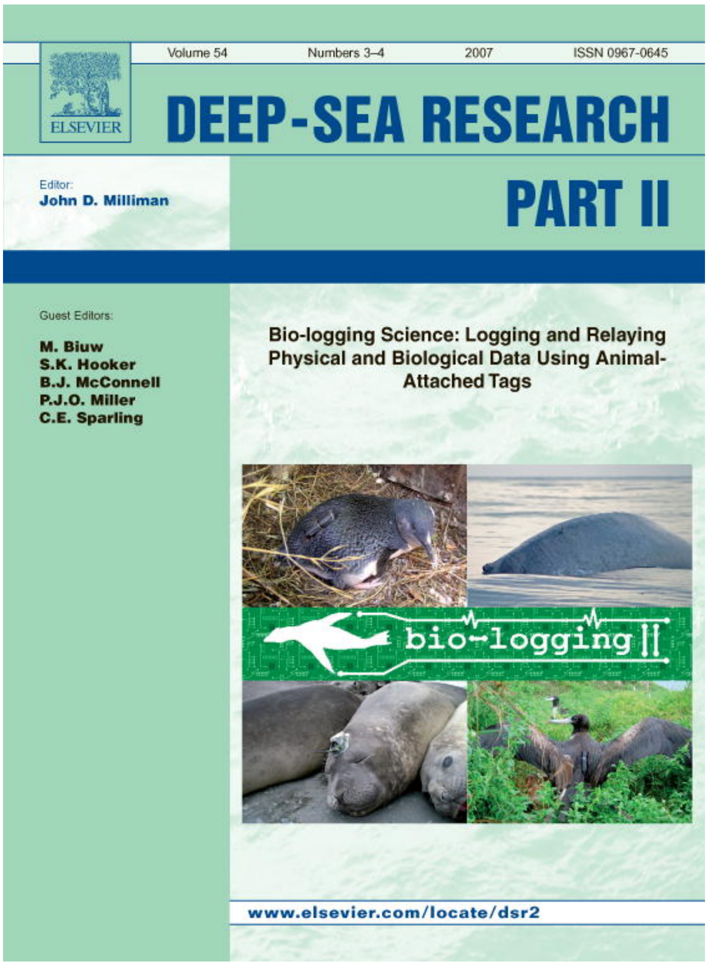
Volume 54
Numbers 3–4
2007
ISSN 0967-0645
ELSEVIER
DEEP-SEA RESEARCH
PART II
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Deep-Sea Research II 54 (2007) 290–297

DEEP-SEA RESEARCH PART II

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Comparison of echolocation behaviour between coastal and riverine porpoises

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Accepted 15 November 2006

Abstract

Echolocation behaviour of a harbor porpoise and six finless porpoises was recorded in open-water systems using acoustic data loggers (A-tag). In total 1359 click trains were recorded during 4.6 h for the harbor porpoise and 46,240 click trains were recorded during 82.3 h for the finless porpoises. The harbor and finless porpoises produced sonar click trains every 12.3 and 6.4 s on average, respectively. During the inter-click-train interval, the porpoises were silent or produced clicks below 148 dB re. 1 μPa, the detection threshold of the tag. Ninety percent of the inter-click-train intervals were 20 s or less in both species. This means that porpoises frequently produce intense click trains. Click-train intervals lasting over 50 s constituted 1% of the total intervals in finless porpoises and 4% in the harbor porpoise. Both species swam without intense clicks for less than 10 m in most cases, but occasionally remained silent or used undetected low-intensity clicks for more than 1 min. During these periods, the porpoises would be susceptible to entanglement in fishing nets.

Keywords: Bioacoustics; Echolocation; Marine mammals; By catch, Finless porpoise; Harbor porpoise

1. Introduction

In recent years, passive acoustic monitoring of odontocete biosonar signals using stationary data loggers has provided valuable data concerning the abundance of animals in their natural habitats. The reliability of detection can be quite high as shown for finless porpoises (*Neophocaena phocaenoides*). For example, 80% of visually detected finless porpoises were also detected acoustically with false alarm rates as low as 1% (Akamatsu et al., 2001; Wang et al., 2005).

In cetacean management, abundance surveys and monitoring of density changes are essential to assess the status of a population and determine the impact of by-catch. For the reliable estimation of abundance, the probability of finding the target animal on the survey cruise line (the so called g(0)) and the

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doi:10.1016/j.dsr2.2006.11.006

detection function are key factors in line transect surveys (Buckland et al., 1993). In visual surveys, g(0) is difficult to estimate because animals cannot be detected during diving and detections are weather- and observer-dependent.

The major challenge in using acoustic instead of visual detections in survey work will be to identify and localise the vocalising animal, and to estimate the probability of detecting an animal within a definable area, which is required to estimate g(0) and the detection function. Acoustic monitoring for cetaceans has a significant advantage over visual methods because it can be automated. Furthermore, data can be collected independent of daylight, weather conditions, and observer skills. Acoustic surveys rely on identifiable sounds made by animals. Many odontocetes are observed to use echolocation (Au, 1993), which assists them in navigation and prey detection. In principle, systematic recordings of odontocete sonar signals will make it possible to estimate abundance and density changes. Acoustical monitoring was used by Carstensen et al. (2006) to estimate the density changes of harbor porpoises during the construction of a wind farm.

Knowing the echolocation behaviour of small odontocetes is essential for understanding by-catch problems, especially in gillnets. Thousands of harbor porpoises (*Phocoena phocoena*) are by-caught yearly in bottom set gillnet fishery throughout their distribution (e.g., Vinther and Larsen, 2004). Little is known about the echolocation behaviour of wild harbor porpoises and their ability to detect gillnets.

Sound production per unit time for each marine mammal species is necessary for both quantitative acoustic surveys and investigation of by-catch mechanisms. Therefore, tagging animals with acoustical monitoring devices is a powerful method to estimate the phonation behaviour of a species (Johnson and Tyack, 2003). Thus far, acoustic tags have been deployed on free-ranging beaked whales (Johnson et al., 2004; Madsen, 2005; Zimmer et al., 2005), sperm whales (Miller et al., 2004), North Atlantic right whales (Nowacek et al., 2004), and finless porpoises (Akamatsu et al., 2005a, b). This technique will certainly be applied to other marine mammal species, especially coastal small odontocetes that are often affected by human activities.

Advances in microelectronics have made it possible to design and build acoustic tags for monitoring biosonar emissions of large odontocetes (Burgess et al., 1998; Johnson et al., 2004). Recently, a miniature stereo acoustic tag (A-tag) was developed to record the echolocation behaviour of small odontocetes (Akamatsu et al., 2000, 2005c). Behavioural data, such as dive depth and times, and potential target distance, can be obtained by using acoustic tags supplemented with additional data acquisition devices. For some captive odontocetes there is a linear correlation between inter-pulse interval and target range as shown by the bottlenose dolphin, *Tursiops truncatus* (Au, 1993), false killer whale, *Pseudorca crassidens* (Thomas and Turl, 1990), and the harbor porpoise (Verfuss et al., 2005). The inter-pulse interval is longer than the two-way sound travel time to and back from the target (Morozov et al., 1972). The extra time is called the lag time and is thought to be used by the animal for processing echo information. The inter-pulse intervals provide an index for range sensing by odontocetes.

The present study is the first attempt to record the biosonar behaviour of a harbor porpoise (*Phocoena phocoena*) in coastal Danish waters for comparison with a related freshwater species, the finless porpoise (*Neophocaena phocaenoides*) using an acoustic tagging system.

2. Materials and methods

2.1. Tagging systems

We used two types of A-tags, a W20-A (monaural hydrophone, Little Leonardo, Tokyo) for a Danish harbor porpoise and W20-AS (stereo hydrophone, Little Leonardo, Tokyo) tags for Chinese freshwater finless porpoises. Both data loggers are ultrasonic pulse event recorders. They record the sound pressure (peak-to-peak re. 1 μPa) and the absolute time of occurrence of each pulse to flash memory. The stereo A-tag (W20-AS) provides additional information of sound source direction by the sound arrival time difference between the hydrophones. The sound source directionality obtained by W20-AS is not relevant for this comparative study and is therefore not included in this paper. W20-A and W20-AS measure 21 and 22 mm in diameter by 96 and 122 mm in length, respectively. They were attached with a suction cup to the back of the animals (see Akamatsu et al., 2005a, for details on attachment). The sampling frequency is 1 kHz for W20-A and 2 kHz for W20-AS, which gives a time resolution of pulse event detection of 1 ms and 0.5 ms, respectively. The hydrophone sensitivity was calibrated in advance, and a detection threshold level in the off-line analysis was set at 148 dB peak-to-peak re. 1 μPa for both tags to facilitate comparisons. All the data have been standardised, using software developed for the present study. Inter-pulse intervals of more than 1 ms were analysed. Additionally, only sonar signals containing more than five pulses in a train were analysed to eliminate possible noise contamination. The detailed description of W20-AS is reported in Akamatsu et al. (2005c).

Diving behaviour of the finless porpoises and the harbor porpoise was recorded by a data logger PD2GT (Little Leonardo, Tokyo) and DST milli (Star-Oddi, Iceland), respectively. The PD2GT tag recorded swimming depth, speed, two axis accelerations, and water temperature. The DST milli tag recorded swimming depth and water temperature. The time resolution of the depth recording of DST milli was set to 4 s whereas PD2GT had 1 s resolution. To reduce splash noise contamination near the surface, pulses recorded within 0.3 m from the surface were excluded.

2.2. Experiment in Danish and Chinese waters

On 8 June 2005 a subadult male harbor porpoise (body length = 120 cm) was accidentally trapped in a Danish pound net placed in the Great Belt. The fisherman immediately reported the catch to the National Environmental Research Institute, Roskilde, Denmark. The harbor porpoise was able to swim freely and was lifted out of the water when the researchers arrived later the same day. After a careful physical examination, the animal was equipped with two tags. One was the acoustic-depth unit combined with the A-tag (W20A), a dive recorder (DST milli), and a VHF radio (MM130, Advanced Telemetry Systems, USA) in a floating package attached in front of the dorsal fin with a suction cup. For positioning the animal, the second tag (a satellite transmitter, SPOT4, Wildlife Computers, USA) was mounted to the dorsal fin with two silicone-covered 5-mm delrin pins (see Teilmann et al., in press, for details). The animal was released after 30 min on the boat. This experiment was carried out under permissions from Danish Forest and Nature Agency (no. SN 343/SN-0008) and Ministry of Justice (no. 1995-101-62).

Six finless porpoises (five adult males and an adult female, body length = 159.0, 147.0, 146.5, 123.0, 148.5, 148.5, and 131.0 cm, respectively) were used for the freshwater experiment in an oxbow of the Yangtze River, China. This oxbow lake, part of Tian-e-Zhou Baiji National Natural Reserve of the Yangtze River, Shishou, Hubei, China, is approximately 21 km long and 1–2 km wide. It was established by the Chinese government in 1992 as a sanctuary for baiji (*Lipotes vexillifer*) and finless porpoises. Finless porpoises were caught by encircling them with a net for this experiment in October 2004 and temporarily housed in a net enclosure beside the oxbow lake. Six animals were equipped with two tags. One was the A-tag (W20AS) and the other a data logger (PD2GT). Each tag was assembled with a VHF radio (MM130), a float, and a suction cup for attachment to the animal. The animals were released in the oxbow on the next day. The procedure of the experiment in China is identical to the experiment in 2003 that is described by Akamatsu et al. (2005a). However, the data from finless porpoises presented in this paper have not been reported earlier. The experiments were conducted under a permit issued by the Fisheries Management Department of Hubei Province, China.

3. Results

In total 1359 click trains were recorded during 4.6 h for the harbor porpoise and 46,240 click trains were recorded during 82.3 h for finless porpoises. The harbor and finless porpoises produced sonar click trains every 12.3 s (S.D. = 39.6) and 6.4 s (S.D. = 14.2) on average, respectively. Comparison of the dive depth profile is shown in Fig. 1. The harbor porpoise constantly dove deeper than 10 m, whereas the finless porpoise dove mostly to less than 5 m and occasionally down to 18 m in depth. These dive depths are consistent with the bathymetric profiles of the two habitats (see Section 4).

Trains of sonar signals from the harbor porpoise are shown in Fig. 2. Click trains were defined as pulse sequences separated by more than 200 ms with no triggered clicks. Ninety percent of the inter-click-train intervals were shorter than 20 s in both species (Fig. 3).

The inter-pulse interval of odontocetes is linearly correlated with target range (Thomas and Turl, 1990; Au, 1993). We calculated the average inter-pulse interval in all click trains for both species (Figs. 2, 4). The mean inter-pulse interval of the harbor porpoise was 80.5 ms (S.D. = 41.1); while the average inter-pulse interval was shorter for finless porpoises, 60.4 ms (S.D. = 29.7).

The lag time (signal processing time of an echo in biological sonar) of captive harbor porpoises is 26–36 ms for difficult tasks and 14–19 ms for simpler tasks with individual differences (Verfuss et al., 2005). Here we use a 20 ms lag time for both species to standardise the comparison. Half of the average interval minus the lag time multiplied by the speed of sound in water will represent the average distance to the perimeter of an animal's "active space". This would be about 45 m for the harbor porpoise and about 30 m for the finless porpoise assuming 1.5 m ms^{-1} for the velocity of sound and assuming they can hear a returning echo. The calculated sonar ranges for all inter-click intervals are shown in Fig. 5. Also shown in Fig. 5 is the distance travelled with no triggering of the A-tag. Here we assume a mean swimming speed of 0.89 m s^{-1} based on finless porpoise data (Akamatsu et al., 2005a), on body size (Sato et al., 2006), and on harbor porpoise swimming speeds during diving (Westgate et al., 1995). The distance swam without the A-tag being

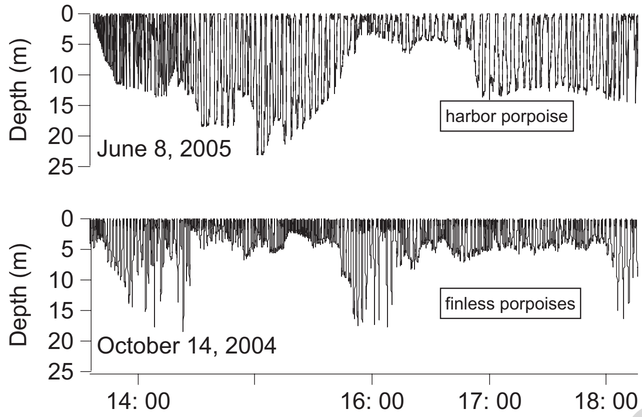

Fig. 1. Comparison of depth profile of the harbor porpoise (upper inset) and a finless porpoise (lower inset). Entire observation duration is indicated in the harbor porpoise. The depth profile of the finless porpoise is a sampled section of data obtained from one of the six animals. The hour of day is identical, but the date of the observation is different (8 June 2005 for harbor porpoise (upper) and 14 October 2004 for finless porpoise (lower)).

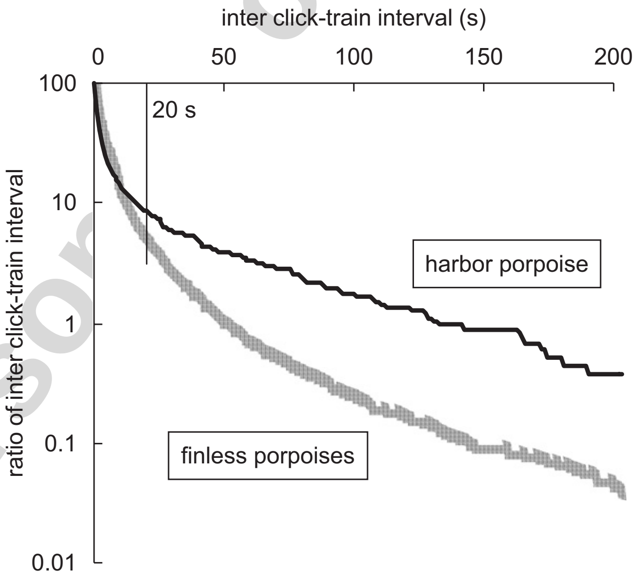

Fig. 3. Ratio of inter-click-train intervals over 200 s (abscissa). Harbor porpoise (dark line) and finless porpoise (light line). Note that the decay of the ratio in each species is similar up to 20 s. After this the harbor porpoise showed longer intervals.

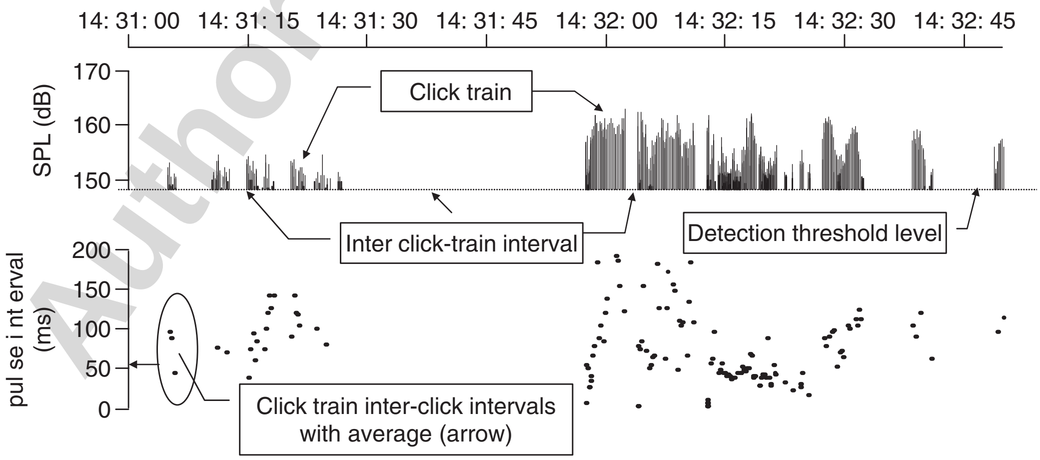

Fig. 2. Sonar pulse trains of the harbor porpoise. Many short and several long inter-click-train intervals were observed. The A-tag is not triggered during the inter-click-train intervals indicating either a click level below threshold (148 dB re. 1 μPa indicated by a horizontal dotted line) or no sound emissions from this animal. Inter-click intervals are shown in the lower trace with the average of the first click train indicated with an arrow.

triggered is usually less that the calculated sonar range (Fig. 5).

Fig. 6 shows an assumed approach sequence for the harbor porpoise and for one of the finless porpoises where the inter-click interval reduces monotonically with time. The inter-pulse interval changed 5.8 ms during 2.6 s for the harbor porpoise and 53 ms during 22 s for a finless porpoise.

4. Discussion

This is the first study of the sonar behaviour from a free ranging harbor porpoise and offers the opportunity for comparison with freshwater finless porpoises. The harbor and finless porpoises produced sonar click trains on average every 12.3 and 6.4 s, respectively. The off-axis sound intensity at the position of A-tag had to be stronger than 148 dB re. 1 μPa peak-to-peak to be recorded. This shows that both species frequently produce intense sonar signals.

Two major limitations should be addressed. First, the 148 dB threshold level could miss recording low-level clicks. During the inter-click-train intervals, the tagged animals might have produced low-level clicks. Therefore, results of this study provide conservative estimates of the animals' biosonar abilities. When investigating by-catch problems, a conservative criterion is preferable, as only intense signals will provide detectable echoes from remote gillnets (Hatakeyama and Soeda, 1990). Secondly, tagging the animals may affect their natural behaviour. However, the attack area that contributes the resistance of an A-tag to water flow should be rather small (3.8 cm^2 for an A-tag having 22 mm in diameter), still we cannot assess the effect of the tags. Geertsen et al. (2004) studied the behaviour of a satellite-tagged captive harbor porpoise over a month that showed only a limited influence on swimming behaviour during the first few hours. Although the tags may have affected the behaviour of the harbor porpoise in this study, we continuously recorded dives to the bottom and no obvious change in behaviour was seen during tag attachment and release of the animal. We therefore believe that the results reflect natural (or close to natural) behaviour.

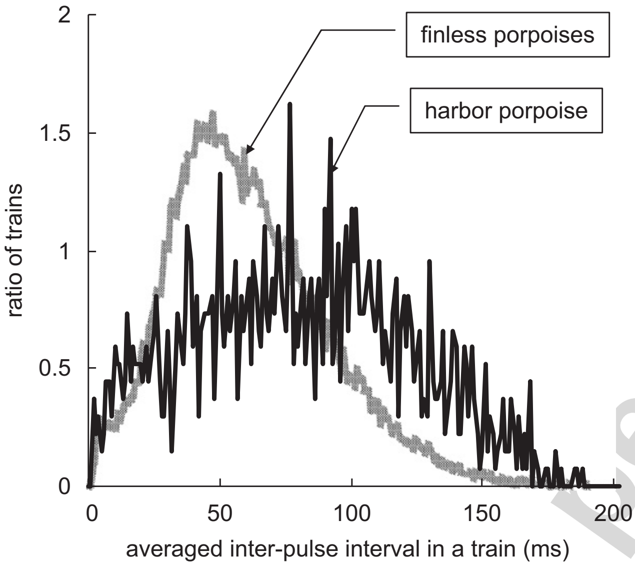

Fig. 4. Distribution of averaged inter-pulse intervals in a train. The finless porpoises used 60.4 ms inter-pulse interval in average whereas the harbor porpoise used 80.5 ms mean inter-pulse interval.

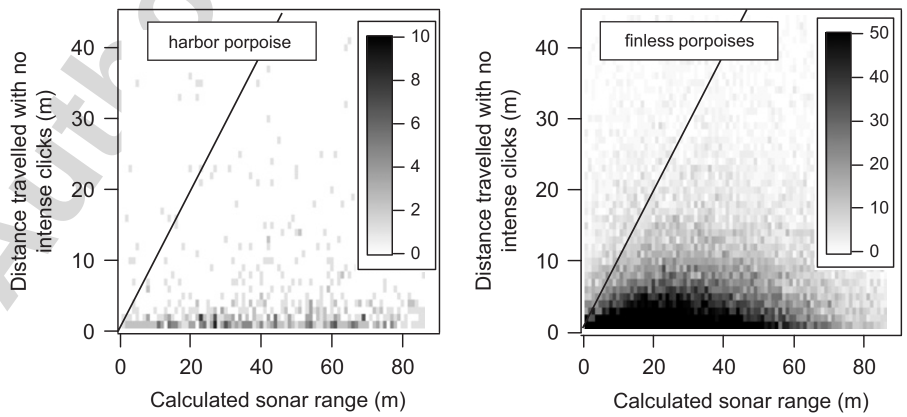

Fig. 5. Distance travelled with no triggering of the A-tag as a function of sonar range. For both the harbor porpoise and finless porpoises, calculated sonar range was much larger than the distance travelled with no intense clicks. Note that the data of finless porpoises was obtained in 2004, which is different from the similar figure reported in Akamatsu et al. (2005a).

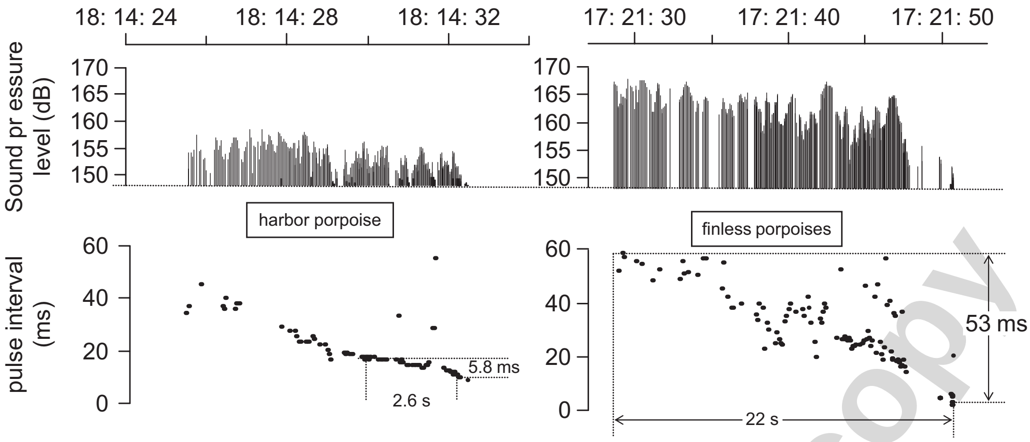

Fig. 6. Details of sonar signals during approach phase in the harbor porpoise (left) and a finless porpoise (right). The swimming speed calculated from the change in inter-click intervals over a defined time period indicates that the harbor porpoise swam at $1.7\,m\,s^{-1}$ and the finless porpoise at $1.8\,m\,s^{-1}$ during the respective approach phases. The speed of the finless porpoise corresponds to that recorded earlier with instrumentation (Akamatsu et al., 2005a).

The sound level at the position of the acoustic tag deployed on the harbor porpoise is about −20 to −30 dB relative to the outgoing signal 1 m in front of the animal (L.A. Miller, personal communication). These values were measured at the dorsal fin of a trained, captive harbor porpoise with a miniature hydrophone attached to a suction cup. This means that the recorded clicks were between 168 and 178 dB re. 1 μPa at 1 m, which is somewhat higher than ranges reported in the current literature (e.g., Teilmann et al., 2002).

Gillnet fishery results in high levels of by-catch of harbor porpoises (e.g., Vinther and Larsen, 2004). The detectable ranges for lead-line and netting of a gillnet were estimated at 9 and 2 m, respectively, for harbor porpoise sonar (Hatakeyama and Soeda, 1990). As seen in Fig. 5, both of the species swam without using intense clicks for no more than 10 m in most cases. This estimated swimming distance is critical, since a harbor porpoise could easily collide with a gillnet if they swim without using the sonar or only use low-intensity clicks. Inter-click-train intervals longer than 1 min. rarely occur in both species (Fig. 3). Fig. 5 shows almost the same trend for the two species: longer range scanning before swimming silently or using low-intensity sonar. This suggests that the harbor porpoise might stop echolocating or reducing levels of echolocation signals for more than 1 min. in about 1% of the inter-click-train intervals. Thus both species were potentially at risk of entanglement during the observation duration of data logger deployments.

Calculated sonar ranging was mostly longer than the distance travelled silently for both species (Fig. 5). The harbor porpoise and the finless porpoises in the present study presumably inspected an area ahead of themselves before using weak clicks or swimming silently. However, the distribution of average inter-pulse intervals of the harbor porpoise was longer than that of finless porpoises. Visibility in Danish waters is often less than 5 m whereas in the oxbow of the Yangtze River it is less than 1 m. The depth of the Danish Belt varies between 5 and 40 m in shallow slopes. The oxbow lake had a steep slope along the high current side of the old course of the main stream of the Yangtze River extending down to 20 m. However, most of the oxbows were less than 5 m in depth. These bathymetric factors consist of the depth profile indicated in Fig. 1 that shows relatively deeper dive depth for the harbor porpoise. This might explain the difference in sonar range estimated by the inter-pulse intervals. A captive harbor porpoise used 59 ms (mean value) inter-pulse interval independent of target range during target detection experiments (Teilmann et al., 2002). The free-ranging harbor porpoise produced inter-pulse intervals from a few ms to 150 ms (Fig. 4). The inter-pulse interval depends more on the size of the swimming environment rather than species differences (Akamatsu et al., 1998). This suggests that the tagged harbor porpoise in the present study scanned various distances, while the captive porpoise might only have used its sonar ranging to cover the distance of the enclosure (Verfuss et al., 2005).

The approach phase is characterised by linearly decreasing inter-pulse intervals observed in both the porpoise species (Fig. 6). Verfuss et al. (2005)

showed that captive harbor porpoises adjusted the click intervals to the target range during most of the approach. In the later part of the approach phase of the present study, the inter-pulse interval changed by approximately 5.8 ms during 2.6 s indicating an estimated change in sonar range of 4.4 m. If the porpoise locked its sonar on a target at this time, the approaching speed would be 1.7 m s^{-1}. This is higher than the assumed cruising speed of 0.89 m s^{-1} and close to the upper limit of the descent and ascent speeds of wild harbor porpoises (Westgate et al., 1995). The animal might increase swimming speed during the final stage of approaching a potential target and reduce the speed thereafter. When approaching a potential target, finless porpoises decreased the inter-pulse interval linearly (Akamatsu et al., 2005a). The body acceleration of the tagged animals showed quick changes after the linear approach speed of about 1.7 m s^{-1} (see Akamatsu et al., 2005a, Fig. 3A) and finally the swimming speed dropped, which was interpreted as a turning (possible prey capture) behaviour. The harbor porpoise in the present study did not carry any acceleration or speed sensors that would allow description of behavioural details during and after the linear decrease of inter-pulse intervals.

In conclusion, the coastal harbor porpoise in the present study and the freshwater finless porpoises produced intense sonar signals almost continuously. The intense biosonar signals facilitate passive acoustic survey methods. Both species swam without using intense sonar signals for less than 10 m in most cases, but could remain silent or possibly use undetected low-intensity clicks for more than 1 min. During these ‘less observant’ periods, the porpoises would be susceptible to entanglement in fishing nets.

Acknowledgements

We thank Q. Zhao, Z. Wei, X. Zhang, X. Wang, B. Yu, J. Xiao, S. Li, J. Zheng, J. Xia, K. Lucke, K. Sato, A. Takahashi, V. Deecke, A. Kato, H. Tanaka, M. Suzuki, H. Muramoto, N. Sugiyama, K. Oda, A. Matsuda, S. Suzuki, T. Ishida, M. Ota, M. Nakamura, H. Hiruda, S. Numata, T. Sakai, M. Soichi, and H. Katsumata for their help in conducting this research. This work was funded by the Program for Promotion of Basic Research Activities for Innovative Biosciences of Japan, National Environmental Research Institute, Denmark, The Danish Research Council for Natural Sciences, and Forschungs- und Technologiezentrum Westkuste, University of Kiel, Germany. We thank the constructive comments from two reviewers.

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