

Grey seal attacks on harbour porpoises in the Eastern Scheldt: cases of survival and mortality

Annemieke E. Podt¹ & Lonneke L. IJsseldijk^{2*}

¹ Stichting Rugvin, Jeruzalem 31a, NL-6881 JL Velp, the Netherlands

² Faculty of Veterinary Medicine, Department of Pathobiology, Utrecht University, Yalelaan 1, NL-3584 CL Utrecht, the Netherlands, e-mail: L.L.IJsseldijk@uu.nl

Abstract: In the southern North Sea, hundreds of mutilated harbour porpoise carcasses (*Phocoena phocoena*) are found each year on beaches. Recent studies have confirmed that these concern the remains of predation by grey seals (*Halichoerus grypus*). A retrospective study of post mortem photos helped to further characterise grey seal induced wounds and indicated that grey seal predation is currently one of the main causes of death of harbour porpoises in the Netherlands. In addition to direct mortality, non-lethal interactions also occur. Both outcomes could play a significant role in ecosystem dynamics. The Eastern Scheldt has a resident group of harbour porpoises and also grey seals can be found in this semi-enclosed tidal bay, making this a suitable area for studying inter-specific interactions. The Rugvin Foundation collects photographs of harbour porpoises in the Eastern Scheldt in a database for photo-identification purposes. Four individual harbour porpoises within this database presented bilateral tailstock lesions and additional body scarring that matched descriptions of lesions induced by grey seals. These lesions appeared to be completely healed and the sighting of these scarred animals in multiple years demonstrate complete recovery from the attacks. In addition, post mortem research revealed that over the last decade at least ten porpoises found in this tidal bay died from wounds inflicted in grey seal attacks. This apparent predation threat in combination with the scarce food sources available for harbour porpoises imposes significant pressure on the survival of this species in the Eastern Scheldt. Knowledge about the interaction between grey seals and harbour porpoises is currently increasing, mainly through the investigation of stranded harbour porpoises. Our findings demonstrate that the scope of this phenomenon goes beyond direct lethality and that behavioural adaptations in harbour porpoises, aiming to prevent detection, encounter, and, eventually capture by grey seals, are to be expected.

Keywords: *Phocoena phocoena*, *Halichoerus grypus*, interspecific interaction, predator-prey relationship, body scarring, tidal bay, Eastern Scheldt, the Netherlands.

Introduction

Predator-prey interactions play a vital role in ecosystem dynamics and almost all aspects of decision-making in prey are influenced by the risk of predation. Research on the interactions between predators and prey and the behavioural aspects involved, therefore provide

valuable knowledge on species ecology, distribution and abundance (Lima 1998a, 2002). Recently, a probably novel predator-prey interaction has been described in the southern North Sea, where hundreds of severely mutilated harbour porpoises (*Phocoena phocoena*) wash ashore each year. The lesions and lacerations present on mutilated harbour porpoises

© 2017 Zoogdierverseniging. Lutra articles also on the internet: <http://www.zoogdierverseniging.nl>

*corresponding author

were matched to the inter-teeth-distance of grey seals (*Halichoerus grypus*), implicating this species in these interactions (Haelters et al. 2012). This theory was proven thanks to documentation of field observations of (fatal) interactions between grey seals and harbour porpoises (Bouveroux et al. 2014, Stringell et al. 2015) and the retrieval of grey seal DNA from bite marks on mutilated harbour porpoises (Jauniaux et al. 2014, van Bleijswijk et al. 2014). The characteristics of the bite marks on harbour porpoises were assessed by Leopold et al. (2015) in a retrospective study evaluating post mortem photos of harbour porpoises and it was concluded that predation by grey seals is one of the main causes of death among harbour porpoises in the Netherlands. Leopold et al. (2015) reported that besides direct mortality, non-lethal attacks are also likely to occur, with 46 'possible escaped harbour porpoises' (6% of the studied sample) which lacked large mutilations but presented bite marks with associated infections that were often believed to have contributed to the death of these individuals (Leopold et al. 2015). Interactions between grey seals and harbour porpoises along the southern North Sea coastlines have undoubtedly become more common in the past decade due to the increasing numbers of both species in this area (Reijnders 1995, Camphuysen 2004, Brasseur et al. 2010, Camphuysen 2011, Leopold et al. 2015).

In the Dutch semi-enclosed tidal bay 'the Eastern Scheldt' (Province of Zeeland), the focus area of this study, harbour porpoises and grey seals co-exist. Historical reports of harbour porpoise sightings and strandings are not available for this area and only started to emerge in the late 1990s (Zanderink & Osinga 2010, waarneming.nl). Nowadays, porpoises are resident in the Eastern Scheldt (Zanderink & Osinga 2010), as demonstrated by field observations, including re-sightings of well-recognisable individuals (Bakkers et al. 2016, rugvin.nl) and by stable isotope analysis of tissues obtained from stranded por-

poises (Jansen et al. 2013). Photo-identification techniques are used by the Rugvin Foundation to investigate the occurrence and abundance of this species in these waters (Strietman 2012, Bakkers et al. 2016). This is a widely used method for studying cetacean abundance and also provides data on the life history of individuals (Würsig & Jefferson 1990). Although harbour porpoises were previously thought to be less suitable for photo-identification methods (Evans & Hammond 2004), recent studies proved it to be feasible (Keener et al. 2013, Bakkers et al. 2016, Elliser & MacIver 2016). In the south-western part of the Netherlands, grey seals are found in the Voordelta, the coastal area west of the islands of the Zeeland and Zuid-Holland provinces. Tens of individuals are also reported to haul-out on sandbanks within the borders of the Eastern Scheldt (Arts et al. 2016). The accessible area of the Eastern Scheldt therefore presents a suitable area for studying the interspecific interactions of grey seals and harbour porpoises.

Knowledge about the frequency and consequences of non-lethal interactions is important when aiming to understand the behaviour of prey within an ecosystem (Lima 2002). Documented survival with complete recovery of harbour porpoises after a grey seal attack is, however, still lacking. Here, we present photographs of re-sighted harbour porpoises in the Eastern Scheldt that present body scarring consistent with descriptions of lesions induced by grey seals. Additionally, based on post mortem data of stranded harbour porpoises found in the Eastern Scheldt we investigate whether any of the deaths are attributable to grey seal attacks. Although we cannot quantify and generalise our findings to the whole population, we elaborate on the possible effects of this non-lethal interaction on the behaviour of individual porpoises and the resident population of the Eastern Scheldt. Currently, much research into harbour porpoise - grey seal interactions is being carried out across the North Sea. This study adds to our knowledge of the scale of this phenomenon.

Methods

To study survival and mortality of harbour porpoises in the Eastern Scheldt after a grey seal attack, we focussed on data available from live harbour porpoises observed in this area as well as data from deceased stranded individuals here. Photographs of individual animals were assessed for the presence of (healed) wounds which matched the description of grey seal induced lesions. In detail:

Non-lethal cases: Photographs of harbour porpoises in the Eastern Scheldt were opportunistically collected by the Rugvin Foundation for identification purposes, with photos dating back to 2007. Efforts to collect photographs intensified in the summer of 2015 and 2016, with dedicated photo-identification surveys in the north-western part of the Eastern Scheldt between the harbours of Burghsluis and Zierikzee. All available photographs of harbour porpoises within the photo-identification database of the Rugvin Foundation were examined for evidence of scarring consistent with lesions induced by grey seals as described by Leopold et al. (2015). Harbour porpoise tailstocks, an area often targeted by attacking grey seals, are typically visible when they surface and could therefore be assessed on the photographs. Individual harbour porpoises were included in the study when photographs of both sides of the tailstock were available and of sufficient quality, and when bilateral scarring was seen on the tailstock.

Lethal-cases: The Faculty of Veterinary Medicine (Utrecht University) database of post mortem-investigated harbour porpoises was used to provide supporting evidence of lethal grey seal attacks on animals found in the Eastern Scheldt in order to further assess the scale of this threat on the resident harbour porpoise population. Cases investigated between 2006-2016 were selected when stranding locations were at the entrance or inside the Eastern Scheldt, and when the post mortem results indicated that a grey seal attack was the most likely cause of death. Two

groups were distinguished: *direct lethal cases*, those cases with large, sharp-edge mutilations which did not show signs of healing or infection, often accompanied by suspect bite marks and scratches; and *non-direct lethal cases*, or 'the escaped porpoises' - those cases with suspect bite marks with associated inflammation, whilst large mutilations were lacking, according to Leopold et al. (2015).

Stranding date, location, age class and sex were recorded for each case. Carcass freshness was scored using the decomposition condition code (DCC): the DCC has five categories, with DCC1 including very fresh carcasses, and DCC5 including remains of carcasses (Kuiken & García Hartmann 1993). The nutritional condition code (NCC) was judged by the blubber thickness (measured at three locations at the cranial insertion of the dorsal fin: dorsal, lateral and ventral), amount of musculature, and the presence or absence of internal fat: the NCC has six categories, with NCC1 including porpoises in a very good body condition and NCC6 including porpoises in a very poor body condition. The characteristics and incidence of grey seal-associated wounds found on stranded harbour porpoises were evaluated according to Leopold et al. (2015).

Results

Non-lethal cases

Four individual porpoises from the Rugvin Foundation database met the selection criteria. These four cases are described and of each case four photographs are presented: the left lateral side (A), the right lateral side (B), the left side of the tailstock (C) and the right side of the tailstock (D).

HPI (figure 1):

The first photographs of this individual were taken in 2012. At that time, no scars were present on the lateral sides or the tailstock. The



Figure 1. Photographs of harbour porpoise 'HP1', taken on 22 July 2016 (A, B, C), and 30 August 2016 (D). Photos: Annemieke Podt.

individual was photographed again in 2015, with healed scars visible on its flanks and bilaterally on the tailstock. There was a notch on the dorsal side of the tailstock with bilaterally healed scars (figure 1C and 1D). There were two large scars on the right lateral side, one of which seems to extend towards the ventral side (figure 1B). Smaller scratches were present around the horizontally curved scar. There were five re-sightings of this individual in the summer of 2016. The animal obtained two new minor markings on its left lateral side in 2016, close to the already present scars (figure 1A).

HP2 (figure 2):

The first photographs of this individual were taken in 2011. The animal was scarred on both sides of the posterior part and the tailstock (figure 2C and 2D) and it had a nick in the dorsal fin. Since 2011, this individual was encountered yearly, except in 2014. The scars present on the right side of the head and flank in 2016 (figure 2B) were not observed in 2015. In 2013, no scars were visible on the left side

of the head (figure 2A). A photograph of this part of the body, made in July 2016, revealed new markings. This individual was seen twice during this summer.

HP3 (figure 3):

The first photographs of this individual were taken in 2014. Only the left side of the body was photographed, showing a scar crossing the dorsal side cranial to the dorsal fin and markings on the tailstock (figure 3A and 3C). The scar on the dorsal side was also visible on a photograph of the right side, taken in 2015 (figure 3B). No photos of the right side of the tailstock were available prior to 2016. This individual was seen twice in the summer of 2016. Photos of both sides of the tailstock were taken and showed clear scars (figure 3C and 3D), including a parallel zigzag scar on the right side of the tailstock.

HP4 (figure 4):

The first photograph of this individual was taken in 2007. More sightings followed in 2009-2012 and in 2014-2015 and there were



Figure 2. Photographs of harbour porpoise 'HP2', taken on 30 July 2016. *Photos: Annemieke Podt.*



Figure 3. Photographs of harbour porpoise 'HP3', taken on 30 August 2016 (B, C), and 31 August 2016 (A, D). *Photos: Annemieke Podt.*

four re-sightings in 2016. Markings on the tailstock were photographed for the first time in 2015, and were not present during the sighting in 2014. This individual had a notch on the

top of the tailstock. On the left side of the tailstock, parallel scars were present (figure 4C). However, the markings were not parallel on the right side and converged at the notch on



Figure 4. Photographs of harbour porpoise 'HP4', taken on 19 August (B, C), 30 August (A), and 31 August 2016 (D). Photos: Annemieke Podt.

the dorsal side of the tailstock (figure 4D). A small indentation cranial to the dorsal fin became apparent in 2014 (figure 4B).

Lethal cases

Ten cases from the post mortem database of Utrecht University met the selection criteria. These included three individuals in the 'direct lethal' group (figure 5, case TX046), and seven individuals in the 'non-direct lethal' group. All cases were juveniles, with the exception of one neonate (case UT1525) and both sexes were represented with six targeted females and four males. Most cases were very fresh (DCC1) to fresh (DCC2), with two cases in a more advanced state of decomposition (DCC3: UT125 and DCC4: UT1542). A more advanced state of decomposition often hampers the assessment of the cause of death, therefore it cannot be excluded that the mutilation and bilateral tailstock lesions on case UT1542 could have been induced post mortem. The bilateral tailstock lesion on case

UT125 presented a clear inflamed wound, which strongly points towards a previous grey seal attack based on the morphologic appearance. The cases in the non-direct lethality group in general appear in a moderate to poor nutritional condition suggesting an overall deteriorated health (average NCC of 4). Direct lethal cases present a lower NCC, representing a better nutritional condition, although numbers here are too low to make a solid judgement. The basic case characteristics including the lethality category are presented in table 1. Five carcasses were discovered at the entrance of the Eastern Scheldt, while the other five cases were found inside the Eastern Scheldt (figure 6).

Discussion

This study investigated whether the small resident population of harbour porpoises in the Eastern Scheldt is currently facing a predation pressure by grey seals. To our knowledge, there has been no direct observation of

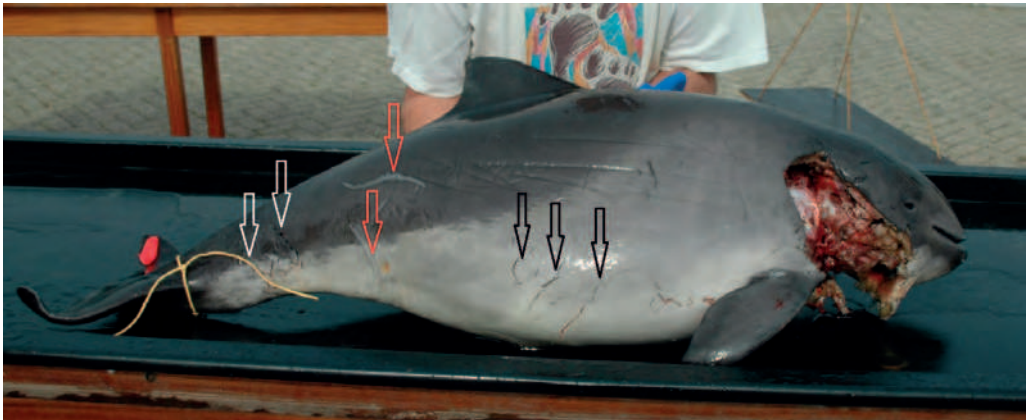


Figure 5. Harbour porpoise carcass ‘TX046’, showing sharp edge mutilation on the throat area, bite marks on the tailstock (white arrows) and scratches on the mid-ventral body side (black arrows). In addition, two healed scars of unknown origin are present (red arrows). *Photo: Kees Camphuysen.*

Table 1. Data of stranded harbour porpoises found at the entrance of and inside the Eastern Scheldt and which most likely died directly or non-directly from a grey seal attack based on post mortem findings.

Idcode	Date	Location	Age class	Sex	DCC	NCC	Lethality category
TX046	15-03-2006	Burgh	Juvenile	Male	2	1	Direct
TX059	23-04-2006	Scherpenisse	Juvenile	Female	1	4	Non-direct
UT125	16-08-2008	Oosterland	Juvenile	Male	3	2	Non-direct
UT159	05-08-2008	Stavenisse	Juvenile	Female	2	3	Non-direct
UT391	31-03-2010	Neeltje Jans	Juvenile	Female	2	5	Non-direct
UT442	13-03-2011	Neeltje Jans	Juvenile	Female	2	6	Non-direct
UT1129	10-03-2013	Neeltje Jans	Juvenile	Male	2	3	Direct
UT1513	22-03-2016	Kats	Juvenile	Female	1	4	Non-direct
UT1525	25-06-2016	Burghsluis	Neonate	Female	2	4	Non-direct
UT1542	11-04-2016	Oostdijk	Juvenile	Male	4	2	Direct

grey seal attacks on harbour porpoises within the Eastern Scheldt. However, at least ten harbour porpoise carcasses demonstrating bite marks and/or mutilations consistent with a grey seal attack were found in these waters. Photographs of four live harbour porpoises in the Eastern Scheldt show parallel, bilateral scarring on the tailstocks which is consistent with injuries reported to be inflicted by the teeth of grey seals (Haelters et al. 2012, Leopold et al. 2015), making a grey seal attack the most probable cause of these scars. Our study suggests that grey seal attack harbour porpoises within the borders of the Eastern Scheldt and whilst in some cases this attack

was fatal, other porpoises survive and completely recover.

In addition to the tailstock lesions on the live individuals that were the focus of this study, other markings such as bite marks on the head and the pectoral fins and nail rake marks anywhere on the body (up to five parallel scratches) have also been reported in relation to grey seal predation (Haelters et al. 2012, Leopold et al. 2015). However, in live animals, only a limited part of the porpoise’s body is visible when it surfaces to breathe, and as such, scarring on the ventral side and extremities could not be assessed. Three of the four live porpoises described in



Figure 6. Map of the Eastern Scheldt area with stranding locations of ten harbour porpoises (black dots) in the Eastern Scheldt which died directly or non-directly from a grey seal attack. Five individuals were found at the entrance of the Eastern Scheldt, whilst the other five were found more inland.

this study show clear markings on the dorsal to dorsolateral sides. Also, consecutive photos of HP1, HP2 and HP4 taken during several years, demonstrate that not all lesions could have been inflicted in a single event. Moreover, it is possible that not all of the lesions on the four described porpoises can be explained by grey seal attacks. Other causes cannot be ruled out, such as contact with Japanese oysters (*Crassostrea gigas*), an invasive species with a razor-sharp shell that have colonised tidal flats in the Eastern Scheldt (Troost 2009), or temporary entanglement in fishing gear (Read & Murray 2000). Boat propeller injuries are unlikely, due to the superficial nature of the injuries on the four harbour porpoises described here (Read & Murray 2000). Other species reported to harass and kill harbour porpoises in European waters, including killer whales (*Orcinus orca*) (Cosentino 2015) and bottlenose dolphins (*Tursiops truncatus*)

(MacLeod et al. 2007), are only very rarely found in the southern part of the North Sea.

It is possible that the lesions seen on the four porpoises from the Rugvin Foundation database were inflicted outside the Eastern Scheldt, as some markings were present when animals were photographed for the first time in these waters. However, HP1 was photographed without the scars in 2012 in the Eastern Scheldt, and also HP4 was seen without tailstock lesions in 2014. Passage through the storm surge barrier that separates the Eastern Scheldt from the North Sea is possible but suggested to occur only rarely (Korpelshoek 2011). Stable isotope studies of stranded harbour porpoises from this area revealed a distinct $\delta^{13}\text{C}$ signature in muscle tissue, demonstrating that these animals foraged there for a longer period. This distinct signature was lacking in bone samples of the same individuals, suggesting a relatively recent but per-

manent shift (Jansen et al. 2013). The study of Jansen et al. (2013) suggests that the semi-open barrier may form a passage barrier and that the Eastern Scheldt would, therefore, be an ecological trap for harbour porpoises. If the porpoises do not leave the Eastern Scheldt, this would also suggest that grey seal predation is occurring in these waters. Nevertheless, grey seal attacks occur also in the coastal and deeper water of the North Sea, with stranding records of fresh, mutilated cases from anywhere on the Dutch coastline (Leopold et al. 2015). Escapes and subsequent complete recovery of harbour porpoises after grey seal attacks may also very likely occur elsewhere in the North Sea, however, the collection of good quality photographs over a period of time to prove this is considered too challenging given the elusive nature of these relatively small marine mammals.

Further evidence in the form of the mutilated carcasses found inside the Eastern Scheldt reveals that in addition to the non-lethal attacks, fatal attacks indeed occur within its borders. No clear difference was found in sex of the targeted porpoises, however the majority of them were juvenile animals. The harbour porpoises which die acutely of a grey seal attack present a better nutritional condition than those dying as a result of a previous, failed attack, where a deteriorated general health status is a common finding. These findings correspond to the results presented by Leopold et al. (2015), who concluded that the affected animals were mostly healthy juveniles.

Survival after a grey seal attack possibly allows a porpoise to learn from this predatory attempt and adapt its behaviour to try to prevent detection, encounter and eventually (fatal) capture. The result is an everlasting trade-off between energy intake and the costs of mortality due to predation; to this end, long-term behavioural changes with impacts on entire ecosystems can be expected (Lima 1998b). Changes can be seen in the abundance, habitat use, and hunger-depend-

ent risk-taking behaviours associated with energy intake (Lima 1998a, 1998b). Harbour porpoise numbers in the southern North Sea were recently reported to have decreased and it was suggested that prey availability, as well as predatory pressure played a role in this drop (Haelters & Geelhoed 2015). Harbour porpoise prey availability is reported to be low in the Eastern Scheldt (Tulp 2015) and concerns have been raised about the energy intake of the porpoises living in these waters (Jansen et al. 2013, rugvin.nl). Recently, a study by van Dam et al. (2017) on Eastern Scheldt porpoises demonstrated that their diet (especially that of adults) differs only slightly from that of North Sea stranded animals. No significant difference was found in general nutritive condition (body condition, e.g. blubber thicknesses) between Eastern Scheldt and North Sea stranded animals and therefore van Dam et al. (2017) concluded that Eastern Scheldt-bound porpoises may have developed specialised feeding skills to cope with low prey availability. This could mean that juveniles face increased competition for prey within the Eastern Scheldt with adults of their own species (van Dam et al. 2017). Nutritional challenges also include feeding adaptations as a result of predator presence. Porpoises that co-exist in areas with bottlenose dolphins adapt by losing weight to allow efficient manoeuvrability (MacLeod et al. 2007), and this phenomenon is reported in many other organisms at risk of predation (e.g. Lima 1986, Houston et al. 1993, Lima 1998b). Hunger-dependent risk-taking makes porpoises more prone to emaciation (Leopold et al. 2015). For harbour porpoises in the Eastern Scheldt - an environment where food availability is already scarce (van Dam et al. 2017) - the combination of this hunger-dependent risk-taking and a predation risk could result in a population reduction, of which the highest minimum population size was estimated at 61 individuals in June 2011, but reported to have decreased to around 30 individuals in the following five years (Bakkers & Tuhuteru 2016, rugvin.nl).

Conclusion

The documentation of complete recovery after a probable grey seal attack reveals that besides mortality, non-lethal interactions should also be considered when investigating and assessing the extent of this phenomenon, both in the Eastern Scheldt and in the North Sea. Harbour porpoises present in the Eastern Scheldt are believed to be 'trapped' and therefore resident (Jansen et al. 2013). We show that these resident porpoises are faced with a predation risk due to co-existence with grey seals, which could induce significant behavioural and distribution changes, as well as negatively affect population numbers in this area. Besides continuing the research on the wild porpoises in the Eastern Scheldt in order to estimate the abundance, post mortem research of stranded animals and subsequent stable isotope and diet analysis are also useful tools for evaluating the status of this population. To understand and eventually predict spatial and temporal changes in harbour porpoise abundance and distribution here and elsewhere, assessment of fine-scale habitat use and abundance of their prey as well as their predators would be recommended.

Acknowledgements: Fieldwork of Rugvin Foundation was funded by the World Wide Fund for Nature. We thank all the volunteers conducting the fieldwork for their help with the data collection. Special thanks go to Wouter Jan Strietman, who started with the photo-identification research on harbour porpoises in the Eastern Scheldt and collected many photographs in the first years of the project. We would also like to thank Sanne Bakkers and Naomi Tuhuteru for their data collection in the summer of 2015 and Frank Zanderink for his input on an earlier draft of this manuscript. The cases collected for post mortem research were available thanks to the volunteers of the Dutch stranding scheme. We would like to thank all students, volunteers, technicians and veterinary pathologists who helped conducting harbour porpoise necropsies at IMARES/NIOZ (2006-2007) and the department of Pathobiology (Utrecht University, 2008-2016). The post mortem research was financed by the Dutch

Ministry of Economic Affairs under grant number 140000353. Finally, we thank Steve Geelhoed, Jan Haelters and Mardik Leopold for their helpful comments and suggestions on a previous draft of this manuscript, and Rachel Thomas for her final guidance in the setup of this manuscript.

References

- Arts, F.A., S. Lilipaly & R.C.W. Strucker 2016. Watervogels en zeezoogdieren in de Zoute Delta 2014 / 2015. Report BM 16.09. RWS Centrale Informatievoorziening, Lelystad, the Netherlands.
- Bakkers, S. & N.A.M. Tuhuteru 2016. Photo-identification of harbour porpoises in the Eastern Scheldt. Internal report. Stichting Rugvin, Velp, the Netherlands
- Bakkers, S., N.A.M. Tuhuteru, W.J. Strietman & F. Zanderink 2016. Harbour porpoise photo-ID in the Eastern Scheldt, the Netherlands. Poster presented at the 30th Conference of the European Cetacean Society, Madeira, 14-16 March 2016.
- Bouveroux, T., J.J. Kiszka, M.R. Heithaus, R. Jauniaux & S. Pezeril 2014. Direct evidence for gray seal (*Halichoerus grypus*) predation and scavenging on harbor porpoises (*Phocoena phocoena*). *Marine Mammal Science* 30: 1542-1548.
- Brasseur, S., T. van Polanen Petel, G. Aarts, E. Meesters, E. Dijkman & P. Reijnders 2010. Grey Seals (*Halichoerus grypus*) in the Dutch North Sea: Population ecology and effects of wind farms. Report C137/10. IMARES Wageningen UR, Wageningen, the Netherlands.
- Camphuysen, C.J. 2004. The return of the harbour porpoise (*Phocoena phocoena*) in Dutch coastal waters. *Lutra* 47 (2): 113-122.
- Camphuysen, C.J. 2011. Recent trends and spatial patterns in nearshore sightings of harbour porpoises in the Netherlands (Southern Bight, North Sea), 1990-2010. *Lutra* 54: 39-47.
- Cosentino, A.M. 2015. First record of Norwegian killer whales attacking and feeding on a harbour porpoise. *Marine Biodiversity Records* 8: 1-5.
- Elliser, C. & K. MacIver 2016. Who is that? Identifying individuals and creating a regional ID catalogue for the harbor porpoise in the Salish Sea. Poster

- presented at the Salish Sea Ecosystem Conference, Vancouver, 13-15 April 2016.
- Evans, P.G.H. & P.S. Hammond 2004. Monitoring cetaceans in European waters. *Mammal Review* 34 (1): 131–156.
- Haelters, J. & S. Geelhoed 2015. Over enkele jaren weer zeldzaam? Minder bruinvissen in de zuidelijke Noordzee. *Zoogdier* 26 (4): 1-3.
- Haelters, J., F. Kerckhof, T. Jauniaux & S. Degraer 2012. The grey seal (*Halichoerus grypus*) as a predator of harbour porpoises (*Phocoena phocoena*)? *Aquatic Mammals* 38: 343-353.
- Houston, A.I., J.M. McNamara & J.M.C. Hutchinson 1993. General results concerning the trade-off between gaining energy and avoiding predation. *Philosophical Transactions of the Royal Society B* 341: 375–397.
- Jansen, O.E., G.M. Aarts & P.J.H. Reijnders 2013. Harbour porpoises *Phocoena phocoena* in the Eastern Scheldt: a resident stock or trapped by a storm surge barrier? *PLoS ONE* 8 (3): e56932.
- Jauniaux, T., M.M. Garigliany, P. Loos, J-L. Bourgain, T. Bouveroux, F. Coignoul, J. Haelters, J. Karpouzopoulos, S. Pezeril & D. Desmecht 2014. Bite injuries of grey seals (*Halichoerus grypus*) on harbour porpoises (*Phocoena phocoena*). *PLoS ONE* 9 (12): e108993.
- Keener, W., I. Szczepaniak, J. Stern & M. Webber 2013. Porpoises and dolphins find new habitat in San Francisco Bay. State of the San Francisco Estuary Conference, Native Wildlife and Invasive Species Session, Oral Abstracts.
- Korpelshoek, L.D. 2011. Resident harbour porpoises *Phocoena phocoena* in the Oosterschelde (Netherlands): their behaviour compared to the behaviour of migratory harbour porpoises in the southern North Sea. MSc thesis. Leiden University, Leiden, the Netherlands.
- Kuiken, T. & M. García Hartmann (eds) 1993. Cetacean pathology: dissection techniques and tissue sampling. Proceedings of the European Cetacean Society Workshop, Leiden, the Netherlands.
- Leopold, M.F., L. Begeman, J.D.L. van Bleijswijk, L.L. IJsseldijk, H. Witte & A. Gröne 2015. Exposing the grey seal as a major predator of harbour porpoises. *Proceedings of the Royal Society Biology* 282: 20142429. DOI: 10.1098/rspb.2014.2429.
- Lima, S.L. 1986. Predation risk and unpredictable feeding conditions - determinants of body-mass in birds. *Ecology* 67: 377–385.
- Lima, S.L. 1998a. Stress and decision making under the risk of predation: Recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27: 215-290.
- Lima, S.L. 1998b. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48 (1): 25-34.
- Lima, S.L. 2002. Putting predators back into behavioral predator-prey interactions. *Trends in Ecology & Evolution* 17 (2): 70-75.
- MacLeod, R., C.D. MacLeod, J.A. Learmonth, P.D. Jepson, R.J. Reid, R. Deaville & G.J. Pierce 2007. Mass-dependent predation risk and lethal dolphin-porpoise interactions. *Proceeding of the Royal Society Biology* 274: 2587–2593.
- Read, A.J. & K.T. Murray 2000. Gross evidence of human-induced mortality in small cetaceans. NOAA Technical Memorandum NMFS-OPR-15. U.S. Department of Commerce, Washington D.C., USA.
- Reijnders, P.J.H. 1995. Recolonization of the Dutch Wadden Sea by the grey seal *Halichoerus grypus*. *Biological Conservation* 71 (3): 231-235.
- Rugvin.nl. Available at: <http://rugvin.nl>.
- Strietman, W.J. 2012. Photo-identification of harbour porpoises in the Oosterschelde estuary, the Netherlands. Poster presented at the 26th Conference of the European Cetacean Society, Galway, 26-28 March 2012.
- Stringell, T., D. Hill, D. Rees, F. Rees, P. Rees, G. Morgan, L. Morgan & C. Morris 2015. Predation of harbour porpoises (*Phocoena phocoena*) by grey seals (*Halichoerus grypus*) in Wales. *Aquatic Mammals* 41 (2): 188-191.
- Troost, K. 2009. Pacific oysters in Dutch estuaries. Causes of success and consequences for native bivalves. PhD thesis. University of Groningen, Groningen, the Netherlands.
- Tulp, I. 2015. Analyse visgegevens DFS (Demersal Fish Survey) ten behoeve van de compensatiemonitoring Maasvlakte2. Rapport C080/15. IMARES Wageningen UR, Wageningen, the Netherlands.
- van Bleijswijk, J.D.L., L. Begeman, H.J. Witte, L.L. IJsseldijk, J.D.L., L. Begeman, H.J. Witte, L.L. IJsseldijk

- seldijk, S. Brasseur, A. Gröne & M.F. Leopold 2014. Detection of grey seal *Halichoerus grypus* DNA in attack wounds on stranded harbour porpoises *Phocoena phocoena*. *Marine Ecology Progress Series* 513: 277-281.
- van Dam, S., L. Solé, L.L. IJsseldijk, L. Begeman & M.F. Leopold 2017. The semi-enclosed tidal bay Eastern Scheldt in the Netherlands: porpoise heaven or porpoise prison? *Lutra* 60 (1): 5-18.
- Waarneming.nl. Available at: www.waarneming.nl.
- Würsig, B. & T.A. Jefferson 1990. Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission, Special Issue* 12: 43-52.
- Zanderink, F. & N. Osinga 2010. De bruinvis is terug in de Oosterschelde. *Zoogdier* 21 (3): 12-15.

Samenvatting

Aanvallen van grijze zeehond op bruinvissen in de Oosterschelde: ontsnappings- en sterftegevallen

In het zuidelijke deel van de Noordzee worden jaarlijks honderden verminkte, dode bruinvissen (*Phocoena phocoena*) aangetroffen. Recente studies tonen een relatie aan met predatie door grijze zeehonden (*Halichoerus grypus*). Door middel van een retrospectieve studie van sectiefoto's kon aangetoond worden dat aanvallen van grijze zeehonden een van de meest voorkomende oorzaken zijn van sterfte onder bruinvissen in Nederland. Naast dodelijke aanvallen worden ook niet-dodelijk aanvallen gerapporteerd, die een grote rol kunnen spelen in de dynamiek van het ecosysteem, in het bijzonder in gebieden waar veel grijze zeehonden en bruinvissen samen voorkomen. De Oosterschelde heeft een residente populatie bruinvissen en ook grijze zee-

honden komen in dit gebied voor. Dit maakt de Oosterschelde een geschikte locatie om de interactie tussen deze twee soorten te onderzoeken. Foto's van bruinvissen in de Oosterschelde worden verzameld door Stichting Rugvin voor foto-identificatiedoeleinden. In deze database werden bij vier individuen bilaterale littekens vastgelegd op de staartaanzet en op additionele delen van de flanken. Deze littekens vertoonden sterke overeenkomsten met de beschreven wonden die door grijze zeehonden kunnen worden toegebracht bij een predatiepoging. De wonden waren genezen en bovendien waren deze bruinvissen ook in voorgaande jaren geobserveerd met deze littekens. Dit bewijst dat deze vier dieren volledig hersteld zijn na het veroorzaakte trauma. Daarnaast heeft postmortaal onderzoek aangetoond dat in de laatste decennia minimaal tien in dit gebied gestrande bruinvissen gestorven zijn als gevolg van een aanval door grijze zeehond. Deze predatiedreiging, in combinatie met de schaarse voedingsbronnen die beschikbaar zijn voor bruinvissen, impliceert een aanzienlijke druk op het overleven van de bruinvis in de Oosterschelde. Gedragsaanpassingen bij bruinvissen zijn daarom te verwachten. De interactie tussen grijze zeehonden en bruinvissen in de Noordzee en elders wordt intensief bestudeerd, maar de studies richten zich in veel gevallen op het onderzoek van gestrande, dode dieren. Onze bevindingen laten zien dat, naast de interacties waarbij bruinvissen direct worden gedood, ook niet-dodelijke interacties in beschouwing moeten worden genomen bij het onderzoek naar de schaal van dit fenomeen, zowel in de Oosterschelde als in de Noordzee.

Received: 8 May 2017

Accepted: 16 August 2017