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Predator-borne acoustic transceivers and GPS tracking reveal spatiotemporal patterns of encounters with acoustically tagged fish in the open ocean

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ABSTRACT: Pinnipeds are abundant upper trophic level predators in many marine ecosystems. Top-down effects of their consumption can play important roles in ecosystem structure and functioning. However, interactions between pinnipeds and their prey remain poorly understood due to their inaccessibility while foraging at sea. This uncertainty has fueled debate on the impact of seal predation on fish stocks of commercial or conservation interest. Here, we show that a novel combination of acoustic (Vemco Mobile Transceiver, VMT) and GPS technology can be used to determine the spatial and temporal pattern of interactions between grey seals *Halichoerus grypus* and fish species in 2 large marine ecosystems, the Eastern Scotian Shelf and the southern Gulf of St. Lawrence, Canada. During 4 yr of study, the VMT on 9 of 64 adult grey seals recorded detections from 3 species of fish, namely 17 adult Atlantic cod *Gadus morhua*, 7 Atlantic salmon *Salmo salar* and 1 American eel *Anguilla rostrata* implanted with coded acoustic tags. An examination of the temporal and spatial pattern of these seal–fish interactions suggested that 1 salmon and 2 cod might have been predated on. However, to have confidence in the occurrence of a predation event, more conclusive evidence is required, which may be gathered through validation experiments. These preliminary results provide proof-of-concept that large upper trophic level marine predators fitted with VMT and GPS tags can provide information on species locations in areas where fixed receiver arrays are not present and allow new insights into the nature of interspecies interactions in otherwise inaccessible environments.

KEY WORDS: Interspecies interactions · Grey seal · *Halichoerus grypus* · Predator–prey interaction · Southern Gulf of St. Lawrence · Eastern Scotian Shelf

INTRODUCTION

Food webs are a complex and dynamic network of inter- and intraspecies interactions across multiple temporal and spatial scales. An understanding of how ecosystems function requires an understanding of food web (i.e. predator–prey) interactions (May et al. 1979, Christensen et al. 1996, Matthiopoulos et al. 2008). However, relative to terrestrial, freshwater and coastal marine ecosystems, predator–prey interactions in the open ocean are poorly understood due to the difficulty of sampling free-ranging predators and their prey and of conducting controlled experiments.

Apex and other upper trophic level predators are fundamental in shaping and stabilising ecosystems, with respect to both their abundance and behaviour

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(Estes et al. 2011, Ritchie et al. 2012). Technological advances in telemetry have contributed towards a greater understanding of movement, foraging behaviour and habitat use of marine upper trophic level predators, such as pinnipeds (e.g. Le Boeuf et al. 2000, Matthiopoulos et al. 2004, Aarts et al. 2008, Breed et al. 2009). Nevertheless, little remains known about how marine mammals interact with their prey (Holland et al. 2009, Hayes et al. 2013). This limits our ability to address questions concerning the impact marine mammal predation may have on fish populations of conservation or commercial interest, and the roles played by these predators in ecosystem structure and functioning (Bowen 1997, Matthiopoulos et al. 2008).

Since the late 1980s and early 1990s, Atlantic cod *Gadus morhua* stocks in eastern Canada have declined dramatically (Hutchings & Myers 1994, DFO 2003a). Similar trends have been observed for other fish species, e.g. winter skate (Swain et al. 2013). Despite greatly reduced or halted fisheries, Atlantic cod stocks have not recovered or are recovering at a pace slower than expected (Bundy & Fanning 2005). Several theories have been proposed, (e.g. Swain & Mohn 2012), but none can account for the failure of the stocks to recover, although causes are likely multifaceted (Neubauer et al. 2013). In contrast to the poor state of fish stocks, the eastern Canadian grey seal *Halichoerus grypus* population has increased from 13 000 in 1960 to 410 000 in 2010 (Thomas et al. 2011). Several studies have attempted to evaluate the impact of the grey seal on the recovery of depleted fish stocks, with a focus on the Atlantic cod (Mohn & Bowen 1996, Fu et al. 2001, Trzcinski et al. 2006, 2011, Bundy et al. 2009). Among other things, these studies have shown that model outcomes are highly sensitive to estimates of the proportion of cod in the grey seals' diet.

The northwest Atlantic salmon *Salmo salar* in Canada has also been in decline and suffers from unknown sources of high at-sea mortality (Gibson et al. 2006, ICES 2008). Many Atlantic salmon populations are listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, www.cosewic.gc.ca), and commercial fisheries for Atlantic salmon have been closed since at least the early 2000s (DFO 2008). Like Atlantic cod, salmon are known to be consumed by grey seals (Beck et al. 2007, Bowen et al. 2011); thus, understanding the level of grey seal predation will contribute towards better evaluation of the sources of salmon mortality.

Recent advances in acoustic telemetry may help to reduce uncertainty surrounding the interactions with and impact of marine mammals on commercial or vulnerable fish species (Holland et al. 2009, Stokesbury et al. 2009, Lidgard et al. 2012, Hayes et al. 2013). Traditionally, miniature acoustic transmitters and stationary receivers (Voegeli et al. 1998) were used to study interspecific interactions. A significant limitation with this design is the restricted geographical area within which information can be collected, e.g. rivers or intertidal systems, where species movements are relatively limited and easily monitored. A more recent advancement is the animal-borne video camera that provides detailed observations of prey (Davis et al. 1999, Bowen et al. 2002, Hooker et al. 2002, Heaslip et al. 2012). However, due to memory and battery-life limitations the deployment period is short and variation in video quality can lead to difficulties in identifying prey. The Vemco Mobile Transceiver (VMT; www.vemco.com) overcomes these problems. The VMT is a 69 kHz coded transceiver that alternates between transmitting a coded acoustic signal and listening for transmissions from other Vemco 69 kHz coded acoustic transmitters. Acoustic codes are unique due to the time interval between pings and the length of time it takes to transmit the full code. By attaching the VMT and a Fastloc™ GPS satellite transmitter to a marine predator, such as a seal, and tagging fish species with Vemco transmitters, time-stamped, georeferenced records of interactions between seals and fish can be collected over extended periods of time. Thus, in principle, one could examine species interactions, including predation, in the open ocean and seek to better understand the role of upper trophic predators in marine ecosystems.

In this study, we sought to determine whether the VMT combined with Fastloc™ GPS telemetry could be used to examine interactions between grey seals and several of their potential prey in 2 marine ecosystems off Eastern Canada.

MATERIALS AND METHODS

The study was conducted between 15 October 2009 and 21 January 2013 on the Eastern Scotian Shelf and the southern Gulf of St. Lawrence, Canada (see Fig. 1A). Both regions are important foraging areas for the grey seal (Breed et al. 2006). The Eastern Scotian Shelf is a continental shelf (108 000 km^2) composed of a series of offshore shallow banks and inshore basins separated by deep gullies and canyons (DFO 2003b). The southern Gulf of St. Lawrence (80 000 km^2) is a semi-enclosed sea connecting the St. Lawrence estuary with the Atlantic Ocean through 2 outlets, Strait of Belle Isle and Cabot Strait.

Sable Island (43° 55′ N, 60° 00′ W) is situated on the Eastern Scotian Shelf ~300 km ESE of Halifax, and is the location of the world's largest breeding colony of grey seals (Thomas et al. 2011). Between 1969 and 2002, groups of male and female grey seals at this colony were branded at weaning, providing a pool of individually identifiable, known-age adults. From this pool, 44 female and 19 male adults, in addition to 9 non-branded female adults were captured over a 4 yr period: October 2009 (n = 15), September 2010 (n = 20), June 2011 (n = 20) and June 2012 (n = 17). Seals were weighed using a 300 kg (±1 kg) Salter spring balance and then immobilised using the chemical anaesthetic Telazol (males 0.45 mg kg^{-1}; females 0.90 mg kg^{-1}; Bowen et al. 1999) to equip each seal with telemetry and data-logging devices. These comprised a VHF transmitter (164 to 165 MHz, www.atstrack.com), MK10-AF Fastloc™ GPS tag (www.wildlifecomputers.com) and a VMT tag. The VHF tag was used to locate animals returning to Sable Island to breed in the following December and January. The MK10-AF tag was programmed to transmit ARGOS and GPS positional data and to archive GPS data that were downloaded on recovery of the tag. These units were programmed to record a GPS location every 15 min. GPS attempts were suspended when the unit was dry for >20 min and a location had been attained. The VMT was programmed to transmit on an irregular schedule, every 60 to 180 s (to avoid VMTs transmitting at the same time and causing code collisions and false detections), to blank the receiver for the complete code transmission ~3.6 s (to prevent the tag from receiving its own transmission) and to remain in listening mode for the remainder of the time. Peak sensitivities for hearing in phocids is between about 10 and 50 kHz with a high frequency limit of ~100 kHz (Kastelein et al. 2009). Given the power output of the transmitters (146 to 149 dB re 1µPa source pressure level measured 1 m from the source), seals could likely hear the 69 kHz transmission pings (Bowles et al. 2010). However, if motivated, it is not clear whether a seal could localise other VMT-tagged seals or prey due to ambient background noise, reflection and refraction of the signal, and decline in sensitivity with the duration and frequency of the ping (Bowles et al. 2010). Seals in this study exhibited similar foraging and breeding patterns to seals previously tagged with satellite transmitters but with no acoustic tag (Mellish et al. 1999, Lidgard et al. 2005, Breed et al. 2006).

The VHF transmitter was attached to the MK10-AF unit using a stainless steel hose clamp and the whole unit was attached to the hair on the top of the head using a 5 min epoxy (Bonessl et al. 1994). The VMT was attached in the same manner as for the MK10-AF, but was located on the lower back of the animal to maximise the likelihood that the tag remained underwater when the animal was at the surface and to minimise electromagnetic interference with the MK10-AF unit. The tag mass burden (total mass of tags / average body mass) was 0.30% for males and 0.39% for females. Individuals were recaptured during the subsequent breeding season (Dec–Jan 2009–2010, 2010–2011, 2011–2012, 2012–2013) to determine returning body mass and recover instruments.

A total of 623 Atlantic cod were tagged with a Vemco V13 acoustic transmitter in the southern Gulf of St. Lawrence (249 between May 2009 and May 2011) and the Eastern Scotian Shelf (374 between November 2010 and November 2012) (see Fig. 2). The V13 tag is 13 mm in diameter, 35 mm in length and weighs 6 g. Cod ≥40 cm in length were used in this study since they are at a size that can accommodate a V13 tag (tag burden ~1.3%) and are both sexually mature and of commercial size (DFO 2009). In 2009 to 2011, the V13 tags were programmed to transmit a unique acoustic code on an irregular schedule every 60 to 180 s, while in 2012 the transmission interval was reduced to every 40 to 80 s to increase the likelihood of detection. V13 tags were placed in a sealed plastic bag and gas-sterilised using ethylene oxide. Between surgeries, all instruments were kept in a pan of 95% ethanol. Cod were captured using longlines set in waters <40 m deep baited with mackerel on #14 circle hooks. Cod that were ≥40 cm in length were placed in a 1000 l holding tank with seawater circulation until they had acclimated to the new conditions. After 90 min, fish that were not swimming strongly or having trouble maintaining their position near the bottom of the tank were released. Individuals were then transferred to a 40 l tank with MS 222 (tricaine methanesulfonate; 40 to 50 mg l^{-1}) until anaesthesia stage III.2 (i.e. analgesia and muscle relaxation sufficient for most surgical procedures) was reached (~15 min). The tag was implanted in the peritoneal cavity of the fish as follows. Fish were removed from the anaesthesia bath and their length measured using an offset measuring board. A small incision (2 cm) was made in the ventral wall of the peritoneal cavity midline and posterior to the pelvic fins. After inserting the transmitter, the incision was closed using two 3 mm nylon sutures and a 19 mm reverse cutting needle and sealed using Vetbond™ (www.3m.com) and then covered with Polysporin® (www.polysporin.ca). The procedure took ~1 min to complete. Fish were then placed in a 1000 l circulating recovery tank for between 45 and 90 min and released when they were swimming strongly. Fish were released close to their site of capture. To avoid attracting predators and minimise predation risk, releases were staggered. All field procedures were conducted in accordance with guidelines for the use of animals in research (ASAB 2006) and with those 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: 08-088, 10-065, 11-020, 12-64) and Fisheries and Oceans Canada (animal care permits and licences: 08-16, 09-40, 11-09, 11-10, 12-13, 12-14).

During the same period of years, Atlantic salmon — n = 298; in collaboration with the Ocean Tracking Network (OTN, www.oceantrackingnetwork.org) and the Atlantic Salmon Federation (ASF, www.asf.ca); see Cooke et al. (2011), Halfyard et al. (2013) — and American eel *Anguilla rostrata* — n = 17; in collaboration with the OTN, University of Laval (www.bio.ulaval.ca) Fisheries and Oceans Canada (DFO; www.dfo-mpo.gc.ca) and Quebec Ministère des Ressources Naturelles et de la Faune (www.mrn.gouv.qc.ca); see Cooke et al. (2011) — were tagged with V9 or V13 Vemco acoustic transmitters to describe their distribution and movement patterns, thus providing other fish species that could potentially be detected by instrumented grey seals (see Fig. 2).

Data analysis

Archival GPS data provided more locations and of higher accuracy compared with the data transmitted to Service Argos; thus, we report only those data here. Propriety software from the manufacturer (WC-DAP; www.wildlifecomputers.com) and archival ephemeris data (www.cddis.gsfc.nasa.gov) were used to determine GPS locations. Locations acquired from <5 satellites and/or with a residual error >30 were removed from the dataset due to their lower accuracy (Byrant 2007, Hazel 2009). VMT detections comprised a date–time stamp and the identities of the Vemco transmitters detected; these were downloaded and visualised using the dedicated software VUE (www.vemco.com). False detections, e.g. the production of legal codes from the collision of multiple codes from other active transmitters, were identified using proprietary software (Vemco) and deleted (1.6% of the total number of detections). Using the date–time data from each VMT and the seal's GPS record, the location of each seal–fish encounter was estimated using linear interpolation between GPS locations. Multiple detections were expected when a seal encountered a fish; therefore, it was necessary to operationally define a seal–fish encounter. Inspection of times between detections showed that 93.6% of the data were <10 min; thus, a period >10 min between detections was considered to constitute the end of an encounter. For encounters that involved only a single detection (n = 12), the duration of the association was set at 2 min, since after this time, based on the least frequent transmission rate of the Vemco transmitters, another detection would have occurred if the 2 individuals were still together.

Bottom depth and travel rate were assigned to each seal location (Lidgard et al. 2012). Bathymetric values were obtained from the Canadian Hydrographic Service (www.dfo-mpo.gc.ca) with a 0.25 min resolution. We used the same approach as in Lidgard et al. (2012) for modelling the travel rate data. To discriminate between 2 behavioural states (travel vs. foraging) along each seal track, and determine the activity of the seal during interactions with fish, a hidden Markov model (HMM; Patterson et al. 2009, Zucchini & MacDonald 2009) was used. We assumed that seal travel rate is conditional on 2 discrete, unobserved movement states: fast and slow movement, where slow movement (probability of area-restricted search, p(ARS) >0.5) is assumed to be associated with foraging or resting behaviours (Barraquand & Benhamou 2008).

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

RESULTS

A total of 72 seals were studied during 4 field seasons (Table 1). Of these, 64 (89%) returned to Sable Island during the following breeding season and their GPS transmitter and VMT recovered. Seals were studied for an average of 79 d in 2009 to 203 d

Table 1. Number of grey seals equipped with telemetry instruments and recovered on Sable Island, Nova Scotia from 2009 to 2012 and details of seal–fish encounters

Year	No. of seals tagged (recaptured) Female	Male	Mean (±SE) deployment (d)	No. of seals with detections	Fish species detected	No. of fish detected	No. of detections	No. of encounters
2009	8(8)	7(5)	79 (±0.6)	0	–	–	–	–
2010	14(14)	6(6)	109 (±1.7)	2	Atlantic salmon smolt	2	13	2
2011	20(16)	–	203 (±2.0)	3	Atlantic salmon kelt	2	34	4
					Atlantic cod	11	51	15
2012	11(11)	6(5)	196 (±1.6)	11	Atlantic salmon smolt	1	2	1
					Atlantic salmon kelt	2	9	2
					Atlantic cod	6	14	7
					American eel	1	2	1

in 2011 (Table 1). In all 4 yr, the movement of seals was confined to the Eastern Scotian Shelf and the southern Gulf of St. Lawrence, with most seals using the former during repeated trips to and from Sable Island. As estimated by the HMM, seals exhibited fast movement when moving between Sable Island and shallow offshore areas, and slower area-restricted movements over these shallow areas, suggesting seals might be foraging (Fig. 1). These movement patterns are typical of grey seals from Sable Island (Austin et al. 2004, Breed et al. 2006).

Nine of the 64 seals from which VMTs were recovered recorded 125 detections during 32 encounters with Atlantic cod, Atlantic salmon and American eel (Table 1, Fig. 2). One Atlantic salmon smolt was believed to be dead (J. Carr pers. comm.) since it was detected in September when all smolts are expected to have departed the Gulf, and was excluded from further analyses. There were no encounters with fish in 2009, likely due to the low number of fish tagged (n = 100) and the spatial distribution of the tagged seals that did not overlap with the general area where the fish were tagged. Seal–fish encounters occurred in both the southern Gulf of St. Lawrence (n = 16) and on the Eastern Scotian Shelf (n = 16) (Fig. 2). The location of 3 additional seal–cod encounters was unknown due to battery failure in one of the satellite and GPS transmitters.

The temporal nature of encounters between seals and fish varied considerably (Fig. 3A–D). During the majority of encounters with Atlantic cod, Atlantic salmon (smolt or kelt) and American eel, seals exhibited low p(ARS) values, suggesting that they were moving relatively quickly, and encounters were brief, involving a single or relatively few detections (Fig. 3A,B). Presuming that if a fish is ingested so is its acoustic tag, fish encounters that involved seal predation are expected to show a continuous series of detections occurring over several hours or more as the acoustic tag passes through the digestive tract of the seal. None of the encounters described above had this expected pattern, and it is more likely that they involved a seal moving through an area used by a tagged fish.

A single encounter with an Atlantic salmon kelt (Gulf of St. Lawrence), and 3 encounters with 2 Atlantic cod (Canso Bank, Eastern Scotian Shelf) shared a similar pattern, which was different to those described above. In these cases, the encounters were longer (25.3, 17.6, 20.6 and 38.5 min, respectively), involved frequent detections (21, 6, 7 and 21, respectively) and the seals exhibited high p(ARS) values (0.78, 1.0, 1.0 and 0.97, respectively), suggesting area-restricted search behaviour. The characteristics of these encounters suggest either the seal predated on the tagged fish but did not consume the transmitter, which may have fallen to the sea floor but remained within detection range of the VMT, or the seals were foraging in the same area as the tagged fish.

In another case, a seal engaged in multiple interrupted encounters with the same fish over an extended period of time. In 2011, a single female grey seal detected the same Atlantic salmon kelt 3 times over a 33 d period. The distance between the first and second encounter was 7 km, whereas the distance between the second and third encounter was 1 km. The last encounter was the potential predation event described above.

All seal–fish encounters occurred when the seal was diving at depths from 4 to 74 m (Fig. 3C). Encounters with cod occurred when the seal was off the sea floor (Fig. 3C,D). The mean depth of all dives for all 16 seals was 32.0 ± 8.0 m.

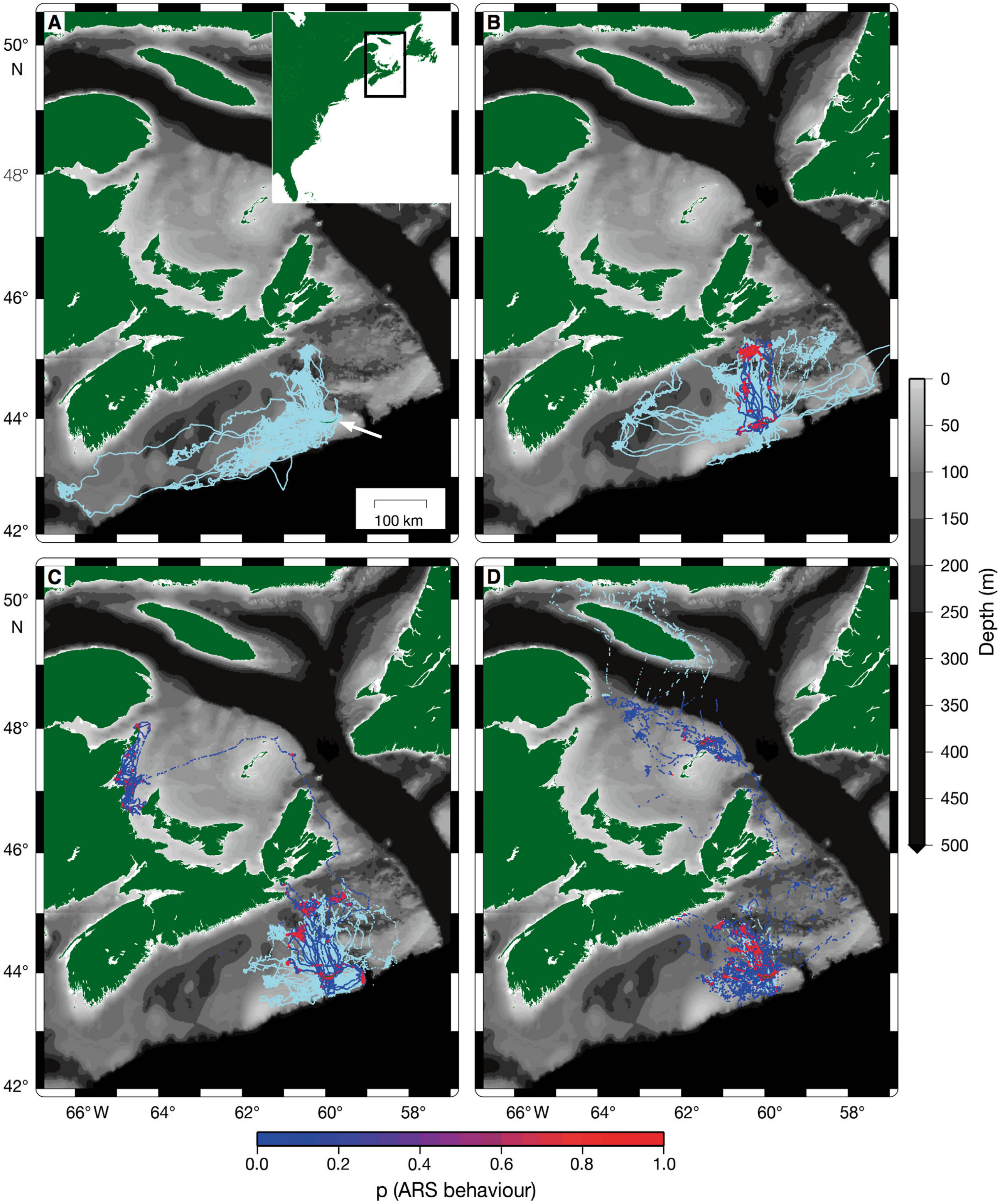

Fig. 1. (A–D) Study area and GPS movement tracks for grey seals deployed from Sable Island in (A) 2009, (B) 2010, (C) 2011 and (D) 2012. The light blue lines show the tracks of all seals. The dark blue to dark red lines (coloured according to p(ARS) behaviour — a continuous measure of the probability [p; 0 dark blue to 1 dark red] of exhibiting area-restricted search behaviour according to the hidden Markov model) show the movement tracks of those seals that detected fish. The white arrow indicates the location of Sable Island

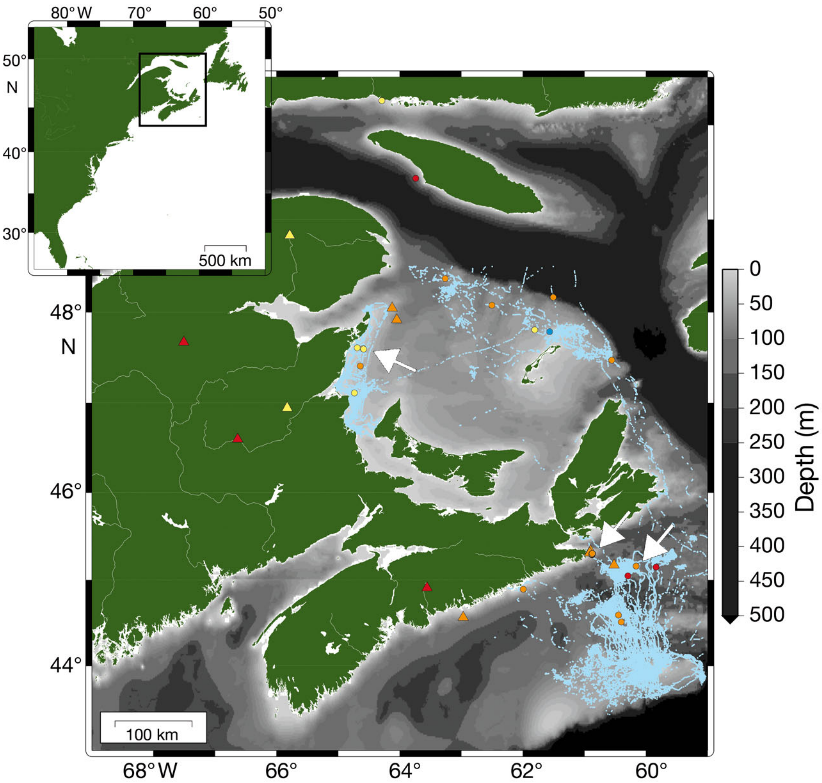

Fig. 2. Distribution of fish deployments (△), grey seal–fish encounters (○) and movement tracks (light blue) for 16 grey seals on the Eastern Scotian Shelf and in the southern Gulf of St. Lawrence from 2010 to 2012. Atlantic cod are represented by orange symbols, Atlantic salmon smolts by red, Atlantic salmon kelts by pale yellow and American eel by blue. The white arrows indicate the location of a possible predation event

DISCUSSION

We have shown that mobile acoustic transceivers and GPS technology deployed on an upper trophic level predator can be used to collect spatial and temporal distribution data on tagged fish over an extended period of time in a large marine ecosystem. The spatial and temporal pattern of these grey seal–fish encounters provides new opportunities for inferring the nature of interspecies interactions in large inaccessible environments.

Our findings complement and extend previous studies using Vemco acoustic telemetry. In a pilot study, Holland et al. (2009) deployed 4 VMTs on free-roaming Galapagos sharks *Carcharhinus galapagensis*. Although only 2 VMTs were recovered, both units collected records of absence and presence from several species of shark, some of which occurred outside of a monitoring acoustic arena, demonstrating the effectiveness of using mobile receivers. Twenty-one VMTs recovered from northern elephant seals *Mirounga angustriostris* after their annual migration across the northeast Pacific Ocean, collected 9 detections from 2 species of sharks and 3 species of fish (Hayes et al. 2013). In addition to inferences of between-species interactions, VMT-equipped seals have revealed an unexpectedly high number of conspecific associations during foraging trips on the Eastern Scotian Shelf, which may provide new insights into grey seal foraging behaviour (Lidgard et al. 2012).

Grey seals are abundant and wide-ranging predators that are known to eat Atlantic cod (Breed et al. 2006, Beck et al. 2007, Hammill 2010, Stenson et al. 2010, Bowen et al. 2011, Thomas et al. 2011). Thus, it is certainly possible that grey seals may be partly responsible for the lack of or slow recovery of cod stocks in the southern Gulf of St. Lawrence and on the Scotian Shelf. However, a key uncertainty in tests of this hypothesis is the proportion of total cod mortality accounted for by grey seal consumption (e.g. Mohn & Bowen 1996). This question has been difficult to answer (e.g. Trzcinski et al. 2006, 2011) because of the limitations of the methods used to estimate the diets of grey seals and other pinnipeds and the difficulty in obtaining a representative sample of the diet from which to draw firm conclusions (Bowen & Iverson 2013). This has led to the search for other approaches, such as the extent of spatial and temporal overlap between the distribution of prey and the foraging effort of the predator (Matthiopoulos et al. 2008, Harvey & Hammill 2010, Harvey et al. 2012). Although such overlap is necessary, it is not a sufficient basis to conclude that predation has occurred or to estimate the extent of predation.

Given the absence of direct observation, a degree of speculation will be required to assess the likelihood of a predation event using acoustic telemetry. To determine the most likely predator of 6 silver American eels tagged in the Gulf of St. Lawrence with miniature satellite pop-up tags, Béguer-Pon et al. (2012) used temperature and depth profiles generated post-predation to determine the most likely predator. In our case, we expect that predation should be evident in the continual pattern of acoustic

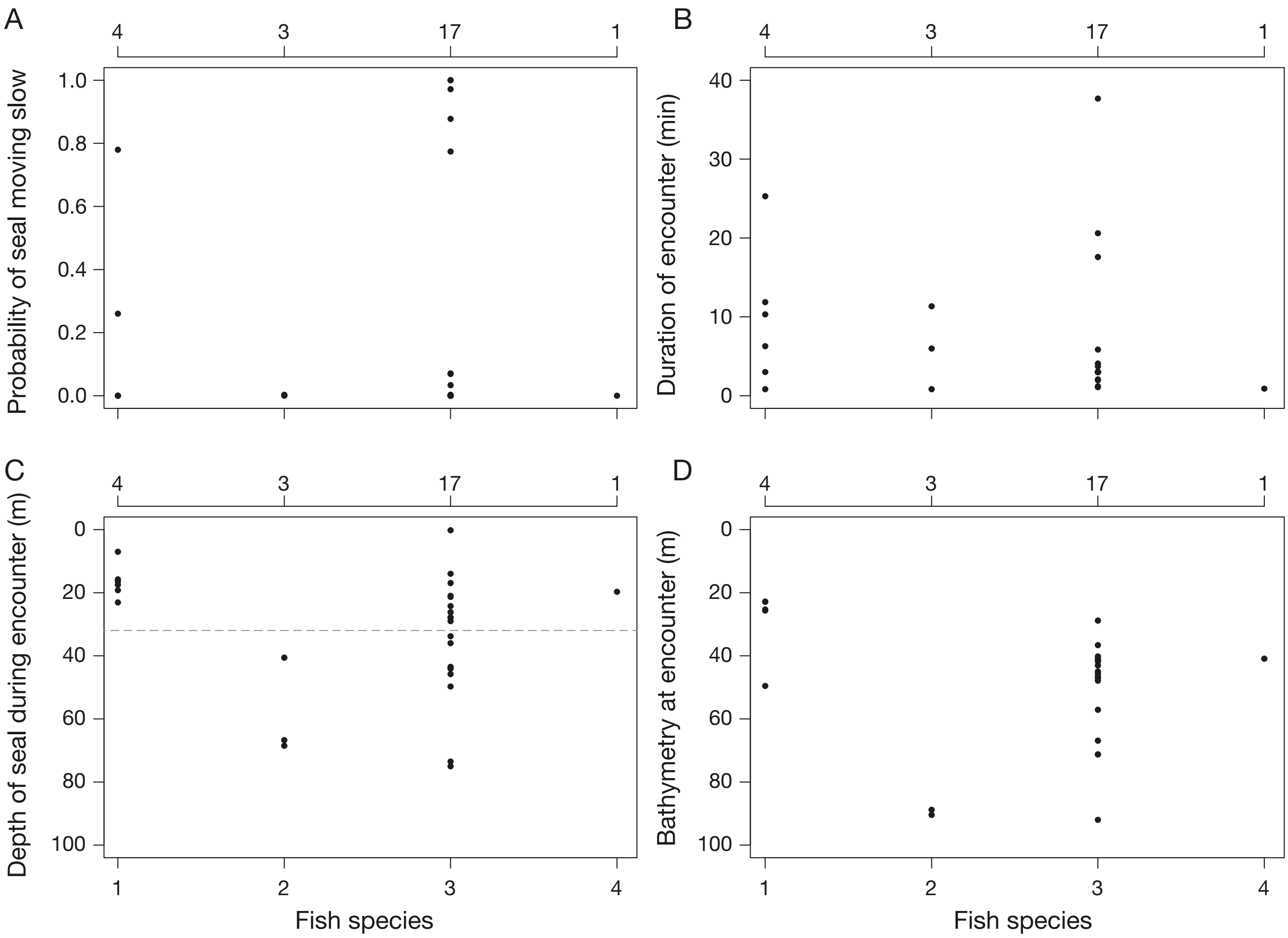

Fig. 3. Plots describing seal–fish encounters for grey seals on the Eastern Scotian Shelf and southern Gulf of St. Lawrence from 2010 to 2012. (A) Probability of seal exhibiting 'slow movement' during an encounter, (B) duration (min) of encounter, (C) depth (m) of seal during encounter (dotted line signifies the mean dive depth of all 16 seals) and (D) bathymetry at encounter. Fish species 1: Atlantic salmon kelt; 2: Atlantic salmon smolt; 3: Atlantic cod; 4: American eel. The upper horizontal axis gives the number of unique seal–fish encounters; note, the number of dots may not correspond with the number of unique seal–fish encounters due to overlapping data points and unique seal–fish events comprising of multiple encounters

detections of individual prey during the pursuit and time taken for the prey, and the ingested acoustic tag, to pass through the predator's digestive tract and be expelled in faeces. In the case of grey seals, captive feeding experiments using herring *Clupea harengus*, cod, whiting *Merlangius merlangus* or haddock *Gadus aeglefinus* (Prime & Hammond 1987, Marcus et al. 1998) found that the passage time for the majority of prey remains was between 24 and 48 h. Thus, during this time, we would expect a regular and frequent pattern of detections. However, it is possible during the handling of large fish, such as salmon kelts and adult cod, that the transmitter may dislodge from the peritoneal cavity and fall to the sea floor, or that the seal may not consume all parts of the fish (Rae 1968). In these cases, and given that the mean bathymetry of the areas where seals encountered tagged fish was 49 ± 3.5 m, we would still expect to see a continual pattern of detections, but for a much shorter duration while the tagged seal remained within proximity of the tag. Although there were no extended periods of time that would indicate ingestion of the fish and tag, there were 3 instances when the seal spent between 25.0 and 48.5 min within proximity of a tagged Atlantic salmon and 2 Atlantic cod and recorded frequent detections indicating possible predation.

The speed of movement of the seal may also help determine the likelihood that predation occurred. When foraging, grey seals most likely engage in area-restricted search behaviour, typical of many animals during foraging (Kareiva & Odell 1987, Wallin 1991, Bergman et al. 2000), whereby the seal moves slowly and turns frequently such that it remains in the prey patch. In this study, during the majority of encounters between grey seals and

Atlantic cod, Atlantic salmon or American eel, the seal was moving relatively quickly in a directed manner, suggesting travelling rather than foraging. Furthermore, although encounters occurred in relatively shallow waters, they were often not associated with the shallow offshore banks where Sable Island grey seals are thought to forage. However, in those encounters with salmon and cod that were longer in duration with frequent and regular detections, the seals were moving slowly, suggesting area-restricted search behaviour, and the encounters with cod occurred at Canso Bank, an area favoured by grey seals for foraging. These observations therefore support the possibility of a predation event. However, without a strong predation signature that involves the seal consuming the tag, the occurrence of a predation event would need more conclusive evidence, such as that gathered through validation experiments conducted under controlled conditions.

We believe our findings demonstrate that there is added value to the combined use of GPS or other tracking technologies and mobile acoustic receivers to contribute towards our understanding of the extent that top predators associate with potential prey and support of conclusions from dietary analyses. For species such as Atlantic cod, Atlantic salmon and American eel, this information is critical for identifying the sources of at-sea mortality. Animal-borne video cameras have also provided insight into the foraging ecology of marine mammals and their diet (Davis et al. 1999, Bowen et al. 2002, Hooker et al. 2002, Heaslip et al. 2012). However, although they can provide detailed observations of interactions with prey, deployments are often one or a few foraging trips in length due to memory or battery limitations. Variation in video quality may also make it difficult to identify prey (Hooker et al. 2002). The VMT has a longer life span (~8 mo), providing greater spatial and temporal coverage, but, compared with video, at the cost of less detail.

In the same spirit of using marine mammals to collect oceanographic data (Biuw et al. 2007, Simmons et al. 2007), VMTs deployed on top predators could be used to collect data on the spatial and temporal distribution of acoustically tagged prey. Although we have some understanding of the gross movements of Atlantic cod in the southern Gulf of St. Lawrence (Campana et al. 1999, Comeau et al. 2002), fine-scale movements and the movement of cod on the Eastern Scotian Shelf are poorly understood. A better understanding of cod seasonal distribution relative to that of grey seals will be valuable in evaluating the opportunity for grey seal predation. Many populations of the northwest Atlantic salmon in Canada have been in decline for the last few decades, with high at-sea mortality, for reasons largely unknown (Gibson et al. 2006, ICES 2008), and are listed as endangered by COSEWIC (www.cosewic.gc.ca). There is also concern that rising sea temperatures may accentuate the decline (Todd et al. 2008). The oceanic lifestyle of cod and salmon makes it difficult to assess the spatial and temporal movement of individuals, foraging areas and sources of mortality. The size of satellite transmitters limits their use on adults and their cost limits the number that can be deployed (Thorstad et al. 2011). Acoustic transmitters, however, are much cheaper and of a sufficient size to be deployed on young as well as older life stages. In contrast to the traditional use of stationary acoustic receivers, grey seals range widely and thus can provide valuable data on spatial and temporal patterns of fish movement as well as survival. Furthermore, a recent advancement is the development of a Bluetooth link between the satellite transmitter and the VMT, thus allowing for data logged by the VMT to be transmitted to the satellite tag for eventual retrieval through system ARGOS (authors' unpubl. data). This removes the necessity to recapture animals for instrument recovery and allows deployments to occur on a wider range of species, e.g. other pinnipeds, cetaceans and turtles, and in more inaccessible environments.

Given the integrative nature of this work, the effort required for this study and its success need to be evaluated within the context of the network within which it operates (Cooke et al. 2011). For example, VMT-tagged grey seals collect not only records of fish detections, but also detections from other VMT-tagged seals to provide a better understanding of grey seal foraging tactics (Lidgard et al. 2012), and oceanographic data to help identify the variables that influence habitat choice by grey seals and fish species. Strategically positioned fixed acoustic receiver arrays have collected a large volume of detection data from passing tagged fish and contribute towards understanding seasonal changes in movement and distribution patterns. Similar to the grey seal, autonomous gliders collect detection data, and thus expand the sampling effort for detecting acoustically tagged fish and collecting oceanographic data.

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