

## The impact of glide phases on the trackability of hydrodynamic trails in harbour seals (*Phoca vitulina*)

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### SUMMARY

The mystacial vibrissae of harbour seals (*Phoca vitulina*) constitute a highly sensitive hydrodynamic receptor system enabling the seals to detect and follow hydrodynamic trails. In the wild, hydrodynamic trails, as generated by swimming fish, consist of cyclic burst-and-glide phases, associated with various differences in the physical parameters of the trail. Here, we investigated the impact of glide phases on the trackability of differently aged hydrodynamic trails in a harbour seal. As fish are not easily trained to swim certain paths with predetermined burst-and-glide phases, the respective hydrodynamic trails were generated using a remote-controlled miniature submarine. Gliding phases in hydrodynamic trails had a negative impact on the trackability when trails were 15 s old. The seal lost the generated trails more often within the transition zones, when the submarine switched from a burst to a glide moving pattern. Hydrodynamic parameter analysis (particle image velocimetry) revealed that the smaller dimensions and faster decay of hydrodynamic trails generated by the gliding submarine are responsible for the impaired success of the seal tracking the gliding phase. Furthermore, the change of gross water flow generated by the submarine from a rearwards-directed stream in the burst phase to a water flow passively dragged behind the submarine during gliding might influence the ability of the seal to follow the trail as this might cause a weaker deflection of the vibrissae. The possible ecological implications of intermittent swimming behaviour in fish for piscivorous predators are discussed.

Key words: harbour seal, vibrissae, hydrodynamic reception, burst-and-glide trail, particle image velocimetry.

### INTRODUCTION

The marine environment contains different sources of information allowing aquatic animals to orient themselves and localize their prey under water. One potential source of information is given by water disturbances – that is, flow events in the water, which can be of biotic and abiotic origin. To detect these hydrodynamic events, most aquatic and semiaquatic animals have developed hydrodynamic receptor systems (Bleckmann, 1994). Although hydrodynamic receptors such as the lateral line of fish (Bleckmann, 1994; Coombs et al., 1989) as well as diverse hydrodynamic receptor systems in many invertebrate phyla (Heinisch and Wiese, 1987; Laverack, 1962; Tautz and Sandemann, 1980; Wiese, 1976) are well studied, nevertheless little work has been done regarding the capabilities of hydrodynamic perception in marine mammals. After it had been shown that the vibrissae of harbour seals (*Phoca vitulina* L.) respond to vibrations mediated by a rod directly contacting the vibrissae (Dykes, 1975; Mills and Renouf, 1986; Renouf, 1979), Dehnhardt and colleagues (Dehnhardt et al., 1998) demonstrated their function as a hydrodynamic receptor system sensitive to sinusoidal water movements as low as  $245 \mu\text{s}^{-1}$  caused by an oscillating sphere (hydrodynamic dipole). Owing to the rapid attenuation of hydrodynamic dipole stimuli with distance, it was assumed that hydrodynamic information could only be important in the vicinity of the receiving animal (Kalmijn, 1989). However, the wakes of fish contain water movements persisting for up to several minutes after their generation (Hanke and Bleckmann, 2004; Hanke et al., 2000), thus representing trackable hydrodynamic trails of considerable length. In further experiments, it has been demonstrated that blindfolded harbour seals can track hydrodynamic trails of biotic

(Schulte-Pelkum et al., 2007) and abiotic origin as far as 40 m (Dehnhardt et al., 2001) by means of their vibrissae. Further investigations using fin-like artificial stimuli recently showed that harbour seals can detect the movement direction of a trail-generating object after more than 30 s (Wieskotten et al., 2010). These results showed that seals can use hydrodynamic information for long-distance object localization, which is a useful ability while foraging on pelagic fish in dark or turbid water.

In the experiments on hydrodynamic trail tracking, trails were generated by means of a miniature submarine, driven exclusively with constant thrust and speed (Dehnhardt et al., 2001) or a conspecific that continuously flicked its hind flippers (Schulte-Pelkum et al., 2007). Contrary to these experiments, the majority of fish species do not usually swim in a constant way. They commonly use ‘burst-and-glide’ (‘burst-and-coast’) swimming behaviour (Blake, 1983). This locomotion comprises cyclic bursts of swimming movements followed by a glide phase in which the body is kept motionless and straight. The fish starts off the burst phase when a certain velocity lower than the average velocity is reached. It accelerates during the burst to a final velocity that is higher than the average velocity. The cycle is completed when the initial velocity is reached again at the end of the deceleration during gliding (Videler and Weihs, 1982). Such a swimming behaviour is suggested to be energetically advantageous. Weihs (Weihs, 1974) and Videler (Videler, 1981) predicted theoretical energy savings of approximately 50% if burst-and-glide swimming is used instead of steady swimming at the same average speed. These predictions are supported experimentally by a recent study by Wu and colleagues (Wu et al., 2007). In quantitative measurements on the swimming

kinematics and flow patterns of koi carp (*Cyprinus carpio* L.), the authors suggest that nearly 45% of energy is saved when burst-and-glide swimming is used compared with steady swimming at the same average speed.

An additional advantage of this swimming behaviour could be the prevention of the generation of a constant hydrodynamic wake behind a swimming fish and thus the reduction of a trackable hydrodynamic trail. Although several studies describe the hydrodynamic trails of actively swimming fish starting out as clear vortex structures (Blickhan et al., 1992) and containing water velocities significantly higher than background noise up to several minutes after their generation (Hanke and Bleckmann, 2004; Hanke et al., 2000), little is known about the temporal and spatial changes in hydrodynamic trails of gliding fish. The initial results of Hanke and colleagues [fig. 3k in Hanke et al. (Hanke et al., 2000)] confirmed the obvious conjecture that, in contrast to hydrodynamic trails of actively swimming fish, which contain a high proportion of vortices, the trail of a gliding goldfish (*Carassius auratus* L.) consists mainly of a narrow street of gross water flow directed towards the direction of movement of the fish. As far as these results are transferable to other fish species using the intermittent swimming style, potential piscivorous predators, such as harbour seals, would be confronted with weaker and faster-decaying parts of hydrodynamic trails during glide phases that could impair their ability to follow trails.

Based on the first indications described by Hanke and colleagues (Hanke et al., 2000), we hypothesize that the hydrodynamic trails generated by gliding objects impair the ability of harbour seals to follow trails. In the present study, we test this hypothesis by using a combination of psychophysical experiments and particle image velocimetry (PIV). As fish are not easily trained to swim along certain paths and with predetermined burst-and-glide phases, a modified miniature remote-controlled submarine was used to generate hydrodynamic trails, including burst-and-glide phases.

## MATERIALS AND METHODS

### Experimental subject

The experiments were conducted at the Marine Science Center at Cologne, Germany (recently relocated to Rostock, Germany). The experimental animal was an 11-year-old male harbour seal (*Phoca vitulina* L.) named 'Sam'. The subject was kept with seven other male harbour seals in a concrete outdoor pool, filled with fresh water. Only one experimental animal was available at the time of the experiments because the other animals were involved in different studies. The seal was familiar with psychophysical experiments but not versed in hydrodynamic trail following. During experiments, the seal received 3–5 kg of cut herring supplemented with vitamins, which was approximately 90% of the daily food amount. Experiments were performed twice a day, on 5 days per week. During the experiments, the other seven seals of the group were separated in an enclosure in a corner of the holding pool. The experiments were performed under the guidelines established by the European Communities Council Directive of 24 November 1986 (86/609/EEC).

### Stimuli and test apparatus

The experiments were conducted in the large kidney-shaped outdoor pool of our laboratory, using an area of approximately 50% of the pool, with an average depth of 1.5 m. The animal started each trial in a hoop station attached approximately 10 cm above the water surface on the lowest level of a concrete island in the middle of the pool (Fig. 1). A remote-controlled miniature submarine (length

64 cm, diameter 13 cm; see Fig. 2) steerable in all directions and with an average driving speed of  $>2\text{ ms}^{-1}$  was used for trail generation. Thrust was generated with a three-blade propeller. The propeller was 63 mm in diameter and rotated at 6000 rpm, resulting in an advance ratio of 0.32. The swimming direction was controlled with the moveable rear 25% of the fins, which were pin-jointed to the unmoveable front 75%. The fins did not significantly interact with the propeller because only a thin steel wire bridge was positioned within the propeller stream, acting as a protective cage. The submarine was remote-controlled by a pilot sitting on top of the island (Fig. 1), where this person was not visible to the seal waiting in its station. In order to avoid acoustic cues produced by the submarine after trail generation, all servos were switched off by an interrupter.

The submarine was started at a depth of  $50\pm 10$  cm. It was equipped with a position controller that helped the pilot to keep it away from the bottom or the water surface. Trials where the boat came in contact with the bottom or the water surface were aborted before the seal started its search. As the hydrodynamic trails of the submarine were less than 50 cm wide, any influence of the bottom or the water surface on the strength of the trail would be insignificant.

The trials were conducted double-blind. The person handling the seal was not informed about the decision of the submarine pilot to steer a left or a right curve, and no details of the path were given.

### Experimental procedure

Before each trial, the seal was blindfolded by an opaque stocking mask, leaving its mystacial vibrissae uncovered. To test for complete blindfolding, a herring or a hand was waved in front of the animal. No reaction was shown, contrary to the situation without a mask where the seal, even if trained to take herring only on command, followed the movement with its head. The blindfolded animal then placed its head into the hoop station, where it was supplied with headphones transmitting pink noise for acoustic masking. While the animal was waiting in its station, the submarine started underwater from a position in front of the seal. The submarine was driven in predetermined paths, including trials with left or right curves, as well as trials where no curves occurred (linear trails). Given that the angle the seal hits a hydrodynamic trail (Schulte-Pelkum et al., 2007), as well as the angle of curves, does not affect the capability of the seal to follow a trail (Hanke et al., 2004), the angles of curvature, as well as the angles of the starting submarine, were randomly chosen. The angles of linear trails ranged between  $+50$  and  $-50$  deg relative to the direction straight ahead from the animal. After a running time of approximately 4 s, the servos of the submarine were switched off, so that no motor noise was produced any more. In order to investigate how trail aging influences the trackability of burst-and-glide trails, delays between the generation of the hydrodynamic trail and trail following ranging from 5 to 30 s were introduced. After the respective delay, the headphones were removed from the head of the animal, and the animal started to search for the hydrodynamic trail.

In the first block of experiments (30 sessions), the submarine was driven with constant thrust and speed to its end-point ('burst'), where it was stopped by a short reverse thrust of the propeller. Thus, the submarine generated a hydrodynamic trail of length approximately 8–10 m. The hydrodynamic trail was defined as the sum of the points that the submarine had passed and where thus it had caused hydrodynamic events, independently of the magnitude of hydrodynamic events remaining after a specific time. All lengths were estimated to an accuracy of 10% or better by using the length of the submarine as a scale. In the second block of 30 sessions, the

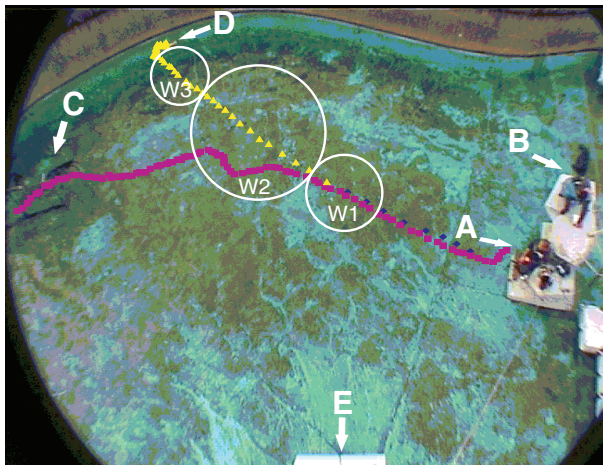


Fig. 1. Example of the analysis of a trail-following exercise. The graphic shows a top-view of the experimental set-up. Blue dots represent the path of the submarine during the burst phase, and yellow dots represent the path of the submarine during gliding. The path of the seal is marked by purple dots. The white circles (W1–W3) represent the three observation windows. (A) hoop station; (B) submarine pilot; (C) seal during tracking; (D) submarine at end-position; (E) platform bearing the camera mast of height 8 m.

motor of the submarine was stopped after 3–5 m (randomized in each session) – thus, it was moving without thrust for the rest of the way ('glide'). To aid video analysis, the submarine-pilot raised their right leg to show when the glide-phase started. During both experimental blocks, the direction (linear, left curve, right curve) of the submarine as well as the delays were presented in a pseudorandomized order, where the same parameters were never presented more than three times in a row, following the principles established by Gellermann (Gellermann, 1933).

A total of 1079 trail followings was recorded. In 895 of these trail followings, the seal reached the first observation window (see below); these cases were evaluated further. A hydrodynamic trail following was counted as successful when the seal either followed the trail accurately over the whole distance, thereby never deviating for more than 0.5 m from the path (for examples, see Fig. 3), or deviated only shortly from the trail, then retrieved it and accurately followed it again. While burst trails had to be followed over the whole distance until the point where the submarine was stopped by a reverse burst, glide trails had to be followed over a comparable length of 8 to 10 m (where the boat was not stopped). For a successful trail following, the seal was reinforced by a whistle signal presented immediately and by pieces of herring presented after return to the station. The seal was not required to find the boat at its end-position as the submarine was affected by natural water movements and drifted away a little after stopping. Between each trial, a break of approximately 3 min was introduced to ensure that the following trial was not affected by water disturbances remaining from the trail before.

To verify the role of the vibrissae of the seal in trail following, control experiments were performed during which the vibrissae were covered by a water-permeable stocking mask. The experimental procedure in control trials was in accordance with that of test trials.

#### Data recording and analysis

The experiments were video-taped with a digital camera (Canon XLIS; Canon Deutschland GmbH, Krefeld, Germany) equipped

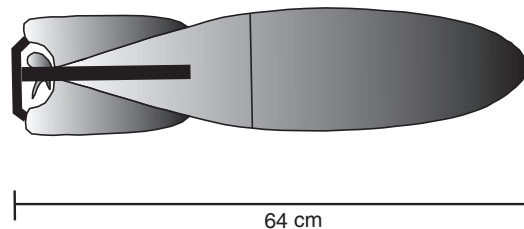


Fig. 2. Remote-controlled miniature submarine used for generation of trails. The submarine was equipped with a position controller that helped the pilot to keep it away from the bottom or the water surface. Direction was controlled with the moveable rear 25% of the fins. The pilot steered the submarine to generate both straight and curved trails in the behavioural experiments. The wakes of the propelled and the gliding submarine were quantified in separate trials using digital particle image velocimetry.

with a wide-angle lens (3.4–10.2 mm, camera aperture: 1.8–2.2). The camera was mounted at a height of 8 m on a mast, vertically above the pool. The recordings were digitally sequenced at a frequency of 5 frames  $s^{-1}$  using 'Main Actor for Windows' (MainConcept GmbH, Aachen, Germany), V. 3.65. Using 'Scion Image for Windows' (Scion Corporation, Frederick, MA, USA), Beta 4.02, frame-by-frame analysis was conducted to mark the swimming path of the submarine on subsequent pictures, as well as the path of the seal. The obtained coordinates were plotted in 'Excel' (Microsoft) and superimposed for comparison. The results were reviewed for trail-following behaviour. Trail-following behaviour was defined as a search behaviour where the seal did not deviate from the path of the submarine by more than 0.5 m – and it was usually even more accurate than that.

To compare the performance of the seal in following burst-and-glide trails at different stages of the pursuit, three observation windows were defined. In glide trails, the first observation window covered an area approximately 3–5 m away from the hoop station at the island, depending on the point where the motor was switched off, containing the transition zone between the burst-and-glide phase of the submarine. The second observation window covered the following 5 m of the trail. Within this window, the submarine decelerated from  $>2 \text{ ms}^{-1}$  to typically  $0.4 \text{ ms}^{-1}$  while gliding. The last window covered approximately 1 to 2 m of the trail of the submarine, where it was gliding with an average speed less than  $0.4 \text{ ms}^{-1}$ . In burst trails, comparable observation windows were defined, covering areas of the same sections of the trail. Trials in which the seal lost the hydrodynamic trails within the first 3 m, or never found them at all, were excluded from further analyses (they were discarded because they would not add information on the comparison between burst and glide trails).

#### Stimulus measurements

Digital particle image velocimetry (DPIV) (cf. Westerweel, 1997; Willert and Gharib, 1991) was used to analyse the hydrodynamic wakes generated by the submarine during burst-and-glide phases. We used two-dimensional single-plane DPIV. The set-up was adapted to the special requirements, regarding object size and speed, width of the hydrodynamic wake and flow speed within the wake. Measurements were conducted in a small outdoor pool of dimensions  $5 \times 2 \times 1 \text{ m}$  (L  $\times$  W  $\times$  H), which provided relatively calm water conditions (water velocities typically less than  $10 \text{ mm s}^{-1}$ ). Neutrally buoyant seeding particles (Vestosint 1101, Degussa-Hüls AG, Marl, Germany) were added to the water and illuminated in a 2 mm thick

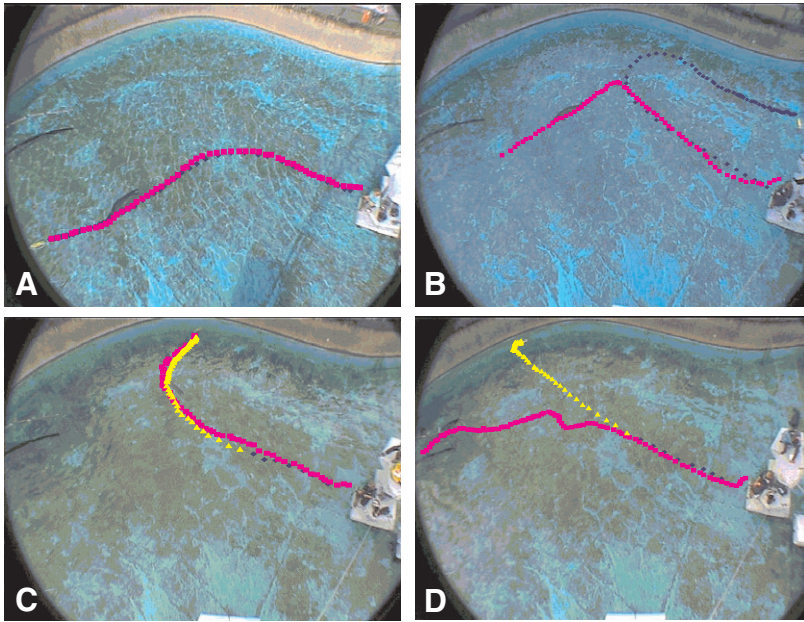


Fig. 3. Four examples of typical experimental trials. Pictures (A) and (B) show trials with constantly driven submarines (burst trials), whereas (C) and (D) represent the trials where the propeller was switched off after 3 to 5 m (glide trials). The blue dots represent the path of the submarine during the glide phase, the yellow dots the submarine during the burst phase and the red dots the path of the seal during trail following. (A) Trail following with a delay of 10 s. The seal followed the trail of the submarine accurately, never deviating more than a few centimetres from the path. (B) Example of a trail following of a burst trail that was 20 s old. The seal was not able to follow the trail until the end; it lost the trail of the submarine in the middle stage of the pursuit. (C) Successful glide trail following (age of trail: 20 s). (D) An example where the tested animal lost a glide trail that was 15 s old in the zone of transition between burst and glide.

horizontal plane by a fanned-out diode pumped solid-state laser (light source: 500 mW-DPSS-Laser, Entertainer 500, Quantum Physics, Newcastle, UK; optical fiber: Laserlight Showdesign, Berlin, Germany). The height of the horizontal laser-light plane below the water surface was adjusted to illuminate the mid-point of the submarine, which was steered at a height comparable to that of the behavioural experiments. The water surface was smoothed by a Perspex screen. A CCD camera (DMK2001, The Imaging Source, Bremen, Germany), mounted 20 cm above the water surface, filmed a section of 32×24 cm of the illuminated fluid layer. To measure water velocities of the order of several centimetres per second with our standard video camera (50 half-frames per second), relatively large interrogation areas (cf. Willert and Gharib, 1991) of 64 by 64 pixels were required. With an overlap of 50%, velocity vectors were spaced 28 mm, resulting in vector fields of 21 by 17 vectors. The video signal was stored digitally on a DV camera (Canon XL1S). Measurements of each trial include recordings of the background flow for 3 s. Then the submarine was driven through the layer of illuminated particles. The hydrodynamic trails of driving, as well as those of gliding submarines were recorded over a time of 30 s. The video recordings were digitally sequenced at a frequency of 50 half-frames per second and analysed using custom-designed correlation programs in MatLab 6.5 (Hanke and Bleckmann, 2004) that followed the principles of DPIV (Hart, 2000; Willert and Gharib, 1991).

## RESULTS

As soon as the headphones were removed from the head of the seal, the animal instantly left its station and started to search for the trail, thereby abducting the mystacial vibrissae to an extreme forward position. Trail following occurred in the vast majority of trials.

Fig. 4 illustrates the performance of the seal in tracking hydrodynamic trails as a function of the delay. The performance in trail following of continuously driven submarines ('burst trails') is compared with the performance of non-continuously driven submarines ('glide trails') for each delay. Numbers at each point indicate the total number of trials. The general run of both curves shows that the ability of the seal to follow the trails decreased with increasing delay. After delays of five seconds, the seal was able to

track burst-trails successfully in 93.2% of all trials. With increasing delays, the performance of the seal in tracking burst trails dropped almost linearly (10 s, 79.5%; 15 s, 62.3%; 20 s, 45.5%; 25 s, 33.3%) and reached a value of 20.6% at a delay of 30 s. The ability to follow glide trails was similar to that in following burst trails after delays of 5 and 10 s (5 s, 95.4%; 10 s, 78.2%). However, an increase of delays up to 25 s was accompanied by a faster decrease of successful tracking than found for burst trails (15 s, 43.1%; 20 s, 32.9%; 25 s, 21.1%). After 30 s delay, the tested animal was able to follow glide trails in 22.9% of all trials. According to a  $\chi^2$ -homogeneity-test, the tested animal was significantly less successful in tracking glide trails when trails were 15 s old (15 s,  $P < 0.05$ ). At an age of 20 to 25 s, the decrease of success rate in glide versus burst trials was statistically not significant, but substantial (it was statistically significant at the 10% level at an age of 25 s).

Further analysis showed that the seal, in cases of no success, lost the burst as well as the glide trails mostly in one of the first two observation windows. In most configurations, the tested animal lost

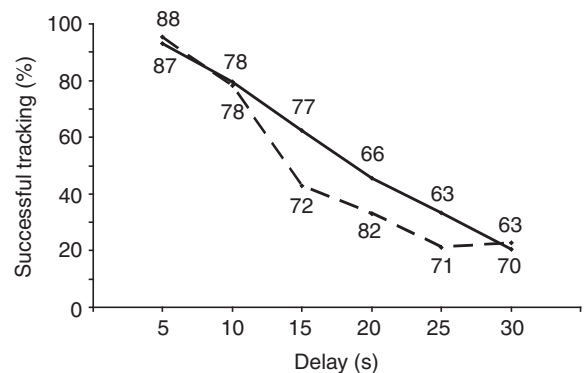


Fig. 4. The performance of the seal in following burst and glide trails plotted against the delay between the start of movement of the submarine and the start of the pursuit of the seal. Numbers at each point indicate the total number of trials (numbers above the graphs for burst trials, numbers below the graph for glide trials). A decrease of performance in glide trials in comparison with burst trials was found after delays of 15 to 25 s. Solid line: burst trails; broken line: glide trails.

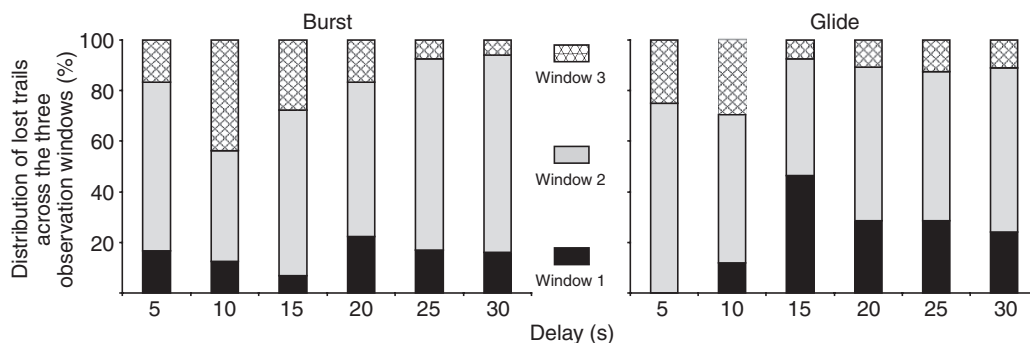


Fig. 5. Comparison of the distribution of lost trails for burst- and glide trials across the observation windows for delays of duration 5–30 s. The obtained values represent the ratio of losses in a specific observation window to the total number of losses.

the trails within the last stage of pursuit in less than 30% of all unsuccessful cases (exception: after 10 s delay in following burst trails). Fig. 5 shows the comparison of this distribution of lost trails for burst and glide trails within the different windows for each delay. A  $\chi^2$ -test revealed that, within the first observation window, the seal lost the hydrodynamic trails significantly more often after delays of 15 s when glide phases were introduced. Within the second observation window, the glide trails were lost more often than the burst trails after delays of 20 s – however, after delays of 15 and 25 s, glide trails were lost less often than burst trails. In the last stage of the pursuit (observation window 3), the biggest differences were found after delays of 15 and 20 s. Here, the seal lost the glide trails less often than the burst trails.

The results of the control experiments are in accordance to those of other studies concerning hydrodynamic trail following (Dehnhardt et al., 2001; Schulte-Pelkum et al., 2007). During control experiments with covered vibrissae, no trail following was observed. In fact, the tested seal refused to leave the hoop station, not starting the hydrodynamic trail following. In cases where the seal was forced to leave its station, it never moved away. After a few seconds, it then pulled off its mask. This behaviour did not change after several sessions of training.

#### Stimulus measurements

PIV measurements revealed some basic differences in parameters between hydrodynamic trails generated by burst-mode and glide-mode submarines. Hydrodynamic trails of the submarine during the burst phase consisted mainly of a narrow street of water disturbance with an approximate horizontal extent of up to 50 cm. The trails consisted of a turbulent structure with a jet-flow in a direction mainly opposite to that of the motion of the submarine (see Fig. 6). After a delay of 5 s, the hydrodynamic trail contained water velocities that could reach approximately  $100 \text{ mm s}^{-1}$  (see Fig. 7). After this delay, the width of the wake was approximately 25 cm. During the next 10 s, water velocities still could reach approximately  $50 \text{ mm s}^{-1}$  (see

Fig. 7) and the width of the trail increased to maximally 40 cm. After delays of 30 s, water velocities decreased to approximately  $30 \text{ mm s}^{-1}$ , whereas the width reached up to 50 cm. As hydrodynamic trails were generated by a torpedo-shaped submarine equipped with one circular propeller, a rotational symmetry of the wake can be assumed – thus, the vertical extent of the wake had a similar dimension.

In contrast to burst trails, hydrodynamic wakes generated by gliding submarines consisted mainly of a narrower street of water flow passively dragged behind the submarine and reached a maximum width of less than 30 cm. After 5 s, these hydrodynamic trails contained water velocities of up to approximately  $80 \text{ mm s}^{-1}$  and were 20 cm wide. During the next 10 s, a distinct decrease of water velocities was measured ( $<40 \text{ mm s}^{-1}$ ), whereas the width increased slightly up to 25 cm. After a delay of 30 s, water velocities finally reached less than  $30 \text{ mm s}^{-1}$ , whereas the horizontal width did not exceed 30 cm.

#### DISCUSSION

The results of the present study provide the first experimental evidence that the ability of seals to track the hydrodynamic wakes of a moving object can be affected by gliding phases during trail generation. By contrast, the still-high success rate in following the trails of gliding objects is remarkable.

Although the results of the control experiments do not show that the seal would do everything else but follow the trail, they show that covering of the vibrissae made the animal, which was highly motivated, expect an unsuccessful trial. The results from Dehnhardt and colleagues (Dehnhardt et al., 2001), where another harbour seal ('Henry') actively searched for a trail generated by a miniature submarine but was unable to find it, support our conclusion that the vibrissae were indispensable for following trails.

Our results demonstrate that, besides the age of the trail, the performance of the seal in tracking hydrodynamic trails can be negatively affected by glide phases during trail generation. Although the tested animal was able to track burst as well as glide trails with

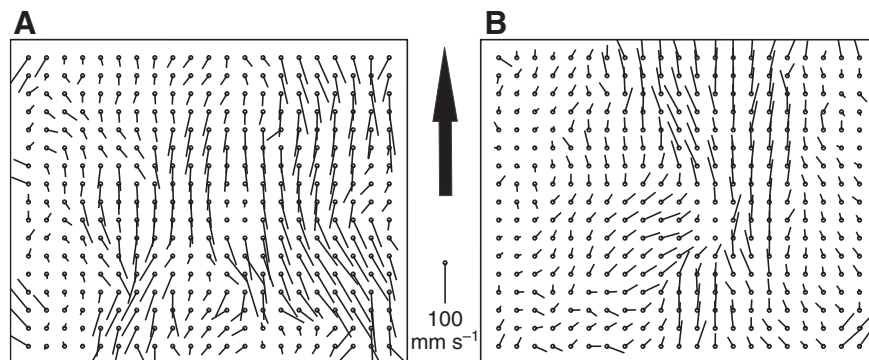


Fig. 6. Water velocities shown as vector fields in a typical example for burst (A) and glide trails (B). Both examples show a hydrodynamic trail 5 s after the passage of the submarine. The hydrodynamic wake of burst trails consists mainly of a rearwards-directed jet flow of turbulent water, whereas the wake of a glide trail contained primarily water flow passively dragged behind the submarine. The large arrow indicates the direction of movement of the submarine.

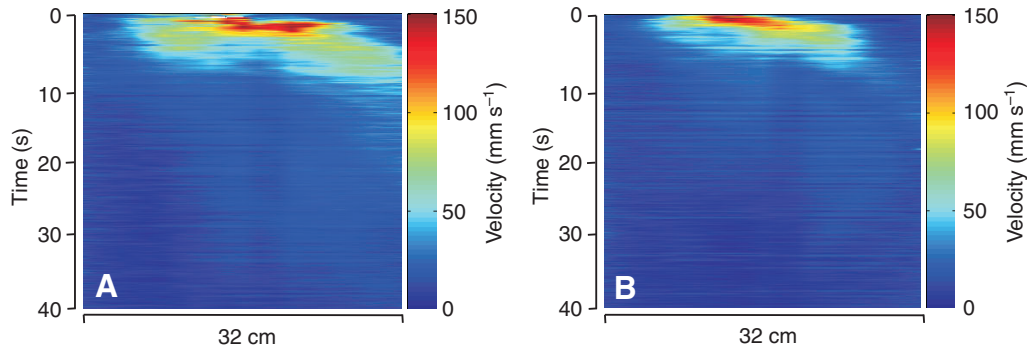


Fig. 7. Colour-coded representation of water velocity distribution behind the submarine. The examples (A,B) compare the temporal development of the lateral spread of burst-and-glide trails in a horizontal plane. Velocity is encoded by colour, where dark red encodes the highest and dark blue the lowest velocity. Note that the velocity scale in (A) does not cover the complete upper range of obtained values. Thus, velocities higher than  $150 \text{ mm s}^{-1}$  are shown in dark red. For this illustration, each vector field was reduced to a row by averaging over the columns of the vector field, and rows resulting from this procedure were assembled in temporal order.

about the same reliability within the first 10 s, it lost the glide trails significantly more frequently when these were aged 15 s. Comparisons between the performance of the seal during burst-and-glide trials within different stages of the pursuit revealed that the ability of the seal is not simply affected by the decreased speed of the submarine during the last stages of the following of the trail. In fact, the animal lost the trails by contrast in earlier stages of the pursuit. Especially the zone of transition between the burst and the glide moving pattern seems to have an effect on the capability of the seal to follow glide trails after delays of 15–25 s. The reason for the impaired performance when trails were generated by a gliding submarine can be related to the results of the PIV flow measurements. When trails are not older than 10 s, the water movement in glide trails is not that different from that of a burst trail. Both types of trails contain water velocities of considerable speed, which allows a tracking seal to detect and follow a glide trail as well as a burst trail with about the same reliability, even when gross water flow in the wakes is not equally directed. The biggest differences between the hydrodynamic parameters of burst and glide trails can be found in wakes aged between 15 and 20 s. While maximum water velocities of burst trails were approximately  $50 \text{ mm s}^{-1}$  and the lateral spread extended to 40 cm, the velocities of glide trails as well as their lateral spread are considerably lower (velocity:  $<40 \text{ mm s}^{-1}$ ; width:  $\sim 25 \text{ cm}$ ). Thus, a seal is confronted with a weaker and smaller water flow passively dragged behind the gliding submarine. Water velocities in burst and glide trails were more similar to each other after longer delays (30 s) because their approximately logarithmic decay leads to decreasing differences in absolute values.

The negative impact of glide phases on the trackability of hydrodynamic trails of age 15–25 s within the transition zone between burst and glide can be explained through a theoretical basis. The PIV set-up used did not allow the taking of data of the hydrodynamic trail when the boat changed from burst to glide phases because of the small field-of-view of our optical system. Nevertheless, it is safe to assume that, when the propeller was stopped, the backwards-directed water-stream ceased abruptly and the velocity of gross water-flow quickly reached a value of approximately zero. Afterwards, the gross water flow changes its direction and flows into the direction of the gliding submarine. The transition between burst and glide phases and thus the change from a rearwards-directed stream in the burst phase to a water flow passively dragged behind the submarine during gliding could confuse a tracking animal in a way that it loses the hydrodynamic trail within this area more frequently.

The ability of a seal to follow fish, their natural prey, is probably impaired more strongly when burst-and-glide swimming behaviour occurs than demonstrated here. The hydrodynamic trail of a swimming fish is more complex than the trail of the submarine used in this study. While a hydrodynamic trail of a submarine primarily consists of the narrow street of a backward-directed water stream, the trail behind a swimming fish shows clear vortex structures, and vortices at approximately the size of the fish tail can persist for a minute or longer in still water (Hanke et al., 2000; Hanke and Bleckmann, 2004). The structure of a hydrodynamic trail, as well as its persistence after generation, depends on the body shape and the swimming style of the species (Hanke and Bleckmann, 2004; Nauen and Lauder, 2002a; Nauen and Lauder, 2002b). By contrast, the live fish will drag less water behind in the gliding phase than our submarine did as most fish have very low drag coefficients (e.g. Anderson et al., 2001; McHenry and Lauder, 2005). This way, the trails of gliding fish differ much more strongly from the trails of actively swimming fishes, compared with the differences in trails of our propelled submarine. In comparison to actively swimming fish, the trails of gliding fish can decrease faster and have considerably smaller dimensions (Hanke et al., 2000), thus making it more difficult for a seal to find and to track this kind of trail. Therefore, the ability of a seal to track the hydrodynamic trail of a gliding fish will probably differ from its ability to follow the trail of an actively swimming fish even more than found in our experiments.

Harbor seals are generalist predators and feed on a wide variety of prey, including gadoids, salmonids, clupeids and pleuronectids (Andersen et al., 2004; Hauksson and Bogason, 1997; Sharples et al., 2009). Burst-and-glide swimming occurs in gadoids and clupeids (Blake, 1983; Videler and Weihs, 1982) as well as salmonids (Hinch et al., 2002; Standen et al., 2004). Flatfish can cease tail beating and glide to the ground (S.W. and W.H., unpublished observations in flounder *Platichthys flesus*) in a way similar to burst-and-coast swimming, although the role of this behaviour in predator avoidance needs to be investigated.

In summary, the results of the present study are consistent with the hypothesis that glide phases in fish not only play a role in energy saving during locomotion but might also constitute a strategy to avoid piscivorous predators through the reduction of a constant trackable hydrodynamic trail. By contrast, we found that harbour seals can follow gliding objects, and selective pressure should have been effective in tuning this ability to the hydrodynamic

characteristics of their prey. Experiments with live fish as trail generators are needed to obtain a better quantitative estimate of the effect of this potential hydrodynamic camouflage against predators that follow hydrodynamic trails.

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