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RESEARCH ARTICLE

Hydrodynamic detection and localization of artificial flatfish breathing currents by harbour seals (*Phoca vitulina*)

Benedikt Niesterok, Yvonne Krüger, Sven Wieskotten, Guido Dehnhardt and Wolf Hanke*

ABSTRACT

Harbour seals are known to be opportunistic feeders, whose diet consists mainly of pelagic and benthic fish, such as flatfish. As flatfish are often cryptic and do not produce noise, we hypothesized that harbour seals are able to detect and localize flatfish using their hydrodynamic sensory system (vibrissae), as fish emit water currents through their gill openings (breathing currents). To test this hypothesis, we created an experimental platform where an artificial breathing current was emitted through one of eight different openings. Three seals were trained to search for the active opening and station there for 5 s. Half of the trials were conducted with the seal blindfolded with an eye mask. In blindfolded and non-blindfolded trials, all seals performed significantly better than chance. The seals crossed the artificial breathing current (being emitted into the water column at an angle of 45 deg to the ground) from different directions. There was no difference in performance when the seals approached from in front, from behind or from the side. All seals responded to the artificial breathing currents by directly moving their snout towards the opening from which the hydrodynamic stimulus was emitted. Thus, they were also able to extract directional information from the hydrodynamic stimulus. Hydrodynamic background noise and the swimming speed of the seals were also considered in this study as these are aggravating factors that seals in the wild have to face during foraging. By creating near-natural conditions, we show that harbour seals have the ability to detect a so-far overlooked type of stimulus.

KEY WORDS: Vibrissae, Pinniped, Benthic prey, Foraging, Hydrodynamic sensory system

INTRODUCTION

Harbour seals are food generalists and feed on pelagic as well as benthic prey fish (Bowen et al., 2002; Sharples et al., 2009). A seal's diet can vary seasonally and spatially, but usually contains a high percentage of benthic fishes (Harkonen, 1987; Pierce et al., 1991; Rae, 1973; Thompson et al., 1996; Tollit and Thompson, 1996). However, foraging on benthic prey fish should be challenging for a predator as benthic fish are often cryptic. Furthermore, harbour seals also hunt during dusk or at night, when vision is limited or precluded. Another factor that affects vision is turbidity (Weiffen et al., 2006), which usually occurs in the waters of the Baltic and Northern Sea.

To date, it has not been investigated how foraging harbour seals perceive their benthic prey. One possibility, suggested by the underwater behaviour of southern sea lions (Lindt, 1956) and walruses (Fay, 1982), is active touch with the vibrissae. Active touch has been well studied in harbour seals (Dehnhardt and Kaminski, 1995; Dehnhardt et al., 1998b), but its relevance to benthic feeding is not known.

Pinnipeds also use hydrodynamic stimuli – that is, the water movements the prey generates – to capture prey. They perceive and analyse these hydrodynamic stimuli using their vibrissae (reviewed by Hanke et al., 2013). A basic type of hydrodynamic stimulus is the dipole stimulus, i.e. the water movements produced by a small sphere oscillating sinusoidally in the water. Stationary harbour seals are very sensitive to dipole stimuli (Dehnhardt et al., 1998a), which are often a good model of the hydrodynamic stimuli produced by fish (Bleckmann et al., 1991).

Hanke et al. (2000) showed that the wake of a goldfish can persist for more than 3 min, forming a hydrodynamic trail. Harbour seals can track fish-like hydrodynamic trails (Dehnhardt et al., 2001), which allows them to detect pelagic fish over extended distances. The water movements from fast-starts in fish are especially strong and remain above background noise for several minutes (Niesterok and Hanke, 2013).

Benthic fish generate hydrodynamic stimuli even when they lie on the substrate apparently motionless: they emit water through their gill openings while breathing (breathing currents). Breathing currents are within the detection range of harbour seals and are especially strong in flatfishes (Hanke et al., 2015).

Here, we tested the hypothesis that harbour seals use breathing currents to detect benthic prey. We show that harbour seals are able to detect and localize artificial breathing currents, providing evidence that harbour seals can utilize this currently overlooked type of hydrodynamic stimulus during foraging. We further show that seals can use the direction of an impinging artificial breathing current to localize the stimulus generator without additional search effort and that this also holds true under natural conditions while the seal is swimming around freely and while the seal encounters hydrodynamic background noise. This is the first study to show that harbour seals can use weak water currents, such as those produced by fish, to detect benthic prey.

MATERIALS AND METHODS

Animals

Three male harbour seals (*Phoca vitulina*, Linnaeus 1758) were used in this experiment: Luca (12 years old), Filou (8 years old) and Henry (18 years old). They were kept in a netting enclosure in the Marina Hohe Düne, Rostock, Germany, in the Baltic Sea. All three harbour seals were experienced in experiments concerning hydrodynamic detection. The experiments were carried out in accordance with the European Communities Council Directive of 24 November 1986 (86/609/EEC).

Experimental setup

An experimental platform (2 m×4 m) was suspended 1 m below the water surface. Eight nozzles were mounted on the platform in an array

Institute for Biosciences, Chair of Sensory and Cognitive Ecology, Albert-Einstein-Straße 3, Rostock 18059, Germany.

*Author for correspondence (wolf.hanke@uni-rostock.de)

W.H., 0000-0003-1682-4525

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of 1.35 m×3.30 m (Fig. 1A). Water flow (hereafter called artificial breathing current, or breathing current for short) was produced by a gear pump (Junior Puppy Drive, Jabsco, Gloucester, MA, USA) driven by a brushless electromotor (Smartmotor SV3450D-PLS, Moog Animatics, Milpitas, CA, USA) (Fig. 1A,B). One of the eight nozzles was selected to expel water by manually operating eight ball valves (Fig. 1A,C). From the valves, eight hoses led the water to eight PVC tubes which penetrated the PVC platform from underneath. Each tube ended in one of the nozzles (Fig. 1C). The nozzles were bent at an angle of 45 deg to the platform (Fig. 1C), as this approximated the angle found in real flounders emitting a breathing current (Hanke et al., 2015). A mesh-wire grid was mounted 30 cm above the platform to keep the animals at a minimum distance from the nozzles. The mouths of the nozzles were 2–3 cm beneath the grid and 135 cm crosswise and 110 cm lengthwise apart. For each nozzle, a camera (CMOS colour camera, YC260, B&S Technology GmbH, Eutin, Germany) was installed laterally at a distance of about 30 cm in a waterproof housing (Fig. 1A). These cameras were used to record the animal's behaviour and to clearly determine whether the animal had found the active nozzle and stationed correctly at that position. Additionally, a top-view camera (XC229SR, B&S Technology GmbH) positioned 3.5 m above the experimental platform was used to record the animal's swimming trajectory. This allowed the experimenter to decide whether the seals crossed the breathing current and to evaluate the swimming speed of the animals. To increase visibility, the nozzles were marked with a coloured circle on the platform (Fig. 1A). A hoop station was mounted near the edge of the platform as a starting point for the animal.

Hydrodynamic stimuli

Breathing currents were generated artificially instead of using real flounders in order to have a controlled stimulus. The rotational speed of the motor (see above) was externally controlled using the software Smart Motor Interface (Moog Animatics, version 2.4.3.7). Breathing currents were quantified using particle image velocimetry (PIV; Westerweel, 1997).

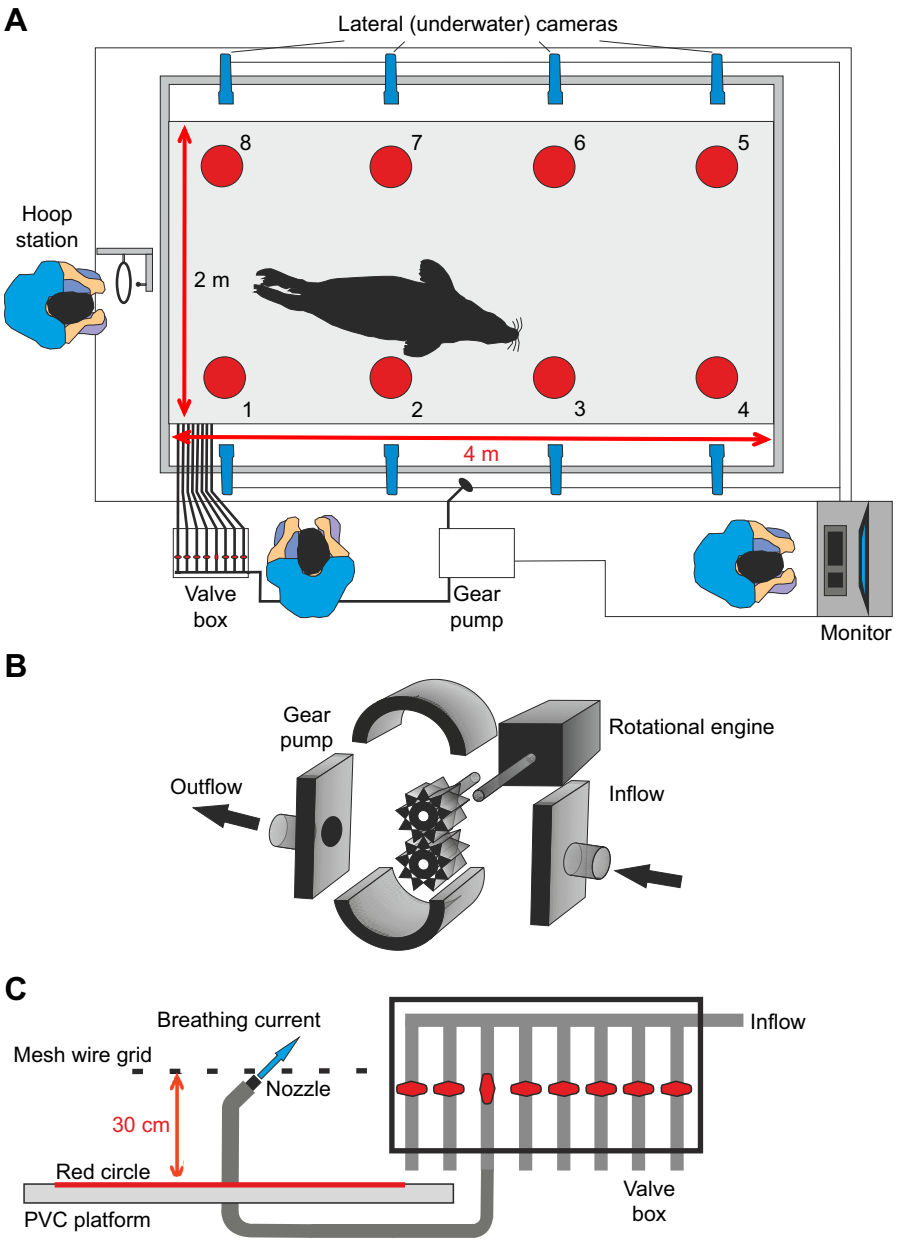

Fig. 1. Experimental setup. (A) Top view. Experimental platform (2 m×4 m) with eight nozzles (within red circles, numbered 1–8). Lateral (underwater) cameras were mounted next to each nozzle. Nozzles, and hence breathing currents, were oriented at a 45 deg angle to the platform, pointing to the right in A (see C). The trainer remained near the hoop station. The experimenter controlled the stimulus and monitored the animal's response. The experimenter (or an assistant) operated the ball valves. (B) Expanded view of the gear pump and the rotational brushless motor. The motor controller was integrated in the motor housing. (C) Box with valves leading the water from the gear pump to each nozzle via hoses (only one nozzle is given here as an example). The nozzle is shown in lateral view with the PVC platform and the mesh wire grid. The nozzle is oriented at a 45 deg angle to the platform.

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Animal training

The three harbour seals were trained to start from the hoop station, dive over the platform and station at the active nozzle, i.e. to put their snout at the mesh grid at the position of the nozzle for at least 5 s. Correct stationing was reinforced with a short whistle (acoustic bridging stimulus) followed by a food reward. Initially, the experimental animal did not wear an eye mask, and a ball target (10 cm sphere mounted on a hand-held pole) was used to indicate the position of the active nozzle. The active nozzle emitted a breathing current at least twice as strong (in terms of flow velocity) as during data acquisition. Training started with the active nozzle to the right of the animal (nozzle 1) in order to initiate a counter-clockwise swimming pattern over the experimental area. The counter-clockwise swimming pattern was introduced to improve comparability between the animals with regard to swimming direction, and to increase the probability of the animal encountering all of the nozzles. Within 1 week, an eye mask was introduced, which the animal had to wear during the task to preclude vision. In the initial training with eye masks, the position of the active nozzle was indicated acoustically by tapping the mesh grid at that position with a metal rod. All animals learned to find the active nozzle and to station at it without acoustic cues within 3–5 training sessions (72–120 trials).

Subsequently the flow velocity of the breathing current was gradually reduced between sessions, with occasional exceptions to maintain motivation, until the testing stimulus was reached (gear pump operated at 50 rpm). Testing started after the animal had positively detected this stimulus in 75% of the trials within one session with 24 trials (12 blindfolded, 12 non-blindfolded).

Experimental procedure

General

In general, one session per day was run 5 days per week. A session consisted of 24 trials, and the animal was blindfolded with an eye mask in 12 of these. In a few cases, the number of trials in a session was reduced because of a lack of cooperation from the animal; missing trials were then performed in subsequent sessions. The sequence of nozzles and blindfolded/non-blindfolded trials was changed pseudorandomly.

Experiments were run by an animal trainer, who handled the animal, and an experimenter, who selected the active nozzle, operated the cameras and decided whether the animal's response was correct or not (double-blind experiment). In some cases, an assistant supported the experimenter by operating the ball valves. Before each trial, the experimenter opened the valve for one nozzle while the seal was waiting in the hoop station next to the trainer. Then the trainer blindfolded the animal in the case of a blindfolded trial. The experimenter switched on the pump and, after a short whistle (start signal) from the trainer, the animal started to dive. Once the animal found the site of the active nozzle, it had to station there for 5 s to give a clear behavioural response. The experimenter watched the seal via the lateral and top cameras and signalled to the trainer by hand whether the animal's response was correct. Correct responses were defined as the seal's snout or vibrissae being positioned above the active nozzle. If the animal was correct, the trainer gave a longer whistle tone as a secondary reinforcer, and the animal returned to the trainer and was rewarded with fish. In the case of a wrong decision or if the animal surfaced without success, it was called back and received no fish.

Constant breathing currents

Data were collected from all three harbour seals during the first part of the study (constant breathing currents). Filou and Luca each performed 54 trials per nozzle, 27 of these while blindfolded (total: 432 trials in 18 sessions per seal). A total of 560 trials were conducted with Henry (70 trials per nozzle, 24 sessions).

Pulsed breathing currents

During the second part of the study, pulsed breathing currents were applied. Two harbour seals (Luca and Henry) were used. Each seal performed 54 trials per nozzle, 27 of these while blindfolded (total: 432 trials in 18 sessions per seal).

Measuring hydrodynamic background noise

After daily sessions, background flow velocities were measured using a custom-made PIV device (Fig. 2). A horizontal light sheet was produced by a battery-operated 1 W laser (Spartan Series SBW1W, Dragon Lasers, Changchun, China) in combination with a cylindrical lens. A GoPro Hero 3 (black edition) camera (GoPro Inc., San Mateo, CA, USA) running at 50 frames s^{-1} with a resolution of 1920×1080 pixels recorded the horizontal light sheet from above at a distance of 30 cm. The camera was placed in a waterproof housing (GoPro Inc.) and equipped with a bandpass blue light filter (450±2 nm centre frequency, 10±2 nm full width at half maximum, FWHM; FB450-10, ThorLabs, Newton, NJ, USA). The blue light filter reduced background light and enabled operation of the device using naturally occurring floating particles even under bright daylight conditions. All measurements were made using naturally occurring particles, as initial experiments where tracing particles were seeded into the water were affected by artificial disturbances. Flow velocity vectors were calculated using the PIV software DaVis 7.2 (LaVision GmbH, Göttingen, Germany). Three sequences (each with 100 frames) with

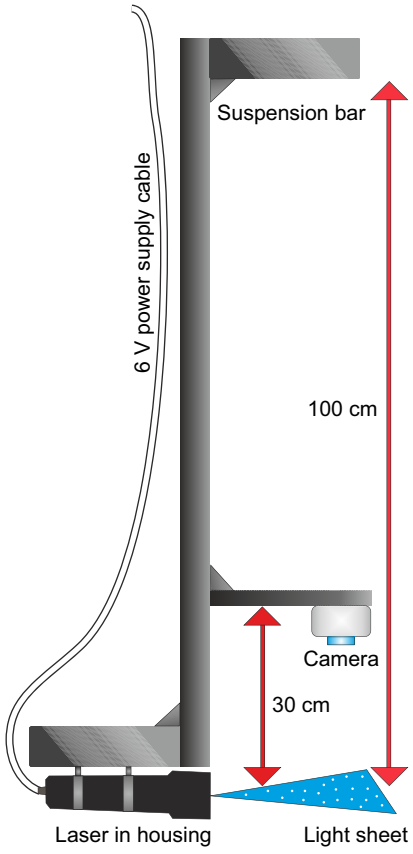

Fig. 2. Particle image velocimetry (PIV) device for measuring the background water flow in the experimental area. An underwater camera filmed naturally occurring particles in a light sheet produced by a 1 W laser.

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good particle density were chosen for evaluation. The mean magnitude of the three highest velocity vectors from each frame was plotted over time. The maximum of each time plot was used to calculate the mean of the three sequences. Recordings with too little particle density were not evaluated, to avoid calculation errors.

Control measurements/experiments

Acoustic cues that might have been generated by an active nozzle were checked by recording sound with a hydrophone (Brüel & Kjær 8103) behind, right in front of, and 1 m away from a nozzle. Additionally, a human observer listened to the underwater sound using a stethoscope.

Behavioural control experiments were performed by covering the eyes and vibrissae with a stocking mask. For each nozzle and each animal, two trials were performed mixed with some non-blindfolded trials to keep the animal motivated. The two trials for each nozzle were performed in two different sessions.

Data evaluation

Statistics were run in R (R Development Core Team 2008) and Matlab (MATLAB and Statistics Toolbox Release 2012b, The MathWorks, Inc., Natick, MA, USA).

Detection rates

Detection rates were calculated for each animal and experimental condition (blindfolded, non-blindfolded, constant breathing current, pulsed breathing current). Because our animals had a minimum of eight different response locations, we assumed (as a very conservative criterion) that the animals had a 0.125 (one out of eight) probability of detecting the correct nozzle by chance. This probability was used to calculate the significance of detection rates using a cumulative binomial distribution. The actual probability of detection by chance was even lower, as the animal was moving freely and was not confined to the eight response locations.

Hydrodynamic background noise

A linear regression model in R was used to correlate background noise data with detection rates of the animals. As detection rates for a specific day could be based on fewer than 24 trials in a small number of cases, the regression model was weighted. The significance of the regression model was tested using *F*-statistics.

Swimming speed

For each animal and stimulus type (constant or pulsed breathing current), swimming speed was measured in three sessions (15 sessions altogether). Recordings taken by the top-view camera were evaluated in the tracking software Tracker (version 4.91, Open Source Physics). The position of the animal was marked 0.5 s before and at the moment of detection of the stimulus. The moment of detection was defined as the first frame in which the animal showed a head movement towards the origin of the stimulus. The time interval of 0.5 s was sufficient to distinguish between the two positions clearly and set the markings accurately. The sessions used for evaluation were chosen because of their good light conditions and visibility. The middle of the animal's head was used to mark its position. Only successful trials were considered for evaluation. Swimming speeds were analysed using a two-sided *t*-test.

Head movements during localization

Using the recordings from the lateral cameras, we classified three different head movements in response to the breathing current. They consisted of rapid yaw and pitch rotations of the head.

The first class of movement was primarily a pitch rotation and a yaw rotation not exceeding an angle of 90 deg ('straight-down' response). The second class of movement was a pitch rotation and a yaw rotation of more than 90 deg ('U-turn' response). If the animal did not meet the position of the nozzle with its snout or vibrissae after the initial head movement and subsequently corrected the head position, this was classified as a 'correction' response, the third type of movement.

Only the blindfolded trials were considered for this classification to exclude the possibility of orienting visually towards the nozzle. Forty-four out of 756 blindfolded trials (5.8%) could not be analysed as a result of the failure of the corresponding lateral camera.

RESULTS

Characterization of hydrodynamic stimuli

Flow velocities of the artificial breathing currents (Fig. 3A) were measured using PIV and were matched to flow measurements (also using PIV) of breathing currents in real flounders (Fig. 3B) from a previous study (Hanke et al., 2015). During the first part of the study, constant breathing currents were generated using a constant rotational speed of the gear pump (50 rpm) (Fig. 3C). During the second part of the study, pulsed artificial breathing currents that simulated even more realistic flatfish breathing patterns were generated, using the same rotational speed of the gear pump (50 rpm) with rotations of 90 deg repeated at 0.7 Hz (Fig. 3D). The breathing currents contained maximal flow velocities of 20–25 cm s^{-1} and reached a spatial extension of 1–3 cm at the level of the harbour seal's vibrissae.

Detection of artificial breathing currents

General

All harbour seals performed a counter-clockwise swimming pattern along the edge of the platform, staying in contact with the grid using some of their longest vibrissae. This applied to the non-blindfolded trials as well as to the blindfolded trials. Fig. 4 shows an example of a harbour seal detecting the active nozzle and responding by stationing, as viewed by the lateral camera. For examples of top and lateral camera views, see Movies 1 and 2.

Constant breathing currents

The overall detection rate of the active nozzle for all three harbour seals is shown in Fig. 5A; the data are from all trials including those where the seal did not cross the active nozzle during its search. In non-blindfolded trials, Filou crossed the active nozzle in 194 out of 216 trials, Henry crossed the active nozzle in 275 out of 280 trials, and Luca crossed the active nozzle in 208 out of 216 trials. In blindfolded trials, Filou crossed the active nozzle in 161 out of 216 trials, Henry crossed the active nozzle in 224 out of 280 trials, and Luca crossed the active nozzle in 193 out of 216 trials. The overall detection rates for all three animals under blindfolded and non-blindfolded conditions were highly significant (cumulative binomial distribution, $P \ll 0.1\%$). In both conditions (blindfolded/non-blindfolded), seal Luca had the highest success rate, followed by Henry and Filou.

Because all animals followed the counter-clockwise swimming path and all nozzles pointed in the same direction (to the right in Fig. 1A), the animals crossed breathing currents from different directions. At nozzle 1, the direction of the breathing current was approximately the same as the swimming direction in most cases, but it could impinge more from the right; at nozzles 2–4, swimming direction was approximately the same as the direction of the

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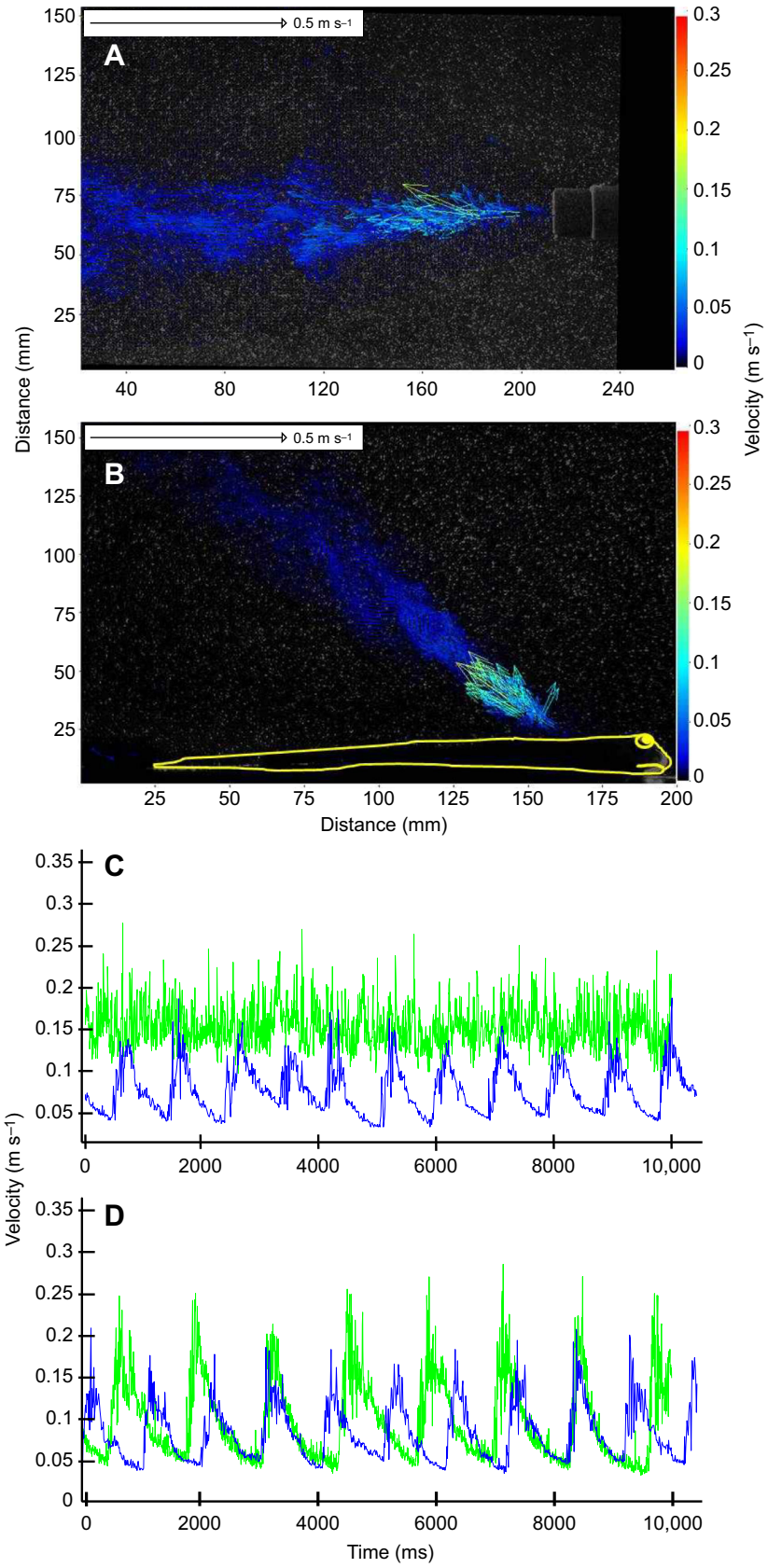

Fig. 3. Comparison of artificial and natural breathing currents. (A) Vector graphic representing the flow field of the artificial breathing current. (B) Vector graphic representing the flow field of a breathing current produced by a real flounder (marked by the yellow outline). Flow velocities are colour coded on the same scale in A and B. (C) Time course of maxima of flow velocities in the constant artificial breathing current (green) and the natural breathing current of a flounder (blue). (D) Time course of maxima of flow velocities in the pulsed artificial breathing current (green) together with the natural breathing current of a flounder (blue).

breathing current; at nozzle 5, the breathing current impinged from the left; at nozzles 6–8, swimming direction was opposed to the direction of the breathing current. To determine whether crossing the artificial breathing currents from different directions affected the detection rate, we evaluated the detection rate for each nozzle for the blindfolded trials (Fig. 5B).

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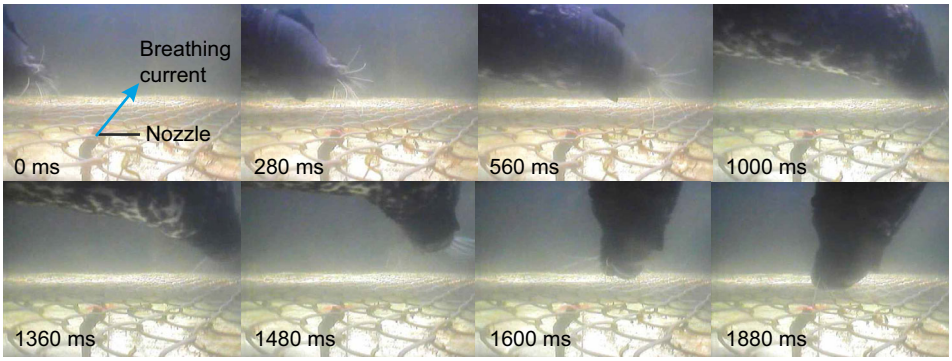

Fig. 4. Time sequence of a U-turn. Time is given in each panel. A harbour seal wearing an eye mask encounters a breathing current (indicated by the light blue arrow) that is directed in its swimming direction. The seal overshoots the position of the nozzle. At 1360 ms, the seal initiates a directed U-turn towards the nozzle. Then it positions itself accurately within half a second.

The detection rates for each nozzle were, with one exception, highly significant (cumulative binomial distribution, $P \ll 0.1\%$) and were usually between 48% and 100%. The animals showed no clear preference for any of the breathing current directions. The ranking of the animals in terms of performance was not constant across nozzles. In one case (Filou, blindfolded, nozzle 5), performance was not significant. However, nozzle 5 was not crossed by Filou in 21 out of 27 trials.

Fig. 5C,D shows the same performance data when only the trials where the animal crossed the position of the active nozzle are included. The performance of all seals is higher in this depiction, as all seals, regardless of whether they were blindfolded, performed some trials where they did not cross the active nozzle (included in Fig. 5A,B, but not in Fig. 5C,D). This effect was strongest in Filou. In most cases, the ranking between seals with regard to detection rates remained the same. Detection rates were again highly significant in all except one case (Filou, blindfolded, nozzle 5, which comprised only 6 trials).

Pulsed breathing currents

The panels shown in Fig. 6 for the overall detection rate (Fig. 6A,C) and the detection rate for each nozzle (Fig. 6B,D) for pulsed breathing currents are arranged in the same way as the panels for the constant breathing currents in Fig. 5. In non-blindfolded trials, Henry crossed the active nozzle in 211 out of 216 trials and Luca crossed it in all 216 trials. In blindfolded trials, Henry crossed the active nozzle in 198 out of 216 trials and Luca crossed it in 203 out of 224 trials. For both seals, the overall detection rate ($P<2\times10^{-6}$) and the detection rate for each nozzle ($P \ll 0.001$) are highly significant. For Luca, the detection rates for pulsed breathing currents even exceeded detection rates for constant breathing currents. Data for all trials (Fig. 6A,B) and for only the trials where the position of the active nozzles was crossed (Fig. 6C,D) show the same general pattern: detection rates for Luca were higher than those for Henry with the exception of nozzle 6 (blindfolded). In the non-blindfolded trials (Fig. 6A,C, left), Luca achieved 100% detection rate. This was due to a shift in strategy in this experimental phase: when not blindfolded, Luca, by contrast with Henry, started to wait at individual nozzles for the breathing current pulse to occur.

Control measurements/experiments

Acoustic control measurements with the hydrophone or by listening with the stethoscope did not reveal any differences between an active and inactive nozzle at any of the measuring points.

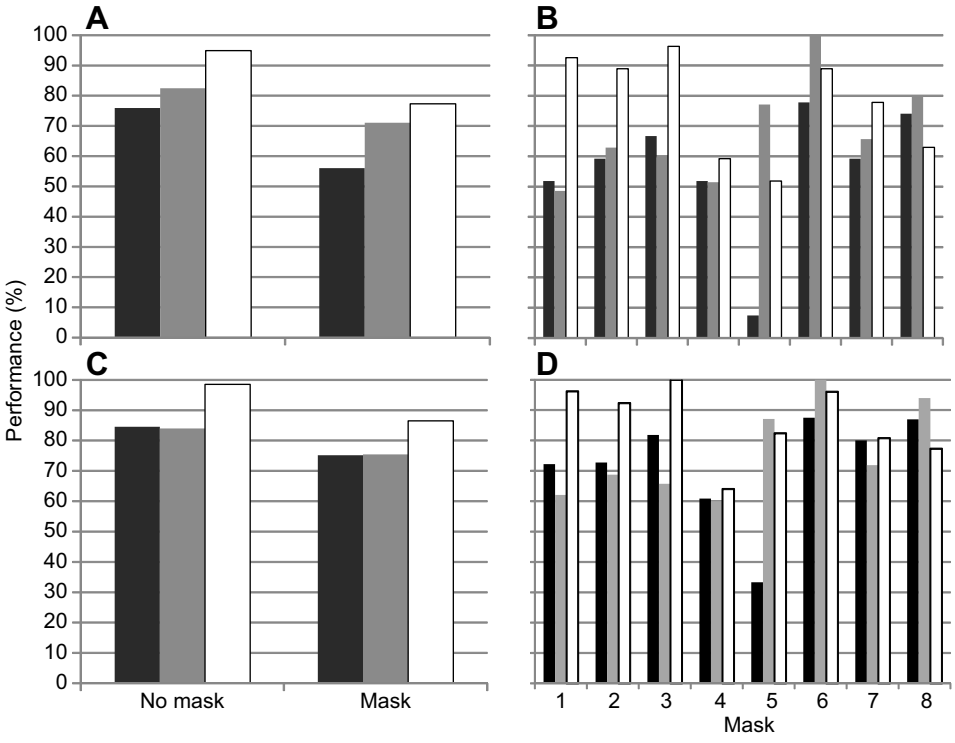

Fig. 5. Detection rates for constant breathing currents. Overall performance (all nozzles pooled; A,C) and performance distinguished by the active nozzle (nozzles 1–8; B,D) are given as percentages of all trials (A,B) or percentages of only those trials where the seal's vibrissae crossed the breathing current (C,D). A and C represent detection rates for both experimental conditions: blindfolded (with eye mask) and non-blindfolded (without eye mask), whereas B and D represent only blindfolded trials for a better overview. Black bars represent detection rates of seal Filou, grey bars represent detection rates of seal Henry and white bars represent detection rates of seal Luca. All detection rates except for Filou at nozzle 5 are highly significant.

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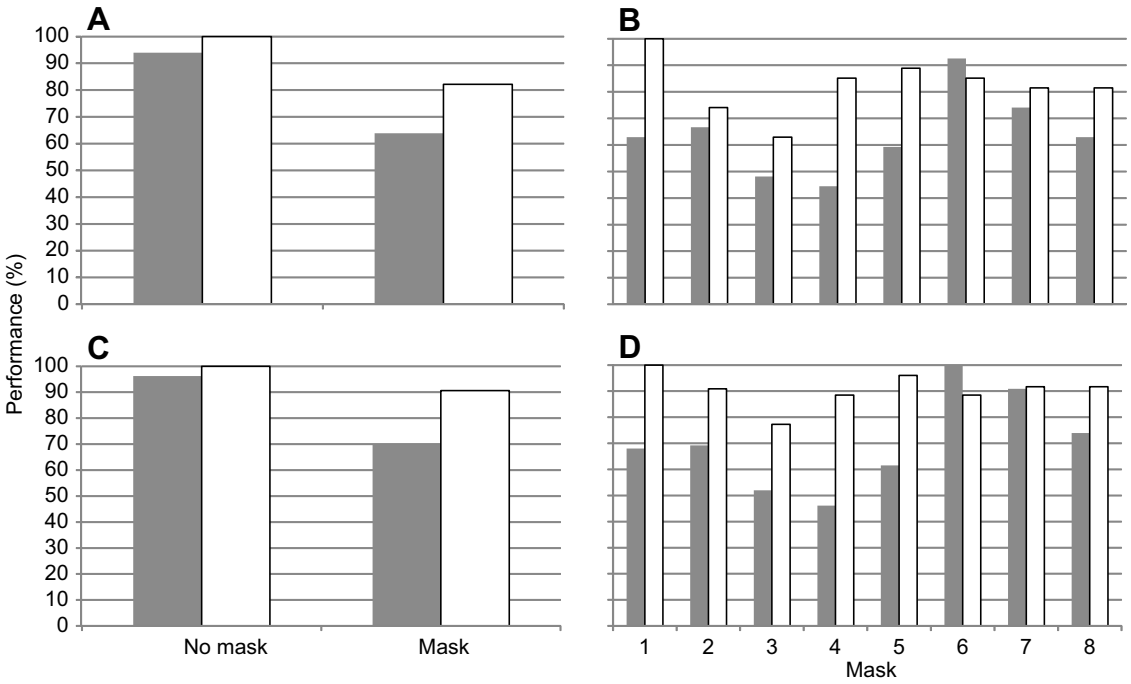

Fig. 6. Detection rates for pulsed breathing currents. Arrangement of panels is as in Fig. 5. Only two harbour seals were used in this part of the study: grey bars represent detection rates for seal Henry, white bars represent those for seal Luca. All detection rates are highly significant.

During the control sessions with eyes and vibrissae covered, the animals did not find any of the active nozzles. In most cases, they drifted on the water surface, refusing to search for the breathing current. When attempting to search, they never found an active nozzle.

Influence of hydrodynamic background noise

Background noise was in the range of 0.5 to 7.2 cm s^{-1} (mean of three video sequences of 100 frames each). On a windy day, the maximum flow velocity found in one sequence reached up to 8.3 cm s^{-1}. Seal performance tended to decrease with increased background noise in constant breathing current trials (Fig. 7A–C). However, we found a significant relationship between background noise and performance of the animal in only one case (Luca, P=0.025; Fig. 7C). By contrast, seal performance for pulsed breathing currents considering background noise revealed no such tendency (Fig. 7D,E); however, in the experiments with pulsed breathing currents, maximum background flow did not reach more than 4.5 cm s^{-1}.

Swimming speed

Fig. 8 shows swimming speed for all seals in successful trials with constant and pulsed breathing currents in blindfolded and non-blindfolded trials. The swimming speeds in successful trials were normally distributed (Shapiro test; P>0.05), except for non-blindfolded trials with Henry when constant breathing currents were presented (Shapiro test; P<0.05; Fig. 8B, grey bars). The median swimming speeds of all seals are given in Table 1.

Swimming speeds where the breathing current was detected ranged from 40 to 130 cm s^{-1} for Filou, from 20 to 100 cm s^{-1} for Henry, and from 20 to 70 cm s^{-1} for Luca for constant breathing currents (Fig. 8A–C). For pulsed breathing currents, the swimming speed ranged from 10 to 80 cm s^{-1} for Henry or from 20 to 70 cm s^{-1} for Luca (Fig. 8D,E). Only Filou chose to swim at speeds above 130 cm s^{-1} in four trials (constant breathing currents, unsuccessful). Swimming speeds with pulsed breathing currents were significantly lower (t-test) than those with constant breathing currents for Henry in blindfolded (P=4.3×10^{-6}) and non-blindfolded trials (P=1.5×10^{-5}) as well as for Luca in non-blindfolded trials (P=0.020), but not significantly lower for Luca in blindfolded trials (t-test; P=0.089). However, in the last case, the P-value exceeded the level of significance only by 4%.

Trials in which Filou's swimming speed was above 110 cm s^{-1} were only successful when he was not blindfolded. In these cases, he briefly reduced the forward speed of the vibrissal array at the nozzles by retracting his head (Movie 3).

The seals swam significantly slower when blindfolded (t-test/Wilcoxon–Whitney U-test; P<0.05) except Luca with pulsed breathing currents. Luca's non-blindfolded swimming speeds were only slightly higher than his blindfolded swimming speeds with both constant (Fig. 8C) and pulsed breathing currents (Fig. 8E). With pulsed breathing currents, his non-blindfolded swimming speeds were so low that the difference to blindfolded swimming speeds became insignificant (Fig. 8E; t-test, P=0.2023).

Head movements during localization

Constant breathing currents

The harbour seals were able to accurately localize the origin of the constant breathing currents. All animals mainly performed U-turns and straight-down head movements (Fig. 9A–C). These head movements strongly depended on the flow direction: seals performed mostly U-turns for nozzles 2–4, and mostly straight-down head movements for nozzles 6–8 (Fisher's exact test; $P \ll 0.001$ for each individual animal). When approaching the breathing currents from the side (nozzles 1 and 5), both straight-down and U-turn head movements were observed (Fig. 9A–C). For examples of head movements, see Movie 2.

The proportion of head movements defined as correction was low (Filou 4.7%, Henry 7.7%, Luca 4.3%). We hypothesized corrections to occur more often for nozzles 2–4 (preference for U-turns) than for nozzles 6–8 (preference for straight-down

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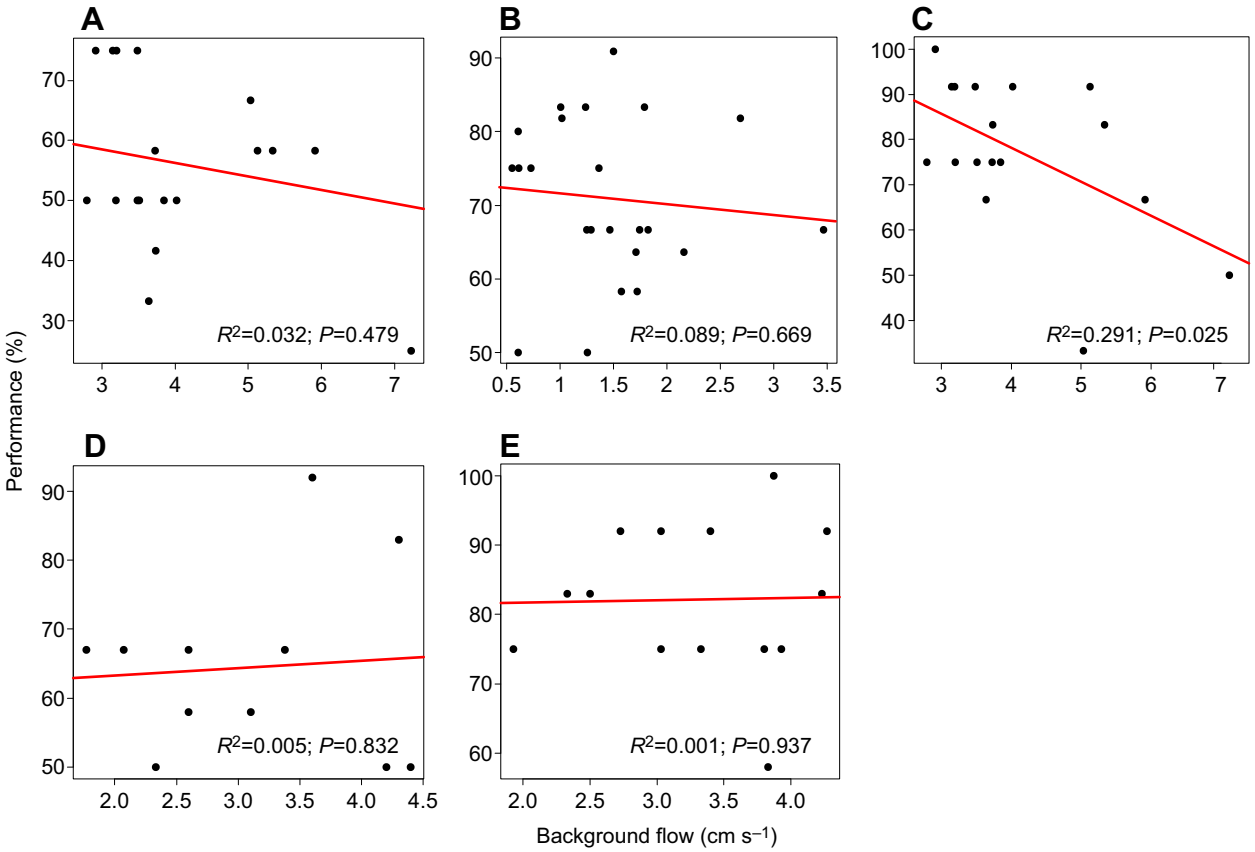

Fig. 7. Correlation between detection rates (performance) and hydrodynamic background noise (flow velocity). Upper row: experiments with constant artificial breathing currents; (A) Filou, (B) Henry, (C) Luca. Lower row: experiments with pulsed artificial breathing currents; (D) Henry, (E) Luca. Red lines show the linear regression in each panel. A–C show a tendency of decreasing performance with increasing background flow (significant only in C).

movements), because U-turns involve larger head movements. For constant breathing current trials with Henry, significantly more corrections for nozzles 2–4 than for nozzles 6–8 were found (Fig. 9B) (one-sided Fisher's exact test; P<0.0001). For seals Filou and Luca (Fig. 9A,C), this correlation was not found (one-sided Fisher's exact test; Filou: P=0.125; Luca: P=0.950).

Pulsed breathing currents

While Henry (Fig. 9D) performed straight-down as well as U-turn head movements for nozzles 2–4, he performed only straight-down head movements for nozzles 6–8. These differences between nozzles 2–4 and 6–8 were significant (Fisher's exact test; P=2×10^{-9}). For Luca (Fig. 9E), this pattern (nozzles 2–4: U-turn

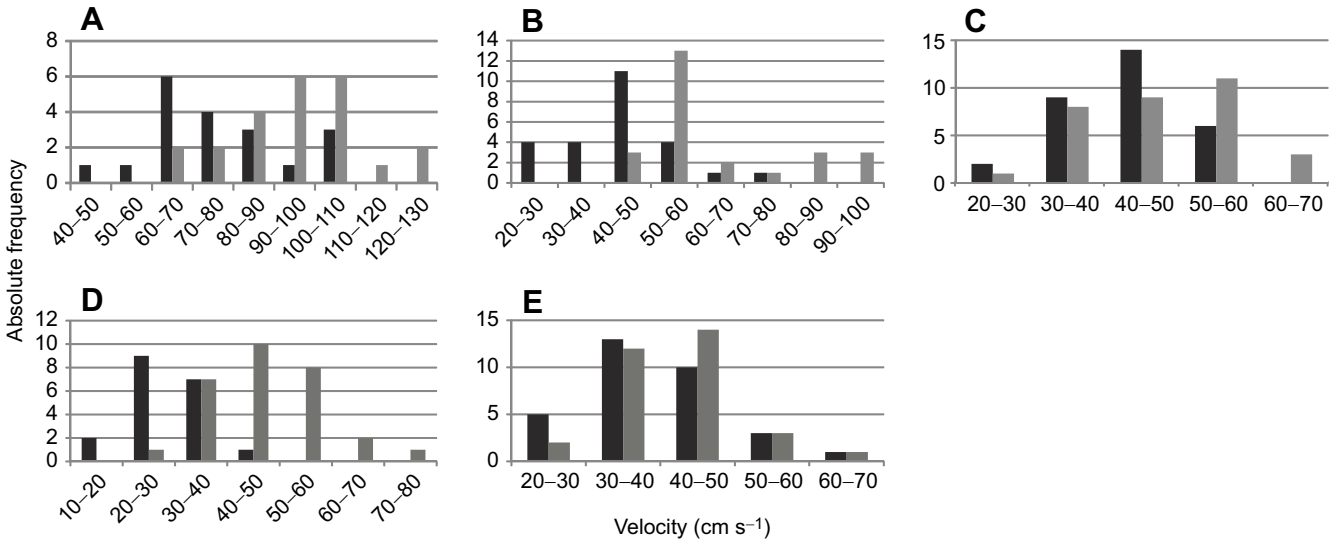

Fig. 8. Frequency distribution of swimming velocities during detection of artificial breathing currents. Upper row: experiments with constant artificial breathing currents; (A) Filou, (B) Henry, (C) Luca. Lower row: experiments with pulsed artificial breathing currents; (D) Henry, (E) Luca. Black bars represent swimming velocities when seals were blindfolded, grey bars represent swimming velocities when seals were not blindfolded. Each panel is based on three typical sessions.

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Table 1. Median swimming speeds of the different seals when successfully detecting a constant or a pulsed breathing current, for blindfolded and non-blindfolded trials

	Constant (cm s^{-1})		Pulsed (cm s^{-1})	
	Non-blindfolded	Blindfolded	Non-blindfolded	Blindfolded
Filou	95.9	77		
Henry	58.6	43.8	48	29.8
Luca	47.5	44.1	41.4	38.9

Each value is based on three representative experimental sessions.

head movements only, nozzles 6–8: straight-down head movements only) was fulfilled without exceptions and was therefore highly significant (Fisher's exact test; $P=2\times10^{-16}$). With pulsed breathing currents, the proportion of corrections increased slightly to 8.2% for Henry (Fig. 9D). For Luca (Fig. 9E), it increased more considerably to 16.8%. Both seals performed more corrections for nozzles 2–4 than for nozzles 6–8 (Fig. 9D,E) (one-sided Fisher's exact test; Henry: $P=0.042$; Luca: $P=0.001$).

DISCUSSION

Benthic prey detection by pinnipeds

Pinnipeds have so far been assumed to use vision or direct touch by means of the vibrissal system for benthic prey detection. For example, Lindt (1956) observed southern sea lions (*Otaria byronia*) searching in the benthos (not providing details of vibrissal use). Laboratory studies on sea lions (Dehnhardt and Dücker, 1996) and harbour seals (Dehnhardt and Kaminski, 1995) have shown tactile discrimination abilities similar to those of the human hand and suggest that pinniped vibrissae are used for direct touch in the wild. Fay (1982) describes the function of vibrissae as tactile organs in walruses (*Odobena rosmarus*) for exploring the sea bottom for benthic organisms. Hawaiian monk seals (*Monachus schauinslandi*) consume mainly benthic prey (Cahoon et al., 2013). Recordings from animal-borne cameras document feeding on cryptic, benthic prey; in a feeding ground with sandy substrate, 70% of the numerical prey abundance (assessed with bottom trawls) were flounders (*Bothidae*) (Parrish et al., 2005). The present study shows for the first time that harbour seals detect benthic hydrodynamic stimuli, namely breathing currents such as those produced by flatfish, with their vibrissae. Therefore, breathing currents are an additional source of sensory information. They are generally produced by benthic prey fish and should consequently be universally used by harbour seals, and probably other pinnipeds as well.

Additional experiments that we propose would include having a harbour seal search for a live versus a dead flounder. However, chemosensory cues might be given by a real flounder that were absent in the present study as it focused on pure hydrodynamic detection.

Detection rates

Constant breathing currents

For all three harbour seals, the detection rate was highly significant for both blindfolded and non-blindfolded trials. Detection rates were significant even when including the rare trials where the seals did not encounter the nozzles.

Any differences in the detection rates between nozzles were not consistent between individual seals. Altogether, detection rates were highly significant for all nozzle positions and seals except for one position and seal, namely Filou at nozzle 5. Filou crossed this nozzle, which was situated in a corner position, only marginally most times, so only a few (estimated three to four) vibrissae could be stimulated. This was also observed in the other two seals in some trials. However, Filou swam at the highest speed on average and also at this nozzle. A combination of these two aspects – fewer vibrissae in contact with the breathing current and higher swimming speed – might be the reason for Filou's poor detection rate at this nozzle.

The data for constant breathing currents show that harbour seals would be able to localize a flatfish by its breathing current with high accuracy at least if they encounter the current in a favourable phase of the respiration cycle; however, we decided to repeat the experiments with pulsed breathing currents to mimic a live fish even more closely.

Pulsed breathing currents

Detection rates for pulsed breathing currents were also highly significant for all nozzles for the two participating animals. Luca performed even better for both conditions (blindfolded and not

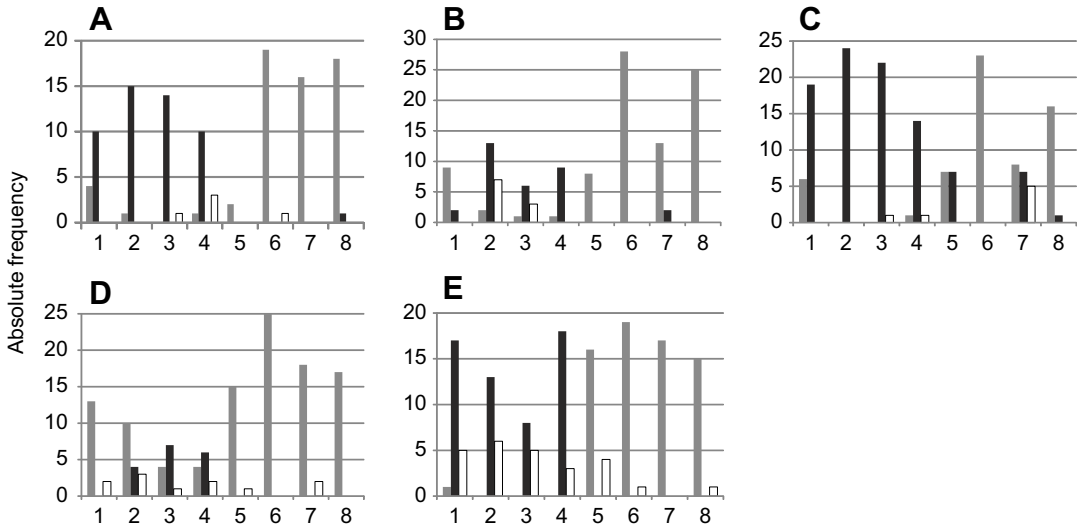

Fig. 9. Frequency of different head movements. Black bars represent straight-down head movements, grey bars represent U-turns and white bars represent head movements involving correction. Upper row: constant breathing currents; (A) Filou, (B) Henry, (C) Luca. Lower row: pulsed breathing currents; (D) Henry, (E) Luca. Head movements in each panel are given for nozzles 1–8.

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blindfolded) than for the constant breathing currents (Fig. 6A,C). This increase in detection rate is probably due to learning. Luca's rate of missed nozzles clearly decreased after 6 sessions after testing conditions had been reached (each session consisting of 24 trials). He tended to wait at the position of a nozzle that he perceived visually in non-blindfolded trials or guessed in blindfolded trials, thereby increasing the probability of encountering a water pulse. This behaviour does not seem to correspond to real prey capture behaviour in the wild. Henry, by contrast, did not change his search behaviour by waiting at promising positions, but showed the same general strategy as with constant breathing currents, which is probably more representative of natural search behaviour in the wild. His performance decreased when pulsed breathing currents were used and he was wearing a mask. When not visually restricted, his performance increased, albeit less than Luca's (Figs 5A and 6A); this may be related to his reduced swimming speed.

Altogether, from our data for pulsed breathing currents, we can conclude that a seal in the wild would be able to accurately detect a flatfish by the use of its breathing current, no matter from which direction the seal approaches the fish.

Role of hydrodynamic detection versus hearing

Measurements with a hydrophone showed no indication of acoustic cues being emitted from the active nozzle; however, acoustic cues below the self-noise of the hydrophone and still within the hearing range of the seal could not be excluded. Therefore, we listened to underwater noise near the nozzles with a stethoscope, in our experience a more sensitive device than the hydrophone; again, there was no indication of acoustic cues. The animals' behaviour in itself constitutes the strongest reason to believe that exclusively hydrodynamic and not acoustic detection was utilized in this study: during training with acoustic cues at the active nozzle, the animals took a shortcut to the correct position. By contrast, during test trials, the animal followed its usual search pattern and only after crossing the position of the active nozzle with its vibrissae did the animal show a behavioural response.

Hydrodynamic background noise

Furthermore, this study shows that harbour seals have the ability to detect breathing currents even when hydrodynamic background noise is present. As no significant correlation between detection rate and background noise was found in most cases (Fig. 7), we conclude that the level of background noise that could affect a seal's hydrodynamic sensory system was not reached during the experiments. Even the highest background noise level measured (7.2 cm s^{-1}) did not result in a complete failure of the seal to fulfil the task, but rather a reduction of the seal's detection rate. Therefore, this noise level may approximately mark the point where background noise starts to affect the seal's performance. Noise level was a quarter to a half of the strength (in terms of flow velocity) of the presented hydrodynamic stimulus. Other types of hydrodynamic background noise that were not measured in this study, but which were still present, were water movements caused by fish that had entered the netting enclosure and the water disturbance from the seal's own swimming movements (fin strokes, head turns). The fish we observed in the experimental area were three-spined sticklebacks and two-spotted gobies a few centimetres in body length. Fish of this size can produce flow velocities of up to 6 cm s^{-1} when performing successive tail strokes (Bleckmann et al., 1991). On at least two occasions, a seal was observed to be distracted by a fish. In addition, harbour seals themselves can generate flow velocities exceeding 20 cm s^{-1} during the first 5 s after the seal has passed by, and at least 3 cm s^{-1} after 30 s (Schulte-Pelkum et al., 2007). Hence, the actual background noise that the seals encountered in some trials may have been even higher. It would be worthwhile to further investigate at what hydrodynamic background noise levels the actual hydrodynamic stimulus can still be detected, i.e. the change of detection rate with decreasing signal-to-noise ratio.

Swimming speed

The male harbour seals that were investigated in the wild in the study of Bowen et al. (2002) had an estimated average speed of 1.9± 0.1 m s^{-1} during their foraging trips. This swimming speed is higher than that in our study, but still of the same order of magnitude. One difference between these two studies is that the seals in our study were tested in a confined space and were not required to cover large distances. In our blindfolded trials, vision was completely absent, whereas in the wild it may be completely absent, merely limited or, as in Bowen et al.'s (2002) study, fairly favourable. In the present study, the blindfolded seals decreased their swimming speed further compared with that when not blindfolded. The estimated swimming speed value from Bowen et al. (2002) does not specifically refer to benthic feeding, where speed may have been significantly reduced. We conclude from our experiments that swimming speeds of more than 1 m s^{-1} (Fig. 8A) still allow seals to detect breathing currents, but lower swimming speeds are preferred and can be considered more representative of benthic feeding in the wild.

Statistical analysis indicates that swimming speeds of seals are slower when searching for pulsed than for constant breathing currents, with one caveat: experiments with constant versus pulsed breathing currents were grouped in time, as for technical reasons all experiments with pulsed breathing currents were performed in a later experimental phase. This limits statistical independence if swimming speeds should have shifted over time as a result of an unknown factor not related to the question of pulsed versus constant breathing currents. However, we worked intensely with the animals outside of the experiments described here, and observed no general shift in behaviour. Learning during the course of experiments, as discussed above, could be a factor that shifts swimming speed over time; however, it seems more plausible that increasing experience with the experiment would enhance, rather than reduce, swimming speed, contrary to the present findings.

Localization of breathing currents

This study shows that harbour seals can detect the direction of an artificial breathing current, as they usually moved their snouts accurately to the origin of the stimulus with a straight-down or a U-turn movement (Fig. 9). The seals rarely required corrective movements to accurately station over the nozzle opening. These corrections occurred more frequently when crossing nozzles 2–4 (swimming along with the emitted breathing current) than when crossing nozzles 6–8. This may be explained by the larger movement they performed to reach the nozzle when using a U-turn and does not necessarily mean that directional resolution is different for different flow directions.

Harbour seals are able to obtain directional information from a hydrodynamic stimulus that has been generated by a fin-like paddle drawn through the water (Wieskotten et al., 2010). The hydrodynamic trail caused by the paddle consisted of a chain of counter-rotating vortices and a jet flow between these vortices. The artificial breathing current of the present study differed from the stimulus used by Wieskotten et al. (2010) in that it was smaller in

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diameter and did not consist of vortices, but rather was a unidirectional turbulent flow. Wieskotten et al. (2010) describe two flow parameters that the seal could use to analyse the movement direction: the spatial arrangement of vortices and the jet flow in between. The present study indicates that the jet flow alone may have been sufficient for the harbour seal to determine the direction of movement of the hydrodynamic trail generator. As shown in this study, the direction of an isolated water jet not surrounded by vortices can be detected.

Directional sensitivity of an array of mechanoreceptors such as the vibrissal field of a seal could be achieved based on the directional sensitivity of the single mechanoreceptor, on the interaction of mechanoreceptors, or both. For example, in surface-feeding vertebrates, directional sensitivity is assumed to be a result of time-of-arrival cues of different neuromasts (Bleckmann, 1985; Görner and Mohr, 1989). Single receptors of a hydrodynamic sensory system can vary in sensitivity depending on flow direction, e.g. in a cosine-type response pattern, as exemplified by the fish lateral line (Coombs et al., 1988; Bleckmann 1994, 2008). However, this basic directionality does not allow for angular resolution as long as only one receptor is involved. Electrophysiological data on the responsiveness of the subdermal mechanoreceptors within the follicle–sinus complex at the base of seal vibrissae are lacking. Another approach to investigate the basic mechanism of directional sensitivity in the pinniped vibrissal system is to conduct further behavioural studies in which specifically one single vibrissa versus several vibrissae are stimulated from different directions. Sensory feedback from an array of several vibrissae may be needed to obtain directional information. Furthermore, as exemplified by the present study, future investigations of absolute and directional sensitivity of the seal vibrissal system should be carried out at different levels of hydrodynamic background noise, as a hydrodynamic sensory system is only as good as its ability to cope with the conditions it encounters in the wild.

An explanation for respiratory suppression in fish as a response to aversive stimuli

Fish can respond to aversive stimuli by holding their breath for several seconds. This response can occur without prior conditioning and has in its conditioned form been used in psychophysical experiments to assess sensory thresholds, generalization and discriminatory abilities (e.g. Fay, 1969, 2009). It seems conceivable that the detection of breathing currents by predators is one of the evolutionary drivers for this respiratory suppression in fish that try to avoid being detected via hydrodynamic stimuli.

Comparison of benthic hydrodynamic detection by the pinniped vibrissal system and the fish lateral line

Experiments on benthic feeding fish

Benthic prey detection by use of a hydrodynamic stimulus has recently been described for fish using the lateral line system (Schwalbe et al., 2012, 2016). Schwalbe et al. (2012) described the behaviour of the cichlid *Aulonocara stuartgranti* feeding on brine shrimp under light and dark conditions. The authors concluded that *A. stuartgranti* uses its lateral line to detect the water flow caused by tethered brine shrimp (*Artemia*), especially under dark conditions. Schwalbe et al. (2016) used artificially generated stimuli emitted from holes in the sandy bottom of an experimental tank that resembled the water currents caused by *Artemia* or other invertebrates. One out of six holes (each one paired with a visually identical sham hole) emitted a current. The hydrodynamic stimuli emitted contained water velocities of up to 3 cm s^{-1}. The fish were able to identify the active hole with currents down to 1 mm s^{-1}. In comparison, the flow velocities in our artificial breathing currents were between 20 and 25 cm s^{-1} maximum. This velocity corresponds to the hydrodynamic stimulus of a much larger animal, a flounder (e.g. up to 20 cm s^{-1} in a small flounder of 18 cm total body length).

Comparison of the hydrodynamic sensory systems of fish and seals

The lateral line system in fish can be 10–100 times more sensitive to hydrodynamic dipole stimuli (Bleckmann et al., 1989; Coombs and Janssen, 1990) than the vibrissal system of harbour seals (Dehnhardt et al., 1998a). The lateral line system of fish consists of two subsystems, the superficial lateral line and the canal lateral line, where the basic components, the neuromasts, are located on the skin or in canals within the skin, respectively. The canal lateral line system detects pressure gradients rather than flow velocity and is believed to be responsible for the lowest sensory thresholds reported so far, which have been measured using dipole stimuli (Coombs and Janssen, 1990). By contrast, the vibrissal system of seals does not consist of two subsystems; however, when thresholds are measured using dipole stimuli, the response characteristics switch from an acceleration detector for frequencies below approximately 50 Hz to a displacement detector at higher frequencies (Dehnhardt et al., 1998a). The nature of the hydrodynamic stimulus for a swimming seal is mixed: even with constant water velocity in the artificial breathing current, the seal encounters a relative acceleration of its vibrissae as it enters or exits the stimulus. This acceleration will be even stronger for pulsed breathing currents. The relative contribution of water acceleration versus water velocity to the detection of benthic prey has not yet been shown conclusively for fish (Schwalbe et al., 2016) or seals (present study). However, acceleration, as detected by the lateral line canal system as well as the vibrissal system, probably plays a significant role. Benthic hydrodynamic detection by fish lateral lines and pinniped vibrissal systems is an example of the convergent evolution of fundamentally different hydrodynamic sensory systems both well adapted to their corresponding ecologically relevant stimuli.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

W.H. and B.N. conceived the project, built the setup and quantified stimuli. B.N. performed the experiments with the aid of Y.K. and S.W., who trained and guided the experimental animals. B.N. and W.H. analysed the data and wrote the paper. G.D. provided constructive scientific input.

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Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.148676.supplemental

References

Bleckmann, H. (1985). Perception of water surface waves: how surface waves are used for prey identification, prey localization, and intraspecific communication. In *Progress in Sensory Physiology* (ed. O. Ottoson), pp. 147-166. New York: Springer.

Bleckmann, H. (1994). *Reception of Hydrodynamic Stimuli in Aquatic and Semiaquatic Animals*. Stuttgart, Jena, New York: Gustav-Fischer-Verlag.
Bleckmann, H. (2008). Peripheral and central processing of lateral line information. *J. Comp. Physiol. A* **194**, 145-158.
Bleckmann, H., Weiss, O. and Bullock, T. H. (1989). Physiology of lateral line mechanoreceptive regions in the elasmobranch brain. *J. Comp. Physiol. A* **164**, 459-474.
Bleckmann, H., Breithaupt, T., Blickhan, R. and Tautz, J. (1991). The time course and frequency content of hydrodynamic events caused by moving fish, frogs, and crustaceans. *J. Comp. Physiol. A* **168**, 749-757.
Bowen, W. D., Tully, D., Boness, D. J., Bulheier, B. M. and Marshall, G. J. (2002). Prey-dependent foraging tactics and prey profitability in a marine mammal. *Mar. Ecol. Prog. Ser.* **244**, 235-245.
Cahoon, M. K., Littnan, C. L., Longenecker, K. and Carpenter, J. R. (2013). Dietary comparison of two Hawaiian monk seal populations: the role of diet as a driver of divergent population trends. *Endangered Species Res.* **20**, 137-146.
Coombs, S. and Janssen, J. (1990). Behavioral and neurophysiological assessment of lateral line sensitivity in the mottled sculpin, *Cottus bairdi*. *J. Comp. Physiol. A* **167**, 557-567.
Coombs, S., Janssen, J. and Webb, J. F. (1988). Diversity of lateral line systems: evolutionary and functional considerations. In *Sensory Biology of Aquatic Animals* (ed. J. Atema, R. R. Fay, A. N. Popper and W. N. Tavolga), pp. 553-593. New York: Springer-Verlag.
Dehnhardt, G. and Dücker, G. (1996). Tactual discrimination of size and shape by a California sea lion (*Zalophus californianus*). *Anim. Learn. Behav.* **24**, 366-374.
Dehnhardt, G. and Kaminski, A. (1995). Sensitivity of the mystacial vibrissae of harbour seals (*Phoca vitulina*) for size differences of actively touched objects. *J. Exp. Biol.* **198**, 2317-2323.
Dehnhardt, G., Mauck, B. and Bleckmann, H. (1998a). Seal whiskers detect water movements. *Nature* **394**, 235-236.
Dehnhardt, G., Mauck, B. and Hyvärinen, H. (1998b). Ambient temperature does not affect the tactile sensitivity of mystacial vibrissae of harbour seals. *J. Exp. Biol.* **201**, 3023-3029.
Dehnhardt, G., Mauck, B., Hanke, W. and Bleckmann, H. (2001). Hydrodynamic trail-following in harbor seals (*Phoca vitulina*). *Science* **293**, 102-104.
Fay, R. R. (1969). Behavioral audiogram for goldfish. *J. Audit. Res.* **9**, 112-121.
Fay, F. H. (1982). *Ecology and Biology of the Pacific Walrus, Odobenus rosmarus divergens Illiger. North American Fauna 74*, pp. 1-279. Washington, DC: US Department of the Interior, Fish and Wildlife Service.
Fay, R. R. (2009). Sound source segregation by goldfish: two simultaneous tones. *J. Acoust. Soc. Am.* **125**, 4053-4059.
Görner, P. and Mohr, C. (1989). Stimulus localization in *Xenopus*: role of directional sensitivity of lateral line stitches. In *The Mechanosensory Lateral Line: Neurobiology and Evolution* (ed. S. Coombs, P. Görner and H. Münz), pp. 543-560. New York: Springer.
Hanke, W., Brücker, C. and Bleckmann, H. (2000). The ageing of the low-frequency water disturbances caused by swimming goldfish and its possible relevance to prey detection. *J. Exp. Biol.* **203**, 1193-1200.
Hanke, W., Wieskotten, S., Marshall, C. and Dehnhardt, G. (2013). Hydrodynamic perception in true seals (Phocidae) and eared seals (Otariidae). *J. Comp. Physiol. A* **199**, 421-440.
Hanke, W., Bublitz, A. and Niesterok, B. (2015). Breathing currents of prey fish quantified to predict their role in benthic predation. In 21st Biennial Conference on Marine Mammals. San Francisco, CA: Society for Marine Mammalogy.
Harkonen, T. (1987). Seasonal and regional variations in the feeding habits of the harbor seal, *Phoca vitulina*, in the Skagerrak and the Kattegat. *J. Zool.* **213**, 535-543.
Lindt, C. C. (1956). Underwater behavior of the southern sea lion, *Otaria jubata*. *J. Mammal.* **37**, 287-288.
Niesterok, B. and Hanke, W. (2013). Hydrodynamic patterns from fast-starts in teleost fish and their possible relevance to predator–prey interactions. *J. Comp. Physiol. A* **199**, 139-149.
Parrish, F. A., Marshall, G. J., Littnan, C. L., Heithaus, M., Canja, S., Becker, B., Braun, R. and Antonelis, G. A. (2005). Foraging of juvenile monk seals at French Frigate Shoals, Hawaii. *Mar. Mamm. Sci.* **21**, 93-107.
Pierce, G. J., Boyle, P. R. and Diack, J. S. W. (1991). Identification of fish otoliths and bones in faeces and digestive tracts of seals. *J. Zool.* **224**, 320-328.
Rae, B. B. (1973). Further observations on the food of seals. *J. Zool.* **169**, 287-297.
Schulte-Pelkum, N., Wieskotten, S., Hanke, W., Dehnhardt, G. and Mauck, B. (2007). Tracking of biogenic hydrodynamic trails in harbour seals (*Phoca vitulina*). *J. Exp. Biol.* **210**, 781-787.
Schwalbe, M. A. B., Bassett, D. K. and Webb, J. F. (2012). Feeding in the dark: lateral-line-mediated prey detection in the peacock cichlid *Aulonocara stuartgranti*. *J. Exp. Biol.* **215**, 2060-2071.
Schwalbe, M. A. B., Sevey, B. J. and Webb, J. F. (2016). Detection of artificial water flows by the lateral line system of a benthic feeding cichlid fish. *J. Exp. Biol.* **219**, 1050-1059.
Sharples, R. J., Arrizabalaga, B. and Hammond, P. S. (2009). Seals, sandeels and salmon: diet of harbour seals in St. Andrews Bay and the Tay Estuary, southeast Scotland. *Mar. Ecol. Prog. Ser.* **390**, 265-276.
Thompson, P. M., McConnell, B. J., Tollit, D. J., Mackay, A., Hunter, C. and Racey, P. A. (1996). Comparative distribution, movements and diet of harbour and grey seals from Moray Firth, N. E. Scotland. *J. Appl. Ecol.* **33**, 1572-1584.
Tollit, D. J. and Thompson, P. M. (1996). Seasonal and between-year variations in the diet of harbour seals in the Moray Firth, Scotland. *Can. J. Zool.* **74**, 1110-1121.
Weiffen, M., Möller, B., Mauck, B. and Dehnhardt, G. (2006). Effect of water turbidity on the visual acuity of harbor seals (*Phoca vitulina*). *Vision Res.* **46**, 1777-1783.
Westerweel, J. (1997). Fundamentals of digital particle image velocimetry. *Meas. Sci. Technol.* **8**, 1379-1392.
Wieskotten, S., Dehnhardt, G., Mauck, B., Miersch, L. and Hanke, W. (2010). Hydrodynamic determination of the moving direction of an artificial fin by a harbour seal (*Phoca vitulina*). *J. Exp. Biol.* **213**, 2194-2200.