

Transmitting species–interaction data from animal-borne transceivers through Service Argos using Bluetooth communication

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Summary

1. Interactions between upper trophic-level predators and their prey remain poorly understood due to their inaccessibility during foraging at sea. This uncertainty has fuelled debate on the impact of predation by species such as the grey seal (*Halichoerus grypus*) on fish stocks.
2. The Vemco Mobile Transceiver (VMT) has provided us with new knowledge on interactions between pinnipeds and fish species. However, the necessity to recover the VMT for data retrieval has limited deployments to locations where confidence in instrument recovery is high, and has thus restricted both species and geographical sampling.
3. To overcome these limitations, a Bluetooth link was integrated into the VMT and GPS satellite-linked transmitter. The two-unit design allows data collected by the VMT to be transmitted via Bluetooth to the satellite transmitter, which relays the interaction data to the ARGOS satellite system for retrieval.
4. To evaluate in-situ performance, units were deployed on two adult female grey seals on Sable Island, NS in October 2012 and recovered during the subsequent breeding season. Data archived by the VMT were compared with data uploaded via ARGOS.
5. The deployment periods were 76–84 days. The total number of valid detections archived was 179. All detections archived by the first unit ($n = 66$) were transmitted via ARGOS, while all but two of the 113 archived detections from the second unit were transmitted. Detections recovered from both units were from other VMT-tagged grey seals ($n = 173$) and moored V13 transmitters on Middle Bank, Eastern Scotian Shelf ($n = 6$).
6. These preliminary results are proof-of-concept that integrated Bluetooth VMTs can be used on a broader variety of marine predators to collect data on species interactions in otherwise inaccessible environments and without the need to recover instruments.

Key-words: sampling, population ecology, species interactions, monitoring, community ecology

Introduction

Top and other upper trophic-level predators are important components of ecosystems and there is growing awareness of their functional roles (e.g., Estes *et al.* 2011). Knowledge of predator–prey interactions can inform potential resource conflicts (e.g., Mohn & Bowen 1996), and contribute toward an understanding of the potential effects of global environmental change and top predator declines on communities (Heithaus *et al.* 2008; Tylionakis *et al.* 2008; Baum & Worm 2009; Gilman *et al.* 2010; Hollowed *et al.* 2013). However, in comparison to terrestrial and inter-tidal environments, our

understanding of species interactions involving marine top predators is limited due to their wide-ranging and relatively inaccessible nature (Heithaus *et al.* 2008; Baum & Worm 2009). Nevertheless, some studies have taken advantage of these characteristics and employed upper trophic-level marine predators as sampling platforms (‘bioprobes’) of the marine environment collecting both oceanographic (e.g., McCafferty *et al.* 1999; Fedak 2004) and biological (e.g., Holland, Meyer & Dagorn 2009; Lidgard *et al.* 2012; Hayes *et al.* 2013) data.

Satellite-linked conductivity–temperature–depth (CTD) loggers have been deployed on various marine birds (Charrassin *et al.* 2002) and mammals (McCafferty *et al.* 1999) to collect high-resolution oceanographic records along with location and behavioural data (McCafferty *et al.* 1999; Fedak 2004).

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Marine species often access environments, such as ice-covered polar regions (Charrassin *et al.* 2008), that are effectively or completely inaccessible to ships, buoys and/or satellite coverage. Diving animals, such as pinnipeds, can provide valuable horizontal and vertical oceanographic profiles from such remote areas. In the Southern Ocean south of 60 degrees latitude, animal platforms have provided approximately 70% of all oceanographic profiles (Fedak 2013), and have made significant improvements to global ocean circulation models (Roquet *et al.* 2013).

Recently, several studies have used upper trophic-level marine predators to examine intra- and interspecies interactions in large marine ecosystems (e.g., Holland, Meyer & Dagorn 2009; Lidgard *et al.* 2012; Hayes *et al.* 2013). Lidgard *et al.* (2012) employed grey seals with GPS satellite-linked transmitters and Vemco mobile acoustic transceivers (VMT, www.vemco.com) to examine interactions among grey seals (*Halichoerus grypus*) while on foraging trips to better understand foraging tactics and possible at-sea social structure. The same technology was used with northern elephant seals (*Mirounga angustirostris*; Hayes *et al.* 2013) and grey seals (Lidgard *et al.* 2014), to explore the spatial and temporal nature of detections of acoustically tagged fish and thereby better understand predator-prey interactions.

Species that have low mortality rates and reliably return to the same location to feed young (e.g., king penguins, *Aptenodytes patagonicus* Guinet *et al.* 1997), breed (e.g., northern elephant seals, Boehlert *et al.* 2001) or remain within a small geographical area (e.g., shark species, Holland, Meyer & Dagorn 2009), can be used to collect archived location, oceanographic and biological data. However, the necessity to recover tags and retrieve the data limits the number of marine species that can act as biologgers, shortens the deployment period (tags are often removed before the battery is exhausted) and limits the geographical sampling area. To reduce the risks and overcome these limitations, since the late 1980s, marine animal trackers have used the ARGOS satellite transmission system (CLS-Argos) and sophisticated compression algorithms (Fedak, Lovell & Grant 2001; Fedak *et al.* 2002) to remotely collect location, behavioural and more recently oceanographic data from roving marine animals, eliminating the need for their recapture and retrieval of instruments (McConnell *et al.* 1992). However, the VMT is an acoustic transceiver and data logger and thus has no satellite transmission capability and must be recovered from the animal to retrieve the data.

The VMT is being used to record interactions between grey seals and other tagged species such as Atlantic cod (*Gadus morhua*) and salmon (*Salmo salar*) in the northwestern Atlantic as part of the Ocean Tracking Network (OTN), a multinational project using acoustic and complementary technology to examine the movement and survival of marine organisms (Cooke *et al.* 2011). The aim of our study is to gain a better understanding of the importance of specific prey in the grey seal diet and the extent to which predation by grey seals may be limiting the recovery of depleted fish stocks. As the VMT must be recovered, all of the seals have been deployed on Sable Island, Nova Scotia since grey seals reliably return to the island

after capture to breed, providing an exceptionally high tag recovery rate (~90%). However, Sable Island grey seals show a strong fidelity throughout the Scotian Shelf for foraging (Austin, Bowen & McMillan 2004; Breed *et al.* 2006) which limits the amount of sampling in other parts of the species range, most notably the Gulf of St. Lawrence and Cabot Strait where the impact of grey seal predation on cod stocks is thought to be greatest (Benoît *et al.* 2011).

These limitations motivated the development of a Bluetooth communication link between the VMT and GPS satellite-linked transmitter, allowing for data collected by the VMT to be potentially sent to the user via the ARGOS satellite system. This configuration would eliminate the need for recapture and allow VMTs to be deployed at locations used by grey seals that are in or close to the Gulf of St. Lawrence, providing a more balanced spatial sampling design than was previously possible. Additionally, if proven successful, this technology could be implemented with other large marine predators and ecosystems where recapture is not possible.

In this study, we tested the prototype of this new technology on two adult female grey seals deployed in October 2012 on Sable Island, NS to determine the relative success of the Bluetooth link in wild conditions. We recaptured both individuals during the following breeding season and compared the archived data from the recovered tags with the data transmitted via the ARGOS satellite system.

Materials and methods

The study was conducted between 12 October 2012 and 4 January 2013 on Sable Island and the Eastern Scotian Shelf, Canada (Fig. 1a). Sable Island (43°55'N, 60°00'W) is situated on the Eastern Scotian Shelf approximately 300 km ESE of Halifax, and is the location of the world's largest single breeding colony of grey seals (pup production of 61 600 in 2010; Thomas, Hammill & Bowen 2011). The Eastern Scotian Shelf is a continental shelf (108 000 km²) composed of a series of offshore shallow banks and inshore basins separated by deep gullies and canyons (DFO 2003), and an important foraging area for the grey seal (Breed *et al.* 2006) and other species (DFO 2003).

Between 1969 and 2002, samples of male and female grey seals at the Sable Island colony were branded at weaning providing a pool of individually identifiable, known-age adults. From this pool, two female adults were captured on the 12th and 13th of October 2012. Seals were weighed using a 300 kg (± 1 kg) Salter spring balance and then immobilized using the chemical anaesthetic Telazol (0.90 mg kg⁻¹; Bowen, Beck & Iverson 1999) to equip each seal with telemetry and data-logging devices. These comprised a VHF transmitter (164 MHz; www.atstrack.com), a Bluetooth-enabled Sea Mammal Research Unit GPS Satellite Relay Data Logger (SRDL; <http://www.smru.st-andrews.ac.uk/Instrumentation/GPSArgosTag/>) and a Bluetooth-enabled Vemco Mobile Transceiver (VMT; www.vemco.com) (Fig. 2). The VHF transmitter was used to locate the females when they returned to Sable Island in the following breeding season. The GPS SRDL tags were programmed to record and archive a GPS location every 20 min, to transmit positional (ARGOS and GPS) data and archive behavioural (diving and haul-out) data. Archived data were downloaded on recovery of the tag. When the unit was continuously dry for 10 min (i.e. when the seal was on land) and after a location had been attained, the interval between attempts to

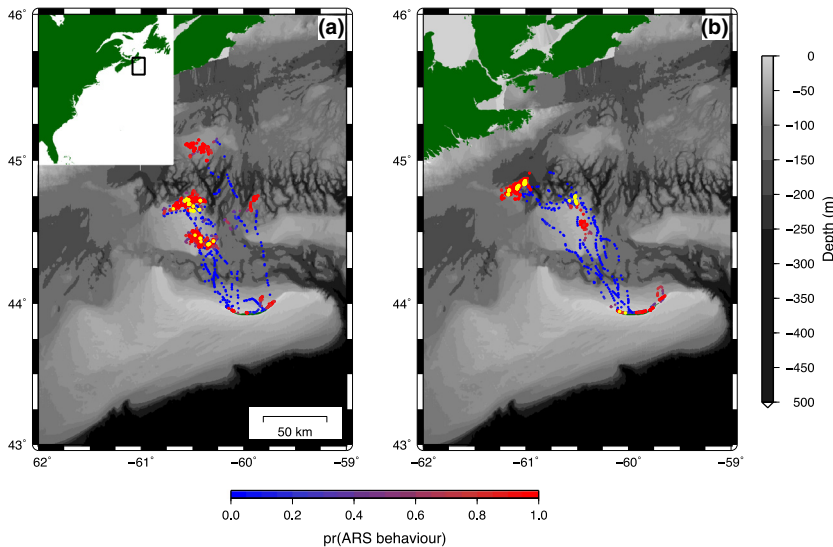


Fig. 1. Map showing the study area, movement tracks and probability of Area-Restricted Search [pr(ARS)] of two adult female grey seals (a: Seal 1; b: Seal 2) and the locations (yellow dots) of interactions with other tagged seals.



Fig. 2. Photograph showing the position of the Bluetooth enabled Sea Mammal Research Unit GPS Satellite Relay Data Logger and Bluetooth enabled Vemco Mobile Transceiver on an adult female grey seal deployed from Sable Island. Photo credit: D.C. Lidgard.

obtain a GPS location was increased 12 times to save battery energy. The VMT was programmed to transmit at 69 kHz on an irregular schedule, every 60 to 180 s (to avoid VMTs transmitting at the same time as another transmitter and thus causing code collisions and false detections), to switch off the listening mode during transmission (~3.6 s) to prevent the tag from recording its own code, and to remain in listening mode for the remainder of time. The high frequency limit for hearing in phocids is ~100 kHz with peak sensitivity between ~10 and 50 kHz (Kastelein *et al.* 2009). It is therefore possible that seals could hear the 69-kHz transmission pings from the VMT and other tagged individuals (Bowles, Denes & Shane 2010a; Bowles, Graves & Shane 2010b). Nevertheless, due to the position of the tag on the lower back of the animal, ambient background noise, reflection and refraction of the signal, and habituation to the ping (Bowles, Denes & Shane 2010a), it is not clear what proportion of the pings from the VMT the seal would hear, nor whether a seal could localize other tagged seals or fish. However, the movement and breeding patterns of seals in the current study (and other VMT studies, that is, Lidgard *et al.* 2012, 2014) were similar to those in previous studies that were tagged with a satellite transmitter but with no acoustic tag (Mellish, Iverson & Bowen 1999; Lidgard *et al.* 2005; Breed *et al.* 2006, 2009).

The VHF transmitter was attached to the satellite-GPS unit using a stainless steel hose clamp, and the assembled unit was attached to the hair on the top of the head using a 5-min epoxy adhesive (Boness, Bowen & Oftedal 1994). The VMT was attached in the same manner as for the satellite-GPS tag, but was located on the lower back of the animal with the hydrophone pointing to the rear to reduce the likelihood that the seal would hear the acoustic pings, improve the chances of the tag remaining underwater when the animal was at the surface and to minimize electromagnetic interference with the satellite-GPS. The tag mass burden (total mass of tags/average body mass) was 0.39%. Individuals were recaptured during the subsequent breeding season (on the 28 December 2012 and 4 January 2013, respectively), to determine final body mass and recover instruments.

As part of a concurrent study examining interactions between grey seals and tagged fish within the OTN, an additional 17 grey seals were tagged with non-Bluetooth satellite-GPS tags (www.wildlifecomputers.com) and VMT's on Sable Island in June 2012 using the same methods as given here. Through collaborations within the OTN, 623 Atlantic cod and 298 Atlantic salmon were tagged during 2010 and 2012 with Vemco transmitters on the Eastern Scotian Shelf and within the southern Gulf of St. Lawrence (Lidgard *et al.* 2014). All field procedures were conducted in accordance with guidelines for the use of animals in research (ASAB 2006) and of the Canadian Council on Animal Care. The research protocol for the study was approved by the University Committee on Laboratory Animals, Dalhousie University's animal ethics committee (animal care protocol: 12-64) and Department of Fisheries and Oceans, Canada (animal care permit and licenses: 12-13, 12-14).

COMPRESSION ALGORITHM FOR SENDING VMT DATA OVER ARGOS

Argos messages can accommodate a data payload of approximately 31 bytes. The VMT outputs an 11-byte record per detection, which includes a 2-byte code space, 3-byte tag identity and a 4-byte date-time stamp (the code space nomenclature is required by the receiver to decode tag transmissions). Such a coding scheme is simple for the VMT to internally store its data, but lacks entropy and thus is inefficient for transmission over a limited bandwidth. To overcome this problem, a compression algorithm, using a similar approach for transmitting compressed behavioural data from satellite relay data loggers

(Fedak *et al.* 2002), was designed to compress detection data through the use of indices, encoding schemes and removal of unessential data.

When a seal encounters another acoustically tagged animal, one or more detections will be recorded by the VMT along with a date-time stamp. For most situations, it is the timing and duration of the encounter that will be of interest to the researcher rather than the time of single detections. Thus, rather than transmitting individual time-stamped detections, groups of detections from one or more transmitters are transmitted along with a precise start time and duration of the encounter.

Given that many of the tag identities from the tagged grey seals and fish species were already known, a table of tag identities was stored in the tag and the decoder thus reducing the number of bytes required to encode for known tag identities. Unknown (i.e., not listed in the tag identity table) identities (or false identities) can also be encoded although they required more bytes per message. The same logic also applied to the code space as the VMT is programmed to respond only to nine specific values for this field. Time differences were used to reduce the byte length required to encode for timestamps. Thus, for each encounter the first detection receives a precise timestamp and this is transmitted along with the duration of the encounter. A maximum entropy probability-based coding scheme (Huffman coding) was used with the tag identity and code space tables to avoid their need for transmission. The outcome is that each block of data to be transmitted is encoded into a ~1.5-byte identity message and a ~2-byte encounter message that comprises the start time and duration of the encounter(s).

To transmit a block of detection data to ARGOS, the compression algorithm evaluates the size of two sampling windows. The first sampling window is initially 24 h from which all of the detection data are encoded into the identity and encounter messages. If the volume of data within the 24-h period results in either message being too long for transmission, the sampling window is reduced by half to 12 h and the process is repeated. Iterations continue until the length of the two messages is small enough for transmission. At this point, the algorithm attempts to maximize the detail contained within the messages by evaluating the size of a second sampling window, which controls the compression of detections from the same transmitter. The algorithm determines the shortest window that still results in valid (i.e., small enough) messages for transmission. If there are few data, the second window might be one minute, in which case all detections would receive a date-time stamp. In contrast, if there were many detections, the second window might be equal in length to the first window, in which case all detections from the same transmitter would be grouped into a single encounter with a single date-time stamp and duration.

The VMT was designated as the Bluetooth secondary device (lowest power option) while the GPS satellite-linked tag acted as the primary. To optimize power consumption, the primary tag was programmed to attempt communication with the VMT only when the unit had been dry for > 30 secs, that is, when the seal was hauled out or at the surface, and for a period long enough to ensure it will trigger the VMT to respond. On each successful communication, the primary tag re-synchronized the internal clock of the VMT and programmed it with a new schedule.

DATA ANALYSIS

GPS data archived by the SRDL provided more locations and of higher accuracy compared with the data from Argos thus, we report only those GPS data here. Locations acquired from <5 satellites and/or with a residual error >30 were removed from the data set due to their lower accuracy (Byrant 2007; Hazel 2009). VMT detections comprised a date-time stamp and the identities of the tags detected, these were

downloaded and visualized using the dedicated software VUE (www.vemco.com). False detections, for example, the production of existing codes from the collision of multiple codes from other active transmitters, were identified using proprietary software (Vemco) (two of 181 detections) and subsequently removed from the data set. Using the date-time data from each VMT and the seal's GPS record, the locations of detections were estimated using linear interpolation between GPS locations. In some cases, that is, when the seal is moving slowly, multiple detections with other tagged seals or fish might occur. Thus, we operationally defined a seal-seal or seal-fish encounter according to Lidgard *et al.* (2012, 2014), respectively, whereby a new encounter began when the time between detections was <30 min (seal-seal) or 10 min (seal-fish). For encounters that involved only a single detection the duration of the association was set at either three minutes (seal-seal) or 2 min (seal-fish) since in each case after this time, based on the least frequent transmission rate of the respective tag, another detection would have occurred if the two individuals were still together.

We used the same approach as in Lidgard *et al.* (2012) for modelling travel rate data. A hidden Markov model (HMM; Zucchini & MacDonald 2009; Patterson *et al.* 2009) was used to discriminate between two behavioural states along each of the two seal tracks. We assumed that seal travel rate is conditional upon two discrete, unobserved movement states: fast and slow movement, where slow movement (probability of Area-Restricted Search, $pr(ARS) > 0.5$) is assumed to be associated with foraging or resting behaviours (Barraquand & Benhamou 2008).

Analyses were conducted within R 2.14.1 (R Development Core Team 2011). Maps were generated using the Generic Mapping Tools (Wessel & Smith 1995). Standard error is reported as the measure of variability.

Results

Both Bluetooth VMT-tagged seals were recaptured on Sable Island during the subsequent breeding season, on 28 December 2012 (Seal 1) and 4 January 2013 (Seal 2) with duration of deployment of 76 and 84 days, respectively. The behaviour of each seal while at sea was typical of grey seals from Sable Island, exhibiting central place foraging behaviour between Sable Island and shallow offshore sandbanks (Austin, Bowen & McMillan 2004; Breed *et al.* 2006, 2009). The hidden Markov model showed that both seals exhibited fast movement when moving between these two areas, and slower area-restricted movements over the shallow offshore areas suggesting seals might be foraging (Fig. 1).

The two deployed Bluetooth VMTs recorded detections from eight other VMT-tagged seals (Seal 1, number of detections = 61; Seal 2, number of detections = 112) and two V13 acoustic transmitters moored on Middle Bank, Eastern Scotian Shelf (Seal 1, number of detections = 5; Seal 2, number of detections = 1; Table 1 and Fig. 3). The majority of the seal-seal detections (80%) occurred while the seal was engaged in area-restricted search behaviour (mean $pr(ARS)$ at time of detection, 0.76 ± 0.05 ; Fig. 1). The archived VMT record from Seal 1 was the same as that transmitted via satellite, while the transmitted record from Seal 2 was missing two detections during a single encounter. Thus both Bluetooth tags transmitted the same behavioural information as measured from the full archived records.

Table 1. Summary statistics of archived seal–seal encounters ($n = 173$) for two adult female grey seals deployed with Bluetooth acoustic transmitters on Sable Island, NS, October 2012 to January 2013. pr(ARS) is the probability of Area-Restricted Search

Seal Id	Number of detections	Number of seal–seal encounters	Number of detections per encounter	Duration of encounter, min	pr(ARS) at detection
1	61	15	4.1 ± 1.4	15.5 ± 5.7	0.69 ± 0.05
2	112	27	4.2 ± 0.9	17.4 ± 3.7	0.86 ± 0.03

Discussion

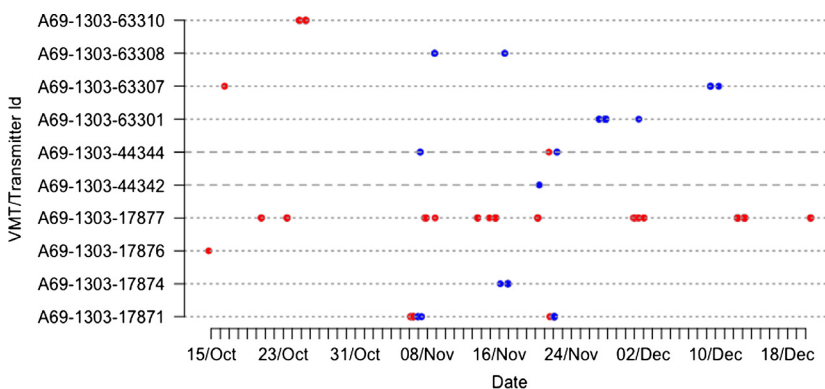
The transmission of behavioural data by free-ranging upper trophic-level marine predators, such as pinnipeds, to users via satellite has become commonplace in the past several decades (Cooke *et al.* 2004). The present study extends this capability by transmitting detections of coded acoustic tags from an acoustic transceiver on the lower back of a seal to a GPS satellite-linked tag on the animal's head. The received data are then transmitted to Service ARGOS for retrieval. Given that this configuration had not been tested in a natural environment, the limited bandwidth available for transmitting data in a single message and the competing need to transmit location, dive behaviour and detection data, there was concern that not all of the detection data from the transceiver would be transmitted. However, this study has demonstrated that a Bluetooth link can be used to exchange data between two physically separate telemetry units deployed on a free-ranging marine mammal. Furthermore, using the compression algorithm, all of the detection data, in addition to location and dive behaviour data, can be retrieved remotely from the acoustic transceiver via satellite.

The main advantage of this configuration is that it eliminates the need to recapture animals to recover data from bio-logging instruments. Grey seals can generally be caught relatively easily at breeding colonies and resting sites for the deployment of instruments, but recapturing the same individual to recover instruments and data is more challenging and often not possible at most locations, and is the case for most other pinnipeds. Thus, a Bluetooth link extends the applicability of the GPS-acoustic tag configuration for use on large upper trophic-level predators that are difficult to recapture. We anticipate that this approach to obtaining bio-logging data could be used on other large (>60 kg), air-breathing or regularly surfacing marine

species, for example, pinnipeds, cetaceans, sea turtles and basking sharks, (see Fig. 2 for tag configuration). Given the frequent transmission of data to ARGOS and our experience with the use of non-Bluetooth satellite transmitters and VMTs, we expect the current Bluetooth configuration to operate for ~8 months.

Although the Bluetooth link configuration extends the list of species that could benefit from its use, there are marine predators that would not be suitable. The transfer of data via Bluetooth occurs when the conductivity sensors on the GPS satellite transmitter have been dry for >30 s and remain so long enough to allow for the transmission of data, thus the animal needs to either be on land or spend an extended period of time at the surface, for example, sharks that frequently surface (Hammerschlag, Gallagher & Lazarre 2011). For many species of pinniped this does not present a problem because they spend time on land in between foraging trips, and many other marine mammals and sea turtles remain at the surface after diving either resting or recovering from an extended dive. However, for species such as large predatory fish, for example, sharks that rarely surface, tuna and small Odontocetes, there likely is insufficient time spent at the surface to allow for the GPS transmitter to achieve a 'dry' status, communicate with the VMT and receive data.

An obvious solution to this problem would be to design an integrated tag that could perform the functions of both tags. An integrated tag would minimize the tag footprint, improve the logistics of deploying tags on large wild animals and reduce production costs, all of which would likely extend the range of animals that could act as marine bioprobes. However, the main obstacle to designing an integrated tag is the conflicting requirements of the two tags. The satellite tag needs to be positioned on an area of the body that will be exposed when the animal reaches the surface to allow for the transmission of data

**Fig. 3.** Temporal pattern of seal–seal detections transmitted from Bluetooth enabled Vemco Mobile Transceivers deployed on two adult female grey seals (Blue: Seal 1; Red: Seal 2), Sable Island, NS. Note transmitter A69-1303-44342 and -44344 were stationary moorings on Middle Bank, Eastern Scotian Shelf.

to ARGOS; in the case of seals, this is the head and neck region. However, this placement is not suitable for the VMT as it needs to remain below water as much as possible to maximize the opportunities for receiving detections from tagged fish or marine mammals; the most suitable location in this case is on the back either toward the rear or near the centre. Further, it is known that seals can hear the transmitted 69-kHz signals from the VMT (although toward the upper limit of their hearing range; Kastelein *et al.* 2009; Bowles, Denes & Shane 2010a; Bowles, Graves & Shane 2010b); thus, placing the unit close to the head could disturb the study animal. A single unit would also place additional demands on battery life that will either lead to a larger battery pack and thus a larger tag footprint or a shorter deployment period, neither of which is advantageous.

Recovering hardware after a deployment is always beneficial to a study. GPS-linked satellite tags and VMTs can be re-deployed with a new battery, thus reducing hardware costs, and provide the user with access to uncompressed archived data. The GPS tag is capable of measuring, at frequent intervals (<4 s), depth and oceanographic descriptors, for example temperature, salinity, providing the user with highly detailed depth and oceanographic profiles. If the transmitter is not recovered, these data are compressed into summary profiles or detailed records are transmitted less frequently using an unbiased sampling strategy (Fedak *et al.* 2002). Uncompressed archived detection data comprise simply the date-time stamp for all detections and the associated receiver and transmitter identity (Table 2A). From these data, the duration of a biolog-

ically meaningful encounter between the tagged animals can be defined and provide greater accuracy when assigning a location to the encounter using interpolation from the bioprobe's GPS or ARGOS track. Compressed transmitted data, due to the limited bandwidth available with the ARGOS satellite system, comprise the receiver and transmitter identities, the start date-time of the first detection in an encounter, the number of detections that have been grouped into the encounter and the duration of the encounter (Table 2B). The number of detections to be grouped is evaluated by the algorithm according to the number of detections received (i.e., volume of data collected) from transmitters in the area, rather than by the biology of the species concerned. In cases where there are few data to transmit during a given period (e.g., 24 h), the sampling window for transmission will be narrow providing more detail (i.e. timestamp for all detections) and therefore minimizing the differences between archived and transmitted data. At the other extreme, if there are a lot of data, all detections for a given transmitter will be grouped into a single encounter with a single timestamp and duration resulting in a loss of detail. Predicting how much detail will be preserved in the transmitted data is not possible but it will be dependent upon the number of animals tagged with VMTs and transmitters, the biology of the species concerned (e.g., seasonal movement patterns) and the size of the study area.

Archived receiver statistics are required to identify false detections (Pincock 2008). All acoustic codes from Vemco transmitters are comprised of eight 69-kHz pings but the duration of intervals between successive pings and the length of time it takes to emit the entire 8-ping code varies to generate unique codes. As with all digital communication systems, transmission errors where the received acoustic signal differs to that which was transmitted are inevitable. The presence of other active transmitters in the area, ocean bottom topography, bathymetry, varying ambient ocean noise and oceanographic features, for example thermocline, can result in code collisions or modified ping sequences that could be accepted as valid detections (Baker *et al.* 2014). To aid in identifying false detections, the VMT archives the time at which it transmits its own code (from which one can assess the likelihood of a collision between transmitted and received codes) in addition to raw data (i.e., number and time of pings transmitted or received) associated with each transmission and valid detection received. If the VMT is not recovered, these supplementary data will not be available to the user simply due to the limited bandwidth available for transmission to the ARGOS system. Thus, single detections logged by a Bluetooth-enabled VMT should be treated cautiously. Access to the raw data can also aid in measuring the proficiency at which the VMT transmits and receives coded data in the environment in which the experiment is conducted, through an examination of the number of pings transmitted and received, and associated variables such as sea temperature, wind speed, depth of tagged animal, distance from transmitter, etc (Baker *et al.* 2014). An estimate of VMT proficiency is critical to interpreting the number of detections received by each receiver.

Table 2. Comparison of archived (A) and ARGOS-transmitted (B) raw data from a Bluetooth-enabled Vemco Mobile Transceiver. The number of detections to be grouped for transmission via ARGOS is evaluated by the algorithm according to how many other transmitters were detected and the duration of intervals between detections from the same transmitter

(A)			
Date-time	Transmitter		
2013-12-12 4:39:02	A69-1303-17877		
2013-12-12 4:42:42	A69-1303-17877		
2013-12-12 4:44:31	A69-1303-17877		
2013-12-12 4:47:04	A69-1303-17877		
2013-12-12 4:49:08	A69-1303-17877		
2013-12-12 4:50:11	A69-1303-17877		
2013-12-12 4:52:18	A69-1303-17877		
2013-12-12 4:54:25	A69-1303-17877		
2013-12-12 4:55:29	A69-1303-17877		

(B)			
Date-time	Transmitter	Number of detections	Duration (s)
2013-12-12 4:39:02	A69-1303-17877	2	60
2013-12-12 4:44:31	A69-1303-17877	8	720

The preliminary results of this study clearly demonstrate the value of integrating Bluetooth technology with the Vemco Mobile Transceiver to transmit species interaction data via ARGOS to the user. This configuration eliminates the need to recapture study animals, extending its applicability to a broader variety of marine predators that inhabit inaccessible environments, and allows one to consider the behaviour of the prey in addition to the predator to provide a starting point for quantifying predator–prey interactions.

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Declaration of interest

Dale Webber and Tim Stone are affiliated with the commercial company VEMCO Ltd, and Bernie McConnell and Phil Lovell are affiliated with the commercial arm of the Sea Mammal Research Unit (SMRU Instrumentation). All four authors were involved in the development of the Bluetooth link between the Vemco Mobile Transceiver and the SMRU GPS Satellite Relay Data Logger. Neither VEMCO Ltd. or SMRU Instrumentation financed the project, nor were they directly involved in the study design and data analysis.

Data accessibility

Data from this study are archived with the Ocean Tracking Network (<http://oceantrackingnetwork.org/>) and are accessible in accordance with the data accessibility policy of the OTN.

References

ASAB (2006) Guidelines for the treatment of animals in behavioural research and teaching. *Animal Behaviour*, **71**, 245–253.

Austin, D., Bowen, W.D. & McMillan, J.I. (2004) Intraspecific variation in movement patterns: modelling individual behaviour in a large marine predator. *Oikos*, **105**, 15–30.

Baker, L.L., Jonsen, I.D., Mills Flemming, J.E., Lidgard, D.C., Bowen, W.D., Iverson, S.J. & Webber, D.M. (2014) Probability of detecting marine predator–prey and species interactions using novel hybrid acoustic transmitter–receiver tags. *PLoS ONE*, **9**, e98117.

Barraquand, F. & Benhamou, S. (2008) Animal movements in heterogeneous landscapes: identifying profitable places and homogenous movement bouts. *Ecology*, **89**, 3336–3348.

Baum, J.K. & Worm, B. (2009) Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, **78**, 699–714.

Benoît, H., Swain, D., Bowen, W., Breed, G., Hammill, M. & Harvey, V. (2011) Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. *Marine Ecology Progress Series*, **442**, 149–167.

Boehlert, G.W., Costa, D.P., Crocker, D.E., Green, P., O'Brien, T., Levitus, S. & Le Boeuf, B.J. (2001) Autonomous pinniped environmental samplers: using instrumented animals as oceanographic data collectors. *Journal of Atmospheric and Oceanic Technology*, **18**, 1882–1892.

Boness, D.J., Bowen, W.D. & Oftedal, O.T. (1994) Evidence of a maternal foraging cycle resembling that of otariid seals in a small phocid, the harbor seal. *Behavioral Ecology and Sociobiology*, **34**, 95–104.

Bowen, W.D., Beck, C.B. & Iverson, S.J. (1999) Bioelectrical impedance analysis as a means of estimating total body water in grey seals. *Canadian Journal of Zoology*, **77**, 418–422.

Bowles, A.E., Denes, S.L. & Shane, M.A. (2010a) Acoustic characteristics of ultrasonic coded transmitters for fishery applications: could marine mammals hear them? *Journal of the Acoustical Society of America*, **128**, 3223–3231.

Bowles, A.E., Graves, S.K. & Shane, M. (2010b) Harbor seals respond with aversion to 69-kHz pings: implications for weighting procedures for marine mammal noise metrics. *Journal of the Acoustical Society of America*, **127**, 1803.

Breed, G.A., Bowen, W.D., McMillan, J.I. & Leonard, M.L. (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 2319–2326.

Breed, G.A., Jonsen, I.D., Myers, R.A., Bowen, W.D. & Leonard, M.L. (2009) Sex-specific, seasonal foraging tactics of adult grey seals (*Halichoerus grypus*) revealed by state–space analysis. *Ecology*, **90**, 3209–3221.

Byrant, E. (2007) 2D Location accuracy statistics for Fastloc® cores running firmware Versions 2.2 & 2.3. Leeds Wildtrack Telemetry Systems Ltd., UK Technical Report Fastloc TR01.

Charrassin, J.B., Park, Y.H., Le Maho, Y. & Bost, C.A. (2002) Penguins as oceanographers unravel hidden mechanisms of marine productivity. *Ecology Letters*, **5**, 317–319.

Charrassin, J.-B., Hindell, M., Rintoul, S.R., Roquet, F., Sokolov, S., Biuw, M. et al. (2008) Southern Ocean frontal structure and sea-ice formation rates revealed by elephant seals. *Proceedings of the National Academy of Sciences*, **105**, 11634–11639.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G. & Butler, P.J. (2004) Biotelemetry: a mechanistic approach to ecology. *Trends in Ecology & Evolution*, **19**, 334–343.

Cooke, S.J., Iverson, S.J., Stokesbury, M.J.W., Hinch, S.G., Fisk, A.T., VanderZwaag, D.L., Apostle, R. & Whoriskey, F. (2011) Ocean Tracking Network Canada: a network approach to addressing critical issues in fisheries and resource management with implications for ocean governance. *Fisheries*, **36**, 583–592.

DFO (2003) Status of the Eastern Scotian Shelf ecosystem. DFO Canadian Science Advisory Secretariat Ecosystem Status Report 2003/004.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J. et al. (2011) Trophic downgrading of planet earth. *Science*, **333**, 301–306.

Fedak, M.A. (2004) Marine animals as platforms for oceanographic sampling: a 'win/win' situation for biology and operational oceanography. *Memoirs of National Institute of Polar Research*, **58**, 133–147.

Fedak, M.A. (2013) The impact of animal platforms on polar ocean observation. *Deep Sea Research Part II: Topical Studies in Oceanography*, **88–89**, 7–13.

Fedak, M.A., Lovell, P. & Grant, S.M. (2001) Two approaches to compressing and interpreting time–depth information as collected by time–depth recorders and satellite-linked data recorders. *Marine Mammal Science*, **17**, 94–110.

Fedak, M., Lovell, P., McConnell, B. & Hunter, C. (2002) Overcoming the constraints of long range radio telemetry from animals: getting more useful data from smaller packages. *Integrative And Comparative Biology*, **42**, 3–10.

Gilman, S.E., Urban, M.C., Tewksbury, J., Gilchrist, G.W. & Holt, R.D. (2010) A framework for community interactions under climate change. *Trends in Ecology & Evolution*, **25**, 325–331.

Guinet, C., Koudil, M., Bost, C.A., Durbec, J.P., Georges, J.Y., Mouchot, M.C. & Jouventin, P. (1997) Foraging behaviour of satellite-tracked king penguins in relation to sea–surface temperatures obtained by satellite telemetry at Crozet Archipelago, a study during three austral summers. *Marine Ecology Progress Series*, **150**, 11–20.

Hammerschlag, N., Gallagher, A.J. & Lazarre, D.M. (2011) A review of shark satellite tagging studies. *Journal of Experimental Marine Biology and Ecology*, **398**, 1–8.

Hayes, S.A., Teutschel, N.M., Michel, C.J., Champagne, C., Robinson, P.W., Fowler, M. et al. (2013) Mobile receivers: releasing the mooring to 'see' where fish go. *Environmental Biology of Fishes*, **96**, 189–201.

Hazel, J. (2009) Evaluation of fast-acquisition GPS in stationary tests and fine-scale tracking of green turtles. *Journal of Experimental Marine Biology and Ecology*, **374**, 58–68.

Heithaus, M.R., Frid, A., Wirsing, A.J. & Worm, B. (2008) Predicting ecological consequences of marine top predator declines. *Trends in Ecology & Evolution*, **23**, 202–210.

Holland, K.N., Meyer, C.G. & Dagorn, L.C. (2009) Inter-animal telemetry: results from first deployment of acoustic-business card tags. *Endangered Species Research*, **10**, 287–293.

Hollowed, A.B., Barange, M., Beamish, R.J., Brander, K., Cochrane, K., Drinkwater, K. et al. (2013) Projected impacts of climate change on marine fish and fisheries. *ICES Journal Of Marine Science*, **70**, 1023–1037.

Kastelein, R.A., Wensveen, P.J., Hoek, L., Verboom, W.C. & Terhune, J.M. (2009) Underwater detection of tonal signals between 0.125 and 100 kHz by harbor seals (*Phoca vitulina*). *Journal of Acoustic Society of America*, **125**, 1222–1229.

Lidgard, D.C., Boness, D.J., Bowen, W.D. & McMillan, J.I. (2005) State-dependent male mating tactics in the grey seal: the importance of body size. *Behavioral Ecology*, **16**, 541–549.

- Lidgard, D.C., Bowen, W.D., Jonsen, I.D. & Iverson, S.J. (2012) Animal-borne acoustic transceivers reveal patterns of at-sea associations in an upper-trophic level predator. *PLoS ONE*, **7**, e48962.
- Lidgard, D.C., Bowen, W.D., Jonsen, I.D. & Iverson, S.J. (2014) Predator-borne acoustic transceivers and GPS tracking reveal spatial and temporal patterns of encounters with acoustically-tagged fish in the open ocean. *Marine Ecology Progress Series*, **501**, 157–168.
- McCafferty, D.J., Boyd, I.L., Walker, T.R. & Taylor, R.I. (1999) Can marine mammals be used to monitor oceanographic conditions? *Marine Biology*, **134**, 387–395.
- McConnell, B.J., Chambers, C., Nicholas, K.S. & Fedak, M.A. (1992) Satellite tracking of grey seals (*Halichoerus grypus*). *Journal of Zoology (London)*, **226**, 271–282.
- Mellish, J.E., Iverson, S.J. & Bowen, W.D. (1999) Variation in milk production and lactation performance in grey seals and consequences for pup growth and weaning characteristics. *Physiological and Biochemical Zoology*, **72**, 677–690.
- Mohn, R. & Bowen, W.D. (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic Cod. *Canadian Journal of Fisheries & Aquatic Sciences*, **53**, 2722–2738.
- Patterson, T.A., Basson, M., Bravington, M.V. & Gunn, J.S. (2009) Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology*, **78**, 1113–1123.
- Pincock, D. (2008) False Detections: What They Are and How to Remove Them from Detection Data. Vemco Application Note Version 01, June 10, 2008. DOC-004691.
- R Development Core Team (2011) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Roquet, F., Wunsch, C., Forget, G., Heimbach, P., Guinet, C., Reverdin, G. *et al.* (2013) Estimates of the Southern Ocean general circulation improved by animal-borne instruments. *Geophysical Research Letters*, **40**, 6176–6180.
- Thomas, L., Hammill, M.O. & Bowen, W.D. (2011) Estimated size of the Northwest Atlantic grey seal population 1977–2010. DFO Canadian Science Advisory Secretariat Research Document 2011/017.
- Tylianakis, J.M., Didham, R.K., Bascompte, J. & Wardle, D.A. (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.
- Wessel, P. & Smith, W.H.F. (1995) New version of the generic mapping tools released. *EOS, Transactions American Geophysical Union*, **76**, 329.
- Zucchini, W. & MacDonald, I.L. (2009) *Hidden Markov Model for Time Series*. Chapman & Hall/CRC, New York.

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