Exxon Valdez Oil Spill
Restoration Project Final Report

Seasonal Movements and Pelagic Habitat Use of Murres and Puffins Determined by Satellite Telemetry

Restoration Project 95021
Final Report

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Study History: In 1994, the National Biological Service (NBS) used in-house funds to conduct a feasibility study of satellite telemetry in common murres on Middleton Island, north-central Gulf of Alaska. Results of that effort formed the basis of a proposed 3-year study at the Barren Islands as an *Exxon Valdez* Oil Spill (EVOS) Restoration Project beginning in 1995. EVOS funding in 1995 ($53,800) supported technician and part-time veterinarian salaries through September 30, purchase of 6 satellite transmitters, contractual data-processing fees, and equipment, commodities, and travel costs associated with field work at the Barren Islands. NBS contributions in 1995 ($24,300) and 1996 ($27,500) supported purchase and deployment of 9 additional transmitters at the Barren Islands (4 common murres, 5 tufted puffins) and salary costs for a technician ($21,500) and principal investigator ($6,000) during preparation of this report. In 1995, NBS also deployed 20 transmitters ($93,600 in-house funding) on common and thick-billed murres at two colonies in the Chukchi Sea. Because the application of satellite telemetry to marine birds is developmental, results from all three study sites are mutually informative. Work at the Barren Islands was not funded by the *Exxon Valdez* Oil Spill Trustee Council for continuation in 1996. The following account of work conducted at three colonies in 1995 is submitted as the Final Report for Restoration Project 95021.

Abstract: Common murres (*Uria aalge*) were the bird species most heavily impacted by the *Exxon Valdez* oil spill. The failure of this species to recover 6 years after the event may be related to a long-term decline in the availability of suitable forage. Elsewhere in the restoration program, tufted puffins (*Fratercula cirrhata*) are being used as samplers of the forage fish community and as indicators of changes that may be affecting murres and other injured resources. Tests of hypotheses concerning food limitation on murre population recovery and the application of puffins as fish samplers require information on the foraging ranges and feeding areas of birds from specific colonies. In July 1995, implantable satellite transmitters were deployed in 10 common murres and 5 tufted puffins at the Barren Islands, Gulf of Alaska. In a related study, 20 transmitters were deployed in common and thick-billed murres (*Uria lomvia*) at two colonies in the Chukchi Sea. Barren Islands murres primarily foraged south to Kodiak Island waters at distances of 40-100 km from the release site. One tufted puffin stayed within 20 km of the islands before departing the colony and moving to a relatively small area of open water some 100 km east of Marmot Island. Murres from Cape Lisburne and Cape Thompson commuted up to 135 km from their colonies while breeding, then migrated to a common wintering area in the southeastern Bering Sea near the Pribilof Islands. The main problems encountered during the study were shorter than expected battery life and the inability of some birds to survive the procedure.

Keywords: Barren Islands, Cape Lisburne, Cape Thompson, common murre, *Fratercula cirrhata*, satellite telemetry, seasonal movements, thick-billed murre, tufted puffin, *Uria aalge*, *Uria lomvia*.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

LIST OF APPENDICES

EXECUTIVE SUMMARY

Introduction

Common murres (*Uria aalge*) were the bird species most seriously injured by the *Exxon Valdez* oil spill. After the spill, fewer breeding murres were found at the Barren Islands compared to historical data, and annual censuses have not detected any recovery. One hypothesis to explain the failure of common murres to recover is that low food availability is limiting the birds' ability to breed successfully or to survive in sufficient numbers during the nonbreeding season. As part of the restoration effort, tufted puffins (*Fratercula cirrhata*) are being evaluated as samplers of the forage fish community and as indicators of changes that may be affecting murres and other injured resources. Information on the foraging areas and seasonal movements of murres and puffins is needed to test hypotheses concerning recovery potential and to validate techniques currently being employed in the restoration program for seabirds.

Satellite telemetry offers a more cost-effective approach for determining foraging patterns and habitat use by seabirds than conventional survey methods. In this study, we used implanted satellite transmitters to assess the movements of common murres and tufted puffins from colonies on the Barren Islands and of common murres and thick-billed murres (*Uria lomvia*) from two colonies in the Chukchi Sea. Results from all three study sites illustrate the utility of this approach, as well as problems that must be overcome through further development.

Objectives

The main objectives of this study were: (1) determine the foraging ranges and primary feeding areas of murres and puffins from colonies in the Gulf of Alaska and Chukchi Sea, and (2) locate important nursery and/or wintering areas of birds from the same colonies and determine the timing of use of those critical habitats.

Study Areas

The Barren Islands lie at the mouth of Cook Inlet, about midway between the Kenai Peninsula and Kodiak Archipelago. We took tufted puffins from burrows on West Amatuli Island and common murres from ledges on the northeast side of East Amatuli. In the Chukchi Sea, we sampled murres at Cape Lisburne and Cape Thompson, lying north and south of Point Hope on Alaska's northwest coast.

Methods

Our telemetry device was a 35-gram transmitter supplied by Microwave Telemetry, Inc. of Columbia, Maryland. Transmitters were constructed according to specifications issued by Argos, Inc., the company that operates receiving equipment aboard NOAA weather satellites and distributes transmitted data to users of its data collection system. Besides location data, transmitters provided running information on battery potential and body temperature of the tagged bird. Fourteen transmitters were programmed to turn on for 6 hours and turn off for 12 hours ('short cycle'). Twenty-one transmitters were programmed to turn on for a 6-hour period every three days ('long cycle'). Long- and short-cycle transmitters were deployed in a 3:2 ratio to emphasize the acquisition of winter location data.

Field work was conducted between 15-18 July at the Barren Islands and between 1-6 August in the Chukchi colonies. Birds were captured off nests and transported to a field camp, where they were surgically implanted with transmitters and released in a matter of hours.

We downloaded data from Argos at 2-3 day intervals and used Arc/Info and Arc/Plot software to analyze and map locations of tagged birds. Information supplied by Argos included a coded index to the accuracy of each location. To cull inaccurate data points, we examined the redundancy of locations obtained close to each other in time, and other biologically meaningful criteria, as well as reported signal strengths.

Results

Implanted birds were released in apparently healthy condition and began transmitting location data immediately. The span of days over which we received messages from each of the 35 transmitters deployed ranged from 0 to more than 250 days. In spite of problems with battery life and post-release mortality of tagged birds, we acquired more than 2,100 locations over the course of the study. One thick-billed murre from Cape Lisburne was still carrying an active transmitter and providing locations as of mid April 1996. On average, we culled about 22% of the data, so the net result for all three species and study areas was about 1,650 usable locations.

Tufted puffins tagged at the Barren Islands ranged up to 100 km west and more than 150 km east of West Amatuli Island during the first 2 months after release. Most puffins appeared to abandon their nests as a result of our disturbance. One bird continued to forage near the colony for several weeks then moved to a limited area of open water about 100 km east of Afognak Island, where it remained through September. Common murres tagged at the Barren Islands stayed within a 100-km radius of the islands for the duration of the study. Movements were mainly in a north-south direction, ranging from the mouth of Kachemak Bay to the northern end of Kodiak Island. Waters along the northern shores of Shuyak and Afognak islands were clearly a preferred feeding area in late summer. There was no indication of differences in habitat use between the sexes. No signals from birds tagged at the Barren Islands were received after 20 September.

Murres in the northern colonies ranged more widely than those at the Barren Islands—up to 200 km during the first month after release. We detected no differences between species at either colony, but foraging areas of murres from Cape Thompson (southwest to southeast and north to Point Hope) overlapped little with areas used by Cape Lisburne murres (mainly northwest to northeast of the colony). The mean distance to foraging sites was 68 km in five murres that appeared to be tending chicks at the colonies. After departure, male murres tended to drift north and west toward Siberia, whereas females flew directly south. All birds eventually reached the vicinity of the Pribilof Islands, which appeared to be their final winter destination.

Mortality in the first month after release was 6 of 10 murres tagged on East Amatuli Island, 6 of 10 birds tagged at Cape Lisburne, and 0 of 10 birds tagged at Cape Thompson. Four of the five tufted puffins we implanted were also believed to have died within 30 days. Another significant problem was shorter than expected battery life.

Discussion

Foraging ranges of Alaskan murres were much larger than some reported from Britain, which implies that murres have considerable flexibility in their time and energy budgets while breeding. We detected no differences between the foraging patterns of males and females, or between thick-billed and common murres in mixed colonies. The fact that murres of both species ranged farther from their colonies at Cape Thompson and Cape Lisburne than murres at the Barren Islands suggests that local environmental factors are more important in determining foraging distances than differences in feeding adaptations between these closely related species. Infrared satellite images of the Barren Islands and vicinity suggest that murres were attracted to areas of upwelling and cold surface temperatures near Shuyak and Afognak islands. The fact that female murres from the Chukchi colonies elected to move into the Bering Sea soon after departure suggests that food resources there in late summer and fall were better than in the Chukchi Sea.

Probability of death was related to the duty-cycle (percentage of 'on' time) programmed into the transmitter a bird carried. This suggests there were unanticipated effects of radio signals on physiology or behavior. More detailed investigation is needed, but we speculate that neural impulses are generated that interfere with normal diving behavior. We are optimistic that the mechanisms of injury can be identified and solved, perhaps by surpressing the operation of the transmitter while a bird is underwater. The reduced battery life we experienced is now known to be caused by self-discharging that occurs when miniature lithium batteries are kept at the high internal temperature of a bird. This problem probably can be solved through further engineering of lithium batteries, or by using a different, larger type of battery in combination with other transmitter components of smaller size and weight.

Conclusions

Our results show that murres fly routinely up to 100 km from their breeding sites, a fact that must be taken into account in designing oceanographic studies of murre foraging habitat. Cold, upwelled water along the north coasts of Shuyak and Afognak islands appears to be a preferred habitat of Barren Islands murres in summer. We were unable to identify the wintering area of murres from that colony as none of our records extended beyond late September. We know that birds from Cape Thompson and Cape Lisburne wintered in the vicinity of the Pribilof Islands in 1995-1996. Given the relatively long distances that murres and puffins traveled to feeding areas, we consider that satellite telemetry, in its present state of development, is well-suited for characterizing both the summer foraging patterns and winter distribution of pelagic birds. Solutions to the problems of bird mortality and battery life are needed to increase the prospects for longer-term data acquisition in the future.

INTRODUCTION

Common murres (*Uria aalge*) were the bird species most seriously injured by the *Exxon Valdez* oil spill (EVOS). About 75% of the 35,000 bird carcasses recovered during the spill were murres, and estimates of murre losses exceeded 100,000 individuals. After the spill, fewer breeding murres were found at the Barren Islands compared to historical data, and annual censuses have not detected any recovery. Based on data from Nord Island, production of chicks was almost zero in both 1989 and 1990, and still low in 1991 and 1992 compared to colonies outside the spill zone.

One hypothesis to explain the failure of recovery in common murres is that low food availability is limiting the birds' ability to breed successfully or to survive in sufficient numbers during the nonbreeding season—an important rationale for ongoing EVOS-sponsored research such as the Alaska Predator Ecosystem Experiment (APEX). In the same context, tufted puffins (*Fratercula cirrhata*) are being evaluated as samplers of the forage fish community and as indicators of changes that may be affecting murres and other injured resources. Validation of those ideas requires that the principal feeding areas of murres and puffins be identified and that oceanographic studies be designed to assess the factors affecting food availability in both summer and winter. Mean foraging ranges must be evaluated, because flight distances have a large influence on calculations of energy expenditure (Gaston 1985). Information on foraging areas, foraging ranges, and migration patterns is difficult to obtain, however, because of the large distances traveled and the difficulty of tracking individuals over the open ocean. Traditional methods entail costly shipboard or aerial surveys (Bradstreet 1979, Nettleship and Gaston 1978, Schneider and Hunt 1984) or indirect calculations based on estimated flight speeds and time-activity budgets (Cairns et al. 1987). Few data are available on wintering populations of murres or puffins—none pertaining to birds from known breeding places in Alaska. Work reported here was funded in part by the EVOS Trustee Council for the purpose of addressing these problems using new technology.

Because of the potential for oil and gas development in the Chukchi Sea, murre populations in that area are an important target of seabird monitoring efforts sponsored by the Minerals Management Service (MMS), Fish and Wildlife Service (FWS), and National Biological Service (NBS) since 1976 (Springer et al. 1985, Fadely et al. 1989, Mendenhall et al. 1993a, b). To date, this monitoring has emphasized measures of population size and breeding productivity. On an annual basis, seabirds spend most of their time at sea, however, and even in the breeding season they are most vulnerable to potential pollution events while they are resting or feeding in marine habitats. Similar to restoration management, risk assessment for murres requires a basic knowledge of foraging and migration patterns year-round. In consequence, this project was partially funded by NBS, in consultation with MMS, to improve our understanding of pelagic movements in murres and our ability to interpret variation in conventional measures of population health.

Small (35 g) satellite transmitters have recently become available for use in wildlife telemetry (e.g., Petersen et al. 1995, Falk and Moller 1995). Implantable devices used by Petersen et al. (1995) are proven effective when deployed on birds in the size range of murres (c. 1 kg). Thus, telemetry now offers a more cost-effective approach for determining foraging patterns and habitat use by seabirds than conventional survey methods. In this study, we used implanted satellite transmitters to assess the movements of common murres and tufted puffins from colonies on the Barren Islands and of common murres and thick-billed murres (*Uria lomvia*) from two colonies in the Chukchi Sea, Cape Thompson and Cape Lisburne (Fig. 1).

Preliminary trials in 1994 using implanted transmitters in common murres (Hatch et al., unpubl. data) encouraged our expanded effort in 1995. Prior to this year, however, no tufted puffins had been subjected to the procedure. Our initial efforts, independently funded by the NBS in 1995, constitute a pilot study to assess the feasibility of the techniques in this smaller (c. 750 g) burrow-nesting species.

OBJECTIVES

Regardless of the impetus for tracking studies (pre- or post-spill issues concerning populations at risk or recovery potential) the main objectives of our work can be stated as follows:

(1) Determine the foraging ranges and primary feeding areas of murres and puffins from colonies in the Gulf of Alaska and Chukchi Sea, and

(2) Locate important nursery and/or wintering areas of birds from the same colonies and determine the timing of use of those critical habitats.

In many populations of seabirds, the majority of adult mortality occurs during the winter months (Hatch 1987, Hatch et al. 1993). Probably there is another critical period in fall, when recently fledged young make the transition to self-feeding (Burger 1980). However, the existence or location of possible ‘nursery areas’ is all but unknown for murres and other populations of seabirds in Alaska. Flightless murre chicks are led to sea by their male parents, who continue to provide parental care for several weeks as the young learn gradually to feed themselves (Harris and Birkhead 1985). Thus, we believe it will be possible to locate key foraging areas of juvenile murres by deploying transmitters on breeding males late in the season.

Murre colonies in the Chukchi region present an additional problem worthy of research. Monitoring at Cape Thompson has revealed a long-term decline in murre numbers (c. 50% since 1960), whereas populations at Cape Lisburne, just 100 km north, increased steadily between 1976 and 1987, and may still be growing (Fadely et al. 1989, Roseneau et al. 1989). The decline at Cape Thompson could have resulted from reduced winter food causing elevated over-winter mortality of adults, as proposed for the murre colony at Bluff in Norton Sound (Murphy et al. 1986). However, if murres from Cape Thompson and Cape Lisburne share a common wintering area, then divergent population trends would not have been predicted. Rather, we would reject the idea of winter limitation in favor of the competing hypothesis that differences exist in productivity and recruitment on the breeding grounds. Satellite telemetry offers the most direct approach to this question, which is typical of many similar situations encounterd in seabird monitoring.

STUDY AREAS

The Barren Islands lie at the mouth of Cook Inlet, an oceanographically dynamic area influenced by strong tidal currents and a low-salinity, rapidly flowing Alaska Coastal Current (Muench et al. 1978). This group of seven islands is situated about midway between the Kenai Peninsula and Kodiak Archipelago, on a ridge bordered on the east and west by deep troughs. Circulation patterns and bottom topography result in a highly productive local system that supports some 600-800,000 pelagic birds of 15 species (Sowls et al. 1978). About 90,000 common murres nest on two islands (Nord and East Amatuli), whereas tufted puffins occur on all the islands in numbers estimated at 200,000. Thick-billed murres are scarce at the Barren Islands. We took tufted puffins from burrows on West Amatuli Island and common murres from ledges on the northeast side of East Amatuli (cliffs adjacent to Lighthouse Rock). The nearest known wintering concentrations of murres to the Barren Islands are found in bays and fjords of the Kodiak Archipelago, Lower Cook Inlet, and the outer coast of the Kenai Peninsula (Forsell and Gould 1981, Agler et al. 1994). Substantial numbers of wintering murres also occur within Prince William Sound in some years (Kosliewski and Laing 1994).

Cape Lisburne and Cape Thompson lie north and south, respectively, of Point Hope on Alaska's northwest coast. Some 100,000 murres, mostly (70%) common murres, nest at Cape Lisburne, while Cape Thompson supports an estimated 390,000 murres of both species (ratio undetermined). Black-legged kittiwakes (*Rissa tridactyla*) are also abundant at both sites; 6 other species (cormorants, gulls, guillemots, and puffins) occur in small numbers (Sowls et al. 1978). We took murres at the eastern end of the Cape Lisburne complex, from ledges easily accessible on foot from the Air Force radar station. At Cape Thompson, we caught thick-billed murres in colony 3 (as designated by Swartz 1966) near the mouth of Ikijaktusak Creek and common murres in colony 4, comprising cliffs surrounding Cape Thompson itself.

Oceanographically, the eastern Chukchi Sea is characterized by the convergence and accelerated northward flow of three major currents through Bering Strait, representing Anadyr, Bering Shelf, and Alaska Coastal water masses respectively (Fleming and Heggarty 1966, Coachman et al. 1975). Each current carries a unique mixture of nutrients, plankton, and fish, and fronts between currents are thought to stimulate local production (Springer et al. 1984, Piatt et al. 1991). Sea ice usually does not move out of the Point Hope region before early to mid July, and because of advancing ice in winter, the nearest potential off-season areas for murres from these colonies are in the southeastern Bering Sea, or possibly in polynyas off the southern coast of St. Lawrence Island.

METHODS

Our telemetry device is a 35-gram platform transmitter terminal (PTT) supplied by Microwave Telemetry, Inc. of Columbia, Maryland. The units are identical in most respects to transmitters used previously (1993-1994) in telemetry studies of spectacled eiders (*Somateria fischeri*) (Petersen et al. 1995). Only the programmed duty-cycle (alternation of transmission and inactive periods) differed between some of our transmitters and those used by Petersen et al. (1995). The rectangular body of the transmitter measures approximately 55 x 35 x 10 mm. The antenna (c.

200 mm) consists of a teflon-coated multistrand stainless-steel wire bent at its base to form a 90° angle between the antenna and long axis of the transmitter body. During manufacture the lithium batteries and other electronic components are dipped in a biocompatible potting material that ensures a hermetically sealed package suitable for implanting.

Transmitters are constructed to meet specifications issued by Service Argos, Inc., the company that operates receiving equipment and distributes transmitted data to users of its 'Data Collection and Location System.' The frequency of all PTTs is required to fall within close tolerances (± 4 kHz) of 401.65 MHz as the calculation of position coordinates is based on the doppler shift in wave frequency detected by a receiver as it approaches and recedes from a transmitter during an overpass. In 1995, Argos had receivers on three NOAA polar-orbiting weather satellites, although one satellite went out of service within a few weeks after we deployed our PTTs. Even so, at the latitudes of our study areas in the Gulf of Alaska and Chukchi Sea, we could expect a satellite overpass every 60-90 min on average. However, not every overpass results in the detection or location of an active transmitter (see below). A PTT in its active mode transmitted a 32-bit message over 360 msec, with a repetition interval of 70 sec. Besides location information (computed from frequency shifts, as noted), each message contained calibrated indices to the internal body temperature of the bird and remaining battery potential. Both pieces of information were vital for determining the cause of eventual signal loss (death of bird versus failure of the transmitter). Mortality was often indicated unequivocally by a marked drop in temperature. If a PTT quit transmitting with no other indication of fate, we sometimes inferred mortality, depending on past transmitter performance or timing of the disappearance as compared to similar occurrences in birds of known fate.

We downloaded data every 2-3 days from the Argos earth station in Fairbanks, Alaska via Tymnet, Argos' online data distribution system. We also purchased cumulative data files on tape at monthly intervals.

Field work was conducted between 15-18 July at the Barren Islands and between 1-6 August in the Chukchi colonies (1-3 August at Cape Lisburne, 4-6 August at Cape Thompson). We used noose poles to catch murres off the nest; we pulled incubating tufted puffins from burrows on West Amatuli Island. The breeding status of murres (egg present or not) was noted whenever possible. Birds were transported to a field camp where they were measured, banded, and implanted with transmitters within a matter of hours after capture. Details of the surgical procedures are provided in Appendix 1. Briefly, the transmitter was inserted into the abdominal cavity through a mid-ventral incision, with the antenna exiting dorsally to one side of the tail. To maximize signal strength, we attempted to have the antenna pointing directly upward when the bird was on the water (see Korshchen et al. 1984). Birds were sexed during surgery by using a fiber-optic endoscope to view the gonads. After surgery, birds were allowed to recover for 2-4 h then released at a shoreline near camp (approximately 1-5 km from the colonies). Our protocol was the same at each site, with one exception—we used picric acid dye to mark our instrumented birds for later recognition at the Barren Islands and Cape Lisburne, but not at Cape Thompson.

PTTs were initially programmed to transmit on one of two duty cycles. Fourteen transmitters were programmed to turn on for 6 hours and turn off for 12 hours ('short cycle'). Twenty-one transmitters turned on for 6 hours and turned off for 66 hours ('long cycle'). Battery life is related to transmission frequency. After 32 days (expected battery life), short-cycle transmitters switched to the long-cycle program, retaining enough battery power in most cases to provide additional data at longer intervals. We chose to emphasize the acquistion of winter location data, hence the 3:2 ratio of long- to short-cycle PTTs. We sought an equal sex ratio among the tagged murres on East Amatuli Island, but were unable to catch as many females as males. Elsewhere, transmitters were deployed in groups of 5 units per species and location. With one inadvertant departure from the intended scheme at Cape Lisburne and Cape Thompson, we used a 3:2 ratio of long- to short cycle PTTs and a 3:2 ratio of males to females at each colony. The final allocation of transmitter types among species, sexes, and locations is shown in Table 1.

Not all of the location data obtained were considered reliable. Information supplied by Argos included the number of messages (32-bit transmissions) received during an overpass and a coded index to the accuracy of each location (Fig. 2). Location accuracy is estimated from a number of parameters internal to the system and is expressed as a probability—two-thirds of the locations in a given class are expected to fall within the stated frequency. Thus, while a point assigned location class 3 probably lies within 150 m of true location, it may in fact be off by a larger, unknown amount. Conversely, a point receiving one of the poorer quality codes (0, A, B, or Z) may in fact be highly accurate. To cull erroneous points, we relied on the redundancy of locations obtained close to each other in time as well as on reported signal strengths. We used the following guidelines to make decisions about the relability of each location: (1) *The point lay outside a group of points*—previous and subsequent locations were in agreement, but the location in question lay conspicuously outside the cluster (> 3.5 km away). The odd location was deleted if signal quality was 0 or worse. After the breeding season, when broader scale migration patterns were more important, we raised this tolerance to 50 km. (2) *The point lay outside of the general path of movement*—a bird appeared to be following a specific course, suddenly moved off path, then returned to the path when next located. The odd point was deleted if signal quality was 0 or worse. (3) *The rate of movement between points was unrealistic*—i.e., greater than 58 km/hr (Tuck 1961, Bradstreet 1982) and the distance between points was more than 3.5 km. The less reliable point (determined by location and signal quality) was deleted. (4) *Constancy of individual behavior*. Some birds were more active than others, so past movements were taken into account when assessing the likelihood of questionable points. (5) *Signal quality*. Unless they were at or very near the colony, locations of quality A, B, or Z lacking redundancy were deleted. Points of quality 0 were usually treated like points of A, B, and Z quality, but were also judged by number of messages used in the calculation and plausibility, as above. Points of quality 1, 2, or 3 were accepted unless they clearly reflected implausible locations.

We found it was inappropriate to apply the above culling criteria in every instance, because that would have led to important information being lost. For example, a long move was often followed by several points separated by distances >3.5 km but much shorter than the length of the original move. Deleting those points because of the 3.5-km rule would erase our record of the long move. Also, depending on plausibility, points that would otherwise have been deleted were sometimes retained if they represented the only data collected for a week or more.

Data retrieved from Argos were analyzed and mapped using Arc/Info and Arc/Plot geographic information systems. Distances were calculated from latitude and longitude, taking the earth's curvature into account. Foraging ranges were calculated by averaging distances from the colony to a locus of points that comprised a foraging bout. In general, we defined a foraging bout as any collection of points that occurred between returns to the colony. However, because trips to the colony were probably missed, we further narrowed the definition to exclude points more than 10 km apart. When a bird moved more than 10 km, subsequent locations were considered to be a new bout. For each bout, the distances from individual locations to the colony were averaged. Ultimately, the sampling unit for statistical comparisons was the grand mean for an individual, i.e., we assume that foraging bouts will not be independent observatons of foraging range because of individual differences.

We used 2-tailed student's *t*-tests and *G*-tests to compare sample mean weights and mortality rates. Body weights were standardized by subtracting the local (colony) mean from each value before analysis. Our analysis of water depths included only locations obtained in the first 30 days after deployment (i.e., before migration). Depths were handled in a manner similar to foraging distances—i.e., we averaged depths during a bout and calculated a grand mean for each bird. Mean differences among study areas and between dead and surviving birds were tested in a 2-way ANOVA.

RESULTS

Quantity and Quality of Data Collected

Both puffins and murres proved hearty enough to withstand the effects of full anesthesia and surgery—we had no losses during the operations or throughout the period the birds were held captive. Implanted birds were released in apparently healthy condition and began transmitting location data immediately. The span of days over which we subsequently received messages from each of the 35 PTTs deployed ranged from 0 to more than 250 (Table 2). In spite of problems with battery life and post-release mortality of tagged birds (see below), we acquired more than 2,100 locations over the course of the study (Table 3). One thick-billed murre from Cape Lisburne was still carrying an active PTT and transmitting locations in mid April 1996.

Overall, we culled about 22% of the data (27% during the breeding season, 14% post-breeding; see Methods), so the net result for all three species and study areas was about 1,650 usable locations (Table 3). In terms of quality codes assigned by Argos (Fig. 2), about 42% of our locations were of classes 3, 2, or 1 (Table 4) and are therefore expected to be accurate to within 1,000 m. Sixty-six percent were based on at least 4 messages received during an overpass (class 0 or better), an encouraging result in the context of animal tracking studies. We were able to use additional data from the A, B, and Z classes based on corroboration among locations, as described above.

Five birds that died washed up on beaches and continued to transmit location data from what we assume were fixed locations. Thus, using the same culling criteria as for live birds, we obtained an additional check on the performance of the transmitters. Among the 5 grounded PTTs, average distance to central location was not significantly different either before ($F = 0.76$, 4 *df*, $P = 0.55$) or after culling the points ($F = 1.91$, 4 *df*, $P = 0.11$), suggesting all the transmitters performed about the same. Before culling, these transmitters yielded 183 locations at a mean distance of 20.6 ± 66.7 (s.d.) km (median 0.80 km) from the source, which we took to be the node of positions for a given transmitter. The range was 0-466 km, and 53% of the locations were within 1 km of the node—similar to the percentage of data from live birds in location classes 0-3 (Table 4). After culling (using criteria applicable to the breeding season of live birds), we had 122 locations (67% of total) at a mean distance of 0.77 ± 0.93 km (median 0.41 km) from source. The range was 0-4.3 km, and 77% of the locations lay within 1 km of their estimated true position. The percentages of locations culled from fixed transmitters (61/122) and from live birds before migration (363/1,337) were similar ($G = 2.96$, 1 *df*, n.s.).

Pelagic Movements by Colony, Species, Sex, and Season

Barren Islands

Tufted puffins tagged at the Barren Islands ranged up to 100 km west and more than 150 km east of West Amatuli Island in the first 2 months after release (Fig. 3). We made no attempt to determine the breeding status of the birds after release. Individual patterns of movement (cf. Appendix 2, Figs. A.1-A.5) suggested that some, possibly all, of the puffins abandoned their nests as a result of our disturbance. This is evident, for example, in puffin (PTT) number 5846 and puffin 7548, each of which made extended trips toward the southwest over several days post-release, with no indication that they were commuting back and forth to the colony on West Amatuli. We got few or no data from two of the tagged puffins (nos. 5848 and 7558). The longest record for any of the five puffins (PTT 5849) suggests a bird that may have continued to attend its nest site. This bird foraged around the Barren Islands until 23 August, when it moved to a limited area of open water about 100 km east of Afognak Island (Fig. A.3). The bird remained in that general vicinity until we lost the signal on 20 September.

Common murres tagged at the Barren Islands stayed within a 100-km radius of the islands for the duration of the study (Fig. 4). Movements were mainly in a north-south direction, ranging from the mouth of Kachemak Bay to the northern end of Kodiak Island. There was no indication of differences in habitat use between the sexes. We know that we caused the failure of most, possibly all, of the birds implanted (due to eggs rolling off breeding ledges or being taken by gulls during the disturbance associated with capture). Thus, the movements of tagged birds are likely to differ from those of actively breeding murres. With two or three possible exceptions (e.g., Figs. A.10, A.15), tagged birds did not appear to commute regularly between distant foraging areas and their nest sites on East Amatuli. A generalization we can make from murre location data obtained at the Barren Islands is that waters along the northern shores of Shuyak and Afognak islands, as far southeast as Marmot Island, were clearly a preferred feeding area in late summer.

Cape Thompson and Cape Lisburne

Murres in the northern colonies ranged more widely than those at the Barren Islands—up to 200 km during the first month after release in some instances. We detected no differences in foraging areas between species at either colony (Fig. 5). There was, however, nearly complete separation of the foraging areas of Thompson and Lisburne murres during the breeding season (i.e., before 1 September). Birds from Cape Lisburne foraged almost exclusively northwest to northeast of the colony, whereas Cape Thompson murres foraged southwest to southeast and north to Point Hope (Fig. 6).

As was true at the Barren Islands, there were no obvious differences between male and female murres during summer at either Cape Lisburne (Fig. 7) or Cape Thompson (Fig. 8). Larger samples will be required to confirm this, however, because of individual differences in foraging patterns. By and large, birds seemed to move independently of one another, but in one instance two birds from Cape Lisburne—a female thick-billed murre and a male common murre—made long distance excursions of notable similarity (Fig. 9). The movements occurred several days apart, and presumably were dictated by physical features, possibly ice edges.

Five murres, including one observed to have fledged a chick (D. G. Roseneau, pers. comm.), appeared to engage in incubution or chick-rearing after release, as indicated by their flight ranges and regularity of foraging trips. Foraging distances during the breeding season averaged 79 ± 36 km (range 8-104 km, n = 6 trips), 53 ± 29 km (range 8-96 km, n = 28), and 63 ± 53 km (range 7-135 km, n = 4), respectively, for a thick-billed murre and two common murres commuting from Cape Thompson (Figs. A.41, A.43, A.31). At Cape Lisburne, the distances to foraging places averaged 66 ± 26 km (range 47-84 km, n = 2) in one commuting thick-billed murre (Fig. A.17) and 79 ± 26 km (range 44-114 km, n = 8) in a single commuting common murre (Fig. A.23).

Breeding murres began leaving the colonies around 1 September. After departure, the birds dispersed widely over the Chukchi Sea or flew directly south through Bering Strait. In either case, all tagged birds eventually ended up in the vicinity of the Pribilof Islands (Fig. 10). There was no difference between Cape Thompson and Cape Lisburne murres in that respect, from which we conclude that birds from both colonies had the same wintering area in 1995. There was, however, a distinct difference between post-breeding males and females. Whereas males tended to drift north and west toward Siberia (Fig. 11), most females flew directly south from the colonies (Fig. 12). Three Thompson females, one Lisburne female, and one Lisburne male stayed in Kotzebue Sound 1-2 months before heading south. Five additional birds appeared in Kotzebue Sound for 1 day during their migration.

Waters around the Pribilof Islands seemed to be the final destination of wintering murres as most birds remained there for the duration of our study. One male thick-billed murre made repeated trips between the Pribilof Islands and St. Lawrence Island, possibly visiting the polynya that forms off the southern coast of St. Lawrence in winter (Fig. A.18).

Problems Encountered

Bird Mortality

In the first month after tagged birds were released, 6 of 10 murres died at the Barren Islands, 6 of 10 birds died at Cape Lisburne, and 0 of 10 birds died at Cape Thompson. Subsequent mortality included one possible death at Cape Thompson 48 days after release (Table 2). All other murres outlived their transmitters. Four of the five tufted puffins we implanted also died within the first month of the study.

Probability of death was influenced by the duty-cycle of the transmitter a bird carried. Excluding one long-cycle PTT (no. 5848, Table 2) from which we received too little information to assess the fate of the bird, only 29% of short-cycle birds survived past day 32 (when short-cycle PTTs switched to the long cycle), versus 75% survival among birds carrying long-cycle PTTs (Fig. 13). The difference between transmitter types was significant ($G = 7.09$, 1 *df*, $P < 0.01$). No other factor we examined (species, sex, body weight, wing-loading, or water depths at feeding locations) was consistently related to probability of survival. At East Amatuli, birds that died (mean weight 1,114 g) were heavier than those that lived (mean 1,042 g; $t = 2.8$, 8 *df*, $P < 0.05$), counter to expectations if the transmitter package was too large. No effect of body weight was indicated in the combined analysis for all three colonies. Although mean water depths where birds foraged differed significantly among colonies (Fig. 14), there was no difference in that respect between birds that lived and those that died at either the Barren Islands or Cape Lisburne.

Battery Life

With one exception, transmitter batteries did not last as long as expected (8 months projected for the long cycle, based on battery potential and load). Among birds that outlived their transmitters, short-cycle PTTs that switched to the long cycle lasted 103-144 days, averaging 119 days of service. Long-cycle transmitters lasted 40-252+ days, averaging 115 days.

Batteries contained in dead, cold-bodied birds lost voltage at a slower rate (Fig. 14a) than batteries in live birds (Fig. 14b). In contrast to either of those linear patterns, most of our long-cycle batteries displayed a sharp drop in voltage at some point between 48 and 66 days after they were deployed. Such batteries continued to transmit data, albeit less effectively (fewer messages received), and in some cases a partial recovery of voltage occurred after several weeks (Fig. 14c). Transmitters then continued to operate well until a second drop in voltage took the units permanently off-line. The same phenomenon (sharp decline in voltage) occurred in 2 of 3 short-cycle transmitters 74-83 days after they switched to the long cycle.

DISCUSSION

Murres foraged at considerable distances from all colonies in summer, although data from the Barren Islands must be interpreted cautiously as those birds were no longer constrained by the need to return regularly to their nest sites. Birds engaged in breeding activities at Cape Thompson and Cape Lisburne appeared to forage routinely up to 100 km from the colonies. That result differs markedly from information on common murres in Shetland, where breeding birds usually stayed within 5-10 km of the colony (P. Monaghan, pers. comm.). This implies considerable flexibility in the time and energy budgets of murres, as anticipated by Burger and Piatt (1991).

Other authors have suggested that thick-billed murres forage farther from land than common murres (Swartz 1966, Drury et al. 1981, Gould et. al. 1982). Our results for birds that abandoned their nesting attempts gave no indication of species differences in foraging areas, but our samples of commuting murres were too small to say whether such differences existed in that group. The fact that Thompson and Lisburne murres of both species ranged farther from their colonies than murres at the Barren Islands suggests that local environmental factors are more important in determining foraging distances than differences in feeding adaptations between these closely related species (Bradstreet and Brown 1985).

Our main conclusion regarding the summer foraging behavior of common murres at the Barren Islands is that nearshore waters along the north coasts of Shuyak and Afognak islands were important feeding areas in 1995. Infrared satellite imagery available for 30 June 1994 indicates a distinct zone of upwelling and cold surface temperatures in that area. We suspect this is a recurring habitat feature generated by strong tidal flows in and out of Cook Inlet, but we are unable as yet to confirm whether cold water is a defining characteristic of feeding habitats used by murres from the Barren Islands.

We did not identify the wintering area of Barren Islands murres as none of our records for that colony extended beyond late September. We can state with some certainty, however, that the wintering area of murres from Cape Thompson and Cape Lisburne in 1995 was the southeastern Bering Sea in the vicinity of the Pribilof Islands. Because birds from both colonies used the same area, we suggest that a decline in winter carrying capacity is unlikely to be responsible for the historical decline of murres at Cape Thompson. The separation we found between summer feeding areas at these two colonies is consistent with the idea that better food resources in the breeding season support higher productivity and recruitment at Cape Lisburne.

Male murres that departed the Chukchi colonies, some no doubt with chicks, appeared to drift north and west toward Siberia, as would be expected given the prevailing currents and flightless condition of the young. Any designation of a nursery area for murres from these colonies would have to include all of the southern Chukchi Sea. After several weeks, when chicks presumably had become flight-capable, all of the tagged birds moved rapidly south through Bering Strait, and they did so well ahead of advancing ice. The fact that some female murres chose to move into the Bering Sea immediately upon departure suggests that food resources there in late summer and fall were better than in the Chukchi Sea.

Before culling our data, one reported location of a fixed transmitter (beached bird) was 466 km from its true position—that example alone underscores the importance of applying suitable criteria to remove misleading information from a database generated by satellite telemetry. Acceptance criteria that are more or less stringent can be developed, depending on the questions one wishes to answer. We feel that our criteria were fairly strict, which means that some good locations may have been discarded. After culling, 77% of locations from fixed transmitters lay within 1 km of true position, but the error was as large as 4.3 km. Given the relatively long distances that breeding murres and puffins traveled to feeding areas, we consider that satellite telemetry, at its current stage of development, is well-suited for characterizing summer foraging patterns . Obviously, the identification of wintering areas is even less demanding of highly accurate location data, and present techniques are more than adequate for the task.

For maximum effectiveness, future applications of satellite telemetry to marine birds will have to overcome several problems. First, methods of capture should be devised that permit birds to be instrumented without disrupting normal breeding activities. This is an inherently difficult problem when working with open-nesting species such as murres, but better outcomes than ours have been achieved elsewhere through judicious timing of the captures relative to stage of nesting (M. P. Harris, pers. comm.). Working at night might also be effective in colonies with less than continuous daylight in summer. For any given species, including murres, some colonies will afford better opportunities than others to catch birds with minimal disturbance, although the location of study sites may be dictated by other considerations, as was true in this study. We doubt whether this problem compromises the utility of winter location data—i.e., it seems likely that birds will go to the same places outside the breeding season whether they breed successfully or not.

The reduced longevity of lithium batteries we experienced is now known to be caused by self-discharging that occurs when the batteries are kept at the constant high temperature (c. 104 °C) in the body cavity of a bird (P. A. Howey, Microwave Telemetry, Inc., pers. comm.). To minimize this discharging, battery terminals are designed to chemically coat themselves while the PTT is off, a process known as passivation. Electrical current breaks down the coating when the PTT comes on. This scheme seemed to work more or less as intended in our short-cycle transmitters, possibly because current was applied frequently enough to clear the coating each time the transmitter turned on. We speculate that long-cycle transmitters spent too little time on for the amount of time they were off, and that the sudden drops in voltage we observed were caused by excessive passivation. We believe these problems can be solved through further engineering of lithium batteries, or by using a different, larger type of battery in combination with other transmitter components of smaller size and weight (see below).

The most serious problem we encountered was the inability of many implanted birds to survive the procedure over the long term. The apparent difference in mortality among study areas suggests environmental variation may have played a part. However, murre breeding success was uniformly high at all three colonies in 1995 (D. G. Roseneau, pers. comm.), contrary to what we would have expected if murres at Cape Thompson (good survival) had more food accessible to them than those at Cape Lisburne or the Barren Islands. Because we refrained from coloring the breast plumage of tagged birds at Cape Thompson, it is possible that treatment with picric acid, not the transmitters, was the principal cause of death. We consider that unlikely, however, as picric acid has long been used for marking the feathers of many kinds of birds, with no reported ill-effects as far as we know. Moreover, any effects of picric acid could not explain the differential response to short- and long-cycle trantsmitters observed at Cape Lisburne and the Barren Islands.

The effect of duty-cycle was certainly unexpected and is difficult to explain. Assuming that outcome was not merely a 'Type I' statistical error—a case of falsely rejecting the null hypothesis of no treatment effect—we conclude that some previously unrecognized effect of radio signals may have caused harm to the birds. The PTTs we used are about 100 times more powerful than conventional radios commonly used in wildlife telemetry. Because the device is implanted, the bird's body effectively acts as part of the antenna system, conducting the signal and possibly experiencing voltages during transmission of up to 500 mV, depending on distance from the transmitter. In any radio, maximum voltage is generated at a point one-quarter of the signal's wavelength away from the source—about 20 cm in this instance (P.A. Howey, pers. comm.).

Based on others' experiences (Calvo and Furness 1992) and our understanding of murre and puffin biology, we compiled a list of possible mechanisms for injury resulting from PTT implants (Table 5). Three broad categories are infection, hypothermia, or impairment of normal feeding behavior. Surgery-related infection, though possibly indicated in one or two of the mortalities we recorded, is characteristically a rapid and acute response that can probably be ruled out for any bird that survived more than 4-5 days. The median age (number of days post-release) at which murres died in this study was 13 days (75% fell within the interval from 11-20 days). However, the possibility that radio transmissions could somehow have compromised the immune system over a longer period cannot be excluded. Other proposed mechanisms are of primary concern to us only if they could explain, in principle, the difference in survival probability between birds carrying short- and long-cycle transmitters. We plan to conduct laboratory studies in 1996 to address the question of possible effects of radio transmission on the physiology and health of birds carrying implanted PTTs. Our working hypothesis is that strong radio signals and associated voltages generated every 70 sec impair the ability of a diving bird to forage normally. If true, the problem clearly would be more severe for birds in which fully one-third of potential foraging time is affected (short cycle), as compared to birds deprived of only 8% of potential foraging time (long cycle).

We are optimistic that the problems leading to mortality of PTT-implanted seabirds can be identified and solved. For example, if PTTs interfere with diving behavior, it may be possible to incorporate a conductivity or pressure-sensitive switch that suppresses the transmitter whenever a bird is submerged. Other developments expected in the near future include a new generation of implantable PTTs (20 g or lighter) available in 1996 and a new, more powerful Argos receiver on the next NOAA satellite to be deployed (originally scheduled for July, now December 1996). Service Argos, Inc. advises its new equipment will have 4 times the sensitivity of older receivers, resulting in more and better quality locations for animal tracking studies. Presently, the NBS Alaska Science Center is working with Microwave Telemetry, Inc. to incorporate a micro-electronic time-depth recorder (TDR), which will greatly increase the functionality of the existing transmitter package. We believe all of these developments will make satellite telemetry the preferred method of acquiring data on pelagic movements and foraging behavior of seabirds.

CONCLUSIONS

This study has answered some questions—and raised others—about the utility of satellite telemetry for tracking seabirds. Murres and puffins appear to tolerate well the necessary anesthesia and surgical procedures. The package size currently available (3-5% of body weight, minimal drag) is within accepted guidelines for telemetric studies of birds. The accuracy of our location data is comparable to previous animal tracking studies employing satellite transmitters and Argos data processing, i.e., errors are generally <1000 m, but unknown for individual locations. Because of redundancy in the locations obtained (i.e., during a 6-hour transmission interval), it is possible to determine with acceptable precision the foraging areas of breeding murres in relation to their nest sites. Seasonal movements and wintering areas are also clearly established by this method. The main issues to be resolved are why some birds were adversely affected over the course of 2-3 weeks and whether an improved battery can be developed that performs well at high temperatures.

Our results show that murres may fly routinely up to 100 km from their breeding sites. In designing oceanographic studies to investigate murre foraging habitat, it is important to realize that the feeding area available to birds in oceanic settings like the Barren Islands may be 30,000 km^2 or larger. One would not expect birds to use that area uniformly, however, and our results suggest that cold, upwelled water along the north coasts of Shuyak and Afognak islands was a preferred habitat of Barren Islands murres in summer—at least for birds whose nesting attempts had failed. We would caution that interannual variation in foraging patterns has not been addressed.

Results from Cape Thompson and Cape Lisburne indicate that murre chicks and their male guardians disperse over a wide area of the Chukchi Sea before the young are independent. Females would seem to have an advantage at that time if their long flights upon leaving the colony can be taken as evidence that better feeding conditions exist to the south. We are reasonably confident in concluding that murres from both northern colonies share a common wintering area in the southeastern Bering Sea. The extent of year-to-year differences in winter distribution remains unknown.

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Table 1. Deployment of 35 satellite transmitters in three species of marine birds at three colonies in the Gulf of Alaska and Chukchi Sea, July-August 1995.

	Number of transmitters				
	Short cycle		Long cycle		
Location and species	Males	Females	Males	Females	Total
Barren Islands					
Tufted puffin	1	1	1	2	5
Common murre	3	1	3	3	10
Cape Lisburne					
Common murre	1	1	1	2	5
Thick-billed murre	2	1	1	1	5
Cape Thompson					
Common murre	1	1	2	1	5
Thick-billed murre	1	0	2	2	5
Total	9	5	10	11	35

Table 2. Details of satellite transmitter deployment by location, species, duty cycle, and performance.

Site	Species[a]	PTT	Sex	Program	Date released	Last contact	Days in contact	Total locations	Usable locations	Outcome
Barrens	TUPU	5849	F	long	18 Jul	20 Sep 95	64	116	86	outlived PTT
Barrens	TUPU	7558	M	short	18 Jul	25 Jul 95	7	9	4	died
Barrens	TUPU	7548	F	short	18 Jul	22 Jul 95	4	34	23	died
Barrens	TUPU	5846	M	long	18 Jul	3 Aug 95	16	16	8	died
Barrens	TUPU	5848	F	long	18 Jul	18 Jul 95	0[b]	0	0	died
Barrens	COMU	5856	M	long	17 Jul	26 Aug 95	40	28	15	outlived PTT
Barrens	COMU	5852	F	long	17 Jul	5 Sep 95	50	36	27	outlived PTT
Barrens	COMU	5851	F	long	18 Jul	21 Sep 95	65	28	19	outlived PTT
Barrens	COMU	5891	M	long	17 Jul	19 Sep 95	64	34	19	outlived PTT
Barrens	COMU	7623	M	short	18 Jul	31 Jul 95	13	39	26	died
Barrens	COMU	6328	M	long	17 Jul	3 Aug 95	18	19	12	died
Barrens	COMU	5853	F	long	18 Jul	1 Aug 95	15	19	11	died

(continued)

Table 2. (continued).

Site	Species[a]	PTT	Sex	Program	Date released	Last contact	Days in contact	Total locations	Usable locations	Outcome
Barrens	COMU	7873	F	short	18 Jul	31 Jul 95	13	45	27	died
Barrens	COMU	7559	M	short	17 Jul	29 Jul 95	12	32	24	died
Barrens	COMU	7875	M	short	17 Jul	28 Jul 95	14	77	58	died
Lisburne	COMU	7879	M	long	3 Aug	29 Nov 95	118	27	21	outlived PTT
Lisburne	COMU	20005	F	short	3 Aug	22 Dec 95	141	241	208	outlived PTT
Lisburne	COMU	7903	F	long	3 Aug	31 Jan 96	181	77	60	outlived PTT
Lisburne	COMU	7884	F	long	3 Aug	7 Aug 95	5	7	6	died
Lisburne	COMU	20838	M	short	3 Aug	5 Aug 95	2	13	9	died
Lisburne	TBMU	7877	M	long	2 Aug	10 Apr 96	252[c]	92	77	outlived PTT
Lisburne	TBMU	7917	M	short	2 Aug	17 Aug 95	15	103	77	died
Lisburne	TBMU	7889	F	long	2 Aug	20 Aug 95	20	23	17	died
Lisburne	TBMU	20836	M	short	2 Aug	18 Aug 95	16	89	78	died

(continued)

Table 2. (continued).

Site	Species[a]	PTT	Sex	Program	Date released	Last contact	Days in contact	Total locations	Usable locations	Outcome
Lisburne	TBMU	20003	F	short	2 Aug	10 Aug 95	8	8	5	died
Thompson	COMU	7901	M	long	5 Aug	27 Nov 95	114	82	69	outlived PTT
Thompson	COMU	20001	F	short	5 Aug	27 Nov 95	114	276	246	outlived PTT
Thompson	COMU	7916	M	short	5 Aug	16 Nov 95	103	194	153	outlived PTT
Thompson	COMU	7876	F	long	5 Aug	22 Jan 96	170	114	93	outlived PTT
Thompson	COMU	7888	M	long	5 Aug	10 Dec 95	127	10	7	oulived PTT
Thompson	TBMU	7880	F	long	6 Aug	27 Oct 95	82	6	4	outlived PTT
Thompson	TBMU	7915	M	long	6 Aug	29 Nov 95	115	87	79	outlived PTT
Thompson	TBMU	7887	F	long	6 Aug	22 Nov 95	108	8	4	outlived PTT
Thompson	TBMU	7882	M	long	6 Aug	23 Jan 96	170	13	4	outlived PTT
Thompson	TMBU	20840	M	short	6 Aug	23 Sep 95	48	147	97	possibly died

[a] TUPU = tufted puffin, COMU = common murre, TBMU = thick-billed murre.

[b] Insufficient data to determine time of death (1 message on day 51 only); excluded from analysis of survival through day 32.

[c] Transmitter still active and sending locations through 10 April 1996.

Table 3. Summary of marine bird location data obtained through 10 April 1996.

	Barren Islands		Cape Lisburne		Cape Thompson		All areas		
Event	Breeding	Postbreeding	Breeding	Postbreeding	Breeding	Postbreeding	Breeding	Postbreeding	Total
Messages[a]	636	159	685	420	807	629	2,128	1,208	3,336
Locations	426	106	436	244	475	462	1,337	812	2,149
Culled locations	145	28	86	36	132	49	363	113	476
Usable locations	281	78	350	208	343	413	974	699	1,673

[a] Satellite passes with at least 1 message received from a PTT.

Table 4. Frequency distribution of data by Argos location classes.

	Before culling		After culling	
Argos quality code	No. locations	% of total	No. locations	% of total
3	63	2.9	63	3.8
2	184	8.6	179	10.7
1	474	22.1	465	27.8
0	478	22.2	394	23.5
A	303	14.1	227	13.6
B	320	14.9	156	9.3
Z	327	15.2	189	11.3
Total	2,149	100.0	1,673	100.0

Table 5. Hypothesized causes of murre and puffin mortality associated with satellite transmitter implants.

A. Infection

- (1) Immediate - associated with surgery
- * (2) Delayed - caused by impairment of immune system by radio transmission (effects on bursa, T-cell production; effects on unhealed membranes)
- (3) Delayed - caused by seawater entering body through abdominal incision or antenna hole

B. Hypothermia

- (1) Exposed skin from plucked feathers causes hypothermia
- (2) Picric acid not fully dry at release causes wetable plumage
- (3) PTT acts as heat conductor to outside

C. Behavioral (feeding) impairment

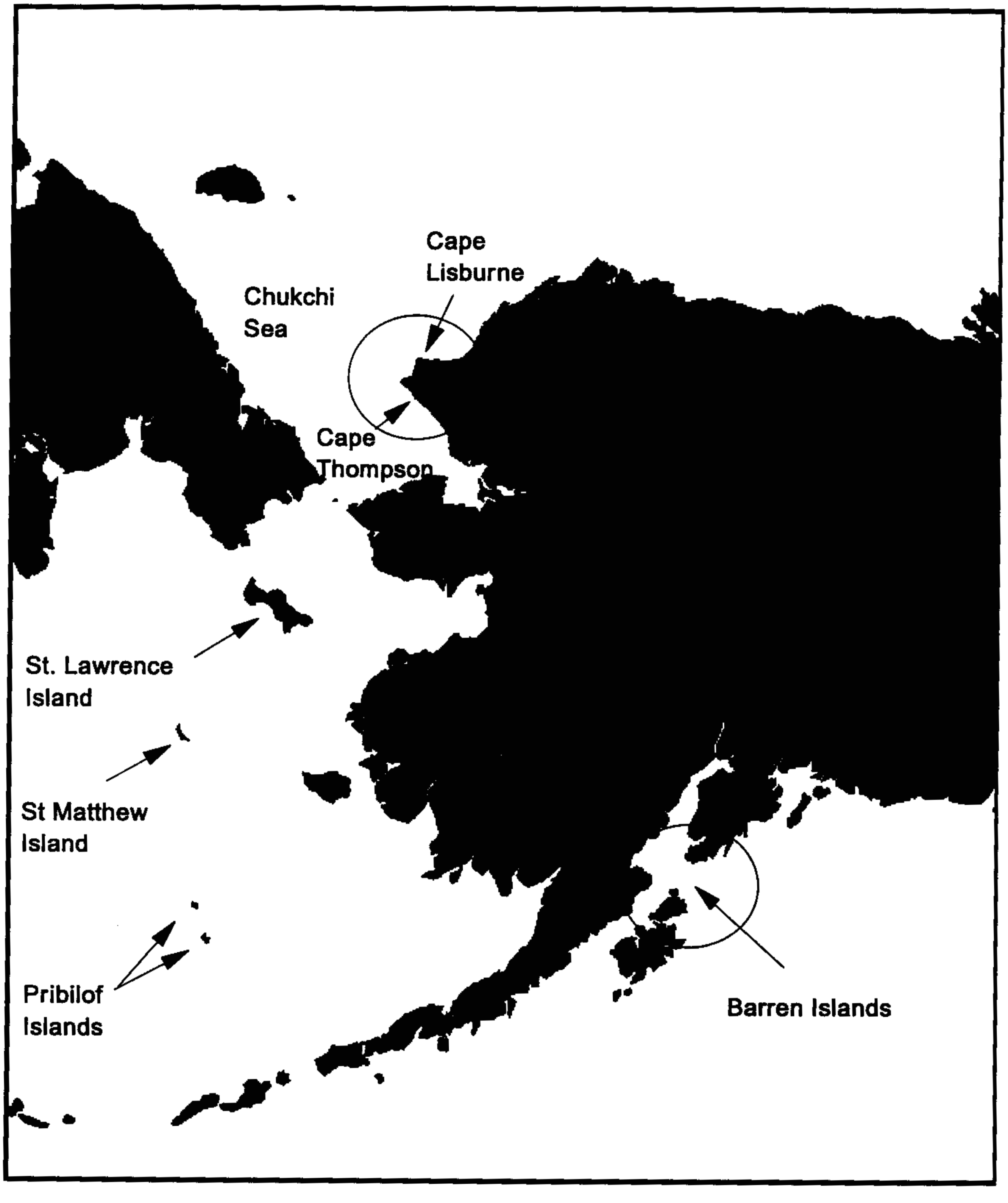
- * (1) Signal causes discomfort or disorientation (neurotransmitter release, heart arhythmia, effects on magnitite in brain, radio frequency 'burns', other?)
- (2) Bulk - PTT introduces mechanical pressures on internal organs, especially at depth
- (3) Bulk - birds have false sense of stomach fullness
- (4) Weight - PTT increases wing-loading beyond tolerance
- (5) Drag - external antenna increases hydrodynamic/aerodynamic drag during diving and flight
- (6) Reduction in air sac volume or puncturing of air sacs affects ability to recover from anaerobiosis
- (7) Unhealed incision causes discomfort at depth; birds abort dives

D. Other

- (1) Toxicity - ingestion of picric acid during preening
- * (2) Prey - detection of radio signals allows avoidance response in fish
- (3) PTTs cause increased risk to predators

Note: Only effects marked with an asterisk could explain the difference between short- and long-cycle transmitters.

Figure 1. Locations of three study areas in the Gulf of Alaska and Chukchi Sea.



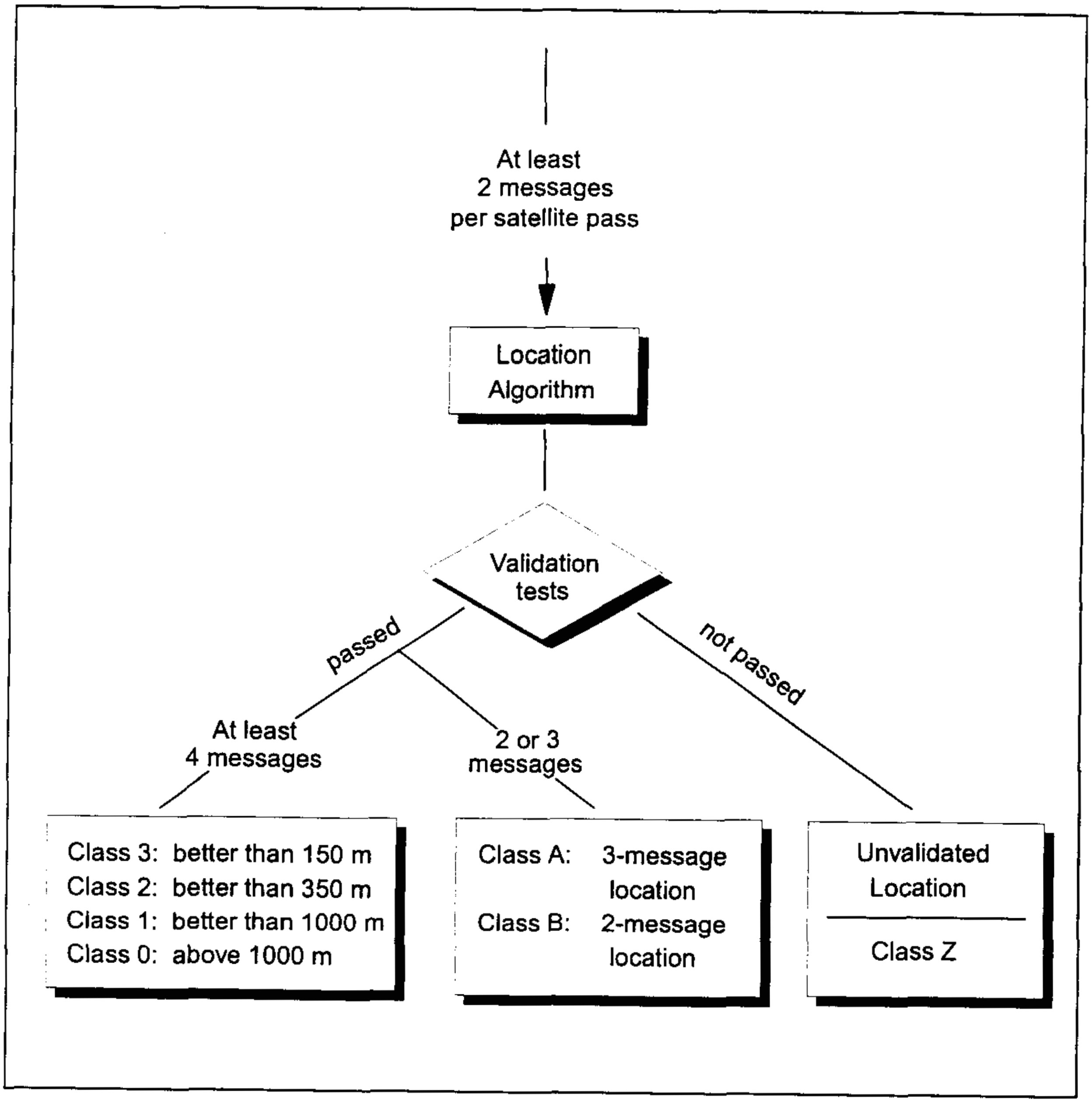


Figure 2. Location quality classes assigned by Argos. (Source: Argos, Inc. Newsletter, October, 1995.)

Figure 3. Distribution of tufted puffins from West Amatuli Island, by sex, 16 July-21 September 1995. Plus signs indicate males and boxes indicate females.

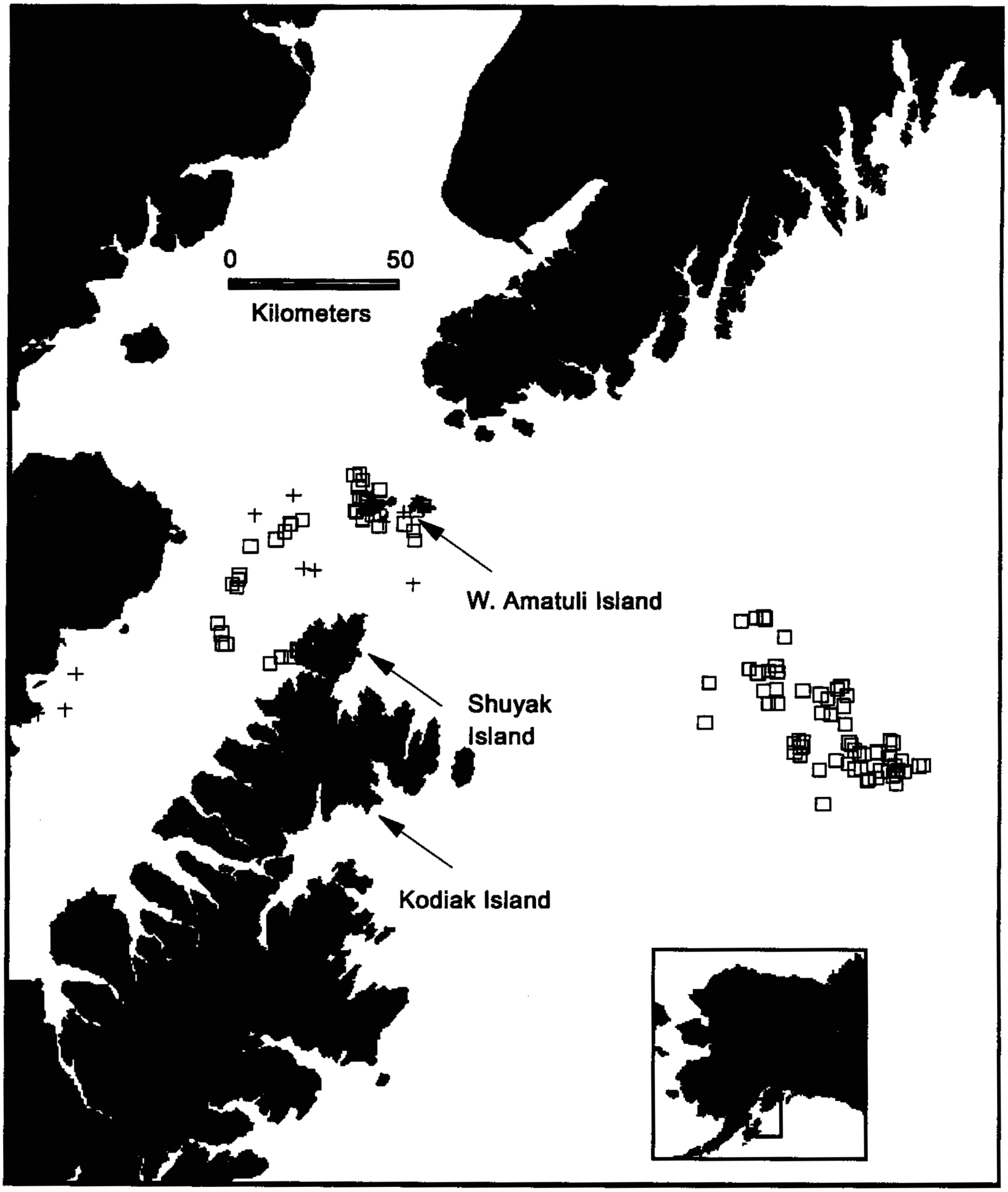


Figure 4. Distribution of common murres from the East Amatuli Island, by sex, 16 July-21 September 1995. Plus signs indicate males and boxes indicate females.

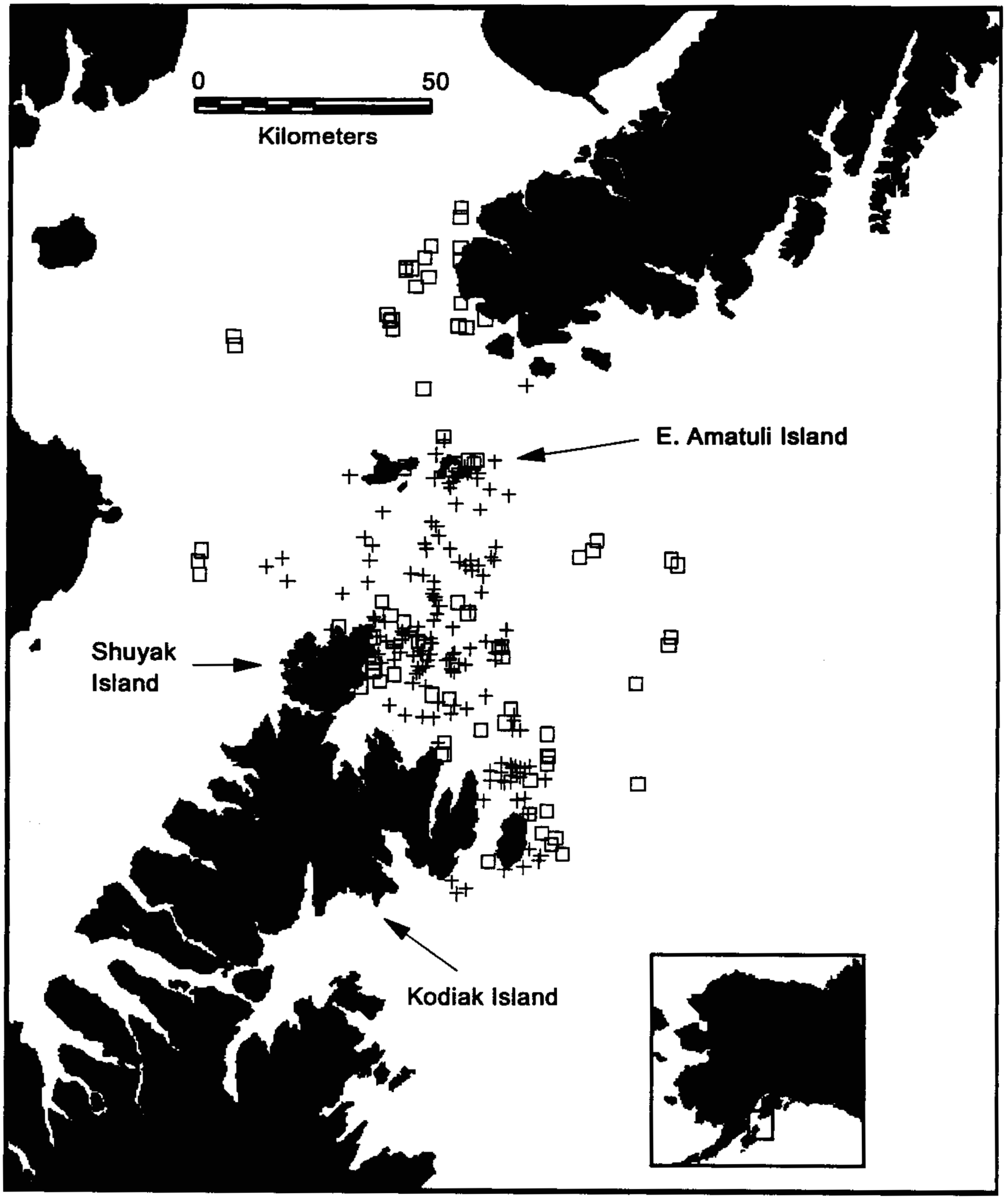


Figure 5. Breeding-season distribution of common and thick-billed murres from Capes Lisburne and Thompson 5-30 August 1995. Plus signs indicate common murres and boxes indicate thick-billed murres.

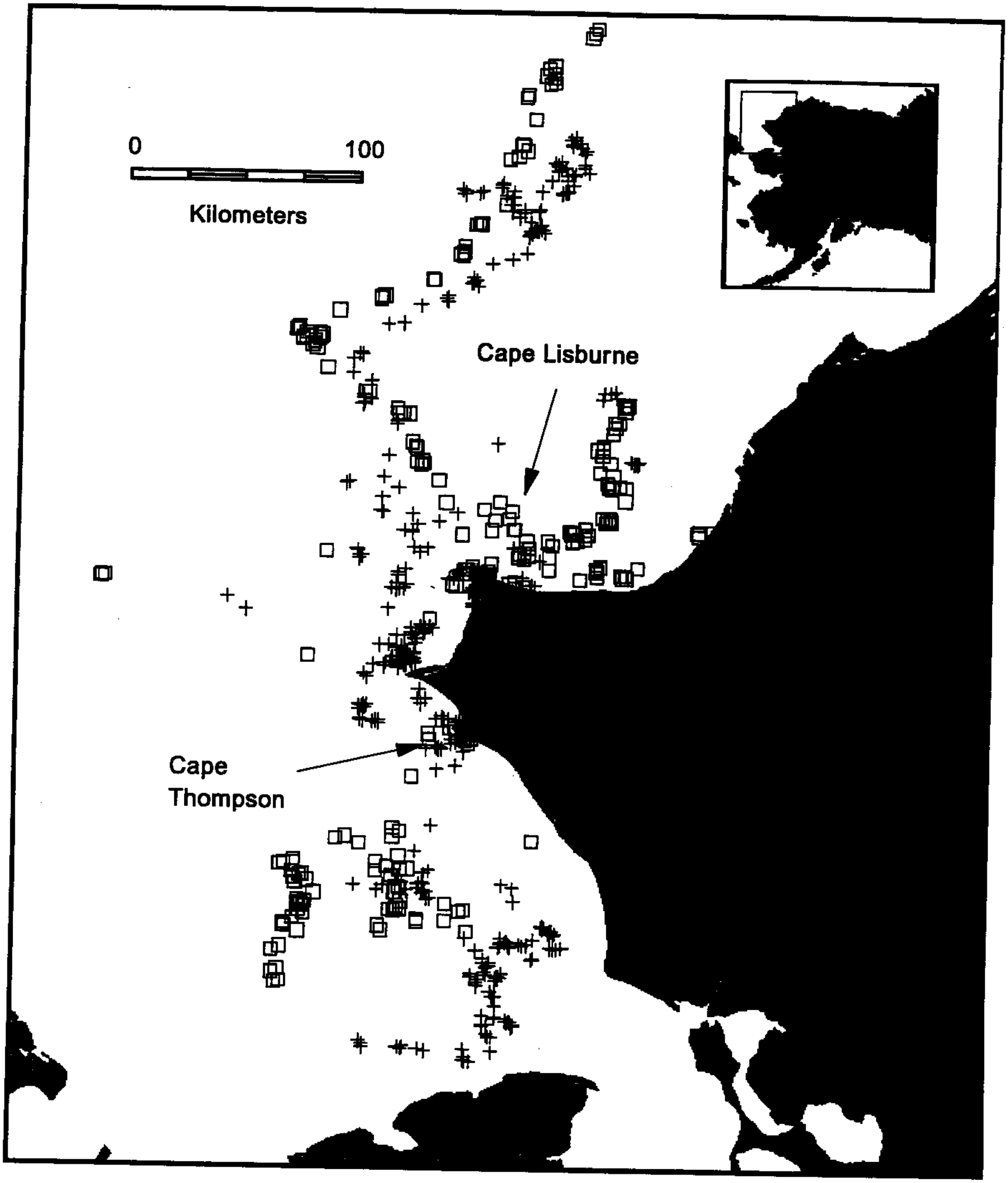


Figure 6. Breeding-season distribution of murres from Capes Lisburne and Cape Thompson 5-30 August 1995, showing non-overlap of summer foraging areas. Plus signs indicate Lisburne murres and boxes indicate Thompson murres.

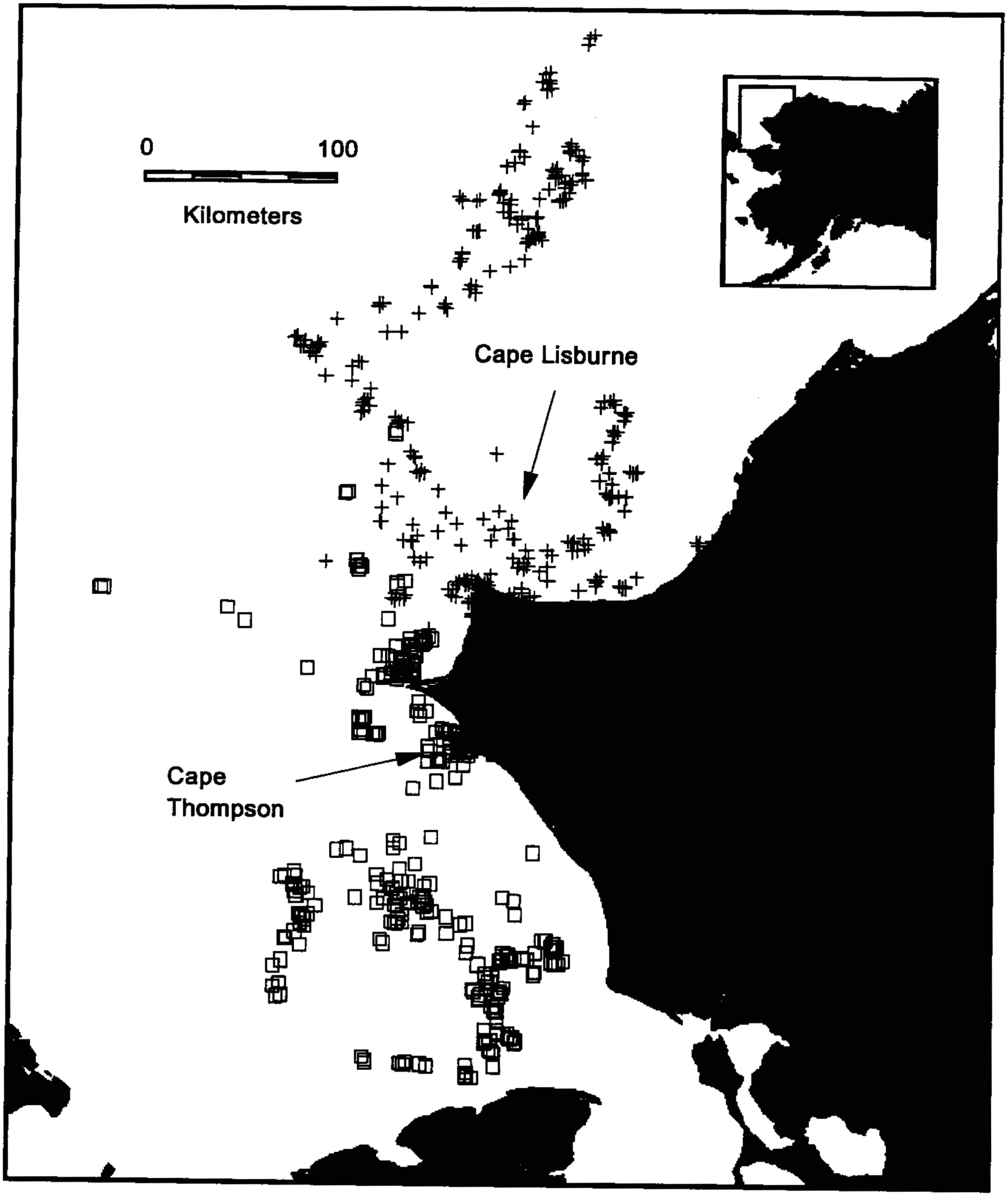


Figure 7. Breeding-season distribution of common and thick-billed murres from Cape Lisburne, by sex, 5-30 August 1995. Plus signs indicate males and boxes indicate females.

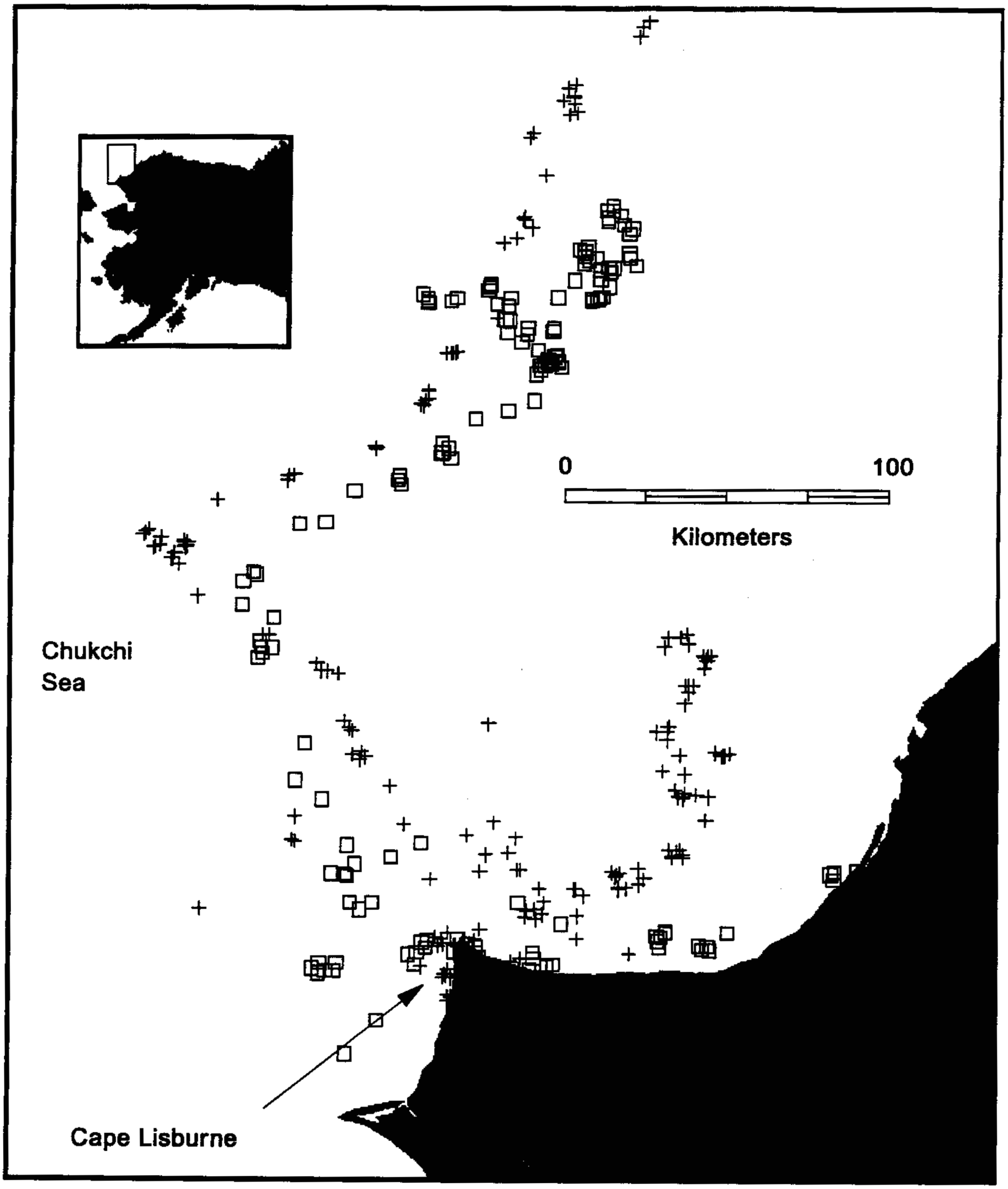


Figure 8. Breeding-season distribution of common and thick-billed murres from Cape Thompson, by sex, 7-30 August 1995. Plus signs indicate males and boxes indicate females.

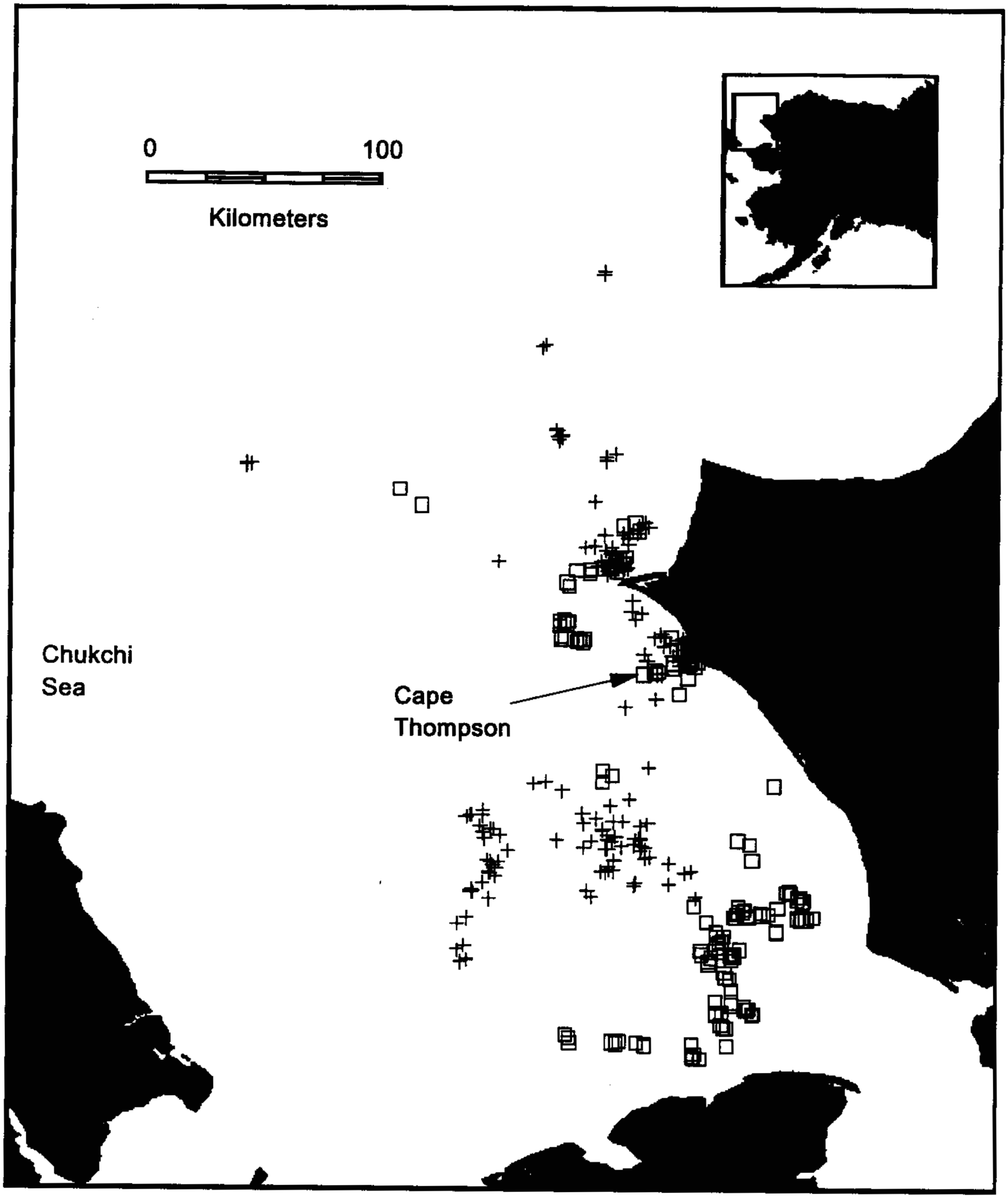


Figure 9. Paths of one common murre (plus signs) and one thick-billed murre (boxes) that abandoned their nesting attempts at Cape Lisburne, August 1995.

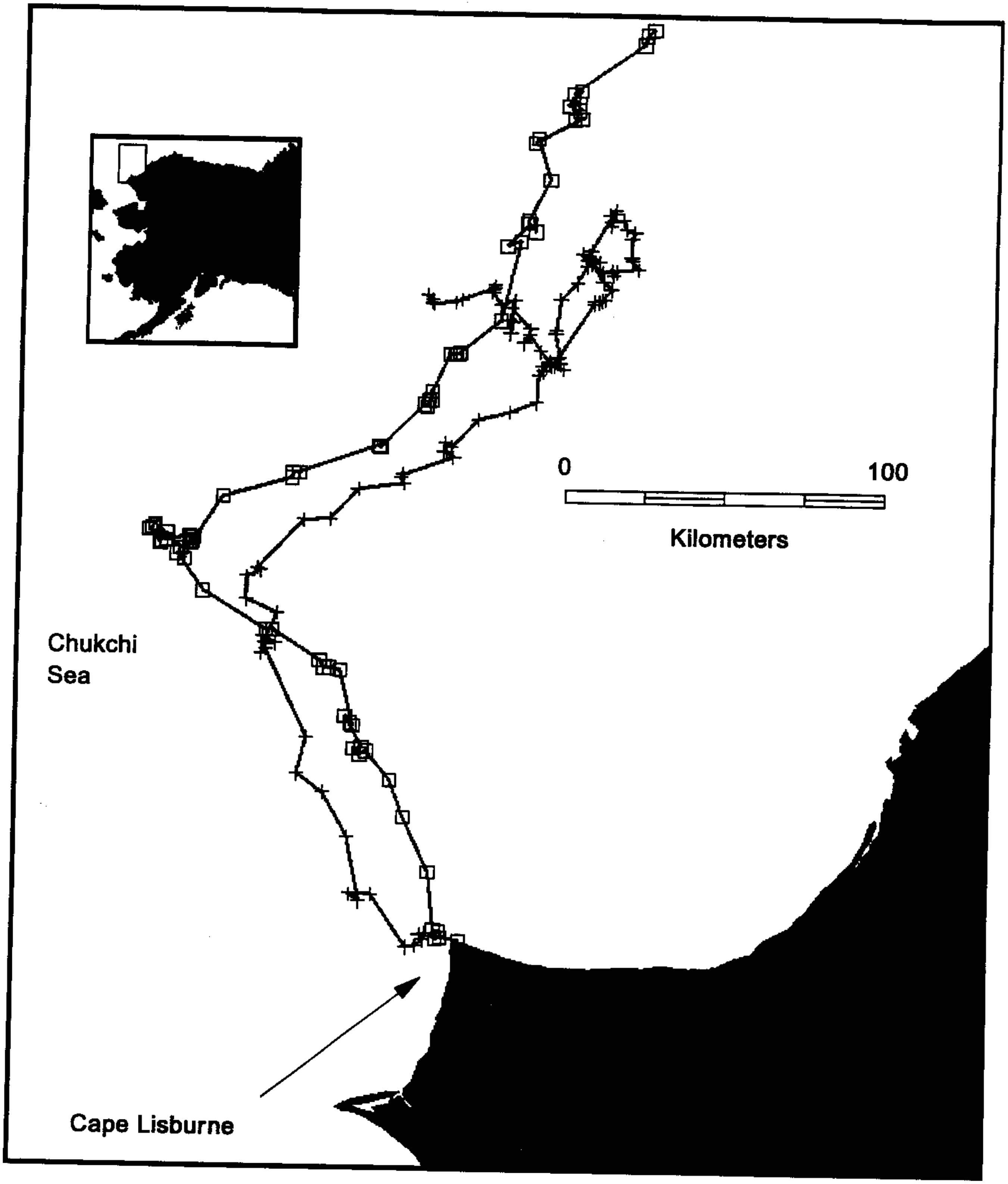


Figure 10. Postbreeding-season distribution of murres from Cape Lisburne and Cape Thompson 1 September 1995-10 April 1996. Plus signs indicate Lisburne murres and boxes indicate Thompson murres.

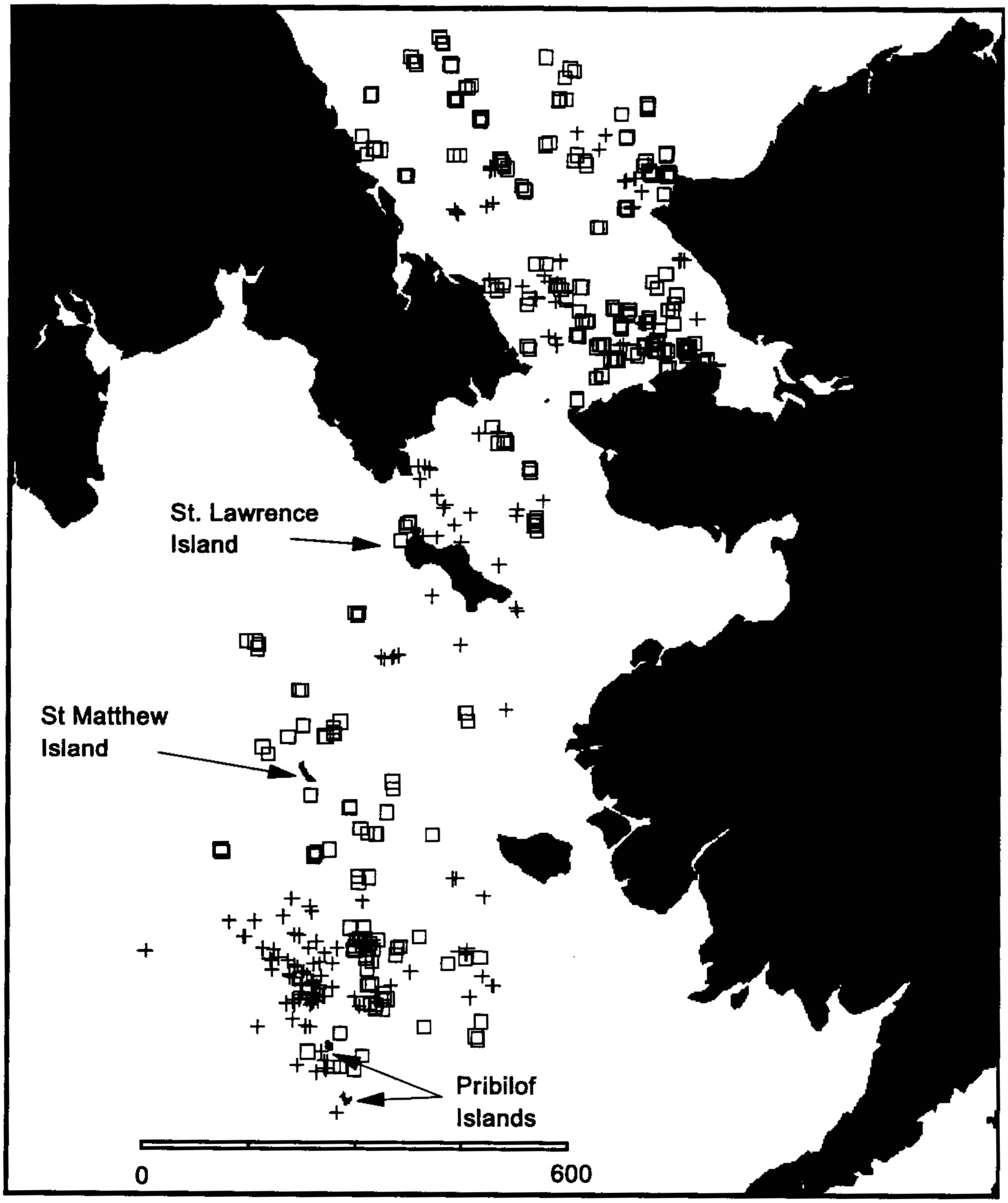


Figure 11. Postbreeding-season movements of male murres from Cape Lisburne and Cape Thompson 1 September 1995-10 April 1996. Each line represents an individual.

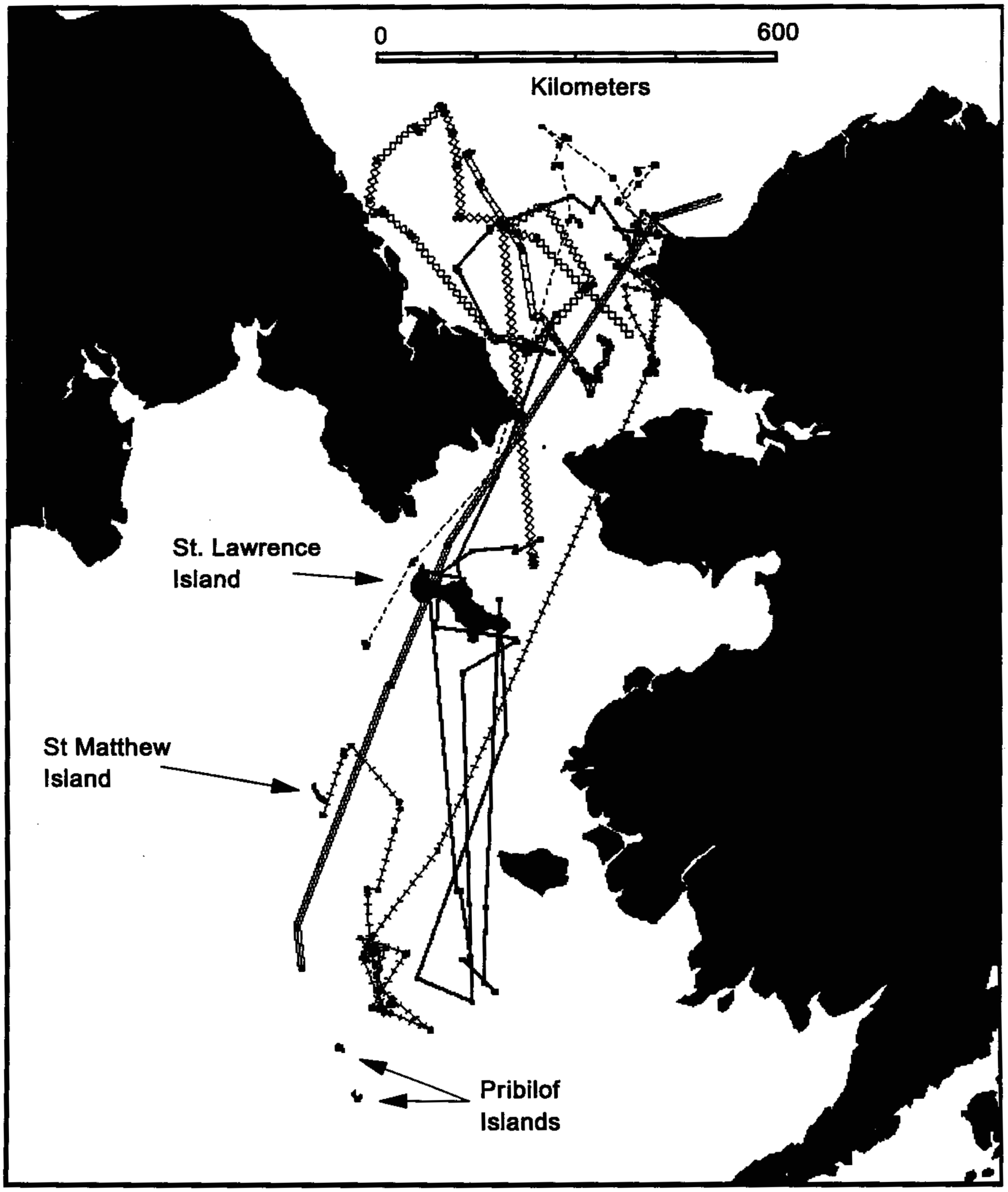
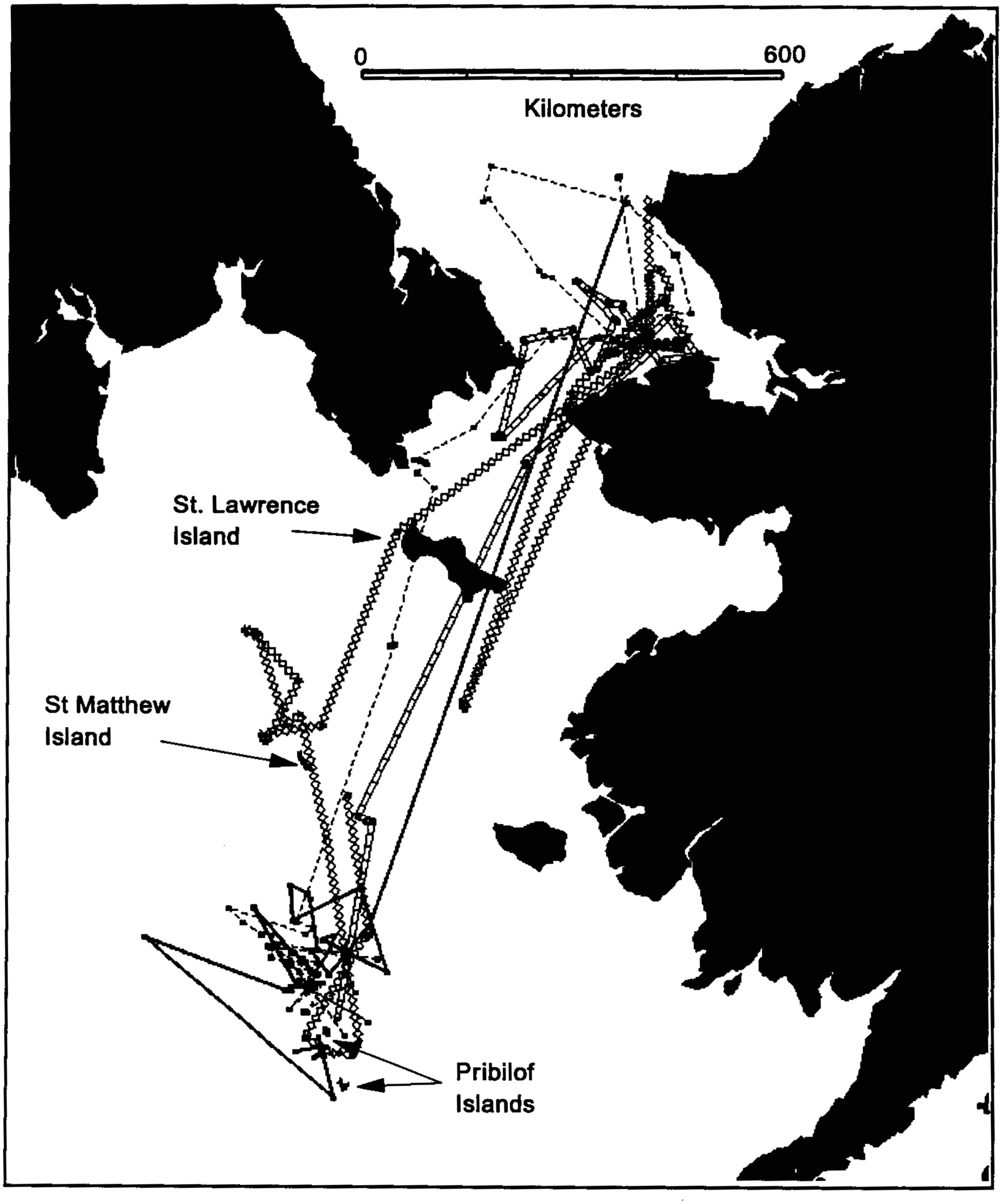


Figure 12. Postbreeding-season movements of female murres from Cape Lisburne and Cape Thompson 1 September 1995-10 April 1996. Each line represents an individual.



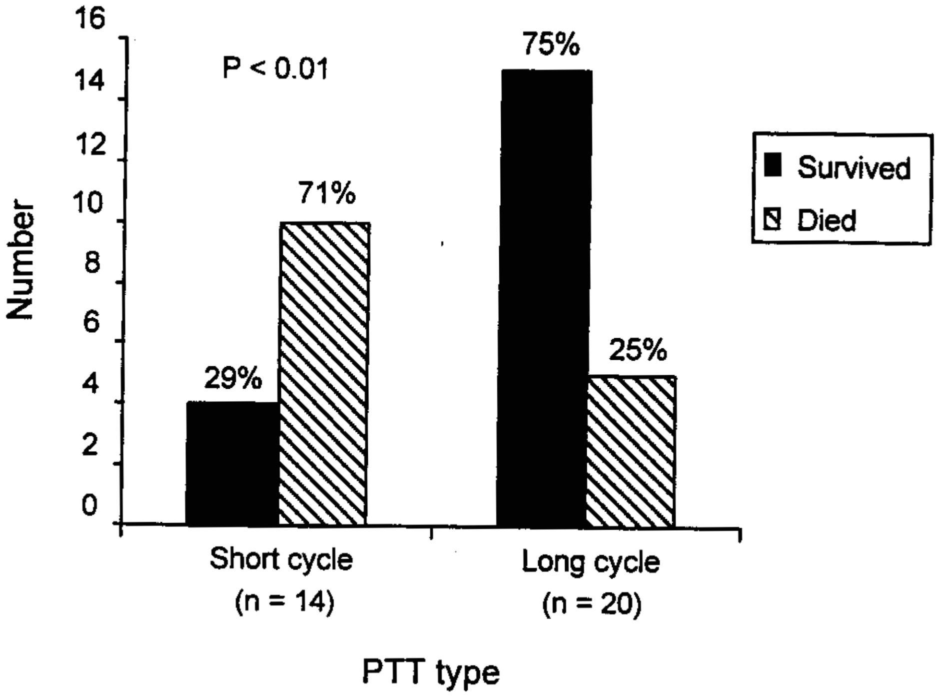
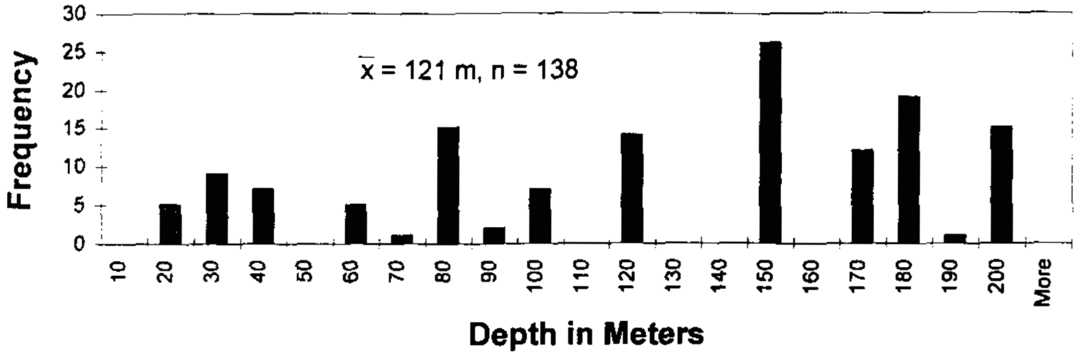


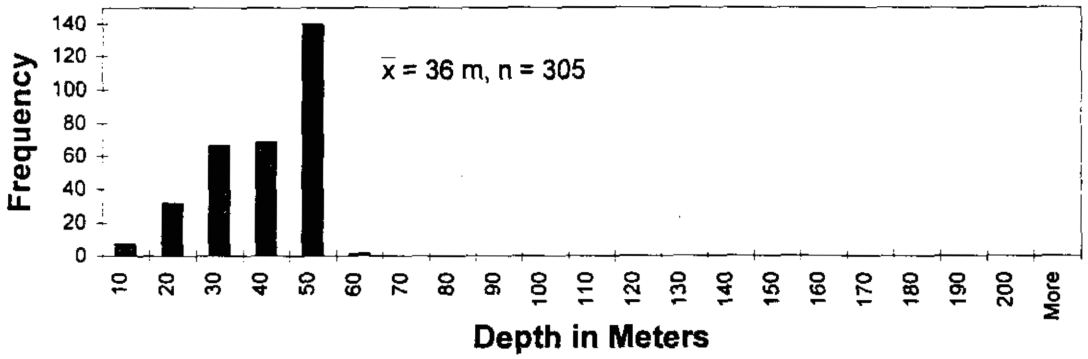
Figure 13. Survival rates of murres and puffins carrying short- and long-cycle transmitters in the first 32 days after release.

Figure 14. Frequency distributions of water depths corresponding to murre locations at three colones through 5 September 1995. Water depths differed among study areas ($\underline{P} < 0.05$, df = 836). Depths of 10 m or less are not depicted.

A) Barren Islands



B) Cape Lisburne



C) Cape Thompson

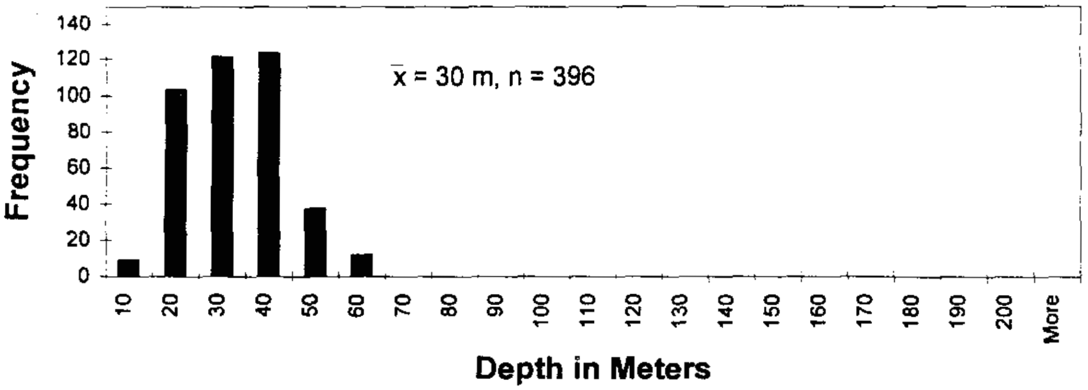
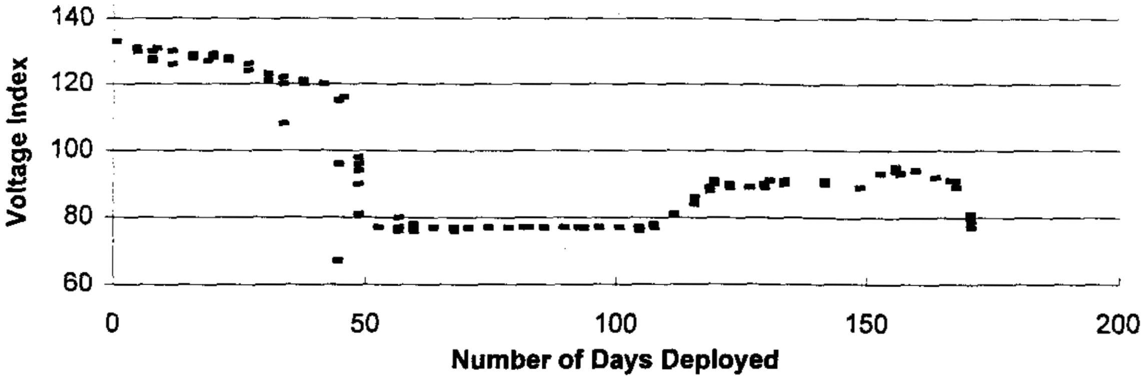
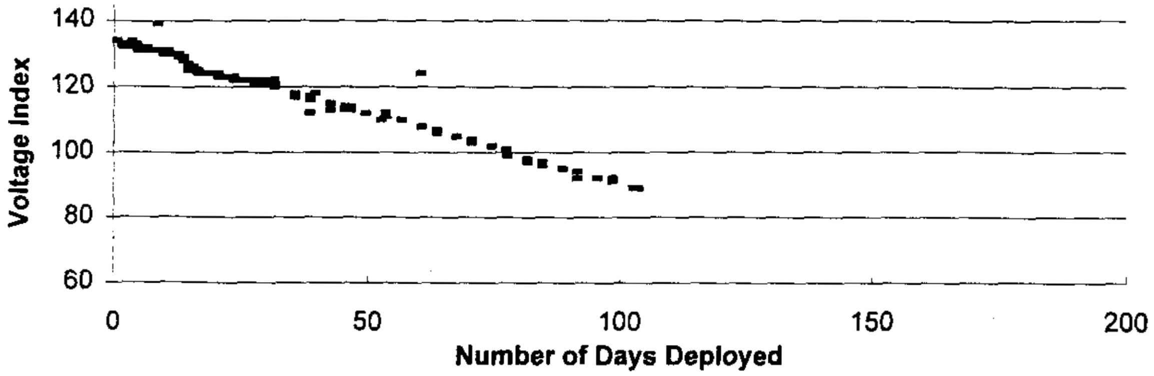


Figure 15. Time-series plots of battery voltage showing effects of temperature and duty cycle on battery life: a) PTT 7873, long cycle; b) PTT 20005, short cycle; c) PTT 7873, long cycle, bird died around day 13.

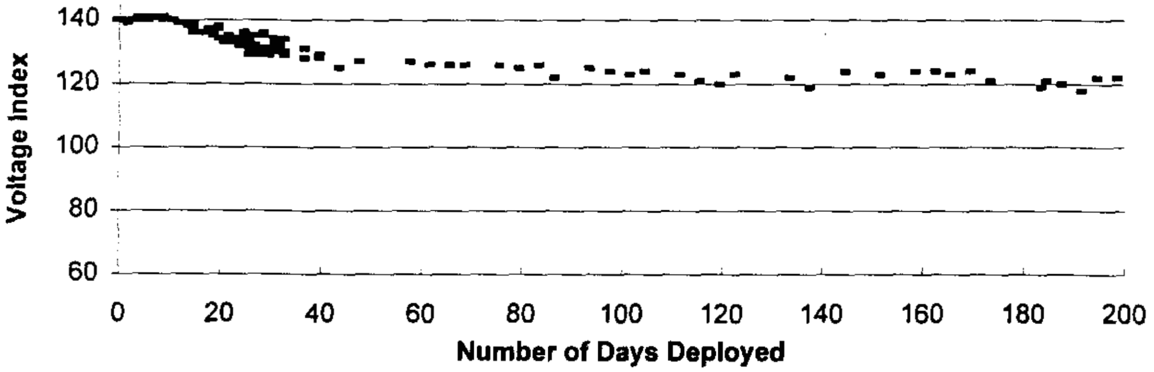
A) Long-cycle PTT.



B) Short-cycle PTT.



C) Short-cycle PTT in bird that died.



APPENDIX 1

NATIONAL BIOLOGICAL SERVICE
ALASKA SCIENCE CENTER
1011 EAST TUDOR ROAD
ANCHORAGE, ALASKA 99503

DATE: 25 JANUARY 1995

STANDARD PROCEDURE

PROCEDURE TITLE: Surgical implantation of transmitters in the abdomens of birds.

SCOPE: This protocol applies to the intra-abdominal surgical implantation of both satellite and conventional radio transmitters in both waterfowl and sea birds.

PRINCIPLE: Diving birds have been a notoriously difficult group of animals to which to attach instrumentation, especially transmitters. Harness and nasal-mounted transmitters have caused alterations in behavior, weight loss, and feather destruction (cf. USFWS Canvasback Telemetry Workshop, held at Patuxent Wildlife Research Center on 24-25 February, 1987; unpubl.). The surgical procedure is adapted from that described by Korschgen et al. (1984).

PROCEDURES:

1. A minimum of three people are required for the procedure: a surgeon, an anesthetist and a person who positions the bird and assists with the passage of the percutaneous antenna.

2. Standard aseptic surgical technique shall be practiced, including the surgeon wearing sterile gloves and a surgical mask. The surgical site will be prepared as for any surgical procedure, including plucking feathers, skin disinfection and the use of a sterile drape.

3. When possible, the transmitters should be gas-sterilized in suitable packaging permeable to gas but not to bacteria. Gas sterilized transmitters should be allowed to outgas for a period of 24 hours before their use. When gas sterilization is not possible, transmitters may be cold-sterilized in a solution of 0.13% (Zephiran®) or chlorhexidine (Nolvasan®) in water for 12 hours.

4. Surgical instruments should be sterilized in an autoclave in suitable packaging. When necessary, instruments may be cold sterilized in the same manner described for the transmitters, above.

5. Position the bird on the surgical table in dorsal recumbancy with the legs extended and the wings folded. A warm water bottle and an insulated (bubble-wrap or equivalent) cover for the surgical table should be used to retard heat loss.

6. Isoflurane gas anesthetic is administered to the bird by face mask. Induction is at 3-4% isoflurane; maintenance is at 1-2% isoflurane in oxygen. Maintenance concentrations may vary depending on the individual bird and environmental variables. Once the abdominal air sacs of a bird are opened, respiration may occur partially through the surgical incision, which may require a higher setting on the vaporizer to compensate.

7. Anesthesia is monitored by use of a respiratory or cardiac monitor, or both. A pulse oximeter or Doppler ultrasound are the preferred monitors. Manual palpation of a tibial or brachial arterial pulse can also be used, but is less preferred to an attached continuous mechanical monitor.

8. The surgical site is between the distal end of the keel and the conjuncture of the distal ends of the pubic bones, palpated through the abdominal wall. The feathers are plucked from the site. An area 1 cm on either side of the incision site should be plucked free of feathers. The feathers around the site are taped back with pieces of microporous tape. A site for the exit of the percutaneous antennae is located by palpating with finger the intersection of the right pubis bone with the synsacrum. A small (1 cm^2) area is plucked free of feathers and the feathers adjacent to the site are taped back using microporous tape. Both sites are swabbed with povidone-iodine or benzalkonium chloride solution. A sterile fenestrated drape is placed over the surgical site.

9. The skin is incised along the ventral midline with a no. 11 sterile blade. The subcutaneous layer and fat are sharp dissected. Once the muscular abdominal wall is reached, the linea alba is identified. The linea alba is seized with a forceps and lifted to permit penetration of the abdominal wall with a blade. The linea alba is then sharp dissected with blade or scissors, avoiding the viscera, to a length of about 4 cm, or a distance sufficient to pass the transmitter body.

10. Using fingers, clear a space on the right side of the abdomen, as dorsally (lateral to the ventriculus) as possible.

11. Maintaining a sterile surgical site, the surgeon lifts the drape, folding it over the abdominal incision. The assistant positions the legs of the bird to permit access to the antenna exit site. The surgeon palpates the site with the right hand and nicks the skin with a blade at the most dorsal position nearest to the intersection of the pubis and synsacrum. Then the surgeon uses a blunt stainless steel trochar to penetrate the abdominal wall, protecting the viscera with his left index finger placed inside the bird. The trochar is drawn inside the bird full length and the assistant holds the exterior end of the trochar in order to maintain its position and to keep the pointed end of the trochar visible through the incision.

12. The surgeon changes gloves and returns the drape to its proper position. The surgeon removes the transmitter from the sterilizing solution or the envelope. While the surgeon

holds the transmitter away from the incision, an assistant rinses the sterilizing solution from the transmitter using at least 10 cc of sterile saline.

13. The surgeon then seizes the end of the trochar and places then end of the antenna into one of the holes in the trochar. Then, as the surgeon guides the antenna into the incision, the assistant slowly withdraws the trochar until the end of the antenna can be seen or felt. Frequently there is a detente as the antenna meets and penetrates the body wall.

14. As the assistant continues to withdraw the antenna, the surgeon guides the transmitter through the incision, which may need to be slightly stretched to pass the transmitter. The antenna is withdrawn until the collar meets the body wall. The transmitter must be positioned on its narrowest edge and fits snugly along the dorsal wall, in a "notch" that can be palpated by the surgeon.

15. The assistant maintains the position of the transmitter for the remainder of the surgery by keeping a firm grip on the antenna adjacent to the body wall, to prevent rotation of the transmitter if the bird moves.

16. The surgical incision is closed in two layers using 3-0 braided absorbable suture on a cutting needle. The linea alba is closed using a simple continuous pattern and the skin is closed using either a simple continuous or simple interrupted pattern.

17. A single simple interrupted suture is used to hold the antenna collar to the body wall. When placing the suture, the needle must penetrate the dacron or plastic of the collar to assure stability. To determine that the collar has been penetrated, the antenna can be moved in and out to see if the suture moves with it, before the knot is tied.

18. The drape is removed and the vaporizer is turned to zero. Oxygen supplementation should continue until the bird recovers. Additional procedures such as obtaining a blood sample or banding may be done during this period.

19. Following recovery, the bird should be placed in a cage or kennel for at least one hour prior to release. Placing the cage partially into a pool of water may permit the bird to rehydrate and begin preening.

EQUIPMENT AND SUPPLIES:

Benzalkonium chloride or chlorhexidine diacetate solution
Sterilizing basin (about 6" x 12" x 2")
Sterile saline
10 or 12 cc syringes and needles
Anesthesia machine with isoflurane vaporizer
Isoflurane
Bain, Ayers T or similar non-rebreathing system
Cat or small dog-sized anesthetic cone
Respiratory monitor

Pulse oximeter or doppler ultrasound cardiac monitor
Surgical masks
Sterile gloves (2 pair per bird)
No. 11 blades
Stainless steel blunt trochars
3-0 braided, absorbable suture (1 pack per bird)
Four-inch fenestrated disposable drapes
Surgical pack for each bird:
    Mayo-Hagar needle holder
    4 inch mosquito forceps
    Brown-Adson tissue forceps
    Scalpel handle
    Scissors
    2-4 2 x2 sponges
Sharps disposal container
Iodophor solution-soaked swabs
Microporous tape

REFERENCES:

Korschgen,C.E., S.J. Maxson, and V.B. Kuechle. 1984. Evaluation of implanted radio transmitters in ducks. J. Wildl. Manage. 48:982-987.

APPENDIX 2

Track-lines showing breeding-season and postbreeding-season movements of each individual included in the study, 15 July - 10 April 1996.

Figure A.1. Track lines of male tufted puffin 5846 from West Amatuli Island. Long-cycle transmitter. Died 3 August 1995, 16 days total.

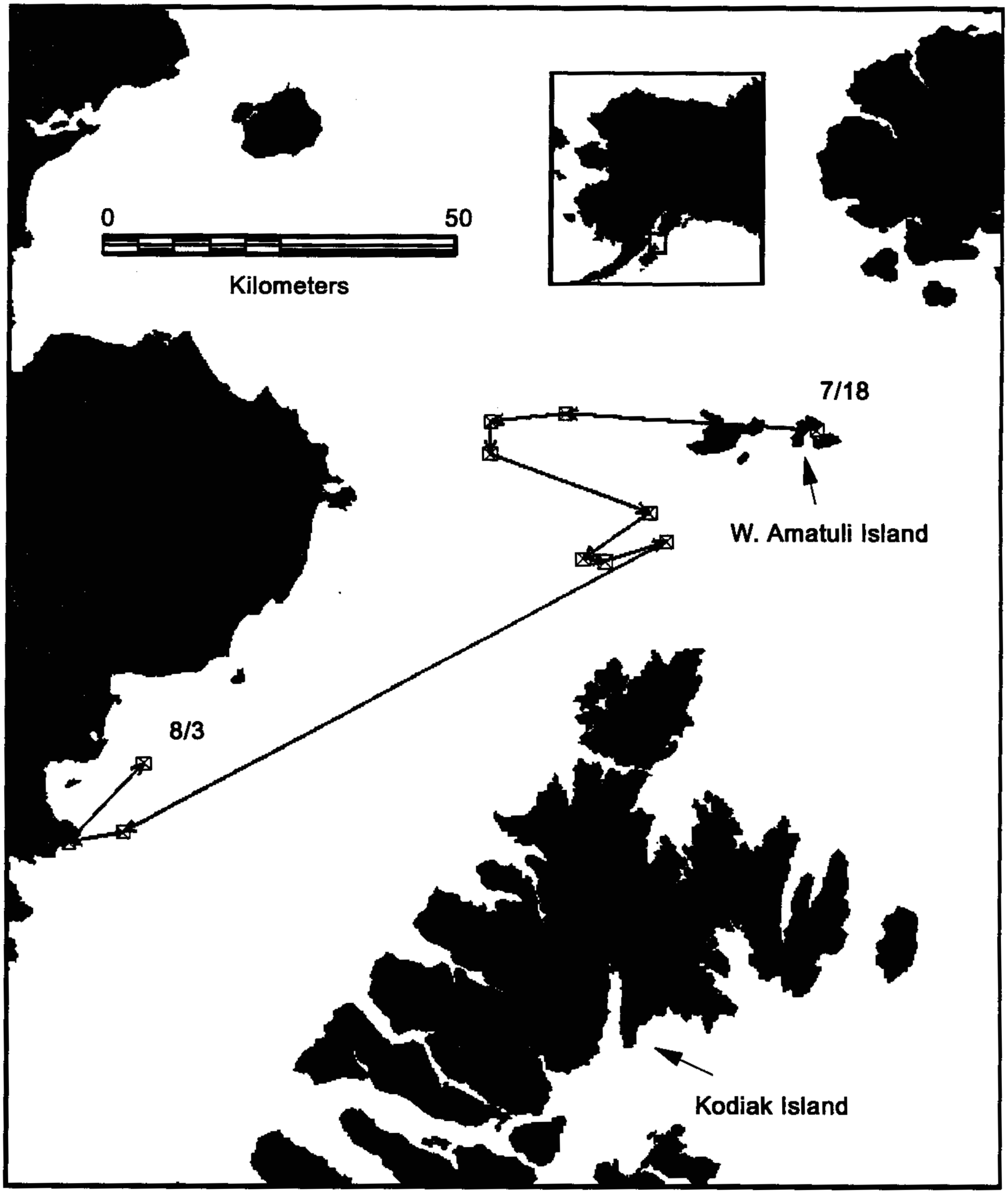


Figure A.2. Track lines of female tufted puffin 5848 from West Amatuli Island. Long-cycle transmitter. Died just after implant. No locations received.

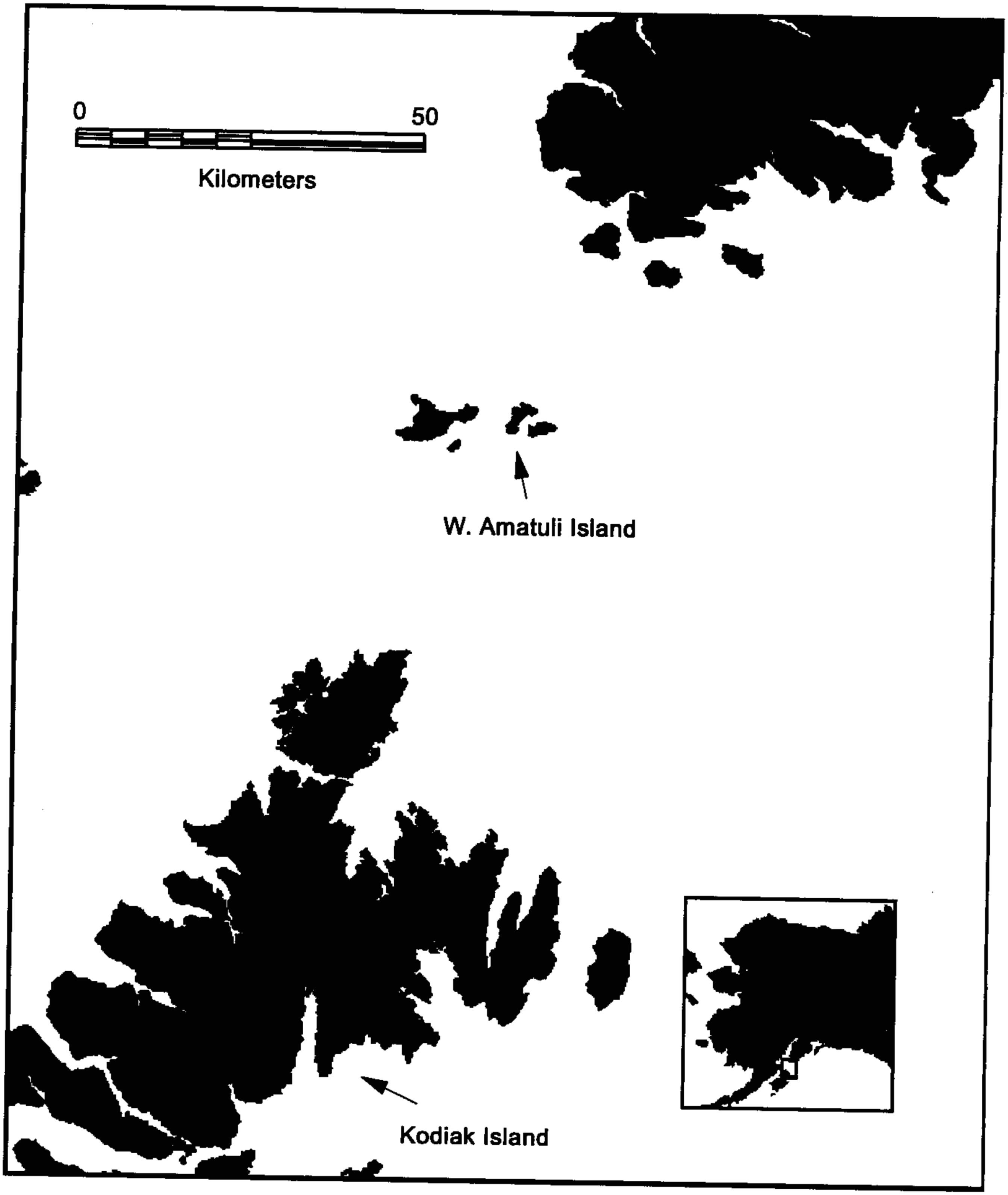


Figure A.3. Track lines of male tufted puffin 5849 from West Amatuli Island. Long-cycle transmitter. Lost contact 21 September 1995, 64 days total. Transmitter turned on continuously around 13 September and subsequently burned out.

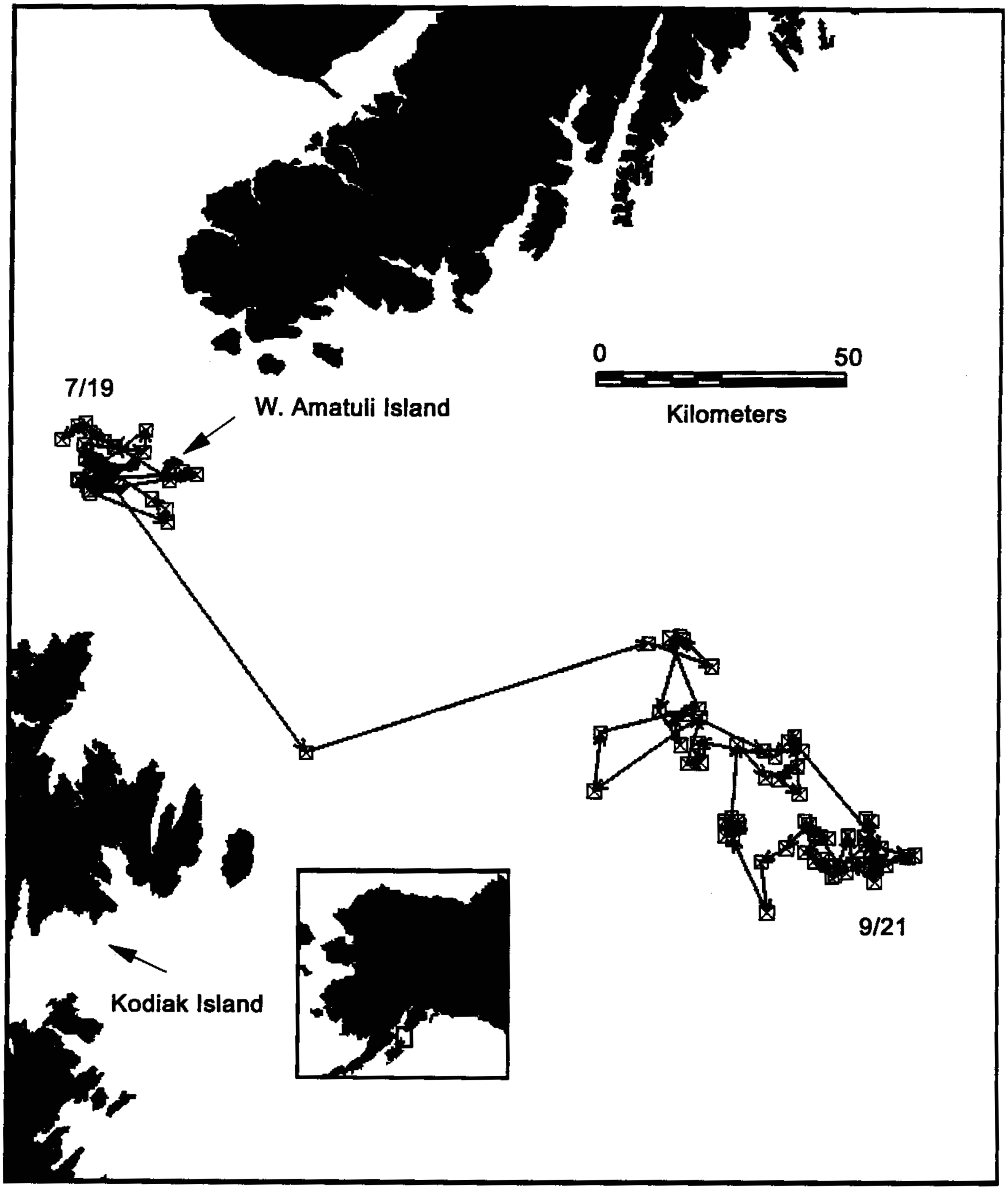


Figure A.4. Track lines of female tufted puffin 7548 from West Amatuli Island. Short-cycle transmitter. Died 23 July 1995, 4 days total.

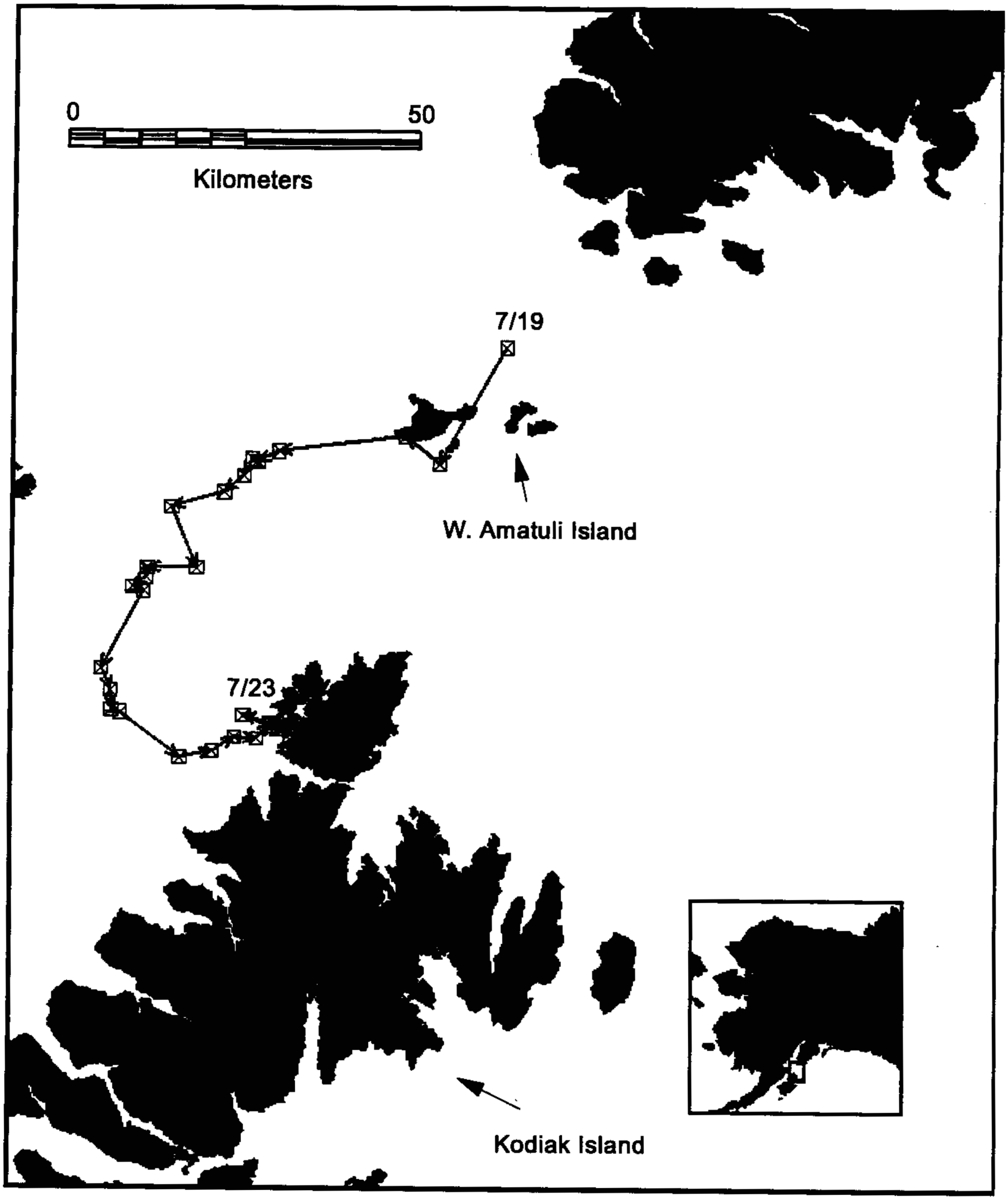


Figure A.5. Track lines of male tufted puffin 7558 from West Amatuli Island. Short-cycle transmitter. Lost contact 26 July 1995, 7 days total. Probably died.

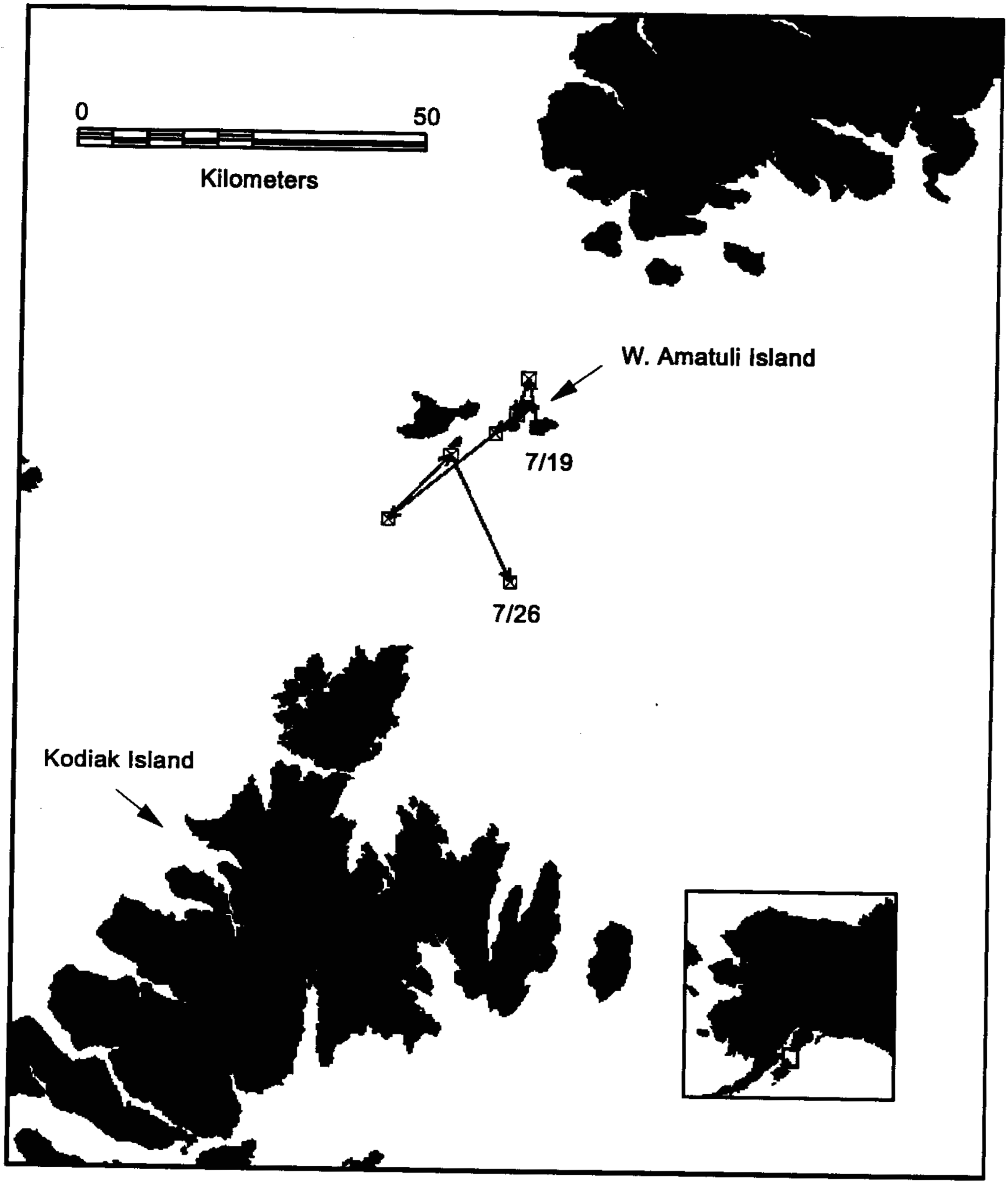


Figure A.6. Track lines of female common murre 5851 from East Amatuli Island. Long-cycle transmitter. Lost contact 21 September1995, 65 days total.

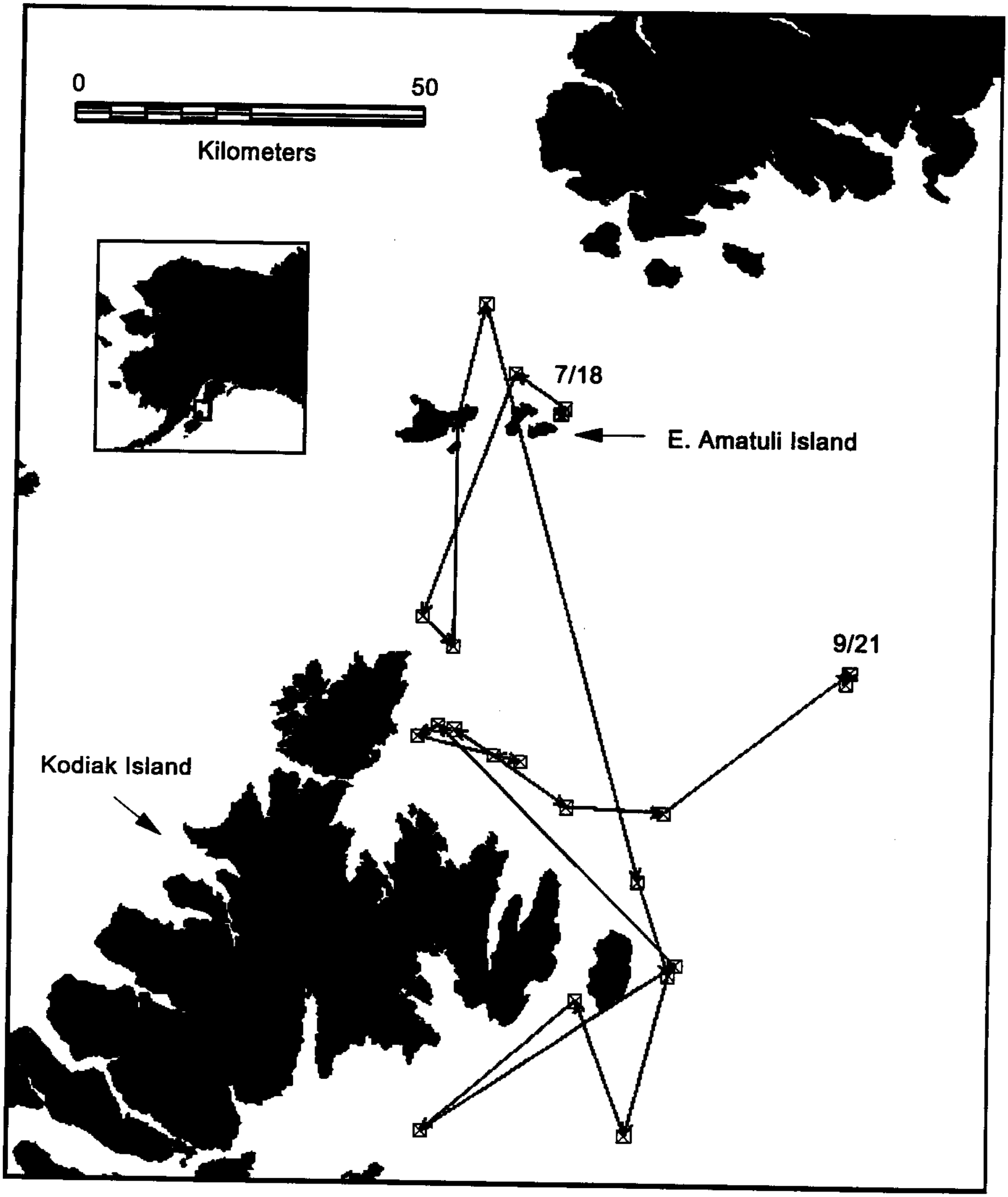


Figure A.7. Track lines of female common murre 5852 from East Amatuli Island. Long-cycle transmitter. Lost contact 5 September1995, 50 days total.

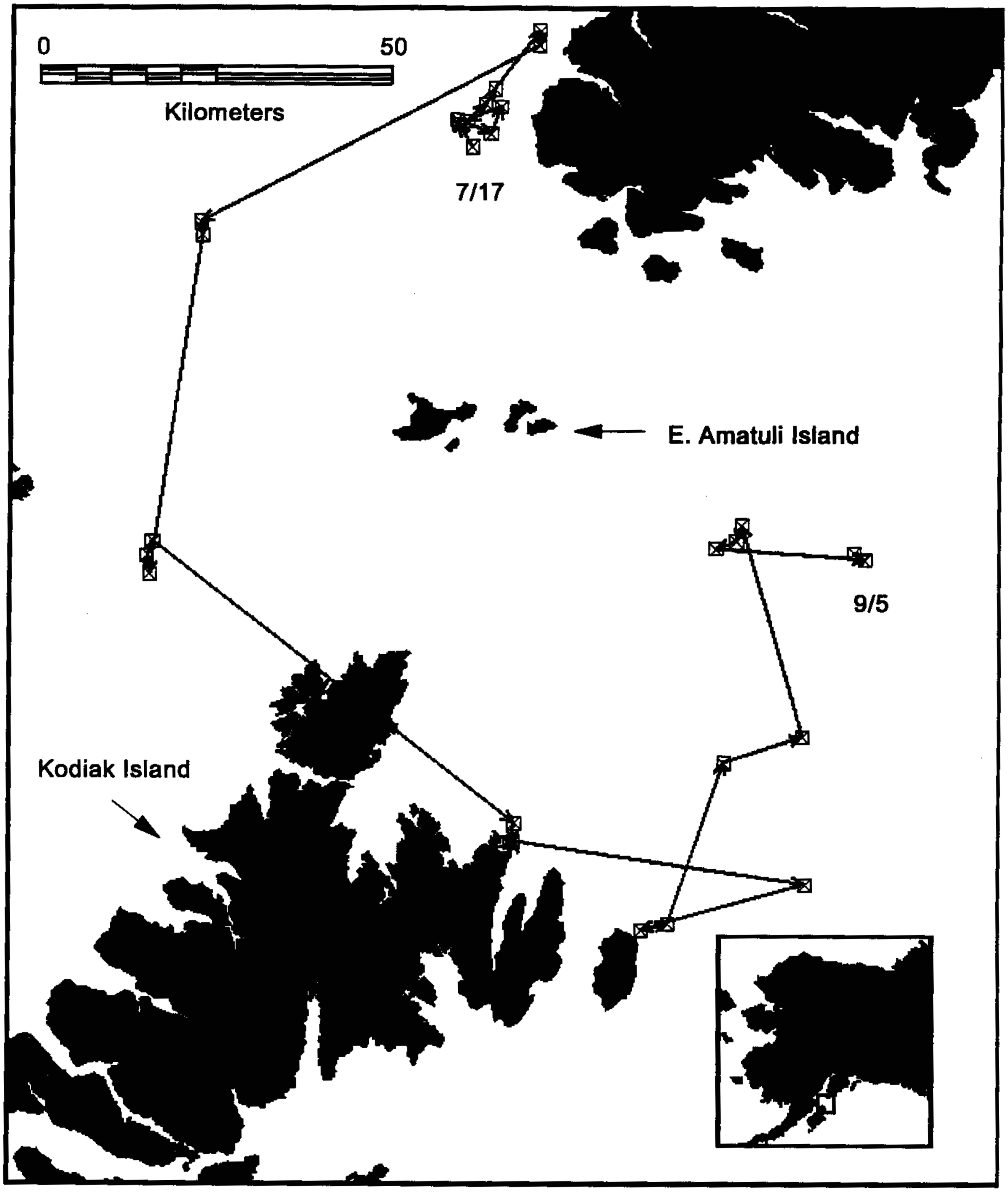


Figure A.8. Track lines of female common murre 5853 from East Amatuli Island. Long-cycle transmitter. Lost contact 1 August 1995, 14 days total. Probably died.

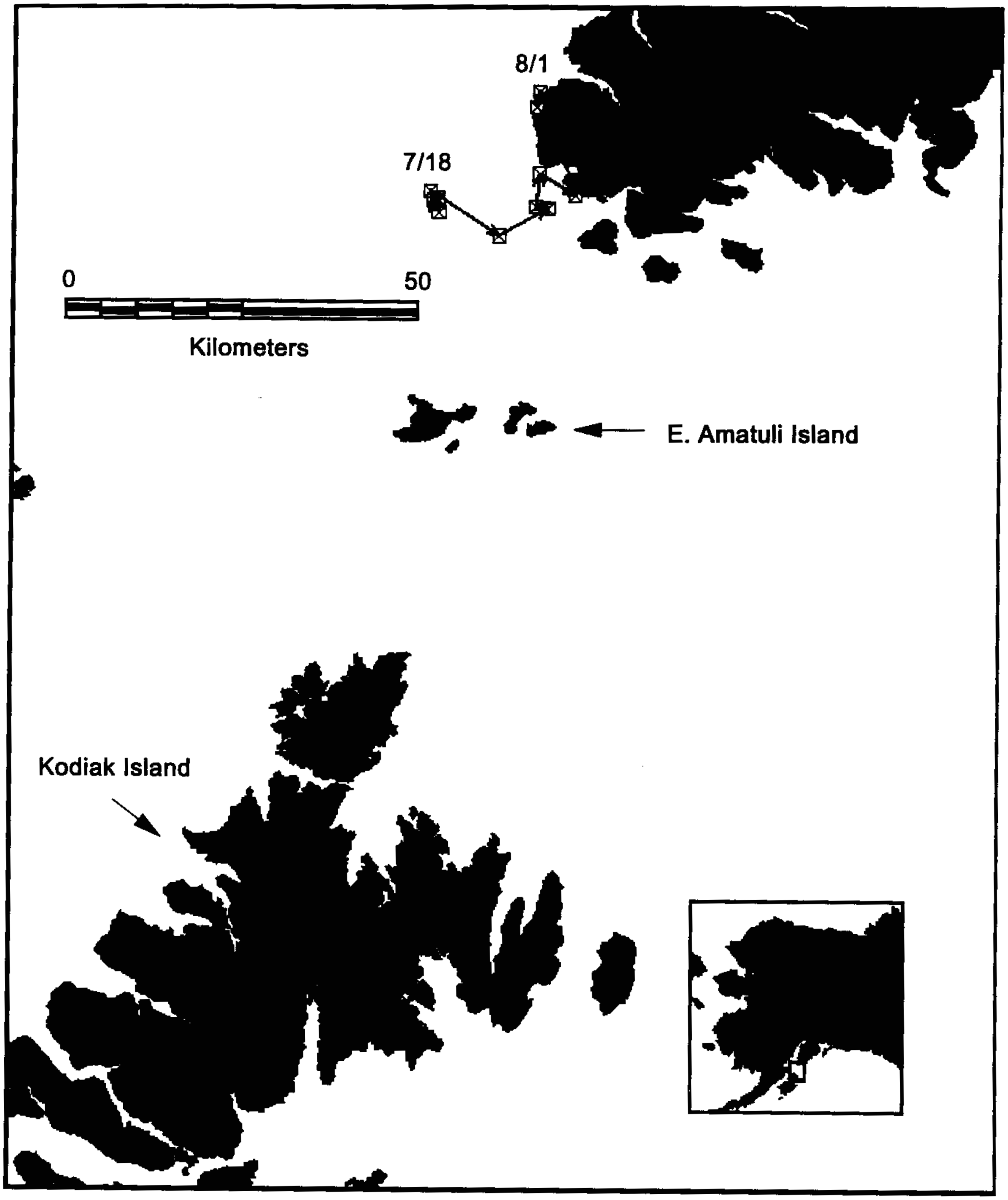


Figure A.9. Track lines of male common murre 5856 from East Amatuli Island. Long-cycle transmitter. Lost contact 26 August 1995, 40 days total.

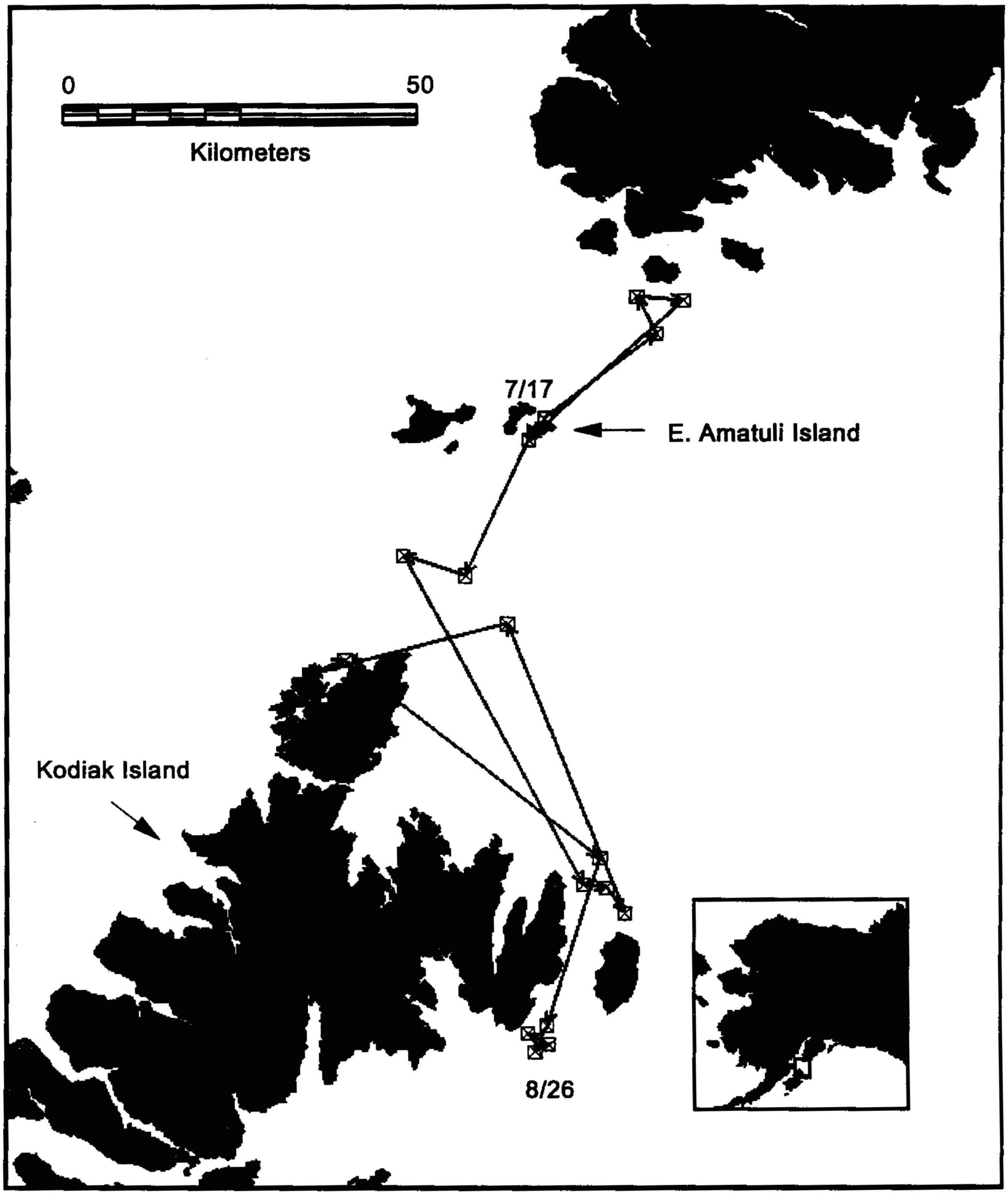


Figure A.10. Track lines of male common murre 5891 from East Amatuli Island. Long-cycle transmitter. Lost contact 19 September 1995, 64 days total.

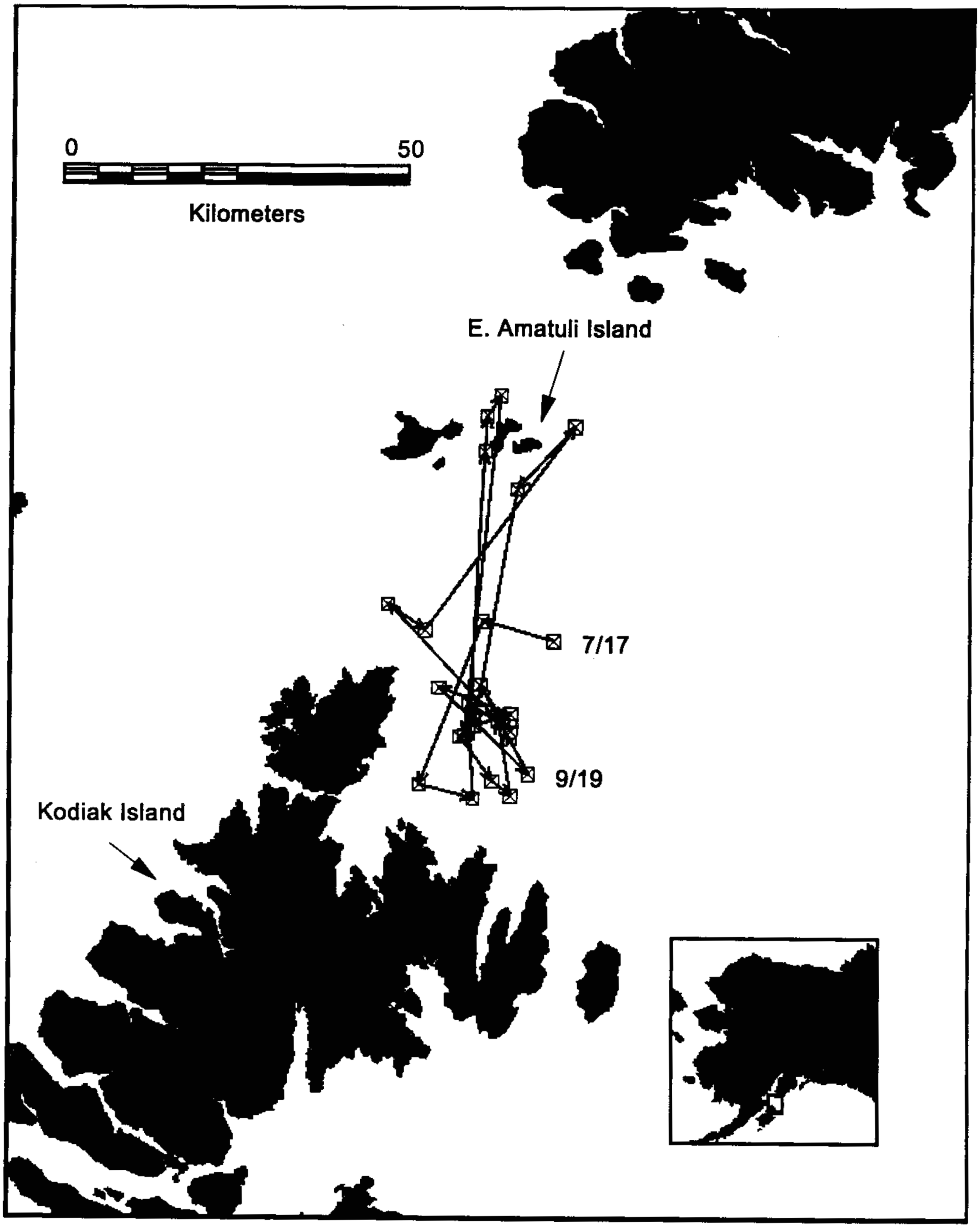


Figure A.11. Track lines of male common murre 6328 from East Amatuli Island. Long-cycle transmitter. Died around 4 August 1995, 18 days total.

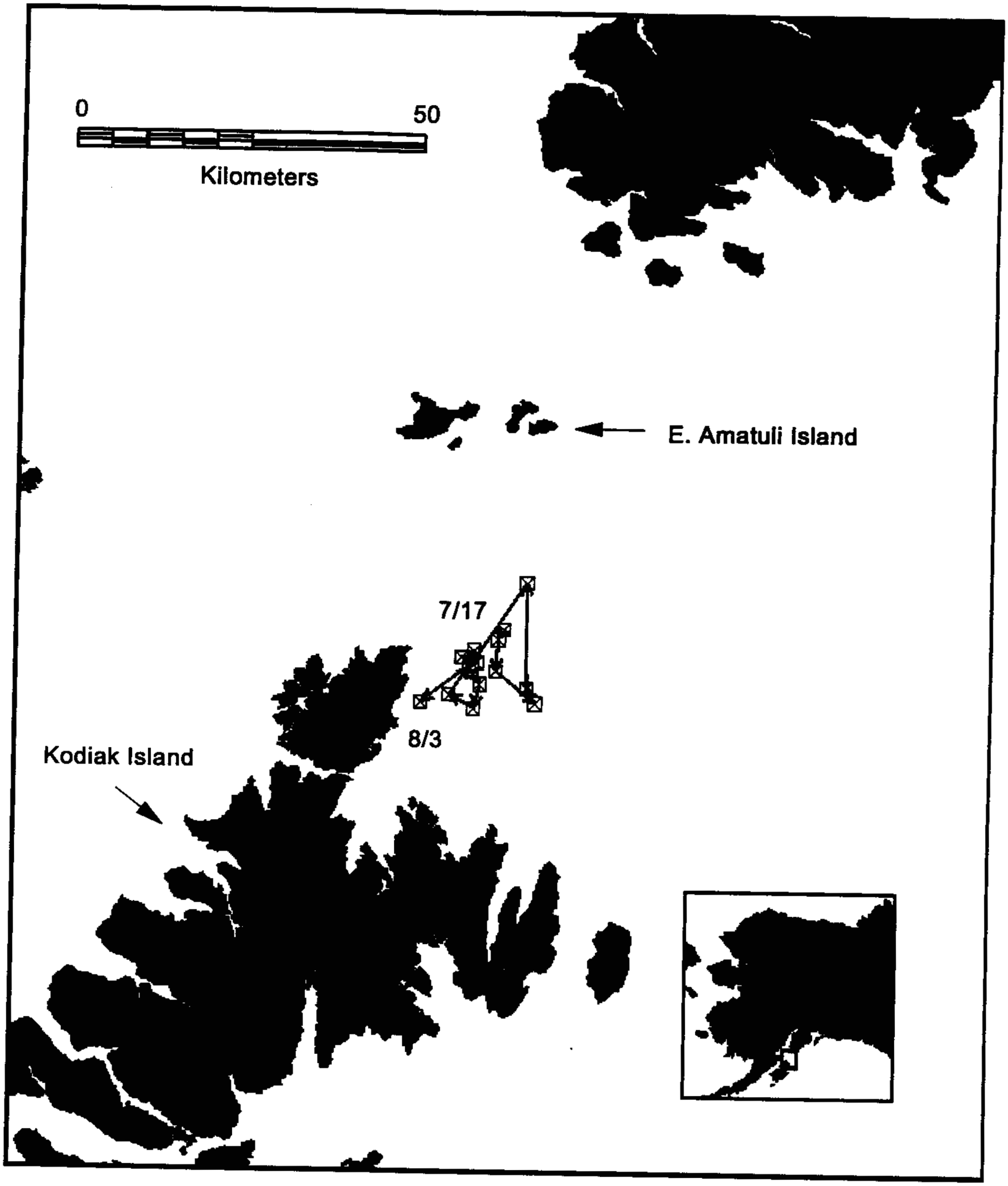


Figure A.12. Track lines of male common murre 7559 from East Amatuli Island. Short-cycle transmitter. Died 29 July 1995, 12 days total.

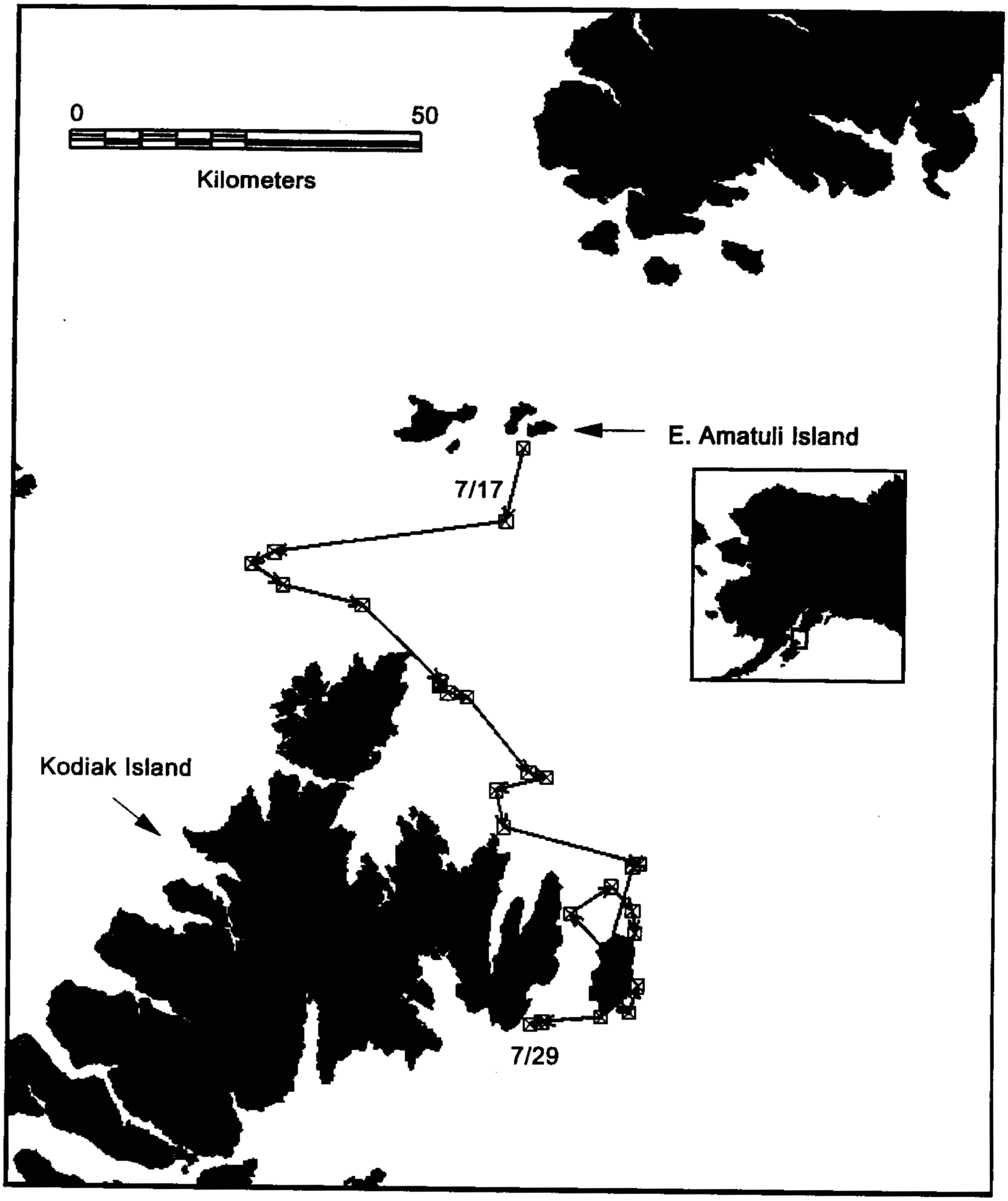


Figure A.13. Track lines of male common murre 7623 from East Amatuli Island. Short-cycle transmitter. Lost contact 31 July 1995, 13 days total. Probably died.

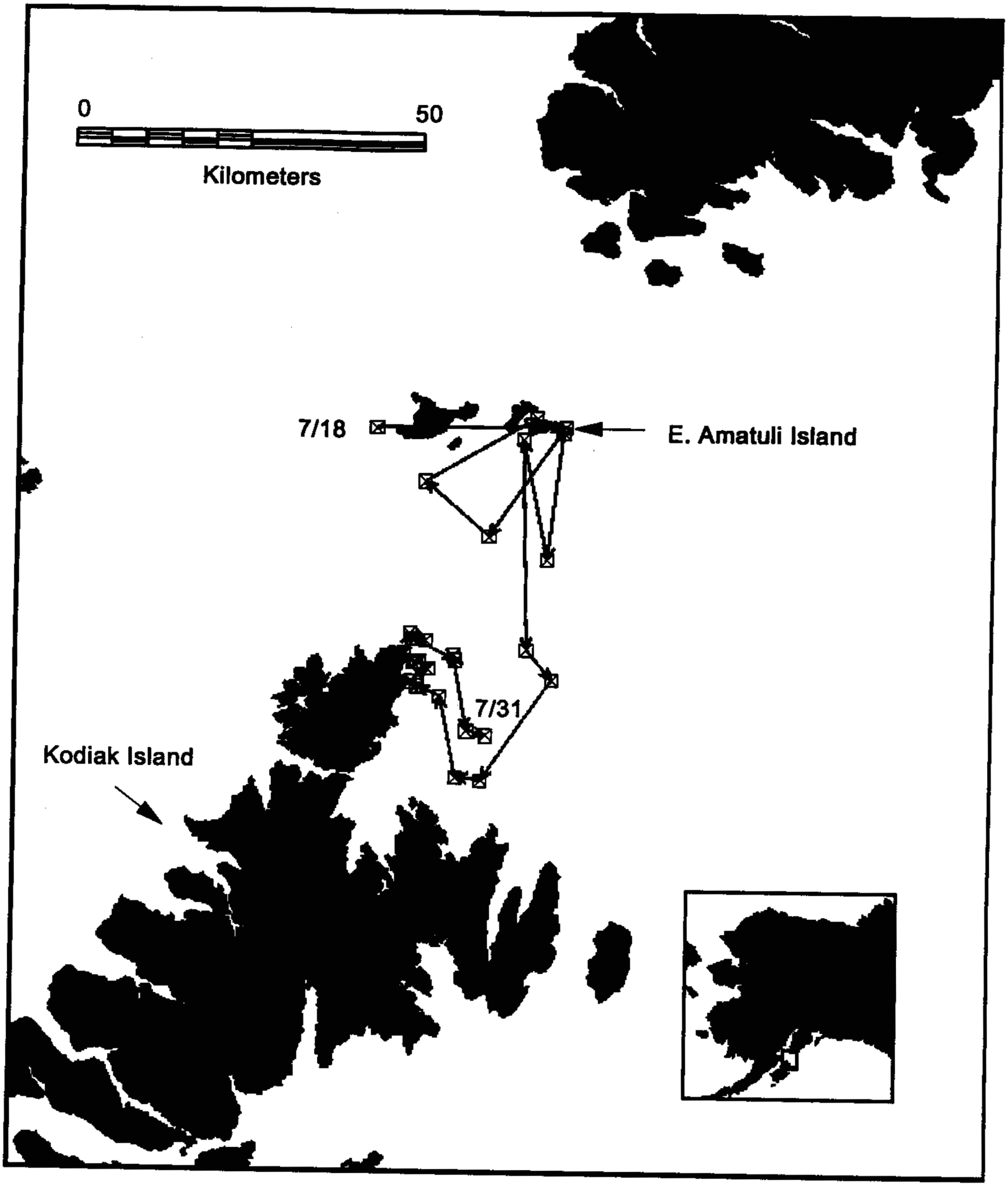


Figure A.14. Track lines of female common murre 7873 from East Amatuli Island. Short-cycle transmitter. Died 31 July 1995, 13 days total.

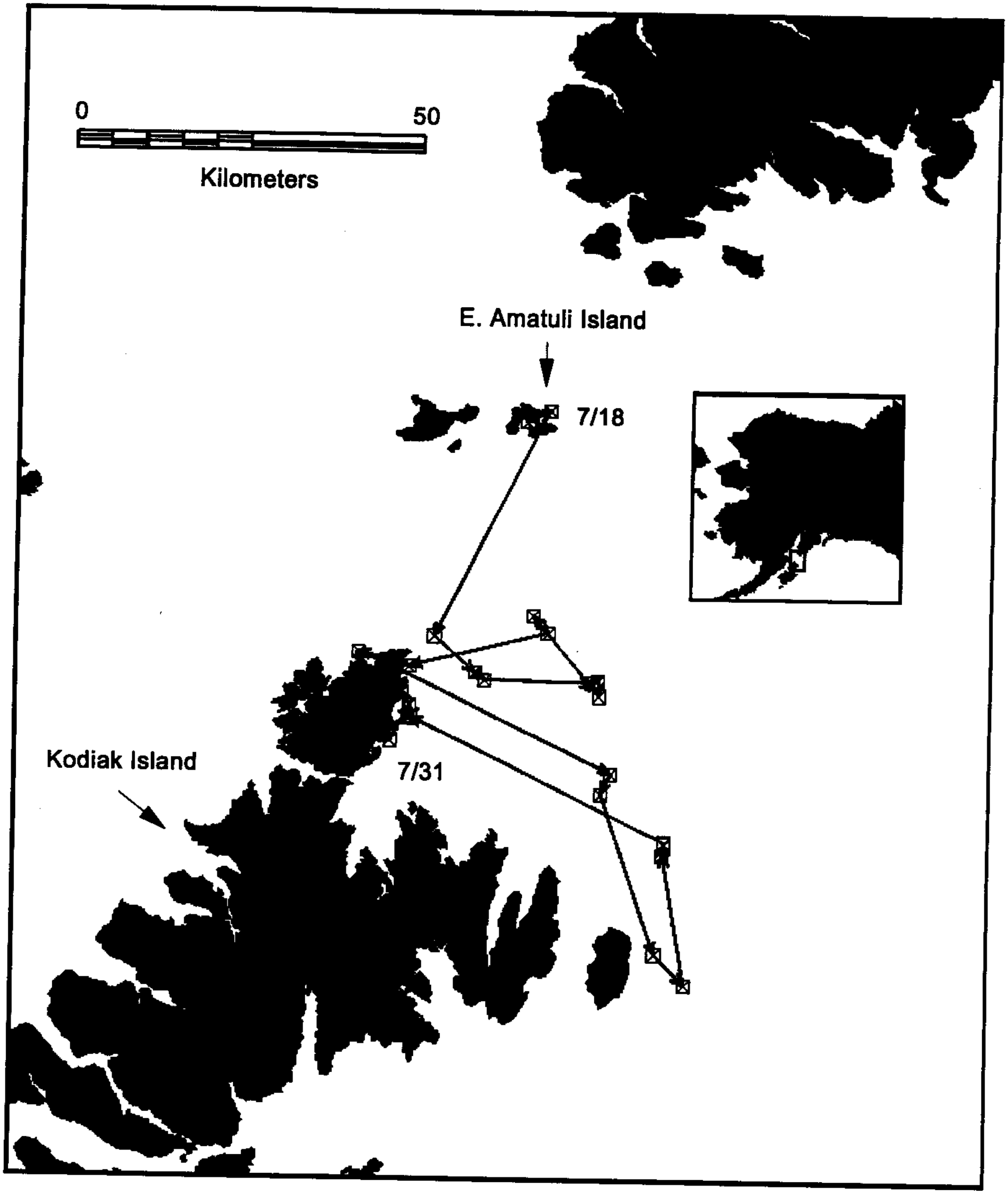


Figure A.15. Track lines of male common murre 7875 from East Amatuli Island. Short-cycle transmitter. Died 31 July 1995, 14 days total.

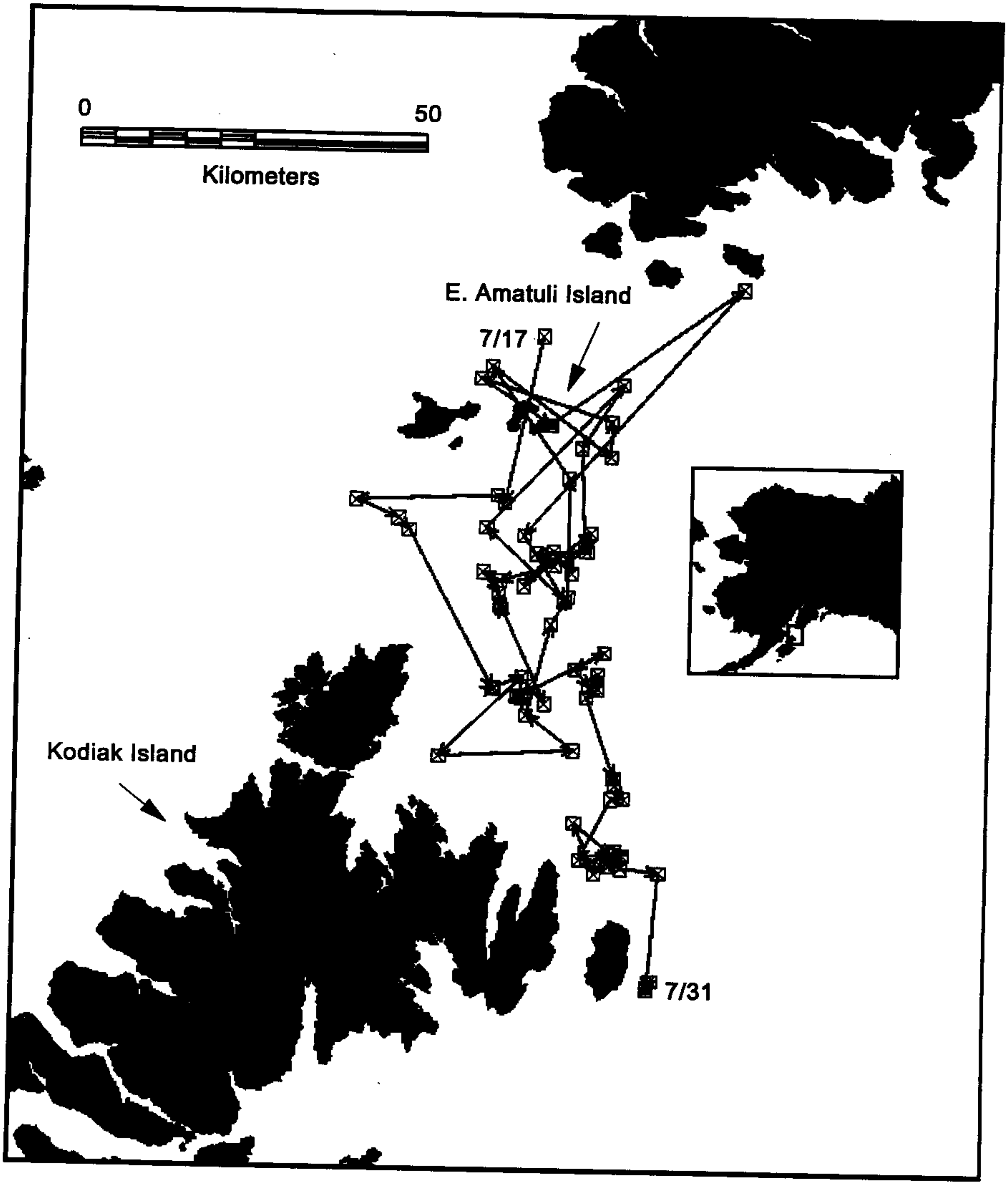


Figure A.16. Track lines of male thick-billed murre 7877 from Cape Lisburne. Long-cycle transmitter. Still alive and transmitting as of 10 April 1996.

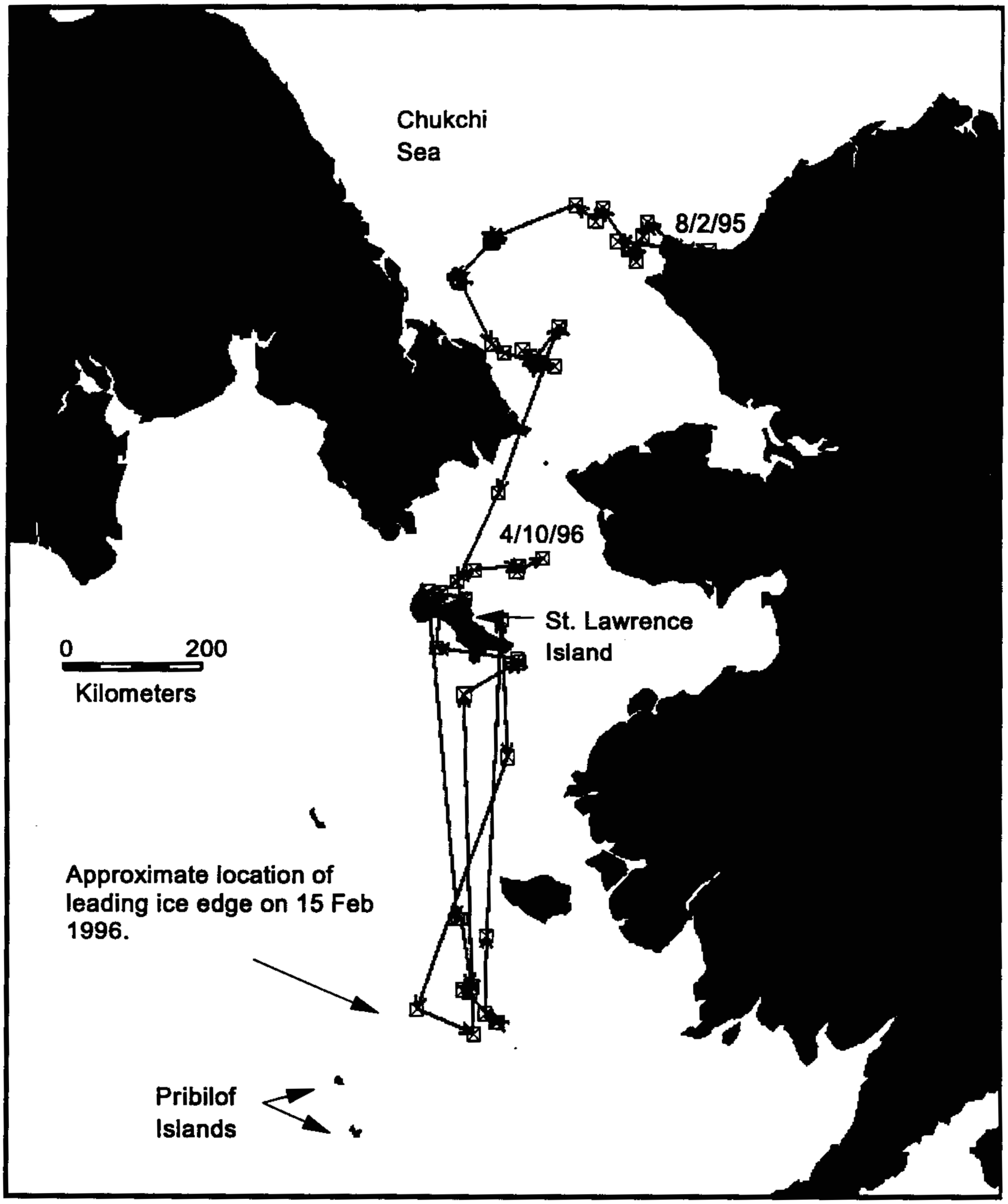


Figure A.17. Breeding-season movements of male thick-billed murre 7877 from Cape Lisburne.

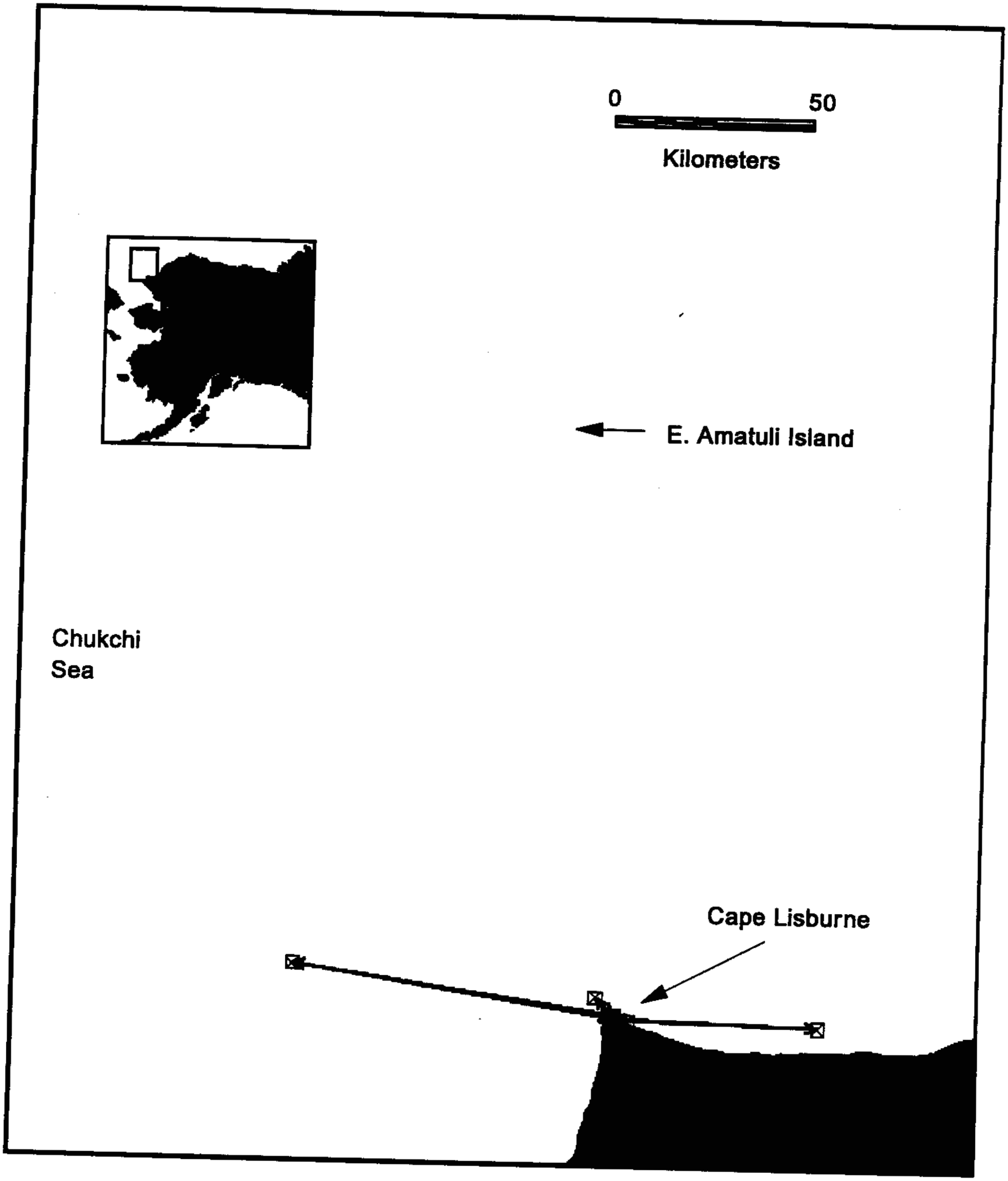


Figure A.18. Track lines of male common murre 7879 from Cape Lisburne. Long-cycle transmitter. Lost contact 29 November 1995, 118 days total. Transmitter sporadic.

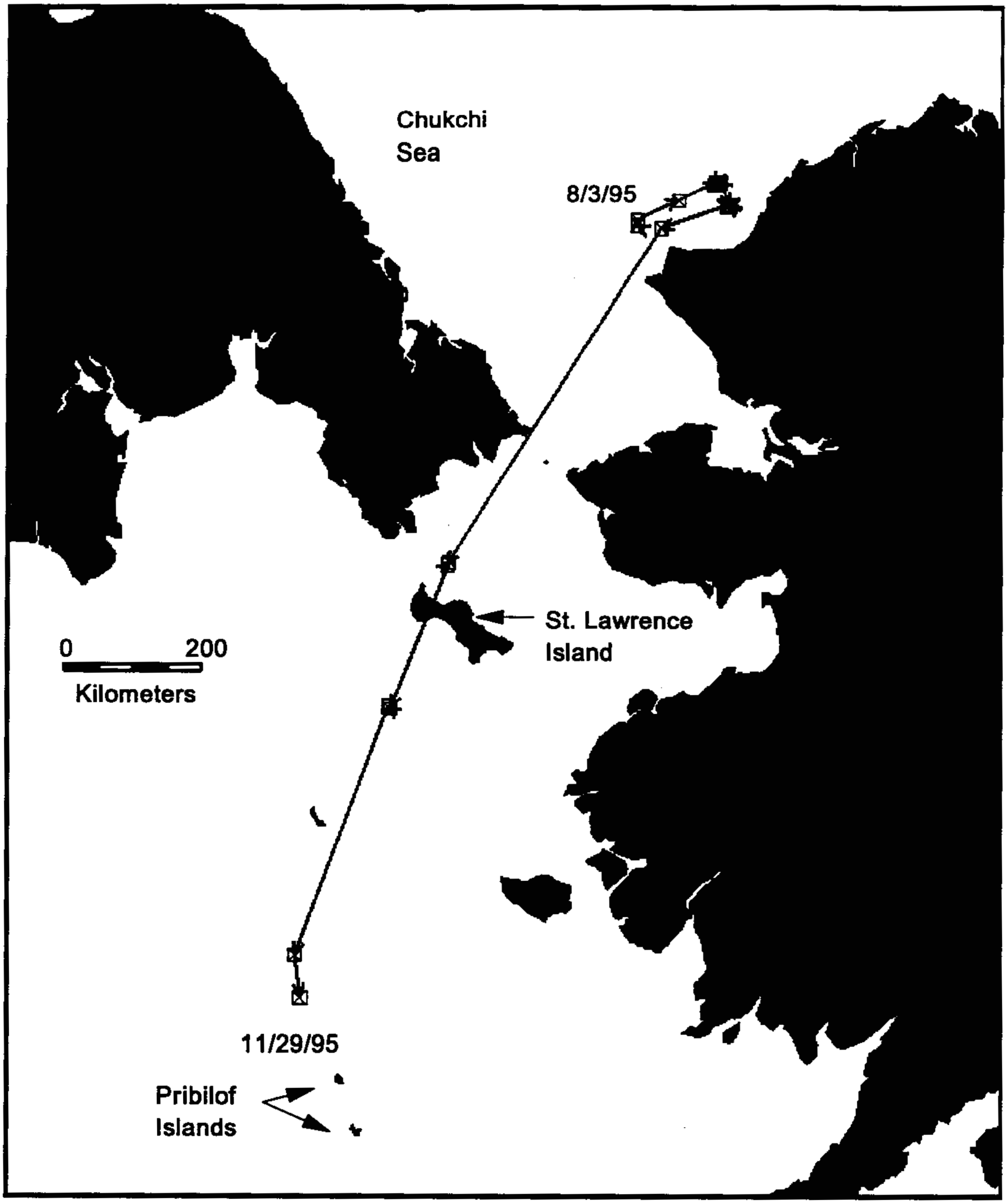


Figure A.19. Breeding-season movements of male thick-billed murre 7879 from Cape Lisburne.

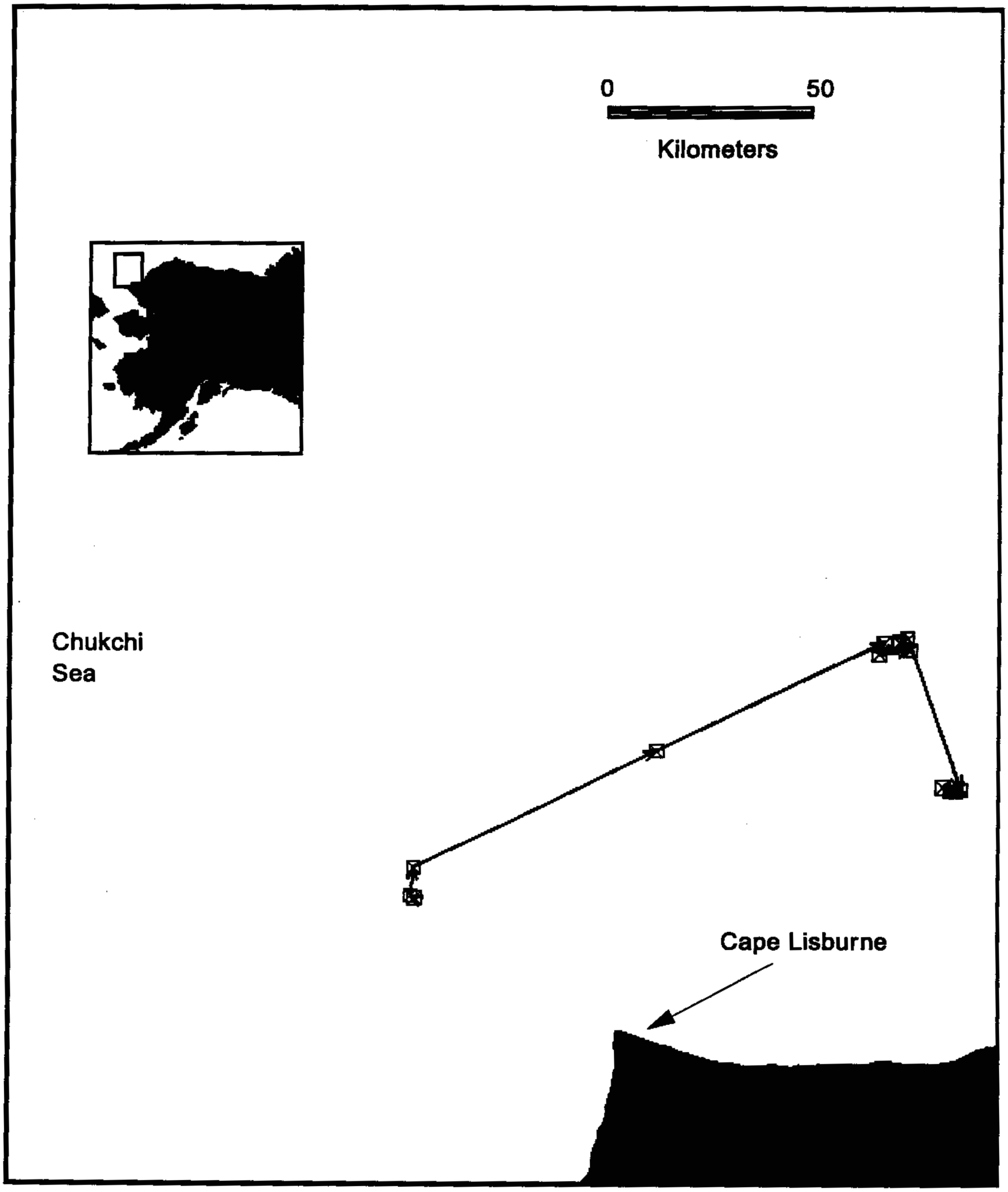


Figure A.20. Track lines of female common murre 7884 from Cape Lisburne. Long-cycle transmitter. Lost contact 7 August 1995, 4 days total. Probably died.

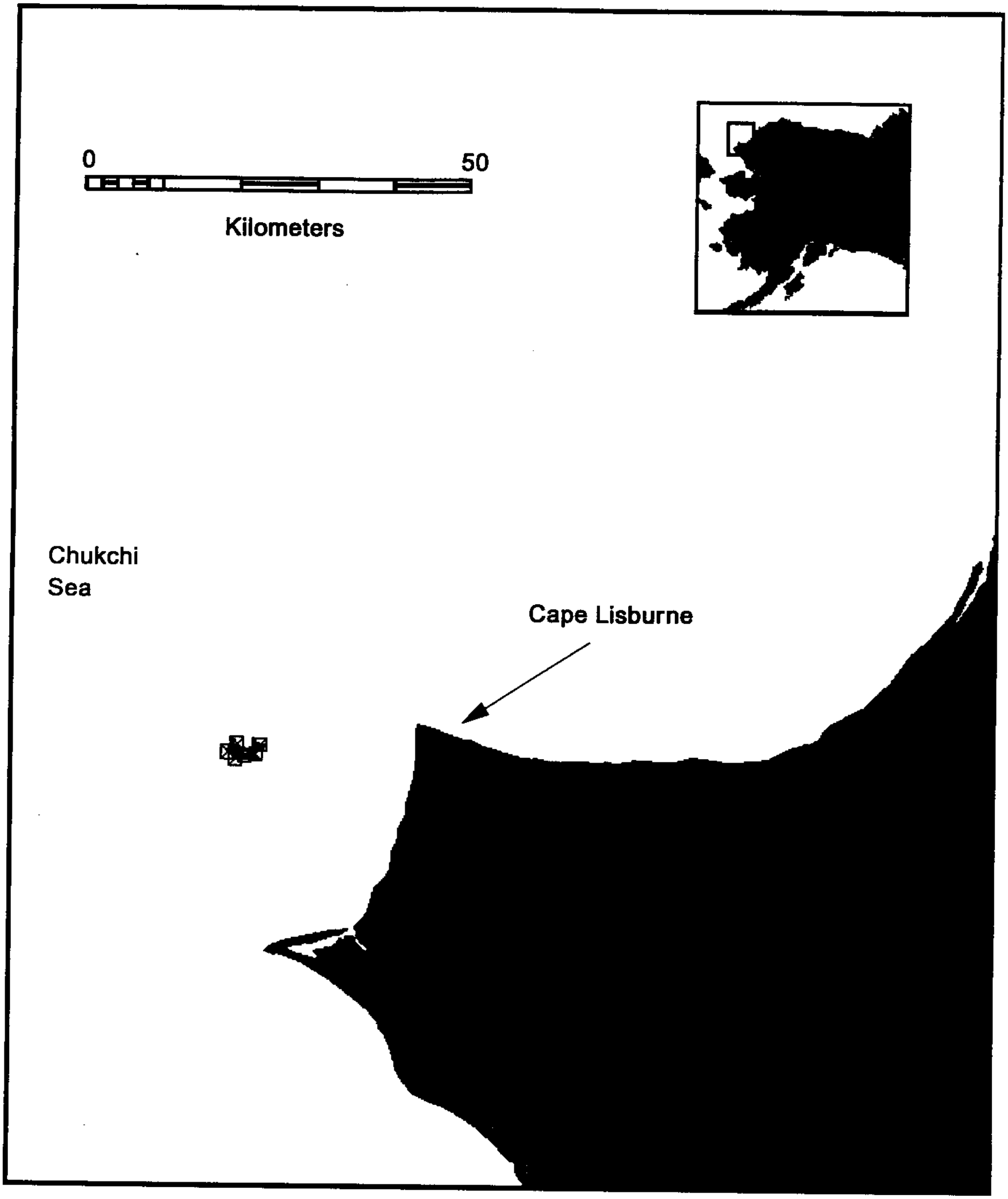


Figure A.21. Track lines of female thick-billed murre 7889 from Cape Lisburne. Long-cycle transmitter. Died 21 August 1995, 19 days total.

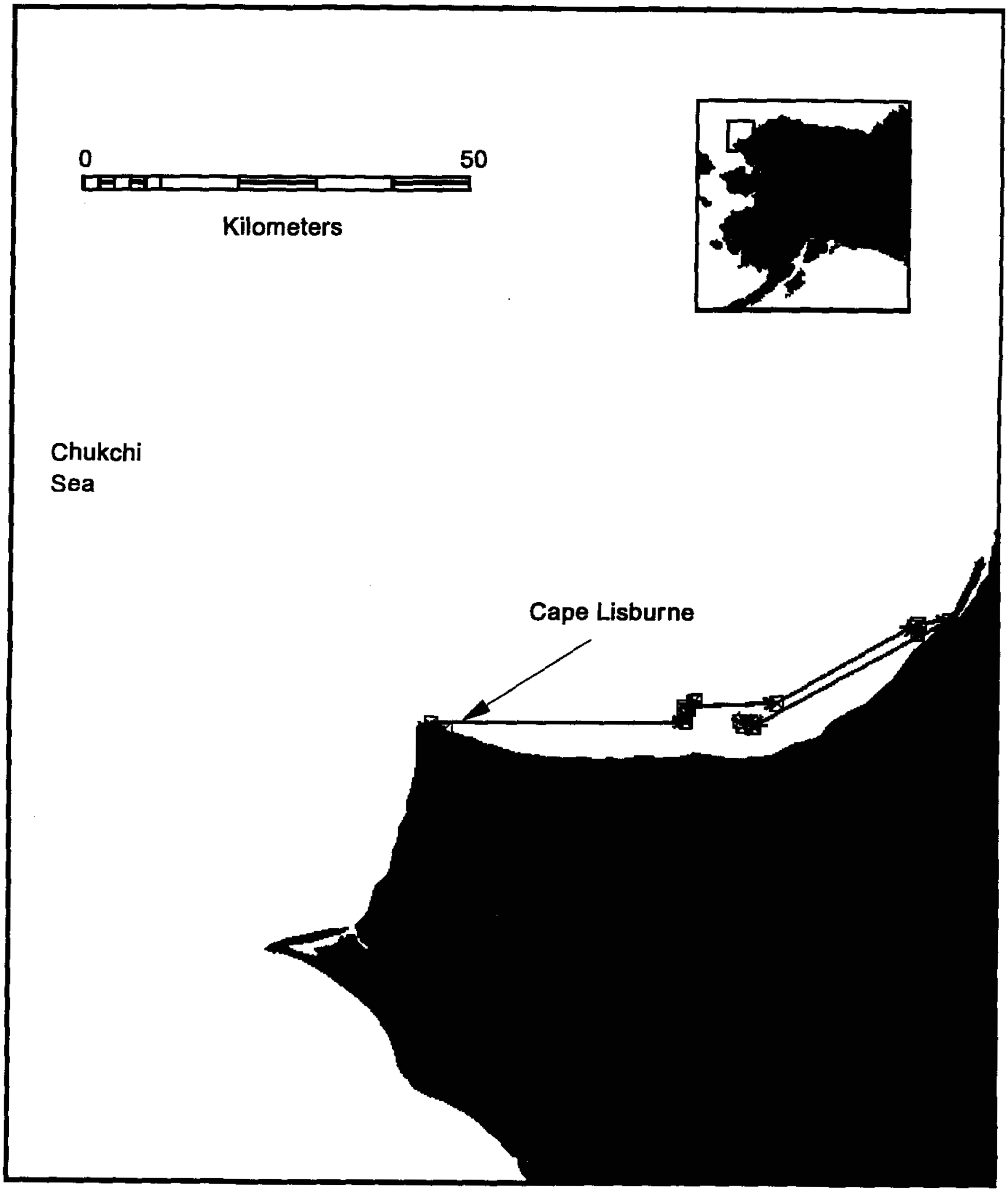


Figure A.22. Track lines of female common murre 7903 from Cape Lisburne. Long-cycle transmitter. Lost contact 31 January 1996, 178 days total.

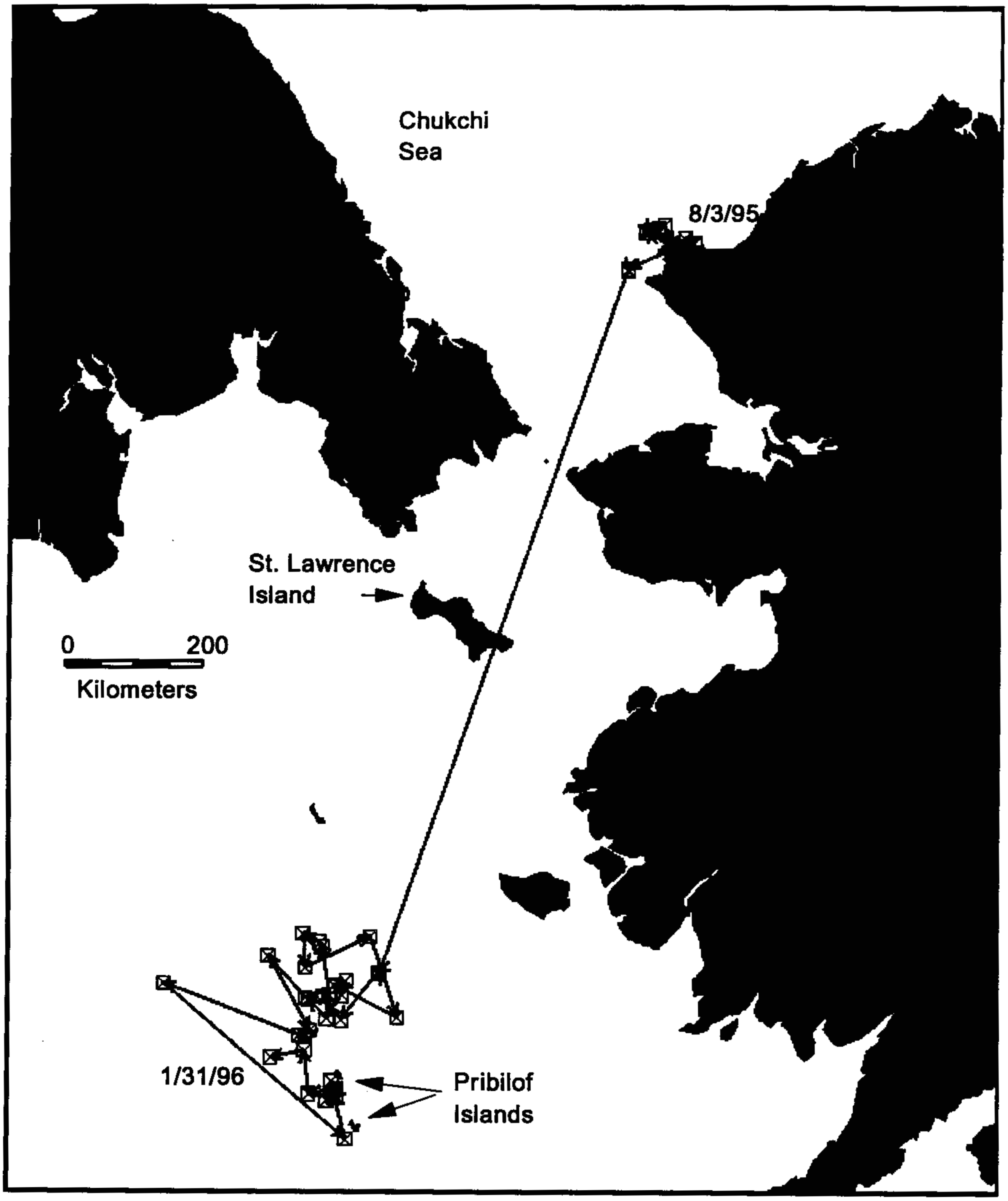


Figure A.23. Breeding-season movements of female common murre 7903 from Cape Lisburne.

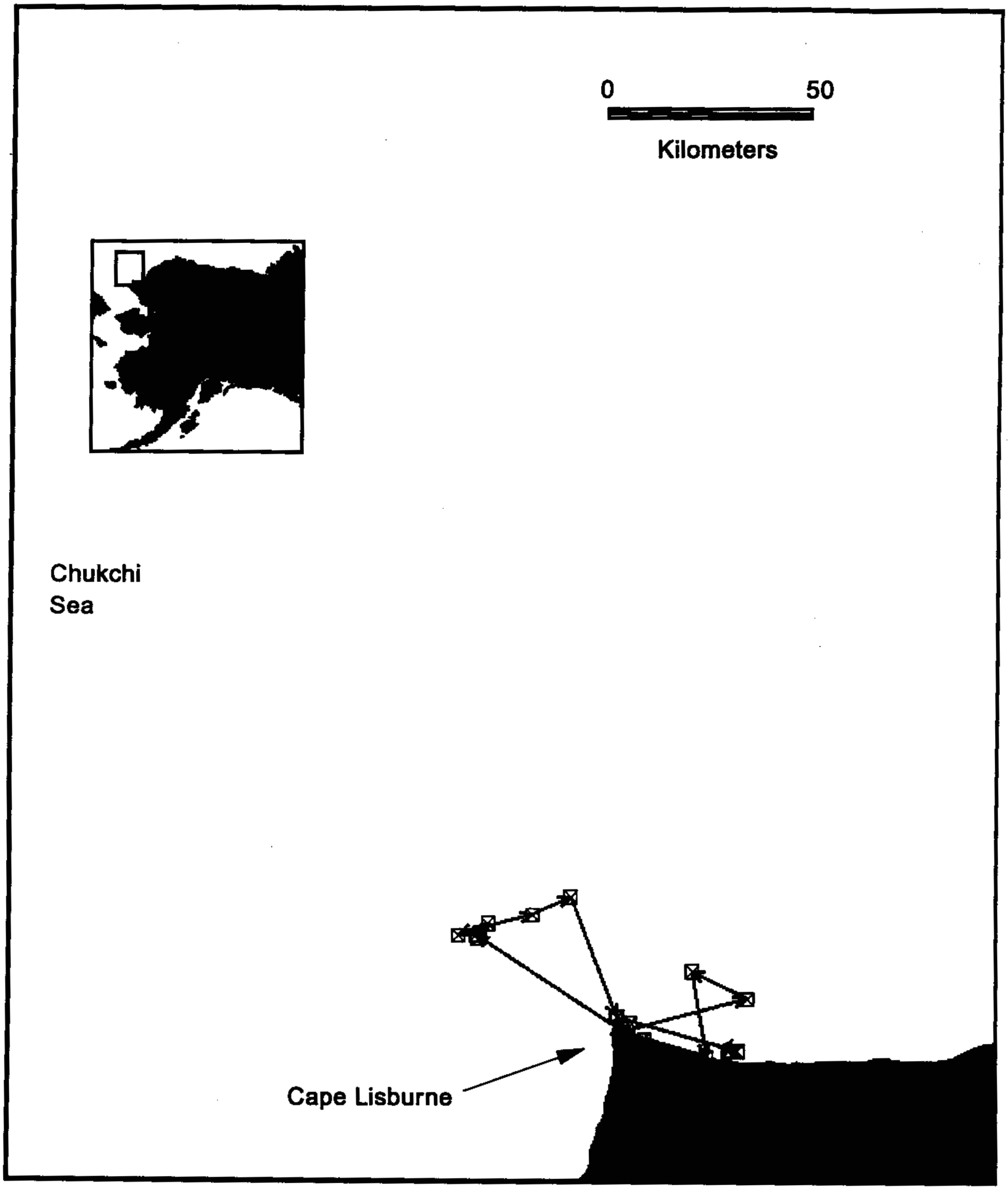


Figure A.24. Track lines of male thick-billed murre 7917 from Cape Lisburne. Short-cycle transmitter. Lost contact 17 August 1995, 15 days total. Probably died.

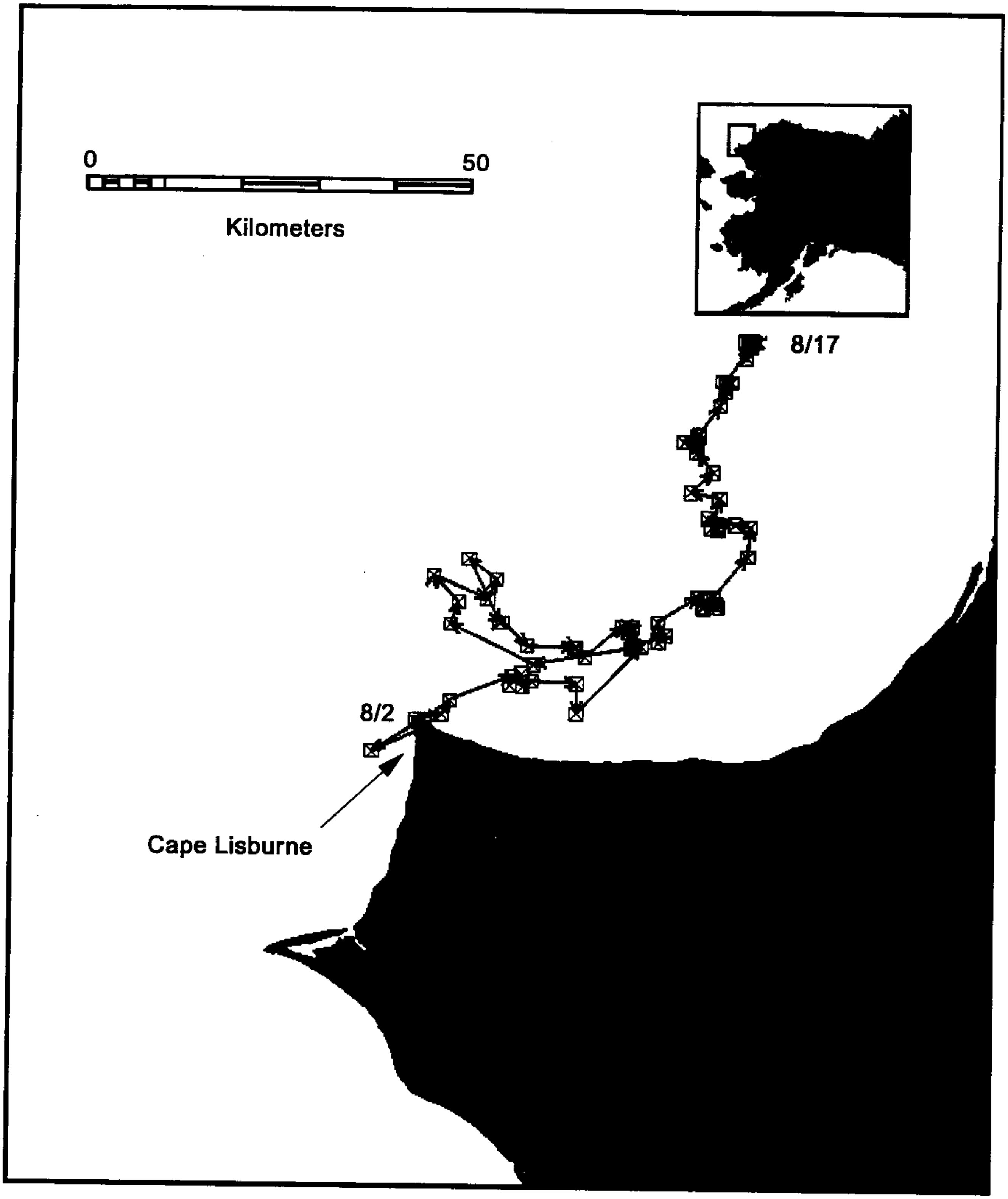


Figure A.25. Track lines of female thick-billed murre 20003 from Cape Lisburne. Short-cycle transmitter. Died 10 August 1995, 8 days total.

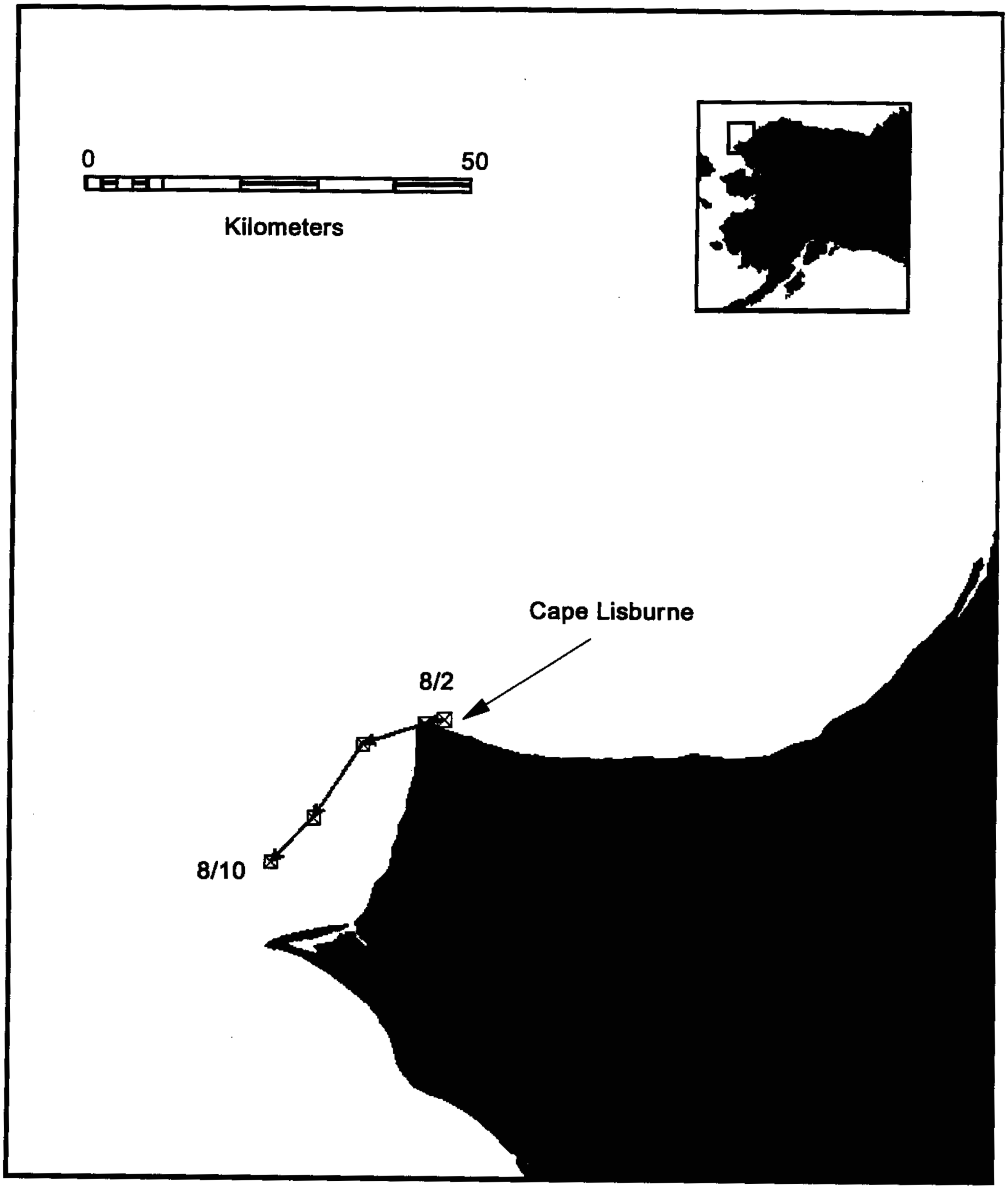


Figure A.26. Track lines of female common murre 20005 from Cape Lisburne. Short-cycle transmitter. Lost contact 22 December 1995, 141 days total.

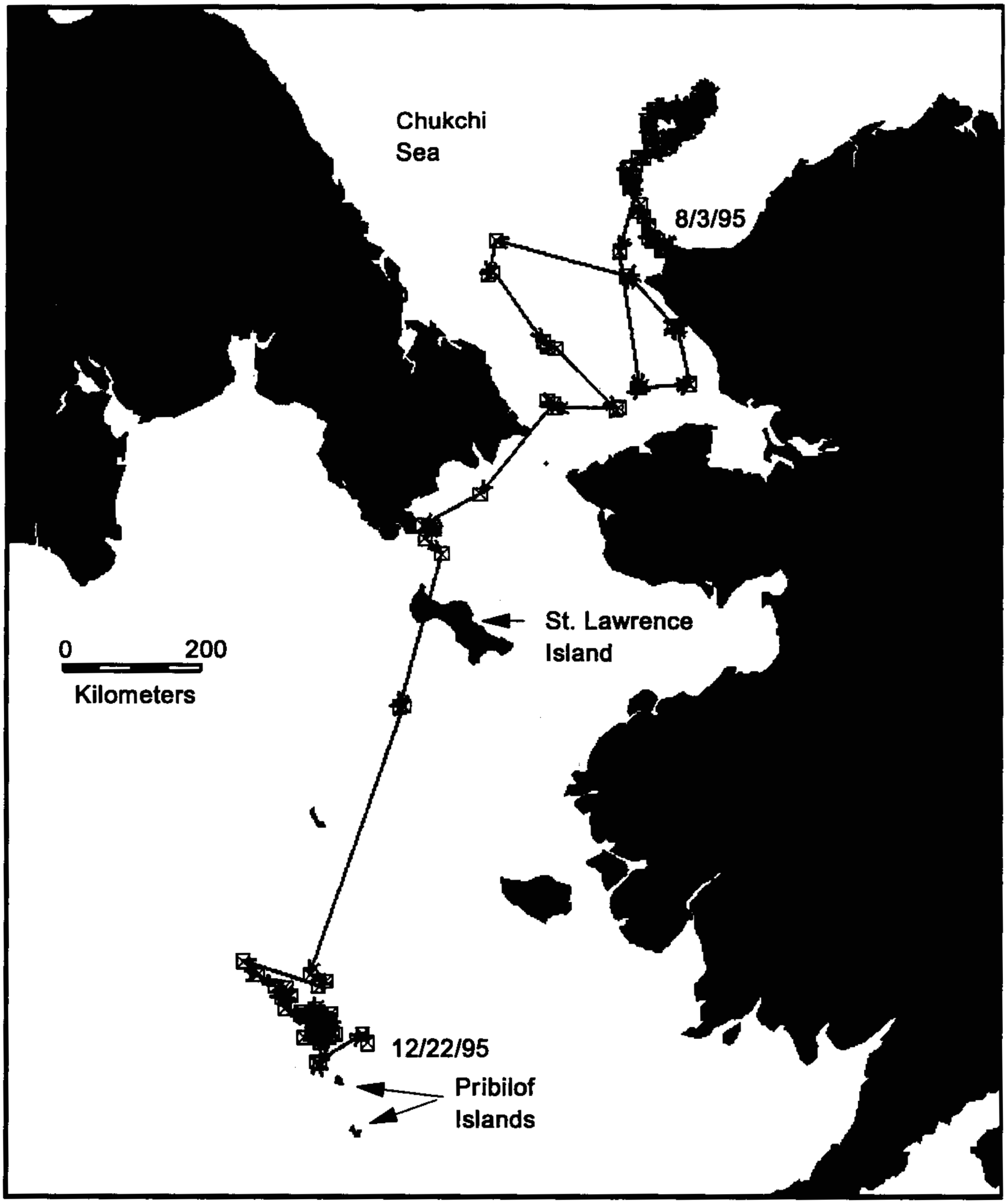


Figure A.27. Breeding-season movements of female common murre 20005 from Cape Lisburne.

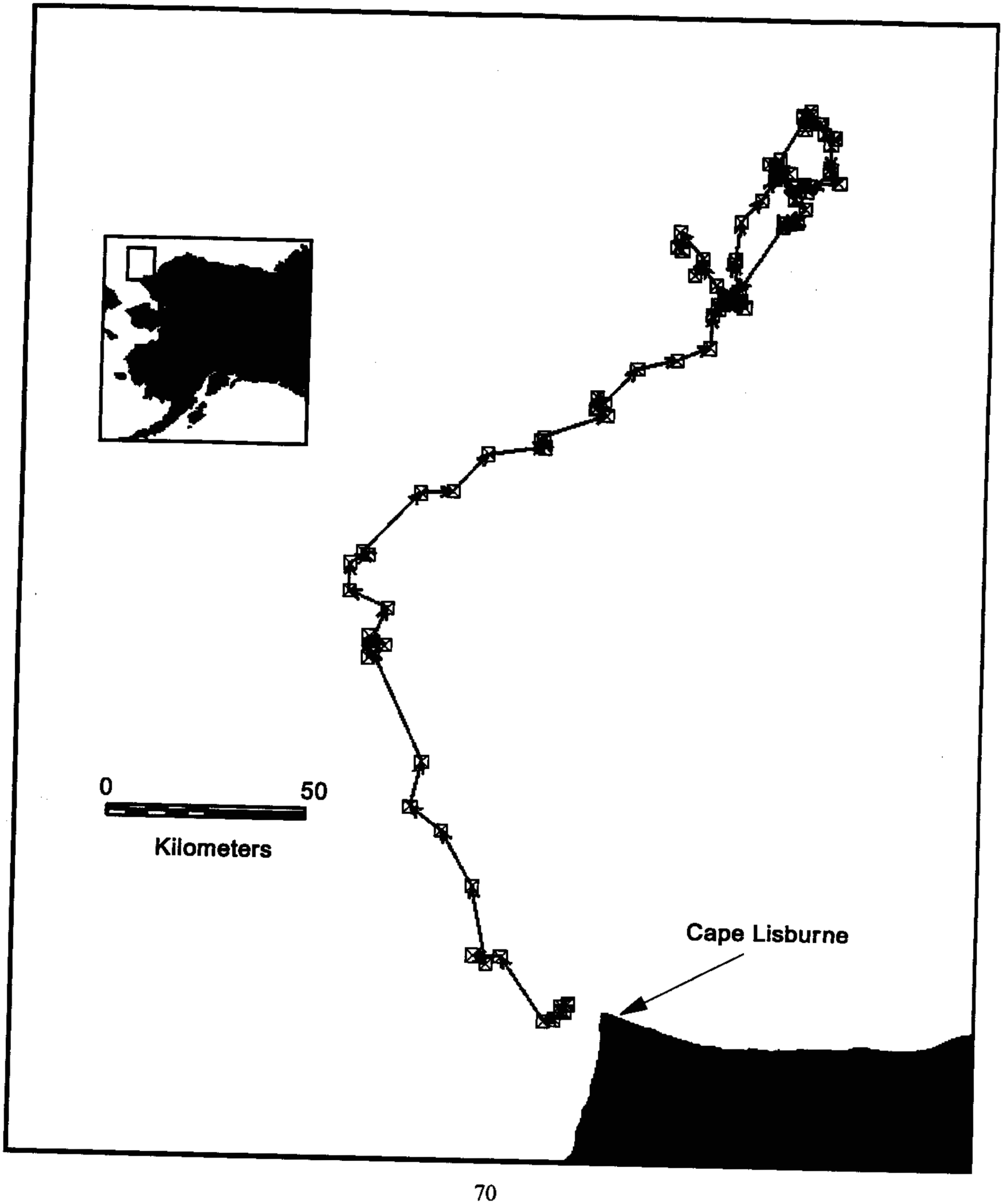


Figure A.28. Track lines of male thick-billed murre 20836 from Cape Lisburne. Short-cycle transmitter. Died 18 August 1995, 16 days total.

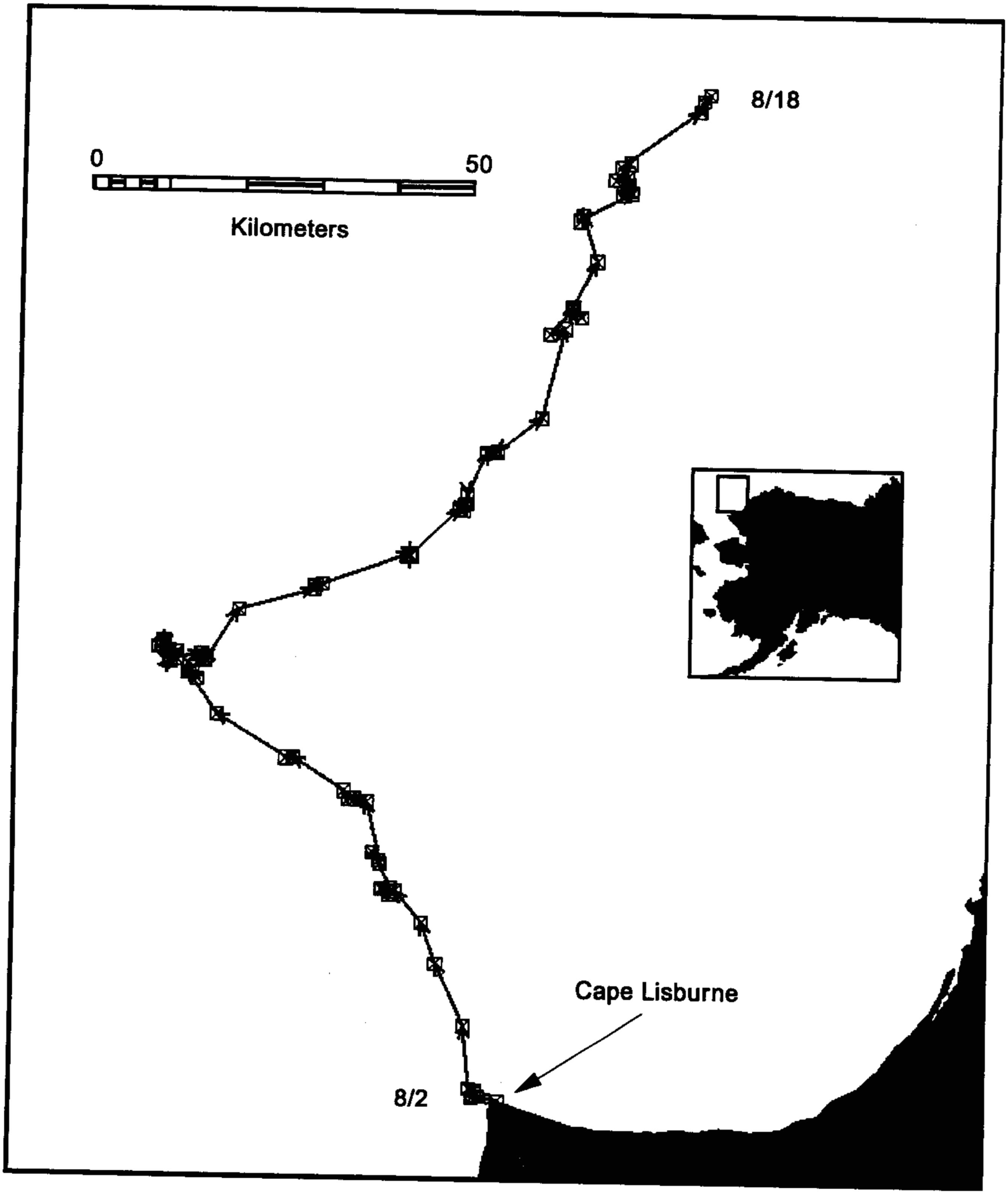


Figure A.29. Track lines of male common murre 20838 from Cape Lisburne. Short-cycle transmitter. Died 5 August 1995, 2 days total.

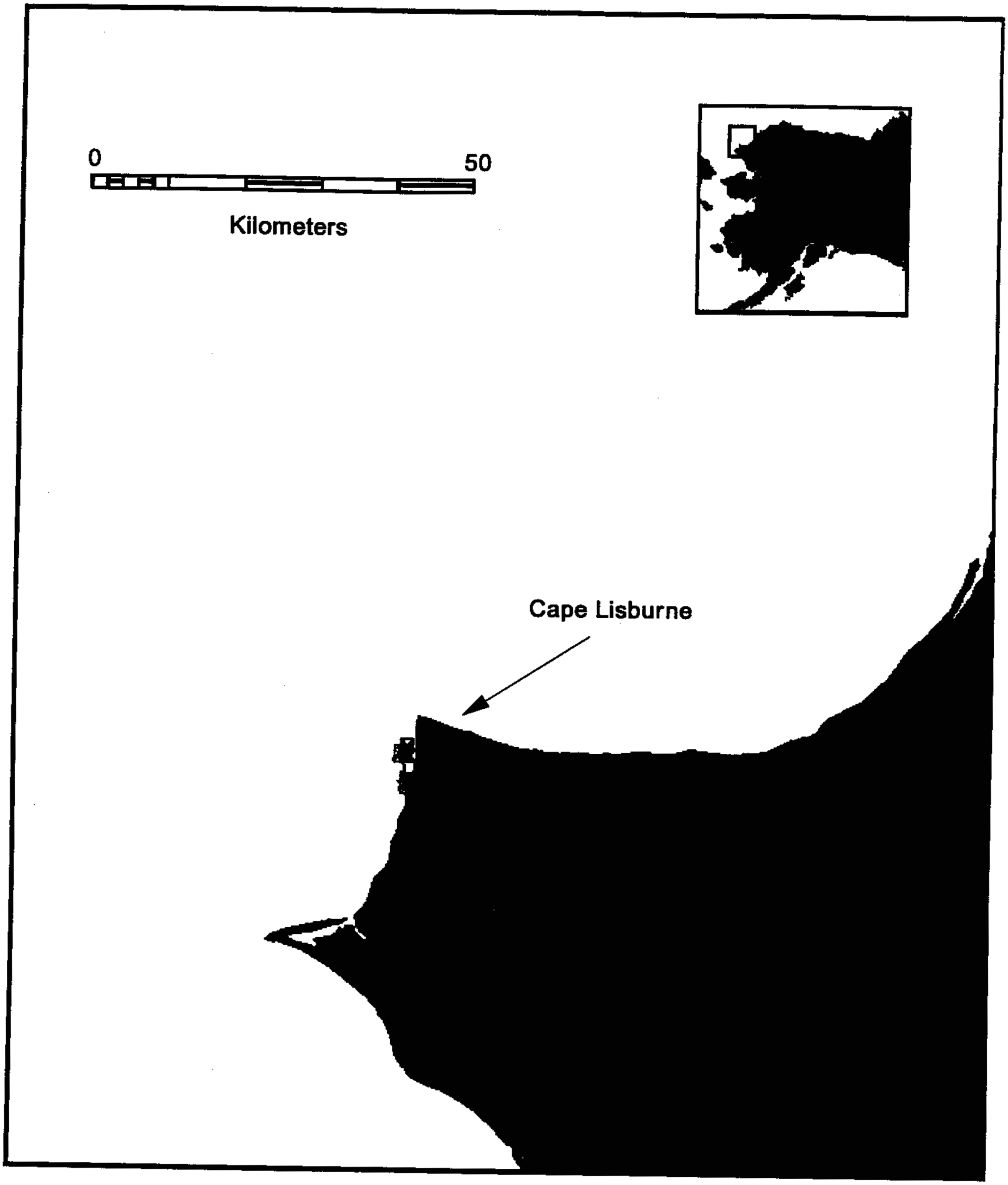


Figure A.30. Track lines of female common murre 7876 from Cape Thompson. Long-cycle transmitter. Lost contact 22 January 1996, 105 days total.

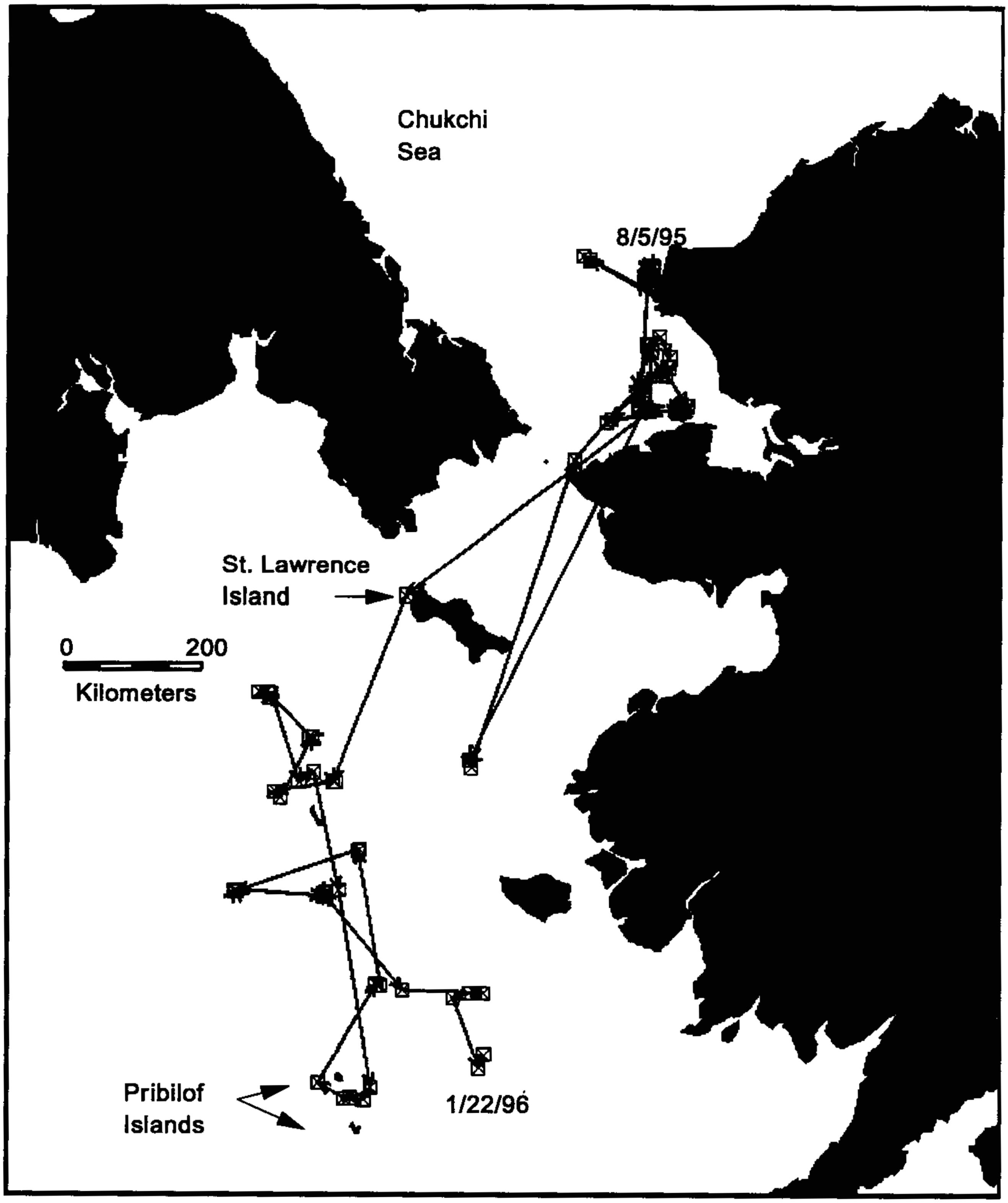


Figure A.31. Breeding-season movements of female common murre 7876 from Cape Thompson.

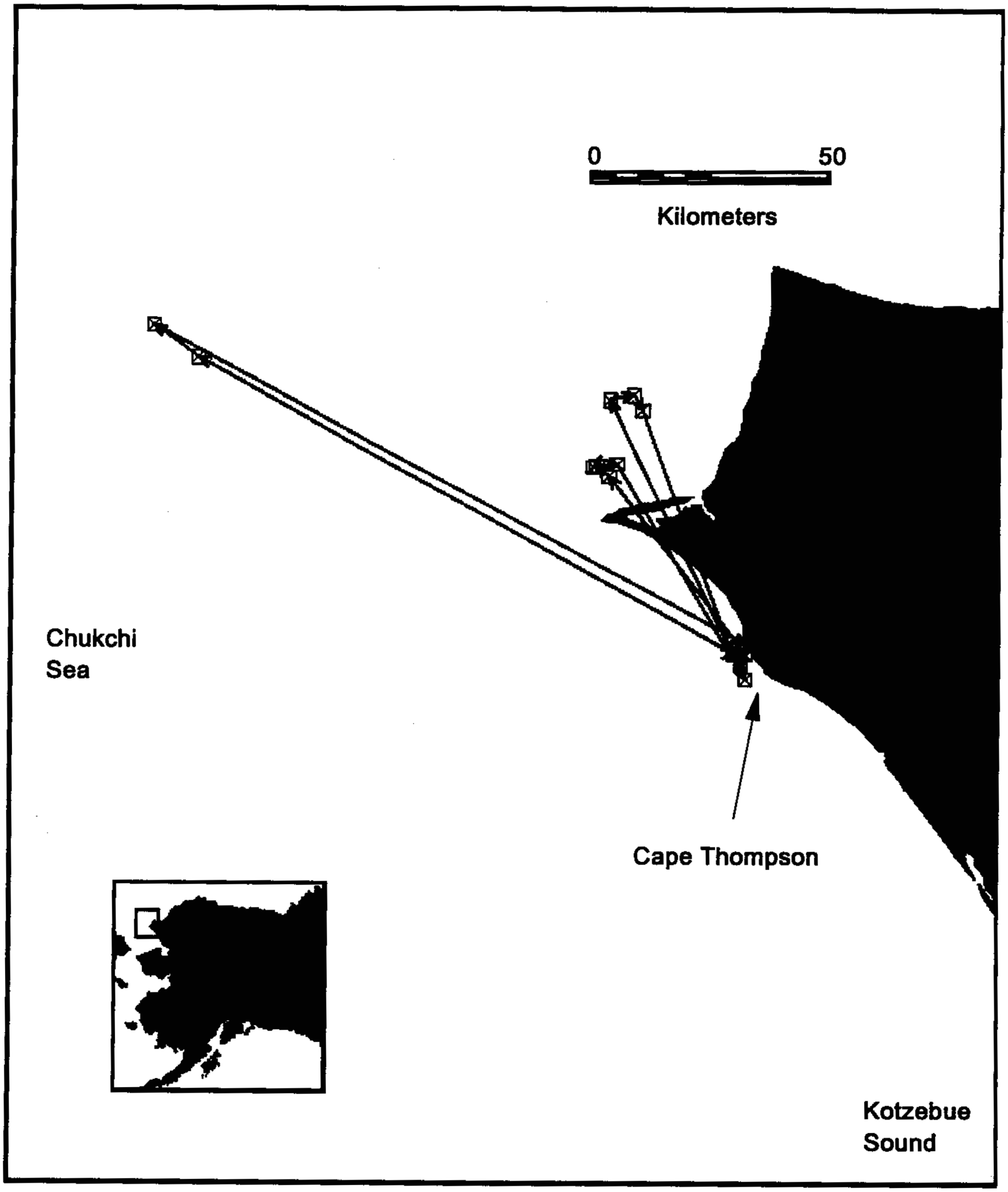


Figure A.32. Track lines of female thick-billed murre 7880 from Cape Thompson. Long-cycle transmitter. Lost contact 27 October 1995, 82 days total. Transmitter sporadic.

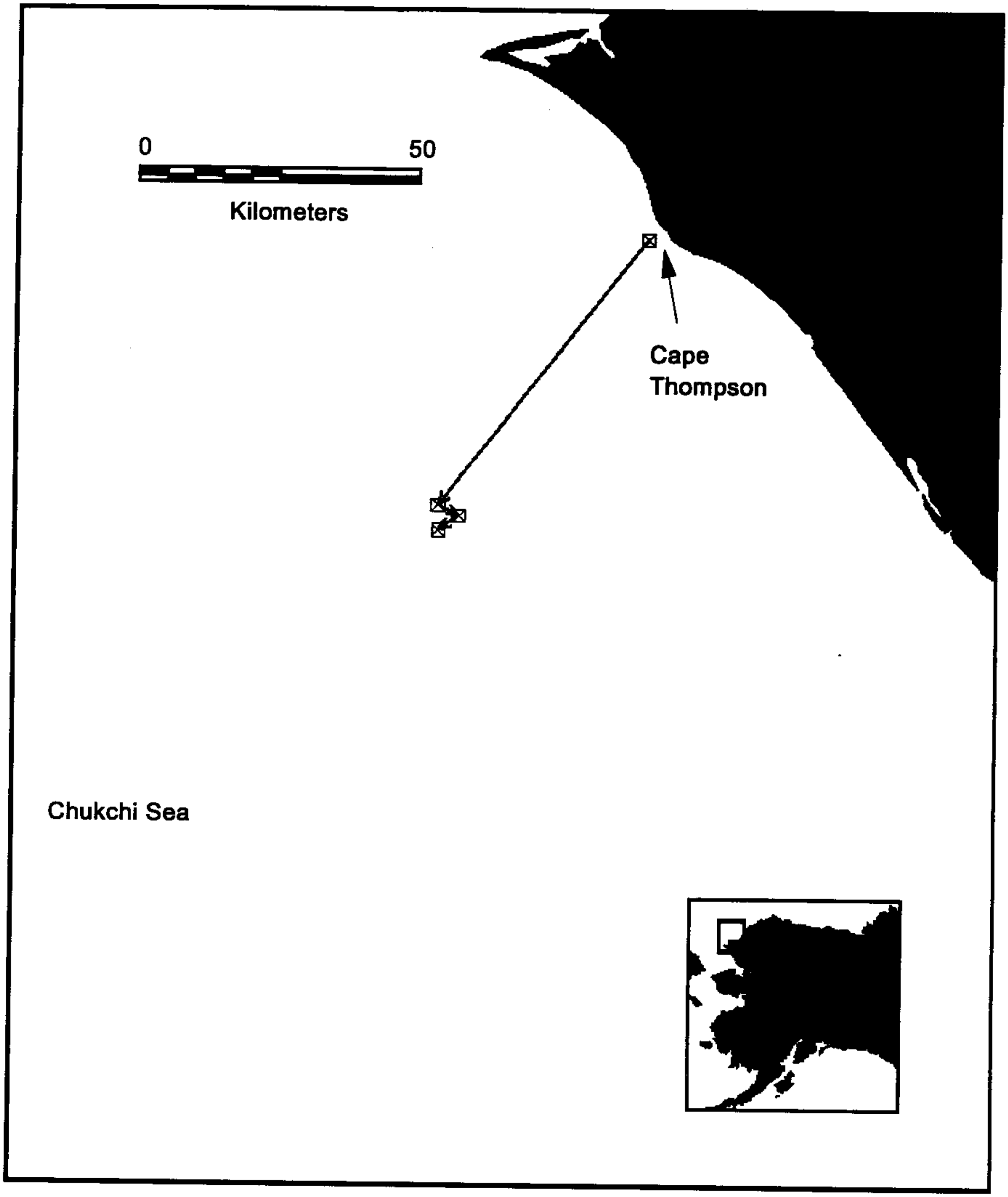


Figure A.33. Track lines of male thick-billed murre 7882 from Cape Thompson. Long-cycle transmitter. Lost contact 23 January 1996, 170 days total. Transmitter sporadic.

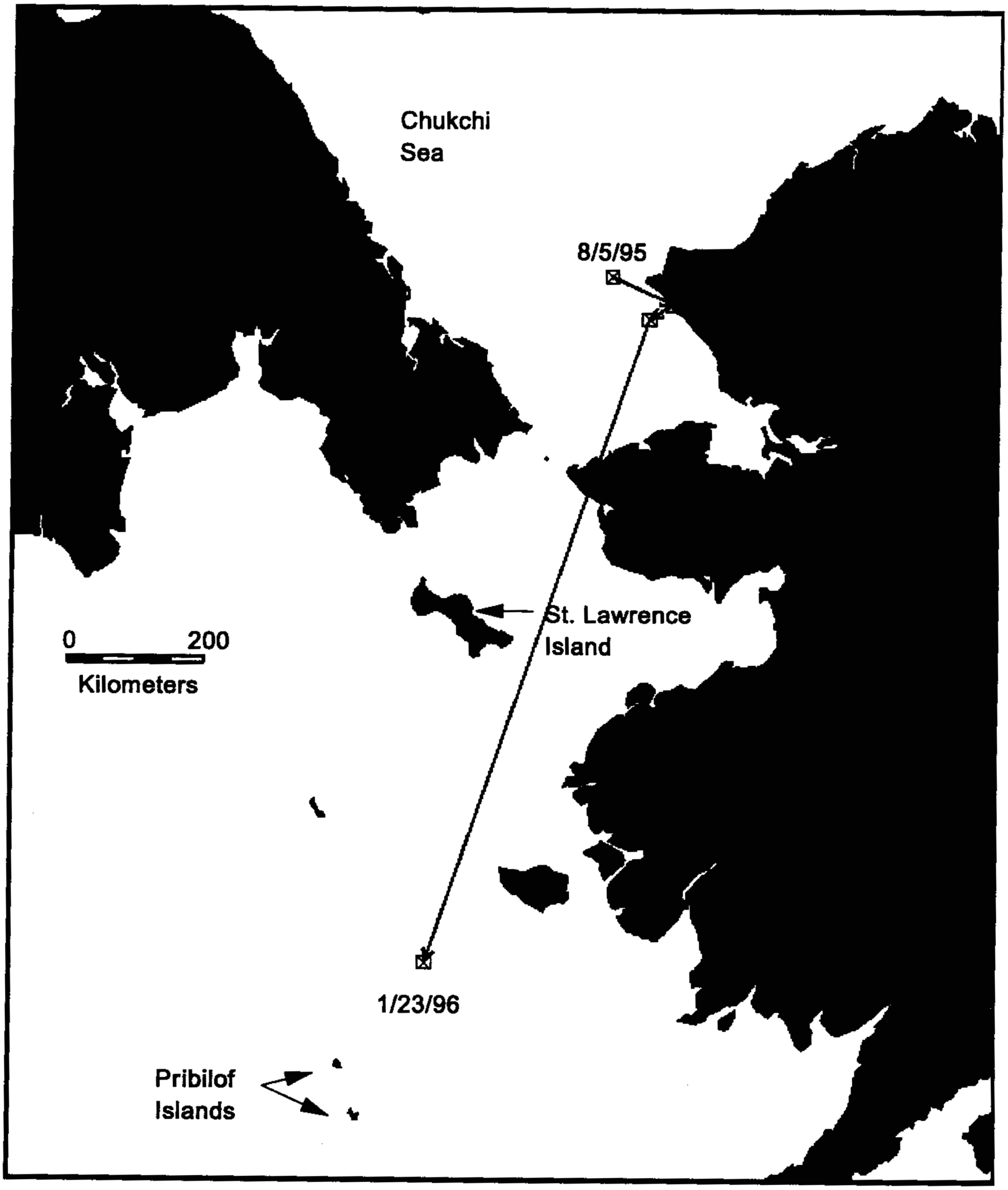


Figure A.34. Breeding-season movements of male thick-billed murre 7882 from Cape Thompson.

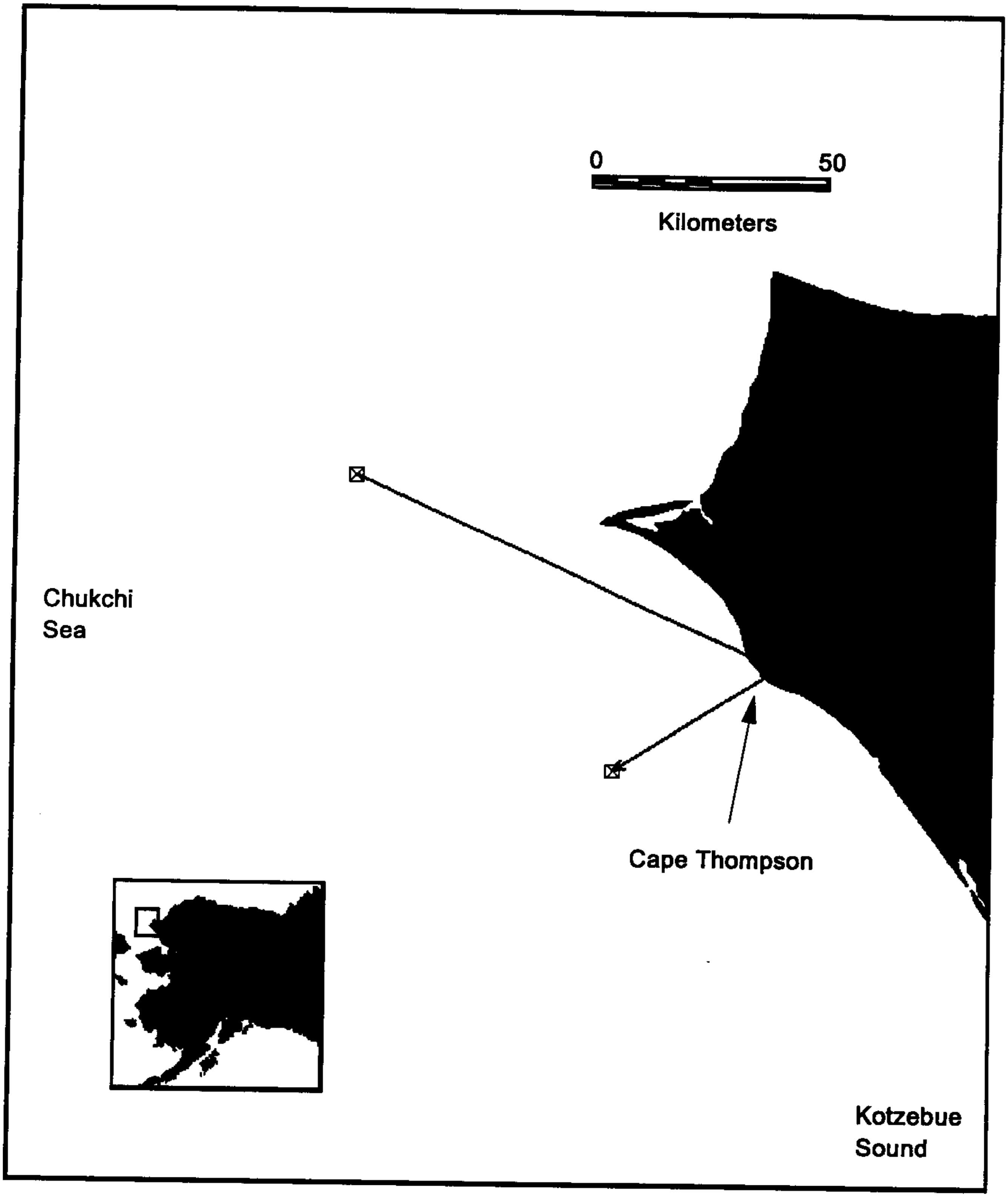


Figure A.35. Track lines of female thick-billed murre 7887 from Cape Thompson. Long-cycle transmitter. Lost contact 22 November 1995, 108 days total. Transmitter sporadic.

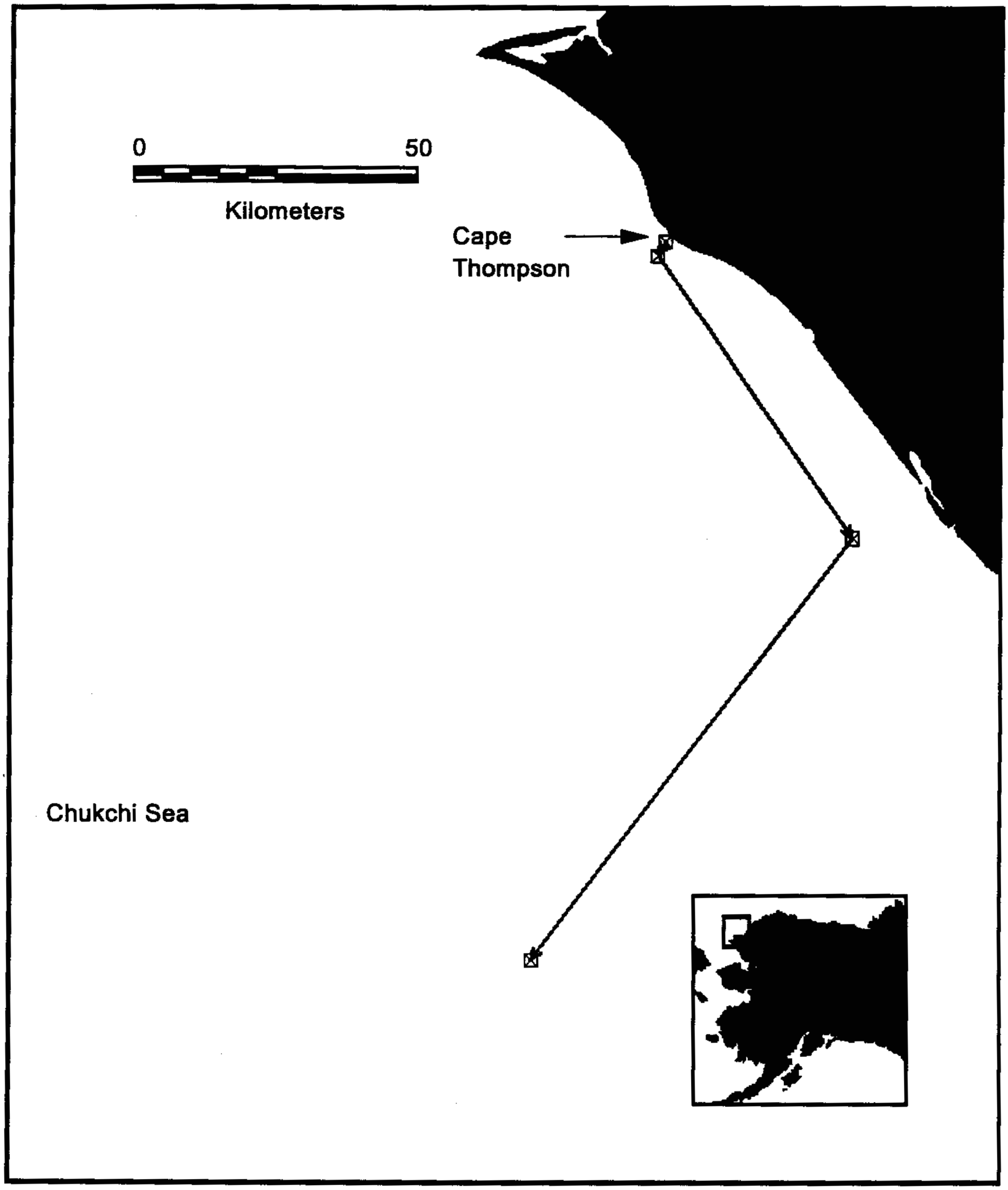


Figure A.36. Track lines of male common murre 7888 from Cape Thompson. Long-cycle transmitter. Lost contact 10 December 1995, 127 days total. Transmitter sporadic.

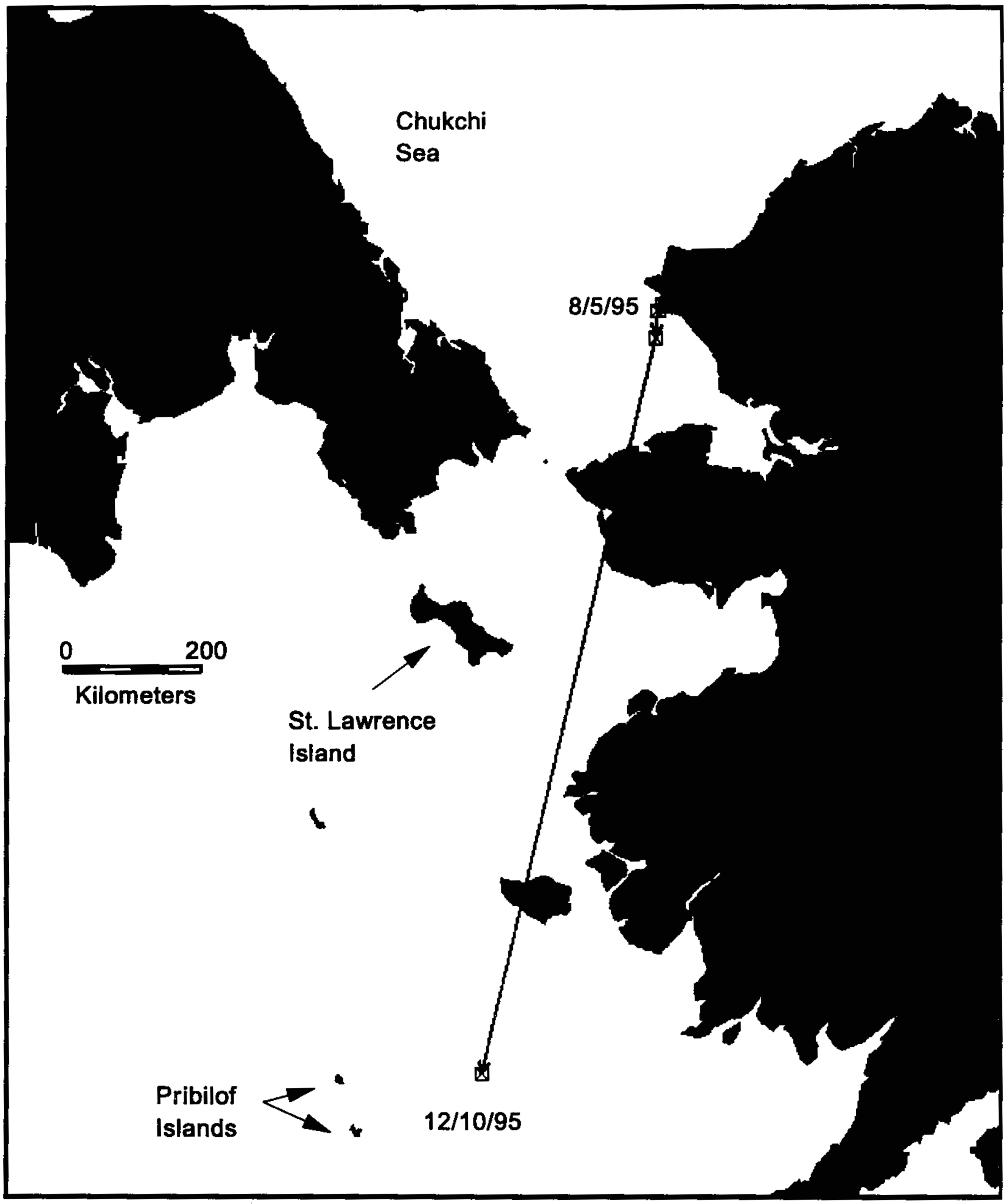


Figure A.37. Breeding-season movements of male common murre 7888 from Cape Thompson. Transmitter sporadic.

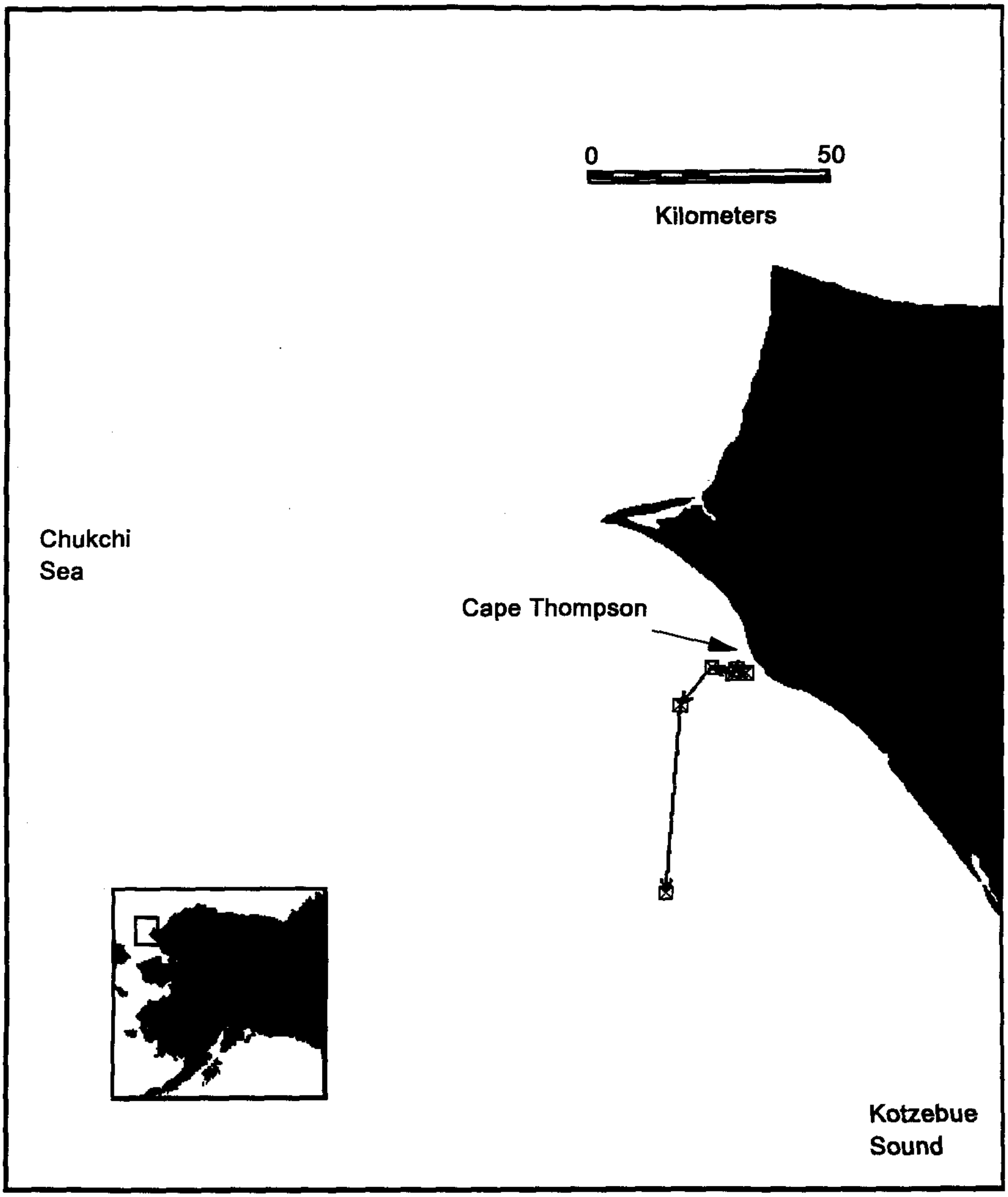


Figure A.38. Track lines of male common murre 7901 from Cape Thompson. Long-cycle transmitter. Lost contact 27 November 1995, 114 days total.

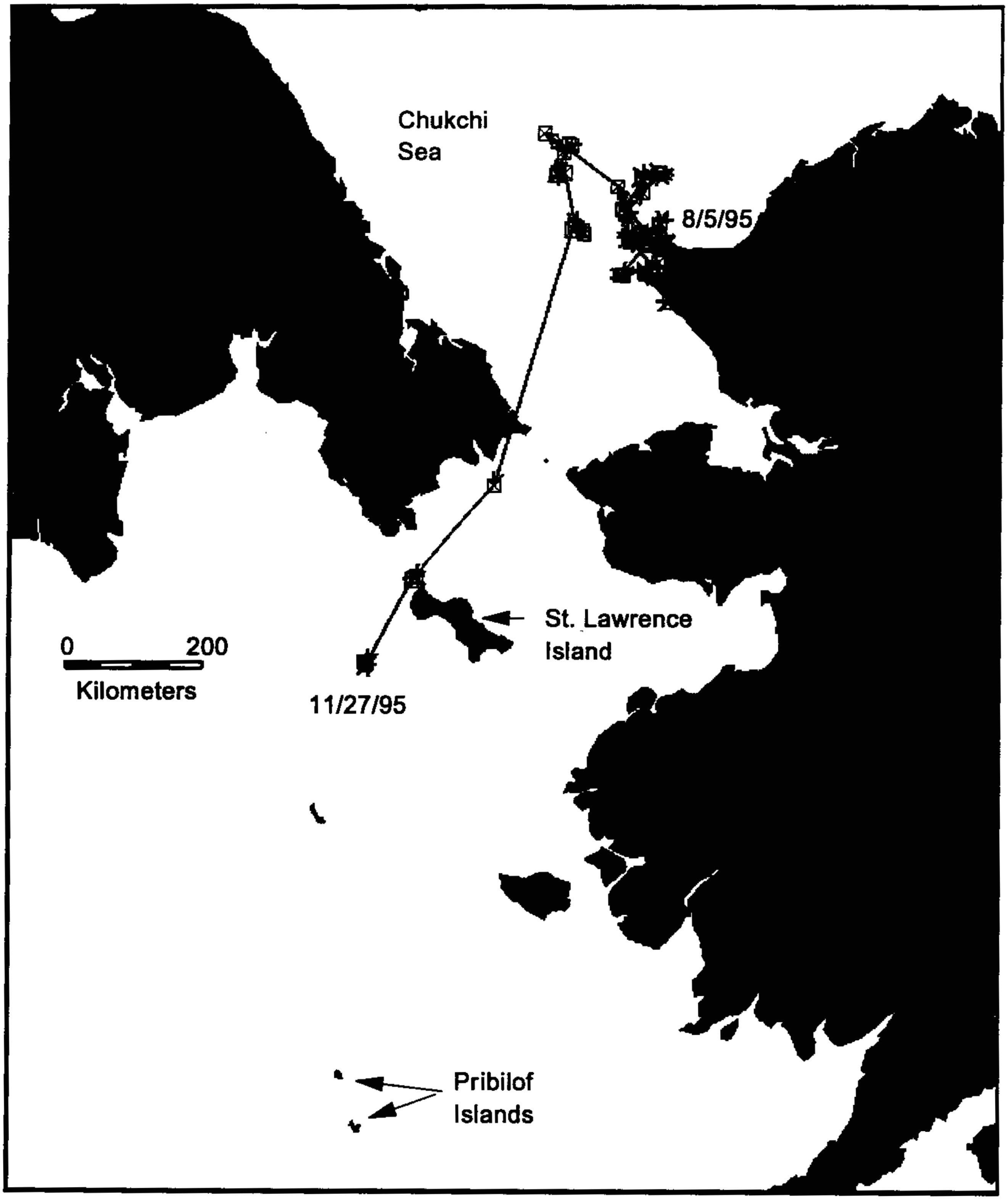


Figure A.39. Breeding-season movements of male common murre 7901 from Cape Thompson.

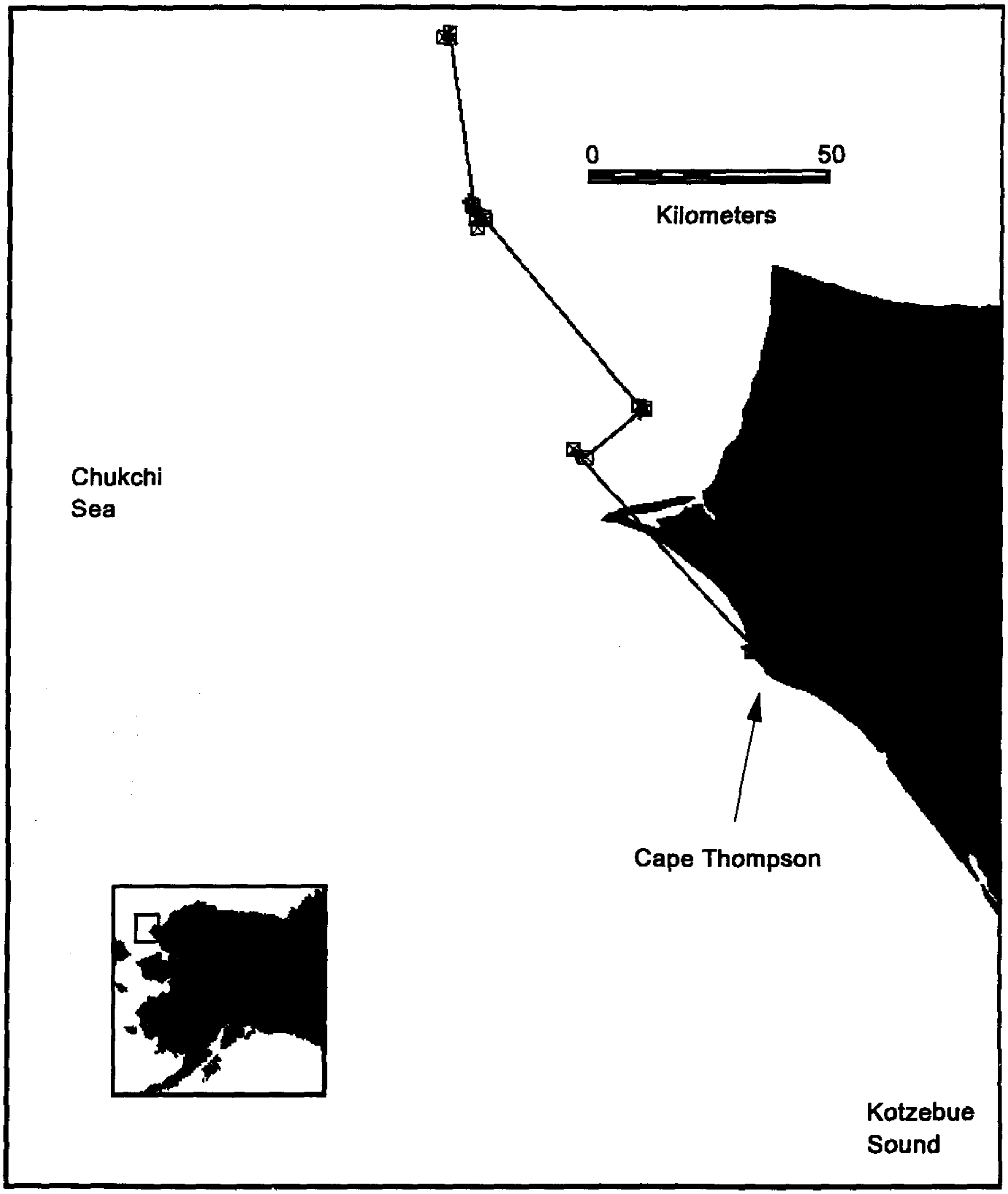


Figure A.40. Track lines of male thick-billed murre 7915 from Cape Thompson. Long-cycle transmitter. Lost contact 29 November 1995, 115 days total.

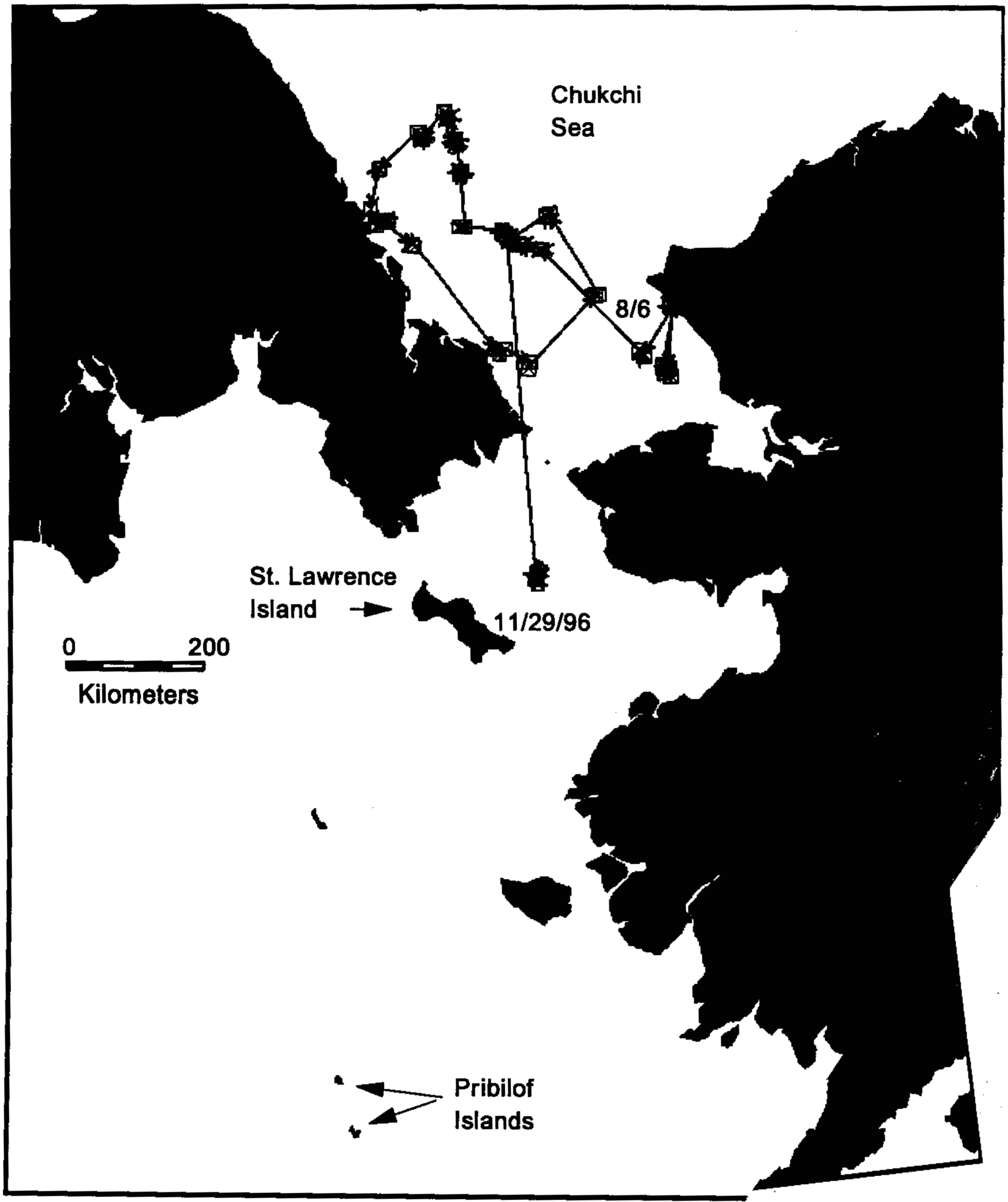


Figure A.41. Breeding-season movements of male thick-billed murre 7915 from Cape Thompson..

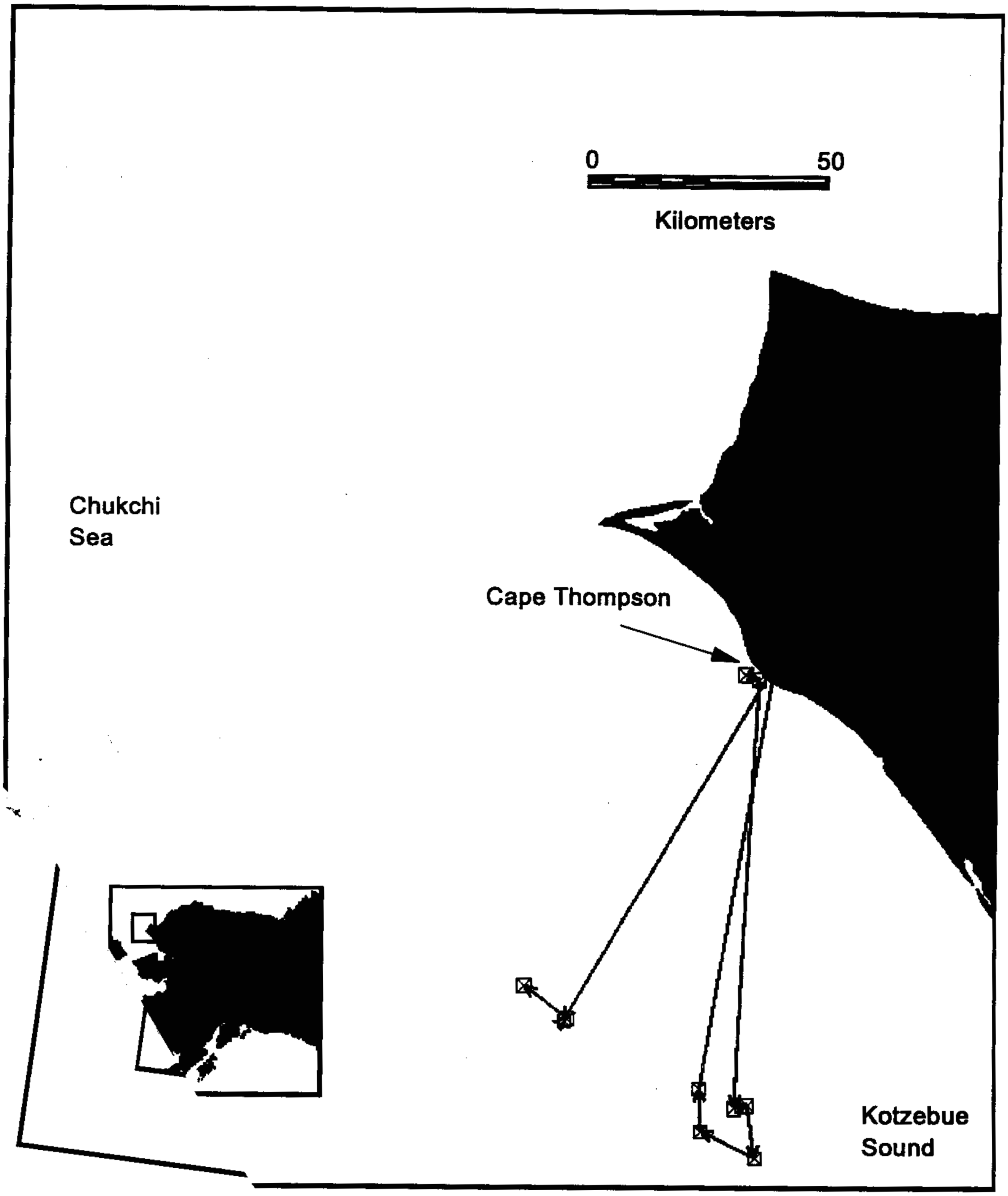


Figure A.42. Track lines of male common murre 7916 from Cape Thompson. Short-cycle transmitter. Lost contact 16 November 1995, 103 days total.

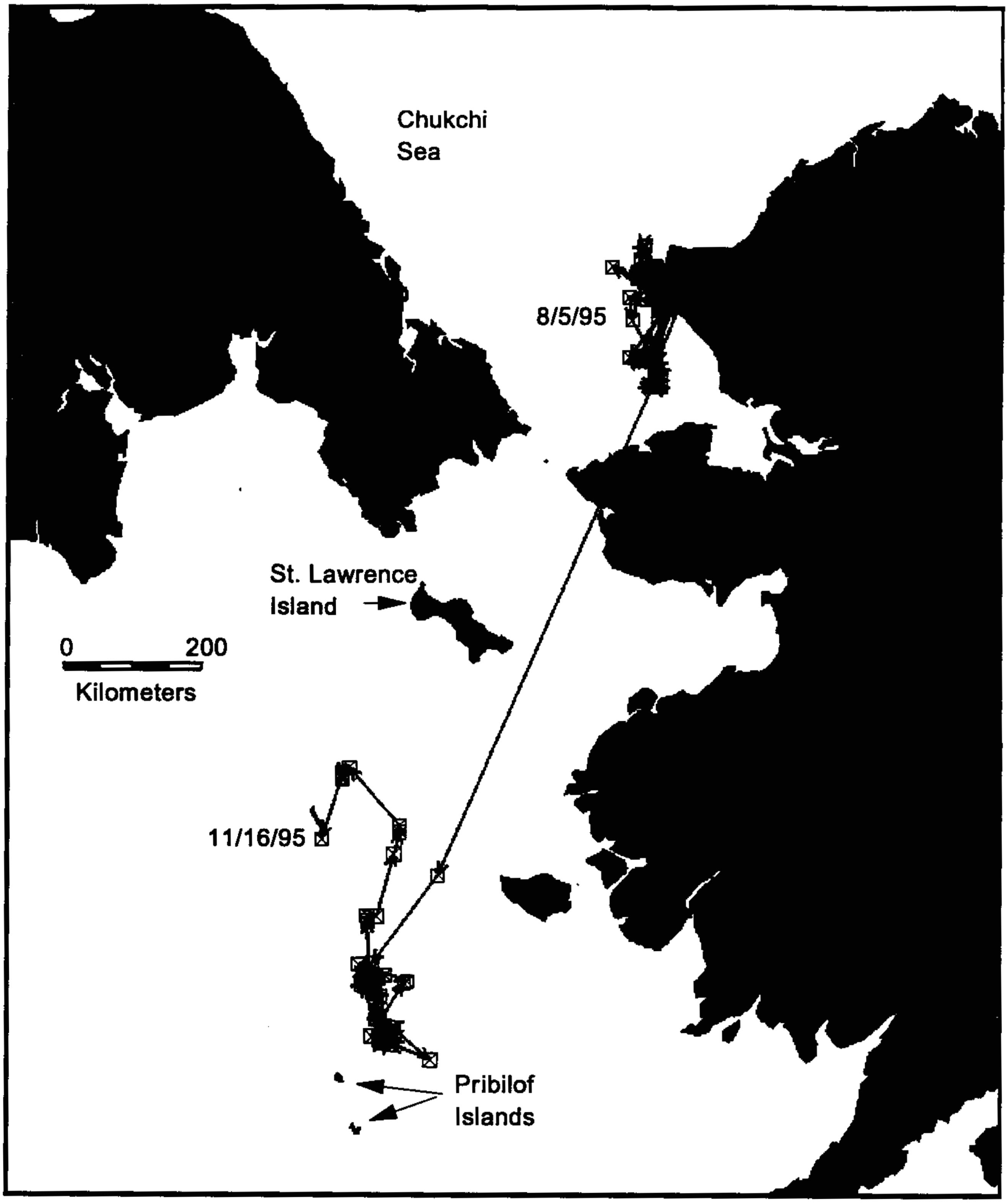


Figure A.43. Breeding-season movements of male common murre 7916 from Cape Thompson.

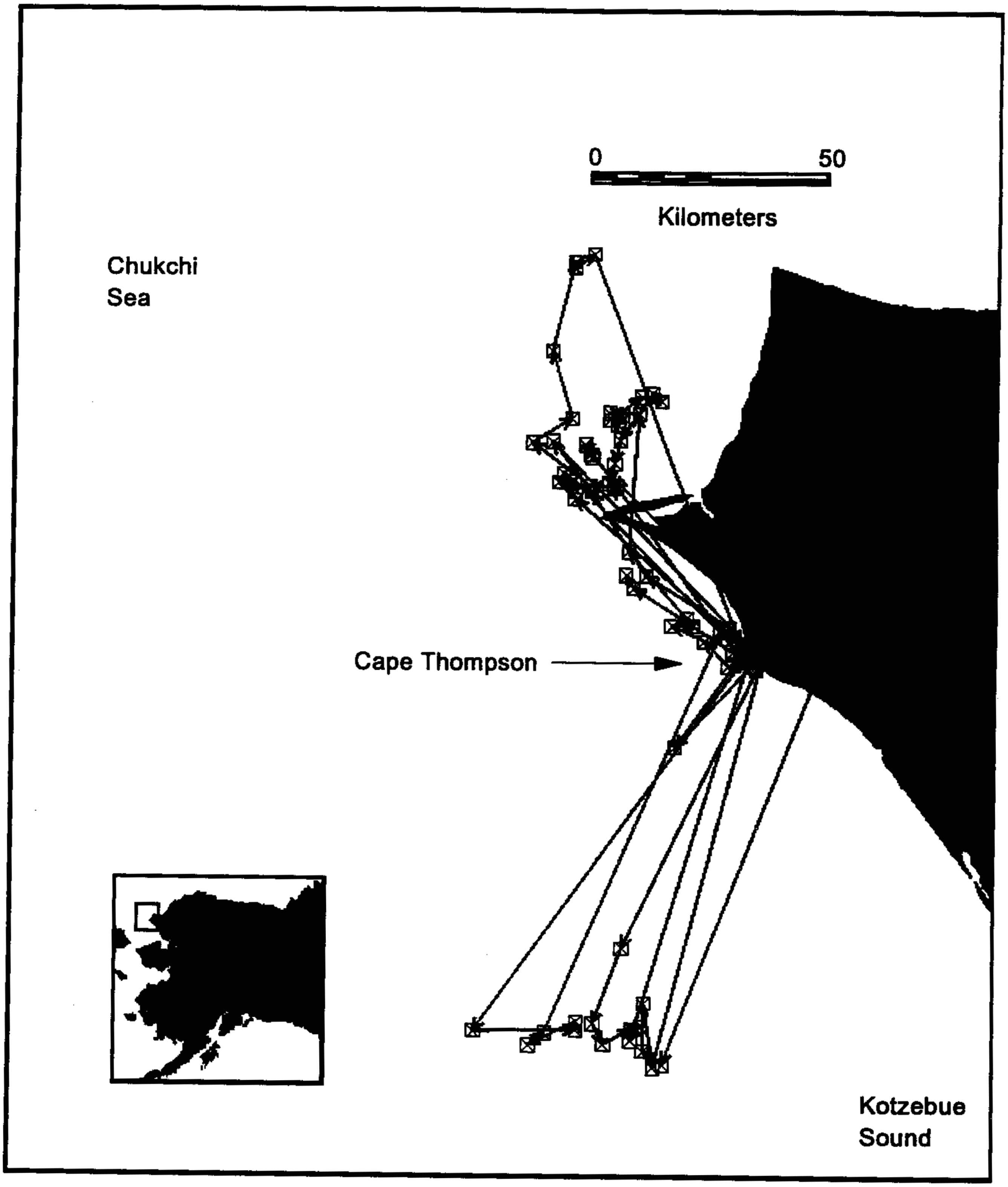


Figure A.44. Track lines of female common murre 20001 from Cape Thompson. Short-cycle transmitter. Lost contact 27 November 1995, 114 days total.

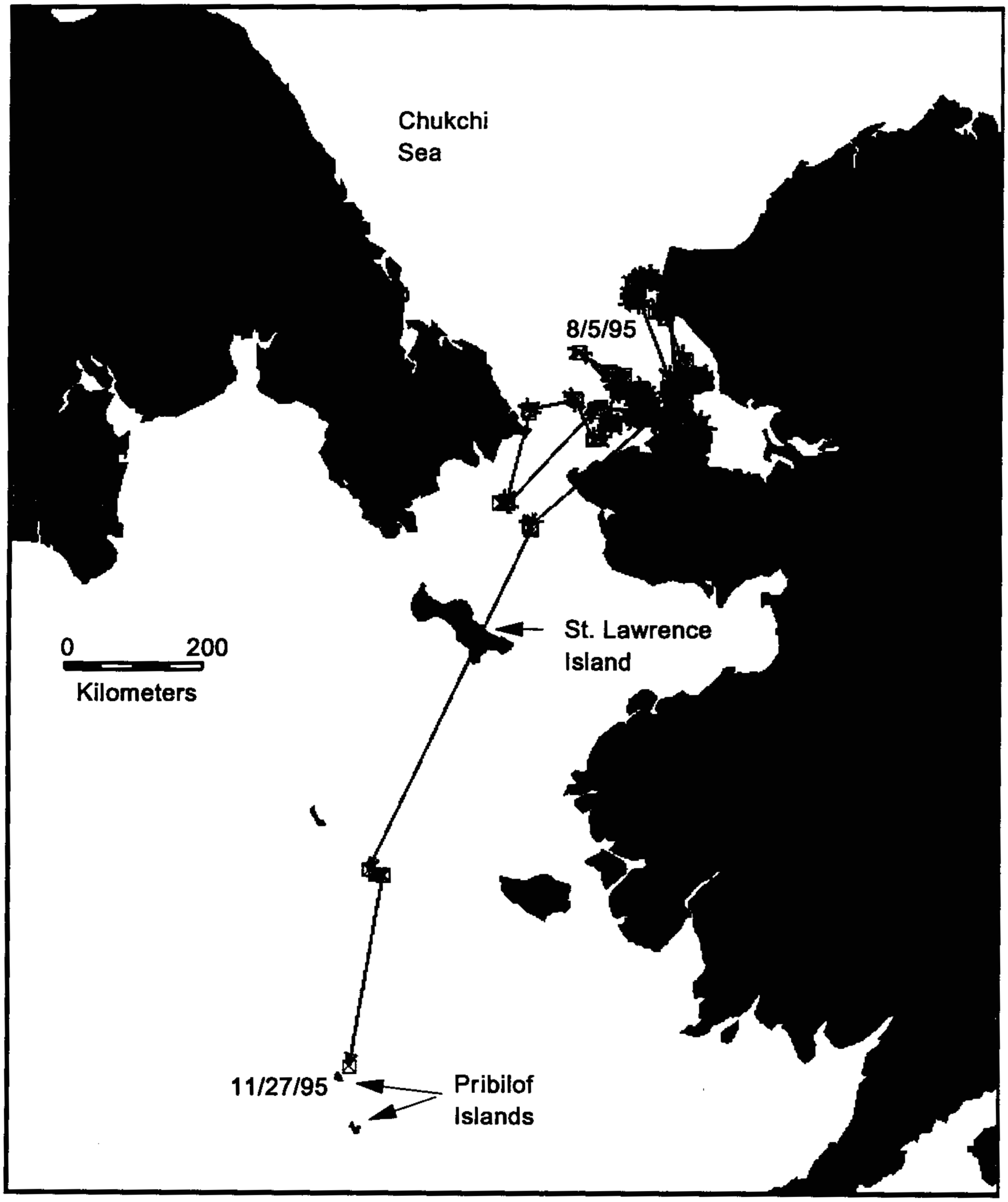


Figure A.45. Breeding-season movements of female common murre 20001 from Cape Thompson.

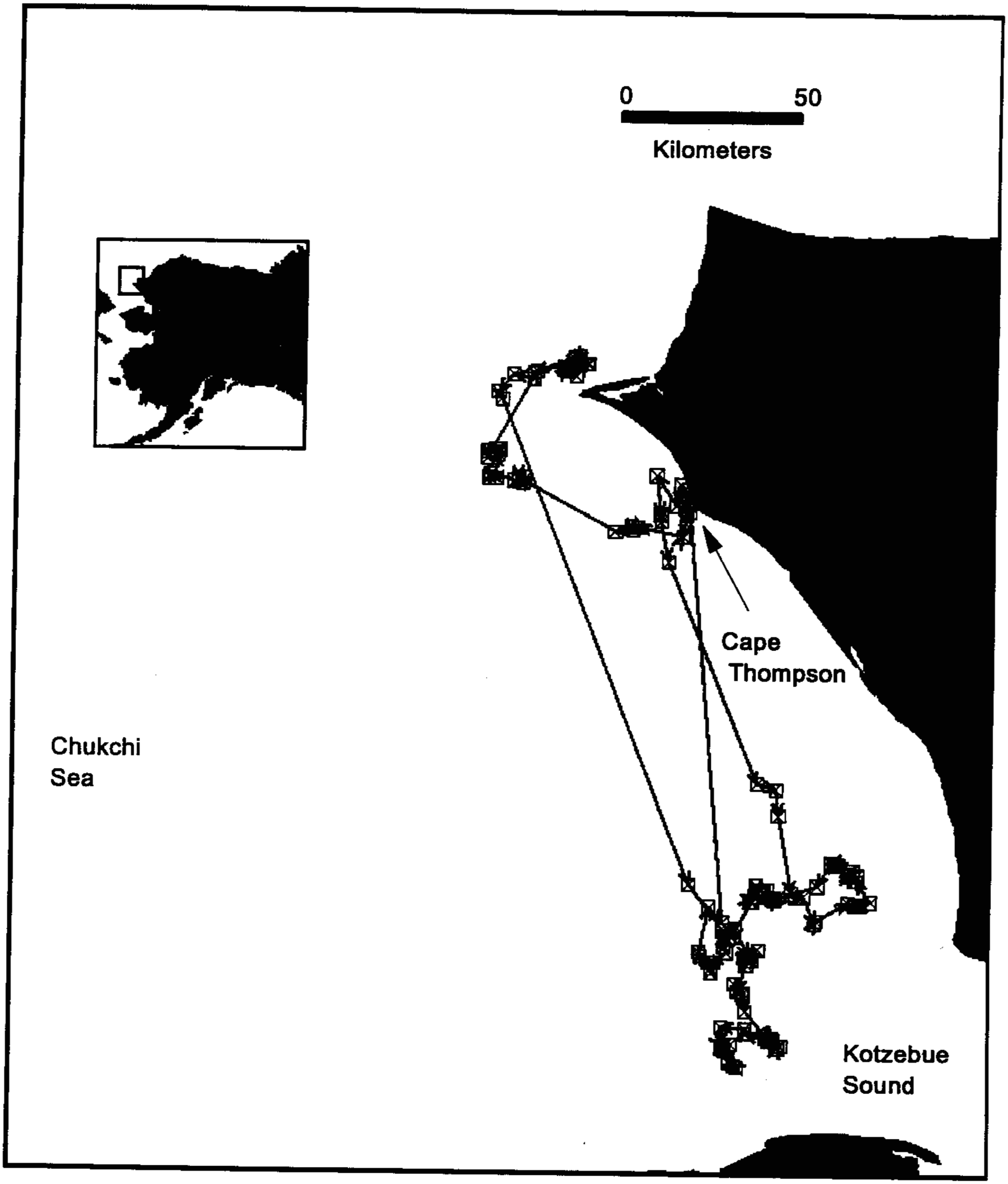


Figure A.46. Track lines of male thick-billed murre 20840 from Cape Thompson. Short-cycle transmitter. Lost contact 23 September 1995, 48 days total. Possibly died.

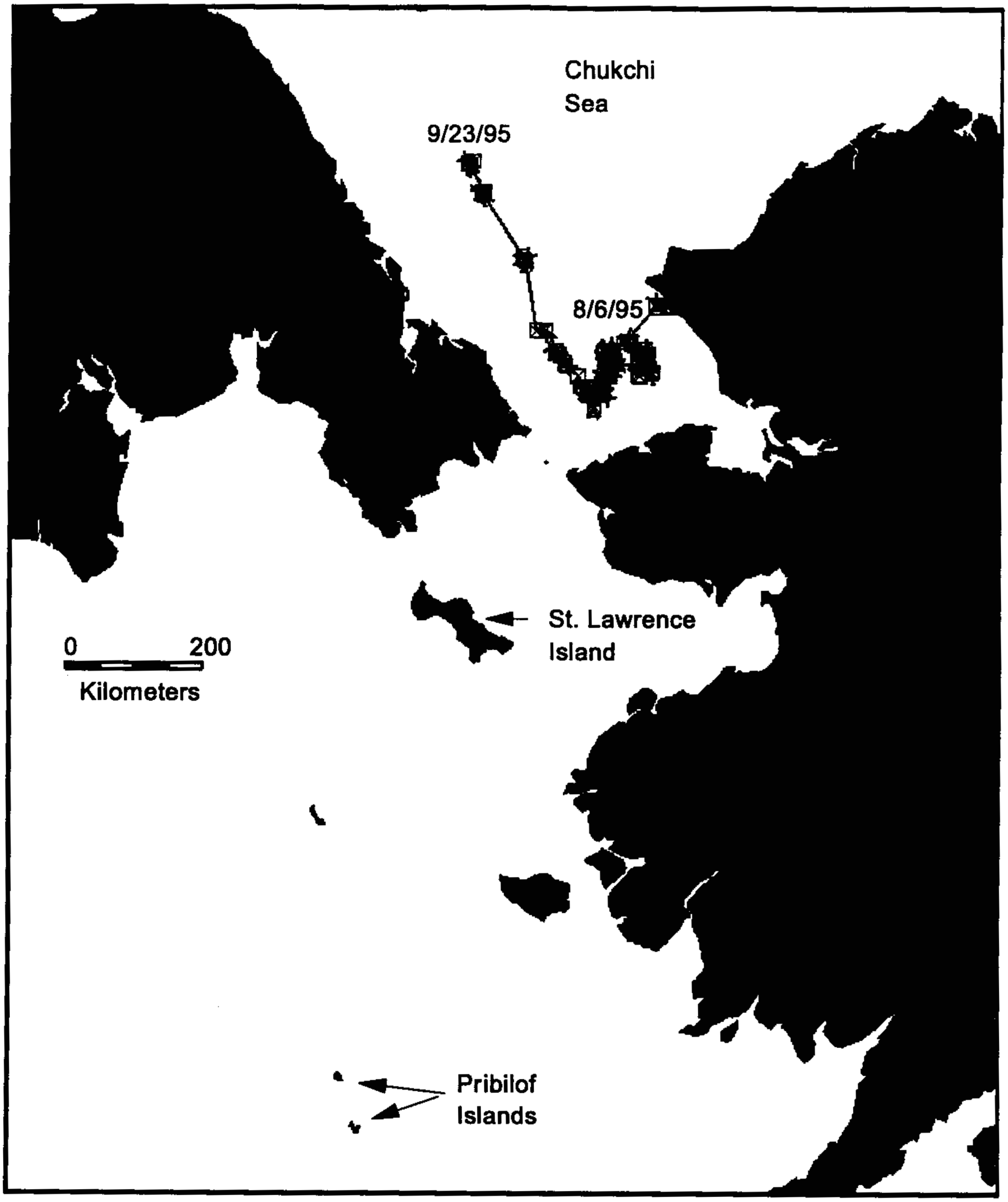


Figure A.47. Breeding-season movements of male thick-billed murre 20840 from Cape Thompson.