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Efficacy of subcutaneous VHF implants and remote telemetry monitoring to assess survival rates in harbor seals

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A long-term study to compare harbor seal (*Phoca vitulina*) survival rates between 2 study areas was conducted in Alaska, in Glacier Bay (GB) and Prince William Sound (PWS). Very-high-frequency (VHF) transmitters with 3.5- to 5-year batteries were subcutaneously implanted into 277 harbor seals; 122 in PWS from 2003 to 2005, and 155 in GB from 2004 to 2006. The presence of radiotagged seals was remotely monitored using VHF data-loggers, which transmitted data via the Geostationary Operational Environmental Satellite (GOES) system. The GOES site is administered by the National Oceanic and Atmospheric Administration, National Environmental Satellite Data and Information Service; data were accessible to researchers via telnet. Initial data-logging was plagued with ambient electronic interference ("noise"); subsequent equipment revisions substantially reduced the noise and resulted in 8,129 total "seal-days" (≥ 1 detection calendar day^{-1} seal^{-1}) of telemetry detections ($\bar{X} = 29$ days/seal $\pm$ 3.4 *SE*; maximum 424 days spanning 4.15 years). Although 84% of radiotagged seals were detected at least once during the year they were radiotagged, the proportion of tagged seals detected in subsequent years dropped to 59%, 28%, 0.9%, and 3% in the 1st through the 4th year, respectively. Tag failure and tag rejection, including 1 tag rejected 11.75 months after implantation surgery, were documented. There was almost no evidence of health problems at the time of implanting the tags in the harbor seals. Survey effort outside the study areas did not detect evidence of high emigration rates. Although subcutaneously implanted transmitters could be radiotracked during and after molt and the long battery life provided multiyear data on a subset of individual seals, this method of subcutaneously implanting radiotags was not effective for assessing the long-term survival rate of free-ranging harbor seals.

Key words: data-logger, Geostationary Operational Environmental Satellite (GOES), harbor seal, *Phoca vitulina*, radiotag, subcutaneous implant, telemetry, very high frequency (VHF)

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The most direct means of understanding fluctuations in population abundance is by estimating survival and reproduction, and quantifying how proximate factors (e.g., health, nutritional stress, and diseases) affect those vital rates (Boyd 2000; Bowen et al. 2003; Pistorius et al. 2004; Beauplet et al. 2006). Harbor seals (*Phoca vitulina*) experienced a long-term population decline (> 63%) in Prince William Sound (PWS), Alaska, since the mid-1980s (Frost et al. 1999; Ver Hoef and Frost 2003). In Glacier Bay (GB) National Park, surveys were initiated in 1992 that documented a decline in harbor seal numbers of similar magnitude (Mathews and Pendleton 2006) that continued through at least 2008 (Womble et al. 2010). The cause of the declines and the relative contribution of emigration, survival, and reproductive rates to the declines are unknown.

Research and modeling have shown that growth rates in pinniped populations are sensitive to adult female survival, and that pup survival, age of 1st reproduction, and reproductive rates may further influence population growth in a density-dependent fashion (Taylor and DeMaster 1993; Harwood and Rohani 1996; Wickens and York 1997; Pistorius et al. 2001; Bowen et al. 2007; Rotella et al. 2012). Delayed age of 1st reproduction or low reproductive rates may result from reduced nutrition (Robbins 1993; Kitaysky et al. 2010). Diminished reproduction also may result from exposure to environmental contaminants or disease (Addison 1989; Ross 2002; Levin et al. 2005; Brodie et al. 2006).

This study was designed to use capture–mark–recapture analysis (Williams et al. 2001) of telemetry data from harbor seals to determine whether vital population parameters could be estimated with sufficient precision and accuracy using subcutaneously implanted very-high-frequency (VHF) transmitters with a long battery life (Lander et al. 2005). Data obtained from radiotracking seals over multiple years, paired with data on diet and health status, and morphometrics of individuals at the time of capture, were expected to facilitate an assessment of factors that differentiated harbor seals that survived from those that did not survive in the declining population of harbor seals at PWS and GB.

Traditionally, radiotransmitters have been attached to the pelage of pinnipeds (Jeffries et al. 1993; Lowry et al. 2001), providing a maximum of 10–12 months of data before the radiotag is shed during the annual molt. Transmitters attached to the webbing of the hind flippers may endure for longer; however, even low-profile plastic identification tags attached to flipper webbing are subject to tag loss (Bradshaw et al. 2000; Pistorius et al. 2000), and the larger bulk of radiotransmitters makes them even more prone to being torn from flippers or suffering a broken antenna and failed transmissions (Williams and Siniff 1983). A subcutaneously implanted transmitter, which requires a relatively simple surgery, is not affected by molting and potentially could provide long-term data for an individual. The duration of data collection is limited only by battery life, retention of the tag by the animal, and the successful function of the transmitter. Subcutaneous implants have been used successfully in a variety of bird species (O'Hearn et al. 2005; Gregg et al. 2007) and with limited success in American black bears (*Ursus americanus*—Echols et al. 2004), European badgers (*Meles meles*—Agren et al. 2000), and sea otters (*Enhydra lutris*—Williams and Siniff 1983). A surgical technique was used in this study that was developed and tested at The Marine Mammal Center to subcutaneously implant VHF transmitters into harbor seals (Lander et al. 2005). To our knowledge, this study was the first to use this tagging method for a population-level study of free-ranging harbor seals.

In addition to telemetry data collected by observers in vessels and fixed-wing aircraft, on-site data-loggers and a remote satellite-linked, land-based tracking system were used to continuously scan for presence of signals from radiotagged seals. Similar equipment had been thoroughly field-tested to successfully track salmon (*Oncorhynchus* spp.) in 2 years of field studies (Eiler 1995), resulting in the collection of significantly more data than would have been possible using standard telemetry methods.

Herein, the efficacy of using subcutaneously implanted VHF transmitters and remote telemetry monitoring to collect data on long-term vital rates from harbor seals are reported for 2 study areas in Alaska.

Materials and Methods

Study areas, seal capture, and seal handling.—Harbor seals were captured, radiotagged, and radiotracked in PWS in south-central Alaska, and GB in southeastern Alaska (Fig. 1). Seals at PWS were captured in 2003–2005 at terrestrial sites that were predominantly rocky areas, and seals at GB were captured in 2004–2006 at terrestrial sites and at Johns Hopkins Inlet, a tidewater glacier inlet (Fig. 1). A multifilament seine net was used for terrestrial captures (Jeffries et al. 1993) and monofilament gill nets were used for capturing seals in the glacial ice (Blundell et al. 2011). Following capture, the seals were transported to a research vessel where the sex and mass (to the nearest 0.1 kg) of the seals were determined, and surgeries were performed.

Surgical methods.—Because population dynamics are most strongly influenced by female survival and reproductive success, and by survival and recruitment of young (Bowen et al. 2007; Rotella et al. 2012), females and young-of-the-year were preferentially selected to receive implanted VHF radiotags. Docile surgical candidates received inhalant anesthesia (Isoflurane or Sevoflurane), administered via a face mask, whereas more aggressive seals received intravenous Telazol (0.8 mg/kg) or diazepam (0.25mg/kg) as a preanesthetic prior to administration of the inhalant. These anesthesia and sedation products are available from Henry Schein Animal Health (Columbus, Ohio). All seals were intubated and maintained on inhalant anesthesia during surgery. As anesthesia began to take effect, a physical exam was conducted and length and girth of each harbor seal were measured to the nearest centimeter. If a seal showed signs of stress from anesthesia or physical ailments were detected, the seal did not undergo surgery to implant a VHF transmitter. This happened on only 1 occasion, when a seal coughed continuously and showed signs of respiratory distress when the face mask was applied to administer inhalant anesthesia.

A surgical site was prepared caudal to the scapula and lateral to the spine on the seal's right side by removing a patch of fur with a #40 blade. Using standard sterile preparation procedures for a surgical site, the shaved area was scrubbed multiple times with alternating applications of iodine-based surgical scrub and isopropyl alcohol, and sprayed with a final iodine-based surgical-preparation solution. Sterile surgical drapes were placed around the prepared surgical site, leaving the seal's head accessible for continuous monitoring of anesthetic level, respiration, and mucous membrane color. A pulse oximeter, capnograph, and flexible rectal temperature probe also were used to monitor the seal during surgery. Once the animal reached a surgical plane of anesthesia, the surgery commenced. An incisor tooth was extracted with a dental elevator and dental extraction forceps for age estimates using cementum annuli (Blundell and Pendleton 2008).

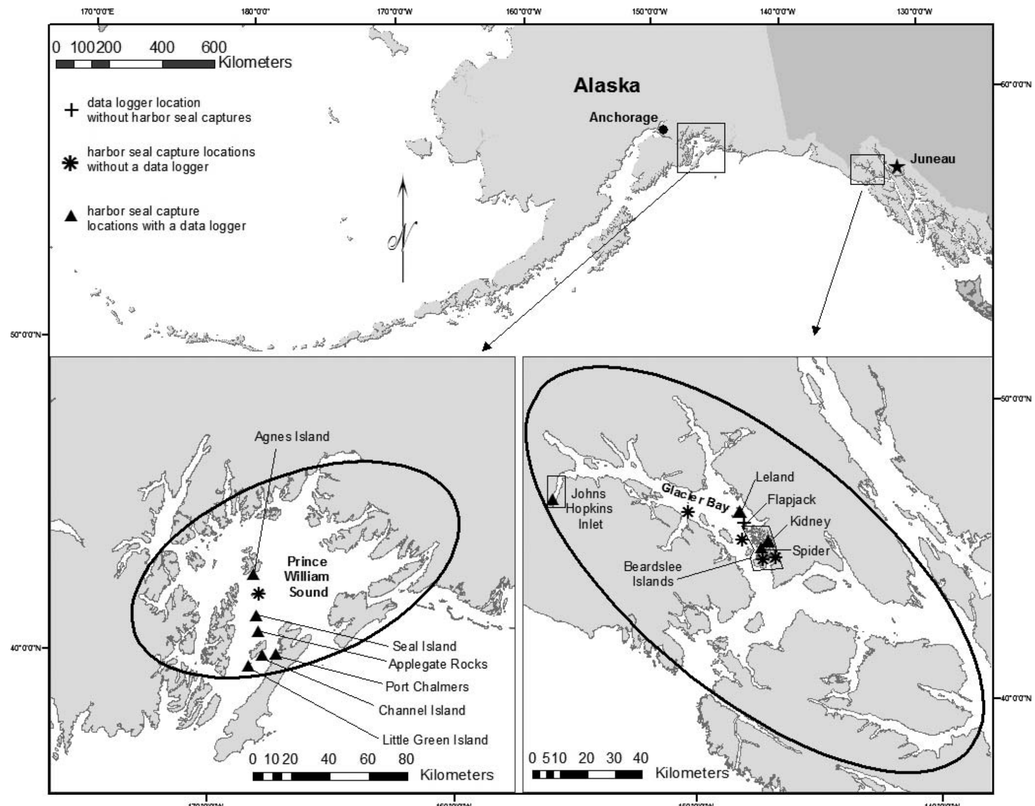

Fig. 1.—Study areas where harbor seals (*Phoca vitulina*) were radiotagged and locations of remote telemetry-monitoring stations. Ovals indicate areas where additional telemetry surveys occurred to search for radiotagged seals that may have emigrated from the primary study areas.

Surgical procedures were identical to those described in Lander et al. (2005) for subcutaneously implanting gas-sterilized IMP-300-L VHF transmitters (Telonics, Mesa, Arizona) into harbor seals (Fig. 2). Prior to this study, veterinary personnel received training on the surgical procedure from Dr. Martin Haulena, a staff veterinarian at The Marine Mammal Center, who was involved in developing the surgical technique used by Lander et al. (2005). Any new veterinary surgeons that joined the research team worked directly with those that had previously performed the surgery to ensure consistency in surgical methods throughout the study.

As the surgery was nearing completion, administration of inhalant anesthesia ceased and the seal was maintained on oxygen until the seal was awake enough to necessitate removal of the endotracheal tube. To alleviate pain and inflammation, seals received an intramuscular injection of flunixin meglumine (Banamine; Henry Schein Animal Health), administered postoperatively at a dosage of 1 mg/kg. Once extubated, the seal was moved to a recovery pen and monitored closely for 30–60 min for signs of respiratory or thermoregulatory distress. Seals were retained until they were sufficiently recovered from effects of anesthesia and alert enough to voluntarily jump out of the boat under their own power (within 1.5–2 h).

All capture, handling, and surgical protocols followed the guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Alaska Department of Fish and Game, Animal Care and Use Committee and the Alaska SeaLife Center, Institutional Animal Care and Use Committee. All procedures were conducted in accordance with National Marine Fisheries Service research permits 358-1585 and 358-1787.

Very-high-frequency implants.—To extend the battery life, all VHF-transmitter implants were duty cycled at 25–30 pulses/min (ppm) and transmission of radiosignals was limited to 4 h

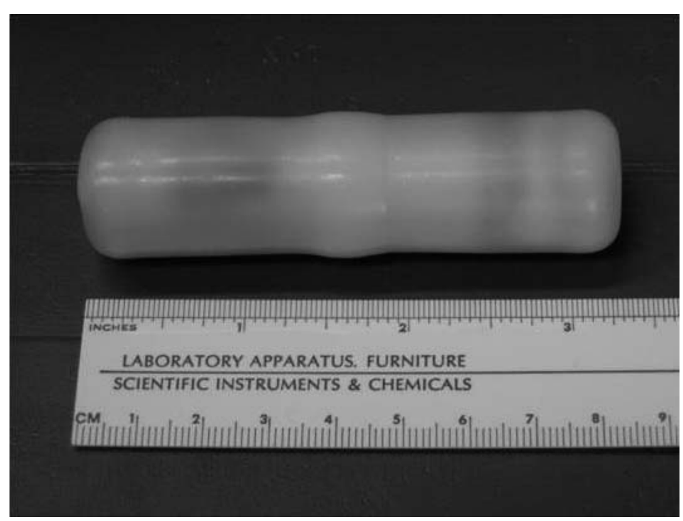

Fig. 2.—Telonics IMP-300-L very-high-frequency transmitter. Transmitters were gas sterilized and subcutaneously implanted into harbor seals.

daily (i.e., 4 h on, 20 h off). Transmitters did not contain actual clocks; instead, they operated on a 24-h time cycle and had to be activated at the beginning of the time period in which they were meant to be transmitting. On the day prior to initial seal captures, 10–15 transmitters were activated by removing the magnet at approximately 1000 h (± 15 min), to allow transmission of signals from ~1000 to 1400 h, when seals were most likely to be hauled out (Small et al. 2003) and more easily located. Transmitters were implanted into seals 1–5 days after activation; function of previously activated transmitters was confirmed as the surgical supplies were prepared for each implantation surgery. Additional batches of transmitters were activated as needed to ensure that transmitters, activated on the proper time schedule, were always available for implantation surgeries.

Transmitters had a temperature-sensitive mortality switch; if a seal's body temperature was ≤ 27°C, the mortality switch activated and doubled the pulse rate of the transmitter. VHF implants deployed at PWS in 2003 were duty-cycled to achieve an anticipated 3.5 years of battery life at 30 ppm. Transmitters deployed in PWS in 2004–2005 and all VHF implants deployed in GB were duty-cycled with a target battery life of 5 years at 25 ppm. All implants transmitted signals for the same 4 h each day; battery life was extended by slowing the pulse rate by 5 ppm. A 5-year battery life was selected to allow tracking of female pups until the average age of 1st reproduction (Pitcher and Calkins 1979; Lydersen and Kovacs 2005). Although this extended battery life was theoretically plausible, Telonics had not field-tested transmitters for long-term function and therefore did not guarantee tag function beyond 3 years.

Other telemetry tags.—During the 1st season in PWS (April 2003) all seals that received VHF implants also were equipped with head-mounted VHF transmitters (MM300; Advanced Telemetry Systems [ATS], Isanti, Minnesota) to facilitate relocations and establish tracking range and function of implant transmitters. A subset of seals with VHF implants in GB also received externally attached Time Depth Recorders (MK9; Wildlife Computers, Redmond, Washington) and ATS MM300 head-mounted VHF transmitters for a companion study (Blundell et al. 2011); this allowed verification of the implanted-tag function on a short-term basis until the external tags were shed during molt.

Radiotelemetry.—Over the course of the study, telemetry tracking was accomplished from boats and fixed-wing aircraft and by using remote data-logging telemetry receivers that either logged data on site or transmitted data via satellite. The 1st year (2003) of subcutaneous radiotagging was considered to be a pilot season; continuation of the study would only occur if the tagging method appeared viable and seals were successfully recaptured via telemetry detection. In 2003, vessel-based radiotracking was conducted from a 6-m skiff using a handheld 3-element yagi antenna and a Telonics TR-5 receiver. Tracking began 5–10 days after each capture trip when signs of acute postsurgical complications would be most apparent. Tracking trips ranged from 4 to 11 days in duration. In subsequent years in both study areas, seals were radiotracked from vessels and fixed-wing aircraft during spring and summer months (Table 1). From 2003 to 2006, for 2–3 days each year, while conducting annual population-trend surveys throughout PWS (Frost et al. 1999), scans for VHF-implant frequencies were conducted well beyond the study area covered by the remote-monitoring stations (Fig. 1), attempting to locate seals that may have dispersed (Table 1). In May 2005 and May and June 2006, extensive surveys were flown throughout PWS (Fig. 1) looking for pupping sites and listening for VHF-implant frequencies, resulting in 79 total days of aerial or vessel-based radiotracking throughout the study. In GB, extensive radiotracking surveys within the study area in 2004–2008 (Table 1) and beyond the study area in 2005 and 2007 (Table 1; Fig. 1) were conducted, for a total of 170 aerial or vessel-based survey days.

In 2004, 3 ATS R4500S receiver–data-loggers (Table 2), which had an integrated noise-reduction unit to filter ambient electronic interference, were deployed. One R4500S was deployed in PWS at Applegate Rocks and 2 were deployed in GB in the Beardslee Islands at Kidney and Leland reefs and later moved to Spider Island and Flapjack reefs (Table 2; Fig. 1), when it became apparent that seals hauled out more often at the latter 2 sites.

Prior to field deployment of these data-loggers, ATS conducted tests of R4500S units to assess performance in conjunction with the VHF implants; the programming was revised to facilitate detection of the narrow pulse width of the transmitters as a result of their slow pulses per minute. VHF transmitters are generally in the 50- to 55-ppm range and have a 20-ms pulse width, whereas the 25- to 30-ppm implant transmitters used in this study had pulse widths of 12–15 ms. Regrettably, ambient electronic interference (hereafter referred to as "noise") also usually has a narrow pulse width and a random pattern. A trade-off of narrow pulse width for weaker signal strength (i.e., decreased reception range) was adopted for the VHF implants to extend the potential battery life to 5 years.

R4500S configuration.—A list of VHF frequencies deployed in each area was created in a spreadsheet and imported into R4500S units deployed in both areas. A combined list of frequencies for both areas was not used because the distance between PWS and GB is > 700 km (Fig. 1) and the distance separating the 2 study areas is farther than harbor seals generally travel. The average maximum distance that harbor seals tagged in PWS in 1992–1996 traveled from their tagging location was 96.6 km for 22 juveniles and 61.3 km for 27 adults; maximum distance traveled by an individual in each age class was 525 km and 189 km, respectively (Lowry et al. 2001). The average maximum distance that 27 harbor seal pups tagged in PWS in 1997–1999 moved was 43.2 km; maximum individual distance was 374 km (Small et al. 2005). Among 37 seals tagged in GB in 2007–2008, 1 seal traveled the longest distance ever reported for a harbor seal, spending time in PWS from late October to early January before returning to the GB area the following spring (Womble and Gende 2013).

Table 1.—Days of effort by month and year for very-high-frequency–telemetry data collected by observers in vessels or fixed-wing aircraft in Prince William Sound and Glacier Bay.

		No. days of vessel or aerial telemetry effort			
Year	Month	Glacier Bay	Outside of Glacier Bay study area	Prince William Sound	Outside of Prince William Sound study area
2003	April			1	
	May	No seals tagged		4	
	June	in 2003		3	
	July			10	
	August			4	3
	September			1	
2004	May	13		2	
	June	15		6	
	July	12		9	
	August	1		3	3
	September	1			
2005	March			1	
	May	13	1		2
	June	15	2		
	July	12			
	August	1		3	3
	September	1			
2006	May	10		5	2
	June	13		6	2
	July	10			2
	August	4		2	2
2007	June	5			
	July	2	3		
	August		8		
	September		1		
2008	June	8			
	July	7			
	August	7			
	September	5			

Each R4500S unit was programmed for a stationary scan and programmed to scan for fixed pulse rates with a continuous scan. The appropriate pulse rates for each type of transmitter deployed in the area were entered into the configuration, and tolerance was set at 0, unless more than 3 pulse rates were deployed in the area and 2 pulse rates could be scanned by increasing the tolerance value. Time-out was set to 10 s, scan-time was set to 20 s, and store-rate was set to 10 s. For further information on these settings, consult the *R4500S User Manual* available at the ATS Web site (ATS 2004).

One or two 4-element directional yagi antennas from ATS were deployed at each site; 1 antenna was used if signals were expected to be received solely when seals were hauled out on that site, 2 antennas were used when seals also might be hauled out on a nearby reef. For 2-antenna stations, R4500S units were originally configured for 2 antennas, and an antenna splitter (available from ATS) or an antenna switch box locked onto both antennas was used. Scanning independently for each antenna did not provide directional data and the extended scan-time required for 2 antennas reduced the total number of scans per animal possible each day. Subsequently, the data-loggers were programmed to scan with only 1 antenna and the antenna splitter was replaced with a 0-degree splitter to allow scanning and logging of data from both antennas simultaneously.

To ensure that each monitoring site was detecting seal presence, rather than logging false positives from noise, several methods were incorporated to verify data integrity. A reference transmitter, which transmitted a signal 24 h/day, was positioned near each monitoring station and the frequency was programmed into the data-logger. The reference transmitter should have been detected on every scan cycle, verifying that the equipment was operational. Three dummy VHF frequencies (i.e., frequencies not deployed in the area) also were scanned. If dummy frequencies were present, any seal frequencies that were concurrently recorded were reviewed; if they were recorded only in conjunction with dummy frequencies, they were rejected as noise.

Geostationary Operational Environmental Satellite transmissions.—In 2005, remote, satellite-linked monitoring was initiated using a Geostationary Operational Environmental Satellite (GOES) to relay logged telemetry data. The GOES system is administered by the National Oceanic and Atmospheric Administration, National Environmental Satellite Data and Information Service. Campbell Scientific (Logan, Utah) TX312 GOES transmitters, together with ATS R4500S data-loggers (Fig. 3A), were installed at 6 sites at PWS and 1 site at GB. The single GOES site at GB was at Johns Hopkins Inlet and the 6 sites at PWS were at Applegate Rocks, Seal Island, Agnes Island, Little Green Island, Channel Island,

Table 2.—Months and years in which land-based remote telemetry-monitoring stations were operating. As of 2005, all Prince William Sound stations and Johns Hopkins Inlet (JHI) in Glacier Bay transmitted data via Geostationary Operational Environmental Satellite.

		No. days remote-telemetry sites were operational										
		Glacier Bay					Prince William Sound					
Year	Month	JHI	Flapjack	Spider	Leland[a]	Kidney[b]	Agnes Island	Seal Island	Applegate Rocks	Port Chalmers	Channel Island	Little Green
2004	January								13			
	February								12			
	March								21			
	April			1	8	4			26			
	May			31	31				28			
	June			14	11				28			
	July		2	20					1			
	August		0	14					13			
	September		0	0					25			
	October		0	0					31			
	November		0	0					24			
	December		0	0					9			
2005	January		0	0								
	February		0	0								
	March		0	0								
	April		0	0								
	May		0	3								
	June	7	15	30								
	July	12	15	31			14	6	15	17	17	17
	August	31	0	31			31	23	31	31	31	31
	September	31	0	24			30	25	30	30	30	30
	October	31	0	15			31	3	31	31	31	31
	November	30	0	7			30	19	30	26	30	30
	December	31	0	2			31	10	31	27	31	31
2006	January	31	2	1			22	16	31	6	30	28
	February	28	0	8			26	10	27	9	26	26
	March	31	0	30			30	10	31	5	30	31
	April	29	0	30			23	2	30	22	22	24
	May	24	13	31			25	20	30	27	29	29
	June	30	30	16			30	30	28	30	28	30
	July	31	14	17			29	29	21	29	31	29
	August	31	10	24			24	14	27	21	28	25
	September	30	4	0			25	5	30	6	20	25
	October	31	0	0			29	1	31	0	28	31
	November	30	0	0			30	18	29	0	30	30
	December	31	0	0			31	4	28	2	26	30
2007	January	31	31	0			25	1	31	1	29	29
	February	28	27	0			23	2	28	2	21	23
	March	31	31	0			23	6	31	2	29	29
	April	30	21	8			24	2	30	10	28	24
	May	31	0	31			2	30	31	21	10	31
	June	30	0	30				27	30	28	21	29
	July	31	7	31				29	31	22	23	30
	August	17	31	31				17	31	21	26	17
	September	30	15	15				28	30	6	30	30
	October	25	0	0				25	30	1	28	23
	November	28	0	0				28	26	1	29	26
	December	19	0	0				16	10	3	21	19
2008	January	31	0	0				30	3	31	12	31
	February	29	0	0				26	10	28	7	28
	March	7[c]	0	0				22	1	27	12	27

and Port Chalmers (Fig. 1; Table 2). Two other data-logging sites at GB (at Spider Island and Flapjack) were maintained without satellite linkage. An engineer from ATS was present during the installation of the 1st GOES R4500S system at GB to assure that the equipment was deployed correctly. The same techniques for deploying identical equipment were used at PWS.

Effective use of GOES equipment required selection of a site that had an unblocked view of the horizon on a direct azimuth to the appropriate satellite in the GOES system. The selected

Table 2.—Continued.

		No. days remote-telemetry sites were operational										
		Glacier Bay					Prince William Sound					
Year	Month	JHI	Flapjack	Spider	Leland[a]	Kidney[b]	Agnes Island	Seal Island	Applegate Rocks	Port Chalmers	Channel Island	Little Green
	April		0	0			29	7	30	4	24	
	May		0	0			25	18	29	11	20	
	June		0	25			26	27	30	6	20	
	July		0	31			22	12	30	14	27	
	August		2	31					31		25	
	September								4		4	
	October								4		4	

[a] Leland station was moved to Flapjack in July 2004.
[b] Kidney station was moved to Spider in April 2004.
[c] The JHI station was destroyed by snow.

site also needed sufficient sun exposure for solar panels and a direct line-of-sight to nearby harbor seal haul outs for positioning of directional yagi antennas. To improve transmission–reception range and increase sun exposure at all GOES sites, towers were built to elevate the antennas and solar panels (Fig. 3B).

From 2005 to 2008, telemetry data were transmitted via GOES and relayed to a receiving station at the National Environmental Satellite Data and Information Service. The R4500S units continually logged telemetry data. Once per hour during a 10-s transmission, each uniquely identified GOES transmitter relayed the time and date of all logged frequencies, along with signal strength, noise levels, and battery voltage of the monitoring equipment.

Power management and equipment protection.—The remote monitoring stations were powered with two 85-W solar panels (Fig. 3B). Six 232-Ah 6-volt deep-cycle batteries were wired in series and in parallel and stored in an enclosed weatherproof container. The electronic equipment at each site was contained in a Pelican case (Torrance, California), along with a wiring panel (Fig. 3A) and an Automatic Sequencing Charger voltage regulator (Specialty Concepts Inc., Chatsworth, California).

Data management.—Large amounts of data were generated by multiple remote-monitoring stations transmitting data hourly. A computer script was written in AutoIt freeware (AutoIt Consulting 2005) to automatically contact the National Environmental Satellite Data and Information Service Web site via telnet, every other day, and download data from each site, merge the data for all sites once weekly, and run encrypted data through a translation program provided by ATS.

A code was written using SAS software (version 9.1—SAS Institute Inc. 2004) to sort and filter data and remove duplicates (e.g., data transmitted via GOES and the same data downloaded directly from the R4500S units). Data were identified as "good" if recorded from 0945 to 1415 h for VHF implant or 24-h for other VHF transmitter, pulse rate was correct (live or mortality), and noise level was < 1. Prior to switching to monitoring both antennas simultaneously, data were considered as good only if frequencies were recorded on > 1 antenna (i.e., antenna 0 initially evaluates both antennas for signal reception before switching to monitoring antenna 1 and then antenna 2, thus data needed to be recorded on more than just antenna 0 to be retained as good data). Error data were sorted into separate files and identified by error type and data-logging location to aid in diagnosing and fixing problems at specific sites.

Data analysis.—Because of large numbers of seals for which telemetry signals were no longer detected (i.e., fate unknown) as the study progressed, data were insufficient for mark–recapture analysis. Alternative methods were used to evaluate factors that might have contributed to poor detection rates. To assess the likelihood of detecting seals with implanted transmitters over time (years), data were fit using generalized linear mixed models (GLMM) in R version 2.15.2 statistical programming language (R Development Core Team 2012) and the linear mixed-effects models package lme4, version 1.0–5 (Bates et al. 2013). Logit link and binomial variance were used to analyze the relationship between the detection of seals tagged with subcutaneous implants and year in which the seal was tagged, age, sex, location, season in which the seal was tagged (tag season), and maximum years detected. Probability estimates of detection were determined using the R package effects (version 2.3-0—Fox et al. 2013). The response variable, Detected, was binary with a "1" indicating a seal was detected during a year and "0" indicating it was not detected. Model covariates included the categorical variables: Year (2003–2006); Age with 4 levels (Young of Year [YY], Yearling [Yrl], Subadult [SA], and Adult [AD]); Sex; Tagging Location (PWS, GB Terrestrial Sites, and GB–Johns Hopkins Inlet); Tag Season (spring, summer, and fall); and Maximum Years Detected. Year Post-Tagging was included as a quadratic effect. Because individual seals were detected in more than 1 year, Animal ID was included as a randomized effect. Reverse stepwise regression was used to sequentially remove least significant variables with $P > 0.05$ after which the model was rerun until all effects significantly contributed to the model. Results reflect the combined performance of transmitters and receivers and survival of all seals that received implanted transmitters over time. A similar analysis was conducted using GLMM to evaluate body condition as an explanatory variable

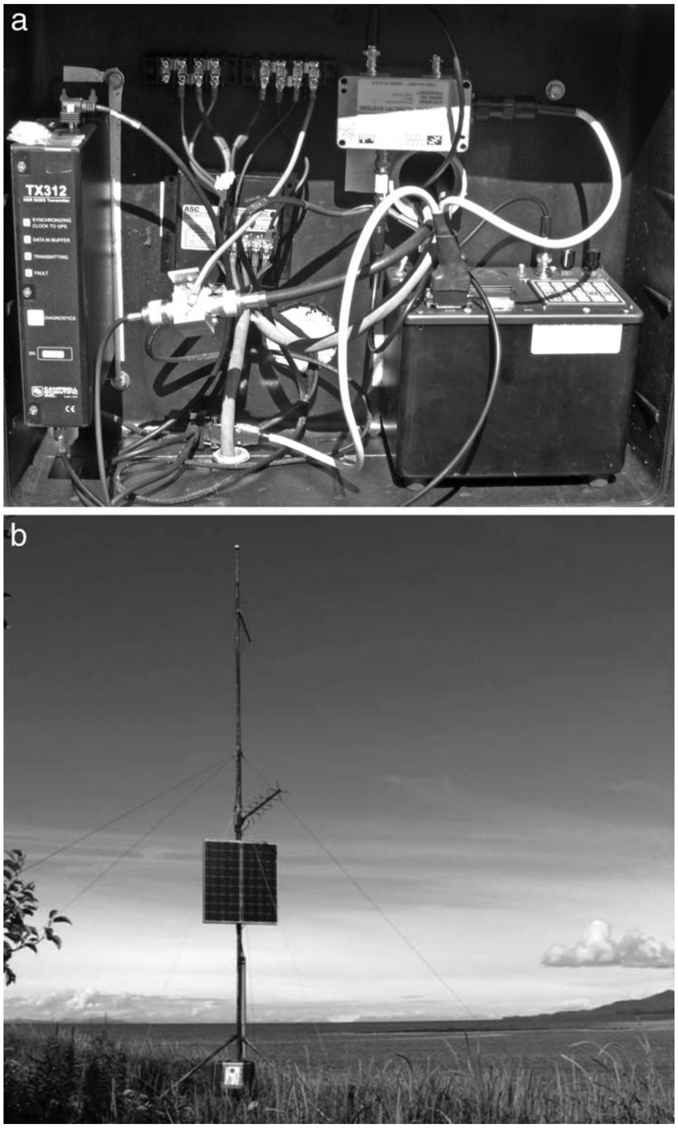

FIG. 3.—Remote telemetry-monitoring equipment. A) Upper photo shows equipment housed within a Pelican case, including TX312 (Geostationary Operational Environmental Satellite [GOES] transmitter) on the left and Advanced Telemetry Systems R4500S very-high-frequency scanner–data-logger on the right. B) The complete tower configuration with a single yagi antenna aimed at the seal haul out (reef) visible in the background on the right, Pelican case mounted on the base of the tripod, and GOES antenna oriented toward the stationary satellite.

in detection of transmitters; we used measurements of blubber depth taken during surgery as an additional covariate. These data were available for a subset of seals ($n = 163$).

For this analysis, only the telemetry data from April through August were used. Seals in GB, particularly those in the glacial habitat of Johns Hopkins Inlet, use the area seasonally, and are present at GB during those months (Mathews and Kelly 1996; Womble and Gende 2013), whereas seals at PWS generally remain within the area year-round (Lowry et al. 2001; Small et al. 2005). Tagging season was included as a covariate because many seals at GB were radiotagged during late summer or fall, shortly before seasonal movements generally occur (Mathews and Kelly 1996; Womble and Gende 2013). Therefore, GB seals may have been less likely to be detected with telemetry during the year in which they were tagged than were seals at PWS. Furthermore, fewer months remain in the year for detection possibilities before the end of the year when seals are tagged in fall, compared to spring and summer.

Year was included as a covariate to account for a reduction in telemetry effort for the predicted life of VHF-transmitter batteries for seals tagged in later years of the study. All PWS seals and GB seals tagged in 2004 had telemetry coverage for the capture year and 4 years posttagging. Seals tagged at GB in 2005 had focused telemetry effort for the capture year and the following 2 years, and partial coverage the 3rd year with remote monitoring at the terrestrial site with the highest use (Spider Island [Fig. 1; Table 2]) and observer tracking throughout GB, including Johns Hopkins Inlet (Table 1). Telemetry monitoring at GB in 2006 was comparable to previous years (Tables 1 and 2); however, when it became apparent that detection levels were too low to achieve the study objectives, further maintenance of malfunctioning remote telemetry stations was not warranted and telemetry effort in 2007–2008 was reduced compared to previous years.

Seals were placed into age categories based tooth cementum annuli estimations as follows: YY $= \leq 0.75$ years; Yrl $= 0.755 <$ age ≤ 1.75 years; SA $= 1.755 <$ age ≤ 3.75 years for females and $1.755 <$ age ≤ 5.75 years for males; AD > 3.75 years for females and > 5.75 years for males. Age divisions for SA versus AD were based on a literature review of the average age of 1st reproduction and sexual maturity for harbor seals (Blundell and Pendleton 2008).

RESULTS

Over the study, 122 subcutaneously implanted VHF transmitters were deployed in harbor seals in PWS and 155 were deployed in seals in GB (Table 3). Seals captured in both areas appeared to be in good body condition, with the exception of females that had recently weaned pups and, as a result, were in lower body condition. Seals generally showed no apparent signs of ill health, although coughing was occasionally observed in a few seals over the course of the study in each area, and lungworms (*Otostrongylus* spp. and *Parafilaroides* spp.) were observed when endotracheal tubes were extracted following surgery (Herreman et al. 2011).

Pilot season.—During the 1st capture trip (April 2003), 1 seal was opportunistically recaptured at 5 days after the implant surgery. The incision showed no evidence of infection and the seal's behavior and movements in the net were typical (fast and alert) as opposed to lethargic, which might indicate poor health from postsurgical complications. Four additional seals were observed within the 1st few weeks after surgery from a distance of 35–150 m using Leica 7× or 10× binoculars (Glazer's Camera, Seattle, WA); all seals exhibited normal body postures and movements when hauled out, or when they entered the

TABLE 3.—Number of harbor seals (*Phoca vitulina*) tagged with subcutaneous very-high-frequency implants by year and study area. Age estimates based on cementum annuli of incisor teeth and divided into 4 categories: YY (young of the year) = ≤ 0.75 years; Yrl (yearling) = 0.755 < age ≤ 1.75 years; SA (subadult) = 1.755 < age ≤ 3.75 years for females and 1.755 < age ≤ 5.75 years for males; AD (adults) > 3.75 for females and > 5.75 for males.

		Female					Male					
		Age class					Age class					
Study area	Year	YY	Yrl	SA	AD	Total	YY	Yrl	SA	AD	Total	Grand total
Prince William Sound	2003	4	14	7	7	32	6	2	1	7	16	48
	2004	11	6	3	8	28	5				5	33
	2005	8	7	4	7	26	14		1		15	41
Total		23	27	14	22	86	25	2	2	7	36	122
Glacier Bay	2004	11	11	3	5	30	5	3	2	10	20	50
	2005	23	13	2	5	43	15	2	2	5	24	67
	2006	24	4	3	5	36	2				2	38
Total		58	28	8	15	109	22	5	4	15	46	155
Grand total		81	55	22	37	195	47	7	6	22	82	277

water, swam at the surface, and dove, indicating no obvious signs of postsurgical discomfort.

A total of 92.6% of seals were detected at least once during the 2003 telemetry tracking, including 1 pup that had traveled 40 km from his capture site. No mortality signals were detected during any radiotracking trips during the 1st year. Given the high telemetry-detection rate and apparent normal behavior of harbor seals tagged with VHF implants during the 1st season in PWS, radiotagging of seals with VHF implants continued in PWS in 2004–2005 and a similar study in GB was initiated in 2004–2006.

Very-high-frequency implant function.—Two of the 31 VHF implants intended for deployment at PWS during the summer in 2003 were nonfunctional prior to surgical implantation; 1 could not be activated when the magnet was removed, the other transmitter was activated, but the signal transmission ceased 2 days later prior to implantation. Problems with activating transmitters, and subsequent predeployment failures, did not occur after 2003. Five seals that received implants in 2003–2006 (age at surgery: 2 male pups, a yearling male, a yearling female, and an adult female) were recaptured 7–12 months after their surgery. All had functional transmitters and completely healed incision sites, although 1 surgical site had no hair and another retained old hair after the rest of the coat had molted.

During vessel-based radiotracking, telemetry signals from harbor seals with VHF implants were reliably detected from a distance of 2.2 km (direct line-of-sight) and 1.3 km when seals were on the backside of a reef system (≤ 6 m high). During aerial surveys, VHF-implant signals could be detected from 2.3 km, flying at ~305 m in altitude.

During the 1st radiotracking fieldwork at PWS in 2004, a mortality signal was detected from an implanted transmitter of a yearling female, tagged in June 2003. The transmitter was buried in substrate below the mean high tide level, resulting in a signal that was only detectable during lower tides. Because her last nonmortality signal was documented the previous July, existing data could only confirm that the transmitter was retained and functional for a period of 9 days after the implant surgery. A 2nd transmitter, implanted in June 2004 in a yearling female, was unearthed from rocky substrate on a PWS haul out in August 2005. Again, due to gaps in telemetry surveys, transmitter function and tag retention for that seal could only be confirmed for ~1 month postsurgery. Tag retention and function for a 3rd transmitter, recovered from a haul-out site at PWS in 2005 following a 2004 deployment in a male pup, could also only be confirmed for ~1 month. One end of this transmitter was badly damaged. A 4th transmitter was recovered on a haul-out site at PWS in July 2006; a subadult female received that transmitter in 2003 and was last known to be alive in November 2005, confirming 19-month tag retention and function. Fate of the seals that had received these transmitters was unknown; no carcass remains were found anywhere near the tag recovery sites.

In 2004, a male seal was recaptured at PWS, 11.75 months after it received a subcutaneous transmitter as a yearling. The transmitter was partially exposed but held firmly in place in a

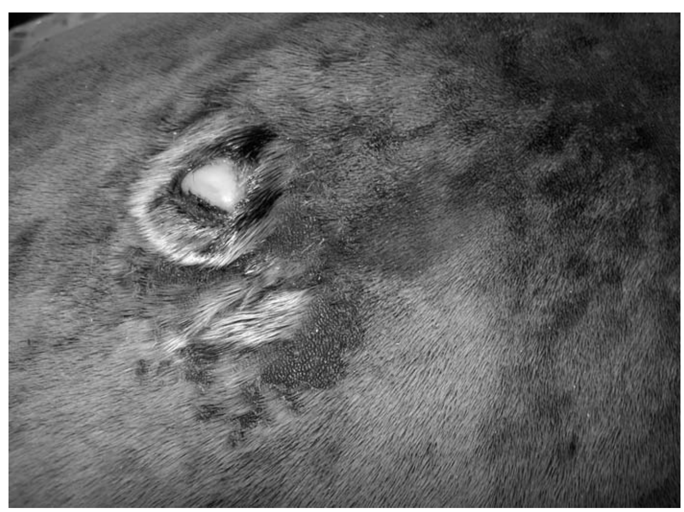

FIG. 4.—Partially extruded very-high-frequency–implant transmitter discovered when a harbor seal (*Phoca vitulina*) was recaptured 11.75 months after surgery for subcutaneous implantation of the transmitter. At the time of surgery the seal was a yearling (Yrl).

walled-off, uninfected, open wound (Fig. 4). The transmitter was easily removed by surgically expanding the size of the opening; no adhesions were evident, the wound was debrided and sutured closed. The seal appeared to be in good condition and had increased in mass, length, and girth during the intervening year. It had a normal white blood cell count indicating that a systemic infection was not occurring. The seal's white blood cell count was = 10,755 white blood cells/μl; average white blood cell count for 669 free-roaming harbor seals captured in Alaska is 11,542 white blood cells/μl (*SD* ± 3,775 white blood cells/μlG. M. Blundell, Alaska Department of Fish and Game, pers. comm.).

Remote telemetry-monitoring stations.—No data collected from the remote telemetry station established at PWS in 2004 were considered useful due to recording of excessive error data, which cast doubt about the few potentially legitimate records of seals noted as present. Poor-quality data were presumably a result of electronic interference from passing vessel traffic. Remote telemetry stations collecting data in 2004 at GB were confined to sites where motorized vessel traffic was prohibited; electronic noise was evident, but approximately half of those data were legitimate detections of radiotagged seals.

Beginning in 2006, GOES transmission of data was intermittent, particularly during winter, as a result of various problems with GOES equipment, including broken antenna elements, shifted antenna position, and problems with GOES transmitters that may have been caused by short circuits in the system as a result of dampness in the instrument case. During maintenance visits, data not transmitted via GOES were downloaded directly from functional R4500S units.

In the 1st few months of 2005 when GOES sites were collecting data at PWS, an unacceptably high occurrence of error data was identified. On average 70% of frequencies and 65% of hits (i.e., recorded data points including multiple records of presence of the same animal throughout the day) per day were filtered out as error data. In late September, an ATS engineer worked in the field to troubleshoot and conduct on-site modifications to reduce the prevalence of error data. Reference transmitters placed near each data-logging site were emitting overly strong signals that resulted in excess noise and caused interference on surrounding frequencies. The signal strength was reduced by moving the reference transmitters farther away from each station, or modifying the effective antenna-length by burying the transmitter with only a portion of the antenna exposed, or by shortening the antenna. Reference transmitter modifications were specific to each site; solutions were tested until the strength of the signal received from the reference transmitter was similar to VHF signals received from tagged seals.

Signal amplifiers originally installed in association with the antenna switch boxes were removed from each station and signal attenuators (3-dB and 5-dB in combination, or 10-dB) were added to modify the signal-to-noise ratio, thereby increasing the signal and dampening the noise. Sensitivity settings on each receiver were set to the middle of the range. Because seals were hauled out in close proximity to the R4500S units, it was unlikely that those strong transmitter signals also would be rejected as noise, despite having narrow pulse widths similar to the noise.

Revisions to equipment resulted in a reduction of the amount of error data to 56.8% of frequencies and 43.6% of hits. Although still unacceptably high, further modifications were not possible during fall and winter due to inclement weather. All stations at PWS remained functional (i.e., 2–31 days of telemetry data logged per month) throughout the 2005–2006 winter, along with the GOES site at Johns Hopkins Inlet in GB and 1 of the 2 sites without GOES (Table 2). Despite the large amount of data relegated to error files, the remaining error-free data yielded 824 total days when individual harbor seals in PWS were detected at least once on a haul-out site during that 1st year (July–December) of GOES tracking. The incidence of error data logged in GB was much lower, likely due to considerably less vessel traffic in that area. Nonetheless, the total seal-days logged (i.e., ≥ 1 detection in a calendar day for an individual seal) in GB ($n = 337$) were less than in PWS, which likely reflected seasonal use patterns for seals in GB (Mathews and Kelly 1996; Womble and Gende 2013).

Subsequent to the considerable error data logged in 2005, ATS engineers modified the programming to improve the R4500S units filtering of noise. The upgraded programming, installed in 2006, resulted in substantial improvement in the quality of the data collected; only $< 7\%$ of the frequencies logged by the monitoring equipment were rejected as error data, and $< 5\%$ of the hits were rejected. Cross-matching of data logged on site and radiotelemetry data collected by observers conducting aerial or skiff-based telemetry surveys in 2006 confirmed that data logged by the R4500S units were accurate (i.e., reference and seal transmitters that were present were logged as present, rather than being rejected as noise). Similarly, low occurrences of error data were noted for all subsequent years of remote telemetry monitoring for this study.

Total telemetry detections.—Land-based monitoring stations provided $> 80\%$ of the telemetry data in this study. A total of 8,129 seal-days of detections (i.e., ≥ 1 detection in a calendar day for an individual seal) were logged for all seals in both areas. Individual seals averaged 29 (± 3.4 *SE*) calendar days of telemetry detections; the median number of days detected was 8.

A total of 7,293 days of seal detections were logged during summer months (April–August), whereas only 836 days of seal detections occurred during winter months (September–March). The difference in number of detections was not a result of disparity in telemetry effort between seasons; there were 3,513 possible days of detections during the summer for all years using all telemetry methods (i.e., days from Table 1 and Table 2 combined), compared with 3,548 possible days of detection during winter. Although most seals were last detected during summer months, 24.6% of radiotagged seals were detected for the last time during the winter. Only 2.2% of radiotagged seals were detected only in the winter months; however, those seals had a total of only 1 location each.

Table 4.—Fixed effects influencing detection of telemetry signals from harbor seals with subcutaneous transmitters implanted from 2003 to 2006 in Prince William Sound and Glacier Bay, Alaska.

Effect	Estimate	*SE*	*z*-value	Pr(>|*z*|)
Intercept	0.56531	0.19542	2.893	< 0.0001
Tag season summer	−0.20933	0.19283	−1.086	0.27765
Tag season fall	−0.78529	0.20042	−3.918	< 0.0001
Year posttag	−1.32303	0.07586	−17.44	< 0.0001
Maximum year detected	1.15523	0.08322	13.882	< 0.0001

Multiple years of telemetry data were logged for 72 seals, with detections through at least the 2nd year after tagging. Detections spanned an average of 540 days (± 26.4 *SE*) from capture to last-known-alive location. A maximum of 424 days of detections was recorded for 1 individual, spanning 1,515 calendar days (4.15 years). Twenty-four seals (8.7% of all seals with VHF implants) were never detected via telemetry after they were radiotagged; 20 of those seals were tagged in GB.

Blubber depth was not a significant explanatory variable to explain probability of detecting telemetry signals from harbor seals with subcutaneous implants. In the GLMM analysis with multiple covariates, 3 terms—Tag Season, Maximum Years Detected, and Year-Post-Tagging^2—were included in the final GLMM (Table 4). Not surprisingly, due to lower surveillance times, seals tagged in fall were less likely to be detected that year than seals tagged in spring and summer, and seals tagged in spring had the highest likelihood of detection. Detection of seals diminished as the number of years posttagging increased but increased as maximum year detected increased. Effects of year, the seal's age, sex, and tagging location did not significantly contribute to the model.

Figure 5 summarizes changes in detection over time. For all seals in the study, 84% (95% confidence interval [95% *CI*] = 0.80–0.87) were detected during their capture year. During the 1st year posttagging, only 59% (95% *CI* = 0.55–0.63) were detected and in years 2, 3 and 4, respectively, 28% (95% *CI* = 0.25–0.31), 0.9% (95% *CI* = 0.07–0.11), and 3% (95% *CI* = 0.02–0.04) of seals were detected.

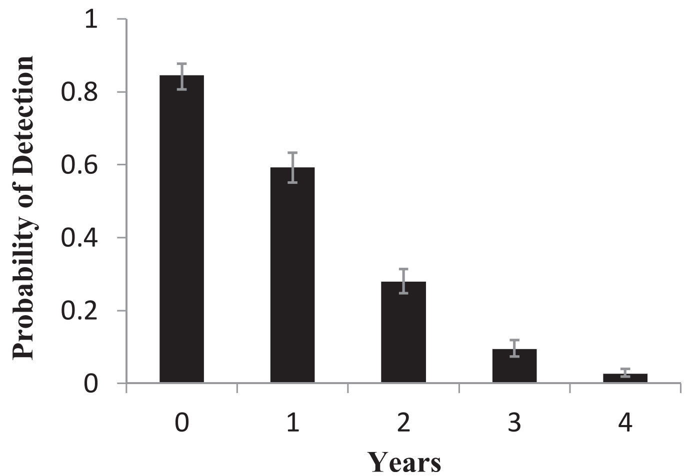

Fig. 5.—Probability of detecting telemetry signals of harbor seals (*Phoca vitulina*) with subcutaneous transmitters for both study areas combined. Year 0 represents the year seals received subcutaneous implants. Error bars represent the 95% confidence interval around estimates.

Discussion

Elucidating factors that affect population dynamics requires long-term monitoring of vital rates; the most influential of which is survival (Pistorius et al. 2004; Bonenfant et al. 2009). Estimates of survival probability are enhanced by following individuals through time, a task that is difficult with marine mammals that spend the majority of their time underwater. Intraperitoneal implantation of VHF-telemetry transmitters has occurred for decades in some species, allowing for successful, multiyear tracking of diving mustelids (Williams and Siniff 1983; Reid et al. 1986; Blundell et al. 2002). Implanting those same transmitters subcutaneously, using a method developed by Lander et al. (2005), offered a potential means of radiotracking harbor seals for multiple years that was less invasive than abdominal implants.

After deploying numerous subcutaneously implanted VHF transmitters during the 1st year of this study, telemetry data for almost all harbor seals were successfully collected during the summer. Encouraged by these results, a large-scale telemetry study was launched in 2 study areas. Initial radiotracking from airplanes and boats was labor-intensive and expensive, due to the remote location of the study areas. Furthermore, surveys could only be accomplished in fair weather, resulting in large gaps in collection of telemetry data. The 1st efforts to use land-based, data-logging equipment were plagued by excessive electronic noise, largely due to the similarity in narrow pulse widths of the slow pulse rate of the implant transmitters and ambient electronic noise. The receiver–data-loggers used in this study were slightly different from those used successfully by Eiler (1995); the equipment in this study scanned for specific VHF frequencies whereas theirs logged pulse-coded transmitters. The specific, repetitious patterns of a pulse-coded transmitter are not likely to be misinterpreted as noise. Unfortunately, pulse-coded transmitters exhaust battery life more rapidly than standard VHF transmitters and were not suitable for this long-term study on vital rates of harbor seals. A short battery life would have eliminated the possibility of assessing interannual survival, pup survival, and survival to reproductive age, all of which affect population dynamics. We accepted the trade-off of problems associated with slow pulse rates to extend the battery life of the transmitters and found effective methods to filter out noise and retain telemetry detections.

Thereafter, continuous telemetry monitoring using land-based, data-logging equipment substantially increased telemetry detections beyond what was possible from aerial and boat-based surveys. We were confident that, if a harbor seal with a functional VHF transmitter was present on or near a site and the remote monitoring station was functional, the harbor seal would be reliably detected.

Harbor seals show a high degree of fidelity to haul-out sites (Harkonen and Harding 2001; Lowry et al. 2001; Cunningham et al. 2009) and telemetry stations were erected in both study areas at haul-out sites used by harbor seals and it was anticipated that tracking the apparent survival of large numbers of seals through time was feasible. Nonetheless, although telemetry detections in the capture year and the 1st year after tagging looked promising, the detection rates were unacceptably low by the 2nd year after surgical tagging, despite extensive telemetry efforts within and beyond each study area. Although population declines had been reported in both study areas (Frost et al. 1999; Ver Hoef and Frost 2003; Mathews and Pendleton 2006; Womble et al. 2010), the rapidly diminishing numbers of radiotagged harbor seals detected over successive years of the study far exceeded the loss rates that could potentially be explained by a declining population.

Diminished detection of young seals could have been influenced by lower survival rates. Generally, survival probability is lower during the 1st several years of life in pinnipeds (Hernandez-Camacho et al. 2008; Hastings et al. 2012; Rotella et al. 2012). Accordingly, the detection of diminishing proportions of YY and Yrl seals during the year of tagging and the following year was expected, whereas older tagged seals should be detected in higher proportions. In contrast, age was not a significant factor; seals detected in all age class declined at similar precipitous rates as the study progressed.

Reduction in telemetry effort toward the end of the study also had the potential to explain the diminishing rate of telemetry detection for seals that were tagged in the last year or two of the study; however, year was not a significant factor in telemetry detection. In fact, the only variables that were significant in influencing whether seals were detected or not were those that can be explained by simple mathematical relationships. Seals tagged earlier in the year (the Tag Season covariate) were more likely to be detected that same year because there were more possible days in which they could be detected. Similarly, seals detected for more years (covariate Maximum Years Detected) were more likely to be detected over that longer time span. The only other significant factor in the model (Year-Post-Tagging^2) revealed that the number of seals detected decreased as the number of years posttagging increased, yet the declining tag-detection rate was not commensurate with survival rates reported for harbor seals. Tag-detection rates during the 2nd through 4th year posttagging were substantially lower for all age classes in this study compared to estimates of survival rates for harbor seals in Alaska (Pitcher and Calkins 1979; Hastings et al. 2012). Both of those studies also reported a lower apparent survival for males than for females, whereas this study found that sex was not a significant factor in telemetry detections.

At the onset of tagging, some tag failure occurred and, at various times during the study, evidence suggested that radiotags may have migrated from the incision and been expelled by some seals. Initially beach-cast transmitters were believed to be all that remained of some seals that died on shore over the winter; however, during thorough searches of the surrounding area, no remnants of a harbor seal carcass were recovered. Discovering 1 harbor seal with a partially extruding transmitter, at 11.75 months after the implantation surgery, cast doubt on interpreting beach-cast transmitters as possible mortality events and provided a plausible explanation for low detection rates, after the 1st year, for seals with subcutaneously implanted radiotransmitters. A transmitter in the process of migrating out of a seal could be expelled while hauled out on land; however, because seals spend $> 70\%$ of their time in the water during most of the year (Frost et al. 2001, 2006), transmitters were more likely to be expelled when the seal was in the water. Transmitters expelled in the water would sink, preventing further detection of telemetry signals.

Subcutaneous implants of radiotransmitters have been used in a variety of species. Echols et al. (2004) reported high ($>$ 64%) rejection rates of radiotransmitters subcutaneously implanted in American black bear cubs. Results of that study, however, are not directly comparable to this study because implant transmitters in the American black bears had an external antenna, which are known to have a higher likelihood of rejection in pinnipeds than transmitters with an internal antenna, potted in the tag (Lander et al. 2005). Moreover, transmitters were deployed in young bear cubs (66–73 days old), which are subject to maternal grooming and sibling interactions, which could have affected suture persistence and incision healing.

Different species may have a higher likelihood of tissue reaction and transmitter rejection. Green et al. (2009) reported that, whereas California sea lions (*Zalophus californianus*) healed well after receiving subcutaneous heart-rate dataloggers, northern elephant seals (*Mirounga angustirostris*) exhibited a pronounced inflammatory response requiring removal of the instrument. Attempts to surgically implant subcutaneous tags in European badgers met with similar results (Agren et al. 2000). Incisions for subcutaneous implantations made along the chest wall were well healed 1 week after surgery; however, within 2 months all 6 badgers had lost their transmitters as a result of pressure necrosis of the skin over the implants. Instruments implanted in the necks of badgers fared slightly better; however, aggressive interactions with conspecifics resulted in damage to and removal of those transmitters, leading to the conclusion that intra-abdominal implants were more effective in badgers than subcutaneous implants. Williams and Siniff (1983) experimented with surgical implantation of transmitters in sea otters, deploying transmitters in 10 sea otters as intraperitoneal implants using 3 different surgical techniques, and deploying 5 transmitters as subcutaneous implants using a single surgical technique. Telemetry signals were monitored for 1 month; 2 of the 5 otters that received transmitters implanted subcutaneously died within a week of surgery and their deaths may have been associated with the subcutaneous transmitters, whereas the intraperitoneal implants were well tolerated in all 10 sea otters for that study and in other studies of sea otters (Ralls et al. 1989).

In this study, there was no means by which to definitively distinguish between emigration, mortality, tag failure, or tag rejection as potential causes of failure to detect telemetry signals of seals in subsequent years of radiotracking. Nonetheless, given the direct and indirect evidence of tag rejection in this study, tag loss may potentially explain a substantial portion of the failure to detect telemetry signals of seals. Expanded telemetry surveys beyond the study areas did not find evidence of high emigration rates, nor was there direct evidence of mortality in either area. The original study design incorporated the use of capture–mark–recapture analysis to determine whether health covariates were predictors of the probability of telemetry detections in the year following tagging. Although telemetry data in this study were insufficient for capture–mark–recapture analysis, at capture, seals tagged in this study appeared healthy, and initial evaluation of health data did not reveal anything overtly indicative of compromised health. Detailed interpretation of clinical health data including disease titers and serum chemistry and hematology data will be presented elsewhere.

The use of subcutaneously implanted VHF tags in this study did not provide a reliable means of tracking a sufficient number of harbor seals for multiple years, and therefore addressing population-level questions pertaining to vital rates was not possible. However, telemetry signals emitted from subcutaneous radiotags were detected when a seal was floating high on the surface of the water, whereas flipper-mounted VHF tags can only be heard when a seal is hauled out. Subcutaneous tags also allowed approximately half of the tagged harbor seals to be radiotracked through at least 1 molt season. Therefore, depending on the objectives of the study, this tagging methodology may be a viable option for other types of research on harbor seals, or perhaps for other species, less prone to rejection of implanted tags.

Remote telemetry-monitoring stations were useful in detecting harbor seals that rarely visited a study site, or hauled out during inclement weather or at times of the day or year when personnel would not be actively radiotracking. Methods of improving filtration of noise, and efficient ways to handle large amounts of data were developed during this research. The vast majority of harbor seals were detected primarily during the summer months and little was gained by year-round telemetry monitoring. Telemetry stations required regular maintenance, especially during the winter, to keep them functional; perhaps creating drip loops in the cables before inserting those cables into the weatherproof case would reduce moisture problems in a wet maritime climate.

Lander et al. (2005) developed the technique for subcutaneously implanting radiotags in harbor seals; they radiotracked 15 seals and survival–tag retention was confirmed for a period spanning an average of 330.5 days ($\pm$ 70.8 *SD*; minimum $= 0$ days, maximum $= 786$ days). Two seals were never located following release after radiotagging and 1 was only tracked for 9 days; however, 6 seals were tracked for $>$ 1 year (including 4 seal tracked for $>$ 600 days). Results from that study indicated that the tagging technique held great promise for multiyear telemetry studies of harbor seals. In this study, multiyear telemetry data for individual seals was obtained for 72 of 277 tagged seals, which will allow analysis of haul-out site use and short-term movements of seals. Furthermore, the study provided a thorough test of the efficacy of using subcutaneously implanted transmitters in harbor seals, which should facilitate a more-informed decision for other researchers contemplating the use of subcutaneous implants in this species.

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