Techniques for Real-Time, Active Tracking of Sea Lions

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Abstract

The movements of otariids at sea are generally studied by satellite telemetry. At fine scales (1-20 km), however, the level of precision provided by this technique (± mean 1.5-19 km) may be insufficient to accurately reconstruct the track of an individual and/or integrate such movement data with habitat and environmental features. An alternative technique is the boat-based active tracking of individuals by very high frequency (VHF) or acoustic telemetry. By following an individual equipped with transmitters, detailed observations of habitat use, predator occurrence, social context, behavioral state, and prey availability may be integrated to provide a real-time context in which to place the animals' movements. For species such as the Steller sea lion (Eumetopias jubatus), which are difficult to recapture, such techniques enable the collection of much needed contextual information. Here we describe the methods we applied to actively track Steller sea lions. Twenty-one juveniles were captured in Southeast Alaska during October 2003 and February 2004. They were fitted with a variety of VHF, satellite, and/or acoustic tags and were tracked through the winter and spring of 2003-2004. The use of ship-based VHF telemetry in conjunction with real time navigation plotting software was highly successful and provided 37 fine-scale tracks of coastal and pelagic

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sea lion movements covering a total distance of 482 km. Acoustic telemetry techniques were less successful because of the suspected overlap in tag transmission frequency and sea lion hearing. The study represents the first active tracking of a sea lion species, highlighting the high-resolution tracks and contextual behavioral and habitat information that can be obtained using VHF telemetry at sea.

Introduction

Understanding the behavior of marine mammals at sea is critical for identifying key relationships between habitat use, foraging preferences, predation risk, and the availability of prey sources. In recent decades, a many kinds of telemetry devices have been developed as tools to provide much needed information on marine mammal distribution and behavior at sea.

Over the last 15 years, the technology of satellite tracking marine mammals has proliferated (Stewart et al. 1989; McConnell et al. 1992a,b; Harcourt and Davis 1997; Stewart et al. 2000; Boyd et al. 2002). More recently, satellite telemetry data have been combined with remotely sensed data on the animal's environment (Hindell et al. 1999, Loughlin et al. 1999, Georges et al. 2000, Goebel et al. 2000, Field et al. 2001, Guinet et al. 2001, Lea and Dubroca 2003, Staniland and Boyd 2003, Beauplet et al. 2004). Static (e.g., bathymetry) and dynamic environmental variables (e.g., chlorophyll a; sea surface temperature, SST; and sea surface height, SSH) have both been integrated with animal movement data at varying temporal and spatial scales providing insights into the oceanic features influencing foraging behavior (Fedak et al. 2002, Lydersen et al. 2002). The ecological significance of such an approach is influenced by the scale of movements and the temporal and spatial resolution of environmental parameters (Bradshaw et al. 2004). For example, seasonal directed migrations of thousands of kilometers made by southern elephant seals (Mirounga leonina) across the open ocean can be effectively tracked with satellite telemetry (McConnell et al. 2002). In contrast, juvenile Steller sea lions (Eumetopias jubatus) often conduct short trips (<15 km) in coastal regions (Raum-Survan et al. 2004). At these scales the precision of data provided by conventional satellite telemetry (Stewart et al. 1989, Raum-Survan et al. 2004) is insufficient to fully understand the relationships between individual movements and the features encountered on these smaller scale foraging trips.

An alternative to satellite telemetry involves using tracking equipment in much closer proximity to the animal. Equipment may be fixed or mobile depending on the circumstances. Fixed gear can include arrays of radio or acoustic receivers that register the presence and location of individuals nearby (Wartzok et al. 1992, Hammond et al. 1993, Harcourt et al. 2000, Hindell et al. 2002). Fixed equipment methodologies are ideal if the range of the tagged animals is known a priori. However, if the animals are more mobile then it may be necessary to use a moving platform to follow tagged individuals, a technique known as "active" tracking (Holland et al. 2001). Under these conditions, the platform (usually a boat) carries the receiving gear and is moved relative to the location of the target animal.

Active techniques, including VHF and acoustic telemetry, have proven successful in fish (Holland et al. 1992, 1999, 2001; Block et al. 1997; Meyer et al. 2000; Voegeli et al. 2001), and whale studies (Goodyear 1993, Watkins et al. 1993, Baird et al. 2002) over short time periods (<3 days). These boat-based techniques also have been used to track grey seals (Halichoerus grypus) and harbor seals (Phoca vitulina) (Fedak et al. 1988, Thompson et al. 1991, Hammond et al. 1993, Thompson and Fedak 1993, Bjørge et al. 1995, Suryan and Harvey 1998), while northern fur seals (Cal*lorhinus ursinus*) have been radio-tracked using fixed wing aircraft (Ragen et al. 1995). Active tracking methods offer several advantages over more remote techniques. Besides providing data to produce a high-resolution two-dimensional path, active methods provide the opportunity to collect ancillary data such as an animal's behavior at sea (e.g., behavioral state, dive durations), physiological state (e.g., cardiac rate, Thompson and Fedak 1993) or more broadly, the physical and biological context in which the behaviors occurred.

Recent Steller sea lion telemetry research efforts have focused on the behavior of juvenile animals (Loughlin et al. 2003, Raum-Suryan et al. 2004), partly because of the logistic challenges in capturing adults (Loughlin 1998, Andrews et al. 2002), but primarily because of the importance of reduced juvenile survival in influencing the dramatic decline in population numbers (Pascual and Adkison 1994, York 1994, Trites and Larkin 1996). Here we describe the techniques that we applied to actively track juvenile Steller sea lions from a boat during the winter and spring of 2003-2004 in Southeast Alaska. Our aim was to determine where the sea lions went on their trips to sea and how these trips were executed. Study methods were chosen that did not necessitate recapturing individuals to retrieve archival tags. Additionally the lack of road access in Southeast Alaska precluded active VHF tracking from land (Tollit et al. 1998). We tested the efficacy of a variety of techniques (including boat-based VHF and acoustic telemetry) and show for the first time that it is possible to track sea lions at sea, both in daylight and darkness, and under a range of sea conditions. We outline both problematic and successful methods.

Materials and methods

Young Steller sea lions were captured during October 2003 and February 2004 at three haul-out sites (Benjamin Island, 58.560°N, 134.916°W; Little Island, 58.542°N, 135.045°W; and Gran Point, 59.132°N, 135.239°W) in



Figure 1. a. Study area and sea lion capture sites, Southeast Alaska. b. The VHF telemetry locations (•) during an 8 hour period and all Argos satellite (0, class A and B) for that day are plotted for a 35 month old female Steller sea lion in Berners Bay, 24 April 2004.

Lynn Canal, Southeast Alaska (Fig. 1a), as part of ongoing studies of Steller sea lion biology by the Alaska Department of Fish and Game (ADFG). Sea lions were captured using the underwater dive capture technique and moved to a larger boat for immobilization and processing (ADFG, Anchorage, unpubl.; Raum-Suryan et al. 2004). The combination of tag(s) that each sea lion received was scaled such that the smaller animals were not burdened by multiple or bulky tags. All animals received VHF transmitters (MM300 Series, 30 ms pulse length, reinforced stainless steel antennas, frequency range 150-152 Mhz (Advanced Telemetry Systems [ATS], Isanti, Minnesota, USA). Two of these instruments were mounted on the back with whip antennas lying along the animal's back, whereas the remaining 19 were mounted on the head with vertical antennas. Nine animals also received back-mounted satellite transmitters (three Kiwisat tags, Sirtrack Pty Ltd., Havelock Nth, New Zealand providing locations; and six series-7000 satellite relayed data loggers [SRDL], Sea Mammal Research Unit, St Andrews, Scotland, UK, providing locations and diving information). Six of the satellite-tagged Steller sea lions also carried a back-mounted acoustic transponder (VX32TP CHAT tags, VEMCO, Shad Bay, Nova Scotia, Canada).

Nylon mesh with a radius approximately 1.5 cm larger than the transmitters was attached to the bottom of each tag and then glued to the fur of the Steller sea lions using Devcon[®] 10-minute, clear epoxy (ITW Devcon[®], Danvers, Massachusetts, USA). Back-mounted tags were placed on the dorsal mid-line slightly anterior of the shoulder blades. Following tag attachment, Steller sea lions were allowed to regain mobility and return to the water unassisted. Steller sea lions were actively tracked during 7 November–3 December 2003, 29 February–13 March 2004, and 1-30 April 2004, for a total of 10 weeks.

VHF tracking protocol

To track animals we traveled to an area highlighted by previous satellite fixes. One of two approaches was then used to detect and track animals at sea: (1) the boat approached within VHF range of the nearest haul-out site and tagged sea lions were monitored until they entered the water; or (2) VHF signals were listened for on a 4-8 s scrolling cycle while the boat was at sea engaged in other operations. Detected sea lions were then located and tracked.

We used an 18 m single propeller motor yacht fitted with an inboard diesel engine. VHF antennas were mounted on the wheelhouse roof at a height of 10.5 m above sea level (ASL). An omni-directional antenna (ATS) connected to an SRX-400 VHF receiver (Lotek Wireless Inc., Newmarket, Ontario, Canada) was used when manually searching for tagged Steller sea lions. After a signal was detected, bearings to the signal were determined using an arrangement of four directional ATS Yagi antennae mounted in a horizontal-cross formation routed to an automatic direction finder (ADF; ATS). The ADF unit compared the output from the antennas to give a display of signal strengths on a corresponding LED display. To improve the performance of the ADF, we used VHF tags with relatively long pulse lengths. Bearings were obtained from single VHF pulses using the combination of ADF and tags. The derived bearings were then drawn, in real time, as lines on a chart plotter display (Nobeltec Visual Series 2.0). This mapping software showed the position and heading of the boat on either a standard navigation chart or a high-resolution aerial photograph of the region. The boat's position on the chart was obtained from a GPS (Garmin International Inc., Olathe, Kansas, USA) and updated once each second. As the boat moved, sequential bearings to the tagged sea lion were plotted. The sea lion position was then estimated using triangulation from two or more of these bearings. Bearings from adjacent surfacings and at angles at around 90° to each other were preferred. Fixing the location of stationary animals was relatively straightforward. Moving animals were more challenging and were most easily tracked by keeping pace with them (i.e., maintaining bearings abeam and at a relatively constant angle) then periodically moving to cross their track from behind to obtain a cross bearing on their trajectory. The field VHF-derived sea lion positions were given a subjective quality rating to allow subsequent filtering. These scores ranged from 1 (excellent cross bearings and sea lion sighted) to 3 (unreliable estimate of location).

In areas of strong currents, or if the boat was stationary, the GPS system could not produce accurate estimates of the boat's heading. On these occasions, landmarks were used to determine the correct heading. Visual observations were made during the day, while RADAR was used at night. Because we were concerned that our presence might disturb the animals we were tracking, we aimed to maximize our distance to the animal while maintaining sufficient proximity to be able to see the sea lion with binoculars.

Because VHF radio waves travel well through air but not through seawater we were able to use the pauses in the VHF pulses to register the animal's diving activity. The tags transmitted approximately one pulse per second and pulses were logged manually with event recording software. The human ear is typically more sensitive than electronic signal detection systems. Though tedious, this approach also ensured that a constant vigil was kept on the strength of the radio signal. In so doing, signal loss and radio interference were dealt with immediately and any periods of known loss could be noted for exclusion in later analyses.

When tracking, attempts were made to estimate the animal's position at least four times an hour. Periods of tracking were terminated when (1) the weather deteriorated; (2) we felt that our presence might be disturbing the animal; (3) the boat was required for other studies; (4) the sea lion hauled out; or (5) the signal was lost. Two tracking crews and skippers (when available) were rotated so that 24-hour effort could be maintained.

Acoustic telemetry

Tracking studies necessarily assume that the methods used to track the animals do not overtly impact the behavior of their subjects. Disturbances stem from multiple sources including handling, the subsequent researcher presence, and the tracking devices themselves. While VHF and satellite transmitters rely on seemingly imperceptible radio waves, the high frequency acoustic transmitters that have been used to study a variety of fish and marine mammals (Hawkins et al. 1974, Holland et al. 1992, Goodyear 1993, Thompson and Fedak 1993, Dewer et al. 1999) may well be perceptible to some species. Most acoustic telemetry studies use constantly emitting acoustic tags; however, in regions inhabited by acoustically sensitive predators or prey the possibility of impact on the tagged animal needs to be considered. Killer whales (Orcinus orca) represent significant predators for many marine animals, including Steller sea lions, and studies of captive killer whales have shown that they can reliably hear at frequencies used by most acoustic tags (Szymanski et al. 1999). Thus, the researcher using these tags is faced with two options: (1) using purpose-made tags emitting at frequencies too high for these predators (>150 kHz) with consequent losses in signal transmission distances or (2) using transponders which, because they are responsive, only broadcast when they themselves receive a signal from an onboard receiver. Thus these tags can be silenced if the tags are under the temporal control of the researchers and so can remain silent if predators are present.

The acoustic transponder tags we used were VEMCO CHAT tags (VX32TP; Voegeli et al. 2001) which transmitted at 32.8 kHz (163 dB) when signals (27 kHz) were received from a boat-based VR-28T set and towed hydrophones (VH-41) mounted on a fiberglass fin (VFIN, see Block et al. 1997). One cycle of transmission and reception lasted approximately 19 ± 3 s (n = 25). The hydrophones were connected to the receiver by an 18 m hairy, fared Kevlar conducting cable (Cortland Cable, Cortland, New York), which permitted the towing of the VFIN at approximately 1 m depth off an outrigger. The "chatting" communication between the transponder and the towed directional hydrophones enabled range and direction to be calculated. Sensors on the tag also recorded depth and temperature data, which were transmitted as a coded acoustic signal to the receiver.

The limited data on the auditory capabilities of Steller sea lions (Kastelein et al. 2005) suggested that the broadcast frequency of the CHAT tags (32.8 kHz) might be near the high frequency limit of the hearing range of this species. To test whether these tags might cause measurable disturbances to Steller sea lions, we carried out trials on two captive animals in July 2003 at a University of British Columbia/Vancouver Aquarium facility. The trained female sea lions (aged 4 and 6 years old) were housed in a floating mesh pen with surrounding pontoons that allowed them to haul out at will. The pen was moored in a sheltered bay, floating several meters over a soft mud bottom. An active CHAT tag was lowered into the water next to the pen and the behavior of the swimming sea lions was monitored. In a second trial, the active tag was placed in a harness on the back of the sea lions and their behavior was again observed.

Behavioral context

While tracking in daylight we were able to observe the focal sea lion and collect additional data with respect to behavior. Parameters measured included the presence of other sea lions, humpback (*Megaptera novangliae*) and killer whales, foraging birds, fishing boats, and specifics of the habitat and water conditions (tidal fronts etc). Night-vision binoculars (Generation 3, ITT Industries, White Plains, New York, USA) enabled us to observe the presence of other sea lions, foraging birds, and whales.

Real-time, fine-scale animal movement data were combined with simultaneous acoustic surveys of prey distribution to provide the threedimensional context for at-sea behavior (MacClennan and Simmonds 1992). To identify and quantify potential prey we used a fin-mounted SIMRAD EK60 scientific echosounder (Kongsberg Maritime Inc., Lynnwood, Washington, USA) towed from an outrigger on the research vessel. To examine the behavior of the sea lion in context with the prey field we conducted acoustic surveys at two spatial scales. The first were large transects encompassing Benjamin Island and Favorite Channel in Lynn Canal, Southeast Alaska, and the second were smaller transects targeting, in real time, the areas used by the tagged sea lions. The results of these analyses will be presented elsewhere.

The majority of animals in this study regularly used the Benjamin Island haul-out site in Lynn Canal (58.560°N, 134.917°W, Fig. 1). To retrospectively determine their use of the haul-out before and after our tracking sessions we placed an automatic VHF receiving station (R2100 VHF receiver and D5041A Data Collection Computer, ATS) directly behind the haul-out, which recorded the presence or absence of the seal lion VHF tags for 15-30 s every 15-30 minutes depending on the season. All hauled-out sea lions hauled out were within 150 m of the receiving station antenna, located ~20 m ASL. The receiving station operated successfully under adverse weather conditions on 12 V external deep-cycle batteries.

Results

Twenty-one juvenile sea lions (5 females, 16 males), ranging from 5 to 29 months in age and weighing 50 to 206 kg (Table 1), were fitted with either a VHF tag (n = 13), or a VHF/satellite transmitter combination (n = 8). Six of the satellite-tracked individuals also carried a back-mounted acoustic CHAT tag.

VHF tracking

Initial trials confirmed that we were able to detect and localize sea lions using the VHF telemetry equipment. The "running fix" technique proved highly effective. The ADF/VHF tag combination was able to produce bearings from single VHF pulses to within approximately 15° of the true bearing. In a blind trial, with a hidden stationary tag using typical tracking effort, we were able to estimate its position to within 50 m of the actual location. Wild, particularly moving, animals were harder to track than stationary ones but we were frequently able to validate the precision of the technique by estimating the sea lion positions and then directing a rooftop observer to visually confirm the presence of the tagged animal. This was sufficiently effective that we were able to spot the tagged animals for half of all the VHF derived locations in 2004 (49.8%, n = 801).

Using the VHF tracking equipment we followed 15 individual sea lions on 37 occasions (Table 1). Tracks ranged in duration from 12 minutes to 57 hours with the median track lasting a little over 3 hours. During these efforts we followed sea lions over a total distance of 482 km and kept a median distance between animal and boat of 522 m (n = 548 fixes). It proved possible to track animals leaving the haul-out and also to follow them on their return.

Age (months)	Male n	Female n	Mass range (kg)	No. of tracks	Duration (min)
5	1	1	53-71	2	265
8	2	1	79-97	1	25
17	6	2	101-146	14	2,460
20	5	_	115-149	6	2,515
29	2	1	140-206	14	7,021
Total	16	5	120 ± 33^{a}	37	12,286

Sex, mass, age, and radio-tracking duration of juvenile Steller Table 1. sea lions tagged and actively tracked in this study.

All captures were made in October 2003 or February 2004 in Lynn Canal, Southeast Alaska. Morphometric data courtesy of Alaska Department of Fish and Game. ^aMean value + sd

Undamaged VHF tags were audible at up to 13 km on calm days and we could obtain useful bearings within 5 km of the sea lion. Headmounted tags provided clear signals when the animal surfaced to breathe, whereas back-mounted tags were generally only audible during a small portion of each surfacing event, and the reliability of their reception was potentially dependent on the behavior of the animal at the surface. During tracking, care had to be taken in areas with steep cliffs or rock outcrops as these structures tended to interfere with signal detection. Meteorological state, wave height, and the condition of the tag all influenced the range over which we were able to track animals. For the shipboard antennas, freezing rain, sea spray, and corrosion reduced reliability, while strong auroras substantially impacted the noise level on the receivers. It was possible to work in waves up to 2 meters in height with our vessel but fixes became inaccurate in greater sea states. The greatest influence, however, was the condition of the tags. Within two months of tag deployment, the whip antennas of the VHF tags began to break off at the base with the epoxy housing leaving an antenna stump of approximately three to five cm. We were still able to track animals with these damaged antennae, but the range of detection was considerably reduced (<2 km).

Satellite/VHF precision comparisons

During the twenty occasions that we tracked satellite tag-equipped sea lions, only forty-four concurrent at-sea satellite locations were obtained during ten focal follows periods. The proportion of quality ranked sea lion fixes at sea was 2% class 3, 11% class 2, 5% class 1, 2% class 0, 30%

	Steller sea llons actively tracked in Southeast Alaska.								
SAT location class	Distance (km), <20 min elapsed time	n	Distance (km), 20-45 min elapsed time	п	Distance (km), combined elapsed time (<45min)	n			
3	1.8	1	_	-	1.8	1			
2	1.3 (0.6)	3	1.3 (0.5)	2	1.3 (0.5)	5			
1	-	_	1.9 (1.6)	2	1.9 (1.6)	2			
0	1.7	1	-	-	1.7	1			
А	6.7 (6.7)	13	-	-	6.7 (6.7)	13			
В	16.3 (19.3)	21	13.9	1	16.2 (18.9)	22			

Table 2.	A comparison of mean great circle distances between concur-
	rent VHF and satellite-derived (SAT) positions for juvenile
	Steller sea lions actively tracked in Southeast Alaska.

Distances are displayed by satellite location class and are compared by time elapsed between SAT and VHF locations. Standard deviations in parentheses.

class A. and 50% class B. The distance between satellite-derived and VHFderived positions was subsequently compared (1) for locations obtained within 20 minutes of each other (n = 39) and (2) for those locations obtained up to 45 minutes of each other (n = 5). The best agreement in location between satellite and VHF locations was obtained for the few location class 0-3 fixes obtained within 20 minutes of each other (Table 2). On these occasions satellite locations were, on average, within 1.3 to 1.8 km of the sea lion (n = 9). However, 80% of satellite fixes for moving sea lions were the lower quality A and B location classes. Figure 1b illustrates the large differences (4-8 km) in location between satellite derived A and B quality fixes and the actual location of the sea lion during one VHF tracking and visual observation period. Only two of the satellite locations received during the 8-hour tracking period were in the water and only one location was within the area actually used by the sea lion. The level of precision derived from the satellite tags was therefore insufficient for the fine-scale focus of this study; however, these tags did allow us to narrow down a search area to find tagged animals and focus the VHF/acoustic tracking efforts.

Acoustic telemetry

Captive trials

The 6 year old female Steller sea lion showed no overt responses to the sound emitted by the CHAT tag, when lowered into the pen or carried in a harness. The 4 year old female, however, exited the water on 5 of 15 transmitter emissions. The responses of the younger animal were ambigu-



Figure 2. The two-dimensional record of a 29 month old female Steller sea lion on 10 November 2004, retrieved from an Mk9 time depth record (Wildlife Computers, Redmond, USA). Depth was recorded every 2 seconds for 6 months. Larger black dots represent those depths also identified simultaneously by the acoustic transponder (CHAT, VEMCO, Canada).

ous and suggested that if she could perceive the tag she did not show a consistent or severe response.

Field trials

Acoustic tracking of young sea lions using CHAT tags was successful at distances up to 800 m. We found that engine and propeller noise of the tracking boat could reduce this distance, probably by masking reception of the acoustic pulses returning from the tag. The engine was therefore engaged intermittently or when possible the vessel was allowed to simply lie stationary. This approach also had the effect of reducing potential acoustic disturbance for the sea lion. Onboard echosounders of similar operating frequencies (e.g., SIMRAD EK60 at 38 kHz) also produced acoustic interference.

One 29 month old female sea lion was tracked acoustically underwater for 1.5 hours on 10 November 2003; the transmitted real-time dive profiles are shown in tandem with archival time depth recorder data (Wildlife Computers) retrieved after the study (Fig. 2). The maximum dive depths (60-94 m) coincided with the depths of dense, overwintering herring schools (*Clupea pallasii*). No obvious changes in behavior occurred in response to the acoustic transmissions for either the individual or members of the associated group of ~20 adult and juvenile sea lions. However, we suspect that the acoustic transmissions were altering her behavior on two subsequent occasions. In these instances the sea lion either changed from long to short dives or broke her diving sequence to surface immediately after the acoustic signal was transmitted from the vessel.

Two separate attempts were also made with a 30 month old male and an 18 month old female. In both instances we observed apparent responses to the acoustic tracking equipment from both the tracked individual and surrounding sea lions. In one case, a group resting at the surface startled and immediately dived. During several other occasions the group surfaced with splashing and commotion immediately after the CHAT tag was signaled. Due to concerns that this equipment disturbed the natural behavior of the tagged sea lion and those around it, and the potential that the sea lions might associate these sounds with the presence of our boat, no further transmissions were conducted.

Behavioral context

During the VHF tracking, we maintained a near continuous chronicle of the VHF tag pulses. These data provided records of 157 hours of the tracked sea lions' presence above and below the surface of the water. The temporal occurrence of the VHF pulses was variable, which when combined with contextual and behavioral data were valuable in describing the activity states of juvenile sea lions on their foraging trips.

Being in physical proximity to the focal sea lion made it possible to observe a wide variety of associated events. Tracked sea lions were observed alone and with other sea lions. Group sizes ranged from a few individuals to groups greater than a hundred. On several occasions our focal individuals were seen in close association with an adult, possibly its mother. Inter-specific interactions with humpback whales and seabirds were also witnessed. Sea lions were seen bringing fish to the surface and one track was cut short when killer whales attacked another sea lion in close proximity. Observations were heavily influenced by the weather, distance from the animal, and time of day. On two clear nights while tracking an individual Steller sea lion it was possible to also observe the presence of other sea lions and humpback whales using night vision goggles.

Discussion

In this study, we assessed the feasibility of actively tracking the movements and behavior of Steller sea lions at sea. Using the methods outlined, it proved possible to follow tagged individuals over extended periods (up to 57 hours), through darkness and adverse weather conditions. Using a combination of ADF and VHF equipment, and a moving platform, we were able to obtain real-time fixes on animals carrying head-mounted VHF tags with sufficient precision that in calm weather conditions we could see them with binoculars on their subsequent surfacings. Surface and dive durations recorded while tracking individuals showed discrete patterns, which may indicate specific behavior classes (e.g., foraging, shore navigation, and open water crossings). Dive duration data collected in this way augments and informs information collected by remote studies of foraging behavior and the ontogeny of diving. The surface interval of seal lions was often short (<3 seconds), so alternative VHF tracking methods that rely on physically maneuvering single or paired antennae to determine the best signal strength would have been unsuccessful during this study.

While at sea, the individuals we tracked spent the majority of their time underwater. We tested acoustic transmitters and found them to work over ranges insufficient to initially locate animals, but certainly sufficient to track animals within 800 m. We selected acoustic transponder tags, rather than continually broadcasting tags for this study because of concerns for potentially elevated killer whale predation risk. An additional advantage of responsive tags was that they also provided a range in addition to a bearing. Because the location of the boat was known, the position of the sea lion could be calculated. By combining this with the coded depth information from the tag, it was possible to produce a threedimensional location for the sea lion.

The hearing capabilities of Steller sea lions are little known; however, recent underwater audiograms of a captive 8 year old male Steller sea lion and a 7 year old female indicated that hearing sensitivity rapidly declined above 16 kHz and 25 kHz respectively (Kastelein et al. 2005). Similar studies of California sea lions (Zalophus californianus) indicate their hearing thresholds drop off quickly above 28 kHz with an upper threshold at 34 kHz (Schusterman and Moore 1978), close to the transmission frequency of CHAT tags (32.8 kHz). Trials of CHAT tags near and attached to captive sea lions elicited few overt responses. However, our observations of startle reactions in the wild suggested otherwise. The ultrasonic tags, therefore, appear to be within the upper limit of juvenile Steller sea lion hearing range. Whether the higher behavioral sensitivity of the wild sea lions was due to better high-frequency hearing among these younger animals or simply a more flighty response to sounds of unknown origin is unknown. However, as a result of the observable responses by the wild animals we discontinued use of these tags. Given the ease of tracking animals using these tags, the future development of acoustic transponder tags that operate at frequencies clear of the hearing range of these animals could provide a valuable tool for future studies using active tracking techniques.

The choice of research platform and crew for these tracking techniques had a considerable impact on the results. Larger platforms provide a more stable working platform, better equipment protection, opportunities for elevated antennae, the capacity for larger crews, the capacity for longer at-sea endurance and operating ranges, and the capability to withstand adverse weather. However, larger platforms also have higher operating costs, are often electrically more complicated, and so are prone to electrical interference. Their physical presence, engine exhaust, and noise may also have a greater likelihood of disturbing the target animals or their prey. As a precaution, in this study we attempted to maximize our distance from the focal animal while maintaining our ability to observe context. However, we cannot exclude the possibility that our presence disturbed the animals. To assess any disturbance it might be possible to use data from other remote telemetry devices to identify unusual sea lion behavior. We therefore tested our fine-scale tracking results against the data derived from the satellite tags but these analyses only served to emphasize the inaccuracy of satellite derived positions for fine-scale studies of sea lion behavior at sea.

As with other telemetry studies, we were limited to relatively small sample sizes given the finances and effort invested. This problem was further accentuated because it was only possible to track one sea lion at a time. With smaller sample sizes, the selection of sea lions in which to invest tracking effort becomes critical to the objective of the study. For example, searching for swimming sea lions in the immediate vicinity of haul-out sites could bias the tracking data away from individuals that make long-range trips. The comparison of the individuals included in the active-tracking data with the range of behaviors exhibited in the satellite telemetry data offers one opportunity to validate this.

The value of real time tracking methods for a particular species is dependent upon several factors relating to the foraging environment and behavior of the species. We found that active tracking was successful with juvenile Steller sea lions in Southeast Alaska. The sheltered nature of the region undoubtedly increased the number of days within which we could work compared to the more exposed coasts occupied by the species elsewhere. Furthermore, the frequent islands and fjords constrained the sea lion movement paths and in so doing, made our searches easier for animals once they had left the haul-out. Because movements were generally localized (1-20 km) we were able to minimize our search time and validate the accuracy of concurrent satellite derived locations. Sea lions that forage in pelagic environments would pose greater, but not insurmountable, logistical problems unless tracked exclusively from a haul-out.

The study also provided a rare opportunity to assess the precision of satellite-derived locations for sea lions at sea through comparisons with concurrently recorded VHF locations. Very few high quality Argos locations (classes 3-0) were recorded for animals at sea, with 80% of locations being from the poorer quality A and B classes. Consequently mean errors of 6.7-16.2 km (range 0.6-74.5 km) were recorded for the majority of satellite-estimated locations at sea (Table 2). Only nine high precision

locations (classes 3-0), accurate to within \sim 1.5-2 km, were recorded. This level of precision, however, while acceptable for large, trans-oceanic migrations, is still insufficient to elucidate direct relationships between prey dynamics and predator behavior, particularly for patchy, highly mobile prey such as herring.

Geographic Positioning System (GPS) tags, however, may provide an alternative to conventional satellite tags for high-resolution tracking studies. A recent study evaluating the use of satellite-linked GPS tags on Pacific walrus (Odobenus rosmarus divergens) indicated that infrequent and short surface intervals, and the proximity of cliffs limited the success of this technique (Jay and Garner 2002). However, the faster signal detection and alternative processing strategies of GPS-Fastloc (Wildtrack Telemetry Systems, UK) has radically improved the effectiveness of GPS in marine mammal tracking. Recent development and trials of Fastloc-GSM tags [Sea Mammal Research Unit, UK]) on grey seals in the North Sea have proved successful, providing an average of 40 locations per day at sea over a period of 100 days (B. McConnell, Sea Mammal Research Unit, UK, pers. comm.). However, if we are to understand the behavior of foraging marine mammals at the scales relevant to their decision processes and the factors influencing them, then fine-scale active tracking is necessary. One of the greatest advantages active tracking offers is the opportunity to put the behavior of individual animals in the context of their often highly dynamic prey and predators, at temporal and spatial scales that are generally unobtainable through the use of remote telemetry, or archival tags.

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