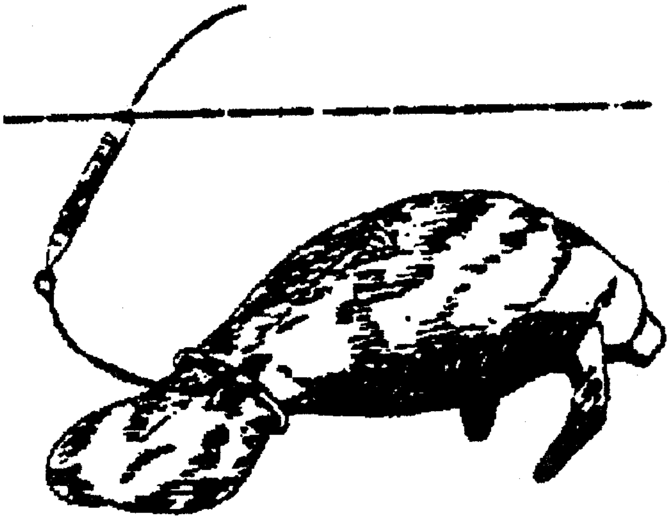
Seasonal Movements, Migratory Behavior, and Site Fidelity of West Indian Manatees along the Atlantic Coast of the United States as Determined by Radio-telemetry

CHARLES J. DEUTSCH
U. S. Geological Survey, Florida Caribbean Science Center, Sirenia Project
and
Florida Cooperative Fish and Wildlife Research Unit,
University of Florida, Department of Wildlife Ecology and Conservation
Gainesville, Florida

JAMES P. REID, ROBERT K. BONDE, DEAN E. EASTON, HOWARD I. KOCHMAN
U. S. Geological Survey, Florida Caribbean Science Center, Sirenia Project
Gainesville, Florida

THOMAS J. O'SHEA
U. S. Geological Survey, Midcontinent Ecological Science Center
Ft. Collins, Colorado



Final Report of the Florida Cooperative Fish and Wildlife Research Unit
under Research Work Order No. 163
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Charles J. Deutsch[1,2], James P. Reid[1], Robert K. Bonde[1], Dean E. Easton[1],
Howard I. Kochman[1], and Thomas J. O'Shea[3]

[1] U.S. Geological Survey, Florida Caribbean Science Center, Sirenia Project, 412 NE 16th Ave.,
Rm. 250, Gainesville, FL 32601

[2] U.S. Geological Survey, Florida Cooperative Fish and Wildlife Research Unit, and University of Florida, Department of Wildlife Ecology and Conservation, P. O. Box 110450,
Gainesville, FL 32611

[3] U.S. Geological Survey, Midcontinent Ecological Science Center, 4512 McMurray Ave.,
Ft. Collins, CO 80525

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U.S. Geological Survey, Sirenia Project, 412 NE 16th Ave., Rm. 250, Gainesville, FL 32601
or
Florida Cooperative Fish and Wildlife Research Unit, P. O. Box 110450, University of Florida, Gainesville, FL 32611

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ABSTRACT

The West Indian manatee (*Trichechus manatus*) is endangered by human activities throughout its range, including the U.S. Atlantic coast where increasing coastal development and manatee deaths from watercraft collisions have been particularly severe. We radio-tagged and tracked 78 manatees along the east coast of Florida and Georgia over a 12-year period (1986-1998). Our goals were to characterize the seasonal movements, migratory behavior, and site fidelity of manatees in this region in order to provide information for the development of effective conservation strategies. Most study animals were tracked remotely with the Argos satellite system, which yielded a mean (SD) of 3.7 (1.6) locations per day. We also tracked manatees in the field an average of 2 days per week using VHF telemetry. The combined data collection effort yielded >93,000 locations over nearly 32,000 tag-days. The median duration of tracking was 8.3 months per individual, but numerous manatees were tracked over multiple years (maximum = 6.8 years) by retagging or replacing tags in the water without recapturing the animal.

Most manatees migrated seasonally over large geographic areas (median = 280 km, maximum = 830 km) between a northerly warm season range and a southerly winter range, but 12% of individuals were resident in a relatively small area (<50 km) year-round. The movements of one adult male spanned >2300 km of coastline between southeastern Florida and Rhode Island. No study animals journeyed to the Gulf coast of Florida. Regions heavily utilized by tagged manatees included: lower (northern) St. Johns River, FL to Brunswick, GA in the warm season; northern Biscayne Bay to Port Everglades, FL in the winter; and central coastal Florida (especially Brevard County) in all seasons. Daily travel rate, defined as the distance between successive mean daily locations, averaged 2.5 km (SD = 1.7 km), but this varied with season, migratory pattern, and sex. Adult males traveled a significantly greater distance per day than did adult females for most of the warm season, which corresponded closely with the principal period of breeding activity, but there was no sex difference during the winter.

The timing of seasonal migrations differed markedly between geographic regions. Most long-distance movements in the southern half of the study area occurred between November and March in response to changing temperatures, whereas most migrations in the northern region took place during the warmer non-winter months. Manatees left their warm season range in Brevard County in response to cold fronts in early winter that dropped water temperatures by an average of 2.0 °C over the 24-hr period preceding departure to a mean of 19 °C. Water temperature at departure from the warm season range varied substantially among individuals (16 - 22 °C) but was not related to body size or female reproductive status. The presence of industrial warm-water effluents permitted many manatees to overwinter north of their historic winter range, and for some migrants this delayed fall migrations and facilitated earlier spring migrations. Southward "fall" and northward "spring" migrations lasted an average of 10 and 15 days at mean rates (SD) of 33.5 (7.6) and 27.3 (10.5) km/day, respectively. The highest documented rate of sustained travel during migration was 87 km/day (3.6 km/hr over 32 hr) during winter. Manatees overwintering in southeastern Florida often traveled north during periods of mild weather in mid-winter—sometimes reaching their warm season ranges—only to

return south again with the next major cold front.

Manatees were consistent in their seasonal movement patterns across years, showing strong fidelity to warm season and winter ranges. Individuals were not nomadic in their movements, usually occupying only 1 or 2 core use areas (as identified by cluster analysis) within a season that encompassed about 90% of daily locations. Site fidelity across years was also strong: the median distance between location clusters within a region from one year to the next was 3.4 and 4.8 km for the winter and warm seasons, respectively. Most manatees with multiple years of tracking data returned faithfully to the same seasonal ranges year after year. Seasonal movements of 4 immature manatees that were tracked with their mothers as dependent calves and then after weaning as independent subadults provided evidence for strong natal philopatry to specific warm season and winter ranges, as well as to migratory patterns. Traditional movement patterns mediated by mother-offspring transfer could maintain the inter-individual variation that we observed in seasonal movement patterns, annual range extent, and migratory behavior (e.g., temperature threshold) across generations. There was striking variation in warm season use of Brevard County waters as a function of an individual's overwintering region and seasonal movement pattern. Manatees overwintering in Brevard County and migrating in spring to Georgia or the St. Johns River preferentially used the northern Indian River when they returned in summer or fall, while those overwintering in southeastern Florida and migrating to Brevard for the warm season typically occupied ranges in the Banana River.

Seasonal movement patterns of manatees along the Atlantic coast were largely driven by seasonal changes in temperature, but seasonal and spatial variation in the abundance and quality of forage was probably also an important factor. Individuals generally occupied a few, relatively small seasonal ranges that were linked by lengthy travel corridors used briefly during migrations. The wide-ranging movements revealed in this study indicate that manatees living along the Atlantic coast (including the lower St. Johns River) need to be managed as a single unit; loss of habitat or elevation of mortality in one locale, for example, is likely to have repercussions for the entire subpopulation. The existence of traditional migrations and of strong philopatry to specific areas must be considered in the design of any protected area networks for manatees along the east coast. Despite these "conservative" behavioral traits, individual manatees showed variability in the timing of migrations, in time spent in different regions within a winter, and in other movement parameters. This behavioral flexibility has permitted Florida manatees to exploit human habitat alterations to their advantage; for example, by using industrial thermal outfalls to extend their stay in northerly regions. Recovery of this endangered species will depend on our ability to reduce human-caused mortality and protect key manatee habitats in waterways essential to manatees (e.g., northern Brevard County), and to keep the pace of habitat alteration within the time frame of the manatee's ability to adapt.

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INTRODUCTION

Sirenians (manatees and dugongs) are unique among completely aquatic mammals in having an herbivorous diet. Reliance on an abundant but low-energy food source is thought to have led to the evolution of a unique suite of morphological, physiological, ecological, behavioral, and life-history traits that characterize this order of mammals (O'Shea and Reep 1990). Chief among these features are a remarkably low mass-specific metabolic rate and high thermoneutral zone (Gallivan and Best 1980, Gallivan et al. 1983, Irvine 1983), which limit the extant species to tropical, subtropical, and warm temperate waters (Reynolds and Odell 1991). The West Indian manatee (*Trichechus manatus*) is distributed in coastal, estuarine, and riverine systems of the southeastern United States, the Greater Antilles, eastern Mexico and Central America, and south to northeastern Brazil (Lefebvre et al. 1989). The Florida subspecies (*T. manatus latirostris*) occupies the northern end of the species' range; its winter distribution is restricted to peninsular Florida, where most manatees aggregate around warm-water sources (natural springs, industrial effluents, or thermally buffered waterways) during cold weather periods (Hartman 1974, 1979; Irvine and Campbell 1978, Beeler and O'Shea 1988). During the warm season, manatees disperse along the Florida and Georgia coast and small numbers move into neighboring states (Rathbun et al. 1982, Powell and Rathbun 1984).

The West Indian manatee is endangered by human activities throughout its range (Lefebvre et al. 1989, Marsh and Lefebvre 1994). In Florida manatees face anthropogenic problems of 2 types: direct threats, such as strikes by watercraft, crushing in water control structures, and entanglement in fishing line, that result in death or injury (O'Shea et al. 1985*a*, Beck and Barros 1991, Ackerman et al. 1995, Wright et al. 1995); and threats to manatee habitat, including propeller scarring of seagrass beds and degradation of water quality due to coastal development, with resulting declines in the abundance of submerged aquatic plants upon which manatees forage (Fletcher and Fletcher 1995, Sargent et al. 1995, see Fonseca et al. 1998 for review). Demographic characteristics of the manatee subpopulation living along Florida's densely populated Atlantic coast indicate cause for concern: a relatively low and variable adult survival rate (Langtimm et al. 1998), a possible decline in the number and proportion of calves counted during aerial surveys at winter aggregation sites (Reynolds and Wilcox 1994), and slow or stagnant population growth (Eberhardt and O'Shea 1995, Craig et al. 1997, Eberhardt et al. 1999). These findings are consistent with analyses of statewide carcass data indicating that the vast majority of deaths from boat collisions have occurred on the east coast (O'Shea et al. 1985*a*, Ackerman et al. 1995), and that 55% of adult manatee deaths in this region were directly attributable to human causes (Florida Fish and Wildlife Conservation Commission, unpublished data, 1989-98). Given that population growth of manatees and other large, long-lived mammals is most sensitive to changes in adult survivorship (Goodman 1981, Eberhardt and O'Shea 1995), the importance of implementing effective conservation measures to reduce human-caused mortality of adult manatees is clear (Marmontel et al. 1997, Langtimm et al. 1998). The need for scientific information upon which managers could base habitat protection strategies, develop boat speed zones, and take other conservation actions to promote recovery of the manatee population (U.S. Fish and Wildlife Service 1996) provided the impetus for this study.

Seasonal shifts in the distribution and relative abundance of Florida manatees along the Atlantic coast have been documented from anecdotal records and sightings (Moore 1951*a*, Hartman 1974, Rathbun et al. 1982) and aerial surveys (Rose and McCutcheon 1980, Shane 1983, Kinnaird 1985, Provancha and Provancha 1988). These studies suggested the existence of a seasonal migratory pattern, with manatees moving south for the winter and returning north for the non-winter months. Resightings of distinctively scarred manatees through the use of photo-identification techniques confirmed that some individuals make long-distance migratory journeys along the Atlantic coast (Shane 1983, Reid et al. 1991). Resighting data on both Atlantic and Gulf coasts have also shown that manatees repeatedly visit the same warm-water aggregation sites within and across winters (Moore 1956, Rathbun et al. 1990, Reid et al. 1991, O'Shea and Hartley 1995), but relatively little research has addressed fidelity to summer ranges (Bengtson 1981, Shane 1983, Reid et al. 1991). These approaches, however, provided gross and incomplete sketches of manatee movement patterns at the individual level.

We employed field-monitored and satellite-based radio-telemetry to investigate questions about seasonal movement patterns, migratory behavior, and site fidelity of manatees along the Atlantic coast. Relatively little was known, for example, of the typical extent of an individual's year-round range and how frequently manatees undertake long-distance travels. We document these aspects of movement behavior, along with areas of high utilization by tagged manatees, variation in seasonal movement patterns among individuals, and degree of interchange with adjacent subpopulations. We describe migratory behavior of manatees in quantitative terms, including information on seasonal timing, trip distance and duration, rate of travel, stopover sites (number and duration), and travel routes. Florida manatees begin arriving at warm-water sources in autumn and winter once ambient water temperatures drop to about 20 - 22 °C in order to avoid cold-related energetic demands and stress (Hartman 1979, Bengtson 1981, Powell 1981, Powell and Waldron 1981, Irvine 1983, Shane 1984). Such a temperature threshold, however, should vary with individual attributes that affect thermoregulatory ability, such as size and nutritional condition. Smaller manatees have a less favorable surface area:volume ratio and are apparently incapable of elevating resting metabolic rate in cold waters (Worthy 1998); furthermore, subadults suffer higher winter mortality from cold stress (O'Shea et al. 1985). We test hypotheses that the ambient water temperature at which manatees move toward warmer waters (1) is inversely correlated with body size, and (2) is higher for adult females with calves than for females without calves. The small size of the calf may make it susceptible to cold stress, and Rathbun et al. (1990) found that cow-calf pairs arrived earlier at warm-water springs than single animals. We also test the hypothesis that the availability and use of power plant thermal outfalls alters migratory timing by allowing individuals to remain in the region of their warm season range for longer periods.

Limited information exists on manatee movements and spatial use patterns during the warm season. Are most manatees nomadic during the warm months of the year, as suggested by Hartman (1979:30), moving from one area to another in search of nutritious seagrass meadows or mates, or do they show fidelity to particular ranges? We investigate the degree of consistency of individuals to migratory patterns across years, and quantify within-season and interannual site fidelity to seasonal ranges. The Florida manatee's mating behavior has been described as "promiscuous" (Hartman 1979), with adult males ranging widely in search of estrous females during the warm season (Bengtson 1981). We test the hypotheses that adult males exhibit higher daily travel rates and lower site fidelity than adult females during the main breeding period, which is diffusely seasonal and roughly corresponds with the months of March through September (Odell et al. 1981, Kinnaird 1985, Ackerman et al. 1995, Hernandez et al. 1995, Marmontel 1995, O'Shea and Hartley 1995, Rathbun et al. 1995, Reid et al. 1995).

Radio-telemetry has been used successfully to track manatees in other regions of Florida (Bengtson 1981, Powell and Rathbun 1984, Lefebvre and Frohlich 1986, Rathbun et al. 1990) and Georgia (Zoodsma 1991), but these early studies relied primarily on conventional VHF (very high frequency) transmitters and were limited in their spatial and temporal scope (see O'Shea and Kochman 1990 for overview). Typically, manatees were tagged at a thermal refuge in the winter and then tracked until the tag detached, usually sometime between the spring and fall of the same year. Our study differs from previous research on manatee movements in several important respects. First, we relied heavily on data from satellite-monitored transmitters using the Argos system, which yielded a substantially greater number of locations and more systematic collection of data compared to previous VHF tracking studies (Deutsch et al. 1998). Second, our tagging and tracking efforts encompassed the entire range of manatees along the Atlantic coast, from the Florida Keys to South Carolina, so inferences were not limited to a small geographic area. Third, we often used freshwater to lure manatees to capture sites, which allowed tagging in all months of the year; this provided more information about summer movement patterns than had previous studies which emphasized capture and tracking at winter aggregations. Finally, the study spanned a decade, and success in retagging animals and in replacing transmitters allowed long-term tracking of many individuals. This provided the opportunity to investigate variation in seasonal movements, migratory behavior, and site fidelity across years for individual manatees.

STUDY AREA

The study area encompassed the eastern coasts of Florida, Georgia, and South Carolina, including inland waterways such as the St. Johns River (Fig. 1). Manatees inhabited the relatively narrow band of water that lies between the barrier beaches and the mainland, occasionally venturing into the ocean close to shore. Between Miami and Fernandina Beach, Florida, 19 inlets provided manatees with corridors between the intracoastal waters and the Atlantic Ocean; the distance between adjacent inlets averaged 32 km (SD = 24 km) and varied from 3 to 88 km. Habitats used by manatees along this 900-km stretch of coastline varied widely and included estuaries, lagoons, rivers and creeks, shallow bays and sounds, and ocean inlets. Salinities in most areas were brackish, but ranged from completely fresh to completely marine. The predominant communities of aquatic vegetation also varied geographically and with salinity: seagrass meadows and mangrove swamps in brackish and marine waters along the southern half of peninsular Florida; salt marshes in northeastern Florida and Georgia; benthic macroalgae in estuarine and marine habitats; and a variety of submerged, floating, and emergent vegetation in freshwater rivers, canals, and streams throughout the region. The depth of most intracoastal waters rarely exceeded 4 m at mean low water, except in Georgia and northern Florida where some rivers and tidal channels were deeper than 10 m. Tidal ranges were typically less than 0.75 m along the central and southeastern Florida coast, but averaged 1.8 to 2.5 m in Georgia and northern Florida. Water levels in inland waterways—especially the St. Johns, Banana, and Indian Rivers—were typically driven more by winds and local precipitation than by tidal influences..

Although none of the study area could be considered pristine, the degree of coastal development ranged from the relatively undisturbed coastal marshes of Georgia to the highly urbanized environments of southeastern Florida. Manatees were attracted to a variety of human-created features, including residential canal systems, marina basins, warm-water industrial discharges (in winter, Fig. 1), and freshwater sewage effluents (in brackish and marine systems). The presence of artificial thermal sources has permitted manatees to overwinter north of their historic winter range, which is generally thought to have been south of the Sebastian River (Y = 3080, Fig. 1) on the Atlantic coast (Moore 1951*a*).

The study area was divided into 3 regions for some analyses, with the north-central and central-south borders set at Flagler Beach and St. Lucie, Florida, respectively (Fig. 1). In addition to the geographic variation in habitats, aquatic vegetation, and human activities mentioned above, there are marked differences among regions in coastal physiography. The intracoastal waterways are generally quite narrow in northern Florida (north of the Halifax River) and provide little suitable manatee habitat south of the St. Johns River; further north the coastal zone is dissected with numerous tidal creeks and rivers that provide manatees access to abundant salt marshes at high tide. The intracoastal waterways are widest and provide the most extensive manatee habitat in the central region, which includes the Mosquito and Indian River Lagoons. The waterways narrow again in the southern region (south of St. Lucie inlet) until one reaches the open waters of Biscayne Bay (Fig. 1).

METHODS

Radio-tag Deployment and Tracking

We radio-tagged and tracked 78 manatees along the Atlantic coast over a 12-year period between 8 May 1986 and 31 May 1998 (Appendix A). Tagging occurred throughout the study area, from the Florida Keys to Brunswick, Georgia (Fig. 1). About half of the animals (N = 41, 53%) were initially tagged in the Indian River lagoon system along the central Florida coast; most (N = 37) of these tagging events took place in Brevard County. The rest were tagged at numerous sites in southeastern Florida (N = 12, 15%) and in northeastern Florida and southern Georgia (N = 25, 32%) (Fig. 1). Manatees were tagged in all months of the year, but more were tagged in the spring (Mar-May, N = 36, 46%) and fall (Sep-Nov, N = 22, 28%) than in the summer (Jun-Aug, N = 10, 13%) and winter (Dec-Feb, N = 10, 13%).

The sample of radio-tagged manatees included 46 adult females, 21 adult males, 5 subadult females, and 6 subadult males; 4 of the subadults were tagged as large dependent calves and then tracked after weaning. Individuals were considered adults if they were: (1) at least 265 cm standard length, based on size-specific reproduction data (Marmontel 1993); (2) known from photo-identification studies (Beck and Reid 1995) to be at least 5 years old; or (3) females observed with a nursing calf. The mean length at tagging was 298 cm (SD = 24, range = 260 - 350 cm) for adults and 244 cm (SD = 17, range = 210 - 260 cm) for subadults and calves.

Capture Methods

Most study animals (N = 48) were captured alongshore and restrained with nets, using standard shore-based capture techniques for manatees (Reid et al. 1995, Deutsch et al. 1998). About half of these captures (N = 23) were of animals lured to freshwater bait stations in Brevard County; 22 captures took place in the warm-water effluents of pulp mills in Fernandina Beach, Florida and Brunswick, Georgia; and 3 involved rescues and on-site releases of manatees trapped in isolated water bodies. No adverse effects of capture and handling on the animals were observed (O'Shea et al. 1985*b*). We were able to radio-tag 17 other free-ranging manatees without capture or restraint by snorkeling and attaching the belt and tag assembly underwater (Rathbun et al. 1990).

In addition to the 65 manatees tagged in the wild, 13 individuals (11 adults and 1 mother-calf pair) that had been rescued and rehabilitated in oceanaria for short periods (median = 3.6 mos., range = 0.2 - 15.5 mos.) were radio-tagged at release. Seven of these manatees were released in the general region where they had been captured; 6 were released at least 100 km from their rescue site in order to remove them from a threat (e.g., power plant intake entrapment, cold water) or to place them where they were expected to be at that time of year, sometimes based on prior sightings of the individuals using photo-identification. The post-release monitoring of captive-born and captive-reared manatees are not considered in this paper, with 1 exception. One of the wild, net-captured adult females (TNC-13) was identified by a passive integrated transponder (PIT) implant (Wright et al. 1998) as having been a former captive. She had been rescued as a 205-cm calf, rehabilitated in captivity for 27 mos., and then released in the Banana River, Brevard County as a large subadult (264 cm) without a radio-tag; 3 years later she was captured and tagged in northeastern Florida. Her migratory movements and use of manatee aggregation areas were indicative of successful adaptation to the wild.

Radio-tag and Attachment System

The tag assembly consisted of a buoyant, cylindrical housing containing the transmitter(s) that was attached with a flexible, nylon rod to a padded belt which fit snugly around the manatee's peduncle at the base of its tail (Reid et al. 1995). The 1.3 - 2.0 m-long tether permitted the tag to float at the surface and transmit in air while the animal was submerged at depths of up to 2 m. This enabled us to track manatees in brackish and saltwater environments, which would otherwise have been extremely difficult due to the attenuation of radio signals by saltwater. Other tracking methods (e.g., sonic) and attachment alternatives have not proved suitable for effectively monitoring manatees (Irvine and Scott 1984). A weak link was built into the base of the tether to allow the manatee to free itself if the tag became entangled. Corrodible nuts and bolts were used in the belt so that the entire tag assembly would fall off after a period of 2 to 4 years.

Two types of radio-tags were used in this study. The smaller tag design (6 cm diameter x 33 cm long housing) housed a VHF (very high frequency) radio-transmitter that emitted pulsed signals at specific frequencies in the 164-MHz band. The most frequently used tag type (9 cm diameter x 39 cm long housing) contained a UHF (ultra-high frequency, 401.650 MHz) transmitter, referred to as a platform transmitter terminal (PTT), that was monitored by the Argos space-based data collection and location processing service. This tag also incorporated a VHF transmitter and an ultrasonic acoustic transmitter (72 - 79 kHz) to facilitate tracking in the field. Battery life was approximately 2 years for VHF transmitters and 6.5 to 9 months for PTTs. An ultrasonic beacon was also built into the belt assembly in order to localize and identify belted manatees that had lost their tags. Additional technical information on the radio-transmitters and the tag attachment system used in this study can be found in Rathbun et al. (1987), Reid and O'Shea (1989), Reid et al. (1995), and Deutsch et al. (1998).

Retagging Methods

Tag detachments at the designed weak link were common (Reid et al. 1995), often leading to interruptions in tracking bouts. Most study animals were radio-tagged more than once (median = 3.0, maximum = 43 tagging bouts), typically to replace a tag that had reached the end of its battery life, had malfunctioned, had been struck by a boat propeller, or had detached. Only 11 (3.0 %) of 363 retagging events required recapture of the animal, sometimes to replace a worn belt. In the vast majority of cases, manatees were retagged by researchers snorkeling quietly up to the animal and attaching a new radio-tag and tether to the peduncle belt (Reid et al. 1995). The median duration of continuous bouts of tracking was 95 days (maximum = 3.6 years) in this study.

Radio-tracking Methods

Standard radio-tracking methods (Kenward 1987) were used to home in on VHF signals in the field at a distance of up to 15 km from shore or boat and up to 50 km from aircraft.

Directional hydrophones were used, as needed, at close range (< 400 m) to detect signals from ultrasonic transmitters. Manatees carrying VHF tags were located an average of 3 days per week, while those with PTT tags were located in the field an average of once per week. Most VHF-determined locations (73.4%) were based on visual observation of the tagged manatee; non-visual locations were determined by triangulation (8.2%) or by delineating the general area the manatee was in (18.4%). Field observations provided information on manatee activity, reproductive status, tag condition, and other variables (Deutsch et al. 1998). Over 1000 sightings of tagged manatees by the public were verified, identified to individuals, and used to supplement the dedicated field observations. Locations were plotted on maps in the field and later digitized on U. S. Geological Survey quadrangle maps (1:24,000 scale) for entry into a geographic information system (GIS).

The Argos satellite system (Service Argos 1996) provided a means of determining the locations of tagged manatees, regardless of weather conditions or time of day. The system is comprised of UHF receivers onboard 2 near-polar-orbiting NOAA weather satellites that receive transmissions from PTTs within their field of view; PTT locations are calculated from the Doppler shift in the carrier frequency as the satellite passes over the transmitter. Information is relayed to processing centers on Earth and made available to users via telephone links to personal computers within a few hours. In addition to locations, the PTT transmitted a variety of sensor data, included the temperature of the tag at the time of transmission. Data received from Service Argos on monthly diskettes were used to develop the manatee PTT database. The manatee PTTs were programmed to transmit 8 hr per day, over 4 2-hr time periods that corresponded to the peak periods of satellite overpasses in Florida. Excellent descriptions on the use of Argos for tracking wildlife can be found in Fancy et al. (1988) and Harris et al. (1990); Deutsch et al. (1998) provide details on its application for tracking manatees.

Argos assigned a location class (LC) code to each record that denoted the relative accuracy of the location fix. According to Service Argos (1996), 68% of locations should lie within the following distances from the actual latitude and longitude of the PTT: LC3, 150 m; LC2, 350 m; and LC1, 1000 m. Locations with poorer accuracy (> 1000 m) were assigned LC0 or, starting in June 1994, LCA or LCB. Field experiments have shown that locational error is somewhat greater than expected and that latitudinal error is less than longitudinal error (Keating et al. 1991, Deutsch et al. 1997).

Water Temperature Recording

Automatic water temperature recording stations were maintained at sites in the Banana Creek and the northern Banana River of Brevard County, Florida from February 1988 through May 1998; units were anchored at a depth of about 1 m. These instruments (Tempmentor RTM 2000, Ryan Instruments, Richmond, WA; Stowaway and Tidbit, Onset Computer Co., Pocasset, MA) stored electronic records of hourly temperatures over several months and were periodically downloaded to computers. The manufacturer's stated accuracy was ± 0.2 °C. Temperature differences between these sites were minor (mean difference in mean daily temperatures = 0.2 °C, SD = 0.6 °C); the data were probably representative of temperatures of other shallow-water areas in the region. Temperatures were recorded weekly in the lower St. Johns River at Jacksonville from November 1994 through October 1998 at 0.7 m above the substrate (Jacksonville University, unpublished data).

Data Processing and Analysis

In addition to the VHF (field) and PTT (satellite) telemetry databases of locations and associated information, 2 other databases were developed: an identity database stored data on the attributes (e.g., sex, size) of tagged manatees; and a tagging history database provided information on all tagging and retagging events for each individual (Deutsch 1996). Because tags were frequently redeployed on different manatees, the latter database was necessary to assign a given Argos record to the correct manatee and to filter out records from non-deployed or detached tags. Database management and statistical analyses were accomplished with SAS for Windows v. 6.12 (SAS Institute, Inc., Cary, NC). Development and GIS analysis of spatially referenced databases were done using ARC/INFO and ArcView software (Environmental Systems Research Institute, Inc., Redlands, CA). Geographic coordinates of manatee locations and study area features were converted to the Universal Transverse Mercator (UTM) coordinate system (zone 17 North) and the North American Datum of 1983 (NAD-83).

Censoring Criteria

The telemetry databases were subjected to a series of manual and automated error-scanning routines to eliminate duplicates, flag locational outliers, and correct other types of errors (Deutsch 1996). Outliers were identified as those lying outside of a series of latitude-longitude windows defining the study region. These putative outliers were checked against temporally adjacent Argos records and field sightings to determine whether the locations were plausible. The combined PTT (LC1-3 only) and VHF databases were also passed through a movement rate filter to flag unrealistic travel rates between consecutive locations. Rates greater than 2.6 km/hr (2.0% of 77,328 records for all time intervals) based on Euclidean distance were inspected using the ArcView Tracking Analyst extension; most rates greater than 3.6 km/hr were generated either by inaccurate Argos locations that were then classified as outliers or by incorrect field sightings that were then corrected or deleted. Application of the outlier windows and the movement rate filter resulted in the elimination of 1.7% of Argos records from the database, as follows: 6.4% LC0/A/B, 2.4% LC1, 0.1% LC2, and 0.01% LC3. Argos locations with poor precision (LC0/A/B) were excluded from most analyses; they were sometimes useful in determining the timing of long-distance moves, because higher-quality locations were less frequent during the periods of prolonged tag submergence associated with rapid travel (Deutsch et al. 1998).

The databases were censored prior to certain analyses to exclude data from tagged manatees with insufficient tracking histories. For analysis of distribution, classification of seasonal movement patterns, and calculations of maximum range and of distance between warm season and winter ranges, the following censoring criteria were established: the animal must have been tracked for at least 90 days, of which 30 days must have occurred during the winter season (Dec. - Feb.) and 30 days during the warm season (Apr. - Oct.). March and November were transitional months, in which temperatures could be quite mild or could drop precipitously upon the passage of strong cold fronts.

Distribution and Range

The distribution of locations for individual animals was analyzed after a four-step process of data aggregation. First, the Argos and VHF databases were merged, excluding non-guaranteed Argos locations. Second, only 1 record was kept for an individual when there were multiple locations within 2 hr of each other. A location was chosen based upon the following order of preference: Visual observation, LC3, LC2, LC1, triangulation, and general area. Third, a mean location per day was calculated for each individual from the X-Y coordinates of the selected locations for each day. Finally, the number of days that a manatee was tracked in each 25-km section of coastline (based on daily mean Y coordinates) between the Florida Keys and southern South Carolina was computed (Fig. 2). Frequencies were adjusted for animals tracked over 365 days, so that the numbers represent the average number of days tracked in each 25-km area per year. Mean daily locations in the lower St. Johns River (Fig. 1)—south of the Trout River mouth where the St. Johns River bends sharply south (30° 23.4' N, 81° 37.8' W)—were tallied and displayed separately from records which shared the same Y coordinates but were located along the coast.

The extent of a tagged manatee's range was quantified in 2 ways. "Annual range" denoted the average distance between seasonal ranges; it was defined as the greatest distance between the center of a warm season location cluster (see below under Site Fidelity analyses) and the most distant mean daily location in winter. In most cases, this measurement was taken between the most northerly warm season cluster and the southern terminus of the winter range. Annual range was quantified for each temporally adjacent winter to warm season pair and then averaged to yield a single value per individual. "Maximum range" was measured as the distance between the most distant locations (Argos LC1-3 and visual locations only) over the individual's entire tracking history, providing a measure of the amount of coastline covered by an individual over this time period. Annual and maximum range measurements were computed in ArcView from the intracoastal waterway (ICW) distance, as determined from mile markers on NOAA nautical charts. Waterway distances of annual range were a median of 19.5 km (7.8%) greater than straight-line measurements, which greatly underestimated range for certain individuals (maxima = 122 km and 44.4% difference), such as migrants using the St. Johns River and residents of Brevard County.

Daily Travel Rate

An individual's daily travel rate was defined as the straight-line distance between successive mean daily locations divided by the time interval between successive mean date-times (hrs), standardized to a 24-hr period. For consistency, only manatees tagged with satellite-monitored PTTs were included in this analysis. Mean daily locations were computed as in the distributional analysis (see above), except that non-visual field locations and public sightings were excluded. Of 21,696 successive daily locations within a tracking bout, 95.2% were separated by 1 day (i.e., continuous tracking) and 1.0% by more than 2 days. Travel rates for adult male TBC-42 north of Georgia were excluded from analyses, as he sustained high rates of directed travel on his journey to New England over most of the summer, which was atypical for manatees in Florida and Georgia.

Median travel rates were calculated for each individual for each time period of interest (i.e., months, seasons, or all year); use of the median statistic minimized the effect of high travel rates associated with long-distance migrations. Mean travel rates by age-sex class, seasonal movement pattern, season, and month were then computed from these individual values. Individuals with at least 30 daily travel rate measurements within a season (winter or warm season) were included in the analysis of seasonal variation. Data for all individuals were used in the plot of travel rate by month, but the means and variances were weighted by the number of days sampled per month; manatees tracked in a given month over multiple years were given a weighting factor equal to the number of days in that month.

Migratory Behavior

In this paper we use the term migration to mean "a regular round-trip movement of individuals between two or more . . . seasonal ranges" (White and Garrott 1990, p. 121). The following variables were determined for each southward "fall" and northward "spring" migratory trip using the ArcView Tracking Analyst extension:

1. "Fall" ["Spring"] Departure Timing = the date and time of the animal's last location in its warm season [winter] range. To differentiate the true start of a southward "fall" migration from "false starts" or localized movements, the move must have continued for at least one-quarter of the total migratory distance and the animal must not have returned within 7 days.

2. "Fall" ["Spring"] Arrival Timing = the date and time of the animal's first location in its winter [warm season] range. To differentiate the true end of a northward "spring" migration from that of mid-winter migrations, the animal must have remained in its warm season range.

3. Migratory Stopover = a pause in directed linear movement for at least 1 day; stops short of the final destination that lasted over 25 days were considered the endpoint of the first stage of a two-stage migration and were not included in stopover statistics. The total number and duration of stopovers were calculated for each migratory trip.

4. Migration Distance = the distance between departure and arrival endpoints, computed as the intracoastal waterway distance. Distance along the coast was used for migratory segments that took an oceanic route.

5. Use of Industrial Warm-water Sites = presence at a power plant or pulp mill thermal effluent prior to initiation of "fall" southward migration or after termination of "spring" northward migration, between 1 October and 30 April. Presence was determined by 1 of the following: (a) a visually determined location occurring within 200 m of the warm-water aggregation area, (b) a satellite-determined location within 1 km of this area, or (c) a PTT temperature that was elevated well above ambient temperature combined with a location in the proximity of the plant.

6. Travel Route = movement in the intracoastal waterways or in the Atlantic Ocean close to shore. On a few occasions, manatees were observed and tracked along the ocean side of barrier islands. Oceanic travel was also inferred from the following types of information: departure

from and arrival at oceanic inlets; rapid rate of travel between inlets; paucity of Argos locations between inlets, suggesting continuous travel; and, in some cases, Argos locations within 1 km of shore.

The following variables were computed from the above measurements for each trip:

7. Total Migration Duration = arrival date-time - departure date-time.
8. Mean Stopover Duration = total stopover duration / number of stopovers.
9. Migration Travel Time = total migration duration - total stopover duration.
10. Migratory Travel Rate = migration distance / migration travel time. This was typically slower than an actual travel rate because the travel time often included brief (<24 hr) stopovers and the trip sometimes involved reversals in direction as, for example, when a manatee responded to rapid changes in temperature.

Winter Migrations

In addition to the annual migrations between winter and warm season ranges, manatees sometimes made long-distance movements during the middle of winter. Winter migrations were defined as round trips of at least 50 km in each direction that occurred during the months of November through March and between the individual's southward "fall" and northward "spring" migrations. The following variables were calculated for each winter migration using the ArcView Tracking Analyst: number of round-trip migrations per winter; distance of northbound and southbound legs of trip (measured along the ICW); distance of northbound trip expressed as a percentage of the distance to the center of the individual's warm season cluster; round-trip distance and duration; duration spent on warm season range; and travel routes of northbound and southbound movements. For descriptive statistics on the number of migrations per winter, the percentage of individuals that made winter migrations, and the total migratory distance traveled per winter, the data were censored by excluding years with less than 70 days of tracking between December and February (maximum = 90-91 days).

Migratory Timing in Relation to Temperature

Water temperature at fall departure from the warm season range was determined for tagged manatees in northern Brevard County, within 40 km of the temperature recording stations. For animals that moved to local power plants before initiating their southward migration, the temperature at the time of this move was used instead of at the later departure date from the power plant. Timing of movement of Brevard County resident manatees from the Banana River to the Indian River power plants was also included in this analysis. Departure times with an uncertainty greater than 16 hr were excluded from these analyses; most departures were known to have occurred within a 6 - 12 hr time period.

In addition to water temperature at the time of departure, 3 other temperature metrics—including mean, minimum, and temperature change—were calculated over each of 3 time periods: 24 hr prior to departure, 24 hr after departure, and the 48-hr period that comprised these 2 24-hr periods.

Site Fidelity to Seasonal Ranges

Site fidelity to seasonal ranges was measured for manatees with at least 30 days of locations between April and October (for the warm season) or between December and February (for the winter season) of a given year. We employed cluster analysis to identify the number, locations, and sizes of concentrations of mean daily locations (as determined under Distribution above). This approach revealed the structure underlying an individual's spatial use patterns within each season, with the clusters representing separate components of an animal's home range. The analysis was implemented with SAS' Proc MODECLUS (method = 1), a non-parametric clustering method based on non-parametric density estimation that can detect clusters of unequal size, dispersion, and with highly irregular or elongated shapes (Koontz et al. 1976, Mizoguchi and Shimura 1980, SAS Institute, Inc. 1993). A non-parametric method was selected because it has the least bias (Silverman 1986:130-146) and because much of manatee habitat along the Atlantic coast is linear or elongate in shape. Density estimation was based on circular uniform kernels of fixed radius set to 7 km. The choice of this smoothing parameter appeared to provide the optimal balance between many small clusters (at a small radius) and 1 extensive cluster (at a large radius). The clustering algorithm calculated an approximate *p*-value for each cluster by comparing the estimated maximum density in the cluster with the estimated maximum density on the cluster boundary. Clusters with the highest *p*-values were hierarchically joined with neighboring clusters until all remaining clusters were significant at $P \leq 0.10$. Non-significant clusters and clusters with less than 10 days of locations were dissolved.

The number of significant clusters and the percentage of mean daily locations that were assigned to significant clusters within a season provided indices of intraannual site fidelity. The 90th percentile of distances between mean daily locations and the centroid (i.e., arithmetic mean) of the corresponding cluster provided a linear measure of the size of each cluster in km.

Interannual site fidelity to seasonal ranges was quantified in 2 ways. First, cluster locations were compared from one year to the next year with sufficient data, and the percentage of comparisons with overlap between the polygons formed by the clusters was computed. Second, the Euclidean distance between the arithmetic means of clusters in corresponding regions across years was calculated. When there was 1 cluster in 1 year and multiple clusters within the same region in the comparison year, the inter-cluster distance was calculated for each cluster pair across years; the mean of these distances, weighted by the number of records in each cluster (for the year with multiple clusters), was then computed to yield a single data value (in km) for interannual site fidelity for that animal, year span, and region. A mean value across years and regions was calculated for each individual.

Statistical Analyses

To avoid biasing descriptive statistics of seasonal ranges, migratory behavior, site fidelity, and other parameters toward values of those study animals that were tracked over multiple years, mean (or median) values were calculated for each animal and these data were then used in calculating means, medians, and standard deviations across animals (denoted as sample size N). To document the range of observed values, however, minimum and maximum values were based on the raw data (denoted as sample size n). All statistical tests were based on only 1 mean value per animal. To test hypotheses about the effects of individual attributes (e.g., age class, sex, female reproductive status) or environmental variables (e.g., geographic region) on movement parameters, we usually employed two-sample t-tests or Wilcoxon two-sample tests (using a normal approximation and a continuity correction of 0.5). Non-independence sometimes resulted from individuals contributing to data in both categories (e.g., with calf and without calf; northern and southern regions; visit or did not visit power plant). In these cases, we used paired t-tests or Wilcoxon matched-pairs signed-ranks tests when sample sizes were sufficient; otherwise, data were eliminated from the larger class to ensure an independent data set before performing the standard two-sample tests.

RESULTS

Radio-tracking Effort and Telemetry Performance

Over the course of the study, 63 manatees were tagged with PTT tags and 15 others carried only VHF tags. VHF tags were also frequently deployed on a temporary basis on satellite-tracked animals until a replacement PTT could be attached. An average of 18.5 ± 4.4 manatees (range = 9 - 23) were radio-tracked in each full year of the study (Table 1). The median duration of tracking was 8.3 months, but this varied widely among study animals (interquartile (IQ) range = 4.0 - 16.1 mos; range = 2 days - 6.8 years, Appendix A). Twenty-nine individuals (37%) were tracked for a cumulative duration of at least 1 year. Considering the total tagging period from first to last deployment, including time intervals when the manatee was not carrying a transmitter, the median duration was 13.4 months and the maximum period was 9.7 years (Appendix A); the tagging period extended over 1 year for 41 (53%) manatees. Manatees carried functioning radio-transmitters for a cumulative total of 31,983 tag-days (equivalent to 87.6 tag-years), of which 73.7% were based on PTTs (Table 1). Tracking effort was fairly evenly distributed throughout the year, with a somewhat greater number of animals tagged and number of tag-days in the spring than in the fall seasons (Table 2).

This effort yielded 83,276 Argos-determined locations and 10,539 field observations of tagged manatees. Since October 1989, when LC0 records were incorporated into the telemetry database, the PTTs generated a mean ± SD of 3.7 ± 1.6 locations per day (maximum = 10), distributed among Argos location classes as follows: 24.2% LC3, 36.6% LC2, 19.0% LC1, and 20.1% LC0/A/B. Good quality Argos locations (LC1-3) were obtained on 94.0% of PTT tag-days; days without any locations were rare (2.5%).

General Distribution

Most of the 78 tagged manatees were distributed in the intracoastal waters between Biscayne Bay in southeastern Florida (SE FL) and the Brunswick River in southeastern Georgia (SE GA) (Fig. 1). Three adults ventured north of Georgia during the warm season: 2 females used southern South Carolina, and 1 male journeyed as far north as Rhode Island. Three other adults restricted their movements to the upper Florida Keys.

Tracking histories of 48 study animals (37 female, 11 male) met the criteria for inclusion in analyses of distribution and seasonal movement patterns (see Methods); their median tracking duration equaled 14.1 months. Three areas were heavily utilized by manatees in our study (Fig. 2): (1) northeastern Florida (NE FL) and SE GA between Fernandina Beach and Brunswick ("FL/GA" in Fig. 2); (2) the Banana and northern Indian Rivers in Brevard County ("BC"); and (3) SE FL, primarily northern Biscayne Bay and Port Everglades ("PE"). The intracoastal waters and coastline between these core use areas were used less frequently and primarily as a migratory corridor (Fig. 2). The lower St. Johns River south of Jacksonville was another important area, being visited by 18 tagged manatees (11 meeting seasonal movement criteria) in this study; 1 adult male (TBC-21) traveled as far inland as Palatka, 139 km upriver from the

Atlantic Ocean. The intracoastal waters between the Sebastian River (southern border of Brevard County) and Riviera Beach (Fig. 1) were also used regularly by several manatees (Fig. 2). The northern region was generally used during the warm season, the southern region was typically used during winter, and the central region—particularly Brevard County—was frequented throughout the year. Body size of adult manatees, as measured by standard length at tagging, did not vary significantly by overwintering region (central: mean ± SD = 288 ± 17 cm; south: 302 ± 25 cm; $t = -1.722$, $df = 38$, $P = 0.09$) or summering region (north: 301 ± 24 cm; central: 296 ± 26 cm; $t = 0.720$, $df = 49$, $P = 0.48$).

Seasonal Movement Patterns and Range

Nearly all tagged manatees migrated seasonally between winter and warm season use areas, which were separated by a median waterway distance of 280 km; this measure of annual range extent varied widely among individuals (min - max = 11 - 831 km) (Fig. 3A, Appendix A). The maximum extent of coastline that manatees covered over their entire tracking histories varied from 44 km to approximately 2360 km (median = 309 km); 92%, 56%, and 15% of tagged manatees had maximum ranges of at least 100, 300, and 500 km, respectively (Fig. 3B). Neither measure of range differed significantly by sex or age class (Wilcoxon two-sample tests, $P > 0.40$; Table 3) or was correlated with body size ($r_s = -0.02$ and $r_s = 0.03$, respectively, $N = 48$, $P > 0.80$).

Four principal types of seasonal movement patterns were evident, as characterized by the distance between winter and warm season ranges, and these types could be further grouped by geographic region (Figs. 2 and 4). These patterns showed no apparent relation to the manatee's sex, age class, body size, or reproductive status. The north-south movements of each tagged manatee over their entire tracking period are shown in Appendix B.

Medium-distance Migrants

Most manatees (N = 29, 60%) migrated 150 - 400 km one-way between a northerly warm season range and a southerly winter range (Figs. 2A,B and 4A). The most common pattern in our sample—termed the *central-south (C-S) migratory type* (N = 18, 38%)—was exhibited by 12 adult females (ADF), 2 adult males (ADM), and 4 subadults (SUB). These animals spent most of the year (about 9 months) in central Florida; they typically migrated south in late fall or early winter, overwintered in SE FL, and then returned north to their warm season range in late winter or early spring. Their median annual range was 282 km (min - max = 209 - 349 km) and their median maximum range was 316 km (min - max = 225 - 630 km). All C-S migrants traveled as far south as Riviera Beach and 16 (89%) reached Port Everglades or points further south during at least part of the winter season; all used power plant effluents to thermoregulate during cold periods and some visited natural warm-water sites or thermally buffered waterways. All but 2 individuals (89%) summered in Brevard County.

The other type of medium-distance seasonal movement pattern—termed the *north-central (N-C) migratory type* (N = 11, 23%; 7 ADF, 2 ADM, 2 SUB)—also involved a north-south trek over the annual cycle, but shifted about 250 km to the north (Figs. 2A and 4A). N-C migrants typically spent the spring and summer months in NE FL (lower St. John's River to Fernandina Beach) or SE GA (Cumberland Sound to Brunswick). Unlike C-S migrants, however, most of them migrated south to central Florida (Brevard County) in late summer to fall. After spending all or part of the winter in Brevard County, where they relied on 2 power plants in the Indian River for warmth during cold weather, these animals returned to their northern ranges in spring. The median annual range of N-C migrants was 294 km (min - max = 176 - 373 km) and the median maximum range was 350 km (min - max = 257 - 394 km).

Long-distance Migrants

Six (12%) manatees (4 ADF, 1 ADM, 1 SUB) made seasonal migrations of over 400 km between SE FL in the winter and NE FL (including the lower St. John's River), SE GA, or points further north during the warm season (Figs. 2A and 4B). The median annual range of these migrants was 595 km (min - max = 575 - 831 km) and the median maximum range was 631 km (min - max = 586 - 2360 km). Long-distance migrants exhibited a seasonal movement pattern that was a combination of the N-C and C-S migratory patterns. Like the C-S migrants, all 6 manatees moved at least as far south as Port Everglades and visited power plant effluents in SE FL. They made a two-stage migration in spring: (1) movement north from SE FL to Brevard County, usually in February or March, where they resided for a average duration of 74.0 days (SD = 28.6, range = 28 - 112, N = 5); and (2) the second stage of movement north from Brevard County to NE FL or SE GA, usually between mid-March and May. Similar to the N-C migratory pattern, all N-S migrants spent parts of the warm season in both the northern region and Brevard County. Two manatees made a two-stage southward migration, arriving in Brevard from the north in late spring to mid-summer, spending most of the remainder of the summer and fall there, and then completing the southward journey in December. Two others made a fairly continuous southward migration, leaving the northern region in November or December and not pausing more than a few days at any site along the way until reaching Port Everglades (e.g., Fig. 4B). Adult male TBC-42 ("Chessie") added a third stage to his northward migrations in each of 2 years; after departing his NE FL spring range in early June, he reached Rhode Island in August 1995 and at least as far as Virginia, where his tag detached, in summer 1996. Details of this record-breaking migration will be presented elsewhere.

Short-distance Migrants

Seven (15%) manatees (5 ADF, 2 ADM) undertook seasonal migrations over a distance of 50 - 150 km between their winter and warm season ranges (Figs. 2C and 4C). These animals were distributed in the NE FL - SE GA region (N = 2) and the region between Brevard County and Riviera Beach (N = 5). The seasonal movement patterns of the latter 5 animals were similar to that of the C-S migrants, except for a shorter distance between seasonal ranges. Their median annual range was 97 km (min - max = 80 - 148 km) and their median maximum range was 175 km (min - max = 109 - 266 km). Two of these individuals made at least 1 additional round-trip migration between their northerly and southerly core ranges during the warm season. As shown in Fig. 4C, for example, male TFP-02 occupied 2 core ranges: the Sebastian River area in spring, south to Jupiter and Hobe Sounds in summer, back north to Sebastian in autumn and early winter, and then back south to the Jupiter area in winter, where he used the Riviera Beach power plant during periods of cold weather. The 2 short-distance migrants that overwintered near pulp mills in NE FL and SE GA dispersed away from these thermal refugia in the spring (March - May) to the north (as far as Brunswick, GA) or to the south (to the lower St. John's River).

Year-round Residents

Six (12%) manatees traveled <50 km between winter and warm season ranges, which typically overlapped each other (Figs. 2C and 4D). Year-round residents (4 ADF, 2 ADM) were found throughout the study area, including NE FL and SE GA (N = 1), Brevard County (N = 3), and the upper Florida Keys (N = 2). The median annual range was 21 km (min - max = 11 - 36 km) and the median maximum range was 50 km (min - max = 44 - 107 km). The winter range was usually smaller than and often a subset of the warm season range, even in the Florida Keys where temperature plays a lesser role in constraining winter movements. One Brevard County resident occasionally made brief excursions during the warm months up to 100 km north of its normal range.

Unclassified Movement Patterns

Thirty manatees did not meet the criteria for inclusion in analyses of seasonal movement patterns, because their tracking periods were either too brief (<90 days, N = 16) or did not sufficiently span both winter and warm seasons (N = 14). Nevertheless, many of these individuals showed movements that were similar to the above patterns, including the following: 6 probable C-S migrants, 5 probable N-C migrants, and 3 probable year-round residents. Most of the animals with unclassified movement patterns (N = 18, 60%) traveled over 100 km of coastline during their relatively brief tracking periods. Some of the 11 manatees that apparently made medium-distance migrations between summer and winter ranges may have actually been long-distance migrants whose tracking histories were truncated by tag loss. Another manatee (TNC-03) covered a range of approximately 280 km during the warm season entirely within the northern region; limited sighting and tracking data suggest that she overwintered in the north as well. Of the 8 additional animals tracked only in the northern region during the warm season (generally tagged in March), it is likely that some resided there year-round. The 3 individuals that appeared to be year-round residents were located in Brevard County (TBC-29, June - December), the upper Florida Keys (TFK-03, October - February), and SE FL (TPE-02, February - September). Adult female TPE-02 was tracked or sighted at Little River, northern Biscayne Bay, and Port Everglades during the winter, but her warm season movements over a 5-month period (April - September) were restricted entirely to the rivers and canal system around Miami; she moved as far inland as Homestead, 77 km by canal from the Miami River mouth.

Daily Travel Rate

The distance that manatees shifted their mean location from one day to the next varied with seasonal movement pattern, season, and age-sex class. Daily travel rate varied significantly among manatees with different seasonal movement patterns during the winter months (Kruskal-Wallis test, $\chi^2 = 18.619$, $df = 4$, $P < 0.001$), but not during the warm season ($\chi^2 = 4.161$, $df = 4$, P

= 0.38, Table 4). During the winter season, year-round residents moved significantly shorter distances (mean ± SD = 1.1 ± 0.3, N = 6) than did migrants (all types combined, 3.2 ± 3.4, N = 34; Wilcoxon two-sample test, $P < 0.001$). Movement rates during the warm season, however, did not differ significantly between residents (1.9 ± 1.0, N = 5) and migrants (2.3 ± 1.2, N = 38; Wilcoxon two-sample test, $P = 0.40$). The maximum single measurement of distance moved per day was 77.3 km during winter and 59.5 km in the warm season (Table 4).

Analysis of covariance of daily travel rate of adult manatees during the warm season, controlling for body size (length at tagging), revealed that adult males moved at a significantly higher rate (mean ± SD = 3.8 ± 1.6 km/day, N = 11) than adult females (2.0 ± 0.8 km/day, N = 35; $F = 23.82$, $df = 1, 41$, $P < 0.0001$). Larger adult manatees traveled at higher rates ($F = 4.46$, df = 1, 41, $P = 0.04$), but body size accounted for little of the total variation. Daily movement rates during the winter season were similar for adult males (mean ± SD = 3.2 ± 4.7, N = 9) and adult females (2.9 ± 2.9, N = 28; Wilcoxon two-sample test, $P = 0.18$). The sex difference in movement rate occurred during the months of April through September, which corresponds closely with the principal period of reproductive activity (Figure 5). The sample for subadults was small but rates were similar to that of adult females during the warm season (mean ± SD = 1.7 ± 0.9, N = 3) and less than that of adults during winter (1.7 ± 0.8, N = 3).

Migratory Behavior

Timing of Seasonal Migrations

The initiation of migrations between summer and winter areas was typically abrupt and followed by a rapid, directed move (Fig. 4). The timing of seasonal migrations differed markedly by region, with most movements north of Brevard County occurring during the non-winter months and most migrations south of Brevard County taking place between November and March (Fig. 6A). Manatees that spent the warm season in central Florida generally departed for southerly overwintering sites in early winter (mean ± SD departure date = 12Dec ± 25 days, N = 25 manatees, n = 48 migrations), whereas those animals that established ranges in NE FL and SE GA during the warm season typically moved back south to Brevard County during the summer to fall months (28Aug ± 65 days, N = 12, n = 21). Manatees overwintering in SE FL returned to their warm season ranges in the central region during late winter to early spring (mean ± SD arrival date = 16Mar ± 22 days, N = 27, n = 62), whereas those migrating to NE FL and SE GA from Brevard County arrived an average of 5 weeks later (19Apr ± 49 days, N = 19, n = 28). The timing of migrations between northern and central regions was considerably more variable than that between central and southern regions (Fig. 6A). The differences in migratory timing across regions resulted in temporal and spatial overlap of manatees exhibiting different migratory patterns in Brevard County during a short period in March and April and a longer period in the fall (Fig. 4A and 6A).

The artificial warm-water refugia created by power plants influenced the timing of fall and spring migrations for some individuals. Manatees that visited the thermal effluents of power plants in the central region (primarily Brevard County), prior to migrating to SE FL, departed their autumn range an average of 4 weeks later (mean ± SD = 27Dec ± 26 days, N = 12) than those that did not visit a power plant (29Nov ± 15, N =13; two-sample t-test, $P = 0.003$). Likewise, manatees visiting power plants after their return to the central region arrived earlier in spring (mean ± SD = 1Mar ± 19, N = 11) than those that did not do so (24Mar ± 20, N = 15; two-sample t-test, $P = 0.007$). All migrants to the northern region that arrived by 15 March (N = 6, n = 8)—including 3 that migrated north in early to mid-winter—used industrial warm-water refugia after their arrival.

Timing of "fall" southward and "spring" northward migrations did not vary significantly between sexes (two-sample t-tests, $P > 0.40$ for all comparisons) or by adult female reproductive status (two-sample t-tests or paired t-tests comparing females with and without calves, $P > 0.40$ for all comparisons) for both N-C and C-S migratory regions. For the C-S region, departure timing of southbound migrations was not significantly correlated with body size ® = 0.18, N = 25, $P = 0.37$), but during northbound spring migrations larger manatees arrived significantly earlier than smaller ones ® = -0.46, N = 26, $P = 0.02$).

Migratory Timing in Relation to Temperature

There was a clear relationship between migratory timing and mean monthly water temperature in Brevard County for manatees migrating seasonally between central and southeastern Florida. The approximate threshold temperature for these movements was 20 °C (Fig. 6). Likewise, the bulk of spring migrations north of Brevard County occurred after water temperatures had warmed to 20 °C in the northern region; most return southward migrations back to central Florida, however, occurred when waters were still quite warm (Fig. 6).

The temperature regime at the beginning of winter directly affected migratory timing for manatees in the central region, as illustrated in Figure 7 for 2 years with contrasting weather patterns. Manatees migrated south or moved to local power plants early in the season when major cold fronts arrived in November (Fig. 7A), but they remained on their warm season ranges through mid-December when mild weather prevailed in early winter (Fig. 7B). Consequently, much of the within-individual variation in departure date across years can be explained by interannual variation in weather patterns (*cf.* Fig 7A and 7B for individuals 1 and 3).

Most tagged manatees left their warm season range in Brevard County in response to cold fronts that dropped water temperatures below 20 °C (Fig. 7). At the time of departure, water temperatures had declined by an average of 2.0 °C over the prior 24 hr to a mean of 19.1 °C (Table 5). This temperature drop was significant compared to the known distribution of 24-hr temperature changes in November and December during the study period (Wilcoxon one-sample signed-ranks test, $P = 0.002$). Water temperature continued to decline an average of 1.4 °C over the 24 hr subsequent to departure. For the 48-hr period that spanned 24 hr before and after departure, the mean temperature was 19.2 °C and the minimum temperature averaged 17.1 °C (Table 5). On average, water temperatures dropped 3.5 °C over this 48-hr period, from 21.1 to 17.7 °C. For all 3 time periods considered, 93% of tagged manatees (N = 14 - 15) departed while temperatures were falling.

The water temperature at which manatees in Brevard County initiated their fall migration was not significantly correlated with body size ($P > 0.10$, Spearman rank correlations with 7 temperature metrics, N = 14 - 15). Sample sizes were insufficient to examine variation with age class or sex. Departure temperature in autumn was similar for adult females with calves (mean ± SD = 20.0 ± 2.0, N = 6) and those without calves (19.0 ± 2.3, N = 8). The 4 females that were tracked both with and without calves did not initiate their migration at different temperatures when in the presence of a calf. This is consistent with the finding that departure date did not vary with female reproductive status.

There was considerable variation among individuals, however, in the water temperature at which departure from the warm season range was triggered (Fig. 8). Some individuals (e.g., TBC-09, denoted as no. 1 in Fig. 7A,B) consistently headed south with one of the first cold fronts to drive water temperatures toward 20 °C, whereas others (e.g., TRB-01, denoted as no. 6 in Fig. 7B) often remained in the Banana River until water temperatures plummeted to 15 °C (Fig. 8). This variation in departure temperature across individuals with multiple years of data was highly significant (one-way ANOVA for 48-hr mean temperature, $r^2 = 0.74$, $F = 8.04$, $df = 6, 17$, $P < 0.001$).

The timing of return migrations from southern to central Florida in late winter and early spring was also influenced by the prevailing temperature regime (Fig. 6). Manatees frequently turned back south in mid-migration after encountering a cold front, such as occurred during the severe "Storm of the Century" in mid-March 1993 (Fig. 9). Such round-trip migrations are considered further under *Winter Migratory Behavior* (see below). Other individuals responded to cold fronts during their northward migration by seeking shelter at warm-water refugia provided by power plant effluents (Fig. 1) or by thermally buffered waterways such as the Sebastian River.

Duration of Migrations

Southward "fall" migrations lasted an average of 10 days, of which approximately 8 days were spent traveling and 2 days were spent at stopover sites along the way (Table 6). Durations of short-distance migrations were about half that of medium-distance migrations (Table 6). The longest recorded fall migration was made by adult female TNC-13, who traveled 812 km in 2 stages between the Broad River, South Carolina and Savannah, Georgia, and then south continuously to Port Everglades (Fig. 4b); the combined trip lasted 46 days and included 31 days spent traveling and 15 days spread across 9 stopover sites (excluding 36 days spent in Savannah). The total duration and travel duration of medium-distance fall migrations did not vary significantly by sex of adult (Wilcoxon two-sample tests, $P > 0.10$), but adult males spent an average total of 2 days longer in stopovers than adult females (Wilcoxon two-sample test, $P = 0.04$). There was no significant variation in total, travel, or total stopover durations during fall migration as a function of adult female reproductive status (Wilcoxon two-sample tests, $P > 0.40$).

The duration of northward "spring" migrations averaged 15 days, of which about 10 days were spent traveling and 5 days were spent at stopover locations (Table 7). This varied across regions, however, with N-C migrations lasting a mean of 12 days and C-S migrations taking a mean of 19 days to complete (Table 7). All long-distance spring migrations between southern and northern regions occurred in 2 distinct stages, with the northern Indian or Banana Rivers in

Brevard County being used for at least 1 month in the spring. The lengthiest spring migration lasted 52 days between Port Everglades and the Banana River, of which at least half was spent at 4 stopover sites. Spring migrations took twice as long to complete as fall migrations for the C-S and short-distance migrants because the animals spent both more time traveling and more time at stopover sites in the spring (*cf.* Tables 6 and 7). Migration durations in the N-C region were similar in the fall and the spring.

The spring migrations of adult males were significantly longer than those of adult females for the N-C region (male: mean ± SD = 15.1 ± 4.5 days, N = 5; female: 8.9 ± 3.9 days, N = 10; Wilcoxon two-sample test, $P = 0.01$), but not the C-S region (male: 18.2 ± 11.5 days, N = 6; female: 16.9 ± 4.9 days, N = 13; $P = 0.69$). The sex difference in migration duration for the N-C region apparently stemmed from adult males spending more total time in stopovers than females (Wilcoxon two-sample test, $P < 0.01$), and perhaps also from more time spent traveling (Wilcoxon two-sample test, $P = 0.052$). The total duration of spring migrations for females with calves averaged 4.0 days longer than for those same females without calves (paired t-test, $P = 0.07$), apparently because females spent more total time at stopover locations when they were accompanied by a dependent calf (paired t-test, $P = 0.08$).

Migratory Travel Rate

The average rate of travel between origination and destination points during fall migration was 25 and 36 km per day for short- and medium-distance migrations, respectively (Table 6). Travel rate was substantially slower in spring (23 km/day) than in fall (36 km/day) for the C-S region, but was similar across seasons for the N-C region and for short-distance migrations (*cf.* Tables 6 and 7). Of the 6 trips that averaged over 50 km per day, 5 occurred during winter months; the 3 highest rates (up to 58 km/day) involved northward migrations from Brevard to the Florida-Georgia border in the middle of winter.

Migratory travel rate of adults did not differ significantly between sexes in either the fall (male: mean ± SD = 29.4 ± 7.2 km/day, N = 5; female: 34.7 ± 7.8, N = 20; two-sample t-test, $P = 0.18$) or the spring (male: 22.9 ± 5.7, N = 8; female: 29.5 ± 11.5, N = 24; Wilcoxon two-sample test, $P = 0.11$). Presence of a calf did not significantly affect travel rate of adult females in either the fall (no calf: mean ± SD = 35.8 ± 7.5, N = 14; with calf: 31.6 ± 7.7, N = 7; two-sample t-test, $P = 0.26$) or the spring migrations (C-S and short-distance migrants, no calf: 24.0 ± 4.4, N = 12; with calf: 22.3 ± 7.3, N = 14; paired t-test for 9 females, $P = 0.43$). Migratory travel rate was not significantly correlated with body size (fall: $r = 0.24$, N = 27, $P = 0.22$; spring: $r = 0.12$, N = 34, $P = 0.50$).

The above estimates of travel rate during migration were affected by the manatee's swimming speed, the directness of travel, the number of brief (< 24 hr) stopovers, and the extent of backtracking that occurred. The highest rate of travel during a migratory segment in which there was no evidence of stopovers or backtracking was exhibited by adult male TRB-01 moving south in the Atlantic Ocean between inlets at Port Canaveral, Brevard County and Ft. Pierce during the winter: a distance of 116 km in ≤32 hr, for an average travel rate of at least 3.63 km per hr (87.2 km/day); other southbound winter trips by TRB-01 between these locations also yielded high rates of travel (2.7, 2.8, and 3.6 km/hr). Manatees often migrated without pause between Brevard County and the St. Johns River (Fig. 2A), traveling at average rates of up to 2.6 km per hr (62 km/day) over periods of 2 to 4 days. Over shorter time periods (8 - 10 hr), we have recorded migratory movements using boat-based VHF telemetry as high as 4.1 km per hr.

Migratory Stopovers

Most migrations were direct with few, if any, stops lasting more than 24 hr between destinations. The percentage of trips that were non-stop was 52% for "fall" migrations (n = 52) and 36% for "spring" migrations (n = 74). Non-stop migrations were more frequent between northern and central regions (fall, 60%; spring, 50%) than between central and southern regions (fall, 42%; spring, 32%). The average number of stopovers per migratory trip was small (Tables 6 and 7), with only 4% of fall trips and 11% of spring trips involving more than 2 stopovers. The median duration of stopovers was 2.0 and 2.8 days in the fall and spring, respectively; stopovers tended to be more variable in duration, including longer stops, in the spring (*cf.* Tables 6 and 7).

Particular stopover sites were favored by tagged manatees during migration. We identified 19 areas as stopover locations in the fall, including 8 used by at least 2 tagged manatees. In the spring 31 stopover sites were identified, including 11 used by at least 3 animals. The most important migratory stopover area in the central region was the Sebastian River and adjacent intracoastal waters, used by 8 tagged manatees during fall migration and by 9 during spring migration. Of 26 tagged manatees that migrated past the Sebastian River mouth between the months of November and April, 18 (69%) were located at least once in this river. Because of its importance to manatees, this waterway was designated a year-round slow speed zone for boats, and a manatee winter aggregation site in the C-54 canal off the river's north fork was designated a no motorboat sanctuary. Frequently used stopover sites during spring migration were also located in the 25-km stretch of intracoastal waters between Ft. Pierce and Vero Beach, where 16 tagged manatees stopped on their way north. The Haulover Canal area separating the Indian River from the Mosquito Lagoon in northern Brevard County was often used as a spring staging area where manatees (N = 8) paused before continuing on the 200-300 km journey northward. The Tomoka River was the next frequently used stopover site (fall, N = 3; spring, N = 4) for manatees migrating between central and northern regions. We sometimes observed numerous untagged manatees at these stopover sites during field tracking of study animals.

Although the number and duration of stopovers did not vary with sex or reproductive status, individual variation and consistency in use of particular sites was apparent. This can be illustrated with a few examples from individuals with multiple years of migration data: (a) adult female TBC-03 visited the Sebastian River in all 5 fall trips, and she made 1 or 2 stops in each of 3 spring trips, typically in Lake Worth and between Sebastian and Vero Beach; (b) adult female TBC-09 made no stops in 5 fall trips and in 4 of 6 spring trips in the C-S region; (c) adult male TFP-02 stopped in the vicinity of Harbor Branch (10 km north of Ft. Pierce) for 2-3 weeks in each of 3 spring migrations before continuing north to his spring range at Sebastian; and (d) adult male TRB-01 made 1 stop, always at Ft. Pierce, after leaving the Banana River in each of 4 southbound trips, yet he made no stops in 5 of 6 northbound trips.

Most of our field observations of manatees during migration occurred during stopovers or brief pauses in traveling. The most common activity was resting (50% of 177 observations), often in the warmth of power plant effluents or thermally buffered waterways during cold weather. Tagged animals were observed with other manatees in 59% of 163 observations during fall or spring migrations. Limited observational data suggest that manatees usually traveled alone or in small groups during migrations but joined conspecifics in larger groups at stopover sites.

Winter Migratory Behavior

Manatees often traveled north from their overwintering areas during periods of mild weather in the middle of winter, only to return south again with the next major cold front (Fig. 9). Figure 9 illustrates the synchrony of winter migrations across individuals in the central and southern regions; despite geographic separation, they responded in similar ways to changes in air and water temperatures associated with the passage of cold fronts and subsequent warming trends. The round-trip duration of such winter migrations lasted an average of nearly 3 weeks—including time spent in stopovers and at northern destinations—but varied from a few days to 2 months (Table 8). Round-trip distances varied from a minimum of 100 km to over 500 km. The northbound leg of winter migrations extended a mean of 62% of the way to the center of the warm season range, but this varied from as little as 18% to areas well north of the warm season range (Table 8). Of 58 winter migrations, 43% reached the individual's warm season range; 12 (71%) of the 17 manatees that migrated in winter (and were tracked at least 70 days) reached their warm season range at least 1 time. Once on their warm season range, manatees stayed for a variable amount of time (up to several weeks), typically until the arrival of the next cold front.

There was a strong regional difference in winter migratory behavior. Manatees overwintering south of Brevard County were more than twice as likely to make round-trip migrations during the winter season than were those spending the winter in Brevard or further north ($\chi^2 = 3.882$, $df = 1$, $P < 0.05$; Table 8). Manatees overwintering in southeastern Florida engaged in longer trips and traveled greater distances than those few individuals that migrated north of Brevard County during winter (Table 8). In contrast to the frequent, extensive migrations that occurred during winter south of Brevard County, no manatees made round-trip migrations between Brevard and the northern region during the period of November through March. Three adult females made one-way northward migrations along this stretch of coastline during winter, however, remaining in close proximity to industrial thermal effluents for the remainder of the cold season; 1 individual (TBC-23) maintained this "reverse" migratory pattern over a 10-year period (Fig. 10F).

Presence of a calf did not significantly affect the frequency with which adult females made winter migrations south of Brevard County (no calf: mean ± SD = 0.9 ± 1.0, N = 8; with calf: 0.6 ± 0.8, N = 7; Wilcoxon two-sample test, P = 0.61). Likewise, duration and distance of winter migrations did not vary significantly with female reproductive status (Wilcoxon two-sample tests, P > 0.50). As with other aspects of manatee movement patterns, there appeared to be variation among individuals in the frequency with which they made mid-winter migrations.

At opposite ends of the spectrum were some manatees that never migrated north over several winters of tracking (Fig. 10A), versus others that made round-trip within-season migrations during nearly every winter they were tracked (Fig. 10B,C).

The total distance traveled during winter migrations averaged over 400 km, nearly as much as the fall and spring migratory distances combined (*cf.* Table 8 vs. Tables 6 and 7). The record distance was made by adult female TNC-01, who traveled more than 1400 km over 4 winter migrations between SE FL and Brevard County; she reached her warm season range in Brevard County on 2 of these trips (Fig. 10G). Adult female TBC-09 migrated a total distance of 1050 km with a first-year calf (3 mos. old in December) during the 1990-91 winter (Fig. 10C), in addition to the 550 km traveled in fall and spring migrations.

Travel Routes during Migration

Although tagged manatees spent the vast majority of their time in intracoastal waters, rivers and bays, they occasionally ventured into the Atlantic Ocean close to shore. Migratory routes apparently included travel along the ocean side of the barrier islands in the following cases: 6 (14%) of 42 fall migratory trips, 2 (3%) of 75 spring migratory trips, 3 (11%) of 27 southbound legs of winter migrations, and 1 (2%) of 40 northbound legs of winter migrations; 6 individuals made these trips. These estimates are probably conservative, as the route could not be determined in many cases (20% in spring, 44% in fall, and 73% in winter) due to a paucity of high-quality locations during rapid travel and to the proximity of the coastal and ICW routes. Seven of these oceanic trips started at Port Canaveral and 6 terminated at Ft. Pierce, about 115 km to the south. Adult male TRB-01 frequently migrated between these 2 points during fall, mid-winter, and spring migrations; at least 5 of his 8 southbound trips between the northern Banana River and the Ft. Pierce power plant apparently took a coastal route (3 were unknown), but all 10 of his northbound trips were via the intracoastal waterway. Tagged manatees were also occasionally observed traveling along Atlantic beaches during other long-distance moves and while in mating groups.

Site Fidelity

Interannual Consistency in Seasonal Movement Pattern

Thirty-three of the 48 tagged manatees that met the criteria for assignment of seasonal movement patterns (see above) had tracking histories that were long enough to assess the level of consistency in these patterns. The vast majority of these animals (N = 27, 82%) maintained fidelity to their seasonal migratory patterns, including principal summer and winter destinations, across all years of tracking (Figure 10). The 6 documented cases of a shift in seasonal movement pattern represented 8% of the 72 opportunities (i.e., manatee-years) in which we could have observed such a change. Five cases involved a shift in the southernmost extent of the animal's winter range. Two long-distance migrants (TNC-10, TNC-13) that traveled as far south as the Miami River and Port Everglades in their first winter shifted their overwintering area by 260-300 km in the next year to the northern Indian River in Brevard County (Fig. 11A). According to the distance criterion, TNC-13 was still a long-distance migrant in the second year

(430 km between winter and summer ranges), but the movement pattern was essentially that of an N-C migrant. Three other manatees (2 short-distance migrants in the central and southern regions, TBC-36 and TFP-04, and 1 N-C migrant, TJX-02) shifted their winter destination to the south, thus becoming C-S migrants in the next year (Fig. 11B). For example, TBC-36 spent much of the first winter in Sebastian (moving briefly as far south as St. Lucie, Fig. 9), and occupied 2 core areas to the south during the second winter in Vero Beach and Riviera Beach. One year-round resident in the northern region (TGA-03) added a new warm season core area about 60 km north of her winter range in the second year of tracking (Fig. 4D); this shift placed the animal's movements into the short-distance migrant category for year 2.

Intraannual Site Fidelity to Warm Season Range

Most tagged manatees demonstrated strong within-year fidelity to a warm season range. Fifty-seven manatees were located on an average of 106 days per year (SD = 48 days, range = 30 - 213 days, n = 127 manatee-years) during the months of April through October. All long-distance migrants (N = 5) and most N-C migrants (70%, N = 10) possessed core warm season use areas in both central and northern regions (Figs. 4B, 10F,G). Only 1 C-S migrant (6%, N = 17) had a cluster of locations outside of the central region, however, and this one was just south of the regional C-S boundary in Hobe Sound. Within a region, the warm season movements of individual manatees were typically focused in only 1 area, as indicated by the fact that there was only 1 cluster of locations in 82.5% of 143 cases (all years and animals pooled). The maximum number of location clusters that a single animal occupied within a region was 3, occurring just twice in the northern region. For 19 animals with multiple clusters of locations within a region in a given warm season, the straight-line inter-cluster distance varied from 18 to 221 km; 68% of these individuals moved between core areas that were less than 60 km apart (median = 41.1 km).

Cluster size, as measured by the 90th percentile of distances between the cluster center and daily locations, averaged 8.0 km (SD = 3.9 km, range = 1.0 - 44.7 km, N = 57, n = 170 clusters). Cluster size did not vary significantly across regions, age classes, or sexes (Wilcoxon two-sample tests, $P > 0.10$ for all). The size of clusters was weakly correlated, however, with the individual's length at tagging ($r_s = 0.27$, N = 56, $P < 0.05$). Manatees were located on a mean ± SD of 75 ± 42 days (range = 12 - 210 days, N = 57, n = 170) within an identified warm season cluster.

A strong degree of within-season site fidelity was indicated by the fact that a median of 91% of daily locations (IQ range = 83 - 98%, range = 24 - 100%, N = 57 manatees, n = 127 manatee-years) were within significant clusters. Clearly, manatees were not nomadic in their movements during the warm season. Adult females had a significantly greater percentage of daily locations assigned to clusters (median = 91%, IQ range = 83 - 98%, N = 35) than did adult males (median = 76%, IQ range = 66 - 90%, N = 13; Wilcoxon two-sample test, $P < 0.01$). Subadults were similar to adult females in the percentage of locations found in clusters (subadult female: median = 92%, IQ range = 88 - 96%, N = 4; subadult male: median = 97%, IQ range = 85 - 100%, N = 6; Wilcoxon two-sample test between adult female and subadult classes, $P = 0.20$). This result is consistent with the finding from the daily travel rate analysis that adult males moved more extensively than adult females and subadults during the warm months

(Figure 12), probably in their search for and associations with estrous females.

Interannual Site Fidelity to Warm Season Range

Data on 32 tagged manatees indicated a high degree of interannual site fidelity to warm season range. Of 70 comparisons of cluster locations across successive years, 66 (94%) showed overlap in at least 1 cluster. The median interannual distance between the centers of warm season clusters within the same region was 4.8 km (IQ range = 2.0 - 11.3 km, range = 0.2 - 38.0 km, N = 31, n = 76). Seventy-four percent of these animals shifted the center of their warm season use areas by an average of less than 10 km between successive years (Fig. 13A). Interannual site fidelity did not vary significantly between adult males and females (Wilcoxon two-sample test, $P = 0.44$), between north and central regions (Wilcoxon two-sample test, $P = 0.61$), or with body size ($r_s = 0.23, P = 0.20$).

When a manatee's spatial use pattern was characterized by 1 cluster of locations in year A and by multiple clusters within the same region in year B, 1 of the clusters in the latter year always corresponded with the single cluster in the former year. In 9 of 12 such cases, the manatee returned to within 5 km of year A's cluster. That is, the animal showed strong fidelity to a given location, but also expanded its range to include 1 or 2 additional focal areas. Using the closest instead of the mean inter-cluster distance for these cases, median site fidelity within a region was 3.7 km; 61% of 31 animals returned to and used core areas within 5 km and 81% within 10 km of the previous year's location cluster.

Two manatees shifted regions from one year to the next for at least part of the warm season. Adult female TNC-13 was tagged in Fernandina Beach, Florida in March 1997, spent about 1 month in the Satilla River, Georgia during the spring, and then moved to southern South Carolina (Broad River and Hilton Head Is.) for the remaining 5 months of the warm season (Fig. 4B). In 1998, she used the Indian and Banana Rivers in Brevard County from April through July (285 km south of the 1997 Satilla River cluster) before returning to the same area in South Carolina (interannual site fidelity = 1.6 km) in mid-August, where she stayed through the rest of the warm season. In the second case, adult female TMI-02 was stranded in a Miami golf course pond by Hurricane Andrew in August 1992; after an on-site rescue and release into Biscayne Bay, she remained in the area until April and spent the entire subsequent warm season, including fall of 1993, in the Banana River of Brevard County, 321 km north of the previous year's autumn range (Fig. 12B). It is possible that she had migrated to SE FL early in the 1992 warm season or that she had been trapped upstream of water control structures in spring of 1992, thus preventing her northward migration.

Manatees remained faithful to their warm season ranges over several years (Fig. 10). The distance between warm season range centers from one year to the next did not vary with the number of intervening years (Fig. 14A). Three adult females that were tracked over a period of 6 to 10 years consistently returned to the same areas each year (Fig. 10A,C,F, 15A).

Intraannual Site Fidelity to Winter Range

During the months of December through February, 45 manatees were located an average of 65 days per winter (SD = 15 days, range = 31 - 90 days, n = 89 manatee-years). Site fidelity within a winter varied with migratory pattern. Most short- and medium-distance migrants between the central and southern regions (60%, N = 20) formed significant winter clusters in both regions at some time during their tracking histories. In contrast, only 15% (N = 13) of migrants between northern and central regions formed clusters in both regions during the winter. This reflects regional differences in both the timing of seasonal migrations (Fig. 6A) and the frequency of mid-winter migrations (Table 8). Within a given region, there was only 1 significant cluster of locations in 86.1% of 101 cases (all years and animals pooled). Four manatees formed no significant location clusters during a winter season because of frequent north-south movements and brief stays at warm-water refugia and other sites. The maximum number of location clusters occupied by an individual within a region was 3. For 9 manatees with multiple clusters of locations within a region in a given winter, the inter-cluster distance ranged from 18 to 116 km (median = 27.5 km) and was less than 50 km for all but 1 individual.

The average size of winter clusters (90th percentile of distances from daily locations to cluster centroid) was 6.4 km (SD = 3.2 km, range = 0.3 - 23.0 km, N = 44, n = 116 clusters). Cluster size was significantly larger in the central region (mean ± SD = 7.6 ± 3.1 km, N = 31) than in the southern region (4.6 ± 3.2 km, N = 23) (Wilcoxon matched-pairs signed-ranks test, N = 13, $P < 0.001$); cluster size for 5 manatees in the northern region (5.6 ± 3.8 km) was similar to that of manatees in the south. The size of clusters did not vary significantly with sex of adult or age class (Wilcoxon two-sample tests, $P > 0.05$) or with body size ($r_s = 0.20$, N = 44, P = 0.19). Individual winter clusters contained a mean ± SD of 43 ± 20 days (range = 12 - 90 days) of locations.

Site fidelity within a winter season was generally high, as evidenced by a median of 87% of daily locations (IQ range = 66 - 99%, range = 0 - 100%, N = 45 manatees, n = 89 manatee-years) that were members of significant clusters. Unlike the warm season, the percentage of daily locations assigned to clusters in the winter did not differ significantly between adult males (median = 92%, IQ range = 42 - 100%, N = 10) and adult females (median = 87%, IQ range = 75 - 99%, N = 30; Wilcoxon two-sample test, $P = 0.97$). Subadults were similar to adults in the percentage of daily locations found in clusters (median = 80%, IQ range = 66 - 99%, N = 5). The percentage of daily locations assigned to clusters during winter varied significantly across seasonal movement patterns (Kruskal-Wallis test, $\chi^2 = 24.095$, $df = 4$, $P < 0.0001$): year-round residents (median = 100%, N = 6), N-C migrants (99%, N = 15), short-distance migrants (89%, N = 9), C-S migrants (75%, N = 15), and long-distance migrants (43%, N = 6). Residents and individuals overwintering in Brevard County were generally sedentary during the winter, but migrants overwintering in southern Florida typically made considerable long-distance movements during the winter (e.g., Fig. 9) and so a smaller proportion of their locations were in significant clusters.

Interannual Site Fidelity to Winter Range

Data on 20 tagged manatees indicated strong interannual fidelity to overwintering areas. Of 39 comparisons of cluster location across successive years, 32 (82%) showed overlap in at least 1 cluster. The median interannual distance between the centers of winter season clusters within the same region was 3.4 km (IQ range = 1.6 - 9.6 km, range = 0.2 - 109.4 km, N = 17, n =

40). For most (76%) of these animals, the center of their winter use areas remained within 10 km of the previous year's cluster (Fig. 13B). The distance between cluster centers from one winter to the next was significantly greater in the central region (median = 9.5, range = 2.1 - 109.4, N = 8) than in the southern region (median = 2.1, range = 0.2 - 12.4, N = 8; Wilcoxon two-sample test, $P = 0.04$). Data were insufficient to analyze by sex of adult or age class, but interannual site fidelity was not significantly correlated with body size ($r_s = -0.09$, $P = 0.74$).

For several manatees, the region of winter location clusters changed from one year to the next; these shifts are not reflected in the above statistics on within-region site fidelity. Two individuals (TBC-36, TNC-10) included in the winter cluster analyses altered their migration pattern by overwintering in a different region, as noted above (Fig. 11A). Winter cluster locations did not change, however, for another short-distance migrant (TFP-04) that changed its seasonal movement pattern in the fourth year of tracking; this female traveled south 200 km from Ft. Pierce to northern Biscayne Bay in response to a cold front in early March 1996 (Fig. 11B). Four manatees that maintained fidelity to their seasonal movement patterns and southerly winter destinations nevertheless showed regional shifts in winter cluster locations due to variations in migratory timing and duration spent at overwintering sites. C-S migrant TBC-03, for instance, showed strong fidelity to the Port Everglades power plant effluent canal, visiting the site in each of 8 consecutive years; however, she spent relatively little time there in most winters, and her location clusters varied greatly from year to year, as follows: no significant clusters in 1987-88, Sebastian in 1988-89, Port Everglades in 1989-90, northern Indian River (near Brevard power plants) in 1990-91, Vero Beach to Ft. Pierce in 1992-93, and Little River (northern Biscayne Bay) in 1993-94 (Fig. 10D). This adult female accounted for 4 of the 7 cases of non-overlap of location clusters between successive years. N-C migrant TBC-23 journeyed from the northern Indian River to pulp mills in the Florida/Georgia border region in each winter but the timing of the moves (and resulting cluster locations) varied as follows: early February 1991 (1 cluster near Brevard County power plants), late January 1992 (clusters at the Brevard County power plants and the pulp mill in St. Mary's, GA), and mid-December 1997 (1 cluster in the FL/GA border region) (Fig. 10F). Likewise, C-S migrant TPE-01 utilized the Port Everglades power plant effluent in 6 consecutive winters, but headed north in early January of 1 year, resulting in only 1 significant cluster near her warm season range in the Banana River that winter. Finally, C-S migrant TFP-06 spent most of the 1992-93 winter in the Vero Beach to Ft. Pierce area, but in 1993-94 her locations formed 2 clusters, 1 in this same area and 1 to the south in Riviera Beach; she also regularly but briefly visited Port Everglades in each winter (Fig. 10H). Some manatees formed significant winter clusters on their warm season range, in addition to clusters in their southerly winter range (e.g., Figs. 9, 10B,C).

Most manatees that we tracked over multiple years returned faithfully to the same winter ranges (Fig. 10) and the same warm-water refugia. The distance between clusters within a region from one winter to the next did not vary with the number of intervening years (Fig. 14B). Five adult females and 1 adult male that were tracked over 6 to 8 winters consistently returned to the same areas (Fig. 10A-D,F, 15B), though the amount of time spent at these destinations often varied among years.

Natal Philopatry

To determine whether seasonal ranges and movement patterns were similar in mothers and offspring, we tracked 4 cow-calf pairs for periods of 24.0 (TBC-09/TBC-25), 20.6 (TBC-09/TBC-35), 23.6 (TBC-24/TBC-43), and 9.5 months (TPE-04/TBC-29), representing the entire dependency period from birth to weaning for the first 3 pairs. The calves (3 male, 1 female) were tagged with VHF radio-tags a few days to several months before weaning and then were tracked after weaning as independent subadults for 15.0, 8.8, 2.4, and 6.5 months, respectively; the VHF tags were replaced with PTT tags on 3 individuals. After tag detachment, sightings of these subadults were confirmed by photo-identification of unique scar patterns (Beck and Reid 1995) and by observation (and sonic identification) of animals wearing belts.

Three subadults clearly adopted the C-S migratory patterns of their mothers (Fig. 16A,B). Although the fourth calf (TBC-29) lost his tag and belt to a boat strike 3 weeks into his first December as an independent subadult, his movements between his warm season range in the Banana River and winter range near the Indian River power plants suggest that he was continuing the year-round resident pattern that he had experienced as a second-year calf (Fig. 16C). Sightings of this calf with his mother (TPE-04) prior to tagging indicate that he was born in the 1989 warm season and that the pair migrated from the Banana River to SE FL in December 1989 (Fig. 16C). The mother-calf pair became trapped in the Port Everglades power plant intake canal in March 1990, where they remained until their rescue in July. Based on the history of warm season sightings of TPE-04, the pair was released in Brevard County in August 1990, and they remained in this area throughout the rest of their tracking histories.

The 4 subadults showed strong philopatry to the specific warm season ranges in the Banana River that they had occupied as dependent calves. Site fidelity within the same warm season, measured as the distance between location cluster centroids before and after weaning, was quantified as 0.6, 3.3, 3.7, and 4.7 km for the 4 animals. Interannual site fidelity, measured as the distance between warm season clusters from the last year as a dependent calf to the first year as an independent subadult, was 1.5 km for TBC-25 (Fig. 17A,B); this male was photo-identified in the same area several times during the warm seasons of 1991 and 1993, 2 and 4 years after weaning. Interannual site fidelity for TBC-43 was 1.7 km for the pair's principal range in the Banana River and 5.3 km for a secondary cluster in the Indian River where he was weaned. TBC-29 and TBC-35 were photo-identified on their natal warm season ranges up to 1 and 2 years after weaning, respectively.

These subadults were also philopatric to their natal winter ranges, including repeated use of specific warm-water refugia. Both of TBC-09's calves returned to the Port Everglades power plant effluent canal, 275 km south of their warm season range (Fig. 16A,B), and were photo-identified there 4 years after weaning. TBC-25 also used the inland Ft. Lauderdale power plant discharge canal and basins, as he had previously done as a nursing calf with his mother (Fig. 17C,D); his interannual site fidelity to natal winter range was 0.9 km. As noted above, TBC-29 returned as a subadult to the Brevard power plants during early winter—as he had as a second-year, dependent calf—rather than migrating south as he had in his first winter; interannual site fidelity was 8.5 km for this animal, but his locations as a subadult coincided with those from the previous year at the power plants. Lastly, TBC-43 was not tracked in winter after weaning, but was photo-identified in his first and fourth winters as a subadult at SE FL sites that he frequented with his mother, including Coral Gables Waterway, Little River, and Port Everglades. Unlike his mother, TBC-43 visited a Brevard County power plant in December of his first independent winter before migrating south; furthermore, the most recent sightings of TBC-43 at Brevard County power plants in January and February 2000 suggest that he may have changed his overwintering region at the age of 6.5 years.

Differences in the timing of migrations between female TBC-09 and her 2 newly independent calves indicate that the juveniles did not migrate between seasonal ranges with their mother. TBC-25 and TBC-35 initiated their southward fall migration within 1 and 3 weeks, respectively, after their mother's departure from the Banana River. TBC-25 began a slow (52-day) spring migration with several stopovers in mid-winter (30Jan90), at which time his mother was nearly back on her warm season range (Fig. 16A). While this northward movement during the middle of winter was similar between mother and offspring, the female's migration was rapid and direct, without stopovers. Unlike his mother, TBC-25 responded to a late winter cold front with a short, southward move to the Vero Beach power plant rather than returning all of the way back to Port Everglades (Fig. 16A). TBC-25 reached his natal warm season range in the Banana River on the same day in late March that he and his mother had in the previous spring.

Migratory Pattern and Seasonal Range Use in Brevard County

Brevard County waterways were major destinations of our radio-tagged manatees, as evidenced by the fact that 85% (N = 41) of the 48 manatees meeting seasonal movement criteria visited Brevard waters, and all but 1 of these spent at least 1 month there (Fig. 2). This percentage is significantly greater than that expected based simply on tagging location, given that 44% (N = 21) of these manatees were originally tagged in Brevard County (single classification goodness of fit test, $\chi^2 = 33.862$, $df = 1$, $P < 0.001$). In fact, 80% (12/15) and 67% (6/9) of manatees tagged in the northern and southern regions, respectively, that had sufficient data to include in the seasonal movement analysis traveled long distances to and occupied seasonal ranges (i.e., formed significant location clusters) in Brevard County during their tracking periods.

The Indian and Banana Rivers are shallow, sheltered, brackish lagoons that lie on either side of Merritt Island and are connected at 2 points: the narrow, man-made Barge Canal that bisects the island, and at the southern tip of Merritt Island where the mouth of the Banana River meets the Indian River (Fig. 15A). There was striking variation in warm season use of these 2 water bodies as a function of an individual's overwintering region. Manatees that spent the winter in Brevard County occupied core warm season ranges in the northern Indian River (57%) more often than in the Banana River (21%), whereas the converse was true for manatees overwintering south of Brevard (27% in the northern Indian River and 73% in the Banana River) (Table 9). Excluding manatees with core ranges in both rivers (N = 3) or in neither river (N = 4), the difference in river use by overwintering region was significant (likelihood ratio chi-square test of independence, $G = 8.474$, $df = 1$, $P = 0.004$). Considering the entire warm season range (i.e., all locations) rather than just the core range, 79% and 36% of manatees wintering in Brevard County were present in the northern Indian and Banana Rivers, respectively, between April and October; for manatees wintering to the south, the corresponding values were 58% and 92% (Table 9).

This strong association between warm season and winter ranges was related to differences between the 2 principal seasonal movement patterns. N-C migrants preferentially used the northern Indian River over the Banana River during the warm season; only 3 of these 11 manatees ever visited the Banana River during their tracking periods (Table 9). In contrast, 70% of the 20 C-S migrants that visited these waters occupied core warm season ranges in the Banana River; only 1 settled exclusively in the northern Indian River, and 2 formed clusters that spanned both lagoons (Table 9). While 95% of C-S migrants moved through the Banana River during the warm season, only 50% visited the northern Indian River (Table 9). This finding is all the more remarkable given the fact that the mouth of the Banana River is so narrow (~300 m) relative to the width of the Indian River (~2420 m) where the 2 water bodies meet (Fig. 15A). Most long-distance migrants utilized both lagoons (Table 9), which was not surprising since their seasonal movements were a combination of the N-C and C-S migratory patterns.

DISCUSSION

The Florida manatees tracked along the Atlantic coast of the United States in this 12-year study were highly mobile, migrating seasonally over extensive geographic areas (Figs. 2 and 3). They exhibited a diversity of seasonal movement patterns, ranging from some individuals that took up year-round residence in a localized area to others that migrated over several hundred kilometers of coastline each year (Fig. 4). Although the extent and timing of these migratory movements varied considerably among individuals, this variation was not related to sex, body size, age class, or reproductive status. The diversity of observed movement patterns over the annual cycle was underlain by common processes that reflected the animal's physiological and behavioral adaptation to its environment. Chief among the environmental factors driving long-distance movements was seasonal fluctuation in water temperature (Figs. 6 and 7), but temporal and spatial variation in the abundance and quality of forage was probably also important. Behaviorally, manatee movement patterns were structured by strong philopatry to the same seasonal ranges year after year (Figs. 13-15). From a landscape-level perspective, the result was that individual manatees typically occupied a few, relatively small core areas linked by lengthy travel corridors that passed either through mostly unsuitable habitats (e.g., northeastern coast between Brevard County and the St. Johns River) or through suitable habitats occupied by other manatees.

Seasonal Migrations

Moore (1951*a*) and Hartman (1974) speculated on the existence of seasonal migrations by manatees along the Atlantic coast based on reviews of historical accounts, interviews with local people, and a limited number of sightings by correspondents. Further evidence for this phenomenon was gathered through repeated aerial surveys of selected regions over the course of a year and through resightings of distinctly marked individuals on their winter and summer ranges (see references in Introduction). This study provides the first, clear, detailed demonstration of regular, long-distance, seasonal migrations in manatees.

Role of Temperature

The timing of most migrations was closely tied to changes in water temperature, with sharp drops in temperature below 20 °C during November and December precipitating a southward move to the winter range and warming trends in late winter and early spring associated with a northward return to the warm season range (Fig. 6). This corresponds well with previous observations on the timing of manatees' first appearance at winter aggregation sites, including warm-water springs and industrial thermal effluents, in relation to ambient water temperature (Hartman 1979, Rose and McCutcheon 1980, Bengtson 1981, Packard 1981, Powell 1981, Powell and Waldron 1981, Shane 1984).

Other environmental variables that are temporally correlated with seasonal variation in temperature, such as photoperiod, might also provide proximate cues to initiate migrations. A variety of evidence, however, points strongly to changes in temperature as the primary driving force behind most migrations: year-to-year variation in the initiation of fall migration from central Florida was related to the timing of the first major cold fronts (Fig. 7); about 90% of individuals left their warm season range in central Florida within 1 - 2 days of a rapid drop in water temperature (Table 5); many individuals that migrated northward from SE FL during mild periods in mid-winter or early spring quickly returned south upon encountering a cold front (Fig. 9); and regional variation in the timing of northward spring migration was associated with a temporal lag in warming of waters between northern and central regions (Fig. 6). Furthermore, this conclusion is entirely consistent with what is known of the Florida manatee's physiological intolerance to cold temperatures (Irvine 1983) and susceptibility to cold-related stress and mortality (O'Shea et al. 1985, Ackerman et al. 1995).

In the United States, selection pressure on the manatee's ability to find and move to warm waters during winter cold periods is strong. A number of cold-related mortality events have been documented over the past quarter century (Campbell and Irvine 1981, O'Shea et al. 1985, Ackerman et al. 1995), and historically there has been an association between periods of extreme cold and the subsequent discovery of manatee carcasses, even in southern Florida (Moore 1951*b*, 1956). This strong selection pressure, combined with the spatial distribution of suitable habitats, has resulted in the phenomenon of seasonal migrations along the Atlantic coast. In other parts of Florida, including the upper (southern) St. Johns River (Bengtson 1981), the Big Bend area on the northwest Gulf coast (Powell and Rathbun 1984, Rathbun et al. 1990), and southwest Florida (Lefebvre and Frohlich 1986), manatees also exhibit a seasonal pattern of movement between their warm season and winter ranges. Rather than making directed, long-distance migrations, however, manatees in these regions generally disperse shorter distances both northward and southward from warm-water aggregation sites in spring. Most individuals radio-tagged in winter at artesian springs in the upper St. Johns River and in northwest Florida remained within 100 km (waterway distance) of their winter aggregation sites throughout the warm season (Bengtson 1981, Rathbun et al. 1990, U.S. Geological Survey, unpublished data). Likewise, most tagged manatees dispersing in late winter and early spring from waters warmed by a Ft. Myers power plant moved down the Caloosahatchee River and into sounds, bays, and rivers within 100 km (waterway distance) of the plant (Lefebvre and Frohlich 1986). In all three regions the warm season range was north of the winter range for most tagged manatees, but some individuals migrated south from their overwintering site.

Role of Habitat

In addition to the seasonal fluctuation in water temperature, spatial and seasonal variation in habitat quality probably also contributed to the occurrence of seasonal migrations. Cold winter temperatures forced manatees to move to warmer waters and precluded access to northerly regions and habitats, except in proximity to reliable warm-water sources. When not constrained by temperature, manatees returned northward to their spring and summer ranges, apparently attracted by habitat that was of higher quality than that in their winter range. Physical and biological features of the habitat that affect manatee distribution during warm weather include currents and shelter from wave action, salinity and access to freshwater sources, bathymetry, and availability of aquatic vegetation (Hartman 1979, Lefebvre et al. 1989). Variation in physical characteristics of habitats across regions was unlikely to be sufficient to motivate the manatee's northward spring migration. Barrier islands provided shelter from ocean waves along nearly the entire east coast of Florida, and residential canal systems, marinas, coves, and creeks provided sheltered resting areas used by manatees throughout the intracoastal waters. The association between West Indian manatee distribution and freshwater sources (e.g., rivers, estuaries) is strong and consistent throughout the species' range (Lefebvre et al. 1989), and a variety of behavioral, ecological, and physiological evidence suggests that freshwater intake may be necessary to reduce the osmotic stress of feeding on hypertonic vegetation (Hartman 1979:58-59, Powell and Rathbun 1984, Ortiz et al. 1998). Manatees overwintering in SE FL had access to numerous sources of freshwater—including rivers, canals, and human-provided sources (e.g., hoses, storm water runoff)—so the idea that they migrated long distances in order to reach areas with more abundant or accessible freshwater seems untenable.

Regional and seasonal variation in the quantity or quality of aquatic vegetation may provide the ultimate explanation for the manatee's northward spring migrations. As a large herbivorous mammal dependent on a low-energy and low-protein diet, the manatee must spend a considerable proportion of time foraging to meet metabolic requirements. Estimates for free-ranging adults range from 5 to 8 hr per day spent feeding, thereby consuming an average of 7% of their body weight in wet vegetation daily (Hartman 1979:42, Bengtson 1983, Etheridge et al. 1985). Manatees have evolved a variety of physiological and morphological adaptations to efficiently process these large volumes of food, including a remarkably long retention time in the gut (Lomolino and Ewel 1984, Larkin 2000) and very high digestive efficiency (Burn 1986). Natural selection should also have led to the evolution of foraging strategies that maximize rate of energy or protein intake, subject to potential constraints such as acquisition of essential nutrients and avoidance of high salt loads (Birch 1975) or toxic secondary plant chemicals (Zapata and McMillan 1979). These behavioral strategies could include seasonal movements to areas with the most productive or nutritious vegetation, selection of plant species and organs with the highest nutritional value, and use of different feeding behaviors such as grazing versus rooting (Provancha and Hall 1991, Lefebvre et al. 2000). On a local scale (i.e., 10's of km), there is a strong association between the locations of manatees sighted on aerial surveys and the distribution of submerged aquatic vegetation (SAV) (Kinnaird 1985, Provancha and Hall 1991). This association has also been noted qualitatively from radio-telemetry studies in Florida (Lefebvre and Frohlich 1986, U.S. Geological Survey, unpublished data) and Puerto Rico (Deutsch et al. 1998, Lefebvre et al. 2000). In the northern Banana River manatee density was positively correlated with seagrass abundance (*Halodule wrightii*, *Syringodium filiforme*) and negatively related to abundance of the attached macroalga *Caulerpa prolifera* (Provancha and Hall 1991). Support for the hypothesis that spatial variation in food resources drives the spring migrations of manatees, when freed from temperature constraints, would require information on the abundance and nutritional value of forage summed over large regions. This would be an enormous task, but a qualitative assessment of the areal extent of SAV along the east coast indicates that the southern region has relatively little benthic vegetation compared to the central region, despite their roughly similar linear distances of shoreline, until one reaches the central and southern portions of Biscayne Bay (Florida Fish and Wildlife Conservation Commission 2000), which were not used by most of our tagged manatees.

Movements of manatees are likely to be influenced by seasonal fluctuations in standing crop (biomass), energy content, epiphyte load, and proximate constituents (e.g., protein) of their principal forage plants. Seagrass communities (including drift and attached macroalgae) on both coasts of north-central Florida undergo a major dieback in winter, followed by a spring growth flush, and maximal biomass and energy content by mid- to late summer (Gilbert and Clark 1981, Dawes et al. 1985, Dawes 1987). Because productivity and growth of seagrasses are positively related to irradiance and water temperature, seasonal variation is less pronounced in lower latitudes (Gilbert and Clark 1981, Hillman et al. 1989); seagrass beds in southern Florida, for example, do not show a major winter dieback (Jones 1968 cited in Dawes 1987). Manatees migrating north in spring left areas in the vicinity of warm-water refugia where vegetation resources may have been depleted by large aggregations of manatees. Packard (1984) determined that over a 2-month winter period manatees disturbed 40% of the seagrass beds in Jupiter Sound—a feeding area about 25 km north of a major warm-water aggregation site at the Riviera Beach power plant; the undisturbed beds were generally either too shallow to be accessible or were used regularly by fishermen. She estimated that manatees removed from half to two-thirds of the total biomass of seagrass communities showing evidence of manatee feeding. Within the feeding scars themselves, over 90% of the total biomass was removed (Packard 1984). Lefebvre et al. (2000) likewise found substantial reductions in seagrass biomass in patches grazed by manatees in the same region. Localized depletion of food resources may explain why manatees overwintering in SE FL showed such a strong preference for summering in the Banana River, which experienced little manatee use during the winter, rather than in the northern Indian River, where large numbers of manatees overwintered in the vicinity of two power plants (Table 9). Upon arriving on their warm season range at the end of the spring migration, most manatees were able to utilize beds of aquatic vegetation that had only been lightly grazed over the winter season. However, seagrass biomass and energy content in central Florida are typically at their annual winter low until April (Gilbert and Clark 1981, Dawes et al. 1985, Dawes 1987), about 1 month after the arrival of most manatees in this region. Manatees may have been attracted by the abundant sprouting of new shoots over extensive seagrass beds; although low in biomass, these young shoots would provide high nutritional value (e.g., protein), low ash content, and scarcity of epiphytes (Dawes et al. 1979, Zieman et al. 1984).

A striking exception to the temperature-induced seasonal migrations was the southward migration from northeastern Florida and Georgia to Brevard County, which took place over an extended period in the late summer and fall while water temperatures were still quite warm (Fig. 6) (Zoodsma 1991; see Rathbun et al. 1982 for monthly temperatures in Georgia). Rathbun et al. (1982) noted a similar seasonal pattern in the relative abundance of manatees north of Florida, with reported sightings being rare in the winter, increasing from spring through summer, and then declining rapidly from late summer (Jul-Aug) to early fall (Sep-Oct). They were surprised that manatees did not visit a warm-water effluent at a wood processing plant in Brunswick, GA during cool weather in the fall, although small numbers used it regularly during the spring. This matches findings from an aerial survey study of manatees in the narrow intracoastal waterways between SE GA (Kings Bay) and Volusia County (Oak Hill, Florida): winter sightings were rare; counts increased through the spring (Mar-May), declined through summer (Jun-Aug), spiked in September, and were nearly non-existent from late fall through winter (Nov-Feb) (Kinnaird

1985). The early fall decline in manatee sightings north of Florida corresponds nicely with the early fall peak in numbers in the ICW, which is clearly utilized as a migratory corridor between preferred habitats in NE FL/SE GA and Brevard County. Manatees summering in the lower St. Johns River may not follow the same fall migratory schedule, however. Kinnaird (1985) found a seasonal rise in the number of manatees using this broad stretch of river starting in April, with relatively constant numbers from May to November, followed by a dramatic decline and low numbers through the winter. A similar seasonal pattern in manatee abundance for this region has been documented in more recent years (Jacksonville University 1999). Although our data on fall migratory timing of tagged manatees using the St. Johns River were limited, 4 of 5 individuals departed after 25 October. In contrast, only 1 of 10 individuals summering north of the St. Johns River (n = 3 of 19 trips) had an average departure date this late in the season; most migrants (N = 7 of 10, n = 14 of 19 trips) had departed by 15 September.

We suggest that this apparent difference in "fall" migratory timing between manatees spending the warm season in the St. Johns River versus those summering to the north may stem from regional differences in their primary forage plants. In the lower St. Johns River manatees feed mostly on submerged beds of brackish or freshwater aquatic vegetation, such as eelgrass *Vallisneria americana* (Kinnaird 1985) whereas north of the river mouth they forage primarily on emergent shoreline vegetation, especially smooth cordgrass *Spartina alterniflora,* in salt marshes (Baugh et al. 1989, Zoodsma 1991). The arrival of manatees in the FL/GA border area in March, when water temperatures were usually cool enough to require the regular use of industrial warm-water effluents, and their subsequent return to Brevard County in summer or early fall suggest that seasonal changes in the abundance or nutritional quality of *Spartina* may play a role in the timing of these migrations. In an investigation of the seasonal dynamics of production, mortality, and mineral composition of a Georgia salt marsh plant community, Gallagher and coworkers (1980) found considerable fluctuation in the living biomass of the tall, creek-bank form of *S. alterniflora*, with the highest standing crop occurring in the early summer to fall. The nitrogen content of the above-ground tissues peaked between late winter and early spring when biomass was low, and the growth rate was maximal between early spring and early summer. Manatees migrating northward to the salt marshes of northeastern Florida and Georgia in spring were likely attracted to the rapid growth of young *Spartina* shoots rich in nitrogen. Given that the living standing crop of *S. alterniflora* remains high through October, and that the tissue nitrogen content is relatively stable but lower from May through January (Gallagher et al. 1980), there is no clear explanation for the departure of manatees from this region in summer to early autumn. Perhaps variation in other chemical constituents of *Spartina*—such as calcium, magnesium, or iron, all of which decline in tissue concentration during this time of year (Gallagher et al. 1980)—is involved. The biomass of seagrass communities in the northern Indian River increases steadily from April to September (Gilbert and Clark 1981), so migrant manatees may depart Georgia salt marshes before the end of the warm season because the nutritional value of foraging on seagrasses has risen above that of continued feeding on salt marsh grasses.

Long-distance Winter Movements

Winter movements of manatees along the Atlantic coast were dynamic and variable across individuals and years. About half of the tagged manatees made round-trip excursions of over 100 km in the middle of winter, sandwiched between their southward "fall" and northward "spring" migrations (Fig. 9). Regional and temporal variation in these winter migrations again demonstrate the importance of temperature as a constraining environmental factor. Long-distance winter movements were uncommon north of Brevard County but frequent to the south (Table 8). Manatees overwintering in Brevard waters were sedentary, most remaining in the northern Indian River within a day's swim of the power plants. The few individuals that migrated from the central to the northern region in winter remained near warm-water sites at their destination. The 260-290 km stretch of coastline between warm-water refugia apparently deterred most manatees from making these journeys in winter, when water temperatures in northern areas were consistently below the manatee's thermoneutral zone. South of Brevard County, the temporal correlation between temperature and winter migrations was clear: manatees that moved north in winter did so during periods of mild weather, and they returned south upon the passage of a cold front that sharply dropped water temperatures (e.g., Fig. 9).

The energetic cost incurred by winter migratory behavior may be substantial, given the large distances traveled (mean = 434 km) and the associated cost in loss of time spent foraging. Two adult females, one with a 3-month-old calf, covered over 1000 km in mid-winter migrations! Manatees reached their warm season range on nearly half of these round-trip excursions, yet remained there an average of only 3 days (Table 8). How can we explain the regular occurrence of individuals migrating long distances into cooler waters in the middle of winter? Some of these long-distance movements were actually spring migrations aborted by cold weather (e.g., March 1993 in Fig. 9). Cold fronts occurring in late winter or early spring often caused manatees en route to their summer range to reverse course, and sometimes stimulated manatees that had already reached their warm season range to head back south to a portion of their winter range. Towards the end of mild winters, on the other hand, some manatees returning north to their warm season range in the central region were able to remain there through the rest of the winter and spring without visiting heated water sources; 3 such individuals arrived as early as late January and numerous others arrived in mid- to late February. Thus, northward migration from SE FL in mid-winter can be viewed as a gamble that temperatures will remain mild enough for the remainder of the winter that the animal will not need to return south. Why would so many manatees take such a gamble?

We hypothesize that habitat quality on the warm season range, even in winter, is sufficiently greater than that on the winter range to offset the energetic costs associated with long-distance migration. Spatial and seasonal variation in the quantity and quality of food resources were discussed above. If depletion of forage in the vicinity of winter aggregation sites provided the main impetus for northward migrations, then such movements should have become more frequent as the winter season progressed. Of 52 round-trip winter migrations occurring between December and February, 31% were initiated in the month of December, 40% in January, and 29% in February. If spring migrations were included in the totals, the relative proportion of February departures would be higher. Nevertheless, the fact that nearly one-third of these trips started in December, presumably before there was substantial impact of manatee aggregations on local food resources, does not support the idea that food depletion was driving these movements. This does not imply that availability and quality of aquatic vegetation were unimportant, however. Seagrass availability was limited within 25 km to the south and 75 km to the north of the Port Everglades power plant, which was the principal winter destination for many tagged manatees in SE FL and one of the most heavily used manatee aggregation sites along the Atlantic coast (Reynolds and Wilcox 1994). Of 48 mid-winter migrations from SE FL, 27 (56%) started from this area, 14 (29%) from Lake Worth (location of the Riviera Beach power plant), and small numbers from other locales between Biscayne Bay and Hobe Sound. These figures may simply reflect the relative abundance of manatees in the region during winter, but they may also imply that resource limitation around the major aggregation sites promotes northward migration in winter.

From the manatee's perspective, another factor that may affect habitat suitability is the type and frequency of human activities in an area, especially vessel traffic. An alternative hypothesis for the occurrence of winter migrations is that manatees prefer and move to areas of lower watercraft traffic when their movements are not constrained by cold temperatures. We are unaware of studies on winter boat density that provide comparable data for central and southern regions. But the number of registered vessels, which may provide a crude index of watercraft traffic, was much greater for densely populated SE FL (146,430 for Martin to Miami-Dade counties) than for central Florida (76,538 for Flagler to St. Lucie counties) in 1998 (Florida Marine Patrol 1999). This probably underestimates the difference in actual boat density for two reasons: there is a seasonal influx of out-of-state boaters to SE FL for the winter; and the intracoastal waterways are generally much narrower in the southern region, resulting in greater congestion and nearly 4-fold more boating accidents (338 reported in 1998) than in central Florida (90 in 1998) (Florida Marine Patrol 1999). In addition to the potential for collisions with manatees, boating causes underwater noise pollution and may disrupt manatees while feeding, resting, or nursing (O'Shea 1995). A number of studies have noted shifts in manatee distribution on a local scale to areas less disturbed by recreational or industrial watercraft. In the presence of more recreational boaters and divers, manatees increased their use of no-entry sanctuaries around Crystal River's warm-water springs (Buckingham et al. 1999). The number of manatees using Blue Spring as a winter thermal refuge in the upper St. Johns River increased after boats were excluded from the narrow run in the late 1970's (Bengtson 1981). Provancha and Provancha (1988) detected a shift in the warm season distribution of manatees in the northern Banana River away from areas with increasing industrial activities, primarily boat and barge traffic engaged in space center operations. Manatees have also been found to decrease use of an area around an inactive marina shortly after it was reopened (Kadel and Patton 1991). Packard (1981), on the other hand, did not find that manatees overwintering between St. Lucie and Palm Beach inlets avoided areas of high boat density. Data are unavailable to adequately test these two hypotheses. Given the historical evidence for seasonal migrations (Hartman 1974) and the manatee's ability to adapt to and even exploit human-altered and urbanized environments (O'Shea 1988), however, it is unlikely that such long-distance movements into cooler, northerly waters were motivated primarily by a desire to avoid human activity or harassment. It seems most parsimonious to assume that whatever habitat factors attracted manatees to the central and northern regions in spring were also operating during the winter months.

Individual Variation in Migratory Timing

The timing of fall and spring migrations varied considerably among individuals following the same seasonal movement pattern (Fig. 6A). We were unable to detect any significant differences between female reproductive classes (with vs. without calf) or between the sexes in the timing (departure or arrival dates) of southbound or northbound migrations in both north-central and central-south regions. Ambient water temperature at fall departure from their warm season range in northern Brevard County was similar for lactating and single cows, contrary to expectation. Based on the percentage of calves sighted in aerial surveys over the Crystal River warm-water springs, Rathbun et al. (1990) inferred that cow-calf pairs arrived earlier in the fall and departed later in the spring than single animals. Despite the energetic demands of lactation (Oftedal 1985), the body condition (i.e., blubber thickness, girth, and mass/length ratio) of lactating female manatees is similar to that of non-pregnant, single females (Ward-Geiger 1997). Dependent calves have a greater ratio of blubber thickness to body radius than independent manatees (Ward-Geiger 1997), thus compensating for their lower surface-area-to-volume ratio. This may partly explain why calves, unlike independent subadults, are spared high mortality during freeze events (O'Shea et al. 1985), and why females do not alter their migratory timing when rearing a calf.

The timing of fall migration between central and southeastern Florida was also not significantly related to body size, over the size range in this analysis (225 - 350 cm). This result held true for both the absolute calendar date of departure and the various measures of water temperature at departure. During the return spring migrations, however, larger manatees arrived earlier on their warm season range than did smaller ones. Thermal inertia associated with larger size may have been an advantage as the manatees moved north into cooler waters, given the uncertainty of late winter cold fronts and the likelihood of poorer body condition at the end of winter. Use of warm-water effluents from power plants also affected migratory timing and this topic is discussed later under the section on *Management Implications.*

One of the most striking features of migratory timing along the Atlantic coast was the considerable variation among tagged individuals. The water temperature at which manatees in northern Brevard County departed from their warm season range varied substantially among individuals (16.2 - 22.3 °C). The "threshold" temperature range that stimulated migration was fairly consistent for those individuals tracked over multiple years (Fig. 8). This inter-individual variation in apparent "cold tolerance" may have a behavioral or physiological basis. While some individuals immediately started migrating south in response to the passage of a moderate cold front, others appeared to move to dredged basins or other deep-water sites that presumably cooled more slowly than the surrounding shallows. We hypothesize that manatees departing at lower temperatures took advantage of spatial variation in bathymetry or other physical features during cold fronts to select habitats with higher water temperatures, hence prolonging their stay on their warm season range. Verification of this idea will require a detailed analysis of PTT temperature data in relation to ambient water temperature at monitoring stations; alternatively, local movements of manatees in response to cold fronts could be mapped onto contours of surface and bottom temperatures determined from high-resolution infrared imagery or intensive field measurements. Although departure temperature did not vary with body size, variation in insulation (i.e., composition and thickness of blubber) or metabolic rate may have underlain the observed behavioral variation.

The focus on water temperature at departure may obscure a more complex response of manatees to cold fronts. Some evidence suggests that tagged manatees also responded to air temperature or to the rate of temperature change. Adult male TRB-01, for example, remained in the northern Banana River until water temperatures had dropped to about 15-16 °C in 2 years (no. 6 in Fig. 7B), yet departed at milder temperatures (19 °C) in 2 other years (Fig. 8). In both of the latter occasions, he departed soon after the arrival of a strong cold front that dropped the water temperature by 4.5 °C over the next 48 hr; in 1 case water temperatures fluctuated between 10-15 °C for nearly 10 days. Manatees may be able to assess the severity of the cold front by sensing the rate of decline in air and water temperatures or perhaps changes in other meteorological conditions (e.g., barometric pressure), and then deciding whether to seek local shelter or to initiate a long-distance migration. In the vast majority of cases, manatees departed only after there had been a noticeable drop in water temperature, which continued to decline after migration was initiated (Table 5). One further complication is that manatees appeared to vary in the sensitivity of their response to temperature change, just as household thermostats can vary. The movements of adult female TBC-09 are indicative of a sensitive "internal thermostat": despite being 1 of the first tagged manatees to leave the Banana River every fall (Fig. 8), she frequently returned north in mid-winter during periods of mild weather; declines in temperature, however, quickly sent her back to Port Everglades (Fig. 9, 10C). Relatively minor changes in temperature stimulated TBC-09's movements, whereas other animals (e.g., those that remained in SE FL for the whole winter) may have integrated temperature over longer time periods before initiating long-distance moves.

Movement Polymorphism

This tracking study has revealed a diversity of seasonal movement patterns among individuals, in terms of both the distance between warm season and winter ranges and the regions of migratory destinations. Most tagged manatees (87.5%) migrated between seasonal ranges separated by over 50 km, but at least 6 individuals were year-round residents of a particular area (Figs. 3A and 4). Among migrants, there was considerable variation in the distance traveled between northerly and southerly ranges (80 - 830 km), and one adult male traveled as far as Rhode Island, more than 2300 km north of his winter range (Fig. 3)! A majority of migrants traveled 250-350 km between seasonal ranges (Fig. 3A) because this represented the distance between the most highly used areas along the Atlantic coast (i.e., SE FL to Brevard County to NE FL/SE GA).

Long-term tracking of individual manatees showed great consistency in seasonal movement patterns over multiple years (Fig. 10). A qualitative examination of sighting records based on photo-identification (prior to and after tracking) for the manatees in our study corroborated the year-to-year consistency of movement patterns for the vast majority of individuals (U.S. Geological Survey, unpublished data). There were several exceptions, however, with some manatees shifting their overwintering regions (e.g., Fig. 11). One "year-round resident" of Brevard County (TPE-04, Fig. 4D), for instance, was known from photo-identification studies to have migrated to SE FL (Port Everglades) in 3 of the 6 years prior to tracking and to have apparently overwintered in Brevard County for 2 years (U.S. Geological Survey, unpublished data). The flexibility in movement patterns exhibited by some individuals potentially allowed them to respond adaptively to variation in winter severity and power plant operation, and to take advantage of the best foraging habitat during the winter season.

The existence of migrants and residents within the same population, a phenomenon termed partial migration, is not uncommon (Dingle 1996:304-310). It has been found in a wide variety of taxa, including insects, fish, tortoises, birds, and mammals (Sinclair 1983, Swingland 1983, Lundberg 1988). In populations of terrestrial herbivorous mammals exhibiting partial migration, as in Florida manatees, the relative proportion of migrants is much greater than that of residents (Schoen and Kirchhoff 1985, Tierson et al. 1985). Corkeron and Connor (1999) present evidence suggesting that some baleen whales in "migratory" populations remain in high-latitude waters year-round, although this may reflect individual flexibility from year to year rather than fixed differences in movement behavior among whales. The theory of evolutionarily stable strategies (ESSs) has been invoked to account for the maintenance of movement polymorphism within some populations (Sinclair 1983, Swingland 1983). At equilibrium, the ESS proportions of migrants and residents would be determined by frequency-dependent selection, so that the lifetime fitness of the alternative strategies should be equal. This theory has been applied to genetically-based polymorphisms, which is unlikely in the case of manatees, but it also seems applicable to polymorphisms stemming from transmission of learned behavior patterns from mother to offspring (see Natal Philopatry below). An alternative hypothesis that is supported for some bird species is that the movement polymorphism represents a conditional strategy, with dominant or territorial individuals maintaining residency in high-quality habitat and subordinates migrating to other areas (Adriaensen and Dhondt 1990). This idea can be dismissed for manatees, given their lack of territoriality and aggression (Hartman 1979) and their extensively overlapping ranges (Bengtson 1981, this study). The variability in migratory movements shown by some manatees, however, suggests that their behavior may be conditioned on environmental factors (e.g. winter severity).

We have categorized the seasonal movement patterns of Florida manatees along the Atlantic coast into several "types" that, for the most part, were fairly discrete (Fig. 4). This discreteness likely resulted from the disjunct nature of suitable manatee habitat on the east coast. Nevertheless, there was a gradation of distances between seasonal ranges from year-round residents to short-distance migrants to medium-distance migrants, especially in the C-S region (Fig. 3A). An alternative approach is to view the range of variation in seasonal migratory behavior as a continuum rather than as discrete forms. Taking this perspective, we see that the seasonal movement patterns of year-round residents (excluding 2 in the Florida Keys) resembled that of seasonal migrants on a compressed spatial scale: they moved to industrial warm-water sites upon the onset of cold weather in late fall to early winter; they restricted their winter movements to areas around these thermal refugia, but sometimes migrated to warm season areas during mild periods in mid-winter; and they dispersed away from the warm-water sites in the late winter to early spring. Essentially, the residents in the central and northern regions made temperature-related migrations between warm and cold season ranges, though the distance was as little as 20 km and the overlap between seasonal ranges was sometimes extensive. These similarities indicate that migrants and residents were responding to the same environmental cues in similar ways, but over different spatial scales.

Fidelity to Seasonal Ranges

Florida manatees exhibited strong within-season fidelity to relatively small home ranges, as indicated by the results of the cluster analyses: most individuals used only 1 or 2 core areas within a winter or warm season, and approximately 90% of their mean daily locations were encompassed within these spatial clusters. These findings argue forcefully against the notion that manatees are nomadic in their movements. While individuals occasionally made long-distance excursions outside of their normal seasonal range (e.g., Fig. 10E), the general pattern was one of directed movements to specific areas that were used for prolonged periods. Migrants to the northern region typically possessed warm season ranges in both Brevard County and in the north, whereas migrants overwintering in SE FL often had winter location clusters in both Brevard County and in the south.

Although manatees showed flexibility in the timing of seasonal migrations across years (e.g., Fig. 7), they were remarkably faithful to the destinations of their long-distance moves from one year to the next (e.g., Fig. 15). Within a region, the median distance between the centers of location clusters across successive years was <5 km in both seasons (Fig. 13). Long-term tracks of individuals demonstrated that this site tenacity was maintained over multiple years (Figs. 10, 14 and 15). Given that most tagged manatees (71%) regularly traveled >200 km between winter and summer ranges (Fig. 3A), the year-to-year distance between clusters represented a very small fraction of the individual's annual range.

Exceptions to the general pattern of strong philopatry yield further insights into the movement behavior of these animals. Several tagged manatees changed their overwintering region between years, either by completely shifting their winter range (e.g., Fig. 11A) or by altering the proportion of time spent in different regions (e.g., Fig. 10D,F). Shifts in warm season range occurred even less often than during winter. One of the 4 cases in which there was no overlap of warm season clusters across successive years was particularly revealing. This involved the release of adult female TBC-23 in the northern Banana River after 4 months of rehabilitation in captivity, following her rescue in the Halifax River. She remained in the Banana River for about 1 month after her release before traveling to the Indian River and migrating to NE FL/SE GA. This N-C migrant never returned to the Banana River during 1244 days of tracking over a 10-year period, suggesting that the release site was outside of her established range; this pattern of differential lagoon use in Brevard County was consistent with that of other N-C migrants (Table 9). A long-distance migrant (TNC-13) changed her spring and early summer use areas from the Satilla River, GA and the Broad River, SC in 1997, to the northern Indian River in 1998, to the Banana River in 1999; in each year she spent at least part of the summer and all of the fall in the same stretch of the Broad River (Fig. 4B). The familiarity that these long-distance migrants have with most of the Atlantic coastline may give them greater flexibility in selecting optimal foraging habitats compared to conspecifics with more limited annual ranges. Dramatic shifts in range use within the warm season were sometimes associated with reproductive events. On several occasions adult females rapidly swam 90 - 150 km north or south of their main range in the Banana River to give birth in sheltered canal systems, boat basins, or narrow rivers; they typically returned to the female's normal range about 1 month after birth (Reid et al. 1995, this study). These cases of intra-individual variability indicate that manatees have the potential to alter their movement behavior, at least within the geographic range of their experience, in response to environmental change.

Moore (1956) provided the first evidence of interannual fidelity to a cold-induced aggregation site: 7 of 10 identifiable individuals were sighted at an industrial effluent in the Miami River in more than 1 winter, and 4 were sighted at the same warm-water site 5 years apart. Over the course of 1 winter, these 10 manatees were resighted multiple times over a 50-day period, indicating within-season fidelity to this site. Long-term fidelity to warm-water aggregation sites in winter has since been well-documented using photo-identification methods at natural springs in the Crystal and Homosassa Rivers and in the upper St. Johns River (Powell and Waldron 1981, Powell and Rathbun 1984, Rathbun et al. 1990, 1995, Beck and Reid 1995, O'Shea and Hartley 1995). The probabilities of sighting a particular cataloged individual sometime during the winter at these sites were 0.74 and 0.95, respectively (Langtimm et al. 1998), indicating a high return rate to these natural winter refugia. Resightings of distinctively scarred manatees along the Atlantic coast documented high site fidelity across years to major winter aggregation areas (Reid et al. 1991). The resighting patterns were complex, however, as movements among all east coast aggregation sites were observed within and across winters. Reid et al. (1991) concluded that many of the within-season changes in overwintering sites could be attributed to manatees stopping at thermal refugia along their migratory routes. Although we did not analyze manatee use of specific warm-water aggregation sites, our findings of strong fidelity to winter ranges and the dynamic nature of manatee movements between central and SE FL in winter, corroborate those of Reid and coworkers (1991) and flesh out the interesting details of movements that are hidden from the photo-identification approach.

Prior to this study, limited information was available on manatee movements and site fidelity during the warm season because the animals are more dispersed over a greater area than during the winter months. Despite the accuracy of most of Daniel Hartman's conclusions about Florida manatee ecology and behavior, his thoughts about fidelity to their warm season range proved incorrect: "I doubt that manatees return to the same summer range year after year or that the movements of each individual follow a repetitive pattern" (Hartman 1979:30). Opportunistic photographic efforts at 3 to 4 aggregation sites in the Banana River recorded the summer return of several individuals to the same or nearby locations following winter absences (Shane 1983, Reid et al. 1991). More intensive photo-identification work by Koelsch (1997) has also documented individual fidelity to warm season ranges in Sarasota Bay on the Gulf coast. Although Bengtson (1981) did not attempt to quantify interannual variation in use of the upper

St. Johns River by individual manatees, the temporal-spatial patterns of movements for 8 radio-tracked animals appear similar from the first to the second year. Zoodsma (1991) found that 3 radio-tagged manatees (also included in our study) showed strong site fidelity to warm season ranges in SE GA. Shane (1983) speculated that site fidelity in the warm season might be nearly as strong as that in the winter. Our telemetry data indicate that an individual's fidelity to its warm season range is usually even stronger than to its winter range. This probably reflects the more predictable environmental conditions in summer compared to the vagaries of weather and power plant operations in winter.

No comparable long-term data on individual movements exist for other sirenian species, but interannual fidelity to breeding or feeding grounds has been well-documented for other marine mammal species that migrate seasonally (e.g., pinnipeds: Baker et al. 1995; whales: Clapham et al. 1993; sea otters: Jameson 1989). Large terrestrial herbivores (e.g., deer) in the temperate regions of North America exhibit a similar pattern of strong long-term fidelity to seasonal home ranges (Hoskinson and Tester 1980, Edge et al. 1985, Schoen and Kirchhoff 1985, Tierson et al. 1985, Garrott et al. 1987). As in manatees, fidelity in these species is stronger to summer than to winter ranges because the latter are affected by the distribution of snow cover, which varies from year to year.

The fitness advantage accruing to manatees that return repeatedly to the same, reliable thermal refugia in winter is obvious, given their vulnerability to cold-related stress and mortality (Irvine 1983). This has undoubtedly generated strong selection pressure for site fidelity to traditional warm-water sites (Bengtson 1981, O'Shea et al. 1985). Less clear are the benefits to manatees of returning to the same river system, lagoon, or section of ICW each warm season. Familiarity with the locations of essential resources, including aquatic vegetation and freshwater sources, probably increases an individual's efficiency in energy acquisition by reducing time spent searching. Although the locations of seagrass, salt marsh grass, and other manatee food plants are fairly predictable and easy to locate, recent findings on sirenian feeding ecology and their impacts on seagrass communities suggest that quality of food resources may be more spatially and temporally heterogeneous than we realize. Dugongs (*Dugong dugon*) have been observed to repeatedly graze the same seagrass meadows in large herds, causing a shift in species composition towards preferred pioneer species that are more nutritious (less fiber, more nitrogen) than the less preferred dominant species (Preen 1995). Preen (1995) coined the term "cultivation grazing" for this foraging strategy. Although the West Indian manatee is much more of a generalist herbivore than the dugong, Lefebvre and coworkers (2000) suggest that manatees may return repeatedly to previously grazed areas and that, as in dugongs, this grazing activity may promote the growth of the early successional species (*H. wrightii*) apparently preferred by manatees. Regardless of the effects of herbivory on seagrass community structure, leaf cropping seems to improve the nutritional quality of the regenerated seagrass blades by increasing nitrogen content and decreasing ash and fiber content (Dawes et al. 1979, Zieman et al. 1984). The intimate knowledge of seasonal and spatial variation in forage plants in a particular area provided by long-term site fidelity may improve the quality and quantity of an individual's diet relative to an inexperienced individual.

The other major environmental challenge affecting manatee survival has historically been hunting by coastal peoples, and this is still a serious threat in some parts of the species' range (Lefebvre et al. 1989). In Florida this hazard has been replaced by the threat of collisions with speeding watercraft (Wright et al. 1995). It is conceivable that manatees reduce the risk of being struck by selecting habitats for resting, feeding, and traveling that have lower vessel traffic or deep waters for escape. This may explain why manatees commonly forage on the fringes of grassbeds adjacent to deeper water (Lefebvre and Frohlich 1986, Lefebvre et al. 2000). Familiarity with the subtleties of an area's bathymetry, watercraft traffic patterns, and safe travel corridors is likely to enhance an individual's chances of survival, whether the threat be hunting or boat strikes. Thus, warm season site fidelity may have evolved in response to environmental pressures that included fine-scale spatio-temporal variation in food plant quality and in risk of "predation."

Natal Philopatry

The hypothesis that manatees acquire their migratory patterns and seasonal ranges from their mothers during the 1.5 - 2.0 year dependency period has been stated so many times in the literature (e.g., Bengtson 1981, O'Shea and Kochman 1990) that it is sometimes accepted as fact. There has been little solid evidence to support it, however, except for the return of independent individuals to the warm-water springs that they used as calves (O'Shea and Hartley 1995, Rathbun et al. 1995). The movement pattern of 1 tagged manatee in the upper St. Johns River before and after weaning also supports this contention (Bengtson 1981). The seasonal movements and ranging patterns of 4 immature manatees that we tracked with their mothers as dependent calves and then after weaning as independent subadults provide strong evidence for natal philopatry to warm season and winter ranges, as well as fidelity to migratory patterns (Figs. 16 and 17). The fact that most captive-raised manatees released as subadults along the Atlantic coast did not undertake typical seasonal migrations (Bonde et al. 1998), despite the overwhelming occurrence of migratory behavior in the wild population (this study), also supports the idea that calves learn seasonal movement patterns from their mothers.

Traditions include patterns of movement and behavior that are transmitted from generation to generation and maintained in a population through non-genetic means (Hochbaum 1955, Wilson 1975:168). Traditions may play an important role in manatee movement patterns and habitat use, including use of warm-water refugia (Bengtson 1981, O'Shea and Kochman 1990). The available evidence indicates that calves learn the locations of key resources and migratory routes from their mothers, but the frequent, transient formation of groups could also promote the spread of information among unrelated animals (O'Shea and Kochman 1990). Traditional movement patterns mediated by mother-offspring transfer could maintain the inter-individual variation that we observed in seasonal movement patterns, annual range extent, and migratory behavior (e.g., temperature threshold) across generations. Another consequence is that matrilineally-related kin, particularly adult females and immatures, should share home ranges (Waser and Jones 1983); this may not apply as rigidly to adult males since they wander more during the warm season (Fig. 5, see Sex Differences in Movement Patterns below). This could explain the partial isolation between C-S and N-C migrants through differential use of the lagoonal waters of Brevard County by different matrilines (Table 9). What effects the existence of such loose kin groups might have on patterns of social behavior, survival, or reproduction are unknown. It also implies the potential for population genetic structure at a much finer spatial scale than has been examined to date. Even lacking genetic variation among matrilines that follow different movement patterns, the behavioral traditions should be subject to selection (through natural means or human activities) if individuals maintain them consistently over time (Avital and Jablonka 1994). The result would be rapid population-level change in the relative frequencies of different seasonal movement patterns in response to environmental change. This reasoning may be too simplistic, however, because a number of our tagged manatees have shown variability in their movements from year to year, suggesting that individuals are able to adaptively modify their behavior. Our tracking investigation has raised many interesting questions on this front and points to the need for more research on the juvenile/subadult life stage, in particular focusing on the development of movement patterns, behavioral response to cold temperatures, and degree of flexibility in straying from maternally-transmitted traditions that are no longer locally adaptive.

Sex Differences in Movement Patterns

The pattern of seasonal movements, extent of annual range, migratory behavior, and degree of interannual fidelity to seasonal ranges were similar between mature males and females. The sexes differed significantly, however, in daily travel rate during the warm season, with adult males moving more than females (Fig. 5). Adult males also spent more time away from their warm season core areas (i.e., location clusters) than did adult females. In general, females were relatively sedentary within one or two principal warm season location clusters, whereas males showed frequent, erratic north-south excursions away from their core areas (Fig. 12). The sex difference in movement rate occurred during the 6-month period from April through September, which corresponds closely with the main breeding season in Florida, as determined by seasonal variation in recovery of perinatal carcasses (Ackerman et al. 1995), carcass analysis of male and female reproductive tracts (Odell et al. 1981, Hernandez et al. 1995, Marmontel 1995), and observations of mating herds and births (Kinnaird 1985, O'Shea and Hartley 1995, Rathbun et al. 1995, Reid et al. 1995). We found no sex differences in movements or travel rates during the winter. Notably, free-ranging males undergo a severe reduction or cessation of testicular activity and spermatogenesis in winter (Hernandez et al. 1995), during which testosterone levels are low in most captive males (Larkin 2000). Thus, the proximate explanation for the increased movements of adult males during the warm season may be related to elevated testosterone levels, but the seasonal pattern of male reproductive activity (including hormonal regulation) probably evolved in response to the seasonality of estrus. The role of environmental factors in generating the Florida manatee's diffusely seasonal pattern of female reproduction is discussed by Rathbun et al. (1995).

These findings reflect fundamental differences between the sexes in reproductive strategy. Adult female life history is characterized by long periods of calf-rearing (Rathbun et al. 1995, Reid et al. 1995) punctuated by short-lived reproductive events (parturition, weaning, and mating) that sometimes result in long-distance excursions outside of the individual's normal range (Reid et al. 1995). As with most mammals, male manatees provide no parental care and invest their reproductive effort into searching for and mating with estrous females. The erratic warm season movements of males probably represent both mate-searching excursions and associations with mating herds, in which a group of up to 20 males closely follows an estrous female for a period of 1 to 4 weeks (Hartman 1979, Bengtson 1981, Rathbun et al. 1995). Mating herds can cover long distances, as illustrated by one focal female that traveled 160 km over 12 days accompanied by several males (Bengtson 1981). Bengtson (1981) noted that tagged adult males traveled the narrow and interconnected waterways of the upper St. Johns River basin in regular "circuits" through their home range that took 6 - 10 days to complete, apparently in search of receptive females. The males investigated creeks and other waterways off the main river channel, interacted frequently with conspecifics, and continued this "patrolling" pattern of movements until an estrous female was encountered. Although his sample of tagged adult manatees used in statistical comparisons was small (3 males, 3 females), Bengtson likewise found that adult males traveled greater daily distances and made long trips with greater frequency than did adult females, but the difference occurred during the summer and fall; both sexes remained close to a warm-water source during winter and dispersed long distances in the spring.

MANAGEMENT IMPLICATIONS

Identification of High-use Areas

At a gross scale of resolution, 3 geographic areas were identified as being important to large numbers of tagged manatees for extended periods: (1) the rivers, tidal marshes, and sounds between Fernandina Beach, FL and Brunswick, GA during the warm season (northern region); (2) the Banana and Indian Rivers in Brevard County year-round (central region); and (3) northern Biscayne Bay and Port Everglades during the winter (southern region) (Fig. 2). Other locales outside of these areas that were also important, but were used by smaller numbers of tagged manatees or for shorter periods, included: the lower St. Johns River, the Sebastian River, the southern Indian River between Sebastian and Jupiter, and northern Lake Worth. Manatees typically traveled directly and rapidly between these favored ranges (e.g., fall migration lasted an average of 10 days, Table 6), using the intervening stretches of coastline primarily as migratory corridors. Two sections of the coast with little suitable habitat that manatees utilized primarily as travel corridors were: (1) the St. Johns River mouth to the Mosquito Lagoon (except for the Tomoka River), and (2) southern Lake Worth to northern Biscayne Bay (with the major exception of the area surrounding the Port Everglades and Ft. Lauderdale power plants). Even areas with considerable suitable habitat that were occupied nearly year-round by some tagged individuals, such as the intracoastal waters between the Sebastian River and Jupiter Sound, were traversed quickly by many other animals during migrations (Figs. 2 and 4). Hence, despite their extensive movements over the annual cycle (Fig. 3), most manatees occupied only a few, relatively small areas on a seasonal basis (e.g., Fig. 15) and treated the intervening waters as travel routes. Manatees were infrequently found on the ocean side of barrier islands, which they mainly used for long-distance movements between inlets. We caution that the distribution of manatees tracked in this study should not be assumed to reflect the population distribution along the Atlantic coast, because we did not tag a random sample of the population. For example, relative use of Georgia waters was probably inflated due to the large number (N = 22) tagged at pulp mill effluents in Fernandina Beach and Brunswick; conversely, use of the lower St. Johns River and the southern Indian River may have been underrepresented in our study. Nevertheless, our findings highlight essentially the same resource areas and migratory corridors as identified using aerial survey and other methods (Hartman 1974, Beeler and O'Shea 1988).

Brevard County stands out in our study as the single most important area for manatees along the Atlantic coast of the United States. Indeed, 70% of 27 manatees tagged outside of this county and tracked during both winter and warm seasons traveled to and occupied seasonal ranges in Brevard waterways (Fig. 2). Earlier investigations of manatee distribution and abundance also concluded that a large proportion of the Atlantic subpopulation resides in this area, at least on a seasonal basis (Hartman 1974, Shane 1983, Beeler and O'Shea 1988, Provancha and Provancha 1988). Aerial surveys for manatees in Brevard County have revealed a distinct seasonal pattern in relative abundance, with counts peaking during the spring (March to April) and, to a lesser extent, during the autumn (Shane 1983, Provancha and Provancha 1988). Shane (1983) suggested that these fluctuations represented waves of migrants moving into the region during these seasons. Our radio-tracking study provides an individual perspective on the use of these water bodies that accounts for the observed seasonal variation in aerial survey numbers. The striking spring peak in abundance resulted from the temporary confluence in Brevard County of manatees with different seasonal movement patterns, including: (1) C-S migrants (and some short-distance migrants) returning to their warm season range from SE FL in late winter to early spring; (2) long-distance migrants similarly arriving in Brevard from SE FL for a 1- to 4-month stay in the spring, before continuing on to their more northerly warm season range; and (3) N-C migrants that overwintered in Brevard County and were waiting for temperatures to warm before departing for their warm season range in NE FL or GA (Figs. 4A,B and 6A). By May most animals migrating to the northern region had left Brevard waters, leaving warm season residents (i.e., C-S migrants) and year-round residents in the county. This explains why aerial survey counts for the entire county were relatively constant for the remainder of the warm season until late autumn (Shane 1983), when presumably there was an influx of manatees that had been summering in the St. Johns River. Manatee numbers in the Banana River, however, did not increase in the fall (Shane 1983, Provancha and Provancha 1988), which makes sense given that most N-C migrants did not visit this waterway (Table 9). The rapid decline in manatee abundance in both the Banana River and the entire county in December (Shane 1983, Provancha and Provancha 1988) is consistent with the timing of southward migration of the tagged animals in this study.

Brevard County provided essential habitat to manatees year-round, with the northern and mid-Banana River being heavily utilized during the warm season and the Indian River (especially in the vicinity of the power plants) supporting a large number of manatees through the winter, as noted by Shane (1983). Because water temperatures in Brevard County frequently dropped below the manatee's physiological limits of tolerance, this region could not sustain these animals through most winters without the existence of artificial warm-water sources. Yet our data on long-distance winter migrations revealed that manatees overwintering 200-300 km to the south sometimes visited Brevard waters for short periods during mild spells; some individuals were even able to remain in the Banana River for the latter half of the winter. These shallow, brackish lagoons also served as a critical link for manatees migrating seasonally between high-use areas in SE FL and NE FL/SE GA. Given that Brevard County was a major hub of manatee activity in all seasons, reduction of human-caused mortality and protection of seagrass and other essential habitats in these waters will be key to ensuring recovery of this endangered aquatic mammal.

Establishment of Protected Areas

One of the tasks identified in the Florida manatee recovery plan is to "establish regional protected area networks containing essential manatee habitat" (U.S. Fish and Wildlife Service 1996, p. 76). This objective can be accomplished through a variety of mechanisms, including expansion of existing national wildlife refuges and state parks or preserves, acquisition of new areas containing key manatee habitat, and designation of manatee sanctuaries (areas where all waterborne activities are prohibited) and manatee refuges (areas where certain waterborne activities are regulated) (U.S. Fish and Wildlife Service 1996). In addition to the critical goal of securing the long-term future of essential habitats (e.g., seagrass meadows, resting areas), these and other management actions, such as posting of boat speed zones, aim to reduce watercraft-related injury and mortality and to minimize human disturbance that may exclude manatees from preferred habitats and adversely affect their energy budgets (O'Shea 1995). Two water bodies that have been off limits to the public for security reasons—Kennedy Space Center (KSC) in the northernmost Banana River and Kings Bay Naval Submarine Base off Cumberland Sound, GA—provide de facto refuges for manatees, even though industrial activity and large vessel traffic present some threats. Both areas were heavily utilized by manatees, including a number of our tagged animals, during the warm season (Provancha and Provancha 1988, Zoodsma 1991). The extent to which exclusion of recreational boat traffic from these areas encouraged high manatee use is not clear, but manatees have been shown to increase use of small sanctuaries at warm-water springs as the number of recreational boats (and divers) increased (Buckingham et al. 1999).

This radio-telemetry study has yielded information on seasonal variation in manatee movements and high-use areas along the Atlantic coast that has been valuable in the development of measures by managers charged with recovering the population and protecting its habitat. Along with aerial survey and other sources of data, our telemetry findings have provided scientific justification for the designation of manatee protected areas. One prominent example was the establishment of a 46 km^2 motorboat-prohibited area within the Merritt Island National Wildlife Refuge in the northern Banana River, an area contiguous with the KSC "refuge" and known to be utilized by large numbers of manatees. Identification of the Sebastian River as an important migratory stopover site and as a "natural" warm-water refuge led to the designation of slow-speed zones in and around this waterway and a motorboat-prohibited area at a manatee aggregation site off the river's north fork. The telemetry data have also been regularly reviewed by managers in evaluating marina siting plans, boat speed zones, and other actions that could impact manatees.

The strong fidelity shown by manatees to seasonal ranges has important implications for the effectiveness of a protected area network in recovering manatee populations. How are manatees likely to respond to the creation of new protected areas, where boat traffic or other forms of human harassment are reduced or absent? The answer probably depends on a number of factors, including season of use, relative habitat quality, sex of the animal, and the time scale over which "response" is measured. Manatees were so tenacious to their warm season range(s), both within and across years (Figs. 13A, 14A), that an animal would probably abandon its home range in favor of a nearby sanctuary only if it became unsuitable for foraging or experienced a high level of human disturbance. Four of 5 tagged individuals with their warm season range in the mid-Banana River, for instance, did not shift their range after the 1990 establishment of a motorboat-prohibited refuge a few km to the north (Fig. 15A). The lack of movement into the refuge by these individuals probably reflects the fact that their home ranges provided excellent habitat (i.e., abundant seagrass beds, ready access to freshwater at a sewage treatment plant, and sheltered areas for resting) and extensively overlapped year-round slow speed zones, so there was no incentive to move. The wide-ranging movements of adult males during the spring and summer suggest that males should have a greater chance than females of encountering new protected areas, but once found, should be less likely to remain there. These findings indicate that the most effective approach (and the one most frequently used to date) is to establish refuges or to take other protective measures in waters that are already heavily utilized by manatees. Given the flexibility that manatees have shown in the timing of their movements, we expect that individuals visiting such high-use areas may increase the amount of time spent there after protection.

Individual manatees were also faithful to their core winter ranges within a given region (Fig. 13B, 14B). They were more likely to change overwintering regions from 1 year to the next, however, than they were to switch summering regions. This finding is consistent with year-to-year variation in the proportion of manatees counted at different east coast power plants (Reynolds and Wilcox 1994, Garrott et al. 1995). The apparently greater lability in overwintering grounds, combined with the dynamic nature of winter movements south of Brevard County (Fig. 9), suggests that manatees may more readily discover and occupy a newly established protected area (within their annual range) in winter than during the warm season. The presence of a reliable warm-water source within or in close proximity to a protected area should greatly increase its attractiveness to manatees in winter. Winter use of industrial heated effluents by manatees throughout much of their range attests to the animal's ability to adapt to and exploit human-altered environments (O'Shea 1988). The time frame in which manatees adopt a new protected area should depend on: (1) their probability of encountering the area, which will increase with its proximity to frequently used travel routes or high-use areas; and (2) the relative difference in habitat quality (including human disturbance) between their currently used range and the new area. If the protected area is already within an individual's seasonal range, we hypothesize that the animal's center of activity would shift toward the protected area.

Implications of Migratory Behavior for Boat Speed Regulations

Manatees share the intracoastal waters of Florida with over 1 million boaters (O'Shea 1995), many of whom visit the state for the winter months. The roughly similar timing of north-south migrations by manatees and humans along the Atlantic coast, both of which travel primarily in the ICW, may place manatees at greater risk of watercraft strikes while migrating. Vessel traffic passing the Palm Valley Bridge in the ICW of NE FL, for example, increased in spring (net northward movement) and fall (net southward movement) (Jacksonville University 1999). Ackerman et al. (1995) found that watercraft-related manatee mortality in NE FL was highest during the warm season, but in SE FL it was highest during the winter; this difference may simply reflect the seasonal shift in manatee distribution. Half of the manatees observed during Kinnaird's (1985) aerial surveys of the ICW in NE FL and SE GA were traveling; of those, 82% were swimming within 5 m of shore and the rest were traveling in boat channels.

Our data indicate that seasonal protections for manatees in the ICW should not be applied uniformly across the entire Atlantic coast. In fact, the seasons of greatest use of the ICW were very different for migrations north and south of Brevard County. Pulses of migrants traversed the ICW between central and SE FL from late February to early April and from late November to late December (Fig. 6), but long-distance north-south movements occurred throughout the winter season (Fig. 9). The ICW in NE FL, on the other hand, experienced greatest use during the non-winter months; timing of movements was less synchronized than in the south, but peaks occurred from mid-March to mid-May and from early July to mid-November (Fig. 6). We recommend that the strongest boat speed regulations for the ICW south of Brevard County take effect from November through April, and for the ICW north of Brevard County to apply from March through November. Where currently established boat speed zones or exclusion zones have a seasonal restriction (Florida Fish and Wildlife Conservation Commission 2000), they generally accord well with these recommendations. Of course, much of the intracoastal waterway south of Brevard County was occupied by manatees throughout the warm season as well (e.g., Figs. 2 and 4C), so appropriate protective measures such as boat speed zones need to be in effect year-round in many areas.

The analyses of migratory behavior also highlighted the importance of stopover sites, particularly during the spring migration between central and SE FL. Manatees often took refuge at some of these sites, including the Sebastian River and the Ft. Pierce power plant, during the passage of late winter and early spring cold fronts. Other stopover areas were used for "staging" prior to the main migratory leg (e.g., area around Haulover Canal in northern Brevard County), for resting and nursing in quiet waters (e.g., Tomoka River), or for foraging on seagrass beds (e.g., ICW between Ft. Pierce and Vero Beach). Shane (1983) also noted the temporary aggregation of large numbers of manatees in the spring at certain sites, such as the Banana River Marine Service Marina. The most frequently used areas for migratory stops deserve protection—of manatees from speeding boats and of the resources to which the animals were attracted. Some of these sites, such as the Sebastian and Tomoka Rivers, have received such protection; other areas, such as the northern Indian River near Haulover Canal, may need stronger protection on a seasonal basis.

Protection and Restoration of Manatee Foraging Habitats

Sirenian biologists recognize that the ultimate threat to the long-term existence of manatees in Florida is habitat loss caused by rampant coastal development and associated deterioration in water quality (U.S. Fish and Wildlife Service 1996). One of the common characteristics of high-use manatee areas during the warm season along the east coast of Florida was the presence of abundant submerged aquatic vegetation. These plant communities, particularly the seagrasses upon which manatees thrive, are highly susceptible to reductions in water clarity (Dennison et al. 1993, Stevenson et al. 1993). Increased turbidity can result from urban and agricultural runoff and from physical disturbance of the substrate by dredging and boat propellers; phytoplankton blooms facilitated by excess nutrient inputs from point and non-point sources also reduce the level of photosynthetically active radiation available to benthic vegetation (Kirk 1983, Goldsborough and Kemp 1988). These anthropogenic factors have contributed to the loss of grassbeds in many areas of Florida. The Indian River Lagoon, for example, has experienced a 30% loss of seagrass beds (Fletcher and Fletcher 1995) and Tampa Bay on Florida's Gulf coast has lost over 80% of its grassbeds over the last century (Lewis et al. 1985 cited in Sargent et al. 1995). Salinity changes associated with natural variation in precipitation and with water management activities can also drastically modify the abundance and species composition of SAV beds (e.g., Provancha and Scheidt 2000). The simultaneous occurrence of flooding and a cyclone, combined with poor watershed management practices, resulted in the loss of 1000 km^2 of seagrass beds and in the mass movement and mortality of dugongs in eastern Australia (Preen and Marsh 1995, Preen et al. 1995). Catastrophic loss of seagrass beds has also occurred in Florida, where a massive die-off has impacted the Florida Bay ecosystem since 1987 (Robblee et al. 1991).

The wide-ranging movements of manatees revealed in this study indicate that loss of important foraging grounds, whether chronically through deterioration in water quality or acutely from a natural or anthropogenic event, could have population-level repercussions. The first point is that habitat degradation in one area can affect migrants from throughout the Atlantic coast. This is particularly true for Brevard County, which is utilized by manatees following a variety of seasonal migratory patterns (see above), but the statement applies to nearly all areas of the coast. Secondly, local impacts on manatee habitat could have a cascading effect on habitats 100's of km away through redistribution and consequent elevation of manatee densities in other areas (Sutherland and Dolman 1994, Sutherland 1996:143-145). The potential for increased stress on communities of aquatic vegetation resulting from higher local densities of manatees is probably greatest during the winter, when manatee distribution is restricted by cold temperatures and plant growth is minimal. Investigations of manatee impacts on the biomass, productivity, and species composition of seagrass meadows in the vicinity of warm-water refuges (Packard 1981, 1984, Lefebvre et al. 2000) need to be conducted in other areas. Human activities in the coastal zone must be managed to enhance water quality, in particular the light regime required by submerged plants. Watershed management efforts in Tampa Bay, which included reduction of nitrogen inputs, have reversed the decline in seagrass coverage (Johansson and Lewis 1992 cited in Fonseca et al. 1998). These efforts should be encouraged and implemented elsewhere in Florida.

Effects of Industrial Warm-water Sources

The attraction of manatees to industrial warm-water effluents in winter was first described by Moore (1951*a*, 1956) and has since been well-documented (e.g., Reynolds and Wilcox 1994). These artificial thermal refugia have altered manatee winter distribution, seasonal movement patterns, and migratory behavior along the Atlantic coast by providing access to more northerly habitats where ambient water temperatures were too low to support manatees overwinter. Historical evidence on manatee winter distribution is scant but suggests that northern Biscayne Bay was a major area of concentration (Moore 1951*a*, 1956), although manatees were sighted as far north as Sebastian in some winters (Bangs 1895). The northward shift in winter distribution occurred as increasing numbers of manatees learned to utilize the thermal effluents produced by power plants or other industries in the Indian River of Brevard County (Shane 1984), in the St. Johns River near Jacksonville (Kinnaird and Valade 1983), and in the FL/GA border region near the St. Mary's River (Zoodsma 1991). Manatees aggregated in the thermal plumes of power plants even in southern Florida, however, including Riviera Beach, Port Everglades, Ft. Lauderdale, and the Miami River (Moore 1951*a*, 1956, Reynolds and Wilcox 1994, this study).

Some of the variability in seasonal movement patterns that we observed was certainly a modern artifact of the existence of industrial warm-water sources in proximity to good foraging areas. We venture that the traditional patterns of seasonal movements that existed historically were probably the C-S migrations (short- and medium-distance), the long-distance migrations, and year-round residence in southern Florida. Those seasonal movement patterns with more northerly winter destinations—including the N-C migrations, short-distance migrations within the northern region, and year-round residence in northern and central regions—have probably emerged within the past 40-50 years. This points again to the flexibility and opportunism shown by manatees in their movements and migratory behavior. The year-round existence of manatees in the St. Johns River and further north will soon end, either through mortality or emigration, as existing industrial warm-water outfalls are being phased out.

The creation of artificial thermal refugia has clearly altered seasonal movement patterns and migratory destinations for many individuals. But have they also affected the behavior of those individuals that have maintained traditional migratory patterns? Our data support the hypothesis that the availability and use of power plant thermal effluents altered migratory timing by allowing some individuals to remain in the region of their warm season range for longer periods. Manatees that visited power plants in central Florida departed their autumn range an average of 4 weeks later and arrived in the region of their warm season range an average of 3 weeks earlier than those that did not visit a power plant. Likewise, a number of N-C migrants took advantage of the warm-water refugia at pulp mill effluents to arrive when water temperatures were still quite cool in early spring, as noted by Zoodsma (1991). Few of the C-S migrants that spent the warm season in the Banana River, however, visited the Indian River power plants. Furthermore, fall migrations were generally direct and rapid, with few stopovers; power plants at Vero Beach and Ft. Pierce attracted small numbers of manatees for short periods but did not shortstop our tagged manatees during their southward migrations.

Implications for Demographic and Population Genetic Structure

Seasonal migrations and the extensive movements of adult males during the main breeding season resulted in considerable mixing of individuals, and presumably gene flow, along the entire Atlantic coast. No tagged individuals moved into the upper St. Johns River basin south of Palatka, although such movements are known to occur (Bengtson 1981, Reid et al. 1991). In fact, the growth of the Blue Spring overwintering group was fueled in part by immigration from the Atlantic coast (O'Shea 1988, Ackerman 1995) and, as might be expected from sex differences in movement rates, was highly male-biased (Powell and Waldron 1981). Likewise, no tagged manatees over the course of our 12-year study crossed Florida Bay to the Gulf coast. This is apparently a rare occurrence, as none of the >1000 photo-identified individuals statewide (Reid et al. 1991, Beck and Reid 1995, U.S. Geological Survey, unpubl. data) and only 1 tagged manatee (excluding captive-raised and released individuals) has been documented to make this journey (Wright 1996). The combined findings from radio-telemetry and resightings studies support division of the east coast population into two interacting but demographically separate subpopulations: along the Atlantic coast and in the upper St. Johns River basin. This is the approach that has been taken in recent demographic analyses (Eberhardt and O'Shea 1995, O'Shea and Hartley 1995, Reid et al. 1995, Langtimm et al. 1998) and that is being adopted by federal and state managers.

It follows that genetic variation should be fairly homogeneous within the Atlantic coast subpopulation and similar to that in the upper St. Johns River subpopulation. We might expect to find genetic differentiation, however, between manatees on the Atlantic and Gulf coasts. Protein electrophoresis work revealed a relatively high level of genetic polymorphism and heterozygosity, but little genetic differentiation among 5 geographic regions in Florida (McClenaghan and O'Shea 1988). Garcia et al. (1998) found only a single mtDNA haplotype within the range of the Florida manatee, presumably the result of a colonization event within the last 12,000 years. Analyses of nuclear DNA, however, have uncovered some slight variation between east and west coasts (Garcia 2000). More detailed studies using additional polymorphic primers are planned for the near future.

McClenaghan and O'Shea's analyses (1988) revealed an excess of homozygous individuals within geographic regions, which they noted could result from the pooling of samples from genetically distinct groups. They suggested that this pattern could be generated by natal-area fidelity, which results in geographic clustering of kin (Waser and Jones 1983). The evidence that we have gathered for natal philopatry, albeit limited, supports this interpretation. The different migratory patterns observed in this study may reflect the movements of distinct matrilines, which could represent an important source of genetic variation that is obscured through analyses based simply on geographic region of capture or death. One seasonal movement pattern that has the potential to become genetically differentiated from the others is year-round residence in SE FL. Although residents mix with migrants during the winter, the two groups appear to be geographically separate during the warm season when most breeding takes place.

Behavioral Diversity and the Manatee's Future

Perhaps more important than the potential for genetic substructure within the Atlantic coast subpopulation is the behavioral diversity represented by these matrilineally inherited movement patterns. Bengtson (1981) first called attention to the importance of conserving "behavioral traditions" in manatees and the environmental features associated with them. In addition to the proposition that an individual learns the locations of key resources (e.g., grassbeds, warm-water refugia, freshwater sources) and migratory routes from its mother (Bengtson 1981), a young manatee may also acquire the skills needed to cope with the challenges of its environment through following, observing, and interacting with its mother and perhaps other conspecifics. Such skills may include the ability to navigate and orient in shallow, relatively featureless water bodies where the animals may encounter extensive shoals, strong currents, mazes of islands, and tidal ranges that could strand an unwary marine mammal; the appropriate use of different foraging strategies (e.g., grazing, rooting) to select the most nutritious species and parts of aquatic plants; the development of social and sexual behaviors; and the ability to cope with anthropogenic hazards, such as water control structures, areas with high-speed vessel traffic, ports with large commercial vessel traffic, and power plant intakes.

Lack of these skills in naive captive-raised manatees released into the wild may have been responsible for the disorientation of 2 individuals that became lost at sea (Reid et al. 1999) and for the relatively high human-related problems (including boat collisions and entrapment in power plant intakes and storm water drainage pipes) that this category of animals has suffered along the Atlantic coast (Bonde et al. 1998). If the females of a particular matriline disappear, through locally intensive mortality or through stochastic events (e.g., series of male calves), then the store of knowledge associated with that group may be lost to the next generation and behavioral diversity within the population may be eroded.

One of the striking features of this study was the considerable amount of variation among individuals in movement behavior, including: extent of annual range (Fig. 3), seasonal patterns of movement (Fig. 4), migratory timing in relation to temperature (Fig. 8), frequency and locations of migratory stopovers, degree of site fidelity to seasonal ranges (Figs. 10 and 11), and frequency of mid-winter migrations (Fig. 10). This remarkable variability has two major implications for management. First is the realization that different manatees will respond to environmental stressors in a variety of ways, which complicates predictions of population response to management actions or anthropogenic disturbances. Second, although the fitness consequences and genetic underpinnings of this inter-individual variation are unknown, it potentially provides the raw material for evolutionary change and the phenotypic plasticity to adapt to rapid environmental change. Assuming that the high rate of human population growth along Florida's east coast continues into the foreseeable future, manatees and the habitats they depend on to survive will face escalating pressures from human activities. The behavioral flexibility of individuals and the behavioral diversity among individuals have allowed Florida manatees to adapt to and often exploit the profound changes to their environment that humans have wreaked over the last century. The ability of manatees to modify their behavior in relation to the pace of continued ecological change will be key to determining the future persistence of this unique mammal in North American waters.

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TABLES

Table 1. Radio-tracking effort from May 1986 through May 1998, as indicated by the number of radio-tagged manatees and the number of days manatees were carrying transmitters, by year and type of tag.

	Year of Study													
	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	Total
No. Tagged Manatees:														
All Tag Types	5	18	19	19	22	21	22	22	23	15	9	13	6	78
With PTT Tag[a]	5	5	9	12	17	18	21	22	22	14	8	13	6	63
With VHF Tag[b]	2	16	16	17	16	14	13	11	7	5	2	1	0	53
No. Tag-days:														
All Tag Types	264	1862	2448	2588	2639	4014	4126	3656	3315	2374	1795	2379	523	31,983
% PTT Tag[a]	83	26	26	41	61	55	89	97	96	94	100	98	100	74

[a] Satellite-monitored platform transmitter terminal.

[b] Manually monitored very high frequency radio-tag.

Table 2. Radio-tracking effort by month, as measured by the number of radio-tagged manatees and the number of days manatees were carrying transmitters, from May 1986 through May 1998.

		Month of Study											
		Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
No. Tagged Manatees		53	56	62	63	62	55	48	44	42	43	49	49
No. Tag-days:	Total	2765	2736	3288	3162	3167	2710	2592	2396	2154	2201	2245	2568
	(% of Total)	(8.6)	(8.6)	(10.3)	(9.9)	(9.9)	(8.5)	(8.1)	(7.5)	(6.7)	(6.9)	(7.0)	(8.0)

Table 3. Range of radio-tagged manatees along the Atlantic coast of the United States, by age class and sex of adult. Annual range denotes the mean distance across years between the northerly warm season range center and the southerly winter range terminus. Maximum range refers to the distance between the most distant locations over an individual's entire tracking history. Distances were measured along the intracoastal waterways.

Age-Sex Class[1]	N	Annual Range (km)					Maximum Range (km)				
		Median	25th Percentile	75th Percentile	Min	Max	Median	25th Percentile	75th Percentile	Min	Max
Adult	41	278	102	316	11	831	309	214	394	44	2360
Subadult	7	282	275	300	248	575	292	281	322	257	586
Adult Female	32	281	134	322	11	831	322	218	420	44	850
Adult Male	10	240	96	299	22	580	306	175	362	49	2360
Total	48	280	150	313	11	831	309	224	388	44	2360

[1] Male TBC-06 was included in the subadult (first 2 years) and adult male (last 2 years) categories, but the adult data were excluded from age class totals and from the statistical test between age classes.

NOTE: Wilcoxon two-sample tests showed no significant differences in range by age class (annual range: $S = 197.5$, $Z = 0.7450$, $P = 0.46$; maximum range: $S = 167.0$, $Z = -0.1169$, $P = 0.91$) or sex of adult (annual range: S = 190.0, Z = -0.7237, P = 0.47; maximum range: $S = 186.0$, $Z = -0.8417$, $P = 0.40$).

Table 4. Daily travel rates of manatees tracked with satellite-monitored radio-tags in relation to seasonal movement pattern and season. Travel rate (km/day) was measured as the straight-line distance between successive mean daily locations, standardized to a 24-hr period. Statistics were based on one median value per animal (sample size N); maximum rates in parentheses are for single measurements (sample size n).

	Winter Season (Dec-Feb)				Warm Season (Apr-Oct)				All Year (Jan-Dec)			
Movement Pattern[1]	Mean	SD	Max	N (n)	Mean	SD	Max	N (n)	Mean	SD	Max	N (n)
Long-distance Migrant	7.8	6.0	15.6 (58.0)	4 (382)	2.7	0.9	4.1 (53.7)	5 (1037)	2.9	0.8	4.0 (72.9)	5 (1766)
N-C Migrant	2.0	0.8	3.4 (75.3)	10 (998)	2.6	1.2	5.6 (59.5)	12 (2566)	2.5	1.0	5.3 (75.3)	12 (4371)
C-S Migrant	3.2	3.3	15.1 (77.3)	16 (3172)	2.0	1.4	6.2 (47.4)	18 (5801)	2.0	1.0	4.8 (77.3)	20 (10985)
Short-distance Migrant	1.8	0.8	2.8 (50.1)	7 (699)	1.9	0.7	2.6 (41.7)	6 (1795)	1.8	0.6	2.7 (50.1)	7 (2976)
Resident	1.1	0.3	1.7 (19.5)	6 (439)	1.9	1.0	3.5 (35.1)	5 (633)	1.5	0.4	2.0 (40.2)	6 (1362)
Total[2]	2.9	3.2	15.6 (77.3)	40 (5809)	2.4	1.3	6.2 (59.5)	49 (12936)	2.5	1.7	12.7 (77.3)	55 (22889)

Table 4. Daily travel rate (continued).

[1] Individuals that changed movement patterns are included in two movement categories, but the second pattern was excluded from statistical analyses.

[2] Totals also include individuals with an unclassified movement pattern that had at least 30 measurements of daily travel rate.

Table 5. Water temperature and temperature change (°C) in northern Brevard County (Banana Creek and Banana River) at the time that tagged manatees in this region (N = 15) started their fall migration southward or moved to the local power plants.

	Mean	SD	Min	Max
Temperature at Time of Departure	19.1	2.1	14.5	23.5
Mean Temperature over:				
Previous 24-hr Period	20.1	2.3	14.8	24.4
Subsequent 24-hr Period	18.4	1.7	14.4	21.5
48-hr Period	19.2	2.0	15.0	23.0
Minimum Temperature over:				
Previous 24-hr Period	18.5	2.1	13.4	23.5
Subsequent 24-hr Period	17.2	1.7	13.4	20.1
48-hr Period	17.1	1.7	13.4	20.1
Temperature Change over:				
Previous 24-hr Period	-2.0	1.7	-5.9	2.3
Subsequent 24-hr Period	-1.4	1.3	-4.6	1.5
48-hr Period	-3.5	2.6	-8.8	2.0

Note: Means and standard deviations were calculated from average values per animal; minimums and maximums were based on the 32 records of departure temperatures.

Table 6. Migratory behavior of tagged manatees during the southward "fall" migration, by distance and region. Means ± SD are based on mean values per animal (N); minimum and maximum values shown in parentheses are based on the actual number of migratory trips recorded (n).

	Total Duration (days)	Travel Duration (days)	Distance (km)	Travel Rate (km/day)	Migratory Stopovers			No. of Manatees (N)	No. of Trips (n)
					No. per Trip	Duration per Stop (days)	Total Duration (days)		
North - Central[†]	10.9 ± 5.6 (5.5 - 24.5)	8.6 ± 2.9 (5.5 - 13.8)	286 ± 60 (210 - 437)	35.8 ± 8.3 (18.0 - 51.5)	0.5 ± 0.7 (0 - 2)	1.5 ± 0.2 (1.3 - 2.0)	0.8 ± 1.1 (0 - 3.3)	10 - 11	14 -17
Central - South[†]	10.1 ± 3.6 (4.3 - 20.9)	7.7 ± 2.1 (3.9 - 13.7)	261 ± 47 (158 - 339)	35.5 ± 5.6 (22.1 - 55.7)	0.6 ± 0.7 (0 - 3)	3.3 ± 1.8 (1.0 - 11.7)	2.1 ± 2.6 (0 - 11.7)	14 - 17	31 - 37
Short-distance Migration[‡]	4.9 ± 2.6 (2.7 - 10.0)	3.8 ± 1.0 (2.8 - 5.4)	92 ± 30 (53 - 145)	24.8 ± 5.8 (16.0 - 40.0)	0.2 ± 0.4 (0 - 1)	6.7 (6.7)	1.3 ± 3.0 (0 - 6.7)	5 - 6	6 - 7
Total	9.9 ± 5.3 (2.7 - 46.3)	7.9 ± 4.1 (2.7 - 30.8)	245 ± 103 (53 - 812)	33.5 ± 7.6 (16.0 - 55.7)	0.7 ± 1.0 (0 - 9)	2.9 ± 1.9 (1.0 - 11.7)	1.9 ± 2.6 (0 - 15.5)	26 - 31	52 - 62

[†] All long-distance migrants except one made two-stage migrations and are included separately under the N-C and C-S medium-distance migrations; one animal that migrated continuously from the north to the south region is only included in the totals.

[‡] Short-distance migrations were defined as 50 - 150 km and occurred within a region (central or north) or between central and south regions.

Table 7. Migratory behavior of tagged manatees during the northward "spring" migration, by distance and region. Means ± SD are based on mean values per animal (N); minimum and maximum values shown in parentheses are based on the actual number of migratory trips recorded (n).

	Total Duration (days)	Travel Duration (days)	Distance (km)	Travel Rate (km/day)	Migratory Stopovers No. per Trip	 Duration per Stop (days)	 Total Duration (days)	No. of Manatees (N)	No. of Trips (n)
North - Central[†]	11.8 ± 6.9 (4.7 - 30.6)	9.4 ± 3.3 (4.8 - 16.0)	290 ± 45 (224 - 413)	34.9 ± 12.3 (16.5 - 58.3)	0.8 ± 0.8 (0 - 3)	4.0 ± 5.4 (1.0 - 17.0)	2.9 ± 4.7 (0 - 17.0)	14 - 17	19 - 24
Central - South[†]	19.4 ± 10.4 (5.8 - 51.6)	11.7 ± 3.3 (5.1 - 22.6)	269 ± 49 (166 - 361)	23.2 ± 5.7 (11.8 - 37.6)	1.6 ± 1.1 (0 - 6)	3.6 ± 2.6 (1.0 - 24.0)	5.8 ± 5.6 (0 - 26.3)	20 - 23	41 - 50
Short-distance Migration[‡]	9.6 ± 6.0 (3.8 - 22.4)	4.8 ± 2.3 (2.0 - 10.3)	96 ± 26 (63 - 133)	22.6 ± 7.3 (9.4 - 31.2)	0.9 ± 0.7 (0 - 3)	5.4 ± 2.8 (1.0 - 14.5)	4.9 ± 4.6 (0 - 15.5)	7	10 - 11
Total	15.0 ± 8.9 (3.8 - 51.6)	9.7 ± 4.0 (2.0 - 22.6)	250 ± 79 (63 - 413)	27.3 ± 10.5 (9.4 - 58.3)	1.2 ± 1.0 (0 - 6)	3.9 ± 3.2 (1.0 - 24.0)	4.5 ± 4.4 (0 - 26.3)	34 - 40	71 - 84

[†] All long-distance migrants made two-stage migrations and are included separately under the N-C and C-S medium-distance migrations.

[‡] Short-distance migrations were defined as 50 - 150 km and occurred within a region (central or north) or between central and south regions.

Table 9. Number of tagged manatees tracked in Brevard County waters (between the southern tip of Merritt Island and Haulover Canal) that used the Indian or Banana Rivers (or both rivers) during the warm season (April to October), as a function of seasonal movement pattern and overwintering region. Entire range includes all locations during the warm season, whereas core range refers to the predominant location of warm season clusters.

		Entire Warm Season Range			Core Warm Season Range		
	N	Indian R.	Banana R.	Both Rivers	Indian R.	Banana R.	Both Rivers
Seasonal Movement Pattern*							
N-C Migrant†	11	6	0	3	7	1	0
Resident	3	1	1	1	1	2	0
Long-distance Migrant	6	1	1	4	3	2	1
C-S Migrant‡	20	1	10	9	1	14	2
Overwintering Region*							
Brevard County†	14	7 (50%)	1 (7%)	4 (29%)	8 (57%)	3 (21%)	0 (0%)
SE Florida	26	2 (8%)	11 (42%)	13 (50%)	4 (15%)	16 (62%)	3 (12%)

[*] Data for only the first seasonal movement pattern and winter region is tallied for three individuals that changed movement patterns.

[†] Two N-C migrants were not present in Brevard County during the warm season.

[‡] The C-S migrant category includes both short- and medium-distance migrants between the central and south regions.

Table 8. Winter migratory behavior of tagged manatees by overwintering region. Means ± SD are based on mean values per animal (N); minimum and maximum values shown in parentheses are based on the number of animal-years (for frequency) or the number of migratory trips recorded (for duration and distance) (n).

	FREQUENCY			DURATION (days)		DISTANCE (km)				
Wintering Region	% Animals Migrating†	No.per Winter†	N (n)	Round Trip	On W.S. Range	Round Trip	Total per Winter	% Distance to W.S. Range	% Migrations to W.S. Range	N (n)
Brevard & North	27	0.6 ± 1.1 (0 - 3)	11 (13)	9.4 ± 3.0 (4 - 17)	0.4 ± 0.3 (0 - 2)	146 ± 17 (122 - 215)	346 ± 119 (256 - 481)	47 ± 36 (22 - 90)	29	3 (6-7)
South of Brevard	64	0.8 ± 0.7 (0 - 4)	22 (47)	20.6 ± 12.4 (4 - 60)	3.3 ± 5.1 (0 - 42)	251 ± 116 (101 - 569)	452 ± 353 (101 - 1416)	65 ± 30 (18 - 133)	45	14-17 (50-51)
Total	45	0.7 ± 0.9 (0 - 4)	38 (65)	18.9 ± 12.1 (4 - 60)	2.8 ± 4.8 (0 - 42)	236 ± 113 (101 - 569)	434 ± 323 (101 - 1416)	62 ± 30 (18 - 133)	43	17-20 (56-58)

Note: W.S. = Warm season

† Residents and manatees with unclassified movement patterns (N = 5, n = 5) were excluded from the regional subtotals but all animals were included in totals.

FIGURES

Figure 1. Locations of radio-tagging sites for 78 manatees tracked along the Atlantic coast of Florida, Georgia, and South Carolina. The number of manatees tagged at each site is given in parentheses. An additional 363 retagging events took place throughout the study area. Thick lines separate northern, central, and southern regions. Locations of warm-water power plant effluents used by large numbers of manatees in winter are denoted by house symbols.

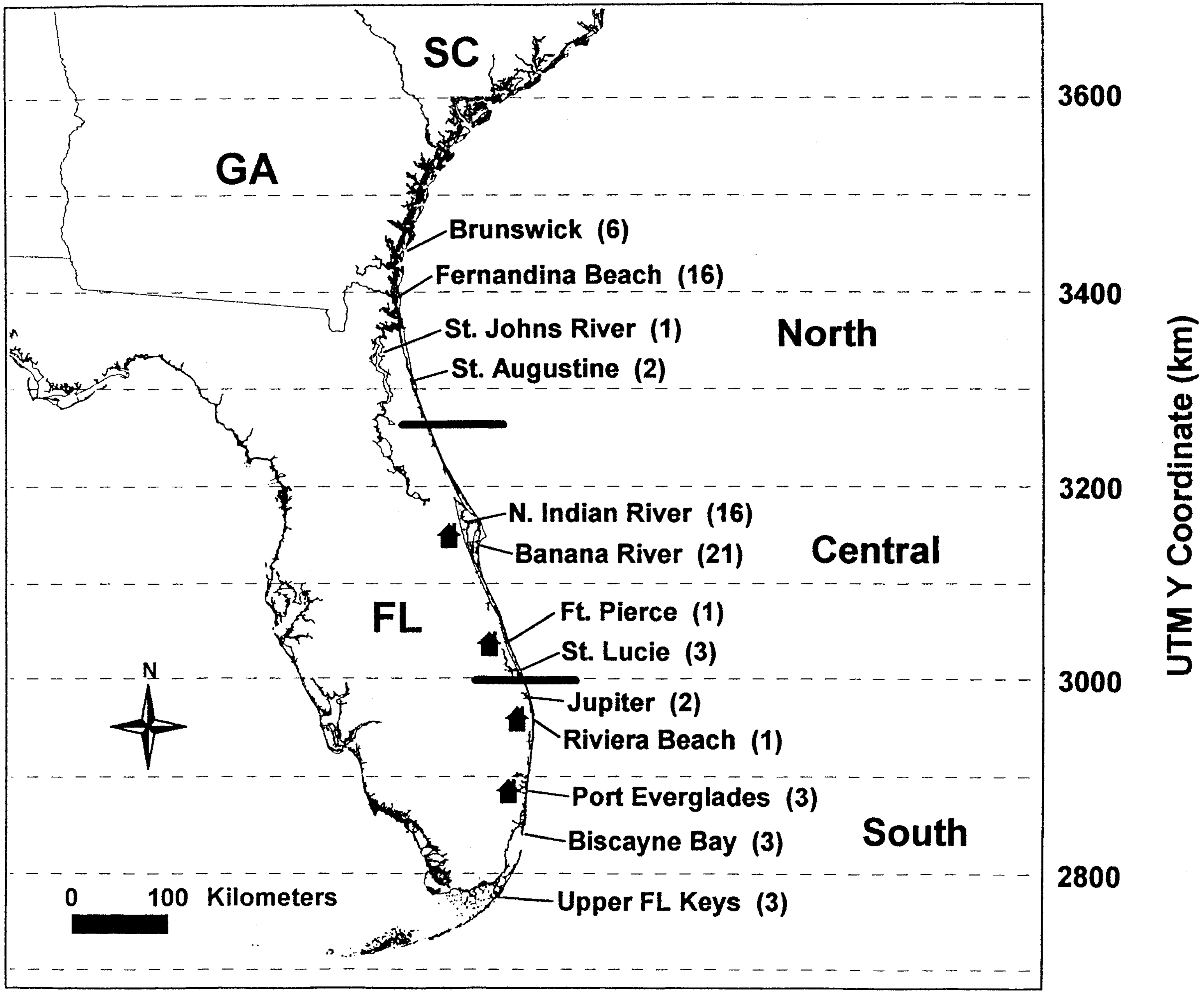
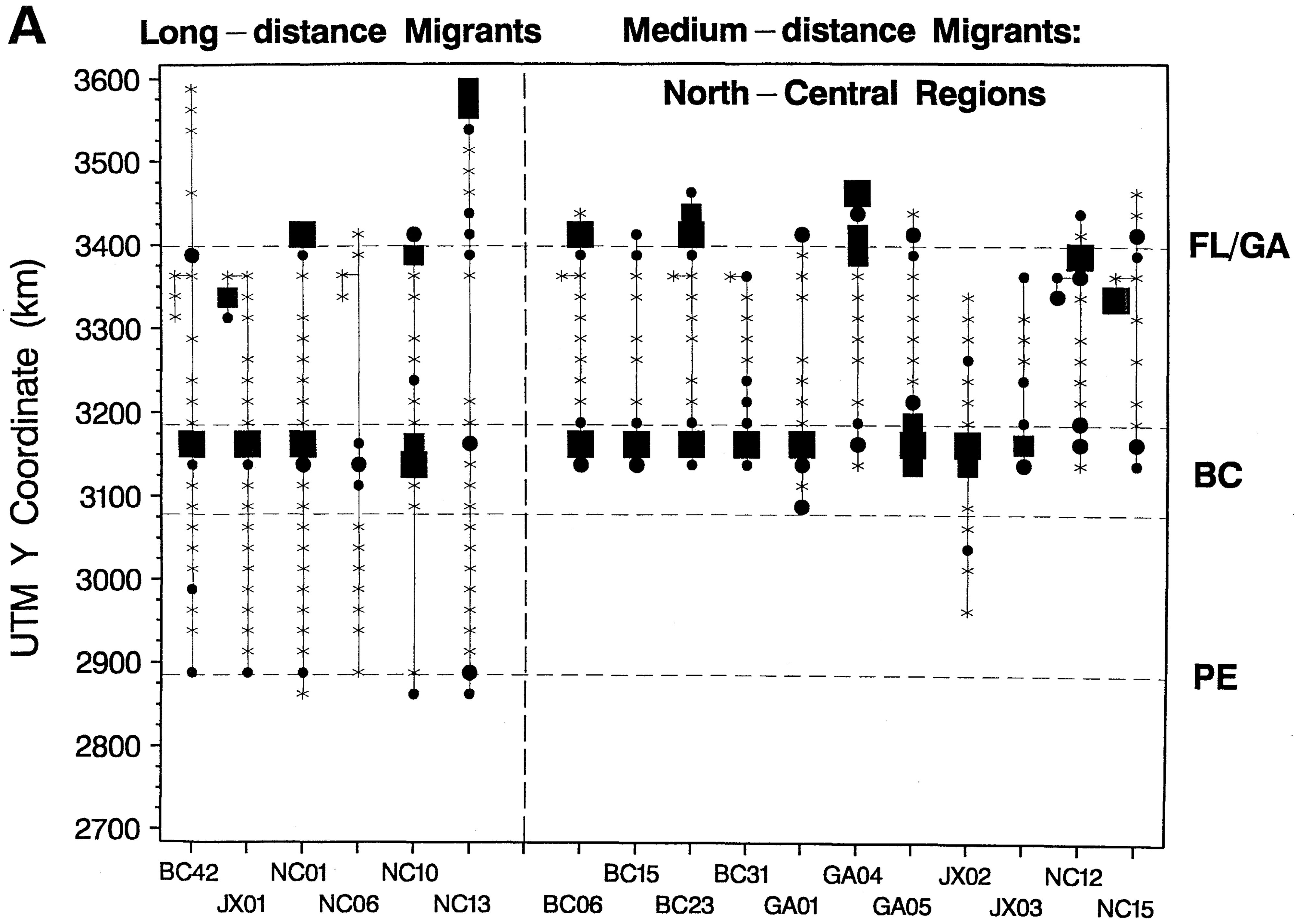
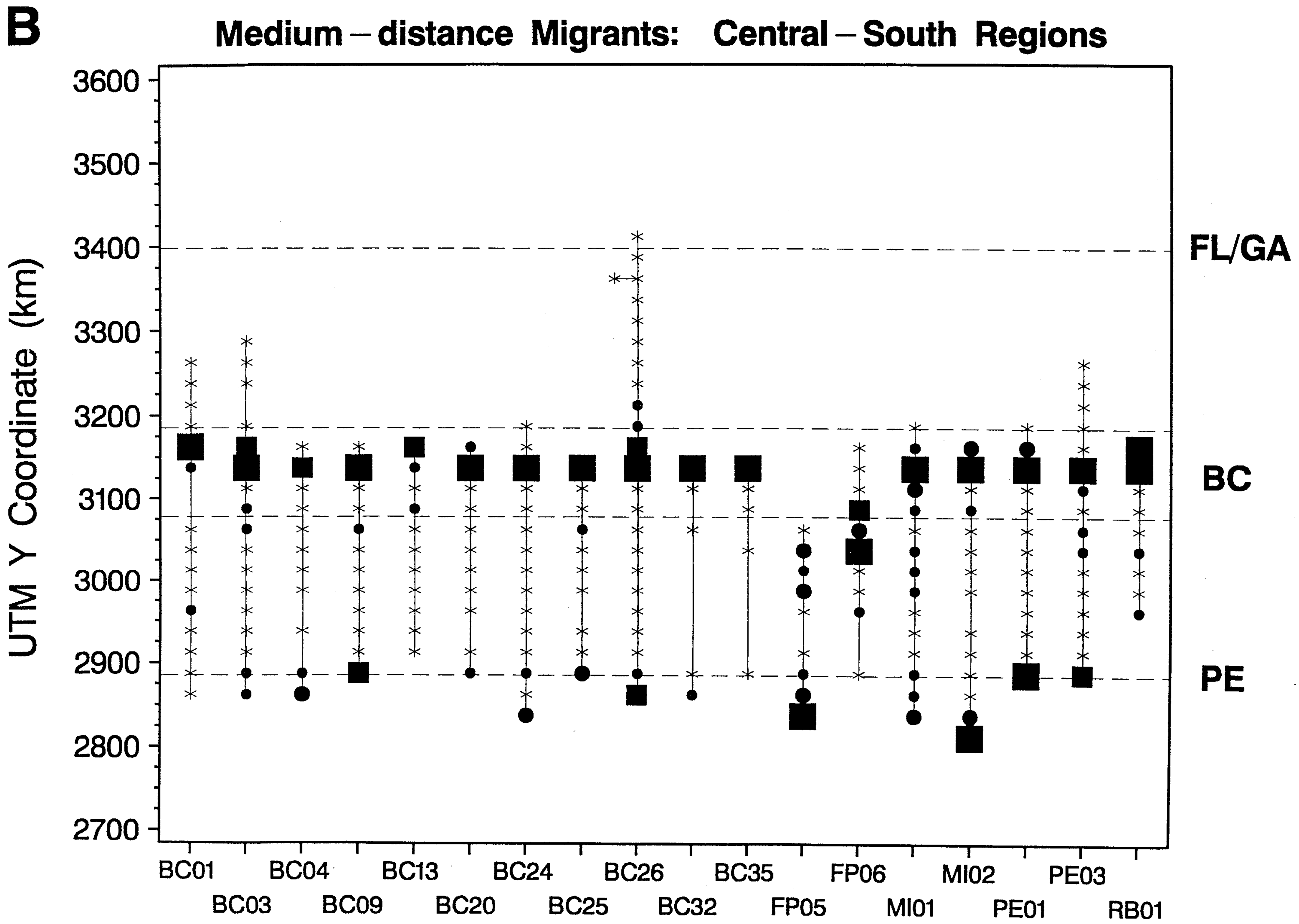

SC
GA
FL
Brunswick (6)
Fernandina Beach (16)
St. Johns River (1)
St. Augustine (2)
North
N. Indian River (16)
Banana River (21)
Central
Ft. Pierce (1)
St. Lucie (3)
Jupiter (2)
Riviera Beach (1)
Port Everglades (3)
Biscayne Bay (3)
South
Upper FL Keys (3)
N
0 100 Kilometers
3600
3400
3200
3000
2800
UTM Y Coordinate (km)

Figure 2. Ranges of 48 tagged manatees, plotted as the number of days tracked in each 25-km section of coastline: 1 - 10 days (∗), 11 - 30 days (•), 31 - 60 days (●), 61 - 90 days (▪), and >90 days (■). Animals are grouped by seasonal movement pattern: (A) Long-distance migrants and medium-distance migrants between northern and central regions; (B) medium-distance migrants between central and southern regions; and (C) short-distance migrants and residents. See Fig. 1 for geographic reference of UTM Y coordinates. Symbols branching off the range lines (Y between 3300-3400) represent use of the St. Johns River. FL/GA = border of Florida and Georgia; BC = Brevard County; PE = Port Everglades.

A
Long – distance Migrants
Medium – distance Migrants:
North – Central Regions
UTM Y Coordinate (km)
3600
3500
3400
3300
3200
3100
3000
2900
2800
2700
FL/GA
BC
PE
BC42
JX01
NC01
NC06
NC10
NC13
BC06
BC15
BC23
BC31
GA01
GA04
GA05
JX02
JX03
NC12
NC15


B
Medium – distance Migrants: Central – South Regions
UTM Y Coordinate (km)
3600
3500
3400
3300
3200
3100
3000
2900
2800
2700
FL/GA
BC
PE
BC01
BC03
BC04
BC09
BC13
BC20
BC24
BC25
BC26
BC32
BC35
FP05
FP06
MI01
MI02
PE01
PE03
RB01

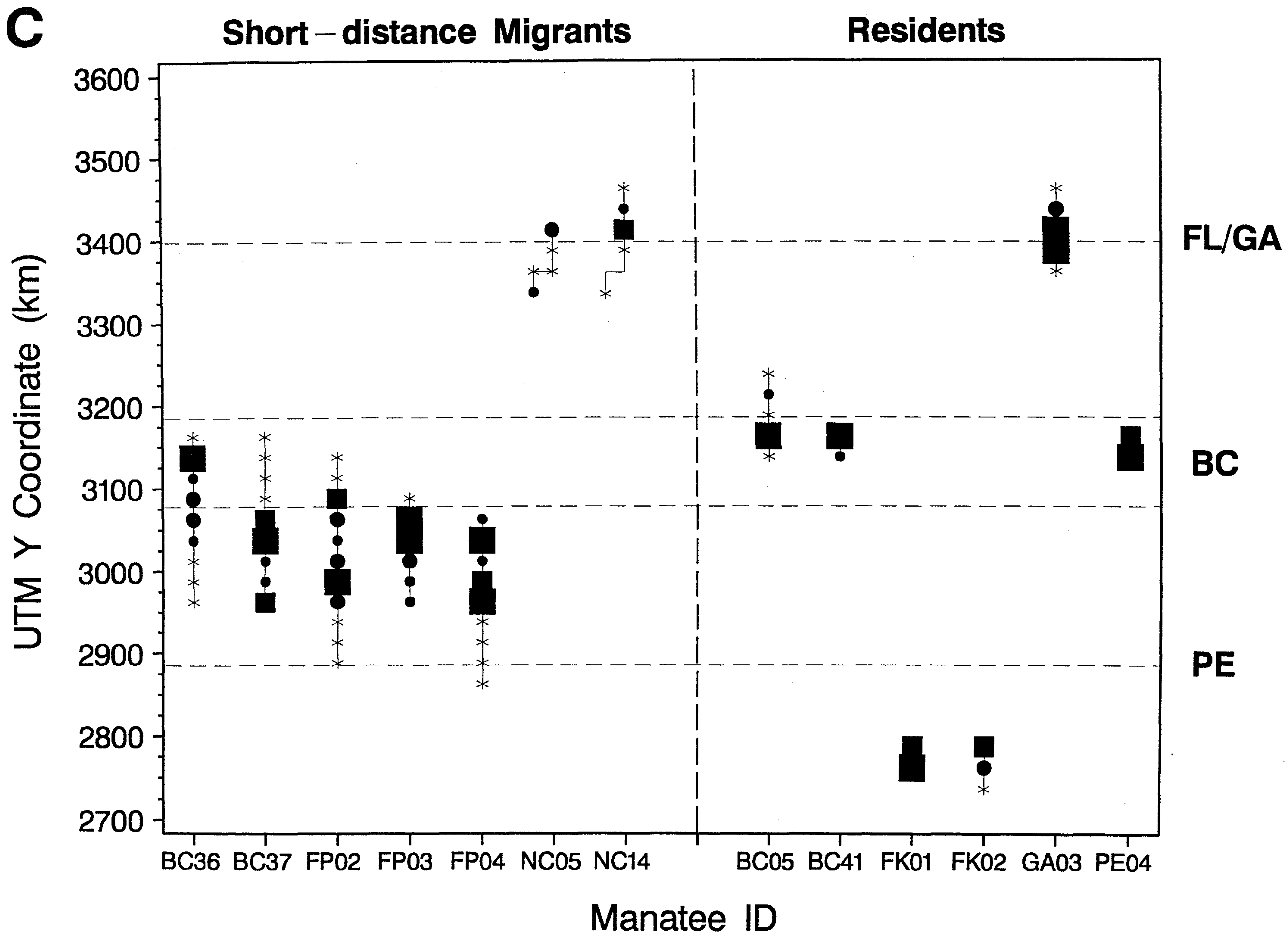

C
Short – distance Migrants
Residents
UTM Y Coordinate (km)
3600
3500
3400
3300
3200
3100
3000
2900
2800
2700
FL/GA
BC
PE
BC36
BC37
FP02
FP03
FP04
NC05
NC14
BC05
BC41
FK01
FK02
GA03
PE04
Manatee ID

Figure 3. Frequency distributions of (A) mean distance between warm season and winter ranges (i.e., annual range), and (B) maximum range over tagged manatees' tracking histories (N = 48). Distances were measured along the intracoastal waterways.

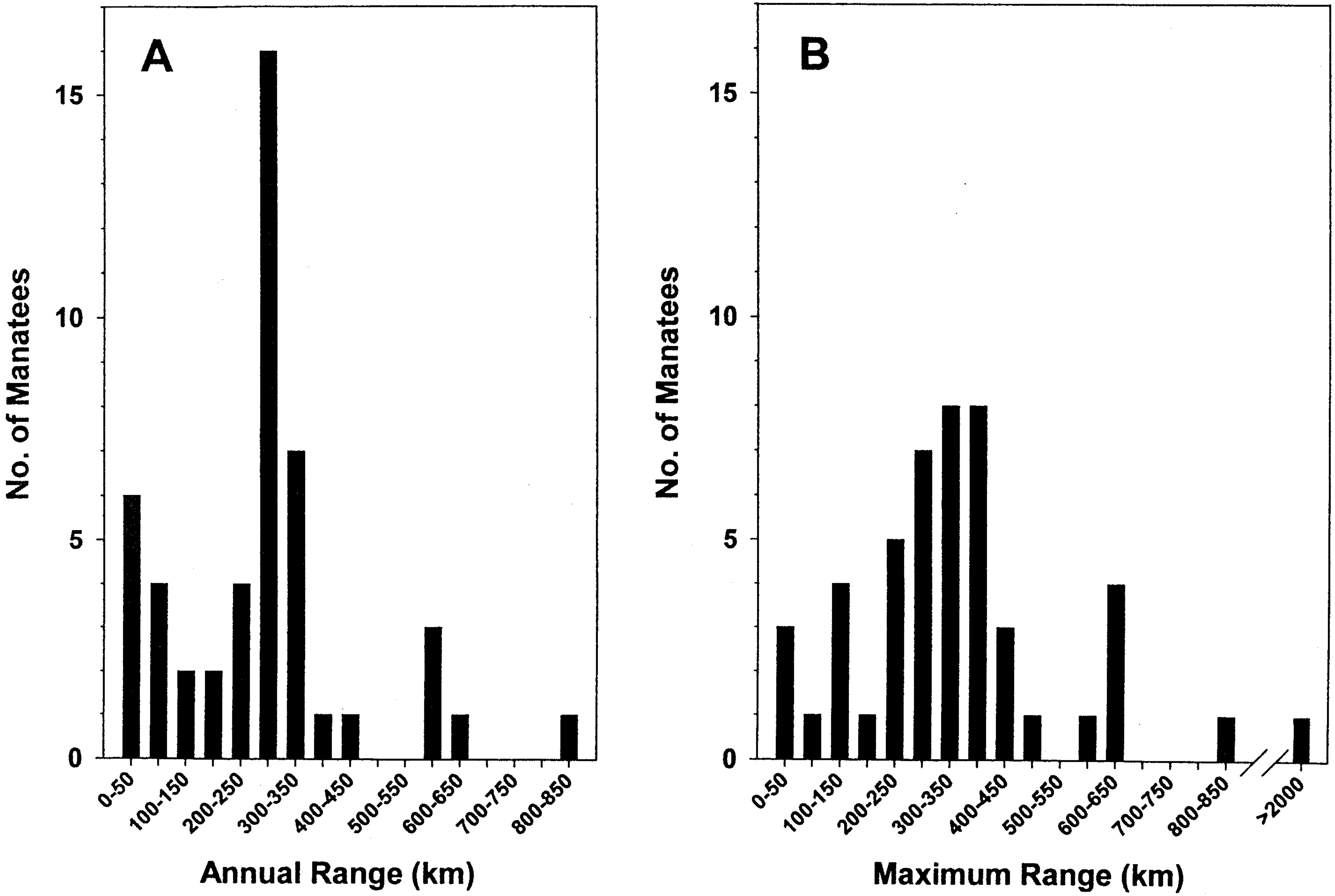

A
B
No. of Manatees
0
5
10
15
0-50
100-150
200-250
300-350
400-450
500-550
600-650
700-750
800-850
>2000
Annual Range (km)
Maximum Range (km)

Figure 4. Types of seasonal movement patterns exhibited by manatees along the Atlantic coast, as shown by plots of Universal Transverse Mercator (UTM) northing coordinates against date for a 15-month period. (A) Medium-distance migrants between northern and central regions (○) (TBC-06, 1987-88) and between central and southern regions (✳) (TBC-24, 1991-92). (B) Long-distance migrant between northern and southern regions (TNC-13, 1997-98). (C) Short-distance migrant (TFP-02, 1991-92). (D) Year-round residents in the northern (○) (TGA-03, 1995-96), central (✳) (TPE-04, 1990-91), and southern (△) (TFK-01, 1993-94) regions. Vertical dashed lines denote the winter season (December through February). GA/SC = border of Georgia and South Carolina; FL/GA = border of Florida and Georgia; BC = Brevard County; PE = Port Everglades.

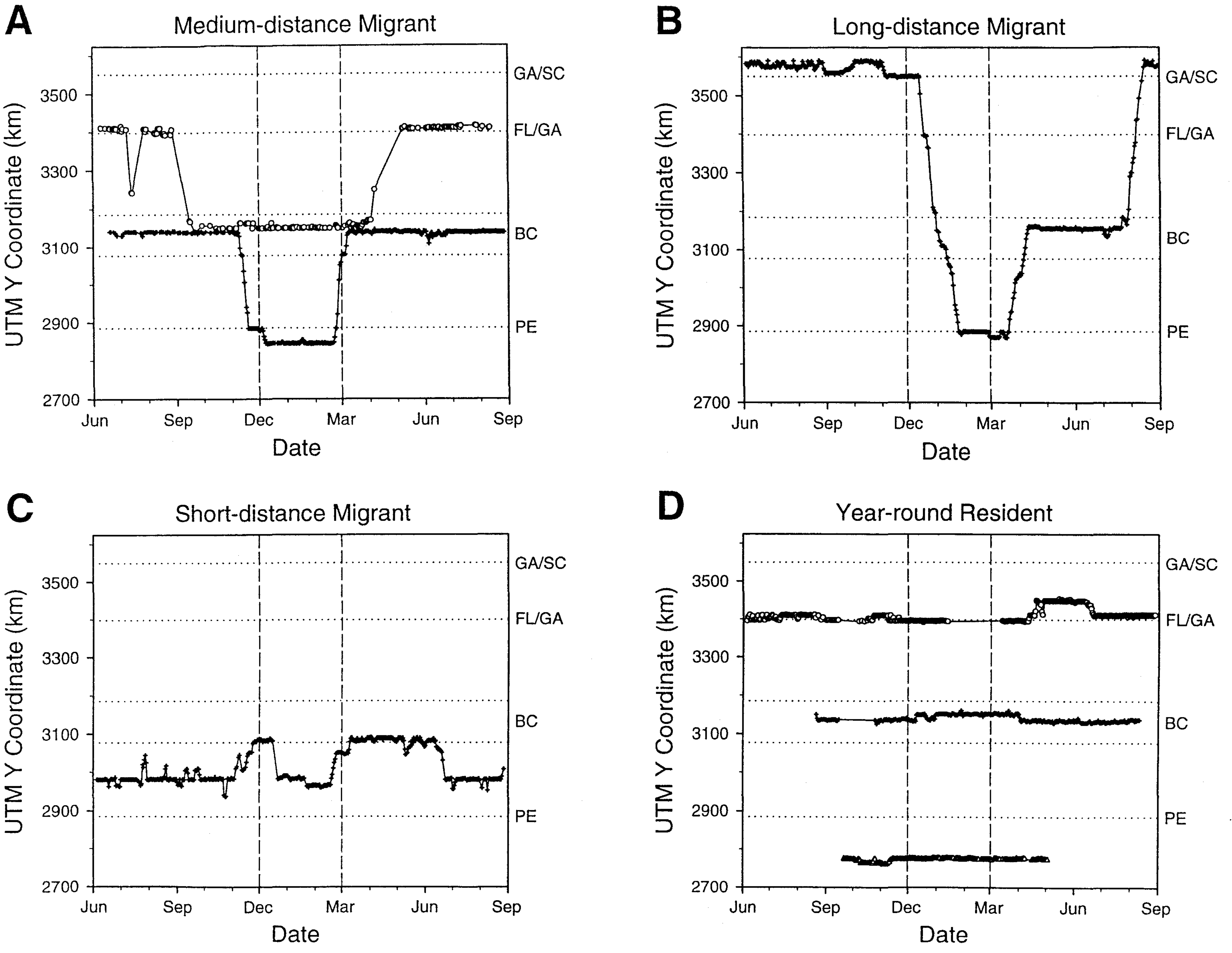

A
Medium-distance Migrant
B
Long-distance Migrant
C
Short-distance Migrant
D
Year-round Resident
UTM Y Coordinate (km)
2700
2900
3100
3300
3500
GA/SC
FL/GA
BC
PE
Jun
Sep
Dec
Mar
Jun
Sep
Date

Figure 5. Seasonal variation in daily travel rate (i.e., distance between successive mean daily locations, standardized to a 24-hr period) of adult male and female manatees that were tracked with satellite-monitored radio-tags. Symbols indicate means ± 1 SE, weighted by the number of measurements per individual per month (see Methods). The hatched bar denotes the main breeding season.

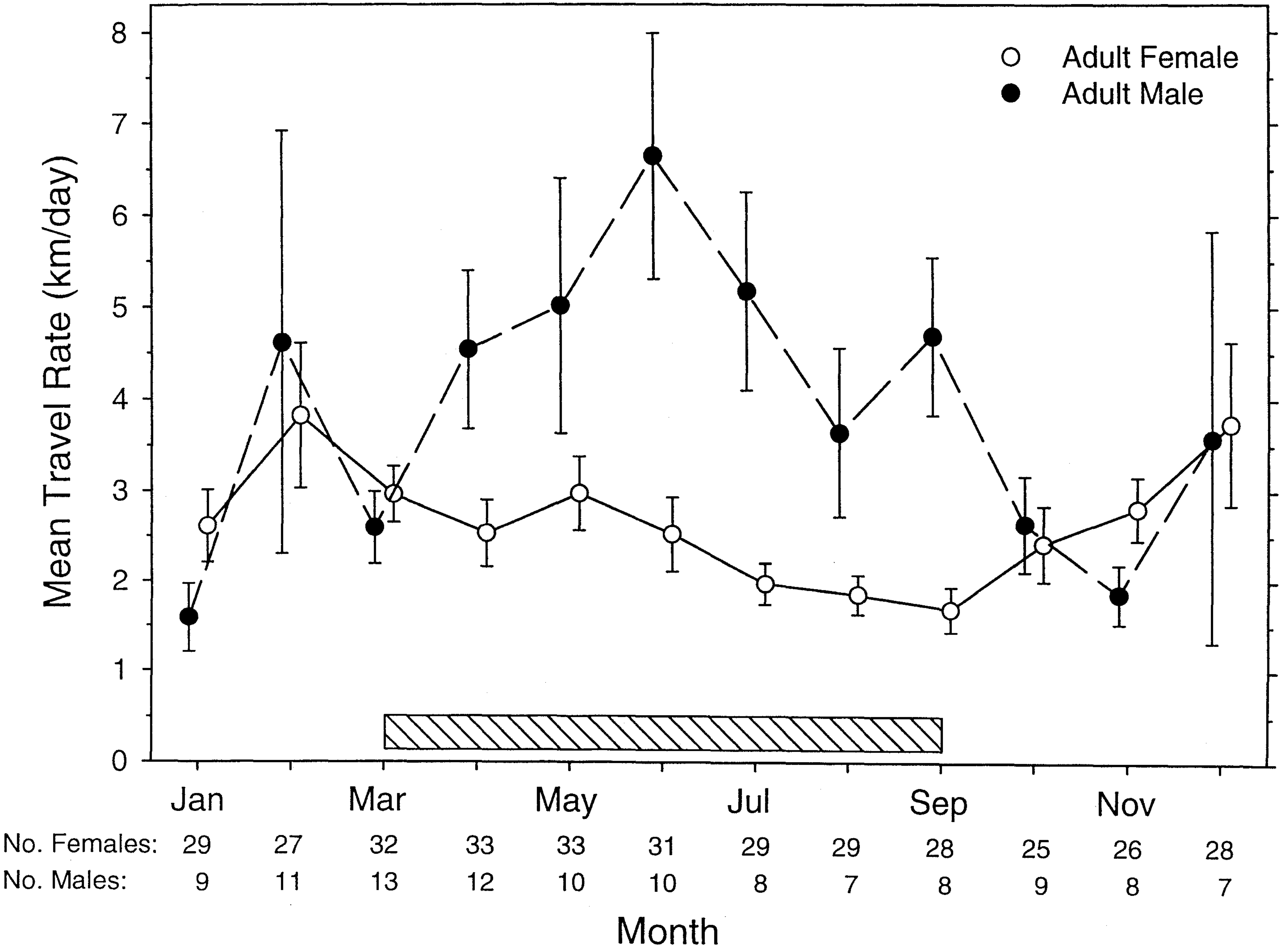

Adult Female
Adult Male
Mean Travel Rate (km/day)
0
1
2
3
4
5
6
7
8
Jan
Mar
May
Jul
Sep
Nov
No. Females: 29 27 32 33 33 31 29 29 28 25 26 28
No. Males: 9 11 13 12 10 10 8 7 8 9 8 7
Month

Figure 6. (A) Timing of "fall" southward migration and "spring" northward migration, as shown by departure date from and arrival date on warm season range, respectively, for the northern and central regions of the study area. The median value is shown as a line within a box bounded by the 25th and 75th percentiles; whiskers denote 10th and 90th percentiles, and points represent minimum and maximum values. See text for sample sizes. (B) Mean monthly water temperature in northern Brevard County, Florida (●) from 1988 to 1998 and in the St. Johns River at Jacksonville, Florida (○) from 1994 to 1998. Whiskers show the minimum and maximum values of the mean monthly temperature across these time periods. The bar denotes the main winter season (solid bar) and adjacent months of transitional weather (hatched bars).

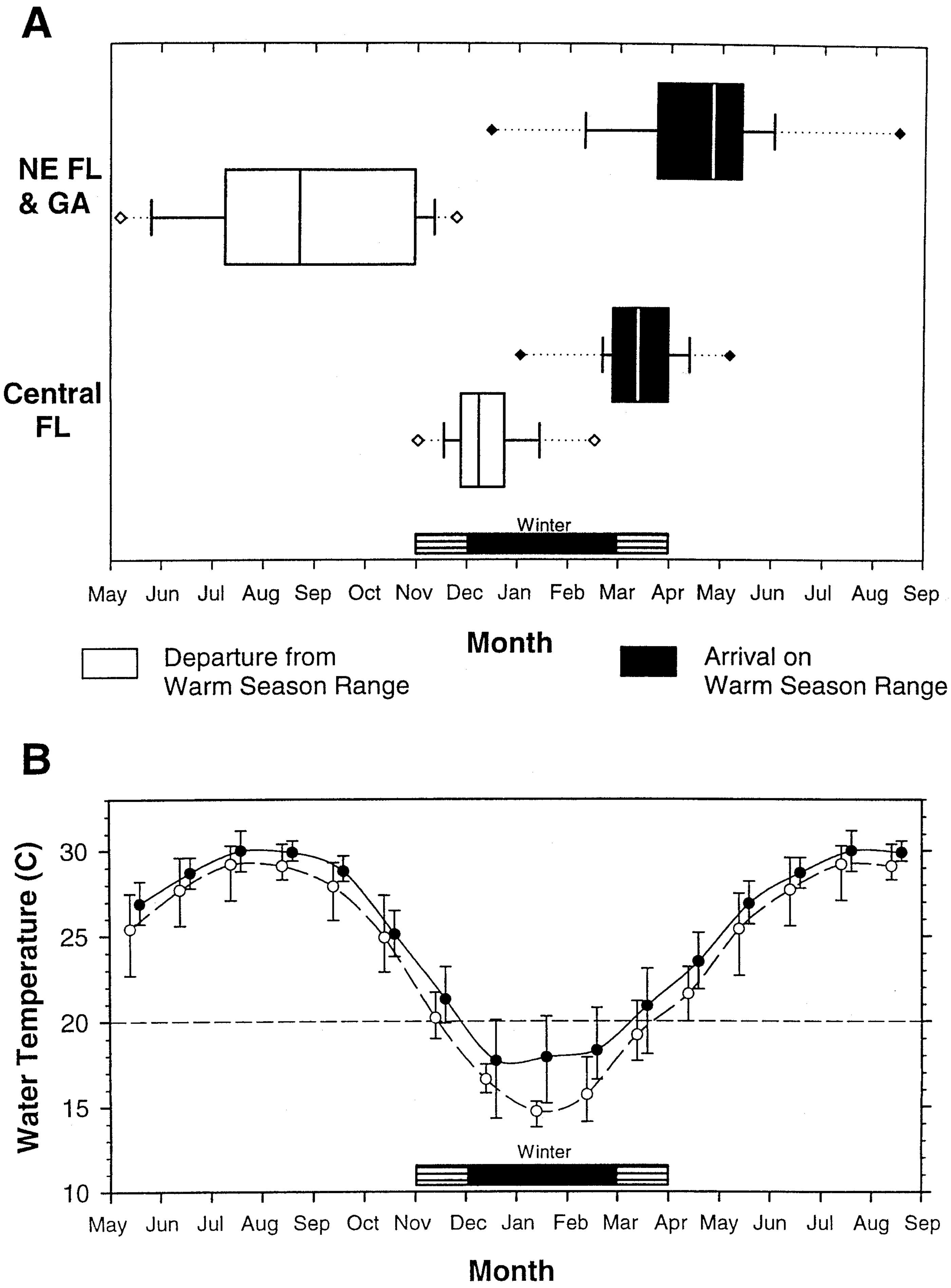
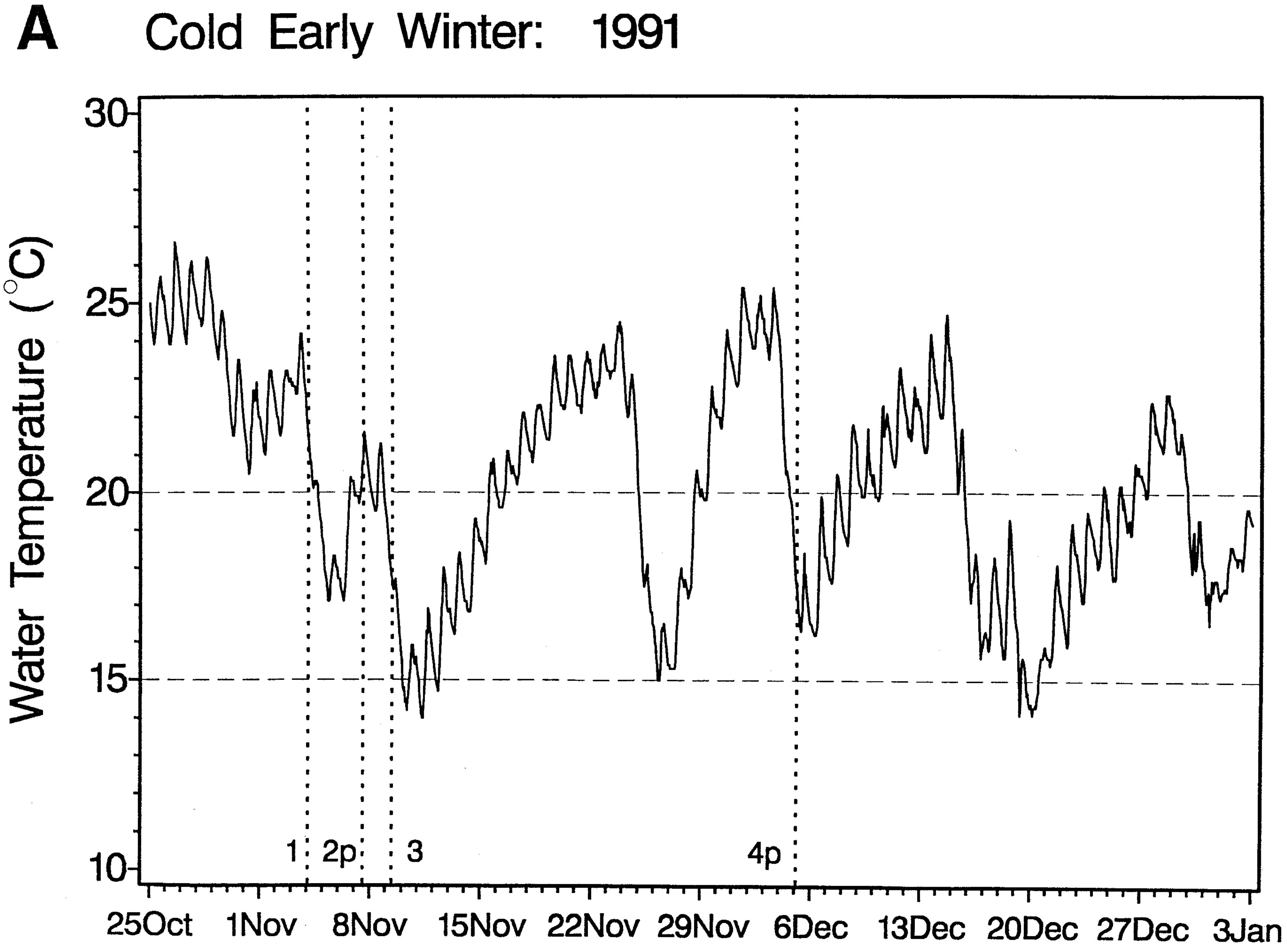

A
NE FL & GA
Central FL
Winter
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Month
Departure from Warm Season Range
Arrival on Warm Season Range
B
Water Temperature (C)
10
15
20
25
30
Winter
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Month

Figure 7. Comparison of fall departure dates (vertical lines) of tagged manatees from their warm season range in Brevard County in relation to hourly water temperature for (A) an early start to cold winter weather (1991), and (B) a late start to cold weather (1994). Numbers denote individual animals, 2 of which (1 and 3) were tracked in both years; the 'p' suffix after the number indicates movement to local power plants in Brevard County.



A Cold Early Winter: 1991

B Mild Early Winter: 1994

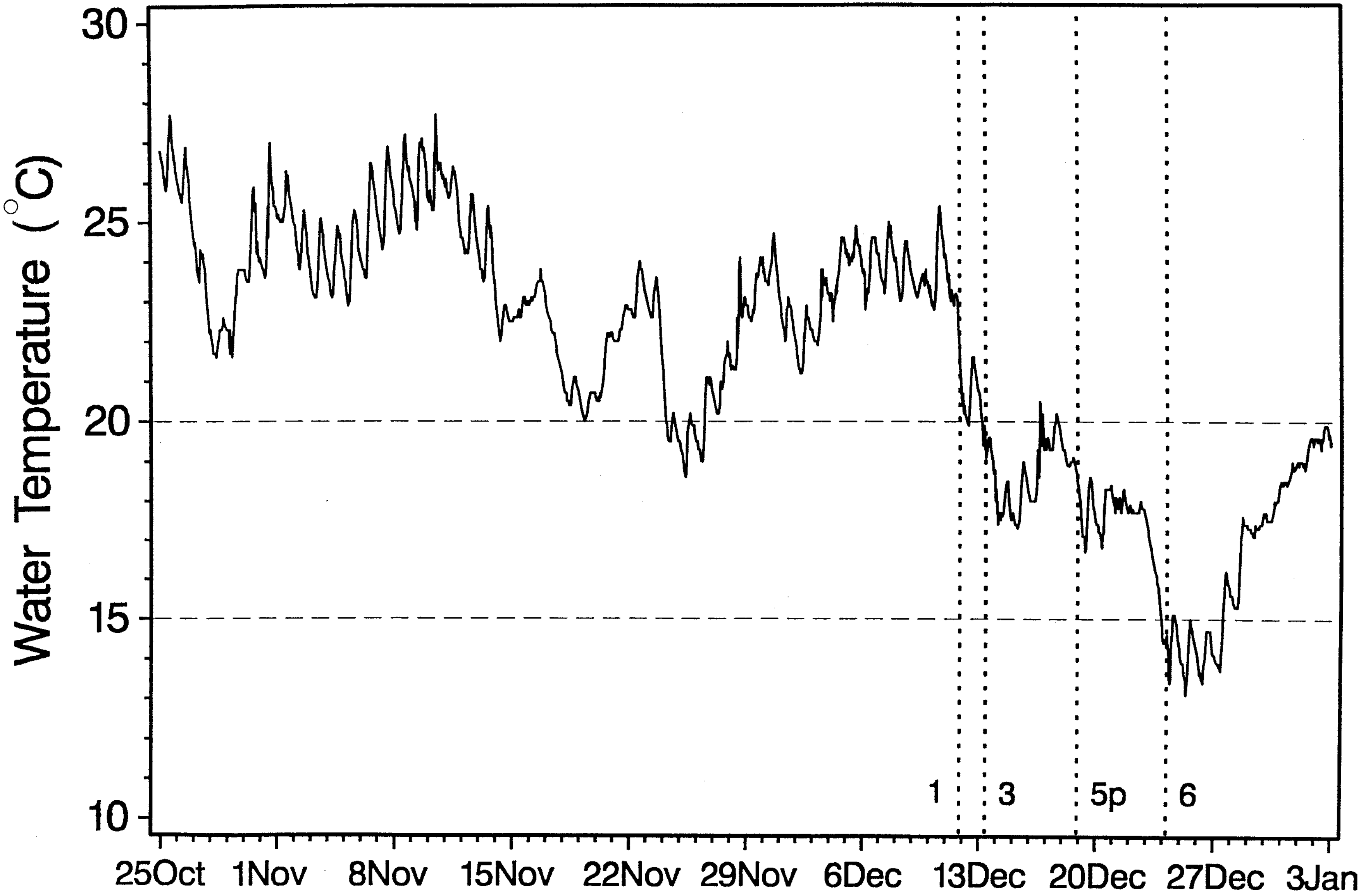


Figure 8. Individual variation in water temperature (°C) at departure from their warm season range in Brevard County, Florida for 7 tagged manatees with multiple years of fall migration data (number of years in parentheses). Symbols represent the individual means across years of the 48-hr mean temperature, which is the average temperature over a 24-hr period before and a 24-hr period after the date-time of departure; lines connect the minimum and maximum values of the 48-hr mean temperature.

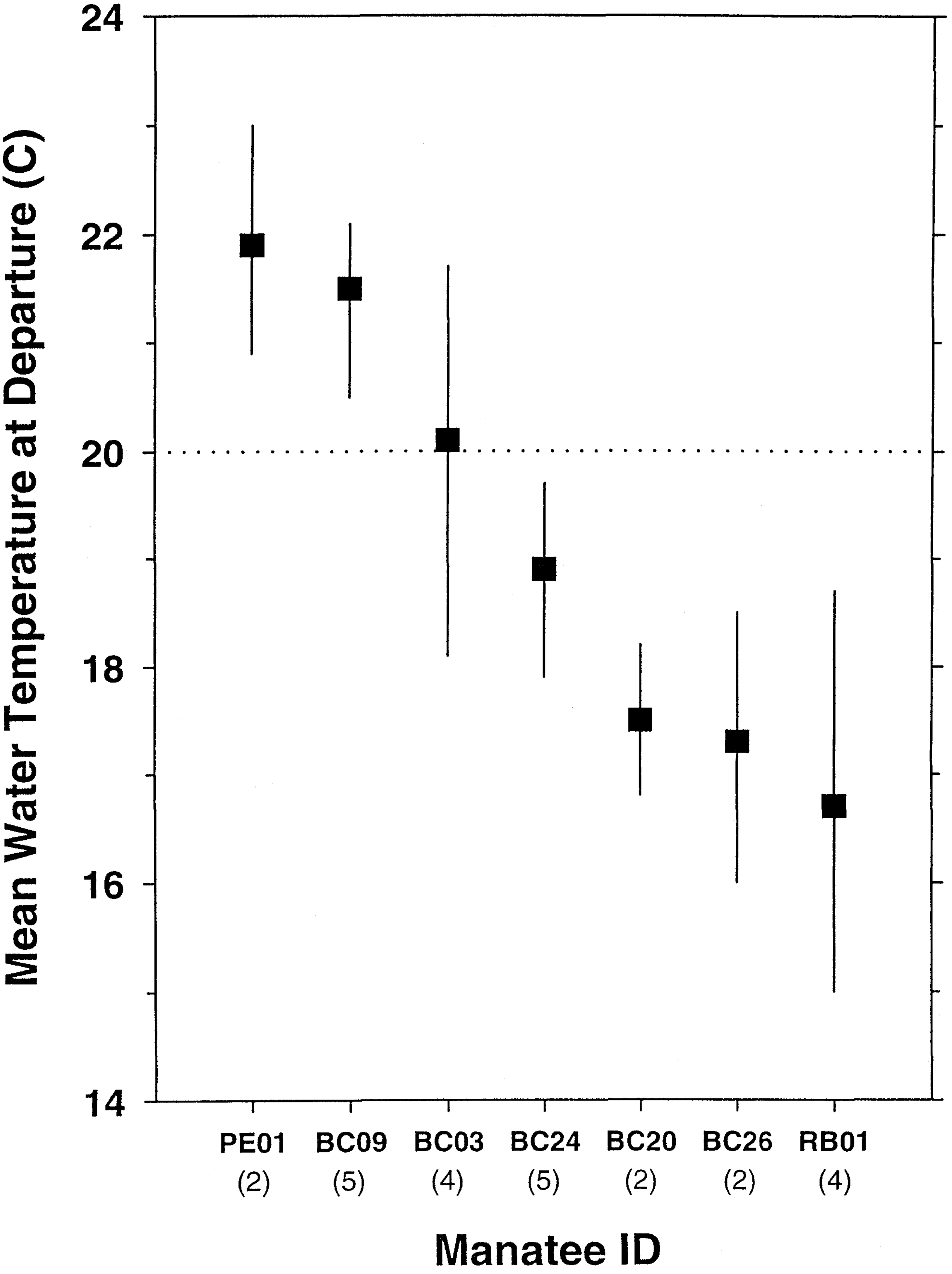

24
22
20
18
16
14
Mean Water Temperature at Departure (C)
PE01
(2)
BC09
(5)
BC03
(4)
BC24
(5)
BC20
(2)
BC26
(2)
RB01
(4)
Manatee ID

Figure 9. Migratory movements of tagged manatees in relation to mean daily water temperature in the Banana Creek, Brevard County (Y coordinate = 3150) during 1992-93. The top figure shows the percentage of tagged animals (N = 9 - 13) initiating northward or southward migrations between Brevard County and southern Florida in each 2-week period. In the bottom figure UTM northing coordinates of mean daily locations for 3 adult females (+ = TBC-09, O = TBC-36, ● = TBC-37) are plotted against date (first of the month) to illustrate synchrony of winter movements in relation to temperature change.

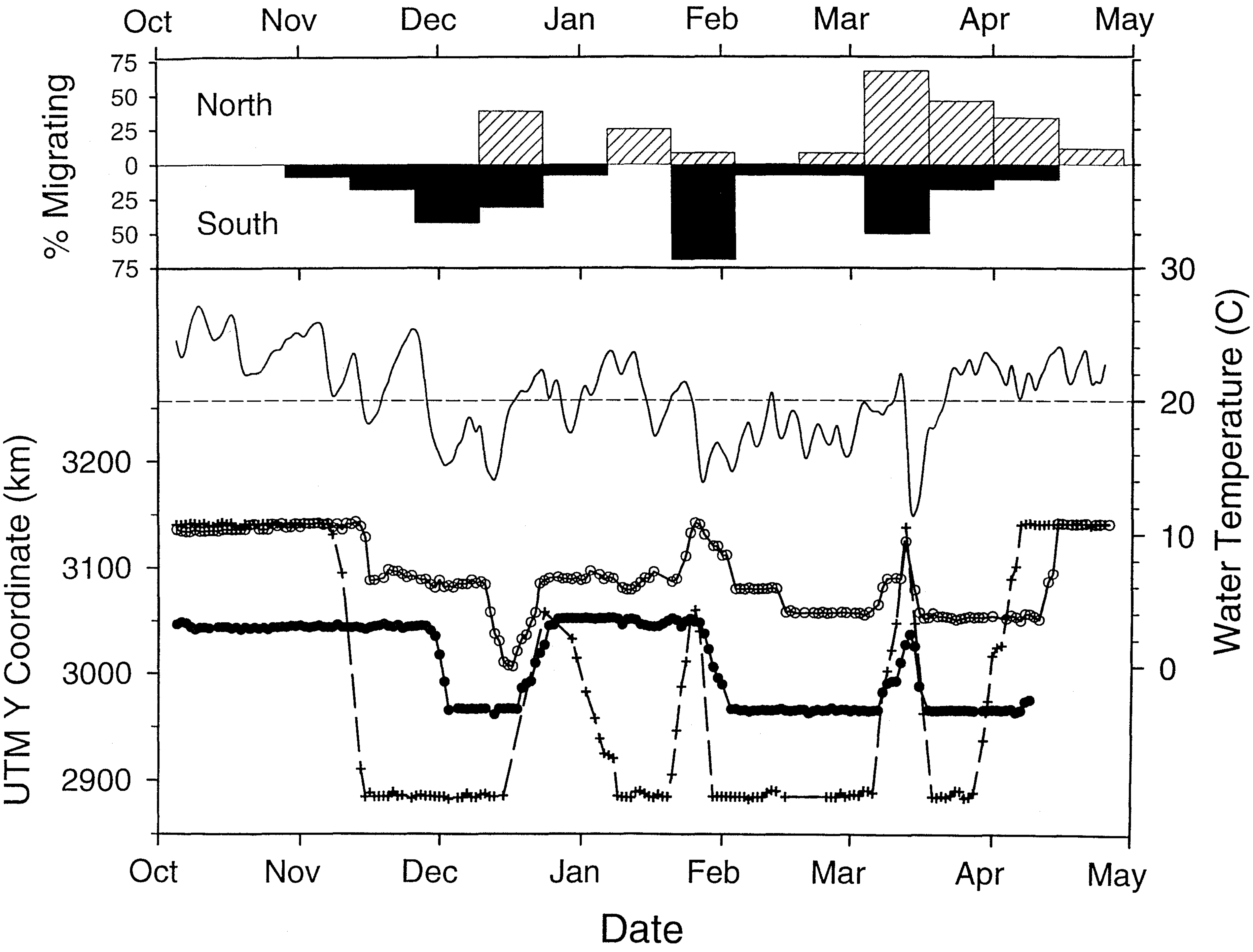
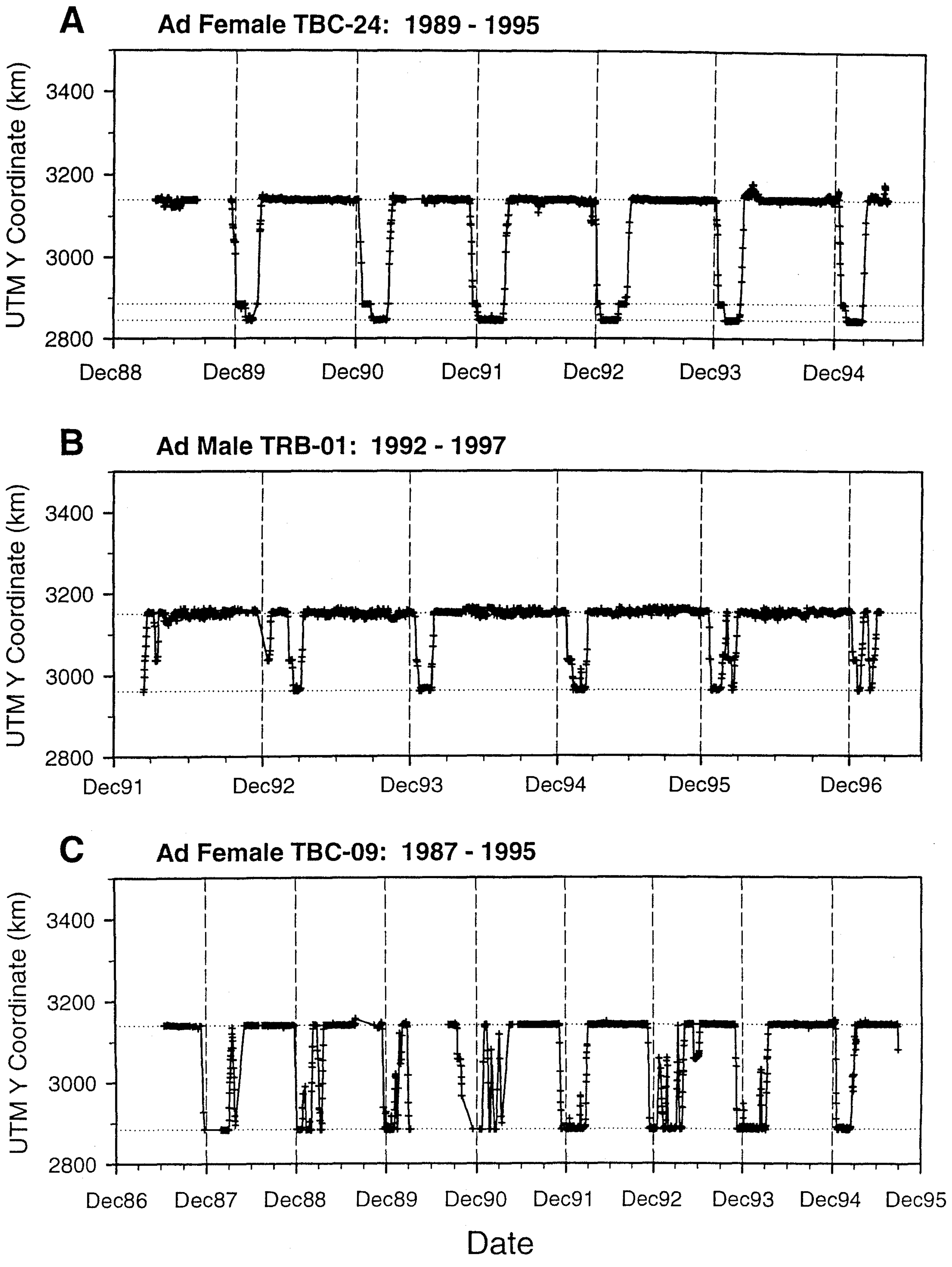

Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
% Migrating
75
50
25
0
25
50
75
North
South
UTM Y Coordinate (km)
3200
3100
3000
2900
Water Temperature (C)
30
20
10
0
Date

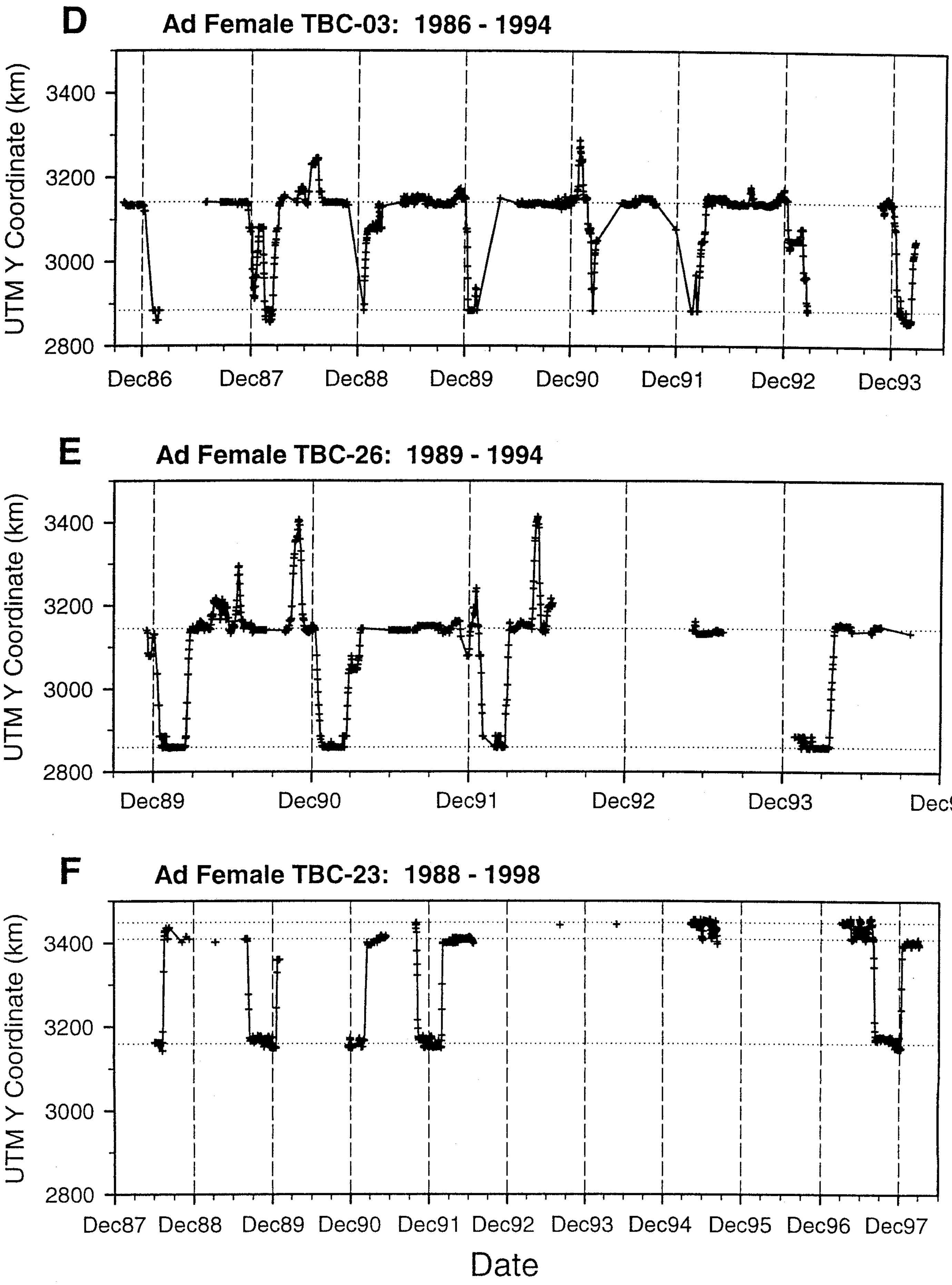
Figure 10. Long-term fidelity to seasonal movement patterns and seasonal ranges, as illustrated by plots of UTM northing coordinates of mean daily locations (+) against date for selected manatees with multiple years of tracking data. (A-C) C-S migrants with high site fidelity to seasonal ranges and strong consistency in movement patterns across several years. (D-E) C-S migrants that made brief excursions north of their warm season range in some years. (F) N-C migrant that regularly migrated to the northern region in early to mid-winter, maintaining this movement pattern over a 10-year period. (G) Long-distance migrant showing consistency across several years. (H-I) C-S and short-distance migrants that occupied 2 core areas during the warm season. Dashed vertical lines denote the start of the winter season (1 Dec.); intervals between minor tick marks on the x-axis represent 3 months. Dotted horizontal lines indicate the principal warm season and winter areas used by each manatee. Successive locations more than 90 days apart are not connected by lines.



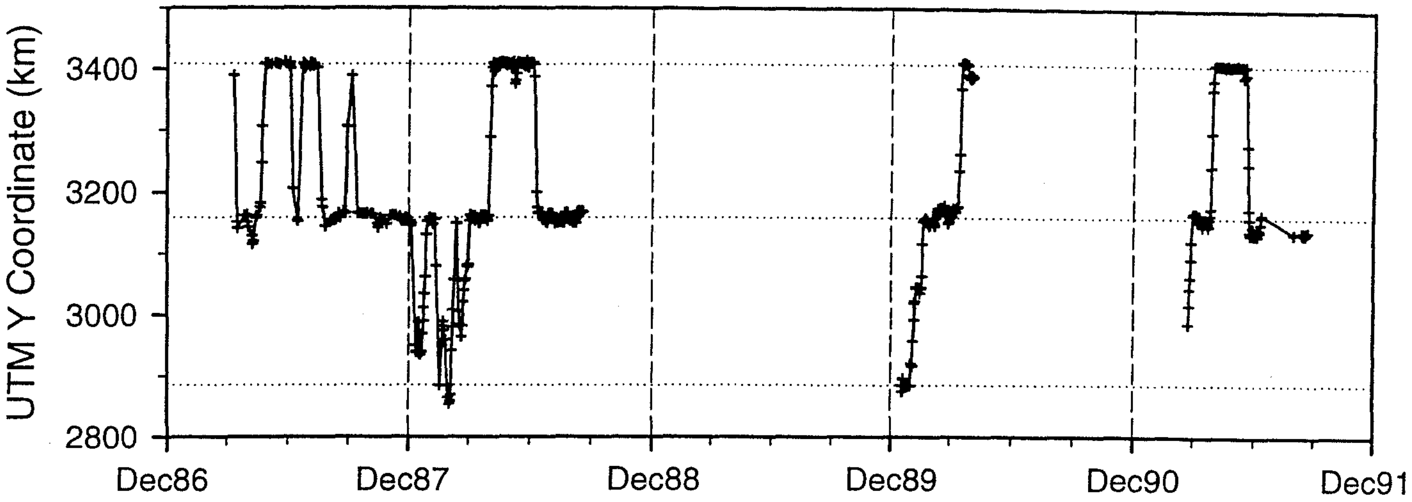
A Ad Female TBC-24: 1989 - 1995

B Ad Male TRB-01: 1992 - 1997

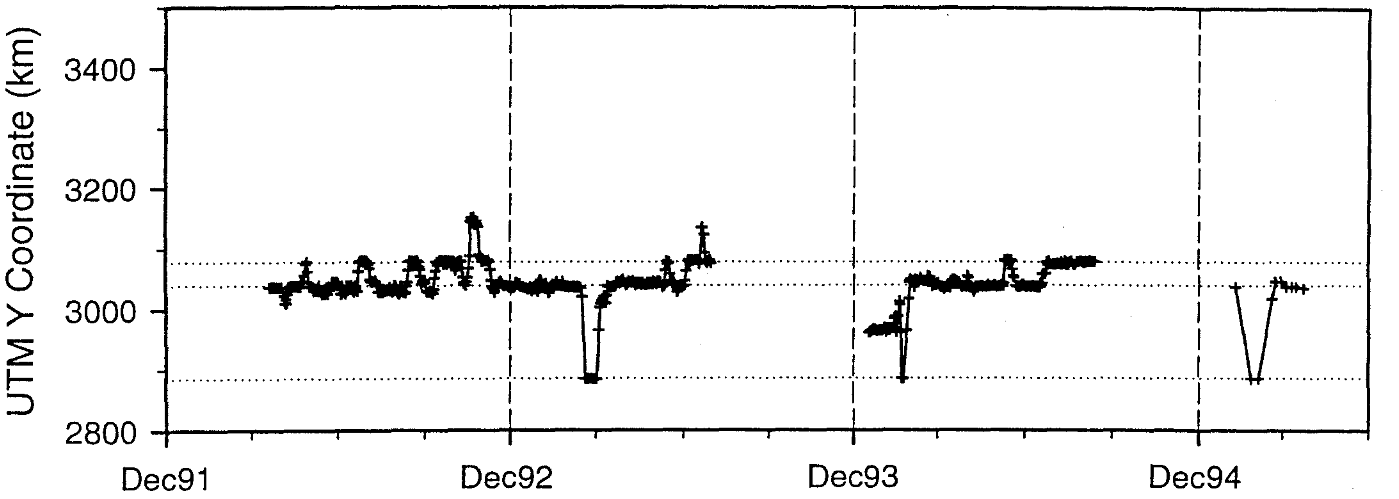
C Ad Female TBC-09: 1987 - 1995


D
Ad Female TBC-03: 1986 - 1994
UTM Y Coordinate (km)
3400
3200
3000
2800
Dec86
Dec87
Dec88
Dec89
Dec90
Dec91
Dec92
Dec93
E
Ad Female TBC-26: 1989 - 1994
UTM Y Coordinate (km)
3400
3200
3000
2800
Dec89
Dec90
Dec91
Dec92
Dec93
Dec94
F
Ad Female TBC-23: 1988 - 1998
UTM Y Coordinate (km)
3400
3200
3000
2800
Dec87
Dec88
Dec89
Dec90
Dec91
Dec92
Dec93
Dec94
Dec95
Dec96
Dec97
Date

G **Ad Female TNC-01: 1987 - 1991**



H **Ad Female TFP-06: 1992 - 1995**



I **Ad Male TFP-02: 1990 - 1994**

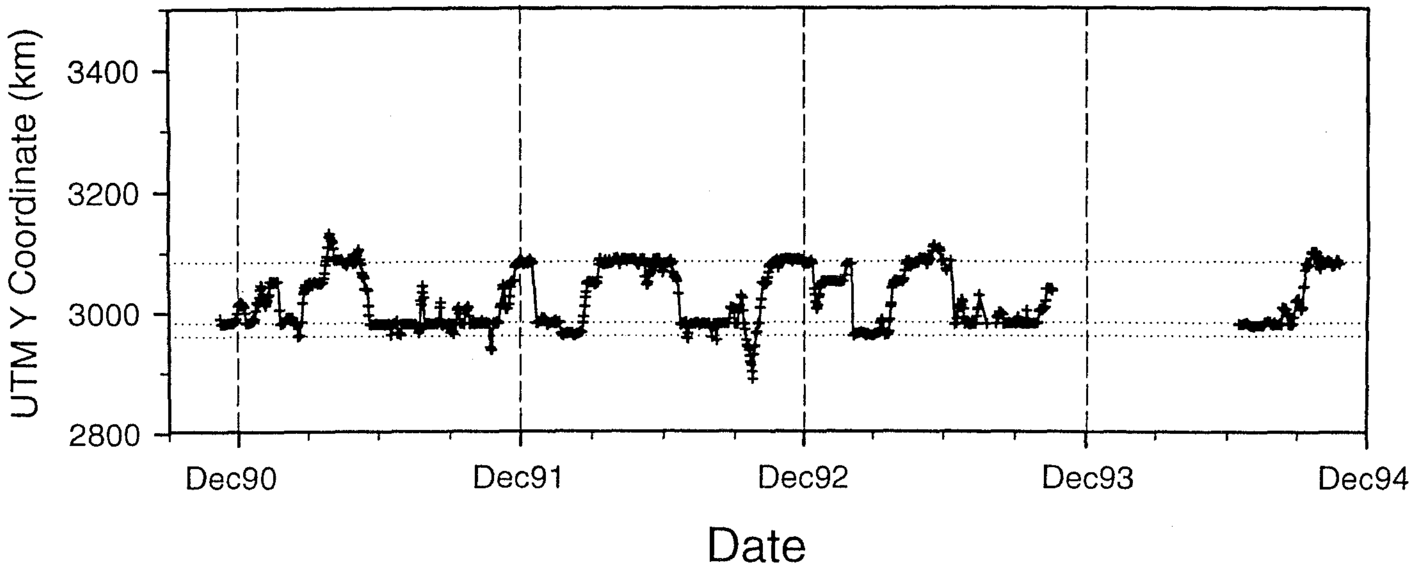
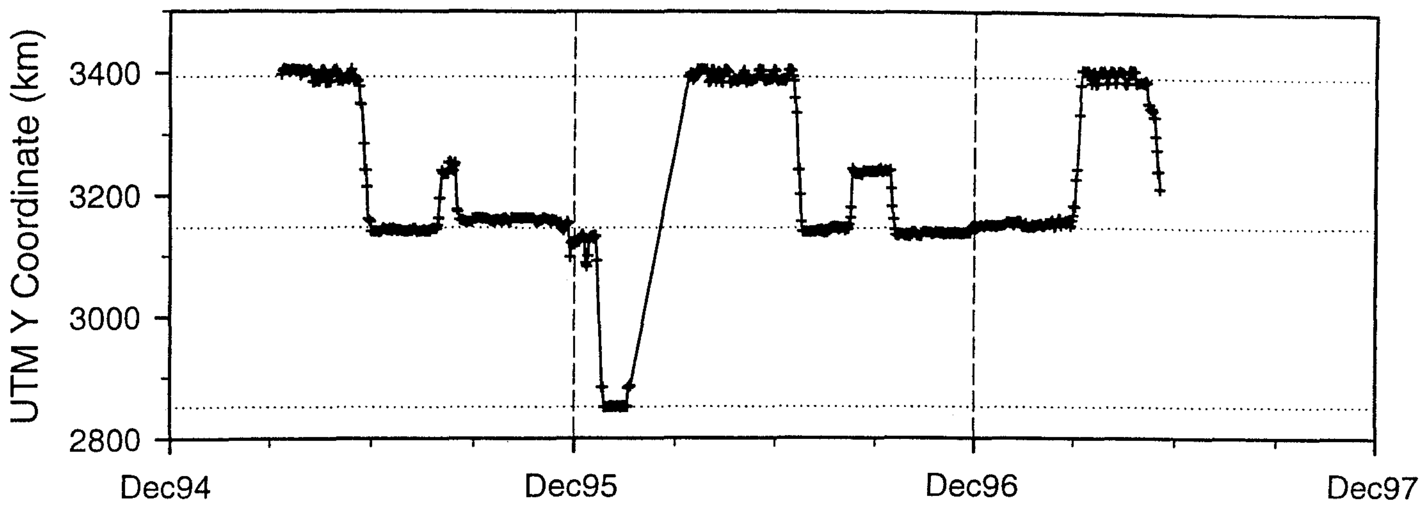
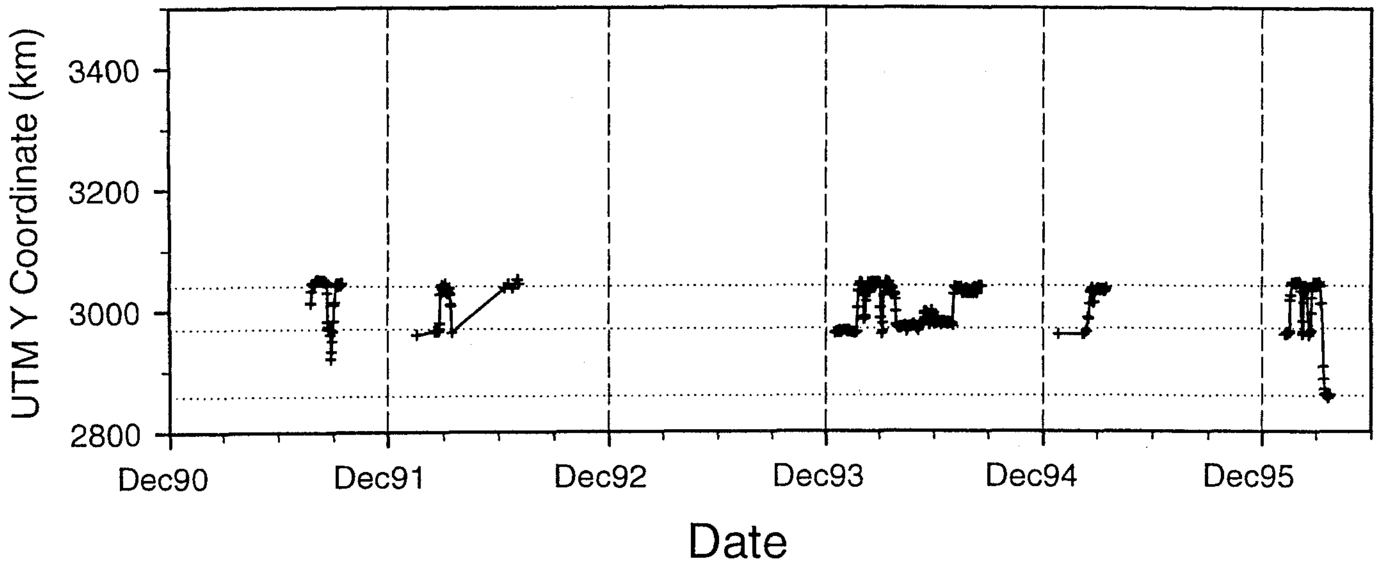


Figure 11. Changes in seasonal movement patterns and overwintering areas for 2 manatees, as shown by plots of UTM northing coordinates of mean daily locations (+) against date. (A) An individual that shifted its winter range from the Miami River (1995-96) to Brevard County (1996-97), thus changing from a long-distance to a medium-distance N-C migratory pattern. (B) A short-distance migrant that typically used the Riviera Beach area during cold winter periods, but migrated 190 km south of her warm season range in late winter of the fifth year of tracking. Reference lines as in Figure 10.



A Ad Female TNC-10: 1995 - 1997



B Ad Female TFP-04: 1991 - 1996

Figure 12. North-south movements of 2 C-S migrants during the 1993 warm season, illustrating the difference in intraannual site fidelity between (A) adult males (TMI-01) and (B) adult females (TMI-02). UTM northing coordinates of mean daily locations (+) are plotted against date over a 9-month period.

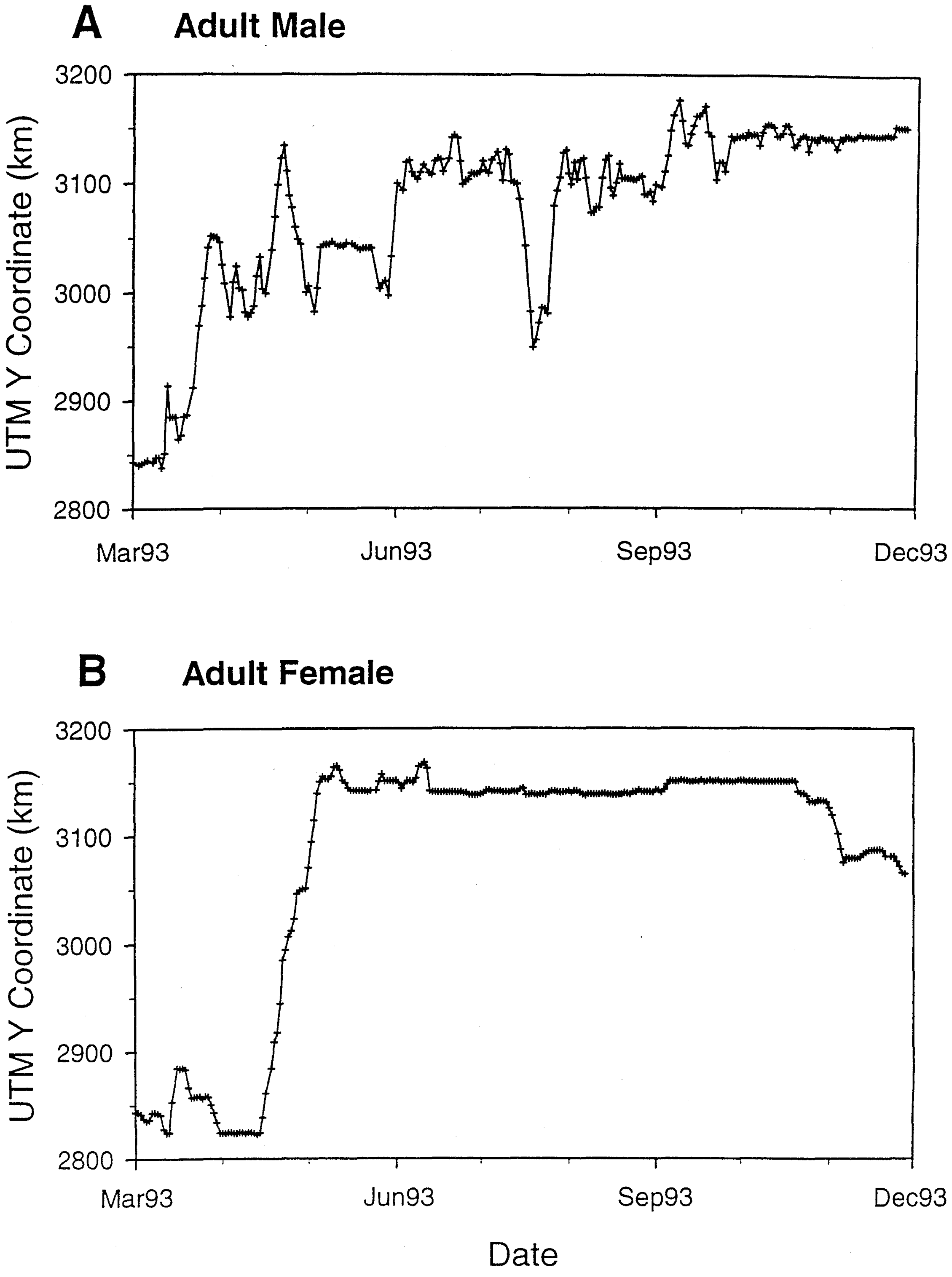

A
Adult Male
3200
3100
3000
2900
2800
UTM Y Coordinate (km)
Mar93
Jun93
Sep93
Dec93
B
Adult Female
3200
3100
3000
2900
2800
UTM Y Coordinate (km)
Mar93
Jun93
Sep93
Dec93
Date

Figure 13. Frequency distribution of mean interannual site fidelity (A) during the warm season (April to October) for 31 manatees, and (B) during the winter (December to February) for 17 manatees. Site fidelity was measured as the distance between the centers of location clusters within the same region from one year to the next (see Methods).

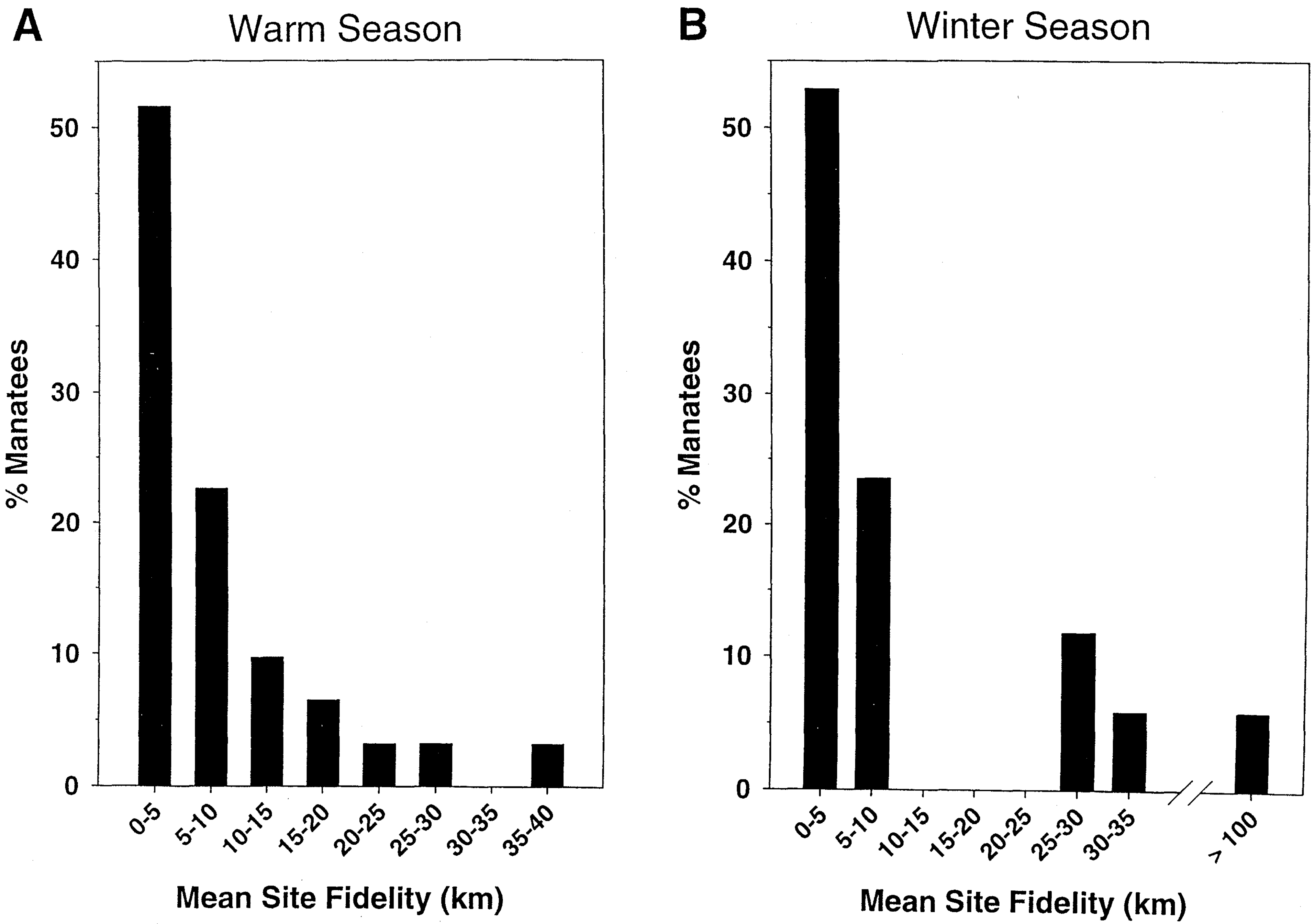
A
Warm Season
% Manatees
0
10
20
30
40
50
0-5
5-10
10-15
15-20
20-25
25-30
30-35
35-40
Mean Site Fidelity (km)
B
Winter Season
% Manatees
0
10
20
30
40
50
0-5
5-10
10-15
15-20
20-25
25-30
30-35
> 100
Mean Site Fidelity (km)

Figure 14. Interannual site fidelity as a function of the number of intervening years (A) during the warm season (April to October), and (B) during the winter (December to February). Site fidelity was measured as the distance between the centers of location clusters within the same region from one year to a later year (see Methods); the 4^+ year category includes time spans up to 9 years in the warm season and up to 7 years in the winter. The median value is shown as a line within a box bounded by the 25th and 75th percentiles; whiskers denote the 10th and 90th percentiles (equivalent to minimum and maximum values for $N \leq 10$). Sample sizes are shown as the number of manatees (N) and the number of year comparisons (n).

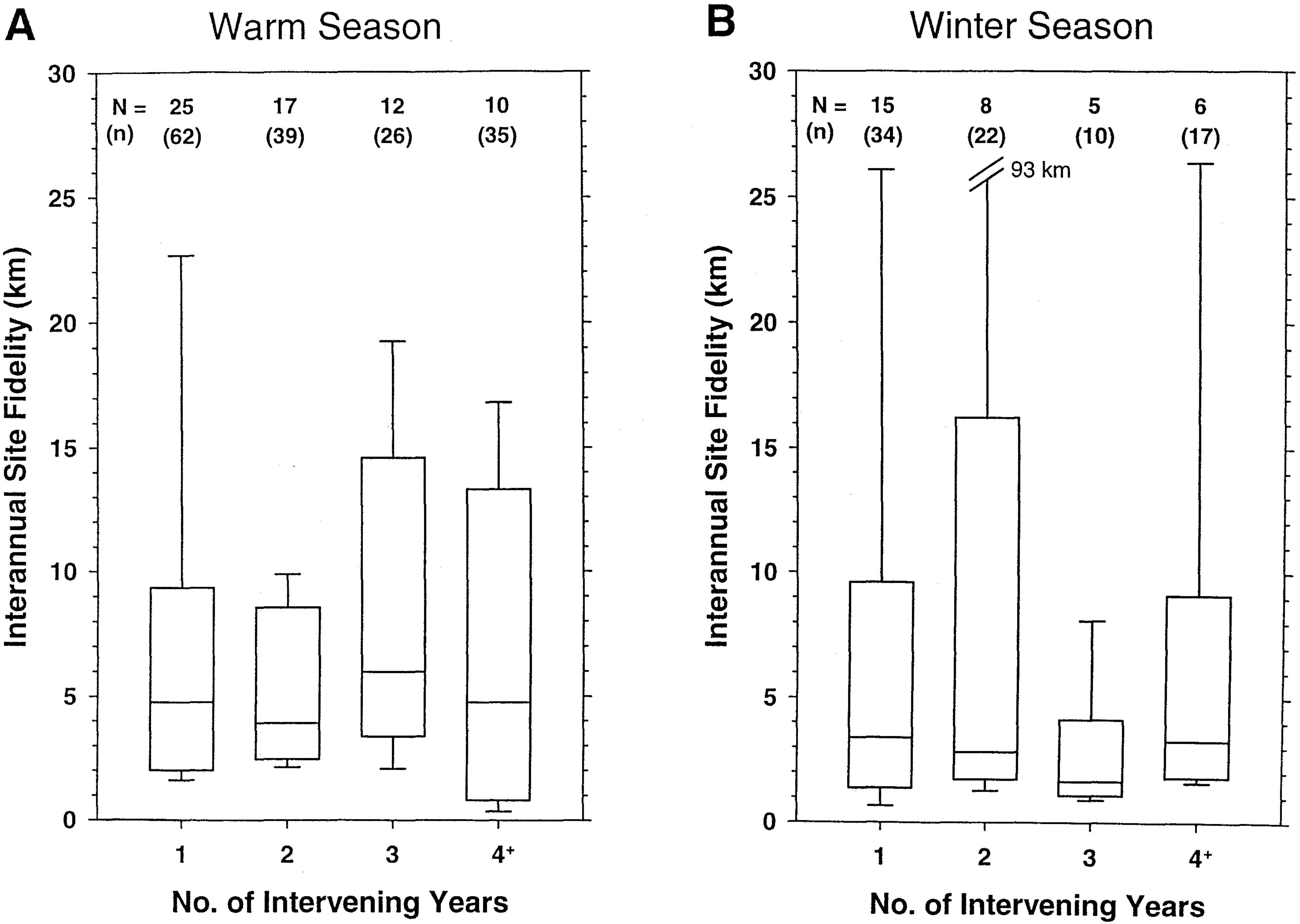
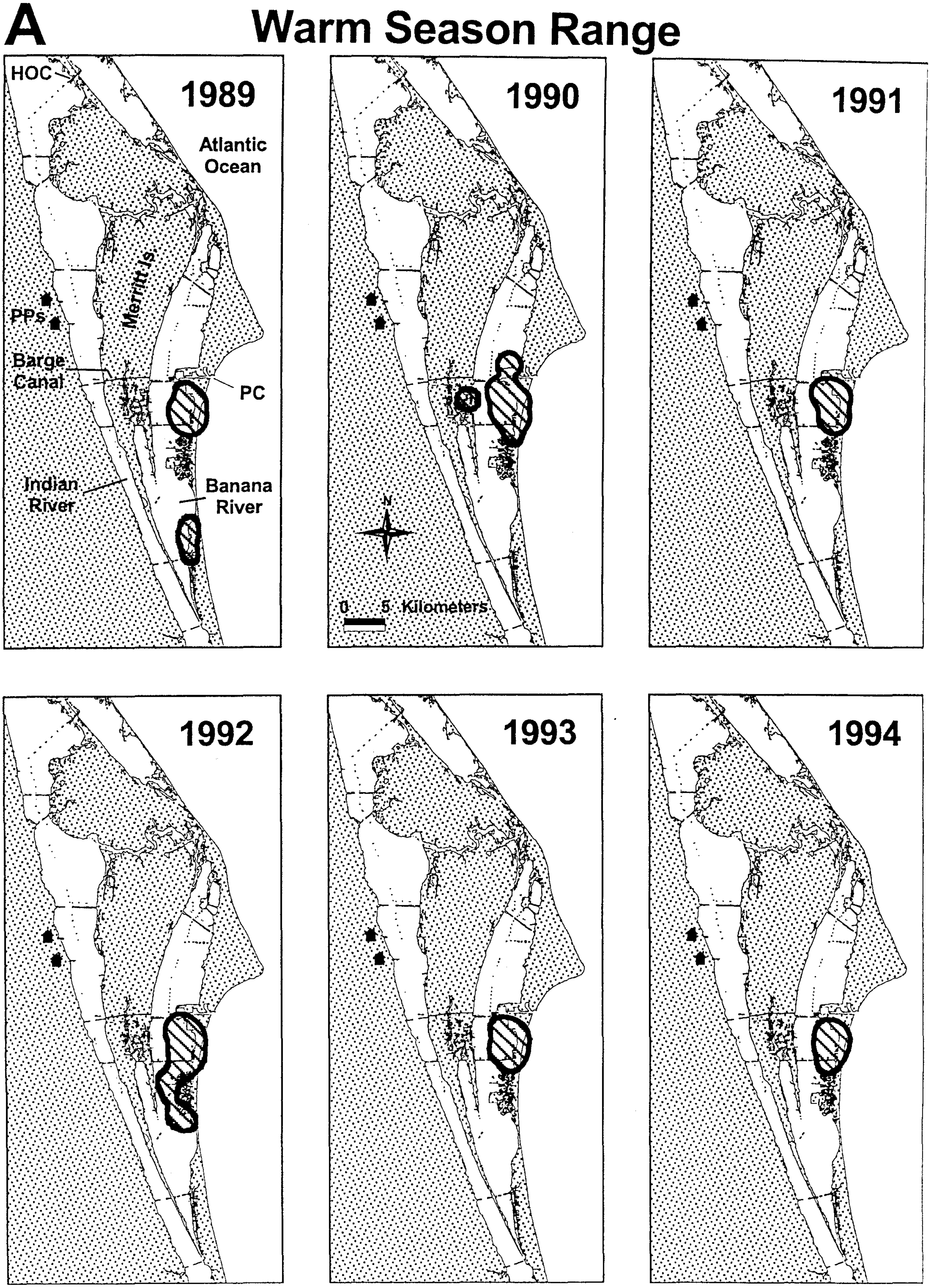
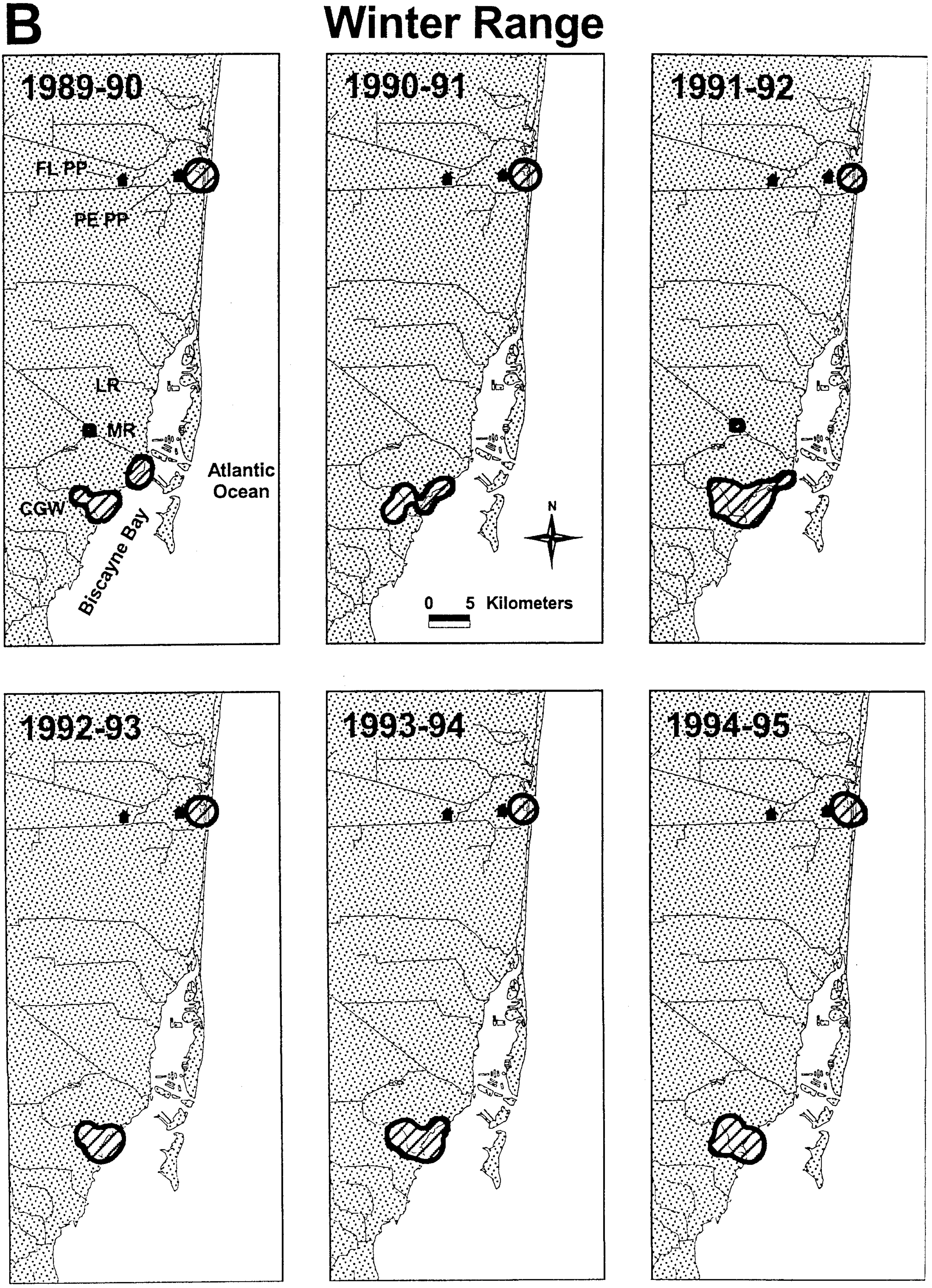

A
Warm Season
B
Winter Season
Interannual Site Fidelity (km)
30
25
20
15
10
5
0
N =
(n)
25
(62)
17
(39)
12
(26)
10
(35)
15
(34)
8
(22)
5
(10)
6
(17)
93 km
1
2
3
4+
No. of Intervening Years

Figure 15. Interannual site fidelity for adult female TBC-24 over six years to (A) warm season range in the Banana River, Brevard County, and (B) winter range at two sites (Port Everglades and Coral Gables) in southeastern Florida, 275 and 320 km south of her warm season range, respectively. Hatched polygons denote 95% kernel home ranges (grid cell size = 100 m, smoothing parameter H = 1000, Hooge and Eichenlaub 1997) based on satellite-determined locations (LC2-3) and visual observations. Locations of warm-water power plant effluents are indicated by house symbols. CGW = Coral Gables Waterway, HOC = Haulover Canal, FL PP = Ft. Lauderdale power plant, LR = Little River, MR = Miami River, PC = Port Canaveral, PE PP = Port Everglades power plant, and PPs = two power plants near Titusville, Brevard County.

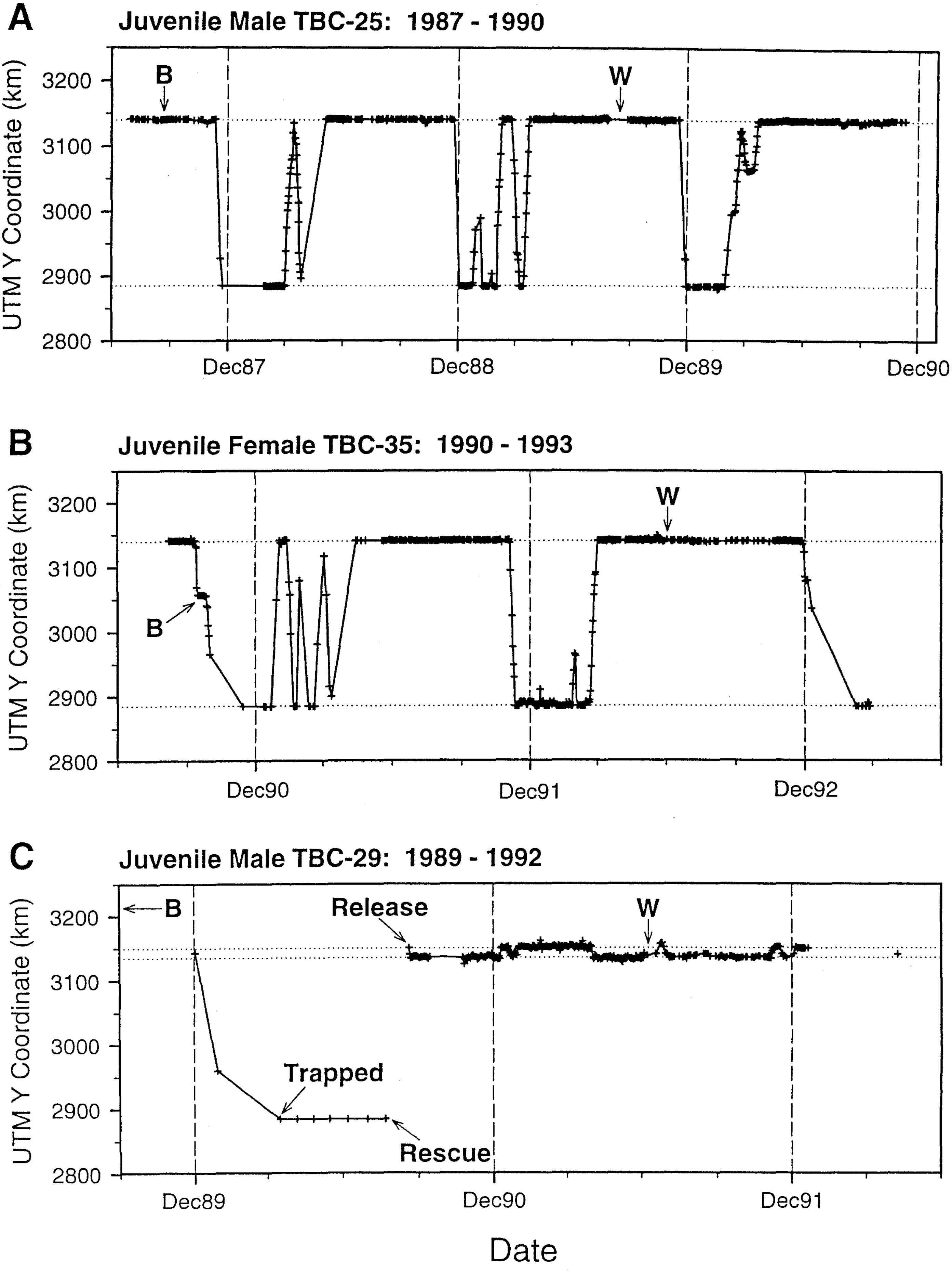

A
Warm Season Range
1989
HOC
Atlantic Ocean
Merritt Is.
PPs
Barge Canal
PC
Indian River
Banana River
1990
N
0 5 Kilometers
1991
1992
1993
1994



B

Winter Range

Figure 16. Natal fidelity to seasonal movement patterns and seasonal ranges, as illustrated by plots of UTM northing coordinates of mean daily locations (+) against date for 3 calves tracked with their mothers and then subsequent to weaning. Birth and weaning events are denoted by the letters B and W, respectively. Dashed vertical lines denote the start of the winter season (1 Dec.); intervals between minor tick marks on the x-axis represent 3 months. Dotted horizontal lines indicate the principal warm season and winter areas used by each manatee.



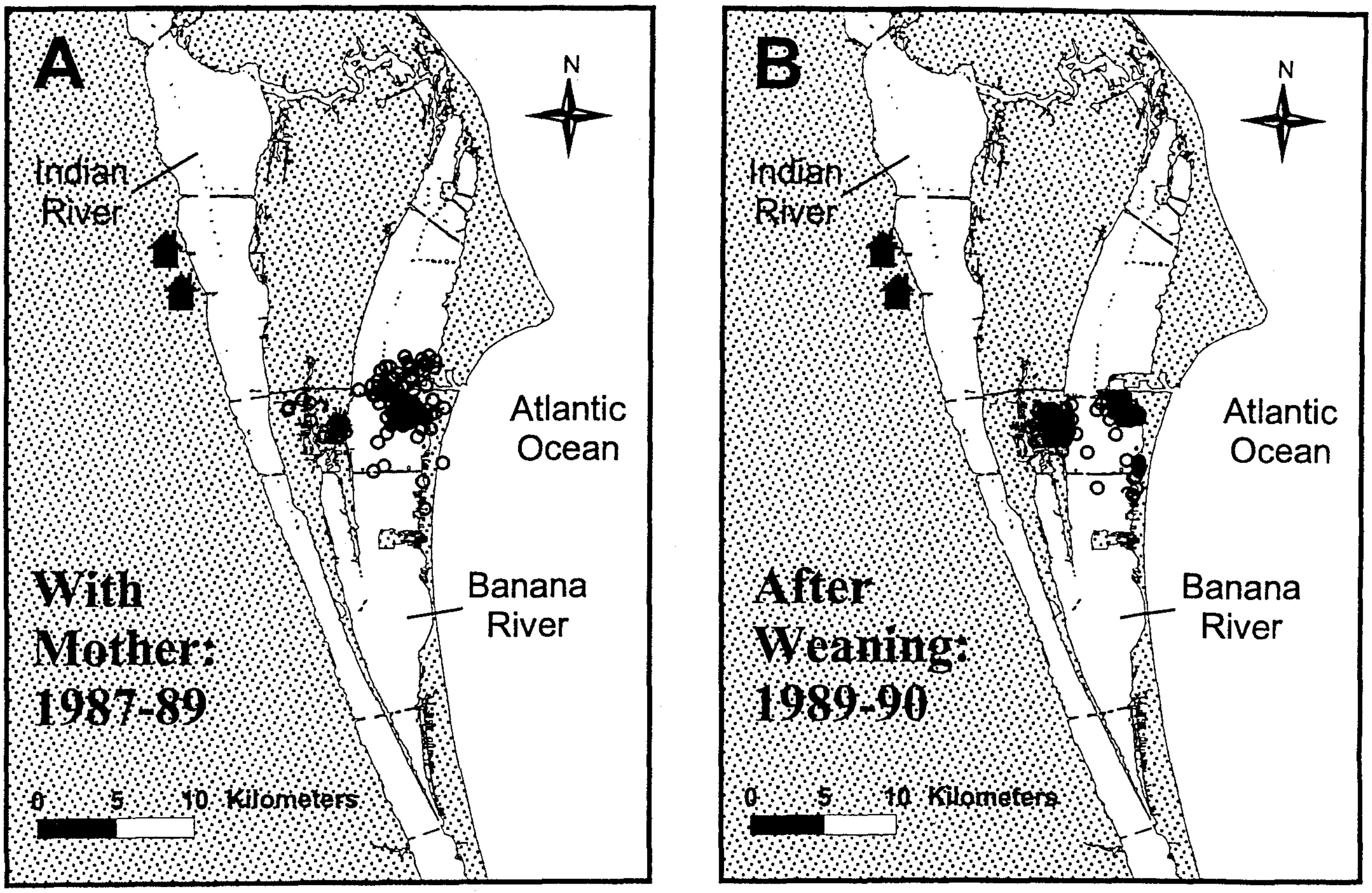
A Juvenile Male TBC-25: 1987 - 1990

B Juvenile Female TBC-35: 1990 - 1993

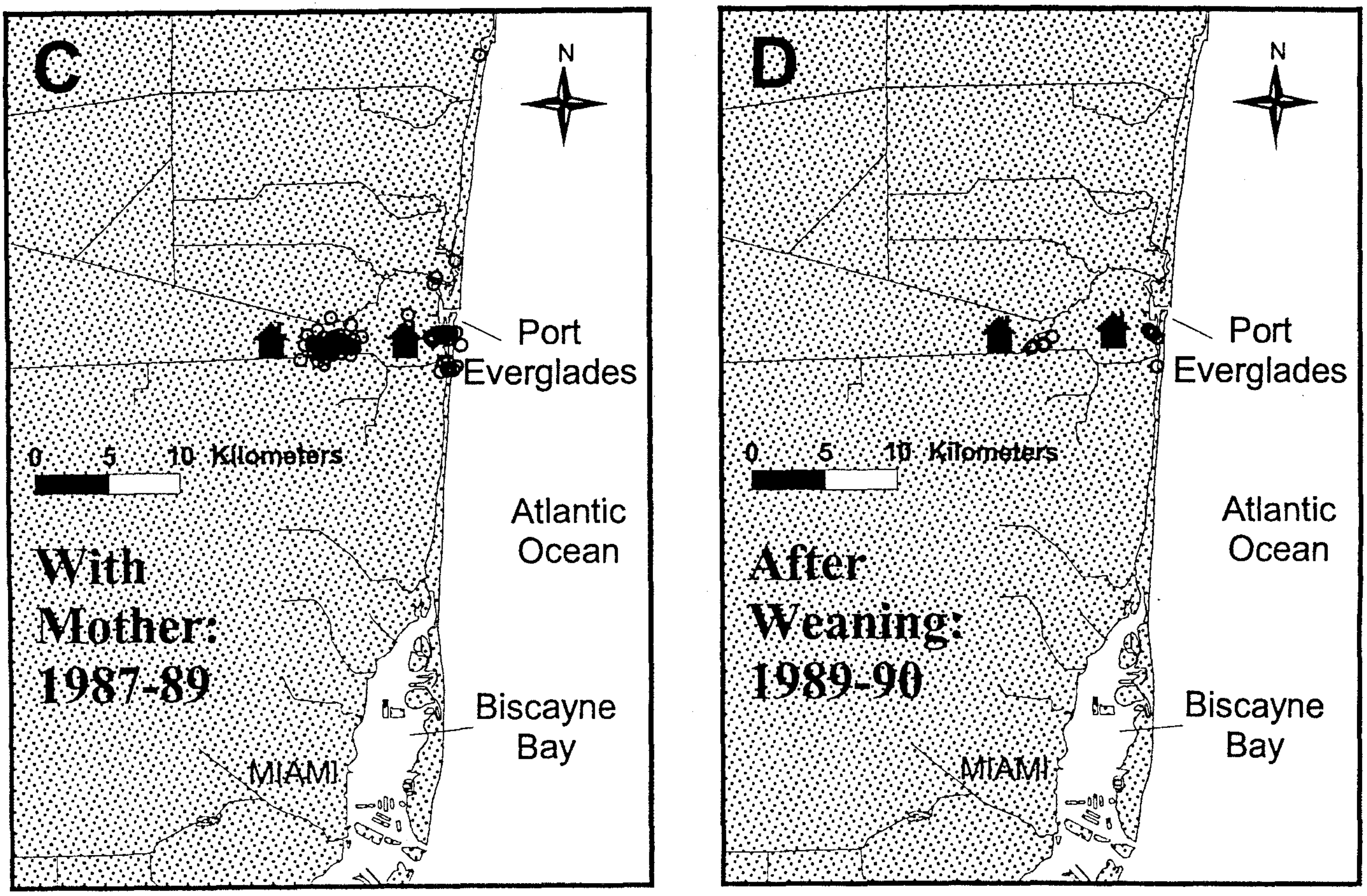
C Juvenile Male TBC-29: 1989 - 1992

Figure 17. Natal philopatry of male TBC-25 to his warm season (April to October) range in Brevard County and his winter (December to February) range in southeastern Florida. (A, C) Locations of the mother-calf pair during the 24-month dependency period over 3 warm seasons and 2 winters. (B, D) Locations of the independent subadult during the 15 months after weaning. Circles (○) represent satellite-determined locations (LC2-3), visual observations, and triangulated positions of TBC-25 or his mother (TBC-09). Locations of warm-water power plant effluents are indicated by house symbols. Linear features in SE FL denote major canals, rivers, and intracoastal waterways. See Figure 1 for geographic reference.

Warm Season



Winter Season



APPENDICES

Appendix A. Attributes of 78 radio-tagged manatees tracked along the Atlantic coast of the United States, including physical characteristics, duration in captivity prior to tagging, tagging information, tracking duration, seasonal movement pattern, and range.

Appendix A.

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TBC-01	Dixie	AD	F	310	--	08May86	17Jun88	C: BR	4	321	C-S	431	310
TBC-02	Trixie	AD	F	270	--	08May86	18Jun86	C: BR	1	41	--	--	--
TBC-03	Moon	AD	F	277	--	30Sep86	22Feb94	C: BR	34	1724	C-S	482	287
TBC-04	Eclipse	SU	F	260	--	03Oct86	30May87	C: BR	3	231	C-S	322	300
TBC-05	Gyro	AD	F	267	--	13Nov86	14May88	C: BCK	3	314	RES	107	20
TBC-06	Moe	SU-AD	M	260	--	20Apr87	09Dec90	C: BCK	6	850	N-C	352	294
TBC-07	Bill	AD	M	270	--	21Apr87	20Jun87	C: BCK	1	59	--	--	--
TBC-08	Angela	AD	F	325	--	23Apr87	15Jun87	C: BR	1	53	–	–	--
TBC-09	C-cow	AD	F	305	--	16Jun87	26Aug95	C: BR	43	2493	C-S	306	282
TBC-10	Fran	AD	F	310	--	16Nov87	21Jan88	C: BCK	1	66	--	--	--
TBC-11	Gloria	AD	F	300	--	16Nov87	13Jan88	C: BCK	1	58	--	--	--
TBC-12	Heike	AD	F	295	--	17Nov87	13Jan88	C: BCK	2	57	--	--	--
TBC-13	Irene	SU	F	260	--	17Nov87	08Jul88	C: BCK	3	234	C-S	281	275
TBC-14	Jerome	AD	M	275	--	17Nov87	26Mar88	C: BCK	1	130	--	--	--

Appendix A (continued).

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TBC-15	Karen	AD	F	280	--	18Nov87	13Jun90	C: BCK	6	272	N-C	301	297
TBC-16	Larry	AD	M	285	--	18Nov87	21Nov87	C: BCK	1	3	--	--	--
TBC-17	Madonna	AD	F	350	--	18Nov87	25Dec87	C: BCK	1	37	--	--	--
TBC-18	Leroy	AD	M	280	--	30Mar88	09May89	C: BCK	3	95	--	--	--
TBC-19	Sharon	AD	F	315	--	21Apr88	01May88	C: BR	1	10	--	--	--
TBC-20	Ruth	AD	F	270	--	21Apr88	20Oct90	C: BR	15	666	C-S	309	280
TBC-21	Willie	AD	M	280	--	22Apr88	06Mar90	C: BR	4	161	--	--	--
TBC-23	Hillary	AD	F	273	4.1	07Jun88	03Mar98	C: BR	22	1244	N-C	394	309
TBC-24	Betty	AD	F	285	--	05Apr89	16May95	C: BR	28	2052	C-S	383	326
TBC-25	D-cow	CA-SU	M	225	--	11Apr89	12Nov90	C: BR	5	552	C-S	292	282
TBC-26	Peewee	AD	F	270	--	16Nov89	22Sep94	C: BR	13	1111	C-S	630	317
TBC-29	Casey	CA-SU	M	210	1.0	21Aug90	22Dec91	C: IRN	10	425	--	--	--
TBC-30	Maria	AD	F	280	--	30Oct90	27Feb91	C: BCK	1	120	--	--	--
TBC-31	Freddie	AD	F	300	--	31Oct90	24Apr92	C: BCK	5	491	N-C	279	251
TBC-32	Tomasina	AD	F	335	--	22May91	25Aug94	C: BR	7	226	C-S	309	297

Appendix A (continued).

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TBC-35	E-cow	CA-SU	F	230	--	05May92	26Feb93	C: BR	5	227	C-S	281	279
TBC-36	Sunshine	AD	F	260	--	15May92	06Mar94	C: BR	5	542	SHT (C-S)	214	165
TBC-37	Pamela	AD	F	263	8.8	28May92	09Apr93	C: BR	2	316	SHT	222	97
TBC-40	Danise	AD	F	280	8.4	08Jun94	10Jun94	C: BR	1	2	--	--	--
TBC-41	Scott	AD	M	274	5.1	09Aug94	08Feb95	C: BR	1	160	RES	52	36
TBC-42	Chessie	AD	M	315	0.2	07Oct94	10Jul96	C: BR	6	373	LNG	2360	580
TBC-43	Robbie	CA-SU	M	240	--	21Apr95	13Jul95	C: BR	2	83	--	--	--
TFK-01	Manny	AD	F	295	0.2	21Sep93	03May94	S: KL	3	216	RES	44	11
TFK-02	Stan	AD	M	280	--	19Oct93	24May94	S: TAV	6	164	RES	49	22
TFK-03	Ollie	AD	M	280	--	19Oct93	15Feb94	S: TAV	1	119	--	--	--
TFP-01	Hutch	AD	M	305	3.4	10Apr90	21Apr90	C: STL	1	11	--	--	--
TFP-02	Ross	AD	M	295	3.3	07Nov90	25Oct94	S: HBSD	12	1187	SHT	266	135
TFP-03	Natalie	AD	F	310	3.7	24Jul91	26Sep94	C: STL	7	394	SHT	138	96
TFP-04	Sophia	AD	F	330	--	26Jul91	24Mar96	C: STL	9	467	SHT (C-S)	212	80
TFP-05	Lani	AD	F	335	--	10Aug91	16Mar93	S: JUP	6	306	C-S	235	210

Appendix A (continued).

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TFP-06	Vanna	AD	F	320	--	20Mar92	23Mar95	C: FP	8	765	C-S	294	215
TGA-01	Mary	AD	F	330	--	26Jul89	29Apr90	N: KB	3	277	N-C	382	373
TGA-02	Tory	AD	M	295	--	10Mar95	16Sep95	N: BRUN	1	190	--	--	--
TGA-03	Marmontel	AD	F	304	--	10Mar95	26Jan97	N: BRUN	6	628	RES (SHT)	112	48
TGA-04	Mercury	AD	F	330	--	12Mar96	10Nov97	N: BRUN	3	608	N-C	375	338
TGA-05	Bailey	AD	M	278	--	17Mar97	29Apr98	N: BRUN	3	408	N-C	362	299
TGA-06	Savannah	AD	F	348	--	17Mar97	27Oct97	N: BRUN	2	224	--	--	--
TGA-07	GP	AD	M	305	--	17Mar97	25Jul97	N: BRUN	1	130	--	--	--
TJX-01	Connie	AD	F	271	15.5	11Sep90	15Jun92	N: SJR	5	353	LNG	613	577
TJX-02	Patience	AD	F	284	--	02May91	01May95	N: STAUG	3	368	N-C (C-S)	419	192
TJX-03	Freckles	SU	F	245	--	19Oct93	23May94	N: STAUG	3	216	N-C	257	248
TMI-01	Bob	AD	M	303	4.8	10Dec90	25May94	S: BB	9	568	C-S	363	316
TMI-02	Fergie	AD	F	265	--	02Sep92	04Dec93	S: BB	3	458	C-S	381	349
TMI-03	Clockwork	AD	M		--	11Feb94	22Aug94	S: BB	1	192	--	--	--
TNC-01	Diane	AD	F	330	--	11Mar87	23Aug91	N: FB	8	754	LNG	623	613

Appendix A (continued).

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TNC-02	Jesse	AD	M	305	--	11Mar87	02May87	N: FB	1	52	--	--	--
TNC-03	Tammy	AD	F	315	--	25Feb88	02Sep97	N: FB	3	315	--	--	--
TNC-04	Pat	AD	F	310	--	25Feb88	21Apr88	N: FB	1	56	--	--	--
TNC-05	Roseanne	AD	F	340	--	18Jan89	31May89	N: FB	1	133	SHT	109	102
TNC-06	Nancy	SU	F	250	--	18Jan89	05Jun91	N: FB	3	188	LNG	586	575
TNC-07	Whitie	SU	M	250	--	16Mar89	24Jul89	N: FB	1	130	--	--	--
TNC-08	George	AD	M	275	--	16Mar89	15May89	N: FB	1	60	--	--	--
TNC-09	Janatee	AD	F	270	--	12Mar95	20Aug95	N: FB	1	161	--	--	--
TNC-10	March	AD	F	330	--	12Mar95	18May97	N: FB	4	746	LNG (N-C)	639	446
TNC-11	Vale	SU	M	257	--	12Mar95	29Apr95	N: FB	1	48	--	--	--
TNC-12	Mossie	AD	M	290	--	13Mar96	16Jun98	N: FB	4	474	N-C	345	271
TNC-13	Knicky	AD	F	280	27.2	06Mar97	01Dec99	N: FB	3	452	LNG (N-C)	850	831
TNC-14	Jeb	AD	M	282	--	06Mar97	25May99	N: FB	2	100	SHT	175	96
TNC-15	Xena	AD	F	278	--	06Mar97	18Feb98	N: FB	3	289	N-C	347	294
TPE-01	Spot	AD	F	315	--	27Jan89	30May94	S: PE	23	1078	C-S	335	275

Appendix A (continued).

ID	Name	Age Class	Sex	Length (cm)	Captive Duration (mos.)	Date Tagged	Last Date with Tag	Tagging Location[a]	Tagging Bouts	Days Tracked	Seasonal Movement Pattern[b]	Maximum Range (km)[c]	Annual Range (km)[c]
TPE-02	Fireball	AD	F	325	--	15Feb89	15Sep89	S: PE	5	163	--	--	--
TPE-03	Sickle	AD	F	335	--	19Dec89	27Sep93	S: PE	11	579	C-S	420	278
TPE-04	Susan	AD	F	304	1.0	21Aug90	25Oct94	C: IRN	5	360	RES	50	36
TRB-01	Sonny	AD	M	315	--	13Feb92	20Feb97	S: RB	14	1805	C-S	225	209

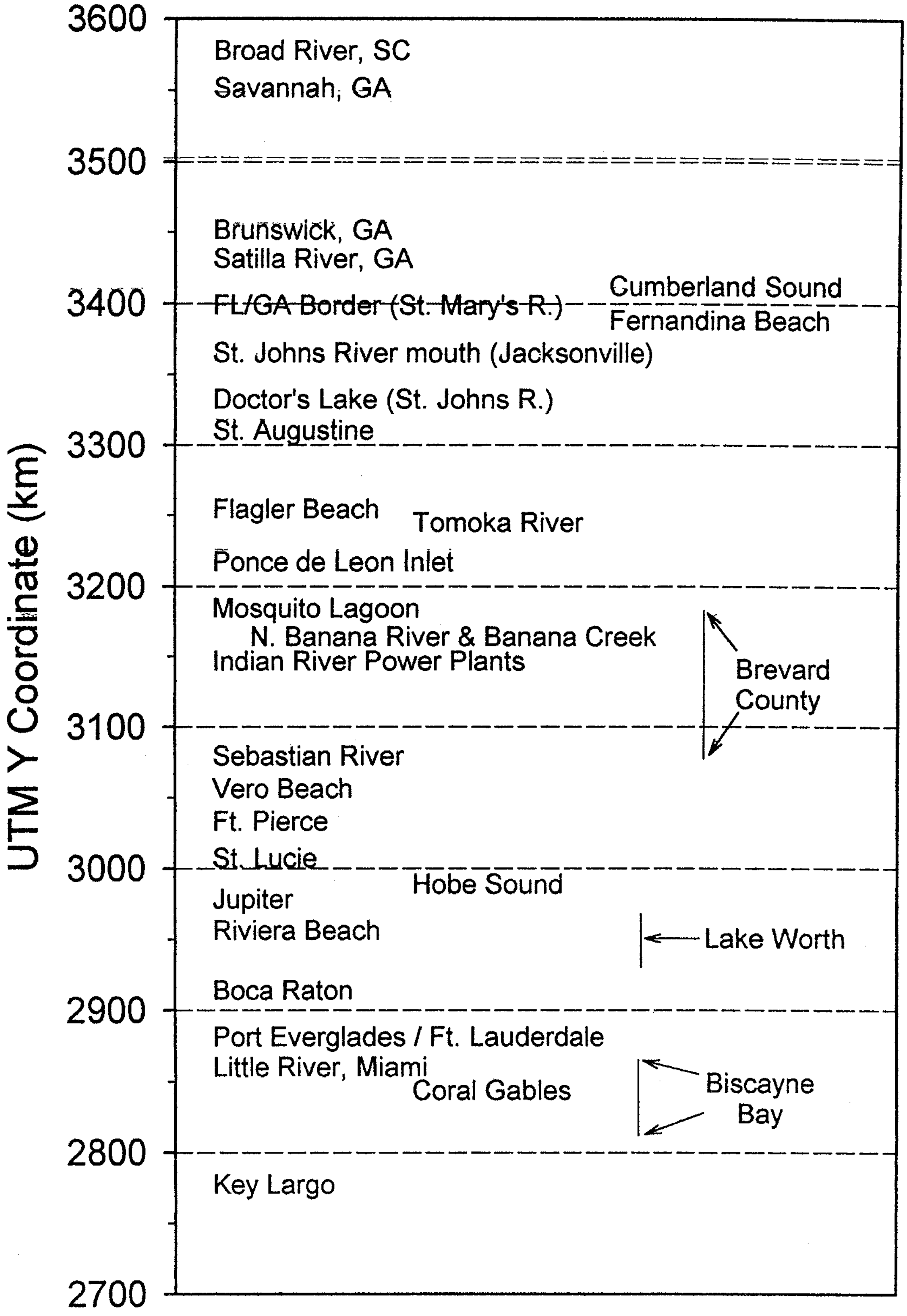
[a] Tagging region (C = central, N = north, S = south) followed by specific location: BB = Biscayne Bay, BCK = Banana Creek, BR = Banana River, BRUN = Brunswick, GA, FB = Fernandina Beach, FP = Ft. Pierce, HBSD = Hobe Sound, IRN = northern Indian River, JUP = Jupiter, KB = Kings Bay, GA, KL = Key Largo, PE = Port Everglades, RB = Riviera Beach, SJR = lower St. Johns River, STAUG = St. Augustine, STL = St. Lucie, and TAV = Tavernier.

[b] Seasonal movement patterns for individuals meeting tracking criteria (see Methods): C-S = central-south migrant, LNG = long-distance migrant, N-C = north-central migrant, RES = year-round resident, and SHT = short-distance migrant (see Results for definitions). For manatees that changed movement patterns over their tracking histories, the second pattern is shown in parentheses.

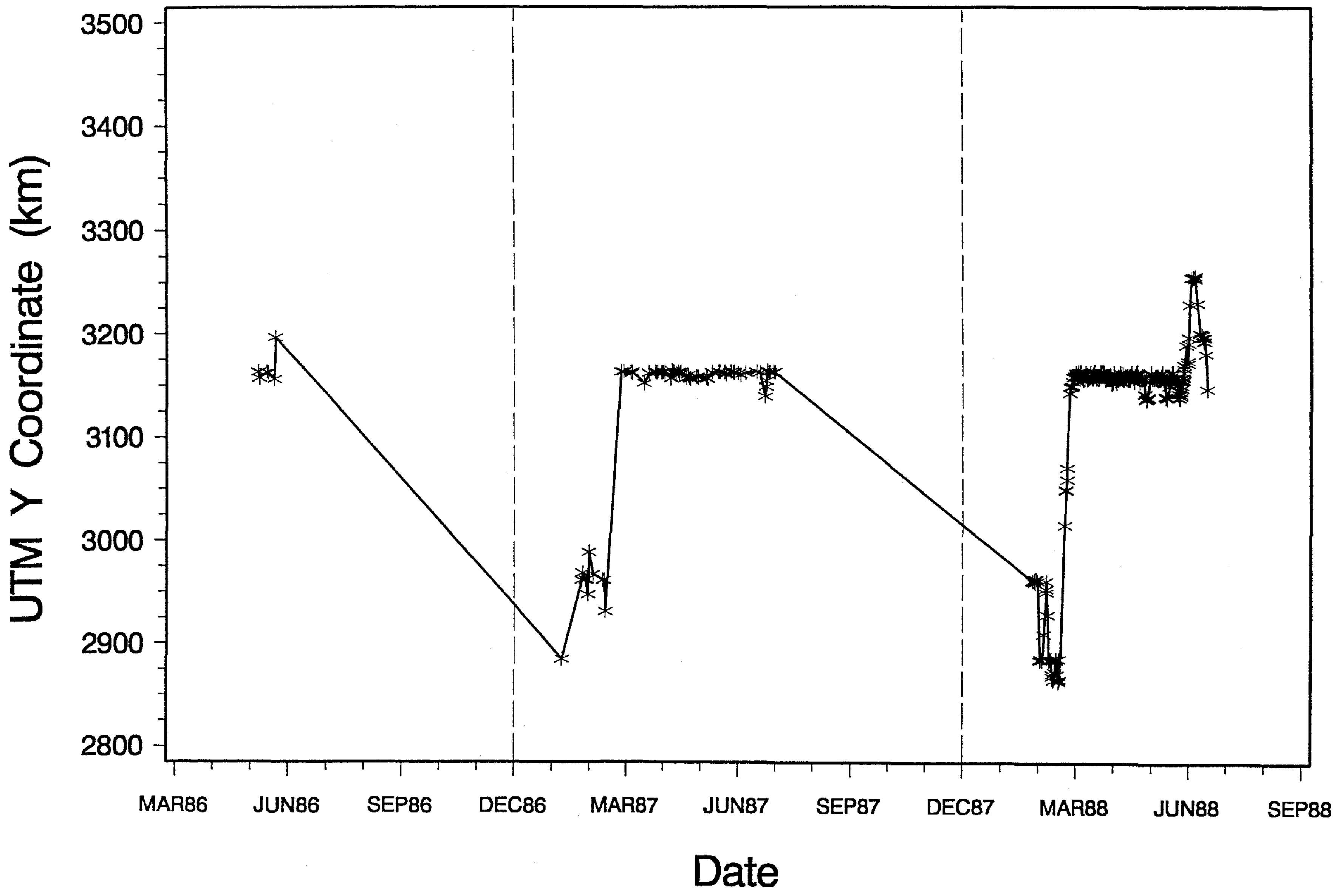
[c] See Methods for definitions.

Appendix B. Movement patterns 78 radio-tagged manatees along the Atlantic coast, as shown by plots of Universal Transverse Mercator (UTM) northing coordinates against date for each individual. Movements of manatees with more than 2 years of tracking data are shown in multiple figures with about 2 years per plot. For geographic reference the first plot shows the UTM northing coordinates of selected places along the Atlantic coast.

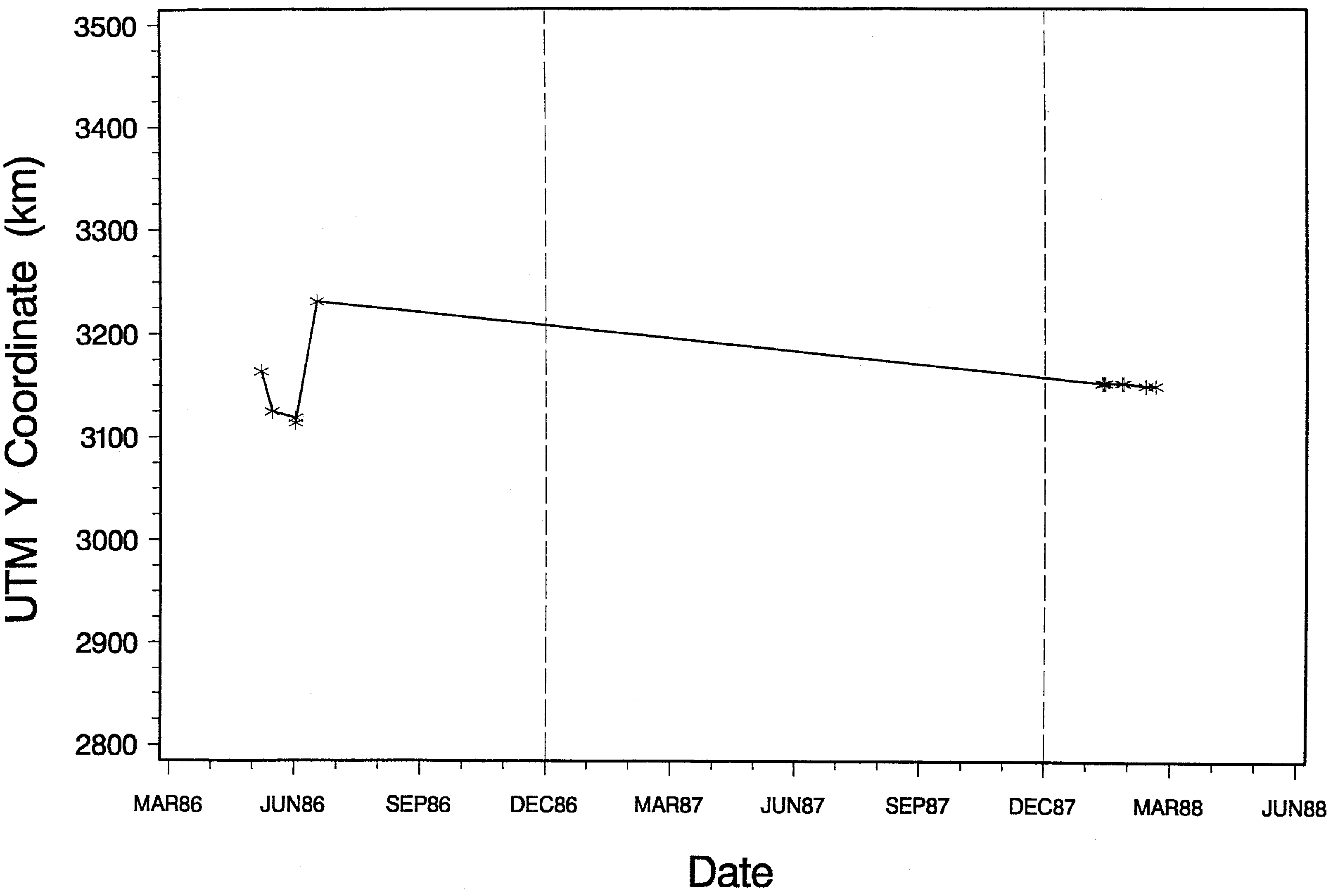
Y Coordinates of Place Names along the Atlantic Coast



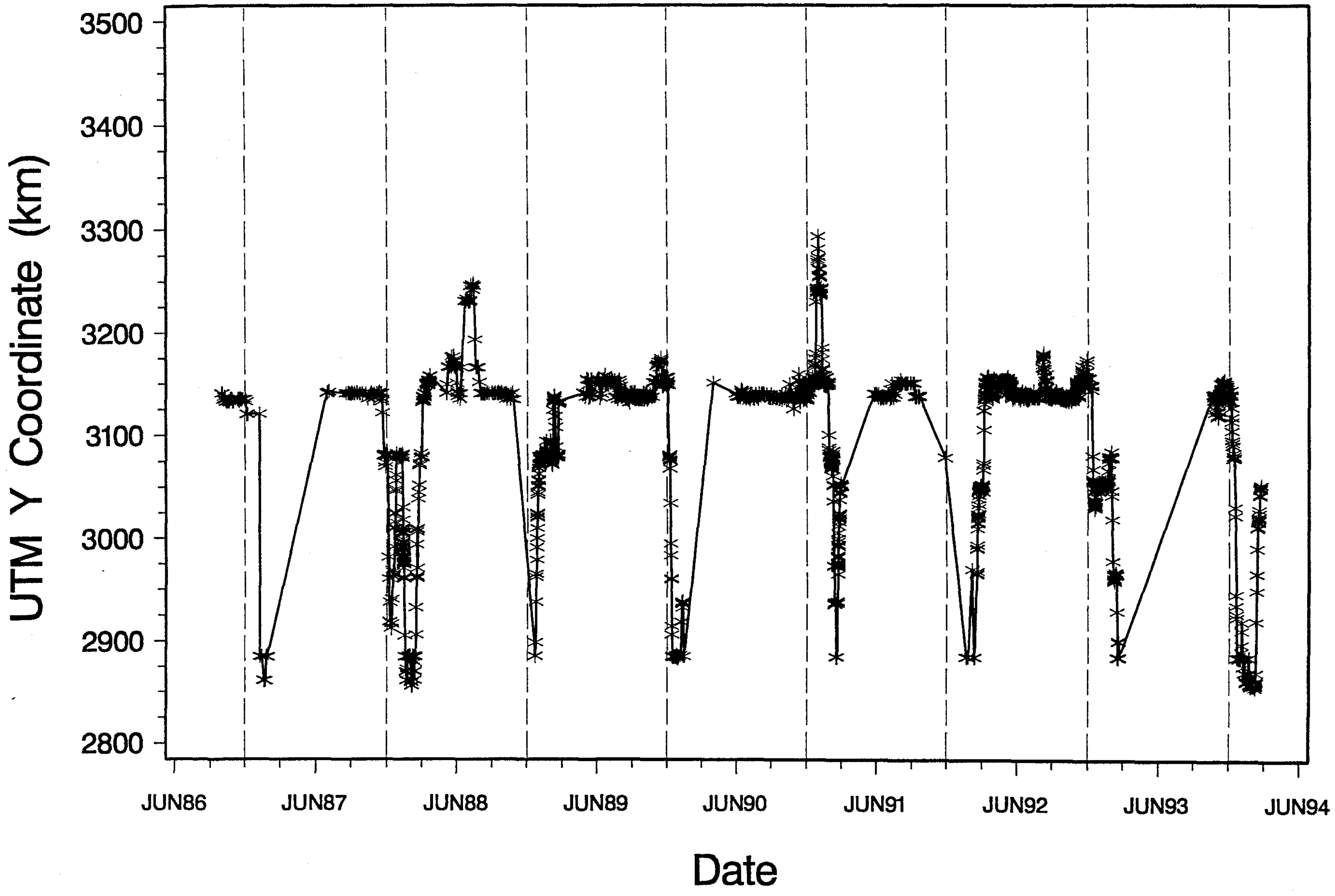
TBC – 01 ("Dixie"): 1986 – 1988



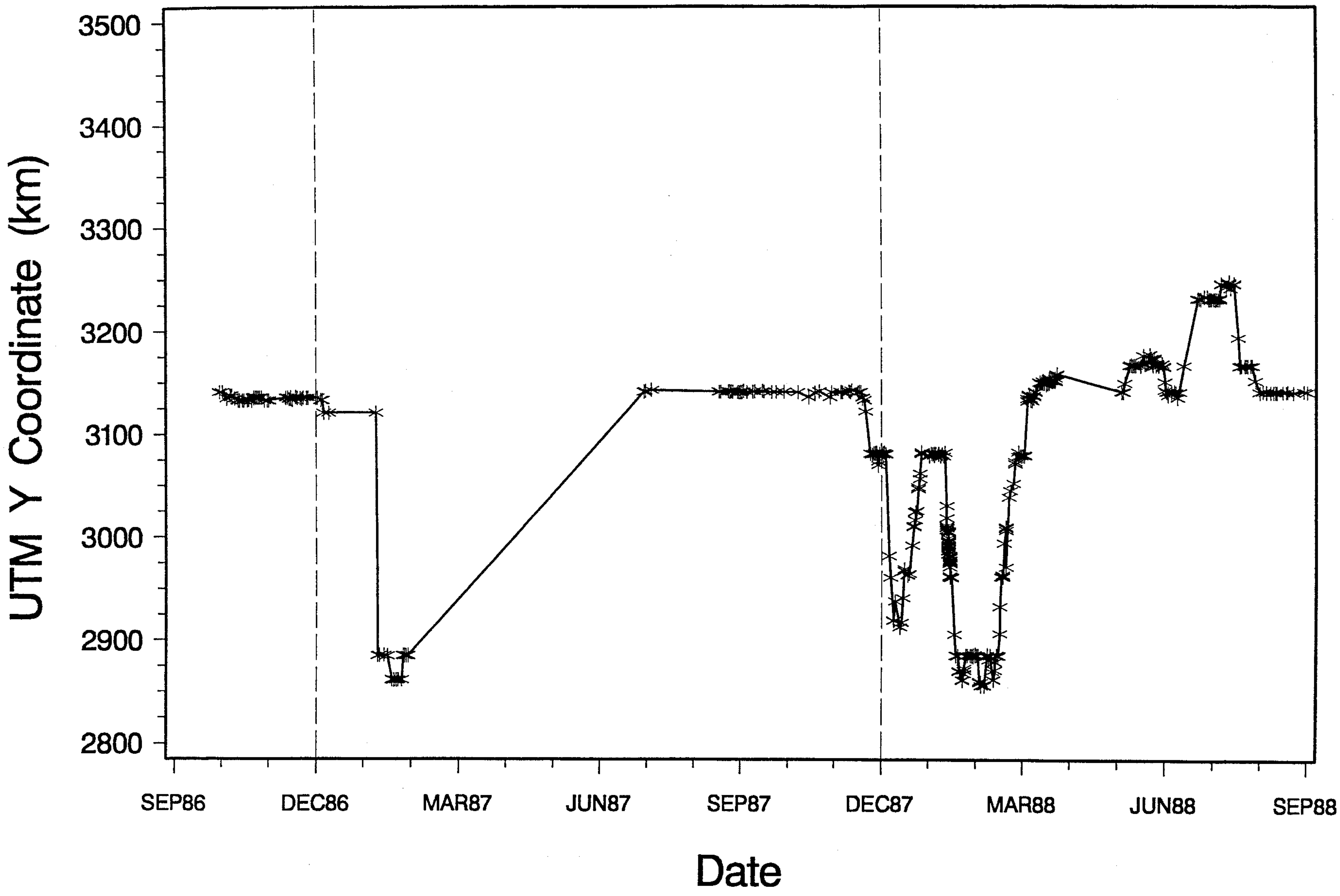
TBC – 02 ("Trixie"): 1986 – 1988



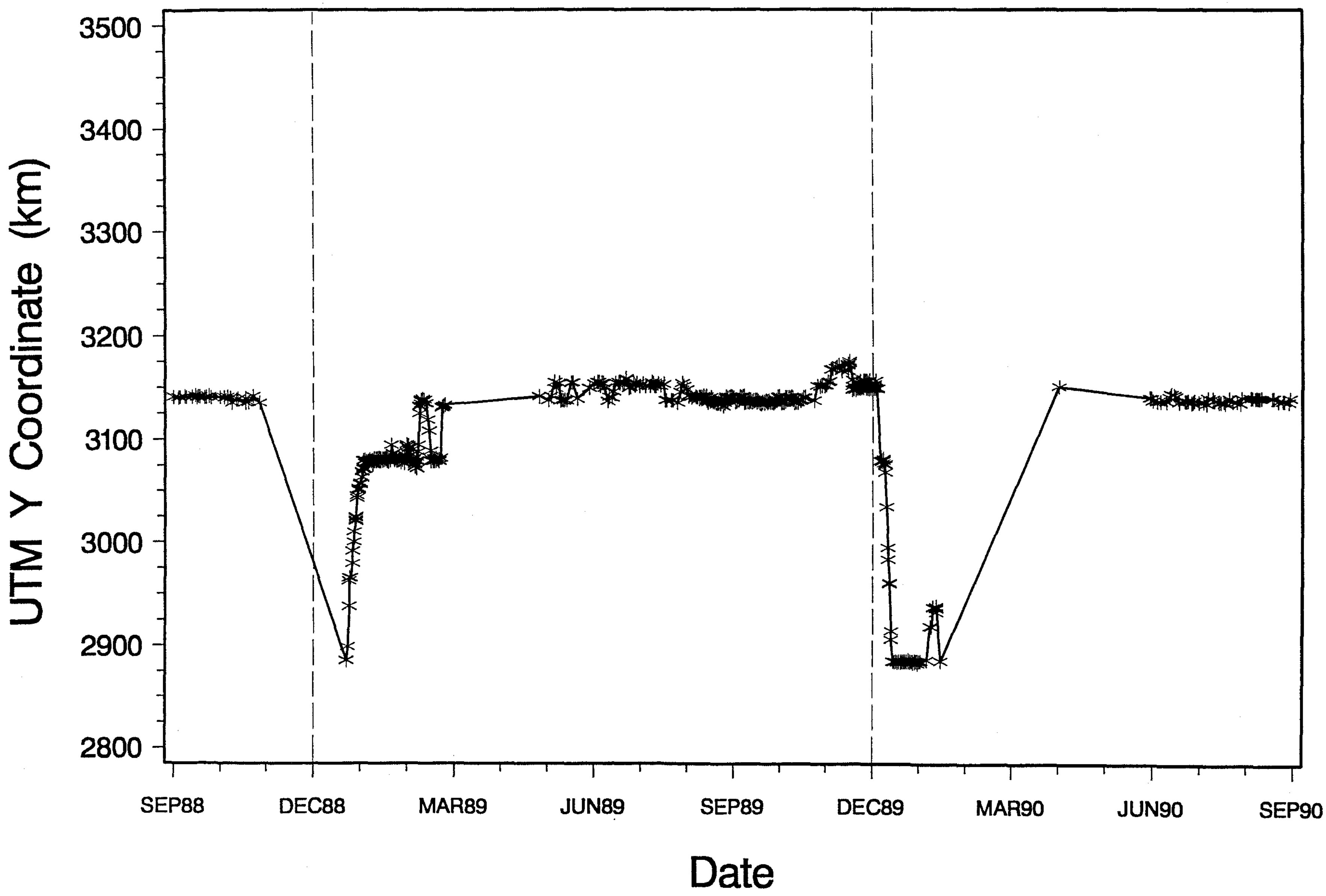
TBC – 03 ("Moon"): 1986 – 1994



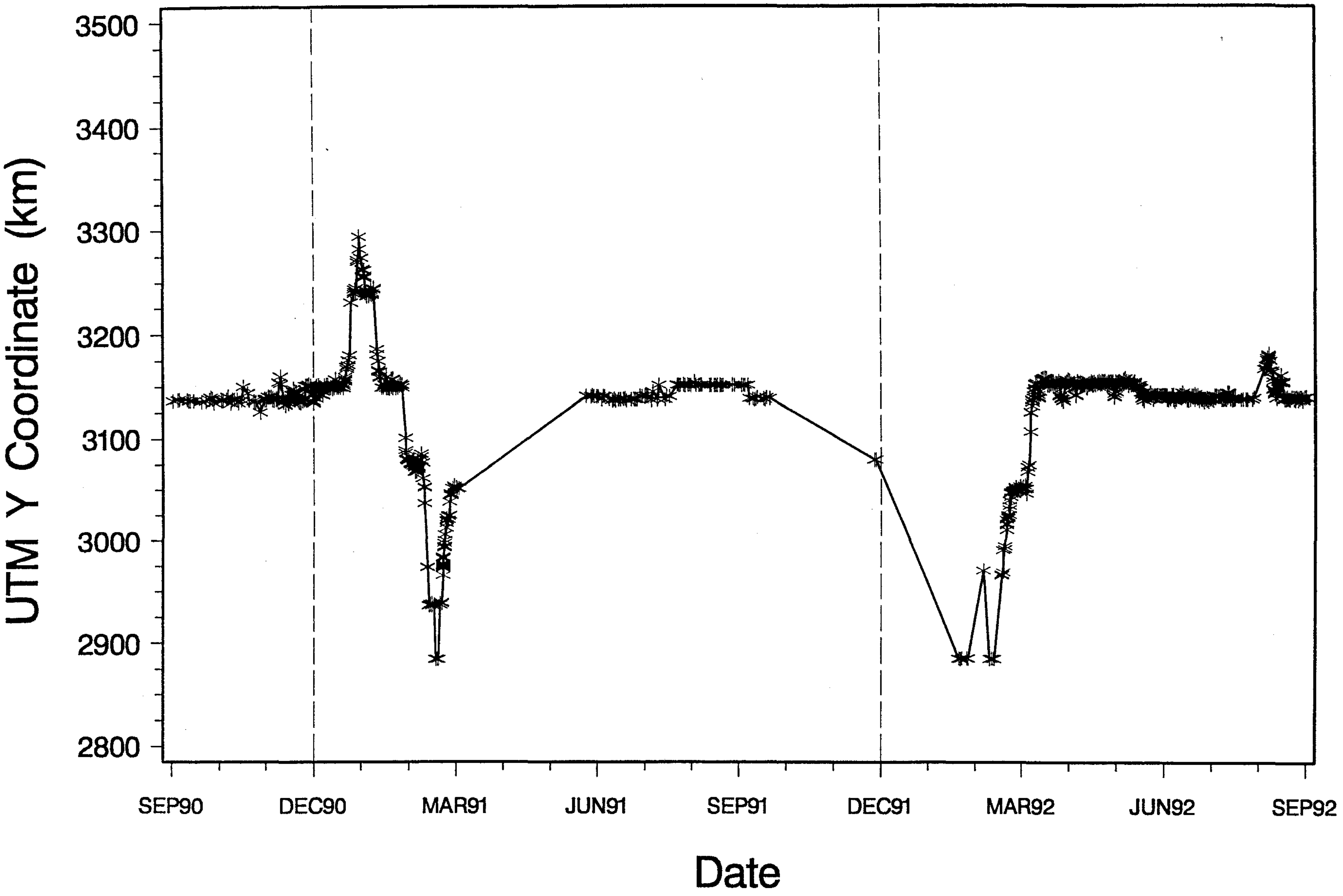
TBC – 03 ("Moon"): 1986 – 1988

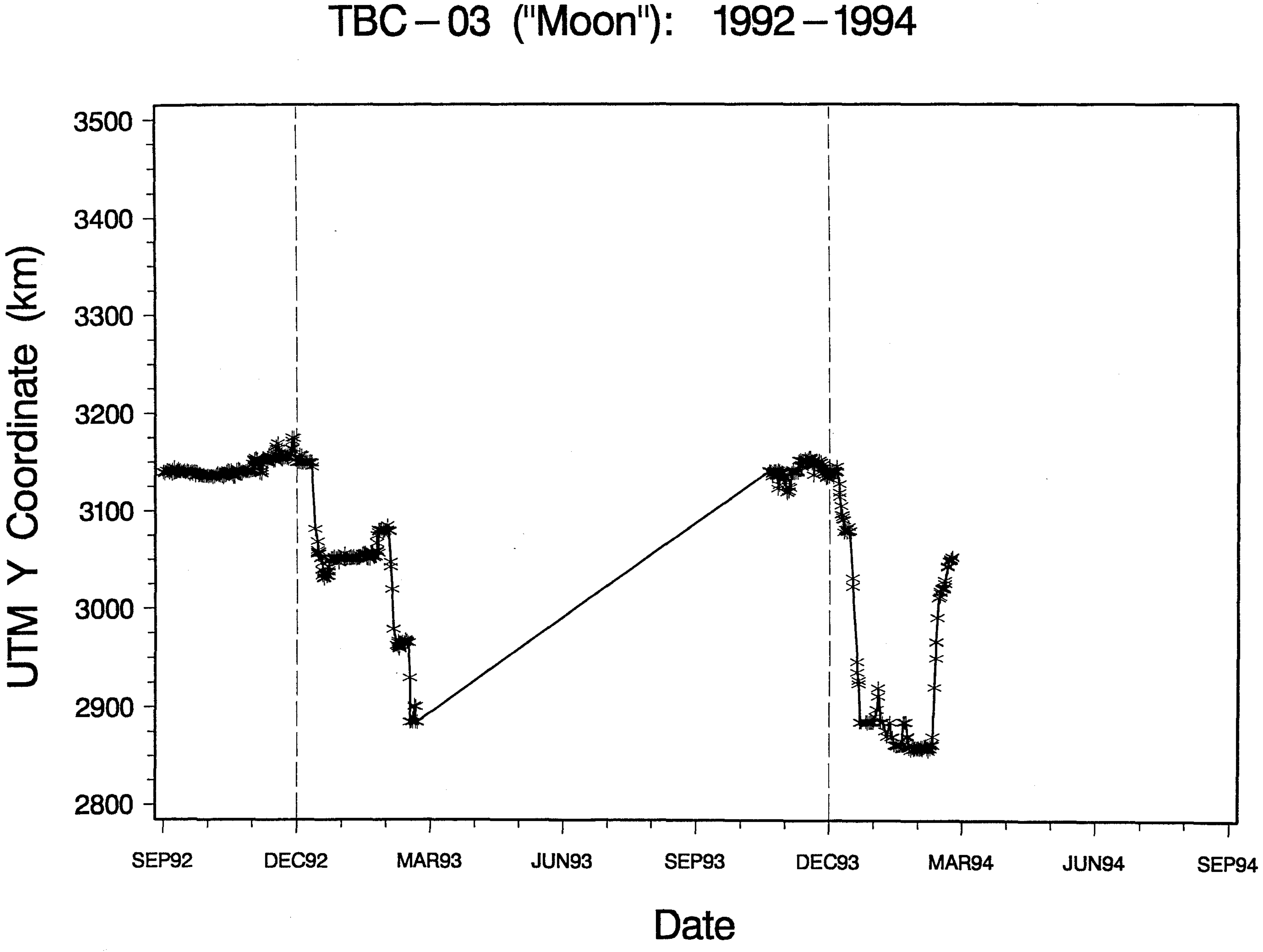


TBC – 03 ("Moon"): 1988 – 1990

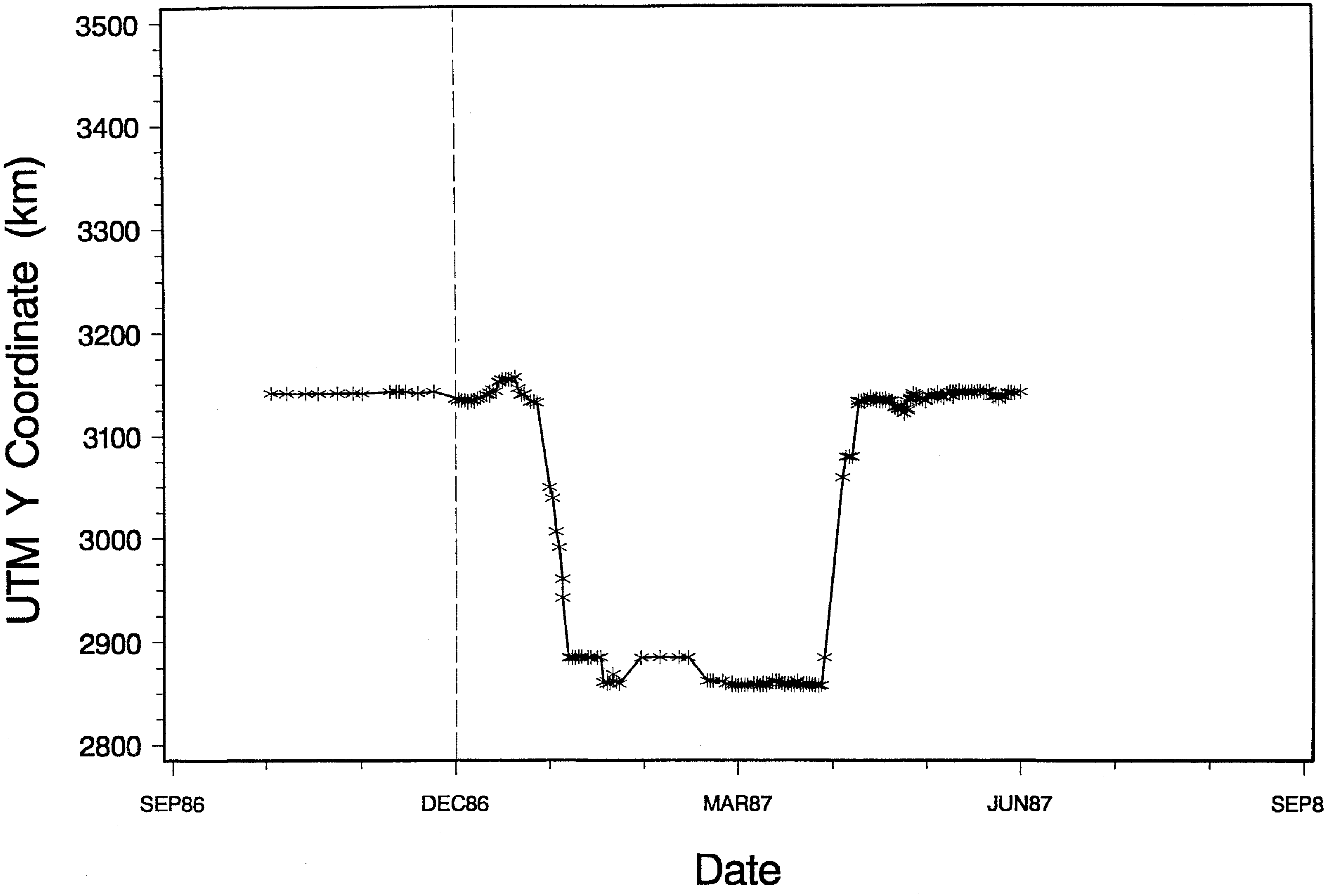


TBC – 03 ("Moon"): 1990 – 1992

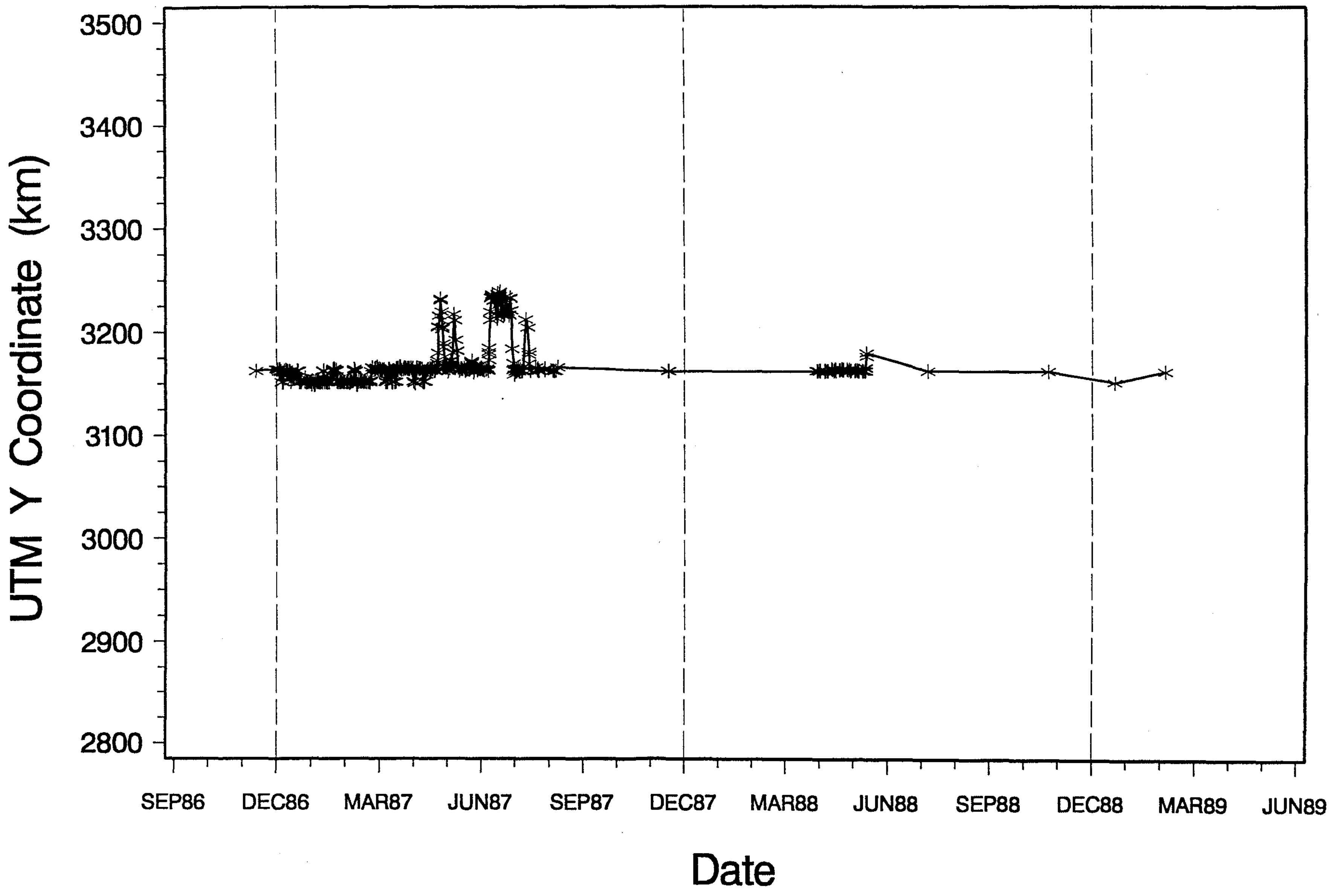


TBC – 03 ("Moon"): 1992 – 1994
UTM Y Coordinate (km)
3500
3400
3300
3200
3100
3000
2900
2800
SEP92
DEC92
MAR93
JUN93
SEP93
DEC93
MAR94
JUN94
SEP94
Date

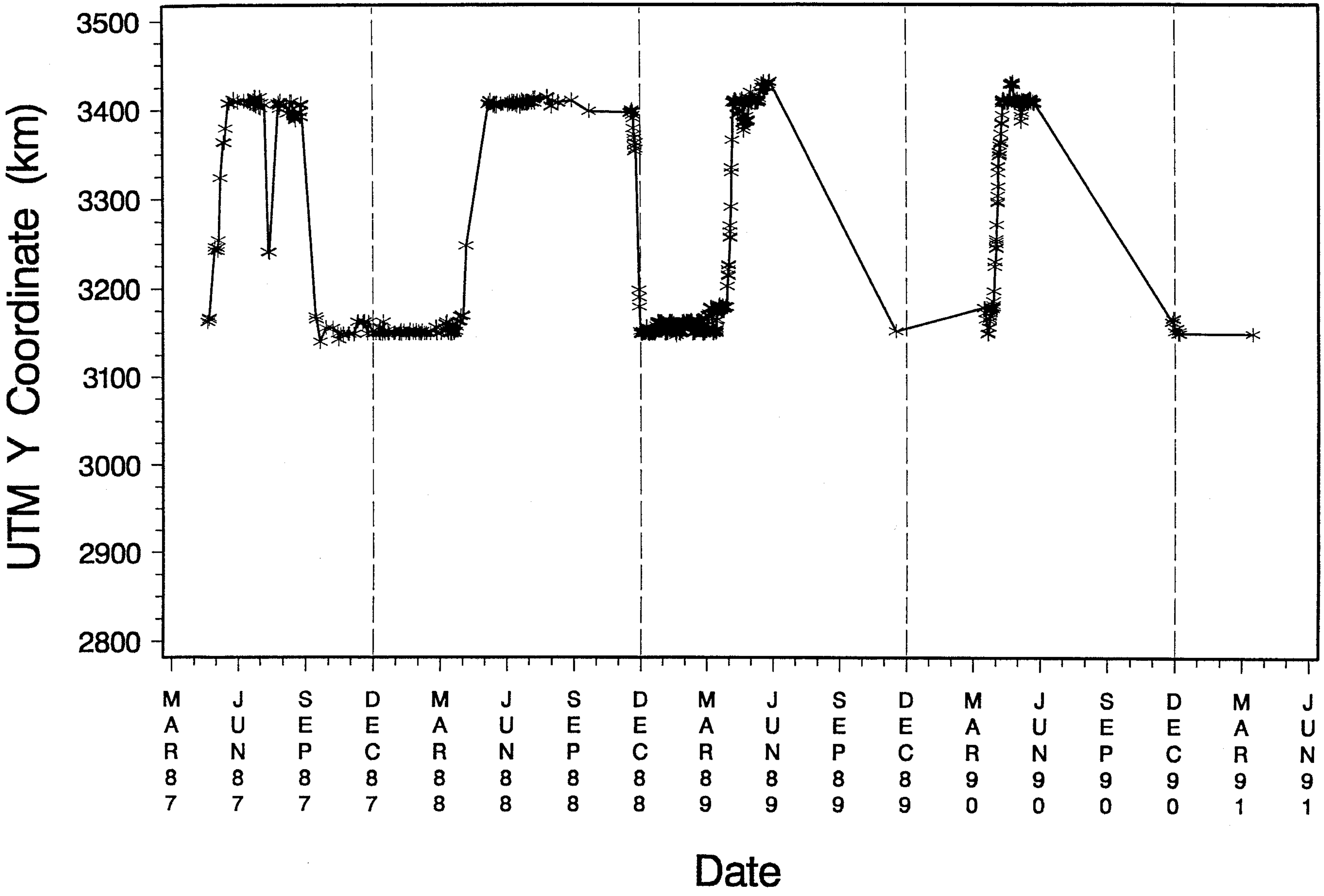
TBC – 04 ("Eclipse"): 1986 – 1987



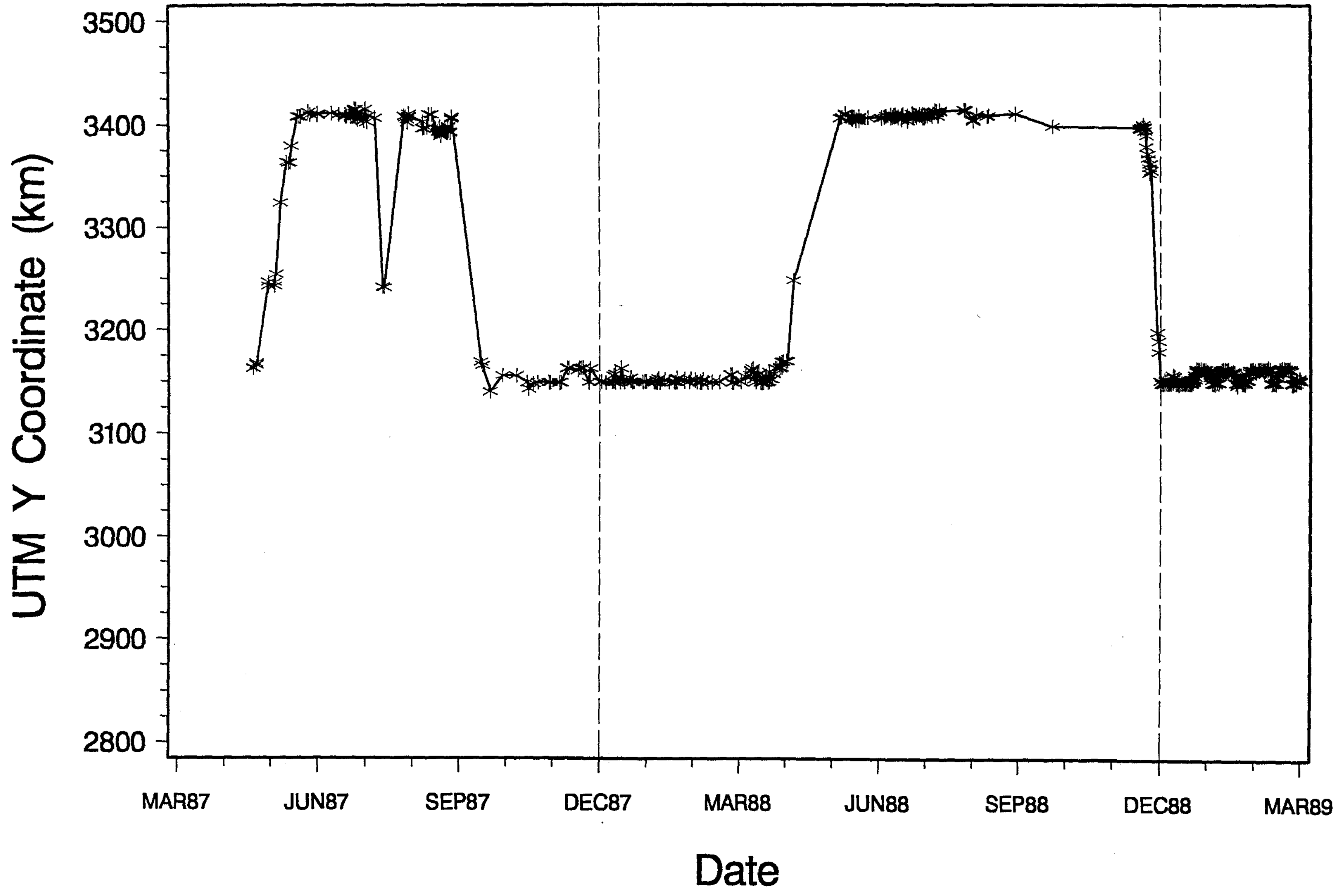
TBC – 05 ("Gyro"): 1986 – 1989



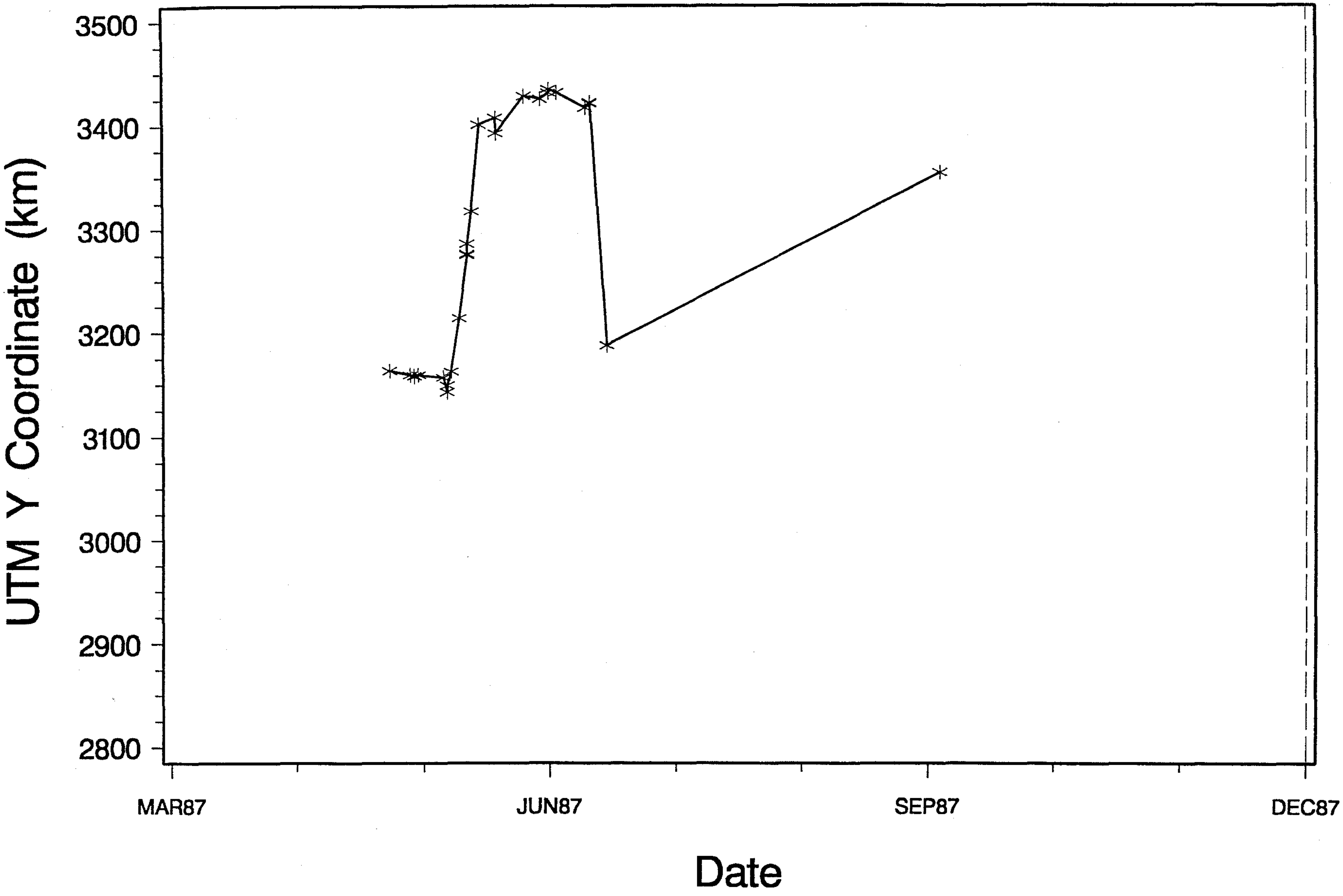
TBC – 06 ("Moe"): 1987 – 1991



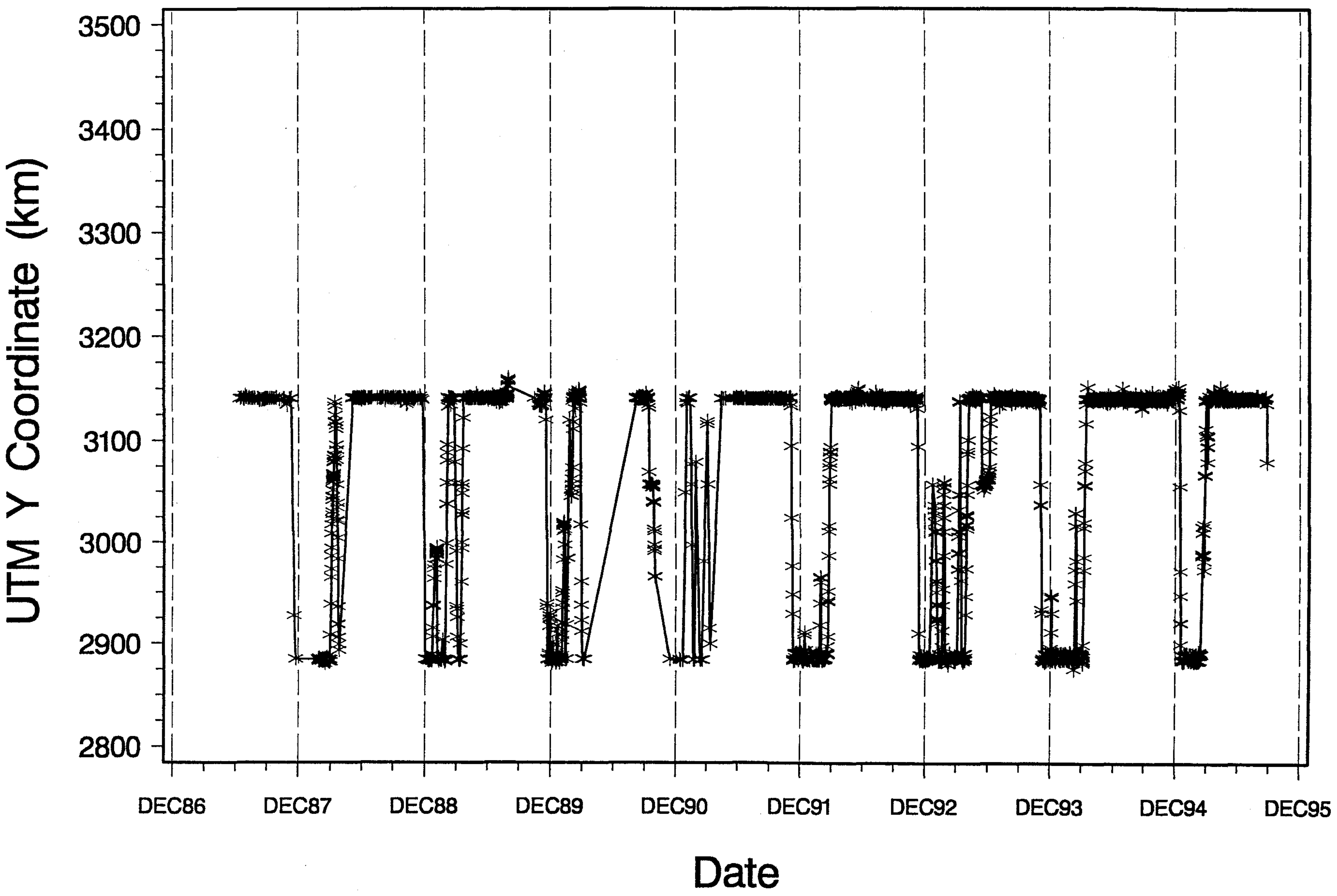
TBC – 06 ("Moe"): 1987 – 1989



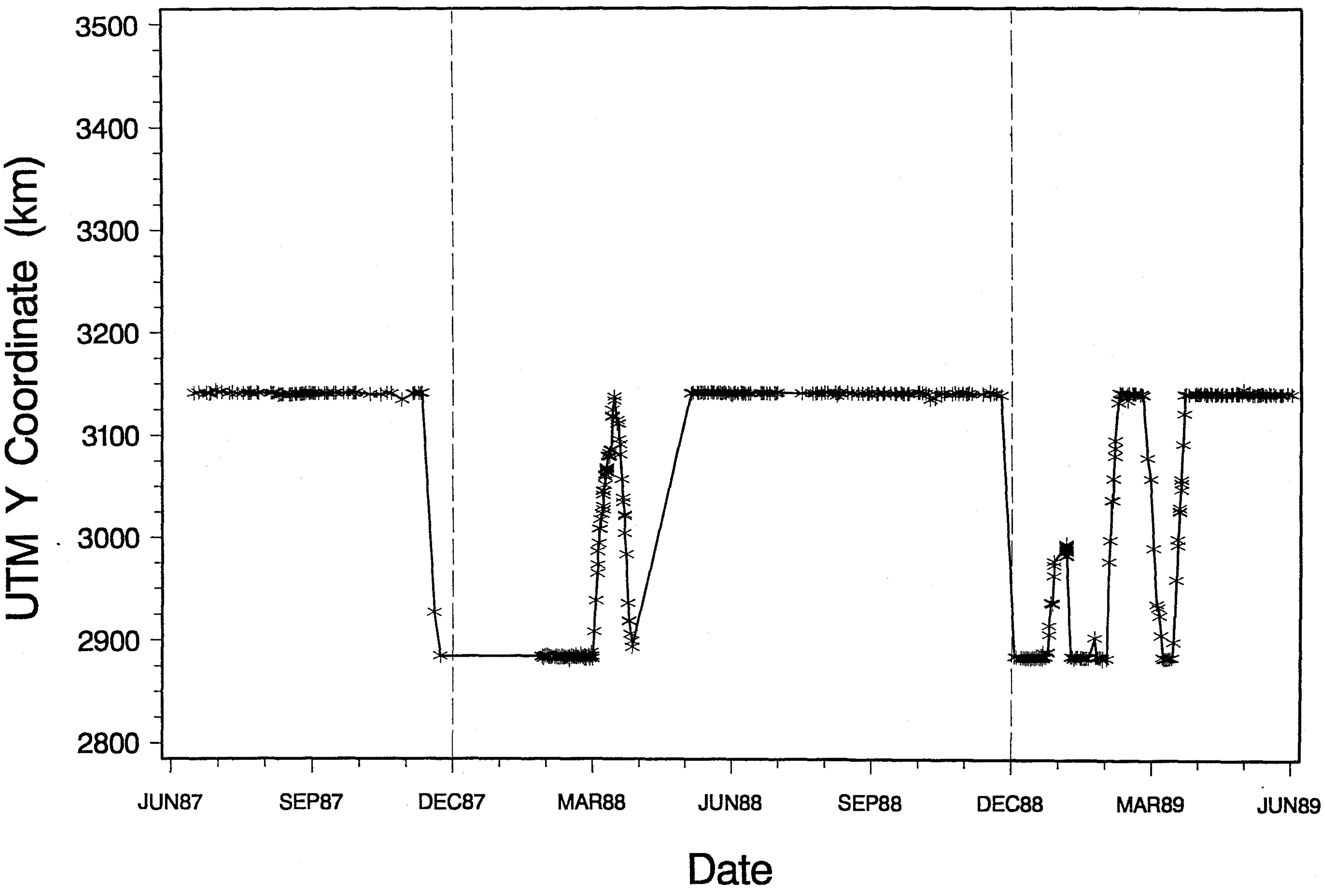
TBC – 08 ("Angela"): 1987



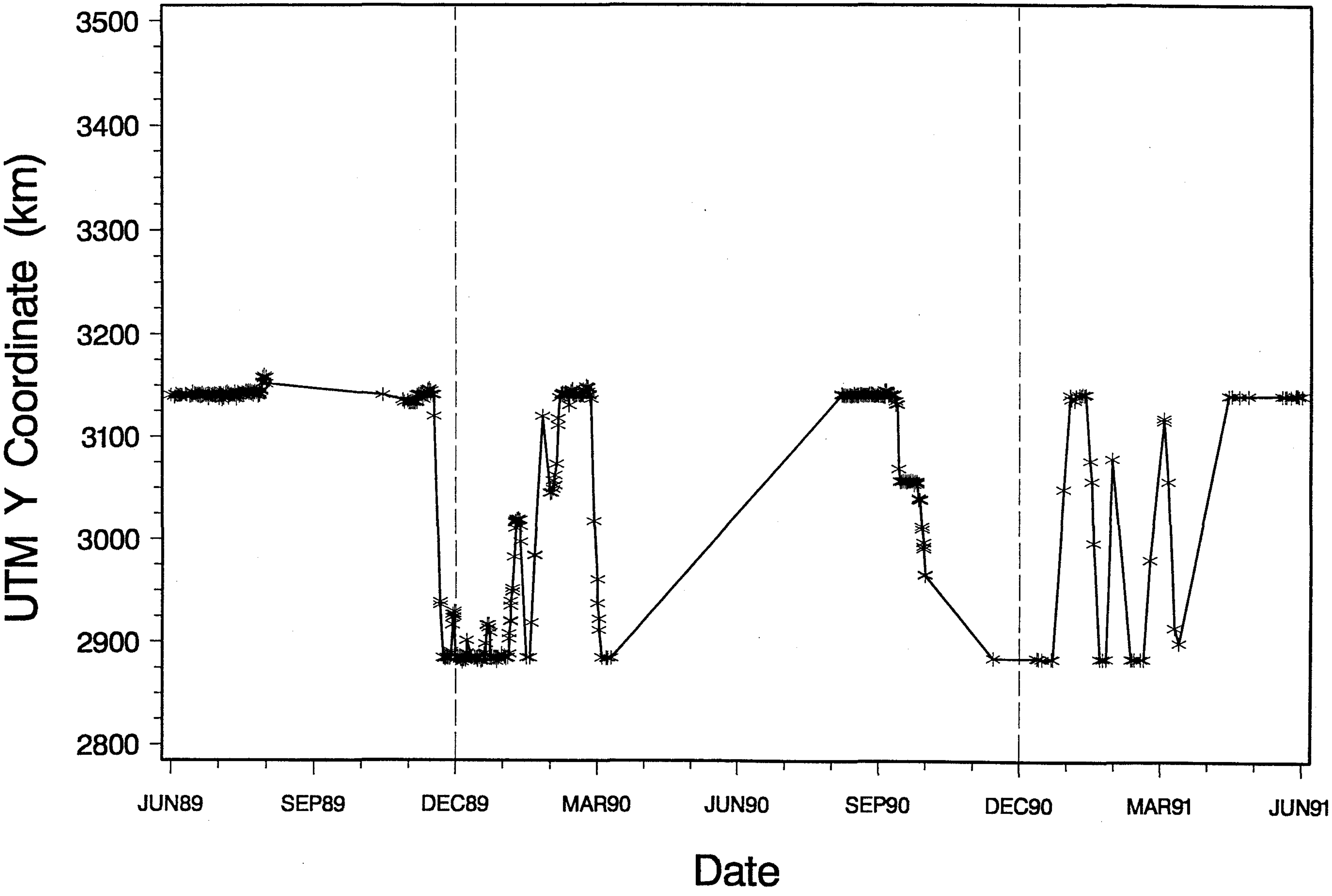
TBC – 09 ("C – cow"): 1987 – 1995



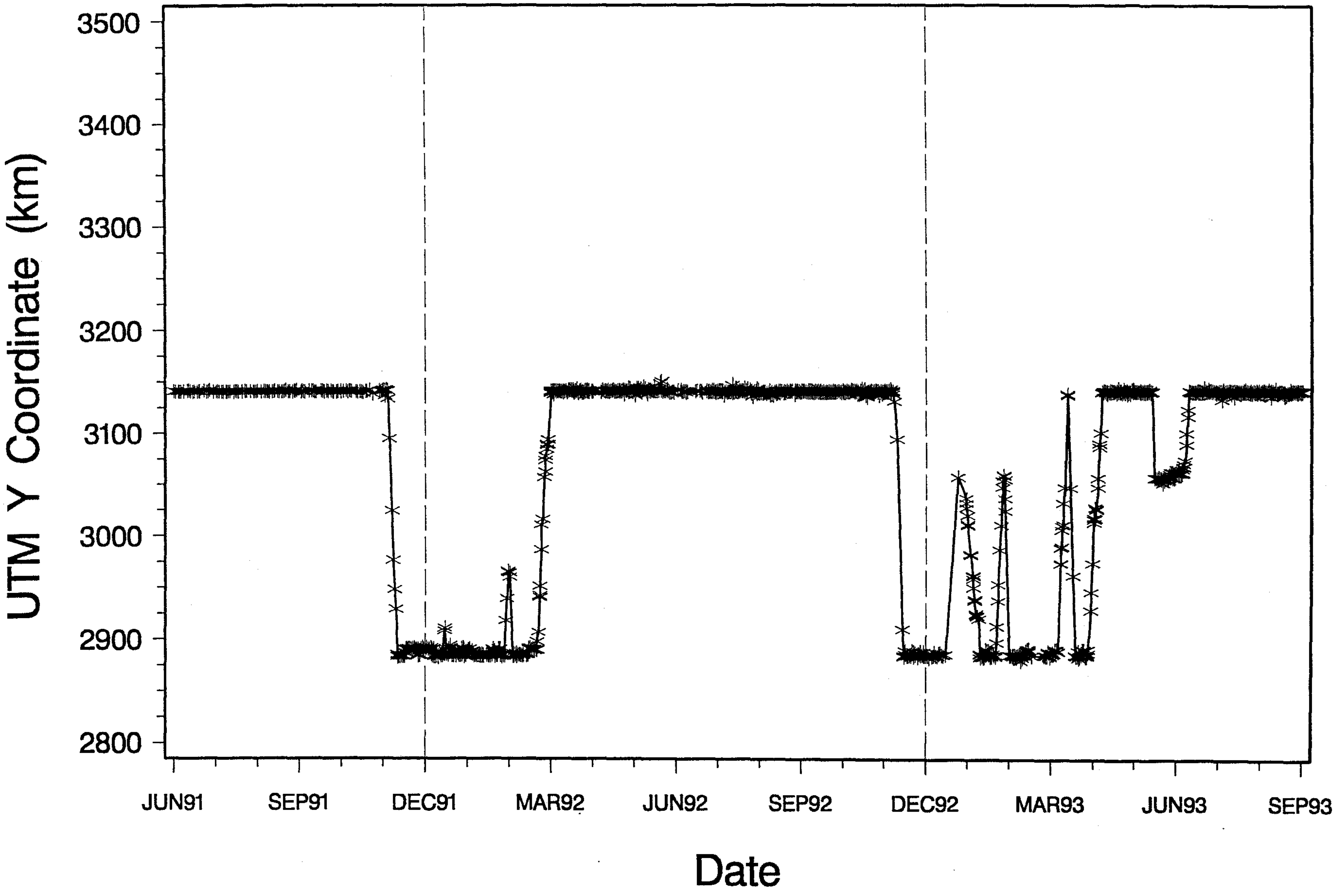
TBC – 09 ("C – cow"): 1987 – 1989



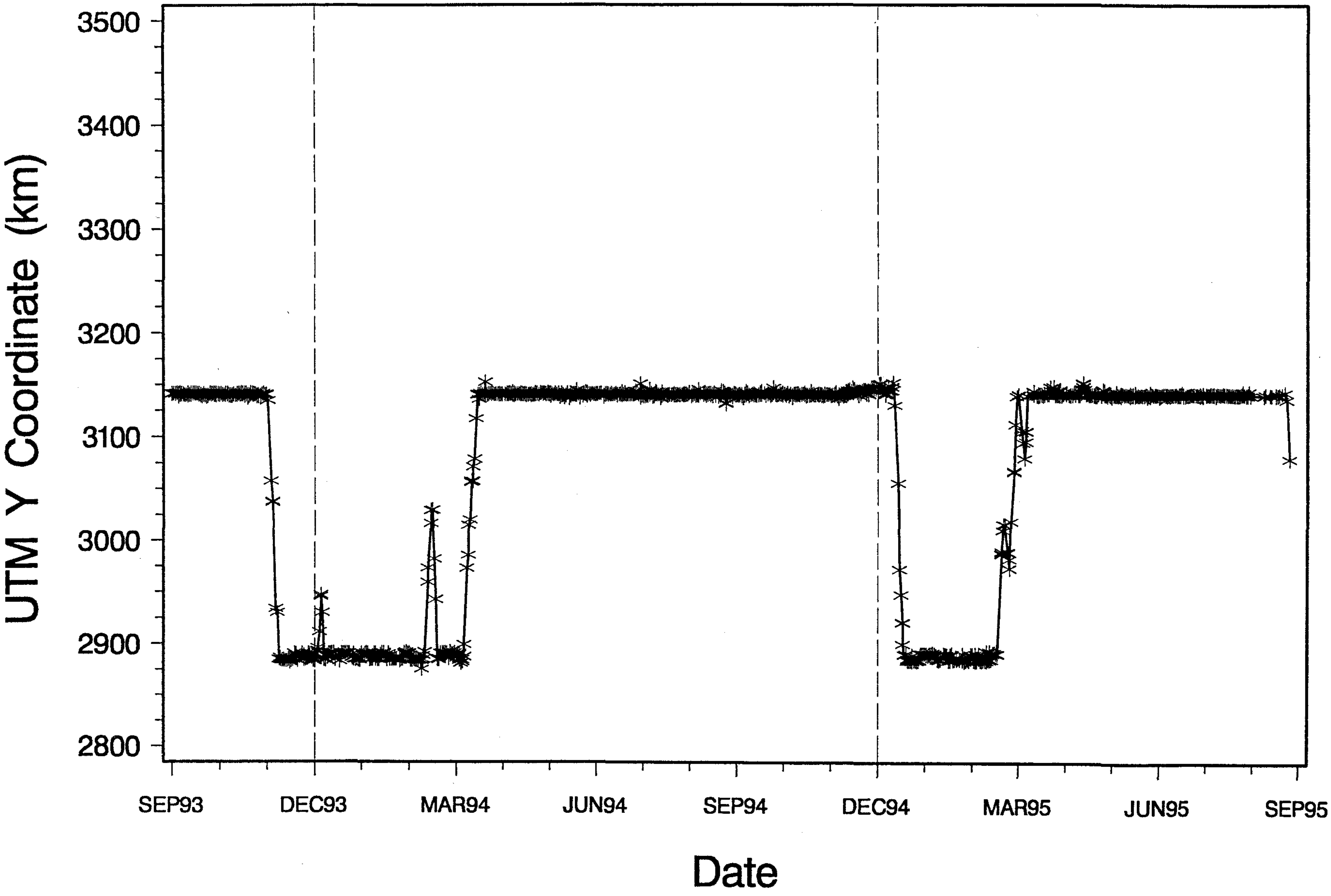
TBC – 09 ("C – cow"): 1989 – 1991



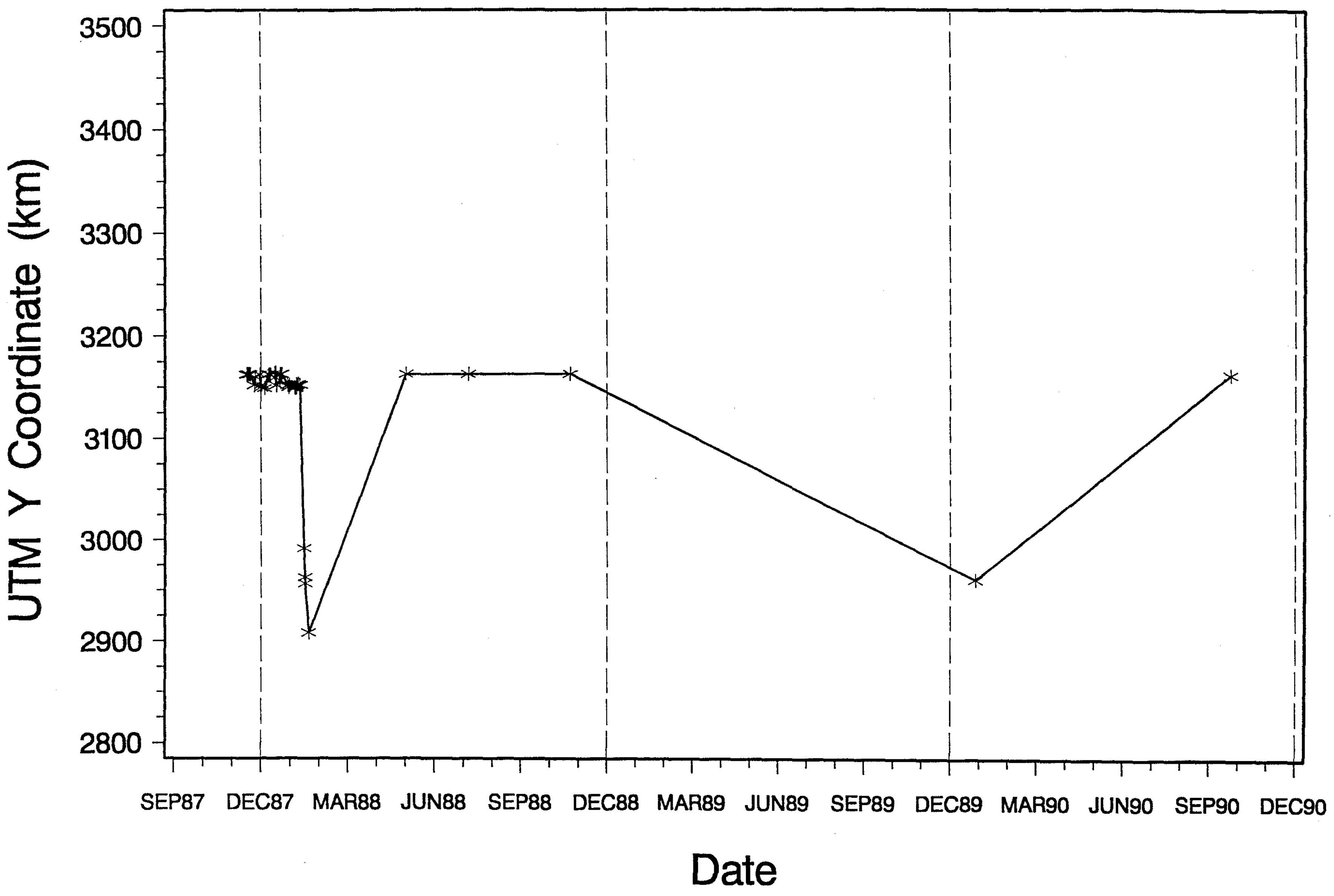
TBC – 09 ("C – cow"): 1991 – 1993



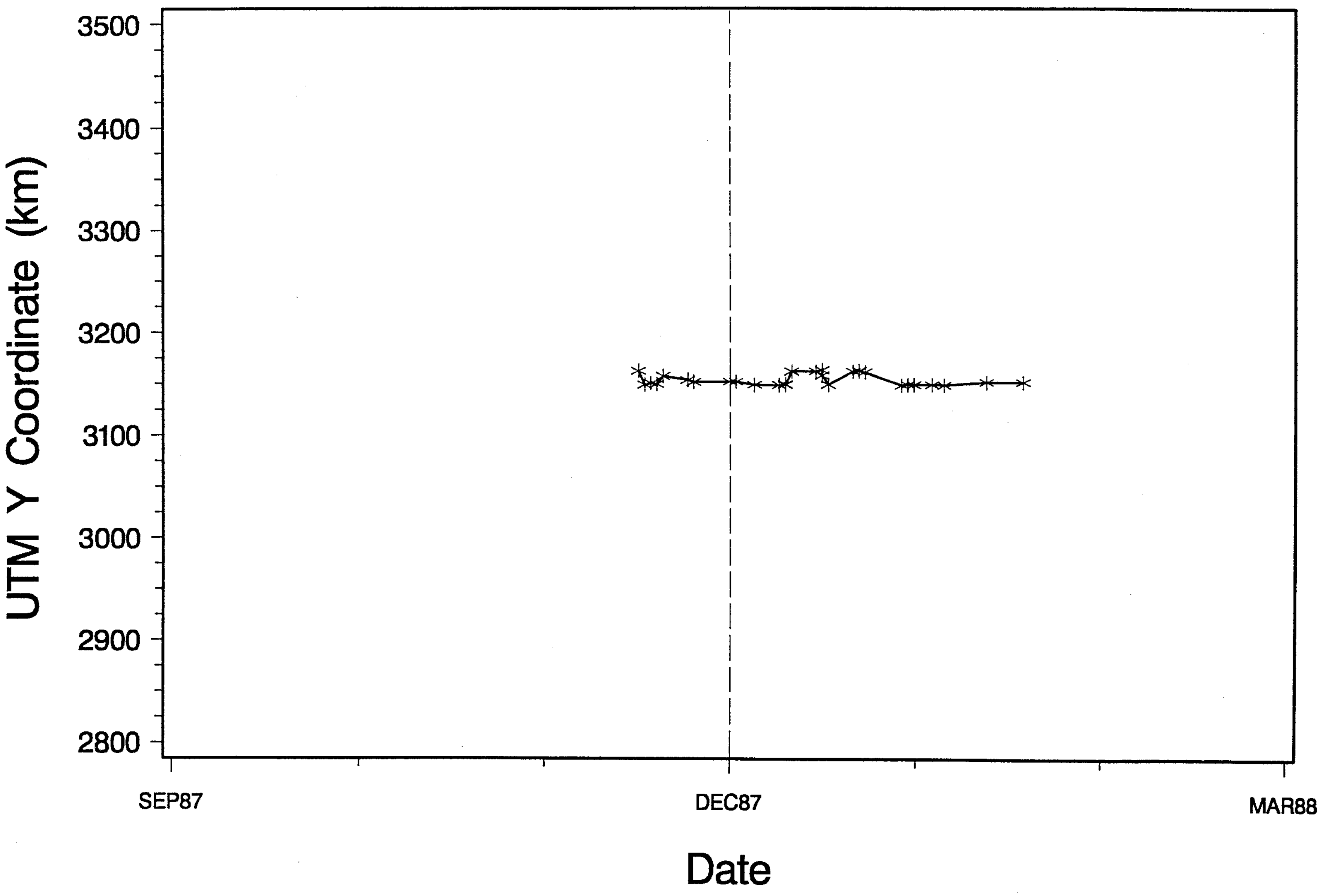
TBC – 09 ("C – cow"): 1993 – 1995



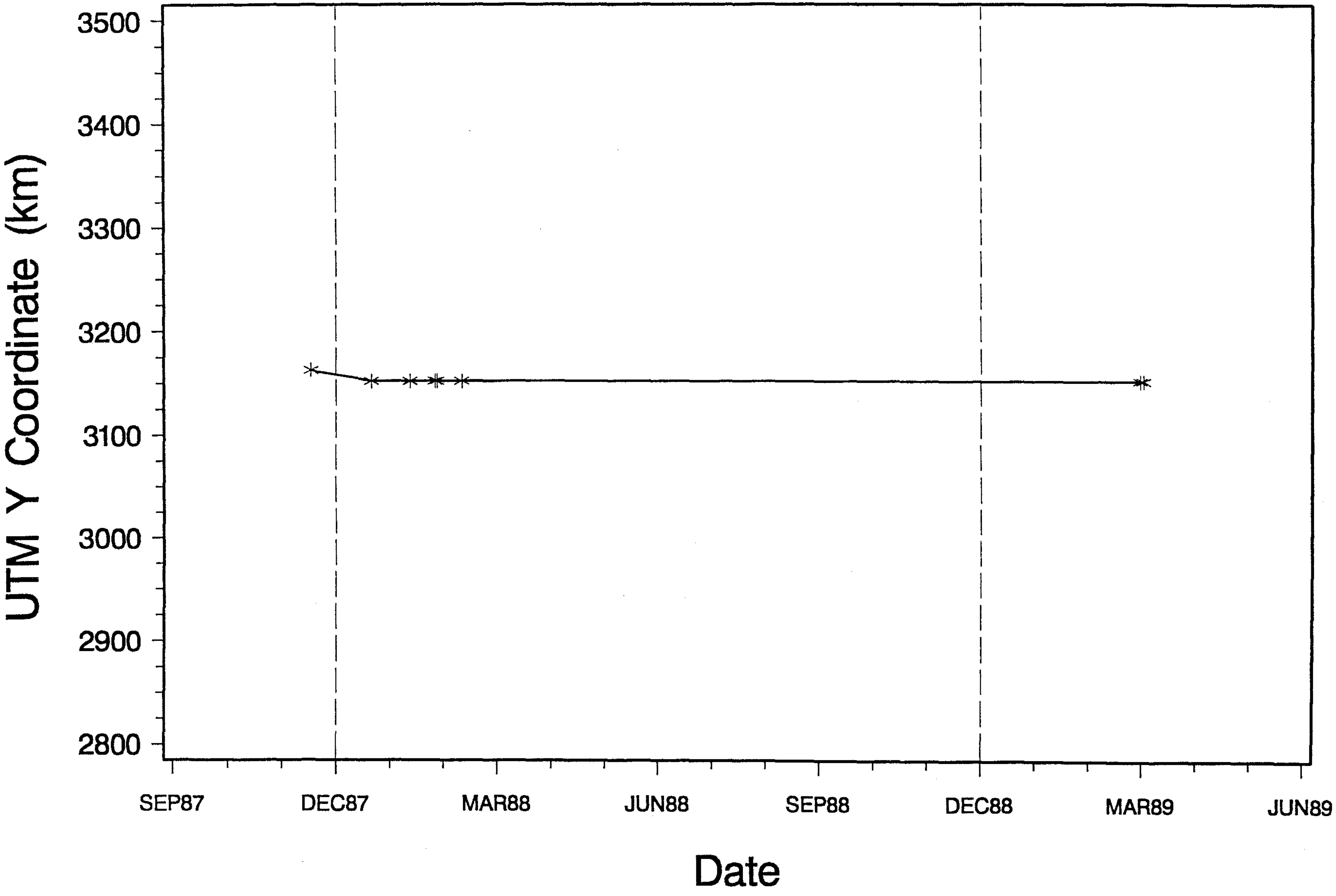
TBC – 10 ("Fran"): 1987 – 1990



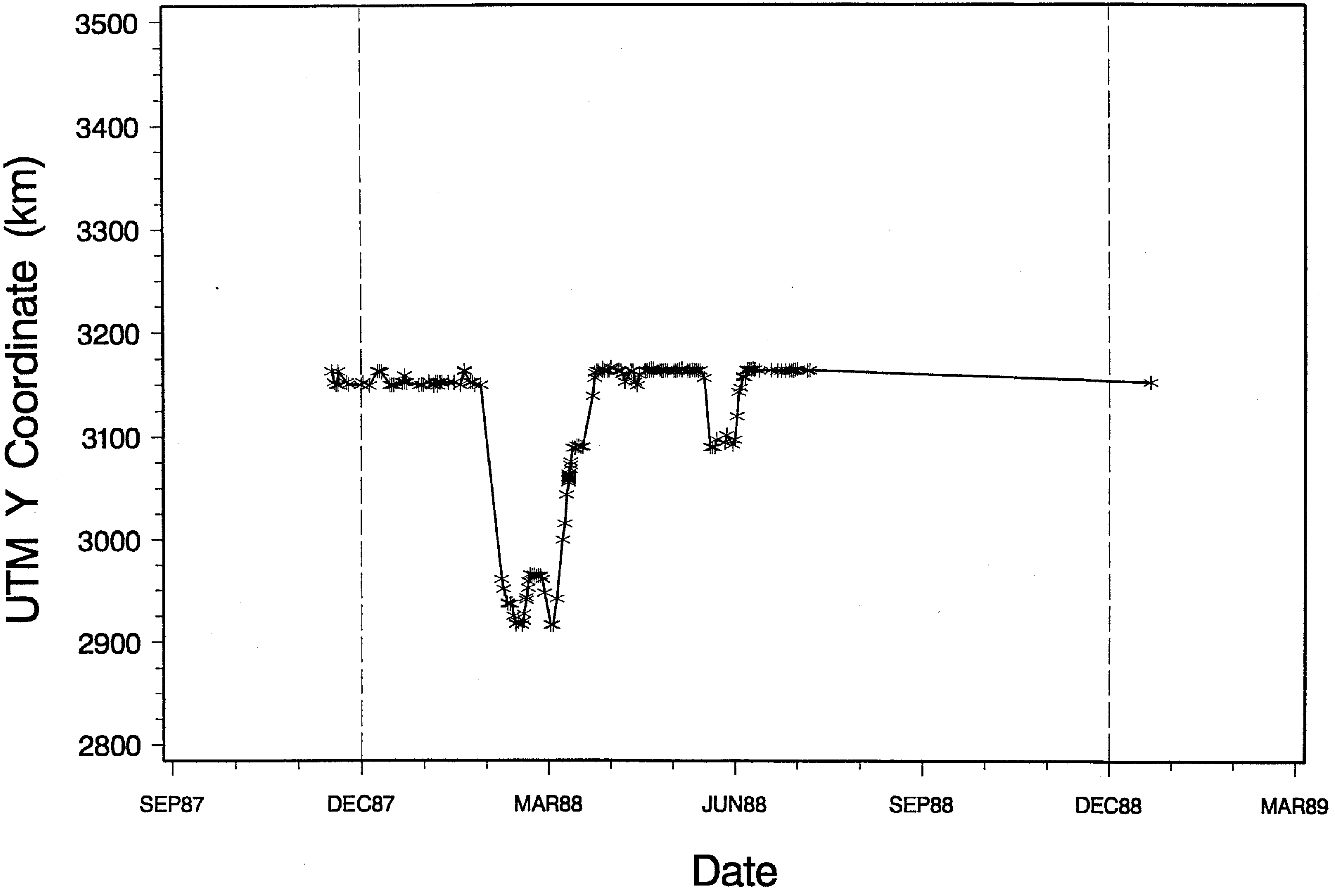
TBC – 11 ("Gloria"): 1987 – 1988



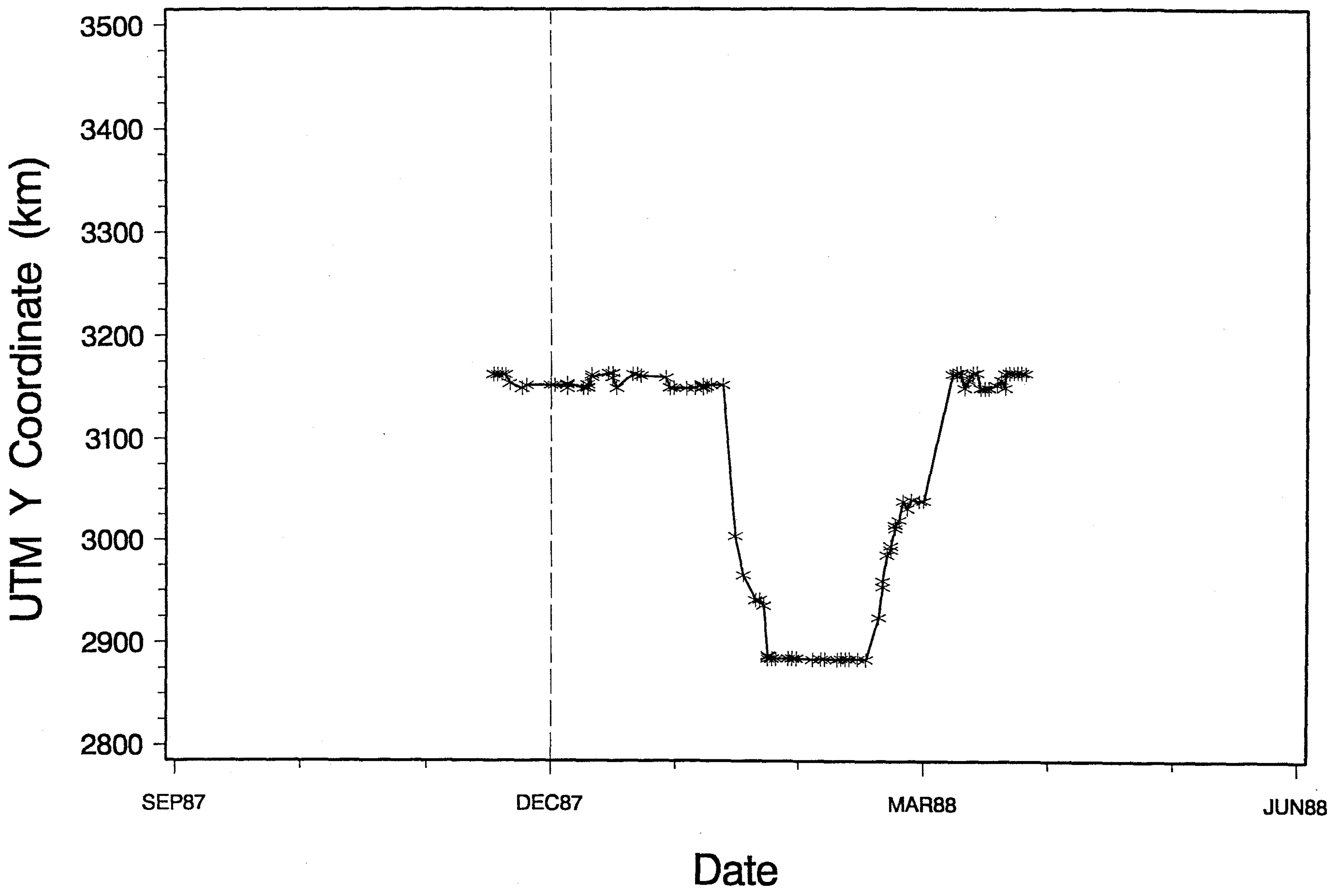
TBC – 12 ("Heike"): 1987 – 1989



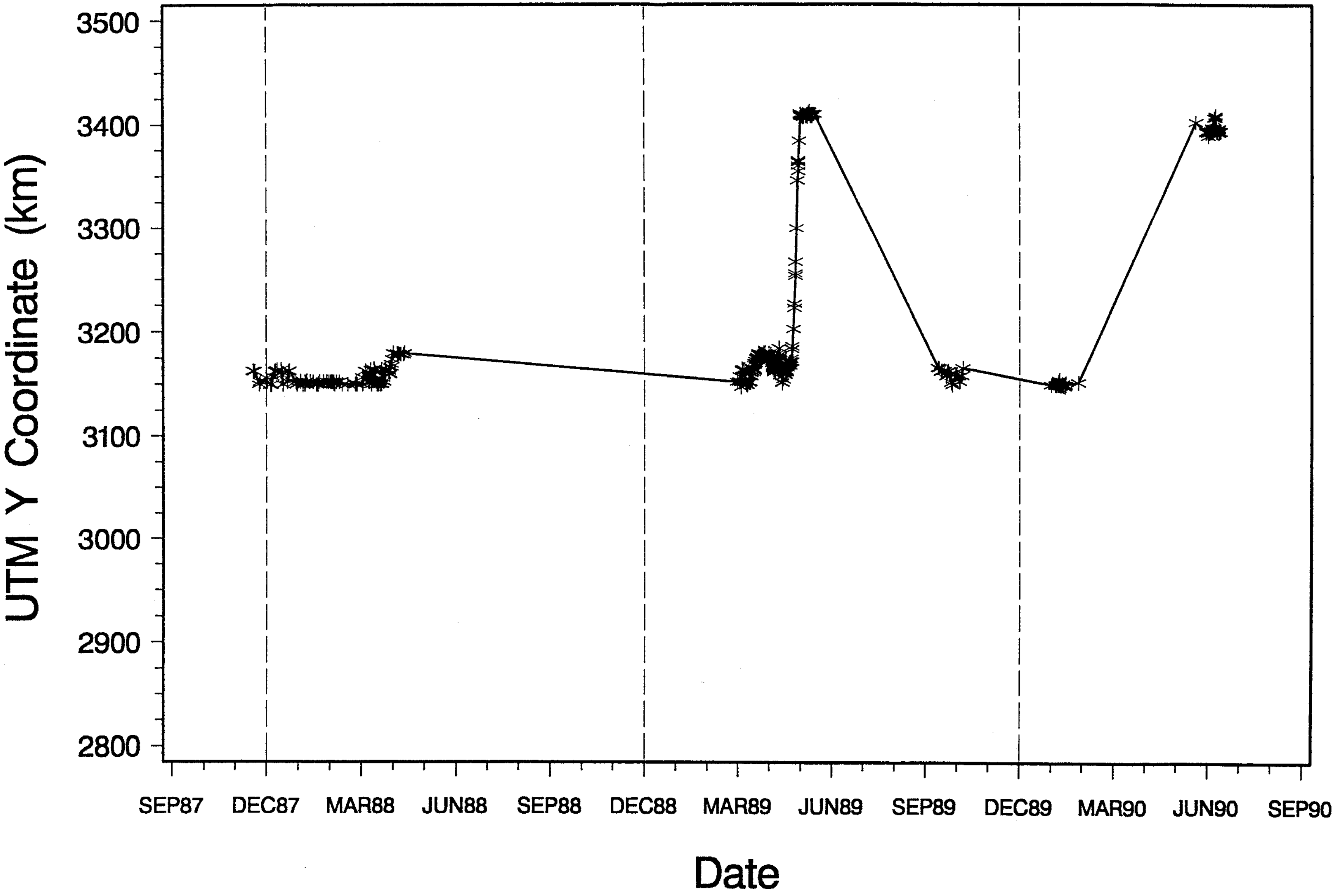
TBC – 13 ("Irene"): 1987 – 1988



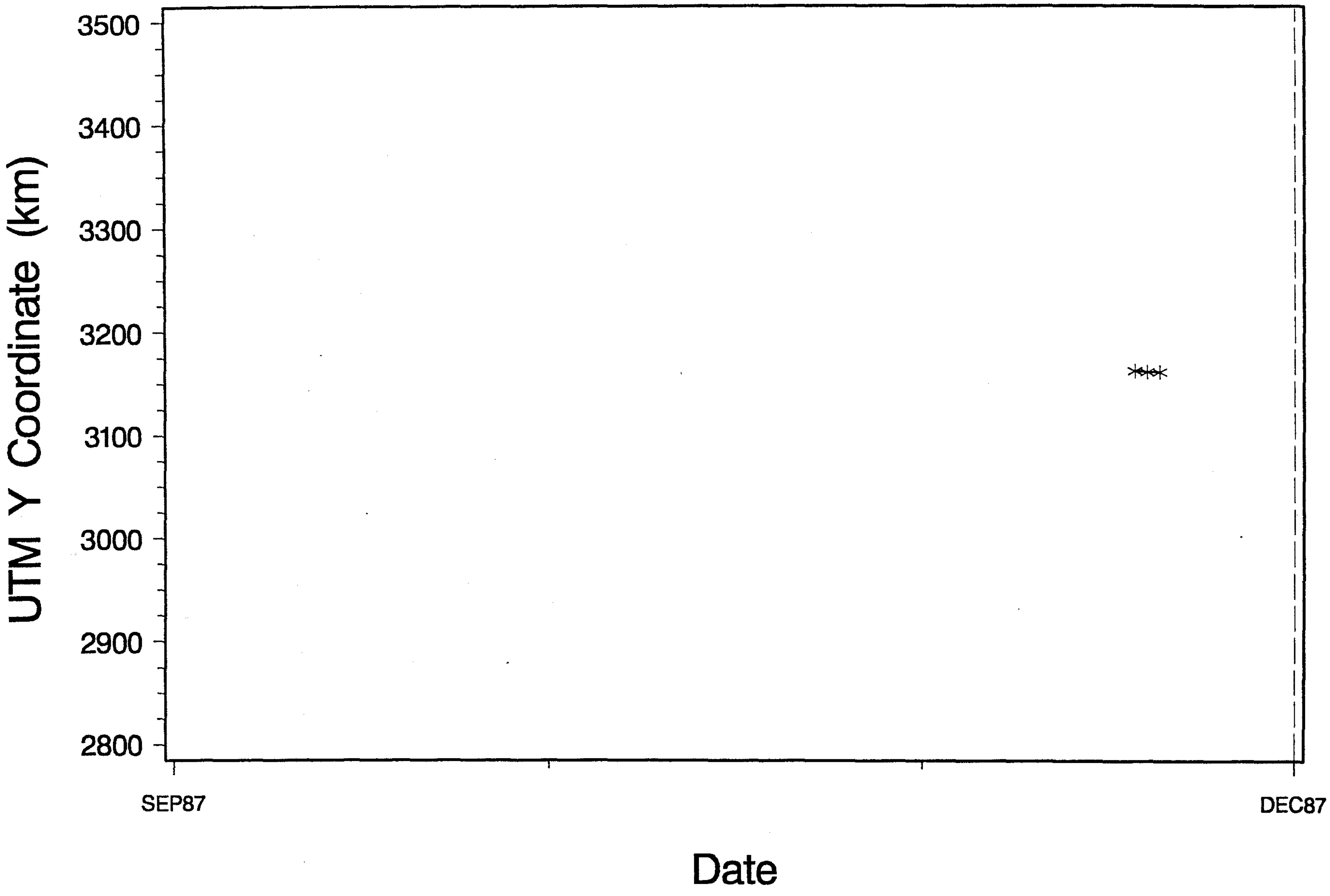
TBC – 14 ("Jerome"): 1987 – 1988



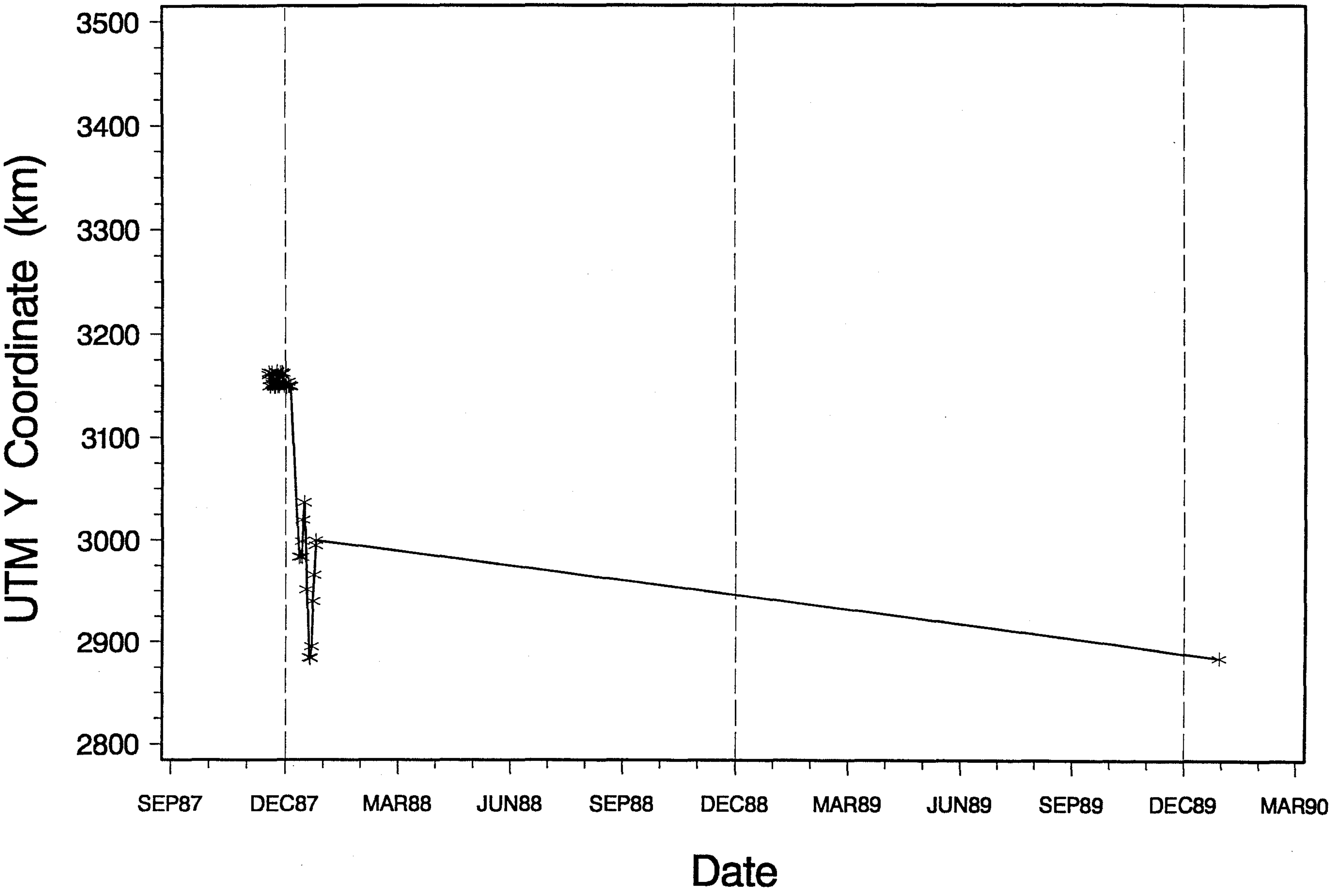
TBC – 15 ("Karen"): 1987 – 1990



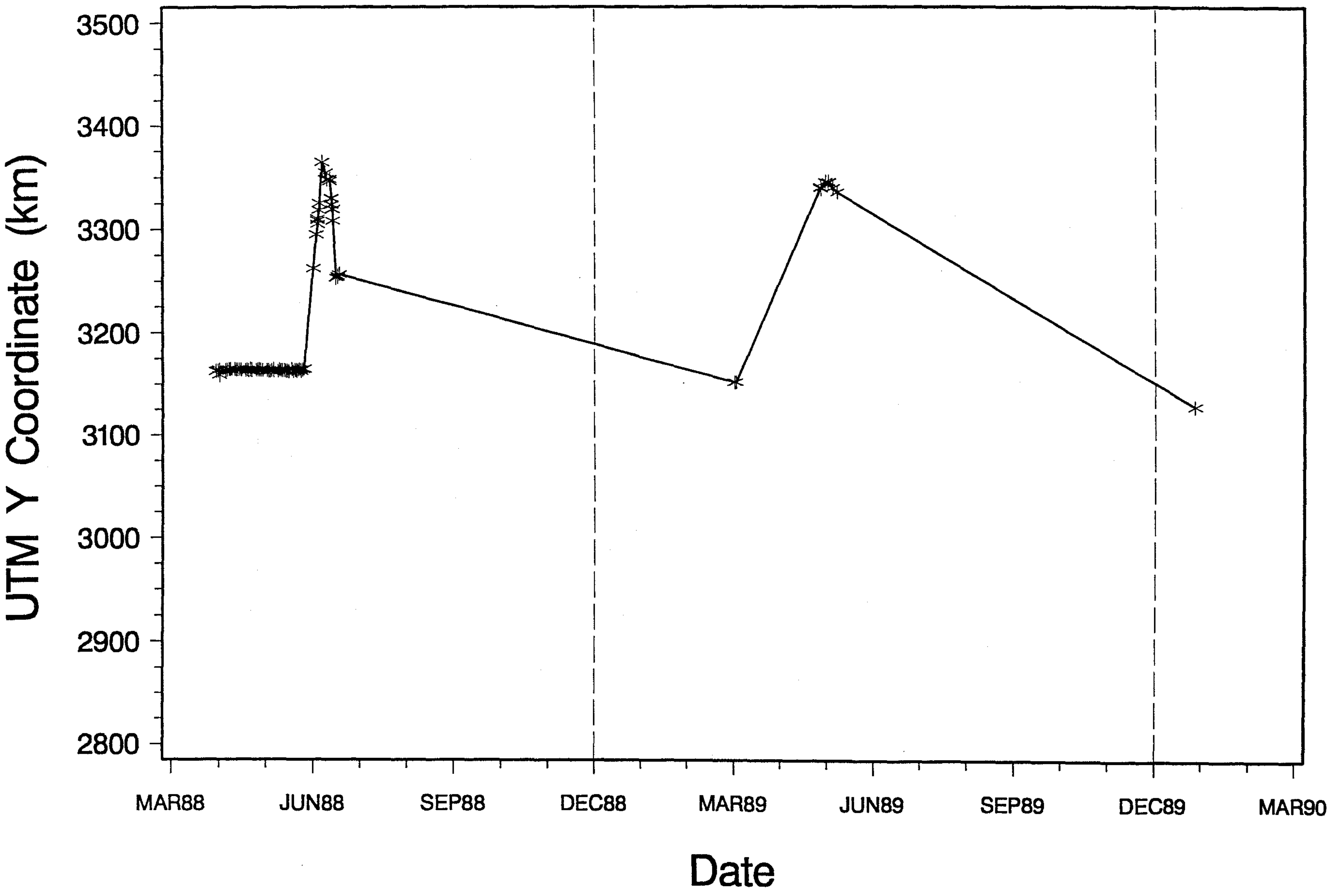
TBC – 16 ("Larry"): 1987



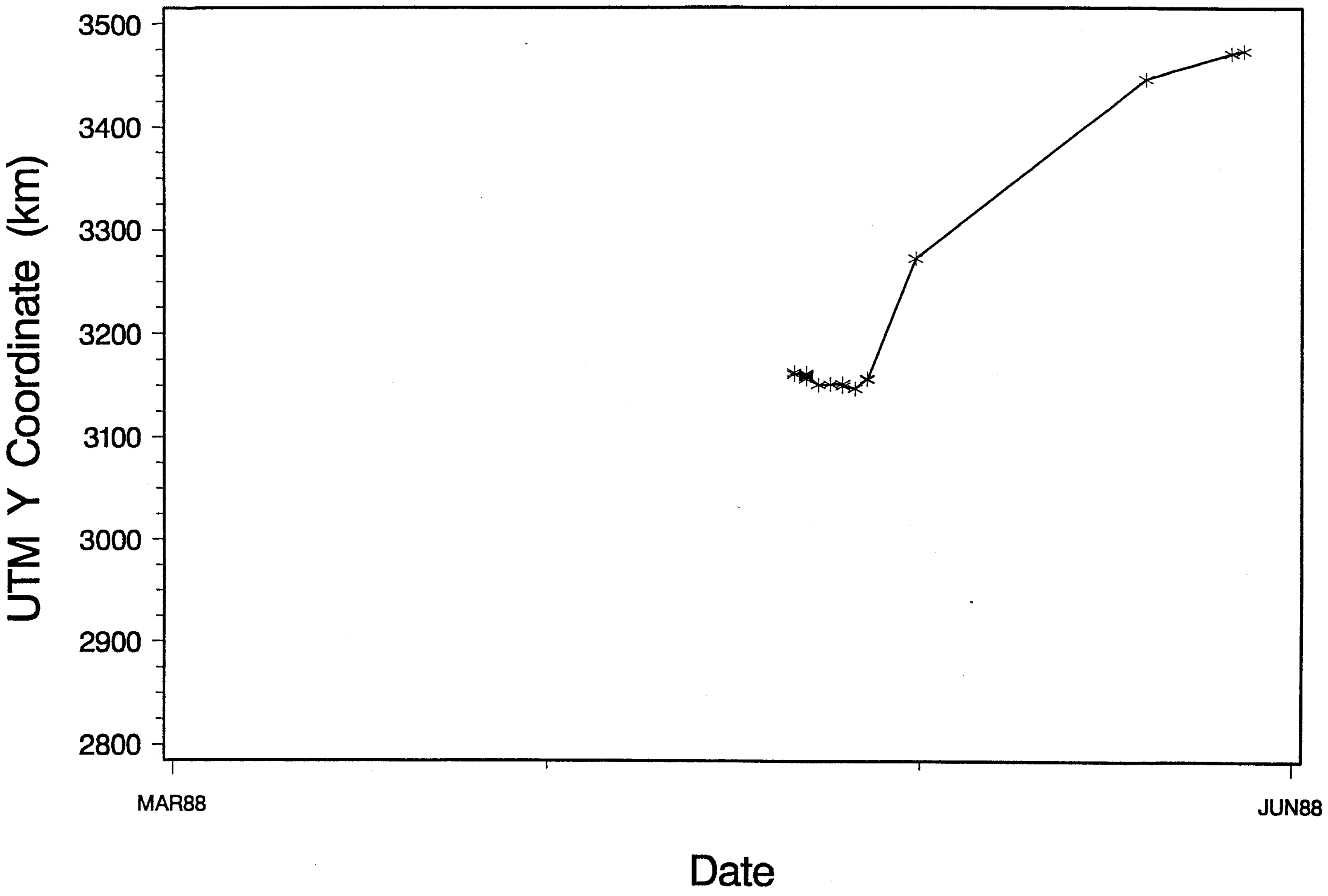
TBC – 17 ("Madonna"): 1987 – 1989



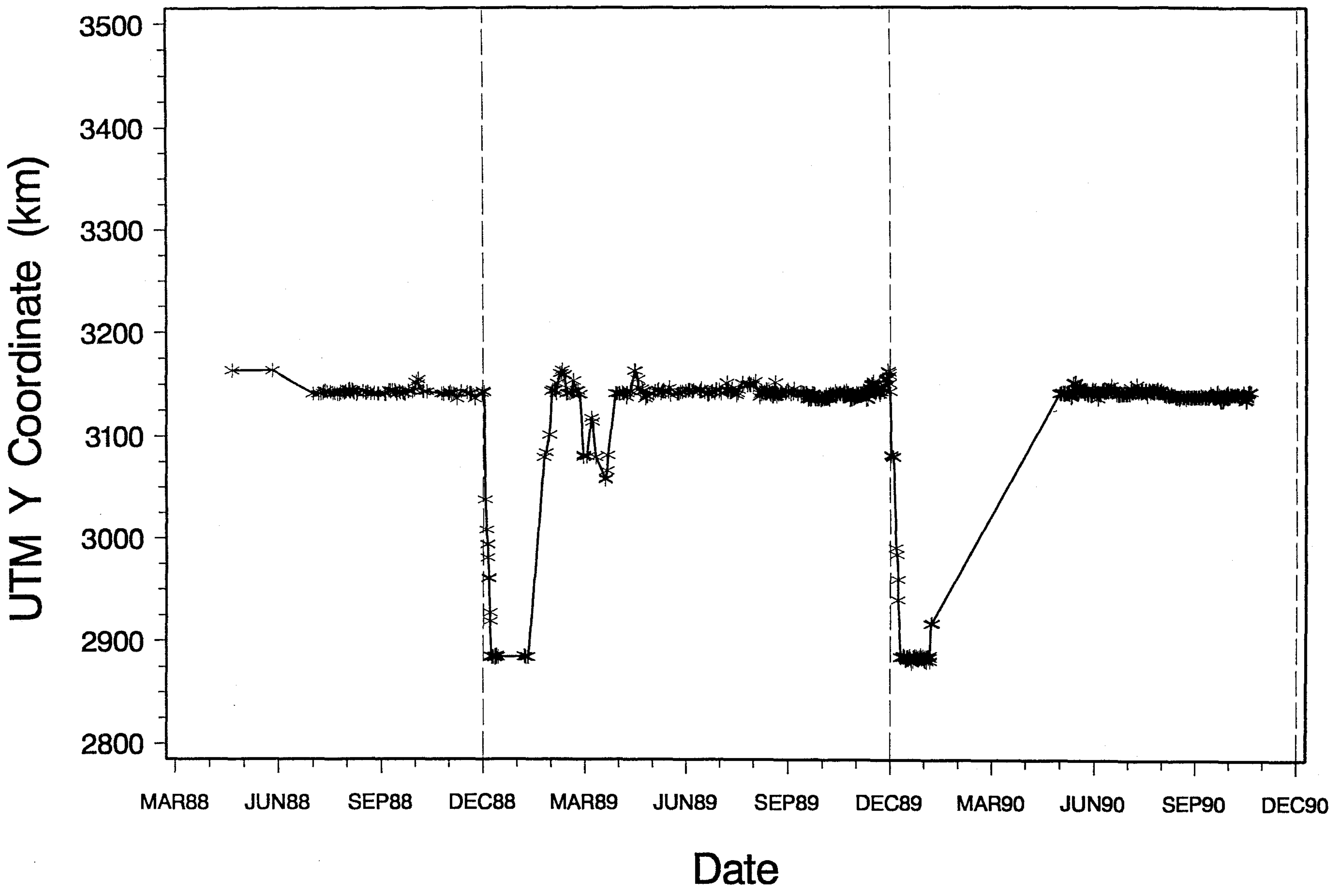
TBC – 18 ("Leroy"): 1988 – 1989



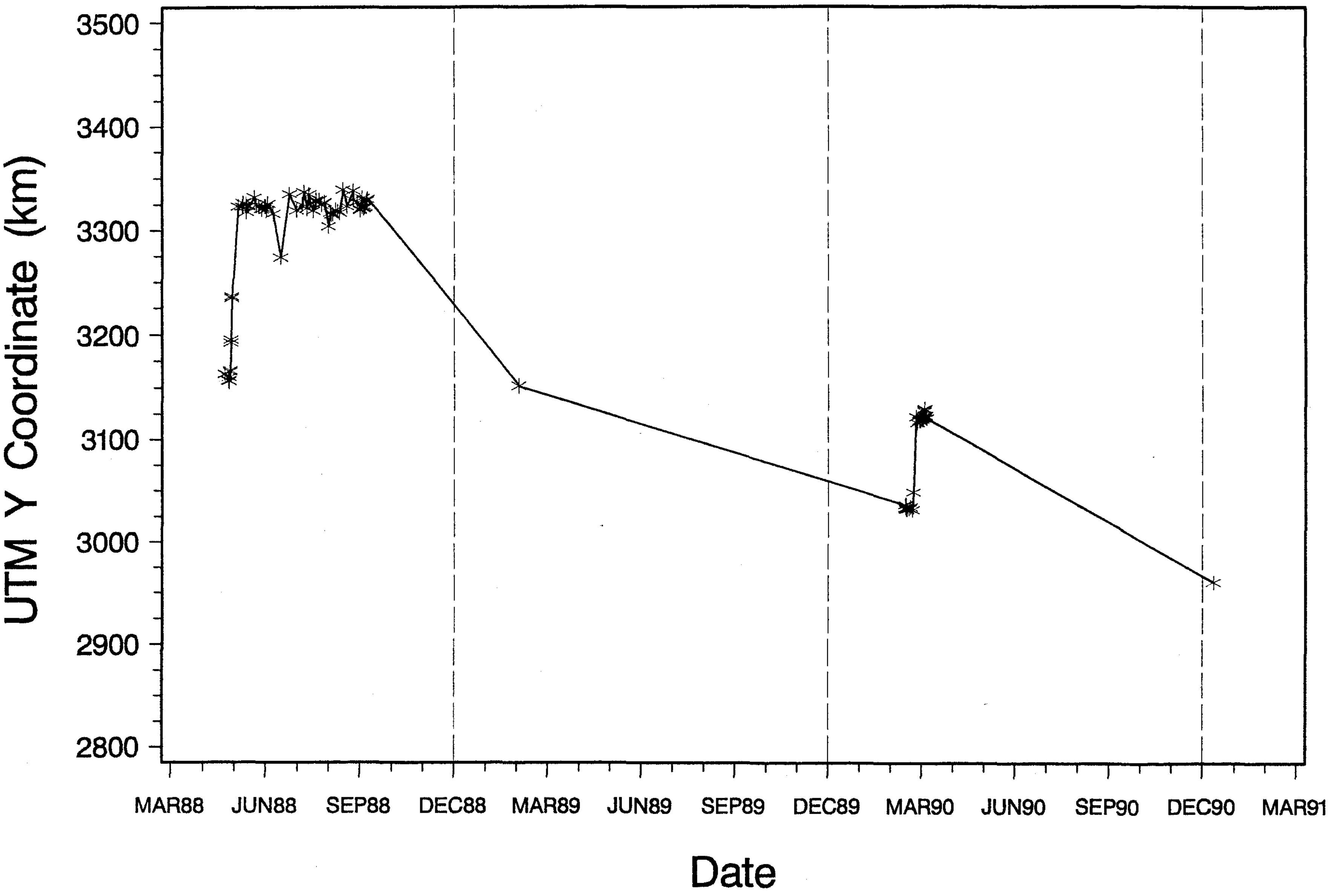
TBC – 19 ("Sharon"): 1988



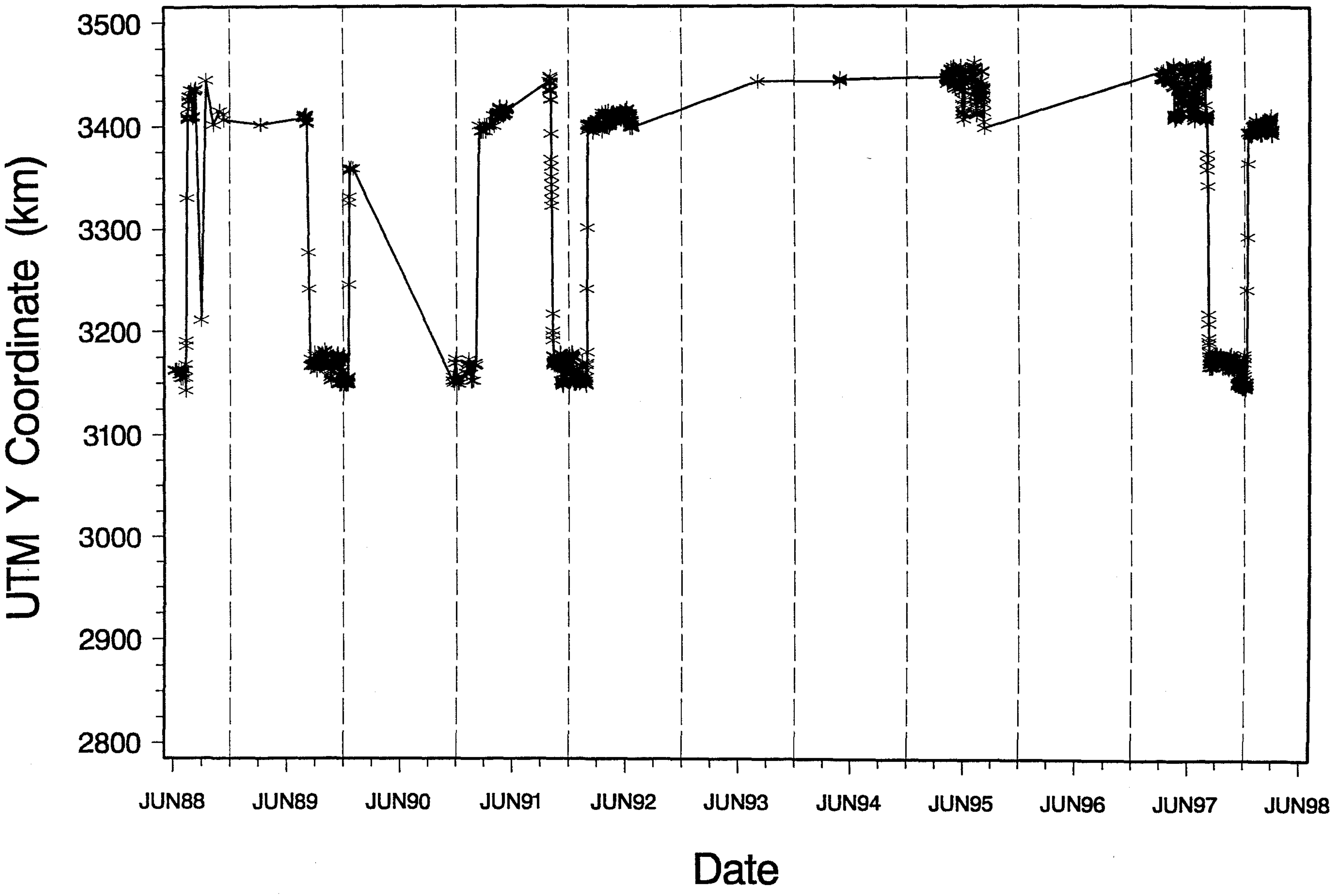
TBC – 20 ("Ruth"): 1988 – 1990



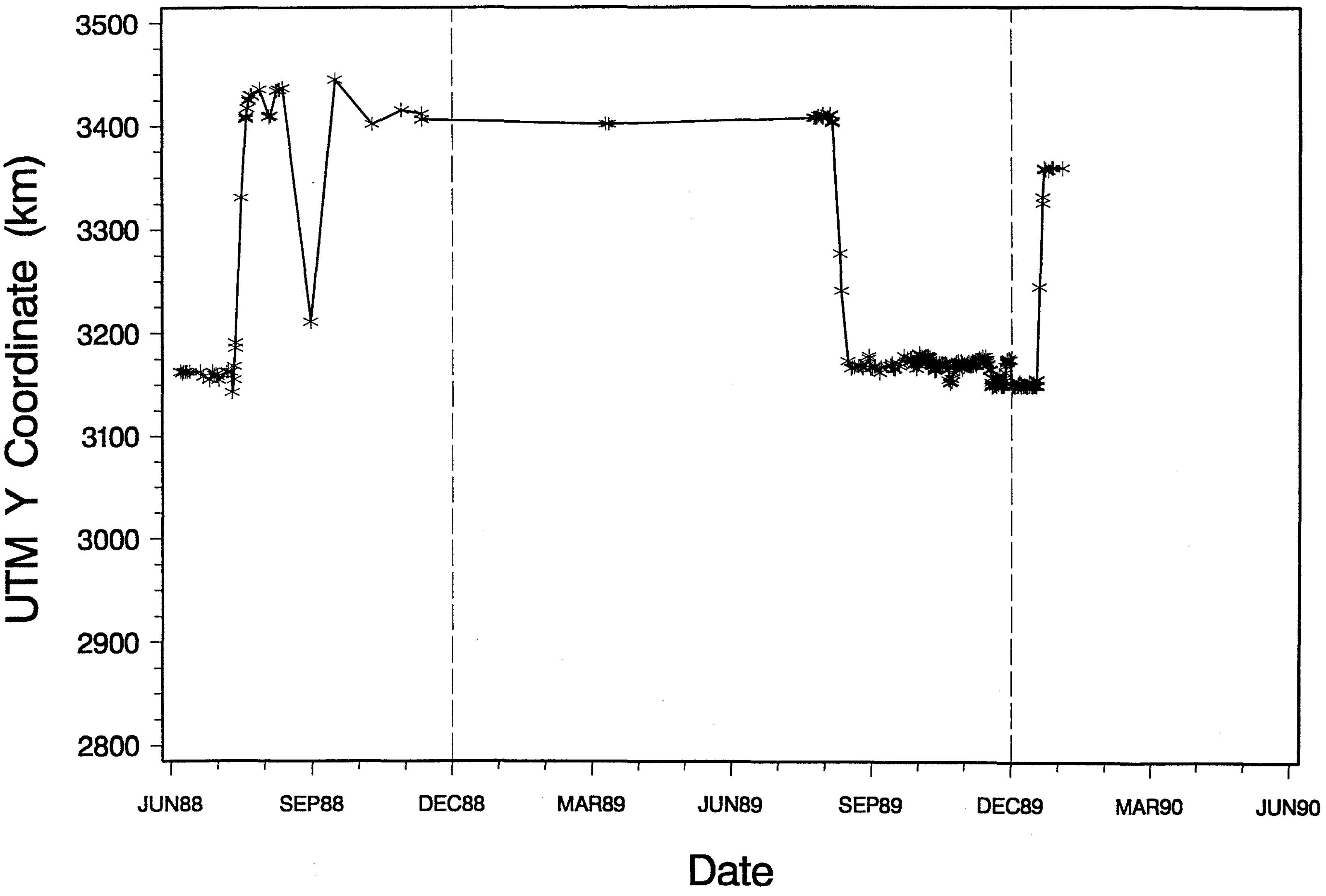
TBC – 21 ("Willie"): 1988 – 1990



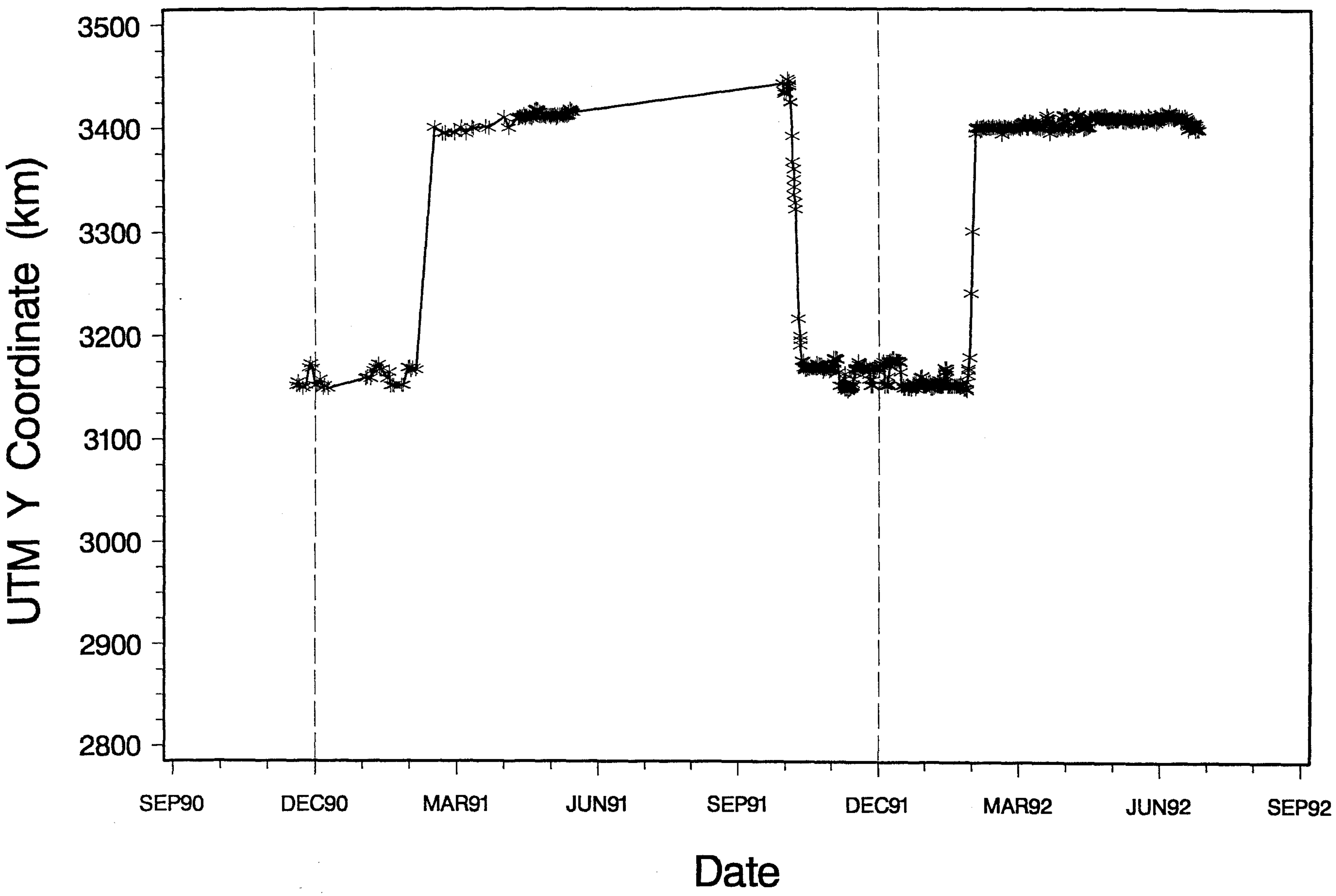
TBC – 23 ("Hillary"): 1988 – 1998



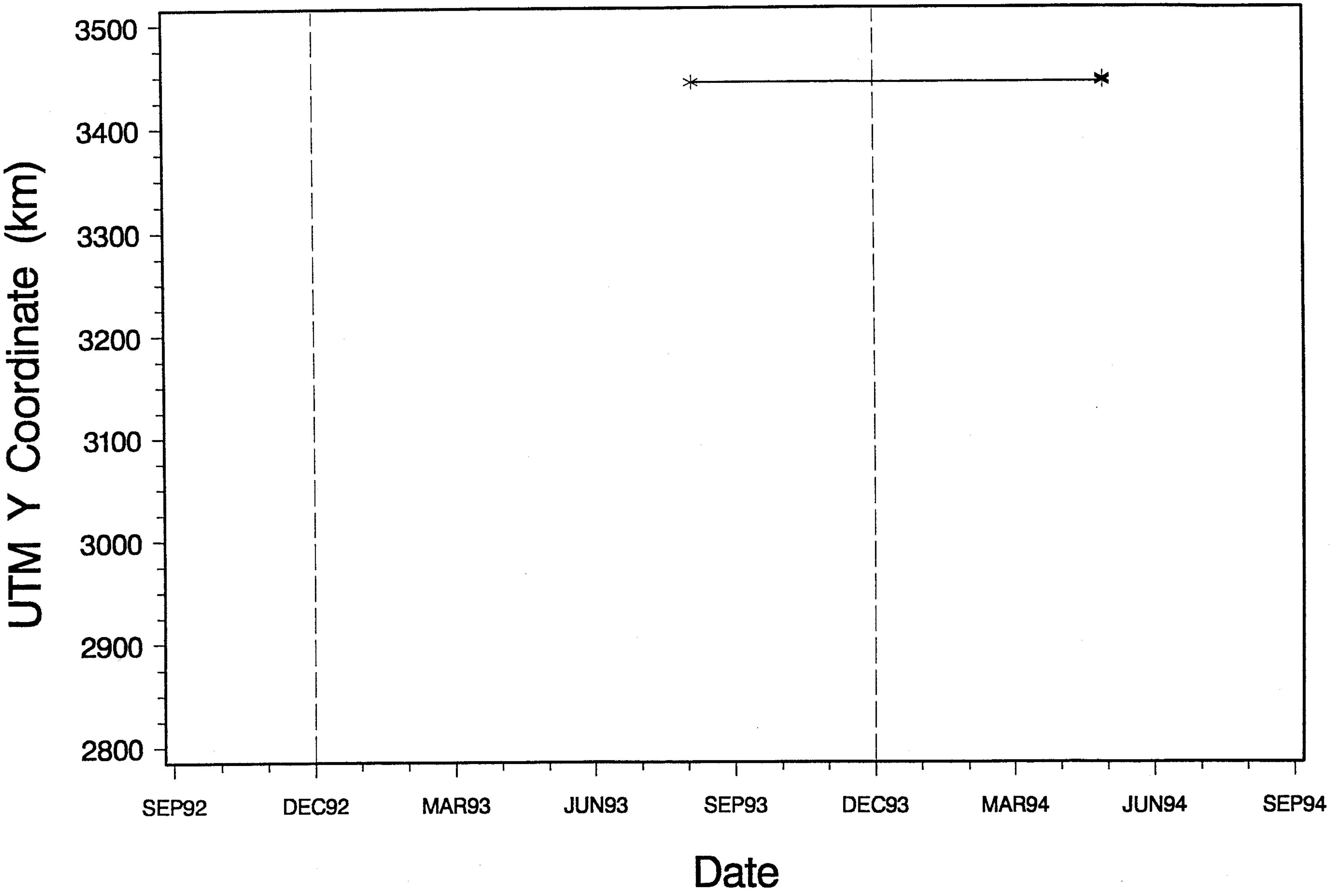
TBC – 23 ("Hillary"): 1988 – 1990



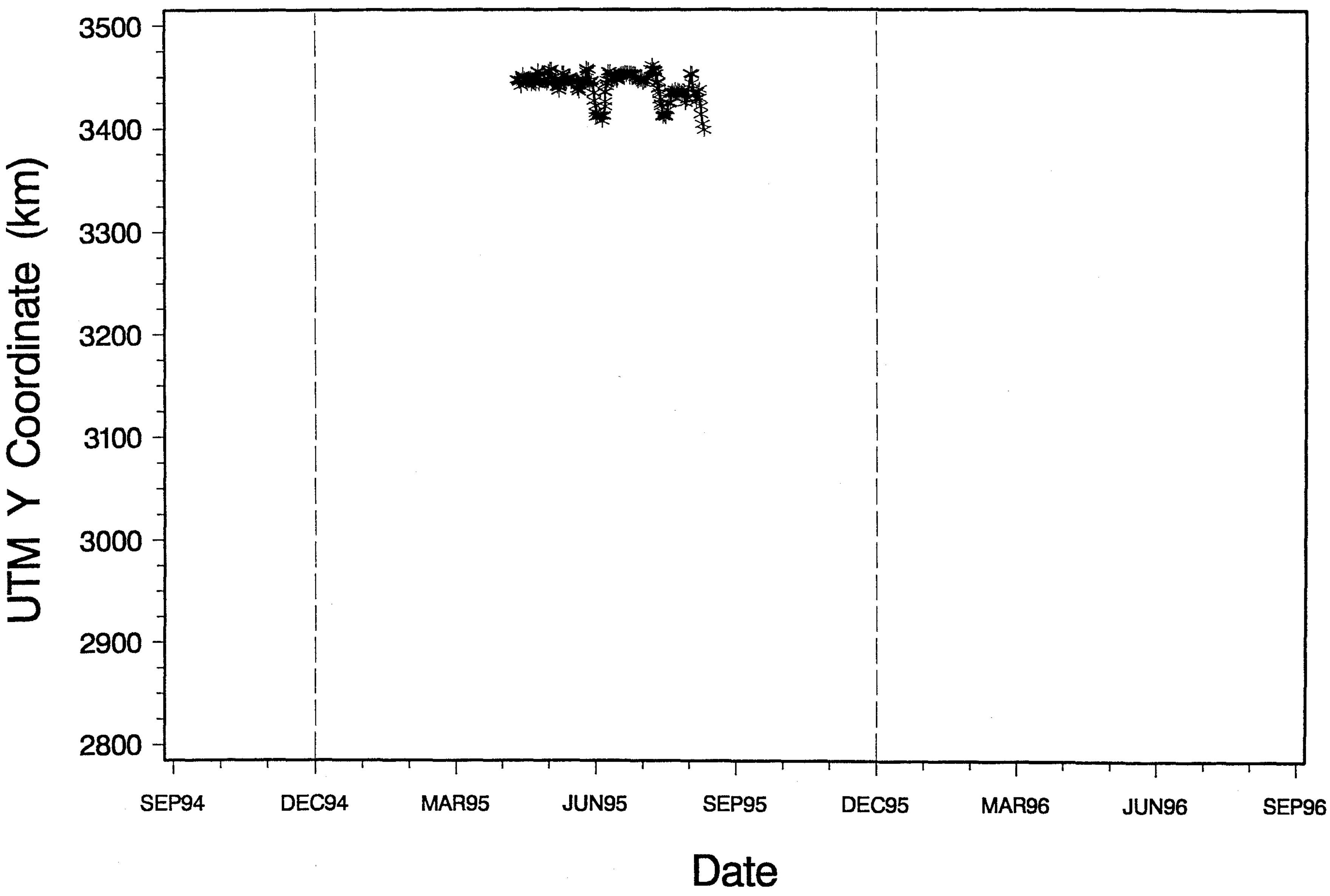
TBC – 23 ("Hillary"): 1990 – 1992



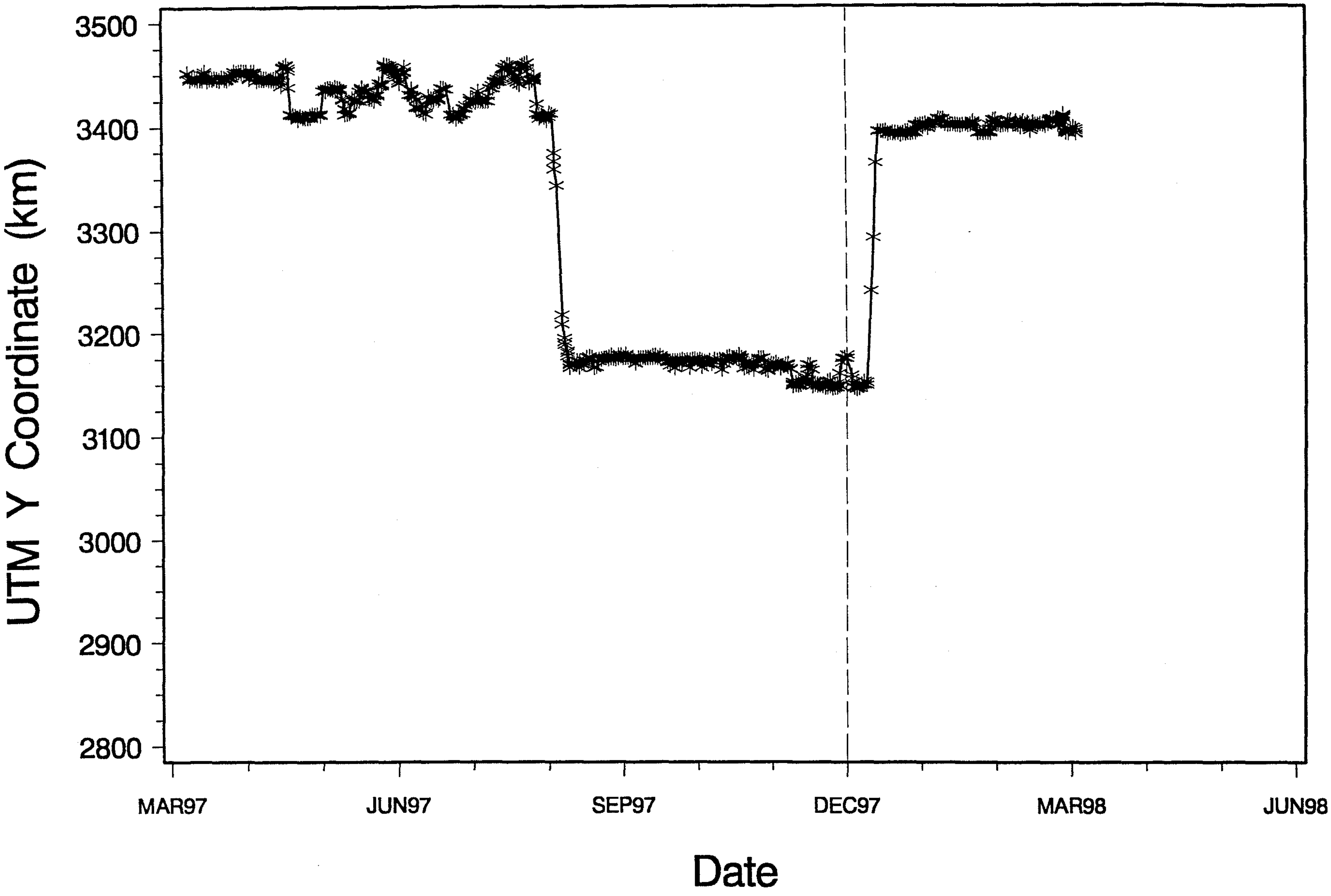
TBC – 23 ("Hillary"): 1992 – 1994



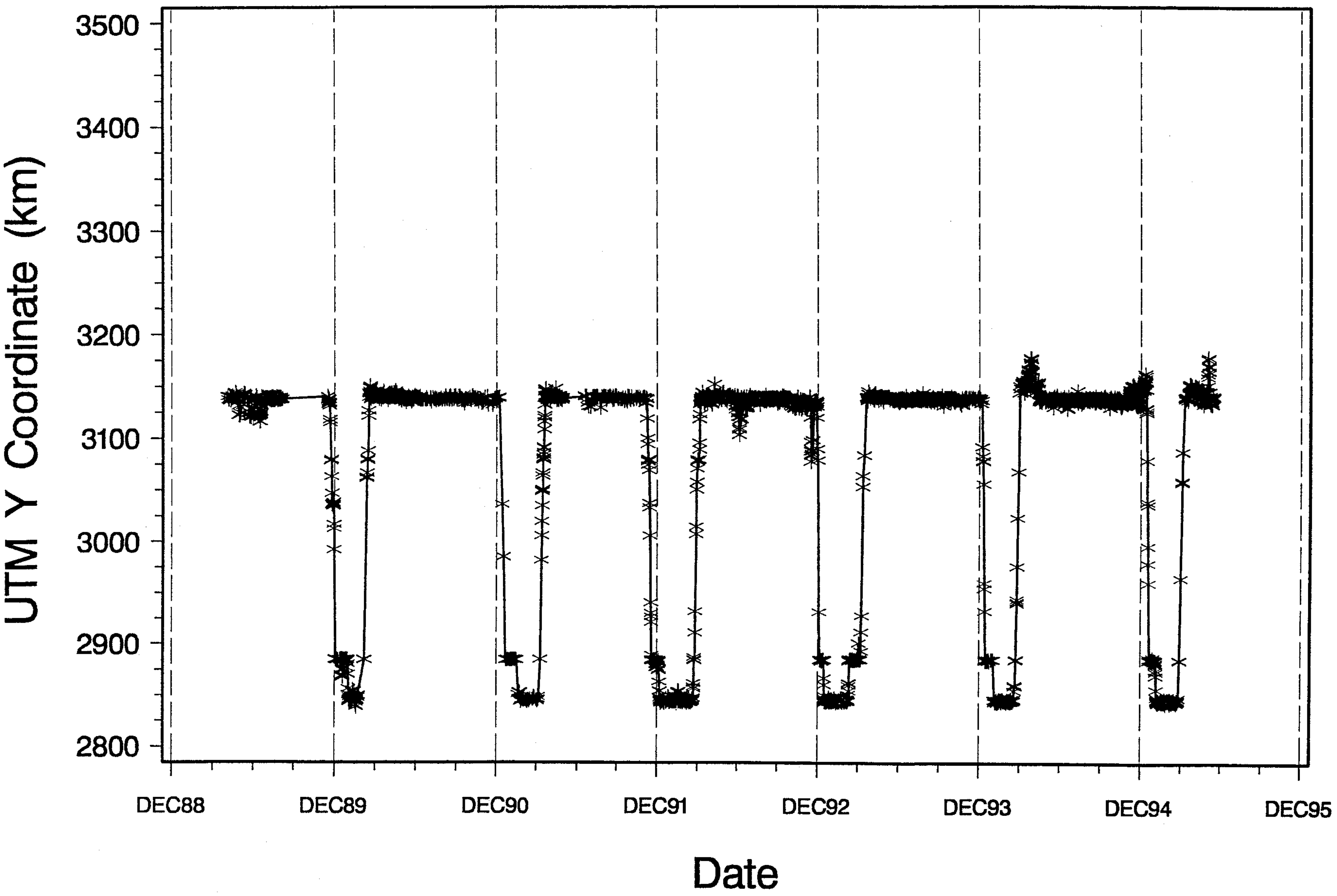
TBC – 23 ("Hillary"): 1994 – 1996



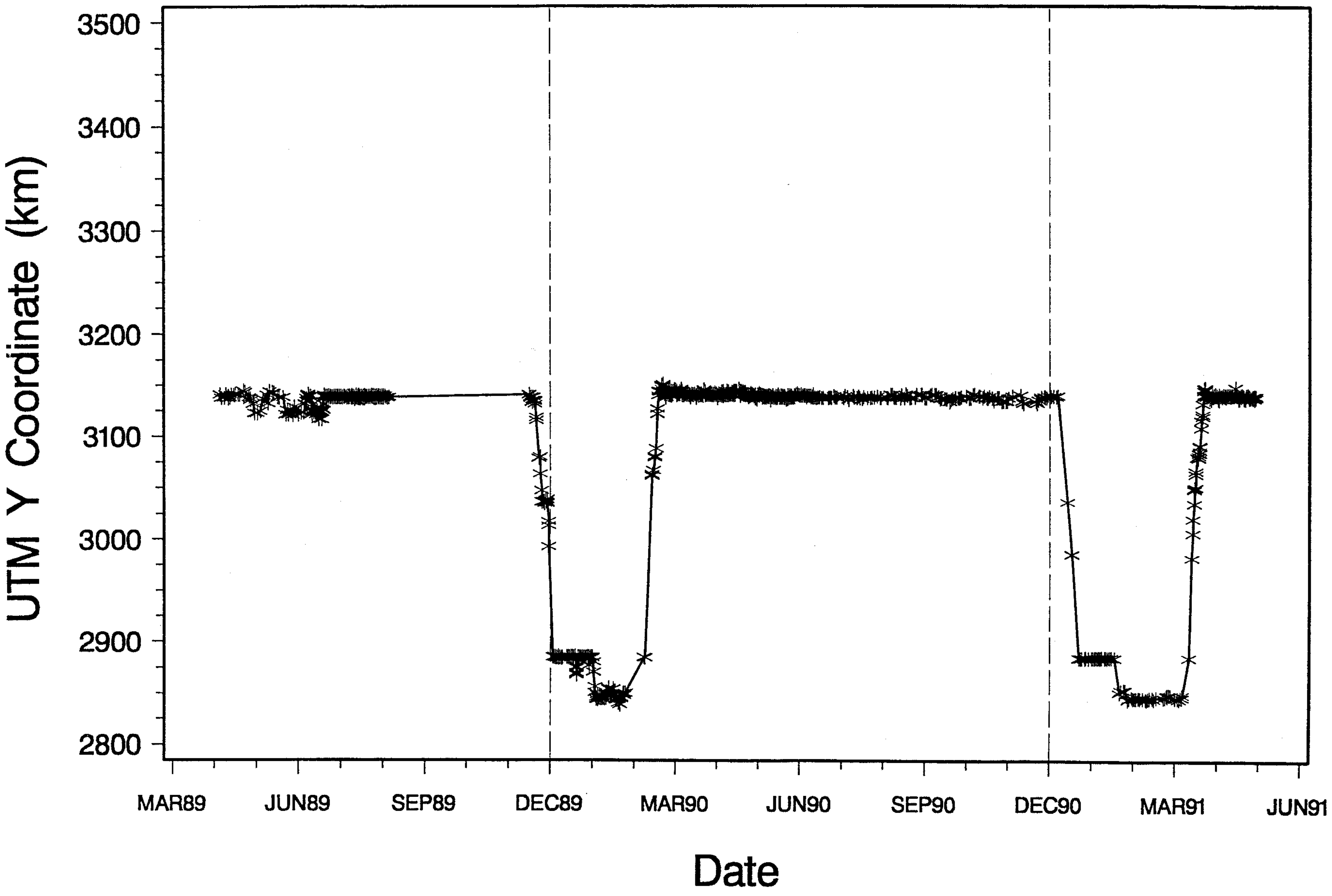
TBC – 23 ("Hillary"): 1997 – 1998



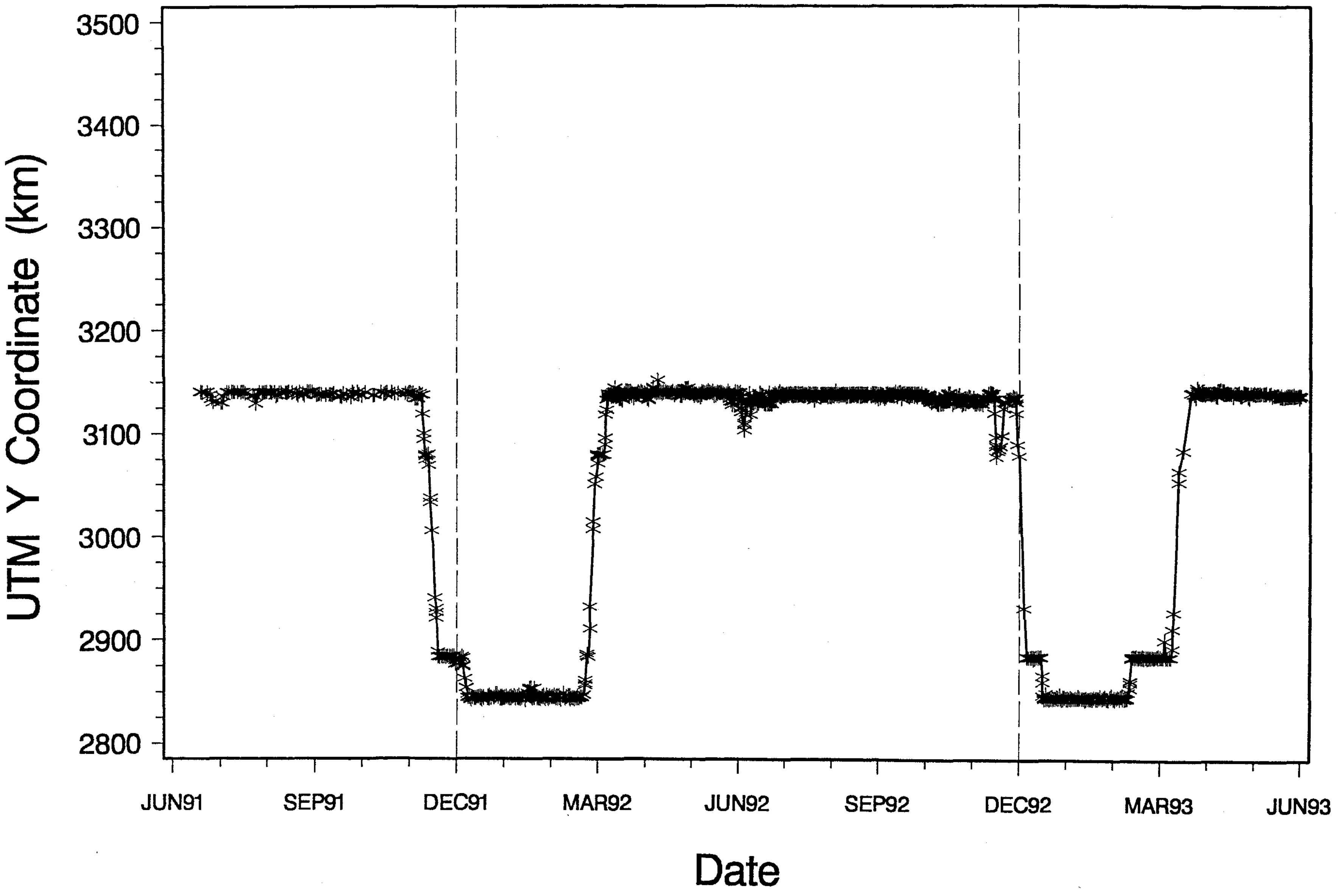
TBC – 24 ("Betty"): 1989 – 1995

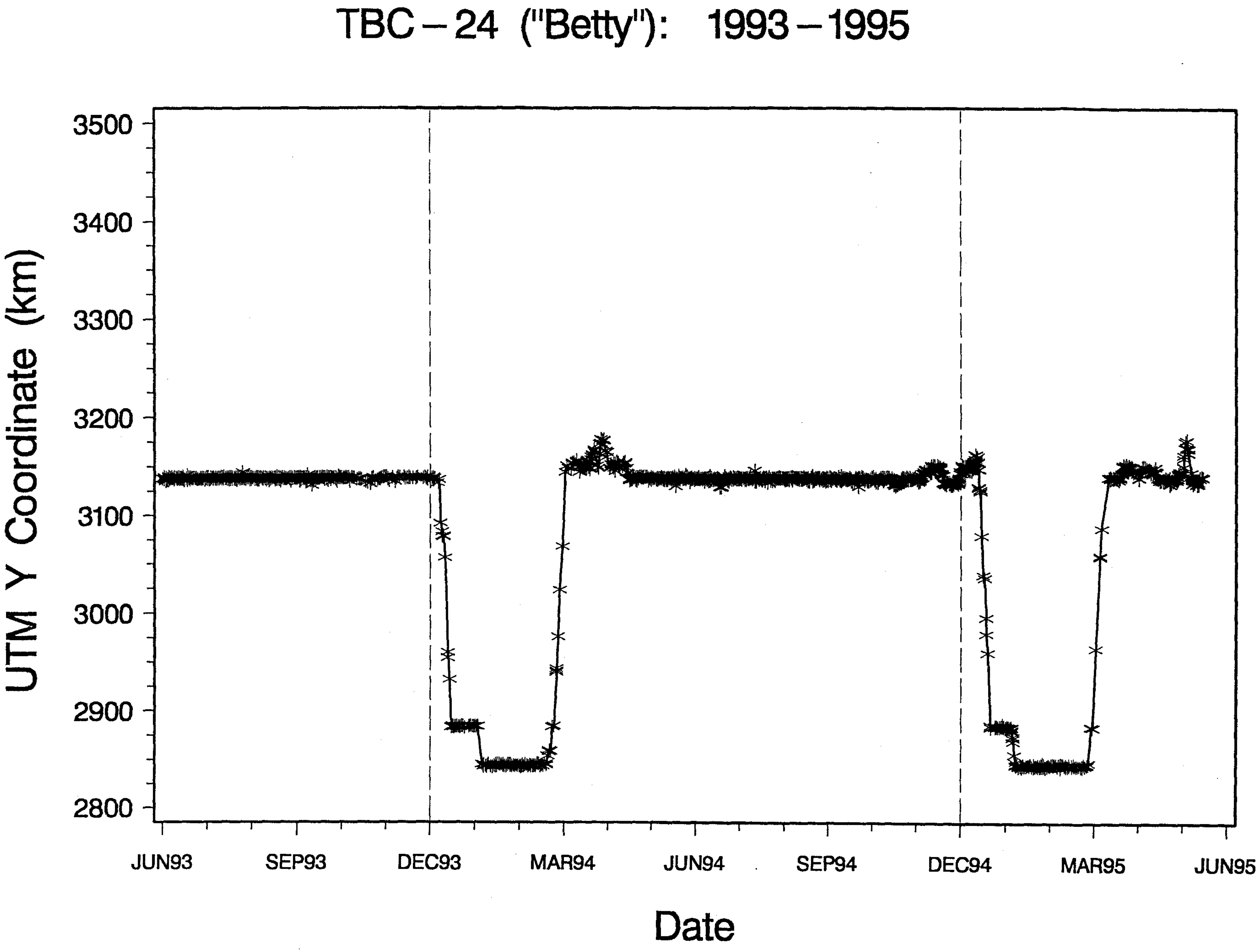


TBC – 24 ("Betty"): 1989 – 1991



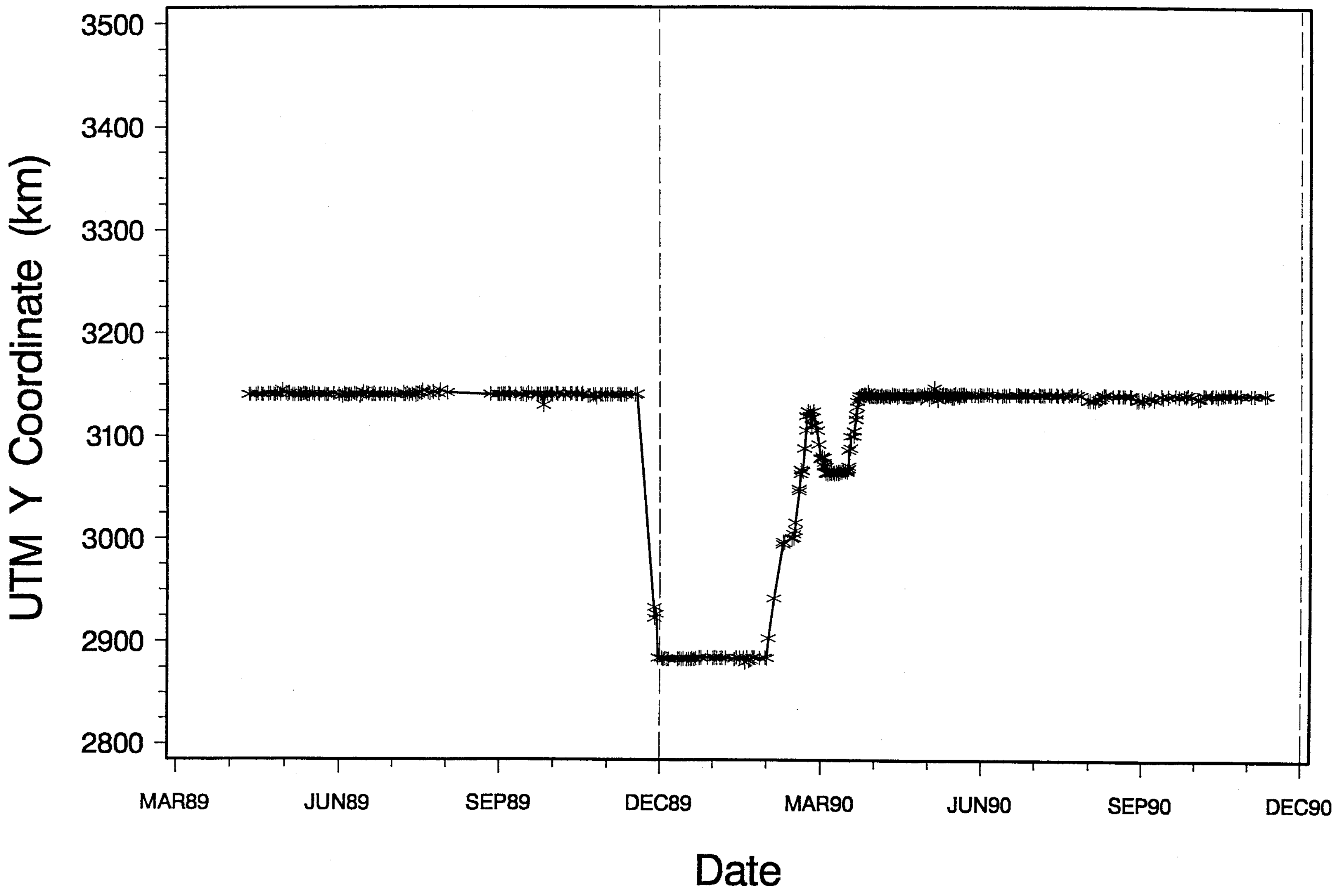
TBC – 24 ("Betty"): 1991 – 1993

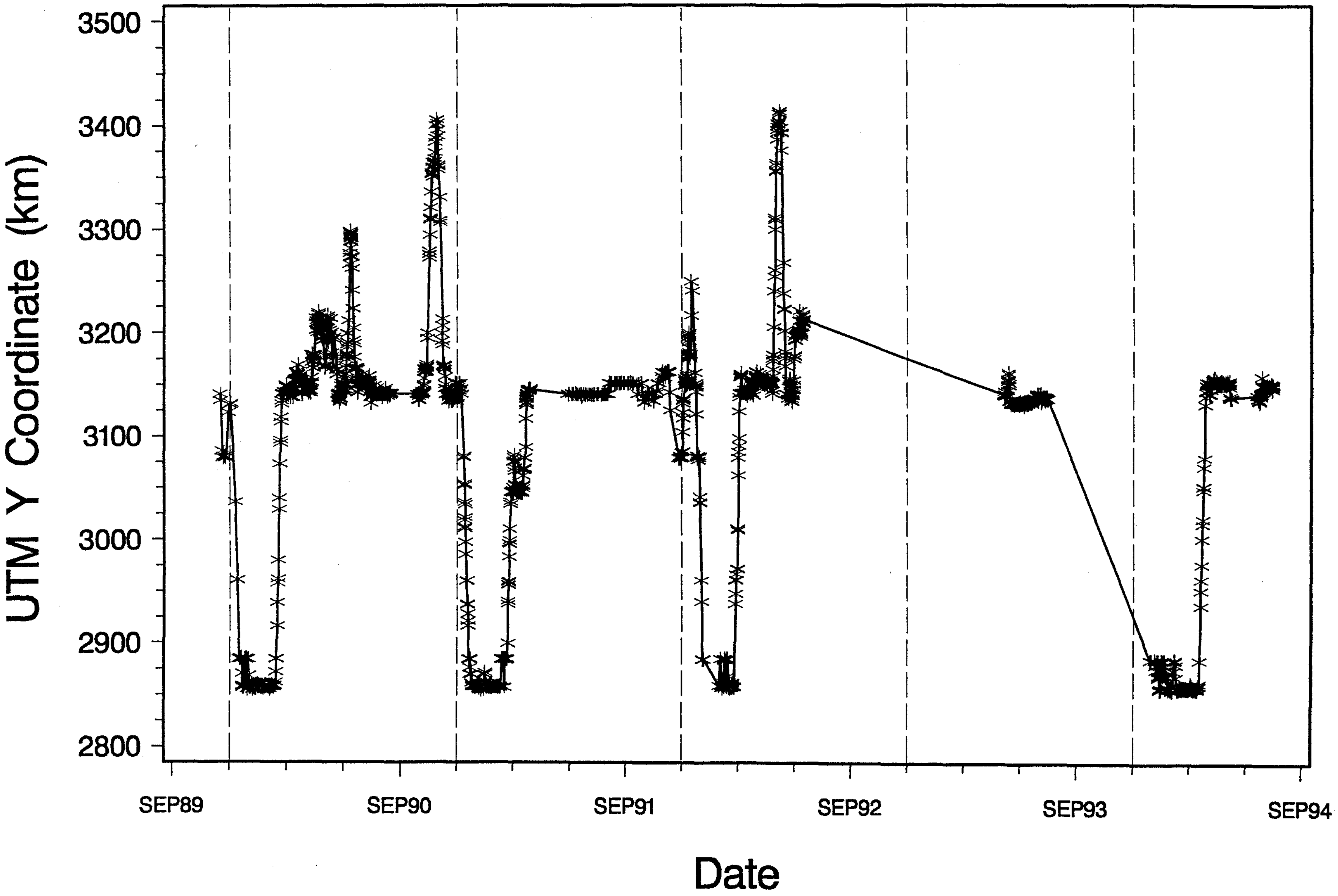




TBC – 24 ("Betty"): 1993 – 1995
UTM Y Coordinate (km)
3500
3400
3300
3200
3100
3000
2900
2800
JUN93
SEP93
DEC93
MAR94
JUN94
SEP94
DEC94
MAR95
JUN95
Date

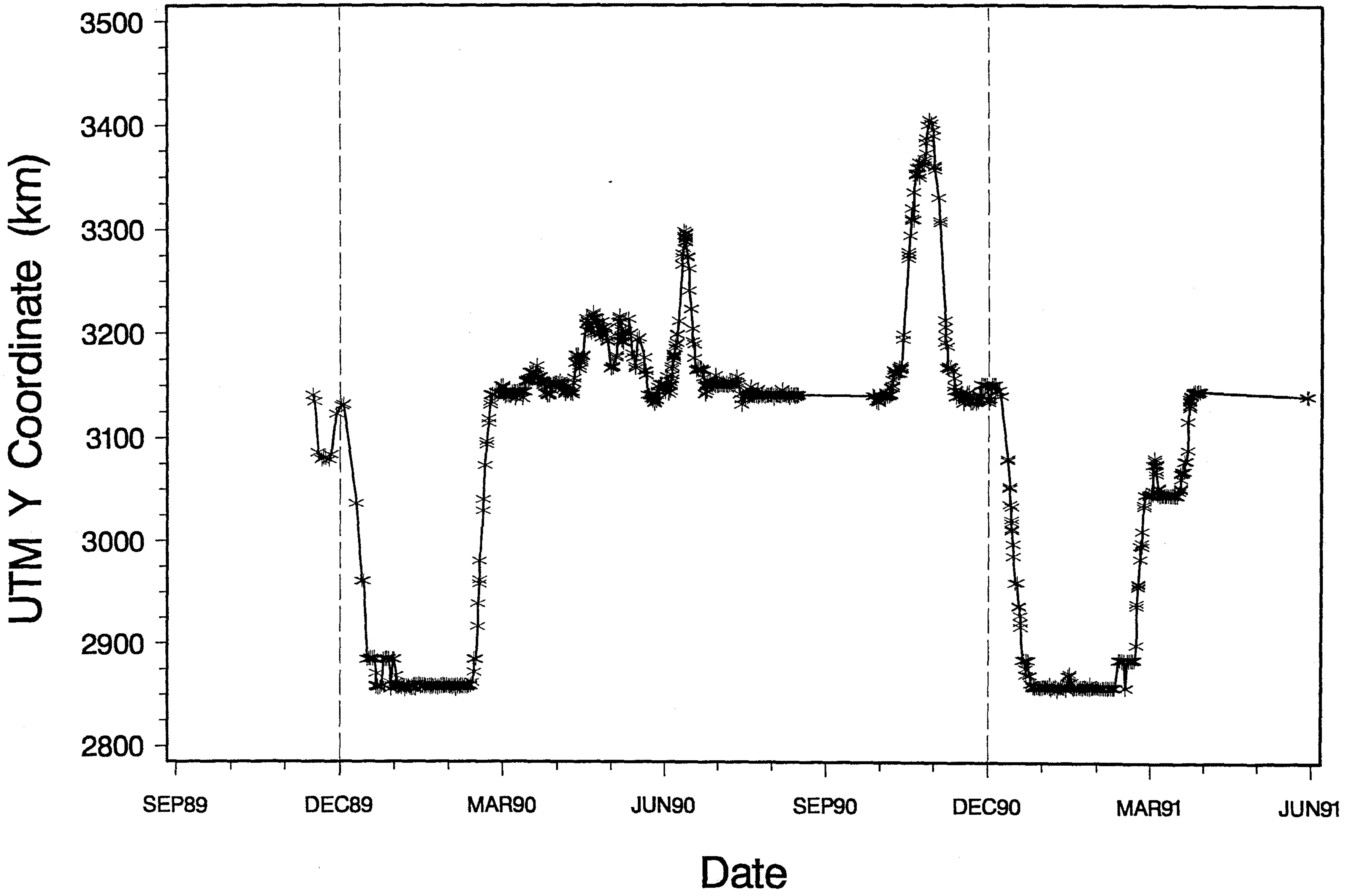
TBC – 25 ("D – cow"): 1989 – 1990



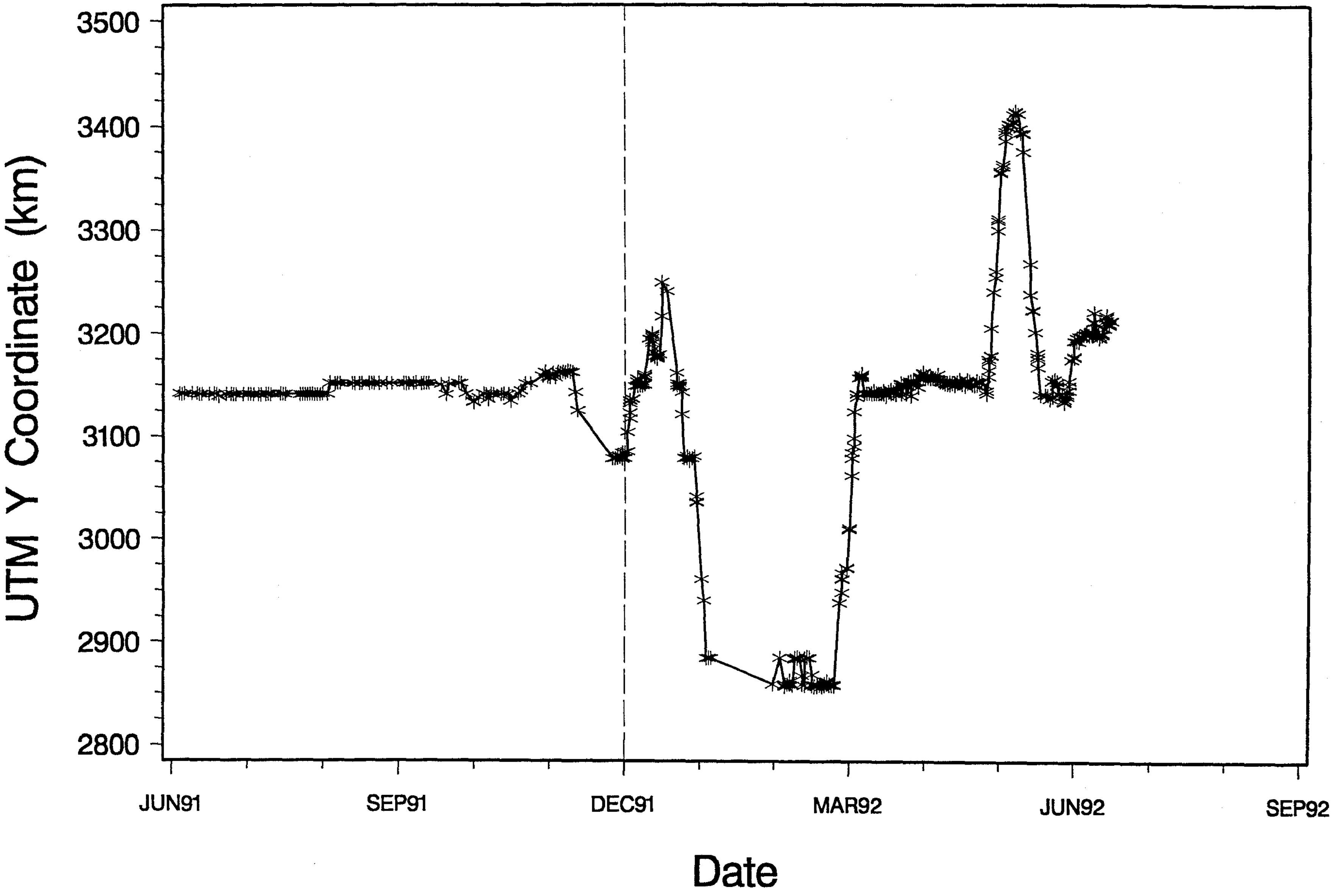


TBC – 26 ("Peewee"): 1989 – 1994

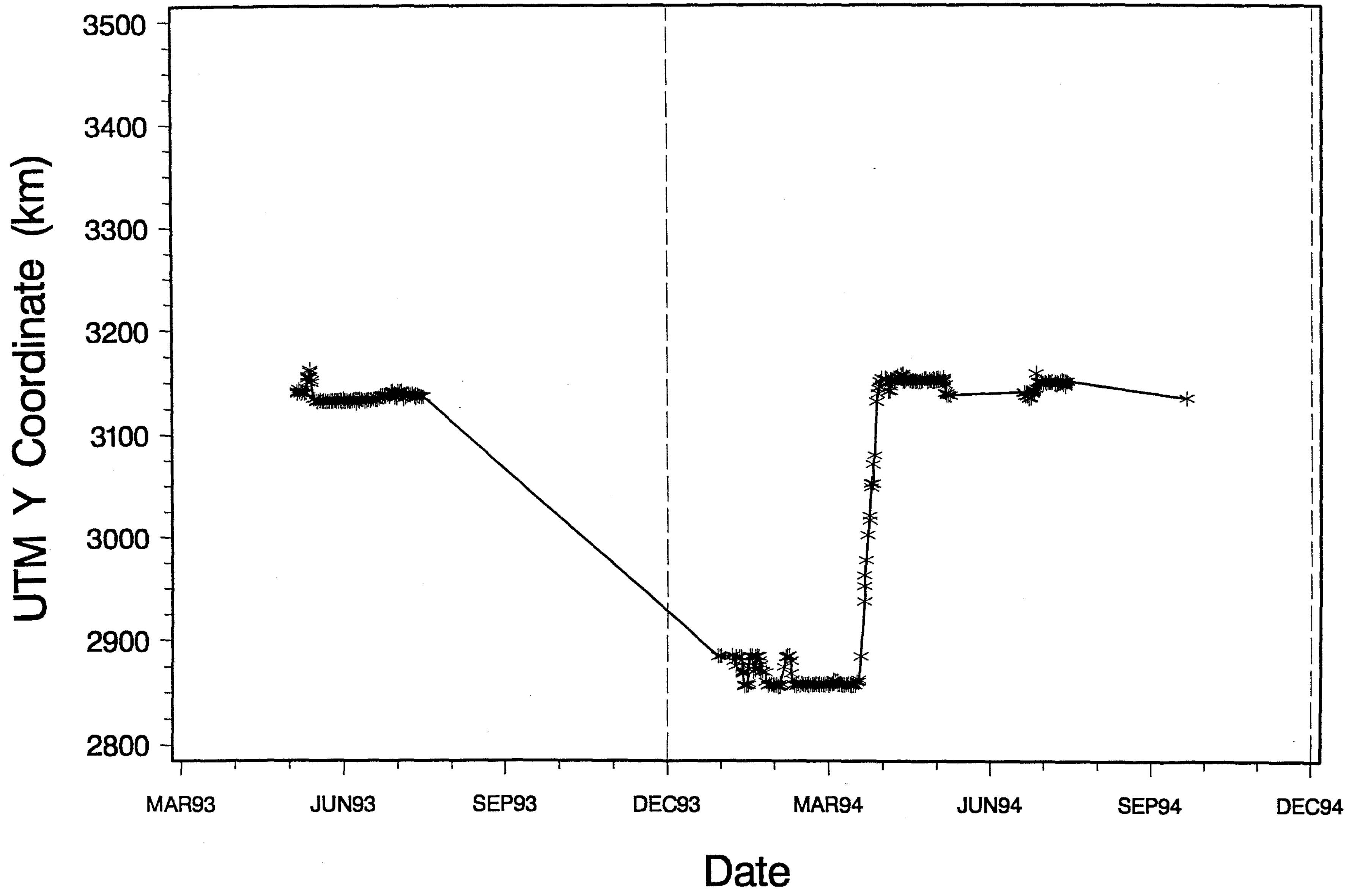
TBC – 26 ("Peewee"): 1989 – 1991



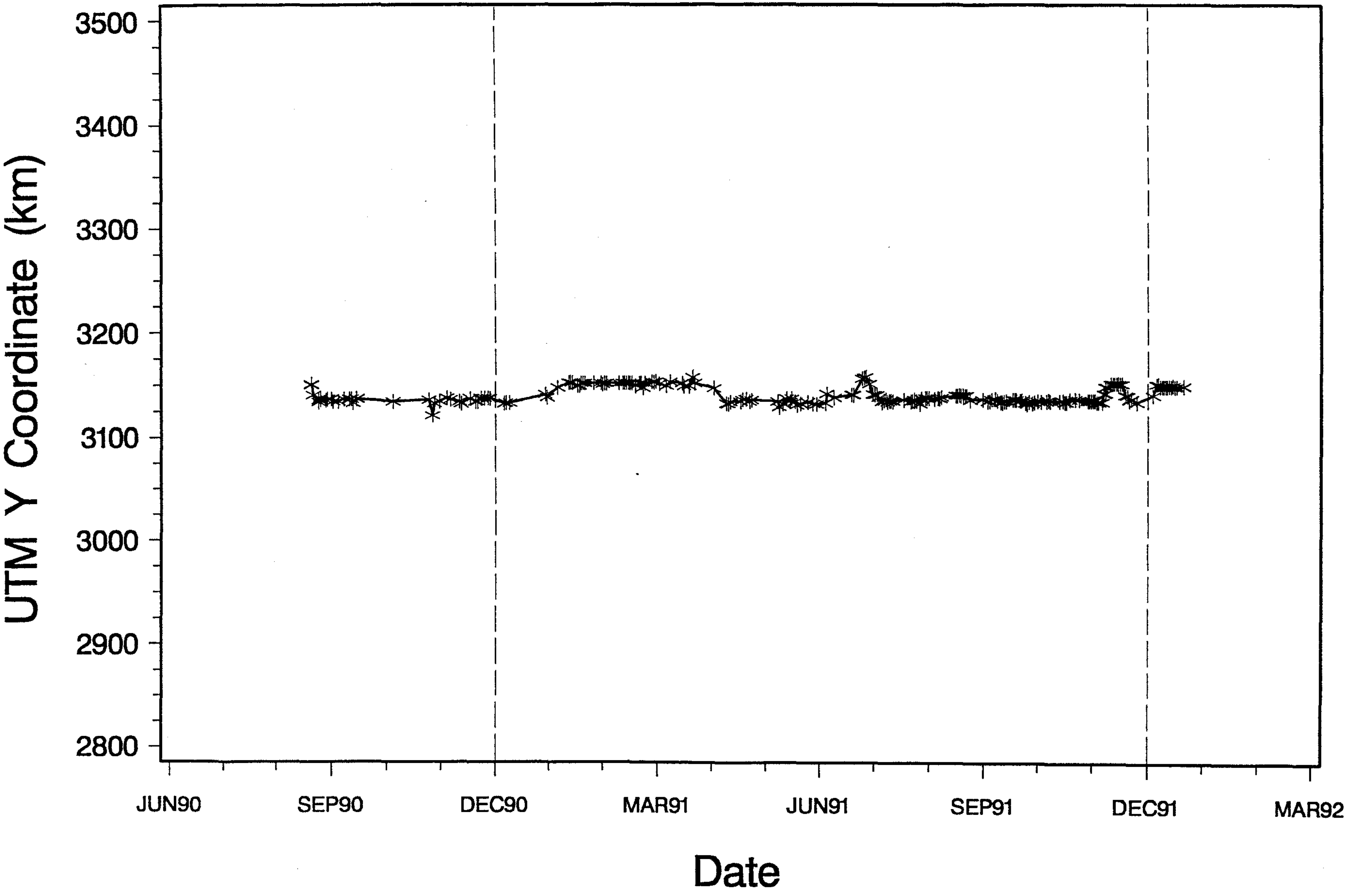
TBC – 26 ("Peewee"): 1991 – 1992



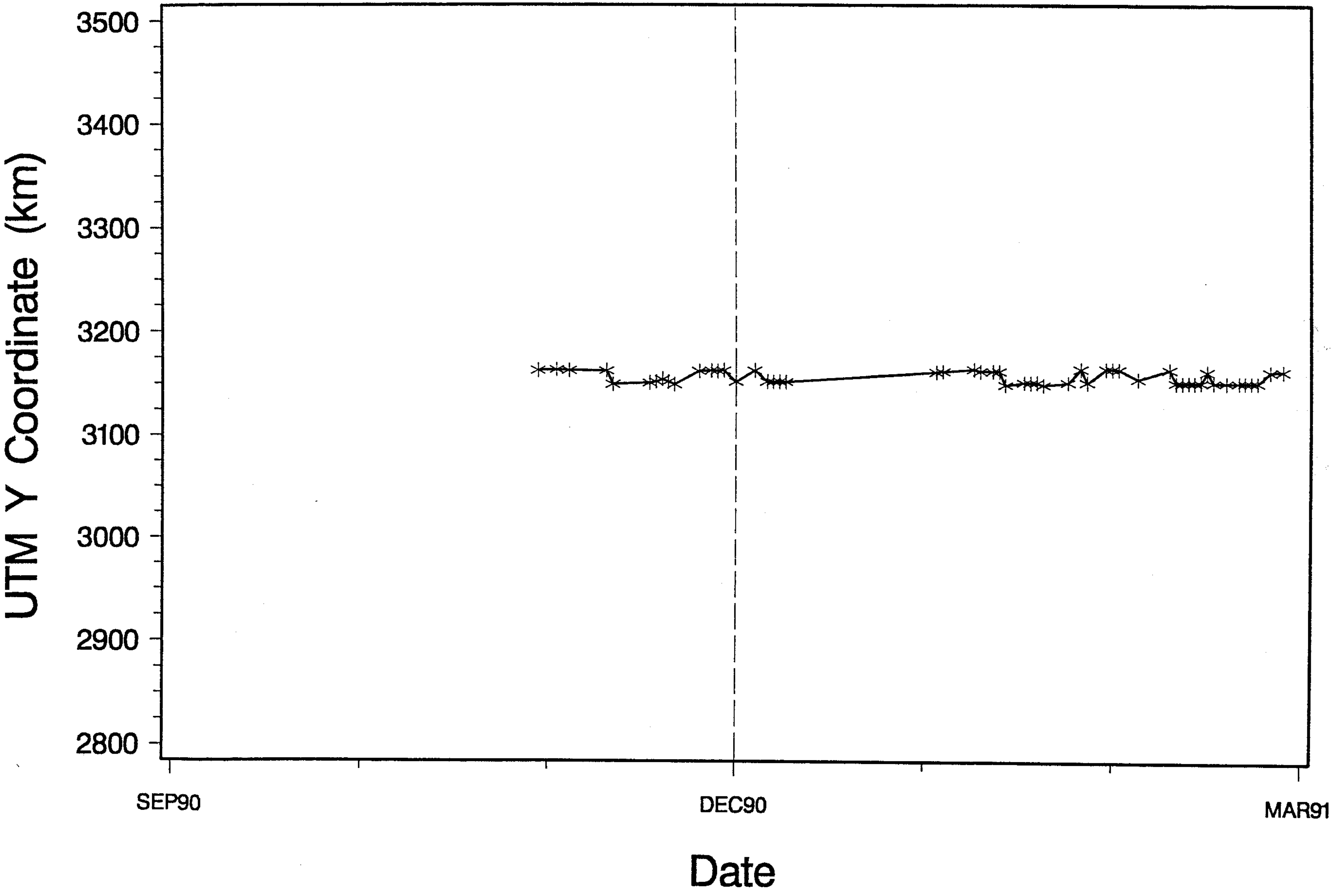
TBC – 26 ("Peewee"): 1993 – 1994

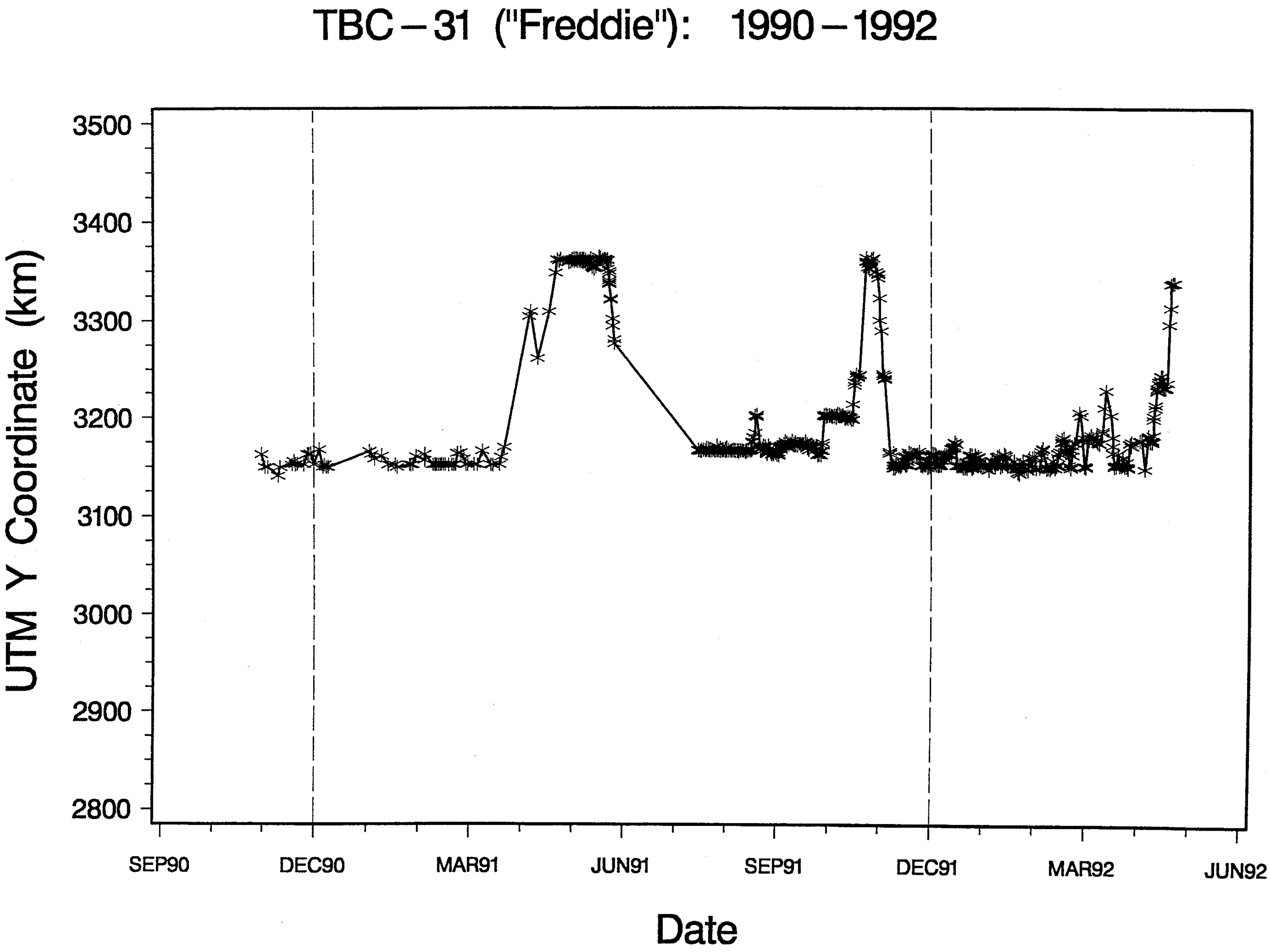


TBC – 29 ("Casey"): 1990 – 1991

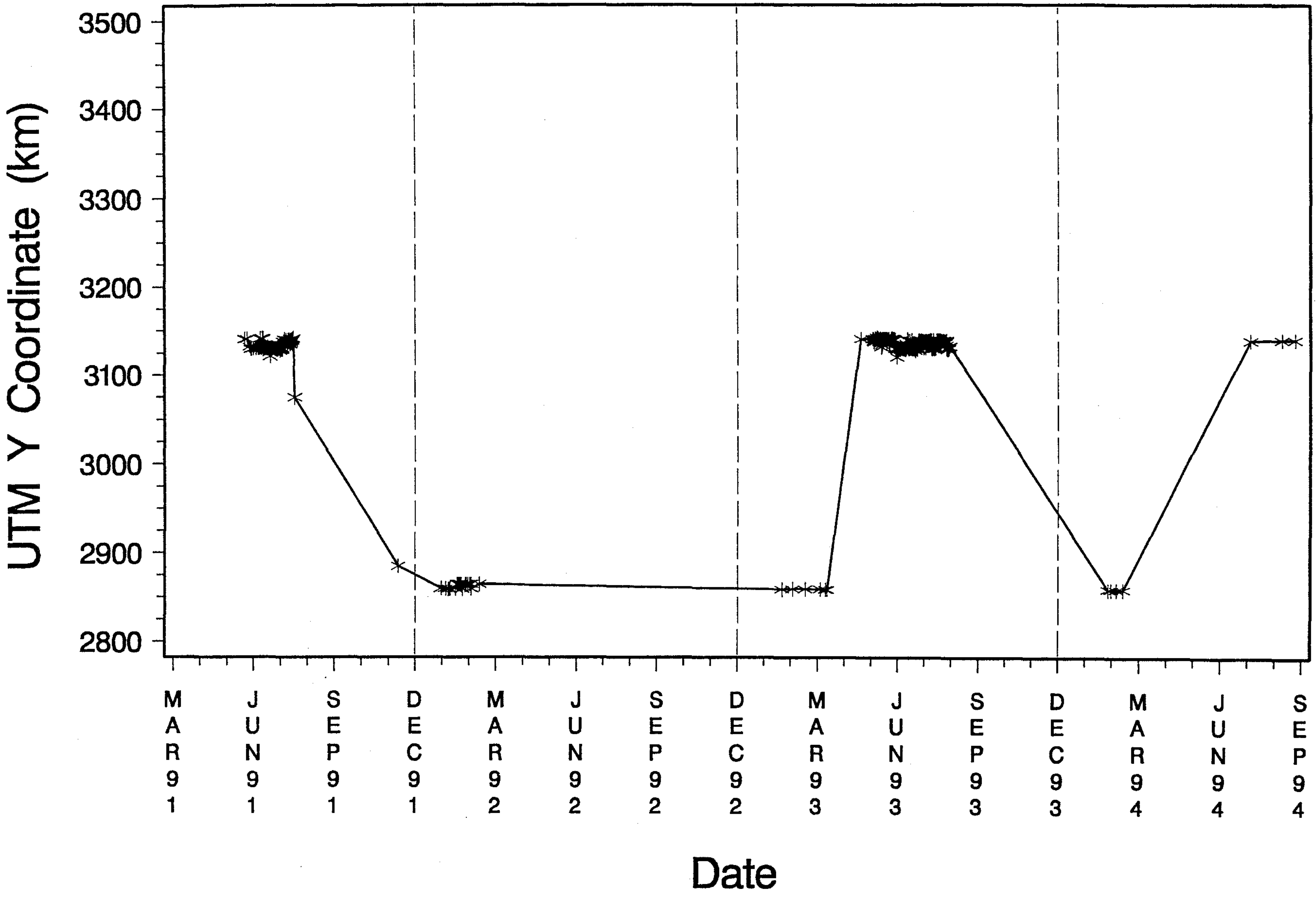


TBC – 30 ("Maria"): 1990 – 1991

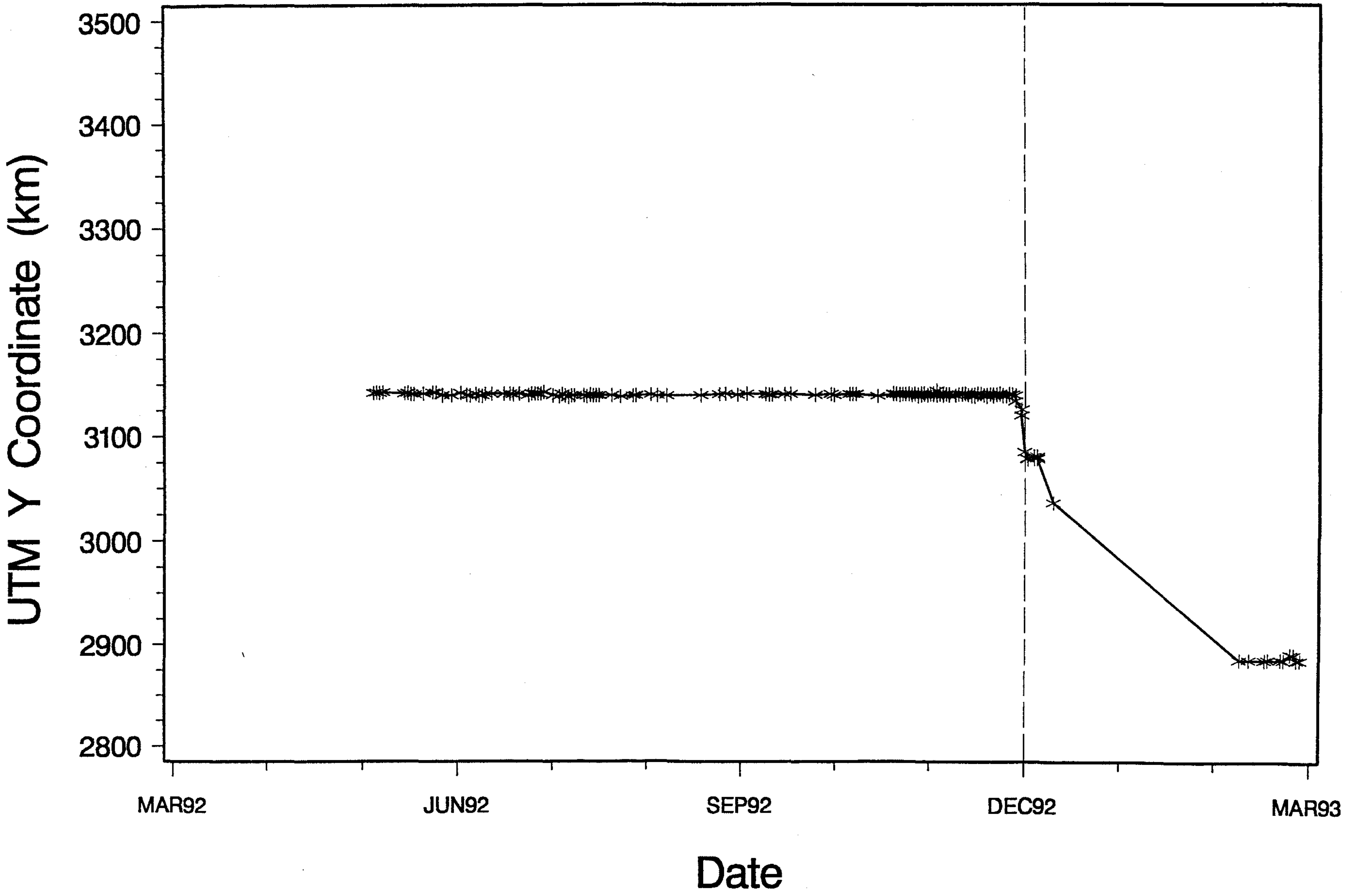


TBC – 31 ("Freddie"): 1990 – 1992
UTM Y Coordinate (km)
3500
3400
3300
3200
3100
3000
2900
2800
SEP90
DEC90
MAR91
JUN91
SEP91
DEC91
MAR92
JUN92
Date

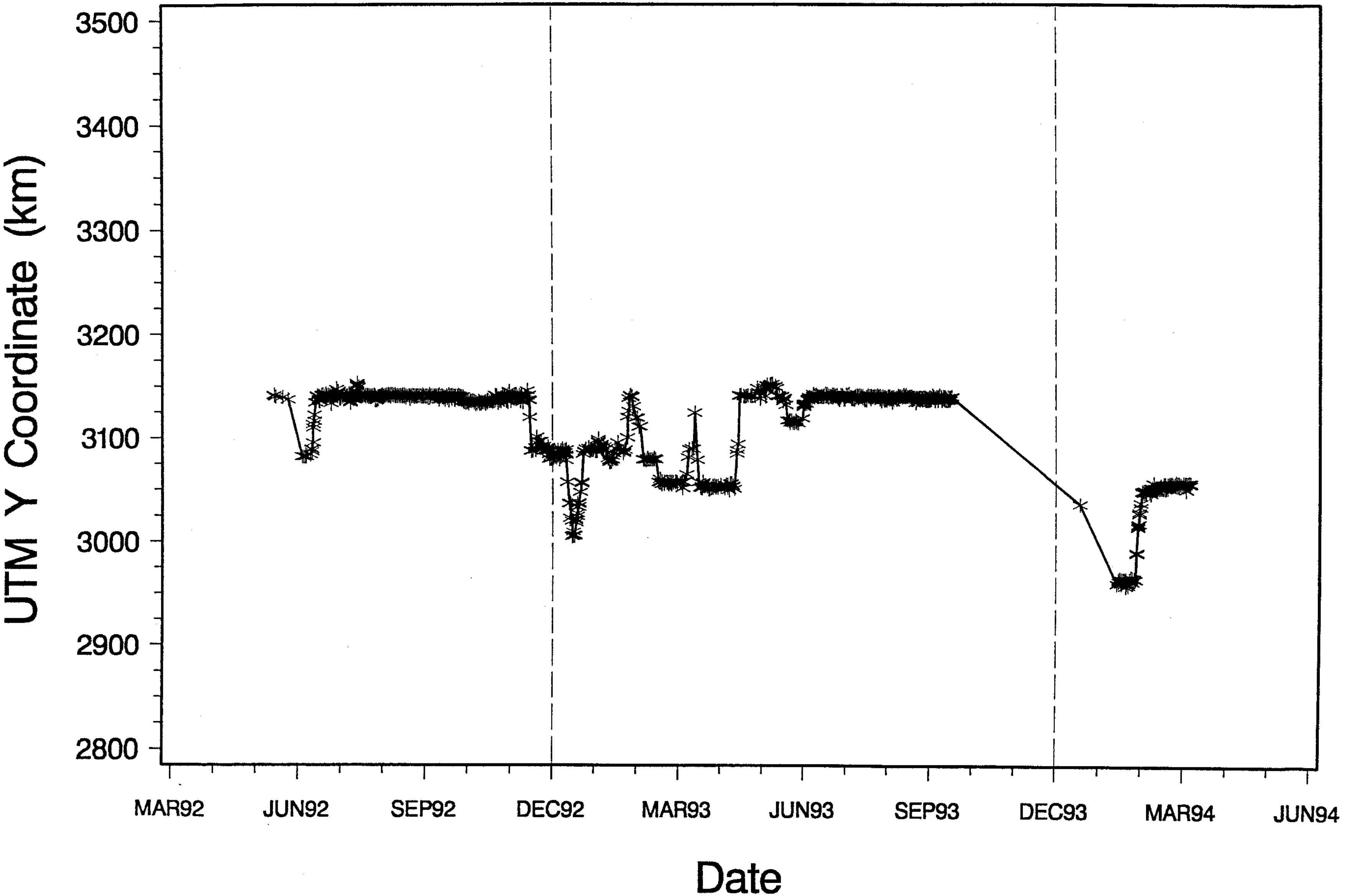
TBC – 32 ("Tomasina"): 1991 – 1994



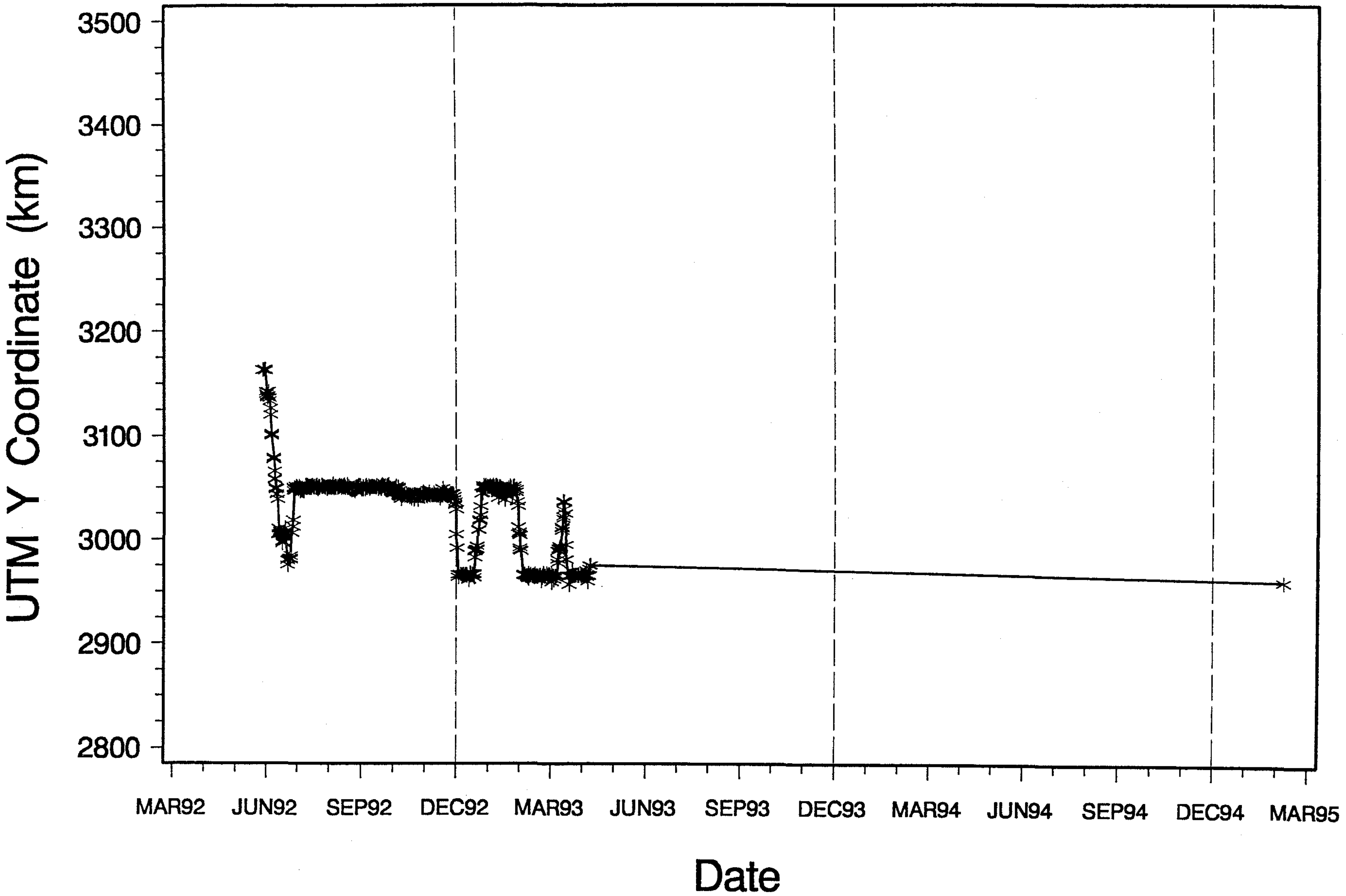
TBC – 35 ("E – cow"): 1992 – 1993



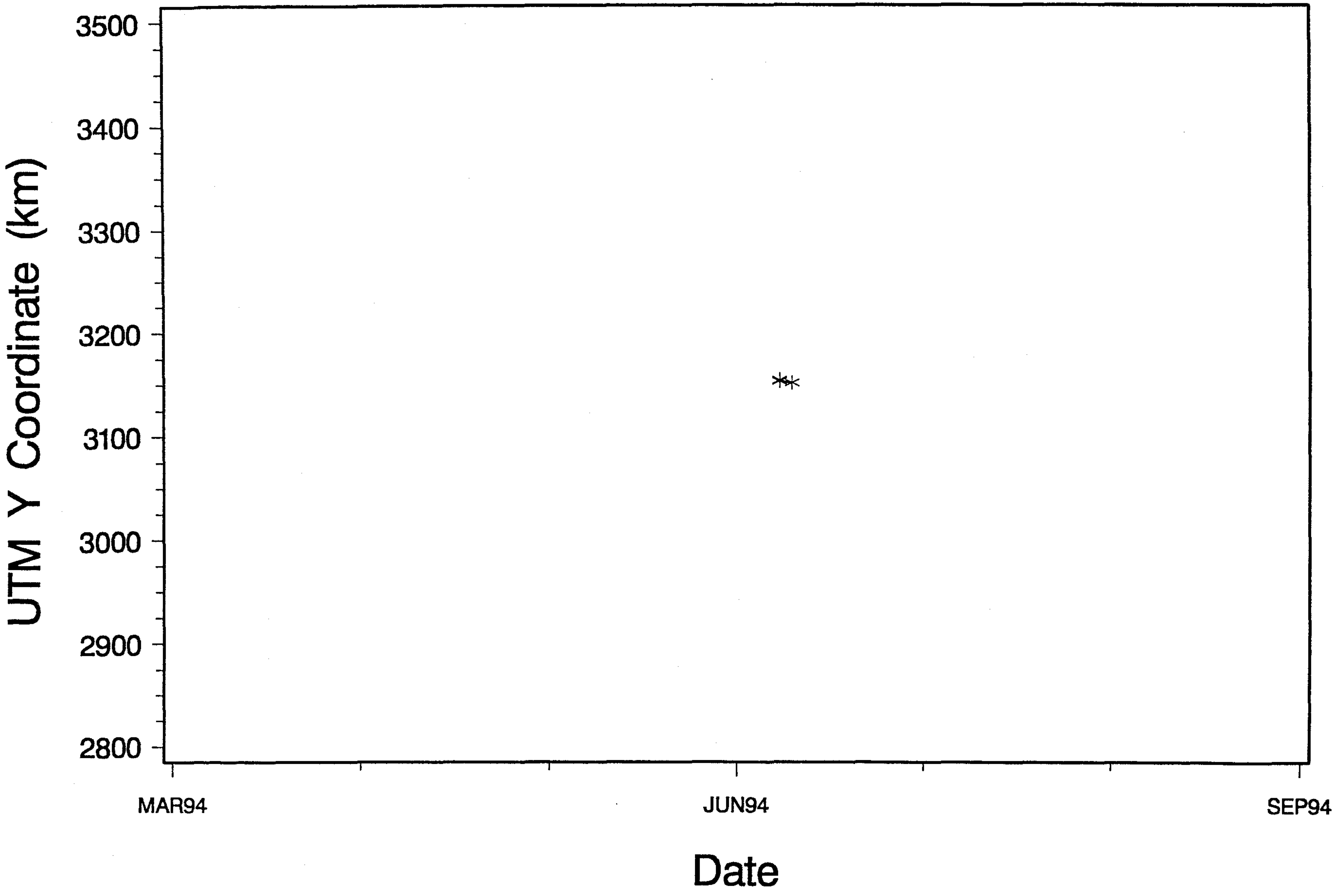
TBC – 36 ("Sunshine"): 1992 – 1994



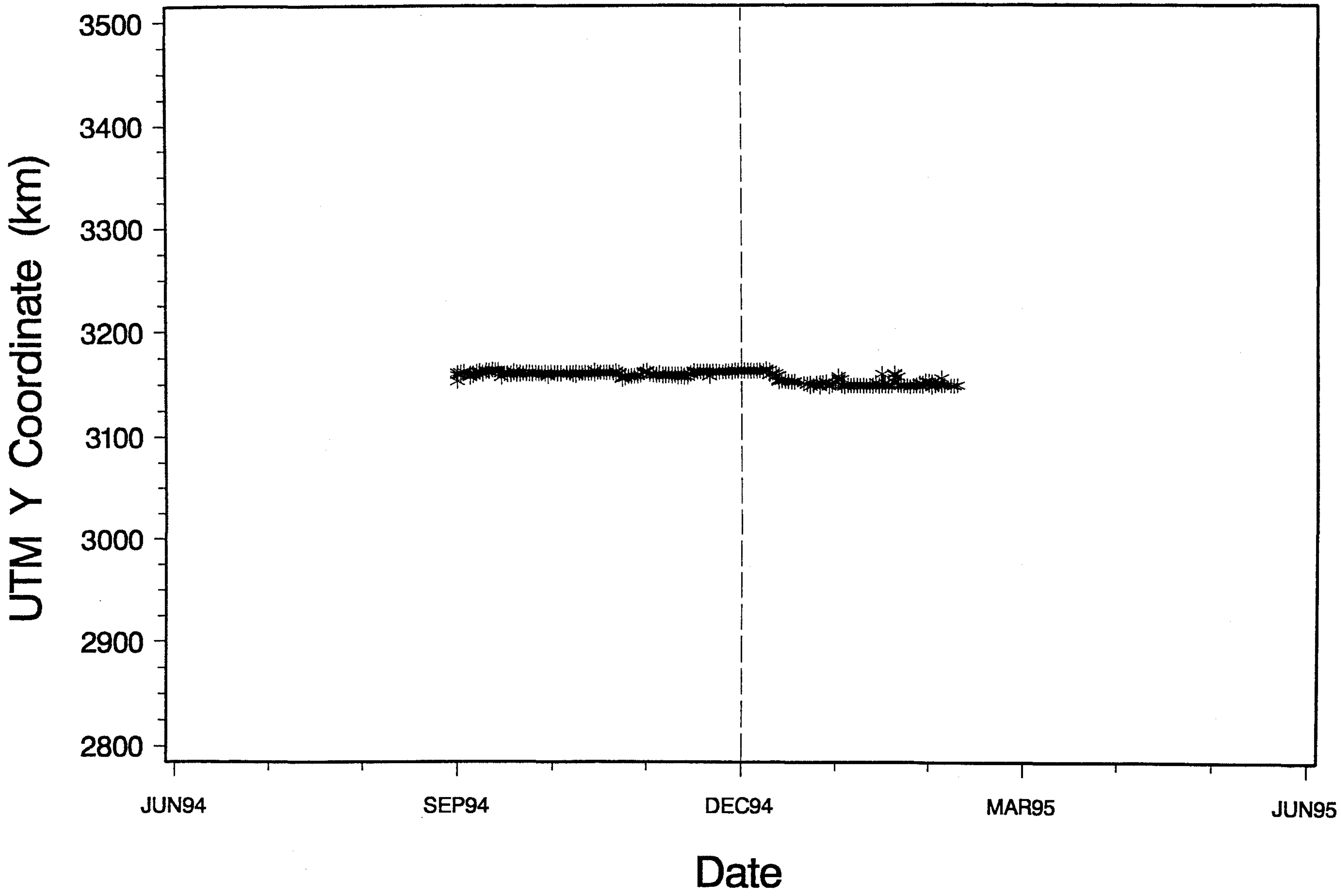
TBC – 37 ("Pamela"): 1992 – 1995



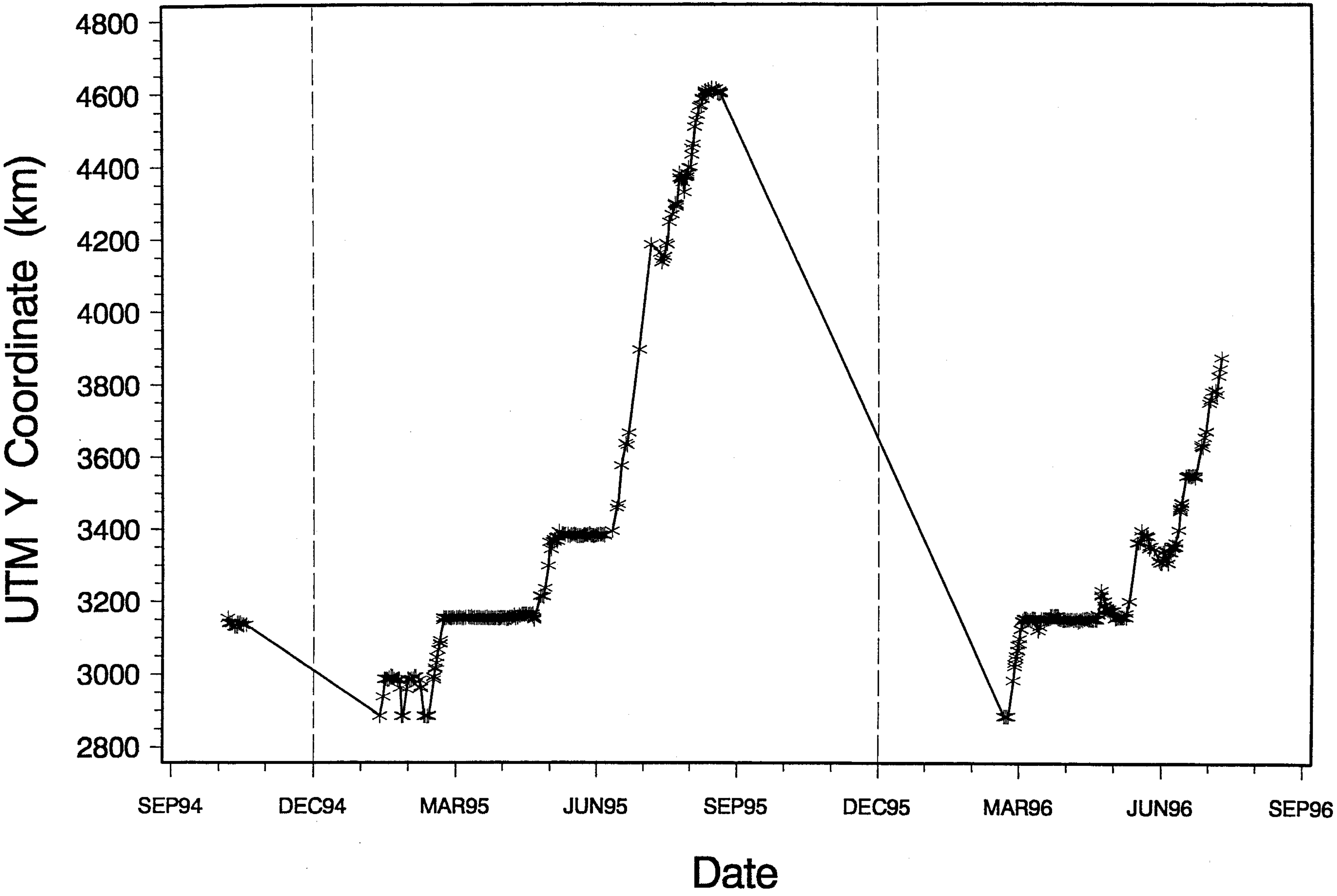
TBC – 40 ("Danise"): 1994



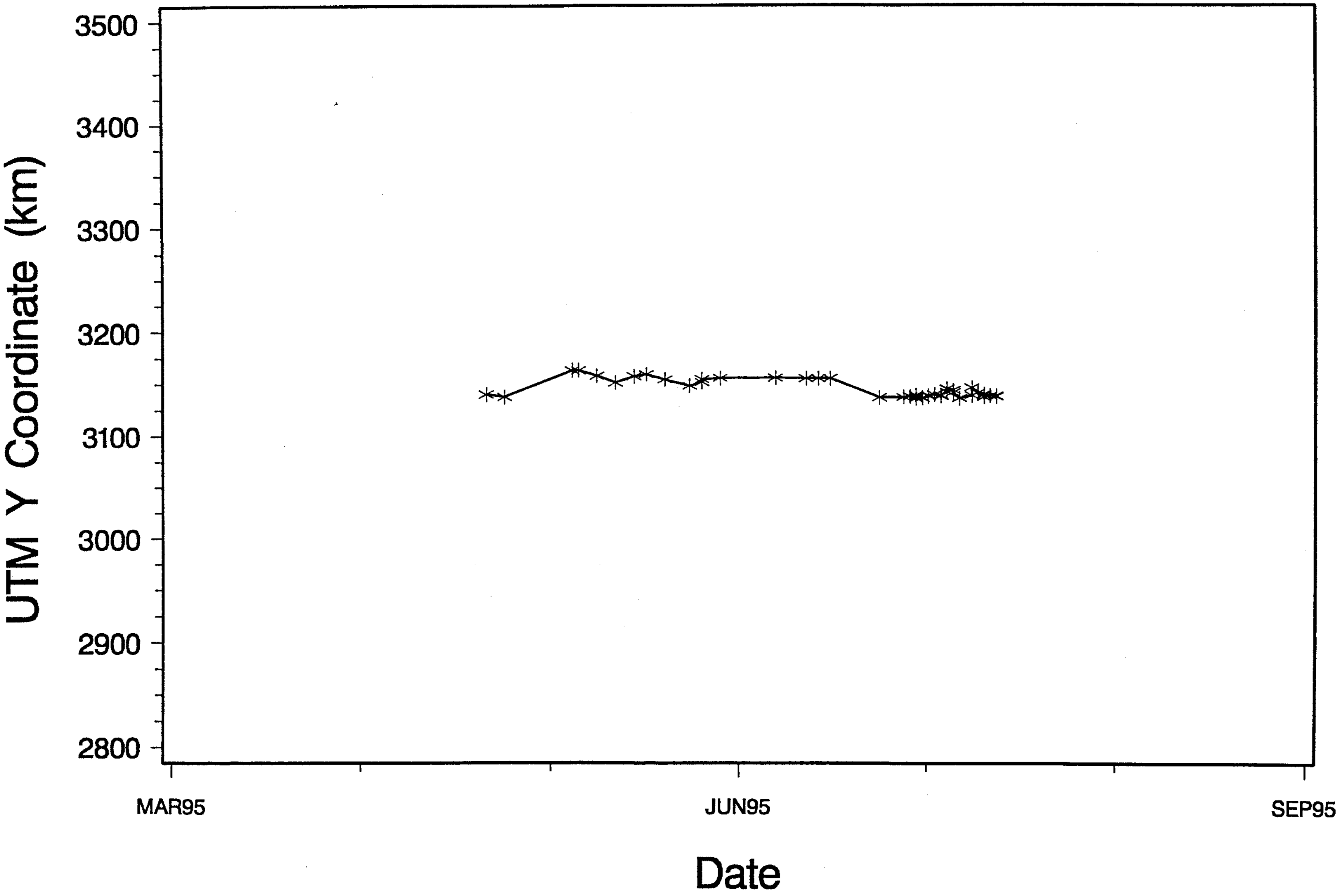
TBC – 41 ("Scott"): 1994 – 1995



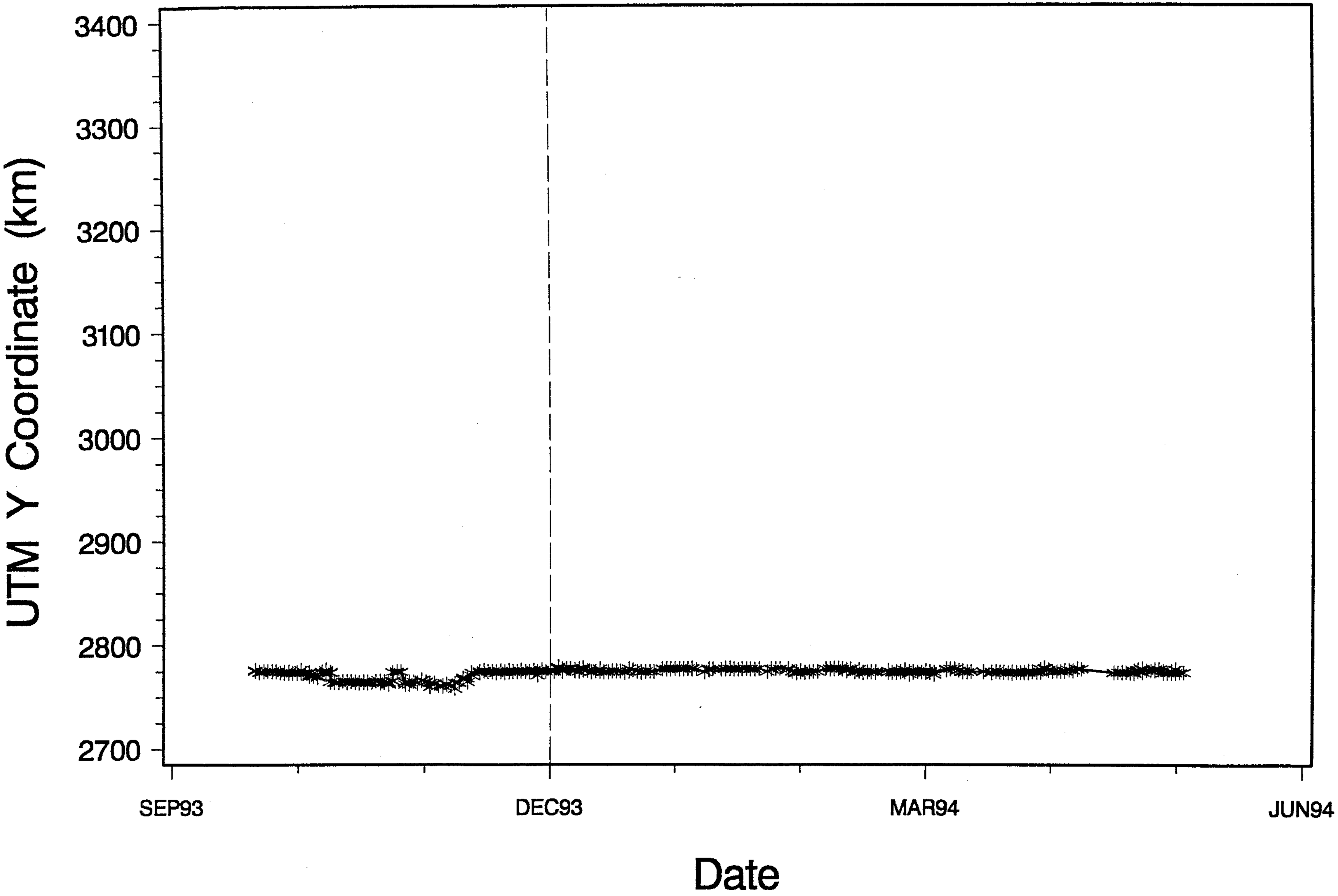
TBC – 42 ("Chessie"): 1994 – 1996



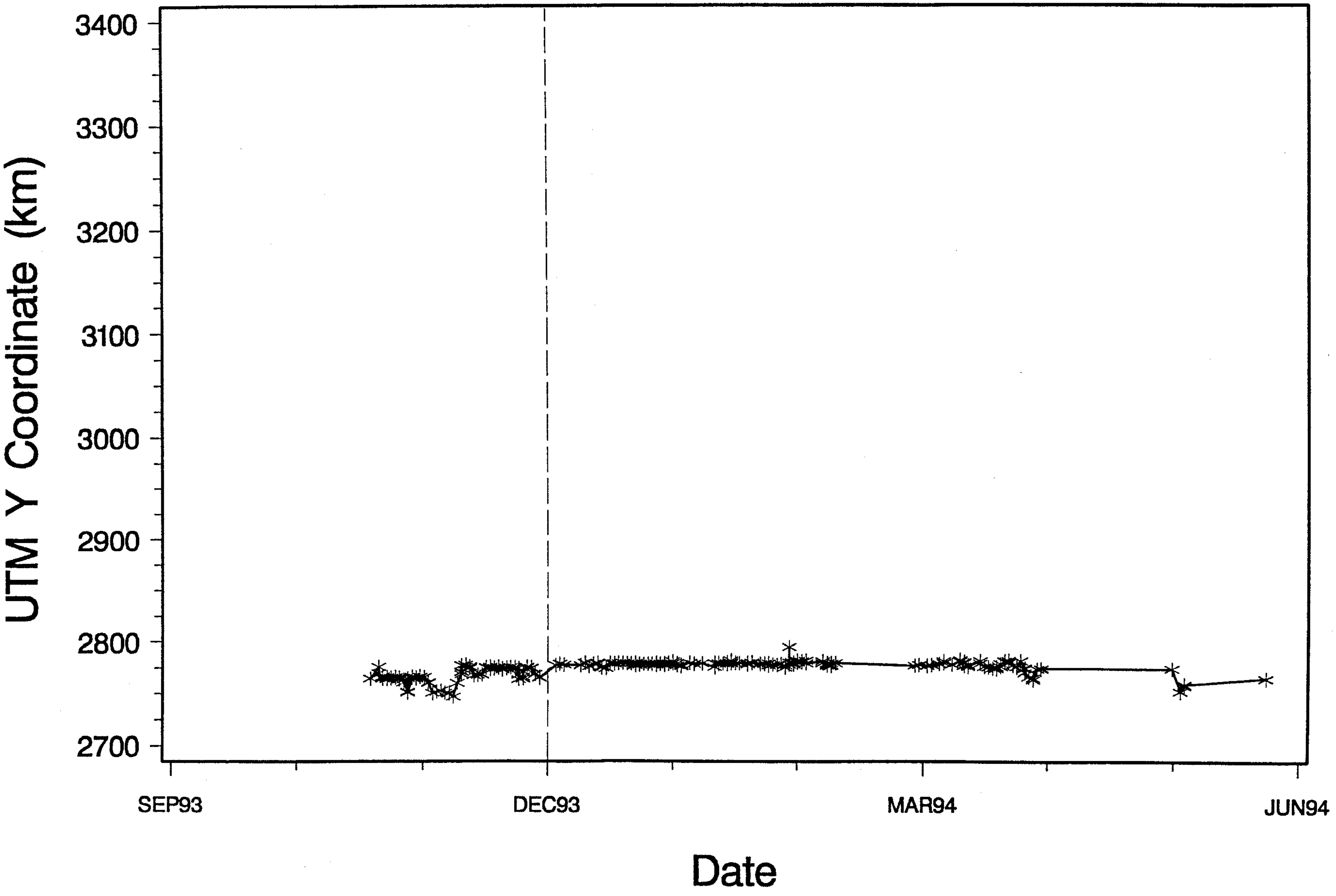
TBC – 43 ("Robbie"): 1995



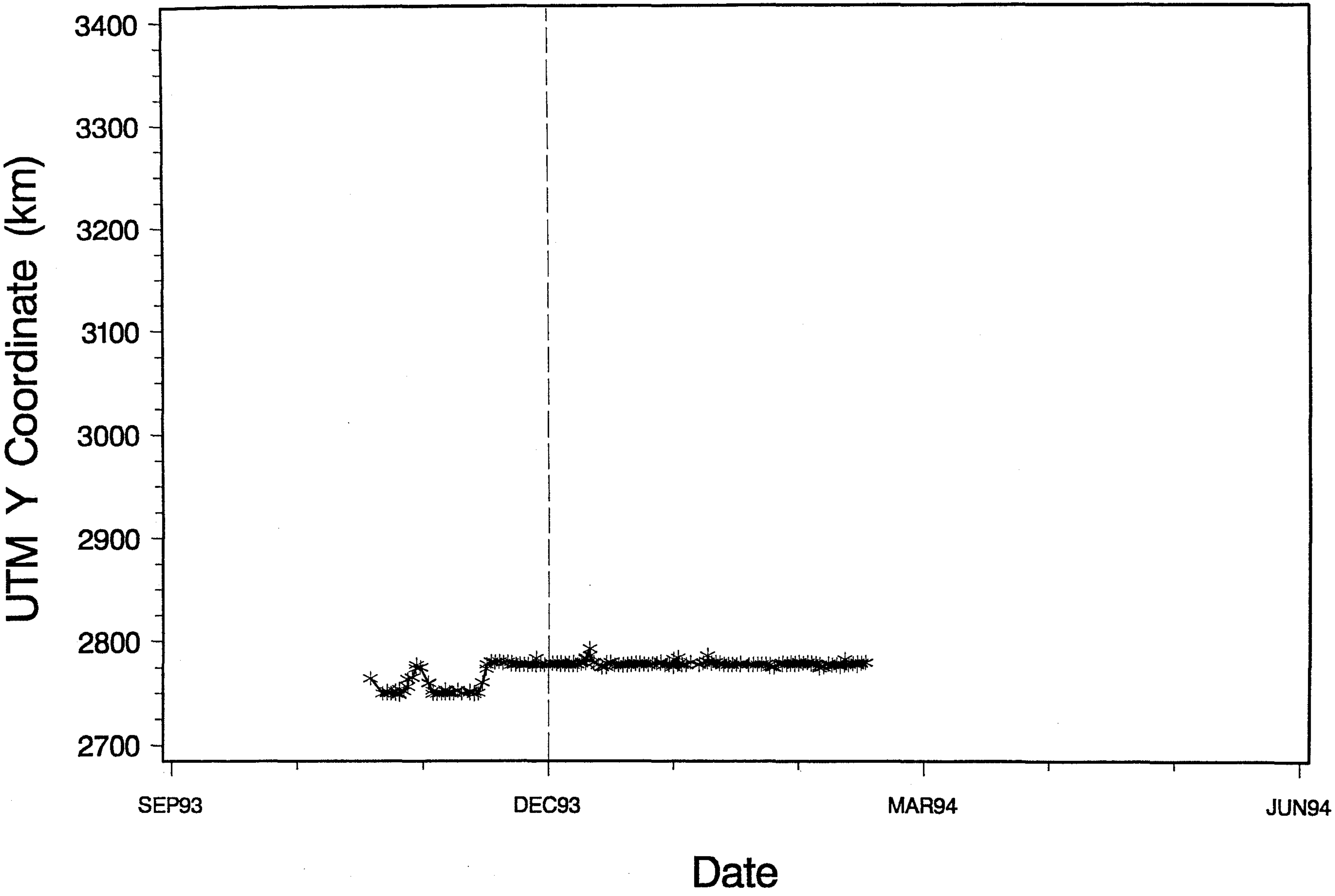
TFK – 01 ("Manny"): 1993 – 1994



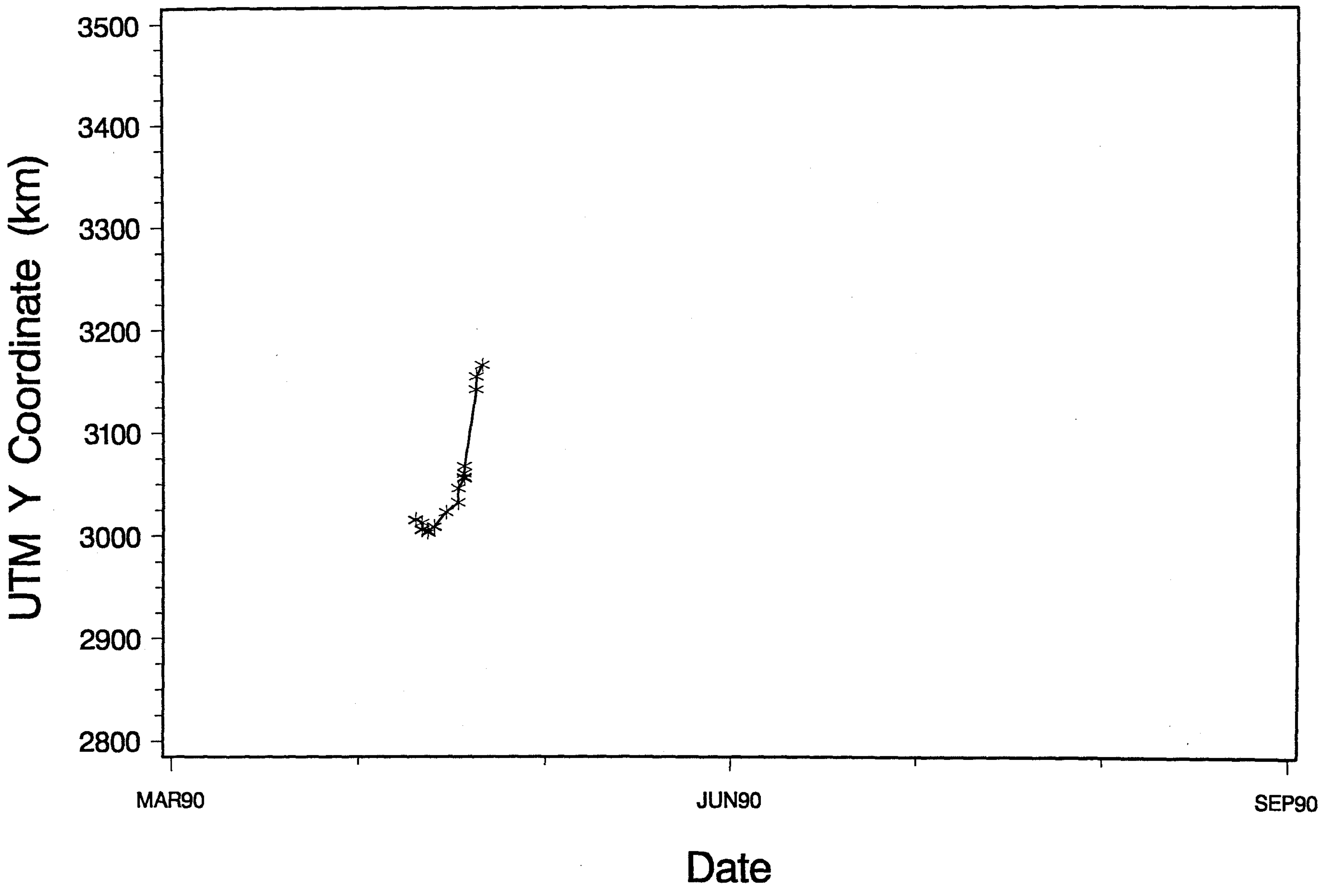
TFK-02 ("Stan"): 1993-1994



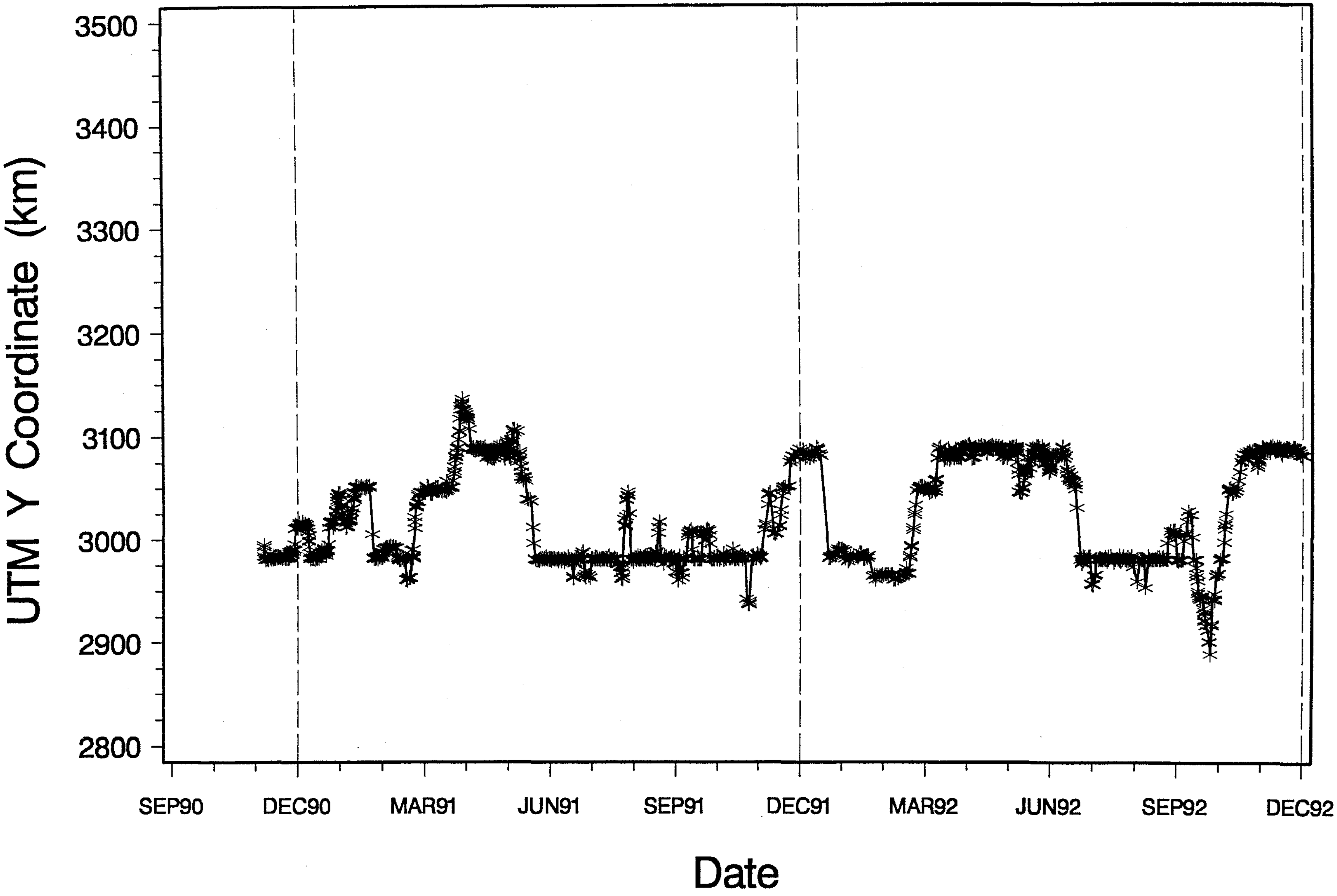
TFK-03 ("Ollie"): 1993-1994



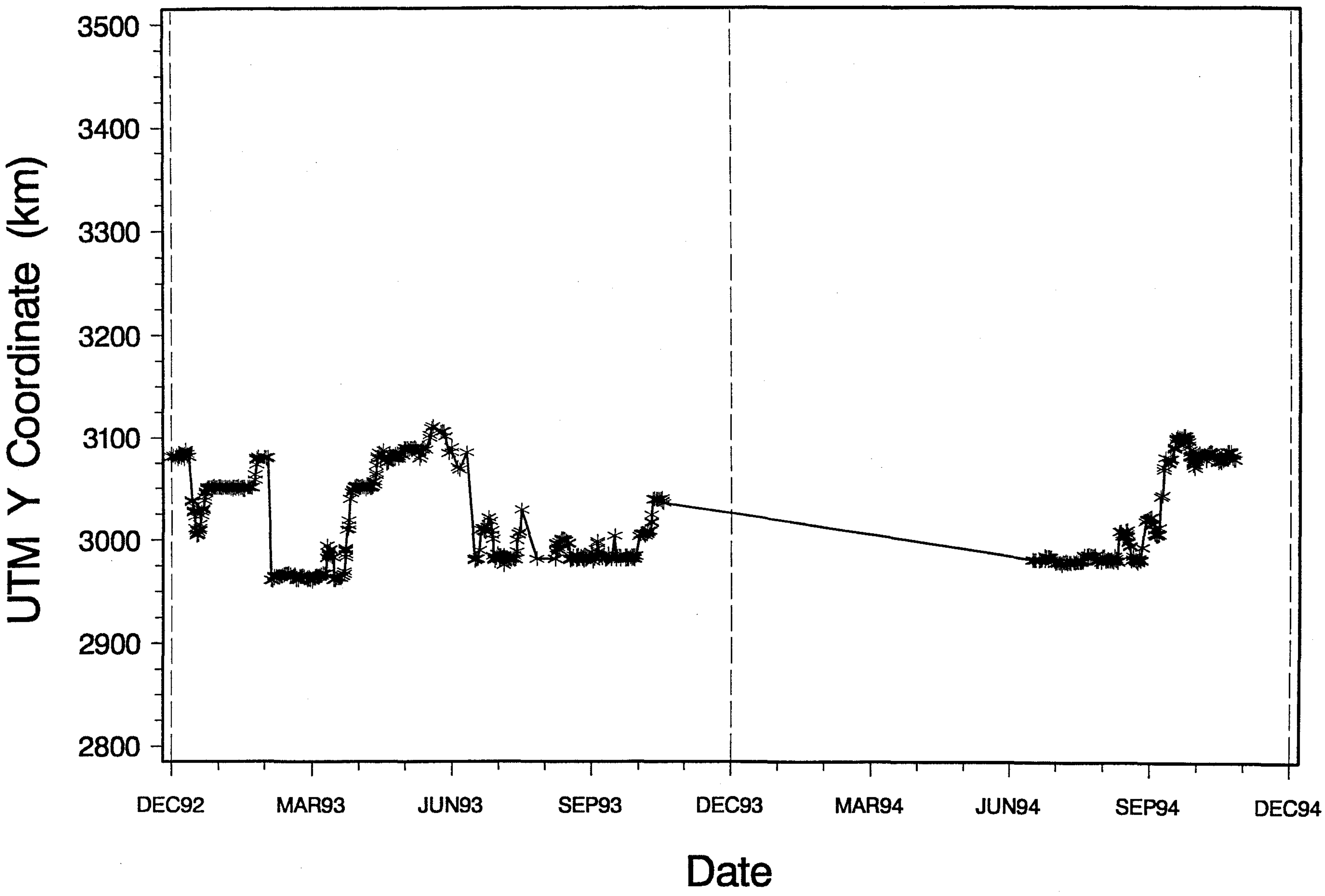
TFP – 01 ("Hutch"): 1990



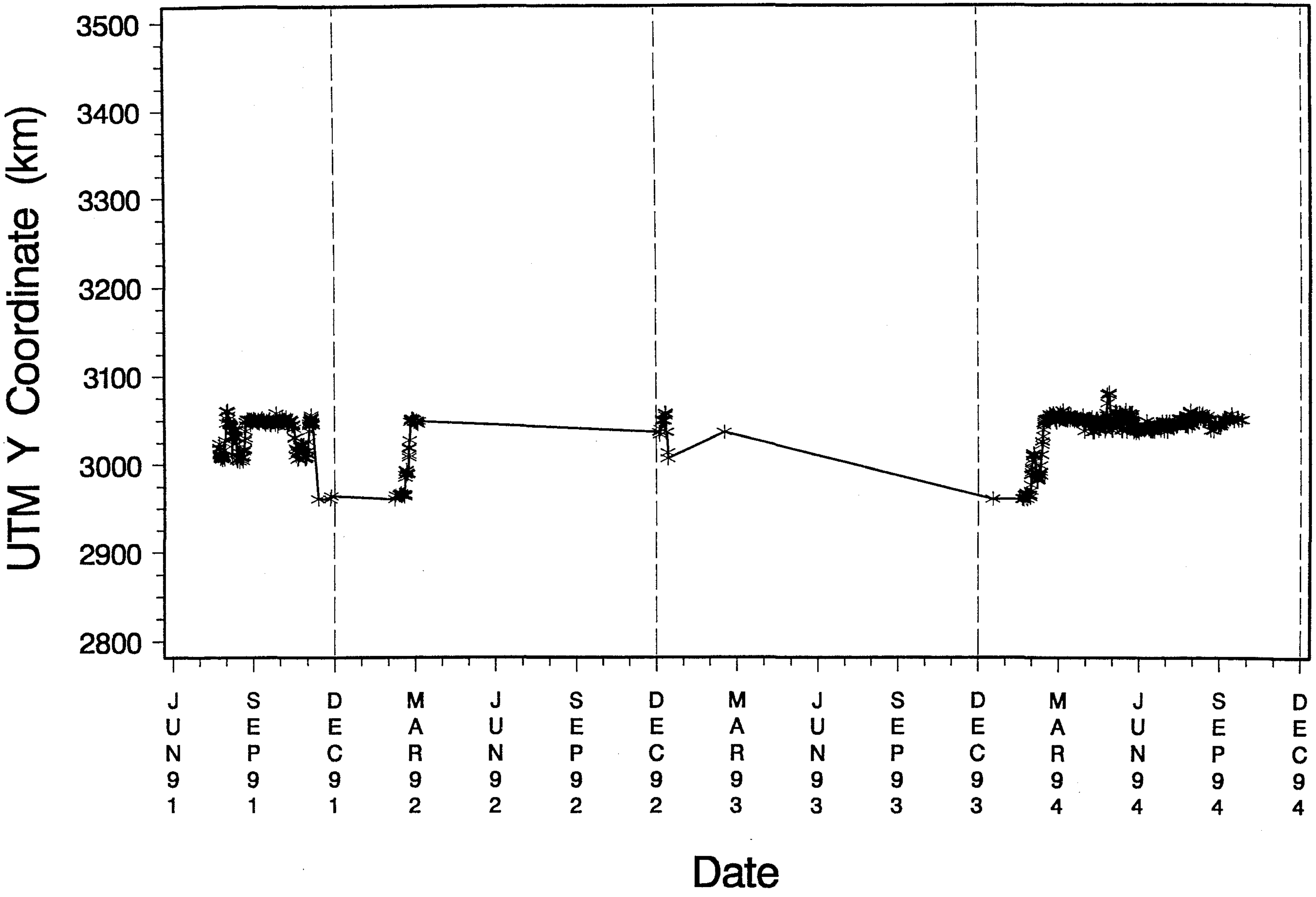
TFP – 02 ("Ross"): 1990 – 1992



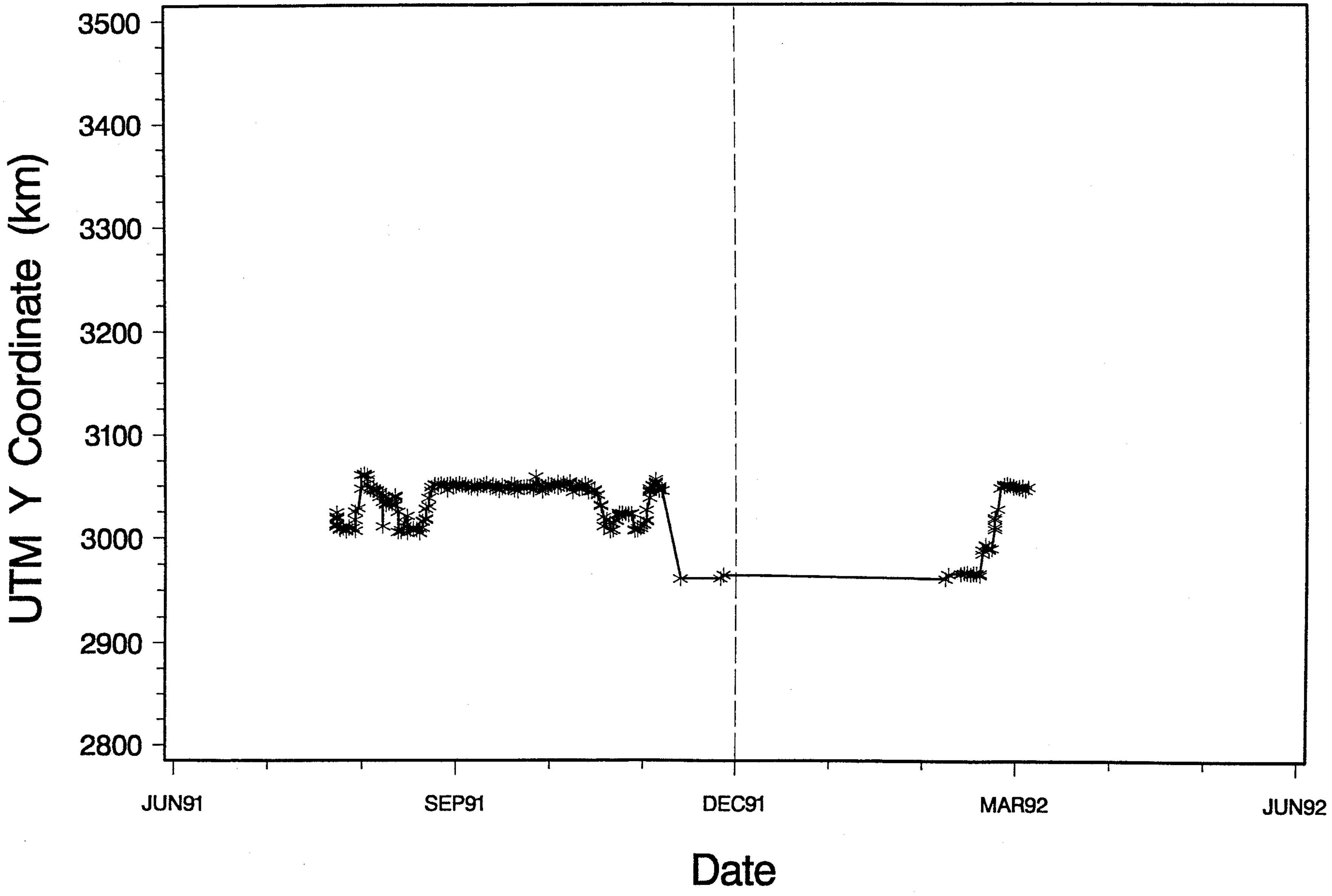
TFP – 02 ("Ross"): 1992 – 1994



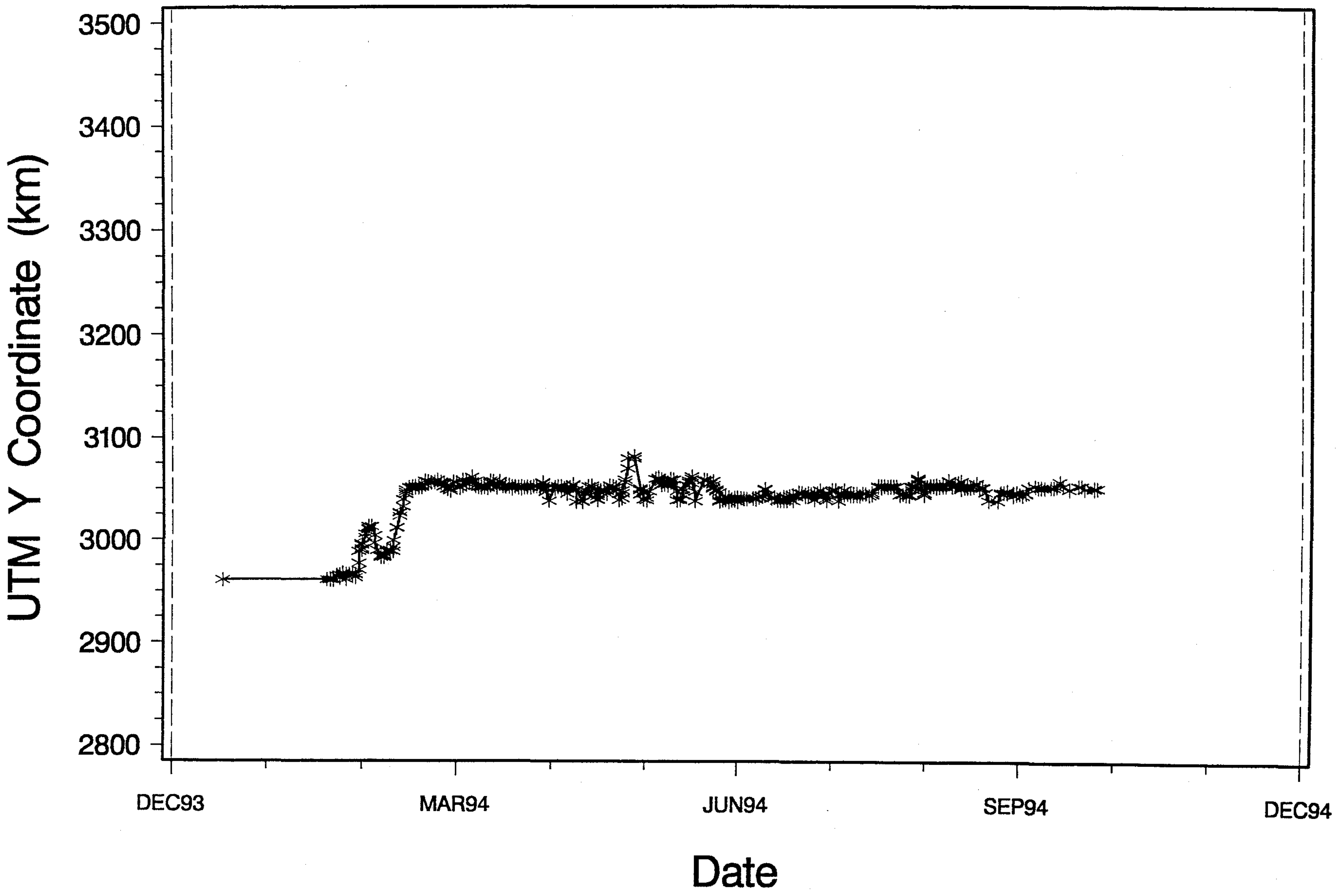
TFP – 03 ("Natalie"): 1991 – 1994



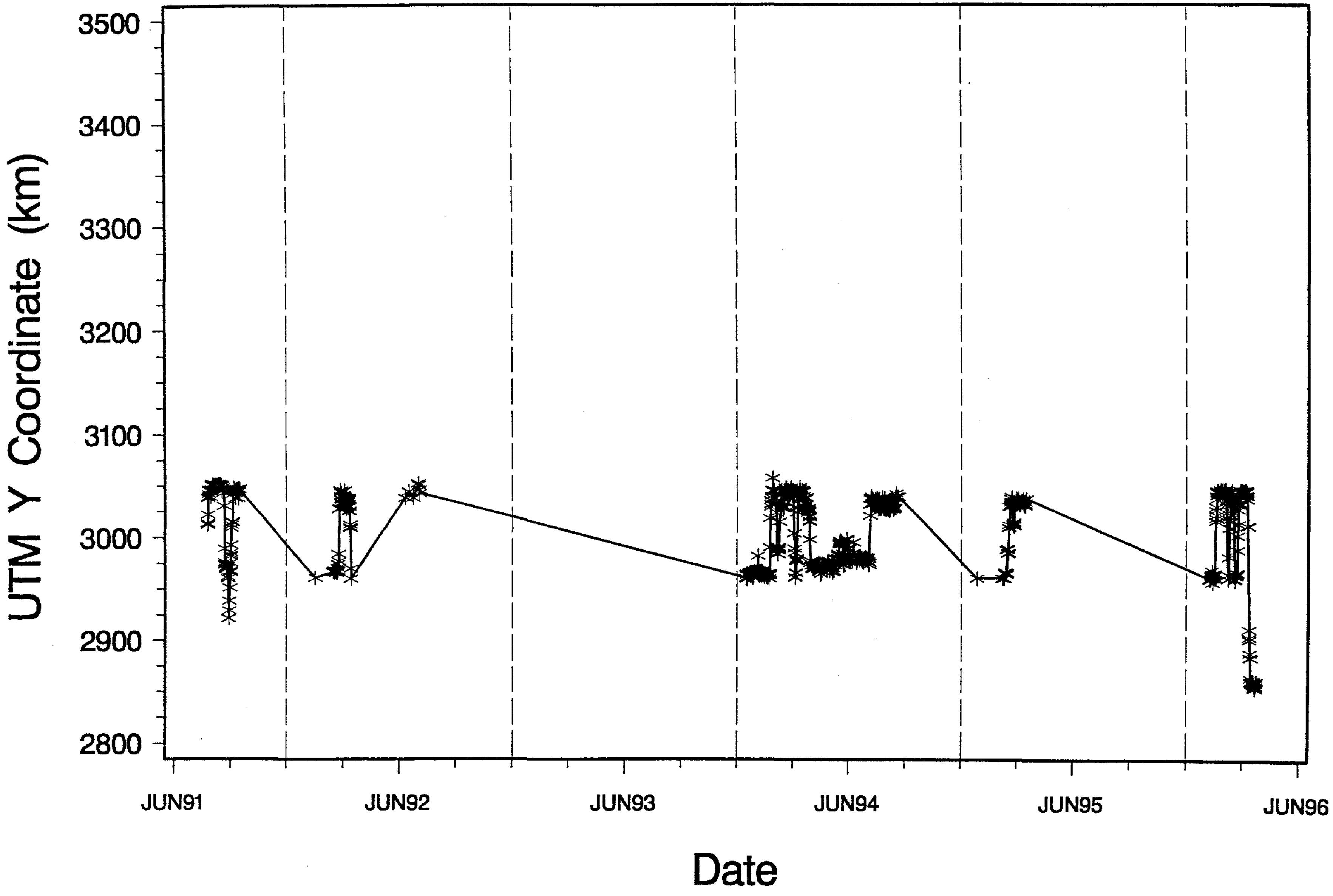
TFP – 03 ("Natalie"): 1991 – 1992



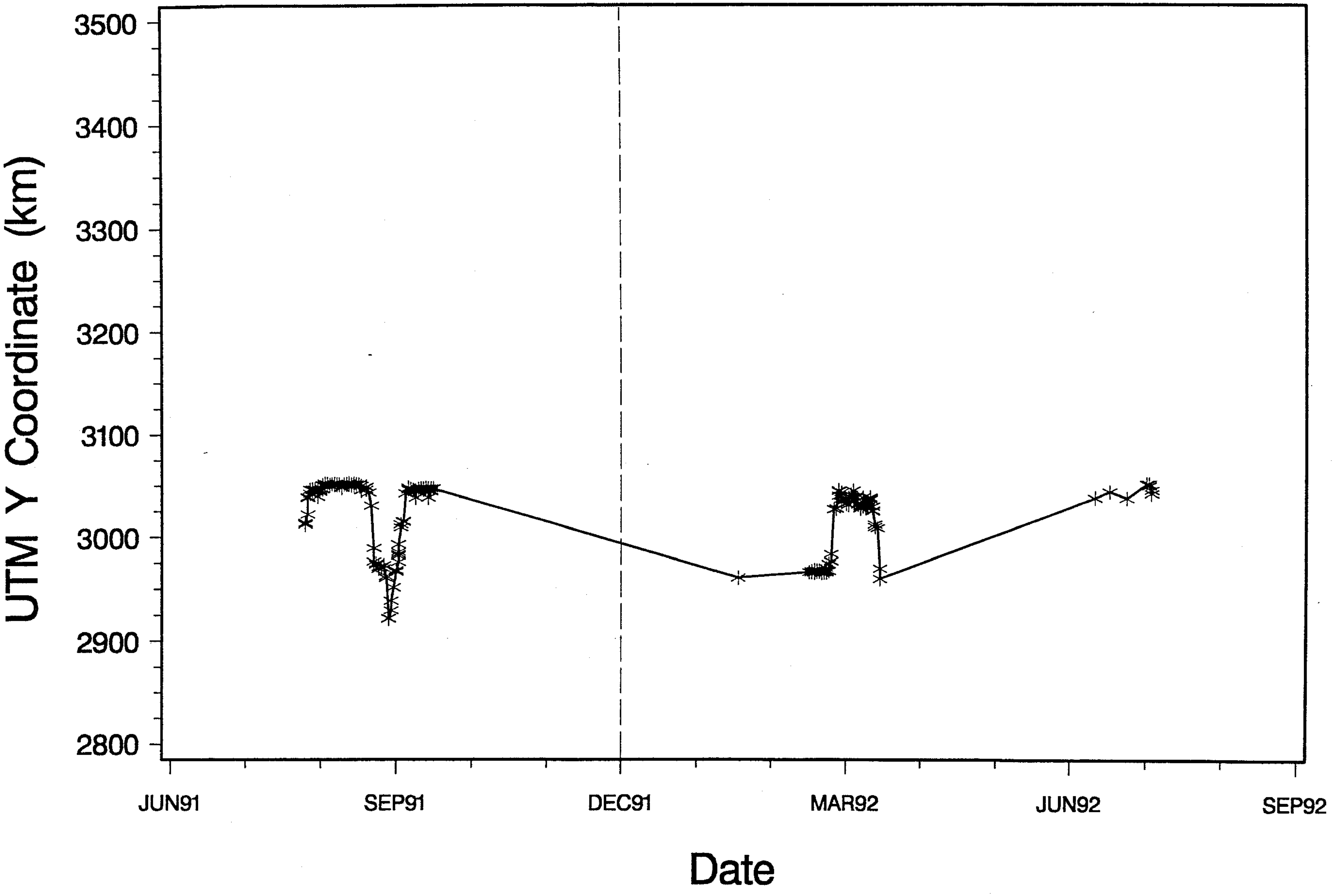
TFP – 03 ("Natalie"): 1993 – 1994



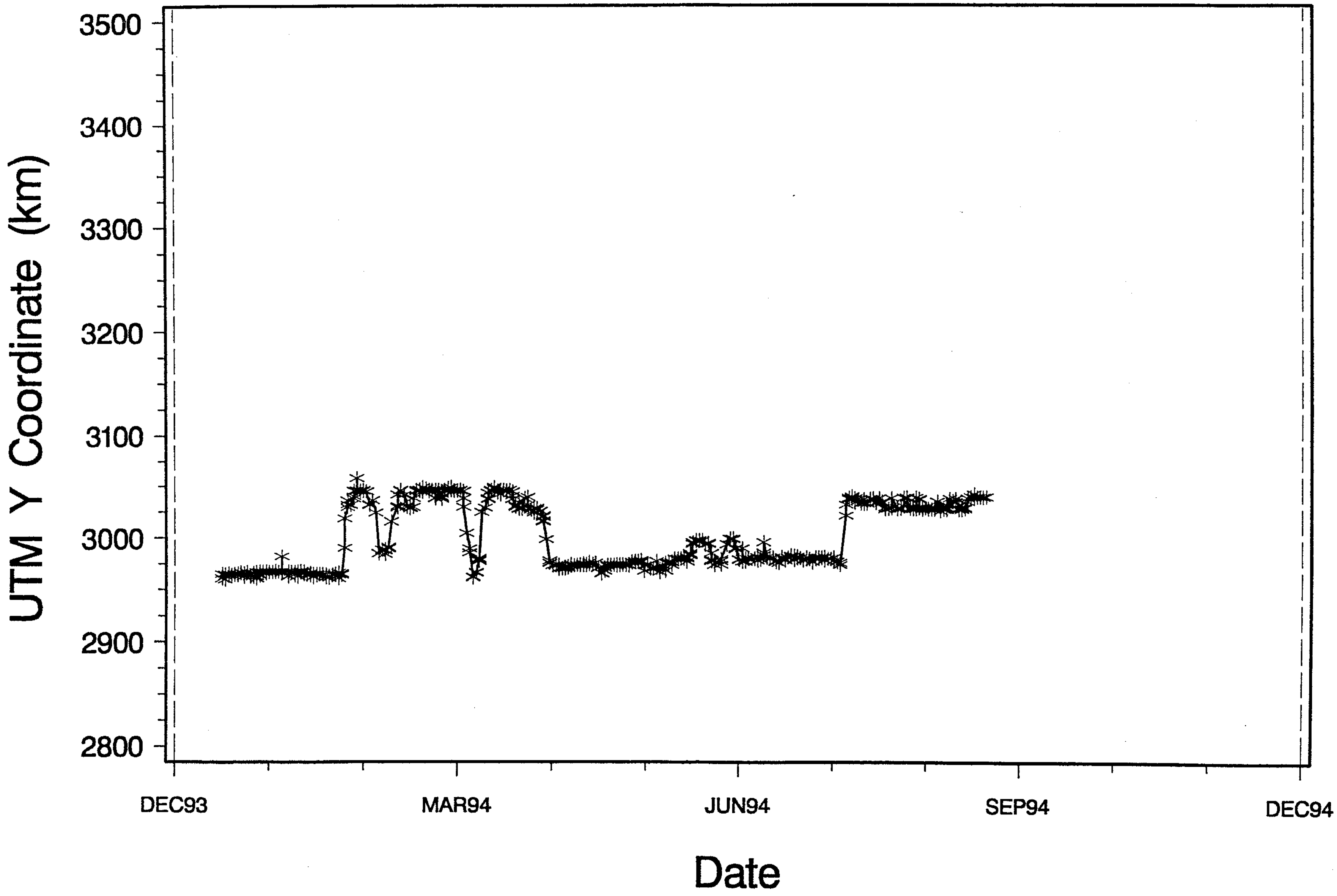
TFP – 04 ("Sophia"): 1991 – 1996



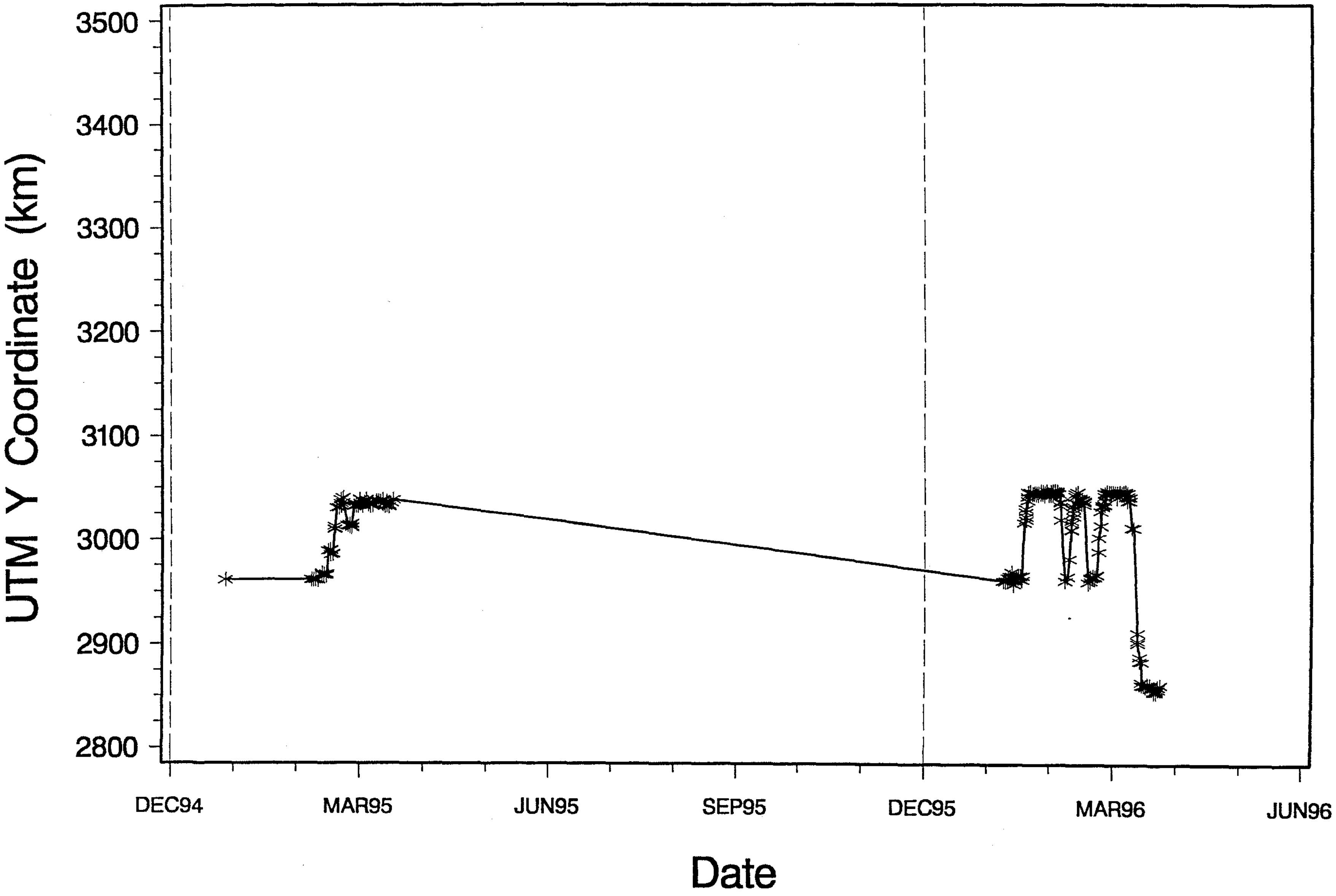
TFP – 04 ("Sophia"): 1991 – 1992



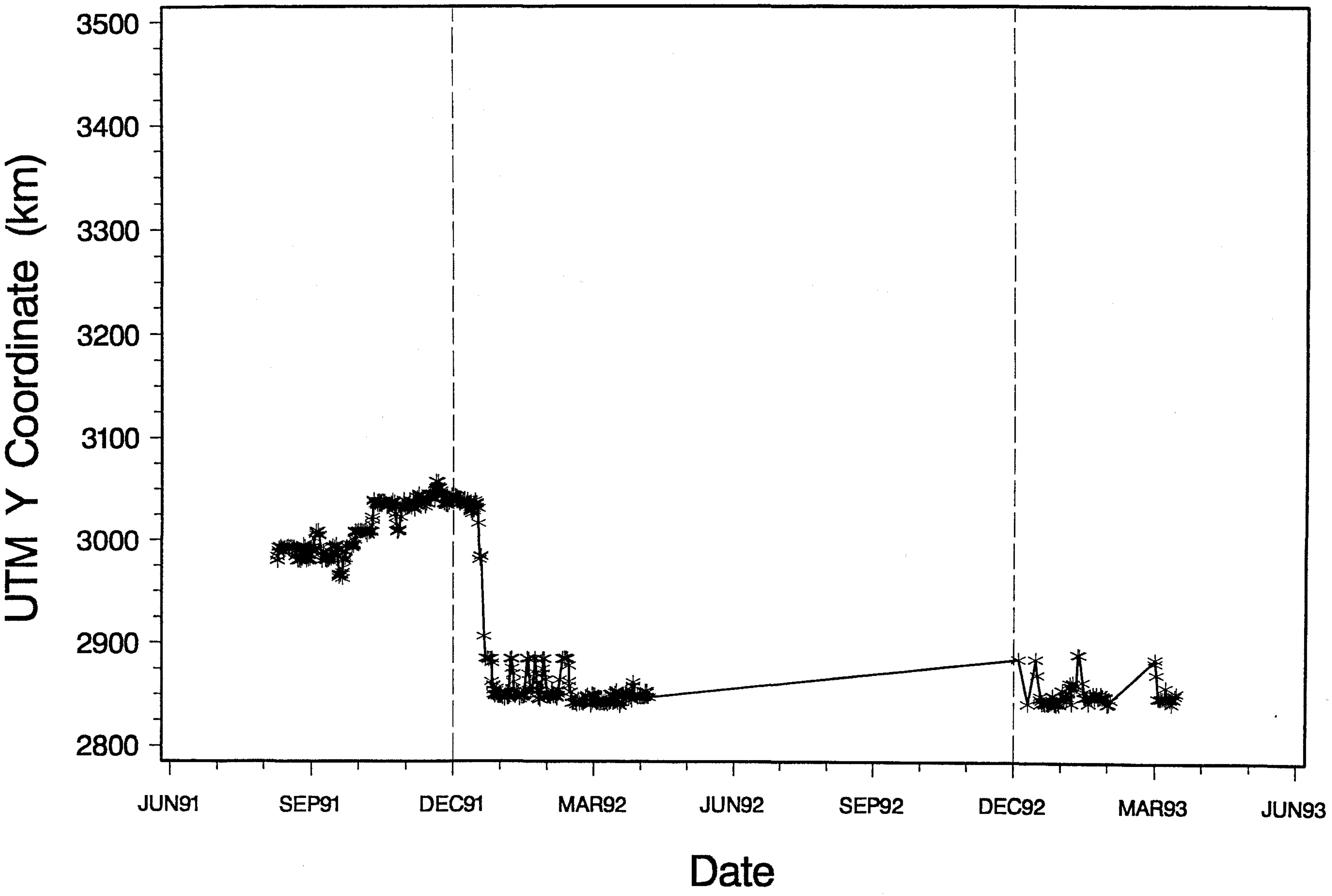
TFP – 04 ("Sophia"): 1993 – 1994



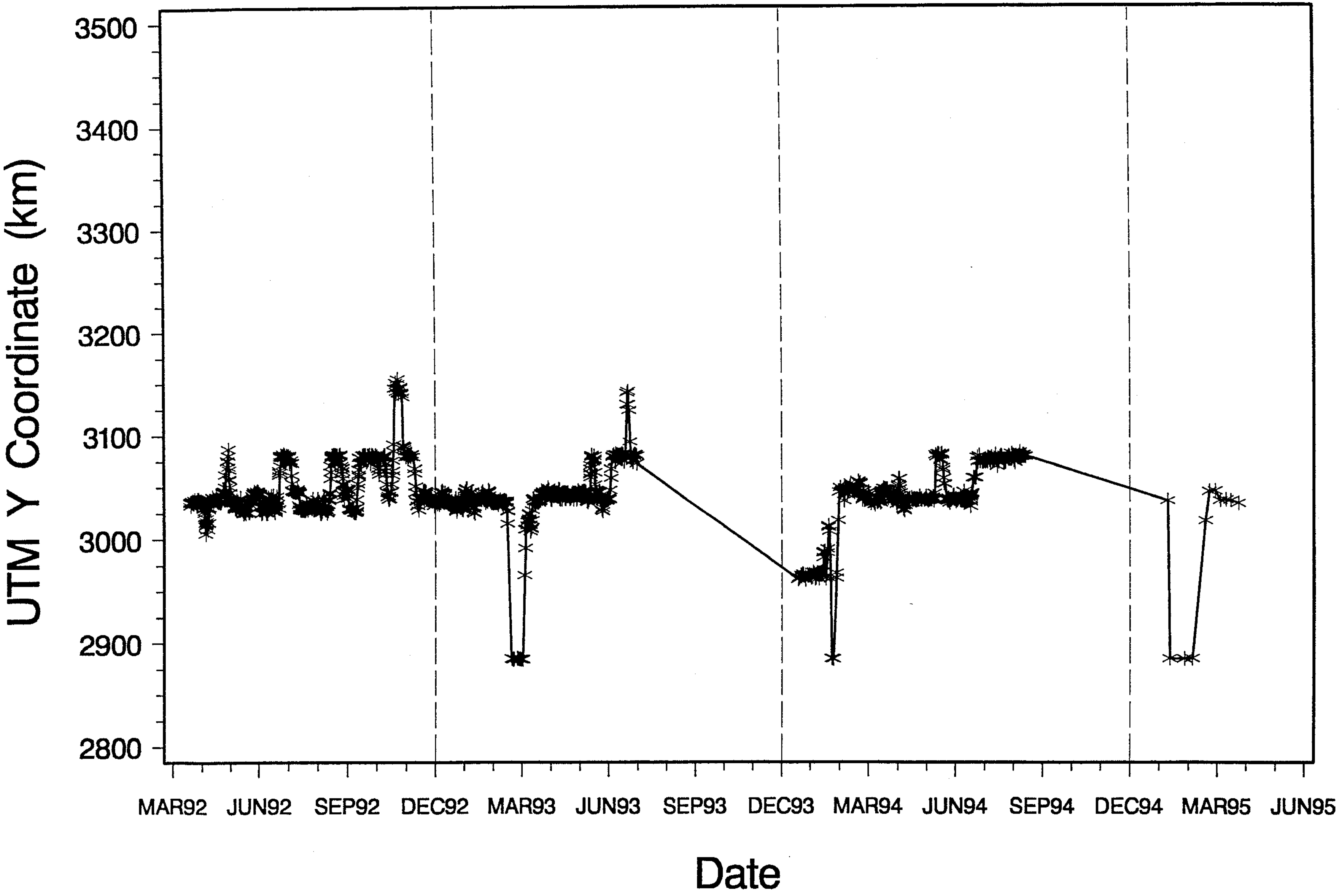
TFP – 04 ("Sophia"): 1994 – 1996



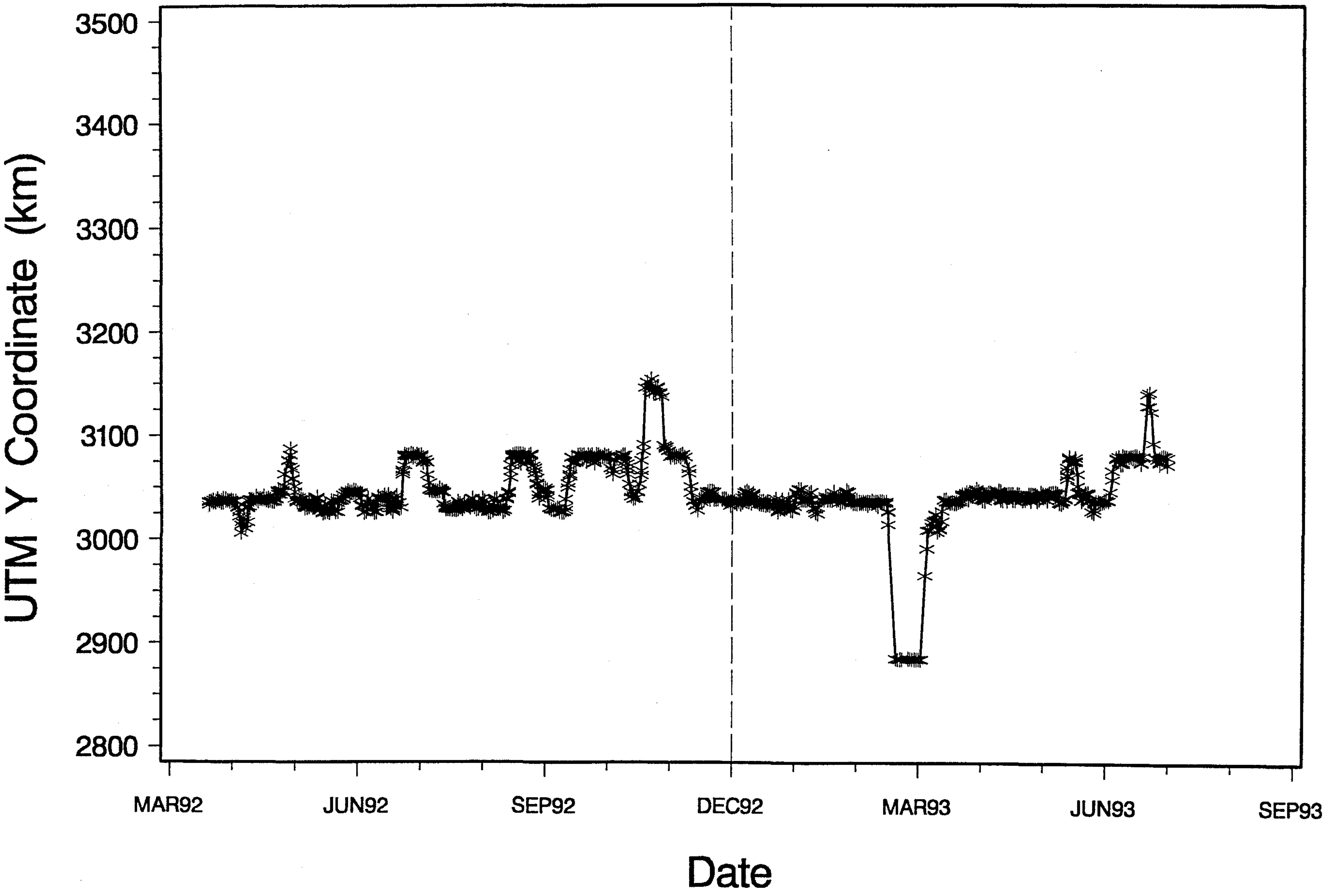
TFP – 05 ("Lani"): 1991 – 1993



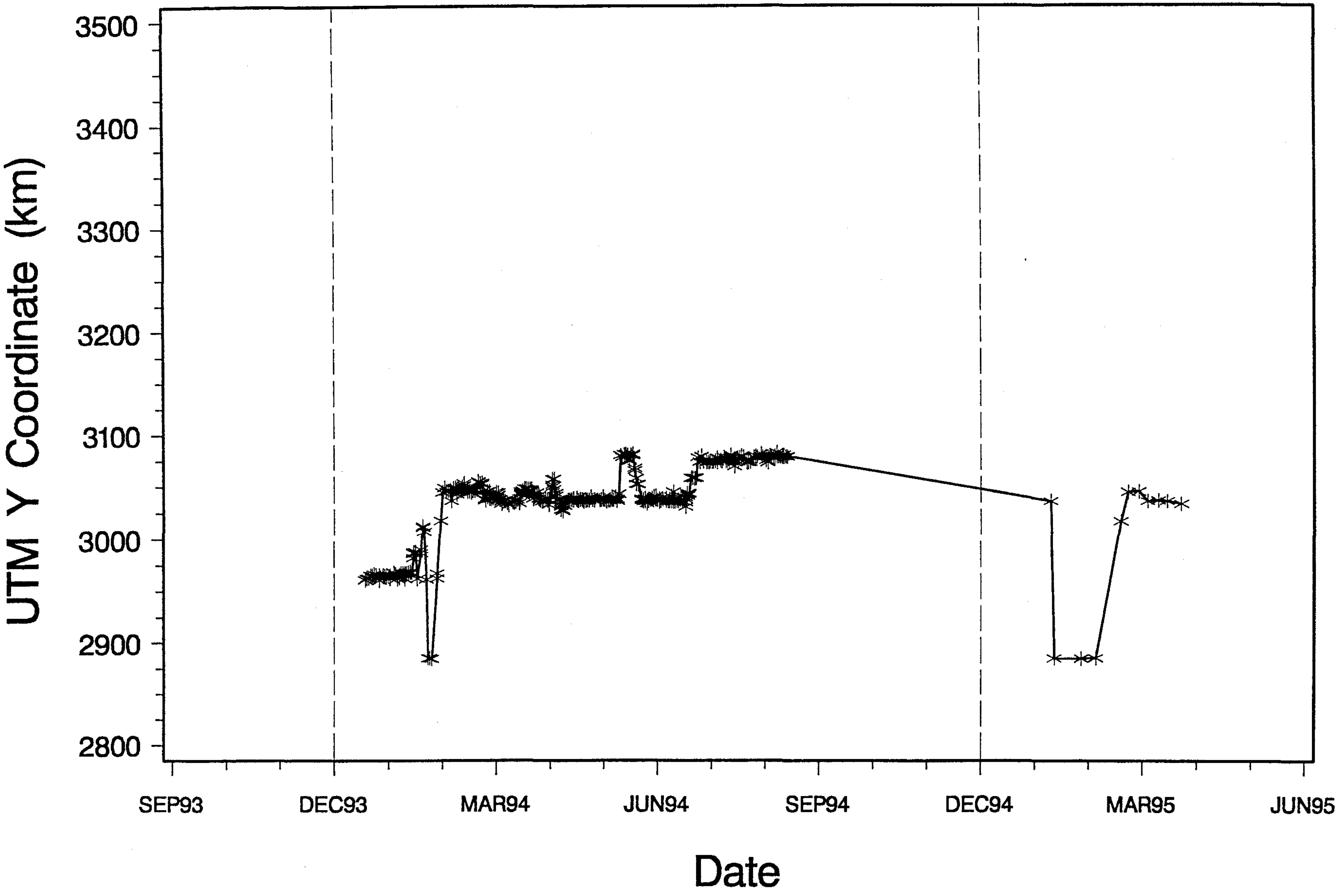
TFP – 06 ("Vanna"): 1992 – 1995



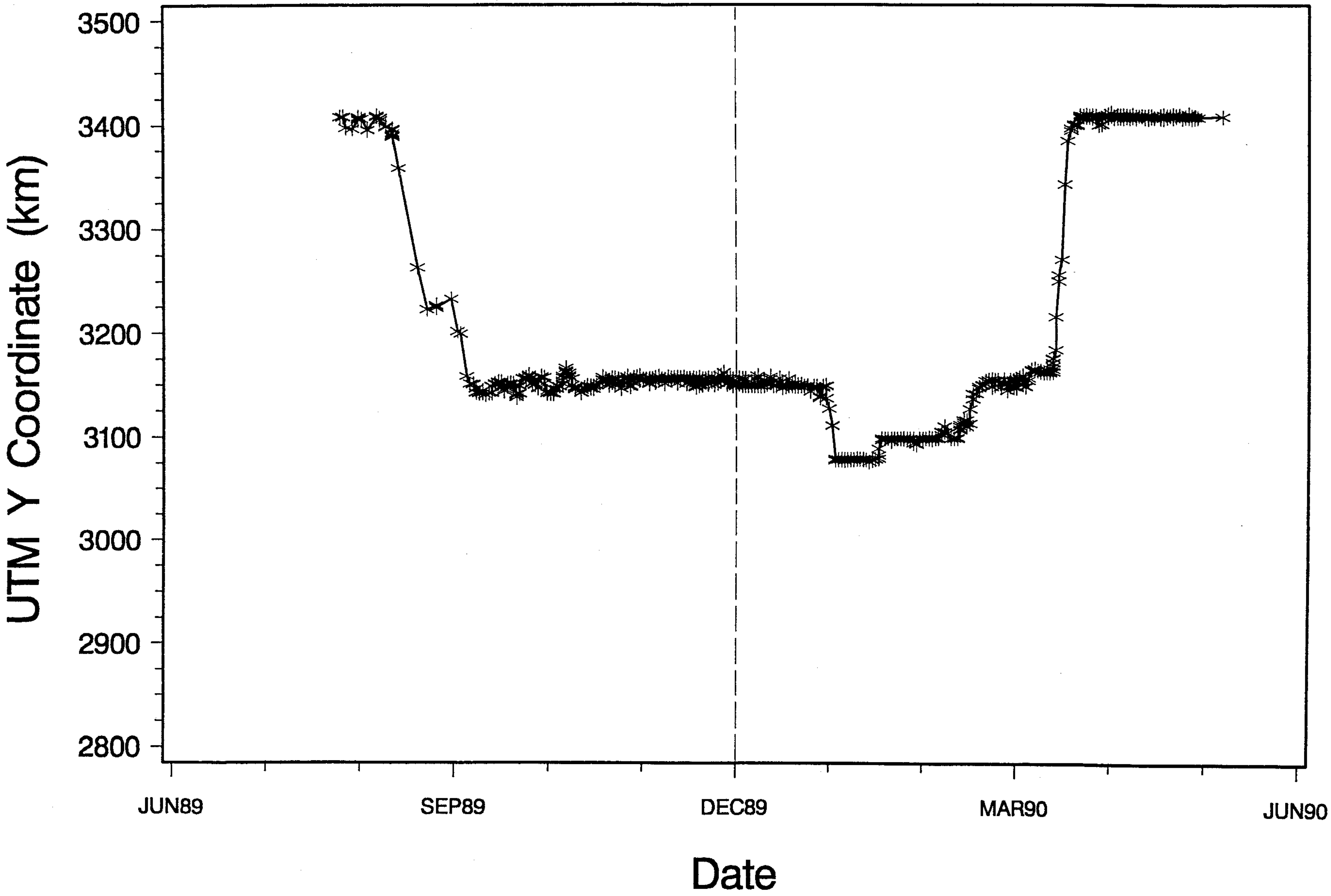
TFP – 06 ("Vanna"): 1992 – 1993



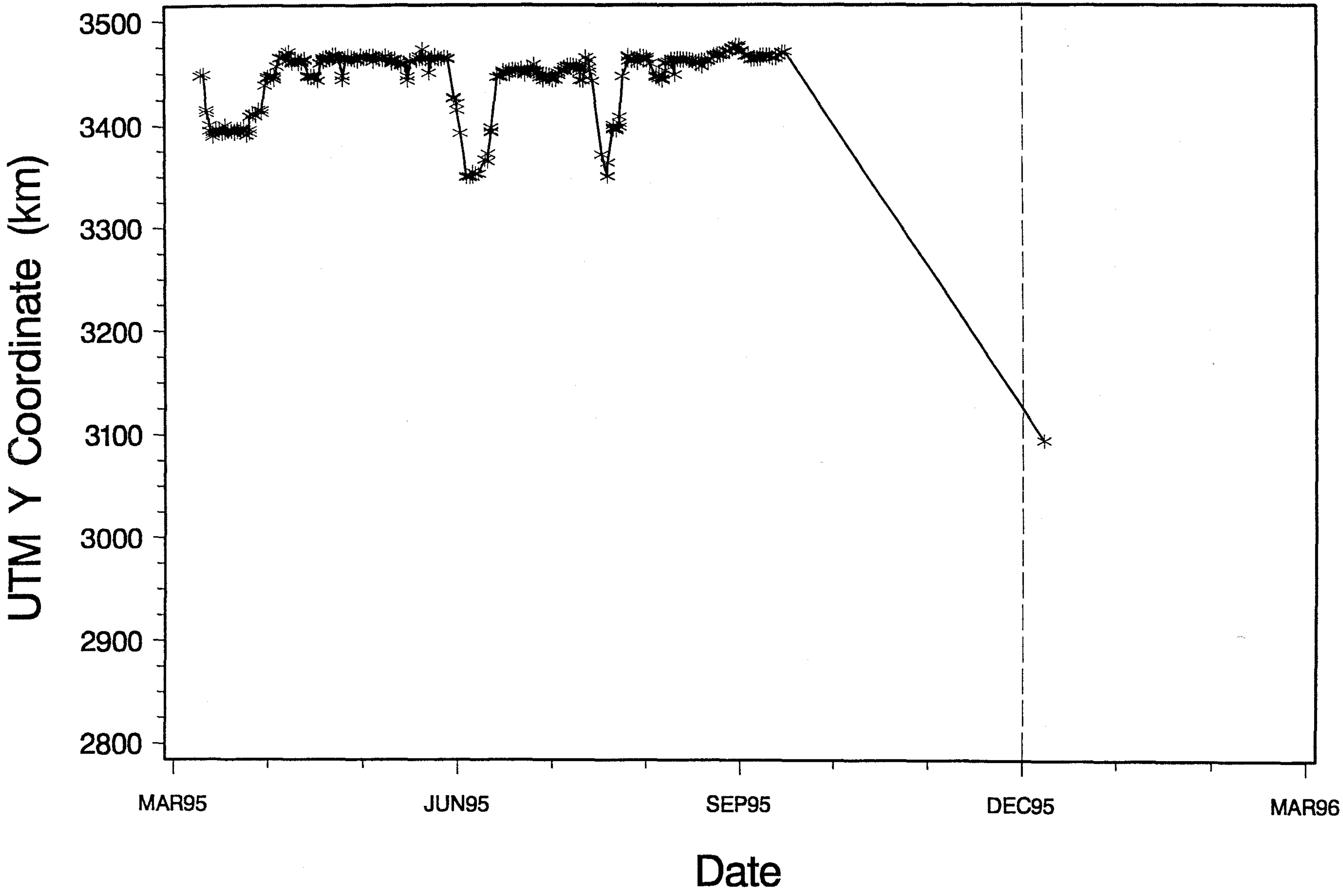
TFP – 06 ("Vanna"): 1993 – 1995



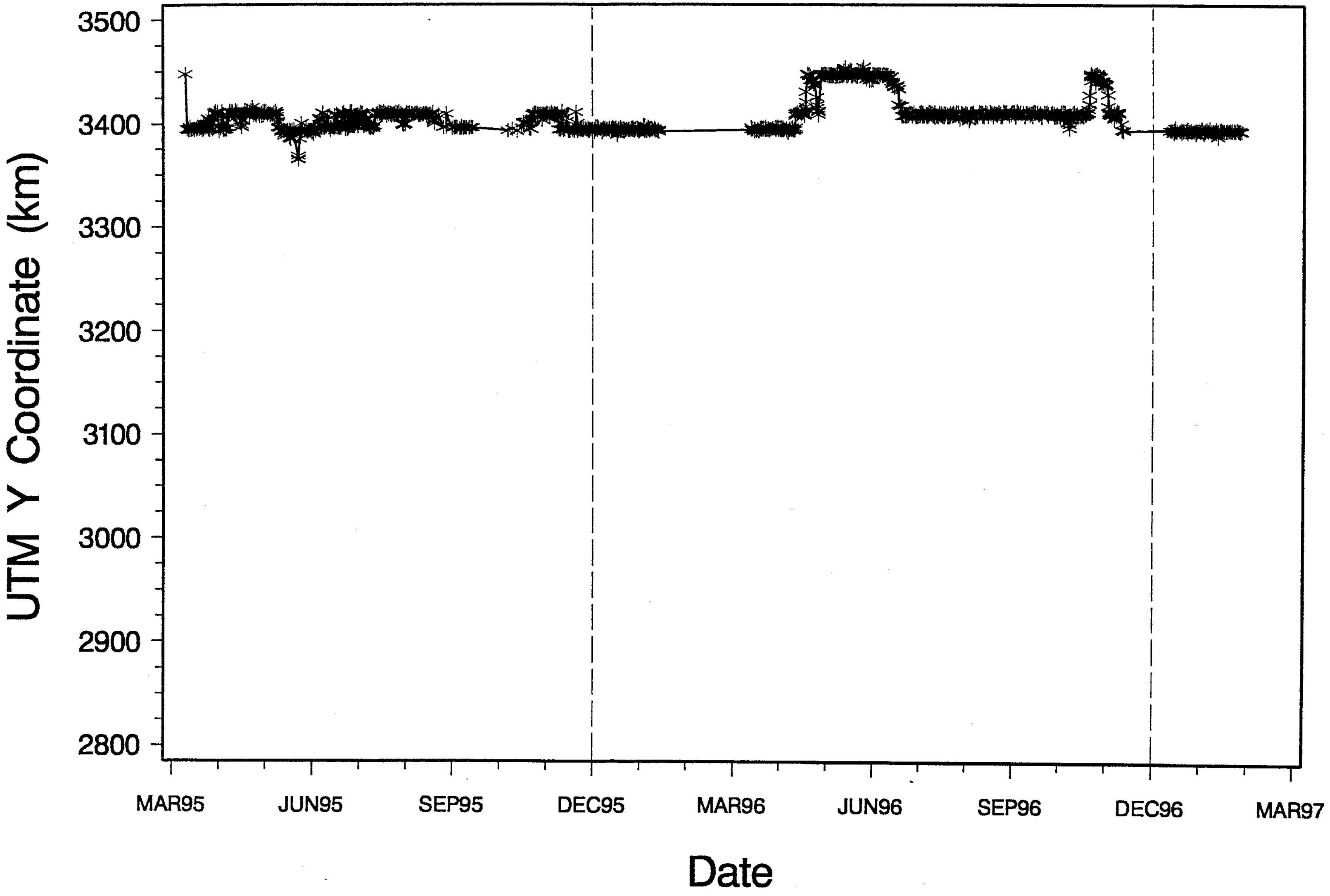
TGA – 01 ("Mary"): 1989 – 1990



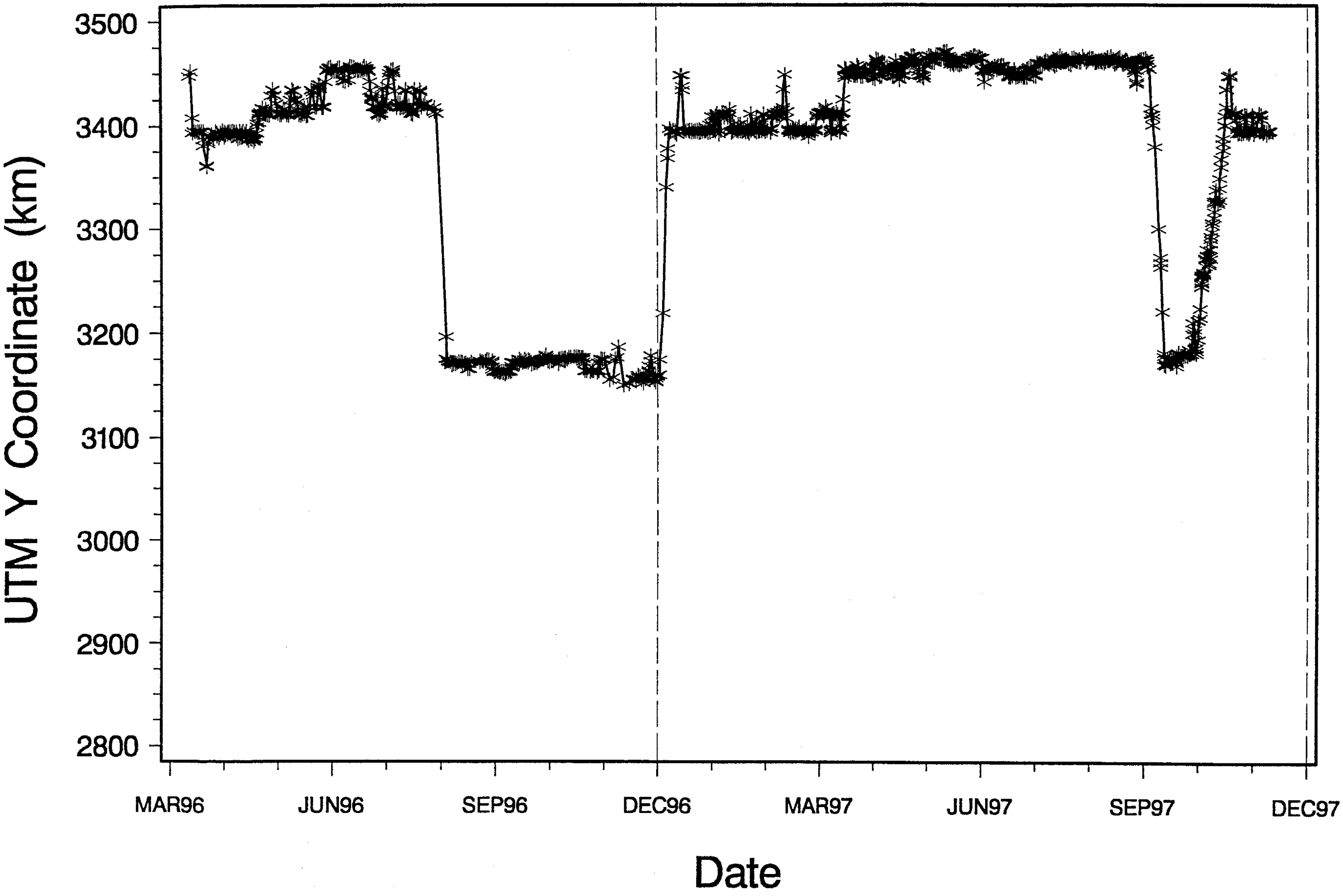
TGA – 02 ("Tory"): 1995



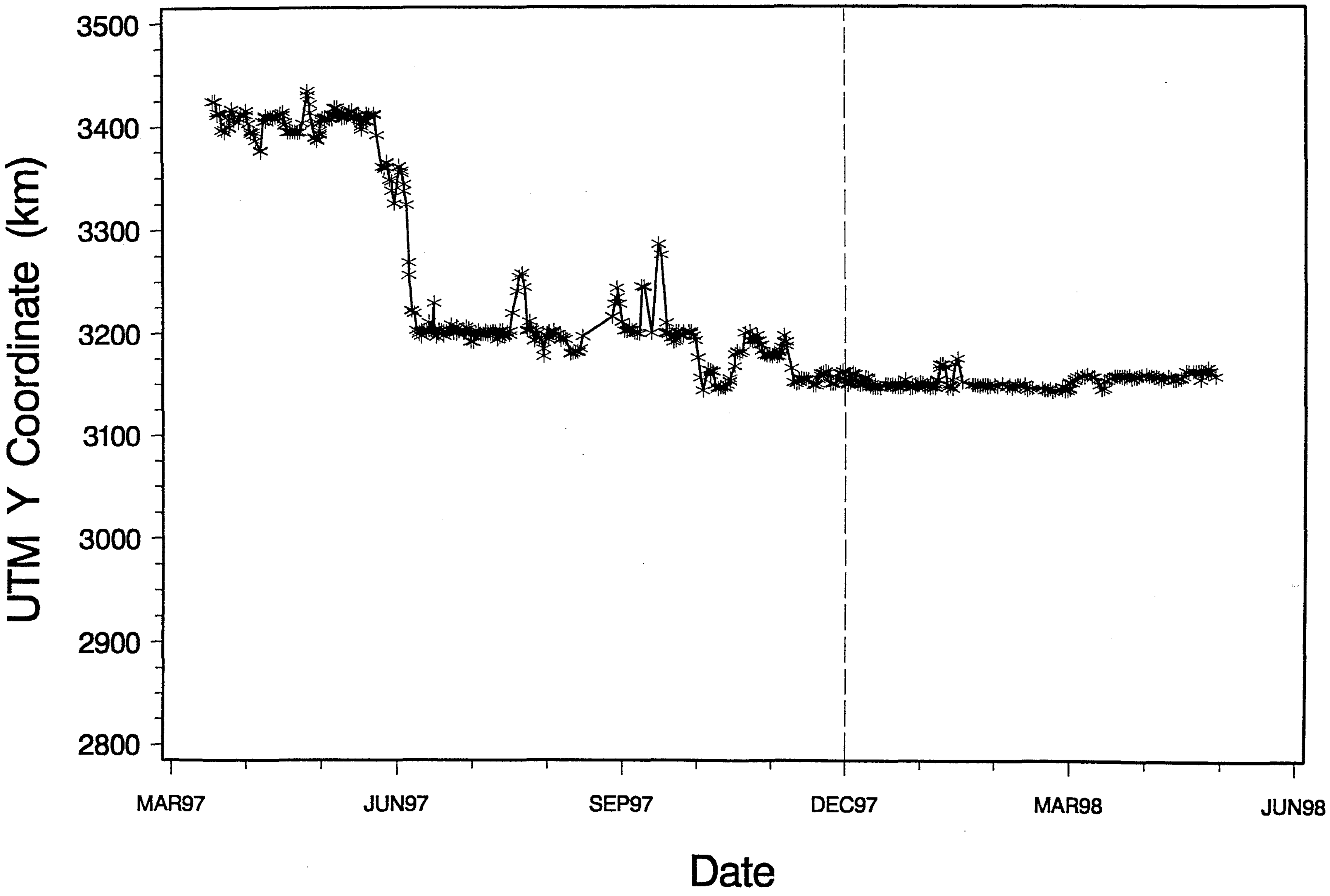
TGA – 03 ("Marmontel"): 1995 – 1997



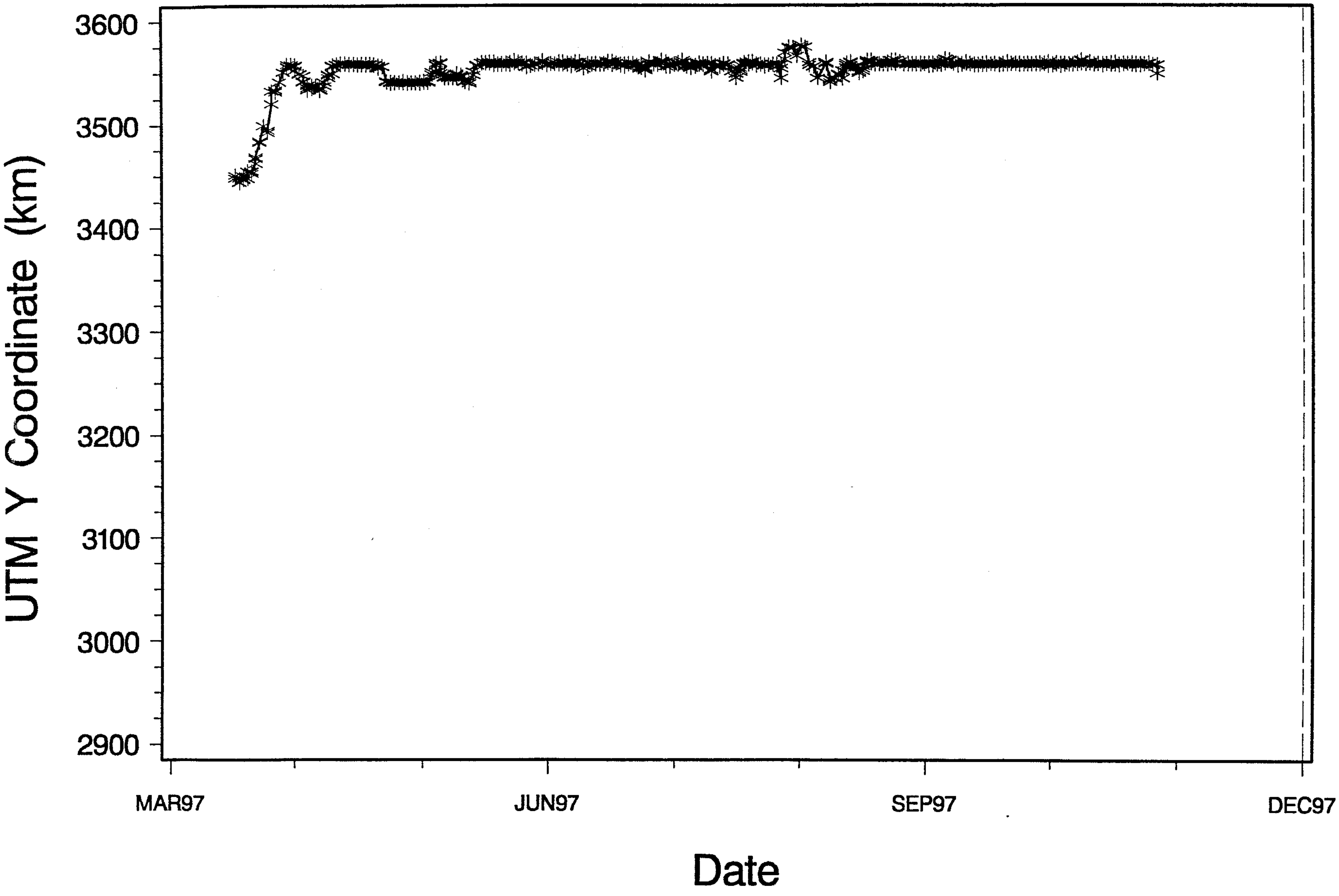
TGA – 04 ("Mercury"): 1996 – 1997



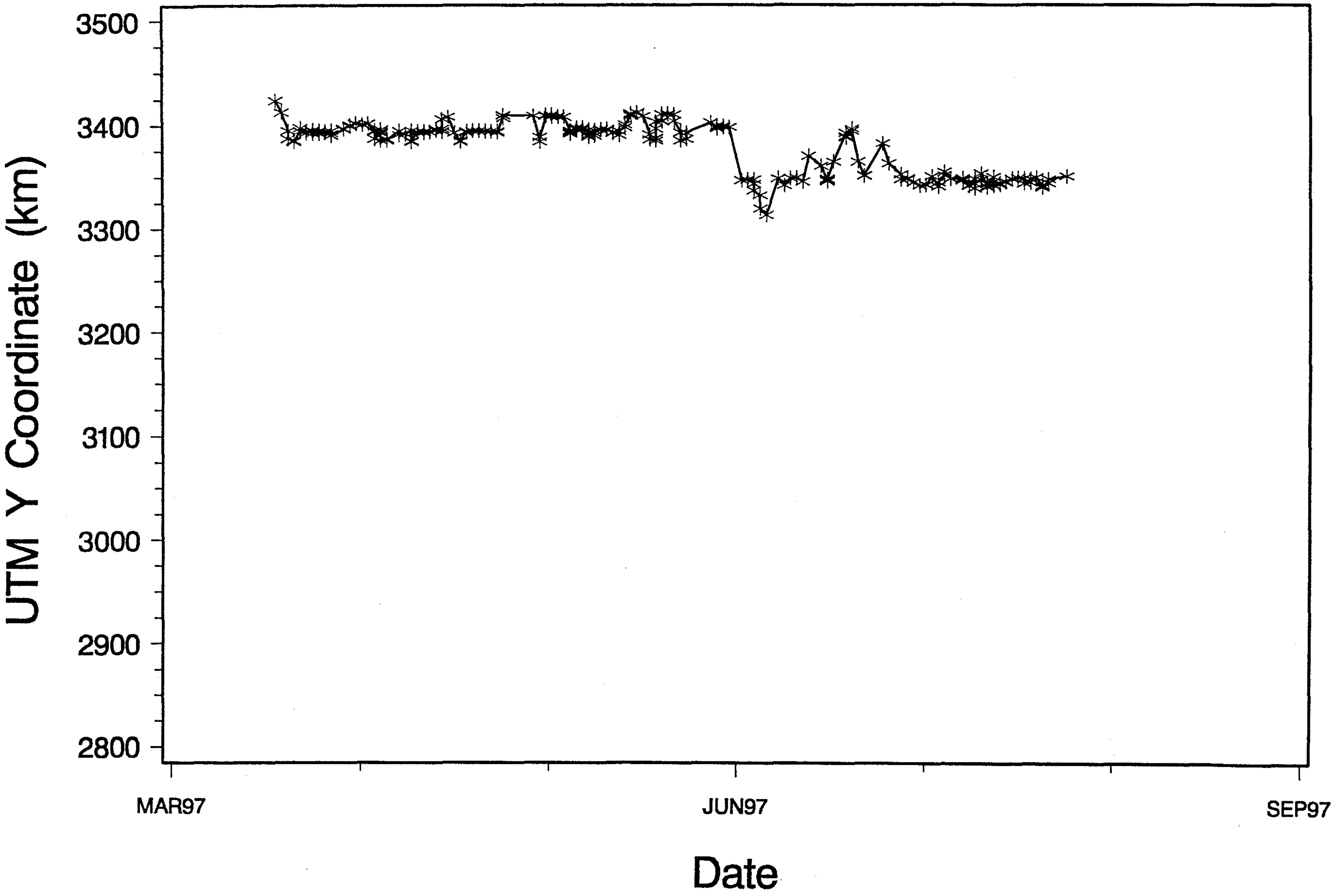
TGA – 05 ("Bailey"): 1997 – 1998



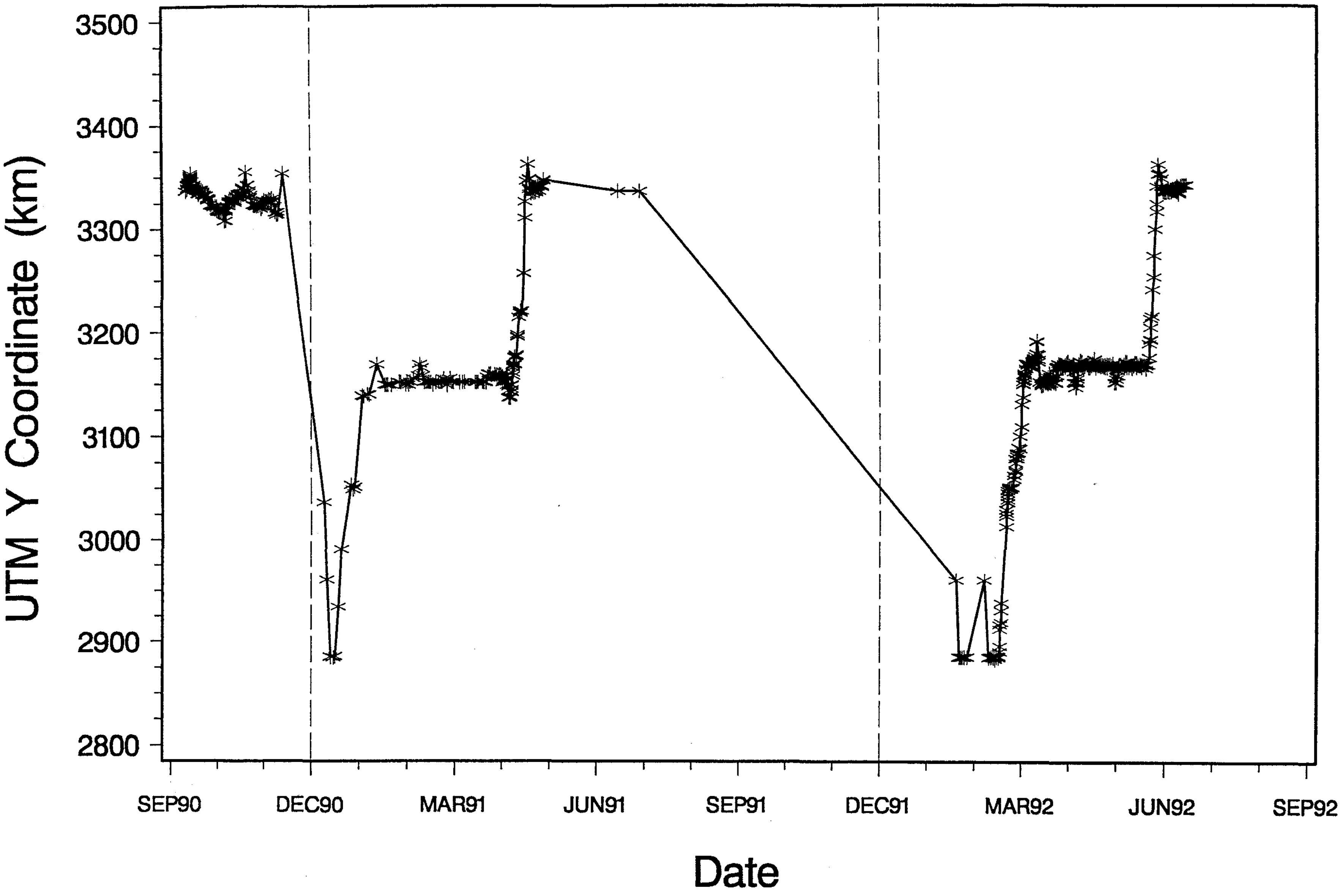
TGA – 06 ("Savannah"): 1997



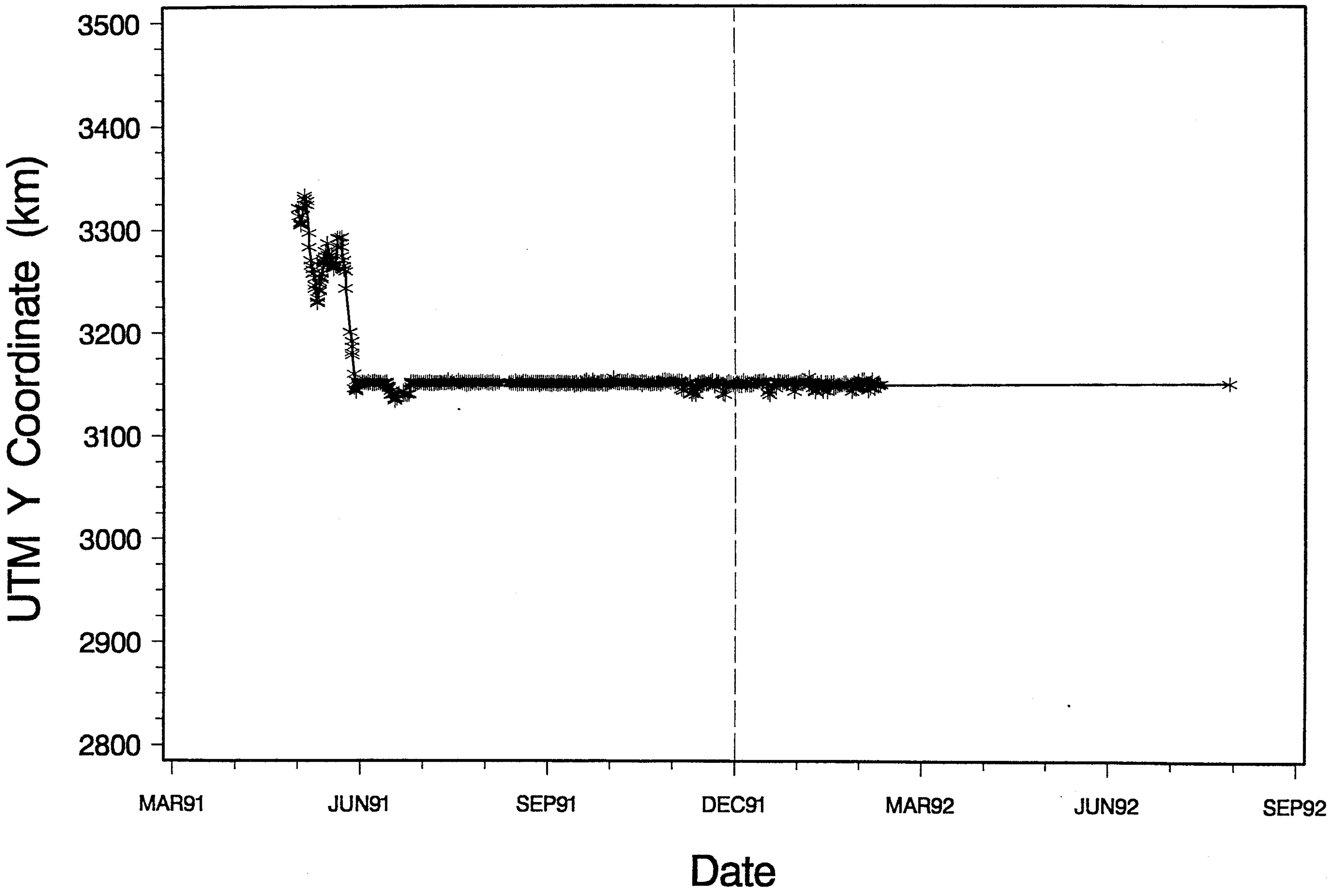
TGA – 07 ("GP"): 1997



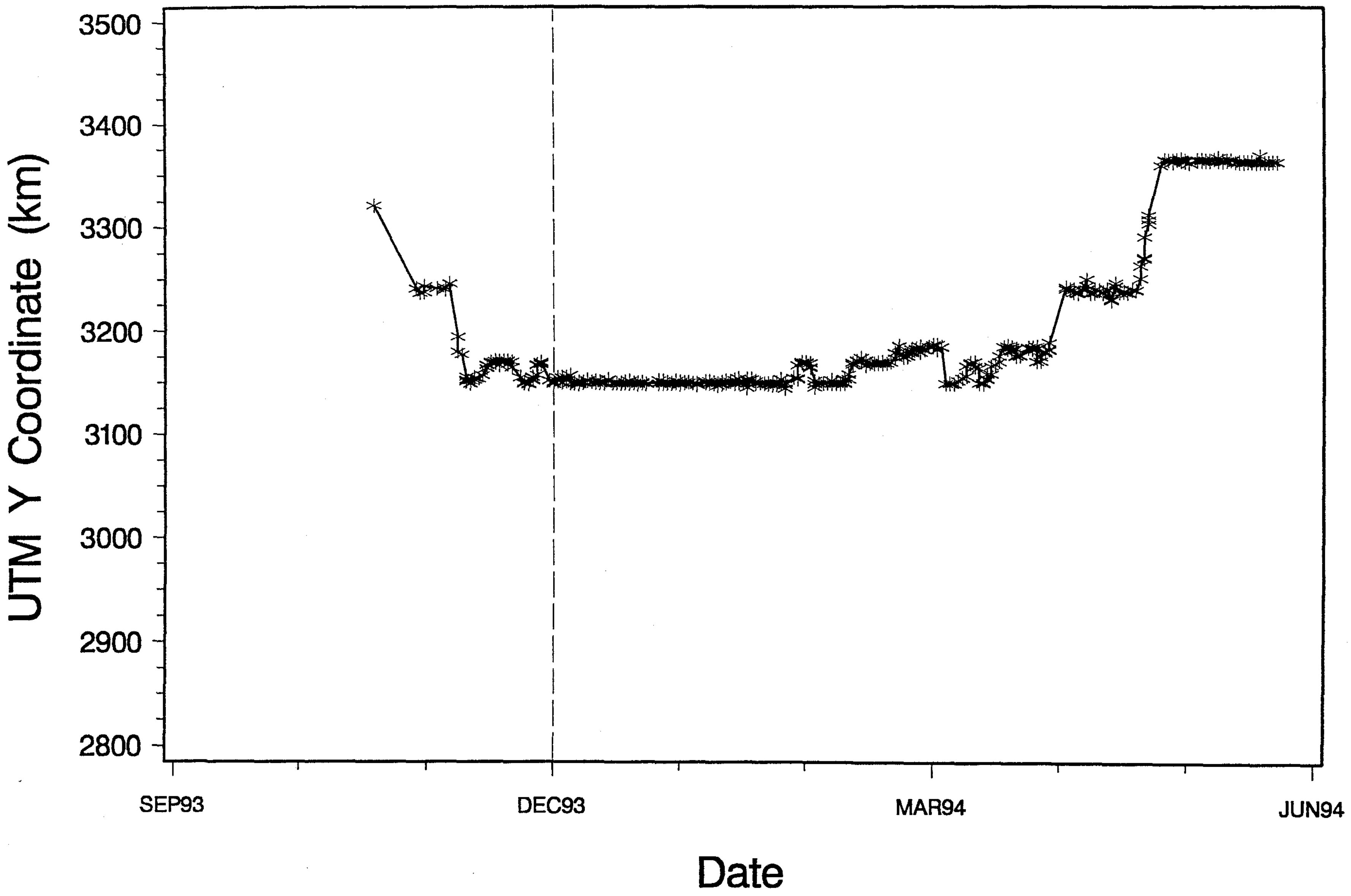
TJX – 01 ("Connie"): 1990 – 1992



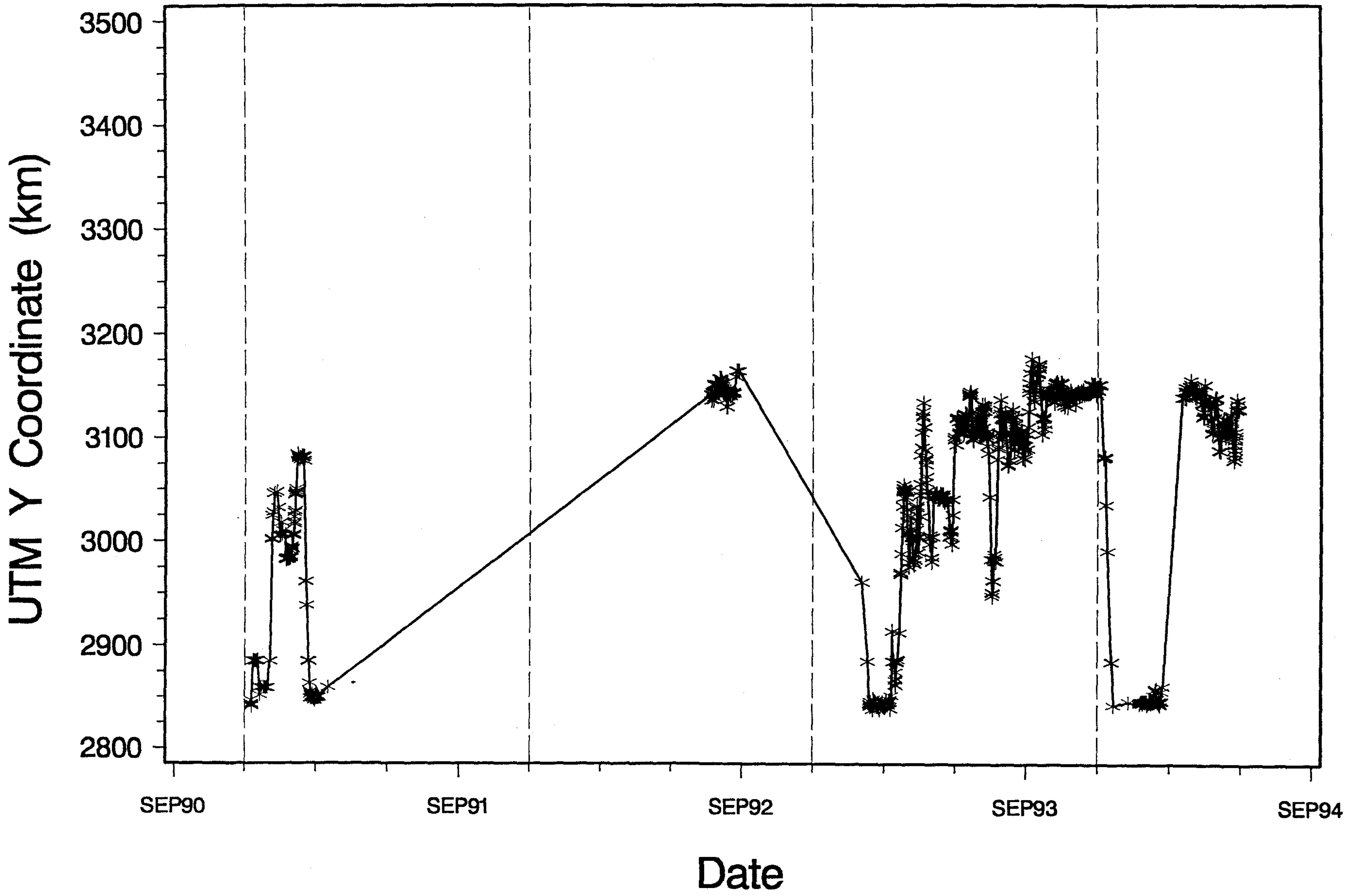
TJX – 02 ("Patience"): 1991 – 1992



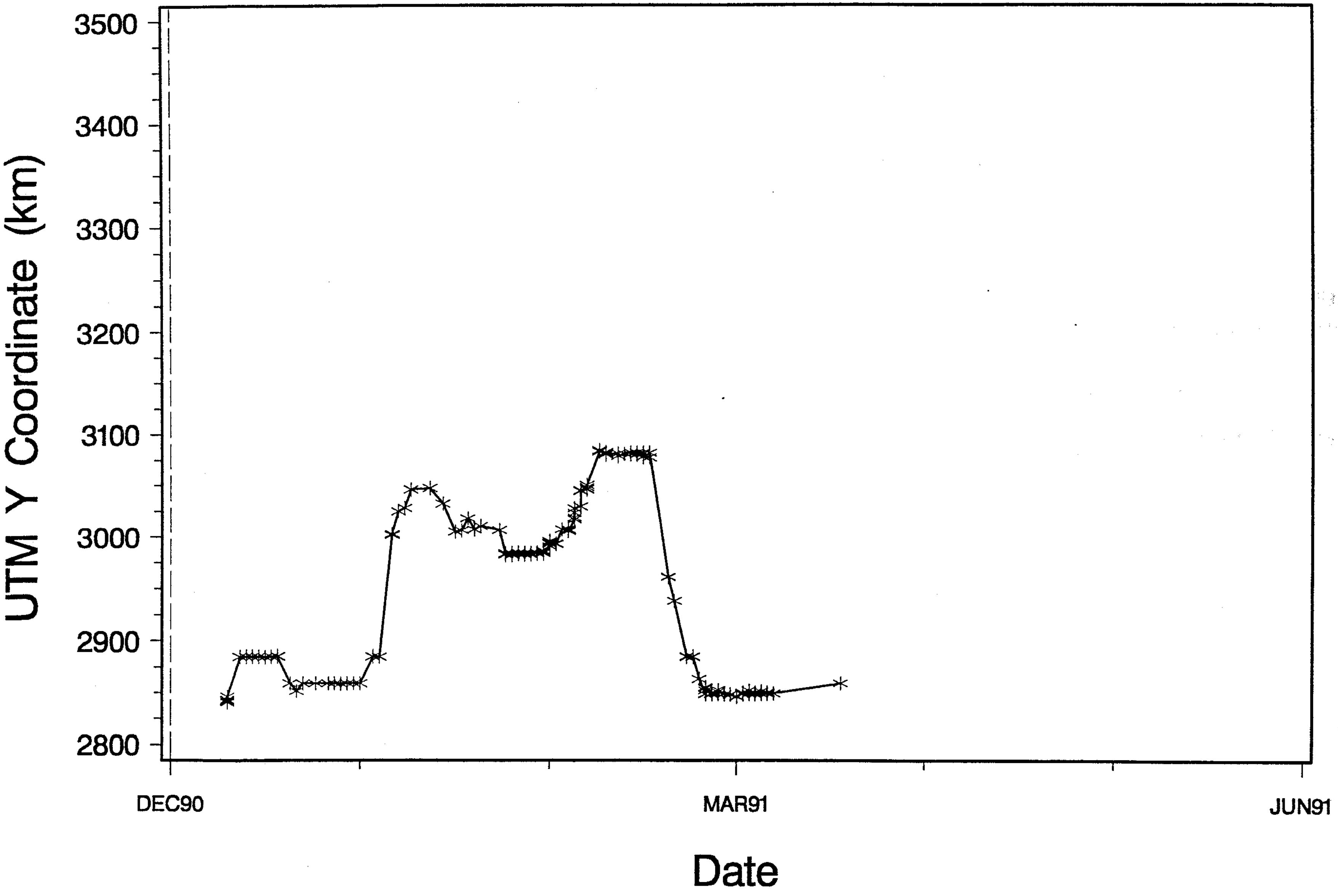
TJX – 03 ("Freckles"): 1993 – 1994



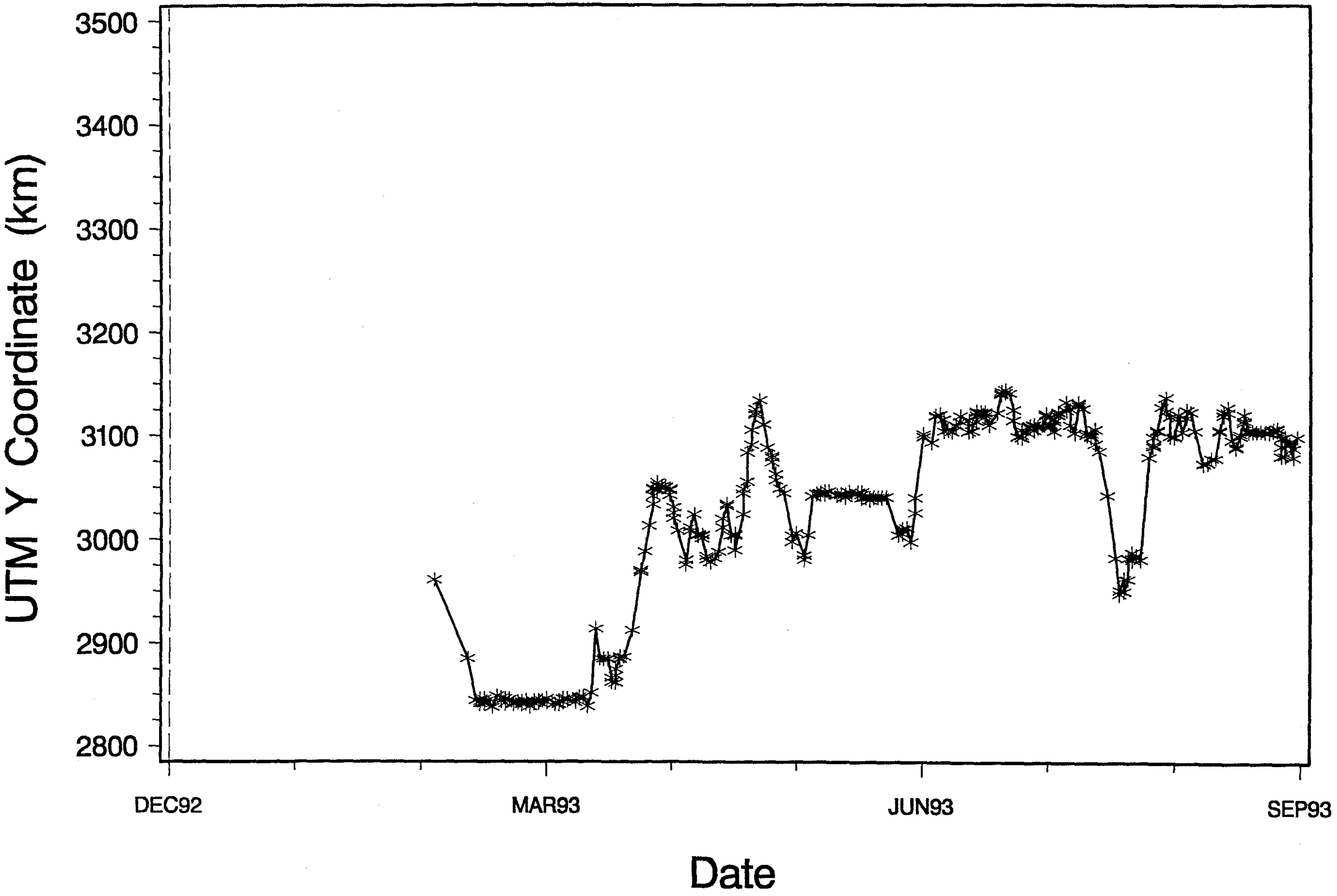
TMI – 01 ("Bob"): 1990 – 1994



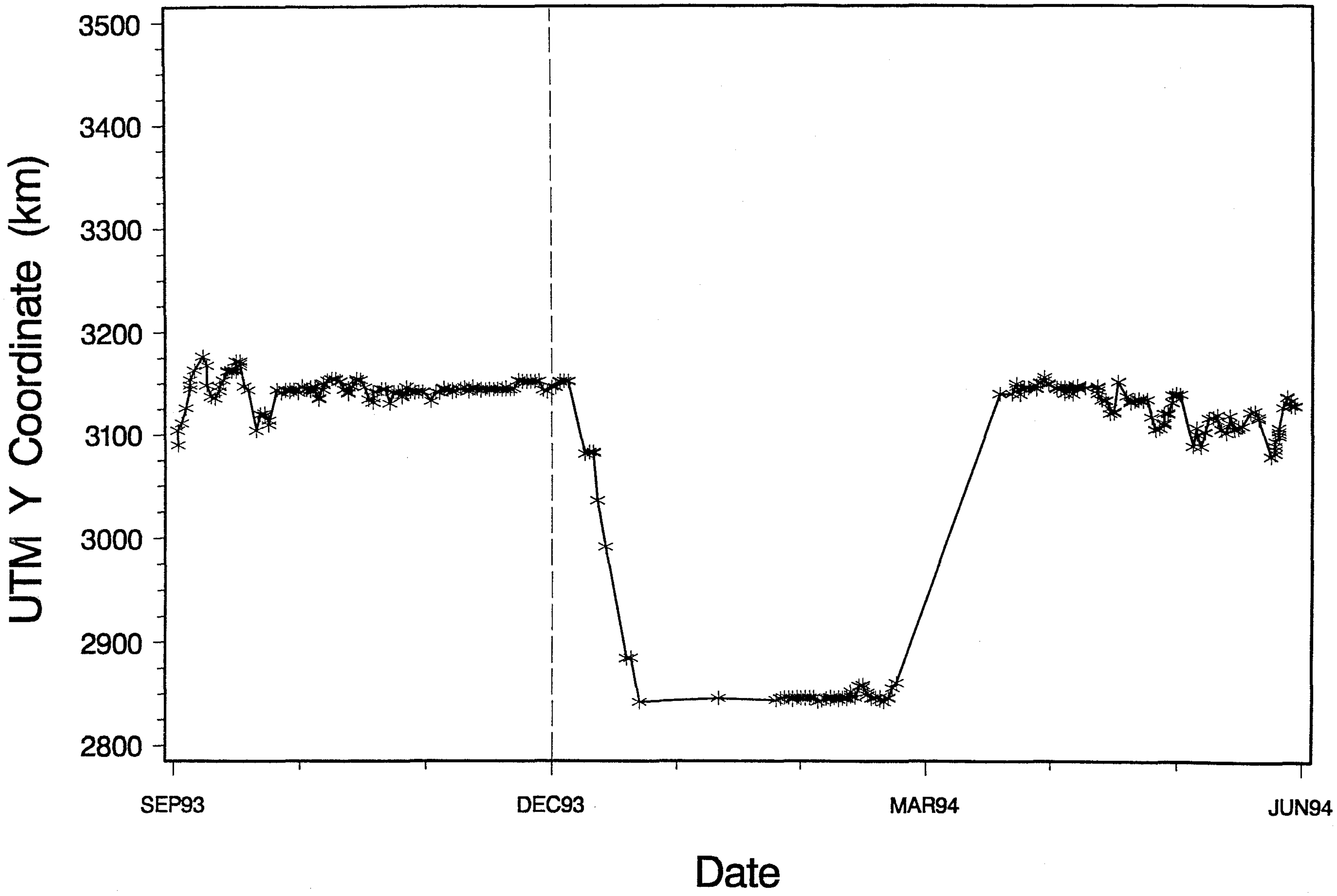
TMI – 01 ("Bob"): 1990 – 1991



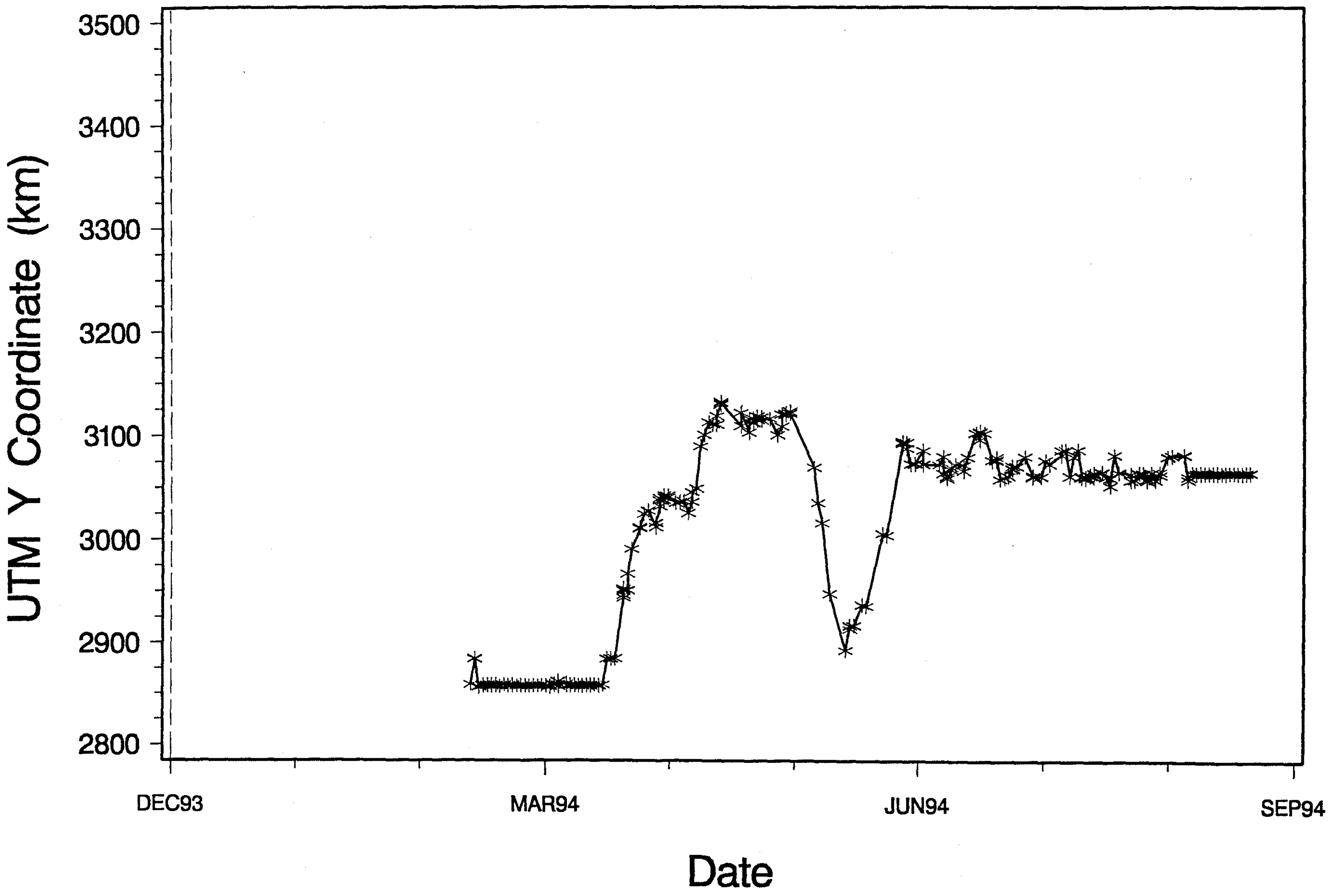
TMI – 01 ("Bob"): 1993



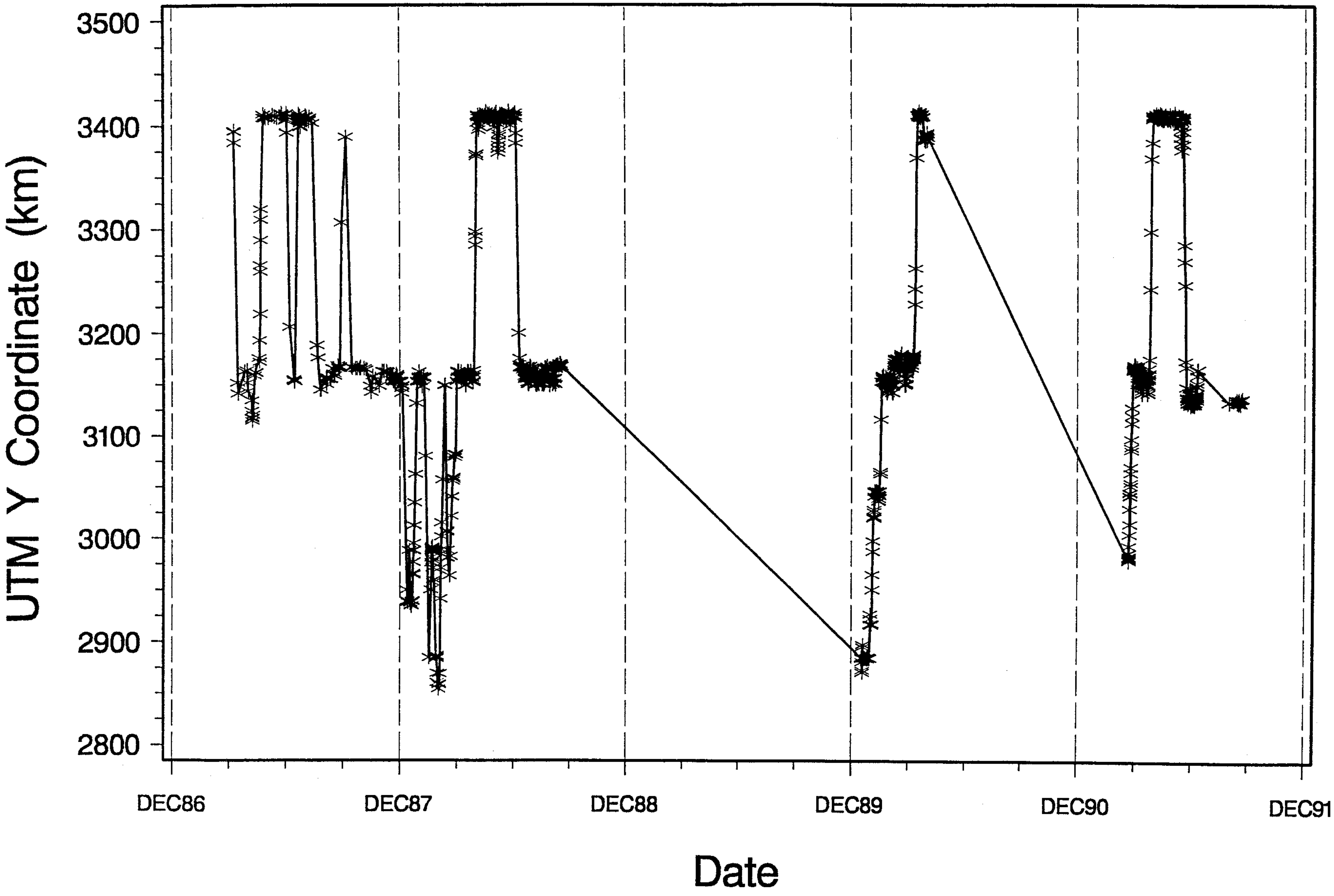
TMI – 01 ("Bob"): 1993 – 1994



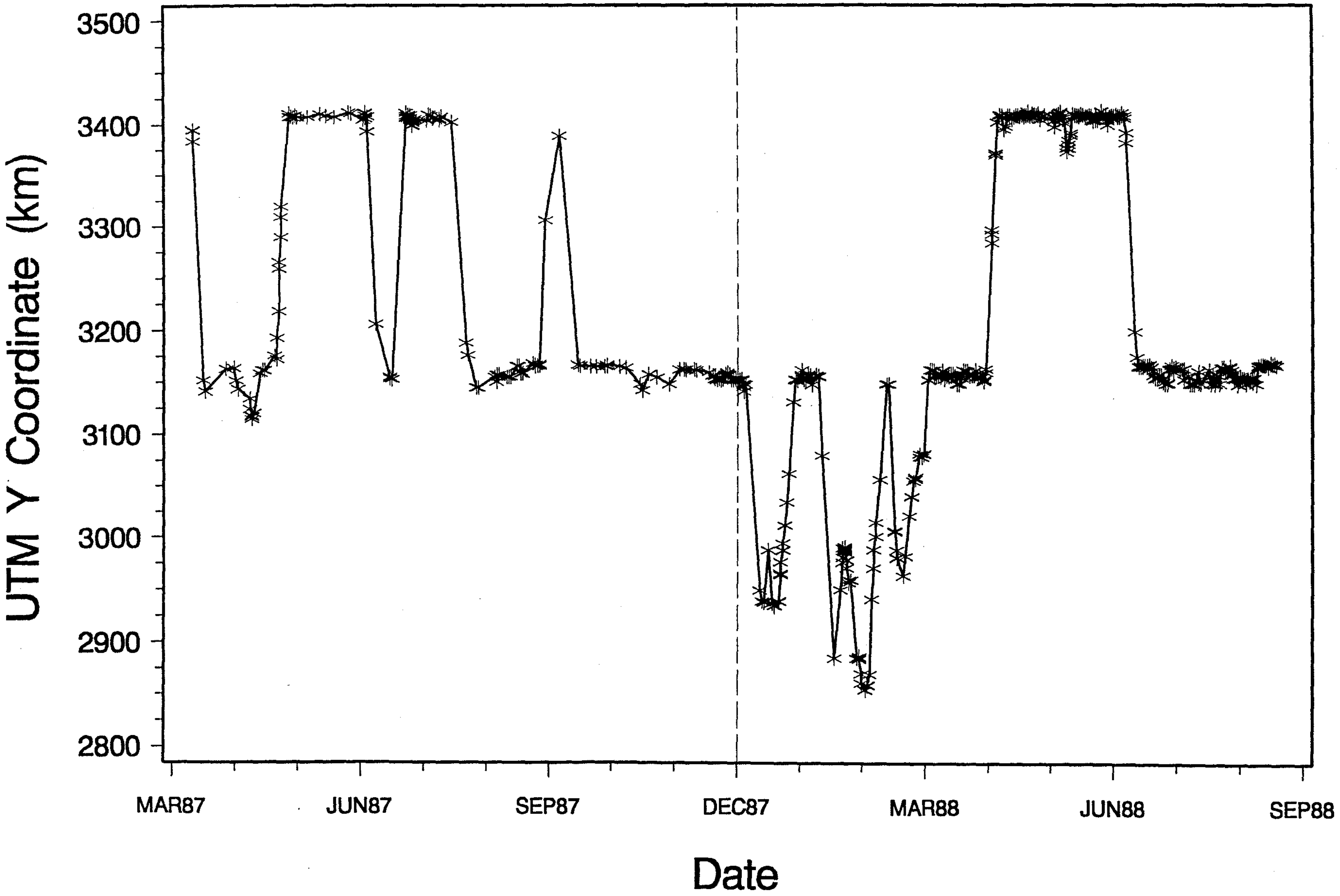
TMI – 03 ("Clockwork"): 1994



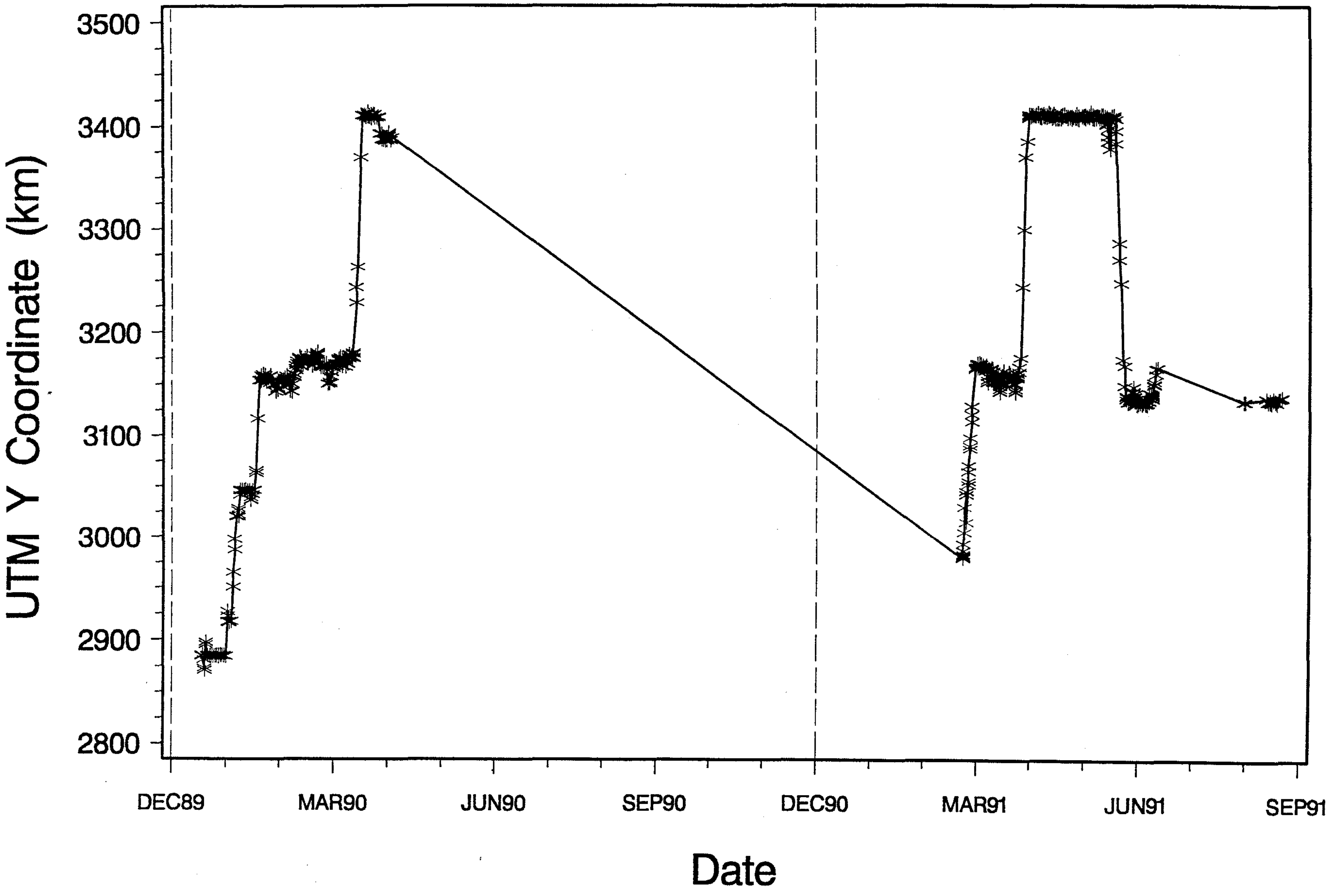
TNC – 01 ("Diane"): 1987 – 1991



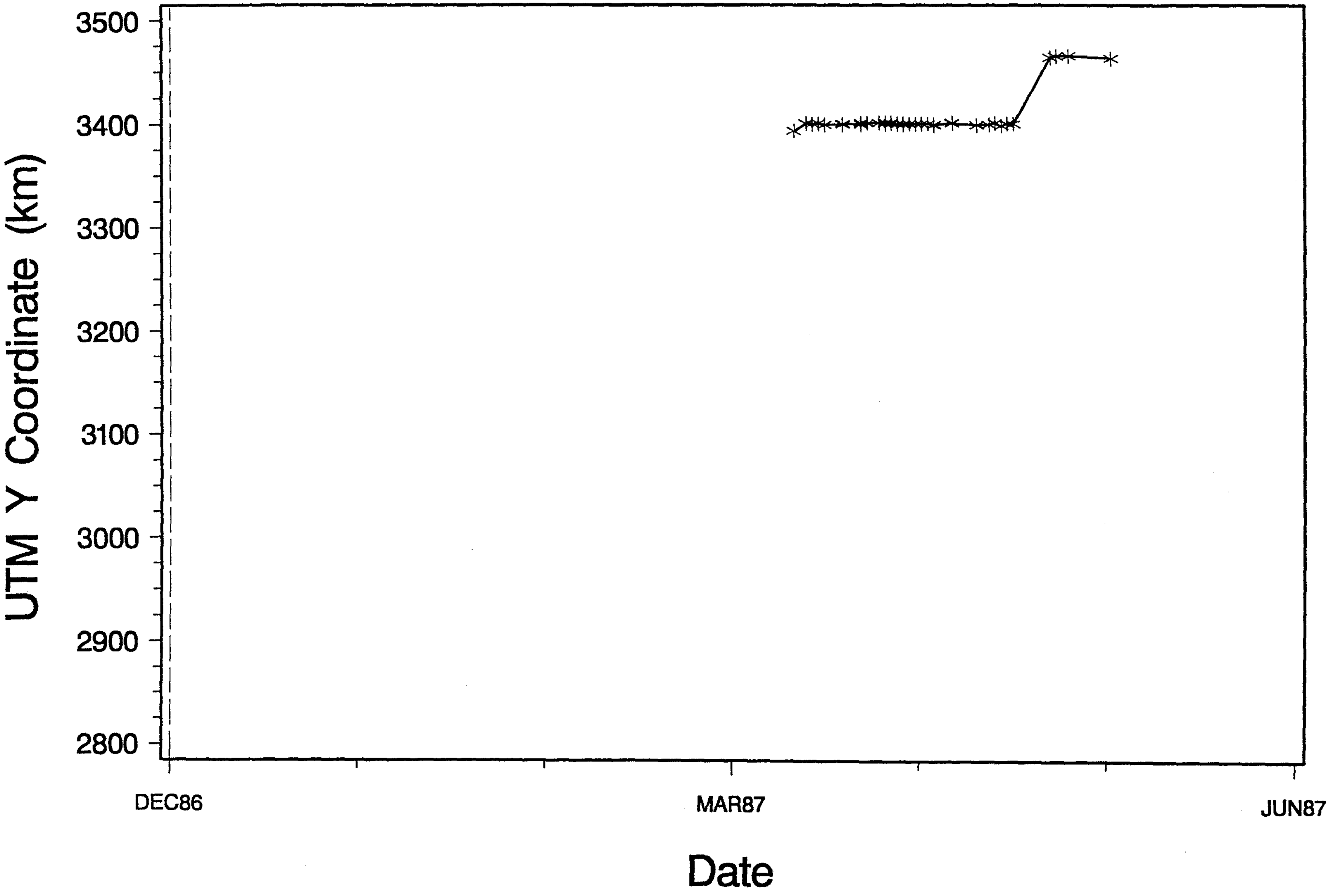
TNC – 01 ("Diane"): 1987 – 1988

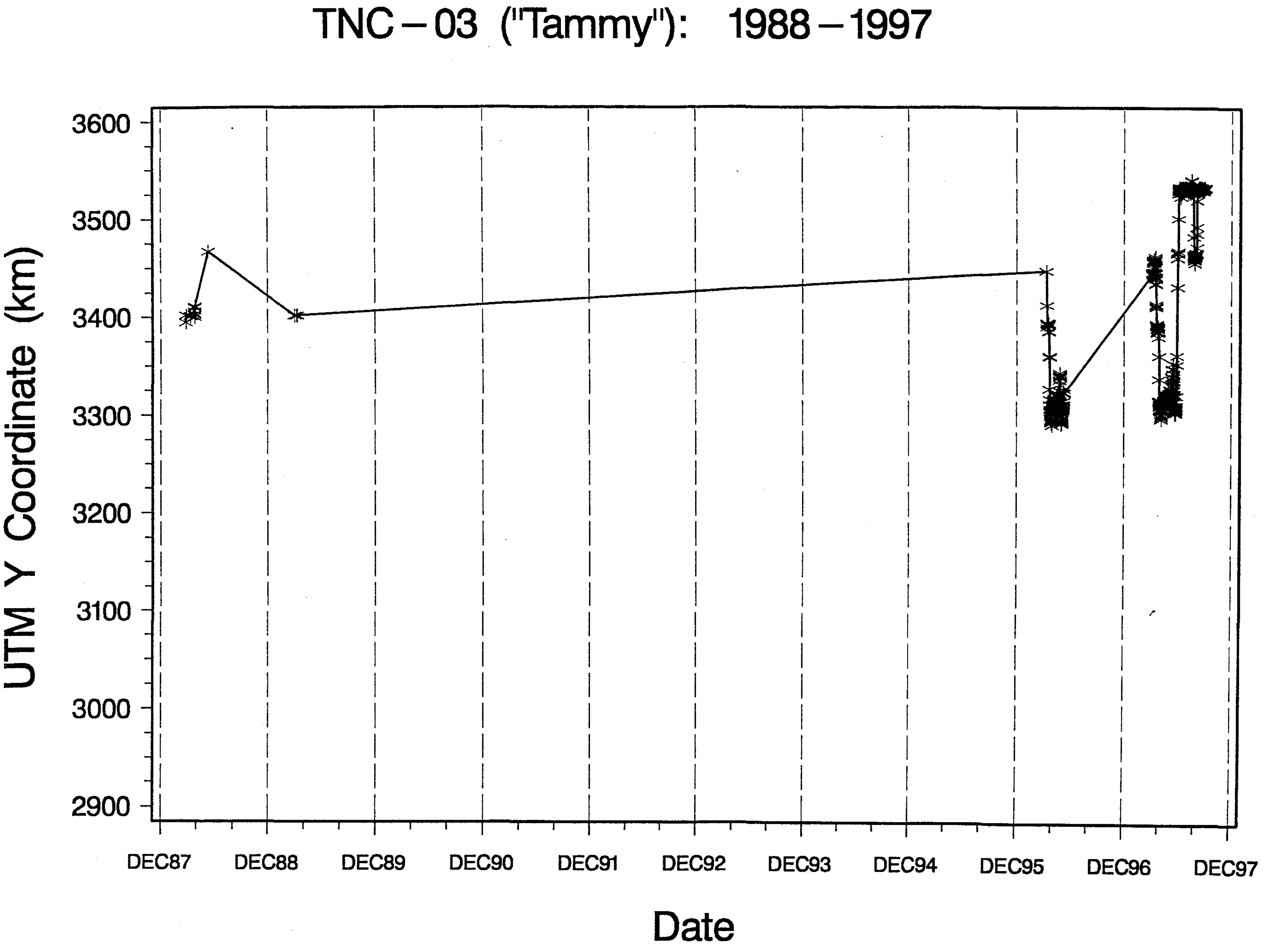


TNC – 01 ("Diane"): 1989 – 1991



TNC – 02 ("Jesse"): 1987




TNC – 03 ("Tammy"): 1988 – 1997
UTM Y Coordinate (km)
3600
3500
3400
3300
3200
3100
3000
2900
DEC87
DEC88
DEC89
DEC90
DEC91
DEC92
DEC93
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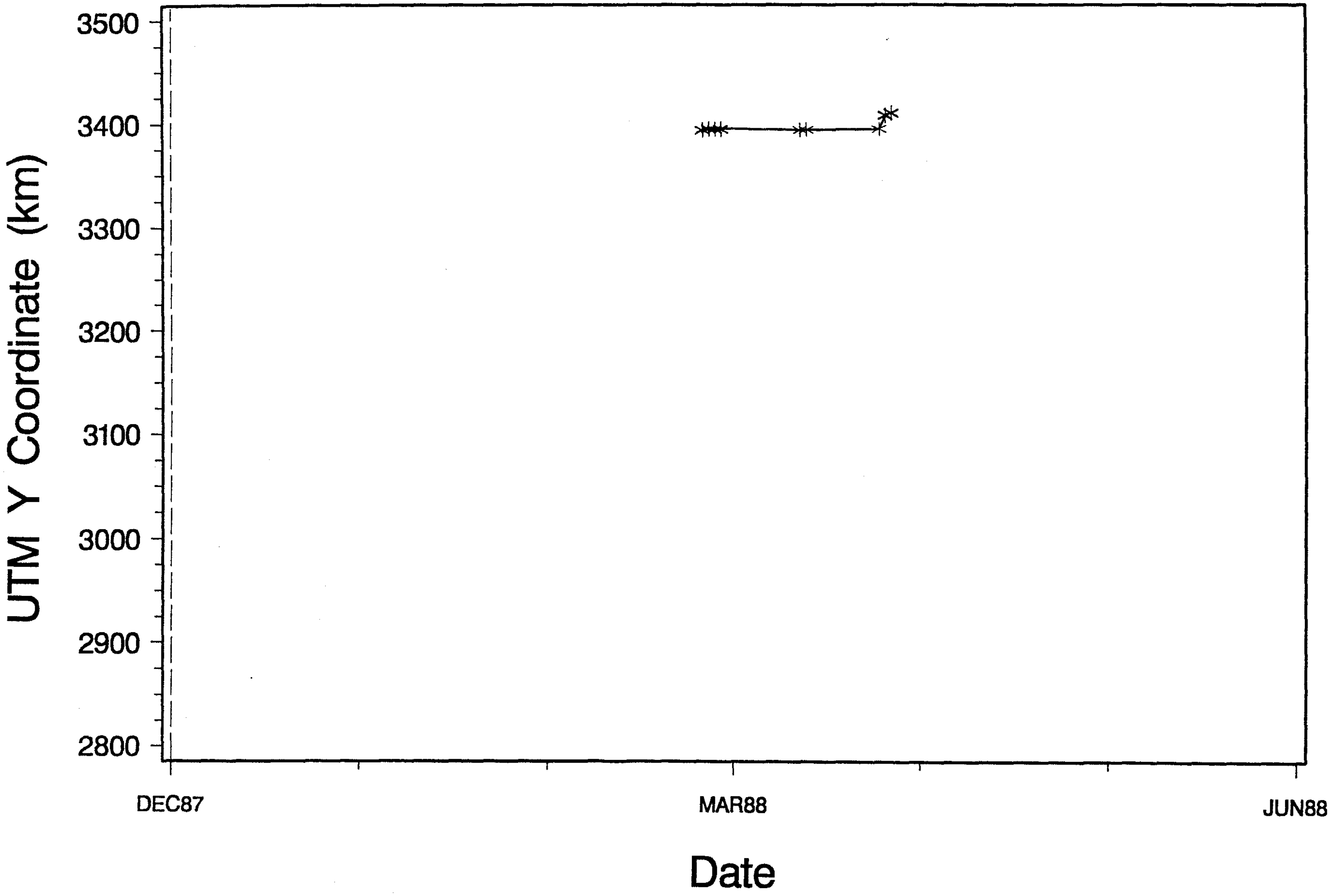
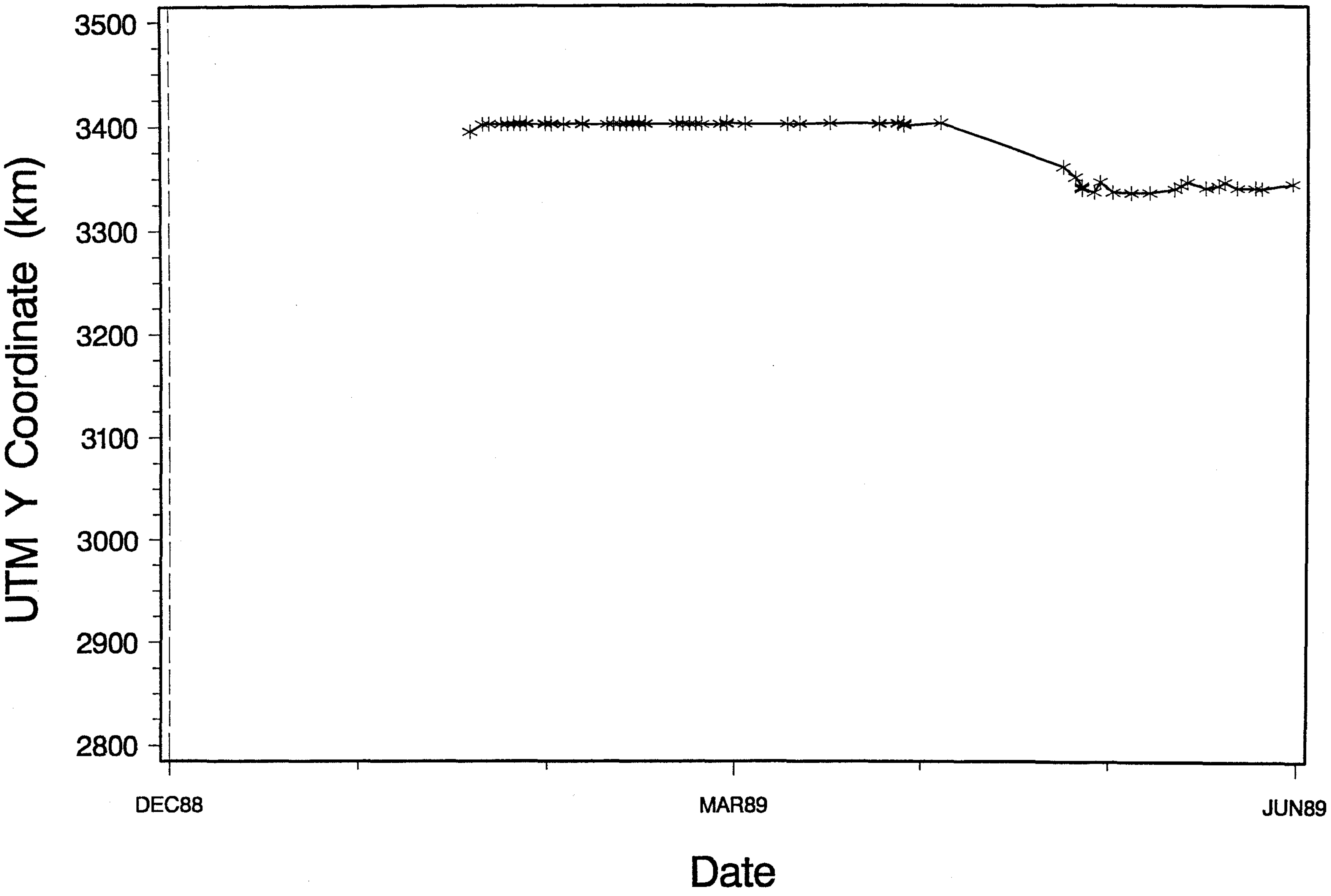
DEC97
Date

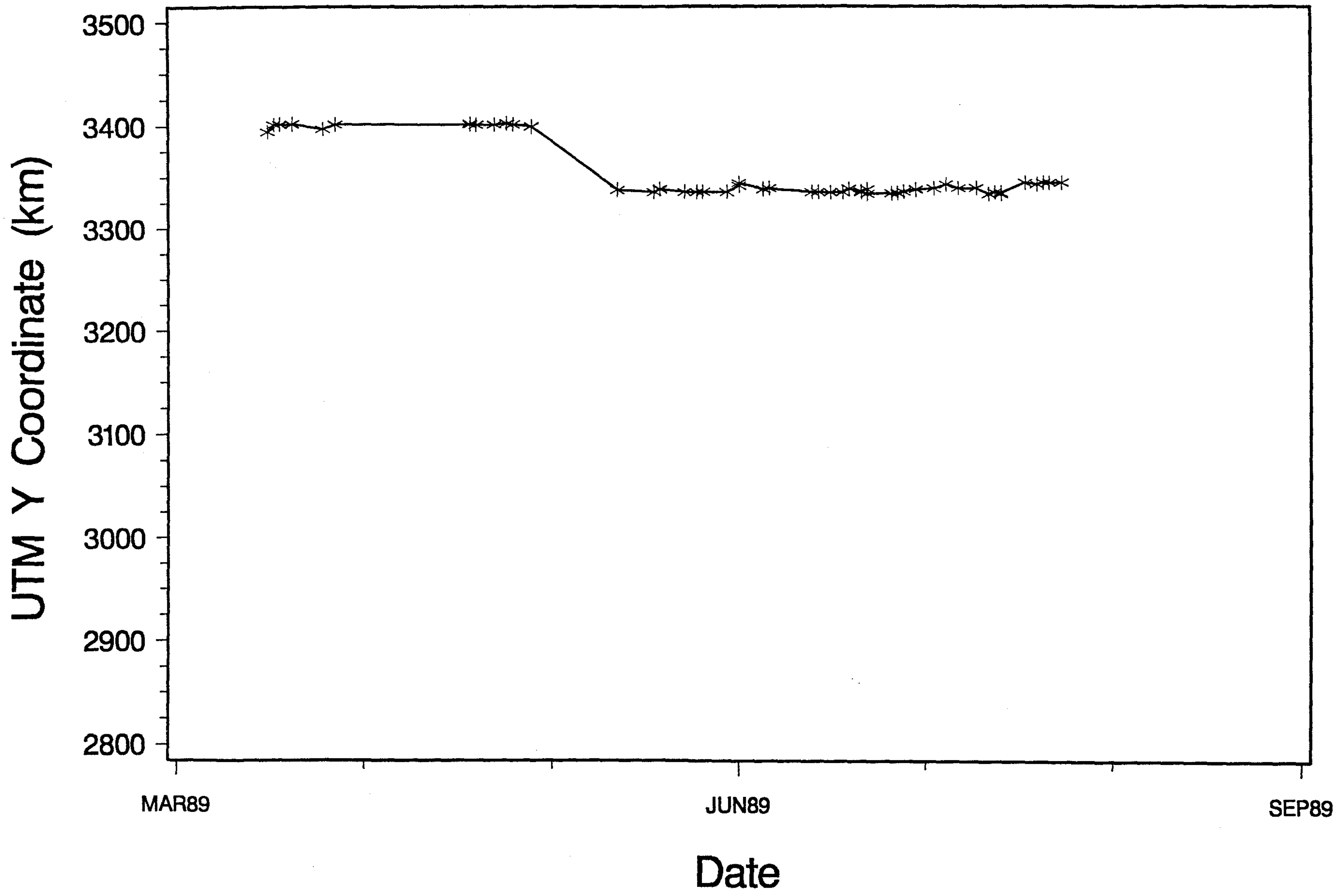


TNC – 04 ("Pat"): 1988

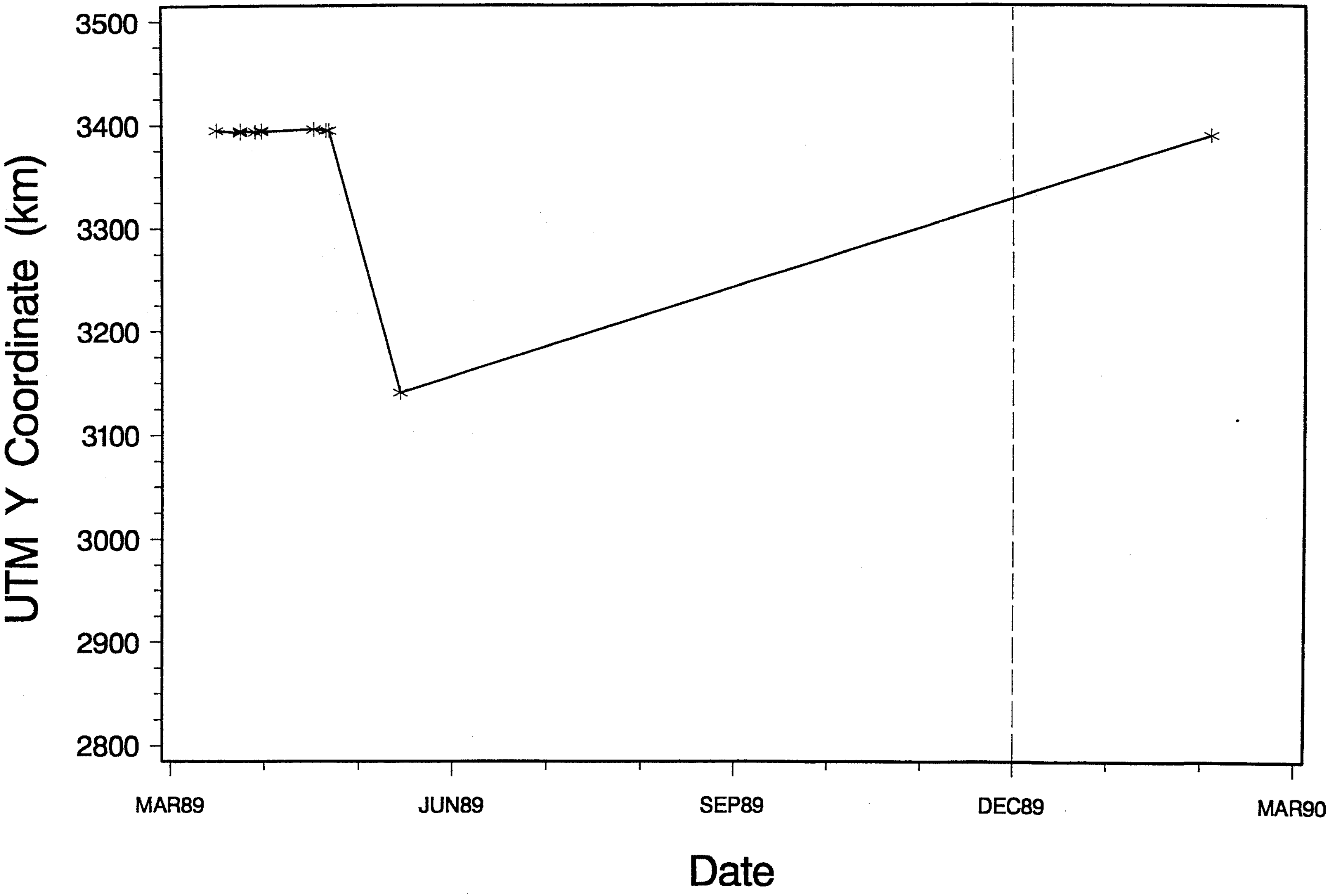
TNC – 05 ("Roseanne"): 1989



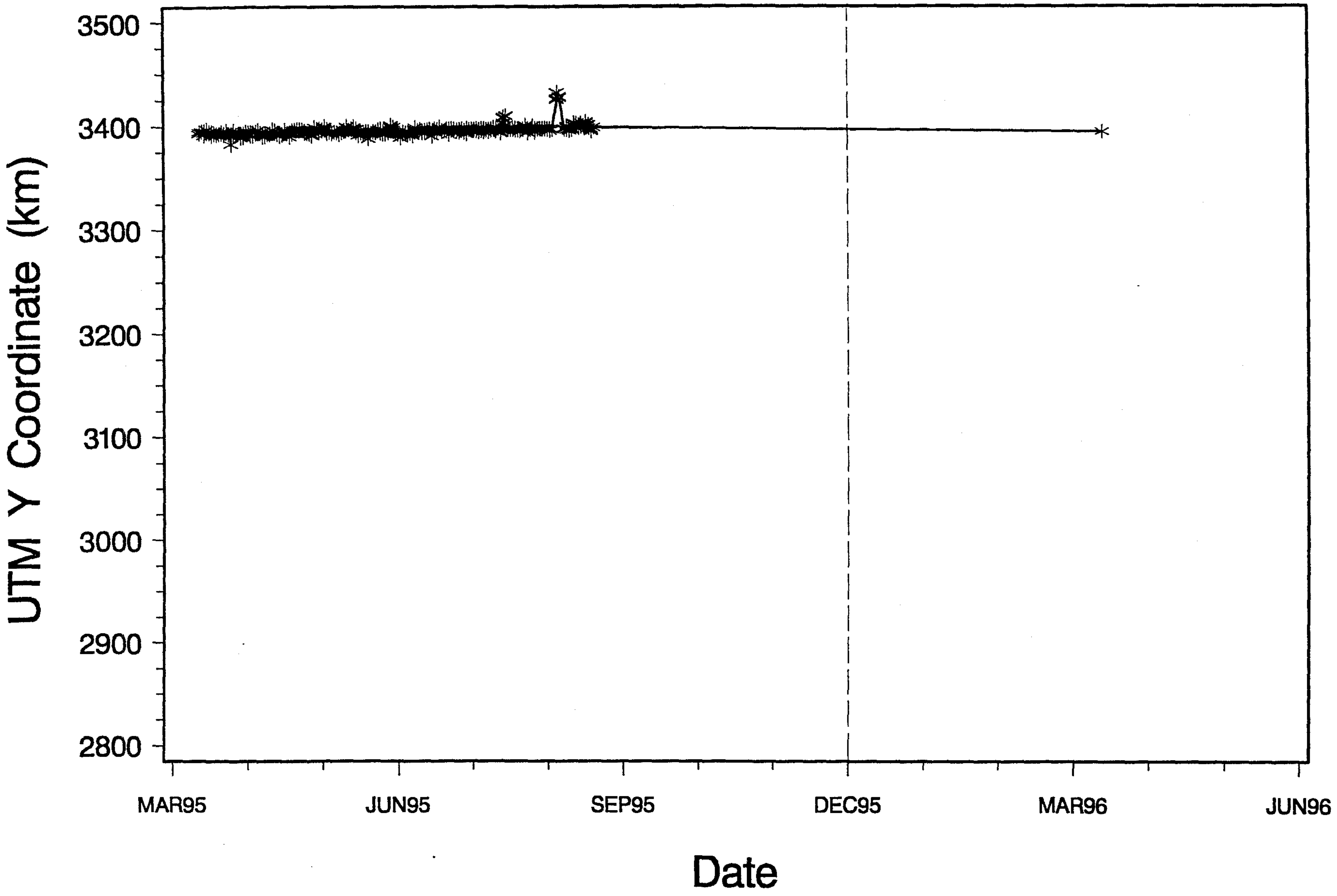
TNC – 07 ("Whitie"): 1989



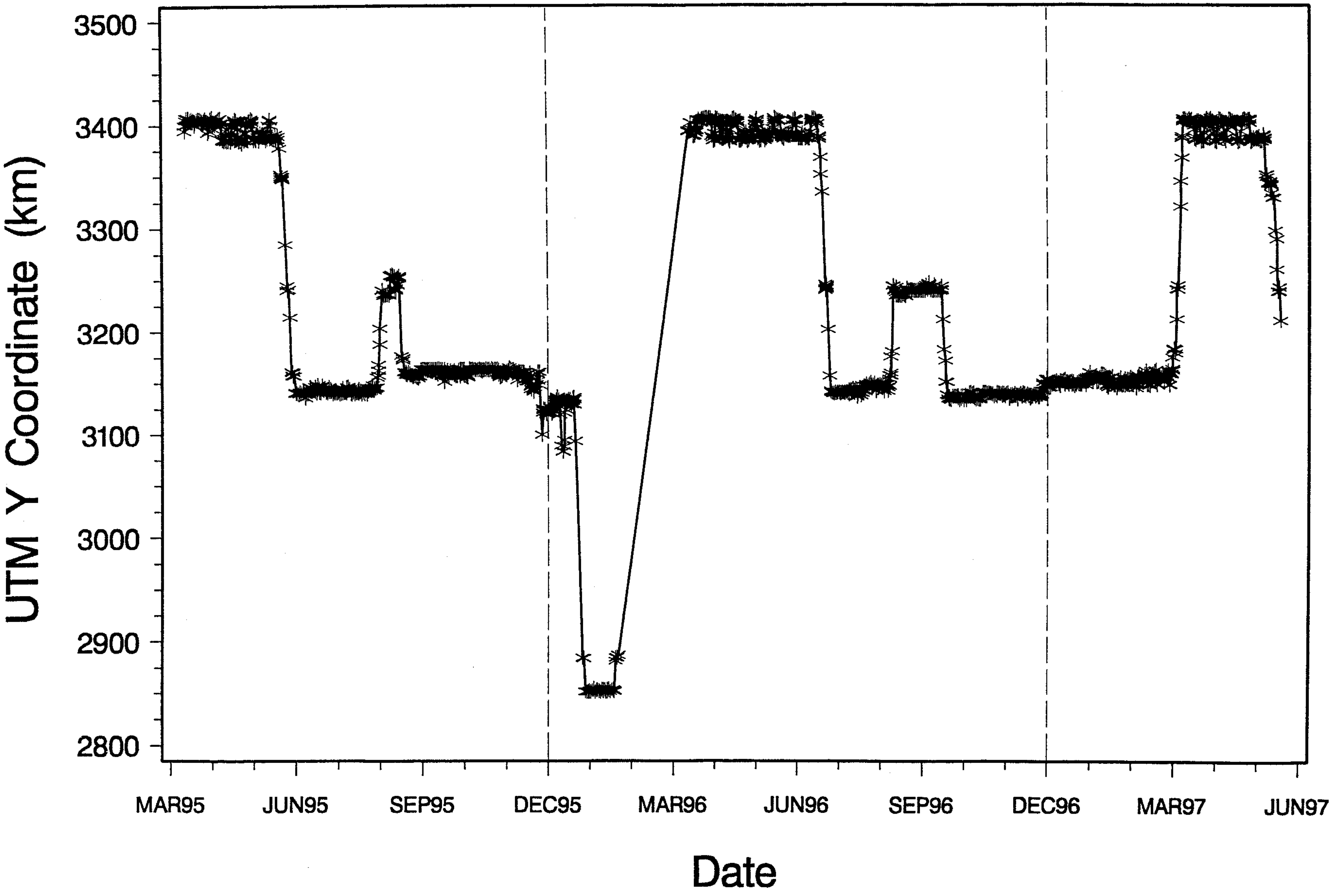
TNC – 08 ("George"): 1989 – 1990



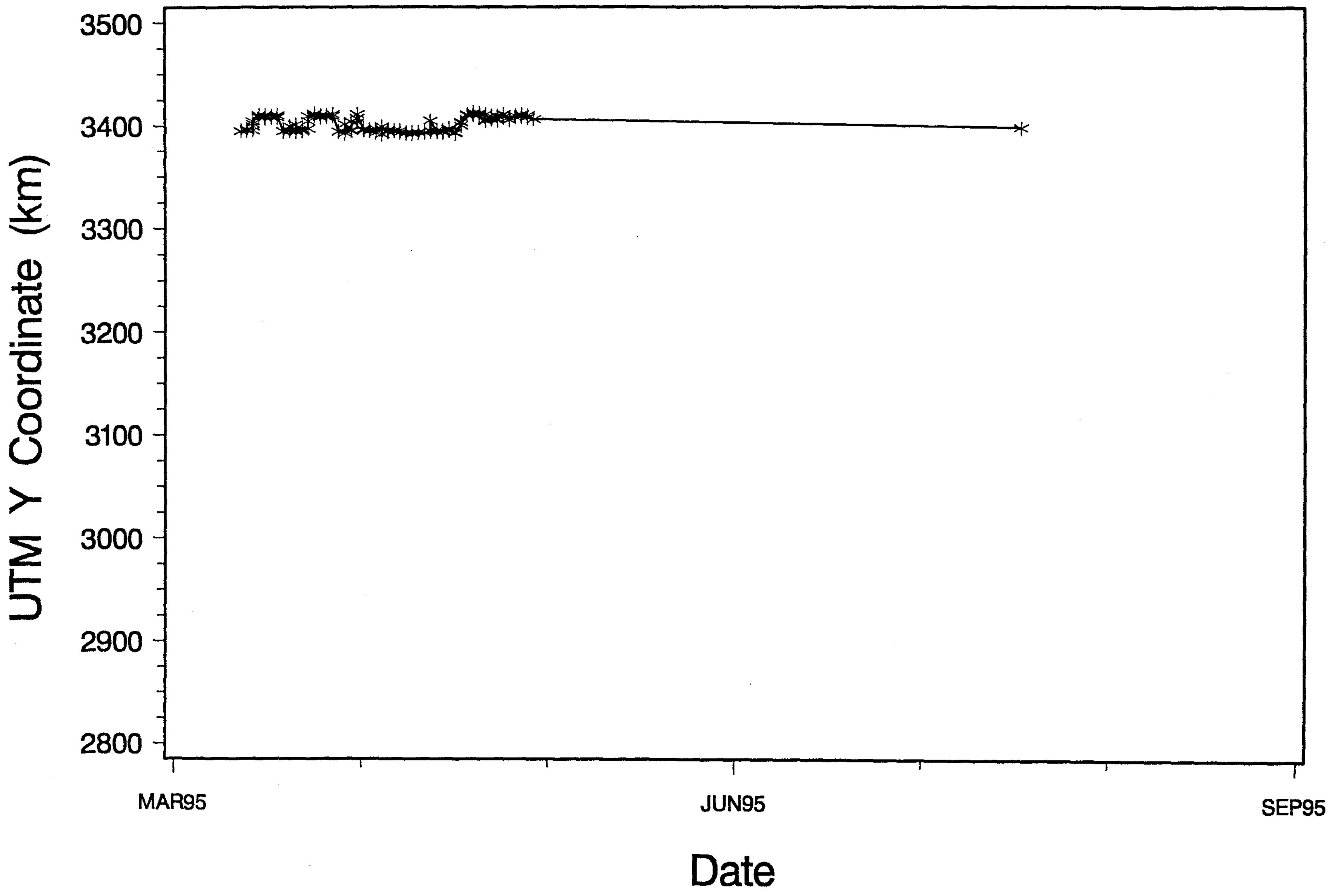
TNC – 09 ("Janatee"): 1995 – 1996



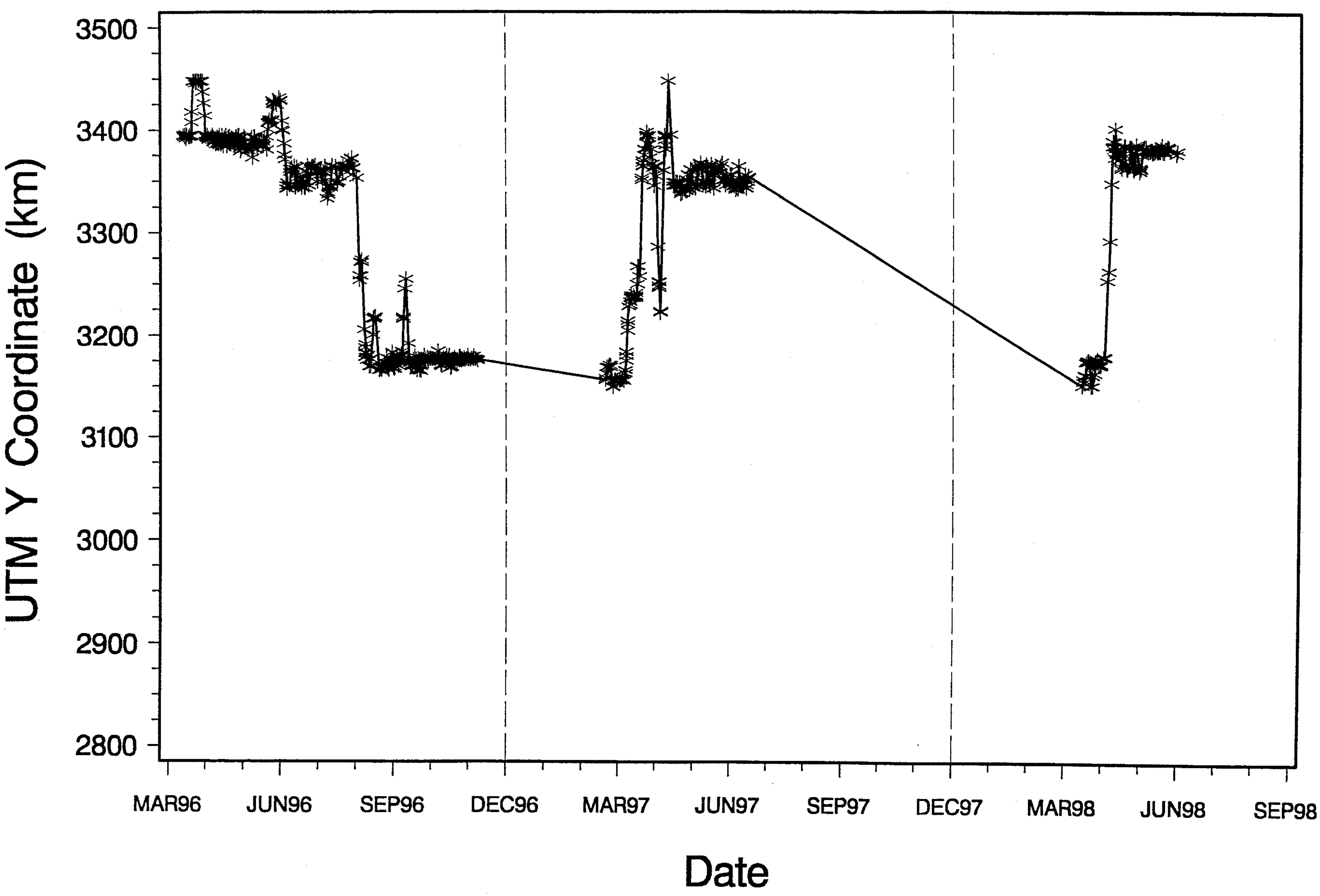
TNC – 10 ("March"): 1995 – 1997



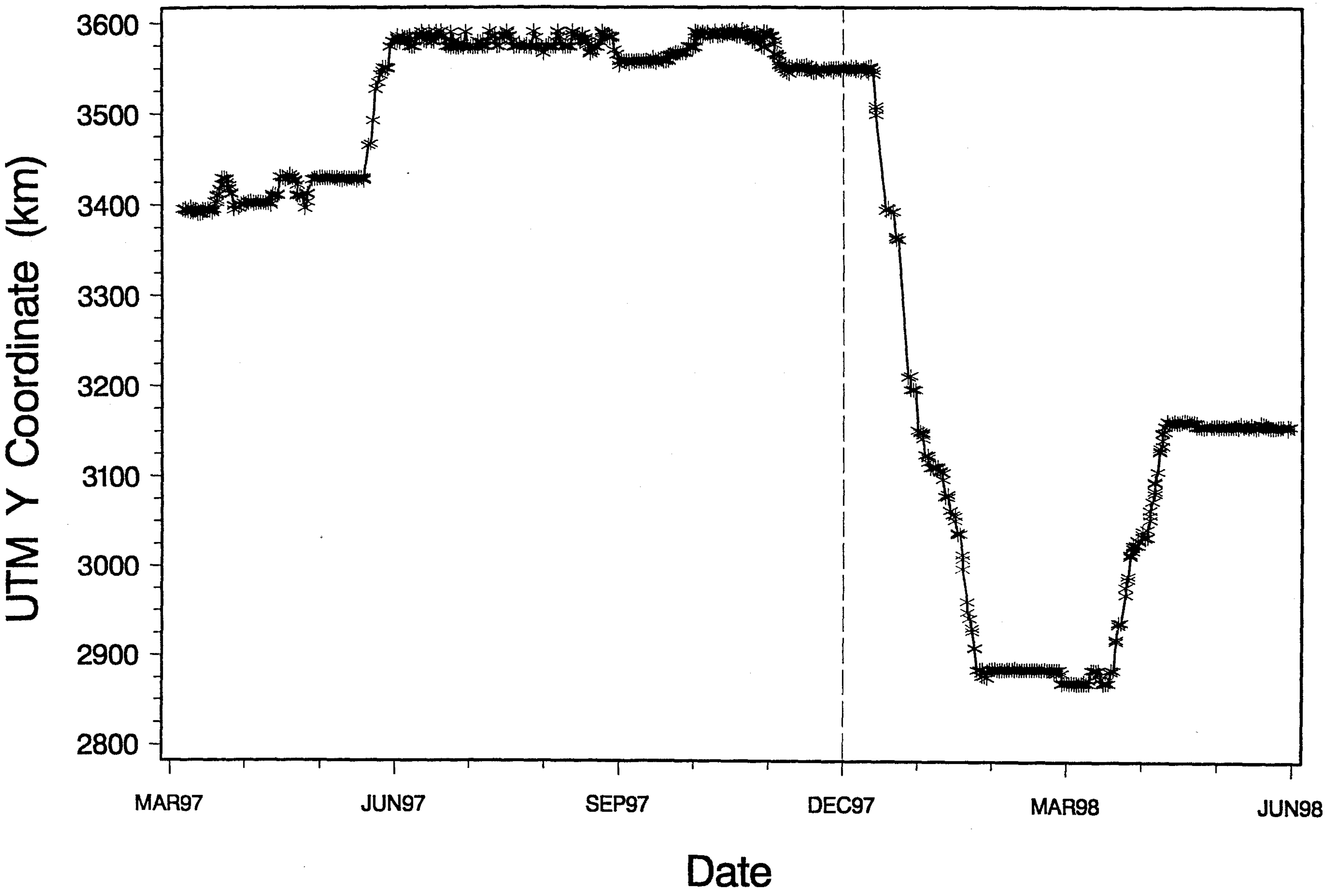
TNC−11 ("Vale"): 1995



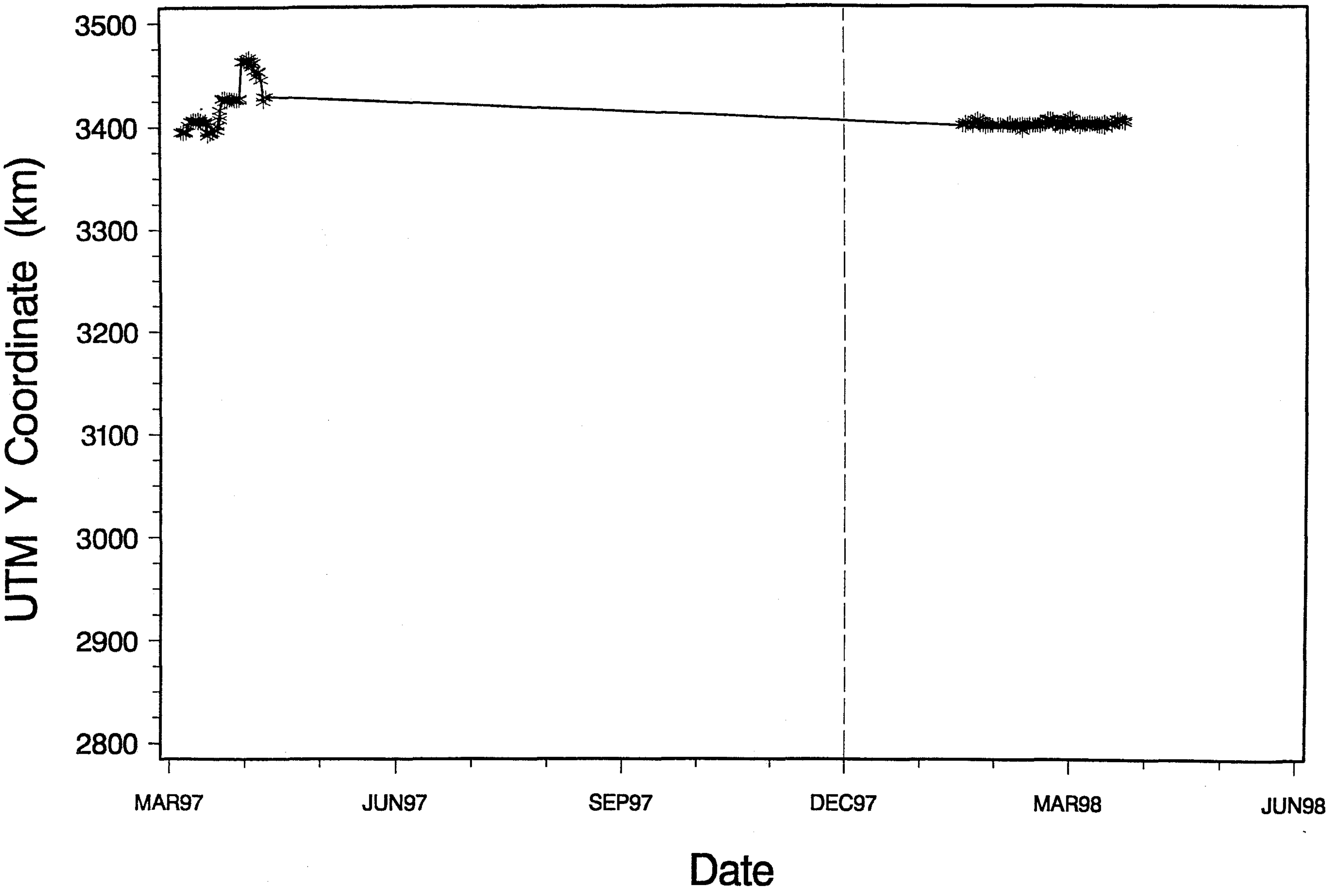
TNC – 12 ("Mossie"): 1996 – 1998



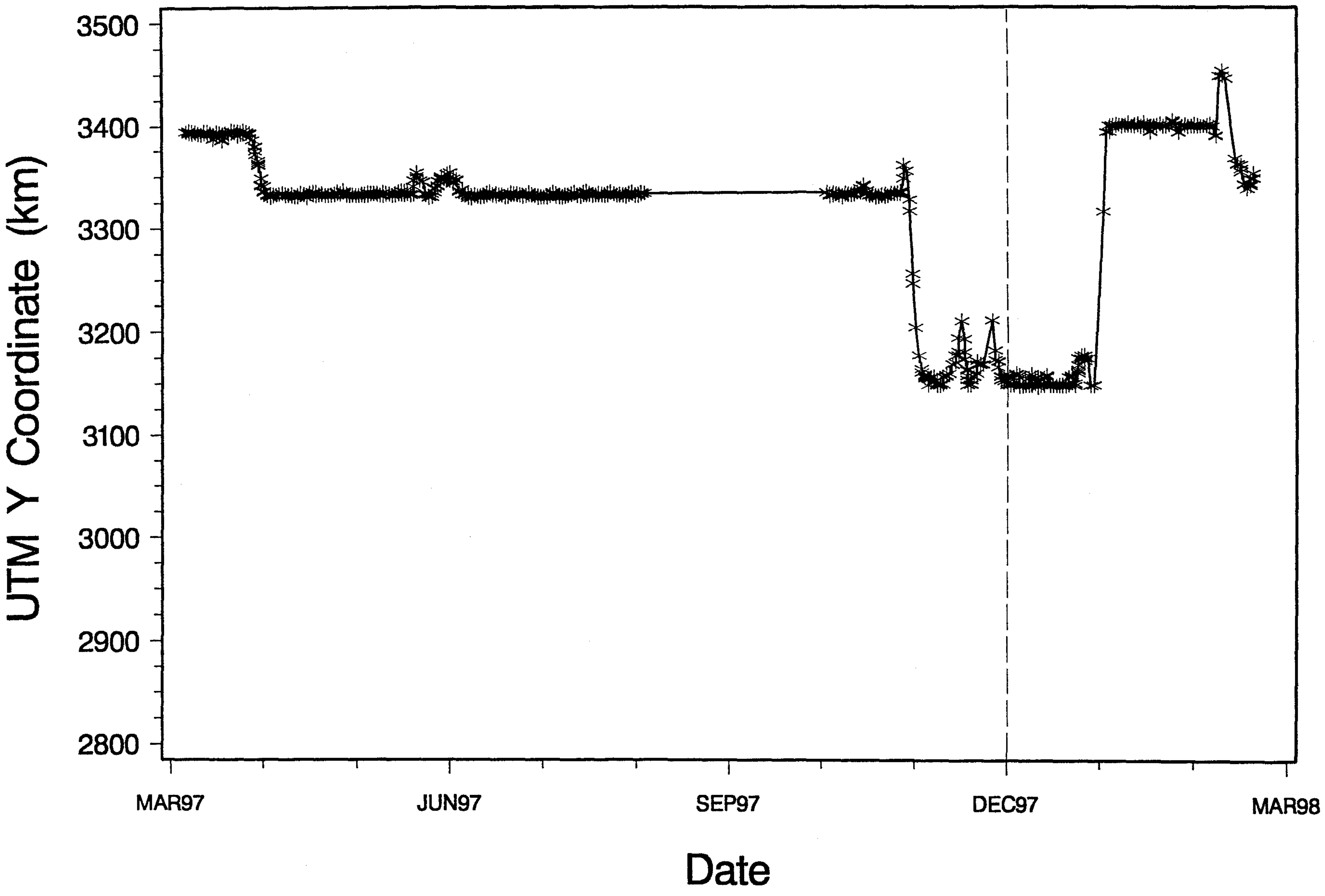
TNC – 13 ("Knicky"): 1997 – 1998



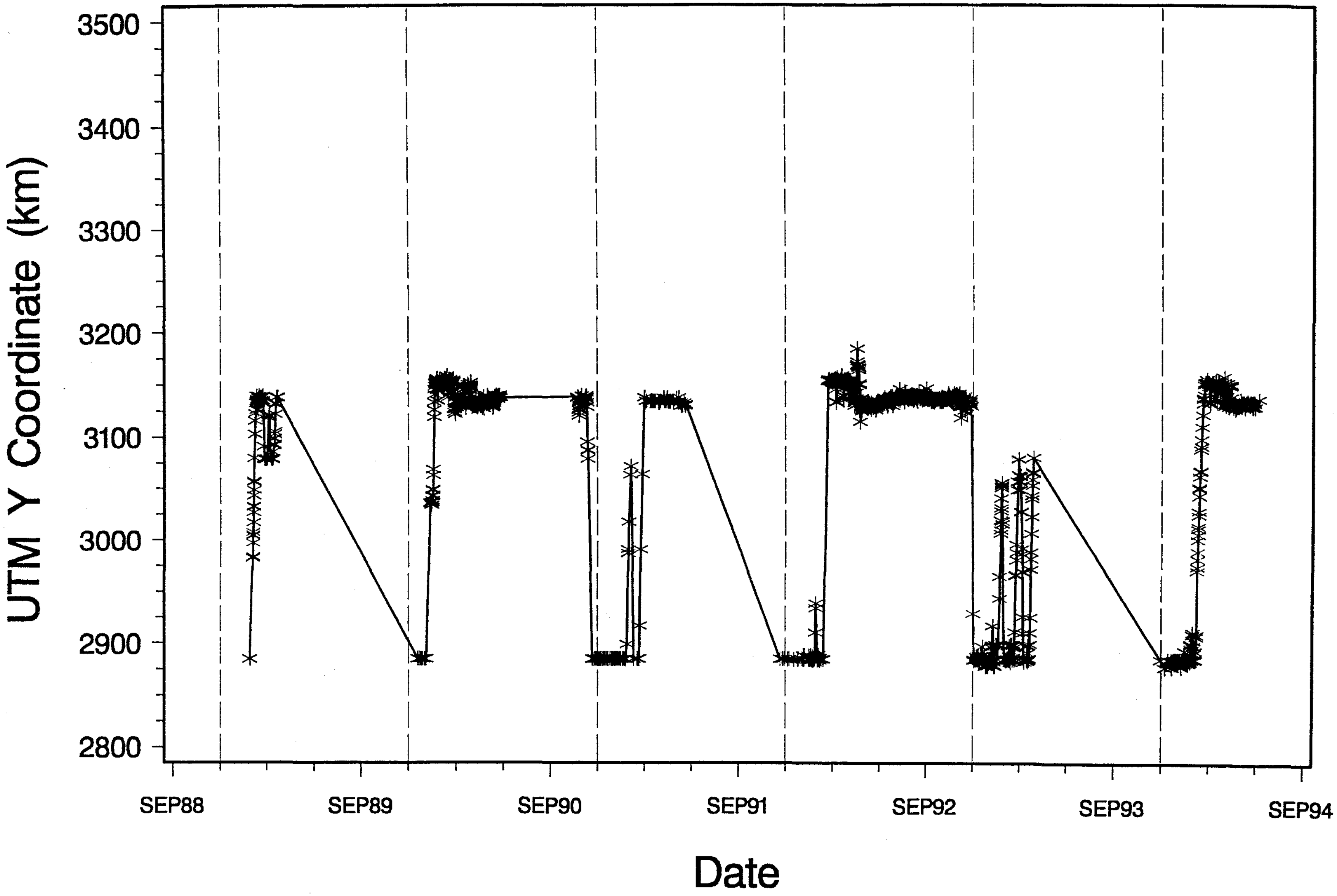
TNC – 14 ("Jeb"): 1997 – 1998



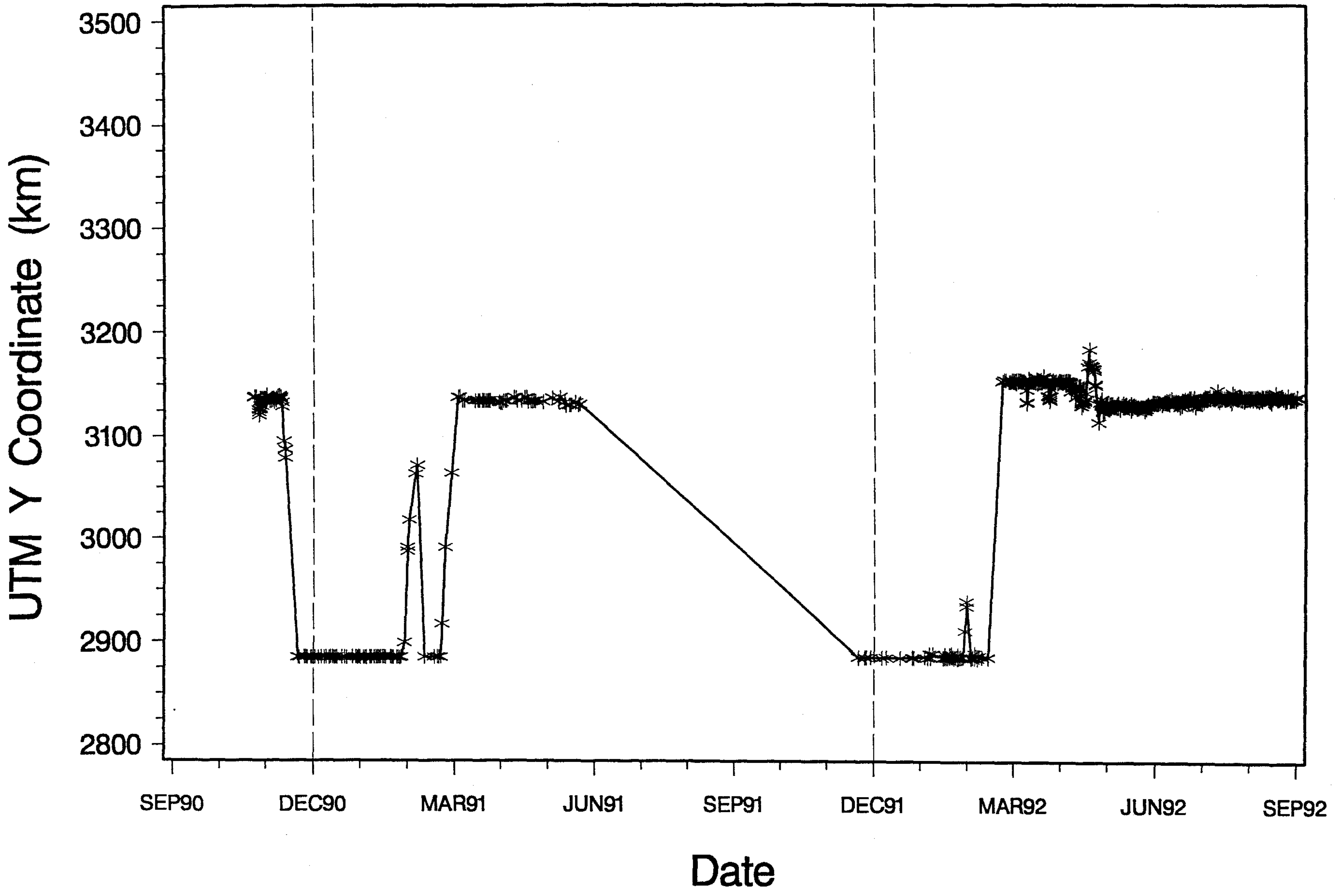
TNC – 15 ("Xena"): 1997 – 1998



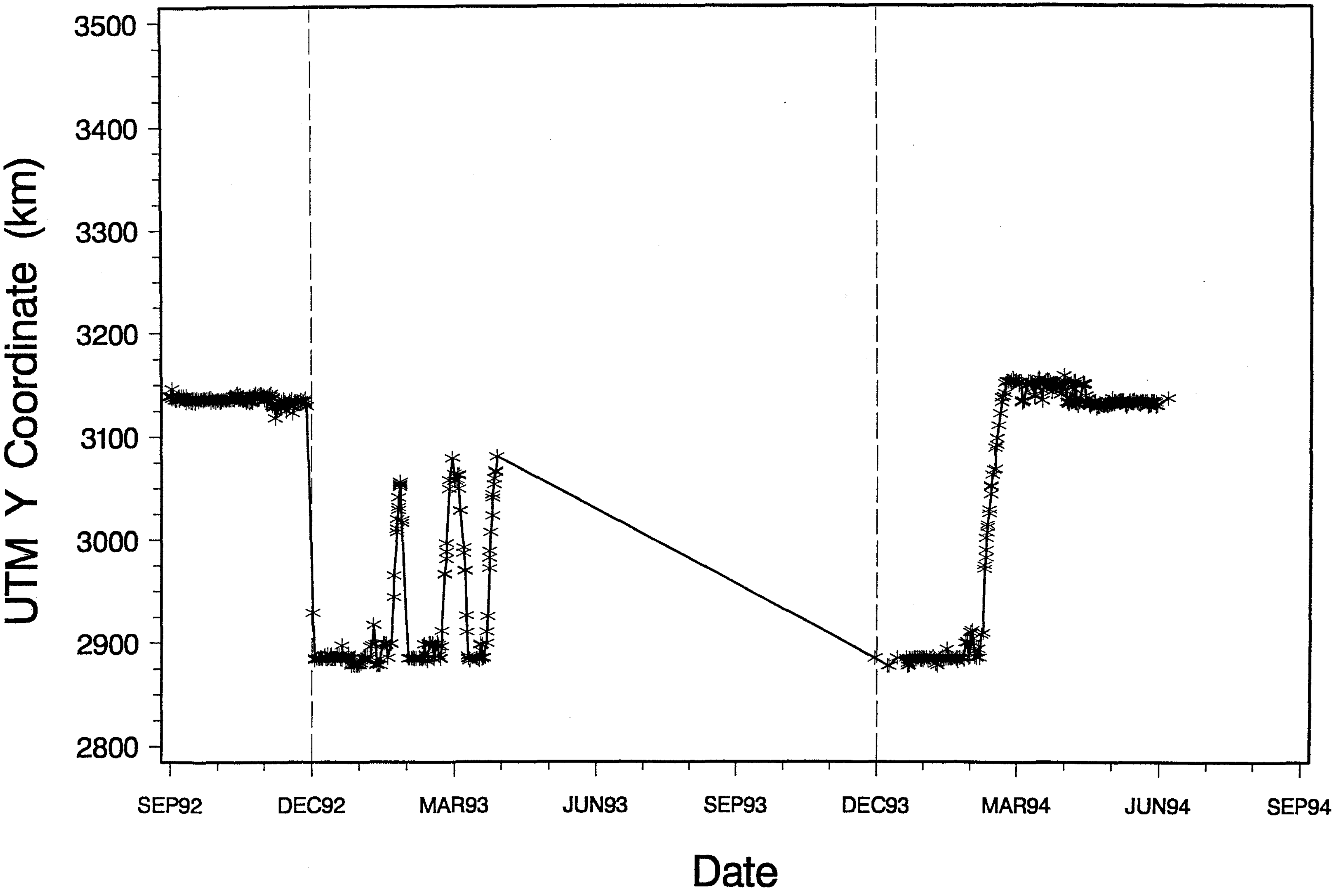
TPE – 01 ("Spot"): 1989 – 1994



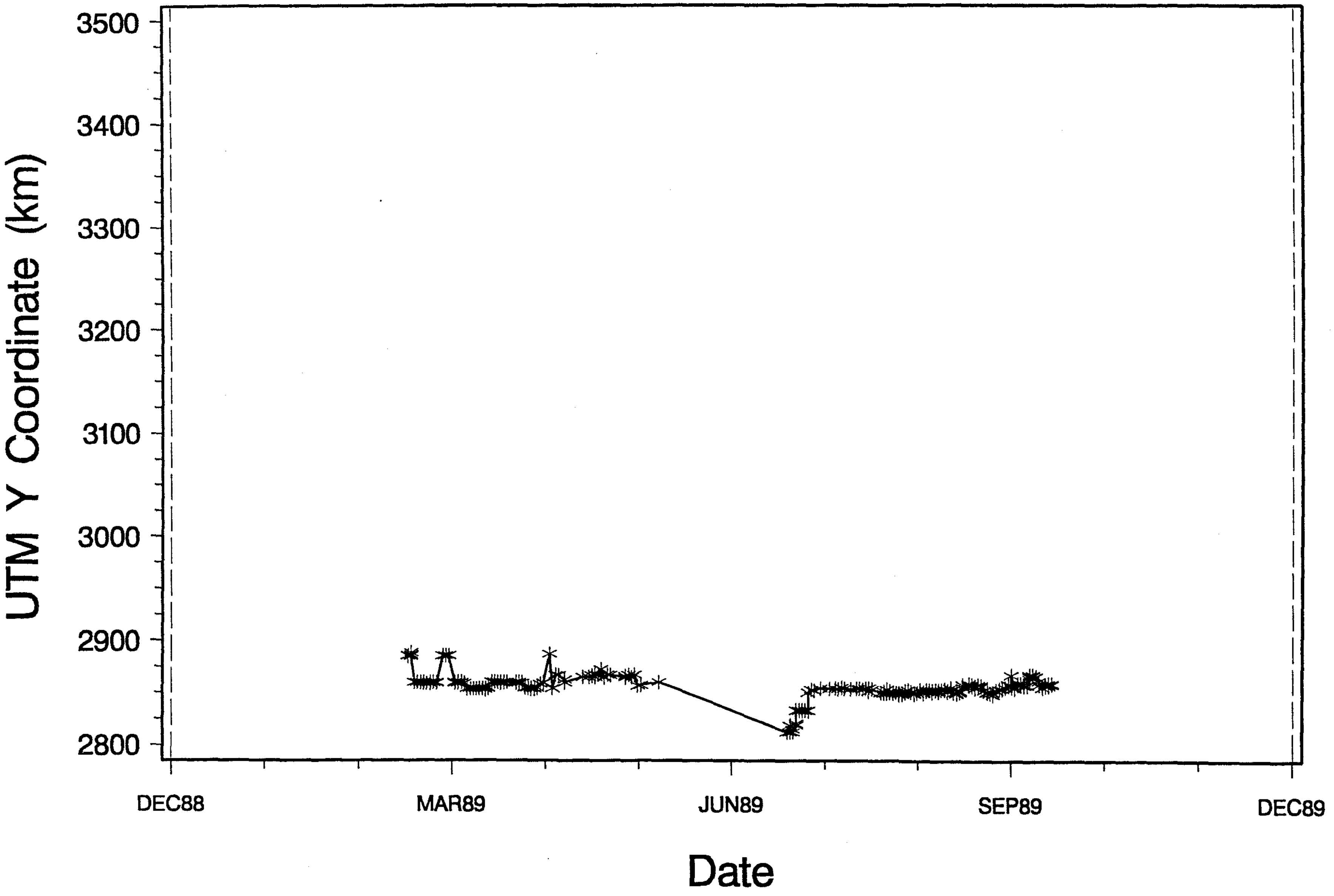
TPE – 01 ("Spot"): 1990 – 1992



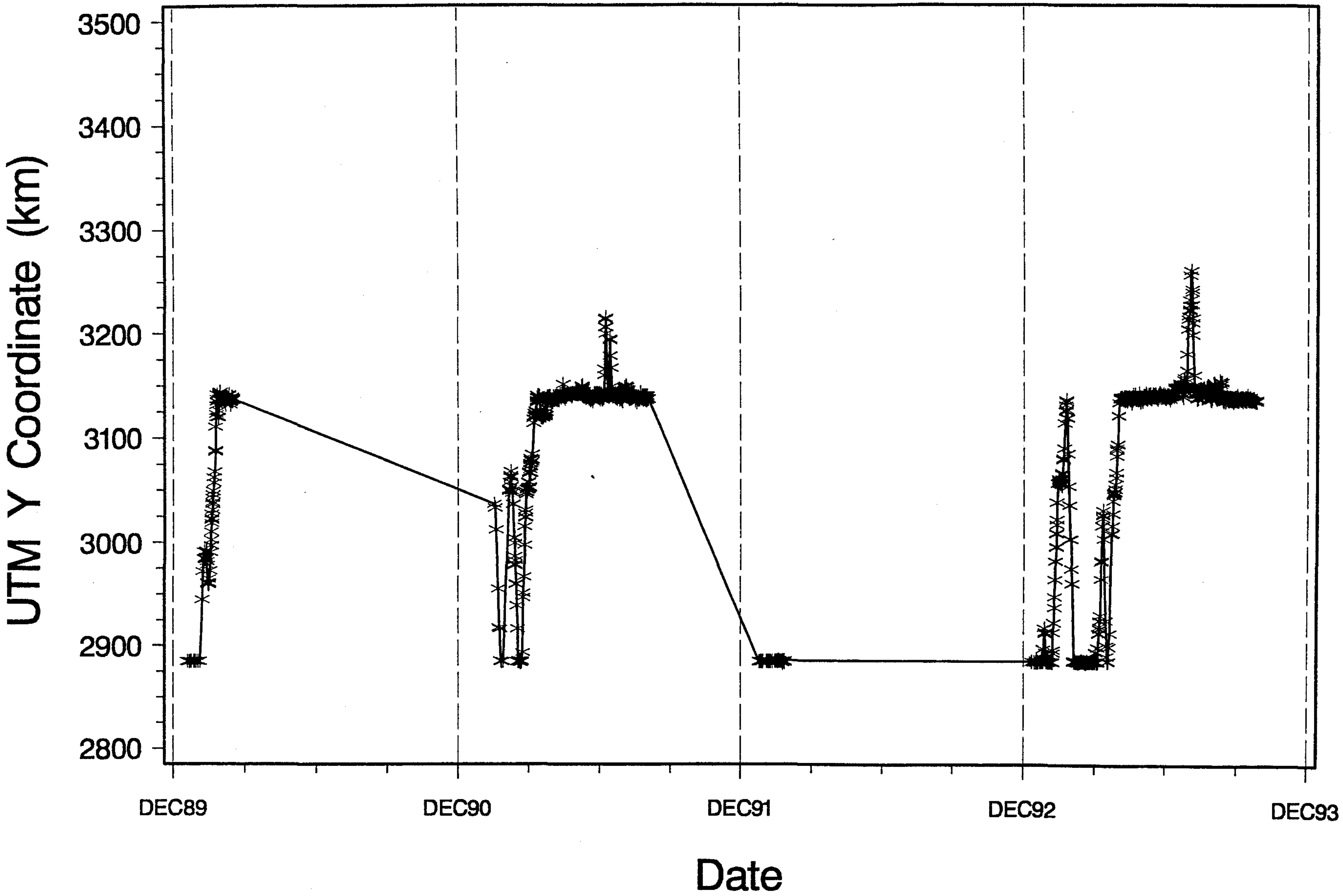
TPE – 01 ("Spot"): 1992 – 1994



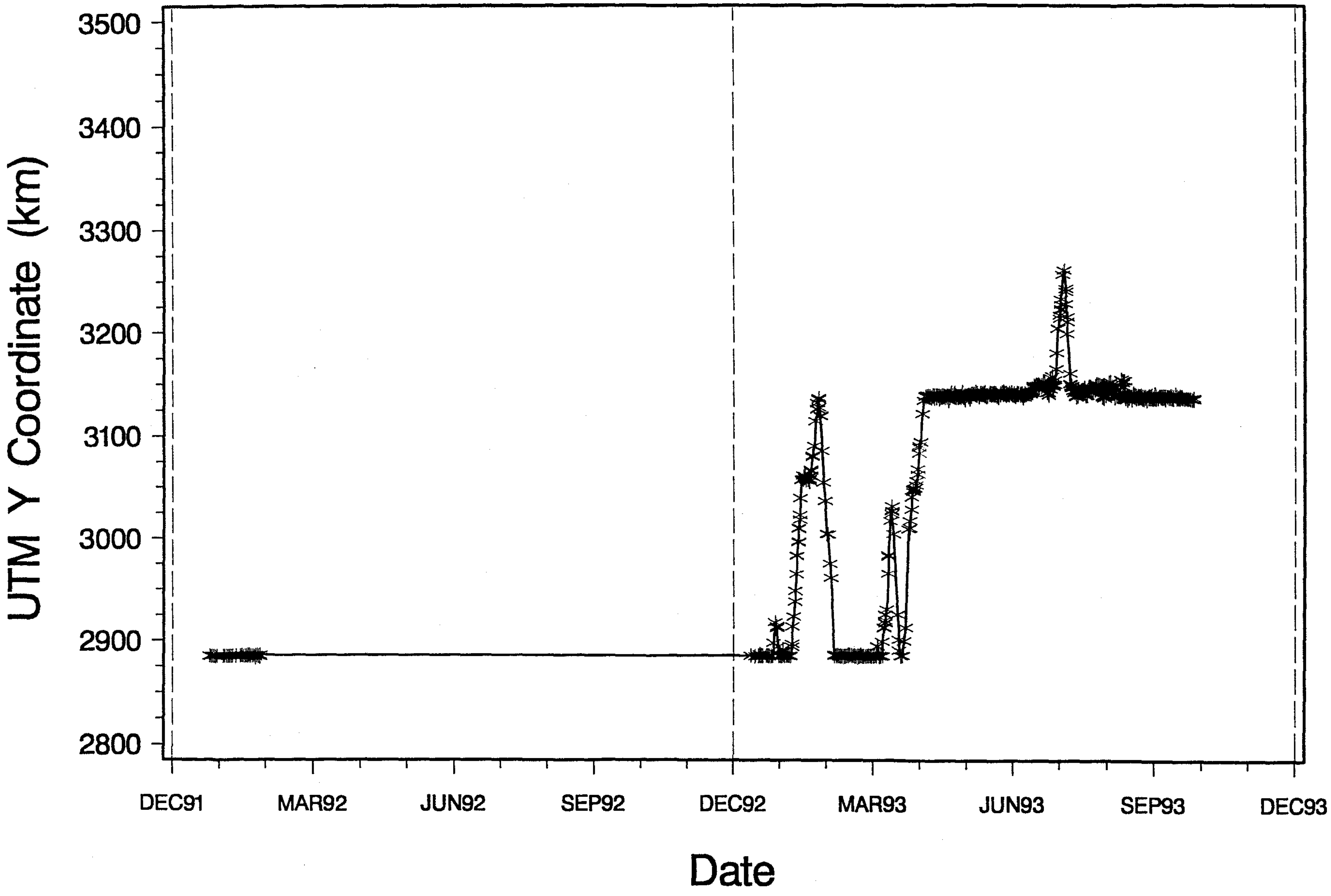
TPE – 02 ("Fireball"): 1989



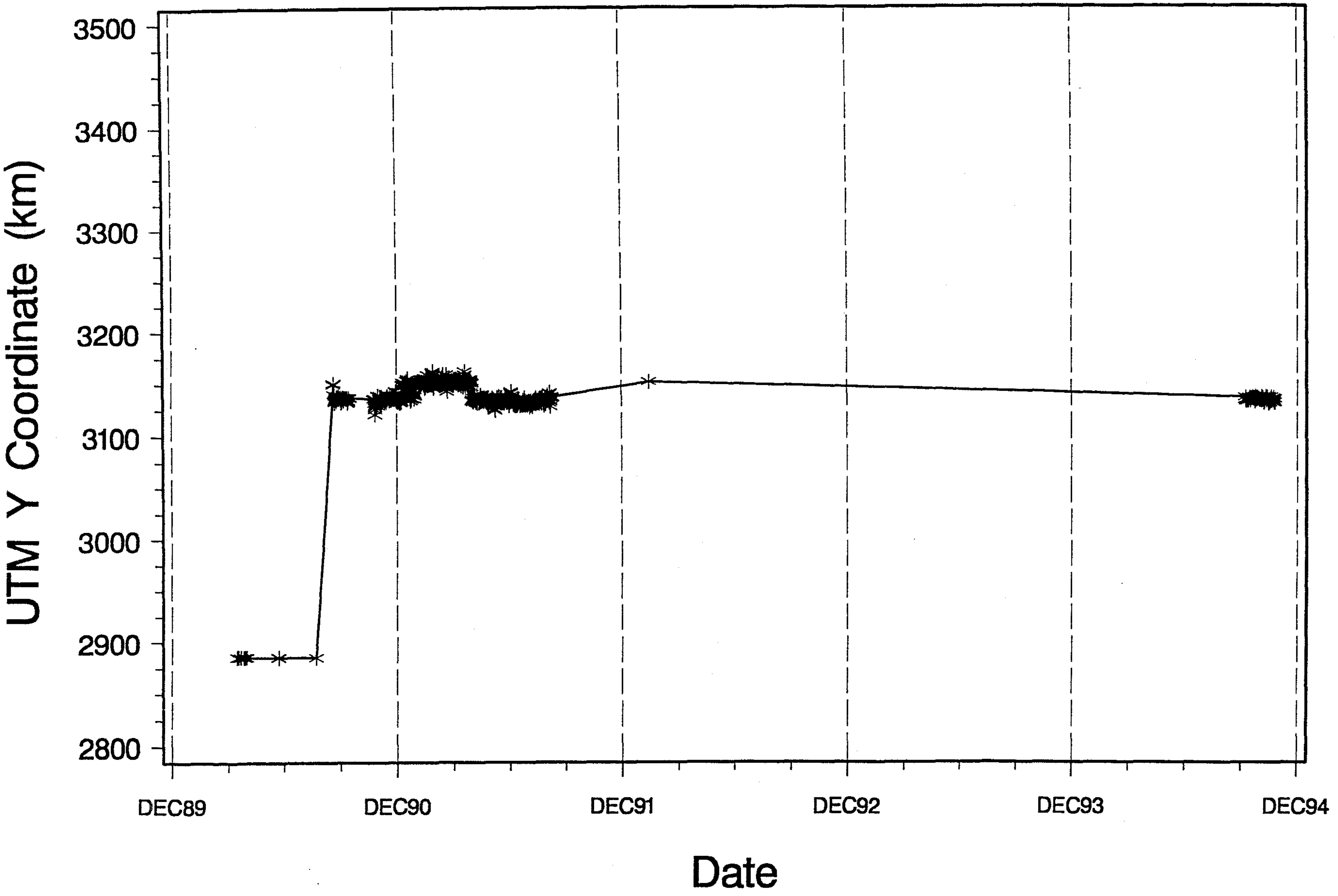
TPE – 03 ("Sickle"): 1989 – 1993



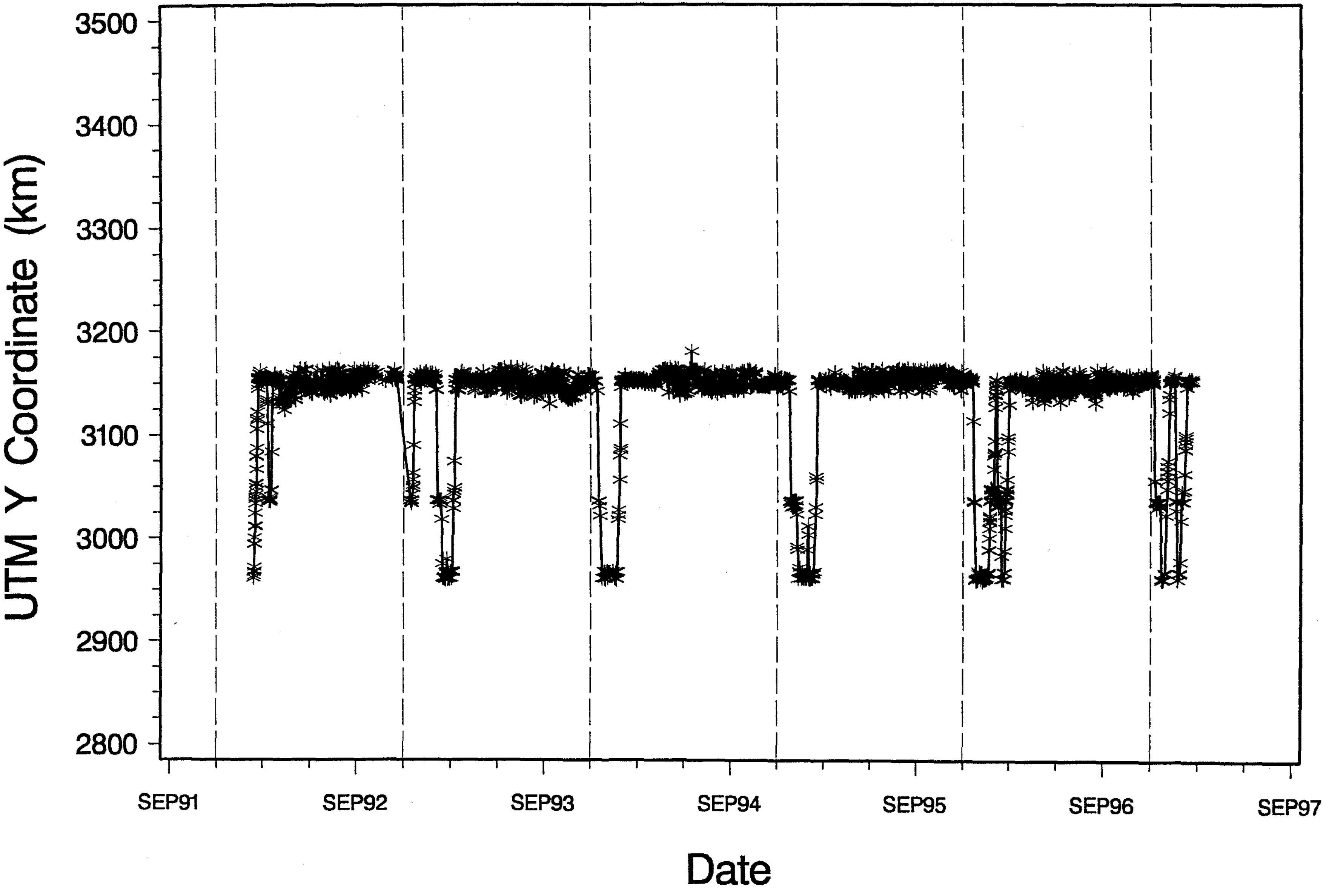
TPE – 03 ("Sickle"): 1991 – 1993



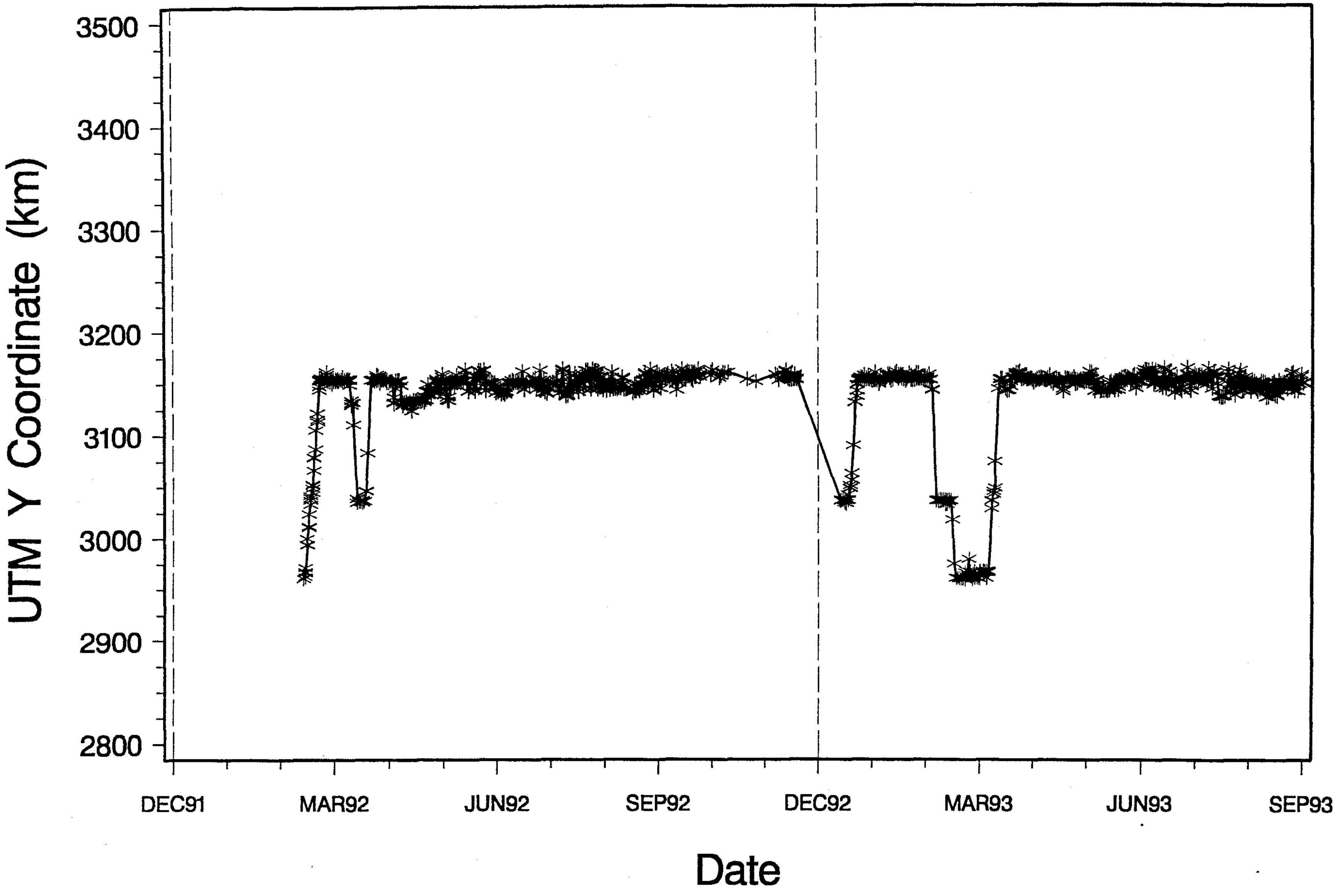
TPE – 04 ("Susan"): 1990 – 1994



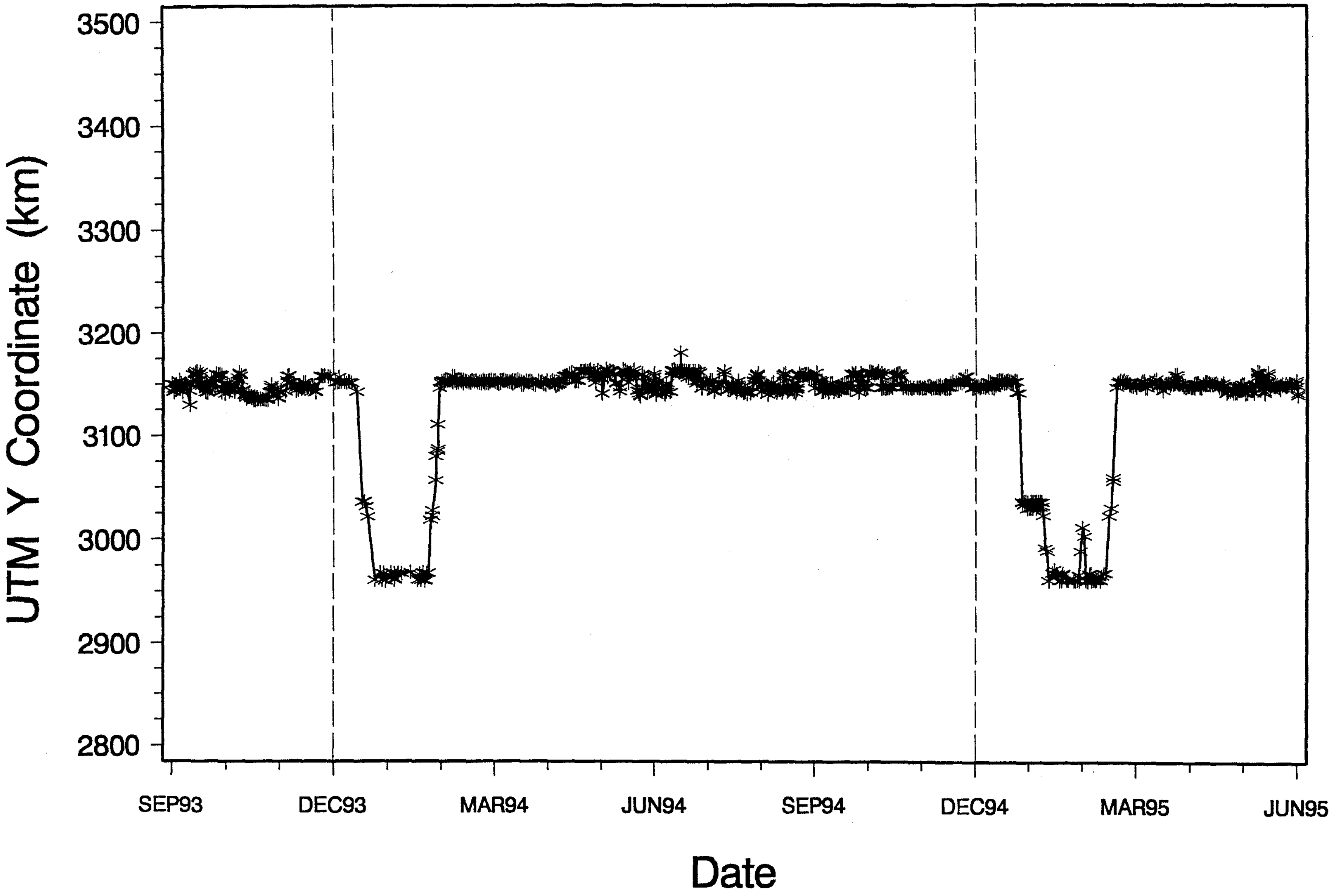
TRB – 01 ("Sonny"): 1992 – 1997



TRB – 01 ("Sonny"): 1992 – 1993



TRB – 01 ("Sonny"): 1993 – 1995



TRB – 01 ("Sonny"): 1995 – 1997