable), where nutrients are recycled extensively, or where energy appears to be used more efficiently. We do not accept the deterministic ideas that these regional or topographic differences in communities can be related in a functional way to the age of the community, to the development of interactions within community members, or to the maturity of the system.

We observe that energy flow through an ecosystem requires only a few basic elements, namely, the primary producers and the decomposers. The additional members of the community, the higher trophic levels, appear to be supernumary, temporary, and opportunistic. Further, observations along gradients of diversity indicate that any one or set of species can be removed without serious (or detectable?) consequences to the energy transfer, hence to the general functioning of the community as a whole. The removal of one species, especially a keystone species, may result either in the increase of some species or in the disappearance of some. The species at higher trophic levels take advantage of the species that exist, for their own benefit; but if those species are absent, the remaining system is just different. It is not in danger of falling apart; nevertheless a simplified system might be seen as damaged by those species (such as humans) who value the species which vanished. We assert that to formulate a model of ecosystem function based on integration and successional trends is to assign to the differences among communities mystical attributes which cannot be understood in Darwinian terms.

Models which assume optimal ecosystem functioning are irrelevant in simplest terms, as Harper (1974) emphasized. They run contrary to the theory of natural selection as we tried to show (Drury and Nisbet 1973). At worst, they inhibit investigations of what is actually happening with energy transfer and with how many species are present in an area, in what numbers, and in what places.

b. The assumption that fluctuations are "normal"

Recently theorists have built models based on assumptions that fluctuations are a general characteristic of population dynamics. One example is Gilpin's (1975) model describing multiphased oscillations. He took account of the fact that fluctuations (and models) become more complex as more species and non-linear effects are included. May and Leonard (1975) emphasized that the effect of non-linearities is to make it impossible to speak even in principle of the equilibrium point of a community. They pointed out that even though a model is deterministic (i.e., assumes that the system will come to equilibrium), the oscillations are so complex that they may appear to be random, and it may be a very long time before the system returns to a position near where the "cycle" started. "On the other hand a truly random ecological system could always be fitted by a suitably ingenious limit cycle. This suggests that ecological analysis which does not consider component processes must be viewed with great suspicion" (Gilpin 1975). May and Leonard (1975) and Gilpin are both making a familiar point--that neither the logic nor the interactions described in a formula will describe biological reality unless the assumptions are correct. They are also making a different point--that an ingenious mathematician can create a formula to describe almost any operation (whether its workings are systematic or random), and the formula may seem to work.

Gilpin's moral is that one cannot learn very much that is helpful by studying population fluctuations as such. One must study the factors controlling populations. This is a very old idea.

It would appear that defining carrying capacity and inherent rate of increase will not be very instructive in managing seabird populations other than in speculating upon what might be ideal upper limits. It can also encourage the musty sophistry that when a population increases beyond this abstract carrying capacity it "needs" to be cropped or hunted to prevent overcropping resources and damage to itself through a population decline. Third, it leads many people to conclude that species whose numbers oscillate, whether wildly or within some limits, are somehow abnormal because their populations are not adjusted to the local carrying capacity.

8. Impact of Deterministic Afterthoughts on a Probabilistic Theory: Island Biogeography

The ideas of independently oscillating populations and recolonization, which we have suggested are consistent with open systems and probabilistically functioning systems, are consistent with the theory of island biogeography in its simplest form (MacArthur and Wilson 1963). The theory encompasses two sets of probabilities: 1) the arrival of colonists varies according to distance from the source, and 2) survival and extinction vary according to the size of the island. This idea was modified by later addenda (MacArthur and Wilson 1967; Wilson 1968) to include concepts of adaptive reproductive rates and turnover rates, both of which carry implications of deterministic thinking.

Reproductive rates were described as strategies (MacArthur and Wilson 1967) with the suggestion that "K" species are selected on islands because they are less liable to extinction than are "r" species. The implication is that oscillation in numbers (resulting from rapid increase with "r" strategy and consequently exceeding the carrying capacity) carries with it danger of extinction. It appears that this argument reflects persistence of concern for Markhovian processes instead of consideration for the possibility that on islands, because seasonal differences in weather tend to be minimal, differences in food supplies between seasons similarly may be minimal. Where seasonal differences in food supply are small, clutch sizes and broods are small because parents cannot collect enough food to raise larger numbers of young. Hence, they have small broods, referred to as "K" adaptation, and are long-lived in a comparatively mild environment, and so invest less in reproductive effort than in competition as living individuals.

Vuilleumier and Simberloff (1980) pointed out that the concept of turnover rate assumes that on an island, competition will result in exclusion of some species when the equilibrium number of species is exceeded. This concept of equilibrium suggests that when one species makes it onto an island another species must go. This suggests fixity of the community structure, the number of "niches," and the integration of community--a very different model than the direct probabilities inherent in the odds of arrival together with the odds of extinction.

Vuilleumier and Simberloff correctly ask (we think): are the numbers of species found on oceanic or mountain islands the results of historical accidents, i.e., probabilistic processes, or is there an equilibrium number resulting from competition for a limited set of resources inherent in the island, its habitats or communities? We identify the calling upon an equilibrium to be deterministic thinking. In contrast, calling upon historical accidents is probabilistic and implies no preferred configuration.

In the next section we review the controversy through geomorphology, plant ecology, and animal ecology and suggest that there have been important influences upon animal ecologists by the assumptions of plant ecologists. In turn, the plant ecologists have built several geomorphological assumptions into their models of the behavior of vegetation.

B. A Consideration of General Systems Models in Geology and Ecology

From: "INTERRELATIONS BETWEEN DEVELOPMENTAL MODELS IN GEOMORPHOLOGY, PLANT ECOLOGY, AND ANIMAL ECOLOGY," by William H. Drury and Ian C. T. Nisbet, General Systems, Vol. XVI, 1971.

1. Introduction: System and Environment

The first step in formulating a theoretical model to describe a natural process is to delimit the scope of the model by making a formal distinction between the system, which is the primary object of study, and its environment--those parts of the external world which interact with it (Hall and Fagen 1956). Except for the special cases of systems which are completely isolated from the external world, as in classical thermodynamics (or which include it in its entirety, as in cosmology), every natural system is affected in some way by the states of its environment. The validity of a model of a system, and of the description of the system which it provides, will then depend not only on the characters of the model but on the assumptions made about the environment and its interaction with the system. In general, it is reasonable to assume that the behavior of the model will not be sensitive to small changes in the behavior assumed for the environment. In particular, the system is likely to be more or less independent of assumptions made about processes in the environment which take place on a sufficiently small scale (e.g., in time or in space). However, the assumption of large-scale order in the behavior of the environment is likely to result in the imposition of large-scale order on the behavior of the model. Such an effect may be mistaken for a deduction within the model if the assumptions made about the environment are not formulated explicitly.

Theoretical models in animal ecology fall into two general types: those in which the system under study is an entire animal community, and those in which it is restricted to one or a few species. In both cases the environment of the system includes the vegetation, climate, and (more remotely) the geology and landscape; in the second type of system it also includes the remainder of the animal community. The validity of the models then depends on the assumptions made, explicitly or implicitly, about the large-scale properties of the vegetation, climate, landscape, and animal communities.

This section includes a brief review of the developmental theories of geomorphology and vegetation and a summary of a case in which the predictions of the theories were compared critically with observation. Although geological processes do not often affect animal communities directly, the examples quoted will show how simplified concepts of geomorphology can affect the formulation of models of plant ecology, and concepts of vegetation can affect models of animal ecology. In other words, while most ecologists nowadays use the developmental terms in a loose and imprecise way, it remains to be shown that the implicit assumptions which they represent about long-term development of landscape and vegetation do not condition the conclusions which are drawn about the long-term behavior of animal communities. For example, succession through seral stages to a stable, efficient, productive climax community, although rarely expressed in Clementsian terminology, appears often as a basic assumption in theories of animal ecology. It therefore seems desirable to review the restrictions imposed by this model on botanical thinking, and to project these restrictions into animal ecology to suggest some of their likely effects.

A number of detailed reviews of contending theories in geomorphology and botany have been published (Chorley 1962; Hack 1960; Whittaker 1965; McIntosh 1968, 1969). We will not discuss at all the concept of climatic constancy that formed one basis for Clements's vegetational concepts, but it should be pointed out that abandonment of this concept has caused difficulties for the developmental theories of vegetation. We begin with an examination of the interrelations between theories of landscape development and theories of vegetation development.

2. Contending Theoretical Schemes in Geology and Plant Ecology

a. A note on terminology

The classical schemes of landscape description (Davis 1909) and vegetation (Clements 1916) are commonly called "dynamic" (Clements's term) because they emphasize progressive change in landscape and vegetation. In what follows, however, we propose to call them "developmental" schemes because they emphasize change towards a stable end-point. We use the term "kinetic" for theoretical schemes which emphasize continuous change and do not require the existence of an end-point.

b. William M. Davis's cycles of erosion

During the nineteenth century, geological controversy had centered on the problem of whether geomorphological forms were the result of present processes or of cataclysmic events in the past. Davis's theory (1909) was built on Lyell's Principle of Uniformitarianism, i.e., that present processes are adequate to explain all of the events which we can see. In applying the principle, however, he went only part way in accepting uniformitarianism. He assumed that present processes are active in only parts of the landscape, and that other parts have been molded by the same processes acting at earlier times. Davis's assumption was that any present landscape reflects the structure of the bedrock outcrops, the geological processes that are in action, and the stage or period of advance of those processes. He built from these assumptions a pedagogical scheme that came to be known as "Cycles of Erosion."

His ideas on the process of formation of landscape were influenced by his experience in the Appalachian Mountains; much of his theory is immediately applicable to the landscape patterns visible there. Davis saw many mountain tops with apparently accordant summits; that is, the tops of the mountains, whatever the kinds of rocks involved, appeared truncated at the same heights. He saw that some meandering rivers had cut down through rock strata so as to flow through deep, steep-sided valleys in mountainous regions. In some places rivers cut across a mountain ridge and followed the structure of the next valley. Unifying these various observations, Davis developed the concept that at some previous time, which he identified with the Cretaceous Epoch, the Appalachian region had been reduced to an essentially level plain, a

Peneplain, across which rivers had flowed wherever they happened to meander. Then renewed uplift of the land mass at the start of the Cenozoic (a period of mountain building) resulted in down-cutting of rivers, oversteepening of the stream beds, and therefore more rapid erosion. However, the courses of many rivers, now rejuvenated, were determined by the patterns they had followed on the previous surface, the Cretaceous Peneplain; hence the rivers follow "entrenched meanders" superimposed upon the topography below.

Each epoch of geological history, Davis reasoned, was a cycle of erosion beginning with the uplift of a block of topography of continental size. Once uplift was complete at the start of a cycle, erosion attacked this uplifted area and lowered the topography towards a Peneplain closely associated with the base level of erosion. This base is controlled by the level of the mouths of the draining rivers and is the surface which is inclined just enough to allow rivers to transport the products of erosion.

The Cretaceous Peneplain, identifiable on the flat tops of the Appalachian Mountains from Georgia to Newfoundland (the "Schooley Surface"), was the product of down-wasting during a previous, Mesozoic, cycle of erosion. This cycle had started with the mountain-building which created the New England Alps in the Permian Revolution (which ended the Paleozoic and introduced the Mesozoic).

Davis's ideas of Cycles of Erosion were consistent with contemporary theories of classification of geological time. Historical geology was built on the idea that there have been major periods of mountain-building in the Cambrian, in the Permian, and at the end of the Cretaceous, thus at the beginning and end of the Paleozoic and at the beginning and end of the Mesozoic.

Within each of the major periods of geological time there were epochs, each of which was defined by a minor period of geological revolution (uplift and mountain-building) followed by erosion.

c. The description of landscape in Davis's terms

At the start of an epoch, following uplift, topography will be, in Davis's allegorical sense, youthful. There will be broad, flat-topped uplands (the remnants of the previous cycle) between the river valleys, and youthful streams, fast-flowing, steep-valleyed, which will have many falls and rapids. The streams erode rapidly at their headwaters. As topography and streams mature, the valley-sides meet at the divides between river systems and then become gentler. The stream, when mature, is graded to its bed throughout its length; that is (i) the grade is steep in the headwaters (streams carry off materials more rapidly than they are produced by erosion), (ii) the grade is at equilibrium in the region of the mature stream (erosion balances what the stream can carry off), and (iii) the grade is low in the lower reaches of the stream (more material is brought to the stream than it can carry away). Stream maturity occurs when the whole system is adjusted. This event is essentially momentary, when all streams in the drainage basin are adjusted to a base level and able to carry off their load. Before the moment of maturity, large areas of slope and surface are still in the erosional context of the previous erosion cycle. After the moment of maturity, many areas are no longer adequately drained and are thus removed from the present cycle of erosion.

In old age, the stream meanders across a broad plain, unable to remove the products of erosion brought down to it from the more youthful portions upstream; i.e., it approaches the base level of erosion. During old age, large areas of the erosion basin have been abandoned by erosion and are stable surfaces, in essence, peneplain elements. The original uplifted surface has been removed except in remnants preserved because of their resistance (hartlings) or their remoteness (fernlings) from the river. The Peneplain, once established, persists until it is eroded by processes set in motion by further uplift in the next cycle of erosion.

d. Plant Succession

The concept of Succession to a stable, self-perpetuating community is the intellectual analogue in botany of the development of landscape to a stable peneplain.

Cowles (1899, 1901) described differences among plant communities on the Indiana sand dunes, correlated with distance from the Lake Michigan shore. In so doing, he assumed that distance from the lakeshore was correlated with the age of the dunes. This correlation is built on the assumption that spatial differences in vegetation and soil are a mirror of temporal events, not merely of stability and shelter.

Cowles described in detail the sequence of vegetation types: (i) the vegetation of the active, blowing sand of the beach, (ii) the vegetation of the dunes where Marram Grass consolidates the sand, (iii) the vegetation of the sheltered backs of these dunes, and so on. He concluded that through the years the vegetation consolidated the sand; then dead vegetation collected, building up soil; on this soil other plants were able to grow, their remains further leading to the development of better soils, allowing forest trees to grow. He reasoned that with increasing age there was an increasing soil stability, development of the soil profile, and a succession of vegetation.

e. Frederick E. Clements's developmental scheme of vegetation

Clements grew up in the sand hills of Nebraska and formulated the concept of the prairies as natural vegetation, in contrast to the traditional American view of the grasslands as "the Great American Desert." He developed the idea that the great vegetational regions were not only natural but keyed to the climate of the region. Clements was influenced by Cowles's studies of plant Succession. But his ideas of evolution toward stability were probably also influenced by the general late nineteenth century assumptions of determinism and of social evolution and adjustment toward balance of political power and stability. Davis's stable old landscape surfaces, uniformly and thickly carpeted with matured soils in which local soil and rock differences were eliminated, provided the substrate upon which competition among plant communities would determine which will finally dominate the landscape. The idea that the Schooley Surface had existed since Cretaceous time had great impact upon botanists, who took the concept literally: if the surface existed during the Mesozoic, it must have been available for the persistence and development of vegetation. In Clement's scheme, plant succession is:

> . . . the process through which tightly organized groups of species called associations interact with their substratum to modify their habitat and pave the way for occupation by other associations not previously able to occupy the habitat. According to this generalization, the outcome of successional developments is determined primarily by the climate because the characteristics of the substrate undergo extremely slow and orderly change related to the formation, uplift and dissection of one or more peneplains. (Hack and Goodlett 1960, p. 61).

The eventual outcome of this slow and orderly change was supposed to be a fully adjusted, and hence unchanging, vegetational formation, which Clements called Climax. The word Climax was related to regional climate. Its association with the idea of a culmination of a sequence of developmental processes came later, but the analogy between Peneplain and Climax is clear.

The successional sequence, which Clements called the sere, is the second major element in his theoretical scheme. Following disturbance, in the process known as recycling, the vegetation retraces and displays the stages of development and establishment of the normal "mature" formation. The major stream of development Clements called the prisere; the establishment, competition, and replacement of species in plant communities he called ecesis. He considered the effects of disturbance by fire, erosion, and factors such as local soils, temporary; hence the changes resulting from these were called secondary succession, but they also return the vegetation to the normal equilibrium--the Climax.

Clements saw in Succession the maturing of the vegetation, a process similar to the stages of a life cycle of an individual:

> The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures that are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, of which all initial and medial stages are but stages of development . . . a formation, in short,

> is the final stage of vegetational development in a climatic unit. It is the climax community of a succession that terminates in the highest life-form possible in the climate concerned. (Clements 1916, restated 1936, p. 161).

He visualized each vegetation stage preparing the soil for the next vegetation to occupy the site. He hypothesized a system of development whereby communities replace each other in succession until the stable equilibrium vegetation occupied the site. Each formation had its characteristic stages of succession or maturation.

Some botanists, and many zoologists, nowadays use the term Succession in a weaker sense, to refer merely to the sequence of changes which follows disturbance of vegetation. Clements, however, as is clear from the above quotation, used the word to imply progressive replacement of communities, preparation by each stage for the vegetation of the next stage, and progression towards a predictable end-point that is determined by the climate and not by the intermediate stages. Thus the concept of Succession is intimately connected with the concept of Climax, and each is unintelligible without the assumption of the other.

Clements considered plant species as uniform, consistent with the type concept generally held by botanists at that time. If species, according to the type concept, are uniform, the members of the community will have a fixed and consistent relationship with each other. Reasoning from space to time, as he did in considering Succession, he concluded that because the forest or prairie Climax is consistent over a regional extent, it must also be continuous through time; hence the mutual adjustments among organisms in the Climax result from their association together and the selection pressures which make them fit into the organization. This concept is expressed in the idea that the members of a community react among themselves while the community as a whole reacts with the physical environment.

f. Developmental systems of soil classification

The analogy between the developmental theories of landscape and vegetation is obvious, and the dependence of the Climax concept on that of Peneplain has been demonstrated in the extracts quoted above. The direct connection between the two schemes is in the soils, which develop under the influence of both landscape and vegetational processes.

In Davis's scheme, as the erosion cycle starts, bedrock outcrops, falls, and rapids are common, and deep soils persist only on the remnants of the older, higher surface. As the cycle proceeds, soils thicken and develop, especially downstream, so that at the end of the cycle the whole lowland Peneplain is covered with deep erosional and residual deposits. The classical scheme of soil development assumes that mature soil types are associated with mature vegetation types, both being products of a long period of growth and integration under constant environmental conditions.

The mature soils, the Climax vegetation, occur on the deep alluvial or residual deposits of the mature land surface--the Peneplain. Because the Peneplain soils are deep and deposits of the river-borne debris include minerals carried from all parts of the previous drainage basin, they were assumed to be homogeneous, independent of the local rock and spread as a deep blanket over all the surface. Each Climax and soil type is determined by the regional climate which determines the final stable community. Local effects of drainage, topography, and bedrock can only be temporary in the development of mature or climax soils as they are in the development of the Peneplain.

g. The kinetic schemes of Gilbert and Gleason

Even before the presentation of Davis's theory, an alternative theoretical scheme for the description of landscape development had been formulated by Gilbert (1880). His report on erosional processes in the Henry Mountains of southern Utah used a theoretical scheme in which a steady state exists at all times because import of energy and materials is balanced automatically by export. Each disturbance alters the system so that it reaches a new steady state determined by the changed transport of mass and energy. The theoretical framework used is essentially that of the open system (von Bertallanffy 1950, 1956); open system treatment is especially applicable to a drainage basin, because the form of the basin is determined by the rates of inflow and outflow of materials.

Gilbert's description of stream action emphasized reciprocal effects upwards and downwards within the system:

> Of the main conditions which determine the rate of erosion, namely the quantity of running water, vegetation, texture of the rock, and declivity, only the last is reciprocally determined by rate of erosion. Declivity originates in upheaval or in the displacement of the earth's crust by which mountains and continents are formed; but it receives its distribution in detail in accordance with the laws of erosion. Wherever by reason of change in any of the conditions, erosive agents came to have locally exceptional power, that power is steadily diminished by the reaction of the rate of erosion upon declivity. Every slope is a

> member of a series receiving the water and waste of the slope above it, and discharging its own water and waste upon the slope below. If one member of the series is eroded with exceptional rapidity, two things immediately result: first, the member above has its own level of discharge lowered and its rate of erosion is thereby increased; and second, the member below being clogged by an exceptional load of detritus has its rate of erosion diminished. The acceleration above and the retardation below diminish the declivity of the member in which the disturbance originated, and as the declivity is reduced the rate of erosion is likewise reduced.
>
> But the effect does not stop here. The disturbance that has been transferred from one member of the series to the two which adjoin it is then transmitted to others and does not cease until it has reached the confines of the drainage basin. For in each basin all lines of drainage unite in a main line and a disturbance upon any line is communicated through it to the main line and thence to every tributary. And as a member of the system may influence all others, so each member is influenced by each other. There is an interdependence throughout the system. (Gilbert 1880, pp. 117-118).

Reciprocal effects of stream action extend upwards to the point at the very tip of the final division of the drainage which Gilbert considered to be the most sensitive spot of all. Above that, drainage on the slopes is either in sheets or in rills and as a result the shape of the surface changes from concave upward (which is the pattern of a stream) to convex upward (which is the pattern of a divide). The divide is controlled by creep; the stream is controlled by erosion. The reason that the divide is convex is that its motion is most rapid where already steepest. As Gilbert sees erosion, displacement by stream action at the highest tip of drainage has a maximal effect because it changes the focus of the ampitheater, or funnel, of creep and translates its influence throughout that funnel, essentailly 180° around the head of the drainage. Because of the oversteepening involved in creep, instability is greatest at headwaters or where streams pass out of hard rocks onto soft rocks.

Hack (1960) asserted that a moving equilibrium is established almost as soon as erosion starts and that it exists at all stages with no time variation in the forms as they are developed. Leopold, Wohlman, and Miller (1964) have shown that both longitudinal and lateral adjustments of the stream bed are continuous. Immediate adjustment of channel shape and cross-section occurs at every flood or low water flow, so that the river is always and everywhere adjusted to the instantaneous stream volume, whatever may be its longitudinal profile. Furthermore, Leopold and Maddock (1953) have shown that the sediment load is also included in the moving equilibrium, in opposition to Davis's statement that a "senile" river cannot carry the sediment brought down by its headwaters.

Gilbert considered vegetation to be highly important in the process of weathering by discouraging erosion, because its presence interrupts the flow of rain and its roots hold the soil. Thus in the Henry Mountains, the slopes on the higher peaks where there was more rainfall were vegetated and rounded, whereas the ridges on the lower hills, where there was less rainfall and little vegetation, were abrupt and sharp. (In the scheme of Cycles of Erosion, the upper rounded slopes would be identified as uplifted, partially dissected remnants of a previous erosion cycle.)

According to Gilbert (1880), down-wasting of the land surface occurs on all surfaces essentially at the same time; the whole land surface, its valleys and its uplands, are all being eroded simultaneously and constantly, instead of having some elements actively attacked and reduced while other parts of the topography are abandoned. Furthermore, the idea that episodes of mountain building have been intermittent or cyclic has been replaced by a concept of very slow and continuous uplift (Hack 1960). Thus changes in landscape form should not simply reflect processes of running down, but adjustment between rates of uplift and rates of down-cutting.

h. Gleason's individualistic concept of the plant association

At the same time that Clements constructed his developmental model of vegetation, Gleason in the United States, Fournier and Lenoble in France, and Ramensky in Russia formulated kinetic models. Gleason (1926) recognized the usefulness of plant associations:

> Plant associations exist; we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with their environment, we can frequently discover their past history and make inferences about their future . . .
>
> We all readily grant that there are areas of vegetation, having a measurable extent, in each of which there is a high degree of structural uniformity throughout, so that any two small portions of them look reasonably alike. (Gleason 1926, pp. 8, 9).

However, he went on to point out the continuous gradations in the species constituents of associations:

i) Associations are vaguely defined. Where the change in the environment is abrupt, the transition line in vegetation is sharply defined and narrow. Where there is a gradual transition in the environment, there is a correspondingly broad transition zone in the vegetation.

ii) Associations have arbitrary geographic boundaries and no two areas of similar vegetation are identical in species composition. Plants typical of one community are often found in many other types of vegetation; it cannot be told whether these isolates are fragments or embryos of a vegetation association.

Lake shores in the same region, for example, have similar vegetations, yet the glacial lakes from Maine to Saskatchewan differ gradually so that

> . . . westernmost and easternmost of the series, while still containing some species in common, are so different floristically that they would scarcely be regarded as members of the same association.
>
> No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark the boundary between them. (Gleason 1926, p. 14).

iii) Vegetation structure in one spot varies from decade to decade so that associations originate and disappear with varying speed.

> And just as it is often difficult and sometimes impossible to locate satisfactorily the boundaries of an association in space, so it is frequently impossible to distinguish accurately the beginning and end of an association in time. (Gleason 1926, p. 13).

iv) The same environment may have different vegetations, e.g. the deserts of Australia and Arizona and the treeless highlands of Chilean Andes or Oregon Cascades. The same vegetation may occur in different environments, e.g. White Pine forests in Massachusetts and Michigan, prairie grasslands in Illinois and Nebraska, cedar swamps in Indiana and Florida.

The vegetation of an area, Gleason concluded, is the result of two factors: the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment. As a result of constant seed immigration, every plant association is regularly sown with seeds of numerous extra-limital species, as well as with seeds of its own normal population:

> . . . every plant association tends to contain every species of the vicinity which can grow in the available environment . . . Each . . . is fully entitled to be recognized as an association and there is no more reason for regarding one as more typical than another. (Gleason 1926, pp. 18-19).

The last sounds analogous to the appearance of the population concept in modern systematics, as does:

> This diversity in space is commonly overlooked by ecologists, most of whom of necessity limit their work to a comparatively small area . . . (Gleason 1926, p. 15).
>
> Under the individualistic concept, the fundamental idea is neither extent, unit character, permanence, nor definiteness of structure.
>
> It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and,either with or without mutual influence, of the result of causes in continuous operation. (Gleason 1926, p. 25).
>
> In conclusion, it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of their

> normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of definite communities. Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into successional series, has not yet been achieved. (Gleason 1926, p. 26).

i. The kinetic scheme in soil classification

The connection between landscape processes and vegetation is directly mediated by soils in a kinetic scheme, too. Soils develop under the influence of weather, landscape processes, and vegetational activities and products.

Nikiforoff (1942, 1956) has shown that development of a mature soil profile is rapid and closely responsive to the vegetation on the site. Olson's (1958) reanalysis of soil processes on the Indiana dune site of Cowles's classical work emphasizes the same point. Soil profile development in Nikiforoff's scheme is the expression of a steady state of outflow of materials so that organic matter, dissolved minerals, and clay-sized particles are removed as fast as they are added. Within this context we can visualize all hilltops, slopes, and valley bottoms lowered by creep, corrosion, or buried by sediment in a continuum while soil processes, determined by the local vegetation, maintain mature soil profiles in a steady state during down-wasting.

3. A Case History

a. The Appalachian mountains and forest revisited

Braun made a comprehensive analysis of the regional vegetation of eastern North America on a developmental basis (1947, 1950). Her study (1947) of the forests of the Appalachian Mountains, together with Davis's work on the geology of the same region (1909), represents the definitive description of this region in terms of the developmental models of Davis and Clements.

Subsequently Hack, a geomorphologist, and Goodlett, a botanist, have worked together in the center of this classic region, the Shenandoah Valley of northern Virginia. In a comprehensive paper (1960), they have compared interpretations of their observations provided by both "developmental" and "kinetic" models. They contrasted the assumptions of the two schemes and their relative merits in clarifying the observations.

b. The developmental interpretation

According to Davis, the flat tops of the mountains show accordance of summits and discordance of structure. They are remnants of an uplifted, partially dissected Cretaceous Peneplain--the "Schooley Surface." Another partially developed Peneplain is shown by the high shoulders of many valleys, the "Harrisburg Partial Peneplain," the product of a later and incomplete cycle of erosion. These surfaces have been identified in Hack and Goodlett's study area (Stose 1922). On these surfaces one would expect development of deep, mature soils and the mature Climax forest. Expressing this, Braun took the long view of geomorphological and vegetational process:

> Here also, physiographic history seems to have had a profound effect upon the nature of present-day vegetation. On the ravine slopes formed in the latest erosion cycle, the vegetation is developing in response to present forces, both topographic and climatic. Although very limited in extent, it seems logical to assume that mixed mesophytic forest is the potential climax of the area; that by its development the extent of the mixed forest, greatly restricted at one or more times in the Tertiary and early Pleistocene, may expand eastward into what we now know as the Oak-Chestnut region. The outliers are forerunners in a development which would take thousands of years to complete, for it must await development of land surfaces and of soils no longer related to the Harrisburg cycle. That these mixed mesophytic communities are not relics of a former more extensive mixed mesophytic region (mixed forest of the Tertiary) seems certain because of their limitations to surfaces produced in the last (or present) erosion cycle. (1950, p. 242).

c. The kinetic interpretation of landforms

Hack (1960) found that the measured profiles of ridge crests and the convex upper slopes of mountains could be described by simple power functions of the form

$$H = CL^f,$$

where H is the fall from the ridge crest, L is the horizontal distance from the ridge center, and C and f are constants, which define the steepness and curvature of the slope respectively. Although C and f vary over a wide range from ridge to ridge, they were found to obey closely an empirical relationship which was the same for different substrates. Thus the shapes of the upper parts of the mountains follow a universal empirical law and therefore can be understood as resulting from contemporary erosional processes. The assumption that the upper mountains are the remains of an ancient Peneplain is not only unnecessary; it requires that the empirical law be dismissed as a set of coincidences.

Furthermore, other geologists have pointed out the close relation between the altitude of the mountain ridges of the region and the structure and physical properties of the bedrock (Edmundson 1940; Thompson 1940). Hack and Goodlett (1960) showed that all the higher mountains in their study area correspond to the Pocono sandstone, the most resistant rock of the area.

Hack (1965) has subsequently shown that the gradients of the "Harrisburg Partial Peneplain" can also be related to present-day drainage, without invocation of hypotheses of uplift and partial dissection in the past.

d. *The kinetic interpretation of vegetation*

Summarizing studies of the distribution and interrelations of the tree species, Goodlett (1954, 1960) reported that the present distribution of many of the tree species as well as the forest types is closely related to topography, orientation of slopes, and the nature and altitude of the bedrock. The main unifying principle underlying the coincidences is water. Thus on the hot, dry ridges and noses he found a forest type characterized by yellow pines (*Pinus rigida* and *P. pungens*), in the hollows where the microclimate is cooler and moister he found forest characterized by northern hardwoods (Sugar Maple, *Acer saccharum;* Basswood, *Tilia americana*; Yellow Birch, *Betula lutea*), and on the intervening slopes he found varied oak forests containing none of these species. Sugar Maple and Basswood, together with Tuliptree (*Liriodendron tulipifera*) are listed as the three dominant species in the "mixed mesophytic forest" which Braun (1950) regarded as the potential Climax of the region.

> Concave areas on slopes, which characteristically support northern hardwood forest, are the product of the geomorphic process of stream sculpture. However, once formed by stream sculpture, a concavity undergoes erosion and grading largely by creep, which is encouraged by the same moist conditions that seem to determine the distribution of the northern hardwood forest type. Convex areas on slopes characteristically support yellow pine forests; therefore, the distribution of yellow pine forests is related to the distribution of land-forms created largely by the process of creep. Rates of creep probably are extremely slow on these noses and ridge crests because the environment is dry and because the volume of material originating on the slope above is less. Dryness presumably controls the presence of yellow pine forest. Convex areas thus tend to be more stable habitats for plant growth than concave areas, and the yellow pine forest probably undergoes less disturbance than the northern hardwood forest. It can perhaps be said, then, that the yellow pine forest is characteristic of relatively stable areas whereas the northern hardwood forest is characteristic of relatively unstable areas. (Hack and Goodlett 1960).

This, of course, is a contradiction of the idea of Succession through pine stages towards a stable Climax of a complex northern hardwood forest type.

Furthermore, the greater diversity of the hardwood forests on the flood plains appears to be maintained not only in spite of their instability, but because of their instability. Studying an area devastated by a flood six years earlier, Goodlett (1960, pp. 49-51), found that the bare areas created by the flood had been reseeded by nearly all the tree species that generally constitute the bulk of both the forests of the flood plain and slopes, and lacked only a few of the species found in the hillslope (older) forest. He suggested that "in large part, the greater number of species in the damaged flood-plain may be the result of periodic inundation by seed-carrying flood-water." Working in a nearby part of the Appalachian Mountains, Whittaker (1965, 1966) has similarly been unable to confirm by empirical evidence the implications of the developmental sequence; he found no consistent relations between diversity, community productivity, disturbance, and succession. The northern hardwood forests in moist cove valleys are characterized by high rates of primary production, but even higher rates were found in disturbed area (Whittaker 1966). According to the developmental theories, biomass, production, diversity, uniformity, efficiency, and stability should all increase with Succession and reach maxima in the Climax (for review see Whittaker 1953).

e. Vegetation and soil erosion

Hack and Goodlett (1960) began their study to investigate the results of a spectacular local flood which had devastated some of the valleys six years earlier. In the developmental systems, vegetation and stable mature soils combine to offer each other maximum protection. In the study area Braun (1950) had identified the theoretical "mixed mesophytic forest" as the potential Climax and considered all other types of forest as transitional or successional. Most of the area had been logged in the late nineteenth century, so it is thus logical within this system to consider the resulting second-growth forest as "inferior" or "immature." Accordingly, the U.S. Forest Service reported on the flood:

> Most of the landslides started on steep slopes near the tops of hog-backs or divides. In these areas, natural regeneration has been slow. It consisted of inferior young stands of rather open and brushy

> type. In general, slides did not occur where thrifty, normal stands had developed. In fact, when some slides reached better stands, the slide was restricted in width and a few slides stopped altogether.
>
> This storm showed how long it takes land to recover fully from past abuse. It showed the urgency for early initiation of good land use and management practices . . . (Anon. 1950, pp. 31-32).

To attribute the flood damage in this way to the "inferiority" of the vegetation carries the implication that stable mature vegetation would have prevented it. Arguing against this, however, Hack and Goodlett pointed to debris from older landslides which had occurred prior to the disturbance of the forest by logging, and showed that the assumption that undisturbed forest protects the soil from landslides leads to a contradiction.

> Compound debris fans are unequivocal evidence of flood damage to slopes in the past, prior to the period of logging, and probably prior to the time of settlement by the white man. Either the forests mantling the slopes in the past were not all "thrifty normal stands"--a possibility--or the slope forests, regardless of quality, cannot control huge volumes of runoff. There is a limit to the amount of runoff that a forest can withstand. This limit determines the density of drainage channels, and were there no limit to the protective powers of the forest there would be no stream channels at all. (Hack and Goodlett 1960, p. 56).

If the maturation of vegetation were a consistent process, one would expect that, by the effects of Succession, progressively older landslides would contain tree species progressively more similar to the regional norm, but Goodlett found the species composition on the oldest landslides to be indistinguishable from that of the young growth on the newest slides.

f. Summary of kinetic interpretation

Summarizing their results, Hack and Goodlett state:

> The present distribution of many of the tree species as well as of the forest types is closely related to topography, orientation of slopes, and the nature and attitude of the bedrock . . . (Hack and Goodlett 1960, p. 32).
>
> The most important lesson to be learned from the landforms of the Little River area relates to the extraordinary regularity of the landforms and the nicety of adjustment of the soils and vegetation to them. The close relation between these three terrain elements has been demonstrated over and over again in the preceding pages. The correlation extends even to the asymmetry in their distribution pattern. The explanation for the relation is that the mountains are shaped or graded in such a way that the products of decay of the bedrock can be moved across the ground surface and carried off in the channelways out of the area. Various processes that differ in relative effectiveness in different parts of the valley act to transport the debris, so that the graded slope must also be different from one part of the valley to another. The resulting regular forms are the product of this adjustment in a region where the underlying bedrock is rather uniform. As time goes on, the entire landscape is lowered. Though the slopes may flatten through time, the entire mountain mass retains a form graded for the transportation of waste materials.
>
> The vegetation reflects the local differences in process, slope, and environment. Difference in forest type within one valley are often as great as the regional differences between the forests of the northern Appalachians and those of the southern Appalachians. The magnitude of these differences is a reflection of the extreme diversity in the physical environment between different parts of the valley. (Hack and Goodlett 1960, pp. 57-58).

As they pointed out (p. 58), the picture envisaged is that of a steady stage in an open system (Chorley 1962). The steady state is shifted by short-term disturbances, such as flash-floods, by medium-term disturbances, such as changes in climate or in the frequency of floods, and by long-term disturbances, such as the steady reduction in relief produced by continuous erosion. In each case those parts of the system whose time-scale is shorter than that of the disturbance react to produce a new steady state. This type of moving equilibrium is characteristic of open systems (von Bertalanffy 1950).

g. Failures of the developmental interpretation

Of the six major predictions of the developmental theories, all are inconsistent with Hack and Goodlett's observations. The summits are not "discordant in structure": all can be related to the same strata of resistant rock. The form of the upper slopes conforms to a universal law which reflects active erosion and is thus inconsistent with the concept of an older Peneplain, as yet uneroded in the present cycle. The Climax is found on the most unstable areas, not on the theoretical Peneplains. The diversity of the forest type which approximates most closely to the theoretical Climax appears to result from repeated disturbance, not from long development. Mature forests failed to protect mature soils from erosion, even in the epoch before man's interference. There is no evidence of vegetation development on progressively older landslides.

None of these discrepancies necessarily undermines the structure of the developmental theories; each could be attributed to a defect in interpretation within the structure. Thus, for example, it could be argued that the Cretaceous Peneplain lay above the Schooley Surface and has already been fully eroded. Or it could be argued that the theoretical Climax forest has not yet evolved; in other words, that the entire vegetation of the region is Successional. Yet to argue thus, that Peneplain and Climax no longer exist, or do not yet exist, even in the classic area for their identification, would seem to change the concepts almost into the nature of myths. In fact, it is easier to explain the conflict between theory and observation in terms of the structure of the model.

In a kinetic theory, observed forms are analyzed in relation to observable processes; only when discrepancies appear does it become necessary to invoke hypotheses about past events. In the developmental theories, however, the assumption of stable equilibrium is made at the outset; when only change is observed, the assumed equilibria must be placed in the distant future and distant past. It then becomes less important to describe the processes of development than to identify the stage of development and the elements which will become important in the distant equilibria. When attempts are made within the developmental theories to identify frozen or partial equilibrium states in the present landscape, the predictions are often found to be incorrect; but this can be attributed merely to errors in identification. The defect of the developmental theories is, then, not that they fail to make correct predictions, but that they are based on assumptions which are unnecessary and unverifiable.

4. Developmental Models in Animal Ecology

There are two broad types of model in animal ecology which utilize the assumptions of the developmental theories.

a. The first comprises those models in which the animal community is the system and the developmental assumptions are applied (explicitly or implicitly) to the plant community which constitutes the environment. In these theories the vegetation is treated as the habitat background within which the animals interact; the effect of the developmental assumptions is that they prescribe a predetermined sequence of changes and an ultimate stable equilibrium in the environment. This has three important consequences:

i. It results in a substantial decoupling of the system from the environment. Just as the adoption of a deterministic model for the evolution of landforms provided an independently specified description of the environment within which the vegetational system develops, so the inclusion of the vegetation in the same deterministic model provides an independently specified description of the environment. When a correlation is observed between the structure of the vegetation and the complexity of the animal community (MacArthur 1961), this is interpreted as cause and effect respectively (MacArthur 1965): the reciprocal effect of the animals on the structure of the vegetation must necessarily be excluded from the model, because the structure of the vegetation is *ex hypothese* determined by Succession--"a characteristic of the community itself." Clements's insistence (1936) that the Climax vegetation is determined only by the regional climate is the prototype for this decoupling: the distribution of grassland, for example, determines the distribution of the grazing herbivores, but the latter are not considered to affect the distribution of the grassland by eliminating invading plants from other formations. In a rigid extension of the theory to animal ecology, the animals will themselves form a Climax community determined by the regional climate, and no interactions between animals and plants need be considered at all; or the interactions are developed in the course of coevolution towards the goal of optimal functioning.

ii. The assumption that plant associations follow one another in an orderly succession, until a perennial and spatially consistent Climax is reached, leads to the typological concept of habitats as discrete and classifiable units. The task of descriptive animal ecology then becomes the association of animal communities with these habitat units (Pitelka 1941; Shelford 1963), and that of quantitative animal ecology becomes the interpretation of interspecific interactions within the units (MacArthur 1965; Hutchinson 1965; Levins 1968). Evidence which is interpreted to mean that animal communities rapidly reach equilibrium with their habitats (Levins 1968; MacArthur 1967) then predicts that animal communities should form discrete typological units matching the habitats. Within such a scheme the succession of animal communities is regarded as a consequence of plant succession (Shelford 1913), and the interrelations of animals in the Climax communities (where they exist) must be a consequence of interactions (e.g., competition) in the past. In particular, the mature animal communities must be matched with the mature plant communities, ex hypothese perennial, and must migrate with them as climatic conditions change. The habitat requirements of individual species, at least in the Climaxes, must thus be attributed to events in the distant past (Mengel 1964). The limitation of such models is that they preclude enquiry into the reasons for regional differences, or historical changes, in the habitat preference of single species. Further, non-conforming species must be dismissed as anomalous or successional and hence outside the scope of the model. When it is found that the distribution of a group of animals as a whole is not well correlated with that of the habitat units, as was pointed out for birds by Peterson (1942), it can then be argued that the whole system has not yet had time to mature. The assumptions of the model are thus in a sense unfalsifiable, because it leads to specific predictions only for Climax communities, which are identified only by agreement with the predictions, and are projected into the future where agreement cannot be found.

iii. Another consequence of the typological view of habitats is the distinction between "within-habitat" and "between-habitat" structural properties of animal communities (MacArthur 1965). To be self-consistent, such a distinction must remain the same when a larger area is sampled, and this is only possible if the habitats are spatially consistent. However, if an inconsistency is observed, this can be attributed to erroneous identification of the "habitats" (MacArthur 1961, 1965). In practice, there is an almost unlimited number of ways to divide the vegetation of an area into habitats, so it is impossible to falsify deductions from a model that assumes that the diversity of an animal community depends in some functional way on the vegetational units which comprise its environment.

b. The second type of model in animal ecology is that which applies the developmental scheme explicitly to the animal community. As shown above under ii, these models arise logically from the use of the developmental scheme to describe the vegetation, just as Clements's system arose naturally within the developmental scheme of geomorphology. Likewise, all these models require a developmental classification of the vegetation, and many of them include it explicitly.

One limitation of these models is the practical difficulty of identifying Climax formations as consistent associations of animal species in space or time. Partly to circumvent this difficulty, other models identify stages in animal Succession by means of other properties which theoretically change in a deterministic fashion. As Margalef (1968) points out, different authors disagree on the most significant properties to use, but the four most common are diversity, stability, efficiency, and productivity. The limitation of all these models is that special mechanisms have to be devised to accommodate these theoretical properties within the framework of natural selection. Thus the assumption that stable communities are more permanent than unstable ones requires that natural selection should act to prevent protracted increases or decreases in a species' population (MacArthur 1966). Such an action is contrary to orthodox concepts of natural selection (Lack 1966), but these can be circumvented if we invoke some form of group selection (Wynne-Edwards 1962; MacArthur 1967, p. 152). Such mechanisms are necessary under the assumptions of the developmental models, and the assumptions themselves are not in practice falsifiable. If, for example, we go into the field and find that diversity and production reach higher values in early successional stages than in late successional stages (Whittaker 1966), it can always be argued that the successional sequence has been wrongly identified, or that the Climax has not yet had time to evolve to maturity. Again we find the characteristic property of the developmental models, that they make predictions about the behavior of elements of the system which can only be identified by reference to the predictions, and need not be present at all in the present epoch.

5. Conclusion

a. General

We have been concerned with making two main points in this appendix. First, the behavior of the models one makes of systems are conditioned by assumptions made about the long-term behavior of their environments. To assume that landscape develops in a predictable way to a stable equilibrium determines that vegetation, and hence animal communities, will also do so; moreover, the structure of the model excludes reciprocal action of animals on the development of vegetation, and of plants on the development of landforms. Second, the assumptions of the developmental models limit the type of question which can be asked within the framework of the model. This is not to say that the assumptions and the conclusions drawn from them are necessarily wrong, but rather that they preclude their own falsification. The main advantage of the kinetic type of model is, then, that it includes the developmental model as a special case. In general, ecological systems comprise a large number of sub-systems, each proceeding on a different time-scale. The main restrictive feature of the developmental models is that some of these time-scales (e.g., those for reciprocal actions, for orogenesis, for immigration and evolution of new species, for local extinctions and reseeding) are made indefinitely long compared to other time-scales of interest: the effect is to place significant events far into the future or into the past. In the kinetic models, these time-scales remain finite; if any are really very long, this can then be established by deduction and observation. Thus diverse, stable, efficient animal communities may in fact exist now, in the future, or in the past, but this cannot be established by assuming that they must have done so in an ancient Climax, on an ancient Peneplain.

b. Where and when diversity and productivity increase

We have argued against development as an evolutionary or directed process which results in an increase of all of these characteristics of "mesophytic" communities together. We observe that coincidences of climate, topography, sunlight, moisture, and nutrients make some places very favorable for plants and animals. Some places have constant and mild climates and these often have large numbers of species. Areas where climates are subject to wide fluctuations in temperature and rainfall (or low rainfall and low temperature) have fewer species than adjacent areas at whatever latitude. If more species live in a geographic region because it is favorable for coexistence of species, the communities are diverse. More species indicates more favorable conditions, not greater maturity of community. There is no evidence that productivity and diversity will increase in the Arctic until climates moderate; therefore, Dunbar's suggestion (1968) that Arctic systems are immature cannot be used as an explanation. There are many places in the Arctic where there are concentrations of species, such as in the Bering Strait Region, but the reasons can be shown to be related to factors directly observable today, such as relative moderation of climate, diversity of habitat, areas of high primary productivity, accessibility of both Eurasian and New World faunas and floras, and a history relatively free of the exceptional stresses of a major glaciation. A major characteristic assigned to mature, well-developed communities is their stability. The chief mechanism by which stability is achieved and maintained is identified as density-dependent reproductive rates and mortality rates. Darwinian natural selection is not a mechanism by which to develop mechanisms for self-regulation because individuals who cheat against the system of self-regulation and produce more offspring even in the short term will be selected for. The only mechanisms by which self regulation can be selected involve group-selection. For a review of debate for and against group selection see Wynne-Edwards (1959, 1962), Crook (1963, 1965), and Lack (1966).

In an open system individuals are free to move out of areas where populations are uncomfortably dense, hence relieve the pressure of density. In such a system how do populations behave and what are some mechanisms by which populations are regulated? We discuss these questions in the next section.

C. The Relevance of Movements to Theories of Population Regulation

1. Population Regulation in the Herring Gull, *Larus argentatus*[1]

Theories involving self-regulation implicitly consider closed populations, and their deductions would be invalid if applied to dispersing populations without definite boundaries. Closed populations have been studied in the field (Stonehouse and Stonehouse 1963; Snow 1966; Nelson 1969), but even in these cases the regulating factors have been envisaged as acting in an indefinite environment over which the population disperses (Ashmole 1963). Most studies of animal populations have been in areas without discrete boundaries, and in the majority of these studies emigration and/or immigration has been specifically described (references in Elton 1927; Andrewartha and Birch 1954; Lack 1954a, 1966; Watt 1968; Johnson 1969; see also below); we know of no study in which they were demonstrated to be absent. Let us consider the relevance of movements to theories of population regulation, using the Herring Gull as an example.

The three intrinsic factors affecting reproductive rate are: the age at first breeding, the proportion of non-breeding birds, and the clutch-size (Wynne-Edwards 1962). In the population of Herring Gulls which we studied between 1962 and 1969, all these factors have changed only slightly in the 25 years since Gross's observations during the late 1930s and the 1940s (Gross 1940, 1948; Paynter 1949), despite a fourfold

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[1] The following paragraphs are taken from a paper on the importance of movements in the biology of Herring Gulls in New England presented at a symposium at Patuxent, MD, in 1969 (Drury and Nisbet 1972). See that paper for a fuller discussion of the biology of Herring Gulls. This section is taken from the discussion of that paper.

increase in total population ("N"). At present, mean clutch-sizes are somewhat lower than average over the decades and the proportion of non-breeding birds somewhat higher than average in only one area--the outer islands of Maine, where the density of breeding birds is lower than average (Kadlec and Drury 1968). Hence, these factors do not act to regulate the population density. Variations in the rate of production of young, then, depend primarily on variations in the success of hatching eggs and raising chicks; we will use the symbol "b" to denote the number of young raised per breeding pair.

Considering the population as a whole, the average mortality rates ("d") for ages 2-5 have not changed significantly in the period 1920-60, despite a roughly sevenfold increase in "N" (Kadlec and Drury 1968, Table 1). These estimates of mortality are somewhat biased by band loss (Kadlec and Drury 1968, 1969, and later work in progress), but should indicate changes reliably. For ages 0-1 and 1-2, the mortality rates "d_0" and "d_1" were 5-10 percent lower (marginally statistically significant) during 1941-50 when "N_0" and "N_1" (the number of chicks produced) were greatly reduced by Gross's program of spraying eggs to kill the embryos. This suggests a small dependence of early mortality on numbers in the early age groups, but only when "N_0" and "N_1" were small. The net rate of increase "r" was similar in the periods 1900-35 and 1950-68, despite a roughly twentyfold increase in "N" (Kadlec and Drury 1968; unpublished data), but was nearly zero in the period 1938-48, when "b" was greatly reduced by Gross. This suggests that "r" was primarily determined by

Table 1. Age-specific mortality rates (%/year) based on recoveries for first five years[a] following banding

	No. of recoveries	Age		
		0-1[a]	1-2	2-5
Northeast Region				
Banded thru 1935	1,049	62.6	53.8	51.4
" 1936-40	1,448	61.3	47.4	52.3
" 1941-45	308	52.9	40.0	50.9
" 1946-50	353	53.9	42.9	57.1
" 1951-55	311	61.7	47.1	48.1
" 1956-60	1,051	66.9	44.5	50.0
Great Lakes Region				
Banded thru 1930	449	76.4	48.1	52.9
" 1931-35	780	75.5	58.1	52.3
" 1936-40	1,005	71.2	42.9	49.3
" 1941-45	307	71.3	52.3	51.9
" 1946-50	731	76.1	52.0	57.1
" 1951-55	873	74.1	29.6	51.1
" 1956-60	2,082	72.7	28.4	49.6

[a] Years begin at banding.

from: Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

"b" ("d" remaining almost constant), and that both were independent of "N" and have been changed only by man's attempts to keep "N" constant by increasing "d_o".

Considering the populations at individual islands, "r" has consistently decreased with increasing "N", being very high in the early years of colonization and decreasing to zero in subsequent years (Tables 2 and 3). However, both the values of "r" achieved and the numerical dependence of "r" on "N" have varied markedly from island to island (Table 2). On the majority of colonies, "r" is near to zero, irrespective of the number of nests (Table 2) and despite variations in the density of nests "p" (=N divided by occupied area) by a factor of 50 or more between islands. There is a simple positive correlation of "b" with "N" (Table 4), and that with "p" is small and probably nonsignificant. Most mortality takes place when the birds are away from the breeding colonies, as indicated both by the distribution of band recoveries (Kadlec and Drury 1968, Tables 5-8)) and the small number of corpses on the islands (unpublished data). At these times birds from different colonies are mixed together and it is very unlikely that mortality could act differentially on birds from large or dense colonies. In fact, estimates of age-specific mortality rates for birds banded in six different regions (which reflect mainly the results from one or a few colonies in each region) are very similar (Kadlec and Drury 1968, Table 9), the small differences bearing no consistent relation to the numbers or densities of nests on the colonies concerned. Hence, on

Table 2.--Estimated numbers of breeding pairs of gulls in some Massachusetts colonies (from Drury and Nisbet 1972).

(Updated from tables 1 and 2 in Kadlec and Drury, 1968).

Year	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969
A. Long-Established Colonies												
Milk Island-------------------	3,750	3,500	4,000	3,750	4,000	3,500	3,750	3,200	3,200	3,600	3,400	3,400
Straitsmouth Island-----------	NA	NA	NA	2,000	2,000	2,000	2,000	2,800	2,500	(2)	910	[1]300
Outer Brewster Island---------	NA	NA	NA	1,500	1,200	1,200	1,300	(2)	(2)	(2)	206	[1]210
North Gooseberry Island-------	NA	NA	NA	NA	200	225	262	234	(2)	(2)	162	134
Island south of Cat Island----	NA	NA	NA	NA	NA	275	290	294	279	289	297	278
Marblehead Rock---------------	NA	NA	NA	NA	NA	315	296	312	304	259	287	247
Egg Rock----------------------	NA	NA	NA	510	530	470	450	525	530	[1]640	NA	[1]400
Green Island------------------	NA	NA	NA	305	260	258	227	320	(2)	(2)	(2)	130
Little Calf Island------------	NA	NA	NA	NA	NA	231	207	243	310	300	280	265
B. New Colonies												
Thacher Island----------------	0	25	75	300	750	1,200	1,800	2,100	2,400	NA	2,200	3,200
Block Island (Rhode Island)---	0	0	--	225	500	800	1,115	1,400	1,700	2,000	2,250	2,500
Norman's Woe------------------	0	0	0	50	75	200	300	530	508	484	478	462
Tern Island-------------------	0	0	0	3	5	25	250	500	700	NA	1,300	(3)
Monomoy Island----------------	0	0	0	0	0	5	75	420	1,000	NA	NA	8,000
Brush Island------------------	0	0	0	0	50	100	200	400	450	[1]470	NA	NA

NA = Not available

[1] Estimate based on air census, hence less accurate than other estimates in the table.

[2] Colony disturbed by introduction of predators.

[3] Colony reduced by control measures.

Table 3.--Herring gull pairs nesting on Muskeget Island, Nantucket Sound (Various sources)

(from: Drury and Nisbet 1972: Importance of Movements in the Biology of Herring Gulls in New England).

Year	1920	1925	1930	1935	1940	1945	1950	1955	1960	1965
Most probable number of pairs----	2	100	------	350	750	6,500	8,000	------	10,000	[1]11,000
Other estimates[2]----------------------		300	------------------			7,500	9,150	7,000	8,000	------
		Chicks				15,000			12,000	

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[1] C. Andrews of Nantucket thought that there were almost twice as many gulls on Muskeget as there had been in 1950.

[2] These estimates are regarded by us to be less accurate.

Table 4.--Annual production of young on colonies of different sizes

	Islands with >400 pairs		Islands with 40-400 pairs		Islands with <40 pairs	
	Number	Percent	Number	Percent	Number	Percent
Study colonies	11	25	34	75	--	--
Chicks fledged on study colonies	26,871	84	5,285	16	--	--
Total colonies (Long Island to Grand Manan)	76	32	311	55	31	13
Total number of nests	104,700	81	23,600	18	840	0.6
Average productivity (chicks/nest) (extrapolated from study colonies)	1.15	--	0.95	--	0.70	--
Estimated number of chicks fledged (number of nests x average productivity)	120,000	84	22,000	15	600	0.4

from: Drury and Nisbet (1972): The Importance of Movements in the Biology of Herring Gulls in New England.

Table 5. Geographical percentage distribution of band recoveries from Herring Gulls banded as chicks--recoveries from first year

Region	Banded in Great Lakes					Banded in Northeast				
	Fall	Winter	Spring	Summer	Annual	Fall	Winter	Spring	Summer	Annual
Northeast..............	11	5	3	5	8	75	24	27	76	56
New Jersey.............	<1	<1	1	2	<1	7	5	7	5	6
SE coast...............	<1	4	5	3	2	9	17	23	12	13
Florida................	0	3	4	2	1	3	20	15	3	9
Cuba, etc..............	0	1	2	<1	1	<1	<1	0	<1	<1
Gulf Coast.............	<1	15	5	3	4	3	18	11	1	8
Texas-Mexico...........	<1	<1	22	8	4	<1	12	12	1	5
Cent. America..........	0	1	1	<1	<1	<1	<1	1	0	<1
No. N.Y. & Vt..........	5	3	4	2	4	1	<1	1	<1	1
Great Lakes............	79	50	30	62	65	<1	1	1	<1	1
G.L. border............	5	12	15	9	8	1	1	1	1	1
Interior...............	<1	5	8	4	3	<1	<1	1	0	<1
No. of band recoveries..	2,658	1,127	662	528	4,975	1,413	790	364	486	3,053

Northeast=Labrador and Quebec south to southern New York, except Vermont
SE coast=Delaware thru Georgia
Gulf Coast=Alabama, Mississippi, Louisiana
Cuba, etc.=Bahamas, Cuba, Haiti, Antilles, Jamaica, Puerto Rico
Great Lakes=Ontario, Michigan, Wisconsin, Minnesota
G.L. border=Pennsylvania, Ohio, Indiana, Illinois
Interior=remaining noncoastal states

from: Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

Table 6. Geographical percentage distribution of band recoveries from Herring Gulls banded as chicks--recoveries from second year

Region	Banded in Great Lakes					Banded in Northeast				
	Fall	Winter	Spring	Summer	Annual	Fall	Winter	Spring	Summer	Annual
Northeast.............	12	4	4	4	7	79	63	57	86	73
New Jersey............	<1	1	0	0	<1	9	13	7	7	9
SE coast..............	2	3	5	0	3	6	15	22	5	11
Florida...............	1	2	1	0	1	2	3	7	1	3
Cuba, etc.............	<1	1	0	1	1	0	0	0	0	0
Gulf Coast............	<1	1	3	0	1	1	4	2	1	2
Texas-Mexico..........	4	4	4	1	4	1	2	3	0	1
Cent. America.........	<1	0	0	0	<1	0	0	0	0	0
No. N.Y. & Vt.........	6	6	5	27	10	1	1	1	0	1
Great Lakes...........	66	54	54	58	60	1	0	0	1	1
G.L. border...........	7	19	20	8	13	<1	0	0	0	<1
Interior..............	1	3	4	0	2	0	0	0	0	0
No. of band recoveries.	304	180	147	136	767	333	181	134	143	791

from Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

Table 7. Geographical percentage distribution of band recoveries from Herring Gulls banded as chicks--recoveries from third year

	Banded in Great Lakes					Banded in Northeast				
Region	Fall	Winter	Spring	Summer	Annual	Fall	Winter	Spring	Summer	Annual
Northeast.............	6	1	5	1	4	80	67	67	87	76
New Jersey............	0	1	0	0	<1	13	10	16	10	12
SE coast..............	0	1	3	0	1	5	15	14	1	9
Florida...............	0	3	1	0	1	1	3	1	1	1
Cuba, etc.............	0	0	0	0	0	0	0	0	0	0
Gulf Coast............	0	1	1	0	<1	0	1	0	1	<1
Texas-Mexico..........	1	3	0	0	1	2	0	1	0	1
Cent. America.........	0	0	0	0	0	0	0	0	0	0
No. N.Y. & Vt.........	2	3	5	3	3	0	0	0	0	0
Great Lakes...........	84	78	66	92	82	0	1	0	0	<1
G. L. border..........	6	9	16	4	8	0	1	0	1	<1
Interior..............	1	0	2	0	1	0	1	1	0	<1
No. of band recoveries	170	77	95	158	500	118	92	90	104	404

from Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

Table 8. Geographical percentage distribution of band recoveries from Herring Gulls banded as chicks--recoveries from 4 years and older

Region	Banded in Great Lakes					Banded in Northeast				
	Fall	Winter	Spring	Summer	Annual	Fall	Winter	Spring	Summer	Annual
Northeast................	4	2	1	1	2	86	66	78	92	82
New Jersey...............	0	0	1	0	<1	9	14	12	6	10
SE coast.................	<1	1	1	<1	<1	4	15	4	1	5
Florida..................	0	1	0	0	<1	0	2	2	0	1
Cuba, etc................	0	0	0	0	0	0	0	0	0	0
Gulf Coast...............	<1	1	1	0	<1	0	2	2	0	1
Texas-Mexico.............	0	0	0	0	0	0	0	0	0	0
Cent. America............	0	0	0	0	0	0	0	0	0	0
No. N.Y. & Vt............	4	7	5	3	4	<1	<1	1	0	1
Great Lakes..............	86	70	78	95	86	<1	1	1	<1	1
G.L. border..............	6	16	13	1	6	<1	<1	<1	0	<1
Interior.................	0	3	1	1	1	<1	<1	<1	<1	<1
No. of band recoveries....	479	153	185	510	1,327	314	251	251	402	1,218

from Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

Table 9. Age-specific mortality rates (percentage per year) from composite dynamic life tables--based on adjusted band recoveries from flightless young Herring Gulls

	Mortality rate										
	Banded in:										
Age[a]	N.Bruns.	Maine	N.H.	Mass.	So.N.Y.	Quebec	No.N.Y.	Mich.	Ont.	Wisc.	Minn.
0 to 1...........	45.3	49.7	66.3	47.2	48.2	54.8	68.7	56.7	68.1	60.9	43.3
1 to 2...........	30.6	28.4	33.3	21.1	22.9	31.6	35.0	23.0	25.5	27.3	18.2
2 to 3...........	26.1	18.0	18.2	18.0	20.7	17.5	23.1	21.0	24.7	26.2	37.8
3 to 4...........	23.2	26.3	29.6	17.8	14.8	18.2	30.0	24.8	32.8	31.4	28.6
4 to 5...........	26.5	34.0	26.3	28.1	24.0	29.6	28.6	26.6	32.5	26.3	30.0
5 to 6...........	25.7	30.9	32.1	32.2	28.1	28.9		27.4	25.9	33.7	
6 to 7...........	26.9	30.4	21.1	25.9	36.6	25.9		24.1	32.5	26.1	
7 to 8...........	20.5	38.4		40.5	19.2	25.0		25.1	40.7	31.2	
8 to 9...........	26.9	22.2		19.8	42.9	33.3		30.4		30.3	
9 to 10..........	17.2			15.1				28.4		21.7	
10 to 11..........	22.6			37.1				25.6		27.8	
11 to 12..........	29.3			10.3				24.1			
12 to 13..........	27.6			31.8				15.9			
13 to 14..........								27.0			
Total recoveries	1,377	638	294	933	463	902	122	3,794	1,237	1,575	150
Estimated total banded............	55,000	25,000	12,000	38,000	20,000	40,000	5,000	164,000	55,000	65,000	7,000

[a] Years begin 2 months after banding on the average--approximately early September.

from Kadlec and Drury (1968): Structure of the New England Herring Gull Population.

a colony-by-colony basis, "d" and "r" have not been significantly correlated with either "N" or "p". Moreover, "r" has varied, both between colonies and within colonies, much more than ("b-d"): this indicates that emigration and immigration are more important in determining "r" than either "b" or "d".

Regional averages are more difficult to derive, because estimates of "b" are available only for our 61 sample colonies, and estimates of "d" are available only for islands where long-term banding has been performed. However, as for colonies, regional estimates for "r" have varied more than those for ("b-d"): the most spectacular example is illustrated in Figure 1. In each region, "r" has decreased with increasing "N", but not at the same rate in different regions; in the late 1960s, the region with probably the highest value of "r" (Nantucket Sound-Buzzards Bay) also had high values of "N" and "p". We conclude that, at the regional as well as the local level, net movements contribute more to variations in "r" than variations in "b" and "d".

In winter, birds breeding in different areas are mixed. Winter mortality rates of first-year birds appear to be negatively correlated with regional densities; there is no clear evidence for variation in mortality rates of older birds (Table 10).

In summary, "r" and "d" (and hence "b") have not varied with changes in numbers or density in the population as a whole. When "b" was reduced artificially, "d" was unchanged (except for a small decrease in first-year birds); hence "r" was reduced correspondingly. Thus, there has been no sign that density-dependent factors have started to "regulate" the total

Figure 1. Numbers of eggs sprayed on 13 islands in Maine and eight islands in Massachusetts, 1940-1952 (from Gross, 1943-1952).

(Originally printed as Fig. 11 in Drury and Nisbet (1972): The Importance of Movements in the Biology of Herring Gulls in New England).

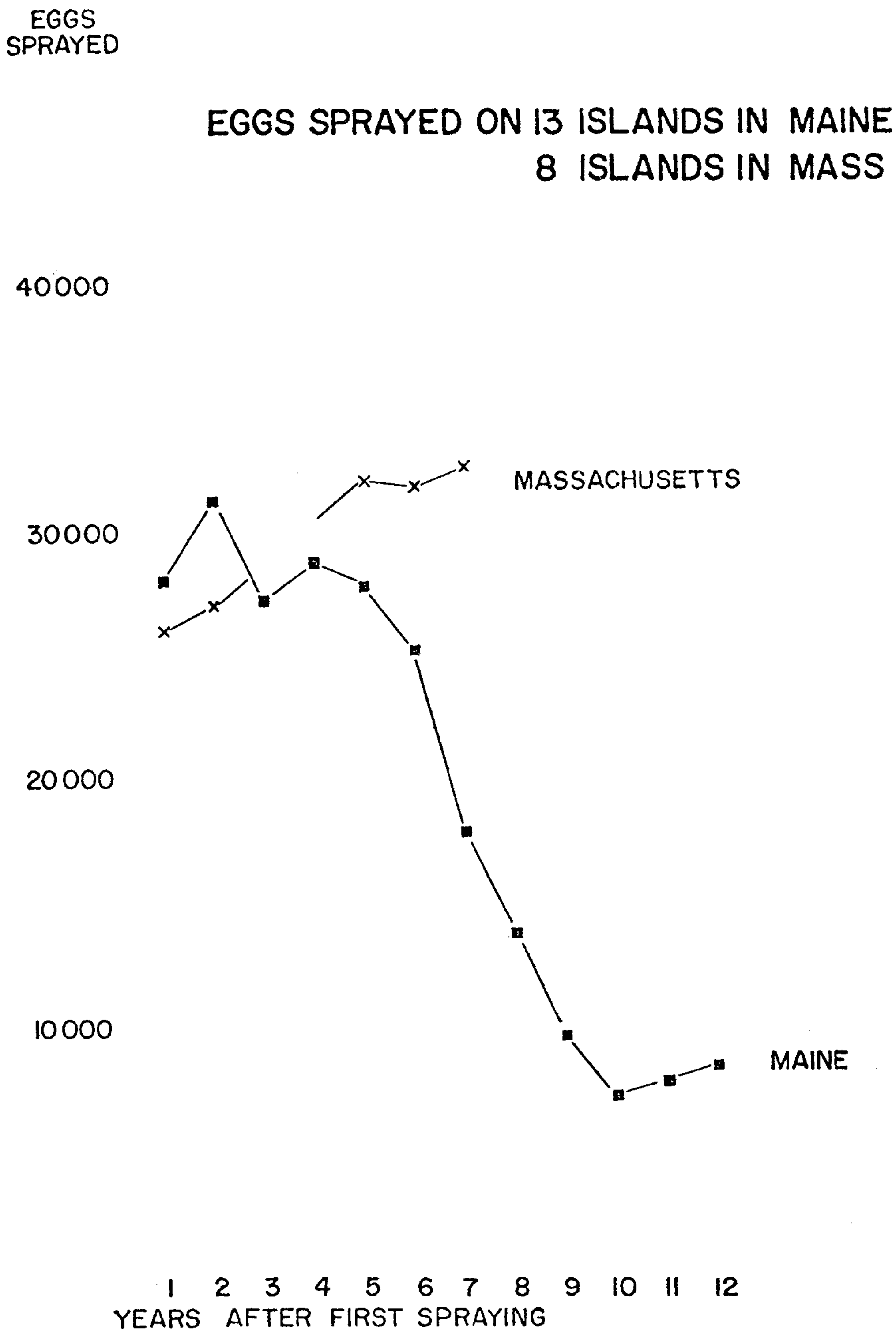


Table 10.--Geographical variation of recovery rates of immature herring gulls relative to recovery rates of adults

Region	1st year: adult ratio			2d & 3d years: adult ratio			No. of 1st year birds X10^3	No. of all age birds X10^3	Tidal shoreline km.X10^3
	Bands[1]	Birds[2]	Recovery rate[3] (bands per 100 birds)	Bands	Birds	Recovery rate (bands per 100 birds)			
Maine-------------------------	1.86	.009	200	1.28	.12	10.3	0.2	21.9	5.6
New Hampshire, Massachusetts, Rhode Island----------------	.78	.025	31	1.13	.14	8.1	18.4	85.8	3.2
Connecticut, New York, New Jersey----------------------	1.16	.16	7.3	1.04	.22	4.7	31.1	271.6	6.9
Delaware, Maryland------------	4.4	.29	15	[4].6	.37	[4]1.6	3.3	19.1	5.8
Virginia----------------------	3.0	.51	5.9	1.15	.66	1.8	9.4	40.0	5.3
North Carolina----------------	4.0	.67	6.0	1.00	.47	2.1	9.2	29.5	5.4
South Carolina-Texas[5]---------	41.1	.72	57	2.61	.32	8.1	39.6	103.5	29.6

[1] Reported through 1965 in the winter months (December-February).

[2] Counted in an air census, January-March 1965. For details see Kadlec and Drury (1958:658-664).

[3] The recovery rate is much lower for adult birds, in part because of their lower mortality rate, but in large part because of band loss.

[4] Based on a sample of only 8 birds.

[5] Data for individual States south of North Carolina are combined here because of the small number of adult recoveries; for details see Kadlec and Drury (1968: table 17).

from Drury and Nisbet (1972): The Importance of Movements in the Biology of Herring Gulls in New England.

population, despite its twentyfold increase. In single colonies and in regional groups of colonies, "r" is strongly density-dependent, but "b" and "d" are not; hence local "regulation" must be achieved by means of emigration correlated with the local density.

2. Imposed Regulation in the Herring Gull

It might be argued that regulation of numbers is not to be expected in the Herring Gull, which is expanding freely because man has removed a "natural regulating factor" by supplying abundant food. Let us therefore conduct two *Gedankenexperimente* to restore the missing factor.

a. Suppose that all food is removed in winter except that which is now used by the present population "N_O", while the summer food supply is unchanged. Then approximately "N_O" birds will survive each winter: if "N_S" die during the summer and "Y" young are produced, the population will be ("$N_O - N_S + Y$") at the start of the winter and approximately ("$Y - N_S$") must die. At present, "Y" is much larger than "N_S", and both are determined by factors which are unlikely to be changed by changes in the winter food. Hence the larger "Y" may be in any year, the more birds will die; the population is "maintained constant by density-dependent mortality."

In a population thus limited by food, it is reasonable to assume that most of the additional mortality (equal to the present overproduction) will fall on the young birds. Calculations based on the model age-structure of Kadlec and Drury (1968) suggest that the number of young dying during the winter will then be increased by a factor of 1.5-2.0. At least in the first few years, the young will migrate to the same areas as they do now. The additional deaths in each area will then be approximately proportional to the numbers in the area, so that the total deaths will remain inversely correlated with numbers. Over the years, the winter distribution of young may shift slowly under the action of differential selection. However, at least in the first few years of the experiment, the population as a whole will be regulated by density-dependent winter mortality, although the winter mortality rates in different regions may be, in fact, either independent of density (adults) or negatively correlated with density (young). This paradoxical result is a consequence of migration, which distributes the adults unevenly, according to the distribution of winter food, while the more vulnerable young winter to a greater extent than adults in less favorable areas.

b. Suppose that all food is removed in summer except that which is now used by the present population, while the winter food supply is unchanged. Then birds in the colonies which are now "full" (type "A") will continue to breed at the present rate, producing more young than are required to replace adult losses; there is a net emigration. At the colonies which are not now "full" (type "B"), including colonies not yet founded, new adults will continue to immigrate, but the number of young produced cannot increase and will probably decrease because an increasing number of adults is competing for limited food. The number of adults in the B colonies will then increase, until their mortality balances the production in the B colonies plus the net immigration from the A colonies.

If for some reason more adults die in any year, more food will be available and more young will be raised. Therefore the entire population is "maintained constant by density-dependent variations in reproductive success," in the manner proposed by Ashmole (1963). In fact, however, the reproductive success rate on any island depends primarily on whether it is type "A" or type "B"; this is determined by the number and size of the islands in the region, in relation to the available food, and may be either positively or negatively correlated with bird density.

The outcome of each experiment is a stationary population in which some colonies export a surplus of young and other colonies import. Suppose that an ecologist were to study one colony of each type. In the first case, he would find that the production of young was dependent on the factors we have mentioned above; in the second case, he would find that it was limited by the food supply. In each case, he would find that the adults are raising as many young as they can, limited only by extrinsic factors. Now, observing that the numbers in each colony and the total number of the species remained constant, and that proportionately fewer young returned to breed in the colony which produced more young, he might conclude that mortality was greater in that colony; i.e., that mortality was "density-dependent." Study of the same colony in different years would support the same conclusion. This incorrect conclusion would result from the neglect of dispersal and migratory movements and the implicit treatment of emigrants as lost to the population.

These examples are somewhat artificial in that the described outcome of the experiments may be only temporary. However, they suffice to show that the population in a restricted study area is not a microcosm of the entire population: regulatory mechanisms observed in one or deduced in the other may differ. A complete theory of population dynamics, at least for gulls, must take account of both.

The above arguments are in no way invalidated by the fact that the population which we have studied is not completely closed. Our references to the "entire population" are to the Herring Gulls which breed on the Atlantic coast of the United States and in contiguous parts of eastern Canada. These are mixed rather freely by dispersive movements, share common wintering grounds, and can therefore be regarded as a unit of population. Gulls breeding in the Great Lakes area form a second unit. The rate of settlement in each unit of birds bred in the other is only about 1 percent (Kadlec and Drury 1968, Table 8), so the time scale for interchange is of the order of 100 gull generations, much longer than that for changes within the units. On this time scale, we would expect the relation of the units to the world population of Herring Gulls to be similar to that of individual colonies to the units, discussed in this paper.

3. Natural Selection for Movement

As the population of Herring Gulls has expanded, there has been a net movement of young birds raised in the more northern colonies to settle and breed in more southern colonies. At the same time, there have been more local net shifts from older to newer colonies and from more productive to less productive colonies. However, movements have occurred in both directions: our file of banding recoveries (not fully analyzed) includes, for example, breeding adults banded in Massachusetts and recovered in Maine in the breeding season, and a number of birds identified at nests on Milk Island, Massachusetts, which had been banded as chicks or as breeding adults on nearby, younger colonies (Table 11).

We have discussed elsewhere the selection pressures acting on the choice of a colony by a young bird for first breeding (Nisbet and Drury 1971a). If it is to settle on an established colony, it has to compete for space not only with resident adults but with other young birds, both from the same colony and from others. The lower the production of young on the colony, the more chance there is for an immigrant to find space, but the less its prospects for success there. On the other hand, if it selects a new or growing colony, its chances of finding space are usually better, but its prospects for success much less predictable. During the period of expansion in the 20th century, conditions have generally favored those birds which tend to shift to young colonies, and their proportion in the population has greatly increased (figure 2). On the other hand, the birds which have a strong tendency to settle on old colonies have not been

Table 11. Sources of banded birds breeding at 2 Massachusetts colonies in 1965

(From data collected during the study reported by Kadlec and Drury, 1968).

Colony where banded	Distance from Milk Island (kilometers)	Date of founding	Years of banding	Age at banding	Bands read on adults breeding[1] at-	
					Milk Island	Thacher Island
Milk Island	0	c.1925	1961-62	Adult	127	11
do	0	c.1925	1958-59	Young	18	
Thacher Island	1	1959	1961-62	Adult	3	2
Straitsmouth Island	4	c.1935	1961-62	Adult	6	3
Kettle Island	14	c.1925	1962	Adult	4	
Cat Island	25	c.1925	1962	Young	1	
Outer Brewster Island	43	c.1940	1962	Young	1	
Martha's Vineyard	140	c.1950	1957	Young	1	
Block Island (R.I.)	175	1961	1962	Young	1	
Trois Pistoles (Quebec)	625	1925	1961	Young	1	
Duluth (Minn.)	1,720	1948	1962	Young	1	
Banded in winter					2	2
Total					166	18

[1] All the birds were present on territories within the colonies and appeared to be breeding, but a few (especially the 3-year-olds) may have been prebreeders.

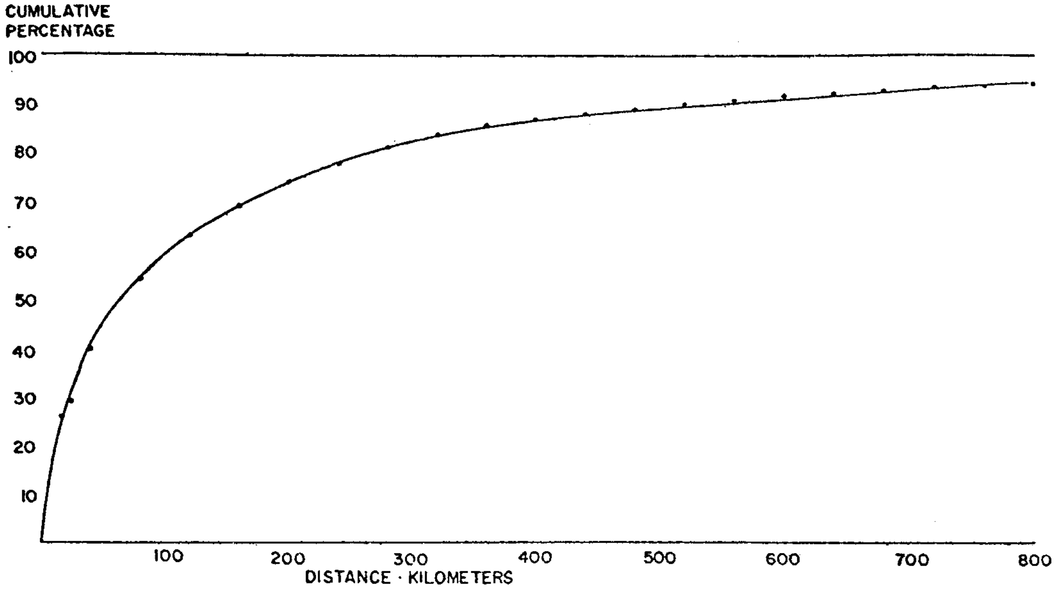


Figure 2. Dispersal of Herring Gulls banded as young and recovered in the breeding season (May-July) when adult (more than 48 months old). Movements indicated by recovery data include: (a) Movement to a breeding-area; (b) feeding-movements within the area; (c) errors dur to imprecise recording of recovery location (usually ±15 km.). Some birds may not have been breeding in the year of recovery.

From: Drury and Nisbet (1972): The Importance of Movements ib the Biology of Herring Gulls in New England.

eliminated from the population, nor even reduced in absolute numbers, because the old colonies have also prospered (Kadlec and Drury 1968, figures 3 and 4). If the environment again becomes unfavorable, as in the late 19th century, the selective balance is likely to shift back to favor those birds which tend to settle on old, secure colonies. However, even if all the colonies founded in the 20th century were to be eliminated, descendants of the birds which founded them would remain in the population, because of the shifts back to the old colonies demonstrated by banding results (see Table 11). Even if the whole population were restricted for a time, as in the 1880s, to a limited group of colonies, natural selection would still be expected to favor shifting short distances between them, because birds which stay on their colony of hatching are more likely to compete with their close relatives (Nisbet and Drury 1971a).

Thus, as a consequence of repeated changes in the environment, different types of behavior are favored at different times and places; as a result, each type of behavior is maintained in the population. When the environment changes again, some types of behavior can then be favored at the expense of others, so that the average behavior over the population can change rapidly. Analogous changes have been demonstrated in a population of voles by Tamarin and Krebs (1969). Hence natural selection, acting in the orthodox way on individuals, can give rise to a population which adapts rapidly to "take advantage of" changing circumstances. The consequences for practical management of such populations are discussed by Nisbet and Drury (1971a).

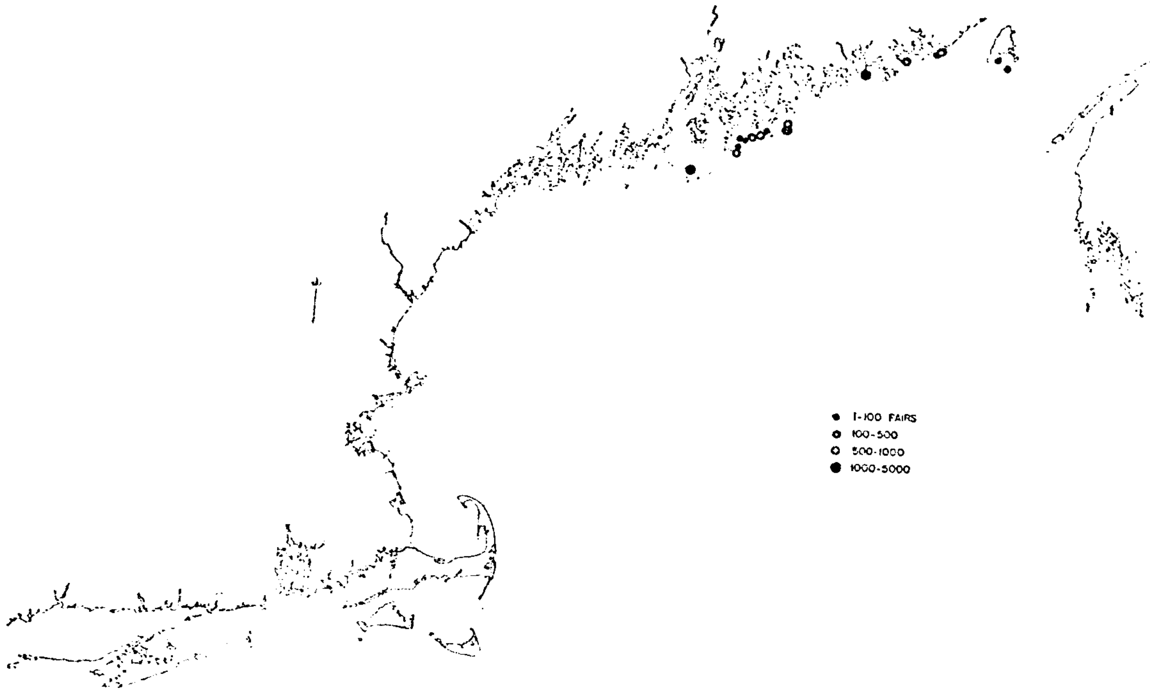
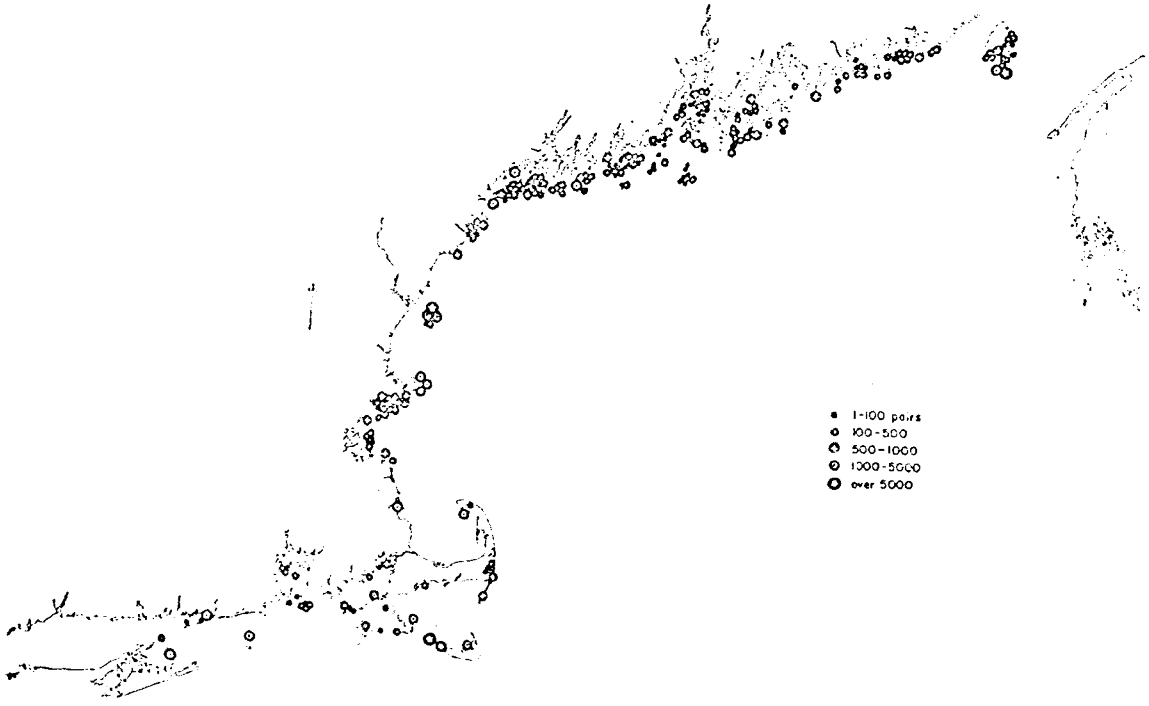


Figure 3. Herring Gull breeding colonies - 1900 (from Norton, in Kadlec and Drury 1968).

Figure 4. Herring Gull breeding colonies - 1965. The coast of Nova Scotia had not been surveyed. (from Kadlec and Drury 1968).



4. Movements and Extinction

The main theoretical argument adduced for intrinsic mechanisms to regulate animal populations is that they are necessary to prevent overexploitation of food supplies (Wynne-Edwards 1962) and extinction (Christian and Davis 1964). However, Herring Gulls do in fact overexploit at least one of their food sources in that they drive away terns and smaller gulls from their favored islands (Drury 1965b; Howard 1968; Nisbet and Drury 1971b). Moreover, extinction by predation is, in fact, a constant threat to all Herring Gull colonies (see especially Axell 1956; Brown 1967). We know of several dozen colonies which have been extirpated one or more times in New England since 1900, while the entire regional population was threatened in the 1880s and was only just saved from extinction. Gaps in the distribution of the species (e.g. in eastern Europe) suggest that regional populations and perhaps entire subspecies have been extinguished in the past (Voous 1960). However, in many of these cases the colonies have been resettled by immigrants (Kadlec and Drury 1968). As shown in the previous section, the existence of two-way dispersive movements between colonies means that such extinction and resettlement does not disrupt genetic continuity.

In a changeable environment, the characteristics are selected of those individuals which, faced with the threat of local extinction, scatter their descendants widely through the population. Even in a constant environment, individuals which limited their reproductive rate in order to regulate their colony's population below the food limit would, under natural selection, be replaced by immigrants from other colonies with higher reproductive rates (Nisbet and Drury 1971a) unless the species were confined to one colony (a special case to be discussed below).

The classic example of animals subject to local extinction because of uncontrolled fluctuations in numbers is the Cladoceran genus *Daphnia*. Some years ago, after promptly receiving several successive orders from a biological supply house, one of us wrote to ask how they could maintain a reliable supply of such an unreliable commodity. They replied that they simply kept the *Daphnia* in two dozen rain barrels out in the yard, and that there was always a flourishing population in at least one. Thus, this species can be (and in nature doubtless is) "protected against extinction" by the simple expedient of dispersing between partially isolated nuclei of population. Extinction is likely to occur only when all the nuclei "crash" simultaneously, the probability of which decreases exponentially with the number of nuclei. An analogous result for a predator-prey system is well known (Huffaker 1958).

It would be difficult to pick a species which exhibits less regulation of numbers within its nuclei than *Daphnia*. In the Herring Gull, the numbers in each nucleus are limited (except on the largest islands) by territorial behavior, which in present circumstances usually promotes emigration before the local food supply is exhausted. However, as shown in this paper, the territorial behavior is not closely matched to the available food; in certain areas, where islands are numerous and artificial food scarce, chick production seems to be low. With this addition of spatial limitation within the nuclei, we suggest that the "rain barrel" mechanism of population regulation suffices to explain the long-term persistence of Herring Gulls.

5. Other Species of Birds in Changeable Environments

We have shown above that the existing deterministic theories of population regulation are not valid for the Herring Gull population in its present state of rapid increase, and that most of them could not become valid even if the population were made constant or decreasing in plausible ways. The three main reasons are: (1) migration, which mixes different populations in winter and exposes them to mortality factors which are independent of their breeding densities; (2) dispersal between colonies, which is expected to be favored by natural selection even in a restrained population and to defeat any intrinsic mechanism to regulate the size of the colonies; (3) communication between different nuclei of the population, which makes the behavior of the entire system different from that of individual nuclei. If these conclusions apply to other species, it will be necessary to construct generalized models of population regulation incorporating these three factors. We will now consider briefly the importance of these factors in other species, using population studies of birds as examples (but without attempting a comprehensive review).

The birds whose breeding dispersion is most similar to that of the Herring Gull are other colonial seabirds (Lack 1968, Chs. 12, 20, 21). Differences in breeding success between colonies have been recorded for Gannets *Sula bassana* (Nelson 1966), gulls *Larus* spp. (Brown 1967; Harris 1964; Paludan 1951), and terns *Sterna* spp. (our data, unpublished). Settlement of new colonies and subsequent immigration has been described for Kittiwakes *Rissa tridactyla* (Coulson and MacDonald 1962; Coulson 1963), Fulmars *Fulmarus glacialis* (Fisher 1952, 1959), Yellow-eyed Penguins

Megadyptes antipodes (Richdale 1949), terns (Salomonsen 1943), and Gannets (Fisher and Vevers 1943-44; Tuck 1960), as well as resettlement of extinguished colonies for Shags Phalacrocorax aristotelis (Potts 1969) and terns (Austin 1951). Two-way movements between breeding colonies have been reported for terns (Austin 1938, 1951), Skuas Catharacta skua (Sladen, et al. 1968), Shags (Potts 1969), and Manx Shearwaters Puffinus puffinus (Harris 1966), and one-way movements in many other species (Serventy 1961; Sladen, et al. 1968; Richdale 1963). Mixing of birds from different breeding colonies in winter has been described for many species in banding reports; segregation of different age groups into different areas has been described for terns (Robertson 1969), Gannets (Thomson 1939), and Skuas (Thomson 1966). Differences in mortality rates between wintering areas have been described for Dovekies Plautus alle (Bateson 1961) and cormorants Phalacrocorax spp. (Coulson and Brazendale 1968; Potts 1969). Hence the phenomena which we have discussed for the Herring Gull appear to be general in seabirds although their numerical importance, of course, varies widely from species to species.

Other species to which our arguments are immediately applicable are those confined to ecological islands, such as lakes, marshes, forest clearings, and mountain tops. One well-studied group is the waterfowl. Hochbaum (1955) has described the dispersion of waterfowl into nuclei and has pointed out differences between species in the speed of recolonization of a nucleus after extinction. Papers on the Mallard Anas platyrhynchos by Bellrose (1972), Dzubin, and Gollop (1972), and Geist(1972) have described mixing of different breeding populations in winter and vice versa, differences in breeding success between nuclei and between regions, and differences in mortality rates between regions. Geis's data suggest only weak correlations of mortality rates with numbers, both between regions and between years. However, annual estimates of the continental population, issued by the U.S. Fish and Wildlife Service, indicate fluctuations with limited amplitude, suggesting a classical type of control by a density-dependent factor.

Another well-studied species is Kirtland's Warbler *Dendroica kirtlandii* (Mayfield 1960). This species breeds in loose but well-defined colonies which persist for only a limited time because the birds nest only in young trees. Extinction of old colonies is thus regular and predictable. Mayfield has described movements of both males and females; females move more freely between established colonies but males appear to found new colonies. Differences between colonies in breeding success have not been measured, but doubtless occur as the suitability of the habitat waxes and wanes. However, the total population of the species has changed only slowly (Mayfield 1962).

In another colonial land bird, the Bank Swallow *Riparia riparia*, Bergstrom (1951) has recorded two-way movements of adults between colonies.

Few other species have been studied in such detail, but Nice (1937) has emphasized the importance of movements in local population balances and has summarized (1957) regional differences in breeding success in various species. Fretwell (1968) has reported differences in survival rates between habitats and has pointed out the effect of migration between habitats on age structure in a population of Field Sparrows _Spizella pusilla_. Hence, we suggest that dispersive movements play a general role in the population dynamics of species with insular or ephemeral habitats. By enhancing gene flow, they may be expected to play an equally important role in the genetic structure of these species.

6. Species of Birds in Stable Environments

However, at least one theory of population regulation has been formulated explicitly for stable environments (MacArthur and Wilson 1967) and most others are so formulated implicitly. If the habitat is stable and spatially uniform ("climax" *sensu stricto*), immigration and emigration may be expected to balance each other and it should indeed be possible to treat a sample population of a species as a microcosm of the whole. It would be difficult, perhaps, to characterize marine species as "successional," but we have emphasized the changeability of the environment in our discussion of the Herring Gull. Therefore, we discuss separately the role of movements in bird populations of "climax" habitat, in particular of mature forests.

The best-studied species is the Great Tit *Parus major* (Lack 1966, Chs. 2-4). This is a hole-nesting species which depends in winter on seeds of characteristic climax trees (Perrins 1965, 1967), but in the areas where it has been studied the mature forest has been fragmented into "islands" separated by less favored habitats. Breeding success and density vary substantially among these islands (Lack 1966; Kluyver 1951; Hublé pers. comm.) and among habitats (Lack 1966; Kluyver and Tinbergen 1953). In an isolated area, adult mortality varied directly with the number of young produced (Kluyver 1966). However, annual fluctuations within an island depended primarily on post-fledging disappearance rates of young, which were correlated not with density but with botanical factors (Lack 1966). Perrins (1963) and Lack (1966) mentioned examples of emigration, but nevertheless equated this disappearance to mortality; however, Kluyver

(1951) suggested that some birds emigrated, and Dhondt and Hublé (1968) confirmed this by capturing birds in neighboring areas. Kluyver and Tinbergen (1953) reported movements from one breeding habitat to another; Kluyver (1966) found that 20-60 percent of the breeding population in one study area consisted of immigrants each year and recorded apparent immigrants even on an island isolated by 20 km. of sea and tidal flats. In these respects, the Great Tit, although noncolonial and nonmigratory, resembles the species discussed earlier. However, three additional points arise:

a) It is not known where the post-fledging mortality takes place, but the fact that net emigration has been recorded from most study areas (selected because they were good Great Tit habitat) suggests that at least part takes place in other habitats; if so, it probably occurs at relatively low numerical densities.

b) The species occurs, not in discrete isolated islands, but in a patchwork of good and bad habitats, which it inhabits at varying densities. Hence dispersion and spacing (in the senses used by Berndt and Sternberg 1968) are not discrete events, but rather statistical shifts of population up or down density gradients.

c) As in the Herring Gull, the Fulmar, and the Mallard, the fluctuations in the Great Tit populations in different nuclei are not independent but are correlated over wide areas (Lack 1966), probably because common climatic factors act to coordinate botanical fluctuations in the different nuclei (Perrins 1967). In moderately good years, the overproduction in the good areas is absorbed as discussed above, whether by mortality *in situ*, by emigration into intervening habitats, or by both. In very good years, however, it cannot be so absorbed, and a large part of the entire regional population may emigrate (Cramp, et al. 1960; Ulfstrand 1962; Cramp 1963; Perrins 1967; Berndt and Henss 1967); the ensuing mortality then takes place outside the usual range, at unknown densities. At these high levels, the regional population then behaves as though limited by density-dependent emigration, but as Perrins (1967) points out, the internal mechanism is not so simple.

Few other species of mature forests have been studied in detail, except for the Blue and Coal Tits *Parus caeruleus* and *P. ater*, whose population dynamics in disturbed European forests are very similar to those for the Cape May Warbler *Dendroica tigrina* (MacArthur 1958), for the Wood Warbler *Phylloscopus sibilatrix* (Svärdson 1948) and for forest birds in general (Huxley and Fisher 1964). Indeed, mature forests are themselves patchy (Whittaker 1952; McIntosh 1967) and as a result of ecological specializations it is to be expected that distributions of birds are correspondingly patchy; this has been demonstrated in detail for two species by Sturman (1968).

For the Pied Flycatcher *Ficedula hypoleuca* breeding success varies between regions (references in Lack 1966). Movements of both adults and young between breeding areas have been recorded in several studies, being more pronounced in a "pioneer" population in Finland than in an established population in Germany (von Haartman 1960); two-way movements have been recorded by Berndt and Sternberg (1966, 1968). In several thrushes *Turdus* spp. differences in density, breeding success, and mortality rates have been recorded, both among habitats and among study areas (Lack 1954b; Snow

1958; Ribaut 1964; Snow and Snow 1963); in two species, calculations show a net movement from one habitat to another (Snow 1968). Differences in average breeding success between study areas have been recorded in a number of other species (Nice 1957).

Winter ecology has been studied for few other woodland species, despite Lack's (1968) generalization that populations even of migratory species should be regulated by density-dependent factors in winter. In the Robin _Erithacus rubecula_, winter mortality is higher in the habitat where the density is lower (Lack 1965). In winter, mixing of birds from different breeding areas is familiar for many species from banding recoveries (Salomonsen 1955).

In these respects, the species of mature forests which have been studied resemble those of successional and island habitats discussed earlier. The main difference is that the patchiness of the breeding distribution in the former is determined not by geographical factors but by the nature of the habitat and by the behavior (habitat selection) of the birds. In those forest species which have a more or less continuous distribution at varying densities, movements between nuclei are not clearly differentiated from dispersal within nuclei, and emigration from a nucleus is not clearly differentiated from change of habitat or movement into marginal habitat. However, the dispersive movements are expected to have the same kind of advantages, under natural selection, as those of colonial species, and their significance for theories of population dynamics is the same: they provide connections between the behavior of a sample population and the behavior of the whole.

7. One-Colony Species

A limiting case of the "rain barrel" model is that of species confined to a single nucleus; there are many such species on isolated mountains and islands, some with flourishing populations.

There are three obvious ways in which one-colony species can arise: (1) evolution *in situ*; (2) extinction of all other colonies by some factor acting everywhere, such as human predation (Grieve 1885) or climatic change (Moreau 1966); and (3) aggregation of the population onto one especially favored island. Brown and Baird (1965) have suggested that process (3) may be taking place in the Great Shearwater *Puffinus gravis*, studied by Rowan (1965), and they proposed a mechanism by which selection could act to favor such aggregation. For this selection to outweigh the selection for dispersal discussed in this paper, several conditions appear necessary: (a) the population should be limited by some factor (e.g., winter food) away from the breeding colony; (b) the best island should be large enough to accommodate the entire population; (c) conditions should be sufficiently constant for (b) to remain satisfied throughout the period of aggregation.

Once a species is confined to a single colony under constant conditions, selection against emigration will be greatly enhanced and if conditions remain stable for sufficiently long, an essentially sedentary population may evolve. (This process could be reversed if the factors limiting the population change, so that a pool of nonbreeders can be built up sufficiently rapidly to overcome the resistance to settling on a new colony; a possible example is provided by the Fulmar (Fisher 1952)). Then emigration may be regarded as a form of mortality, the population forms a closed system, and the assumptions of conventional theories of regulation may become valid. However, if the island is sufficiently large, we would, on the arguments advanced in this paper, expect clumping and dispersive movements between subcolonies to be favored by natural selection. It is perhaps significant that in several one-colony species which have been studied, nests are dispersed into small groups (Stonehouse and Stonehouse 1963; Snow 1966; Nelson 1969). Then the relation of the subcolonies to the single colony is likely to be similar to that of the colony to the total population, which we have discussed. Indeed, structural diversity within colonies is to be expected for the same reason in more widespread species.

Finally, we may comment that a species confined to one colony and with little tendency to form new ones will be in serious danger of extinction if (as is inevitable) the environment changes. On our arguments, this situation is likely to arise as a consequence of environmental stability--in contradistinction to the view that extinction results from instability (Slobodkin 1968).

8. Summary

To summarize these studies: the population of Herring Gulls Larus argentatus breeding in New England and adjacent parts of Canada has been increasing since the 1880s, approximately doubling in size every 15-20 years.

There are marked differences in average nest spacing and breeding success among colonies, correlated with food supply, substrate, and other factors.

On long-established colonies, numbers remain nearly constant because of territorial behavior; many young emigrate. Newly founded colonies increase in size very rapidly, primarily through immigration. Young birds move varying distances away from their colony of hatching; older birds usually breed in the same colony each year, but shift if predators are introduced or if they are repeatedly unsuccessful. Shifts from newer to older colonies have been demonstrated by banding.

Breeding adults commute variable distances, up to 40 km., for food. Birds from different colonies are somewhat segregated into different feeding areas; some segregation persists even in winter. Young migrate long distances and mix freely in winter. Winter mortality rates of first-year birds vary more than those of adults and appear to be higher where regional densities are lower.

Young birds now disperse more widely and winter farther north than they did earlier in the period of increase; there has also been a southward extension of breeding range and a shift from outlying to inner islands. These changes are interpreted as adaptations to new opportunities provided by man. This adaptability is a consequence of variability in behavior within the population, which is maintained by natural selection in a changeable environment.

There is no evidence that any density-dependent factor is yet acting to regulate the population: indeed, breeding success is higher in larger colonies and winter mortality is higher at lower densities. In individual colonies and in groups of colonies, numbers are "regulated by density-dependent emigration", but the limiting densities vary widely between colonies and between regions. If food were restricted, the population as a whole would behave as though restricted by density-dependent mortality, even though regional mortality should remain uncorrelated with density. Current theories of population regulation do not apply to a species in which breeding densities are influenced by dispersive movements and winter densities are determined by migratory movements.

Dispersive movements between colonies appear adequate to explain the persistence of the Herring Gull in the face of the continuing threat of local catastrophes. There is no need to postulate intrinsic regulating mechanisms to protect the species against "overpopulation" or extinction.

Similar phenomena, including spatial variations in breeding success, two-way dispersive movements between population nuclei, differential migration of age-classes, and regional variations in mortality rates, have been recorded in a number of other colonial seabirds, and of landbirds of specialized or insular habitats. The same phenomena have been recorded in many forest species, if the nuclei are identified with favorable patches in a mosaic of habitat. Hence models of population dynamics which incorporate dispersive movements are required for many, if not all, bird species.

D. Populations and Communities: Two Illustrations

1. Population Nuclei of Fish Stocks and Seabird Populations in the Bering Strait

Although the ideas presented above were formulated to describe the behavior of bird populations, they appear to be useful in understanding population phenomena in other groups, most notably fish. Work in progress on Herring (M. Sinclair, Bedford Institute of Oceanography, in press) suggests that stocks of Herring in the Atlantic act in ways very similar to what has been described; the many largely independent stocks of Herring appear to fit the rainbarrel model. Each stock has a discrete spawning ground and there is little exchange of fish between stocks during the spawning season, though they may merge in the open sea. Spawning is highly localized, occurring where strong turbulence mixes the water at all depths in contrast to the surrounding, strongly stratified, water masses. The fish migrate away from the spawning grounds to feed for most of the year; some groups may move long distances, such as from southwestern Nova Scotia to northeastern Nova Scotia, while others appear to be resident.

The average sizes of stocks of Herring appear to vary dramatically in accordance with the size of the spawning area of suitably mixed water and bottom sediments, rather than with the "carrying capacity" of the feeding habitat. Stocks vary enormously around these "averages"; yet the average size of the stock in the upper Saint Lawrence River is relatively small when compared to the stocks off southwestern Nova Scotia, while those are small when compared with the stocks off southwestern Norway.

Characteristic of each stock are the time of spawning, number of eggs laid, size of eggs, and speed of development and growth of larvae. The specificity of these characteristics to the blooms of algal productivity suggests integrity of the stocks, site tenacity or "Ortstreue," and strong local selection.

As Hjort showed for the Norwegian Herring in the early decades of this century, a single year-class may make up a major portion of the fish caught commercially for many years. This indicates that spawning success and larval survival are determinants of population size rather than an indication of the carrying capacity of the fishes' environment when they are numerous. Yet when stocks are low they can be overfished and eliminated, as happened with the stock that formerly spawned on the "Northeast Peak" of Georges Bank.

The patterns of distribution, abundance, and annual changes described in these studies of Atlantic Herring seem applicable to the dynamics of fish stocks in Norton Sound. The populations of Herring, Capelin, Smelt, Arctic Cod, Saffron Cod, Sand Lance, and salmon all seem to conform to the rainbarrel model.

The pattern of year classes among Herring is reminiscent of the breeding of arctic seabirds. A number of authors since as long ago as Bertram, Lock, and Roberts (1934) have observed failure of reproduction among arctic seabirds. Our studies found several years of reproductive failure and one or two of performance high enough to be considered moderate in the northeast Atlantic. It appears that the stocks of seabirds, like those of fishes, may be maintained by occasionally productive years separated by years of general reproductive failure.

The pattern of discrete spawning stocks is reminiscent of the separate identity of seabird cities at distinct locations during the breeding season contrasting with the general mixing of populations on the wintering grounds.

As to population regualtion, we believe that comparison of the enormous variations in the numbers of fish with the relatively small numbers of seabirds suggests that the numbers of seabirds vary within rather narrow limits. We have suggested that among active vertebrates adaptations are selected which allow them to avoid close coupling with fluctuations of their resources, hence for their populations to oscillate less.

In contrast, current ecosystem models such as those influencing the planners of the OCSEAP suggest that the numbers of seabirds vary so widely as the make the seabirds unuseable as indicators. We will now review a widely quoted model of seabird systems (Cody 1973) and the objections to that model offered by an experienced field student (Bédard 1976). We agree with Bédard's statement, "I can only regret, however, that a model developed from such a narrowly quantitative data base and from such a restricted sampling of the field situation should send so many roots into published ecological literature."

2. Review of a Model for Seabird Communities: Cody (1973) and Bédard (1976)

It was a valuable experience for graduate students in the 1960s to read on the one hand Wynne-Edwards' (1958) statement of the overfishing principle together with his arguments for group selection, and on the other hand Lack's (1966) argument against the ideas. By reading the two in opposition, students could grasp the differences and make their own choices. It is useful now to read these two papers by Cody and Bédard which provide a similar contrast in thinking and use of data.

Cody's paper draws broad conclusions suggesting the general operation of a system, basing his conclusions on his data on the attributes of a local seabird population. The conclusions seem reasonable and attractively simple: typical feeding radii, characteristic food species, and mean reproductive rates. It provides an "elegant" model. A major feature of Cody's model is his diagram of the dispersal of feeding auks at sea. This diagram considers only the linear distance to which birds are expected to fly, implying that the sea is a homogeneous habitat. He omits consideration of effects of currents, shallows, fronts, or other oceanographic features of the sea's interior.

Bédard provides the criticisms of a student concerned with how seabirds of different kinds make their livings in different parts of the world, in different conditions, and with different neighbors. He begins by pointing out that Cody's data are inadequate for the conclusions which he has drawn: the few data are not consistently displayed and samples are not comparable. He criticises Cody for comparing a boreal temperate area, the Olympic Peninsula, with a low arctic area, Grimsey Island. If the comparisons were between two boreal temperate areas the comparison would have to be the Olympic Peninsula with the Bay of Fundy; if between two boreal arctic areas, then Grimsey Island with the Aleutian Islands. Bédard observes that within similar climatic areas the community organization and structures are so different as to make parallels impossible. Bédard further points out that the data which Cody uses as representing Grimsey were taken from Belopol'ski (1957), gathered 3000km to the east, and from Bateson (1961), gathered at Spitzbergen 2000km to the northeast. When Bédard arranged the data on feeding to display consistent categories, he did not find patterns of zonation and spatial segregation, but rather considerable overlap.

Cody extends his view of the processes of ecosystem development into the glacial history of the Olympic Peninsula, implying that the communities maintain consistency through time as well as space. His assumption of there being fewer species present along the Olympic Peninsula during the ice advances does not consider that there are full complements of Alcid species found today along heavily glaciated coasts of Greenland or along other coasts of the North Atlantic blanketed with pack ice. Cody omits consideration of several northern species of North Pacific Alcids which one can expect have expanded their ranges south during the advances of the ice.

Cody suggests that Cassin's Auklets developed their adaptations for feeding at great distances at sea because they were forced further offshore as climate ameliorated. Bédard observes that this shift implies that major changes in behavior and anatomy have developed during the last 10,000 years. In that short time, a shift from feeding on fish to feeding on plankton and the development of a gular pouch is improbable.

Models such as Cody's have an attractiveness for people who are interested in the very general functioning or energy flow of a system. For some biologists, the operation of a system or part of a system is "explained" when the amounts and routes of energy flow have been described. The interminable details of activities of each species within trophic levels cloud the issue or are irrelevant to many of these biologists who have fundamentally different interests from ours. As Mayr has often said, there are physiological interests as compared to evolutionary interests. It appears to us that students of trophic-dynamics and ecosystem modeling are interested in the physiological aspects of systems.

To put it another way, some biologists accept the "explanation" of the behavior of female phalaropes when it is established that the endocrine system of the females includes high levels of testosterone. For some biologists, this is an explanation at a fundamental level; for other biologists, this is "how," not "why." Evolutionary biologists require an understanding of the Darwinian fitness of each evolutionary step by which males have been selected to assume increasing responsibility for the eggs while females have become emancipated from the "cruel bind"

(Trivers) of having greater investment in the eggs than do the males. Such an "explanation" is provided by the comparative studies of shorebird behavior (Pitelka, Holmes, and MacLean 1974) combined with the theoretical papers of Trivers (1972, 1974) Orians (1969), and Emlen and Oring (1969).

We do not believe that knowing general patterns of energy flows allows one to predict from lower trophic levels to higher ones. We believe that it is for this reason that successful modeling has been done by those who have used one species or a few species and worked from higher trophic levels downward through the resources which higher level species use, to connections with other species, productivity, nutrients, hydrology, and geology.

In the following pages we discuss how these conclusions apply to the program of research in OCSEAP.

E. Relevance to OCSEAP:

The relation of the theoretical framework presented in Sections A, B, and C to studies of numbers of seabirds and composition of seabird communities in the Bering Strait Region

We have emphasized that we differ with the considerable body of ecological theory which is based on assumptions of stability of numbers and of high orders of integration of the parts of ecosystems. This integration implies functional coupling among subsets of the system, hence consistent interaction, and, therefore, consistent numbers at all levels. This implies in turn that mathematical functions will be distributed according to normal curves. In this section we point out our reservations about this body of conservative ecological theory as applied to the seabirds of the Bering Strait Region.

1. Assumptions about the coupling of subsets of natural systems and about the shapes of functions used to describe natural variability

a. Normal distributions

There is an assumption that biological variables are "normally distributed." We think that it is an oversimplification of the behavior of biological populations to assume that such functions as reproductive rate, mortality rate, and immigration rates conform to bell-shaped curves which, when properly understood, will apply to seabird populations and that the correct values will exhibit relatively small standard deviations. This sort of order is to be expected from physical systems and may appear among some "simple" organisms that appear to be closely coupled to "a" system or to a closed system such as the growth of algae as related to the mineral context of a water column. Among active vertebrates, however, we expect such functions to be multimodal.

Many vertebrates, including fish, appear to reproduce poorly most years and to have spectacular success in a few years. It is our experience that kittiwakes in the Bering Sea follow that pattern. Moreover, the kittiwakes in different parts of Alaska show different patterns. South of the Aleutians, kittiwakes usually reproduce moderately well and occasionally spectacularly well. In any one year in the Pribilof Islands, kittiwakes reproduce moderately well and have not shown peaks of success. In the northern Bering Sea and Chukchi Sea most years would be called disaster years and the years in which kittiwakes have done well would be considered moderate relative to levels of success obtained in other regions. We interpret these patterns as resulting from various adaptations kittiwakes have to make use of the resources available in any area. It would be a misleading simplification to conclude that because kittiwakes in one area use one set of food organisms and feeding behaviors, that that set of behaviors and the "curves" of mortality and reproductive success are "characteristic" of all kittiwakes, let alone of all gulls or all seabirds.

OCSEAP has requested "measurements of the general range of mortality and productivity in order to estimate rates of recovery from impacts," though "detailed understanding of differences in rates are not required" (memo, R. Engelmann, 1978). This implies the existence of a bell-shaped curve of number or rates and seems to assume that one should expect a plot of population size to approach an asymptote, i.e., a model predicting what will happen based on means and equilibria.

We believe that knowledge of geographic differences in reproduction and mortality are important for OCSEAP and that knowledge of the forces influencing these "functions" or of the differences in "strategies" among species which alter the shapes of the "functions" are equally important.

Understanding regional and secular (year to year or decade to decade) differences and changes in numbers will allow us to predict how populations will respond to similar changes in habitat associated with human operations. Regional differences in mortality and life expectancy, while difficult to identify, have emerged from the compilation of ideas during studies of many aspects of the species' biology.

Because the biological functions vary, it is more important to understand the causes and conditions of variation than the means or extremes of variation in the functions. It is important to realize, as pointed out in our report for 1976, that different seabirds have different strategies (Lack 1966) and complexes of adaptations require our separating some "clearly related" species but allow us to lump or categorize disparate taxonomic species groups with similar "strategies." Viz., cormorants, terns, puffins, and Glaucous Gulls may be more similar to one another than kittiwakes are to Glaucous Gulls or than murres are to puffins.

b. Tight couplings

There is an assumption that tight coupling exists between biological variables and the relevant physical forces.

We believe that vertebrates at high trophic levels are selected to moderate or to avoid the direct action of natural forces. In order to avoid coupling they are selected to use as disparate as possible subsystems. We see natural selection as the bringing out of every population those individuals which "carry," to some extent, a "mixed portfolio" whereby individuals can escape the damaging effects of environmental perturbations. Thus, the coupling assumed in ecosystem models may be muted, delayed, or otherwise warped and non-linear.

Therefore, to understand the feeding and reasons for feeding behavior it is necessary to understand the behavior, numbers, and availability or vulnerability of prey species.

It is important to identify prey species which play an important part in the diet of the predator; e.g. i) crucial prey items of last resort to avoid starvation; ii) main prey species used by the predator population in winter and summer for feeding themselves; iii) prey species which are critical for reproductive success (for the female to lay eggs and/or the parents to bring food to their young). Furthermore, variation in the species used for food among regions may be large.

Hence, we disapprove, for example, of the use of the words "feeding radii" except as indicators of the absolute extreme distances to which birds will fly to feed at sea: e.g. about 100 miles, or halfway to the next colony (which becomes meaningless). The sea is not a homogeneous medium. Because of ocean currents, the whole sea moves past the breeding areas in our region (the Bering Strait) at a rate of several knots. Thus, though the food resources may be renewed daily, the seabirds in our area may be very sparse near the nesting area and may commute tens of miles to patches of ocean where they and, one presumes, their prey are temporarily dense. We know already that feeding seabirds and some sea mammals concentrate only in certain areas in the Chirikov Basin. Apparently these concentrations have little relation to accessibility to seabird nesting sites but have close relations to water masses, depth, sediments, and topography of the bottom.

Furthermore, relative to coupling within or between systems, a change in population of one major species may have either a profound effect on other species, or virtually none. Again, we think it is too easy to make predictions from rigorous formulae as if all parts of a system have similar couplings.

It may well be that some commercial fishing activities will affect the food supplies of terns, kittiwakes, murres, and other seabirds, or will affect the populations of large fish which drive bait fish to the surface and make them available as prey items. We would be chary of assuming any direct correlation *a priori*. To put it another way, we think of many subsystems in one "ecosystem" as operating more or less independently of the other subsystems. Occasionally one subsystem may interact with another and these interactions may be direct and important; but it is a mistake to assume that action in one will affect neighboring ones until that has already been established. It is as wrong to assume coupling as it is to assume lack of coupling. We think of systems continuing to operate and to be resilient, not because they are well-integrated but because they are so loose and their elements so redundant that it is hard for disturbance to get a toehold. The members are "accustomed to" extemporizing with changing habitat.

It is through the link of predators to their prey, or other organisms to the resources they need (simple in concept but complex in operation), that fish, mammals, and birds have their major coupling with their "systems." It is by their "tactics" in exploiting, not being shackled to, this linkage that species are "successful," i.e., numerous, widespread, constant in numbers, etc. It is by understanding the nature and operation of these links that we can predict whether or not and how "indicator" species will be affected. The assignment of species to categories such as opportunistic or system-dependent is to simplify the concept to such a degree as to miss the ways in which species compensate for environmental changes. We suspect that the long term failure at "controlling" coyote populations in the United States has been related to a failure of understanding the relationship of the coyote to _its_ systems, not _the_ system.

c. _Stable and healthy configuration of species and ecosystem health_

There is an assumption that there is a stable and healthy configuration of species which will tend to be reestablished after a perturbation has ceased.

Obviously, population size is coupled in some way with various capacities of the habitats occupied to support individuals. If not, populations would increase indefinitely. However, we believe that environmental limitations are expressed sporadically, as we discussed at length in the section on Herring Gulls, not as smooth and steady "regulation." As stated earlier, we believe that "carrying capacity" is an abstraction and that the number of individuals which can make a living may vary greatly with time and space under undisturbed conditions within one "habitat." As a result we hold as a basic tenet that in a state of nature populations may vary dramatically through time and space, i.e., without interference by man.

Similarly, we believe that although the growth of populations may be slowed as their density increases there is no necessary corollary that their growth is stimulated by low densities. Such a reciprocal influence is a logical symmetry unsupported by evidence. It suggests that there is a compensatory mechanism leading to a return to the natural asymptote. We acknowledge that some closeted biologists have assumed this correlation as part of classical ecological dogma, but we believe that it is actually a consequence of "elegant" mathematical formulations, not of the study of nature.

We feel that there is a very important difference between the concept of equilibrium as formulated for the physical sciences and the concept of steady states involving variability and population exchange as formulated by biological scientists studying animals and plants. Even in tropical systems, long thought to epitomize "maturity and hence stability," those populations which have been studied in detail have been found to vary in size tremendously; so seabirds and arctic systems are not special cases in this respect. We have evidence that local populations are in flux and may often go extinct. The "population" is then maintained by influx from other areas where there is population surplus and hence emigration. A considerable literature has developed during the last 15 years treating this topic, "island biogeography" (see page 553).

Hence, we are hesitant to think in terms of the "health of an ecosystem" as if there were a preferred configuration of species and numbers of individuals which once displaced would tend to be reestablished. Although field students see specific linkages, we tend to be much less sanguine about coherent ecological structures than are those who study energy flow and dynamics of ecosystems. Many physical scientists and physiological biologists who have moved into ecology trace their disillusionment with coherent or elegant models to that move (see Slobodkin 1960).

We feel uneasy with blanket statements about negative impact on ecosystems or damage from which systems recover. We expect that negative effects on one species will often be associated with positive effects on others. That differential impact is, after all, the basis of domestication of animals, the cultivation of plants, or management of game species. Cultivation or domestication were tactics by which a successful predator, humans, avoided being coupled to natural decreases or movements of food supplies.

We expect that economic development in coastal Alaska will be accompanied by an increase in Ravens, Glaucous Gulls, Glaucous-winged Gulls, Pintails, and Mallards, among others. We are concerned that this potentially important effect is being largely ignored by OCSEAP. The predictable increase will be accompanied by biological problems, first in the cases where these predators displace other less aggressive species such as raptors from their nest sites, second in cases where their predation on seabirds and waterfowl young will be intensified, and third in cases such as Glaucous-winged Gulls meet and hybridize with Herring Gulls in the Glacier Bay-Copper River area and hybridize with Glaucous Gulls in the Yukon-Kuskokwim delta.

On the other hand, we expect that in many places, conspicuous species are just hanging on with little success locally and can readily be extirpated. This means that a species is in no way an inherent and necessary part of the "community." Kittiwakes may be such a species in the Bering Strait Region.

We expect that it is dangerous to generalize about the behavior of groups of species when individual species follow different "strategies." The word strategy is ecological jargon for sets of interrelated behaviors (including how nests are dispersed, how rapidly young develop, kinds of food used, and distances over which birds seek food) by which a species' ecological adaptations can be characterized. For example, the strategy of mobility of nesting sites among species such as terns which nest on unstable sand islands or gravel bars should not be expected to apply to the strategy of site tenacity among species such as murres or petrels which concentrate at a few rocky nesting islands. There is a field, "game theory," that has proven useful in examining the "strategies" of species using highly variable resources and the "strategies" of species using resources which vary little within seasons, between seasons, or among years.

2. The Variability of Seabird Populations, Their Size, the Forces Affecting Them, and Their Suitability as Indicators for Monitoring Impacts

a. Because variation in bird population sizes can be observed and documented quantitatively, this does not mean that there is more error/scatter and that therefore birds are less suitable as indicators than are other organisms whose variability in populations is not evident. We feel that apparent consistency or clustering of data about averages recorded in some organisms results primarily from lack of ability to make precise measurements within a short time span or area; i.e., the results suggest bogus rigor or precision.

We doubt very much that OCSEAP will find any simple set of variables that can be used to predict changes in biological parts of an environment, especially according to a linear model.

Biological functions are non-linear and, in our experience, logarithmic transformations help to make "quantification" of biological processes tractable. Instead of being summarily discarded, seabirds should be used as organisms especially suitable for numerical monitoring until more useful alternatives are known. We have suggested elsewhere (Species Accounts, Appendix VI) how different species of seabirds can be used for different purposes in monitoring.

We can see and count seabirds, which gives a "ground truth" against which to calibrate our estimates. In contrast, sampling of most other marine organisms requires calibration of blind grabs against speculative models designed to supply consistency.

Specifically, there has been reported a 50 percent decrease in murre populations between the late 1950s and the late 1970s on the Bering Strait and southern Chukchi cliffs. We feel that this offers an incomparable opportunity to a) prepare sampling techniques both for (i) the mathematical and (ii) the biological problems of how breeding birds redistribute on the cliffs following a natural "experimental reduction"; and b) follow future changes.

As to the "sorts of indicators required," it may be that when some processes are better understood some indicator species for parts of systems along parts of the spectrum of changes may emerge. For example, we expect that the growth rates of *Ammodytes* or population changes in *Thysanoessa* might integrate a number of chemical, physical, and biological processes in the northern Bering Sea. The question to be resolved by group research is whether the integrations which these biological processes perform are passed on to kittiwakes and auklets; i.e., we may learn whether, where, and how the systems are coupled and uncoupled.

b. Value of seabird studies

Seabirds are eminently visible and are a center of attention for a large segment of the conservation-minded public. The presence of oiled seabirds, regardless of the longterm effect, generates public outcry.

Seabirds may occur in local concentrations involving millions of birds and thousands of metric tons of biomass. Given that these birds probably consume on the order of 20 percent of their body weight daily, the removal of large segments of the bird population could alter the present ecological structure of the ocean.

Perhaps of more immediate importance, however, is the potential role of seabirds as indicators of environmental quality. They are more conspicuous, hence easier and probably less expensive to study and monitor than other marine species. Since we do not have time or resources to study all areas or all species, we need to make generalizations from a few typical species. To this end we need to select "indicator" species and target areas for concentration of research effort. Because many seabirds are highly vulnerable to floating oil, they can provide indices of contamination through changes in number or distribution. Moreover, these birds as high order consumers at the top of the marine food chain may provide sensitive gauges of the functioning of the marine ecosystem.

3. Linkage Between Marine Birds and the Marine Ecosystem

While it is clear that generalization must be built on "indicator" species, we must nevertheless recognize that the use of certain species as indicators of "environmental quality" or "ecosystem health" depends upon linkage between these species and the ecosystem. We need to learn what the linkages between seabirds and their food resources really are, and we need to learn which of these linkages will be sensitive not only to acute but also to the chronic impact of oil pollution.

Possible Indicator Species

In order to select indicator species it is necessary to ask first what it is we need to know about environmental change and second, which species will supply the answers, i.e., will the species be affected and in what ways.

a. Direct effects of oil on the water:

In order to assess the impact and distribution of oil spills, especially small, chronic losses, we need to have an indicator species that is i) vulnerable to floating oil, ii) that has a widespread distribution, and iii) that occurs in numbers whose changes can be easily measured. Of the breeding seabirds most often encountered in Alaska, the puffins would seem to be a good candidate for this role; they nest in many small to moderate sized colonies well dispersed along most coasts. Murres are often too numerous to allow accurate counts of numbers and tend to be clumped in large colonies. Kittiwake numbers are less likely to be directly affected by spilled oil than alcids because kittiwakes spend relatively little time on the surface of the water.

b. Assessment of local changes or "environmental stress" on food chains:

To the extent that oil development and its attendant activities may cause adverse impact on local food chains or other local ecosystems, it is necessary to have a species for which it is possible to monitor the effects of changes in the availability of food. This can be accomplished through knowledge of the reproductive ecology of a species, including such information as phenology, clutch size, growth of chicks, and fledging success, all of which are sensitive to variations in the availability of resources to breeding adults. For an indicator species of this sort we would choose the Black-legged Kittiwake because the reproductive biology of this species appears to be sensitive to local changes in food supply and because data on reproductive performance can be obtained with relative ease and considerable accuracy; therefore, kittiwakes may be useful as inexpensive yet accurate indicators. They have the further major advantage that considerable background information is available for this species in Alaska and in other parts of its range. Because they are easy to study and probably lack direct sensitivity to spilled oil, kittiwakes are likely to be more useful for gathering information on indirect effects--that is, on the "quality" of the ecosystem--than the alcids.

c. Assessment of spatial patterns of ecosystem productivity and health:

For the purposes of this sort of monitoring, we require a species that is sufficiently widespread and numerous, that is easily located, and for which major changes in numbers and distribution will be detectable.

Also a species will be preferable that is present for most of the year and does not gather in highly mobile, wandering flocks in clumped and erratic distribution. Murres seem suitable for these functions.

4. Planning and implementing programs of research: cooperation among disciplines

We believe that the planning of research programs in NOAA OCSEAP has depended too heavily on the goal of preparing predictive mathematical models of trophics systems and has lacked coordination of this work with the work of field biologists in diverse locations. While these designs may be suitable for physical systems, the approach does not acknowledge that variability in biological systems may involve adaptations by which active vertebrates avoid being coupled to changes in physical systems. The use of redundancy of systems differing in important ways may supply the insurance that keeps populations from extinction during hard times. Thus study of redundancy and of regional differences are of fundamental importance to understanding the operation of systems.

Cooperation among members of research teams from different disciplines encourages understanding and melding of the contributions of those who study different aspects of the systems. Cooperation has been successful in some aspects of the OCSEAP, but has largely been the result of coincidences of personal acquaintance, with the exception of the LGL effort in Simpson Lagoon. Most of the P.I.s in the OCSEAP have operated as if feudal lords in their own feifdom.

If there is future work, it should be directed to specific problems or areas. Principal Investigators should be in groups which formulate problems, plans and carries out the programs. For such programs to be efficient and cost-effective, their efforts should be housed on relatively small vessels. This would allow more parties to work and would avoid the inertia inherent in the operation of overly large vessels whose calendars are planned months in advance. While physical oceanographic work may possibly be planned months in advance, the greatest value of biological research is gained when investigators can interact directly with their study and change programs to test new ideas as the ideas appear. The logistics plans during the OCSEAP so far have favored programs which can be planned months in advance and inhibited many types of effective biological work. Fixed transects and predetermined stations, while they may appear to provide statistical rigor, can result in biological observers spending 95 per cent of their time in sterile areas. Even when it is known where and how subjects are distributed, it is necessary to investigate short-term changes in patterns of distribution which occur according to local short-term effects. Observers must be as opportunistic in pursuing their subjects as the vertebrates are in pursuit of their prey. This means daily changes of plans. The alternative assumes homogeneity of "within-habitat" structure and diversity, the validity of averages , and assumptions of linear patterns. These may make it easier for the model-maker to use the simpler mathematics of deterministic models, but it is our conviction that they do not shed much light on the operation of natural systems.

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