How effectively do horizontal and vertical response strategies of long-finned pilot whales reduce sound exposure from naval sonar?

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Abstract

The behaviour of a marine mammal near a noise source can modulate the sound exposure it receives. We demonstrate that two long-finned pilot whales surfaced in synchrony with consecutive arrivals of multiple sonar pulses. We then assess the effect of surfacing and other behavioural response strategies on the received cumulative sound exposure levels and maximum sound pressure levels (SPLs) by modelling realistic spatiotemporal interactions of a pilot whale with an approaching source. Under the propagation conditions of our model, some response strategies observed in the wild were effective in reducing received levels (e.g. movement perpendicular to the source's line of approach), but others were not (e.g. switching from deep to shallow diving; synchronous surfacing after maximum SPLs). Our study exemplifies how simulations of source-whale interactions guided by detailed observational data can improve our understanding about motivations behind behaviour responses observed in the wild (e.g., reducing sound exposure, prey movement).

Keywords: cetaceans, disturbance, behaviour, environmental impact, noise, risk assessment, individual-based models, sonar

Introduction

Human activities that introduce sound energy in the marine environment have the potential to affect marine mammals on the scales of individuals and populations (National Research Council, 2003, 2005; Tyack, 2008; Weilgart, 2007). Because of the difficulties in studying marine mammals in their natural habitat, the ultimate costs of man-made noise to individual fitness (e.g. survival and reproductive success) are generally inferred from proximate costs (McGregor et al., 2013). Among these proximate costs are masking of the sounds from conspecifics and predators (Clark et al., 2009; Erbe, 2002), stress responses (Rolland et al., 2012), temporary or permanent hearing loss (Finneran and Schlundt, 2013; Kastak and Schusterman, 1996), and changes in vocal behaviour (Miller et al., 2000; Parks et al., 2007) as well as other behavioural responses (Nowacek et al., 2007). For example, tonal sounds from powerful naval active sonars during multi-ship exercises can cause large-scale area avoidance by beaked whales (McCarthy et al., 2011; Tyack et al., 2011) and killer whales (*Orcinus orca*) (Kuningas et al., 2013; Miller et al., 2014); displacement of harbour porpoises (*Phocoena phocoena*) by tens of kilometres from the sound source has been observed following impulsive noise produced by pile driving during offshore wind farm construction (Brandt et al., 2011; Dähne et al., 2013; Tougaard et al., 2009); and continuous noise from vessel traffic may cause chronic stress in endangered North Atlantic right whales (*Eubalaena glacialis*) (Rolland et al., 2012) and reduce their acoustic communication space (Clark et al., 2009).

Recent research on man-made noise has focused mainly upon direct physiological effects such as hearing loss, but behavioural and stress responses that can translate into population consequences may be of greater concern (Bejder et al., 2006). National and international legislation recognise that man-made noise can affect marine mammals, and require that the environmental risks of noise are appropriately assessed and managed (e.g. US Marine Mammal Protection Act [50 CFR 216]; EU Marine Strategy Framework Directive [2008/56/EC]). However, considerable individual and species variation exists in short-term behavioural responses to man-made noise (e.g. Antunes et al., 2014; Goldbogen et al., 2013; Götz and Janik, 2011; Houser et al., 2013a, 2013b; Kastelein et al., 2011; Kastelein et al., 2006a; Miller et al., 2012, 2014; Moretti et al., 2014; Nowacek et al., 2004; Tyack et al., 2011; Williams et al., 2014), and a general lack of information about the biological significance of responses, efficacy of mitigation measures, and how to extrapolate from experimental data, for example, makes impact assessment and management challenging.

One approach that National Research Council (2005) recommended for the assessment of population-level effects of underwater noise, and the interactions between marine mammals and noise sources, is individual-based modelling (IBM). With this technique, the behaviour of individuals within a system and their interactions with the environment and other individuals are modelled to understand the properties and dynamics of the system (Grimm and Railsback, 2004). In the context of man-made noise and marine mammals, this generally means constructing the exposure histories of simulated animals that move through virtual sound fields and evaluating whether levels reach certain risk thresholds (Frankel et al., 2002). Sonar-related mass strandings of beaked whales (Balcomb and Claridge, 2001; Jepson et al., 2003) accelerated the development and use of IBM-based risk assessment models that are designed to investigate the impacts and associated uncertainties of naval sonar on marine mammals (Dolman et al., 2009; Donovan et al., 2012; Gisiner et al., 2006; Houser, 2006). Comparable methods are used in the Environmental Impact Statements of the US Navy to estimate the number of marine mammals that are affected behaviourally or physiologically by noise (Schecklman et al., 2011; U.S. Department of the Navy, 2014; Wartzok et al., 2012). Recently, individual-based methods have also been used to assess the efficacy of operational mitigation procedures for sonar (von Benda-Beckmann et al., 2014), to evaluate interactions between whales and whale-watch boats (Anwar et al., 2007), and to investigate potential impacts of noise on cetaceans from non-sonar sources such as pile driving, seismic surveys, wind turbines and/or vessel traffic (e.g. Gedamke et al., 2011; Nabe-Nielsen et al., 2014; New et al., 2013; NSF and USGS, 2011; Thompson et al., 2013). However, it is necessary to quantify observed behavioural response strategies of cetaceans in reaction to sound sources and to estimate the changes in acoustic exposures that result from these strategies, to increase confidence in the outcomes of quantitative risk assessment models that are based on hypothetical responses (Barlow and Gisiner, 2006).

The avoidance behaviour of a cetacean near a sonar source modulates the sound pressure level (SPL) at the position of the animal (henceforth ‘received SPL’). At close range, movement away from a non-directional sound source will decrease the received SPL in most situations. Therefore, not including rules of repulsion/aversion in IBM will generally be conservative when risk thresholds are high (i.e. it will overestimate the number of times exposure thresholds are exceeded). However, movement away from the source can also increase received SPL in case of a directional sound source, acoustic near field or a complex multipath propagation environment (DeRuiter et al., 2006; Madsen et al., 2006).

Intrinsically, the underlying motivation(s) of the animal will determine the shape of the movement response; for example, a marine mammal could be motivated to: 1) avoid the acoustic intensity and/or energy itself because it is painful or annoying (Culik et al., 2001; Kastelein et al., 2006a, 2006b, 2008; Kvadsheim et al., 2010; McCauley et al., 2000), 2) evade the source by keeping a safe distance without losing visual or acoustic contact with the threat (Lazzari and Varjú, 1990; Williams et al., 2002), or 3) flee or haul out as part of an anti-predator response template (Deecke et al., 2002; Ellison et al., 2012; Ford and Reeves, 2008). In addition, an animal might not have the motivation or option to avoid if the perceived benefit of staying outweighs the cost of leaving (Frid and Dill, 2002). Although the underlying motivations of animals are generally not well understood, avoidance responses of wild and captive cetaceans to various sound sources have been described by a number of studies (see for review: Nowacek et al., 2007; Richardson et al., 1995; Southall et al., 2007) and some studies have measured avoidance movements with sufficient spatial and temporal resolution to be useful for the construction of geometrical models of avoidance (e.g. Curé et al., 2012, 2013; DeRuiter et al., 2013; Dunlop et al., 2013; Goldbogen et al., 2013; Miller et al., 2014; Tyack et al., 2011). Most studies have used stationary sources; however, many anthropogenic noise sources such as towed and hull-mounted active sonar systems, boats, and seismic airguns arrays are moving when they are used.

Many of the detailed observations of behavioural responses of cetaceans were made during field experiments in which the dose of the acoustic stimulus was controlled, called Controlled Exposure Experiments (CEEs; Tyack et al., 2003). Some of these CEEs were conducted with a moving sonar source in 2006 to 2009 on killer whales, long-finned pilot whales (*Globicephala melas*), and sperm whales (*Physeter macrocephalus*) (Miller et al., 2011, 2012). The three species exhibited behavioural responses of various duration and severity (Miller et al., 2012), with clear species differences in avoidance response thresholds (Antunes et al., 2014; Miller et al., 2014). There was a recurring pattern of killer whales moving perpendicular to the source ship's line of approach (Miller et al., 2012, 2014). Pilot whales often switched from deep foraging diving to shallow transit diving, or remained shallow diving throughout the exposure (Miller et al., 2012; Sivle et al., 2012). Pilot whales showed fewer horizontal displacement responses to the sonar than killer whales did, with pilot whales more often slowing down and/or changing orientation, similar to what has been reported for their responses to seismic surveys (Stone and Tasker, 2006; Weir, 2008). In two cases a pilot whale appeared to surface multiple times in near-perfect synchrony with the interval of arriving sonar pulses (Miller et al., 2012).

In the present study we combined an analysis of behavioural data recorded during CEEs with the modelling of three-dimensional (3D) animal trajectories, in order to investigate avoidance responses of cetaceans to approaching sound sources. First, we conducted a quantitative analysis of DTAG (Johnson and Tyack, 2003) data to test the qualitative judgement by Miller et al. (2012) that two long-finned pilot whales responded by surfacing in near-perfect synchrony with the arrival of sonar pulses. Pinnipeds are known to increase their surface durations or haul out in response to underwater noise exposures (Götz and Janik, 2011; Houser et al., 2013a; Kastak et al., 1999; Kvadsheim et al., 2010; Mate and Harvey, 1987), so we hypothesized that the pilot whales' behaviour reported by Miller et al. (2012) could have represented similar attempts to reduce received SPL and/or sound exposure level (SEL) by exploiting lower sound pressures at the sea surface (Jensen, 1981; Weston, 1980). Second, we defined and quantified a number of theoretical response strategies that pilot whales and other cetaceans may use in response to an approaching sound source, and we used IBM to assess how the maximum SPL and cumulative SEL received by a simulated whale differs among these theoretical response strategies. Finally, we compared our simulation results with real-world avoidance responses of marine mammals to man-made noise.

Materials and methods

Data were collected from experiments in northern Norway in May/June 2008, 2009, and 2010, as part of an international project on the behavioural effects of naval sonar on cetaceans. Results of that project are reported elsewhere (Antunes et al., 2014; Miller et al., 2012, 2014). A summary of the experimental protocol and acoustic equipment is given below; detailed methods can be found in Kvadsheim et al. (2009) and Miller et al. (2011, 2012).

CEE methodology

Five controlled sonar experiments with long-finned pilot whales were conducted in 2008 and 2009 in the waters of Vestfjord and Ofotfjord, Norway, at latitudes between 68°N and 69°N.

In each experiment the *H.U. Sverdrup II* functioned as the source vessel. Whales were tracked visually and acoustically by observers on a second vessel (*MS Strønstad*). Multi-sensor suction-cup tags were deployed from small boats using a long pole or a pneumatic remote deployment system (Kvadsheim et al., 2009). When one or two whales were tagged, visual and VHF tracking of one tagged whale was established. One to three vessel approaches with active sonar transmissions (‘exposure sessions’) were performed as part of each experiment. An exposure session started when the source vessel was positioned about 8 km away from the observation vessel. The source vessel moved steadily towards the whale at a speed of 4.1 m/s (8 kn), only adjusting course to continue heading directly towards the animal. At a range of 1 km the vessel maintained a constant heading, passed the whale, and then ceased transmission 5 minutes after the closest point of approach (CPA). To increase the range of SPLs experienced by the tagged whales and to minimise the risk of potentially inducing hearing injury in animals undetected nearby, the source level (SL) was gradually increased over the first 10 minutes of the exposure session (the ramp-up period).

Acoustic source and receivers

Sonar pulses were transmitted using a towed sound source (*Socrates II*, Kvadsheim et al., 2009). The source consisted of a tow body that housed two free-flooded ring transducers for transmitting pulses in the 1-2 kHz or 6-7 kHz bands. The 1-2 kHz projector was horizontally omnidirectional and had a vertical 3 dB beamwidth of 72° at 1.4 kHz. The 6-7 kHz projector was horizontally omnidirectional and had a vertical 3-dB beamwidth of 87° at 6 kHz. Only one of three waveforms was transmitted throughout each exposure session: a 1-2 kHz upsweep, a 1-2 kHz downsweep, or a 6-7 kHz upsweep. All waveforms were hyperbolic frequency-modulated sweeps. Each pulse was 1 s in duration, including rise and fall times of 50 ms duration. The inter-pulse interval of the sonar was 20 s (5% duty cycle). The SL started at 152 and 156 dB re 1 µPa m and was gradually increased in the ramp up period to the maximum SL of 214 and 199 dB re 1 µPa m for pulses in the 1-2 kHz and 6-7 kHz band, respectively.

A multi-sensor movement and audio-recording tag (DTAG version 2) attached to subject whales using suction cups recorded acoustic data at a sample rate of 96 or 192 kHz with a 16-bit resolution sigma-delta analogue-to-digital converter (Johnson et al., 2009). The tag also recorded accelerometer, magnetometer, pressure and temperature data that were synchronised with the acoustic data.

Methods used to calculate the horizontal location and depth of the source and the whale are described in detail elsewhere (Antunes et al., 2014; Miller et al., 2012). Depth was derived from the pressure and temperature data measured by sensors in the source and the animal-attached tag. The geographical location of the towed sonar source was estimated from the cable length, source depth, and GPS location of the source vessel. The geographical location of the whale at the surface was derived from the GPS location of the observation vessel combined with range and bearing to the whale estimated by visual observers. The horizontal speed of the whale was calculated from its visual sighting track by dividing the distance between successive locations by the time difference between the two sightings.

Analysis to identify synchronous surfacing with the sonar

The dive profiles of 10 long-finned pilot whales were part of the analysis of surfacing synchronicity with the arrivals of sonar pulses (Table 1). Six whales were subjects in the five sonar experiments in 2008 and 2009 (i.e. two whales, gm08_138a and b, were exposed simultaneously; Table 1). Baseline data were included for four long-finned pilot whales tagged in 2010 when sonar experiments were not conducted. The baseline period was the period between the time that the tag boat left the whales and either the start of the first exposure session or the time that the tag came off if there was no exposure session.

The length of time each whale spent at the sea surface was automatically determined using an algorithm that identified surfacing periods within the tag record. The algorithm was based upon two threshold criteria; the depth at which the whale was judged to have returned to the surface (0.14 m), and the minimum depth required to identify the start of a dive (0.6 m). The values of these thresholds were estimated based upon a manual analysis in which all surfacing periods were marked after a visual inspection of a subset of dive data (1 h per tag; selected at random). The duration of a sonar pulse was defined as the interval between the first and last time when the received time-weighted SPL (averaging time: 10 ms) in the sonar frequency band exceeded a threshold of 10 dB below its maximum. If the pulse duration could not be determined in this way (for example, when the tag was out of the water), the start and end point of the pulse were estimated from adjacent pulses by linear interpolation.

The duration of received pulses averaged 1.12 s (SD=0.31 s). This average duration was slightly longer than the duration of the transmitted pulse (1 s) because the received signal was a combination of multiple paths that arrived at the receiver at slightly different times.

We identified which of the transmitted pulses arrived when the whale was at the surface. Some inaccuracy in timing due to the tag placement position and/or the behaviour of the whale was expected, so we defined a pulse as overlapped when at least 50% of its duration overlapped with a surfacing (surface duration < 5 s) or a logging period (surface duration ≥5 s). Our main interest was the sequences of successive sonar pulses overlapped by surfacings, termed 'sequential overlaps'. Hence, the number and durations of all sequential overlaps in each exposure session were identified.

To evaluate whether or not a sequential overlap was longer than expected due to chance timing of surfacings relative to the inter-pulse timing of the sonar, we calculated the probability that the sequential overlap could occur by chance in the baseline records (N=9 whales; Table 1) using a randomisation procedure. For each iteration, the full sequence of pulse start and stop times was moved to a new random location in the combined baseline data set and the sequential overlaps were recalculated. The baseline data only included bouts of shallow diving (see next section how these bouts were selected) to avoid potential bias caused by the whale switching from deep to shallow diving in response to sonar. The shallow-dive bouts were placed in a different random temporal order at each iteration. After 100,000 iterations, a P-value was calculated that represented the proportion of randomisations in which a sequential overlap of the observed duration occurred at least once within the source-whale range at which the behaviour was observed. This test design reflected our functional hypothesis that the series of synchronous surfacings occur near the sound source where the received SPL is high. The significance level was adjusted using the Bonferroni method because multiple tests were performed on the same baseline data set (0.05 divided by N=5 tests).

Simulation of behavioural response strategies

Miller et al. (2012) suggested based upon a qualitative assessment that the first behavioural response to sonar during exposure session 3-1 occurred when the tagged long-finned pilot whale (gm08_159a) and his group slowed down and slightly changed heading (Fig. 1a). The source distance (1.24 km), received SPL_{max} (160 dB re 1 μPa) and received SEL_{cum} (168 dB re 1 μPa^2 s) associated with the onset of this response were similar to those for the onsets of other horizontal responses of long-finned pilot whales (Antunes et al., 2014). Five minutes later in the exposure session the tagged whale also surfaced in synchrony with the arrivals of four sonar pulses (Miller et al., 2012; Fig. 1a). We used exposure session 3-1 as a realistic basis for simulating long-finned pilot whale responses to a moving sonar source to investigate the effectiveness of the most common response strategies in terms of reducing sound exposure.

We selected five behavioural response strategies of long-finned pilot whales based upon observations during CEEs (Miller et al., 2012; Sivle et al., 2012) for the simulations. These response strategies were 1) switching from deep foraging diving to shallow transit diving, 2) surfacing in synchrony with the arrivals of sonar pulses, 3) horizontally slowing down, 4) horizontally moving away from the future projected source track, and 5) horizontally circumventing/evading the source. These response strategies were investigated through four model scenarios (A-D). First, we recreated the horizontal trajectories of the real whale and source from the start of the exposure session until the time at which the pilot whales in the experiment started slowing down (defined as the 'behavioural change point'; Fig. 1a). The simulated whale was modelled to perform deep dives during this time interval. Then, the 3D (horizontal and vertical) trajectories of the simulated whale and the source were altered from the behavioural change point onwards according to the movement rules of the specific model scenario.

The four scenarios, labelled by their rule for the horizontal movement of the simulated whale after the change point, were:

A) *Original track*. The source and the simulated whale continued following the horizontal trajectories of exposure session 3-1 (Fig. 1a). The simulated whale remained deep diving, switched to normal shallow diving, or switched to shallow diving with surfacing in synchrony with the arrivals of four sonar pulses. This scenario was used to investigate response strategies 1 and 2.

B) *Fixed position*. The simulated whale stayed in a stationary horizontal location and the horizontal trajectory of the source was straight towards and past the simulated whale's location (Fig. 1b). As in scenario A, the simulated whale remained deep diving, or switched to shallow diving with or without surfacing in synchrony to the sonar. This scenario was used to investigate response strategies 1, 2 and 3.

C) *Linear motion*. The simulated whale moved horizontally with a constant heading relative to the heading of the source (range 10°-170°; 10° steps) and the trajectory of the source was the same as in scenarios B and D (Fig. 1c). Only normal shallow transit diving was modelled as the assumption was that the whale was focusing solely on avoidance at the cost of foraging opportunities. This scenario was used to investigate response strategy 4.

D) *Continuous turning motion*. The simulated whale adjusted its absolute heading continuously relative to the source position (range 10°-170°; 10° steps) and the trajectory of the source was the same as in scenarios B and C (Fig. 1d). As in scenario 3, only normal shallow transit diving was modelled. This scenario was used to investigate response strategy 5.

The four scenarios allowed us to compare the received sound levels across horizontal response strategies (between scenarios B, C and D) and compare across and within dive modes (between scenarios A and B). We changed the trajectory of the source in scenarios B-D because in the real exposure session (and thus, scenario A) the source passed the animal at too great a distance which made the vertical behaviour of the whale less relevant.

To simulate realistic dive behaviour, all baseline records of tagged pilot whales (Table 1) were used to construct composite dive profiles that represented either deep or shallow diving (Fig. 2). A composite horizontal speed profile was also created that corresponded in time to the shallow dive profile (Fig. 2a; only for scenarios C and D). This composite profile for horizontal speed was composed of the whales' speed calculated from the visual sighting tracks.

All periods of at least two consecutive deep dives were identified in the depth data. From a log-frequency analysis of the tags deployed before 2010, Sivle et al. (2012) determined that a depth criterion of 34 m optimally separated deep and shallow dives; we used this criterion as a guide to classify all deep-dive bouts in the baseline records. Single deep dives were omitted because these were often interpreted as probing dives in which the animal was searching for prey, and not foraging dives (Sivle et al., 2012). We measured the average time interval between two consecutive deep dives within all deep-dive bouts, which was 426 s (N=64). The length of each deep-dive bout was then standardised to 0.5 × 426 s before its first deep dive until 0.5 × 426 s after its last deep dive. All deep-dive bouts were placed in chronological order to form the final 21.5 h composite dive profile (Fig. 2b). Because a flat seafloor was assumed, the bottom 10 m of each dive deeper than 322 m was multiplied by a rescaling factor so that the maximum depth became one meter above the seafloor at 323 m and the bottom phase of a dive was generally within 4 m from the bottom. This procedure was based on data for long-finned pilot whales in the same location in Norway: 1) echograms which illustrate the timing of echolocation click returns (Johnson et al., 2009) indicated that whales swam about 2-3 m above the seafloor during benthic foraging (pers. comm., R. Antunes), and 2) photos made with a camera tag attached to whales sometimes showed the seafloor (Aoki et al., 2013). All data other than for deep-dive bouts and single deep probing dives formed the shallow-dive bouts that were used in the randomisation test for the observations of synchronous surfacing. These bouts were placed in chronological order to create the final 55.2 h composite dive profile for shallow diving (Fig. 2a) used in the movement simulations.

The simulation for surfacing in synchrony with the sonar pulses was produced by changing the depth of the whale to 0 m for the first four pulses starting at 1 minute after CPA (the average of the two observations by Miller et al. 2012). This approach was based on the assumption that a simulated whale in shallow diving mode was able to reach the sea surface within one inter-pulse interval (20 s) (dive depths were predominantly <20 m in this dive state; Fig 2a).

Modelling acoustic received levels of the whale

The Gaussian beam-tracing model BELLHOP (Porter and Bucker, 1987; version 09/2010) was used to estimate the acoustic propagation loss (PL; dB re 1 m) at the site of exposure session 3-1. The sound speed profile (Fig. 3a) was based on a conductivity-temperature-depth (CTD)-profile taken near the CPA location, 4 h after the exposure session had ended. The sound speed profile had a minimum at 50 m, and was similar to other profiles collected at inshore locations within Vestfjord in May/June (Wensveen, 2012). The sound speed profile was smoothed to remove insignificant features and then subsampled to decrease computation time. The propagation model assumed a pressure release sea surface and a bottom layer that was a flat, homogeneous fluid layer with constant acoustic properties. Bottom samples were not collected at site, but historical surface sediment data for the Vestfjorden area suggested that fine silt was the most dominant sediment type (Jenserud and Ottensen, 2002; Jenserud, 2002; Knies, 2009). Therefore, bottom reflection coefficients were calculated using reported geo-acoustic parameter values for a fine silt bottom (compressional sound speed ratio: 1.0239, density ratio: 1.513, compressional wave attenuation: 0.17 decibels per wavelength (corresponding to 0.112 dB / (m kHz)); Ainslie, 2010) in combination with the water sound speed and density (derived from CTD data) just above the seafloor.

The modelled sonar source was based upon the properties of the real sonar source. Because the pulse transmitted for exposure session 3-1 was an upsweep in the 1-2 kHz frequency band, we modelled the coherent propagation loss at 41 equally spaced frequencies (25 Hz steps) and calculated the power average of the corresponding propagation factors. The vertical source beam pattern of the real source measured at 1.4 kHz was implemented. The range of beam take-off angles in the vertical plane was ±89°. The number of traced beams ranged from 2000 beams at 1 kHz to 4000 beams at 2 kHz (the number was automatically selected by BELLHOP). The modelled source was horizontally omnidirectional and placed at a depth of 50 m, approximately the actual depth of the source in the exposure session (mean ± SD over 105 transmission locations: 48 m ± 3.6 m).

Propagation loss was modelled for a single two-dimensional slice of 10 km × 323 m (range × depth) with a resolution of 1 m × 0.1 m (Fig. 3b). Water depth was based on the *Marine Primary Data* bathymetry data set of the Norwegian Hydrographic Service, which indicated a reasonably flat seafloor at the experimental site (mean ± SD over the original 104 transmission paths: 323 ± 45 m). An important feature, most noticeable at long range, is the strong increase in PL with decreasing depth as the receiver approaches very closely the sea surface. The presence of this feature suggests a potential sound avoidance strategy involving an animal approaching the sea surface very closely to reduce the sound levels to which the animal is exposed.

The energy source level (SL_E) was calculated from the source level as $SL_E = SL + 10\log_{10}(T/t_{ref})$. The effective duration T of the transmitted pulse was 0.93 s because of its gradual onset and offset, and t_{ref} was 1 s. The SL of the source at full power was 214 dB re 1 µPa m. The received single-pulse SEL and SPL were derived from the propagation loss as $SEL = SL_E – PL$ and $SPL = SL – PL$, respectively. Propagation loss was calculated for the measured and simulated positions of the whale. The received SEL_{cum} for each 3D trajectory of the simulated whale was calculated by cumulative summation of the single-pulse sound exposures; SPL_{max} was calculated over all the received single-pulse SPLs. Both the received SEL_{cum} and SPL_{max} of the simulated whale were used as measures of the efficacy of the behavioural response strategies.

For tagged whale gm08_159a, SELs were calculated from sonar pulses received on the DTAGs by Miller et al. (2012). As a performance check of our propagation model, we compared the measured and predicted SELs based on the position and depth of the actual whale. This comparison used the depth of the whale that was measured closest in time to halfway through the pulse duration.

For simulated whales, statistical distributions of SEL_{cum} and SPL_{max} were obtained each for dive state and whale heading (depending on the model scenario) using an iterative Monte Carlo method. At each iteration, a new 3D trajectory for the simulated whale was generated using the rule for horizontal whale movement and a randomly-selected period of the composite dive profile and, for scenarios C and D, the composite horizontal speed profile. The received SEL_{cum} and SPL_{max} of the simulated 3D trajectory were then calculated and stored. Each Monte Carlo distribution was based upon 10,000 iterations. We used kernel smoothed densities to visualise the probability distributions.

Results

Observations of long-finned pilot whales surfacing in synchrony with sonar arrivals

Out of a total of 1581 sonar pulses that were transmitted during all 12 exposure sessions, 154 pulses arrived at the whale when the animal was at the surface (Table 2). We identified five 'sequential overlaps' of surfacings and sonar pulses in the data set (Fig. 4; Table 2). The randomisation procedure showed that a sequential overlap of two pulses (i.e. one dive of ~20 s duration) was fairly likely to occur due to chance timing of surfacings (P=0.362). Two out of three sequential overlaps of three pulses (i.e. two dives of ~20 s duration each) were relatively unusual, but the null hypothesis of no behaviour response was not rejected (P=0.043 and P=0.053). Only the sequential overlap of three pulses during exposure session 5-1 (Figs. 4i and 4j) and the sequential overlap of four pulses during exposure session 3-1 (Figs. 4c, 4d, and 5a) had P-values that were below the Bonferroni-corrected significance level of 0.01 (P=0.006 and P=0.001, respectively), indicating that these two events were very unlikely to have occurred by chance within the observed range to the source and probably reflected behavioural responses to the sonar.

The dive profile of whale gm08_159a during exposure session 3-1 is shown in Fig. 5a. The synchronous surfacing behaviour started 40 s after the maximum single-pulse SEL of 172 dB re 1 μPa^2 s and SPL_{max} of 175 dB re 1 μPa (level reference values for SEL and SPL omitted hereafter) was reached, at a range of 580 m from the sound source (Table 2; Fig. 5b). Concurrently the received SEL_{cum} became 176 dB. Whale gm09_156b started surfacing in synchrony with the arrivals of sonar pulses at 20 s after the maximum single-pulse SEL of 177 dB and SPL_{max} of 180 dB was reached (SEL_{cum}: 185 dB), at a range of 340 m from the source. Given the relatively high received levels and small distances to the source, it is plausible that the two whales used this response strategy specifically to reduce the received SPL and/or SEL from the sonar.

Modelling behavioural response strategies of long-finned pilot whales

In the second part of the study, we simulated behavioural strategies that long-finned pilot whales may use in response to an approaching pulsed sound source. Exposure session 3-1 with whale gm08_159a was used as a realistic basis of these simulations. Measured and modelled levels were compared to assess the accuracy of the exposure modelling approach by considering the real 3D trajectory of the whale. The modelled single-pulse SEL ranged from 115 dB at the start of the session to 165 dB at the minimum source-whale range (Fig. 5b). The modelled SEL_{cum} at the end of the exposure session was 174 dB. The root-mean-square error between all modelled and measured single-pulse SELs was 4.7 dB, and the modelled SEL_{cum} was 1.9 dB lower than the measured SEL_{cum} at the end of the session. The modelled SEL was generally within the ±5 dB range of the measurement uncertainty for the DTAG (Miller et al., 2012). The largest deviations in single-pulse SEL were observed at the end of the session, when the source was moving away from the animal (Fig. 5b). A number of factors may have influenced these differences between measured and modelled levels; for example, air bubbles may have attenuated the sound near the sea surface, the body of the whale may have blocked direct sound rays from reaching the DTAG hydrophones, the horizontal or vertical beam pattern of the source may have been slightly different *in situ,* or the fine-scale variation in propagation loss may have been larger than the acoustic propagation model assumed.

In model scenario A, the horizontal trajectory of both the simulated whale and the source were the same as during the real exposure session (Fig. 1a). The median SEL_{cum} received by the simulated whale was very similar across dive behaviours (174-175 dB) and the variation was identically small (interquartile range (IQR): 1.1-1.2 dB) (Fig. 6a). Results were similar for SPL_{max}, for which the median values (164-165 dB) also differed by a small amount across dive behaviours, and IQRs were small (2.0-2.6 dB).

In scenario B, the simulated whale was horizontally stationary and the source's line of approach was directly towards and past the whale's location (Fig. 1b). The median received levels for deep diving (SEL_{cum}: 178 dB; SPL_{max}: 171 dB) were somewhat lower than for shallow diving (SEL_{cum}: 180 dB; SPL_{max}: 174 dB), but the variation in received levels for deep diving was three and four times greater (for SEL_{cum} and SPL_{max}, respectively) because of bimodality in the probability density distributions (Fig. 6b). A second mode at a lower received level (SEL_{cum}: 175 dB; SPL_{max}: 163 dB) reflected the relatively high probability that the simulated whale was at the bottom of a deep dive while the source passed overhead.

Surfacing in synchrony with the arrivals of four sonar pulses 1 minute after CPA had a relatively small effect on the received SEL_{cum} for both scenarios A and B. Taking these four synchronous surfacings into account shifted the distribution of SEL_{cum} for normal shallow diving by a very small amount; in both scenarios the median SEL_{cum} received by the simulated whale was reduced by 0.6 dB (Fig. 6). The four synchronous surfacings had no effect on the SPL_{max} as the behaviour started after the minimum source-whale distance.

In scenario C, the trajectory of the source was the same as in scenario B and the simulated whale moved horizontally in a straight line at one of 17 angles away from the projected future path of the source (Fig. 1c). The relative heading of the simulated whale that resulted in the lowest median SEL_{cum} was 100°; the lowest median SPL_{max} corresponded to a relative heading of 110° (Fig. 7a). The angular sectors in which the median SEL_{cum} was within 1 dB and 3 dB from the lowest median were wide; approximately 70° and 120°, respectively (the respective angular sectors for SPL_{max} were slightly narrower: 50° and 100°).

In scenario D, the trajectory of the source was the same as in scenarios B and C but the simulated whale turned continuously because its heading was relative to the position of the source (i.e. the source was at 0°) (Fig. 1d). The horizontal trajectory that resulted in the largest reduction in SEL_{cum} and SPL_{max} had a relative whale heading of 120° (Fig. 7b). The angular sectors in which the median received levels were within 1 dB and 3 dB from the lowest median were comparable to those for scenario C: approximately 60° and 100°-120°, respectively. The median SEL_{cum} for the optimal whale heading for scenarios C and D were almost identical; 175.1 and 175.3 dB (IQRs: 2.6 dB), respectively. The respective median SPL_{max} for scenarios C and D were also very similar: 165.7 and 166.0 dB (IQR: 5.4 and 5.0 dB).

Discussion

Assumptions of the response strategy simulations

Our simulations were based upon an experimental protocol that was designed to recreate a real-world encounter of a cetacean with a closely-approaching naval vessel towing a sonar source. This design influenced the outcomes in several ways. The absolute reductions in received level that could be achieved by the modelled avoidance responses were relatively small because our whale model, like long-finned pilot whales in general, had relatively high response thresholds compared to other cetacean species (Antunes et al., 2014; Stone and Tasker, 2006). As a consequence, the simulated whale had little time to increase its distance from the approaching sonar. The direction of the effect for more responsive species such as killer whales will most likely be the same as for less responsive species but the magnitude of the effect greater (von Benda-Beckmann et al., 2014); therefore, we were mainly interested in the relative effect of the response strategies on the received levels. We used both SEL_{cum} and SPL_{max} for testing the efficacy of behavioural responses because these metrics describe slightly different aspects of the noise (highest amplitude vs. total energy) and there is currently little scientific basis for choosing one or the other. Because SEL_{cum} is calculated over the entire duration of the vessel approach, it resulted here in smoother probability distributions compared to SPL_{max} (Fig. 6). However, the patterns in the data were very similar between SEL_{cum} and SPL_{max} as the sonar pulses received closest to the source strongly influenced both metrics. We should note that there is no simple linear relationship between received SEL_{cum} or SPL_{max} and the risk of causing a potentially negative effect (e.g. hearing loss, reduction in the energy budget); a small decrease at a high level can be of greater significance to the animal than a larger decrease at a low level.

We assumed that the real whale received as much sound exposure near the sea surface as was predicted by the propagation loss modelling at the measured depth (which could be 0 m). Part of the sound energy is expected to propagate through the body of the animal to the inner ear, but it is currently not known by how much the sea surface can reduce the perceived level in any marine mammal. Hearing tests on captive, trained animals might be able to address this question. Because the near-surface pressure release relates to the wavelength of the sound (Weston, 1980; Jensen, 1981), the amount of reduction in perceived level probably depends on the size of the animal as well as the relative position of the ears and hearing pathways of the animal.

Evaluation of the data

The randomisation test quantitatively supported the tentative scoring by Miller et al. (2012) that the series of synchronous surfacings with sonar arrivals during exposure sessions 3-1 and 5-1 represented behavioural responses to the sonar. There were a number of similarities between these two events. In both cases the sonar source had just moved past the tagged whale (the behaviour started 4 vs. 2 pulses after the CPA) at a relative short distance (450 vs. 300 m) and while transmitting 1-2 kHz upsweeps, which resulted in a high SPL_{max} (175 vs. 180 dB) and SEL_{cum} (176 vs. 185 dB) at the position of the whale (Miller et al., 2012). In addition, the shape of the dives between the synchronous surfacings with the sonar were similar (Figs. 4d and 4i). This contrasts with the other two sequential overlaps of three pulses length that were identified, which occurred at distances of 3.8-2.7 km from the source, during transmission of 6-7 kHz upsweeps, and after a much lower received SPL_{max} (123 dB) and SEL_{cum} (126-127 dB). Because the randomisation procedure took into account the timing of surfacings in relation to pulses as well as the distance to the source (which correlates with the received SPL), our results suggest that only during 1-2 kHz exposure sessions did the long-finned pilot whales anticipate the high intensity sounds by timing their surfacings very accurately to coincide with the arrival of sonar pulses. We interpret this behaviour as a vertical avoidance strategy to the received SPL and/or single-pulse SEL of the sonar, as the behaviour occurred after the whales received relatively high sound levels and propagation loss is expected to be very high near the sea surface due to pressure release (Jensen, 1981; Weston, 1980). Fig. 4c illustrates that the vertical propagation loss gradient can be as large as

30 dB in the top 10 m of the water column at the distances of the synchronous surfacings (300-800 m).

However, our simulations showed that surfacing four times in synchrony with the sonar arrivals at 1 minute after CPA was not an effective strategy to reduce SEL_{cum} (Fig. 6), which can be explained by the fact that the received SEL_{cum} for a fast-moving sound source is most strongly influenced by the sound exposures that are received when the source is at a close range. These sound exposures at close range also resulted in no effect of the four synchronous surfacings on the received SPL_{max} (Fig. 6). We only tested one scenario (i.e. four pulses after CPA) that was based upon the observed behaviour, but alternative scenarios (e.g. with a different number of pulses, timings, source characteristics, source distances, propagation conditions) can be explored in future studies.

The relatively high sound levels received prior to the observed responses potentially exceeded a discomfort/disturbance threshold at a received SPL of 175-180 dB, and may have triggered these two animals to try to avoid sounds of similar high intensity from that point onwards. Perhaps a measure such as 'the time that the received SPL exceeded a given threshold' would be better able to predict this type of disturbance. The lack of comparable behavioural responses in the other pilot whales that received SPLs of ≥175 dB (Table 2) does not necessarily contradict this hypothesis. For one of the whales (session 5-3), the level of 175 dB was reached when the animal was still ascending from a deep dive when the source passed overhead; for the other two whales (session 4-3), the source was shut down two pulses after 175 dB was reached because other pilot whales were seen entering the 100-ms safety zone (Miller et al., 2011). Other factors, such as waveform characteristics (upsweeps for sessions with responses; downsweeps for sessions with comparable received levels and no responses), presence of harmonics in the received signal, and the order of the exposure sessions (Table 2), may also have influenced the presence and absence of synchronised surfacings.

The lack of comparable responses to the 6-7 kHz sonar signals may be a result of the lower source level that was used for this signal; the received SPL_{max} never exceeded 150-167 dB during the five 6-7 kHz exposure sessions (Table 2). However, it is conceivable that pulsed sonar signals of 7 kHz and higher can induce similar vertical avoidance responses in long-finned pilot whales when received SPLs are higher than those measured in our 6-7 kHz experiments, as the hearing of pilot whales is probably most sensitive at tens of kilohertz (Greenhow et al., 2014; Pacini et al., 2010; Schlundt et al., 2011).

Comparison of the results for scenarios A and B clearly shows the importance of considering the effects of horizontal and vertical avoidance in combination for deep diving species. In scenario A, there was almost no difference in received level between deep and shallow diving behaviour (Fig. 6a). Although SPL_{max} and SEL_{cum} can be affected by source directivity and acoustic propagation conditions, this result was not entirely surprising because the closest pulse was transmitted at a horizontal range of 440 m and the maximum vertical distance between the source and the simulated whale was 372 m. In scenario B, being at the bottom of a deep dive when the source passed overhead yielded a reduction in median SPL_{max} of about 8 dB (SEL_{cum}: 4 dB; Fig. 6b). If a whale was able to estimate the proximity and speed of an approaching sound source, the animal could time its normal deep-diving behaviour to reduce sound exposure. However, such a response strategy has risk when the source is at close range, which is reflected in a small proportion of high levels received by the simulated whale during deep diving (the 'spurious events' in Fig. 6b). The efficacy of diving deeper than the sound source thus depends upon the diving capabilities and sensory tracking abilities of the species. Here, species-typical behaviour was used to simulate the vertical movement of the whale, but one might predict that animals would extend their diving limits by diving deeper and longer than normally, in order to avoid high sound exposures if sufficiently deep water is available in their habitat (e.g. Tyack et al., 2011).

To horizontally avoid high sound exposures from the approaching source, moving approximately perpendicular (100°-110°) to the source track was always the best strategy when the simulated whale was moving in a straight line (scenario C). This result will be expected for most real-world situations if the sound source moves faster than the animal. For continuous turning motion (scenario D), the optimal starting angle was 20°-30° further away from the source compared to linear motion (Fig. 7), but this starting angle will be affected by the speed of the source relative to that of the whale (Weihs and Webb, 1984). By moving away approximately perpendicular to the source's line of approach (scenarios C and D), the simulated whale reduced its medium received SPL_{max} by 8 dB and the medium SEL_{cum} by 5 dB compared to when it kept diving at the same location (scenario B) (these values were affected by the fact that the closest modelled pulse was at a horizontal range of 40 m, however). Surprisingly, the range of relative headings in which the simulated animal achieved nearly-optimal results was wide. This shows that horizontal avoidance can be effective so long as a whale moves roughly away from the predicted trajectory of the source.

The effect of relative speed on the effectiveness of a response is apparent when comparing the SEL_{cum} for linear whale trajectories that are close to the track line of the source (10° vs. 170°; Fig 7a). A whale that moves directly toward the source will generally receive a lower SEL_{cum} than a whale that is moving in the same direction but is overtaken, as in the example given by Gedamke et al. (2011). In contrast, if that animal is faster than the source, horizontal movement directly away from the source will be optimal in terms of received SPL, SEL and distance. However, moving in the same direction as an incoming source or predator might decrease the ability for the whale to acoustically track the perceived threat, which could potentially speed up. The horizontal trajectories of killer whales and long-finned pilot whales during controlled sonar exposures (Miller et al., 2011; 2012) indicated that these animals can accurately estimate the heading and speed of an incoming sound source if the source is approaching from the side or the front. Keeping an object at an angle of ~90° could therefore be an effective method for these animals to increase distance to the source and reduce sound exposure without completely losing track of the potential treat.

Comparison of simulations with observed avoidance responses

To our knowledge, our detailed report of synchronised surfacing is the first of this type of anticipatory behaviour to high sound exposures for a cetacean in the wild. It is possible that two bottlenose dolphins (*Tursiops truncatus*) exposed to regular series of airgun pulses showed similar behaviour during a captive study on temporary hearing threshold shift (Schlundt et al., 2013). The dolphins oriented their head away from the direction of the sound source when sound was transmitted. Another type of anticipatory behaviour to sound was recently reported; Nachtigall and Supin (2013, 2014) showed that cetaceans are capable of reducing their hearing sensitivity when animals anticipate the rapid onset of a loud sound. Use of the sea surface to reduce SPL has been reported more often for pinniped species (Götz and Janik, 2011; Houser et al., 2013a; Kastak et al., 1999; Kvadsheim et al., 2010; Mate and Harvey, 1987) than for cetaceans.

Besides acoustic quantities (e.g. SEL, frequency, signal-to-noise, signal excess), avoidance responses of marine mammals are likely to be affected by other factors (e.g. the distance to the source, movement of the source, prior experience with the source) (Southall et al., 2007). Especially responses to novel sources that are perceived as a threat are predicted to be shaped by the innate anti-predator response of a species (Ellison et al., 2012; Frid and Dill, 2002). Our simulations suggested that long-finned pilot whales could use deep dives to reduce sound exposure. However, observed behavioural responses to sonar indicate that this was actually not a common response in this species; long-finned pilot whales more often switched from deep to shallow diving, or continued shallow diving during sonar CEEs (Miller et al., 2012; Sivle et al., 2012), which our simulations suggest would increase the received SEL_{cum} and SPL. Pilot whales socialise at the surface in large aggregations but individuals regularly leave their group to forage at depth (Aguilar Soto et al., 2008; Weilgart and Whitehead, 1990); thus, social species such as the long-finned pilot whale may be more likely to respond to noise by returning to their social group at the surface before moving horizontally away from the noise source at higher exposure levels (Visser et al., 2014). In contrast, avoidance with a strong vertical component may be more common in species that forage alone or in small groups such as various species of beaked whales (DeRuiter et al., 2013; Tyack et al., 2011) and northern elephant seals (*Mirounga angustirostris*; Costa et al., 2003).

Some species respond to predators by trying to outswim them (e.g. minke whales; *Balaenoptera acutorostrata;* Ford et al., 2005) and may use this response template also in response to approaching sonar sources (Kvadsheim et al., 2011). Our simulations showed that if the source is faster than the animal, moving perpendicular to the line of approach is an effective solution for the whale to increase distance and/or reduce sound exposure. This is consistent with observations of killer whales moving perpendicular to the heading of the sound source during CEEs (Miller et al., 2014; von Benda-Beckmann et al., 2014). Movement perpendicular to moving anthropogenic noise sources has also occasionally been observed in pilot whales (Miller et al., 2012; Weir, 2008), although their horizontal avoidance responses are generally shorter with higher onset SPL_{max} and SEL_{cum} thresholds (Antunes et al., 2014). Movement relative to the heading of an approaching sound source suggests that a responding animal is not only able to acoustically track the direction the sound is coming from, but also has some ability to estimate the distance to the source and its speed. The horizontal avoidance movements of migrating baleen whales around low-frequency sonar, industrial and seismic noise sources suggest that these whales also have excellent tracking abilities. Gray (*Eschrichtius robustus),* bowhead (*Balaena mysticetus)* and humpback whales (*Megaptera novaeangliae*) are often observed during migration to navigate carefully around the source by making small changes in speed and direction to avoid close encounters (McCauley et al., 2000; Richardson et al., 1986; Tyack, 2009). Such movement patterns were not modelled here, but corresponding trends in received level should be comparable to the results for scenario D.

Conclusion

We combined an analysis of empirical Controlled Exposure Experiment data with the modelling of 3D animal trajectories to gain insight into the avoidance responses of cetaceans to an approaching anthropogenic noise source. Our study showed, for example, that long-finned pilot whales are capable of precisely timed behavioural responses that reduce high SPL. However, these responses had little to no effect on the received SPL_{max} and SEL_{cum} in the specific cases that we observed, because they happened when the source was already moving away from the whale. Our approach of simulating realistic movement was useful to understand possible motivations of cetaceans responding to anthropogenic noise sources, which may not always be as simple as reducing sound exposure alone, and may aid the interpretation of behavioural responses observed in the wild. Individual-based modelling techniques are likely to continue to be an important tool in quantitative risk assessment and management, but more empirical data on avoidance responses (such as distributions of swim speed, distance and received SPL at the onset of response, and relative direction of movement) that can be used as input for these assessment are needed in order to model avoidance more realistically, and thus reduce the uncertainties in impact estimates arising from the effect of avoidance of sound exposure.

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Figure captions

Figure 1. **Horizontal trajectories of the sound source and the simulated pilot whale**. Panels a) to d) correspond to model scenarios A to D, respectively. The horizontal trajectories in scenario A were the same as in exposure session 3-1 with tagged whale gm08_159a. The location of the source and the whale during exposure session 3-1, and the time since the start of the session (in min:s), are indicated for some of the key events.

COLOUR ONLINE ONLY. PREFERED WIDTH: 1-5 COLUMN

Figure 2. **Composite dive profiles for a) shallow transit diving and b) deep foraging diving**. Composite dive profiles were created from the real long-finned pilot whale baseline records (Table 1). The composite horizontal speed profile that corresponded to the profile for shallow diving is shown on the second y-axis. Note the differences in scale between the top and bottom panels. Sections of the profiles for shallow and deep diving are shown in panels c) and d), respectively.

COLOUR ONLINE ONLY. PREFERED WIDTH: 1 COLUMN

Figure 3. **Propagation loss in the water column.** a) The measured sound speed profile for exposure session 3-1 and b) the propagation loss over the entire modelled range and depth. c) Detailed view of the propagation loss in the top 10 m of the water column at distances of 4 km or less from the source.

COLOUR ONLINE ONLY. PREFERED WIDTH: 1.5 COLUMN

Figure 4. **Sequential overlaps of sonar pulses and surfacings**. Sequential overlaps are shown for whales: a-b) gm08_150c, c-d) gm08_159a, e-h) gm09_138b, and i-j) gm09_156b. For each whale is shown a spectrogram (Hann window; 50% overlap; FFT length 8196, 100 dB range) of the acoustic data recorded by the DTAG and in the panel underneath the corresponding depths (z) of the tagged whale. In the dive plots are indicated: surfacings of the whale (upper bars), sonar pulses (lower bars), and which of the pulses temporally coincided with surfacings (stars).

COLOUR ONLINE ONLY. PREFERED WIDTH: 1 COLUMN

Figure 5. **Time series data plots for session 3-1with pilot whale gm08_159a**. a) Depth and horizontal speed (second y-axis) of the whale. Triangles above the dive profile indicate the times of the surfacings that overlapped in time with sonar pulses (top row), sonar pulses (middle row), and whale surfacings (bottom row). (b) The single-pulse and cumulative sound exposure levels (SELs) that were measured by the DTAG attached to the whale and estimated by the acoustic propagation model. The range between the source and the whale is shown on the second y-axis. The time of the first behavioural change (decrease in speed and minor change in direction; Fig. 2) that was judged to be a response to the sonar by Miller et al. (2012) is indicated with a dashed vertical line.

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Figure 6. **Received sound levels of the simulated whale for model scenarios A and B**. The received cumulative sound exposure level (SEL_{cum}) and maximum sound pressure level (SPL_{max}) from a moving sonar source passing the simulated long-finned pilot whale during deep diving, normal shallow diving, and shallow diving with synchronous surfacings (ss) are shown. In scenario A, the simulated whale and source followed their original horizontal trajectories. In scenario B, the simulated whale stayed in the same horizontal location and the source's line of approach was straight towards and past this location.

COLOUR ONLINE ONLY. PREFERED WIDTH: 1 COLUMN

Figure 7. **Received sound levels of the simulated whale for model scenario C and D.** The received cumulative sound exposure level (SEL_{cum}) and maximum sound pressure level (SPL_{max}) of the simulated whale as function of its heading relative to the source position at the onset of the response (scenario C) or relative to the source position throughout the response period (scenario D). For both scenarios, 0° is towards the source and 180° is away from the source at the onset of the response. The black triangle and two vertical lines that are shown on the right side in each panel indicate the optimal relative whale heading (lowest median), and 1 dB and 3 dB ranges.

PREFERED WIDTH: 1.5 COLUMN

Table captions

Table 1. **Details of the long-finned pilot whale tag records**. Year and Julian day are indicated by the first two and last three numbers in the whale ID, respectively. Loggings were defined as periods where the whale was at the surface for 5 s or more. *Tag gm09_138a was excluded as a baseline record because gm09_138b was recorded at the same time so the behaviour of these two whales was possibly correlated. §One data point only for group size because of bad visibility during tracking.

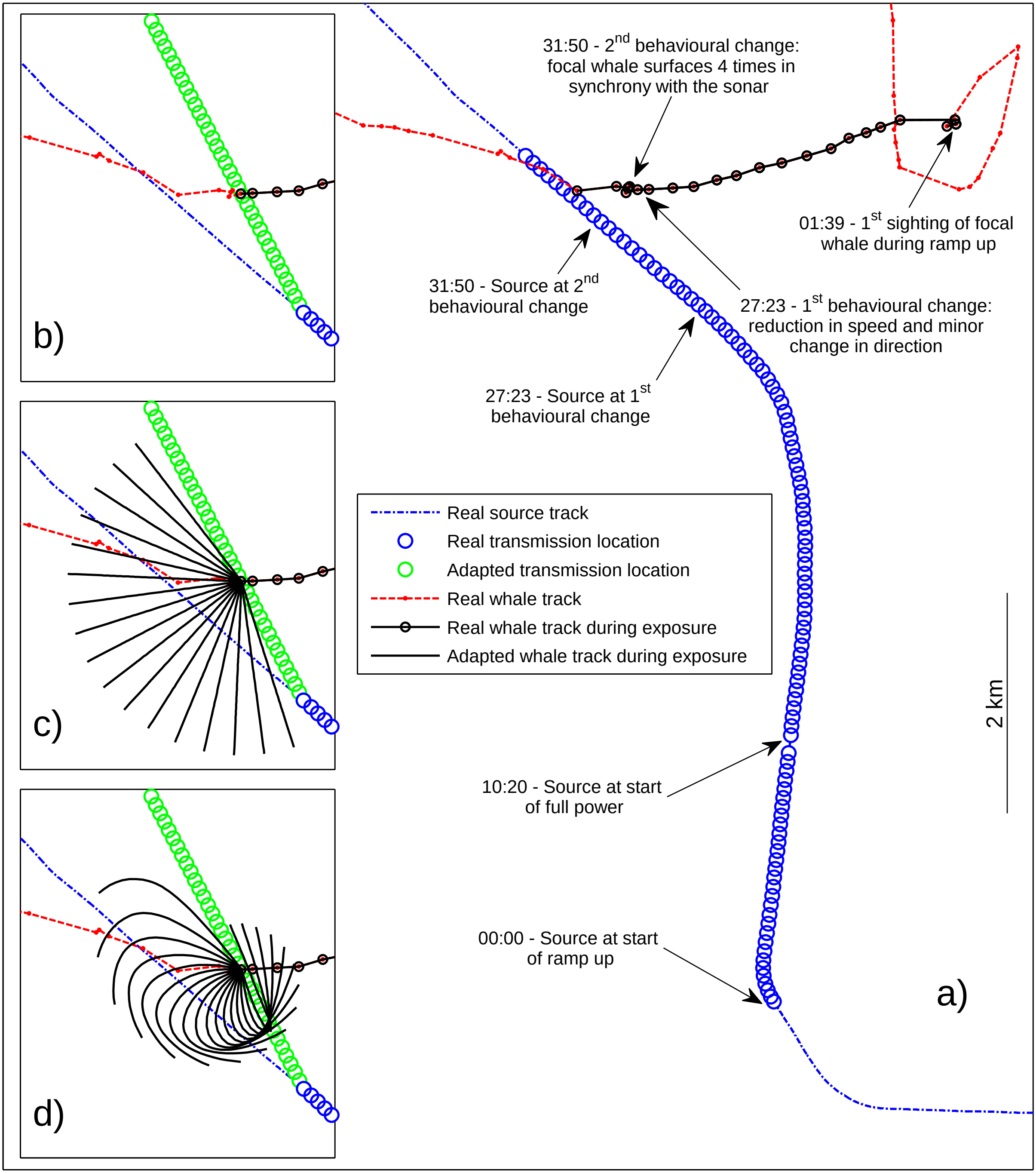
Table 2. **Details of the analysis into synchronous surfacing with the sonar**. For each exposure session are shown the number of transmitted sonar pulses and how many of these were overlapped, number of whale surfacings, number of sequential overlaps, and the received SPL_{max} and SEL_{cum}. For each identified sequential overlap are shown its duration [measured in number of consecutive pulses], the minimum and maximum observed range, the maximum received levels before the behaviour occurred, and the probability that the sequential overlap would occur within the maximum observed source-whale range. The P-values that were below the Bonferoni-corrected significance level of 0.01 are highlighted in bold typescript. Note that Gm09_138a and Gm09_138b were both exposed to sonar during the same experiment. *The transmitted waveform was a downsweep instead of an upsweep.

Table 1

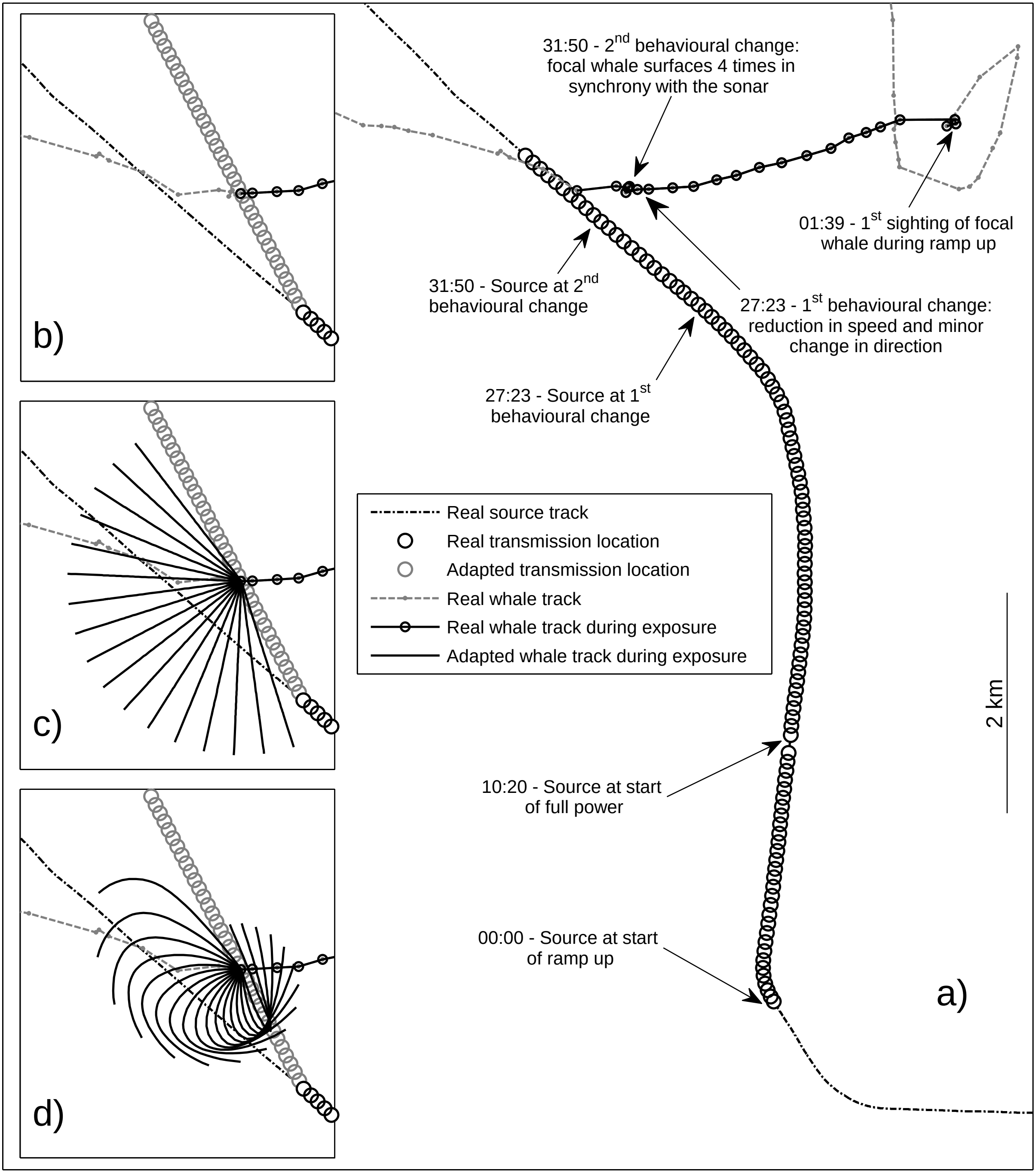
Whale ID	Sonar	Baseline period			Age-sex class	Group size
		Duration	Surfacings	Loggings		
	yes/no	min	#	#		mean [min, max] #
gm08_150c	Y	62	122	1	Female with calf	13 [10, 15]
gm08_154d	Y	129	290	3	Female with calf	30§
gm08_159a	Y	134	245	5	Large adult	15 [10, 20]
gm09_138a*	Y	193	399	6	Medium sized adult	15 [7, 30]
gm09_138b	Y	193	412	5	Female with calf	15 [7, 30]
gm09_156b	Y	305	495	8	Large adult	13 [1, 30]
gm10_143a	N	525	1221	10	Large adult	7 [1, 11]
gm10_152b	N	96	260	6	Medium sized adult	12 [12, 12]
gm10_157b	N	631	1464	7	Female with calf	11 [1, 30]
gm10_158d	N	175	383	7	Medium sized adult	8 [6, 10]

Table 2

Whale ID	Session ID	Exposure session						Sequential overlap				
		Frequency band	Surfacings	Sonar pulses		SPL_{max}	SEL_{cum}	Duration	Range	P-value	SPL_{max}	SEL_{cum}
		kHz	#	# total	# overlaps	dB re µPa	dB re µPa^{2}s	# pulses	km		dB re µPa	dB re µPa^{2}s
gm08_150c	1-1	6-7	67	111	7	150	153	-	-	-	-	-
	1-2	1-2	52	94	9	170	177	2	5.64-5.74	0.362	143	146
gm08_154d	2-1	1-2	187	240	9	163	169	-	-	-	-	-
	2-2	6-7	49	75	7	152	153	-	-	-	-	--
gm08_159a	3-1	1-2	59	105	10	175	176	**4**	**0.58-0.82**	**0.001**	**175**	**176**
	3-2	6-7	38	106	31	159	163	-	-	-	-	-
gm09_138a	4-1	1-2	52	97	4	172	175	-	-	-	-	-
	4-2	6-7	59	106	6	167	166	-	-	-	-	-
	4-3	1-2*	63	86	3	175	176	-	-	-	-	-
gm09_138b	4-1	1-2	63	97	8	167	173	-	-	-	-	-
	4-2	6-7	61	106	17	161	159	3	3.66-3.84	0.053	123	126
								3	2.74-2.87	0.043	123	127
	4-3	1-2*	74	86	6	175	176	-	-	-	-	-
gm09_156b	5-1	1-2	69	100	12	180	186	**3**	**0.34-0.40**	**0.006**	**180**	**185**
	5-2	6-7	51	81	9	156	162	-	-	-	-	-
	5-3	1-2*	60	91	16	177	181	-	-	-	-	-



31:50 - 2nd behavioural change: focal whale surfaces 4 times in synchrony with the sonar
01:39 - 1st sighting of focal whale during ramp up
31:50 - Source at 2nd behavioural change
27:23 - 1st behavioural change: reduction in speed and minor change in direction
27:23 - Source at 1st behavioural change
Real source track
Real transmission location
Adapted transmission location
Real whale track
Real whale track during exposure
Adapted whale track during exposure
2 km
10:20 - Source at start of full power
00:00 - Source at start of ramp up
a)
b)
c)
d)



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Real source track
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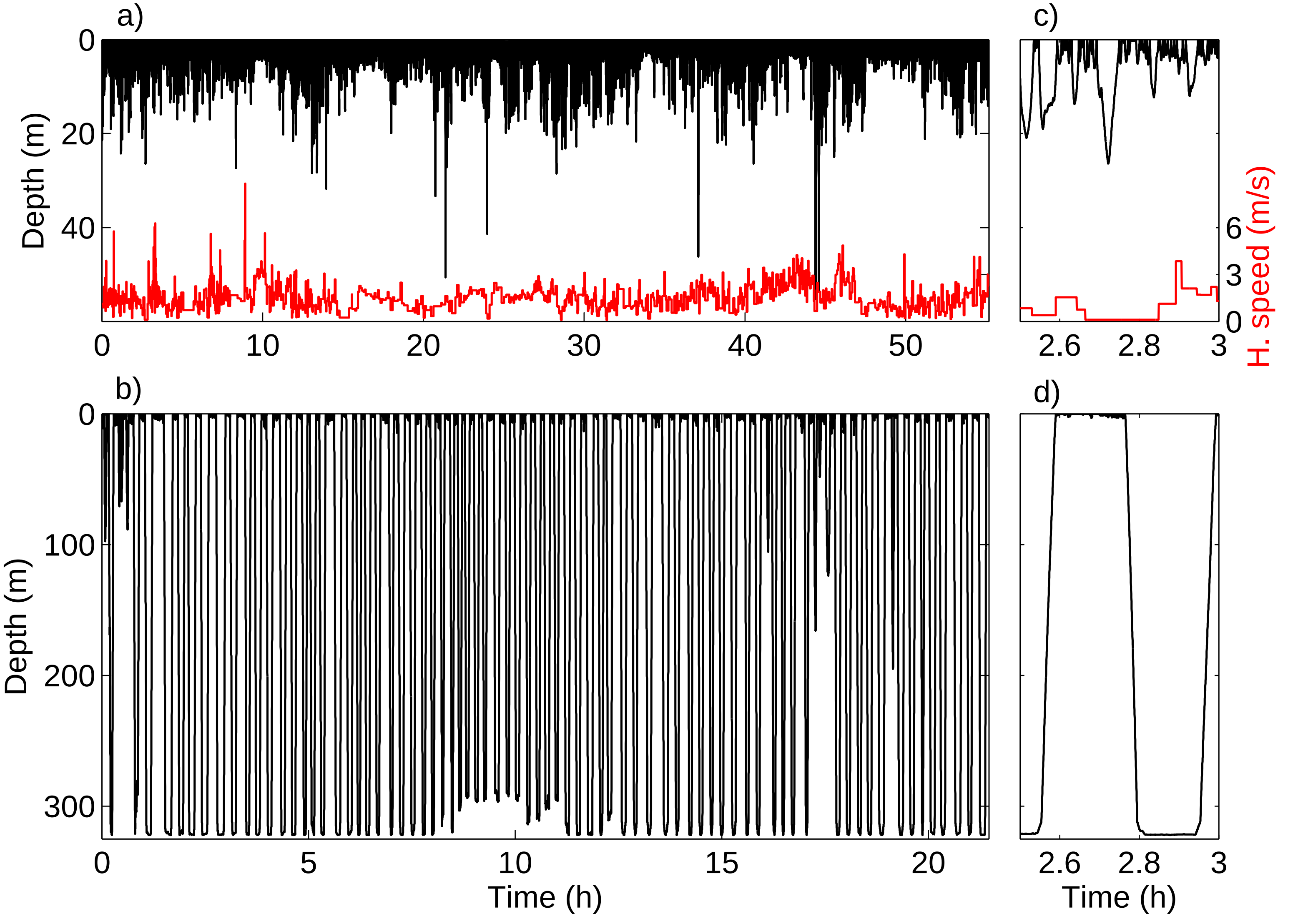
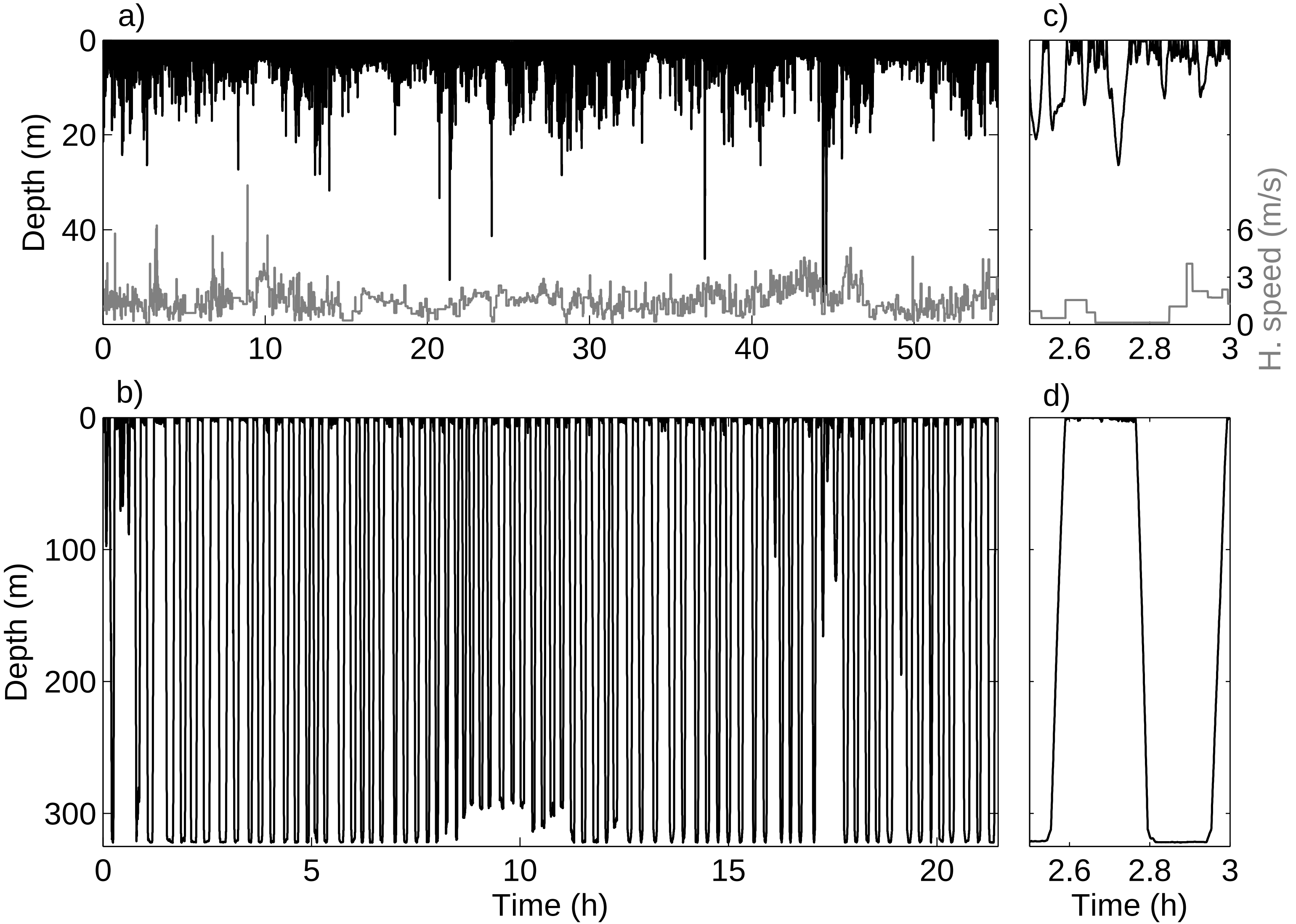
Adapted transmission location
Real whale track
Real whale track during exposure
Adapted whale track during exposure
2 km
10:20 - Source at start of full power
00:00 - Source at start of ramp up
a)
b)
c)
d)


a)
b)
c)
d)
Depth (m)
H. speed (m/s)
Time (h)
0
20
40
0
3
6
0
10
20
30
40
50
0
100
200
300
0
5
10
15
20
2.6
2.8
3



a)
b)
c)
d)
Depth (m)
H. speed (m/s)
Time (h)
0
20
40
10
30
50
100
200
300
5
15
2.6
2.8
3
6

Figure 3 - colour
Click here to download high resolution image

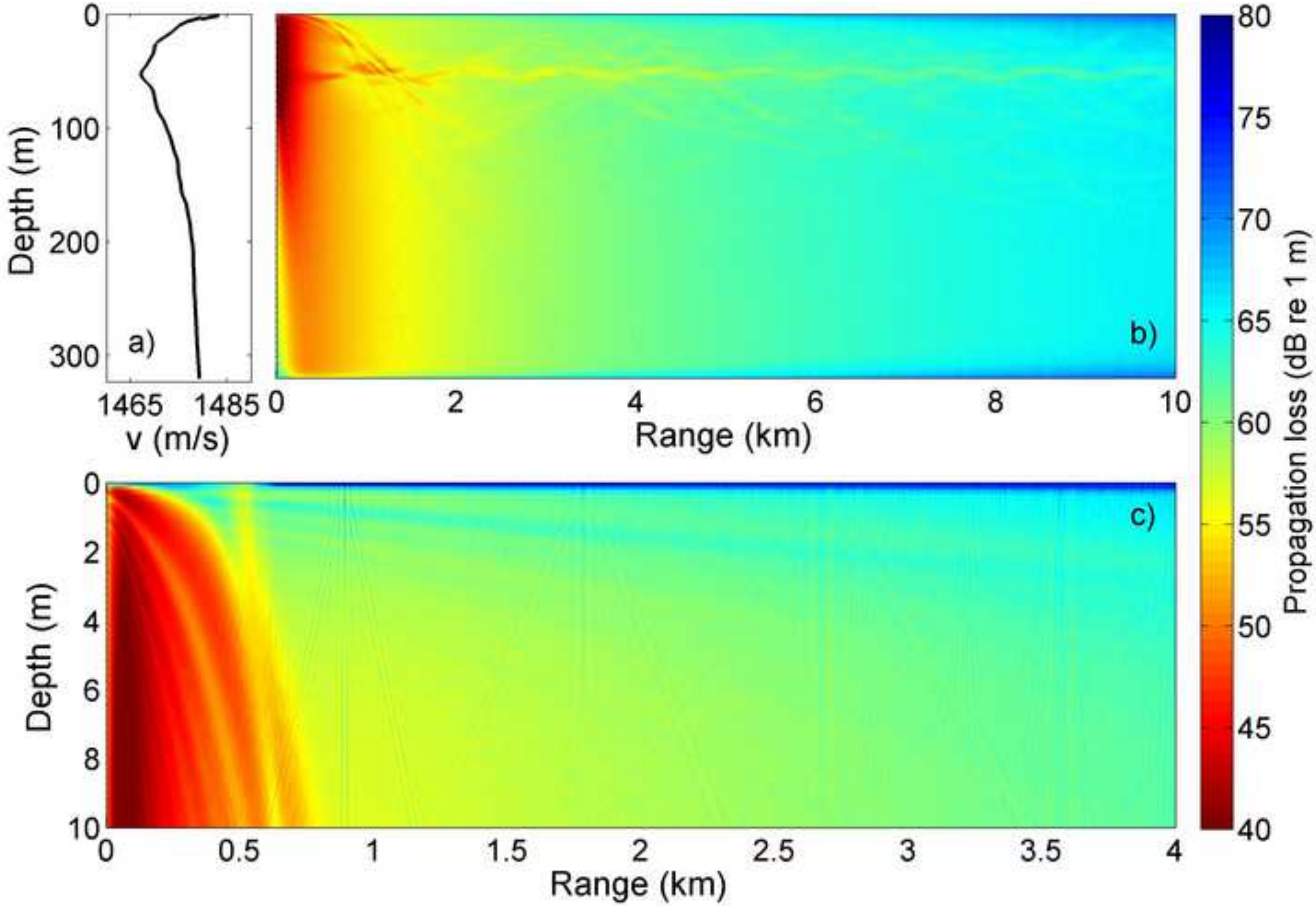


Figure 3 - B/W
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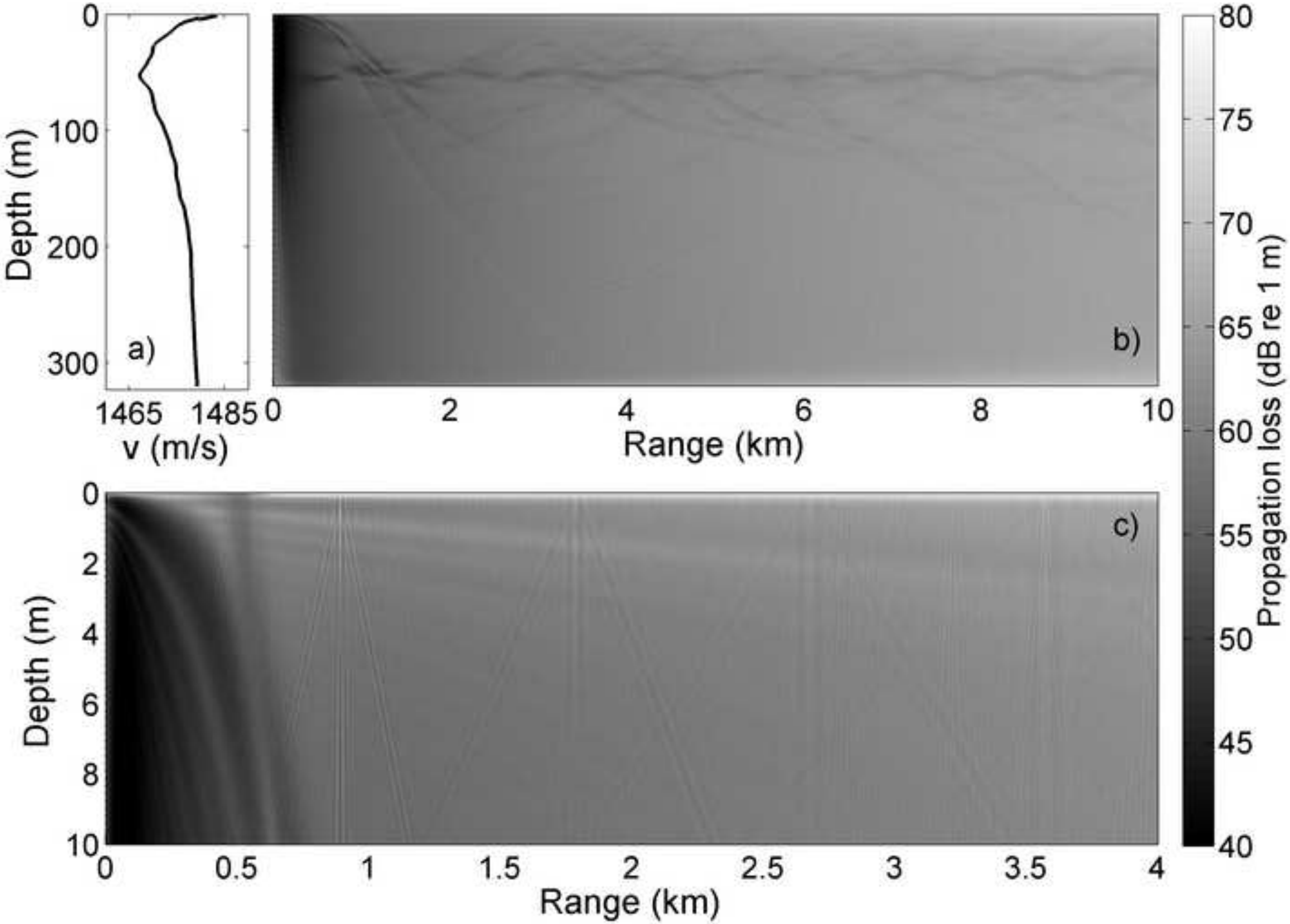

Figure 4 - colour
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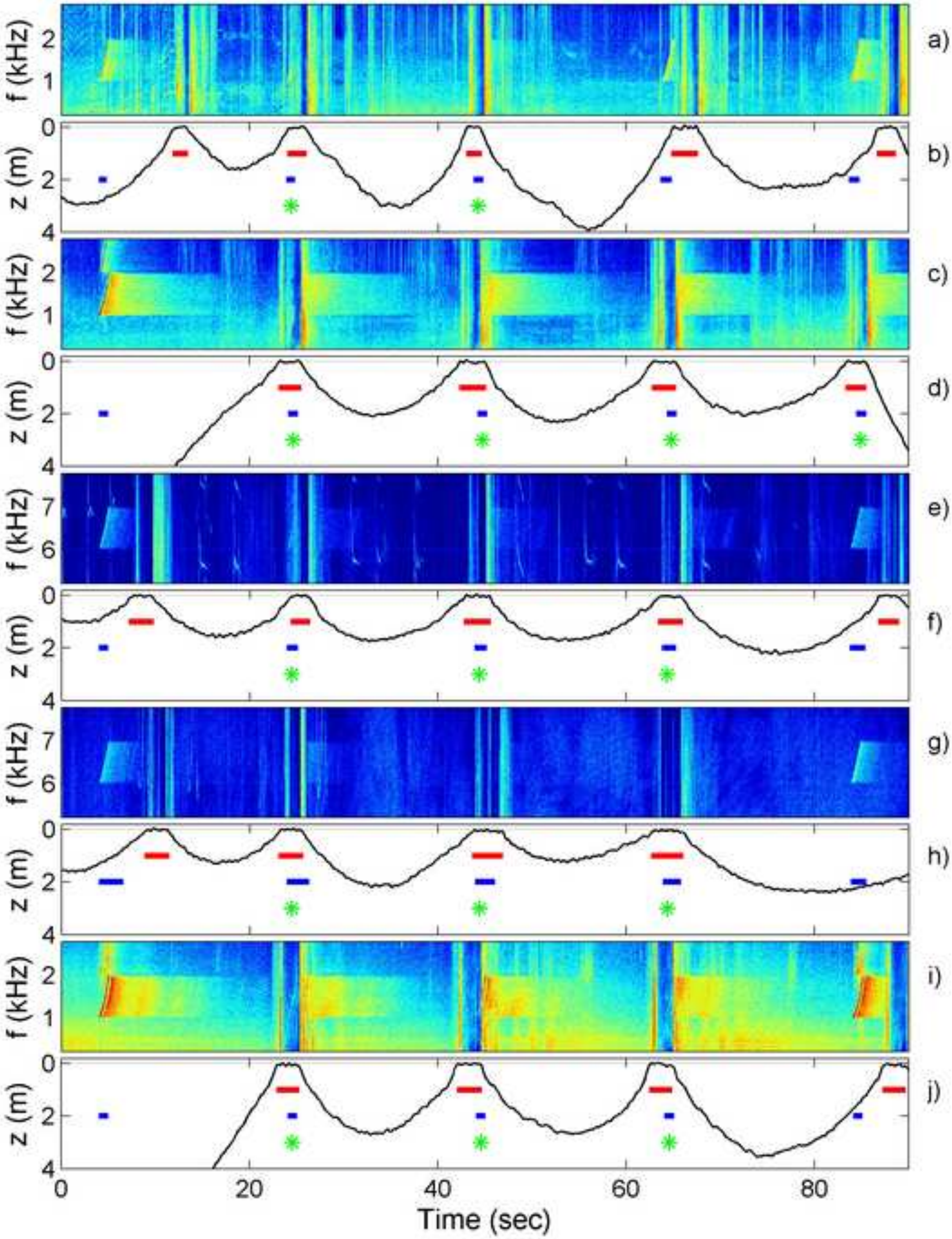

Figure 4 - B/W
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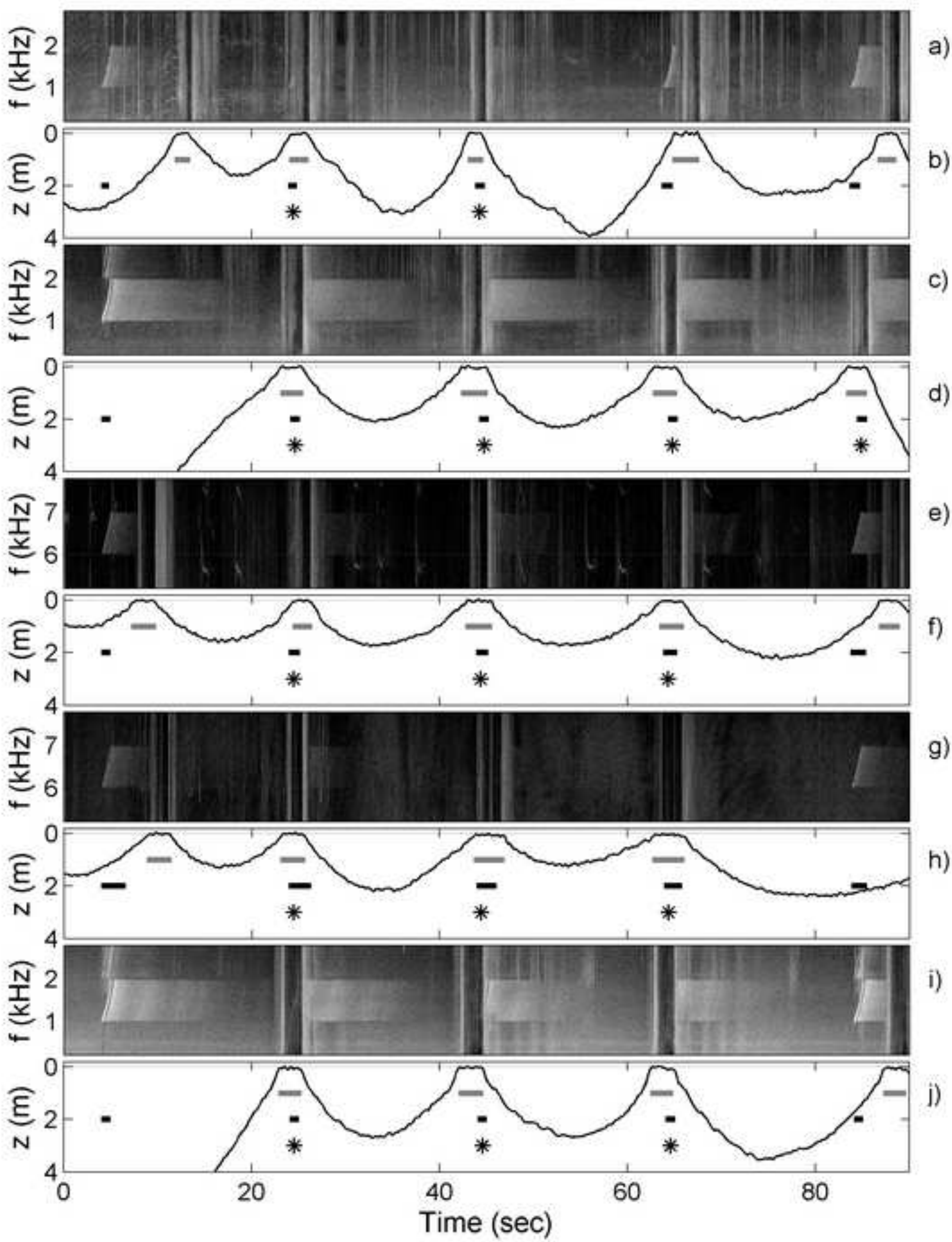
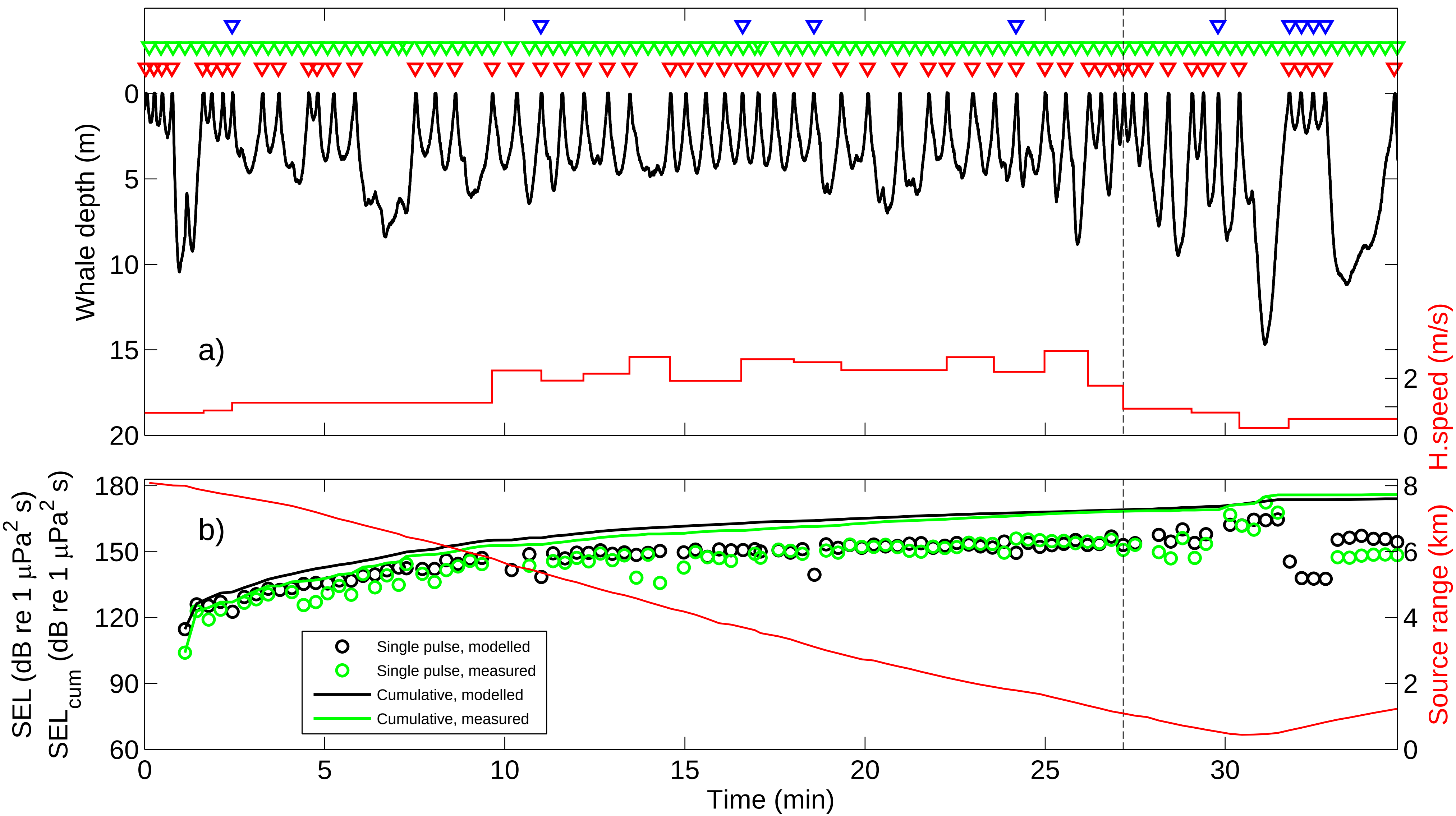
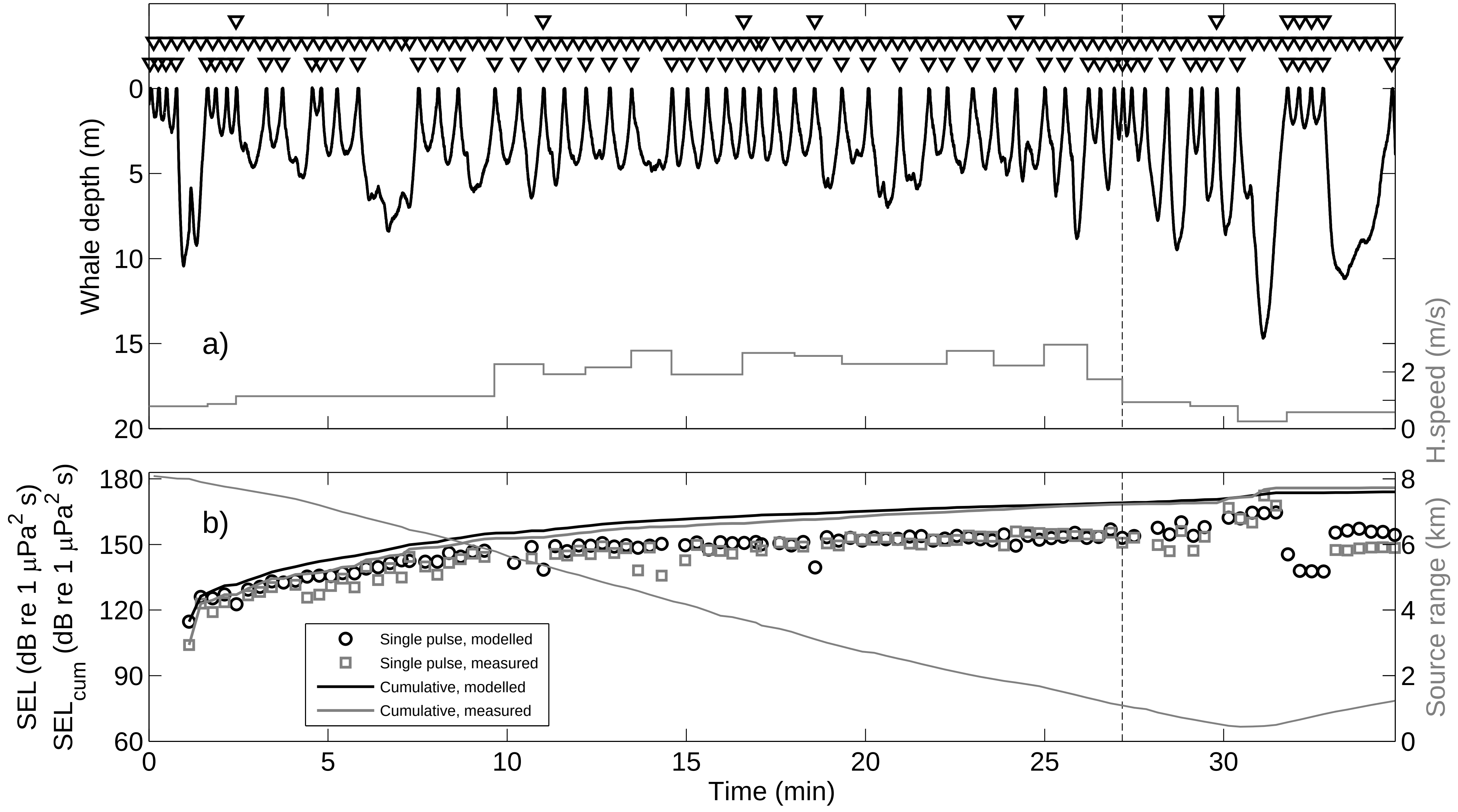
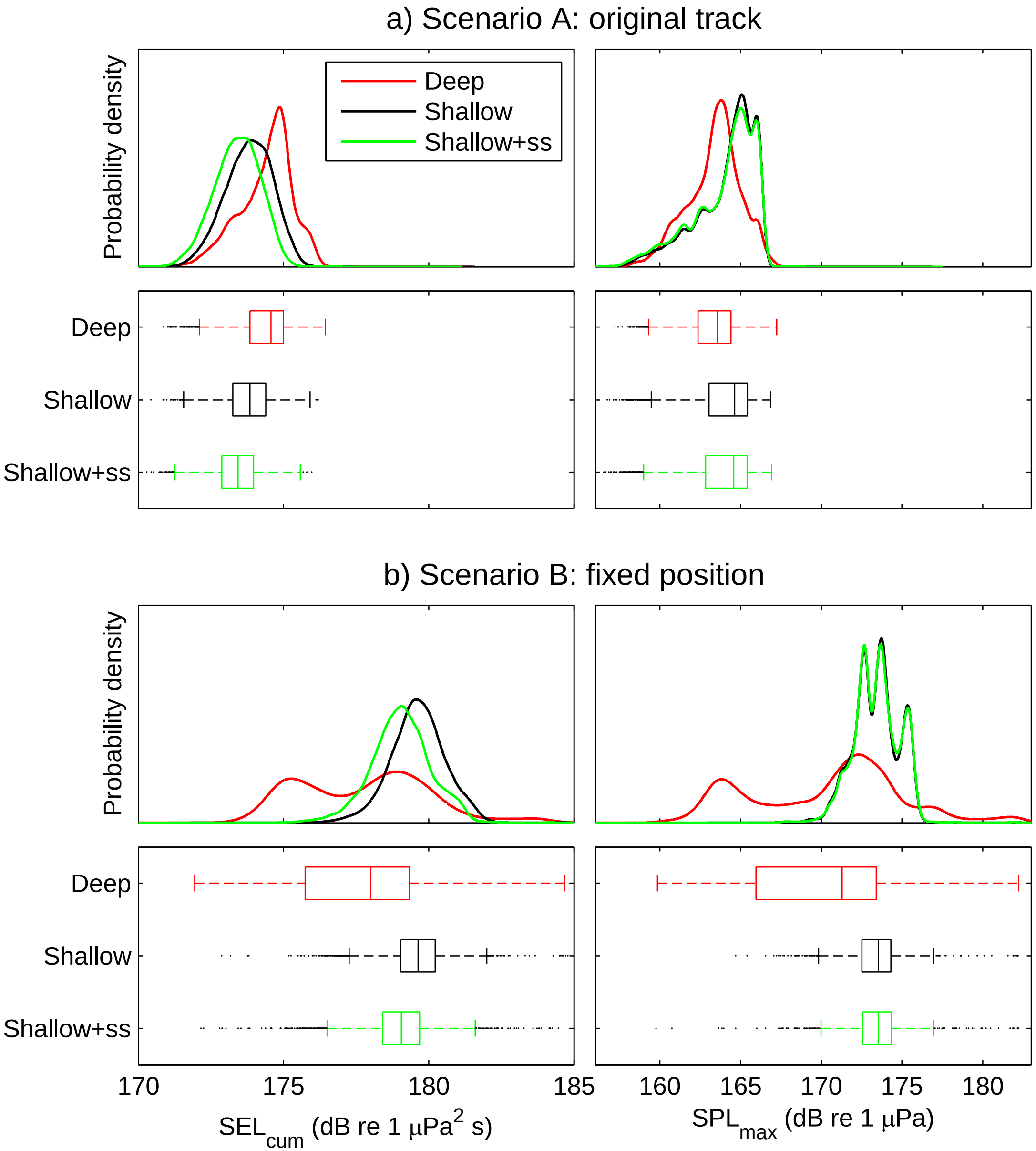


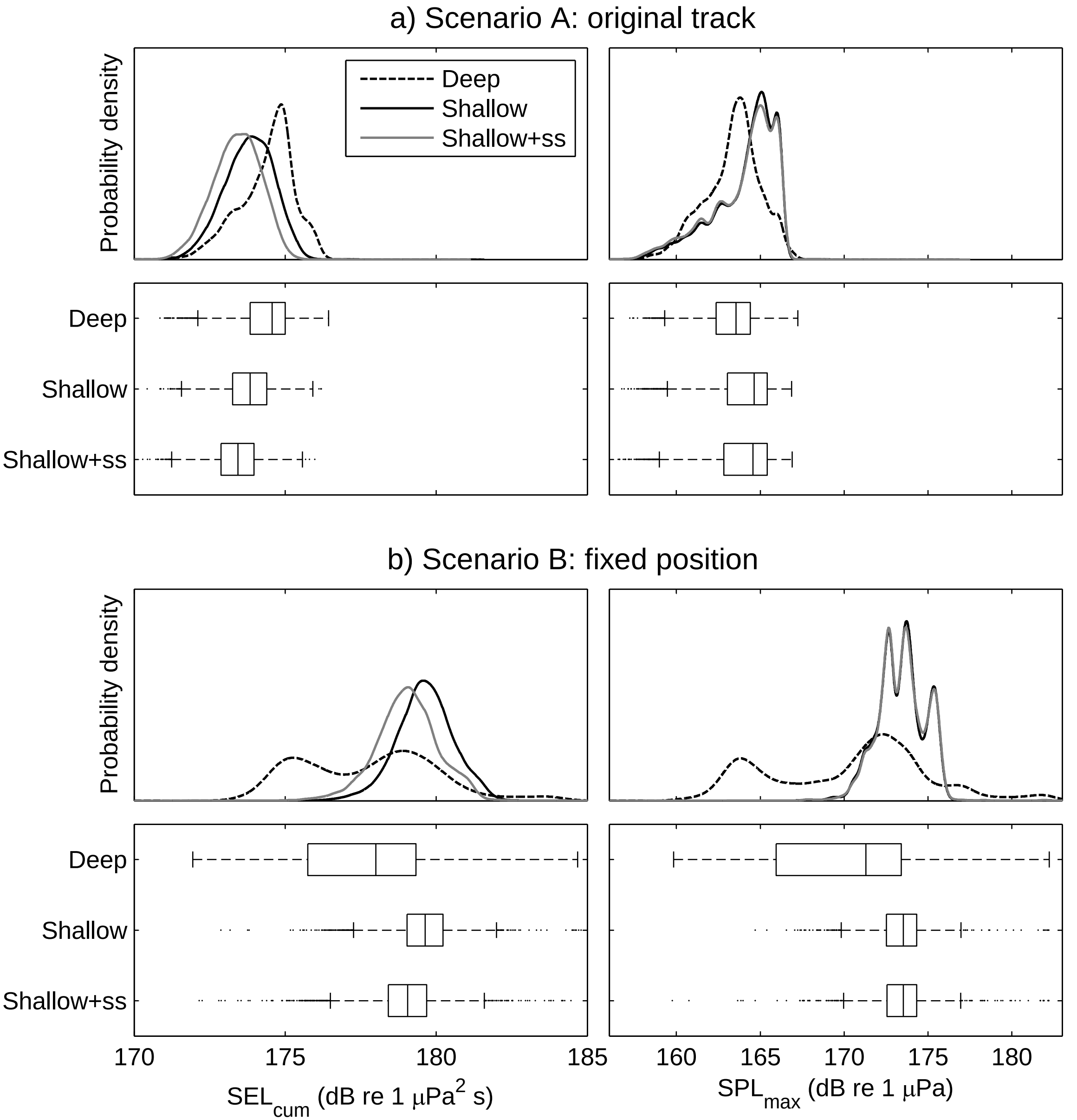


Whale depth (m)
H.speed (m/s)
a)
b)
SEL (dB re 1 μPa² s)
SEL_cum (dB re 1 μPa² s)
Source range (km)
Time (min)
Single pulse, modelled
Single pulse, measured
Cumulative, modelled
Cumulative, measured


Whale depth (m)
H.speed (m/s)
a)
b)
SEL (dB re 1 μPa² s)
SEL_cum (dB re 1 μPa² s)
Source range (km)
Time (min)
Single pulse, modelled
Single pulse, measured
Cumulative, modelled
Cumulative, measured

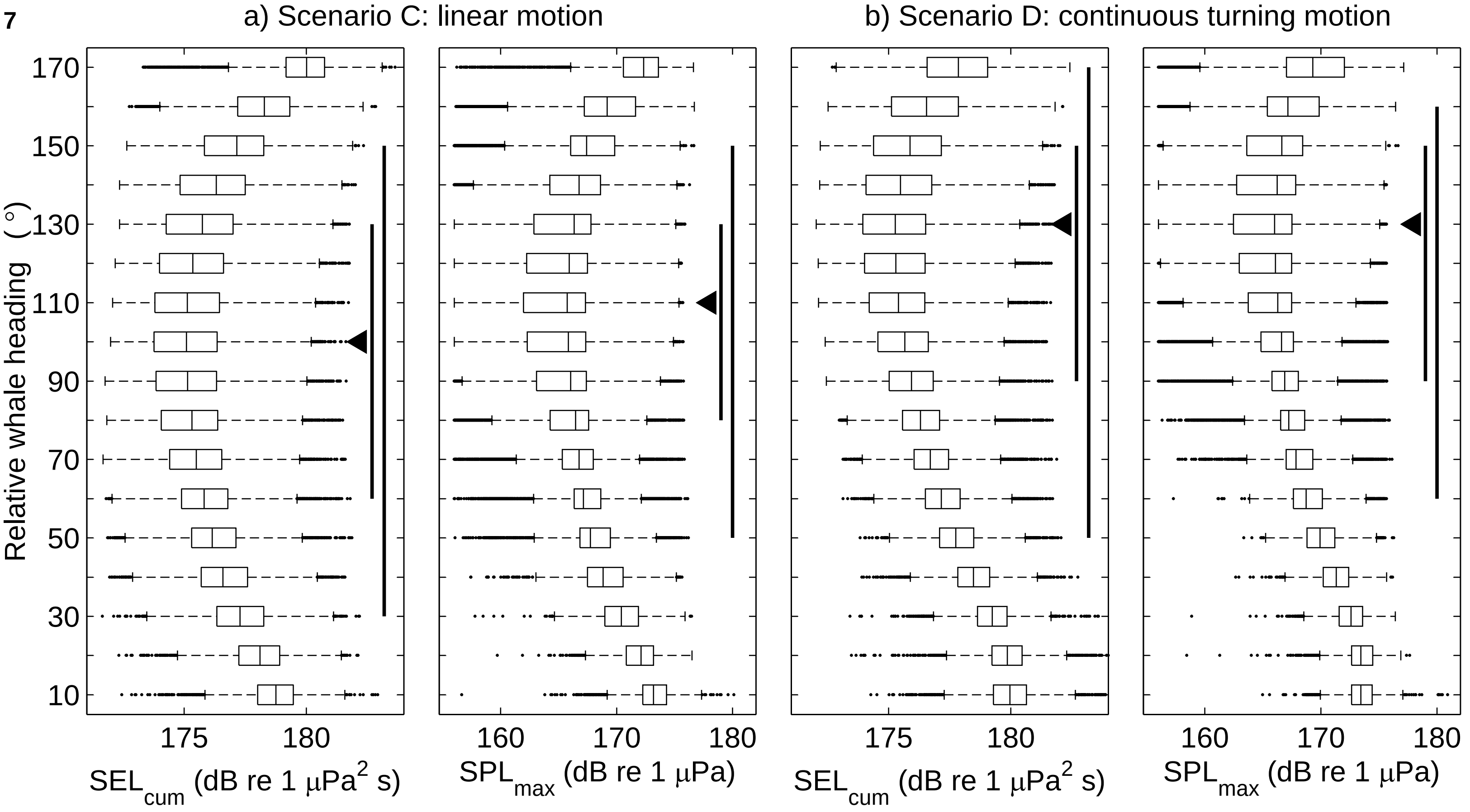


a) Scenario A: original track
Probability density
Deep
Shallow
Shallow+ss
Deep
Shallow
Shallow+ss
b) Scenario B: fixed position
Probability density
Deep
Shallow
Shallow+ss
170
175
180
185
160
165
170
175
180
SEL$_{cum}$ (dB re 1 μPa^2 s)
SPL$_{max}$ (dB re 1 μPa)



a) Scenario A: original track
b) Scenario B: fixed position
Probability density
Deep
Shallow
Shallow+ss
170
175
180
185
160
165
170
175
180
SEL$_{cum}$ (dB re 1 μPa^2 s)
SPL$_{max}$ (dB re 1 μPa)

e 7



a) Scenario C: linear motion
b) Scenario D: continuous turning motion
Relative whale heading (°)
170
150
130
110
90
70
50
30
10
175
180
160
170
180
175
180
160
170
180
SEL$_{cum}$ (dB re 1 μPa^2 s)
SPL$_{max}$ (dB re 1 μPa)
SEL$_{cum}$ (dB re 1 μPa^2 s)
SPL$_{max}$ (dB re 1 μPa)