

HARBOUR PORPOISE BEHAVIOUR NEAR BOTTOM SET NETS AND ACOUSTIC BYCATCH MITIGATION DEVICES

DISSERTATION



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Zur Erlangung des Doktorgrades an der Fakultät für Mathematik, Informatik und
Naturwissenschaften der Universität Hamburg

Vorgelegt von Thaya Mirinda Dinkel

Hamburg 2025

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*This thesis is dedicated to harbour porpoises,
especially to those, whose journey ends too soon*

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Summary

Bycatch in set net fisheries is considered the biggest threat to small cetacean populations worldwide. In the western Baltic Sea or Belt Sea, concerns around elevated bycatch rates of harbour porpoises (*Phocoena phocoena*) have already been raised in the 1980s and are nowadays considered above sustainable threshold levels. One of the primary bycatch mitigation tools employed in gillnet fisheries are acoustic deterrent devices (ADD, so-called pingers), that emit artificial sounds with the aim to keep animals away from fishing gear, and which have proven to significantly reduce harbour porpoise bycatch in set net fisheries worldwide. However, concerns about habitat exclusion of harbour porpoises have been raised around them. To address these concerns, the PAL (Porpoise ALert), an alternative acoustic alerting device that emits synthetic harbour porpoise signals from the Belt Sea population was developed. PAL is currently being implemented in a part of the German fishery in the Belt Sea on a voluntary basis after it showed to be effective in reducing harbour porpoise bycatch in gillnet fisheries. However, even with pingers and PAL, bycatch events persist in the fishery. In fact, despite decades of research going into bycatch mitigation, the mechanisms behind bycatch events in gillnets and in the vicinity of mitigation devices remain poorly understood, particularly regarding animal behaviour, as direct observations are methodologically and logistically challenging. The aim of this thesis was to advance knowledge on harbour porpoise behaviour near bottom set nets and near the alerting device PAL in the Belt Sea, as well as looking at whether porpoises habituate to the PAL signal. It further assessed two land-based methods to observe harbour porpoises providing guidance for method selection for future research, thus addressing issues related to the methodological and logistical challenges when studying bycatch of porpoises.

Harbour porpoises are particularly challenging to observe due to their small size and inconspicuous behaviour. To better understand their behaviour, efficient observation tools are required. The theodolite and the drone are two land-based observation methods commonly employed to observe small cetaceans with near shore distribution. In a first step of this thesis, advantages and disadvantages of both tools were analyzed while studying the harbour porpoise. For this aim, data on their location, behaviour and group sizes of porpoises was collected and compared between methods during a field experiment in Fyns Hoved (Denmark). The theodolite proved to be more adept at rapidly collecting data on the general distribution of porpoises in an area and excelled at gathering data at greater distances. The accuracy of obtained positional data of porpoises at the surface was similar with both methods, but drones revealed a clear advantage in behavioural observations, as they allow recording the animals even under the water surface. Group sizes were also determined more precisely using drones (Chapter 3).

Based on these findings, drones were used to study in more detail the behaviour of porpoises near a bottom set net structure with and without PAL during a targeted experiment in Fyns Hoved (Denmark). These trials were designed to enhance our understanding on underlying behavioural mechanisms leading to entanglement in set bottom nets as well as behavioural reactions of porpoises towards a net equipped with PAL. For this, wild harbour porpoises were recorded with drones and acoustic underwater recorders near a bottom set net structure during an *in situ* experiment in the Danish Belt Sea and different aspects of their behaviour studied: swimming speed, respiration rates, reaction types towards the net and the PAL and apparent reaction distances. Porpoises demonstrated limited behavioral responses when navigating the net, with the most common reaction being swimming over the float line without any apparent reaction, both in the presence and absence of PAL. Porpoises exhibited a consistent pattern of swimming speed, increasing the speed in direct vicinity of the net and slowing down after interacting with the net. This pattern was observed both when only the net was present as well as when the PAL was attached. The echolocation behaviour of the porpoises showed some significant differences when the PAL was present with minimum inter click interval and click train

duration being lower after porpoises crossed the net. In general, during the trials all porpoises navigated the nets efficiently which might suggest that bycatch events could be related to distractions and accidents rather than pure net detection failure (Chapter 4).

To further investigate whether porpoises in Germany might have habituated to the PAL signal since its first implementation in 2017, a long-term experiment was set up in collaboration with some fishers in Germany and Denmark to record the porpoises' echolocation behaviour near nets with PAL. For this aim, two areas inhabited by animals from the Belt Sea population were selected as the PAL signal is a synthetic porpoise sound from this population and has thus far only been successfully tested in this area. As PAL is not employed in the fishery in Denmark, the experiment was conducted under the assumption that porpoises in Denmark are more naïve to the PAL signal, thus considering Denmark as a not-exposed area. To test whether porpoises habituated to PAL in Germany, the echolocation of porpoises on reference stations without PAL and near PAL-equipped nets was compared within Germany and Denmark and between the countries. Four parameters that describe the porpoises' click trains were selected for this aim and investigated using traditional statistics as well as machine learning models: number of clicks within a click train, the median frequency, the average sound and the minimum inter click interval of a click train. The median values for all four acoustic parameters were very similar, both between the reference stations of both countries and between reference stations and PAL-equipped nets within countries. Based on the four selected click train parameters, habituation of German porpoises towards the PAL was not detected (Chapter 5).

The new findings generated in this thesis address several knowledge gaps associated to the study of harbour porpoises and their interaction with bottom set nets and the PAL in the Belt Sea. The evaluation of the two land-based observation methods gives evidence-based guidance for researchers to choose a suitable method in accordance with their research question and sets a base to maintain comparability among different studies that employed theodolites or drones for similar aims. It further revealed that drones are more suitable to study the behaviour of porpoises as they allow recording the animals even under the water surface. This advantage was further highlighted when studying the behaviour of porpoises interacting with a bottom set net structure in the wild for the first time. The interactions revealed that porpoises are able to navigate nets without getting entangled in them and that they do not exhibit a strong reaction either in behaviour, echolocation or swimming speeds when interacting with nets and the PAL. However, despite their ability to avoid nets during the trials, bycatch persists in actual fisheries which might be attributed to distraction or inexperience rather than a lack of net detectability. It is thus recommended that alerting strategies should be combined with materials enhancing the acoustic detectability of nets to further reduce the bycatch risk. Based on previously available information of the PAL and new findings from this dissertation, the PAL seems to be a good alternative to traditional pingers for the Belt Sea, as PAL do not exclude porpoises from their habitat, and signs of habituation to the signal were not detected in the four analyzed click train parameters. Besides these promising findings, they do not yield information on whether PAL still contributes sufficiently to bycatch reduction in the German fishery. To address this question, it is suggested that a long-term bycatch monitoring scheme be implemented to ascertain whether the proven bycatch reduction effect of the PAL persists over time, given the complexity of the real fishery in the Belt Sea. This is especially relevant in light of the limited information available on German harbour porpoise bycatch rates and the fact that current estimated bycatch levels for the Belt Sea exceed sustainable bycatch thresholds.

Zusammenfassung

Der Beifang in der Stellnetzfischerei gilt als die größte Bedrohung für Kleinwalpopulationen weltweit, darunter auch für den in der Ostsee heimischen Schweinswal (*Phocoena phocoena*). In der westlichen Ostsee oder Beltsee wurde bereits in den 1980er Jahren auf die hohen Beifangraten von Schweinswalen aufmerksam gemacht und auch heutzutage liegen die Beifangraten hier über den als nachhaltig angesehenen Schwellenwerten. Eines der verbreitetsten Instrumente zur Vermeidung des Beifangs von Kleinwalen in der Stellnetzfischerei sind akustische Abschreckvorrichtungen (acoustic deterrent devices - ADDs, sogenannte Pinger), die künstliche Töne aussenden, um die Tiere von den Fanggeräten fernzuhalten und deren Beifang somit weltweit nachweislich erheblich zu reduzieren. Dennoch liegen Bedenken hinsichtlich der Vertreibung von Schweinswalen aus ihren Lebensräumen vor. Um der großräumigen Vertreibung von Schweinswalen entgegenzuwirken, wurde der sogenannte PAL (Porpoise ALert) entwickelt. Der PAL ist ein alternatives akustisches Warngerät, das nachgeahmte Laute von Schweinswalen der Beltsee-Population aussendet. PAL hat sich als wirksam bei der Verringerung des Schweinswalbeifangs erwiesen und wird seit 2017 auf freiwilliger Basis von einem Teil der deutschen Fischerei in der Beltsee eingesetzt. Dennoch kommt es trotz Pinger- und PAL-Einsatz weiterhin zu Beifängen von Schweinswalen in der Stellnetzfischerei. Auch nach jahrzehntelanger Forschung im Bereich der Beifangreduzierung sind die zugrundeliegenden Mechanismen hinter den Beifangereignissen in Stellnetzen sowie in der Nähe von technischen Maßnahmen zur Beifangreduzierung nach wie vor nur unzureichend bekannt. Dies betrifft insbesondere das Verhalten der Tiere, da direkte Beobachtungen methodisch und logistisch schwierig sind. Ziel dieser Arbeit war es, das Wissen über das Verhalten von Schweinswalen in der Nähe von Stellnetzen und dem Warngerät PAL in der Beltsee zu erweitern und zu untersuchen, ob sich Schweinswale an das PAL-Signal gewöhnen. Darüber hinaus wurden zwei landgestützte Methoden zur Beobachtung von Schweinswalen bewertet. Die Ergebnisse dieser Bewertung, einschließlich der Betrachtung von logistischen Herausforderungen, stellen eine Orientierungshilfe für die Auswahl von Methoden in künftigen Forschungsarbeiten dar, deren Ziel die Untersuchung des Beifangs von Schweinswalen und seiner Ursachen ist.

Schweinswale sind aufgrund ihrer geringen Größe und ihres unauffälligen Verhaltens besonders schwierig zu beobachten. Um ihr Verhalten besser zu verstehen, sind effiziente Beobachtungsinstrumente erforderlich. Der Theodolit und die Drohne sind zwei Beobachtungsmethoden, die häufig zur Beobachtung von Kleinwalen in Küstennähe eingesetzt werden. In einem ersten Schritt dieser Arbeit wurden die Vor- und Nachteile der beiden Beobachtungsinstrumente für die Untersuchung des Schweinswals analysiert. Zu diesem Zweck wurden während eines Feldexperiments in der dänischen Beltsee bei Fyns Hoved (Dänemark) Daten über die Position, das Verhalten und die Gruppengröße von Schweinswalen gesammelt und zwischen beiden Methoden verglichen. Es zeigte sich, dass der Theodolit besser geeignet ist, um schnell Daten über die allgemeine Verteilung der Schweinswale in einem Gebiet zu sammeln und bei der Erfassung von Daten über größere Entfernungen bessere Ergebnisse liefert. Die Genauigkeit der gewonnenen Positionsdaten der Schweinswale an der Oberfläche war bei beiden Methoden ähnlich, aber Drohnen zeigten einen klaren Vorteil bei Verhaltensbeobachtungen, da sie die Erfassung der Tiere auch unter der Wasseroberfläche ermöglichen. Die Gruppengrößen wurden mit Drohnen ebenfalls genauer bestimmt (Kapitel 3).

Auf der Grundlage der Erkenntnisse aus Kapitel 3 wurden daher Drohnen eingesetzt, um das Verhalten von Schweinswalen in der Nähe einer Stellnetzstruktur mit und ohne PAL vor der Küste von Fyns Hoved (Dänemark) detaillierter zu untersuchen. Diese Versuche sollten das Verständnis für die zum Beifang führenden Verhaltensmechanismen, sowie für die Reaktionen von Schweinswalen auf eine mit PAL ausgestattete Netzstruktur verbessern. Während der Versuche wurden zusätzlich zu Drohnen auch

Unterwasser-Akustikrekorder in der Nähe der Stellnetzstruktur ausgebracht. Verschiedene Aspekte des Verhaltens der Tiere wurden aufgezeichnet bzw. bestimmt: Schwimmgeschwindigkeit, Atmungsraten, Reaktionen auf das Netz und den PAL sowie Reaktionsdistanzen. Schweinswale zeigten in ihrem Verhalten begrenzte Reaktionen bei der Bewegung entlang der Netzstruktur. Die häufigste Reaktion auf das Netz und das Netz mit PAL war das Schwimmen über die Schwimmleine hinweg, ohne eine offensichtliche Abweichung der Schwimmrichtung. Schweinswale zeigten ein einheitliches Muster der Schwimmgeschwindigkeit, wobei die Geschwindigkeit in unmittelbarer Nähe der Netzstruktur zunahm und sich nach der Interaktion mit der Netzstruktur verlangsamte. Dieses Muster wurde sowohl während nur die Netzstruktur im Wasser war beobachtet, als auch wenn der PAL an der Netzstruktur war. Das Echoortungsverhalten der Schweinswale hingegen wies signifikante Unterschiede, je nachdem, ob PAL an der Netzstruktur war oder nicht. Sowohl das kürzeste Intervall zwischen den Klicks in einer Klicksequenz und die Dauer der Klicksequenz waren geringer, nachdem die Schweinswale über die Netzstruktur mit dem PAL geschwommen waren. Während der Versuche gab es keine Anzeichen, dass Schweinswale Probleme hatten, die Netzstruktur zu vermeiden oder darüber hinweg zu schwimmen, was darauf hindeuten könnte, dass Beifangereignisse eher auf Ablenkungen und Unfälle, als auf eine grundsätzlich fehlende Möglichkeit das Netz wahrzunehmen, zurückzuführen sind (Kapitel 4).

Um zu prüfen, ob sich Schweinswale in Deutschland, wo PAL bereits seit 2017 regelmäßig eingesetzt werden, an das PAL-Signal gewöhnt haben, wurde das Echoortungsverhalten der Tiere in einem Langzeitexperiment in Zusammenarbeit mit einigen Fischern durchgeführt. Dafür wurden zwei Gebiete in Deutschland und in Dänemark ausgewählt, die beide von der Beltsee-Population bewohnt werden. Da PAL in Dänemark nicht in der Fischerei eingesetzt werden, wurde bei dem Versuch davon ausgegangen, dass die Schweinswale in Dänemark naiver gegenüber dem PAL-Signal sind, und daher Dänemark als nicht exponiertes Gebiet definiert. Die Echoortung der Schweinswale wurde zwischen Referenzstationen ohne PAL und Stationen in der Nähe von mit PAL ausgestatteten Stellnetzen sowohl innerhalb Deutschlands und Dänemarks, als auch zwischen diesen Ländern verglichen. Zu diesem Zweck wurden vier Parameter, die eine Klicksequenz beschreiben, ausgewählt und mit Hilfe traditioneller Statistikmethoden sowie verschiedener maschineller Lernmodelle untersucht: Anzahl der Klicks, mittlere Frequenz, durchschnittlicher Schalldruck sowie das kürzeste Intervall zwischen den Klicks einer Klicksequenz. Die Medianwerte für alle vier akustischen Parameter waren sowohl zwischen den Referenzstationen beider Länder als auch zwischen den Referenzstationen und den mit PAL ausgerüsteten Netzen innerhalb beider Länder sehr ähnlich. Auf der Grundlage der vier ausgewählten Klicksequenz-Parameter konnte also keine Gewöhnung der deutschen Schweinswale an den PAL festgestellt werden (Kapitel 5).

Die in dieser Arbeit gewonnenen Erkenntnisse liefern wertvolle Einsichten zur Untersuchung von Schweinswalen, ihrer Interaktion mit Stellnetzen und dem PAL in der Beltsee und konnten somit einige bestehende Wissenslücken füllen. Die Bewertung der beiden Beobachtungsmethoden gibt Forschenden evidenzbasierte Anhaltspunkte für die Auswahl einer geeigneten Methode für ihre Forschungsfrage und schafft eine Grundlage für die Vergleichbarkeit verschiedener Studien, bei denen Theodoliten oder Drohnen für ähnliche Ziele eingesetzt werden. Es zeigte sich außerdem, dass Drohnen besser geeignet sind, das Verhalten von Schweinswalen zu untersuchen, da sie Aufnahmen auch unter der Wasseroberfläche ermöglichen. Dieser Vorteil wurde noch deutlicher, als das Verhalten von wild lebenden Schweinswalen zum ersten Mal in der Nähe von einer am Boden befestigten Netzstruktur gefilmt wurde. Die Interaktionen zeigten, dass Schweinswale grundsätzlich in der Lage sind, sich in der Nähe von Netzen aufzuhalten, ohne sich darin zu verfangen, und dass sie weder im Verhalten, bei der Echoortung oder in der Schwimmgeschwindigkeit stark auf die Netze und das PAL reagieren. Trotzdem kommt es in der kommerziellen Fischerei immer wieder zu Beifängen, was eher

mit Ablenkung oder Unerfahrenheit einzelner Tiere als mit einer grundsätzlich fehlenden Möglichkeit, Netze wahrnehmen zu können, zusammenhängen könnte. Es wird daher empfohlen, akustische Warngeräte wie Pinger oder das PAL gleichzeitig mit Strategien zu kombinieren, die die Netze für Schweinswale akustisch wahrnehmbarer machen, um das Beifangrisiko weiter zu verringern. Basierend auf den bisher verfügbaren Informationen über PAL und den neuen Erkenntnissen aus dieser Arbeit, scheint PAL eine gute Alternative zu herkömmlichen Pingern für die Beltsee zu sein, da der PAL Schweinswale nicht aus ihrem Lebensraum ausschließt sowie in den vier untersuchten Klicksequenz-Parametern keine Anzeichen für eine Gewöhnung an das PAL-Signal festgestellt wurden. Die Ergebnisse geben allerdings keinen Aufschluss darüber, ob PAL noch ausreichend wirksam zur Reduzierung der Beifänge in der deutschen Fischerei beiträgt. Zur Beantwortung dieser Frage wird empfohlen, ein langfristiges Beifangerfassungsprogramm einzuführen, um festzustellen, ob die nachgewiesene Wirkung von PAL auf die Reduzierung der Beifänge langfristig und unter Berücksichtigung der Komplexität der realen Fischerei in der Beltsee immer noch besteht. Dies ist besonders wichtig, wenn man berücksichtigt, dass nur wenige Informationen über den Beifang von Schweinswalen in Deutschland zur Verfügung stehen und dass die derzeit geschätzten Beifangmengen in der Beltsee insgesamt über den nachhaltigen Beifang-Grenzwerten liegen.

Chapter 1

General introduction

1.1. Bycatch of Endangered, Threatened and Protected species

In 2022, the global production of marine capture fisheries counted 79.7 million tonnes (FAO 2024). This numbers represent the catch actually landed and does generally not include the amount of discards and discarded bycatch.

Discards are the portion of the total catch that is thrown away or slipped back into the sea (FAO 2011; Regulation (EU) 1380/2013). Reasons for discards are various including species sizes below legal size, absence of quota, low or no market value, damaged captures or that it is prohibited to catch or land that species among others. Discards can include single or multiple species that can be dead or alive (FAO 2011). A standardized definition on bycatch has not been established yet due to the diverse nature of fisheries around the world. Some definitions are:

- I. catch that fishers did not intend to catch but could not avoid (FAO 2011)
- II. unintended, non-target organisms caught while fishing for particular species (or sizes of species) (Gray and Kennelly 2018).
- III. the incidental take of undesirable size or age classes of the target species (e.g. juveniles or large females), or the incidental take of other non-target species. Individuals caught as bycatch can be unharmed, released with injuries, or killed (Lewinson *et al.* 2004)

Bycatch can be divided into captures that are thrown back dead or alive or landed under the EU Landing Obligation¹ (Regulation (EU) 1380/2013)), and non-target organisms that are kept and sold as a by-product (Gray and Kennelly 2018). This by-product of fisheries can in occasions be a substantial source of income for fishers, such as is the case of shark bycatch during pelagic longline fisheries targeting tunas and swordfish in the Atlantic Ocean (Dinkel and Sánchez-Lizaso 2020). Bycatch has been addressed as the ‘fishery management issue of the 1990’ (Tillman 1992; Alverson 1994) and is still nowadays one of the most significant issues concerning fisheries worldwide (Gray and Kennelly 2018) as bycatch occurs in all fishing fleets (Hall *et al.* 2000). This is concerning considering the fishing fleet counted 4.9 million vessels worldwide in 2022 (two-thirds of which are motorized) (FAO 2024).

Endangered, Threatened and Protected species (ETP species) are usually defined by being protected under national or regional legislations and binding international agreements and assessments (Gray and Kennelly 2018). Large marine vertebrates, such as marine mammals, sea turtles, sea birds and a series of elasmobranchs fall within the general definition of ETP species (Good *et al.* 2024). The life history of ETP species (late maturity, low reproduction rates among others) makes them especially vulnerable to unintentional mortality (Rihan 2010). Despite this, ETP species are part of bycatch in fishing activities worldwide (Gray and Kennelly 2018). The most recent annual estimations of ETP species bycatch in marine commercial and artisanal fisheries worldwide estimated around 20 million individuals between 2010 and 2014, including 650 000 marine mammals (Pérez Roda *et al.* 2019). Even with this number, it has to be considered that estimates of ETP species bycatch are often an under representation of the real numbers, as bycatch of ETP species are often not reported as they are considered a controversial event or because they go unnoticed (Gray and Kennelly 2018).

¹ The EU Landing obligation is defined in Article 15 of the Regulation (EU) 1380/2013 and applied to all fishing activities conducted in Union waters or by Union fishing vessels outside Union waters in waters not subject to third countries’ sovereignty or jurisdiction.

1.2. Set net fisheries

Bottom set nets, often referred to as gillnets and entangling nets are passive fishing gears composed of long rectangular walls of netting that catch fish by gilling, entrapping or entangling them in net pockets, by wedging or snagging (He *et al.* 2021). Monofilament nylon is the most common netting material nowadays although multifilament and multi-monofilament are also used (He *et al.* 2021). The replacement of non-synthetic fiber materials occurred in the 1960s and has allowed nets to be more durable and easier to handle while also decreasing their visibility in the water (Gilman *et al.* 2016). The net panels are generally extended vertically by floats attached to the head rope (also called float line) and are pulled down by weights added to the footrope (Figure 1.1.). In some occasions they are also kept open vertically by being attached to stakes (referred to as fixed gillnets), or intentionally leaving a large portion of the net on the seabed with just small floatation provided by polypropylene ropes to allow entanglement of species that move near the bottom (He *et al.* 2021). Generally several net panels are attached together forming a string of nets that can be deployed by small vessels extending from hundreds of meters and up to several kilometers (He *et al.* 2021). Different modalities of gillnets exists but the most commonly used are set gill nets (also referred to as bottom gillnets or set-nets) that are kept in position by anchors or other weights and marked with buoys at the surface. They can either be composed of one net panel or have three layers of netting (two outer layers of larger mesh netting and one inner layer of smaller mesh size) that allow entrapping fish (trammel nets).

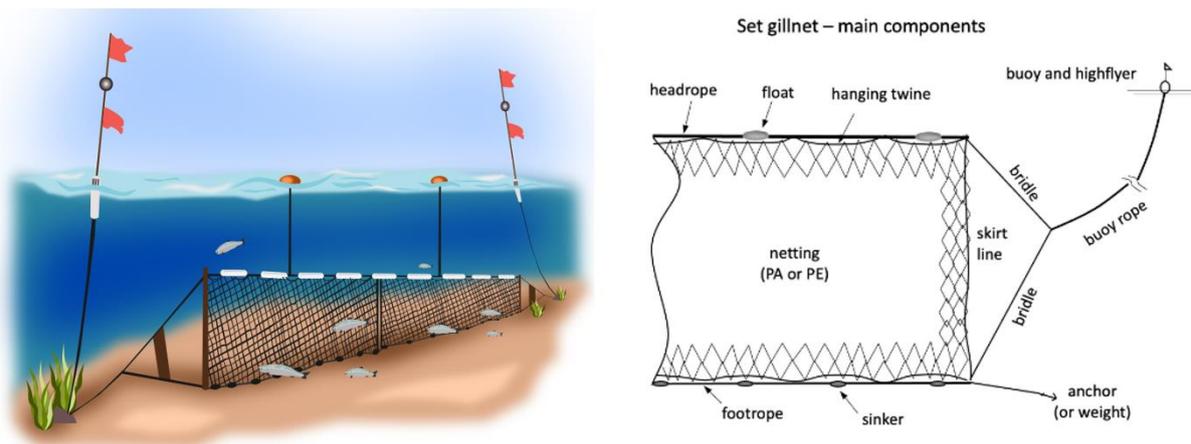


Figure 1.1. Schematic drawing of a bottom set gillnet (left) and main components of a set gill net (right). Sources: Mahela Dinkel (left) and He *et al.* 2021 (right).

Gillnets are used worldwide due to their versatility and fuel efficiency (Suuronen *et al.* 2012), contributing to approximately 10% of global fish landings in weight (He *et al.* 2021). They are considered to have a lower environmental impact compared to towed gear (Suuronen *et al.* 2012) and generally (excluding trammel nets) show a high selectivity for the target species as the catch is largely dependent on the mesh size (Suuronen *et al.* 2012). Despite this, gillnets pose a major threat for many ETP species with regular bycatch reported for all marine megafauna taxa worldwide (Gray and Kennelly 2018) and showing the highest intensity of bycatch of air-breathing megafauna of all fishing gears (Lewison *et al.* 2014). Additionally, gill nets are a substantial part of abandoned, lost and discarded fishing gears contributing to additional fishing mortality often not factored in global estimates of bycatch (Gilman *et al.* 2016).

The gillnet fishery segment is the largest segment in German fisheries in terms of vessel numbers. By the end of 2024, 79 % of fishing vessels registered in the German fleet listed gillnets as their primary or secondary gear (EU 2024b). In 2023, German fishing vessels below 8m length, and between 8 -12 m in length mainly fished in the Baltic Sea and Kattegat (Federal Ministry of Food and Agriculture 2024).

In Denmark, 83 % of the registered vessels indicated gillnets as their primary or secondary gear by the end of 2024 (EU 2024a).

1.3. Harbour porpoise

Harbour porpoises (*Phocoena phocoena*) are small marine mammals that belong to the infraorder Cetacea and superfamily of Odontoceti (toothed whales) (Fordyce and Perrin 2024). They have short rotund shaped bodies with a counter shaded coloration with a dark grey dorsal side and a light grey or almost white ventral side (**Figure 1.2.**) (Bjørge and Tolley 2009).

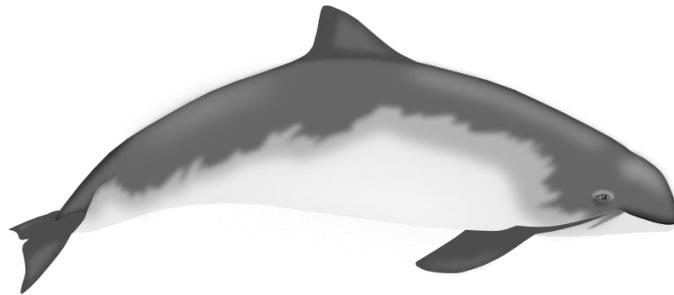


Figure 1.2. Harbour porpoise (*Phocoena phocoena*). Source: Mahela Dinkel.

Harbour porpoises are among the smallest of all cetacean species with females reaching up to 1.6 m in length and weighing around 75 kg and males being even smaller with 1.45 m and weighing about 60 kg (Bjørge and Tolley 2009). They are considered ‘fast life’ species among cetaceans which are characterized by early maturation with males and females reaching sexual maturity at around age three, annual reproduction cycles with short gestation periods estimated to be around 10 months, and dying at a relatively young age generally not exceeding the 12 years life span, despite some findings of older porpoises of up to 23 years of age (Lockyer and Kinze 2003; Read and Hohn 1995).

Diet of harbour porpoise includes a wide range of prey items mainly consisting of fish species, although stomach content analysis have also revealed parts of crabs, shrimps and polychaets (Andreasen *et al.* 2017). While variable, in the Belt Sea, it was revealed that seven main prey categories make up to 91 % of stomach contents of bycaught and stranded porpoises: cod, whiting, herring, sprat, sandeel, eelpout, and gobiid species, with cod and herring constituting on average 70 % of diet mass (Andreasen *et al.* 2017). It is reported that porpoises feed continuously (Wisniewska *et al.* 2016) to maintain their high metabolic demands (Rojano-Doñate *et al.* 2018). The daily prey mass requirement to compensate for daily requirements in the Belt Sea was estimated to range from 3.7 to 3.8 kg of fish per day for juveniles and adults (Andreasen *et al.* 2017).

Distribution and abundance

Harbor porpoises can be found in cold to temperate shelf water in the northern hemisphere (Watson and Gaskin 1983). Based on morphological and genetical differences four subspecies are identified, two in the Pacific Ocean (*P. p. vomerina* and one un-named subspecies), one in the Black Sea (*P. p. relicta*) and one in the North Atlantic Ocean (*P. p. phocoena*) (Gaskin 1984; Rosel *et al.* 1995; Carlén *et al.* 2018).

In the Baltic Sea, where it is the only resident cetacean species (Glemarec *et al.* 2021), three populations of harbour porpoises can be found: i) the North Sea population extending from the northern Kattegat into the North Sea; ii) the Belt Sea population extending from the southern Kattegat through the Belt Sea and The Sound into the southwestern Baltic Sea; iii) and the Baltic Proper population extending into the Baltic Proper (Unger *et al.* 2021) (**Figure 1.3.**). While the harbour porpoise is classified as ‘Least concern’ by the International Union for Conservation of Nature (IUCN)

globally (Braulik *et al.* 2023) and in Europe (Sharpe and Berggren 2023), the Belt Sea population is currently classified as ‘*Vulnerable*’ by the Baltic Marine Environment Protection Commission (Helsinki Commission - HELCOM) (HELCOM 2013) with last population abundance estimations calculating 17 301 harbour porpoises (95 % CI = 11 695-25 688; CV = 0.20) (Unger *et al.* 2021). The Baltic Proper population on the other hand is estimated to have a population of 491 individuals (95 % CI = 71 – 1 105; CV = 68.0) (Amundin *et al.* 2022b) and is classified as ‘*Critically endangered*’ by HELCOM (HELCOM 2013).

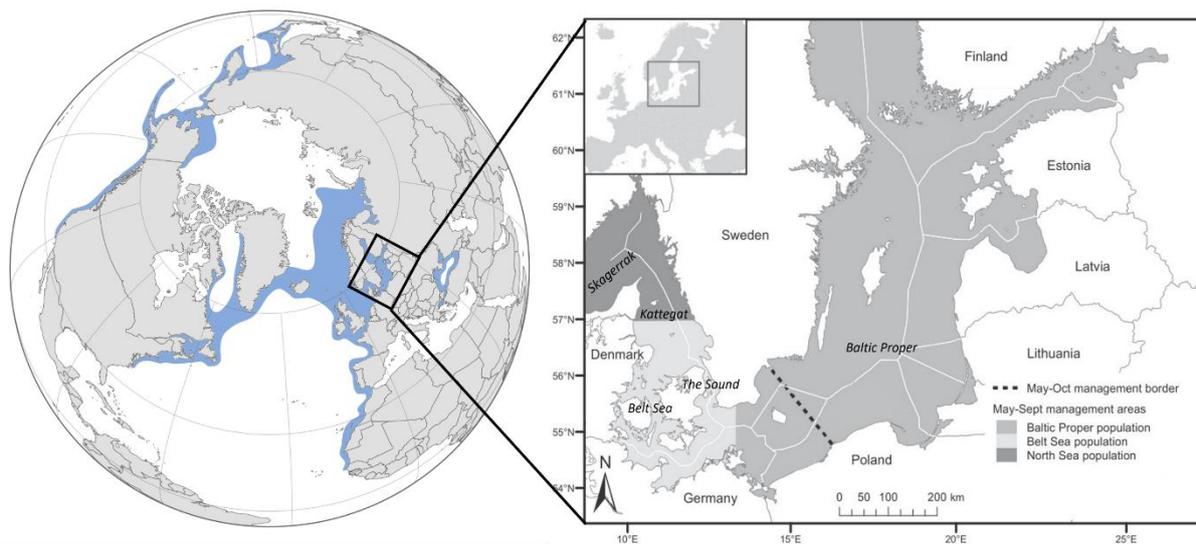


Figure 1.3. Global distribution range of harbour porpoise (left) and (right) management areas for the three Baltic Sea harbour porpoise populations based on Sveegaard *et al.* (2015) and with a proposed summer management border (dotted line) suggested for the Baltic Proper population (Carlén *et al.* 2018). Sources: left: Cephas, adapted from Braulik *et al.* (2023) (Wikipedia Commons); right: modified from Amundin *et al.* (2022).

The SCANS survey (Small Cetacean in European Atlantic Waters and the North Sea) in 1994 was the starting point of a long-term survey series implemented to estimate the abundance and density of small cetaceans in the North Sea and Atlantic Waters through aerial or ship-based line-transect distance sampling surveys (Gilles *et al.* 2022). Since then, six SCANS and miniSCANS surveys have been conducted, providing abundance estimations of harbour porpoises in the Belt Sea. The abundance estimations showed a decreasing tendency over the decades, although with large confidence intervals (**Table 1.1.**).

Harbour porpoises are legally protected under the Bern Convention (appendix II) which is delivered through the European Union (EU) Habitat Directive (Council Directive 92/43/EEC 1992) requiring all Member States of the EU to monitor harbour porpoise and their levels of bycatch. Further, the Marine Strategy Framework Directive (Directive 2008/56/EC) asks Member States to report on whether populations are on good environmental status. They are further included in Appendix II of Bonn Convention also known as the Convention on the Conservation of Migratory Species of Wild Animals (CMS) (CMS 1979), based upon which the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas (ASCOBANS) was concluded and entered into force in 1994.

Table 1.1. Summary table of the six SCANS and MiniSCANS surveys that covered the management area of the Belt Sea population. The surveys were either conducted solely on the distribution range of the Belt Sea population including the Belt Sea, the Sound and Kattegat (marked as BS in the table), or included the Skagerrak (marked as SK in the table). *For ship surveys, effort refers to km in sea condition Beaufort ≤ 2 , and for aerial surveys, under good or moderate conditions. Source: Owen *et al.* 2024.

Year	1994	2005	2012	2016	2020	2022
Survey dates	27 June - 09 July 1994	27 June - 16 July 2005	2 - 21 July 2012	5 - 24 July 2016	24 June - 10 July 2020	28 June - 31 July 2022
Survey	SCANS	SCANS-II	MiniSCANS	SCANS-III	MiniSCANS-II	SCANS-IV
Block (labels)	I + X	S		2	MS A-1	BS A-F
Area	SK/BS	SK/BS	BS	BS	BS	BS
Area (km ²)	55,295	68,372	51,511	40,707	42,244	42,264
Platform	ship + aerial	ship	ship	ship	aerial	aerial
Effort (km)*	2,292	1,279	826	1,028	4,533	4,279
Abundance	51,660	27,901	40,475	42,324	17,301	14,403
CV	0.30	0.39	0.24	0.30	0.20	0.21
CI low (abundance)	29,058	13,387	25,614	23,368	11,695	9,555
CI high (abundance)	91,841	58,149	65,041	76,658	25,688	21,769
Density	0.93	0.41	0.79	1.04	0.41	0.34
CI low (density)	0.53	0.20	0.50	0.57	0.28	0.23
CI high (density)	1.66	0.85	1.24	1.88	0.61	0.52
Reference	Hammond <i>et al.</i> (2021b), revised from Hammond <i>et al.</i> (2002)	Hammond <i>et al.</i> (2021b), revised from Hammond <i>et al.</i> (2013)	Viquerat <i>et al.</i> (2014)	Hammond <i>et al.</i> (2021b)	Unger <i>et al.</i> (2021)	Gilles <i>et al.</i> (2023)

1.4. Echolocation

In the marine environment, sound propagates rapidly and over long distances making it an attractive choice over sight or chemical cues for navigation, foraging or communication (Sørensen *et al.* 2018). Like other toothed whales, harbour porpoises use echolocation or biosonar for foraging, orientation (Verfuss *et al.* 2005; Clausen *et al.* 2011; Villadsgaard *et al.* 2007) and communication (Sørensen *et al.* 2018). Echolocation is the emission of acoustic signals and the reception of echoes that give information on their environment (Verfuss *et al.* 2005) or about direction and distance to potential prey (Villadsgaard *et al.* 2007). The time between emitted sounds and the received echo, is referred to as time lag (Au 1993) and serves to estimate distance to objects as it comprises the double time from emission and travel to an item and the time it takes for the echo to travel back to the receptor. Despite their good vision (Kastelein *et al.* 1990), harbour porpoises have shown to rely on continuous echolocation (Wisniewska *et al.* 2016) even during clear water conditions (Verfuss *et al.* 2005).

The echolocation signals produced by porpoises are termed clicks and described as narrow-band high-frequency (NBHF) signals (Villadsgaard *et al.* 2007). These NBHF signals (or clicks) in harbour porpoises have durations of about 100 microseconds (μ s) with a centroid frequency² around 130 kHz and source levels³ generally below 200 dB re 1 μ at 1 m (Au 1993; Villadsgaard *et al.* 2007). The beamwidth of the

² In acoustics, frequency refers to the number of periods per second or the rate of oscillation or vibration. The unit of frequency is the hertz (Hz), where 1 Hz equals one cycle per second (Todd *et al.* 2015).

³ The sound pressure level of a sound source that would be measured at a standard reference distance, usually 1 m, from an ideal point source and stated as dB re 1 μ Pa @ 1 m or dB re 1 μ Pa m (Todd *et al.* 2015).

clicks is narrow, with a forward beamwidth between 13° and 16° (Koblitz *et al.* 2012; Au *et al.* 2006) and a vertically compressed beamwidth of about 11° at half power (-3dB)⁴ (Koblitz *et al.* 2012). The slightly dorsoventrally compressed beam (Figure 1.4.d.) might reduce bottom reflections while maintaining a larger perception volume on the horizontal plane, which can be an adaptation for species that inhabit shallow areas. This beamwidth can be dynamic with observed variations in the range of 2° (Koblitz *et al.* 2012).

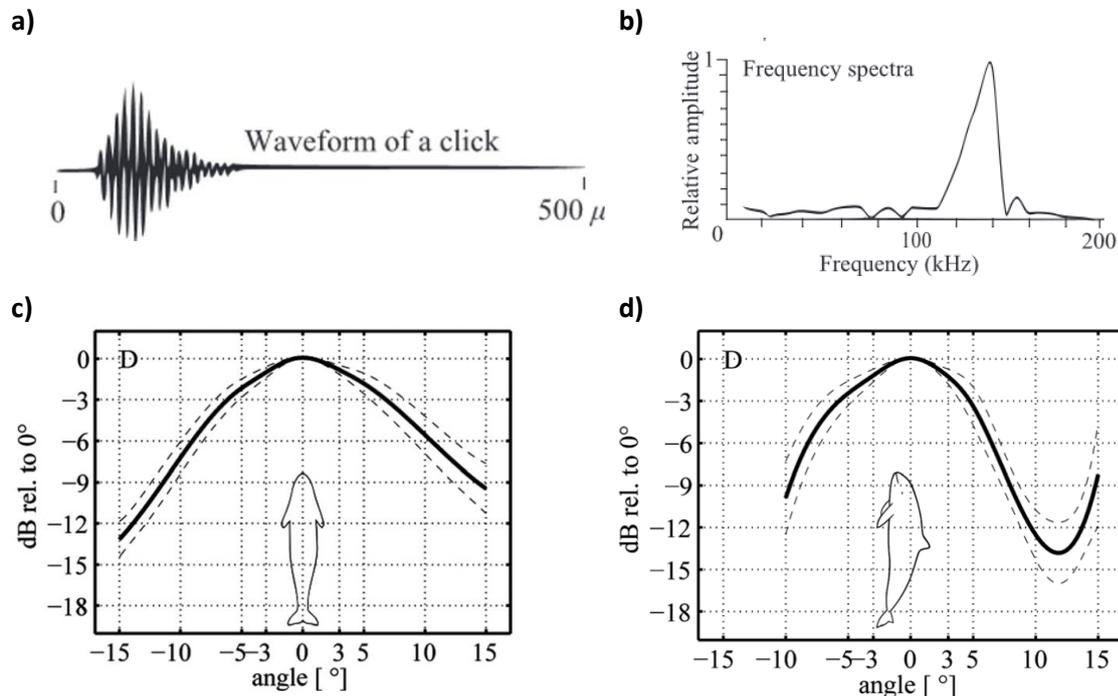


Figure 1.4. a) Echolocation click waveform; b) frequency spectra of a representative narrow-band high frequency (NBHF) click of a harbour porpoise.; c) averaged horizontal beam pattern with standard deviation intervals marked by dashed lines; d) averaged vertical beam pattern with standard deviation intervals marked by dashed lines of harbour porpoise NBHF clicks. a, b) Modified from (Au 1993; Morisaka and Connor 2007); c, d) modified from (Koblitz *et al.* 2012).

The high frequency component make clicks a powerful directional signal (Au 1993) which are generally used for sonar and being less suitable for long-range communication as it requires emitter and receiver to be close or face each other for a successful communication (Clausen *et al.* 2011). Further, the stereotypy of NBHF clicks limits the potential of these signals to encode information compared to frequency modulated acoustic signals such as whistles used by other toothed whales (Clausen *et al.* 2011). Despite this, it has been found that the repetition rates and click patterns within so called click trains (clicks grouped together) rather than individual click structures are used by porpoises to encode the necessary information to communicate (Clausen *et al.* 2011). The selection of a more restricted acoustic repertoire has been hypothesized to be linked to predator avoidance to reduce predation risk by killer whales (*Orcinus orca*) (Andersen and Amundin 1976) with NBHF click frequencies being inaudible to them (Koblitz *et al.* 2012). The small body size of porpoises, reduced group sizes and slower swimming speed are factors that increase predation risk for harbour porpoises (Morisaka and Connor 2007).

⁴ One way to parameterize the beam width is through the -3 dB (half power) beam width (BW) in degrees (-3 dB BW) which is defined as the angle between the direction at which the sound pressure level is reduced by 3 dB to either side of the acoustic axis in the horizontal or vertical plane (Koblitz *et al.* 2012).

1.5. Bycatch of harbour porpoises

Bycatch of porpoises in gillnets has shown to substantially affect porpoise populations worldwide (Jefferson and Curry 1994). The two most critical examples are probably the still ongoing effect of bycatch of two depleted populations, the vaquita porpoise (*Phocoena sinus*) in Baja California (Mexico) (Rojas-Bracho *et al.* 2006) and the Baltic Proper porpoise (*Phocoena phocoena*) in the central Baltic Sea (Carlén *et al.* 2021), both of which are classified as *critically endangered* by the IUCN, despite being subject to active protective measures (Rojas-Bracho *et al.* 2006; Koschinski *et al.* 2024; Carlén *et al.* 2021).

In the Baltic Sea, concerns about harbour porpoise populations were raised already in 1980s based on elevated bycatch events in Danish gillnet fisheries (Lowry and Teilman 1994; Lockyer and Kinze 2003) and evidence of a decrease in distribution and population size (Koschinski 2001). Nowadays, bycatch continues to occur in the Baltic Sea above sustainable thresholds (Kindt-Larsen *et al.* 2023; Owen *et al.* 2024). Despite being a serious concern, bycatch is still under reported and poorly monitored, so bycatch estimates are suggested to be treated with caution as they may not be representative due to the lack of a sampling program (Glemarec *et al.* 2021).

For the western Baltic Sea, only few porpoise bycatch estimations are available, and not for the entire western Baltic Sea. Between 2010 and 2018 it was estimated that around 615 porpoises were bycaught by the Danish fleet in the western Baltic Sea (Larsen *et al.* 2021). For the Belt Sea it was estimated that around 758 porpoises are bycaught per year based on values calculated for the year 2017 (NAMMCO and IMR 2019) and recently, a first fleet-level estimation of porpoise bycatch was conducted for bycatch in commercial fisheries in the Western Baltic Sea, predicting between 862 and 939 porpoises being bycaught by the Danish and Swedish fishing fleet for the year 2020 (Kindt-Larsen *et al.* 2023). Current calculations of bycatch rates in Germany are not available, although different records show that bycatch occurs also in the German gillnet fisheries such as cadavers submitted by fishers (Siebert *et al.* 2006; Dähne *et al.* 2011), bycaught porpoises during scientific studies (Chladek *et al.* 2020) and statements from fishers (Barz 2023).

Methods to estimate bycatch rates include data collected by independent on-board observers, remote electronic monitoring systems which rely on cameras placed on the vessels, as well as voluntary reporting by fishers in their logbooks as part of the mandatory bycatch reporting (ICES 2024c). Indirect estimations can also be made using numbers or port observers (ICES 2024c), although if discards occur at sea, they will be missed by this method; based on interviews with fishers (ICES 2024c); or using *postmortem* examinations of stranded animals, although there are uncertainties when it comes to assessment of bycatch as clear external marks (**Figure 1.5.**) are often not available or not visible due to the state of decomposition when found, although the biggest challenge being the diagnosis of drowning following underwater entrapment (IJseldijk *et al.* 2021). The most reliable methods to quantify real bycatch rates are suggested to be based on electronic monitoring or on-board observers (ICES 2024c).

Besides lack of effective monitoring and under reporting of bycatch of harbour porpoise (Kindt-Larsen *et al.* 2023), a big hurdle to address the problem is the fact that it is still poorly understood which mechanisms underlay bycatch in gillnet fisheries, especially concerning animal behaviour (Northridge *et al.* 2017). Several reasons are regularly mentioned that potentially contribute to animals failing to detect the nets:

- i) **Distraction**, the porpoises fail to pay attention even though emitting clicks (Cox and Read 2004; Larsen *et al.* 2007)
- i) Moments of **sonar inactivity** during which porpoises do not echolocate (Cox and Read 2004; Larsen *et al.* 2007). For instance, it has been measured that porpoises stop or reduce their echolocation activity in some occasions, for example due to boat traffic (Wisniewska *et al.* 2018), while sleeping or resting (Wright *et al.* 2017) or that they experience a startle response in which they stop echolocating (Elmegaard *et al.* 2023).
- ii) **Echolocation beam is not oriented towards the net** while conducting other activities such as bottom grubbing (feeding of prey in the ground) (Larsen *et al.* 2007)
- iii) **Masked echoes from the net** due to free swimming or entangled prey in net material (Kastelein *et al.* 1995; Larsen *et al.* 2007)
- iv) **Masking effect of loud noise**: the auditory capacity of porpoises can be altered in the presence of noise in the sea, such as produced by ships which can mask echolocation echoes at close range (Hermannsen *et al.* 2014)
- v) **Low detectability of the nets** due to the use of transparent fibers in nylon netting and thin material (Northridge *et al.* 2017; Larsen *et al.* 2007)
- vi) Porpoises detect the net but do **not perceive them as a barrier** or make **navigation errors** (Cox and Read 2004)

The sporadic nature of bycatch events and the fact that most occurrences are unobserved and not reported makes the development of bycatch solutions challenging (Rihan 2010). While a large effort has been going into testing mitigation strategies, bycatch still remains a main issue for porpoises. Future progress is thus increasingly dependent on a better understanding of the behavioural interaction of marine mammals with gear (Rihan 2010; Northridge *et al.* 2017).

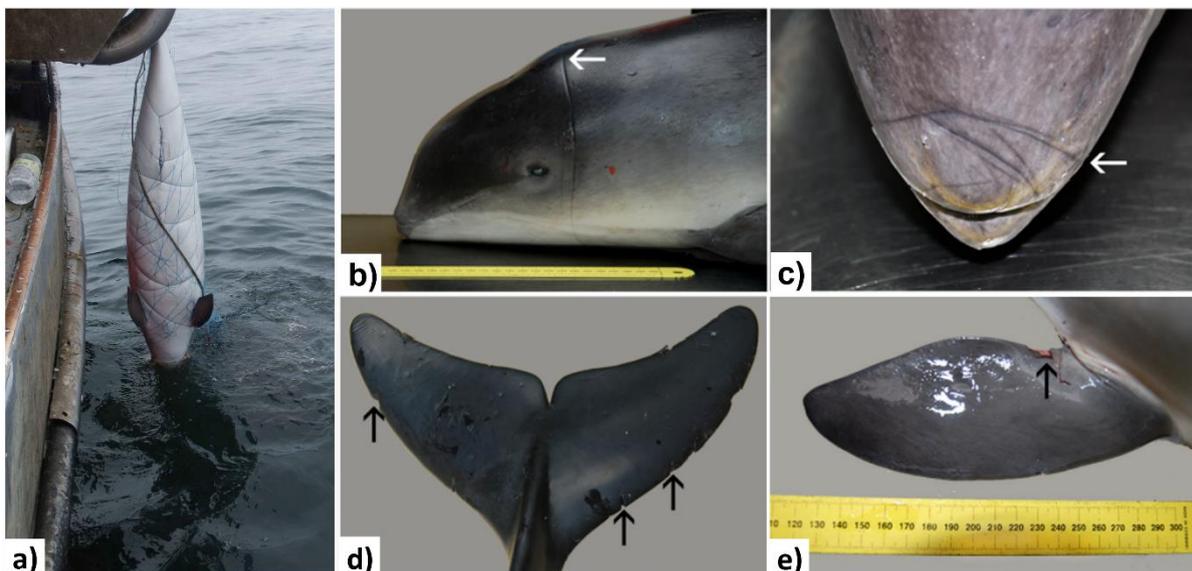


Figure 1.5. a) Bycaught harbour porpoise in a German gillnet fishing net in the Belt Sea. b-e) *Post-mortem* pictures of a bycaught harbour porpoise in the North Sea in a bottom set gillnet: b) encircling imprints around the head (white arrow); c) rostrum with encircling imprints (white arrow); d) incisions in the edges of the flukes (black arrows); e) incision and loss of epidermis in the right pectoral fin (black arrow). Sources: a) Thünen-Institute of Baltic Sea Fisheries (Jérôme Chladek); b-e) Modified from Ijsseldijk *et al.* 2021.

1.6. Bycatch mitigation strategies

Selecting effective bycatch mitigation strategies require several information including data on the life history and distribution of bycaught and target species, the fishing effort and ideally understanding the interaction between bycaught species with the fishing gear. It also requires fishers to be willing to properly implement mitigation strategies despite potential socioeconomic implications (Irvine *et al.* 2024).

Partial and temporal measures

These measures comprise the restriction or prohibition of fisheries in certain areas or seasons (Irvine *et al.* 2024). Risk areas for harbour porpoise bycatch can be defined based on estimations of fishing effort and porpoise distribution (Glemarec *et al.* 2021; Irvine *et al.* 2024) as well as data on occurrences of bycatch events (Read 2013) but require data with sufficiently high spatial and temporal resolution. For mobile species such as porpoises, temporal closures should focus on areas in which they concentrate or that have a key function for some of their life stages (Glemarec *et al.* 2021). An example of implemented temporal closures to protect harbour porpoises is the closure to static net fisheries of eleven marine areas in the Baltic Sea (Commission Delegated Regulation (EU) 2022/303) to protect the Baltic Proper population. Areas of high bycatch risk have also been mapped for the Belt Sea population (Glemarec *et al.* 2021).

Technical measures

Technical measures refer to modifications in already existing fishing gear. They generally find more acceptance in the fishing sector as they mostly allow them to continue fishing in their habitual grounds (Irvine *et al.* 2024). Technical measures may include regulating the mesh size of the nets, reducing the soak time (time a net is in the water) (Irvine *et al.* 2024), reducing the net length (Read 2013) or adjusting net height or hanging ratio of the nets (Lowry and Teilman 1994). Further approaches include increasing the reflectivity of the net twines for example by using high-density fillers such as Barium Sulfate (Mooney *et al.* 2004; Cox and Read 2004; Koschinski *et al.* 2006; Mooney *et al.* 2007) or iron oxide (Larsen *et al.* 2007) which, however, have shown to only increase reflectivity slightly. Reflectors such as air-filled floats (Goodson 1997) or the use of acrylic glass spheres (pearls) (Kratzer *et al.* 2021) have also shown to increase reflectivity of the net, with the pearls showing the potential to reduce bycatch of porpoises, although not statistically significant due to the small sample size (Kratzer *et al.* 2021).

Alternative gears

Substituting set nets with alternative gears has also been an approach in the Baltic Sea using pods or traps with the primary aim to reduce seal interaction or depredation (Hemmingsson *et al.* 2008; Königson *et al.* 2015) but also to reduce the bycatch of harbour porpoises (Chladek 2022).

Acoustic Alarms

Acoustic alarms are devices that emit artificial sounds with the aim to reduce bycatch and reduce depredation of already captured prey on the nets (Dawson *et al.* 2013). Different hypothesis on how pingers may work include: i) displacement from the vicinity of the net because the sound is aversive (Kastelein *et al.* 1995); ii) the alerting hypothesis suggests that pingers encourage echolocation towards the sound source which increases the chances to detect the fishing gear (Dawson *et al.* 2013); iii) interference with the animals sonar which can cause animals to leave the area of ensonification (Dawson *et al.* 2013); iv) pinger sounds disturb the prey (Dawson *et al.* 2013).

Pingers have shown to significantly reduce harbour porpoise bycatch in gillnet fisheries (Palka *et al.* 2008; Larsen and Eigaard 2014; Dawson *et al.* 2013; Kindt-Larsen *et al.* 2019; Omeyer *et al.* 2020) and are one of the primary tools used to mitigate bycatch in gillnet fisheries worldwide (for a review see

Dawson *et al.* 2013). In the Baltic Sea for example, pingers are mandated in some areas to protect the Baltic Proper population (Commission Delegated Regulation (EU) 2022/303).

While concerns around habitat exclusion and noise pollution have been raised around pingers in the past (Kyhn *et al.* 2015; Larsen *et al.* 2013; Culik *et al.* 2001), habituation is considered one of the biggest concern associated to pingers (Kindt-Larsen *et al.* 2019). Habituation can be defined as a “behavioural response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue” (Rankin *et al.* 2009). Several studies on pinger habituation in porpoises have shown different results with some indicating potential habituation (Cox *et al.* 2001; Carlström *et al.* 2009) and others showing no signs of habituation (Kindt-Larsen *et al.* 2019; Palka *et al.* 2008; Omeyer *et al.* 2020).

PAL

The porpoise-PAL (Porpoise ALert) is an acoustic alerting device developed as an alternative to traditional pingers to reduce habitat exclusion effects while alerting harbour porpoises of the risk of set nets (Culik and Conrad 2013; Culik *et al.* 2015). The porpoise-PAL (from here on referred to as PAL) is an acoustic transducer that produces synthetic aversive communication signals of harbour porpoises (Culik and Conrad 2013). The PAL are programmed to synthetically an aversive porpoise communication signal termed ‘F3’ which was recorded in captivity in the Fjord & Belt center (Denmark) from a female (named Freja) towards a male porpoise. Both porpoises belong to the Belt Sea population (Clausen *et al.* 2011). The PAL signal consist of two upsweep chirps beginning with a click rate of 173 clicks/s and ending with 959 clicks/s and has a centroid frequency of 133 ± 8.5 kHz, with a mean source level of 147 dB peak-peak re $1 \mu\text{Pa}@1 \text{ m}$ (Chladek *et al.* 2020). One to three signals are emitted at random followed by a randomised pause of 4-30 seconds thus emitting an average of 5.5 signals/minute (Chladek *et al.* 2020) (**Figure 1.6.a**). The signal repetition pattern fulfils the requirements for acoustic deterrent devices set in (Regulation (EU) 2019/1241). Harbour porpoises should be able to detect the PAL signal within a range of 230-320 m distance with wind conditions of zero Beaufort wind force scale, while detection distance decreases to 90-150 m at seven Beaufort and depending on porpoise orientation and position with respect to PAL (Chladek *et al.* 2020). When tested in the field in the Little Belt (Denmark), wild porpoises reacted to the PAL by increased their echolocation rate by 10 % as well as increasing their distance towards the PAL by 32 m (Culik *et al.* 2015). This reaction agrees with the ‘alerting hypothesis’, which suggests that pinger sounds may alert porpoises about a potential danger and encourages an increase in their echolocation (Dawson *et al.* 2013).

Between 2014 and 2016 PAL were tested in commercial gillnet fisheries in German (waters off Schleswig-Holstein) and Danish waters (Belt Sea) and a significant reduction of harbour porpoise bycatch of up to 79.9 % was observed when PAL were spaced out up to a maximum of 200 m (Chladek *et al.* 2020). This reduction in bycatch was observed in harbour porpoises living in the Belt Sea, the same area from which the porpoise that emitted the so-called F3 signal originated. PAL were also tested in gillnet fisheries in Iceland (Iceland Sea, Atlantic Ocean) where they did not show an effect of reducing bycatch compared to control nets (ICES 2018). Interestingly, bycatch of porpoises in nets with PAL in Iceland had a gender ratio disbalance with eight out of twelve bycaught porpoises being adult males, suggesting a possible attraction towards the PAL devices in this area (ICES 2018). PAL programmed with the F3 signal have not been tested in further areas.

In light of these findings, PAL have been employed by German fishers operating with set nets in Schleswig-Holstein (Baltic Sea) on a voluntary basis since 2017. Fishers are asked to mount the PAL to the floatline of the net along the horizontal axis (**Figure 1.6.a**) with a spacing of maximum 200 m between devices to ensure full acoustic coverage of the net (Chladek *et al.* 2020). In 2018, 1 600 PAL were given to 83 fishers (OIC 2018), 2 270 PAL were distributed between 114 fishers in 2020 following by a decrease in 2021 with 2 037 active PAL distributed between 97 fishers (OIC 2021) and 1 772 PAL handed out to 84 participating fishers in 2023 (OIC 2023). The decreased use of PAL is reported to be associated to retirement of fishers and quota reductions of main target species: cod (*Gadus morhua*) and herring (*Clupea harengus*) (OIC 2023).

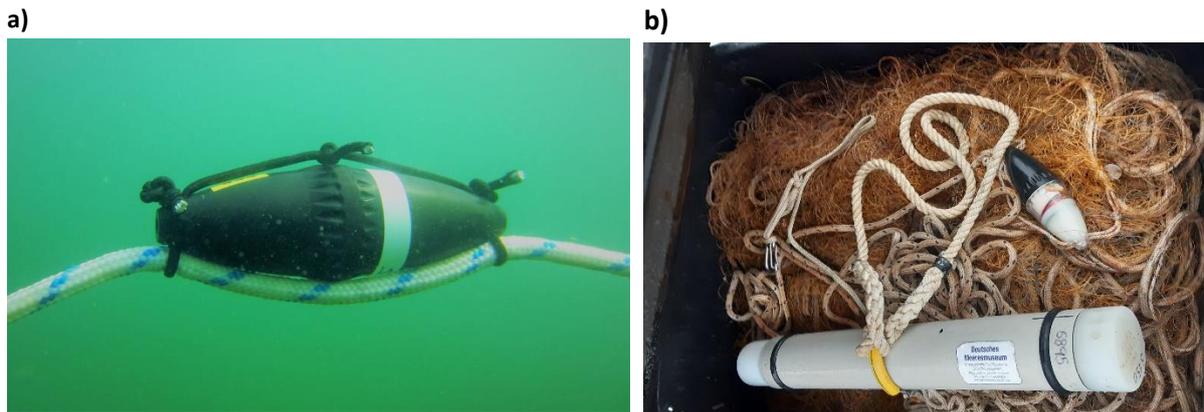


Figure 1.6. a) A PAL device attached to the floatline of the modified net during field trials in Denmark (Chapter 4); b) PAL attached to the floatline of a gillnet together with an acoustic recorder (F-POD) used during trials in fisheries in Germany (Chapter 5). Source: a) Tom Bär; b) Author.

1.7. Monitoring cetaceans

Until the 1960s most studies conducted on cetaceans were based on killed animals or cetaceans kept in captivity. Around this time, the limitation of knowledge that could be acquired by these means as well as ethical concerns around it, gave way to studies based on observations in the wild and methods without focusing on already dead animals or even the need to kill them for research purposes (Tyack and Samuels 2000). In 1983, Payne published the volume '*Communication and behaviour of whales*' which for the first time included only studies based on what he called 'passive observation techniques', results obtained without capturing, confining, killing and not even touching a whale (Payne 1983).

Observing cetaceans is difficult, with the main challenges emerging from the fact that they generally live in the oceans often having offshore distributions or just passing occasionally near coasts (Morete *et al.* 2018), the short period of time that cetaceans spend on the surface, difficulties observing them under the water, large distribution ranges (Piwetz *et al.* 2018), fast swim speeds and the absence of long-lasting traces such as tracks (Mann 1999).

Over the years, a range of research methods have emerged to study cetaceans in the wild without the need of killing them. Methods include visual observations and film or photo recording methods which can be carried out from fixed stations (e.g. shore, oil platforms), from mobile platforms (e.g. boats, aircrafts, unmanned aerial vehicles), to acoustic observations employing underwater acoustic recording equipment or high-resolution acoustic tags, to satellite-linked or animal-borne monitoring instruments to mention just a few (Evans and Hammond 2004; Morete *et al.* 2018; Tyne *et al.* 2016; Nowacek *et al.* 2016; Andrews *et al.* 2019). The choice of method will depend on the species, the research question to be addressed and the budget (Morete *et al.* 2018). For behavioural studies,

methods that do not alter the natural behaviour of the study species are relevant. While many research methods can have an effect on the observed species altering their 'natural behaviour' (Piwetz *et al.* 2018), land-based observation methods and passive acoustic monitoring generally allow for unbiased observations. Reducing modifications of natural behaviour also avoids negative effects of research on the study species as even punctual behavioural changes can have cumulative negative effects for the animals. For example, an interrupted feeding activity will have to be compensated by the animal reducing time for other activities like socializing or resting (Morete *et al.* 2018).

Land-based observation methods

Observations conducted from land are generally restricted to cover species with near distributions often encompassing just a small area of distribution of a species (Evans and Hammond 2004). However, it is a relatively cost-effective method allowing for short, middle and long-term research (Morete *et al.* 2018). Furthermore, land-based observations methods are not restricted to visual data collection, but can include a variety of auxiliary methods such as the collection of visual material (photo or video footage) for post-processing (Aniceto *et al.* 2018), the collection of positional data through the use of theodolites for example (Piwetz *et al.* 2018) and the area of observation from land can even be extended through the use of unmanned aerial vehicles (Fiori *et al.* 2017).

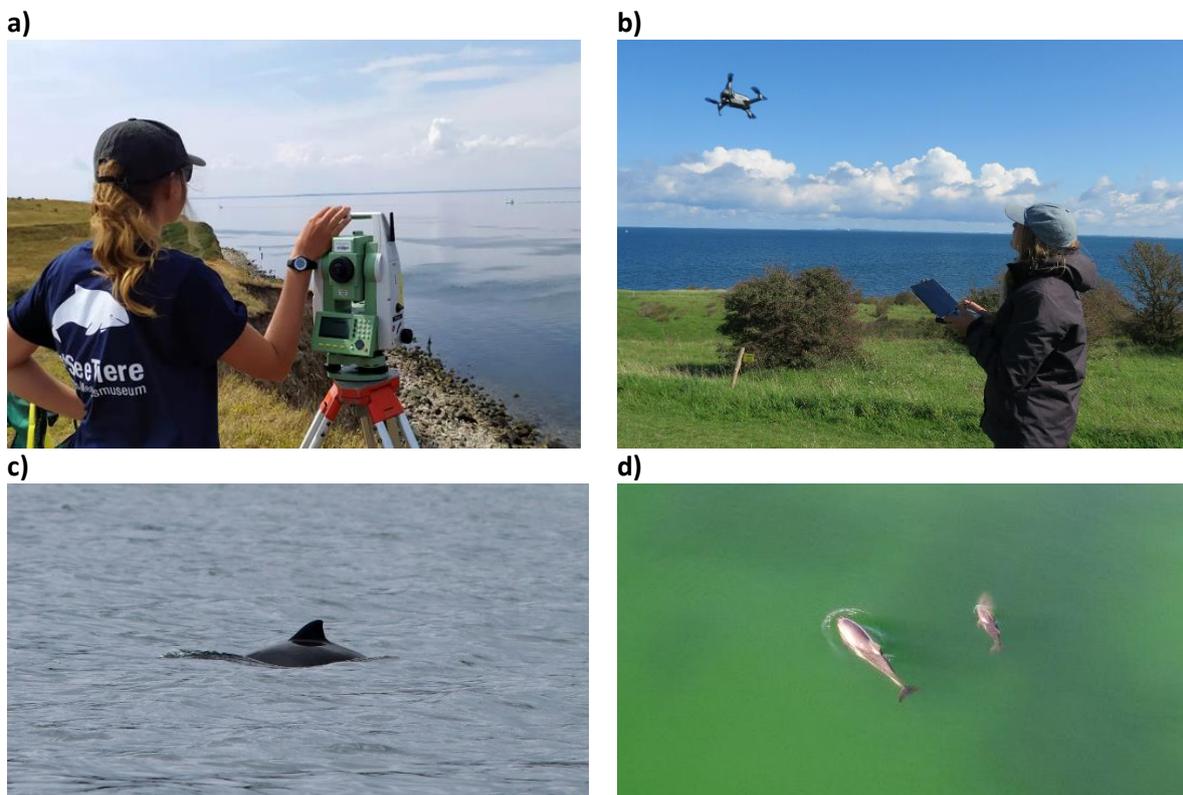


Figure 1.7. a) Theodolite to take coordinates of porpoises while they are surfacing; b) drone being started to record porpoises; c) perspective of a harbour porpoise observed by plain eye, binoculars or though the theodolite; d) perspective of a drone flying above a harbour porpoise mother and calf pair. Photos by a) Tom Bär; b) author; c) Madeleine Berglund; d) author.

Besides plain eye observations and binoculars, probably the most traditional tool used in land-based observation methods is the theodolite or total station. It was first introduced by Roger Payne in 1970s and has since contributed to the research of at least 46 marine mammals worldwide (for a review see (Piwetz *et al.* 2018). Theodolites or total stations are topographic equipment that are used in civic engineering but that allow to obtain positional coordinates with good precision of objects on the water

surface if used from an elevation. On the other hand, unmanned aerial vehicles, often referred to as drones, are increasingly used for visual monitoring of marine mammals and other marine taxa (Aniceto *et al.* 2018; Raoult *et al.* 2020; Fiori *et al.* 2017). Some advantages of drones are their relative low cost compared to other aerial survey techniques such as transects, the reduced risk of operations in dangerous areas such as fjords or difficult to access areas such as polar regions as well as the improved resolution from footage obtained at less altitude without disturbing the animals (Aniceto *et al.* 2018). A thorough analysis of both methods as tools to observe small cetaceans is the core of Chapter 3.

Passive Acoustic Monitoring

Cetaceans spend most of their life underwater and are heavily reliant on echolocation. Passive Acoustic Monitoring (PAM) is an established method to study cetaceans (Todd *et al.* 2023). In contrast to 'active acoustic' methods, in which a sound is transmitted and the returning echo analyzed, PAM devices do not produce any sounds themselves, but only capture sounds (Mellinger *et al.* 2007).

The benefits of PAM are manifold and include reduced cost compared to aerial or ship-based surveys, (Todd *et al.* 2023) which is relevant for low density areas (Kyhn *et al.* 2012), and allows for long term monitoring (Todd *et al.* 2023). Further, undisturbed vocal recordings are obtained (Aniceto *et al.* 2018), the observations are independent of daylight hours, favourable weather conditions or available observers (Todd *et al.* 2023) and automatic classification tools make the data processing fast and efficient (Ivanchikova and Tregenza 2023). PAM is thus generally used to collect information on cetaceans on general vocalizations, determine range and seasonality of species, and helps obtaining abundance estimates (Mellinger *et al.* 2007). Despite this, it has to be considered that there is still generally a lack of understanding around the behavioural context of sound production of many species (Mellinger *et al.* 2007) including the harbour porpoise (Villadsgaard *et al.* 2007).

There are different modalities of PAM system, as they can be fixed in a place (static), towed (such as hydrophones being dragged by a boat) or attached to animals in the form of tags (Todd *et al.* 2015). Static acoustic monitoring systems typically operate autonomously detecting, processing and storing the data as they are generally deployed by mooring them onto a structure where they remain for a period of time (Todd *et al.* 2015). So called 'click detectors' are a common form of static acoustic monitoring system that is regularly employed for monitoring of odontocetes (Todd *et al.* 2015). PODs (Porpoise Detectors) are one form of self-contained click detectors (Tregenza *et al.* 2016) that have become a main tool in harbour porpoise research (Todd *et al.* 2023). The fact that harbour porpoises click almost continuously makes them good candidates for PAM research. Nevertheless, the high frequency of harbour porpoise clicks have a strong seawater absorption loss and can thus be detected only in shorter distances (Mellinger *et al.* 2007). Further, the high directional nature of their clicks pose another challenge as the sound emission is weaker outside of the main click and thus more difficult to be picked up by a recording system if the porpoise is not directly clicking onto it (Ivanchikova and Tregenza 2023).

Limitations observing interactions with fishing gear and bycatch events

This far, research has mainly focused on the determining detection ranges of porpoises in captivity towards nets (Kastelein *et al.* 2000; Culik *et al.* 2001; Mooney *et al.* 2004; Koschinski *et al.* 2006; Mooney *et al.* 2007) and their reaction towards pingers or alternative devices in captivity (Kastelein *et al.* 2001; Teilmann *et al.* 2006) and in the wild (Cox *et al.* 2001; Kyhn *et al.* 2015; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021; Brennecke *et al.* 2022). Relatively little research is available on the behaviour of small cetaceans, and concretely on porpoises, around bottom set nets (Macaulay *et al.* 2022). Probably the most detailed study of the behaviour of porpoises near fishing nets is from porpoises in captivity (Kastelein *et al.* 1995). Behavioural observations of porpoises in the wild are restricted mainly due to the low frequency of entanglements and methodological limitations

(Macaulay *et al.* 2022). Methodological limitations include the limited monitoring ranges of underwater cameras (Macaulay *et al.* 2022) or the fact that while porpoises can be recorded through PAM, the acoustic information reveals little about the interaction and it can generally just be said that porpoises were near nets and if they were feeding (Maeda *et al.* 2021; Higashisaka *et al.* 2018). Visual observation from land are limited to fishing gear deployed near coast and do not give a clear insight into what happens under the water (Nielsen *et al.* 2012) and the low frequency probability of encounters make it a time-consuming task to collect data. Biologging data can provide detail movement information, but over a rather short time span, where again, the probability to encounter a net is small and porpoises may never approach a net at all (Macaulay *et al.* 2022). In Chapter 4 drones were used to record porpoises near a bottom set net, but the relative low frequency of porpoises actually approaching the net made it very time and workforce intensive to even get recordings of a few reactions. The limited availability of data constrains the ability to draw generalizable conclusions and reduces the statistical power of analyzes, thereby increasing uncertainty in findings (Button *et al.* 2013).

In recent years a passive acoustic method was developed to track small cetaceans around marine structures (Gillespie *et al.* 2020) which allowed obtaining 3D tracks of harbour porpoises near a bottom-set fishing net in the UK (Macaulay *et al.* 2022) for the first time. This method is promising especially for environments with murky water where video recording might not be able to give much information such as in the Belt Sea. In the study by Macaulay *et al.* (2022), the passive acoustic records could give detailed information on dive behaviour near nets and approach distances as stated for example in this observation:

[During one encounter] *“a porpoise is initially diving ~100 m from the net and then after the middle of the encounter (>244 s) appears to approach the net. Towards the end of the encounter (at ~300 s), the porpoise dove towards the gillnet and came within 5 m of the floatline, but then surfaced again. After this point, the animal is not detected suggesting that (because of its narrow beam profile) it is facing away from the net (i.e. moving away).”* [In another dive track] *“a porpoise consistently dives close to the net producing buzzes nearby and at a variety of depths. Both examples demonstrate the detailed and varied behavioural information that can be obtained using this PAM methodology.”* (Macaulay *et al.* 2022).

Understanding why porpoises get entangled in gillnets remains an ongoing field of research (Larsen *et al.* 2021). Macaulay and his team were able to produce 3D tracks of the behaviour of porpoises near fishing nets for the first time. The results of Chapter 4 show the first drone recordings of their kind of wild porpoises interacting with a bottom set net structure. While these studies are rare, future advancements to mitigate bycatch is likely to depend on a better understanding of the behaviour of non-target species, in our case the harbour porpoise, near fishing gear (Northridge *et al.* 2017).

1.8. Motivation and outline of the thesis

Among all types of fishing gear, set nets, often referred to as gillnets, are considered the biggest threat to small cetacean populations worldwide (Read *et al.* 2006). While a variety of mitigation strategies are available, pingers have shown to be effective in reducing harbour porpoise repeatedly and are therefore considered the most promising mitigation strategy for developed countries to reduce bycatch in gillnet fisheries (Dawson *et al.* 2013). The ability of pingers to reduce bycatch is nevertheless linked to causing displacement from the nets, which has been raised as a concern in case it causes habitat exclusion (Carlström *et al.* 2009; Kyhn *et al.* 2015). As a response to these concerns the PAL was developed, which is an alternative to traditional pingers as it emits synthetic harbour porpoise sounds based on the Belt Sea population (Culik *et al.* 2015; Culik and Conrad 2013). The effectiveness

of PAL reducing harbour porpoise bycatch was measured in a study comparing the number of bycaught porpoises in nets with PAL to nets without PAL (control) in the Belt Sea (Chladek *et al.* 2020). After demonstrating that their effectiveness is similar to that of traditional pingers (Chladek *et al.* 2020; Dawson *et al.* 2013), PAL have been implemented in Germany on a voluntary basis since 2017 (OIC 2018). The implementation of PAL was not accompanied with a monitoring program to test whether their effectiveness to reduce bycatch is efficient in the long-term. To respond to this question the PAL-CE project (PAL: Current Efficiency and mode of operation, project no. FKZ 3521820700) was launched. The main goal of this project was to understand whether PAL continue to work over long periods of time alerting porpoises and how they affect their spatial distribution. The large sampling effort required to obtain robust statistical power to say whether the efficiency of PAL remains the same as the one detected by Chladek *et al.* (2020) has lead the project to attempt responding to the required questions through alternative methods, and not through the same experiment as performed by Chladek *et al.* (2020). The research presented in this thesis was conducted as part of the PAL-CE project. While it addresses certain key questions, it does not encompass the full scope of the experiments performed within the PAL-CE project, nor does it discuss the final findings, as they were not available at the time of writing. The main objectives of this thesis are presented here.

Chapter 3: It is difficult and work intensive to observe small cetaceans in their natural habitat, with the harbour porpoises being especially challenging due to their small size and their inconspicuous behaviour (Aniceto *et al.* 2018). **In this chapter two land-based observation methods, the more traditional theodolite and the newer drones, were compared identifying advantages and shortcomings.** Both methods were analyzed in their general performance to collect visual observation data, estimating group sizes, obtaining geographical positional data and studying behaviour and fine scale movements of porpoises. While being used on the case study of harbour porpoises, the results are applicable for all small inconspicuous odontocetes with near-shore distribution and provide evidence-based guidance for researchers to choose a suitable method in accordance with their research question. Furthermore, visual observation may be transitioning from the more traditional theodolite to drones. This work sets a base to maintain comparability among studies.

Chapter 4: In general, relatively little knowledge is available of the underlying mechanisms leading to bycatch of porpoises in set nets and it is suggested that the field would benefit from a broader understanding on the behaviour of porpoises near nets (Northridge *et al.* 2017). **This Chapter analyzes the behaviour of harbour porpoises near a set net structure and a net structure with the PAL based on drone and acoustic recordings of wild porpoises.** Different interaction types, reaction distances to the nets and general behaviour patterns were described and analyzed giving some new insight into how porpoises react near nets giving evidence for potential new paths in bycatch mitigation designs.

Chapter 5: Habituation is the main concern associated with pingers as it could lead to reduced effectiveness (Kindt-Larsen *et al.* 2019). **To test whether porpoises in Germany might have habituated to the PAL signal,** a long-term acoustic monitoring scheme was designed in collaboration with commercial fishers to record the echolocation behaviour of porpoises near PAL. This study included fishers in Germany and Denmark operating in areas of the Belt Sea. Echolocation parameters of both porpoise groups were compared to test whether indications for habituation could be found. This chapter (and the PAL-CE project) worked under the assumption that porpoises in Denmark are more naïve to PAL than porpoises in Germany, as PAL are not used in Denmark.

Chapter 2

Methods

2.1. Experimental set ups

Two experimental set ups were used to obtain data for this thesis. While the experimental set ups are described within the corresponding chapters, this section provides some additional visual material that complements the summarized descriptions within the chapters:

- i) **Short-term experimental trials:** two summer campaigns were set up in Fyns Hoved (Denmark) to address different research questions in a more controlled experimental set up. The campaigns took place in 2022 and 2023 with a duration of seven and nine weeks sampling effort respectively. This set up included an observation team stationed on top of a 20 m cliff overlooking the study area below them. Observations were conducted by plain eye and using binoculars. Additionally a theodolite and a drone were used to record porpoises during trials. The cliff overlooked an area in which a modified net (Section 2.2.) was set up together with click-detectors (F-PODs) that recorded the echolocation of porpoises (**Figure 2.1.a**). This set up allowed observing wild harbour porpoises and record data on their behaviour, distribution and echolocation activity near a bottom set net structure and the PAL. Data collected under these conditions was used in **Chapter 3** and **4**.
- ii) **Long-term trials in commercial fisheries:** these trials were intended to record the echolocation of harbour porpoises near commercial fishing nets with PAL over a longer period of time (eight months) compared to the previous short-term trials. Four fishers in Germany and four in Denmark were asked to attach F-PODs to one end of their net near the PAL in a way that the F-POD floated at the same depth as the weightline with the PAL. In Germany, fishers generally attached the F-POD to the anchorline of their nets as seen in **Figure 2.1.b**. This set up allowed recording harbour porpoises in the vicinity of the nets with PAL under commercial conditions to study the long-term echolocation behaviour of porpoises near PAL.

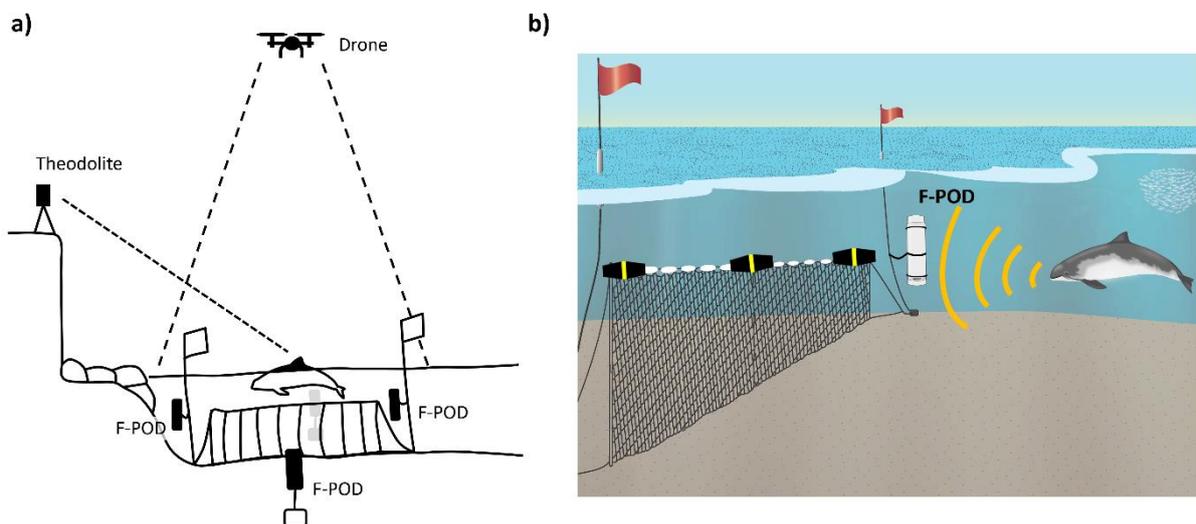


Figure 2.1. a) Experimental set up in Fyns Hoved (Denmark) used for the research in Chapter 3 and Chapter 4. Note that a modified net was used during the trials to reduce the chances of harbour porpoise bycatch while still resembling a bottom set net structure. More details on the modified net can be found in Section 2.2. **b)** Experimental set up for Chapter 5, where fishers in Germany and Denmark attached an F-POD to the anchorline of their nets so that the F-POD floated at the approximate height of the weighline where the PAL was mounted. Graphics by **a)** author; **b)** Thünen Institute of Baltic Sea Fisheries and Mahela Dinkel.

2.2. Modified net

A modified net was designed and built for the field trials to reduce the risk of porpoise bycatch while studying their interaction with a set net (Chapter 4.). Using a modified net in the field experiments that involve vulnerable species may not resemble the real-life fisheries scenario, however it reduces the chances of entanglement during studies using fishing gears like gillnets. This was considered a priority as harbour porpoises in the Belt Sea are currently classified as *vulnerable* by the IUCN (HELCOM, 2013). Similar approaches to reduce the risk of causing a bycatch of harbour porpoises during scientific research have been conducted in other studies such as in (Nielsen *et al.* 2012) where a gillnet was used with all non-vertical filaments cut, or by (Koschinski *et al.* 2006) where the gillnet was cut into vertical strips (2.3 m wide and 7 m long) enabling entangled porpoises to surface and breathe until rescued by observers. To use a modified net was considered necessary as the net was left in the water for prolonged periods of time (hours up to days) without the possibility to attend to a porpoise in case of a bycatch event, especially as the net also remained in the water unattended during night hours.

The modified net is composed of a float line with a diameter of 9 mm and a buoyancy of 0.9 kg/100 m and a weight line weighing 3.2 kg/100 m. Every half a meter (0.5 m) a two meters nylon monofilament longline fishing line with a diameter of 1.6 mm was inserted vertically (**Figure 2.2.**). The 1.6 mm thick longline was used to resemble an echo of a standard gillnet by compensating the lack of netting with a thicker line every half a meter while also reducing the risk of entanglement for porpoises. The total length of the experimental net in the field was 50 m and a height of 2 m. The acoustic properties of a standard gillnet (height: 2 m, mesh size: 140 mm stretched, material: monofilament nylon) and the modified net were examined by obtaining sonar images following the methodology used by (Kratzer *et al.* 2020).

The tests were conducted in the harbour of Rostock (Germany) using the standard scientific echosounder (SIMRAD EK60) of the German fisheries research vessel Clupea. Both nets were stretched under the vessel using an arrangement of metal bars that helped to lower the net simultaneously into the water and pull them under the vessel until they were located in the centre of the sonar beam. Both nets were initially set at 8 m depth. Due to the narrow width of the echosounder beam at this depth, it was not possible to scan the single lines of the modified net at this depth. To solve this issue, the modified net was laid out horizontally using some additional weights, and pulled through under the echosounder. This way the float line passed the beam first, followed by some of the 1.6 mm thick lines and the weight line. Echograms of both nets were made using a 120 kHz hull-mounted transducer. Sonar data were visualized in Echoview Software (www.echoview.com).

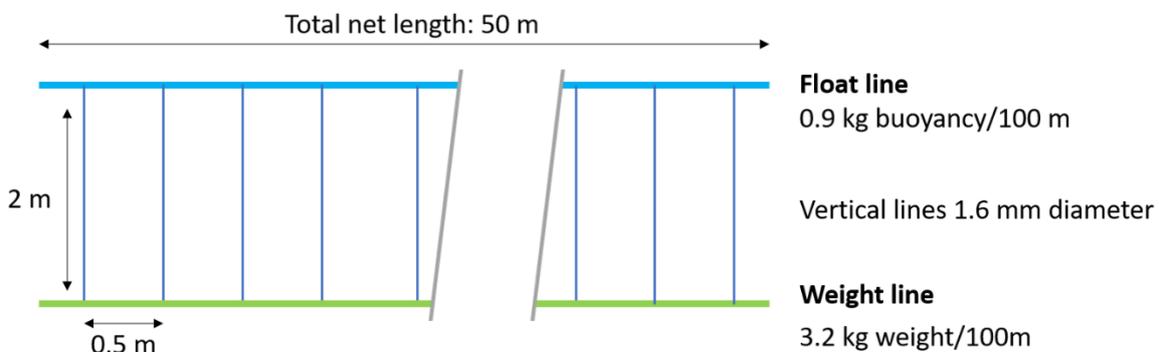


Figure 2.2. Scheme of the modified net with material properties.

The strongest echo in all cases came from the float line and the weight line. The net mesh of the standard gillnet showed lower target strength than the other net elements (**Figure 2.3.**). The 1.6 mm

thick single lines of the modified net were not visible when it was held vertically under the echosounder beam. In that case only the float line and the weight line are visible with a strong echo. The single lines were nevertheless visible when the modified net was pulled horizontally under the echosounder. The single lines showed a similar coloration to the mesh in the standard net, therefore indicating that they produce a similar acoustic image as the mesh of the standard net.

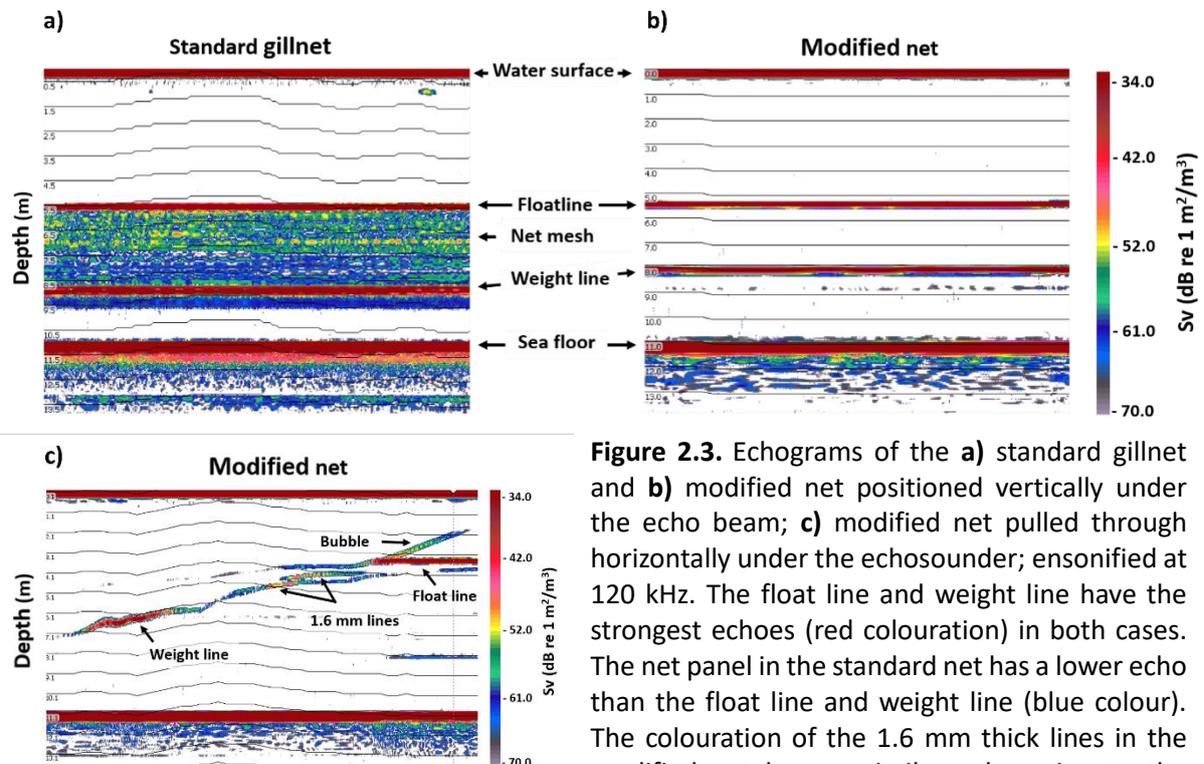


Figure 2.3. Echograms of the **a)** standard gillnet and **b)** modified net positioned vertically under the echo beam; **c)** modified net pulled through horizontally under the echosounder; ensonified at 120 kHz. The float line and weight line have the strongest echoes (red colouration) in both cases. The net panel in the standard net has a lower echo than the float line and weight line (blue colour). The colouration of the 1.6 mm thick lines in the modified net have a similar colouration to the mesh in the standard gillnet.

The modified net was considered an appropriate alternative to a standard gillnet as the echo produced by the individual lines of the modified net is comparable to the echo of the standard gillnet mesh. This will nevertheless only be perceived as such when a harbour porpoise clicks onto a line and not when it targets a space between the lines. The relatively narrow beamwidth of the clicks could increase the chances of missing the individual lines, but porpoises scan their environment with continuous head movements (Kratzer *et al.* 2020) which suggests that they should be able to detect the single lines if they echolocate towards the modified net even if there is a 0.5 m separation between them. The tests further allowed ruling out that the lines produced a much stronger echo than a standard net and does not appear as an acoustically impermeable wall in the water. The float line and the weight line are made of the same materials in both nets and have shown stronger echoes than the other netting materials and are expected to be perceived first by porpoises.

2.3. Software

Two main software were used during the thesis on which not a lot of detail could be provided within the individual chapters. This section gives some additional information on it.

CetTrack

The CetTrack app (www.cettrack.info) was used to extract positional coordinates of porpoises from drone footage during **Chapter 3** and **4**. For this, the drone videos and their associated .srt files (subtitle

files) had to be uploaded together with the flightlog of the corresponding flight. The flightlog is a file containing the information of the drone flight such as the date, time, latitude, longitude position of the drone, the altitude, heading direction, gimbal orientation among others. Once both files are loaded and synchronised (for full instructions see (CetTrack User Manual 2023) the software can be used to manually track porpoises in the drone footage. The drone video can be either played or the user can manually jump from one picture frame to the next one. The drones that were used during trials recorded 27 frames per second. Once a porpoise is seen, the user can click onto the frame and a position will be recorded for the selected point. The software allows giving the selected points different IDs as well as adding notes. The interface will display the track of the porpoise and show details from the flightlog. Once a tracking is completed the information can be downloaded as a .csv file to be further processed. CetTrack was selected to be used in these chapters, as the software was being developed within the project, and input from using it helped further develop it. Positional data from the drones in Chapters 3 and 4 of this thesis were extracted using CetTrack.

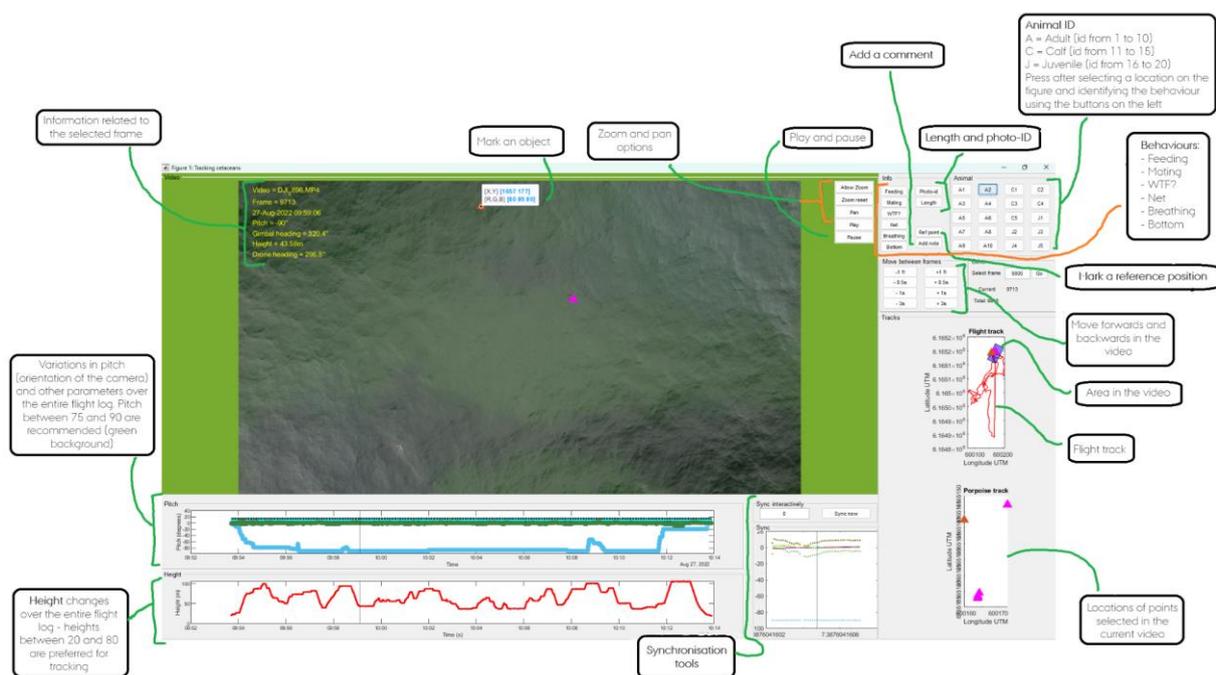


Figure 2.4. CetTrack interface with explanations for different sections. From CetTrack User Manual 2023.

F-POD app

Click loggers such as the F-POD (Full wave capture PORpoise Detector, Chelonia Ltd.) (**Figure 1.6.**) are widely used for PAM as they allow for prolonged data collection on odontocetes clicks through real-time processing and storage of a set of click features for only selected clicks (Ivanchikova and Tregenza 2023). F-PODs have been used to monitor occurrence and distribution of harbour porpoises in the Baltic Sea (HaMoNa Project, Project Number. 3522520300), Black Sea (Paiu *et al.* 2022; Popov 2023), the Belgian part of the North Sea (Calonge *et al.* 2024), to study the acoustic ecology of harbour porpoises in windfarms in the North Atlantic (Holdman *et al.* 2023), their presence in relation to vessel sounds (Van Parijs *et al.* 2023) or other cetacean species (Filatova *et al.* 2024) and to study echolocation behaviour around enhanced nets (Gustafsson 2020) to mention a few. F-PODs were used in Chapter 4 and Chapter 5 of this thesis to record harbour porpoises in the vicinity of an experimental net as well as during commercial fishing activity with and without the PAL. They were selected over other acoustic recorders due to their long-term deployment capacity. The newest version of the PODs was used (F-

PODs) as the software has been further developed and have shown to be exceed its precursor the C-PODs (Cetacean-PORpoise Detector) in their capability to understanding of fine-scale behaviours such as foraging (Todd *et al.* 2023). As the aim in Chapter 4 and 5 was to look for differences in echolocation rates near nets with PAL this was considered important.

F-PODs can detect individual echolocation clicks above 17 kHz sampling at 1 microsecond (μ s) intervals autonomously recording for 4-8 months (Chelonia Ltd. 2024). Together with the instrument a post-processing software is made available to users (F-POD app) that classifies the clicks collected by the F-POD, allows displaying the data (**Figure 2.5.**) analyzing and exporting summarized data as well as detailed information. The F-POD app identifies trains of clicks made by porpoises through a classifier called KERNO-F. In a simplified way, the KERNO-F classifier goes through the recorded clicks and finds click trains of similar clicks at regular intervals (Ivanchikova and Tregenza 2023). The click trains are then classified into four guilds:

- i) NBHF: porpoises or some dolphins that make Narrow-Band High-Frequency type clicks
- ii) Other cetaceans: all those species that produce short clicks
- iii) boat sonar
- iv) unclassified/unclassified: clicks mostly belonging to one of the other guilds but cannot be identified as such with sufficient coefficient.

Then the coherence of the train is assessed giving a threshold value to classify the detected trains into high, moderate, low and doubtful 'quality' classes (Chelonia Ltd. 2024). Click train details (**Table 2.1.**) can then be exported from the F-POD.exe software and used for further analysis. The PAL, being a synthetic harbour porpoise echolocation signal, is detected and classified as NBHF signal by the F-POD and F-POD App.

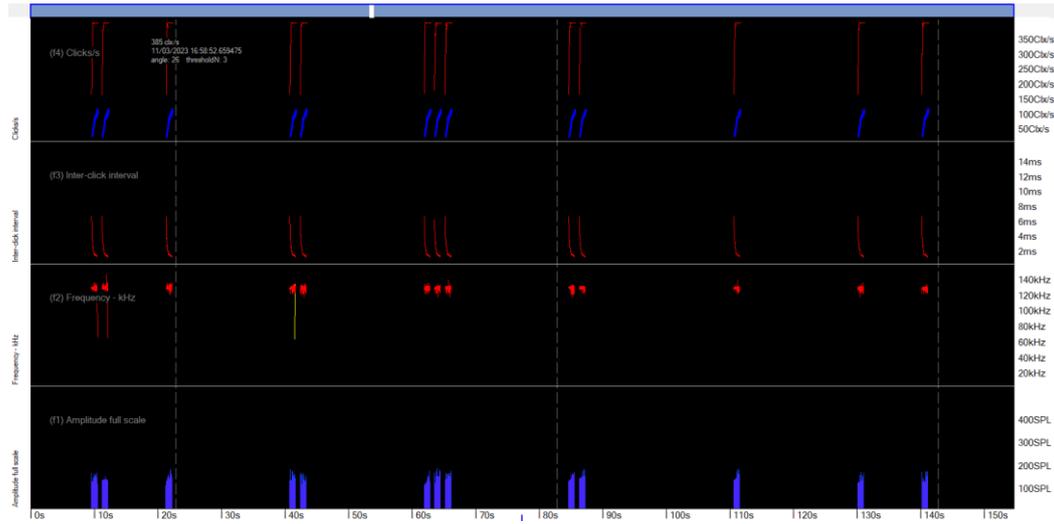
The detection function of F-PODs, tested using simultaneous drone video footage and F-PODs, varied significantly between instruments, with some F-PODS showing a probability of detecting porpoises being below 10 % and others over 80 % (Cosentino *et al.* 2023). The detection function decreased with distance and showed a maximum detection distance of 80 m (Cosentino *et al.* 2023). This range is within the estimated detection range of the T-POD (Timing PORpoise Detector) (22 to 104 m depending on the T-POD type) (Kyhn *et al.* 2012) the first precursor of the F-POD, and is above the estimated detection distance for C-POD (24 m at night and 16 m during day) (Amundin *et al.* 2022) the previous version of the F-POD). The detection function will depend strongly on the swimming direction and depth and the sonar beam behaviour (Amundin *et al.* 2022). Despite this, PODs have been widely used in acoustic research of harbour porpoise (Verfuß *et al.* 2007; Tougaard *et al.* 2009; Koblitz *et al.* 2014; Amundin *et al.* 2022a; Paiu *et al.* 2022; Popov 2023; Van Parijs *et al.* 2023; Calonge *et al.* 2024; Filatova *et al.* 2024).

Table 2.1. Abbreviations and descriptions of click train details exported by the F-POD.exe software.

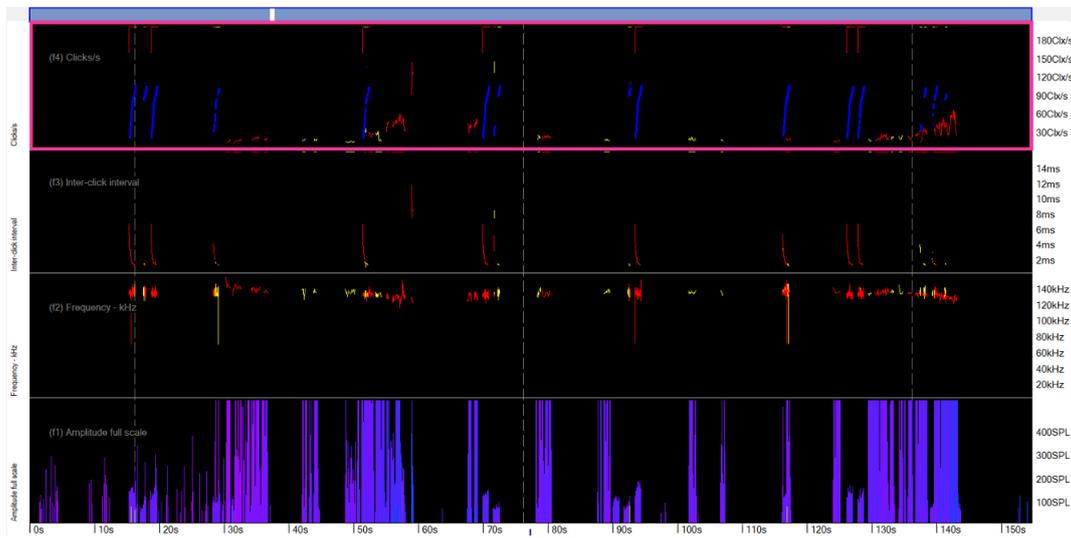
Abbreviation	Description
TrnID	train number
Time	in Excel format
Min	minute number since start of 1900
ON	logging or not
OpThreshold	the F-POD raises this amplitude threshold when it is noisy. It does not change the scale
ClksThisMin	all clicks logged in the minute
SpClass	i.e. NBHF, other cetaceans, boat sonar, unclassified. Set by KERNO-F
Qn	confidence this comes from an actual train source
IClgood	confidence level that the click rate found is correct and not 1/2 etc
tWUTrisk	risk this comes from a weak unknown train source - only evaluated in the sea where these
Marked	.. By the user
Start	time in microseconds in the minute
NofClx	in this train
nActualClx	same but this does not count gaps in which a real click has not been found but has been
medianKHz	of the whole train
avEndF	average of the frequency of the last cycle in all the actual clicks in the train
nRisingIPis	number of clicks in which the cycles around the loudest cycle show no fall in inter-peak-interval
avSPL	average sound pressure level, using raw values that may be clipped
avPkAt	average of the wavenumber of loudest cycle in each click
avBWx8	average of a bandwidth measurement, on an arbitrary scale, for each click
TrDur_us	train duration in microseconds
AvPRF	reciprocal of mean inter-click-interval in seconds
nIClrising	number of inter-click-intervals that are larger than the one before
MinICI_us	Shortest ICI excluding the first and last, as these are more often inaccurate
midpointICI	ICI half way through train of clicks
MaxICI_us	Maximum ICI excluding the first and last, as these are more often inaccurate
ClkNofMinICI	position in train of shortest ICI
ClkNofMaxICI	position in train of longest ICI
NofClstrs	number of train clicks that have an identified multipath cluster following
avClstrNx8	number of clicks in the multipath cluster x 8
avClF0	frequency of loudest cycle within multipath cluster
avClF1	next loudest
BeforeIPratio	av of wavelength before click record starts divided by wavelength of loudest cycle
PreIPratio	av of wavelength of cycle before loudest divided by wavelength of loudest cycle
Post1IPratio	av of wavelength of loudest cycle divided by wavelength of next cycle
Post2IPratio	av of wavelength of loudest cycle divided by wavelength of next+1 cycle
EndIPratio	av of wavelength of loudest cycle divided by wavelength of last cycle
EncSpN	can be used to label the species possibly producing the train
avPkIPI ¹	the average value of the time between peaks (= wave period) of the loudest cycle in each click in a train.

¹ Parameter included in click train export table but missing in the descriptions. Description is personal communication from Nick Tregenza, developer of F-PODs.

a)



b)



c)



d)

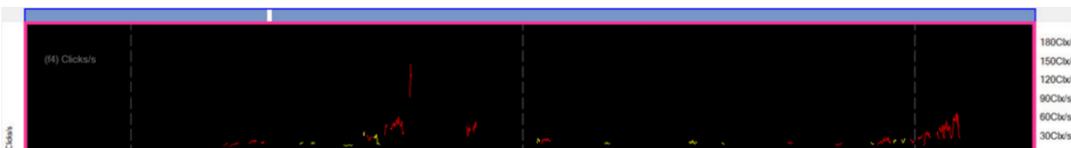


Figure 2.5. F-POD app interface in which click trains recorded by the F-POD can be visualized. The four panels show different qualities of the detected click trains: clicks/s, inter click interval, frequency and amplitude of **a)** clear PAL signals with randomized repetition patterns; **b)** harbour porpoise echolocation signals recorded at the same time as PAL. For an easier understanding of the first panel in **b)** showing the clicks/s (pink box) was modified and both components separated: **c)** PAL recorded during that interval while **d)** shows the porpoise click trains recorded simultaneously. The colours in the first three panels in **a)** and **b)** indicate the quality of the train: red: high quality; yellow: moderate; blue: echoes. The blue to violet coloration in the lowest panel (Amplitude full scale) indicates that the signals are narrow-band high-frequency signal (F-POD software guide: <https://www.chelonia.co.uk/f-pod/existing-user-resources/>).

Chapter 3

Performance of theodolites versus drones in land-based studies of marine mammals

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Title: Performance of theodolites versus drones in land-based studies of marine mammals

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Abstract

Theodolites and drones are key instruments for observing small whales in coastal areas. This study compared their performance while observing the elusive harbour porpoise (*Phocoena phocoena*) in the western Baltic Sea. The methods were used simultaneously providing information on location, behaviour and group size during a field campaign in 2022. Theodolite observers were able to detect surfacing positions during 80.5% of the harbour porpoise sightings while a drone collected data during 50.7% of sightings. The drone footage quality was poor during 47.3% of these sightings. An in-depth analysis of 75:36 hours of good quality footage resulted in 16:55 hours (22.4%) of cetacean appearance. The determination of group size was significantly more precise using drone footage while the theodolite was more accurate in determining the start/end of a sighting. The accuracy of locations was modelled using the distance (D_{t-d}) between recorded theodolite and drone coordinates of the same surfacing porpoise. D_{t-d} varied significantly based on the point quality. Sea state and porpoise to theodolite observer distance did not seem to influence D_{t-d} . Both methods complement each other and should ideally be used simultaneously to obtain both accurate and detailed information on harbour porpoises and other marine mammals during land-based observation studies.

Keywords: Method comparison, land-based observation, odontocetes, cetacean, harbour porpoise

3.1. Introduction

Observing cetaceans in their natural habitat is important and can serve many purposes. Amongst them studying trends in abundance, creating a species inventory, assessing geographical and temporal distribution, mapping behaviours, understanding basic biology and life history parameters as well as targeted experiments (ASCOBANS 2009). This information is not only useful for research but is also fundamental for scientific advice and decision making for effective management measures (Evans and Hammond 2004). Observing cetaceans in their natural habitat can nevertheless be challenging as the animals spend extended periods of time under water, exhibit unpredictable movement patterns with some species only briefly seen at the surface while covering vast distances (Piwetz *et al.* 2018; Morete *et al.* 2018). A variety of visual, acoustic and other survey techniques can be used for this purpose. Visual observations can be land-based (Gutiérrez-Muñoz *et al.* 2021; Dolman *et al.* 2014; Morete *et al.* 2018), boat-based (Brennecke *et al.* 2022; Hamilton *et al.* 2023; Viquerat *et al.* 2014), carried out with aircrafts or drones (Gilles *et al.* 2022; Brennecke *et al.* 2022; Oliveira *et al.* 2023) or using underwater cameras (Patton and Lawless 2021; Morisaka *et al.* 2022). While their cover is limited to the immediate vicinity, land-based observations are a popular method since they allow for a continuous monitoring of an area at relatively low costs with a low risk to alter the natural behaviour of the study species (Piwetz *et al.* 2018). Land-based observation methods can be carried out from dedicated survey platforms or using platforms of opportunities such as light houses or other vantage points, ferries or oil drilling platforms to mention a few. Comparability of such different techniques is not always a given and suggests that comparison experiments are necessary to avoid biased conclusions from differently acquired data.

Theodolites

Since their first use for marine mammal studies in the 1970s by Roger Payne, theodolites and total station theodolites (from here on referred to as theodolites) have been used to study at least 46 marine mammal species in 36 countries (Piwetz *et al.* 2018). They allow recording geographical positions of marine mammals as well as collecting data on their behaviour (Piwetz *et al.* 2018), distribution and relative abundance over time (Frankel *et al.* 2009; Harzen 2002). Some examples of their use are abundance estimates of humpback whales in east Australia (Noad *et al.* 2006), the examination of detection radii of acoustic equipment for harbour porpoises in Denmark (Kyhn *et al.* 2012), estimating approach distances of harbour porpoises to a net and an acoustic alarm in Canada (Culik *et al.* 2001), or to study the effectiveness of seal scarers as deterrent tools for harbour porpoises near construction sites (Brandt *et al.* 2013).

Theodolites are topographical equipment used in civic engineering and cartography to take precise (down to a few mm over hundred meters) measurements within a confined area, usually set up using official survey markers. A traditional theodolite measures only a vertical angle relative to the zenith, the position directly above the theodolite, and a horizontal angle relative to a reference object with known location and bearing from the theodolite (Piwetz *et al.* 2018). A total station theodolite is an optoelectronic geodetic instrument that integrates the function of measuring angles with an electronic distance meter allowing to estimate distances from the instrument to a particular point and computing coordinates through the on-board computer (Kavanagh and Bird 1996). Using the vertical and horizontal angles and the exact height of the station in relation to the variable sea level, the position of targeted object can be calculated based on trigonometric equations.

Drones

Remotely piloted unmanned aircraft systems, commonly referred to as drones, have also become an essential tool for marine mammal observations allowing research on the movement, ecology, behaviour, health and habitat use as well as monitoring activities or during targeted experiments (Raoult *et al.* 2020; Brennecke *et al.* 2022; Aniceto *et al.* 2018). The ability to observe animals from above is especially valuable for analyzing behaviour of cetaceans that spend large amount of their time below but close to the water surface. Most drone platforms are equipped with various modules, such as Global Positioning System (GPS) receivers, accelerometers, magnetometers, ultrasound sensors and barometers, allowing for photogrammetric measurements from drones to produce results with small error levels. Drones thus expand the range of data that can be collected during land-based observations. Further, drones with high precision sensors are now available for a few hundred Euros and are therefore available to everyone. While drone technology has been adopted rapidly by researchers, there is still a shortage of studies that compare visual observations data derived from drones to that obtained by theodolite tracking. Furthermore, the possibility of combining both tools requires the consideration of data set comparability (Godwin *et al.* 2016) and identification of strengths and weaknesses of each method. The aim of this study is to assess these two visual observation methods, reveal their shortcomings and analyze their comparability while studying the rather elusive harbour porpoise (*Phocoena phocoena*) in the western Baltic Sea. We present survey results obtained through a series of field trials and tested the following hypothesis: (1) accurate coordinates of harbour porpoise individual positions can be obtained from both methods, and at close distances they do not differ strongly; (2) drones allow identifying behaviour in more detail and detect formerly unknown behaviours accurately; (3) Visual data collected by both methods overlaps just partially, making the methods complementary rather than alternatives to each other. A SWOT analysis further gives insight into the scope of both methods. SWOT stands for Strengths, Weaknesses, Opportunities and Threats, and is a process in which the internal and external factors that affect a topic or entity are analyzed on its performance (Namugenyi *et al.* 2019). Strengths and weaknesses are considered as internal characteristics that the entity presents itself, while opportunities and threats are considered external properties that can influence the entities success or performance depending on the environment (Namugenyi *et al.* 2019).

3.2. Material and Methods

Study Area

The study was carried out in the western Baltic Sea on the north-western side of the Fyns Hoved peninsula (Island Fyn, Denmark) from June 25 until August 28 2022. Data was collected during a study investigating behavioural responses of harbour porpoises to a temporally activated acoustic alerting device and an experimental net using acoustic and land-based observations. Observations by plain eye of porpoises approaching in one of three quadrants started the theodolite and drone activities (**Figure 3.1.**). At least three observers, but more often four observers worked at the same time. When four observers were present, two drones could be operated simultaneously: one stationary drone at 100 meters above the take-off location that was filming the experimental set up with a ground resolution of 2 cm and a following drone to record porpoises at lower altitude. Activities rotated every 30-40 minutes to add variety to the work hours, keep concentration up and allow rest time for one observer. Different observers on two shifts (< 6 h continuously) operated per day (max 10 hours total) during

daylight hours between 4am – 6 pm UTC. Field work was conducted with authorization from the Danish Nature Agency (Naturstyrelsen).

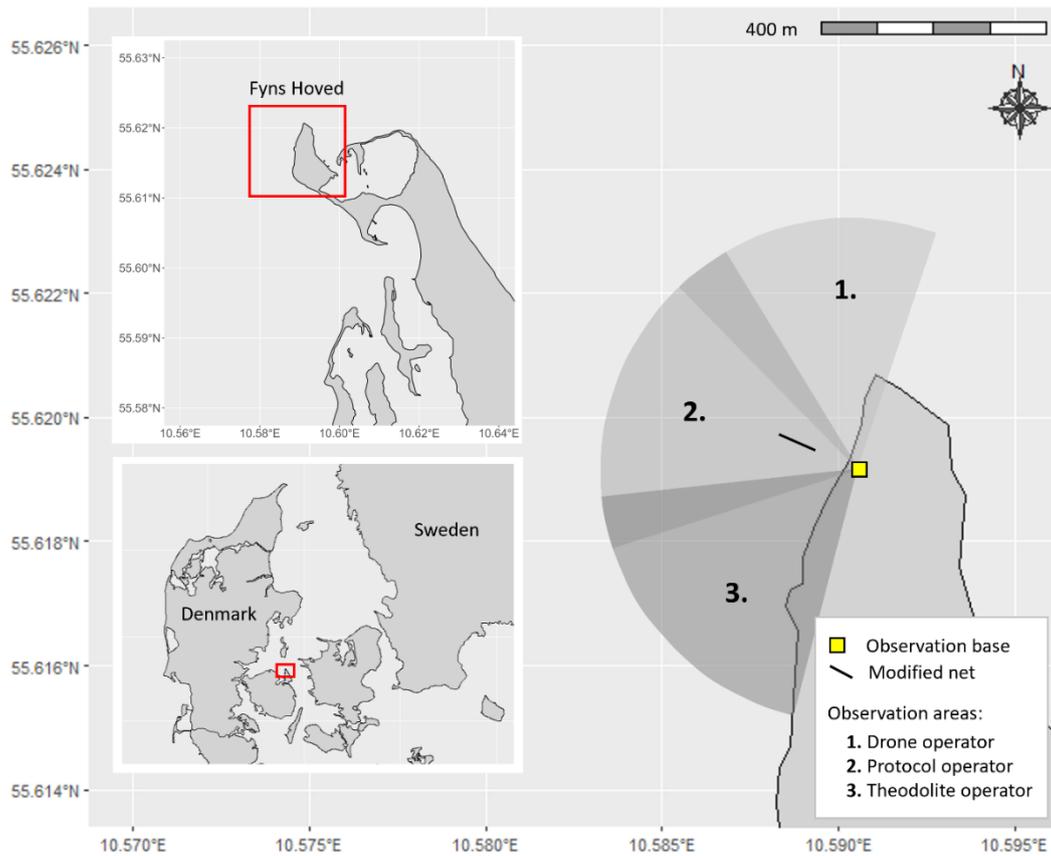


Figure 3.1. Survey area with positions of underwater equipment and three observation quadrants marked in grey shadings (1-3).

Recorded data

A sighting was defined as at least one porpoise or group surfacing at least two times seen by two observers. An event ended when no porpoise was seen for 10 minutes. If an additional (new) porpoise or group was seen during an on-going event it was noted as a new sighting. When several individuals mixed, it was not always possible to tell which porpoise belonged to which sighting. During a sighting event all observers turned to recording data, take theodolite points and flying the drones (**Figure 3.1.**). Observers were asked to briefly scan the area in between individual tasks if time permitted. The time, number of porpoises, general behaviour, initial heading direction, theodolite points, drone activity and the weather were recorded in different protocols (protocols tables as supplementary material *Table S.3.1 – S.3.4.*). Observations were interrupted or terminated when sea state was higher than 3 which corresponds to a wave height between 0.5 to 1.00 m.

Theodolite

The Leica Flexline plus TS06+ total station theodolite was used for the tracking of surfacing points of porpoises from a stationary point on a 20 m cliff. Exact cliff height was measured by stationing the theodolite using three permanently marked large stones with known location on the beach. The height of the stones was calibrated against a sea level meter that was installed behind the cliff in a small lagoon, where wind did not interfere with reading the variable sea level using the theodolite. Horizontal and vertical angles were used to compute the geographic position of the targets. From here

on, the computed positions in UTM will be referred to as theodolite points. The target for the theodolite cross hair when using the ocular was the centre of the animal or its footprint (surfacing turbulences). In some occasions the secondary crosshair on top of the theodolite was used to collect points faster resulting in less accurate positions. All possible surfacings of all individuals were recorded to get an idea of the distribution of the group. If a group of porpoises split up, the theodolite operator concentrated on the porpoises that the drone operator was following. Most observers had no previous experience using a theodolite but had a training session during one day before collecting data in the field. The quality of a point taken was ranked as Q1) porpoise/footprint seen exactly at measured position; Q2) tracking point close to last surfacing; Q3) tracking point was taken as an approximation of the last surfacing point. For each measurement, the observed behaviour, swimming direction and quality was noted.

Drones

Three DJI Mini 2 and one Air 2S drones (www.dji.com) were used. Drones were operated using the Litchi App (<http://www.flylitchi.com>) and flightlogs were automatically synchronized to www.airdata.com. Drones were controlled using either shaded android smartphones or an apple tablet attached to the controller. The following drone was used for detailed focal follows (Altmann 1974) of porpoises. A stationary drone was flown 100 m above take-off location and centred over the experimental set up to record reactions of porpoises towards the net. After July 28th, this drone was continuously in position to avoid missing net interactions. Theodolite and following drone operator were in constant exchange to agree on the individuals to follow. From July 11th on, drone operators assessed the quality of the recorded following drone videos to provide information on the recorded files and to facilitate the post-hoc analysis of the videos. Drone footage quality was ranked as D1: porpoise is on the video nearly full time; D2: porpoise can be seen on the video but with interruptions; D3: porpoise can be seen on the video just for a few seconds or not at all. The altitude of the following drone ranged between 10-90 m above the water surface. Drones were flown during good weather conditions, i.e. no or little precipitation, no fog and wind speed < 10 m/s. The observed sea state and the monitored wind speed were not always in direct relation as the cliff shielded the study area during easterly winds. Flight duration was limited by battery capacity which was about 20-25 min for both drone models. A lead acid battery and inverter provided charging for drones, phones and controllers. Most drone pilots had no previous experience operating a drone except for a training session during one morning. All users operated the drones under the possession of a drone flying certificate, issued by the European Union Aviation Safety Agency for the A1/A3 open sub category.

Video analysis

Drone footage was screened after the field campaign. Mostly following drone videos with quality D1 and D2 were assessed. Those videos were watched at normal speed and played back when necessary. A newly developed software, CetTrack was used to extract geographic positions of porpoises in the footage. The software uses the flight log data (date, time, latitude, longitude, altitude of the drone above medium sea level, heading direction and gimbal orientation), drone data (aperture angle of the camera, and number of pixels of the image recorded) and subtitle information for synchronization purposes.

Comparison data collected by both methods

The number of taken theodolite points during a sighting was compared to the quality of the following drone footage for the respective sighting pairs. A Kruskal-Wallis test was performed for 278 sighting

events. The stationary drone was not included in this analysis as the drone flew continuously on the same position independently if there was a sighting going on or not. All positions from following drones and theodolite were taken into account for producing kernel density plots (Hastie *et al.* 2001) of the location data using the libraries `ggpubr` (Kassambara 2023) and `eks` (Duong 2024) under R version 4.3.1 (R Core Team 2024).

Group size

The estimated porpoise group size recorded by the theodolite observers was compared to the number of individuals observed during the screening of the drone footage for the same sighting played at normal speed. Following drone footage quality D1 and D2 were prioritized as well as stationary drone footage in which porpoise presence was marked in the protocols. 80 sightings were analyzed corresponding to 75:36 hours of drone footage. A Wilcoxon signed-rank test was used to compare the group size counts.

Behaviour

The behaviour recorded by the theodolite operator on the cliff was compared to the behaviour that was observed in simultaneously taken drone footage. For this aim, two exemplary videos were chosen. Videos were selected after initial screening and choosing sightings in which at least 20 theodolite points were taken. The time of occurrence of each individual visible in the footage was noted and each individual was assigned an ID. Sex and age were classified based on the body size and the swimming distance between individuals. Two porpoises with significantly different body sizes swimming very close to each other were classified as a mother-calf pair (MCP); assuming that the bigger individual is the mother and the smaller is the calf. This was verified by observed suckling events. Male porpoises were differentiated from other individuals by observed mating attempts where the penis was visible. Five general behavioural categories (travelling, feeding, socialising, not classified and not visible) were established based on definitions given in previous studies and a larger behaviour analysis for the area (Craul 2023). The exact time stamps for each observed behaviour and surfacing event in the video were recorded for each porpoise that appeared in the footage. All behaviours observed by the theodolite operator and the video analysts were plotted together to allow for a comparison.

Drone and theodolite metrics comparison

Porpoise coordinates were extracted from drone footage to be compared to coordinates collected simultaneously with the theodolite. For this aim 22 sightings encompassing 6:18 h of drone footage were tracked. Sightings were selected based on two criteria: 1) single or MCPs in close proximity to allow for an easy matching process; 2) sightings with more than 20 theodolite points were prioritized. For MCPs, the surfacings of the mother were taken as coordinates for matching. The entire sighting was not always tracked as in some occasions more porpoises joined the sighting which impeded clearly matching theodolite and drone coordinates. In total 153 coordinate pairs could be matched using the date and time allowing for a maximum delay of 30 s between the drone footage and surfacing theodolite point to account for the time it took for manually pointing and measuring surfacings. Once pairs of drone and theodolite coordinates were identified, the Euclidian distance between the Universal Transverse Mercator (UTM) coordinates (D_{t-d} : Distance theodolite - drone) was calculated.

D_{t-d} was used to test if the accuracy of the theodolite coordinates varies with the distance to the instrument, the sea state and the self-assessed theodolite point quality using a generalized linear model (GLM) with Gamma distribution (log link). The variables were reduced by choosing the best

model fit selecting the lowest AIC value. The accuracy of the coordinate position of the drone is affected by the satellite uplink (number of satellites that are in direct line of sight to the drone), and the availability of the different Global Positioning Networks (GPS, GLONASS and GALILEO). The DJI mini 2 drone has a vertical hovering accuracy of ± 0.5 m and a horizontal accuracy of ± 1.5 m (both with GPS Positioning, DJI Mini 2 characteristics, 2023). Precision of the coordinate estimates will vary furthermore with camera characteristics like gimbal angle, movement (abrupt, slow), mode of operation (P-GPS, “Sport-mode”, etc), and if the animals are in the center of the frame or more towards the edges of the image. In the field, drones were usually started when the drone indicated that it had enough satellites to establish a stable GPS connection. Drone footage was tracked when the gimbal was near 90° while avoiding taking points after abrupt movements or rotations in the footage. The precision of the absolute position estimates from the drone is roughly 2 m after first assessment for calibration trials.

Time and distance

The time of the first and last theodolite and drone coordinate during the same sighting were compared to assess if one method is better at capturing the initial or end phase of a sighting event. The distance of the first and last taken coordinate with both methods from the observation based were also calculated for the 22 sightings (**Table 3.3.**). A linear correlation using a square root transformation was performed to explore if the distance data provides a pattern. Sightings with fission-fusion events (Tsai and Mann 2013) were excluded for this analysis due to unclear start/ending times and positions. All analysis were conducted using R version 4.3.1 (R Core Team 2024).

3.3. Results

By plain eye, 576 harbour porpoise sightings were recorded on nearly all observation days (**Table 3.1.**). The mean number of sightings of porpoises per day varied, with more sightings in August than in July.

Table 3.1. Summary of field effort collected by different visual observation methods. *Stationary drone flown continuously after July 28th ** Following drone footage ranking introduced on July 11th.

		Total	June	July	August
SIGHTINGS	Nr of days with sightings	44	3	16	25
	Nr of sightings	576	12	159	405
	Mean Nr of sightings (NS) per day	13.1	4.0	9.9	16.2
THEODOLITE	NS with theodolite points (TP)	464	8	109	347
	NS with ≤ 3 TP	163	5	42	116
	NS with ≥ 4 to 10 TP	141	1	41	99
	NS with ≥ 10 TP	160	2	26	132
DRONE	NS with 100 m drone*	476	1	97	378
	NS with following drone	292	2	65	225
	NS D1**	89	-	3	86
	NS D2**	36	-	12	24
	NS D3**	138	-	42	96
	NS no quality ranking	29	2	8	19

Theodolite

At least one theodolite point was recorded for 80.5 % of the sightings, with a total of 5 058 points taken during the field season. The closest point from the instrument was taken at 55 meters while the furthest point was taken at 1.4 km distance. All three self-assessed qualities of theodolite points can be found over the entire area where data was collected (**Table 3.2.**). Points are distributed near the coast, with more location taken towards the north and south compared to the west (**Figure 3.2.a**). 66.2% of the points were taken closer than 300 m from the instrument.

Table 3.2. Number of theodolite points taken according to distance from the instrument and classified by quality.

Distance from Theodolite (m)	Nr points taken	% of total	Quality of points		
			Q1	Q2	Q3
< 150	1488	29.4	669	599	218
150 – 300	1860	36.8	559	787	507
301 - 450	792	15.6	230	265	292
451-600	531	10.5	240	143	146
601-750	257	5.1	163	50	43
751-900	79	1.6	30	36	13
> 900	51	1.0	29	15	6
TOTAL points	5058	100	1920	1895	1225

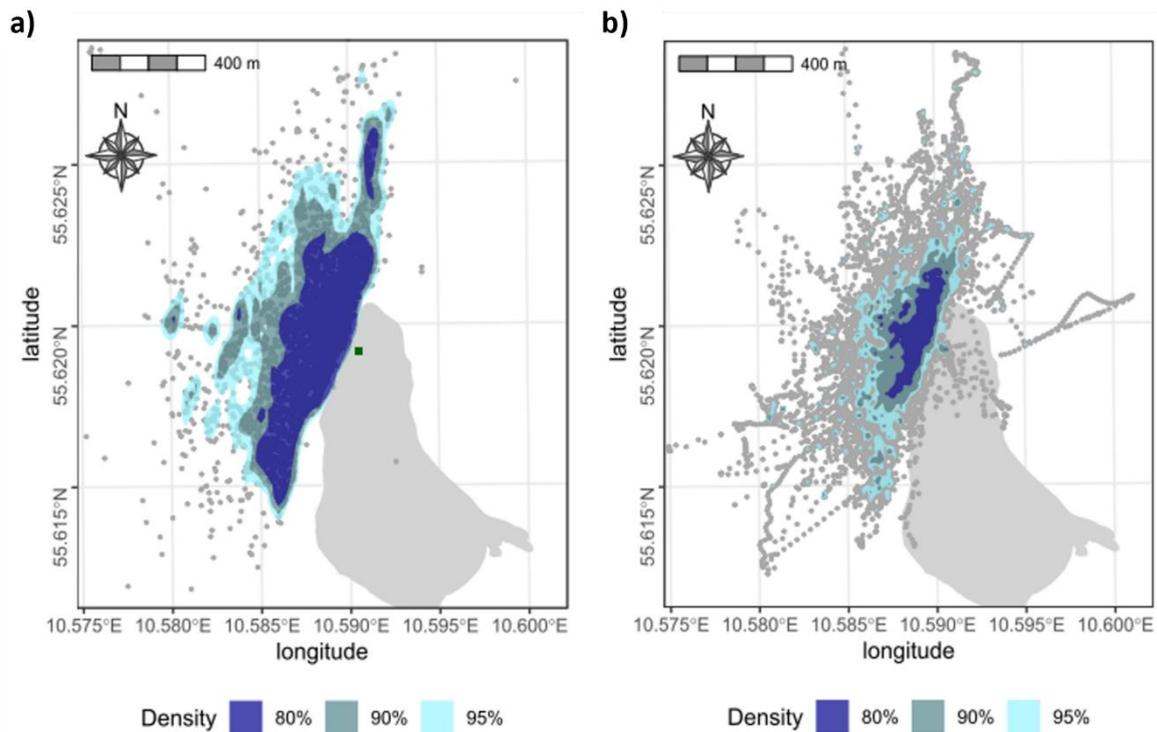


Figure 3.2. Kernel density plots illustrating **a)** the distribution of theodolite points in the study area; **b)** density of drone effort. Core observation areas include 80 % of all theodolite/drone locations (dark blue) 90 % (grey) and 95% (light blue) respectively.

Drone footage

248 hours of drone footage were recorded during the field campaign. Drone effort was concentrated near the coast with the kernel densities covering a smaller area compared to the theodolite points, but showing the same general distribution pattern with more drone locations in coastal areas north and south compared to the offshore areas in the west (**Figure 3.3.b.**).

Video analysis

75:36 hours of D1 and D2 quality footage were screened. Porpoises were seen during 16:55 hours within these videos, corresponding to an appearance rate of 22.4%. Visualizing a 20-minute video and filling in the corresponding data table took between 25-45 minutes as videos had to be frequently paused to confirm a sighting or differentiate between a wave movement, glare, a bird or seal or re-find animals that had submerged under the water surface. 22 sightings were selected for tracking to extract coordinate positions of harbour porpoises (**Figure 3.3.**). Four sightings were tracked taking a coordinate every 0.5 s to showcase how detailed the resolution of the movement pattern can be captured with the drone. The remaining videos were tracked taking points only when the porpoises surfaced to compare those coordinates to the theodolite coordinates.

Comparison of data collected by both methods

Theodolite points were taken during 80.5 % of the sightings while the following drone was started during 50.7 % of the sightings. Significant differences were found in the number of theodolite points taken during flights with different drone footage quality (Kruskal-Wallis test: $p=2.2e-16$). A Dunn-Bonferroni post-hoc test was performed to identify differences between quality categories. Sightings in which the video footage was classified as D1 (mean: 26.6 points, SD: 26.9; min: 0, max: 128) showed no significant differences to D2 footage (mean: 14.0 points, SD: 14.5, min: 0, max: 70) (adjusted $p > 0.05$), but a significantly higher number of taken theodolite points than D3 footage (mean: 6.8 points, SD: 7.9, min: 0, max: 38) (adjusted $p < 0.05$). D2 footage also showed significantly higher number of theodolite points taken than during D3 footage (adjusted $p < 0.05$). Sightings in which the following drone was not flown had a mean number of 3.9 theodolite points (SD: 7.4, min: 0, max: 82) and was significantly lower than all the other drone footage qualities (adjusted $p < 0.05$) (**Figure 3.3.**).

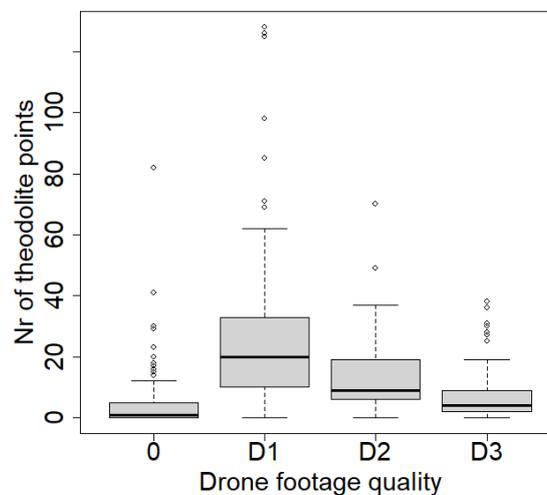


Figure 3.3. Drone footage quality and availability of footage in relation to the number of theodolite points taken during a sighting.

Group size

The group size of porpoises observed by the theodolite operator were significantly lower than counts obtained by analyzing the drone footage for the same sighting (Wilcoxon Signed-Rank Test: $p = 0.023$). Median difference in number of porpoise counts indicated no difference, while the mean showed an underestimation of 0.25 (SD: 1.06) individuals per sighting with the theodolite.

Time and distance

The 22 sightings for which drone coordinates were extracted (**Table 3.3.**) indicated that the theodolite provided first detailed information (smaller difference between start of sighting and first point taken) and remained longer with the porpoises (smaller time difference between the end of sighting and last taken point), compared to the drone coordinates. The distance from the observation station at which the first theodolite point and first drone coordinate was taken varied for most of the sightings without a clear visible pattern (linear regression $R=0.018$, $p=0.596$, **Table 3.2.**). The final points however show a clearer relationship ($R=0.387$, $p=0.004$), with theodolite points being further away than drone points (Supplementary material *Figure S.3.2.*).

Local distribution data

Points collected with the theodolite give a general information on the location of the porpoises in the study area highlighted by three examples in **Figure 3.4.** Theodolite starting points are more accurate in defining where the sighting started than the drone which has to first be started and generally takes some time until it finds the porpoise. In some occasions the theodolite operator was also able to follow the animals for longer periods and at further distances than the drone as can be seen in **Figure 3.4.a** where only the theodolite operator tracked some points that indicate a northward movement of the porpoise. In **Figure 3.4.b** a gap in drone recordings occurred when a sighting was longer than 20 minutes (drone battery capacity limit). In this case, theodolite points could be collected continuously while one drone had to be flown back and a new one started, thus missing a part of the sighting in the northern part of the map. Drone footage nevertheless allows collecting very precise distribution information of the animals especially under the water surface which is missed by the theodolite as can be seen in all graphs. It was feasible to track several animals during one sighting using the drone footage (**Figure 3.4.c**). Nevertheless, drone tracks are often interrupted which occurs when the porpoise dives down deep, its colour merges with the sea floor or the drone operator loses it. Once an individual is lost or exits the frame, it is often not feasible to determine if the same porpoise is seen again in a group once it re-enters the video frame. This hinders a continuous observation of the same individual especially in larger groups where not all the porpoises can be followed at the same time as they often spread out or move into different directions. This is the case in **Figure 3.4.c** where 5 porpoises were present during the sighting but 8 different IDs had to be attributed to the individual tracks as it was not possible to reassign IDs to the porpoises that re-entered the video frame.

Table 3.3. Tracking times and results for drone footage in comparison to the theodolite. Lines with the same colour belong to the same sighting.

#	Date (2022)	Sighting ID	Drone type DJI	Total flight duration (mm:ss)	Time tracked in video (mm:ss)	Nr of animals	Approx. tracking duration (min)	Tracking interval	Nr of tracked surfacings in drone footage	Nr of matching points (theo – drone)	ΔTime 1 st point taken vs start of sighting (mm:ss)		ΔTime last point taken vs end of sighting (mm:ss)		Distance to base, first point (m)		Distance to base, last point (m)		
											Theod.	drone	Theod.	drone	Theod.	drone	Theod.	drone	
1	26.08	21	Mini2	33:02	12:59	2	240	0.5 s	39	14	Several sightings merging								
2	26.08	19		33:09	10:15	2	210		37	10	Several sightings merging								
3	27.08	9		20:51	01:20	2	40		18	7	00:54	28:28	No end time		298,7	279,8	87,2	128,0	
4	16.08	26		21:26	10:36	1	60		26	5	01:31	02:53	03:28	06:21	159,5	103,2	64,2	173,6	
5	21.07	3		19:20	01:18	1	20		5	1	17:20	16:54	00:00	08:23	NA	32,2	115,6	16,0	
6	26.08	11		09:50	01:27	1	20		4	2	00:53	03:20	01:59	03:14	184,1	366,3	407,3	361,0	
7	30.07	3		13:41	02:52	1	30		7	5	01:15	03:34	00:51	07:47	201,5	218,0	805,3	209,9	
8	22.08	15		21:30	04:14	1	50		12	7	01:06	04:12	04:19	09:32	191,5	414,3	770,3	527,4	
9	04.08	3	Air2S	14:16	04:48	2	60	surface	27	5	03:09	02:04	00:36	04:32	208,2	208,6	528,9	341,1	
10	08.08	13	Mini2	13:38	02:00	1	30		5	3	01:26	05:37	00:41	03:26	90,5	441,0	24,7	269,4	
11	14.08	4		14:35	02:20	2	20		8	2	00:09	04:56	01:02	00:00	118,6	155,6	185,0	295,3	
12	14.08	5		12:41	04:05	2	40		27	15	00:20	03:01	04:21	03:15	927,3	314,7	299,3	307,6	
13	26.08	5		15:09	09:03	2	40		60	18	00:12	03:02	00:00	03:35	496,1	241,4	115,3	101,0	
14	27.08	4		20:39	09:58	2	40		46	14	00:00	01:29	03:50	16:35	285,0	100,0	109,2	49,5	
15	25.08	5		17:33	05:55	2	50		30	7	00:00	02:47	01:55	02:29	25,1	285,5	456,2	602,1	
16	25.08	9		19:51	15:00	2	60		48	15	01:10	02:46	01:54	13:54	169,9	85,0	164,1	187,7	
17	22.08	5		18:44	08:23	2	40		59	3	01:40	03:30	00:06	05:14	170,8	72,3	387,2	61,4	
18	20.08	7		21:37	03:27	2	90		23	5	01:37	11:30	10:50	19:36	648,8	302,7	663,2	389,4	
19	20.08	11		20:08	01:47	2	30		8	2	Several sightings merging								
20	22.08	7		20:38	00:56	2	50		8	4	01:06	04:12	02:05	02:14	202,8	246,4	375,1	385,4	
21	15.08	11		07:32	03:52	2	45		14	3	01:51	03:25	No end time		289,5	117,0	63,2	134,6	
22	26.08	8	09:08	00:33	2	30	5		1	07:07	22:36	01:46	04:58	385,1	430,5	506,8	409,5		
Mean (min)				18:08	05:19	1.73					02:15	05:22	02:20	06:46					
Median (min)				19:02	03:59	2					01:10	03:25	01:54	04:58					
S.D. (min)				06:28	04:17	0.46					03:58	05:36	02:37	05:23					

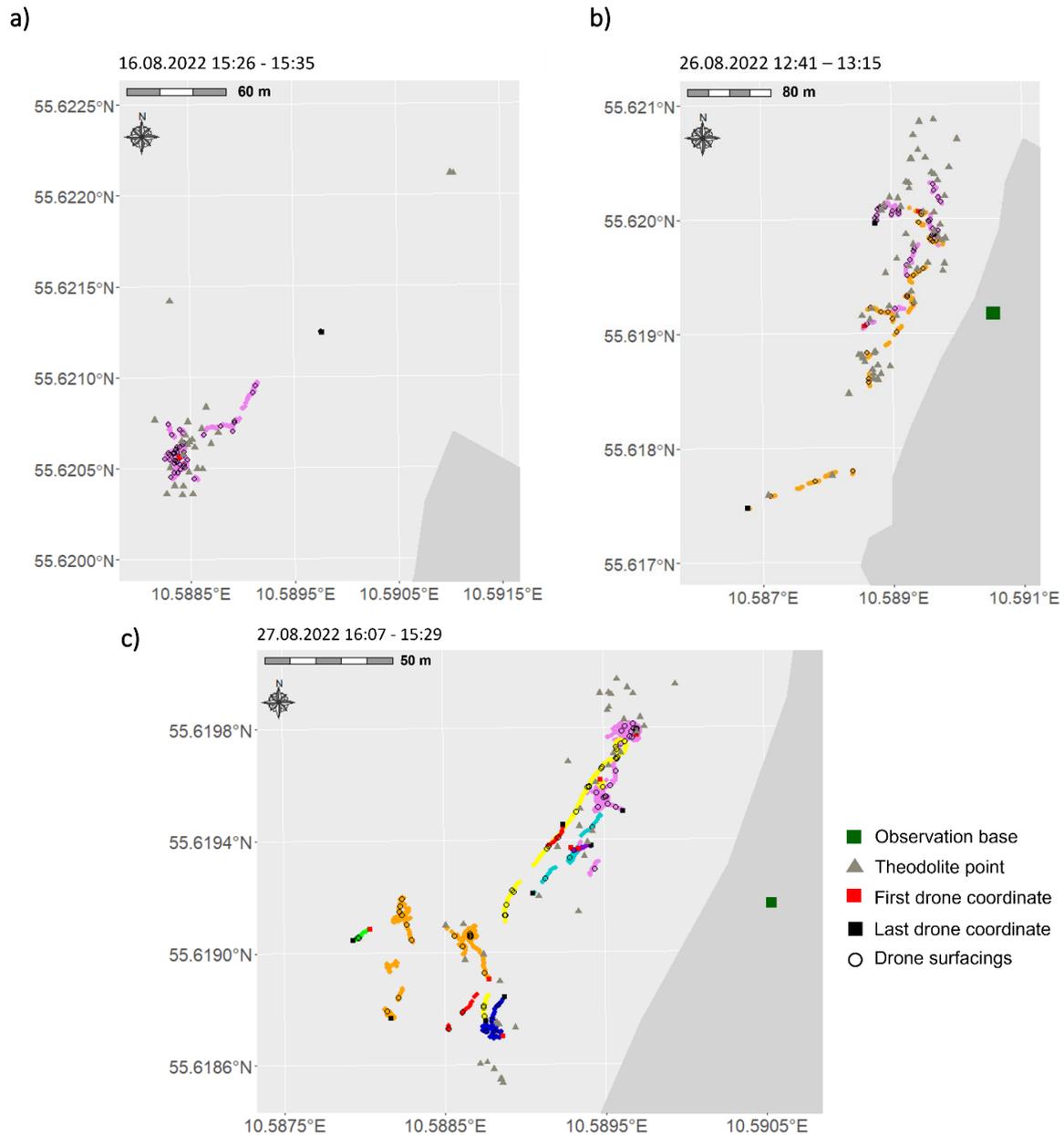


Figure 3.4. Porpoise drone tracks and coordinates from the theodolite for **a)** single adult porpoise recorded during one flight, **b)** a MCP recorded during two flights (pink: first flight, orange second flight), **c)** five porpoises recorded during one flight. Each porpoise ID (8) is marked with a different colour.

Behaviour

While general behaviour observations were recorded by the theodolite observer, these behavioural categories did not always match the drone footage (**Figure 3.5.a**, **Figure 3.5.b**). Further, surfacing events do not align neatly, with theodolite points always being recorded with some delay, probably due to the time that an observer needs to see the animal, adjust the theodolite and take the point and notes. More surfacing events were recorded in the analyzed drone footage compared to the theodolite points taken in the field. **Figure 3.5.a** shows a MCP that was foraging, travelling and socializing. Behaviour categories attributed by both methods do not match, especially not during the first nine minutes of the tracked period. The theodolite operator indicated socializing during the rest of the sighting as it was a MCP and a sort of socializing interaction can to be assumed in this context as animals were also always close to each other. The drone was nevertheless able to discern more

concrete behaviour within this interaction such as foraging intervals and travelling events which were not identified by the theodolite operator. This figure further shows an entire drone flight of around 20 minutes. The theodolite operator took points already before the drone operator had found the animals and also for a longer period as the drone had to fly back limited by drone battery capacity. **Figure 3.5.b** shows a group of five porpoises that were in close proximity to each other which allowed recording them in the same drone frame. Behaviour recorded with the theodolite aligns better in this case but is representing all the surfacing events of the five porpoises without being able to differentiate between the porpoise individuals. Analyzing the drone footage allows attributing individual behavioural categories to each of the five porpoises individually. Fig. 5C shows an example where the behaviour recorded by the theodolite operator matches the drone. Theodolites can thus in occasions provide reliable behaviour information for groups, when all individuals show the same behaviour. Socializing events or assigning MCP cannot be achieved with the theodolite yet can be detected in the drone footage. However, also the drone is unable to give full track information as porpoises are often not visible in murky water. It can be seen in all figures that regular gaps in observation occur.

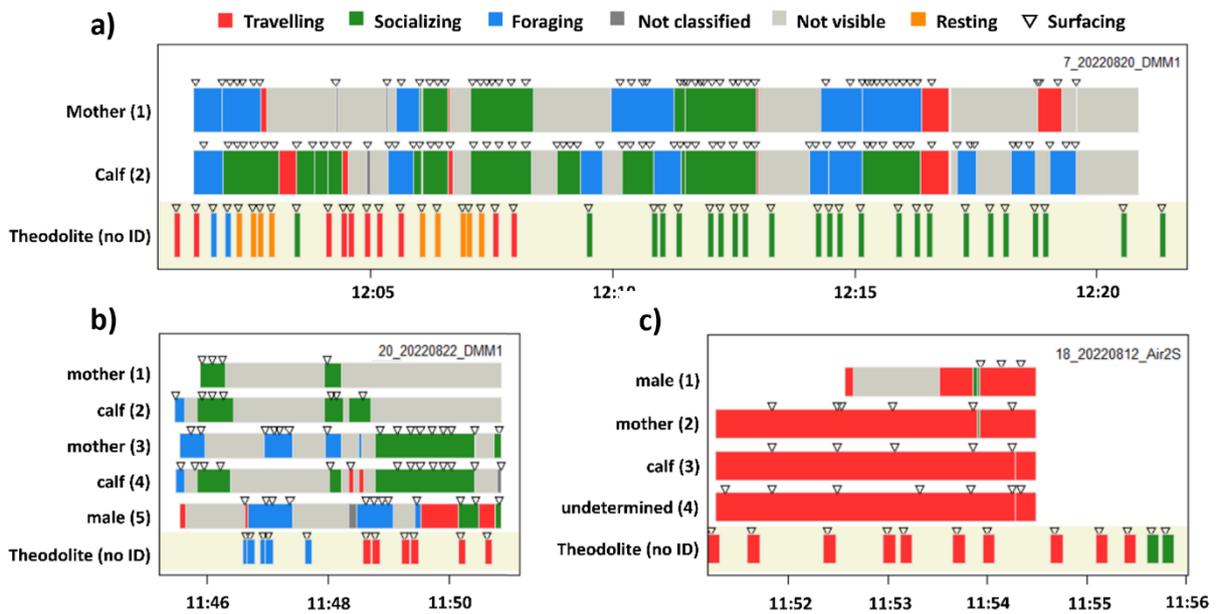


Figure 3.5. Observed behaviour of porpoises in drone footage and simultaneously taken theodolite points.

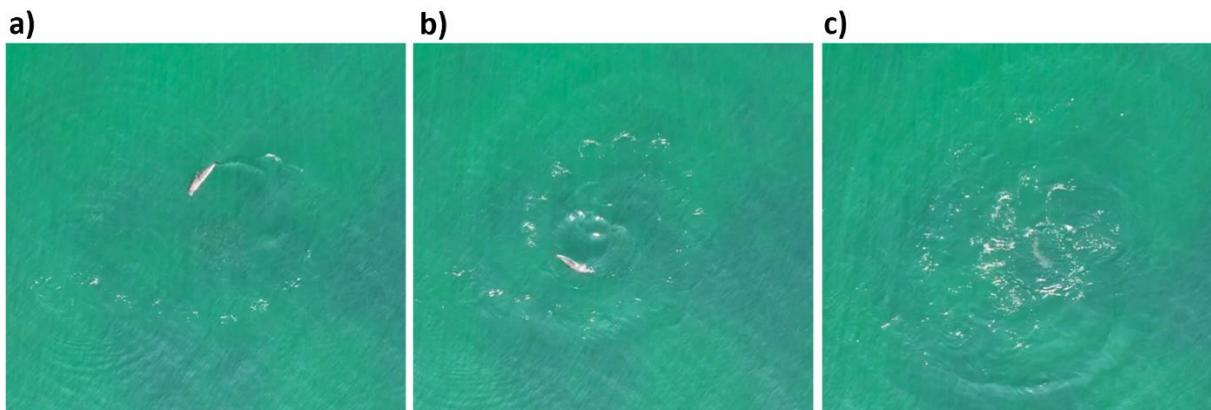


Figure 3.6. Individual harbour porpoise herding a school of small fish: **a)** School of fish visible in centre; **b)** close bordering of school; **c)** diving down in the centre (potential hunting attempt).

Drone footage also revealed that some behaviours are carried out exclusively under the water surface and therefore could not be detected by the theodolite operator. One special behaviour was observed in several occasions of an individual harbour porpoise herding a school of small fish (**Figure 3.6.**), potentially sprat, which has thus far only been described as a group hunting strategy (Torres Ortiz *et al.* 2021).

Modelling location differences

D_{t-d} was calculated for 153 coordinate pairs. The theodolite points that were available to match with drone positions consisted of 83 quality 1 (Q1) theodolite points, 39 quality 2 (Q2) coordinates, 31 quality 3 (Q3) points and were taken from a distance of 82 to 465 meters from the instrument.

None of the interactions in the GLM analysis were statistically significant in explaining the variability in D_{t-d} as well as sea state and distance from the instrument (AIC of full model: 1076.3). While not statistically significant, the mean D_{t-d} slightly increased with the distance of the taken point to the theodolite. Only the theodolite quality showed a statistically significant effect in explaining variability in D_{t-d} . A reduced GLM was performed including only this factor resulting in a lower AIC of 1066.8.

$$\log(D_{t-d}) = \beta_0 + \beta_1 \cdot \text{theo_quality}$$

D_{t-d} was significantly lower for Q1 points (mean: 8.3m, min. 0.4, max. 37.7m, s.d.: 5.99m) compared to Q2 points (mean: 16.3m, min. 0.5m, max. 108.6m, s.d.: 18.88m) (p-value < 0.0009) and Q3 points (mean: 26.6m, min. 4.3m, max. 155.3m, s.d.: 31.30m) (p-value < .0001). No significant difference was detected between Q2 and Q3 points (p-value: 0.087) (**Figure 3.7.**).

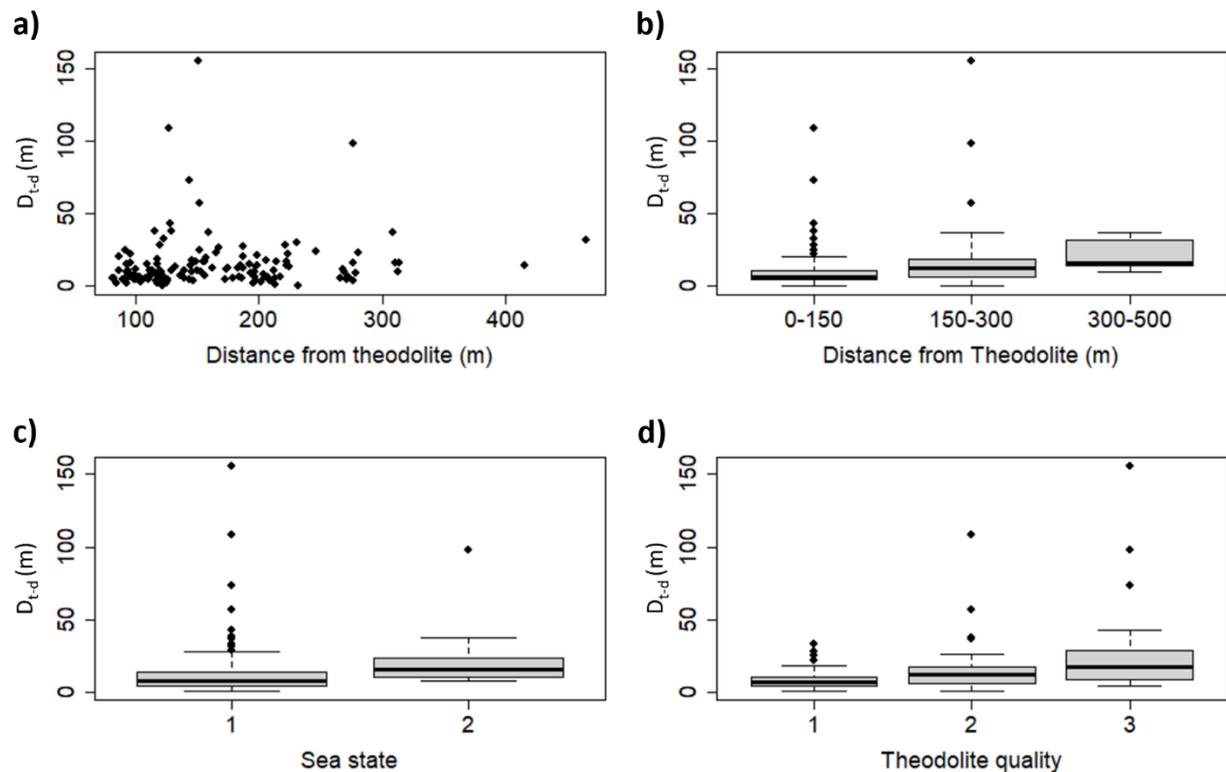


Figure 3.7. D_{t-d} in relation to **a)** Distance from the theodolite; **b)** distance categories from the theodolite; **c)** for Sea State 1 and 2; **d)** for the three theodolite quality categories.

3.4. Discussion

Using harbour porpoise as an example, this study demonstrates that the strengths and weaknesses of theodolites and drones complement each other in a positive way. Drones allow for a detailed assessment of behaviour and life history and collect more precise positional data, but theodolites are faster and cover a larger number of sightings while giving a more complete cover of a full sighting from start to end. The simultaneous use of both methods is recommended to improve the observation studies of harbour porpoises and other coastal marine mammals. Our results can be generalized and put into perspective for smaller whales using a SWOT analysis (**Table 3.4.**).

Method comparison

We observed that none of the methods allowed to fully record all sightings observed by plain eye and thus only a part of the information available could be captured. Theodolites performed better in collecting at least some positional data of many sightings while drones captured more detailed data of fewer sightings. Main reasons for drones not operating for every sighting included 1) very short sightings with animals (dis-)appearing fast, also affecting the success of the theodolite; 2) far out sightings were considered to be hard to find and were hence not attempted to be captured with the drone to preserve operability for better chances; 3) difficult weather conditions such as strong winds or rain. Over half of the videos were classified as D3, showing that it is hard to find and film small porpoises in murky water and low contrast conditions given in the Baltic Sea. D1 and D2 footage further showed a rather small appearance rate of porpoises with only 22.4 % porpoise presence in the screened time. Even when porpoises were in the videos, they were not continuously seen in most cases, even in shallow waters of up to 10 m. Drones nevertheless allowed recording more than one porpoise at the same time if they are in the same frame while collecting more information than the theodolite, which is restricted to taking positional data of one individual at a time.

It has to be considered that collecting drone footage is not always easy (hard to locate and follow the animals, pilot fatigue), requires a lot of storage capacity to film and store high resolution video footage, that the processing of drone footage includes several steps (storing footage correctly and backing it up, screening of the footage, and post-hoc processing if required such as cutting videos, extracting coordinates etc.) and can thus be very time-consuming making it an expensive method when considering time expense of workforce. On the other hand, the theodolite has a long-lasting battery and a large storage capacity for its data. Downloading and processing of the data is fast and takes little time. Some programs such as Pythagoras are further available to help collect, manage and analyze data even in real time in the field.

Group size

Estimating group size in cetaceans is challenging due to fast and unpredictable movement patterns, the time spent under water, the unknown proportion of a group underwater, etc. (Gerrodette *et al.* 2019). In this study, group size estimates made with the theodolite appeared to be less accurate, especially for large groups with significantly lower group sizes obtained with the theodolite compared to numbers counted in the drone footage. The drone footage is deemed to be more reliable since it shows more animals together and especially allows to detect mother calf pairs even when mother and calf swim closely together. A similar result was also observed in dolphin group counts where ship surveys underestimated group sizes compared to aerial photographs (Scott *et al.* 1985) or more

Table 3.4. SWOT (Strenghts, Weaknesses, Opportunities and Threats) analysis of theodolite and drones as land-based observation methods for small odontocetes.

STRENGTHS	
Theodolite	Drone
<p>Effective monitoring tools for large marine fauna(Butcher <i>et al.</i> 2021) (Piwetz <i>et al.</i> 2018); (Butcher <i>et al.</i> 2021) and smaller marine fauna (present study)</p> <p>Non-invasive, non-disturbing methods to estimate precise geographic positions and movement parameters calculable (speed, heading, bearing change, surfacing intervals) in a comparably large area (Piwetz <i>et al.</i> 2018)</p> <p>Easily transported and flexible data acquisition timing, Low cost associated with data collection compared to established techniques (Jiménez López and Mulero-Pázmány 2019), requires little training</p>	
<p>Allows to describe coarse behaviours, collect distribution and relative abundance data (Frankel <i>et al.</i> 2009)</p> <p>Inexpensive for long term use (Morete <i>et al.</i> 2018)</p> <p>Weather resistant and operable in windy and rainy conditions with reduced accuracy (Sagnol <i>et al.</i> 2014)</p> <p>Easy to use, low battery consumption and high data storage capacity, easy download and processing of data</p>	<p>Highly accurate location data can be extracted using CetTrack, Pix4D, Agisoft Metashape (Raoult <i>et al.</i> 2020)</p> <p>Underwater behaviors can be observed (Fettermann <i>et al.</i> 2022)</p> <p>Enables access to sites considered inaccessible such as Marine Protected Areas (MPAs) or remote islands (Fettermann <i>et al.</i> 2022) when permitted</p> <p>Can be operated safely from small research vessels (< 6m) (Fiori <i>et al.</i> 2017)</p>
WEAKNESSES	
Theodolite	Drone
<p>Both methods are weather restricted. Theodolites by the visibility of porpoises and drones by strong winds and rain.</p>	
<p>Limited coverage to animals passing close to shore (Sagnol <i>et al.</i> 2014)</p> <p>Requires an elevated geographically vantage point with unobstructed view of the whole research area (Denardo <i>et al.</i> 2001). Higher observation points lead to more precise positioning (Morete <i>et al.</i> 2018)</p>	<p>Only non-invasive when used properly (Palomino-González <i>et al.</i> 2021)</p> <p>Battery technology and associated limited flight times make it currently difficult to cover large areas (Jiménez López and Mulero-Pázmány 2019)</p> <p>Lithium-polymer batteries can pose a safety risk when they spontaneously overheat while over- or undercharged (Raoult <i>et al.</i> 2020)</p>

WEAKNESSES	
Theodolite	Drone
<p>Only surface behaviours can be observed (Godwin <i>et al.</i> 2016; Piwetz <i>et al.</i> 2018)</p> <p>Challenging when studying elusive animals that surface for only seconds at a time, move quickly, range large distances and have an unpredictable moving pattern (Piwetz <i>et al.</i> 2018)</p> <p>Limited when identifying individuals, sex, age, reproductive status or body conditions (Piwetz <i>et al.</i> 2018)</p> <p>Not appropriate to study group behaviors and spatial structures as it allows observing only one animal at a time, and it is hard to continuously track the same animals once it submerged under the water (Denardo <i>et al.</i> 2001)</p> <p>High initial financial investment (Morete <i>et al.</i> 2018)</p>	<p>Visibility below water is affected by waves, reflections, water turbidity, and objects (Butcher <i>et al.</i> 2021)</p> <p>Requires large data storage: at 4K resolution: ~32 GB per hour (Raoult <i>et al.</i> 2020)</p> <p>Post video processing requires high investment of time, skills, computer programmes and staff (Jiménez López and Mulero-Pázmány 2019) to derive accurate and meaningful information (Manfreda <i>et al.</i> 2018)</p> <p>Requires training, certificate and insurance to be used</p> <p>Unpredictable surfacing patterns and behaviour render odontocetes a difficult target to follow, particularly in deep or turbid water even for experienced pilots (Raoult <i>et al.</i> 2020)</p> <p>Biased group size for many animals</p>
OPPORTUNITIES	
Theodolite	Drone
<p>Both methods can be complemented with other methods</p> <p>Potential to replace more invasive monitoring techniques</p>	
<p>They serve different purposes, and are thus often available for rent or to lend at some academic departments (Morete <i>et al.</i> 2018)</p>	<p>Artificial Intelligence (AI) can help to process data (Jiménez López and Mulero-Pázmány 2019) and (Butcher <i>et al.</i> 2021)</p> <p>Special permits can be requested to fly outside established limits (Raoult <i>et al.</i> 2020)</p>

OPPORTUNITIES	
Theodolite	Drones
<p>A large amount of studies have been carried out using a theodolites to observe marine mammals (Piwetz <i>et al.</i> 2018), there are established workflows on how to use it and recommendations and considerations are available on how to increase the accuracy of data collection.</p>	<p>Drones can be used for a variety of research questions: collect behavioural data, study body conditions, photo-ID, collect samples (breath collection, fecal samples) (Baird <i>et al.</i> 2022)</p> <p>Allows eliminating the research boat bias making it a good tool for shore-based observers (Fiori <i>et al.</i> 2017)</p> <p>Drone images can be used for identifying the number of neonates, calves and juveniles, identifying sexual maturity, mother/calf pairs, body shape and nutritional conditions (Fettermann <i>et al.</i> 2022).</p>
THREATS	
Theodolite	Drones
<p>The accuracy of the geographical position can be influenced by the experience of the observer, the size of the observed species, imprecision in measuring of the elevation of the instrument above the sea level, poor calibration and refraction (Sagnol <i>et al.</i> 2014) sea state, swell and waves (Morete <i>et al.</i> 2018)</p> <p>Challenging when working with small inconspicuous cetaceans such as harbour porpoises where surfacing's are short and can be missed if the observer is looking somewhere else (present study)</p> <p>Collecting drone footage is not always easy (hard to locate and follow the animals)</p>	<p>Common drone airspace rules (Jiménez López and Mulero-Pázmány 2019) and restrictions on where and when they can be flown (Butcher <i>et al.</i> 2021) can limit drone application</p> <p>Large drones can cause life-changing or lethal injuries when they interact with people (Manfreda <i>et al.</i> 2018), smaller drones can produce cuts and bruises.</p> <p>Drones flown continuously during the present study regularly showed malfunction, missions had to be aborted, drones flown back to base due to software or mission failure or batteries drained or malfunctioning. This results in lost research opportunities (present study)</p> <p>Pilot fatigue (Raoult <i>et al.</i> 2020)</p>

recently for boat-based surveys by where counts by plain eye significantly underestimated group sizes of bottlenose dolphins compared to counts conducted on drone footage (Fettermann *et al.* 2022).

The elusive behaviour of porpoises on the surface indicates that the issue should be more pronounced than in *Tursiops*, due to its less active behaviour and smaller body size. The conditions to focal follow animals with the drone are not always convenient, since the water is often murky allowing for only low contrast during cloudy weather or having glare in the image on sunny days. Drone operators thus had to often fly close to the animals (20-30 m) to ensure not losing them. It is possible that at this height not all animals of a group fit in the frame potentially leading to underestimation in group counts also with the drone. Animals were often lost in the video frames, making re-identification challenging, potentially resulting in a low biased group size estimate.

Time and distance

The theodolite was able to capture the initial part of a sighting while drones took more time to be started and to find the animals resulting in lost chances. Gathering data fast is especially important for investigations targeting the initial moments of sightings or those that have to capture full tracks such as detection function studies (Kyhn *et al.* 2012; Nuuttila *et al.* 2013) or reaction studies to permanent sources of disturbances (Koschinski *et al.* 2003; Muir *et al.* 2015; Pirota 2014). The theodolite was further more successful in tracking the animal until the end of the sighting while the drone generally lost them earlier. This can also be explained by the fact that theodolites are able to take far out points while drone operators stopped trying to (re-)find animals or start a new drone when the chances were already low of spotting the porpoises, which is the case when they are further out. The theodolite thus gives a more complete overview of the movement range of the porpoise within the observed area.

Behaviour

While all cetacean species spend only brief times at the water surface, the harbour porpoise is a particular case due to its elusive and random behaviour (Amundin 1973) and their small body size. Wild harbour porpoise behaviour thus remains poorly understood (Elliser *et al.* 2020). Certain behaviours can be detected by theodolite operators, but are always limited to surfacing events which last only a few seconds making a behaviour categorization particularly challenging. The theodolite operator is mostly not able to assign behaviours to specific individuals or establish relationships within a group. This study has also shown that the theodolite operators sometimes provided unreliable information that was not confirmed with drone footage such as resting behaviour. It was nevertheless useful to give early and late information of a sighting in which a drone was not flown and allowed bridging gaps in which drones had to be flown back and re-started due to their limited battery capacity. Theodolite observers can give general patterns of behaviours and have been used in many occasions in the past to study larger coastal occurring whales like humpback whales (Barendse *et al.* 2010), southern right whales (Clark and Clark 1980) and gray whales (Gailey *et al.* 2016) and to a much lesser degree on smaller delphinid species like bottlenose dolphins (Würsig and Würsig 1980). In recent years, technologies that allow recording them under the water surface, have contributed to the description of certain aspects of their behaviour such as mating (Keener *et al.* 2018; Webber *et al.* 2023), group hunting (Torres Ortiz *et al.* 2021) or catching and handling of large fish (Elliser *et al.* 2020), to mention a few. Filming harbour porpoises is however challenging due to the randomness in movement, relatively short surface behaviour, their small body size. This also increases the risk of losing the animals and maintain the identification of the individuals when a group is followed. However, when good footage is available, it allows very detailed observations on their behaviour and the advantage of

providing footage that can be played back many times and analyzed by different observers. In recent years, this has allowed the description of new behaviours that take place completely under the water. This study for instance detected fish herding carried out by individual harbour porpoises, which has thus far only been described as a group hunting strategy (Torres Ortiz *et al.* 2021). Drone footage is a more appropriate tool for behavioural observations in porpoises compared to the theodolite.

Fine scale distribution data

Obtaining precise geographical positional data is essential in target experiments such as estimating the approach proximity of a cetaceans to a net (Culik *et al.* 2001; Cox *et al.* 2003; Koschinski *et al.* 2006), or the reaction towards deterrent devices (Culik *et al.* 2001; Brandt *et al.* 2013; Brennecke *et al.* 2022) and to study the relationship of individuals within a group (Denardo *et al.* 2001) amongst others.

Coordinates of porpoise positions can be obtained from both methods, and at close distances they do not differ strongly. While the theodolite only captures surfacings and the path in between can only be interpolated based on two consecutive surfacing points, the drone can sometimes follow the animals under water. Depending on the interval chosen to extract positional coordinates from the footage an extremely high spatial resolution of movement data can be achieved. In this study, all sightings occurred within 1.4 km distance to the coast. The D_{t-d} of Q1 points was not affected in this distance range from the instrument, showing that the theodolite can take good position estimations in this distance range. The fact that most points were collected within 300 m from the theodolite in this study, is likely not due to a limitation of the instrument, but reflects the near shore distribution of the porpoises in this area during the study period.

While less precise, theodolite points still allow giving an approximation on the location of a porpoise which is especially interesting for short sightings or far out sightings which for instance have often not been recorded with the drone. Therefore, much of the variation in D_{t-d} is likely attributed to position errors in the theodolite. Those arise due to the fast operation mode necessary especially for close range operations. Pointing, fine adjusting and performing the measurement must be carried out in under 5 seconds to then allow a general screening of the study area again. Anyone who has operated a theodolite knows that this is not always feasible using the ocular. This results in a much larger actual error in position estimates for theodolites and challenges the accuracy used in some previous studies (Kyhn *et al.* 2012; Bailey and Thompson 2006). The error range in this study when considering the drone-based coordinates as a reference ranged between 8.3 m (Q1) to 26.6 m (Q3). This accuracy will depend on the calibration of the instrument, accurate stationing, a correct measurement of the theodolite height, the sea level variations in the study area (Bailey and Lusseau 2004) as well as the observers experience, sea state, wind speed and direction, or an error in the positioning of the crosshair on the waterline (Sagnol *et al.* 2014; Harzen 2002). Calculated theoretical distance error ranges when tracking dolphins from a 56 m high cliff in Portugal, ranged from 0.2 m for points taken up to 100 m from the instrument based on 0.002°gon deviation, and 2.7 m for points taken up to 1 km from the instrument. This could be attributed to the higher vantage point; however, our study shows that also 0.002°gon deviation (the error that the lens is causing only) cannot be realistically achieved in the field. Depending on distance a much larger error is always a given. Such error ranges were also observed when studying the precision of a theodolite compared to an on-board GPS of research vessels on sperm whales and dolphins at distances between 2 and 26 km from the theodolite (Sagnol *et al.* 2014). Error in measurements of distances between the theodolite and GPS positions ranged up to ~6000 m with error increasing with distance. Factors that influence the precision of the theodolite in the present study include the comparatively low vantage point (20 m) and the fact that tracking

porpoises is more challenging due to the smaller size of the animal and less active behaviour on the surface which makes its spotting and precise capture with the crosshair more challenging.

Operators had the capacity to take theodolite points with highest quality (Q1) on their first days, showing that it requires little training to obtain good results while also showing good judgement in self-assessing the quality, since distance between simultaneously recorded theodolite and drone coordinates (D_{t-d}) increased with quality class. The variation in D_{t-d} was not influenced by the difference between sea state 1 and 2 although that assessment may differ for larger sea states and more data. It has to be considered that porpoises are small and elusive, while larger whales are easier to spot and provide cues such as blows which will allow better data collection with both drone and theodolite.

Considerations and improvements for future studies

This study was carried out in collaboration with dedicated volunteers calling for a thorough check of each protocol after field work by the responsible scientists. Detailed protocols for observation times in a standard format (like calibrated and synchronized time zones and take off height, etc.) can really help data processing, since a large amount of the drone footage will not contain relevant information (no sightings). Hence, if theodolite observer and drone pilot communicate well in the field, they can note behaviours that cannot be seen from the coast without the time-consuming screening of drone footage by 13 volunteers for 4 months, like carried out here, afterwards. In the future artificial intelligence could help with these tasks too.

3.5. Conclusion

This study shows that even though drones are a new popular tool, they do not supersede theodolites in every regard. When full track information is necessary, theodolites are the preferred method. However, our results also show that already inferred information like surfacing rates and results that rely on high accuracy location data such as acoustic detection functions, have to be reconsidered using drones. Our results are applicable for all small inconspicuous odontocetes with near-shore distribution.

3.6. Acknowledgements

We thank all volunteers that helped us collect data during the field work for their incredible work and dedication. We thank Daniel Steputtis, Thomas Noack and Jakob Tougaard, for their input and support in the conception of the project. Further, the technicians Marko Warmuth from the Deutsches Meeresmuseum Stralsund and Ulf Böttcher from the Thünen Institute of Baltic Sea Fisheries are thanked for their support. We also especially thank Matthias Naumann and the University of Rostock for lending us the theodolite and helping us with the theodolite data.

3.7. Authors contribution

T.M.D., T.B., O.M.K., M.D. conceived, planned and performed the experiments in the field. T.M.D., T.B., O.M.K., M.D., M.C. & A-K.C. contributed to data collection in the field. T.M.D., T.B., A.G., A-K.C., C.v.D and M.D. developed the theoretical frame and performed the analytic calculations. T.M.D. took the lead in writing the manuscript. T.M.D., T.B., M.D., C.v.D., A-K.C. and F.D. provided feedback and discussed the results and contributed to the final manuscript. M.D. conceived the original idea. M.D. and C.v.D. supervised the project and raised the funding.

3.8. Supplementary Material

Figure S.3.1. Group counts. Median is the same, but especially when groups are larger the drone counts more animals.

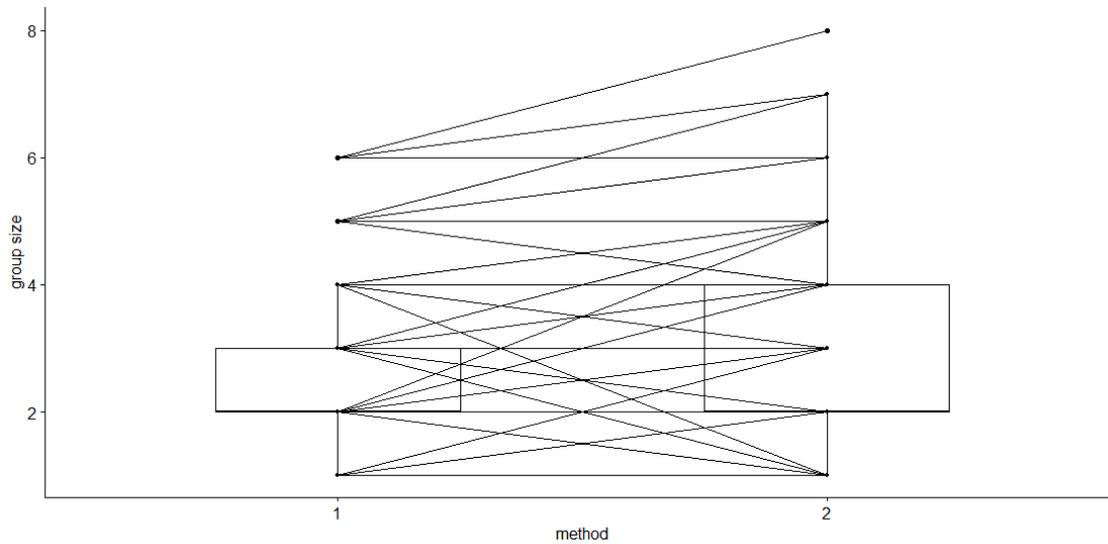


Figure S.3.2. Time and distance. Linear regression using a sqrt transformation.

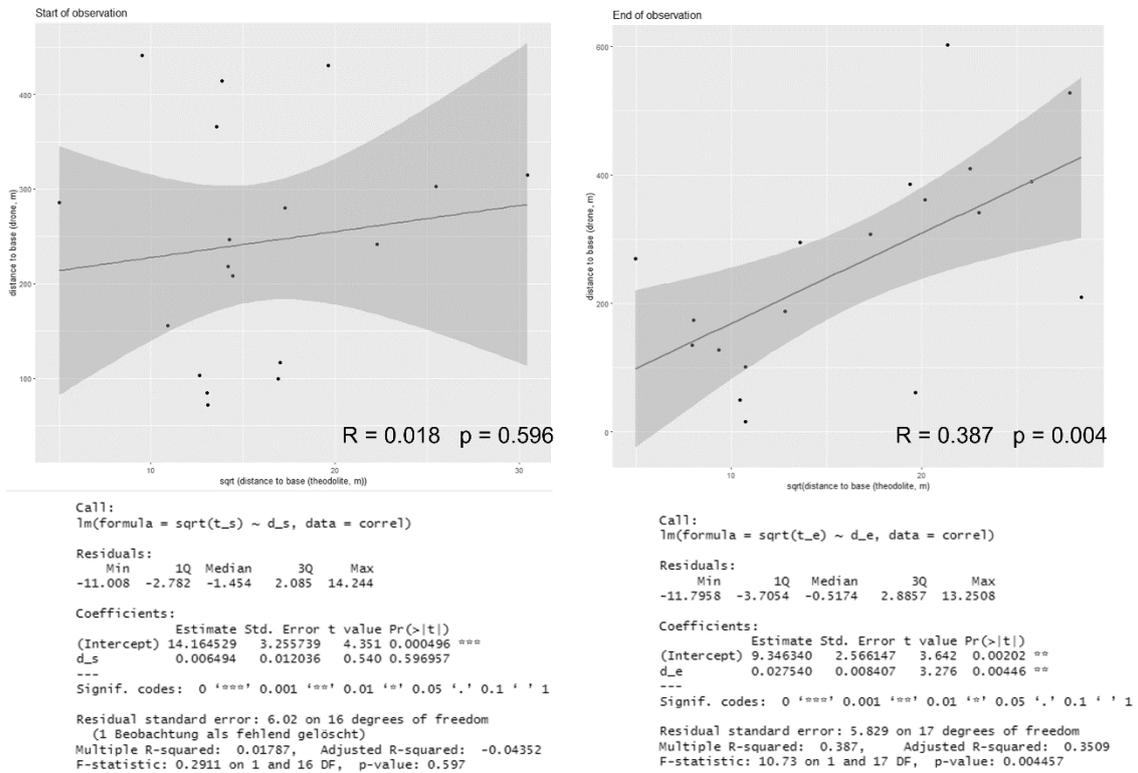


Table S.3.1. Field work protocols.

Harbor Porpoise observations (only fill in when there is a sighting)

Date: _____ Start: _____ UTC End: _____ UTC Net: Yes / No PAL: Yes / No PAL Type: _____

ID	Time (UTC)	Pod size	Heading direct.	Drome 100m (DMM1 or 2)	Drone following (DMM or 2, 3)	Quality Drone following (POor/OK/GOod)	Theod. Y/N	Theod. Start Point	Theod. End Point	Inside exper. Yes/No	PAL Fired? Y / N	Time (UTC) PAL	Observer	Remarks

Drone quality: Poor: HP is just for a few seconds on video; OK: HP can be seen on the video with interruptions; Good: HP is on video nearly full time

Table S.3.2. Theodolite protocol.

Sightings (HP, Net)	ID (Nr sighting HP Protocol)	Theodolite Point Number	Heading direction	Start Behaviour	Data Quality	End Time	Observer

Sighting: HP: Harbor porpoise N: Net **Start behaviour:** travelling, feeding, resting, socializing, mating

Data quality: 1) The porpoise or its footprint was seen by the observer; high accuracy; 2 = The tracking point is close to the last surfacing; good accuracy; 3) The tracking point is further away of the last surfacing / guessed; medium to low accuracy

Table S.3.3. Weather Protocol – Fyns Hoved 2022 (PAL-CE).

Describe weather conditions at the beginning of each observation and whenever conditions change during an observation. Directions are indicated by radicals in binoculars. Weather has to be given at least ones per hour, please set a timer at the beginning as a reminder, please log the Tidal Level at the same time.

Date	Time (UTC)	Sea level	Sea state (0 – 4)	Wind speed (m/s)	Glare direct. (from /to)		% glare cover of study area	Cloud cover (1-8)	Wind direct.	Temp. (°C)	Pressure (hPa)

Table S.3.4. Drone Protocol.

Describe the aerial footage that was collected during a sighting as well as the mode of operation for the drones used. Fill in details on charging level of the large battery.

No.	Drone ID	Time started (UTC)	Time landed (UTC)	Battery start	Battery end	Harbour Porpoise ID (s)	Follow		100 m		Operator	Is-sues? y/n	Remarks (e.g. mother calf pair, PAL remote, issues encountered, solutions)
							Y	N	Y	N			

Chapter 4

Bycatch events of small odontocetes are not directly related to detectability of fishing nets

Title: Bycatch events of small odontocetes are not directly related to detectability of fishing nets

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Abstract

Bycatch is a major threat to cetaceans, yet little is known about how small odontocetes behave around fishing nets. In the first drone and acoustic based in situ experiment on porpoise-net interactions, the response of harbour porpoise to a modified bottom-set net consisting of horizontal monofilament lines only and combined it with a Porpoise Alerting (PAL) device was studied. Porpoises exhibited limited observable response when navigating the net. Four interaction types were identified: crossing, swimming along, swimming around, and turning around. Notably, many mother-calf pairs safely crossed the nets. Contrary to expectations, neither the net nor the PAL device elicited strong changes in swimming speeds. Relative changes in speed followed a consistent pattern: porpoises increased speed in direct vicinity of the net and slowed after crossing. Respiration rates were elevated during net interactions, but click train production, showed no significant changes between treatments. Minimum inter-click intervals decreased, and train durations shortened post-net interaction during PAL exposure, reflecting a potentially increased acoustic vigilance. Visible net reactions occurred at close distances (0.83-16.41 m), within or below detection ranges reported in prior studies. These findings highlight that porpoises avoid nets effectively despite short reaction distances, highlighting that bycatch likely arises from distraction rather than pure detection failure. It is therefore necessary to both increase the awareness of porpoises, which may be achieved by using tools such as PAL, but also work towards increased reflectivity of net structures to avoid high bycatch rates in bottom-set gill nets.

Keywords: pinger, drone, *Phocoena phocoena*, fishery interaction, behaviour near nets, static nets

4.1. Introduction

Many marine mammal species and populations around the world are declining due to bycatch, the incidental and unintentional capture of unwanted target species, and the leading sources of human-induced mortality for marine mammals (Wade *et al.* 2021). While the issues at hand are manifold and depend on the gear type such as traps, trawls, long-lines, purse-seine as well as species of concern (cetaceans, pinnipeds, sirenians); bycatch in gillnets shows the highest intensity of bycatch of air-breathing megafauna of all fishing gears (Lewison *et al.* 2014) and is the largest threat to all endangered small cetacean populations worldwide (Brownell *et al.* 2019; Read *et al.* 2006). The bycatch of harbour porpoises (*Phocoena phocoena*) in the western Baltic Sea, where it is the only resident cetacean species (Glemarec *et al.* 2021), is currently estimated to be above the threshold values for a sustainable bycatch limit (Kindt-Larsen *et al.* 2023). The drivers behind bycatch events are not completely understood, although correlative data analysis suggests an effect of age, area and lunar cycle for porpoises (Brennecke *et al.* 2021).

Bycatch in gillnets occurs when a porpoise comes too close to a static net, of sufficient mesh size; is then unable to avoid flipper or fluke contact; entangles and later drowns due to its inability to resurface and breathe again. If porpoises or small cetaceans in general have developed coping strategies in relation to nets, they are currently unknown due to a general lack of closely observed bycatch events in real time. Since bycatch is in fact a seldom event, animals are mainly found after drowning, when retrieving the fishing gear. While large focus has been put on studying mitigation measures, little attention has been paid to the underlying mechanisms such as animal behaviour near nets, an information on which future progress is likely to depend upon (Northridge *et al.* 2017).

Coping strategies may involve e.g. avoidance, evasive movements, closer inspection of the fishing gear or a startle response. Avoidance towards nets has been observed in harbour porpoises, by turning around (Shimaruma *et al.* 1993; Hatekeyama *et al.* 1988) by moving away from them (Macaulay *et al.* 2022). Active foraging for short periods of time has been detected acoustically in close vicinity (< 10 m) of gillnets (Macaulay *et al.* 2022) and for longer periods of time (9 min to up to 1 hour, < 100 m) (Maeda *et al.* 2021). Harbour porpoises have also been bycaught in large set net arrangements from which they were able to escape without entangling in the netting material (Higashisaka *et al.* 2018). Several hypothesis on why bycatch occurs exist: entanglement during no echolocation periods (Cox *et al.* 2001); entanglement after a startle response (Elmegaard *et al.* 2023); while sleeping or resting (Wright *et al.* 2017); navigation errors even though nets are perceived (Cox *et al.* 2001) and distraction, low detectability of the nets or masked echoes due to swimming or entangled prey or the echolocation beam not being directed towards the net as for example during benthic feeding (Larsen *et al.* 2007).

Harbour porpoises can detect the thin filament of fishing nets acoustically at close distances of at least 3– 8 m during perpendicular approaches (Kastelein *et al.* 2000) and potentially larger distances of up to 26-30 m (Koschinski *et al.* 2006). When different angles of approach were tested, the detection ranges for net filaments were smaller (Mooney *et al.* 2004; Mooney *et al.* 2007). Detection ranges were tested to be potentially larger at 16 m for the thicker floatlines and 12 m for weight lines (Kastelein *et al.* 2000) thus acting as better acoustic reflectors.

Two types of acoustic devices have been successfully used so far to prevent porpoise bycatch: Pingers to displace porpoises and alerting devices to alter their echolocation activity. Pingers are generally designed to prevent the interaction by increasing the distance through deterrence and have shown a significant long-term efficacy in reducing harbour porpoise bycatch in gillnet fisheries (Gearin *et al.* 2000; Palka *et al.* 2008; Larsen and Eigaard 2014; Dawson and Lusseau 2013; Beest *et al.* 2017). To address concerns related to potentially large scale habitat exclusion (Kyhn *et al.* 2015) and noise

pollution associated with traditional pingers (Carlström *et al.* 2009; Larsen *et al.* 2013), the Porpoise-ALert (PAL) (from here on referred to as PAL), an alternative acoustic porpoise alarm was developed (Culik *et al.* 2015; Culik and Conrad 2013) to limit displacement while allowing for effective mitigation of bycatch. PAL emits synthetic signals at 133 kHz, resembling aversive communication sounds produced by a captive porpoise at the Fjord and Belt Center in Denmark (Clausen *et al.* 2011; Culik *et al.* 2015). When tested in the Little Belt (Denmark), wild harbour porpoises reacted to the PAL signal by increasing their echolocation rate by 10 % and by increasing their distance to the PAL from 131 to 163 m (Culik *et al.* 2015). Harbour porpoise bycatch in gillnets equipped with PAL was reduced by 64.9 % and up to 79.7 % depending on the spacing of the PAL in Danish and German gillnet fisheries (Chladek *et al.* 2020). In principle the sounds of PAL should increase awareness in porpoises and should therefore help individuals to associate the porpoise-like signal with the potential danger of the net (Culik *et al.* 2015). Although those results seem to be clear, there is an ongoing discussion whether PALs cause displacement.

In summary, although critically important to develop mitigation concepts, it is still poorly understood how small cetaceans behave near nets or near alerting devices. This study employed drones and acoustic recordings to analyze the behaviour of harbour porpoises near a set net and investigates if aspects of their behaviour vary in the presence of PAL near a newly developed experimental modified net.

4.2. Material and Methods

Study site

Two field campaigns were conducted on the north-western side of the Funen peninsula in Denmark, western Baltic Sea from June 26 to August 28, 2022, and July 7 to August 28, 2023. Data was collected as part of a larger project aiming to study the long-term effect of PAL on harbour porpoise. A land-based observation station was set up on a 20m cliff overlooking the study area. Two red flags marked the start and end of the net or the position of the net during control treatments when no net was in the water. Four click detectors (F-POD, Chelonia Limited, www.chelonia.co.uk) were deployed within the experiment to record the echolocation activity of porpoises near the net. One F-POD was located on each red flagpole of the net and two F-PODs were anchored 30 m north and 30 m south perpendicular to the net from the central position (**Figure 4.1.**). All F-PODs were set at a depth of 2 meters above the sea floor. The depth of the area observed by drone ranged from 5 m to 10 m, with increasing depth towards the west. During PAL treatments, the PAL was attached to the floatline of the net at the western end with its direction towards the net. Three treatments were rotated in a random manner i) Control: no net and no PAL; ii) Net: modified net without the PAL; iii) PAL: modified net with the PAL.

Modified net

A modified bottom set net was built to reduce the risk of harm to or capturing of a porpoise during the trials. This was considered as the net remained in the water for prolonged periods of time without the possibility to assist entangled porpoises. The modified net consisted of a regular float line with a diameter of 9 mm and a buoyancy of 0.9 kg/100 m and a weight line of 3.2 kg/100 m. Every 0.5 m a 2 m nylon monofilament longline fishing line with a diameter of 1.6mm was inserted vertically. The total length of the experimental net in the field was 50 m with a height of 2 m. To compare reflectivity properties of the modified net to a standard gillnet, an echogram (at 120 kHz) was taken of both nets using the echosounder (SIMRAD EK60) of the German research vessel Clupea following the methodology used by (Kratzer *et al.* 2020). Sonar data were visualized in Echoview Software (<http://www.echoview.com>).

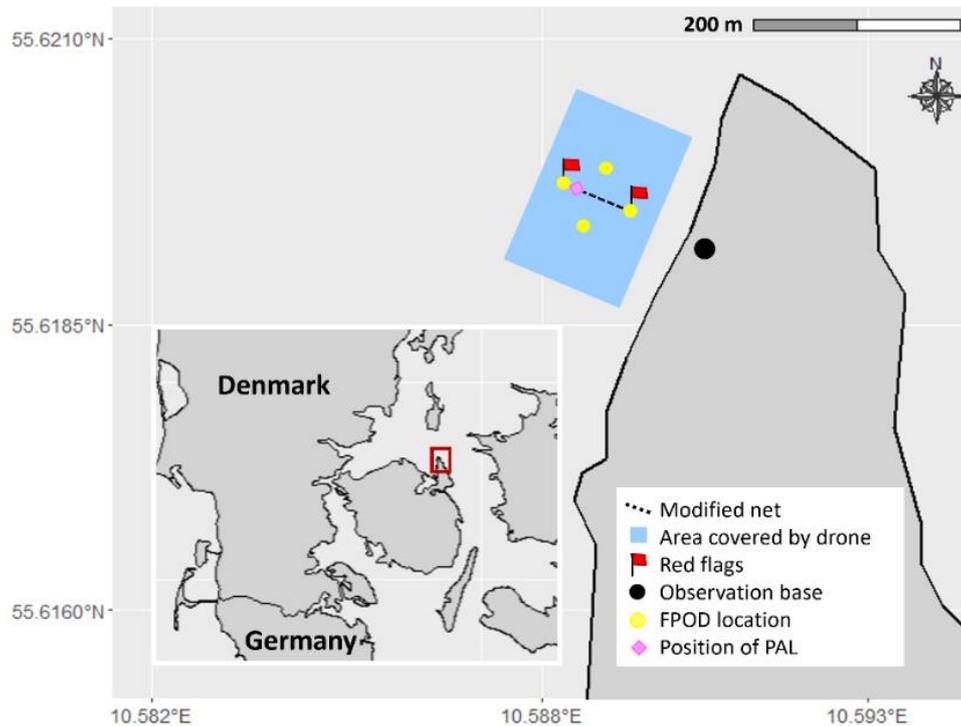


Figure 4.1. Study area and setup of the study at the north-western side of the Funen Peninsula in the Belt Sea (Denmark).

During field trials, the net was deployed approximately in the same location every time between 55.6194796° N 10.5893521° E and 55.6197252° N 10.5883091° E. The orientation was chosen to be perpendicular to the cliff based on previous observations showing regular travelling activities of porpoises alongside the cliff from north to south and vice versa. The net was deployed as a deliberate barrier with the aim of eliciting a behavioral response. The water depth at this location is 5m, allowing porpoises to swim over the net. During all trials two red flags were anchored in the start and end position of the net to define the outline of the experimental setup. This flag poles were also set during trials without net (control) to reduce the potential confounding effects, to mark the limits of the interaction line and as anchoring structure for the F-PODs.

Porpoise-PAL

PAL can transmit different sound types including pinger sounds. The PAL (characteristics described in (Chladek *et al.* 2020), using a synthetic aversive porpoise signal (Clausen *et al.* 2011) was used during the trials. When in use, the PAL was mounted on the western end of the net with its longitudinal axis along the net and the stronger sound beam directed to ensonify the net. This was considered as the source level is not entirely omnidirectional around the PAL and in our case the reaction of the porpoise needed to be observed around the net. Reactions towards the sea were not considered. It is estimated that harbour porpoises can detect PAL in the best cases within distances of 230 - 320 m (during 0 Beaufort wind force scale (Bft)) or 90 – 150 m (at 7 Bft) (Chladek *et al.* 2020). Two versions of the PAL with identical acoustic parameters were used during the study: a) 5-hour PAL that was programmed alternating between on/off every 5 hours to provide a double blind procedure for observers and b) a standard PAL that was on for the full time.

Observations

Observations took place during daytime, between 4 am and 6 pm UTC (Universal Time Coordinated) time and were divided into two shifts of max. 6 hours for each observation team. An observation team

consisted of at least 3 observers continuously scanning the study area by plain eye and using binoculars to detect the presence of porpoises. The study area was divided into three observation areas, south, north and west, with each observer covering one of the areas. Each area had tasks associated like filling in protocols or operating the drones. Observations were interrupted when sea state three was reached which corresponds to a wave height between 0.5 and 1 m and is when whitecaps start appearing. Observers filled in protocols annotating the number of the sighting, pod size, initial travel direction, potential net interaction events, as well as a weather protocol and a drone flight protocol with start and landing times and battery levels. A Secchi disk was used daily to measure the water transparency in the center of the net.

Drone operations

During the observation times, a drone (DJI Mini 2 or AIR2S, www.dji.com) was operated using the Litchi App (www.flylitchi.com). A drone was continuously flown above the center of the net, recording an area of approximately 82 m wide and 178 m long at 100 m above take-off location (standard drone footage frame in supplementary material *Figure S.4.1.*). The drone was changed for the next drone once the battery reached 20 % (after approx. 20 minutes) to provide continuous coverage. In few occasions a second drone was flown to observe porpoises from a closer range when they interacted with the net. The drones were operated under favorable weather conditions, characterized by the absence of precipitation, fog, and wind speeds below 10 m/s. All operators flew the drones in possession of the drone flying certificate emitted by the European Union Aviation Safety Agency for the A1/A3 open subcategory. Flightlogs were stored via Airdata (www.airdata.com).

Analysis

Field protocols were used to select sightings in which potential net interactions could have occurred. Drone footage of these interactions was then screened to find interactions to be analyzed. For our analysis, a *net interaction* was defined as an event in which a harbour porpoise crossed the modified net, swam between the two red flags during control treatment (no net) or showed a clear behaviour of avoidance such as turning around and swimming away from the net or the flag poles. The term *net interaction* will thus refer to any of those circumstances, independently of the treatment. Porpoises passing outside the red flags were not included in the analysis as it can neither be assumed nor excluded that a perception of the net happened. This manuscript will differentiate between 'net interactions' and 'net reactions'. The first refers to the entire response process towards the net/treatment encompassing the encounter of the treatment and the associated navigation decision of the porpoise (e.g. crossing, turning and swimming away) while the term 'reaction' will refer to short behaviours observed in the vicinity of the net such as head movements or turns and changes in direction. Reactions can be thus part of a net interaction. Reactions have previously been described for harbour porpoises (Torres Ortiz *et al.* 2021) although not in association with fishing nets.

Net interactions were classified according to different criteria and to divide the interactions for further analysis. First, net interactions were classified as i) visible: porpoise is visible when crossing the net, or has a swimming path going directly over the net but cannot be seen under the water surface due to murky water, waves or glare and ii) clearly visible: water transparency permits seeing the porpoises below the water surface allowing the observation of fine scale reactions towards the net and tracking the swim path of porpoises.

An ethogram was created describing the types of interactions and reactions observed in porpoises towards the three treatments. In all occasions it was further annotated if porpoises passed the net or the control treatment with: i) a shallow dive in which they dove above the net but remained below the water surface, or ii) surfacing: where porpoises broke the water surface to take a breath exactly above

the net line or control line. The group size of porpoises and if mother and calf pairs (MCP) were present was also recorded. The behaviour of porpoises within the video frame before and after encountering the net, such as travelling (Oakley *et al.* 2017), pelagic feeding or bottom grubbing (Torres Ortiz *et al.* 2021), was annotated for the clearly visible interactions (definitions of behaviours in supplementary material *Table S.4.1.*). Lastly, and as porpoises always approached the set up either from the North or from the South during interactions, the travelling direction of the porpoises (from South to North or vice versa) for each interaction was annotated.

Swimming speed

Videos with clearly visible net interactions where the porpoise is seen for 30s before and after the interaction were used to statistically analyze swimming speed. Individual adults, mothers and also calves or juveniles were tracked when possible. UTM coordinates of porpoises were extracted using the tracking software CetTrack (www.cettrack.info) every 0.5 s marking the most visible frontal part of the animal. In intervals of at least 1 s, the individual swimming speed, and the respective Euclidian distance to the net or control line was calculated. The swimming speed for porpoise movements was obtained by calculating the Euclidian distance between sequential coordinates and divided by the amount of time. The coordinates of the net were extracted for each net interaction as the net configuration varied every day depending on the currents or by variations in where it was set by the boat team on the given day.

A Generalized Additive Mixed Model (GAMM) was performed using the mgcv package v.1.9-1 (Wood 2022) to investigate how porpoises swimming speed is affected by different factors. A logarithmic link function and a quassipoisson family distribution were used to account for overdispersion in the data. Swimming speed (m/s) was set as response variable while distance to the net (m) grouped by treatment (control, net and PAL), swimming direction (North/South), presence of MCP (1/0), visibility (Secchi disk: 0-5), reaction (crossing, swim along, swim around) and dive type (shallow dive/surface) were used as covariates. As there was only one event when a porpoise reacted to the net by turning around, it had to be removed from the analysis. Interaction ID was included as random factor. A backwards-selection was performed, and non-significant variables ($p > 0.05$) were sequentially removed from the initial model by assessing p-values from the model summary. The final GAMM included only treatment and swimming direction as significant covariates. The response variables did not show collinearity using the *vif* function of the car package v.3.1-3 (Fox and Weisberg 2019), with 3 as a cut-off value (Zuur *et al.* 2010). The model used a corAR1 structure.

Reaction distance

In some occasions, porpoises clearly reacted to the presence of the net or a flagpole by showing clear head movements, changing their previously consistent swim direction or turning completely around. For these occasions, the Euclidian distance between the porpoise and the net or buoy was measured at the initial moment of reaction by taking two UTM coordinates within the same video frame using CetTrack: a) coordinate of the closest body part of the harbour porpoise; b) the coordinate of the closest point of the net. Measurement errors when using the same frame to take coordinates are within the range of a few cm (Tuchscherer 2024).

Respiration rate

Mean respiration rate of porpoises before and after the interaction was calculated for events where at least 60s of footage was available either before and/or after the interaction by dividing the number of surfacing events and the respective time duration (as respirations/minute) for both phases. The location when the porpoise was closest to the net was marked and used to divide the net encounter event into 'before net' and 'after net' categories. To test if the phase of interaction (before or after),

the treatment (control, net, PAL), the maximum swimming speed (m/s) or the behaviour (travelling, bottom grubbing, pelagic feeding) were significant predictors of respiration rates, a linear mixed-effects model was performed using the lme4 package v.1.1-35.5 (Bates *et al.* 2014). Respiration rate was the response variable, and interaction ID was included as a random effect to account for individual-based repeated measures. A backwards selection was carried out using anova in the car package (Fox and Weisberg 2019). Non-significant fixed factors ($p > 0.05$) were excluded sequentially from the model based on the highest p-value. The final model included time of crossing and treatment as fixed effects and harbour porpoise ID as random effect. The generalized variance inflation factor was below 3 (Zuur *et al.* 2010) for each fixed effect using the vif function from the car package v.3.1-3 (Fox and Weisberg 2019) indicating no collinearity. The simr package (Green and MacLeod 2016) was used to perform a power analysis on the fixed effects.

Acoustic detections

Click train details of narrow band high frequency (NBHF) click trains with moderate to high quality were exported using the standard KERNO-F classifier of the analysis software F-POD.exe (Chelonia Ltd, UK) with standard settings. Not all porpoise interactions were clearly visible, making it difficult to define a general period during which an interaction occurred. Two minutes before and two minutes after interaction were taken as proxy considering that the mean swim speed of tracked porpoises for all interactions was 1.20 m/s, assuming that a porpoise would need ~3 minutes to travel through the entire video frame (covering approx. 180 m distance) and adding 30 s before and after as a buffer. Acoustic recordings were synchronized using the UTC time stamp of the drone recordings and the F-PODs checking for mismatches using playbacks of porpoise like clicks emitted during servicing of the equipment. Porpoises sometimes traveled together during net interactions. Interactions that occurred simultaneously or close in time (less than a minute time difference) were thus grouped together for acoustic analysis as it was not possible to attribute click trains to specific individuals. Click trains exported during PAL treatment were inspected manually and click trains corresponding to the PAL signal were filtered out manually. The distribution of the data and especially the patchy occurrence of click trains in time did not allow for a detailed GAMM analysis. Therefore non-parametric Kruskal-Wallis tests were performed to conduct a more simplified test for differences in the four acoustic parameters (number of actual clicks (nActualClx), train duration (TrDur_us), median frequency of the train (medianKHz), minimum Inter Click Interval (MinICI_us) between the three treatments and before and after interaction phases for each treatment. All statistical analysis were done using R software v.4.4.2. All visualizations were created using ggplot2 v.3.5.1. (Wickham 2016).

4.3. Results

Modified net

The strongest echo in both standard and modified net came from the float line and the weight line. The net mesh of the standard gillnet showed a lower echo than the other net elements. The 1.6 mm thick single lines showed a similar coloration to the mesh in the standard net, therefore suggesting that the single lines produce a similar acoustic image as the mesh of the standard net.

Types of interactions

Porpoises were recorded swimming through the two red flags or reacting to the flags and net on 88 occasions. 30 interactions occurred during control treatment, 35 during net treatment and 23 during PAL treatment. 61 of these interactions were clearly visible, while the other 27 were difficult to analyze as animals could not be seen under the water surface before and after the net. These 27 interactions were included only in the acoustic analysis. Four types of interactions and three types of reactions

towards the treatments were observed and described (**Table 4.1.**). Porpoises were never been observed to swim into the modified net structure, during all interactions porpoises either swam over the floatline or around the net.

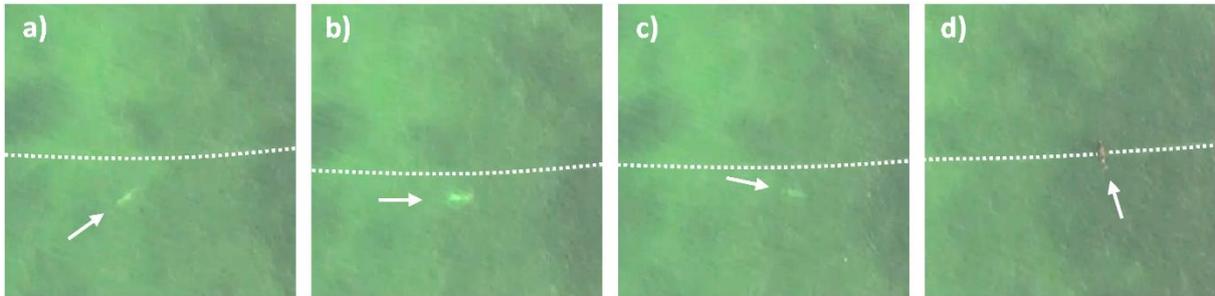
Table 4.1. Ethogram of clearly visible interaction and reactions of harbour porpoise behaviour near the three treatments: C: Control with no net and only the two red flags; N: Net treatment with the net and the two red flags; P: Net with the red flags and with PAL attached at the western end.

	Behaviour	Description	Nr. per treatment			Eg. Figure
			C	N	P	
Interaction types	Crossing	Porpoise swims over the net and/or between the flag poles (control treatment) while only slightly changing its initial swimming direction.	16	26	12	4.6.b HP2
	Crossing with previous swimming along the net	Porpoise changes the initial swimming direction and swims along the net for a short period of time (few seconds) before crossing the net.	0	2	2	4.3., 4.6.b HP1
	swim around	Avoidance of a net structure by swimming around it: One porpoise was observed swimming around a flagpole during a control treatment. One MCP swam around the end of the net avoiding the net panel and swimming over the bridle and buoy rope between the net and the red flagpole.	1	1	0	4.4.
	turn around and swim away	Porpoise turns around in front of the net and swims away from it to a similar direction where it came from.	0	1	0	4.6.c
Reaction types	head scans	Movement of the head towards both sides several times in front of the net. Followed by crossing the net.	0	0	2 ¹	S.4.2.
	Small direction changes	Slight direction changes in front of the net but without a pronounced episode of swimming along. Followed by a crossing.	0	0	1 ¹	
	feeding near net	Porpoises approached the net at a fast speed, taking sharp turns in close vicinity to the net (0.83 and 4.26 m). In both occasions pelagic feeding on non-visible prey was observed before the sharp turns. Porpoises proceeded to cross the net.	0	2 ¹	0	4.2. 4.6.a

¹ Approaches with these reactions are included in the interaction type 'crossing', as the reactions were followed by porpoises crossing the net without changing their direction strongly nor swimming along the net.

Reaction distance

During 12 of the clearly visible interactions, porpoises showed a reaction in the vicinity of the net or the flag poles. Observed behaviours were head scans, changes in direction near the net, turning around and sharp turns near the net (**Table 4.2.**). The reaction distance from the net for these occasions ranged from 0.8 to 16.4 m with median reaction distance of 4.9 m during net treatment, 7.6 m during PAL treatment and 8.95 m for one occasion during control treatment as reaction to a flagpole.



Tabl 4.2. **a)** Fast approach and turn of a porpoise (white arrow) while pelagic feeding near the modified net (dotted line redrawn on net for visibility); **b)** closest point of approach to the net (0.8 m from net); **c)** then turn away **d)** shortly followed by a crossing event. Swim speed track for this interaction in Figure 4.7. Treatment: Net; ID: 20 (Table 4.2.).

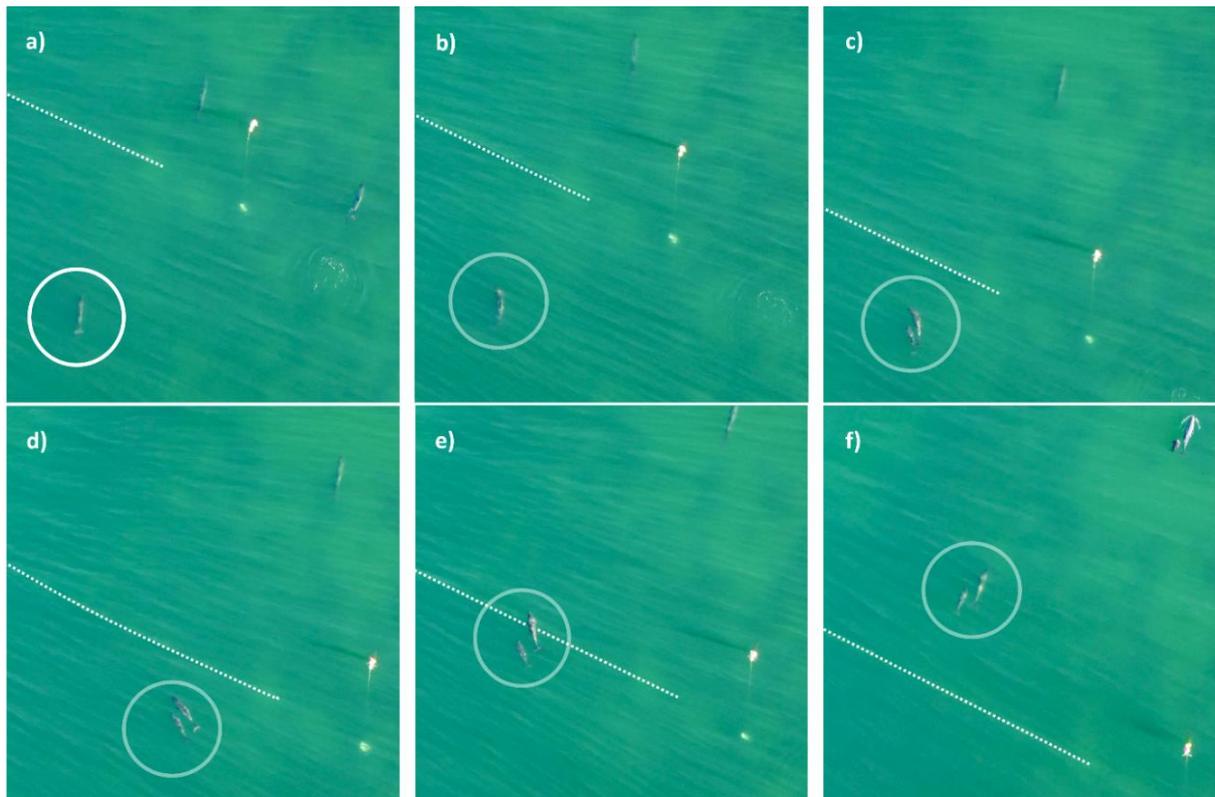


Figure 4.3. **a)** Three mother-calf pairs (MCPs) swimming close to the net with the PAL. Net is marked by the dotted line (redrawn on net for visibility); **b)** visible head movement towards the left for the circled mother; **c)** swim direction change towards the left; **d)** swim briefly along the net; **e)** followed by a crossing with a shallow dive; **f)** re-taking the initial swimming direction. Calf follows the mother. Treatment: PAL; ID 45 (Table 4.2.).

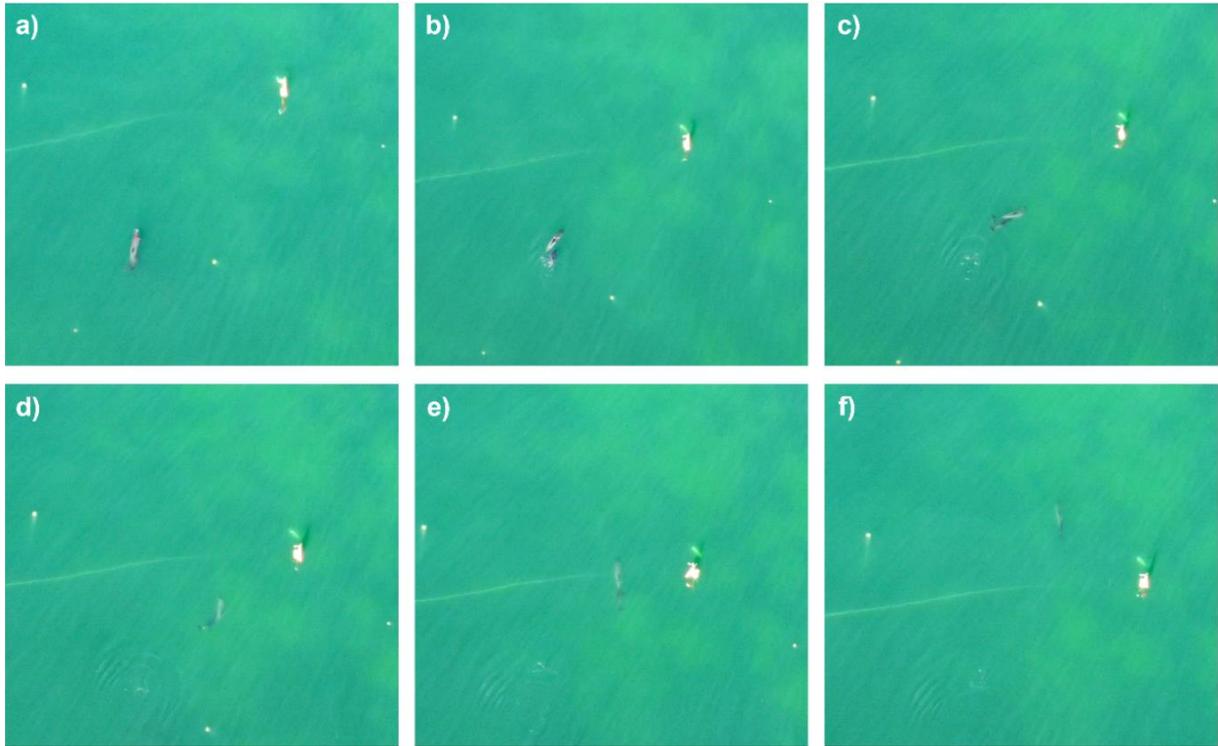


Figure 4.4. **a)** Mother and calf pair (MCP) approaching the net at one end near the flag; **b)** change of direction towards the right; **c)** swim along the net; **d)** turning its swimming direction back towards the net; **e)** swimming around the net avoiding the net and swimming over the bridle and buoy rope between the net and the red flagpole. Treatment: Net; ID: 63 (Table 4.2.).

Table 4.2. Summary of interactions for which 30 seconds before and after interaction are clearly visible (n=25) and/or a reaction towards the net was observed independently on the time the porpoise was seen before and after the interaction (n=12). Surfacing rates are available for interactions where porpoise is visible 60 seconds before and/or after the net encounter (n=26). Only adult porpoises are shown in the table. Mothers travelling with a calve are marked as 1 in the MCP (Mother Calf Pair) column. The table is divided by treatments.

Treatment	ID	Date	Time seen (s)		Behaviour before net	Reaction	Dive type over net	MCP	Secchi Disk visibility (m)	Distance reaction towards net (m)	Crossing direction (towards)	Visible reaction towards net	Max. speed (m/s)		Surfacing rate (surf/min)	
			Bef	Aft									Bef	Aft	Bef	Aft
Control	28	27.08.23	32	35	travelling	cross	shallow		3.5	9.0	North	swim around flagpole	4.66	3.32	-	-
	1	6.08.23	127	103	bottom grubbing (gr.)	cross	surfacing		5	-	South		3.74	4.42	2,36	2,33
	29	27.08.23	187	69	bottom gr.	cross	shallow		3.5	-	South		3.11	3.22	3.53	4.35
	31	28.08.23	95	67	bottom gr.	cross	shallow	1	3.5	-	South		2.05	2.23	4.42	4.48
	33	28.08.23	228	60	bottom gr.	cross	shallow	1	3.5	-	South		2.25	2,05	4.21	4
	34	28.08.23	191	41	bottom gr.	cross	shallow	1	3.5	-	South		1.51	2.18	4.4	-
	58	28.08.23	1320	88	pelagic feed.	cross	shallow	1	3.5	-	South		1.79	2.09	1.73	4.09
	59	28.08.23	1305	87	pelagic feed.	cross	shallow		3.5	-	South		1.73	3.55	1.47	2.07
	64	9.07.23	120	30	travelling	cross	shallow	1	3.5		North		2.62	2.28	4,5	-
Net	20	25.08.23	82	90	pelagic feeding	cross	shallow		4.5	0.8	North	Close turn chasing nonvisible prey	3.47	1.46	4.39	3.33
	21	25.08.23	210	88	pelagic feeding	cross	shallow		4.5	4.3	South	Close turn chasing nonvisible prey	2.97	1.44	4.86	5.85
	24	25.08.23	282	104	pelagic feeding	swim along, cross	surfacing		4.5	4.1	South	Direction change, then swim along	3.4	3.7	1.28	5.77
	37	20.08.22	23	31	travelling	swim along	shallow	1	4.4	1.8	South	swim along	3.08	5.07	-	-
	57	11.07.22	109	10	pelagic feed	turn around	shallow	1	4.5	4.0	North	Turn around, swim away	4.57	7.47	3.85	-

Treatment	ID	Date	Time seen (s)		Behaviour before net	Reaction	Dive type over net	MCP	Secchi Disk visibility (m)	Distance reaction towards net (m)	Crossing direction (towards)	Visible reaction towards net	Max. speed (m/s)		Surfacing rate (surf/min)	
			Bef	Aft									Bef	Aft	Bef	Aft
Net	5	14.08.23	239	40	travelling	swim along, cross	shallow		4.5	3.2	South	turn, slight direction change	3.08	3.36	4.02	-
	63	12.08.23	49	80	travelling	around	shallow		3.5	16.4	South	direction change, avoiding net	3.04	2.61	-	1.5
	19	25.08.23	145	81	pelagic	cross	Shallow		4.5	-	South		3.49	3.77	4.55	4.39
	22	25.08.23	82	81	pelagic	cross	shallow		4.5	-	North		2.61	2.42	5.85	5.19
	44	26.08.22	340	29	pelagic	cross	shallow		4.5		South		2.4	2.77	2.65	-
	9	15.08.23	314	46	bottom gr.	cross	shallow		4.5	-	North		3.9	3.86	4.39	-
	10	15.08.23	43	34	travelling	cross	shallow		4.5	-	North		2.92	2.95	-	-
	11	15.08.23	36	81	travelling	cross	shallow		4.5	-	South		0.98	1.55	-	4,44
	12	17.08.23	45	30	travelling	cross	shallow		-	-	North		3.53	3.35	-	-
61	12.08.23	64	30	travelling	cross	surfacing		3.5		South		4.21	2.21	5.63	-	
PAL	4	14.08.23	131	134	pelagic	cross	shallow		4.5	10.2	North	turn, slight direction change	3.36	2.22	4.12	2.24
	6	14.08.23	58	4	travelling	swim along	shallow		4.5	6.6*	North	Sharp turn then swims along	4.99	2.41	-	-
	45	25.08.22	104	27	bottom gr.	cross	shallow	1	4.5	6.8	North	Head scans	2.93	3.49	1.15	-
	54	25.08.22	17	28	travelling	cross	shallow	1	4.5	5.9	North	Head scans	2.79	3.52	-	-
	46	25.08.22	111	27	bottom gr.	cross	shallow	1	4.5	-	North		4.29	2.75	2.86	-
	3	14.08.23	86	42	travelling	cross	shallow		4.5	-	North		1.42	1.91	2.09	-
	42	25.08.22	57	80	travelling	cross	shallow	1	4.5	-	North		3.57	2.13	-	1.5
	43	25.08.22	48	77	travelling	cross	shallow	1	4.5	-	South		2.18	1.94	-	2.34

*Reaction and reaction distance was potentially influenced by a second drone fastly approaching. The measure was included in any case as the porpoise took a sharp turn and proceeded to cross the net. It was not included when calculating mean distance of reaction during PAL treatment.

Swimming speed

The median swim speed of porpoises during all three treatments are within comparable ranges (**Table 4.3**). Relative changes of swim speed follow a similar pattern during net and PAL treatments with swim speeds increasing as they approach the net reaching maximum swim speed shortly after the net followed by a decrease (**Figure 4.5**). This differs from the control trials with lowest swim speed recorded at the theoretical net location. Differences in swim speeds are more pronounced during PAL treatment, where the effect of the distance is significant ($p = 1.19e-04$) than during net treatment where no significant effects of distance on swim speed were detected ($p = 0.270$). This pattern differs from the control observations in which the distance did show a significant effect on swim speed ($p = 9.21e-06$), with porpoises starting faster, then approaching the center of the experiment slower and then getting faster again. Porpoises swimming towards the south were also observed to be significantly slower ($p = 0.024$) than porpoises travelling towards the north. The model explained 5,27 % of variability in swim speed (GAMM summary table *in supplementary material Table.S.4.2*).

Table 4.3. Median, minimum, maximum and inter quartile range (IQR) for swimming speeds of porpoises during different treatments and swimming directions.

	Swimming speed (m/s)			
	Median	IQR	Min	Max
Control	1.00	0.726	0.009	5.81
Net	1.04	0.789	0.030	7.47
PAL	1.14	0.679	0.051	4.99
North	1.18	0.804	0.085	7.47
South	0.98	0.720	0.010	5.73

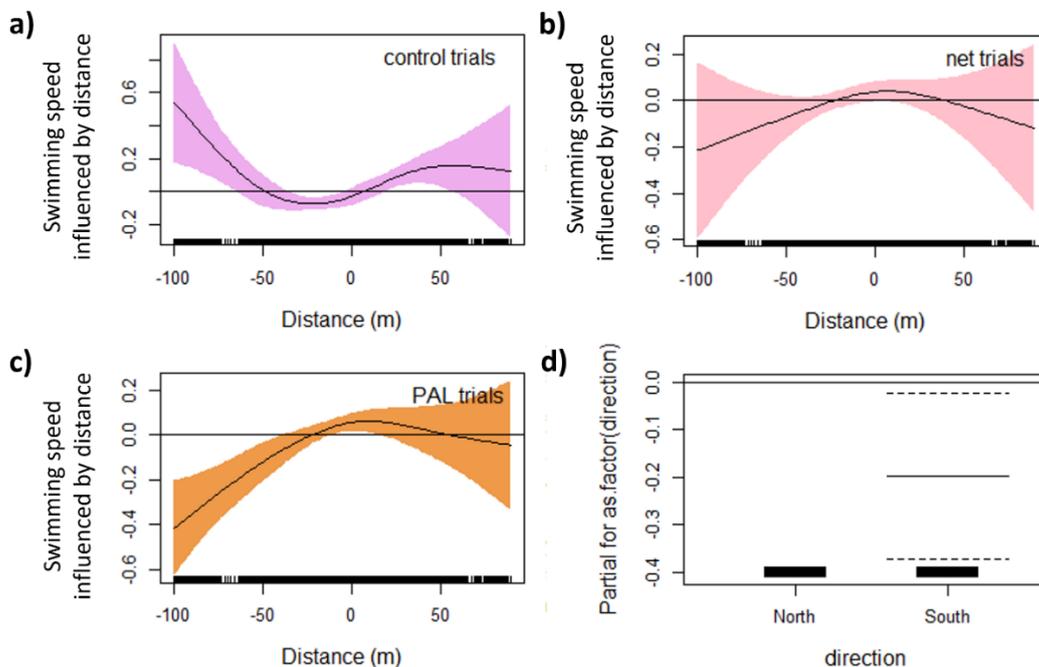


Figure 4.5. Fitted relationships for swim speed of porpoises influenced by distance (0 marks the position of the net) based on the settings of the GAMM. Standard 95% confidence intervals are represented in coloured areas around the relationship for each smooth covariate and as a dotted line for factor variable (d) (swimming direction). The Y axis values displays the change in the log-transformed swim speed as influenced by the treatment.

The analysis of individual swim speed profiles during certain net interactions (**Figure 4.6.**) reveals that variations in swim speed occur during both travelling and pelagic feeding behaviours. Notably, elevated swim speeds are not solely associated with net-crossing events. Specifically, **Figure 4.6.a** illustrates that the highest swim speeds are recorded during pelagic feeding, while the swim speeds during both net-crossing events remain within the lower range for the observed porpoise. **Figure 4.6.b** highlights differing responses among porpoises travelling in tandem; one porpoise maintains a relatively direct trajectory over the net (HP2), while the other exhibits a potentially more cautious behaviour by swimming along to the net before crossing (HP1). Increases in swimming speeds were also observed close to the net **Figure 4.6.c** where a porpoise increases its speed as it approaches the net, subsequently turning to swim away at higher speed.

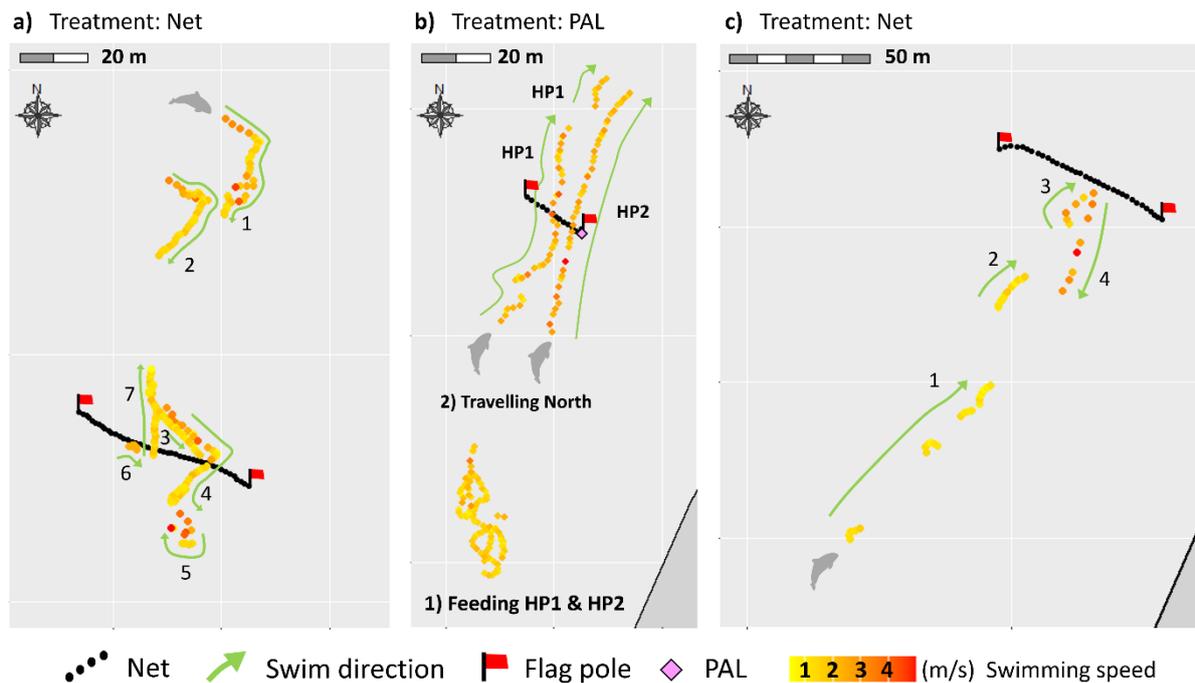


Figure 4.6. Swimming speed tracks of different net interactions: **a)** individual porpoise pelagically feeding near the net in the north (lines 1 - 2), then crossing the net (4), pelagic feeding near net in the south with increased speeds (5), close turn at 0.8 m from the net (6) just before crossing a second time (7). Swim speed track corresponding to images in Figure 4.2.; ID:20 (Table 4.2.); **b)** Two adult porpoises observed bottom grubbing in the south before travelling towards north crossing over the net. One porpoise (HP1) shows a reaction towards the net at 6.8 m from the net swimming along the net and then crossing it. Swimming speed is slightly faster as it crosses the net. The other porpoise (HP2) also crossed the net with a shallow dive. Swim speed track corresponding to images in Figure 4.3; ID: 6 (Table 4.2.); **c)** mother and calf pair pelagic feeding in the south (line 1), then approaching the net (2), sharp turn near net at 4.0 m distance (3) and swim away with increased swimming speed (4). ID: 57 (Table 4.2.).

Respiration rate

The range of respiration rates observed during both control and net treatments were similar, whereas respiration rates during PAL treatments exhibited a narrower distribution (**Figure 4.7.**). Mean respiration rates of porpoises did not differ significantly before and after the interaction within the respective treatments ($p= 0.9997$ for all three treatments). Significant differences were nevertheless found comparing the respiration rates before interaction between the three treatments, with respiration rates being significantly higher before the net treatment compared to before the PAL treatment ($p=0.033$) (**Figure 4.4.**). However, both respiration rates before the interaction did not differ

significantly from the respiration rate before the control treatment (p -values = 0.634 and 0.431, respectively). The same trend was observed for mean respiration rates after the interaction for the three treatments. Porpoises showed significantly higher mean respiration rates after the net treatment compared to after the PAL treatment ($p= 0.033$) while no significant differences in respiration rates after the interaction were detected compared to control treatment ($p= 0.634$ and $p= 0.431$ respectively). It is important to interpret these findings cautiously due to the relatively low statistical power of the model, which had a predictive value of 4.40 % (95 % CI: 2.78–6.59 %).

Table 4.4. Respiration rates calculated for sightings with porpoises visible for at least 60 seconds before or after crossing the two flags.

	Respiration rate (respirations / minute)							
	Mean		S.D.		Maximum		Minimum	
	Before	After	Before	After	Before	After	Before	After
Control	3.33	3.55	1.28	1.07	4.5	4.48	1.47	2.07
Net	4.15	4.35	1.35	1.54	5.85	5.85	1.28	1.28
PAL	2.55	2.03	1.26	0.46	4.12	2.34	1.15	1.50

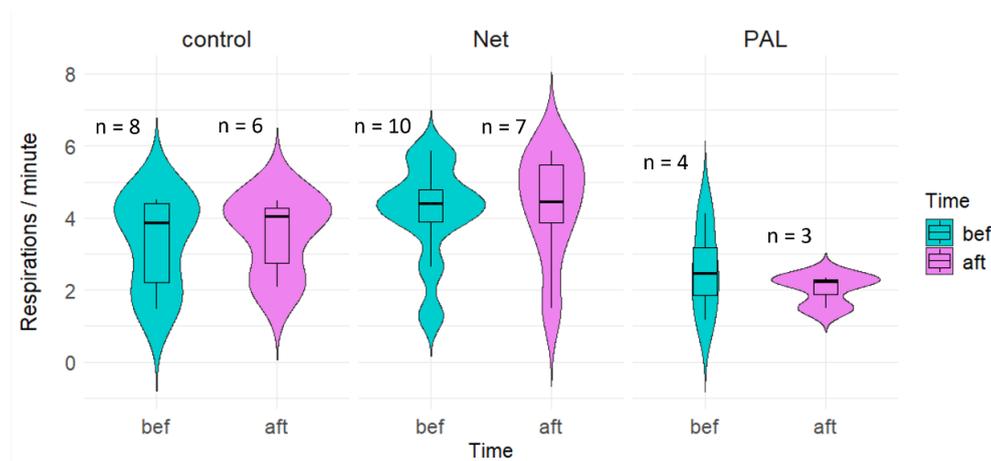


Figure 4.7. Violin plots illustrate the Kernel Density estimation of respiration rates before and after interactions for porpoises during the three treatments. Median and interquartile ranges are indicated by the boxplot within the density plots.

Acoustics

Out of the 88 net interactions, clicks trains were detected during 43.3 % of control interactions (n: 13 out of 30 interactions), 51.4 % of net interactions (n:18/35) and 43.5 % of PAL interactions (n:10/23). The median number of click trains detected during the 4 min period did not differ significantly between the three treatments ($p = 0.826$) with 3.5 clicks/4 min (range: 0 to 20 click trains/4 min, IQR: 8.25) detected during control treatment, 2.5 click trains/4 min (range: 0 to 17, IQR: 6.5 trains/4 min) for net treatment and 2 click trains/4 min (range: 0 to 13 click trains/4 min, IQR: 5) during PAL treatment. No significant difference was found between treatments in the number of click trains recorded before the interaction ($p= 0.545$) nor after the interaction ($p= 0.818$). Detected click trains showed an asymmetric distribution with click trains more often being detected in the two minutes before the interaction (click trains detected 19 times out of 22 interactions with click trains) compared to the two minutes after the interaction (n: 11/22) during all three treatments (Individual interactions in supplementary material Fig.S.4.3.). While not significant for any treatment (Kruskal-Wallis test: Control: $p = 0.077$; Net: $p = 0.332$; PAL: $p = 0.111$) there seems to be a slight tendency for the number of clicks to be lower after interactions for all three treatments (**Figure 4.8.a.**).

No significant differences were detected for most of the combinations of treatments and before and after interactions for the four selected acoustic parameters when performing individual Kruskal-Wallis tests (p-values for each KS-test as supplementary material *Table S.4.3.*). The duration of the click trains (TrDur_us) was significantly shorter after the interaction during PAL treatment compared to before the interaction ($p = 0.022$) (**Figure 4.8.d**). Significant differences were further detected for the shortest Inter Click Interval (ICI) in the click train (MiniICI_us) during PAL treatment showing significantly shorter ICI after the interaction compared to before the interaction ($p = 0.002$) and shorter MiniICI_us during PAL treatment after the interaction compared to after the Control and Net treatment ($p = 0.044$) (**Figure 4.8.e**). Median, minimum, maximum and inter quartile ranges for all parameters and treatments are available in supplementary material *Table S.4.4.*)

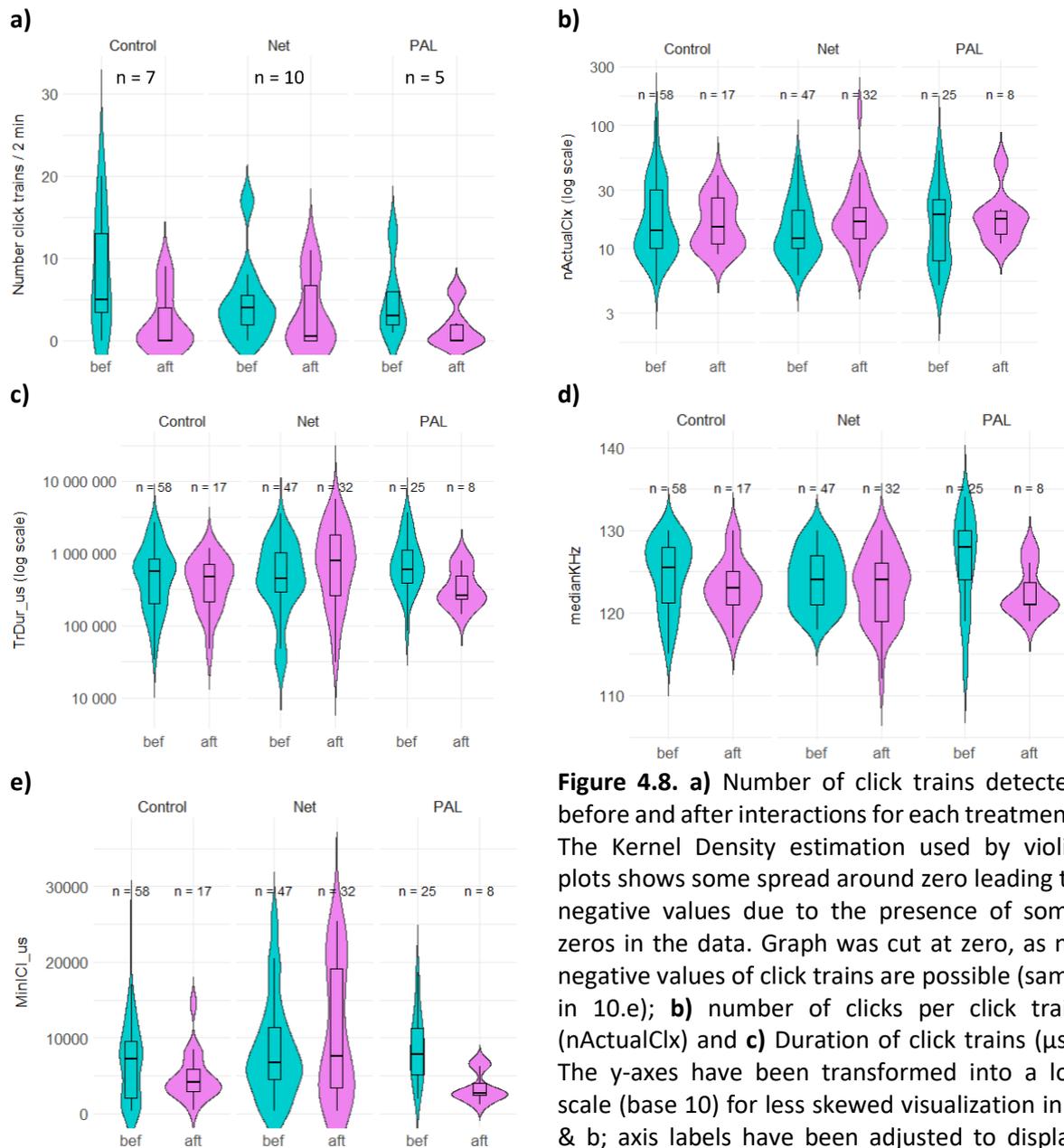


Figure 4.8. **a)** Number of click trains detected before and after interactions for each treatment. The Kernel Density estimation used by violin plots shows some spread around zero leading to negative values due to the presence of some zeros in the data. Graph was cut at zero, as no negative values of click trains are possible (same in 10.e); **b)** number of clicks per click train (nActualClx) and **c)** Duration of click trains (μ s). The y-axes have been transformed into a log scale (base 10) for less skewed visualization in a & b; axis labels have been adjusted to display actual values and not log transformed values. **d)** median frequency (kHz) of the whole click train; **e)** Shortest Inter Click Interval (ICI) excluding the first and last (ms).

4.4. Discussion

Detailed observation effort of small cryptic odontocetes around fishing nets is scarce and therefore mechanisms of how bycatch occurs are of highest value while needing huge sampling efforts in the wild for acquiring small sample sizes. To our knowledge this is the first time harbour porpoises were filmed and acoustically recorded near set net structures in the wild revealing concrete responses of porpoises towards a bottom set net with two precise methods. Differences found between net encounters and control trials were minor. Visible behavioural reaction distances of porpoises towards the net were found to be below or within lower ranges of known acoustic detection ranges for nets. Despite this, porpoises observed made navigation decisions to avoid conflict with the net at very short ranges, suggesting that even with short reaction times and distances porpoises are able to avoid bycatch by swimming above the floatline or around the net. PAL alerting devices evoked different responses in comparison to traditional pingers since porpoises were not deterred and approached the nets and the PAL with only small changes in swimming speed and respiration rates compared to the net treatment. Reaction distances with the PAL were slightly larger than and minimum ICI was shorter in contrast to when only the net was present potentially suggesting more alertness to their surroundings when PAL was active, indicating a slightly increased chance of the porpoise in reacting to a potential danger, when using PAL, potentially mitigation at least some cases of bycatch. These findings however also suggest that a more powerful approach to mitigate bycatch of small odontocetes could come from a combination on increasing awareness of porpoises of their surroundings in combination with enhancements of reflectivity of the net (Larsen *et al.* 2007; Kratzer *et al.* 2021).

Reaction types and distance

The most often observed behaviour towards the net and the net with PAL was crossing the net conducting a shallow dive above the floatline generally without any preceding visible behavioural reaction (head scans, changes in direction). Only three individuals avoided the net by either turning around or swimming around the net or the net with the PAL. The mean visible reaction distances towards the net were lower (4.9 m) than when the PAL was active (7.6 m) indicating that porpoises had more time and distance to react to the net with the PAL. These reaction distances were measured during daytime and could be potentially lower during nighttime when porpoises must rely more strongly on echolocation. The fact that most observed reactions were slight turns away from the net could indicate that they try to avoid the net at first. This is further supported by one observation in which a mother and calf pair completely turned around in front of the net and swam away at increased speed. If porpoises' reaction is avoidance, we would expect them to respond as soon as possible when a barrier is perceived. The fact that the observed avoidance reactions occurred only this close to the net in this study suggests that this is the real range at which they may react in nature. Reaction distances found in this study agree with the lower detection ranges calculated in previous studies assessing the distance at which porpoises perceive set nets (Kastelein *et al.* 2000; Culik *et al.* 2001; Mooney *et al.* 2004; Koschinski *et al.* 2006; Mooney *et al.* 2007) and ranged well below lowest detection ranges from other studies (Villadsgaard *et al.* 2007; Koschinski *et al.* 2006). This suggests a discrepancy between distance of detection and actual distance of reaction towards the net, maybe due to a time lag between perception of the net and reaction. Despite the short range, all porpoises efficiently avoided or crossed the net or the net with PAL with no signs of potential entanglement in the single lines of the modified net. Porpoises are therefore often able to react in an appropriate way to avoid the net despite late notice.

A limitation of this study is that the net was always set in the same location, we can therefore not exclude that individual porpoises got used to the position of the net. The event of the mother and calf pair turning around was in fact towards the beginning of the field season during the first year

(11.07.2022). Despite this one case, all visible reactions towards the net that were associated with avoidance were observed far into the experimental period in August of both years.

Swimming Speed

Swimming speeds followed a similar pattern during net and PAL treatment with slightly increased swim speeds closer to the net followed by a decrease after the net, suggesting a short-term response to the net in both cases. Regardless, the median swim speeds ranged within baseline swimming speeds of porpoises (van Beest *et al.* 2018) and 'before pinger exposure' scenarios of previous studies (Kastelein *et al.* 2001; Brandt *et al.* 2013; Brennecke *et al.* 2022; Elmegaard *et al.* 2023) suggesting that neither the net nor the PAL elicit strong behavioural responses expressed in swim speed. This is different to findings in most pinger studies that generally detect a significant increase in swimming speed or acceleration when porpoises are deterred (Kastelein *et al.* 2001; Teilmann *et al.* 2006; Brandt *et al.* 2013; Brennecke *et al.* 2022; Elmegaard *et al.* 2023) which is suggested to be related to stress.

Respiration rates

While respiration rates were significantly higher during net treatment compared to the PAL treatment, both did not differ from control in this study and were within baseline respiration ranges recorded for wild porpoises of 2.0 to 4.4. resp/min (Rojano-Doñate *et al.* 2018), mean 2.3 resp/min (Watson and Gaskin 1983); and captive porpoises 3 to 5 resp/min (Kastelein *et al.* 2018), 2.4 to 4.0 resp/min (Rojano-Doñate *et al.* 2018). Lower respiration rates detected during PAL exposure may be a result of prolonged diving times with higher echolocation click rate but is difficult to interpret since respiration rates of porpoises vary strongly among studies and even between individuals during the same experimental conditions (Elmegaard *et al.* 2023; Brennecke *et al.* 2022) Similar respiration rates to baseline and control treatments could however suggest that neither the net nor the PAL elicited a response expressed in respiration rate that maybe interpreted as stress. (Summary in supplementary material Table S.4.5.)

Acoustics

The number of click trains per two minutes intervals before and after the interaction did not differ significantly for the three treatments and were within ranges of click train emissions per minute observed in captive porpoises (Carlström 2005). Previous studies showed that the echolocation activity of porpoises can vary during pinger exposure compared to control treatments, with some studies measuring increased activity (Koschinski *et al.* 2006; Culik *et al.* 2015), decreased activity (Culik *et al.* 2001; Carlström *et al.* 2009) or detecting no significant differences (Desportes *et al.* 2006). An increase in echolocation click rate, previously measured to be caused by PAL (Culik *et al.* 2015), was not detected in this study.

The echolocation behaviour of porpoises, measured by different acoustic parameters, was not affected by the presence of the net when compared to the control treatment. In contrast, significantly shorter ICIs and shorter train durations were detected after porpoises interacted with the net ensonified by the PAL, suggesting that the PAL shows potential to modify some acoustic echolocation parameters of porpoises. While shorter ICIs are generally related to feeding activity or communication (Carlström 2005), it has also been observed that when porpoises are not locked onto a target, the ICI can vary, possibly indicating that the animal is exploring the existence of anticipated targets at different distances (Koschinski *et al.* 2008). This could be a possible explanation for decreased ICI after crossing the net, as the porpoise may be anticipating or scanning for more obstacles. A similar trend could not be observed during net treatments.

The echolocation of porpoises was not recorded during all interactions. Tag studies have shown that porpoises echolocate almost continuously (Sørensen *et al.* 2018), thus the reduced number of interactions with click trains is probably due to a limitation of the instrument as the detection function can vary strongly even in short distances and between instruments (Cosentino *et al.* 2023) and not all click trains are actually recorded and/or classified by automated train detection. In fact, studies with TPODs (predecessor of the F-POD) have shown reduced detection ratios ranging from 17 – 30.6 % (Cox *et al.* 2001).

Porpoise-PAL

Our findings suggest that PAL does not strongly alter the natural behaviour of porpoises and does not exclude them from potentially important habitats. While this experiment did not aim to measure the number of porpoises that were deterred by the PAL (this reaction could have occurred at further distances than those covered by the drone footage), it showed that porpoises chose to move within the hearing range of PAL even decided to approach and cross a net close to the PAL (50 m range). This is emphasized as mother and calf pairs were also observed swimming through the experimental set up with PAL active as well as showing feeding behaviour (pelagic feeding and bottom grubbing). This is interesting in the context of concerns related to habitat exclusion and noise pollution of pingers (Carlström *et al.* 2009; Larsen *et al.* 2013; Kyhn *et al.* 2015). At the same time, PAL have shown to significantly reduce the bycatch of porpoises by up to 79.7 % in gillnet fisheries in the Belt Sea (Chladek *et al.* 2020). PAL thus seems to have a much reduced effect on porpoise behaviour compared to pingers. While promising, the application of the PAL in further areas has to be tested before larger applications, as the synthetic signal belongs to a porpoise from the Belt Sea and successful bycatch reduction has this far only been shown there (Chladek *et al.* 2020). No significant differences were obtained in the Icelandic Sea (ICES 2018).

Feeding near nets

In two occasions, porpoises were observed pelagically feeding very close to the net without the PAL, with one porpoise taking a sharp turn at less than a meter distance from the net. Foraging of porpoises near set nets has not been filmed previously but recorded via acoustic methods (Higashisaka *et al.* 2018; Maeda *et al.* 2021; Macaulay *et al.* 2022) with some porpoises being localized foraging up to 5 m from a set net for some time (Macaulay *et al.* 2022). Porpoises have also been filmed swimming behind the cod-end of a Scottish seine capturing fish that escaped through the mesh, indicating that porpoises interact with some fishing gear (Molenaar and Vrooman 2022). Feeding near net structures poses a risk to porpoises as distraction or navigation errors can cause them to entangle (Cox and Read 2004) and free swimming prey has been suggested to potentially mask the echoes from the net (Kastelein *et al.* 1995; Larsen *et al.* 2007). It can be hypothesized that porpoises are either not aware of the nets while feeding beforehand, or that they may benefit from the presence of a net in high risk feeding behaviour if they perceive it earlier. Strategies of cetaceans using already existing barriers such as shores (Lopez and Lopez 1985), the water surface (Heithaus and Dill 2009) or cooperating with fishers (Simões-Lopes *et al.* 1998) have been observed in other cetacean species. Harbour porpoises have also been observed hunting on fish close to the surface, which could indicate that they use the surface as a barrier to push prey towards and often engage in collaborative hunting in which they herd fish as a group (Torres Ortiz *et al.* 2021). Nets could thus potentially be used as a barrier to herd fish by porpoises, which could come in especially useful when hunting alone. In an analysis of stomach content of bycaught porpoises during bycatch trials, bycaught porpoises revealed to often have food remains in the stomach with intact fish potentially suggesting that porpoises had been feeding just before entanglement (Kraus *et al.* 1997). In this study, the modified net could not have functioned as a barrier for herding fish due to the absence of mesh material. However, the extent to which the

porpoises initially perceived the modified net structure remains uncertain. The standard floatline produces the strongest echo and is thus believed to be detected from a further distance (Kastelein *et al.* 2000) and thus may elicit the same hunting strategy in the modified net as in a conventional fishing net. However, dedicated studies and observations during real fishing efforts are needed to be able to support the theory that porpoises potentially use nets as a barrier during their hunting activity in a high risk attempt to catch prey.

4.5. Conclusions

This study represents the first attempt to capture in situ investigation of harbour porpoise interactions visually and acoustically with fishing nets, offering valuable insights into their behavioural responses. Despite their ability to avoid nets at close distances in our trials, bycatch persists in the real fishery, likely due to moments of distraction, exploratory behaviour, or inexperience. These findings underscore the potential of combining acoustic alert systems with innovations in net design to enhance detectability and reduce bycatch risks. These results hold global relevance for improving bycatch mitigation strategies in gillnet fisheries, particularly in regions where such incidents heavily impact cetacean populations.

4.6. Acknowledgements

We thank all volunteers that helped us collect data during the field work for their incredible work and dedication. We thank Tom Bär and Thomas Noack for their input and support in the conception of the project as well as technicians Marko Warmuth from the Deutsches Meeresmuseum Stralsund and Ulf Böttcher from the Thünen Institute of Baltic Sea Fisheries. We further thank Sara Kallmeyer and Angélique Girard for their help screening and tracking videos and we thank Christina Henseler and Christian Wolf Lewin for their input on statistical questions.

4.7. Conflict of interest

Michael Dähne changed employers and now works for the funding body. He initially was the project lead for Meeresmuseum. He is not in charge of any project related tasks at the Federal Agency for Nature Conservation.

4.8. Authors contribution

T.M.D. & M.D. conceived, planned and performed the experiments in the field. J.S.L & M.A.C. contributed to data collection in the field. T.M.D., D.S. and M.D. conceived the idea of the net and tested it. T.M.D., M.D., J.T. & J.S.L. developed the theoretical framework of the paper. J.S.L. & T.M.D. curated the data. T.M.D., M.D. and S.A. performed the analytic calculations. T.M.D. & M.D. created visualizations. T.M.D. took the lead in writing the manuscript. T.M.D., J.S.L., J.D., F.D., D.S., S.A. & M.D. provided feedback and discussed the results and contributed to the final manuscript. T.M.D. & M.D. conceived the original idea. M.D. and F.D. supervised the project and M.D. raised the funding.

4.9. Supplementary material

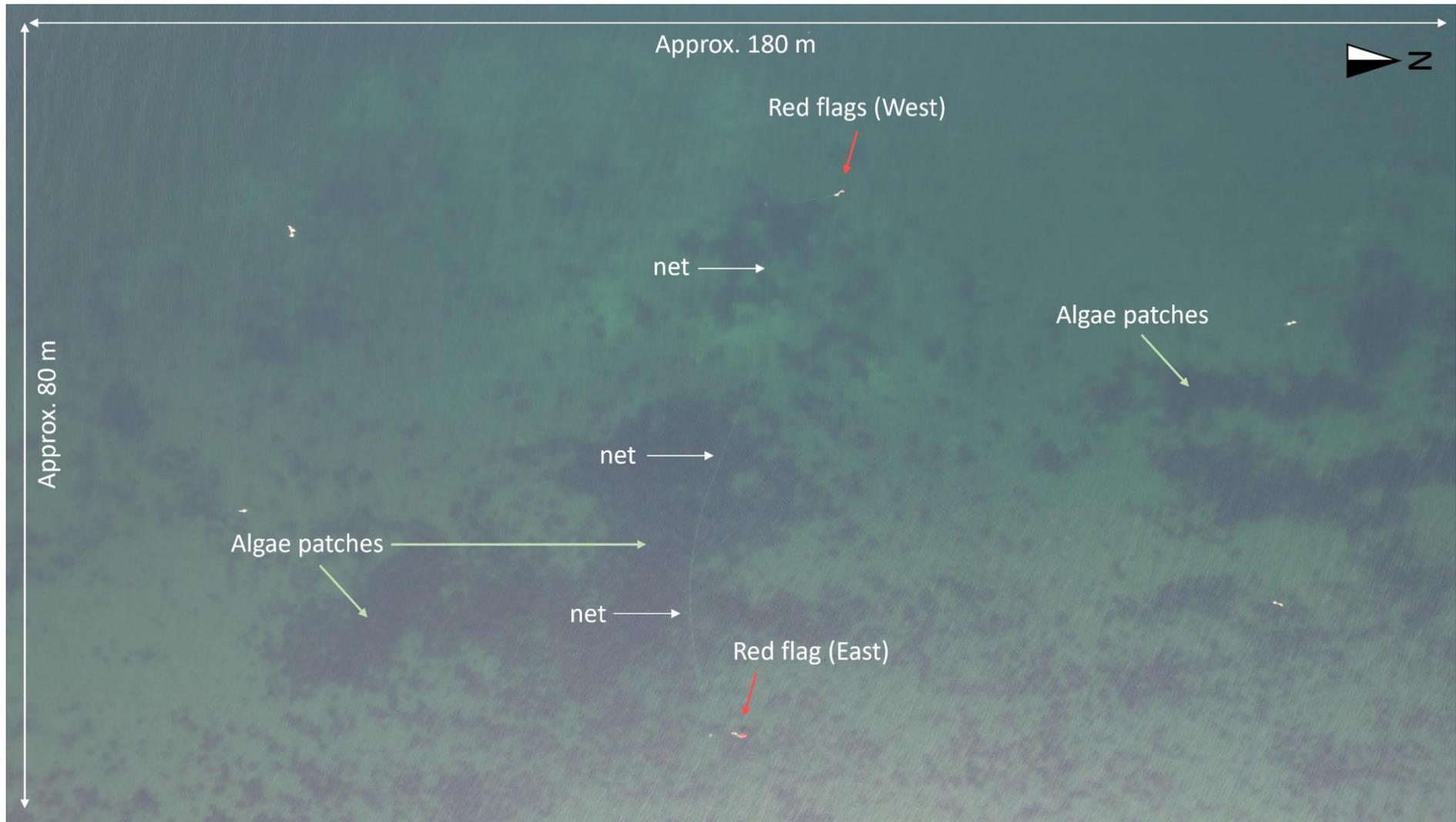


Figure S.4.1. Standard drone footage recording frame with net in the center and good visibility of seafloor composition

Table S.4.1. Description of harbour porpoise behaviours used for drone footage analysis based on other bibliography.

Behaviour	Definition	Source
Head scan	Repeated movement of the head from side to side	Torres <i>et al.</i> 2021
Rapid acceleration	Sudden increase in speed	
Fast turn	Sudden change in direction in movement	
Dive, leap or burst	High arching dives, leaps or burst of directed swimming	
Bottom investigation	Vertical position with head down, close to the bottom, and tail and fluke up; white belly often clearly visible	
Chasing visible prey	Chasing a visible single fish or fish from a school, often includes rapid acceleration, fast turns, and bottom-investigation	
Chasing non-visible prey	Non-visible prey but otherwise same behaviour as above when chasing a visible prey item	
Prey capture	Visible successful prey capture	
Mating	High energy and rapid approached of males towards females with either copulatory attempt or just display that could result in contact or no-contact events. Approaches can occur from all sides but closest contact point during the approach is the left side of the female. Approaches often resulting in male aerial behaviour (including leaps and splashes).	Keener <i>et al.</i> 2018
Travelling	Persistent directional movement at speeds greater than resting	Oakley <i>et al.</i> 2017
Resting	Very slow movements or stationery at the surface	
Feeding	Cooperative hunting, chasing fish, circling, fast directional and synchronised movements, associated diving seabirds	
Foraging	Repeated, unsynchronised dives in different directions in a determined location, erratic movements or splashes	
Socializing	Frequent physical contact, vigorous movements and aerial behaviour such as breaching: playing-rolling at the surface	

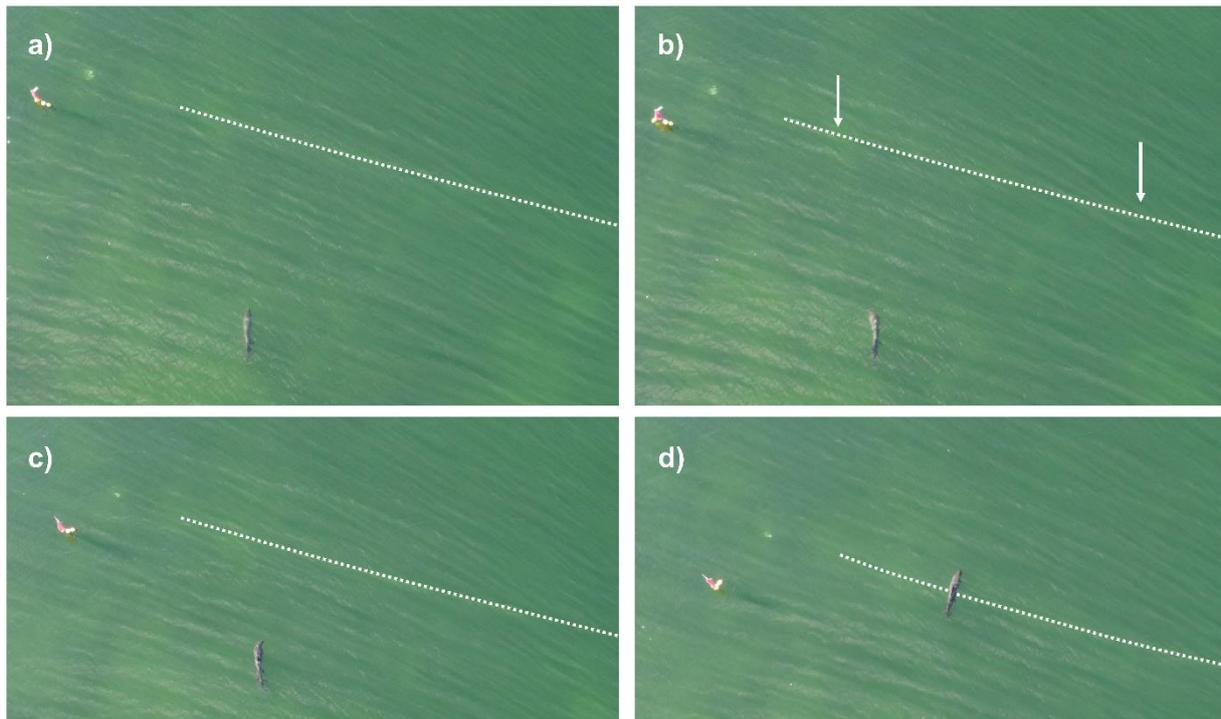


Figure S.4.2. a) Moter and Calf Pair approaching the modified net (marked with two white arrows); b) head scan to their left; c) head scan to their right; d) net crossing with shallow dive.

Table S.4.2. Statistical summary table for the GAMM model for swimming speed of best fit. Adjusted R^2 for this model is 0.0527.

Parametric coefficients:				
	Estimate	Std. Error	t-value	p-value
Intercept	0.32035	0.06553	4.888	1.06e-06
as.factor(direction)South	-0.19815	0.08778	-2.257	0.024
Approx. significance of smooth terms:				
	edf	Ref.edf	F	P-value
s(dist_net2):as.factor(treatment)control	3,285	3.285	6.979	9.21e-05
s(dist_net2):as.factor(treatment)Net	1.626	1.922	0.834	0.269657
s(dist_net2):as.factor(treatment)PAL	2.355	2.355	7.973	0.000198

p-value > 0.05 indicates significant effect of distance on the swim speed.

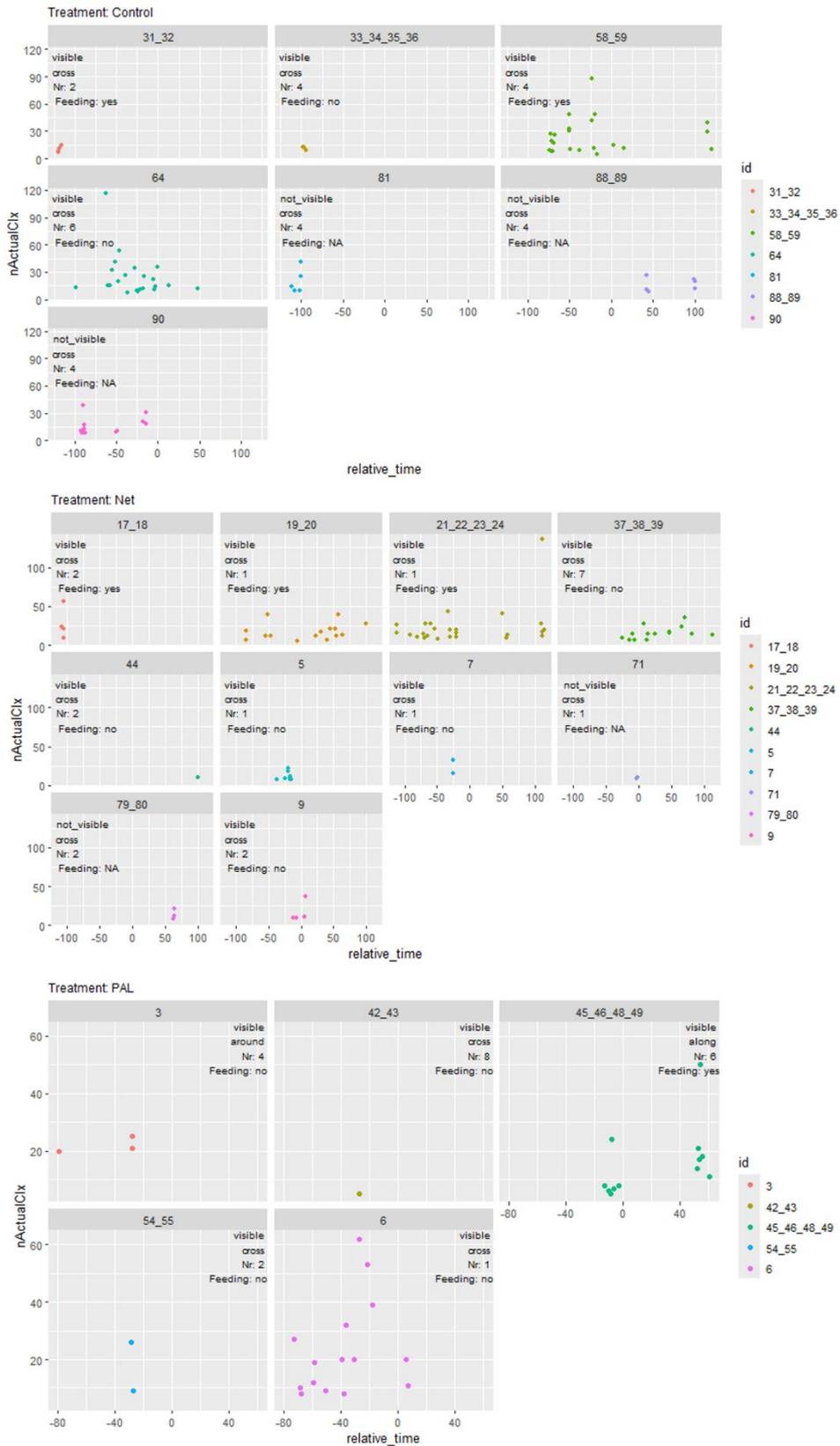


Figure S.4.3. Number of clicks in a click train (nActualClx) detected by the KERNO classifier of the F-POD.exe software for the different net interactions IDs divided by the three treatments. Several interactions may be plotted together as they occurred simultaneously and thus correspond to the same acoustic 20 min data (10 min before interaction to 10 minutes after interaction).

Table S.4.3. P-values obtained from non-parametric Kruskal-Wallis (KW test) tests to compare acoustic parameters between three tree treatments treatments: i) before the interaction and; ii) after the interaction; and iii) before and after within each treatment.

Variable	Description	KW test between treatments (before)	KW test between treatments (after)	KW test (before vs after) for treatments	
		p-value	p-value	Treatment	p-value
nr trains/ 4 min	nr of click trains detected during 2 min before and 2 minutes after the interaction	0.5451	0.8181	Control	0.07736
				Net	0.3332
				PAL	0.1105
nActualClx	number of clicks in train without imputing clicks	0.5314	0.7866	Control	0.9192
				Net	0.07652
				PAL	0.6135
TrDur_us	train duration in microseconds	0.2525	0.07265	Control	0.531
				Net	0.1328
				PAL	0.02203 *
medianKHz	median frequency of the train	0.1068	0.8723	Control	0.08629
				Net	0.2858
				PAL	0.07326
MinICI_us	shortest Inter Click Interval excluding the first and last, as these are more often inaccurate	0.2701	0.04374 *	Control	0.2103
				Net	0.4971
				PAL	0.00188 **

Table S.4.4. Median, min, max and inter quartile ranges (IQR) for the number of click trains detected on the F-PODs two minutes before and two minutes after each interaction divided by treatment, and for different acoustic parameters.

		Control		Net		PAL	
		before	after	before	after	before	after
nr clicks / 2 min	median	5	0	4	0.5	3	0
	Min – Max	0 – 20	0 – 9	0-17	0-11	1-13	0-6
	IQR	9.5	4	3.5	6.75	4	2
nActualClx	median	14	15	12	16.5	19	17.5
	Min – Max	5 – 117	9 – 39	6 – 57	7 – 136	5 – 62	11 - 50
	IQR	20	15	10.5	9.75	17	7
TrDur_us	median	561758	476190	450000	786764	606060	272727
	Min – Max	33950 - 2700000	47318 - 1200000	21868 - 3545454	31088 - 5714285	84745 - 3647058	144736- 793650
	IQR	628509	494805	718056	1559723	728759	475649
medianKHz	median	126	123	124	124	128	121
	Min – Max	115 – 130	117 – 130	118 – 130	112 – 130	113 – 134	119 – 128
	IQR	6.75	4	6	7	6	2.75
MinICI_us	median	7180	4102	6781	7590	7831	2646
	Min – Max	316 - 24599	457 - 14579	357 - 25574	315 - 25372	2004 - 18596	1161 - 6934
	IQR	7521	3001	6806	15746	6133	1618

S.4.5. Summary of literature examining the effect of different acoustic deterrent devices (ADD) on harbour porpoise swim speed and respiration rates.

	ADD	Captive or wild	Reaction	Swim speed (m/s)		Trend swim speed	Respiration rate (respiration / min)		Trend resp. rate		
				before ADD exposure	during ADD exposure		before ADD exposure	during ADD exposure			
<i>(Brennecke et al. 2022)</i>	Pinger	Wild	Escape	Max. 1.1 – 8.4	Max. 0.4 – 10.01	Increase	2.4 – 4.4	1.8 – 4.2	Decrease		
<i>(Kastelein et al. 2001b)</i>	Alarms	Captivity	Swam away	-	-	Increase	-	-	More forceful		
<i>(Lockyer et al. 2001)</i>	Deterrent sound	Captivity	Move away	-	-	-	-	-	Slight increase		
<i>(Teilmann et al. 2006)</i>	Deterrent sounds	Captivity	Avoidance	used acceleration 0.05 – 0.09 m/s ²	acceleration 0.05 – 0.11 m/s ²	Increase in most cases	-	-	-		
<i>(Brandt et al. 2013)</i>	Seal scarer	Wild	Avoidance or no obvious reaction	1.3 – 3.2	average 1.6	Increase	-	-	-		
<i>(Elmegaard et al. 2023)</i>	AHD	Wild	Startle response and fleeing	HP1	1.3	1.4	Increase (average 26 %)	HP4	3.9	3.3	15% decrease to 31% increase
				HP3	1.4	1.8		HP3	3.2	4.2	
				HP5	1.3	1.9					
<i>Present study</i>	PAL	Wild	No obvious reaction	(Control) Median: 1 (0.009 – 5.81)	Median 1.14 (0.051 – 4.99)	Slight increase	Control Mean: 3.42 (1.47 – 4.5)	Mean: 2.33 (1.15 – 4.12)	Decrease		

Chapter 5

Harbour porpoise reaction to PAL (pinger alternative) in the Western Baltic Sea

Title: Harbour porpoise reaction to PAL (pinger alternative) in the Western Baltic Sea

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Abstract

The acoustic alerting device "Porpoise-PAL" (PAL) has been used in Schleswig-Holstein (Germany) since 2017 as a tool to reduce incidental bycatch of harbor porpoises. While the effectiveness of PALs in reducing bycatch has been proven, concerns have been raised about potential habituation to the porpoise-like signal, which could diminish their efficacy over time. Here, we investigated the echolocation behavior of harbour porpoises in response to PAL exposure in previously exposed areas (Germany) and non-exposed areas (Denmark). Using F-PODs, we recorded echolocation behavior of porpoises during two field campaigns at both reference stations without PAL and near set nets equipped with PALs during regular fishing activity. The aim was to detect potential habituation effects by analyzing changes in echolocation parameters. To assess potential differences, we compared four acoustic parameters of detected click trains: number of clicks per train, median frequency, average sound pressure, and minimum inter-click interval. Statistical analysis using non-parametric Kruskal-Wallis tests and machine learning models (gradient boosting) revealed that median values for all four parameters were similar between reference stations and PAL-equipped nets in both countries and within countries. Although statistically significant, the detected differences showed generally small effect sizes (epsilon squared mostly <0.04). In congruence, the machine learning models did not exhibit strong classification ability (AUC < 0.69) further suggesting small variation in acoustic parameters. Porpoises recorded in not exposed areas in Denmark did not show a strong reaction towards the PAL. The reaction of porpoises in previously exposed areas was similar. Evidence for habituation in German porpoises towards the PAL signal was thus not provided using the four parameters in this study. While the absence of detectable changes in echolocation behavior could indicate that PALs remain effective, reliable long-term monitoring of bycatch rates is necessary to confirm their sustained applicability in fisheries management.

Keywords: *Phocoena phocoena*, acoustic deterrent device, bycatch, long-term habituation, F-POD, porpoise management

5.1. Introduction

The harbour porpoise (*Phocoena phocoena*) is the only cetacean species resident in the Baltic Sea (Carlström *et al.* 2023). Here they are regularly bycaught (Glemarec *et al.* 2021), with records of their incidental capture in set net fisheries in the Baltic Sea dating back to the 19th century (Koschinski 2001). The current bycatch rates for the Western Baltic assessment unit are considered above sustainable bycatch threshold limits (Kindt-Larsen *et al.* 2023; Owen *et al.* 2024) despite the harbour porpoise being listed in annexes II and IV of the EU Habitats Directive (92/43/EEG), with the latter requiring Member States to establish a strict protection regime throughout its range.

Pingers, devices that emit an unpleasant signal, have generally proven to be effective at reducing harbour porpoise bycatch in static nets (Palka *et al.* 2008; Larsen and Eigaard 2014; Dawson and Lusseau 2013; Königson *et al.* 2021). However, concerns about habitat exclusion and noise pollution have been raised in relation to pingers (Kyhn *et al.* 2015; Larsen *et al.* 2013; Culik *et al.* 2001). As an alternative, the porpoise-PAL (from here on referred to as PAL: Porpoise ALert) (Culik and Conrad 2013) was designed with the aim to alert porpoises of the presence of a danger without excluding them from their habitat (Culik *et al.* 2015). The PAL is programmed to emit synthetic porpoise communication sounds that are based on aggressive calls of a female in captivity of the Belt Sea population (Culik *et al.* 2015). The PAL signal consist of two upsweep chirps beginning with a click rate of 173 clicks/s and ending with 959 clicks/s and has a centroid frequency of 133 ± 8.5 kHz (Chladek *et al.* 2020). With one to three randomly emitted signals the PAL meets the signal repetition requirements for acoustic deterrent devices (Regulation (EU) 2019/1241). PAL have shown to produce an increase in porpoise echolocation rate of 10 % causing a rather small displacement response in porpoises which increased their distance to the signal by 32 m (from 131 to 163 m) in the western Baltic Sea (Culik *et al.* 2015). PAL have further shown to reduce porpoise bycatch in the western Baltic Sea by up to 79.7 % (Chladek *et al.* 2020). Based on these results, PAL have been used since 2017 in German set net fisheries off of the Baltic coast in Schleswig-Holstein (SH) in the frame of a voluntary agreement (Freiwillige Vereinbarung 2015). In 2023, 1772 PAL devices were distributed between 84 participating fishers (OIC 2023).

Harbour porpoises habituating to pingers (Reeves *et al.* 1996; Dawson *et al.* 1998; Dawson *et al.* 2013) is considered one of the most serious concerns related to pingers (Kindt-Larsen *et al.* 2019). Habituation has been defined similarly in different occasions as “a relatively permanent waning of a response as a result of repeated stimulation” (Thorpe 1956), “behavioural response decrement that results from repeated stimulation and that does not involve sensory adaptation/sensory fatigue or motor fatigue” (Rankin *et al.* 2009). The behavioural response decrement or waning/decrease in response can be observed either in frequency or magnitude or both (Rankin *et al.* 2009). Habituation of harbour porpoises to pingers has been described previously for different pinger types (Cox *et al.* 2001; Carlström *et al.* 2009; Kindt-Larsen *et al.* 2019) while no habituation has been detected during other studies (Palka *et al.* 2008; Carretta and Barlow 2011; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021). In the wild, habituation has been studied acoustically looking at variations in harbour porpoise click rates over time in the presence of a pinger (Kindt-Larsen *et al.* 2019), measuring the encounter rates during periods with pingers on/off (Kyhn *et al.* 2015), or looking at detection positive minutes per hour during and after pinger exposure (Königson *et al.* 2021) as well as in captivity looking at click activity during on/off pinger exposure periods (Teilmann *et al.* 2006).

In the present study, two main experimental set up problems had to be considered: i) no baseline echolocation data on porpoises in Germany was recorded before PAL exposure which started in 2017, thus, to test whether porpoises in Germany might show signs of habituation, in this study, their echolocation was compared to that of porpoises belonging to the same Belt Sea population, but from

an area where PAL is not being used in the fishery, and which is therefore considered as not exposed to PAL; ii) during traditional pinger effect experiments before, during and after pinger exposure are measured in the same area relying on the assumption of a similar density of porpoises. In the present study such as set up was not selected as the aim was to record porpoises during commercial fishing activity comparing an area where porpoises have previously been exposed (Germany) and not exposed to the PAL (Denmark). Considering that units such as detection positive minutes or click rates are influenced by the abundance of porpoises, in this study echolocation parameters of click trains were analyzed as these are more independent from the abundance of porpoises which is expected to vary between Germany and Denmark (Gilles *et al.* 2022).

Previous habituation studies towards pingers have looked at echolocation parameters of porpoises using passive acoustic monitoring (PAM) (Carlström *et al.* 2009; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021). As an acoustic response of porpoises towards the PAL has previously been detected (Culik *et al.* 2015) this study investigated whether certain acoustic parameters of the click trains produced by porpoises near PAL could be a potential indicator for habituation. Acoustic parameters were selected based on the following information: the number of clicks per click train has previously been used to study habituation in porpoises towards pingers (Kindt-Larsen *et al.* 2019); the frequency of clicks has been observed to vary during different calls (Clausen *et al.* 2011), thus, if a specific reaction towards the PAL is elicited, porpoises may adapt their calls which could be reflected in the median frequency of the click train; similarly, variations in Inter Click Interval (ICI) have been detected during different echolocation categories such as dominance and distress calls (Amundin 1991), or threat calls (Busnel and Dziedzic 1966). Further, the ICI can give information on the activity of porpoises, with ICI below 2 milliseconds being indicators for feeding buzzes or communication (Koschinski *et al.* 2008; Verfuss *et al.* 2009); lastly, the sound pressure level recorded on the click-detectors, such as the F-POD, can depend on a variety of reasons, but a clear difference could be an indicator for distance between porpoise and the click detector and thus the noise source (Kyhn *et al.* 2013). In this case consistent higher average sound pressures near PAL-equipped nets in Germany could be an indicator of porpoises moving closer to the nets with PAL compared to Denmark, which could be an indicator for habituation.

Besides the suggested increase in echolocation activity (Culik *et al.* 2015), it is still unknown exactly how harbour porpoises behaviourally and acoustically react to PAL in a real fishery and if potential habituation may occur over longer periods of time. To study whether habituation to PAL might have occurred in Germany, we investigated parameters of echolocation recorded by click-detectors attached to fishing nets with PAL, and on reference stations without PAL in areas where PAL has not been used before (not exposed area, Denmark) and areas where PAL has been used (exposed areas, Germany). Both areas in Germany and Denmark are inhabited by porpoises belonging to the Belt Sea population (Wiemann *et al.* 2010; Lah *et al.* 2016; Galatius *et al.* 2012). The study areas were selected in this manner, as the synthetic porpoise signal programmed in the PAL come from the Belt Sea population, and is assumed to match those used by the same wild population nearby (Culik *et al.* 2015). Furthermore, PAL efficiency has only been tested for the western Baltic Sea (Chladek *et al.* 2020). While some movement of porpoises between the German and Danish areas has previously been observed through satellite tags (Teilmann 2004), porpoises generally seem to show site fidelity (Nielsen *et al.* 2018; Zein *et al.* 2019). In the present study we assume that harbour porpoises in the Danish study site are more naïve to the PAL signal than porpoises in the German study site.

5.2. Material and Methods

Study area

Two measuring campaigns were conducted simultaneously in Germany and Denmark: The first run from March 1, 2023 until May 31, 2023, the second from September 1, 2023 until May 31, 2024. Trials took place in the Bay of Eckernförde (Germany), the central region where PALs have been used since 2017, and around the northern Øresund (Denmark) (Figure 5.1.), where PALs have not been used previously.

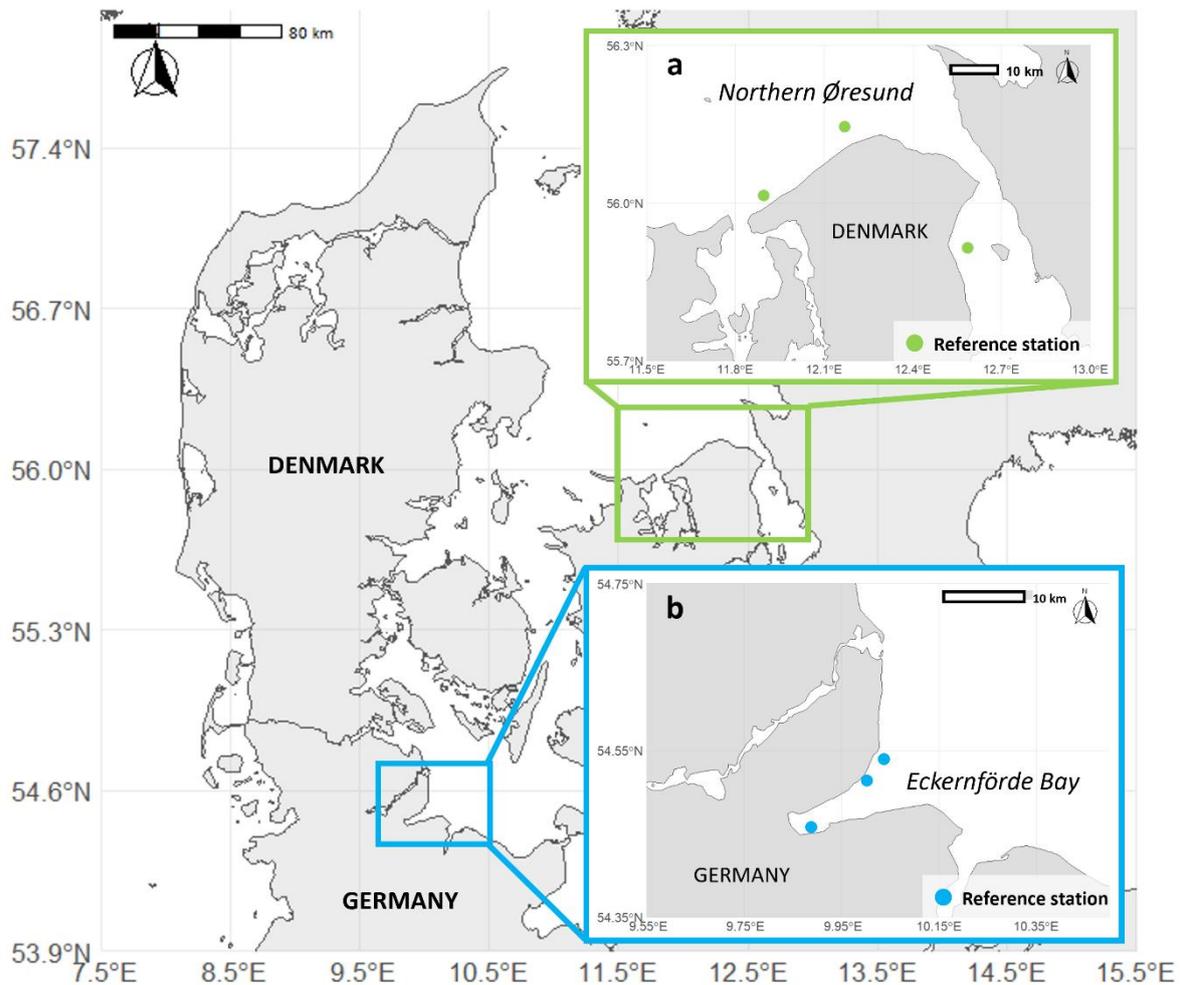


Figure 5.1. Map of the study area in (a) northern Øresund, Denmark; (b) Eckernförde Bay, Germany. The location of the reference stations in both areas is shown on the insert maps.

Acoustic data

Click-detectors (F-POD, Chelonia Ltd. UK) were used to record harbour porpoise clicks near set bottom nets equipped with PAL during regular fishing activity in both countries. Two to four fishers participated both in the trials in Germany and Denmark, with the number of participating fishers fluctuating throughout the campaigns. In Germany mainly trammel nets with mesh sizes between 75 and 180 mm were used as well as herring nets with mesh sizes between 26 and 52 mm. In Denmark, fishers used trammel nets with mesh sizes between 110 – 175 mm as well as gillnets with a mesh size of 240 mm. Fishers in Germany already used PAL on their nets spacing them 200 m covering the entire length of the net. In Denmark, fishers did not use PAL beforehand, therefore one PAL device was given to each Danish fisher to be mounted with its longitudinal axis at one end of the net near the mounted

F-POD. The source level is not completely omnidirectional around the PAL, with a measured 7 % lower source level towards the battery compartment (Chladek *et al.* 2020) which corresponds to about 11 dB. Fishers in Denmark were thus asked to mount the PAL with the stronger sound beam directed onto the net, away from the F-POD. PALs are estimated to be heard by porpoises up to distances of 90 – 320 m (Chladek *et al.* 2020). Each fisher was handed one F-POD to be attached to their nets with PAL during their regular commercial fishing activity. Fishers generally attached the F-POD to the anchorline of the flag pole of the net, in a way that the F-POD stayed at the height of the floatline near the end with the PAL. The position of the nets and the F-POD as well as the time of deployment and retrieval of the nets was registered either with a smartphone app (Mofi - Mobile Fisheries Log, (<http://www.anchorlab.dk>) or via paper protocols.

Only one PAL was attached to the nets in Denmark for two reasons: i) to reduce the chances of porpoises getting used to the PAL as the study area in Denmark is the not exposed area suggested to represent a more naïve behaviour when reacting towards the PAL; ii) the effective detection distance of C-PODs (predecessor of the F-POD) was estimated to be in the ranges of 16 – 24 m (Amundin *et al.* 2022) and to be around 80 m for the F-POD (Cosentino *et al.* 2023). The effective detection range of the F-POD therefore does not exceed the expected ensounded distance by the PAL. Hence additional PALs would have possibly altered the results, but would have not been noticed by the F-POD.

Baseline echolocation behaviour of porpoises in both countries was obtained by deploying three F-PODs in each country at reference stations without PAL. These F-PODs continuously recorded during the two campaigns and helped to determine whether there are already baseline differences in the echolocation parameters across the two countries. The reference stations were placed on main fishing grounds of the participating fishers (**Figure 5.1.**). Three reference stations were deployed in each country during the first campaign while only two reference stations could be deployed in both countries during the second campaign. The reduction in sampling effort in Denmark was due to one fisherman leaving the project and therefore his area no longer had to be covered, while in Germany logistical issues prevented the deployment of the third station. All F-POD were calibrated prior to deployment and between measuring campaigns according to standard methodology (Dähne *et al.* 2013).

Click train classification

The echolocation clicks recorded by the F-PODs were classified using automated analysis algorithm KERNO-F in the F-POD software (technical version 1.06, Chelonia Ltd, UK). Data was filtered for narrow-band high frequency (NBHF) click trains retaining only high and moderate click train categories. Full click train details were exported and four click train parameters were selected to test whether differences in echolocation of porpoises near PAL can be detected in Germany (exposed to PAL) and Denmark (not exposed to PAL): i) nActualClx: the number of clicks in the click train, without imputed clicks in gaps where a real click has not been found; ii) medianKHz: median frequency (kHz) of the whole train; iii) avSPL: average sound pressure (8 Bit values) (Dähne *et al.* 2013), iv) minICI_us: shortest ICI excluding the first and last click (ms), as these are more often inaccurate (definition of abbreviations given when exporting the click train details from the F-POD software).

Filtering out PAL signals

The synthetic harbour porpoise NBHF signals produced by the PAL were often detected and classified by the KERNO-F classifier as harbour porpoise click trains. Therefore, to analyze only real harbour porpoise click trains, the PAL had to be filtered out of the data. As the manual extraction of each PAL click train would have been too time-intensive, an eXtreme Gradient Boosting (XGBoost) binary classification model was trained using the xgboost package v. 1.7.8.1 in R (Chen *et al.* 2024) to differentiate between signals from real porpoises and synthetic NBHF signals emitted by the PAL. To

train the classifier, two experienced and trained independent annotators manually separated PAL click trains from porpoise click trains recorded near PAL-equipped nets collected during the first campaign in Germany. Results obtained by both annotators were merged into one data set keeping only click trains where the classification by both annotators matched. The final training set contained 154 772 click trains (912 harbour porpoises and 153 860 PAL trains). The XGBoost binary classification model was trained using all acoustic parameters of click trains that can be exported from the F-POD software as features (**Table 2.1.**) and using click trains from porpoises as target variable to be mapped to binary labels. The maximum depth of the decision tree was 3 to prevent overfitting, 10 iterations or boosting rounds were used together with a binary logistic function to obtain the output as probability between 0 and 1. The performance of the trained model was tested on a validation data subset in Germany and on a data set from Denmark where one annotator had manually filtered PAL and porpoises for a proportion of the data from the first season (392 278 click trains; porpoise click trains: 22 935; PAL click trains: 369 343). The model was trained using the German training data set, as annotators with experience classified the data, while the Danish data was classified by a student and partly cross-checked by one of the annotators. Thus, the annotations on Danish data were only used to assess model performance on that data, but not for model training. Priority was set on excluding PAL signals. The resulting trained model was then used to predict the probability of each click train belonging to either a PAL signal or a real porpoise in the rest of the data.

Click trains recorded on the reference stations were screened to exclude days on which a net with PAL might have been set in close vicinity. The screening of the reference station data was done manually as the filter did not perform well on the reference data due to the PAL signals being weaker. PAL signals were not detected on the reference stations in Denmark but were detected in some occasions on the reference stations in Germany. Days in which at least one PAL signal was detected on the reference stations were completely excluded from the reference data. To ensure comparability under consistent criteria between click trains in the reference stations and near fishing nets with PAL, the PAL filter was also applied onto the reference station data after manually filtering the PAL signals out, to ensure the same proportion of false negatives (true porpoises classified as PAL) was excluded on the reference stations. After applying the PAL filter to the reference station data a mean of 83 % of click trains remained in both countries. (Proportion of filtered click trains for countries in *supplementary material* Table S.5.3.)

Statistical analysis

The number of clicks in a click train, average sound pressure and the minimum ICI did not follow a normal distribution, and the median frequency of the click train failed to show homogeneity of variances (Levene test: $p\text{-value} < 2.2e^{-16}$). Thus, non-parametric Kruskal-Wallis tests (KW tests) were performed to test for differences in the four acoustic parameters of click trains recorded at reference stations and near PAL-equipped nets within countries and across countries. The epsilon squared (Kelley 1935) was used to quantify the effect size of the observed differences in the KW tests (Tomczak and Tomczak 2014). KW tests were employed as the distribution of the data did not allow to properly fit mixed models. Diagnostic plots and the DHARMA package v.0.4.7. (Hartig 2024) were used to assess residual patterns in mixed models, but problems with the uniformity of residuals, outliers and overdispersion were encountered in most cases, suggesting the models did not adequately fit the data despite using different variable transformations, families and link functions as well as including and reducing the number of fixed factors, random factors and interactions.

Gradient Boosting Model

To assess whether differences in echolocation behavior could be detected between porpoises in Germany and Denmark at reference stations and near PAL-equipped nets, we employed eXtreme

Gradient Boosting (XGBoost) models for multiple classification tasks. The models were trained using the four selected acoustic parameters and evaluated with data from both countries collected in spring 2023 and 2024 (March 1 – May 31), while the remaining data were used for training. Model parameters included a maximum tree depth of 3, 10 iterations for cross-validation, and a binary logistic function for classification.

The first classification task aimed to determine whether click trains recorded at reference stations could be distinguished between Germany and Denmark. This test was conducted to assess potential baseline differences in echolocation parameters between porpoises in the two countries, despite belonging to the same population. The second task examined whether click trains recorded near PAL-equipped nets could be distinguished between the two countries, providing insight into potential habituation effects in German porpoises. Since slight differences were detected between reference stations in Germany and Denmark, additional models were trained to test whether click trains could be distinguished between reference stations and PAL-equipped nets within each country. To further control for potential underlying heterogeneity unrelated to country or PAL exposure, additional pairwise models were trained to test whether click trains could be distinguished across individual reference stations within each country and across individual PAL-equipped net recordings within each country.

The underlying assumption was that if the classifier could accurately distinguish between groups based on the provided acoustic parameters, it would indicate meaningful differences in echolocation behavior. Conversely, if classification performance was close to random chance, this was interpreted as evidence for a lack of discernible differences, supporting the null hypothesis. This machine learning approach allowed for the identification of potential patterns and interactions that may not be apparent through conventional statistical methods.

The classifier performance was assessed using the area under the Receiver Operating Characteristic (ROC) curve (AUC) (Bradley 1997) with the pROC package v.1.18.5 in R (Robin *et al.* 2023). To further interpret model results, SHapley Additive exPlanations (SHAP) values (Lundberg and Su-In 2017) were obtained using the SHAPforxgboost package v.0.1.3 (Liu *et al.* 2023), providing insights into the importance of individual acoustic parameters in distinguishing between groups. All statistical analyzes were conducted using R v.4.4.2, and visualizations were generated with ggplot2 v.3.5.1 (Wickham 2016).

5.3. Results

A total of 4 411 hours of F-POD recordings near PAL-equipped nets were collected by German fishers throughout the two campaign. In Denmark, fishers collected 4 441 hours of F-POD recordings near PAL-equipped nets. Click trains of harbour porpoises were detected both in Germany and Denmark near fishing nets with PAL in both campaigns. After applying the PAL filter, 32 388 click trains were classified as true porpoises in Germany and 29 887 click trains were classified as true porpoises in Denmark. The duration of hauls in Germany was averaged on 21.3 h (8.8 h Standard Deviation (SD)) per haul while the mean duration of hauls in Denmark was longer with 41.6 h (SD: 36.5 h) per haul. The sampling effort in the reference stations was higher both in Germany and Denmark as the F-PODs were continuously deployed, recording a total of 719 days in Germany among all three stations and during 526 days in Denmark combining all three stations. Click trains of true porpoises were detected on all reference stations in both campaigns. After applying the PAL filter, 487 836 click trains remained in Germany and 148 892 click trains in Denmark. The total number of click trains on each position of net with PAL can be seen in **Figure 5.2**. No porpoises were bycaught during the trials in Germany, while

one porpoise was bycaught at a distance of around 64 m from the PAL device in Denmark in spring 2023 (Figure 5.2).

Filtering out PAL signals

Using the 0.8 prediction threshold on the German data, a sensitivity of 0.916 was obtained, indicating that 91.6 % of real harbour porpoises were classified as such (true positives) and a specificity of 0.999, which indicated that 99.9 % of PAL signals are classified as such (true negatives). Predictions made on the training data set classified 891 click trains as real porpoises, out of which 37 had been classified as PAL signals by annotators (4.2 %). When applying the filter onto the manually classified Danish data, a sensitivity of 0.823 and a specificity of 0.999 was obtained. In the manually classified data in Denmark, the PAL filter classified 19 114 click trains as real porpoises, out of which 317 had been classified as PAL signals by the annotators (1.7 %).

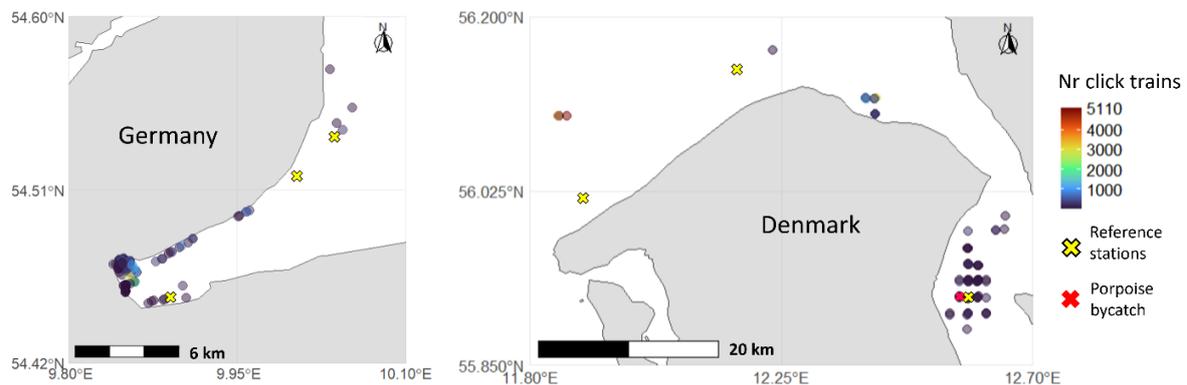


Figure 5.2. Total number of click trains recorded on F-PODs at each PAL-equipped net in Germany and Denmark during the entire measuring campaign. Note that the scales of the maps are different.

Non-parametric tests

Significant differences were found for all four parameters between reference stations when conducting KW tests but with very small effect sizes (epsilon squared, E^2) (Table 5.1.). The median number of clicks per click train ($n_{ActualClx}$) did not vary between both countries, and the difference in the median value of minimum ICI ($MinICI_{us}$) was less than a millisecond. The two largest differences were found between the median average sound pressure ($avSPL$) which showed a difference of 11 Bits between countries and on the median frequency ($medianKHz$) of the click trains which showed a maximum difference in mean values of 2 kHz between countries. In all cases, values on the reference stations in Germany were lower (Table 5.1.).

The KW test for the acoustic parameters recorded near PAL-equipped nets also indicated significant differences between Germany and Denmark for all four parameters, although again with small effect sizes (Table 5.1.). The differences detected near PAL-equipped nets between the two countries followed the same pattern and were in the same order of magnitude as those detected between countries on the reference stations. The median number of clicks per click train detected near PAL-equipped nets was the same in both countries, the median value of minimum ICI varied in less than a millisecond, the median value of average sound pressure differed by 10 Bits between countries and the median frequency of the click trains showed a difference of 3 kHz. Like the reference stations, all values recorded in Germany were lower than those recorded in Denmark. Further, the median values for the four parameters were slightly smaller near PAL-equipped nets compared to the reference stations in both countries (Figure 5.3.).

Significant differences were also found in the KW tests between reference stations within Germany (supplementary material Table S.5.1.) and within Denmark (supplementary material Table S.5.2.),

although with very small effect sizes. In Denmark, despite the large data size, the p-values were close to 0.05 for the number of clicks in click trains and the minimum ICI suggests that the values on reference stations and PAL-equipped nets are very close. The small effect sizes for the other two parameters also suggest only minor differences.

Table 5.1. Summary of acoustic parameters of click trains of porpoises recorded on reference stations (Ref) and near PAL-equipped nets (PAL) in both countries. P-value for Kruskal-Wallis tests (KW test) between countries (DE: Germany and DK: Denmark) and effect size (epsilon squared, E^2) of the test for each parameter.

Parameter	Station	Country	Mean	Median	Q1-Q3	Min - Max	p-value (KW test)	Effect size (E^2)
nActualClx (nr of clicks in click train)	Ref	DE	15.9	11	8-18	5 – 577	2.2e-16	0.000125
		DK	16.4	11	8-18	5-460		
	PAL	DE	15.4	11	8 - 17	5-281	2.2e-16	0.00131
		DK	16.2	11	8 - 18	5-421		
avSPL (8 Bit values)	Ref	DE	84.1	54	34-101	18 - 406	2.2e-16	0.00603
		DK	100.8	65	38-130	17-406		
	PAL	DE	77.3	48	32 - 93	17 - 406	2.2e-16	0.0124
		DK	105.8	58	34 - 146	18-406		
mediankHz (kHz)	Ref	DE	123.4	123	121-126	100-144	2.2e-16	0.0432
		DK	125.2	125	122-128	84-143		
	PAL	DE	122.1	122	119-125	88-144	2.2e-16	0.133
		DK	125.3	125	122-128	109-144		
MinICI_us (ms)	Ref	DE	8.66	7.38	4.98–10.4	0.24-178	2.2e-16	0.00402
		DK	9.98	7.93	5.24–12.0	1.1-158.8		
	PAL	DE	7.79	6.36	4.27-9.4	1.1-97.7	2.2e-16	0.00791
		DK	9.09	7.00	4.59-11.0	1.14-178.4		

Table 5.2. Results of the Kruskal-Wallis tests (KW test) and effect sizes (Epsilon squared, E^2) comparing four acoustic parameters of the click trains between reference stations and PAL-equipped nets within countries.

Parameter	Country	Station	p-value (KW test)	Effect size (E^2)
nActualClx (nr of clicks in click train)	DE	Ref	2.2e-16	0.000235
		PAL		
	DK	Ref	0.04411	0.0000171
		PAL		
avSPL (8 Bit values)	DE	Ref	2.2e-16	0.000962
		PAL		
	DK	Ref	2.2e-16	0.000411
		PAL		
mediankHz (kHz)	DE	Ref	2.2e-16	0.00596
		PAL		
	DK	Ref	2.2e-16	0.0000296
		PAL		
MinICI_us (ms)	DE	Ref	0.0121	0.00275
		PAL		
	DK	Ref	2.2e-16	0.000411
		PAL		

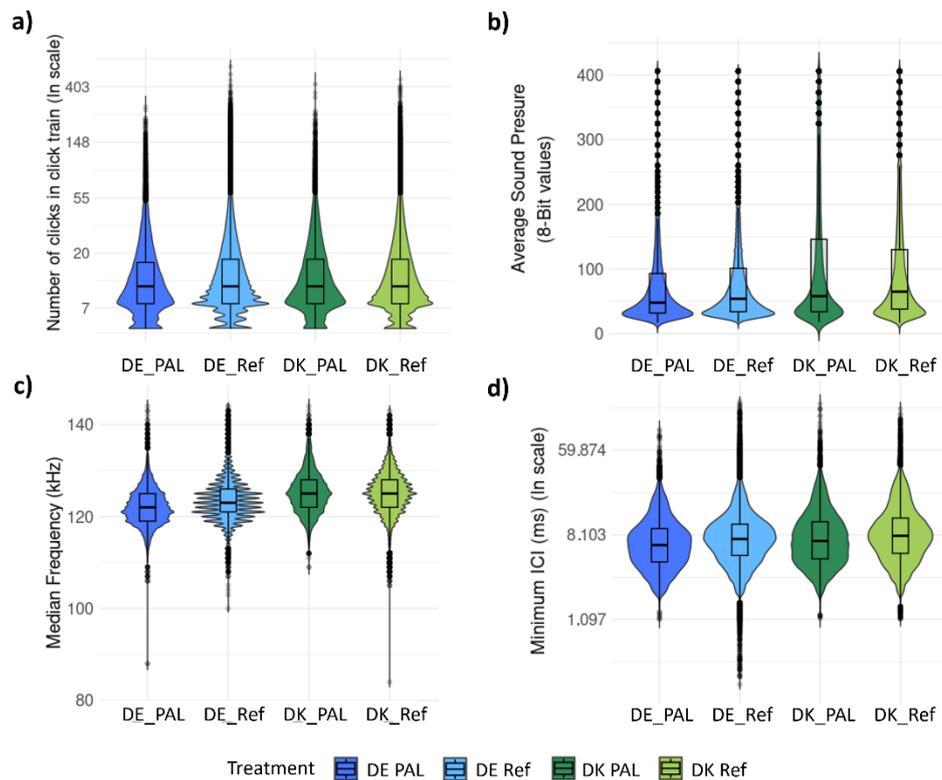


Figure 5.3. Violin plots illustrating the Kernel density of the four acoustic parameters on reference stations and near PAL-equipped nets in Germany (DE) and Denmark (DK). Median and interquartile ranges are indicated by the boxplot within the density plots. **a)** Number of clicks in a click train ($n_{ActualClx}$) (ln scale) (The Kernel density estimation used by violin plots shows some spread below five. Graph was cut at five, as click trains always have five or more clicks); **b)** median frequency of the click trains (kHz); **c)** average Sound Pressure (8-Bit values) of the click trains; **d)** Minimum Inter Click Interval of the train ($minICI_{us}$) log transformed (ms) (ln scale).

Gradient Boosting Model

Reference stations between Germany and Denmark could be somewhat separated with the XGBoost model showing an AUC of 0.655 which is higher than an AUC of 0.5 which represents random class distinction capacity. The feature contributing most to the classification model was the median frequency of the click train (SHAP: 0.277), followed by the minimum ICI and average sound pressure (**Figure 5.4.a**). A similar classification score was obtained for the model separating click trains detected near PAL-equipped nets between countries (AUC: 0.699). i.e., the classification capability of the model improved slightly compared to the reference stations model. The median frequency of the click trains was again the feature contributing most to the model (SHAP: 0.567).

The model aiming to separate click trains between reference stations and PAL-equipped nets within Denmark, showed almost no class separation capacity (AUC: 0.511). The capacity to differentiate click trains between reference stations and PAL-equipped nets in Germany was only slightly higher (AUC: 0.565) than in Denmark, but still suggest rather small differences between the click trains detected on PAL-equipped nets compared to the reference stations. The median frequency of the click train contributed most to the model prediction in Germany. The average sound pressure level and the minimum ICI followed in importance (**Figure 5.4.d**).

When pairwise models were trained to test how well the models could separate pairs of reference stations within countries, the mean AUC for Germany was 0.605 (range: 0.594 – 0.624) while the mean

AUC for Denmark was 0.522 (range: 0.500 – 0.568). These values indicate that already between reference stations within each country the machine learning models can find small differences which allow somewhat of a classification in Germany, and almost no classification of click trains in Denmark. Similar values were obtained when comparing fishers that set the PAL-equipped nets in Germany obtaining a mean AUC value of 0.554 (range: 0.508-0.575) and in Denmark with the mean value of the AUC being 0.507 (no range).

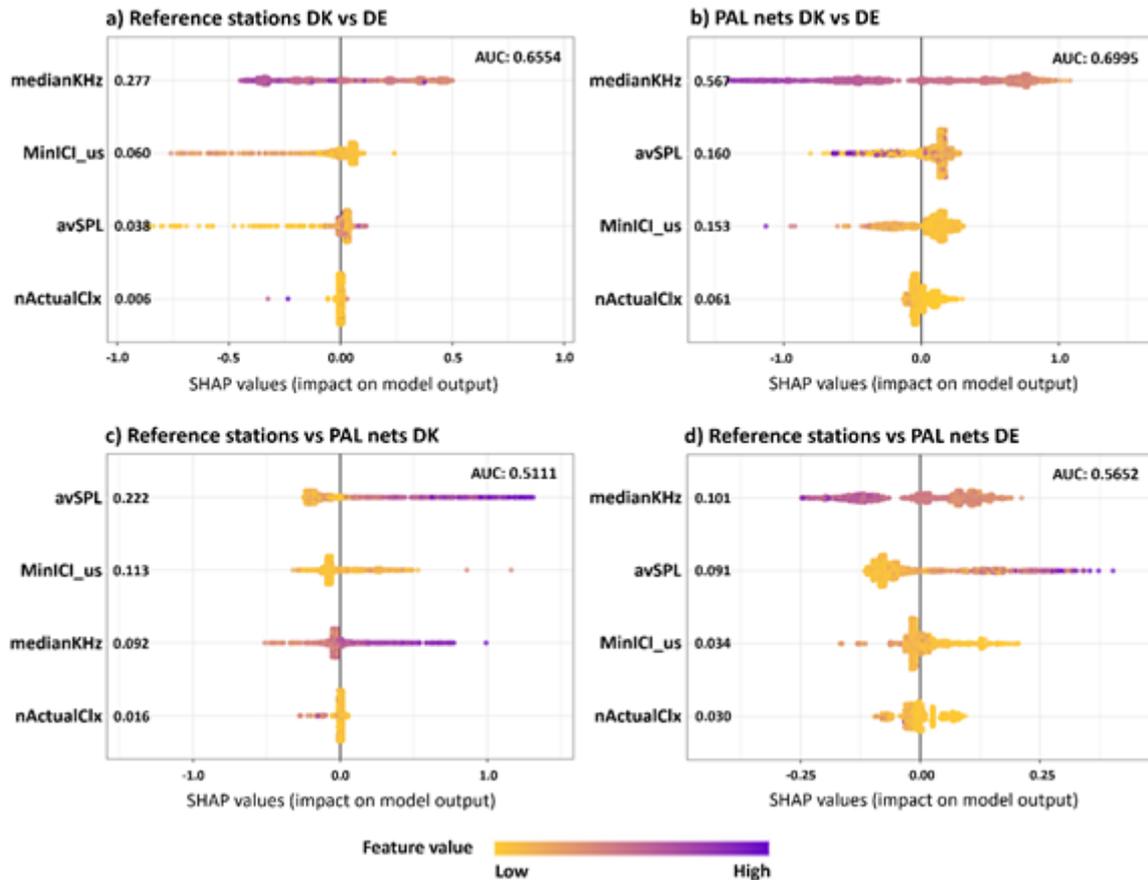


Figure 5.4. SHapley Additive exPlanations (SHAP) values in descending order by importance for model prediction to differentiating different groups between countries and within countries. For plots **a** and **b** the output predicted by the model is Germany, so feature values towards the right of the 0 indicate a positive effect on the prediction of the click train belonging to Germany. In the plots **c** and **d**, the output predicted by the model is PAL.

5.4. Discussion

The results from this study do not reveal a strong echolocation adaptation of harbour porpoises as a reaction to the PAL, whether in areas where PAL have not previously been deployed (Denmark) nor in areas where PAL have been in use since 2017 (Germany). Although non-parametric tests found statistically significant differences for all tested acoustic click train parameters, the effect sizes were consistently small (epsilon-squared < 0.04 in all but one of the cases where epsilon squared was 0.133) (Tomczak and Tomczak 2014). Similarly, machine learning models demonstrated low to moderate classification performance (AUC range: 0.51 - 0.69). The highest differences in echolocation were found across countries, both between reference and PAL-equipped nets. These small but detectable adaptations to individual areas within one population have not been reported previously and reveal information on harbour porpoise capability to adapt their click behaviour. The inter-country variability

was larger than the difference of echolocation parameters between reference stations and PAL-equipped nets within countries. In Denmark, porpoises did not exhibit a pronounced reaction to the PAL signal. Likewise, porpoises in Germany, despite prior exposure to PAL, did not show a clear deviation in their acoustic behavior compared to their Danish counterparts. These results provide no strong evidence of habituation to PAL signals in German waters despite comparably high sampling effort.

Non-parametric tests

It is well known that a large sample size will have a higher power to detect significant differences in statistic tests (Sullivan and Feinn 2012) which is why it is important to report the appropriate effect size together with the p-value (Tomczak and Tomczak 2014). This information is relevant in this study, as all KW tests showed significant differences although with small effect sizes, which indicates that the magnitude of the differences in the parameters were rather small in this context. In fact, the median values of all four parameters in this study vary just slightly between the countries and the reference stations and PAL-equipped nets.

The echolocation of porpoises without the influence of PAL was recorded on reference stations to rule out any potential underlying differences between animals in Germany and Denmark. Depending on the parameter of echolocation under focus it can be assumed that large variability is observed throughout geographic ranges within one population for instance due to specialized hunting behaviour (Schaffeld *et al.* 2016). The larger a dataset is, those variations diminish due to seasonal effects (Schaffeld *et al.* 2016). Therefore it was expected to find at least small to medium differences despite both areas being in the same population range (Schaffeld *et al.* 2016; Gallus *et al.* 2012; Zein *et al.* 2019). Hence it is not surprising that small differences were in fact found between Germany and Denmark on the reference stations which have to be taken into account when comparing the four acoustic parameters across countries near PAL-equipped nets. Indeed, differences detected near PAL-equipped nets in both countries followed a similar magnitude and trend as on the reference stations. Both in Germany and in Denmark, the echolocation parameters were generally slightly lower near PAL compared to the reference stations which can be indicative of a slight reaction of porpoises towards the PAL in both countries (**Table 5.1.**).

When comparing echolocation of porpoises near reference stations with those near PAL-equipped nets in Denmark, only small changes in median values were observed, which suggests that unexposed porpoises did not strongly adapt the investigated four acoustic parameters as a reaction of hearing or reacting to the PAL signal. The same magnitude of differences were also observed between reference stations and PAL-equipped nets in Germany. In both countries, median number of clicks per click train did only show very minor differences as a response to the PAL and was actually equal in median to the values recorded in the respective reference stations. The median frequency of the click train remained the same in Denmark near PAL-equipped nets as on the reference stations and did only decrease by 1 kHz near PAL-equipped nets in Germany. The median value of the minimum ICI in the click trains decreased by less than a millisecond in both countries near PAL-equipped nets. The largest differences were found on the average sound pressure which decreased by 11 Bits near PAL-equipped nets in Germany and by 10 Bits in Denmark which are also of minor relevance in a biological context.

Therefore, the differences detected in parameters are small and do not yield a lot of information in terms of biological implications. A reduced number of click per click trains recorded per hour was previously used to suggest habituation of porpoises towards a pinger (Kindt-Larsen *et al.* 2019), and reduced number of clicks per click train were also mentioned as a possible cause for lower echolocation rates in the presence of a pinger (Kraus *et al.* 1997). Our study did not show a variation in the median number of clicks per click train between reference stations and nets with PAL or between countries, thus a reaction towards the PAL or habituation could not be detected in our study based on this

parameter. The average sound pressure level recorded by the F-PODs can vary due to several factors such as the distance or directionality of clicks onto the recorder (Kyhn *et al.* 2013) as well as the intensity of the emitted clicks by the porpoise which can vary depending on habitat conditions (Dähne *et al.* 2020), noise in the environment (Kyhn *et al.* 2010) and distance to a target, for example prey items when porpoises are feeding next to the F-POD (Atem *et al.* 2009; Verfuss *et al.* 2009). In this study, the average sound pressure was lower near PAL-equipped nets compared to the reference stations in both countries. A possible explanation for this could be that porpoises stayed further away from the F-PODs due to the PAL signal. An increase in distance from the PAL was previously observed by (Culik *et al.* 2015). The PAL sound did not elicit a strong response in the median frequency of click trains in both countries. In fact, the difference between countries on the baseline echolocation was more pronounced than the reaction towards the PAL. Porpoises in Germany showed a 3 kHz lower median frequency compared to porpoises in Denmark. Significant variations in this magnitude of order have been detected for porpoises in the Baltic Sea compared to the North Sea in buzz and landmark sequences (Voß 2017). Lastly, the median value of the minimum ICI were lower near PAL-equipped nets compared to reference stations, but less than a millisecond in both countries compared to their baseline recorded on reference stations. ICI in harbour porpoise trains are highly variable (Koschinski *et al.* 2008) and a variation in ICI could have given an information about different behaviours conducted near PAL (e.g. feeding or communication). However, the small differences detected in this study do not indicate large behavioural changes in this context.

The median values of the four acoustic parameters varied in a similar range already between the single reference stations within the respective countries. This indicates that the four parameters already show differences within countries where reference stations were separated by only few kilometers.

Gradient Boosting model

The machine learning approach generally showed low to moderate classification performance (AUC < 0.69), indicating a limited ability to differentiate between groups based on the four selected acoustic parameters. The weakest classification was observed when distinguishing between reference stations and PAL-equipped nets in not previously exposed areas in Denmark (AUC: 0.511). This suggests that the model performed only slightly better than random chance, providing no indication of a clear adaptation in echolocation due to newly deployed PALs. Similarly, in Germany, where porpoises have previously been exposed to PAL, classification between reference stations and PAL-equipped nets was only slightly better (AUC: 0.565), and median values of acoustic parameters remained very similar. Interestingly, the machine learning model performed better when classifying porpoise echolocation data between countries, both at reference stations (AUC: 0.655) and near PAL-equipped nets (AUC: 0.699), although in a similar order of magnitude. In both cases, the median frequency of the click train contributed most to the classification performance (**Figure 5.4.**). The observed difference in median frequency between Germany and Denmark was 2 kHz at reference stations and 3 kHz near PAL-equipped nets, larger than the differences found within each country between reference stations and PAL-equipped nets, which explains the model's improved performance at distinguishing between countries. Such small but distinguishable adaptations to individual areas within one population have not been reported yet and may indicate that porpoises may have more capabilities to change their click behaviour than currently assumed. The minimum ICI and average sound pressure were the next most important features in separating groups between countries. While the median ICI varied by only 0.59 ms at reference stations and 0.64 ms near PAL-equipped nets, these differences were very small. Similarly, the median average sound pressure varied by 11 Bits between reference stations and 10 Bits between PAL-equipped nets, showing a comparable order of magnitude. Since baseline (reference stations) differences in echolocation parameters already existed between Germany and Denmark, the classification of PAL-equipped nets reflects most probably these pre-existing differences.

Habituation

Habituation, which can be defined as a decrement in a previously existing behavioural response resulting from repeated stimulation (Rankin *et al.* 2009) seems to be a general feature in the animal kingdom (Dawson *et al.* 2013) and is one of the main concerns for pinger use as a bycatch mitigation strategy (Kindt-Larsen *et al.* 2019). By definition, an initial reaction would have to precede a potential habituation to PAL. Looking at the four parameters that were tested in this study, porpoises in previously not exposed areas in Denmark did not show a strong reaction towards the PAL. This was also underlined as the classification capacity of the machine learning model was almost absent when separating click trains between reference stations and nets with PAL in Denmark. Similarly smaller values of each of the analyzed four acoustic parameters were observed for porpoises in Denmark and Germany, suggesting that both naïve and not-naïve porpoises react similarly to the PAL sound. It can be discussed whether all porpoises in the tested sites Denmark are naïve to PAL and all porpoises in Germany already had contact with PAL at least once, but the probability that a higher proportion of animals in Denmark was naïve is a given.

Evidence for habituation in German porpoises towards the PAL signal was thus not provided using the four parameters in this study. Absence of evidence is on the other hand not evidence of absence. In that sense, the results are based on a large dataset, showing significant but generally small differences, that are finally biologically more indicative of regional differences, than an echolocation reaction or habituation to PAL.

Habituation of porpoises towards pingers has been detected previously and described as increases in porpoise encounter rates after an initial drop (Kyhn *et al.* 2015), as a variation in the number of clicks per click train in an hour (Kindt-Larsen *et al.* 2019), as an increase in echolocation rate over time (Carlström *et al.* 2009) or as a decrease in distance towards a pinger after time (Cox *et al.* 2001). On the other hand, several studies have also concluded that no pinger habituation effect could be detected for harbour porpoises as for example temporal trends in bycatch rates did not vary over the years in gillnet fisheries in the Gulf of Maine (Palka *et al.* 2008) or in California-Oregon (Carretta and Barlow 2011), or as no differences in acoustic echolocation parameters could be found after prolonged pinger exposure (Kyhn *et al.* 2015; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021). It is possible that very intense stimuli may yield no significant observable response decrement (Rankin *et al.* 2009) which could be an explanation of why pingers, being a strong deterring sound, may not allow porpoises to habituate. In our study, a strong reaction of naïve porpoises towards the PAL was not detected using the four acoustic parameters and no clear evidence for habituation was detected when comparing the more naïve porpoises in Denmark to porpoises in Germany where PAL have been in use regularly since 2017.

Since habituation is an effect on individual level, our results cannot show completely convincingly that no habituation exists, but from a management perspective it is more important that i) porpoises are not deterred or change their echolocation drastically, which we could show and ii) that bycatch rate stays reduced, which was not the focus of our study. However, having a porpoise bycaught in Denmark one time agrees with the results by Chladek *et al.* (2020) reporting bycatch from all areas also in cases where PAL is deployed. Our study was not intended and cannot be used statistically to calculate bycatch rates. While habituation to pingers or PAL devices is a concern, it does not necessarily lead to increased bycatch if a residual deterrent or in the case of PAL attention effect continues to keep porpoises away from nets (Cox *et al.* 2001). In fact, if habituation reduces habitat exclusion without increasing bycatch, it may even be beneficial (Kindt-Larsen *et al.* 2019). Our results indicate that PALs using the porpoise like signal do not cause large-scale displacement. Further, PAL have previously been shown to reduce porpoise bycatch by 65 – 80 % in German and Danish fisheries in the Belt Sea (Chladek *et al.* 2020). Yet, to fully understand the long-term impact of PAL, a continued monitoring of porpoise bycatch rates would be essential. During such long-term monitoring in the Gulf of Maine (Palka *et al.*

2008) and along the California-Oregon coast (Carretta and Barlow 2011) no consistent increase in bycatch over time was detected with prolonged pinger use, supporting the idea that habituation does not necessarily compromise effectiveness. However, reliable bycatch monitoring requires accounting for fishing effort, fleet characteristics (Kindt-Larsen *et al.* 2023), population abundance, and bycatch rates (Glemarec *et al.* 2021).

Error sources

An automated filter was applied to remove artificial PAL signals as manual extraction was not feasible given the large dataset (8 800 hours) and the complexity of PAL emissions. While necessary, the filter introduced some error by excluding real porpoise signals due to a conservative threshold as well as wrongly attributing some PAL signals by retaining them as harbour porpoises. To ensure comparability, the filter was applied uniformly across all data, maintaining consistent bias across reference stations and PAL-equipped nets. Ideally, reference sites would have retained 100 % of porpoise detections with no misclassification. However, retention at reference stations ranged from 72.7 % to 90.5 %, indicating some loss of real porpoise signals. Additionally, 4 % (Germany) and 1.7 % (Denmark) of PAL signals were misclassified as porpoise clicks, affecting parameter calculations. These discrepancies highlight the filter's limitations but were consistent across datasets.

Further, only one PAL was attached to nets in Denmark, compared to the nets in Germany where PAL are mounted every 200 m for the entire length of the net. The sound field from several pingers might produce a different reaction in porpoises (Königson *et al.* 2021) and could have induced an error in our study. Despite this, nets in Denmark were equipped with only one PAL as it was prioritized to keep the porpoises in Denmark relatively naïve to the sound as long as possible. Further, only one F-POD could be given to each fisher, which means that the reaction to further set PAL would have not been covered by the F-POD due to their limited detection range. Fishers were asked to deploy the F-POD at one end of the net, so that the recorder was near to one PAL only to create similar recording conditions in both countries. Lastly, as in most field studies on harbor porpoises, this study does not track individual responses but instead reflects large scale patterns.

5.5. Conclusions

The four acoustic parameters analyzed in this study are influenced by multiple factors. A pronounced change in any of them would have indicated a reaction to the PAL in Denmark, while a difference between Denmark and Germany could have suggested habituation. However, no such clear and biologically relevant differences were detected. Detecting habituation in wild porpoises is however inherently challenging, and past studies using different methods have yielded varying results. Therefore, ideally, baseline data in terms of echolocation monitoring, but especially bycatch monitoring should always be collected before introducing new bycatch mitigation measures and reporting and hand over for pathological investigations of bycaught animals should always be implemented. However, delaying implementation of bycatch mitigation measures to also implement extended monitoring can be counterproductive when the primary goal is conservation of a declining population like the Belt Sea porpoises. This study provides an extensive dataset indicating that four echolocation parameters of porpoises' click trains do not show evidence of habituation to PAL. This is encouraging, as it indicates that PAL remains a viable long-term bycatch mitigation tool without long term displacement effects. However, we cannot directly link our acoustic findings to whether PAL still contributes to a sufficiently high reduction in bycatch of harbour porpoise in the western Baltic Sea. This is however necessary to fulfill the Marine Strategy Frameworks obligation for monitoring of human induced mortality within the descriptor 1, Marine Biodiversity, to ensure long-term viability of species' like porpoises and in general a good environmental status throughout European Waters. For this aim a reliable long-term bycatch monitoring program, using video surveillance or observer

schemes (ICES 2024c), in gillnet fisheries in Germany or where PALs or pingers are used, is suggested to provide a reliable basis for future conservation and management decisions.

5.6. Acknowledgments

We thank all part-time fishers in Germany and fishers in Denmark that participated in this study and helped in data collection as well as the Ostsee Info-Center in Eckernförde for their help establishing contact with fishers in Germany and their support throughout the trials. We further thank our colleagues Leon Rostock and Hannah Gasterstädt for their assistance going through the click train data and our colleagues Wolf-Christian Lewin and Christina Henseler for their support in statistical questions. We also thank the Deutsches Meeresmuseum, for their input during discussions about the project. We thank Chelonia Ltd. for support when questions about the F-POD software arose. This study was funded by the German Federal Agency for Nature Conservation (Bundesamt für Naturschutz, project no. FKZ 3521820700, PAL Nutzung in Deutschen Gewässern - Derzeitige Effizienz und Einsatz, PAL-CE).

5.7. Conflict of interest

Michael Dähne changed employers and now works for the funding body. He initially was the project lead for Meeresmuseum. He is not in charge of any project related tasks at the Federal Agency for Nature Conservation.

5.8. Authors contribution

T.M.D., C.v.D., M.D. & L.A.K. conceived and planned the experiment. T.M.D. and P.B.J. collected the data in the field. T.M.D., C.v.D., S.L., M.D., J.T. developed the theoretical framework of the paper. T.M.D. curated the data. T.M.D. and S.L. performed the analytic calculations. T.M.D. and S.L. created visualizations. T.M.D. took the lead in writing the manuscript. C.v.D., S.L., M.D., F.D. & P.B.J. provided feedback and discussed the results and contributed to the final manuscript. M.D. conceived the original idea. M.D. and C.v.D. supervised the project and raised the funding.

5.9. Supplementary material

Table S.5.1. Summary of acoustic parameters measured by reference stations in Germany. Kruskal-Wallis test (KW test) to look for differences between reference stations within Germany and Wilcox pairwise comparison to look for differences between the different pairs of reference stations in Germany. The effect size of the Kruskal-Wallis test was measured using Epsilon squared (E^2)⁵.

Parameter	Station name	Min	Max	Mean	Median	Q1-Q3 (IQR)	p- (KW test)	Effect size (E^2) ⁵	p - Wilcox (pairwise)
nActualClx	AS	5	577	16.2	11	8-18 (10)	2e-16	0.00473	All pairs: 2e-16
	LA	5	452	15.5	11	8-19 (9)			
	BoEck	5	322	17.9	13	9-20 (11)			
avSPL	AS	18	406	70.1	44	31-77 (46)	2e-16	0.0271	All pairs: 2e-16
	LA	18	406	87.6	56	36-109 (73)			
	BoEck	18	406	104.0	69	40-138 (98)			
medianKhz ⁶	AS	100	144	123	123	121-126 (5)	2e-16	0.0127	All pairs: 2e-16
	LA	103	144	123	123	120-125 (5)			
	BoEck	110	143	124	124	124-127 (6)			
MinICI_us	AS	0.237	153	8.0	6.78	4.53-9.72 (5.19)	2e-16	0.0122	All pairs: 2e-16
	LA	1.1	178	8.85	7.59	5.15-10.8 (5.6)			
	BoEck	0.354	144	9.34	7.75	5.71-11.0 (5.25)			

Table S.5.2. Summary of acoustic parameters measured by reference stations in Denmark. Kruskal-Wallis test (KW test) to look for differences between Ref stations within Denmark and Wilcox pairwise comparison to look for significant differences between the different pairs of reference stations. The effect size of the Kruskal-Wallis test was measured using Epsilon squared (E^2)⁵.

Parameter	Station name	Min	Max	Mean	Median	Q1-Q3 (IQR)	p- value (KW)	Effect size (E^2)	p - Wilcox (pairwise)
nActualClx	Palle 1	5	373	16.4	11	8-18 (10)	2e-16	0.00115	P1-P2: 0.13 P1-P3: 1.2e-10 P2-P3: 2e-16
	Palle 2	5	393	16.1	11	8-18 (10)			
	Palle 3	5	460	17.2	11	8-19 (11)			
avSPL	Palle 1	18	406	118.0	77	40-170 (130)	2e-16	0.00608	P1-P2: 2e-16 P1-P3: 2e-16 P2-P3: 0.25
	Palle 2	17	406	95.6	62	38-125 (87)			
	Palle 3	17	406	102.0	62	36-130 (94)			
medianKhz ⁶	Palle 1	84	141	125	125	122-127 (5)	2e-16	0.00371	P1-P2: 2e-16 P1-P3: 4.6e-09 P2-P3: 2e-16
	Palle 2	105	142	125	125	123-128 (5)			
	Palle 3	105	143	125	125	122-128 (6)			
MinICI_us	Palle 1	1.1	142	11.1	8.23	5.27-15.0 (9.69)	2e-16	0.0185	All pairs: 2e-16
	Palle 2	1.14	137	9.92	8.10	5.4-11.9 (6.46)			
	Palle 3	1.13	159	9.46	7.40	4.94-11.2 (6.26)			

⁵ Epsilon squared (E^2) coefficient which assumes the value from 0 (indicating no relationship) to 1 (indicating a perfect relationship) Tomczak and Tomczak 2014.

⁶ Kruskal-Wallis test was also used for mediankHz although it does not follow a normal distribution, because the criteria for homogeneity of variances was not met.

Table S.5.3. Summary of sampling effort and click trains detected in Germany (DE) and Denmark (DK) on fisher nets equipped with PAL and reference stations after applying the PAL filter (0.8 threshold).

Data	Description	Country	Spring 2023	Autumn 2023	Winter 23/24	Spring 2024	Total
PAL (Fisher nets with PAL)	Total nr click trains recorded (including PAL signals)	DE	310389	451321	78673	192766	1033149
		DK	391925	95977	223024	681845	1392771
	Nr click trains (after applying PAL filter (0.8 threshold))	DE	2171	3246	3588	23383	32388
		DK	18913	7019	680	3275	29887
	Sampling effort (days, 24 hours periods)	DE	60.19	18	47,86	57.74	183,79
		DK	110.73	14.89	23.75	35.7	185,07
	Click trains/day	DE	36.1	180.3	75.0	405.0	176,22
		DK	170.8	471.4	28.6	91.7	161,49
	Nr fishers	DE	3	4	4	4	3 - 4
		DK	4	2	3	2	2 - 4
Reference stations (no PAL)	Total nr click trains recorded	DE	137305	25127	179112	216142	557686
		DK	116244	12247	48361	10618	187470
	Nr click trains (after applying PAL filter (0.8 threshold))	DE	108273	22744	163563	193256	487836
		DK	92896	8906	38642	8448	148892
	Sampling effort (days)	DE	276	85	182	176	719
		DK	258	20	181	67	526
	Click trains/day	DE	392.3	267.6	898.7	1098.0	678,49
		DK	360.1	445.3	213.5	126.1	283,06
	Nr Reference Stations	DE	BE, AS, LA	BO	AS, LA	AS, LA	2 - 3
		DK	P1, P2, P3	P2, P3	P1, P2	P1, P2	2 - 3

Chapter 6

General discussion

6.1. Aim of the thesis

The aim of this thesis was to advance our knowledge on underlying mechanisms of harbour porpoise bycatch in static bottom set net fisheries and gaining more insight into the behaviour and reaction of harbour porpoises towards an alternative acoustic alerting device implemented in the Belt Sea, the PAL. It further looked at two land-based observation methods and assessed their advantages and shortcomings to observe small cetaceans. The research presented in the previous chapters thus addressed knowledge gaps in this research field in two main areas:

- i) It responds to the need to further investigate underlying behavioural factors that lead to entanglement of porpoises in fishing nets (Northridge *et al.* 2017; Larsen *et al.* 2021). Up to date, these have been relatively unexplored, especially through visual observation methods on wild animals. In an extensive study, porpoises were filmed for the first time in the wild near a bottom set net structure (Chapter 4). The new information inferred in Chapter 4 will be discussed in the frame of existing theories on why bycatch of porpoises occurs. This information gives new insights that could be relevant for the conservation of porpoises and potentially cetaceans worldwide.
- ii) This thesis further investigated the reaction of harbour porpoises towards the PAL, an alternative acoustic alerting device, that has been implemented in German fisheries on a voluntary basis since 2017 (OIC 2018). Up to date, only two research papers have been published on the effect of PAL on porpoises and their bycatch in the Belt Sea (Culik *et al.* 2015; Chladek *et al.* 2020). The behaviour of porpoises was analyzed near PAL through visual observations giving more insight into the spatial distribution of porpoises near the alerting device (Chapter 4). Chapter 5 further addressed concerns around habituation for the first time, looking at harbour porpoise echolocation near commercial fishing nets with PAL. The new information on the effect of PAL on harbour porpoises in the Belt Sea could be useful for decision making bodies and relevant stakeholders to consider the application or testing of PAL in further areas.

Further, within the thesis several methods were used, and Chapter 3 specifically gives guidance to choose between the theodolite and the drone in terms of their suitability to respond to different research questions. The application of the findings in Chapter 3 are not limited to the harbour porpoise but applicable in general on the observation of small cetaceans with near shore distribution.

In this section, the main findings of this thesis will be discussed in relation to already available knowledge, as well as looking out into future towards potential applications of the findings and management considerations.

6.2. Key findings

Behavioural findings of porpoises near a bottom set net structure

The presence of a net structure did not elicit a strong reaction in wild harbour porpoises. Porpoises were filmed for the first time in the wild near a modified bottom set net structure. The porpoises did not significantly adapt their swimming speed, respiration rates or echolocation when approaching and swimming over the net nor when swimming away from the net. Despite this, an increase in swim speed was observed as they approached the net followed by a decrease at around 25 m after the net. Further, porpoises avoided the net only in few occasions, while more often than not the porpoises swam over the floatline. Visual reaction towards the net such as turns or feeding activity were observed in close vicinity of the net.

Bycatch events are likely related to moments of distraction or curiosity. The fact that all porpoises were able to securely navigate the bottom set net suggests that they are able to make correct navigation decisions to avoid entanglement. Bycatch events could therefore potentially be accidents. Combining the findings with previous research it is suggested that a **combination of alerting strategies and net material enhancement may be necessary to reduce porpoise bycatch in set net fisheries.**

New findings around effect of PAL on the harbour porpoise

PAL attached to a bottom net did not elicit a strong reaction in wild harbour porpoises. Porpoises increased their swimming speed significantly as they approached the net with the PAL and decreased it again at around 25 m after the net. Further, changes in click train duration and minimum ICI were measured after they crossed the net with the PAL, potentially indicating a reaction towards the PAL. In any case, porpoises crossed the net swimming over the net with the PAL during all observed interactions and no avoidance attempts were observed. Visible reactions such as head movements or slight changes in swimming direction were observed in close vicinity of the net but at a greater mean distance than when only the net was present.

Porpoises considered naïve to the PAL signal did not strongly adapt selected echolocation parameters near commercial fishing nets with PAL. Porpoises in Denmark were considered more naïve to the PAL as PAL are not being used in the fishery in Denmark. Only slight variations were observed in the number of clicks in a click train, median frequency, average sound pressure and the minimum ICI of the click trains of porpoises in Denmark echolocating near PAL-equipped nets, compared to their baseline echolocation without PAL. This suggests that PAL did not elicit a strong echolocation reaction expressed in the investigated four acoustic parameters in more naïve porpoises in Denmark.

Evidence for habituation in German porpoises towards the PAL signal was not provided using the four parameters in this study. The reaction of more naïve porpoises in Denmark was used as control information to assess whether habituation towards the PAL had occurred in Germany, where porpoises have been exposed to the PAL signal since 2017. Both, naïve and not-naïve porpoises reacted similarly to the PAL sound when looking at the four acoustic parameters mentioned previously. Near PAL all parameters were slightly smaller in both countries compared to their reference stations without the PAL. Evidence for habituation in German porpoises towards the PAL signal could not be provided.

Methodological insights

Drones proved to be the more suitable instrument to study the behaviour of porpoises and their reaction towards the net and the PAL compared to the theodolite. A great advantage of drones is that they allow recording the behaviour of porpoises also below the surface, while the theodolite is limited to taking points when the animals are at the water surface. This makes the drone more suitable for behaviour studies or studies that assess the distance of approximation of porpoises to an object as this can occur under the water surface (detection function studies, pinger reaction studies, net reaction studies). With the new opportunities introduced by drones as a relatively accessible research tool for the observation of small odontocetes, the results suggest that some already inferred information that relies on theodolite measures should be reconsidered.

The accuracy of geographical coordinates collected with a theodolite and extracted from the GPS of the drone footage of porpoises at the surface is similar. Having this baseline on comparability between methods is relevant, especially when a field might be transitioning to a new technology, or to compare results from studies that addressed similar research questions through different methods.

6.3. Understanding bycatch: revisiting theories with new behavioural insight

Static nets, mainly gillnets, entangling and trammel nets, are associated with high bycatch mortality in marine mammals (Northridge *et al.* 2017) and bycatch in static nets is considered the most important threat to populations of small cetaceans (Lewinson *et al.* 2004; Read *et al.* 2006). In fact, static nets have contributed to the decline of populations of odontocetes worldwide (for a global meta-analysis see Sonne *et al.* (2024)) including porpoise populations (Rojas-Bracho *et al.* 2006; Carlén *et al.* 2021). Despite the impact of bycatch on populations and decades of effort to mitigate it, the issue of bycatch of odontocetes in static nets persists (Sonne *et al.* 2024). Further, the most obvious bycatch mitigation measures have already been tested (Northridge *et al.* 2017), yet a lack of understanding on why, when and where marine megafauna are bycaught continue to hinder the further development process of mitigation measures (Kastelein *et al.* 1995; Rihan 2010). It was therefore suggested that the research field of bycatch mitigation would benefit from investigations of underlying factors of bycatch, such as the behaviour of non-target species in relation to fishing gear (Northridge *et al.* 2017; Larsen *et al.* 2021). This is also the case for the harbour porpoise in the Western Baltic Sea. While there are several bycatch mitigation strategies in place, there is almost no knowledge about the exact circumstances of what causes bycatch and how it occurs. On-board observer programs, remote electronic monitoring or fishers self-reporting in logbooks provide information on the number and location of bycatch events, but not on how an entangling event takes place. This is mainly due to the fact that bycatch events are relatively infrequent and difficult to observe as they take place under the water surface. To address the knowledge gap concerning the behaviour of porpoises near set net structures, harbour porpoises were recorded for the first time in the wild near a bottom set net structure to analyze their behaviour near set nets (Chapter 4). Different theories have been formulated in the past on potential causes for bycatch (Section 1.5.) and are revisited here complementing them with newly gained behavioural insight for the harbour porpoise.

Low detectability of the nets

Harbour porpoises have been recorded near fishing nets previously without getting entangled (Macaulay *et al.* 2022; Maeda *et al.* 2021). Little information is available on the degree of interaction between porpoises and set bottom nets or porpoises behaviour around set nets in the wild. Chapter 4 revealed that porpoises did not actively avoid areas where a bottom set net structure was present. While porpoises generally swam over the net in a straight line without changing their swimming direction, in several occasions some behavioural patterns were exhibited that could be interpreted as reactions towards the net, such as head movements (so called head scans), slight turns to swim around the net or turning around. As some of these reactions can be categorized as avoidance behaviour (turning around, swimming around the edges of the net) it is probable that porpoises would try to avoid the net as soon as they detect it. The measured reaction distance towards the net where relatively close to the net (0.8 – 16.4 m, mean 5 m) which suggests that this is the distance in which porpoises may perceive and react to the nets (Chapter 4). The measured reaction distances are slightly below or within net detection distances calculated in previous studies which analyzing the acoustic beam and click intensity of porpoises (Kastelein *et al.* 2000; Mooney *et al.* 2004; Koschinski *et al.* 2006; Mooney *et al.* 2007). Porpoises detect and react to nets at close distances which in turn could be related to the low detectability of fishing nets (Larsen *et al.* 2007; Northridge *et al.* 2017). The observation of porpoises near fishing nets also revealed that porpoises did not increase their swimming speed greatly when approaching and crossing the nets (Chapter 4). This is advantageous because a higher swimming speed would cost them important decision-making time when navigating along a bottom set net. Despite close reaction distances, all porpoises recorded for Chapter 4 were able to successfully navigating the fishing net by either swimming over it, around it or turning around, suggesting, that the short distances provide enough time to respond to the presence of the net. Lastly,

Larsen *et al.* (2007) also suggested that porpoises might be well aware of nets but do not perceive them as hazards in which case increasing detectability of the nets may not reduce bycatch.

Echolocation beam orientation and echo masking effects

Harbour porpoises feeding near nets have previously been recorded acoustically (Maeda *et al.* 2021; Macaulay *et al.* 2022) with prolonged feeding events of up to an hour (Maeda *et al.* 2021) as well as in close proximity of less than 5 m from a net (Macaulay *et al.* 2022). Porpoises were recorded with a drone feeding in the vicinity of a bottom set net (within 30 m of the net) including two events of porpoises fastly approaching the net at less than 5 meters while potentially feeding on a prey item (Chapter 4). It is therefore confirmed through different methods, that porpoises actively feed close to fishing nets.

The analysis of stomach content of bycaught porpoises in the sink gillnet fishery in New Hampshire and South of Maine (USA) revealed that bycaught porpoises often had food remains in their stomach with intact fish, which was related to the idea that porpoises were feeding right before entanglement (Kraus *et al.* 1997). This also goes in hand with the theory that porpoises get entangled during activities in which their echolocation beam is not oriented towards the net such as for example while feeding on demersal species (Larsen *et al.* 2007). The stomach content of bycaught porpoises in the North Sea was composed of 98 % demersal fish species (IJseldijk *et al.* 2021) which can potentially be linked to demersal feeding before entanglement. During bottom grubbing, or bottom investigations, porpoises often take a vertical position in the water with their head down, close to the bottom, and their tail and flukes going upwards (Torres Ortiz *et al.* 2021). With the narrow echolocation beam of porpoises (Au *et al.* 2006; Koblitz *et al.* 2012) pointed towards the bottom while searching for demersal prey, porpoises might get entangled in a net set in close vicinity, because they recognize the net as an obstacle too late or not at all. Further, during experiments in captivity it has been measured that the narrow echolocation beam of porpoises is generally focused on an item while they are targeting a prey, which makes them 'blind' to echoes for surrounding objects (Kastelein *et al.* 1995). This can also occur when locked onto a different group member or nearby obstacle leading them to failing to detect the net (Larsen *et al.* 2021). This can lead to potential bycatch events in nets, if porpoises are hunting in close vicinity to the nets, such as recorded by Macaulay *et al.* (2022) or described in Chapter 4. In fact, during experiments in captivity, it was suggested that the presence of live fish near a set net in a distracted a porpoise increasing its chances of impact with a net (Kastelein *et al.* 1995).

Different causes which were addressed in the previous section can be linked to feeding activity in porpoises such as their echolocation beams not being directed towards the net or the presence of masked echoes and distractions due to prey items. While harbour porpoises are generally not suggested to feed on dead fish in nets, experiments in captivity have shown that harbour porpoises trying to detach dead fish from fishing nets (Kastelein *et al.* 1995). While pulling fish from the net, the net was observed to also be pulled towards the porpoise increasing chances of entanglement, not only for the porpoise pulling the fish, but also for a standby porpoise (**Figure 6.1.**). In fact, during observations within the controlled experiment, both porpoises attempted to pull dead fish from the net and got entangled during some attempts with their flukes. Porpoises had to be disentangled by a rescue team (Kastelein *et al.* 1995). Recent acoustic recordings (Macaulay *et al.* 2022) and visual observations (Chapter 4) have provided new evidence of wild porpoises feeding near fishing nets, highlighting potential consequences of this behavior. Combined with observations of entanglement in captivity, these findings suggest that feeding near nets increases the risk of accidental entanglement.

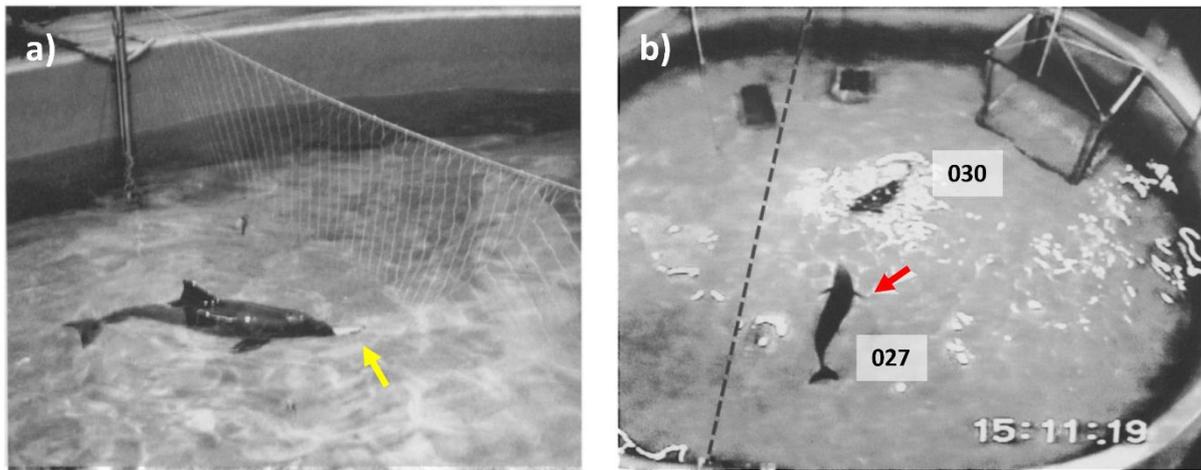


Figure 6.1. **a)** Harbour porpoise 030 pulling a dead herring (yellow arrow) attached to a net in a pool. The net is being pulled towards the porpoise together with the herring; **b)** Porpoise 030 pulling a fish from the net while porpoise 027 maneuvers near the net (dotted line), the extended pectoral fins (red arrow) of porpois 027 increase the chances of entanglement in the net pulled by porpoise 030. (Modified from Kastelein *et al.* 1995).

Distraction and navigation errors

Most porpoises recorded in Chapter 4 navigated the net efficiently by generally swimming over the floatline with only few porpoises avoiding the net by turning around or swimming around the net (Chapter 4). The lack of an apparent avoidance reaction could suggest that porpoises are used to encountering set bottom nets in their habitat. This can be the case, as set nets are regularly deployed in coastal areas within the distribution range of porpoises increasing the chances of regular encounters.

Porpoises were often observed crossing the net with calves, which shows that encounters with nets seems to occur already at an early age (Chapter 4). Despite this early introduction to fishing nets, confirmed bycatch records often have a bias towards juveniles. Between 1990 and 2015, fishers in Schleswig-Holstein and Mecklenburg-Western Pomerania (Germany, Baltic Sea) submitted 150 porpoise carcasses that had been bycaught in their fishing nets, the majority of the porpoises were less than three years of age (Siebert *et al.* 2006). Similarly, bycatch in static nets submitted by fishers in the North Sea, showed ten individuals to be juveniles compared to only two adult females (IJseldijk *et al.* 2021). Postmortem analysis have also shown that bycaught porpoises in the Baltic and North Sea were generally in good to moderate nutritional state (Siebert *et al.* 2006; IJseldijk *et al.* 2021) and were considered healthy, although some porpoises showed signs of disease or debilitation (IJseldijk *et al.* 2021) with some suffering from infectious diseases especially in the respiratory tract (Siebert *et al.* 2006).

The generally good health status and young age of bycaught porpoises, together with the observation of porpoises closely approaching a net and swimming over it without entanglement support the theory, that bycatch events might be accidents related to distraction (Cox and Read 2004). From a broader perspective, human wildlife conflicts often include mortality through accidents, such as wildlife vehicle collisions which are not intentional, often avoided by animals but with incidents occurring regularly (Sáenz-de-Santa-María and Tellería 2015; Abraham and Mumma 2021). Inexperience has also been associated with bird and aircraft collisions (Vaishnav *et al.* 2024). Similarly, distraction was identified as a primary human-factor affecting road traffic accidents despite most of us possessing a valid driving licence (Chand *et al.* 2021).

6.4. Developments in PAL research and comparison of PAL and pingers

A primary aim of this thesis was to broaden the existing knowledge on PAL. In this section we complement available information on PAL with newly obtained data and compare PAL as a bycatch mitigation tool for the harbour porpoise in the Belt Sea to traditional pingers.

PAL was developed as an alternative to traditional pingers for the Belt Sea and has been implemented in the German fishery since 2017 (OIC 2018). Pingers have shown to be effective at reducing harbour porpoise bycatch in static net fisheries worldwide (Kraus *et al.* 1997; Gearin *et al.* 2000; Palka *et al.* 2008; Carretta and Barlow 2011; Larsen and Eigaard 2014; Moan and Bjørge 2023; Lusseau *et al.* 2023) and are the most widely adopted bycatch mitigation strategy for small cetaceans (Omeyer *et al.* 2020). Despite this, concerns about potential habitat exclusion or displacement (Carlström *et al.* 2009; Kyhn *et al.* 2015; Larsen *et al.* 2021) and habituation (Cox *et al.* 2001; Larsen *et al.* 2021) have been raised. In this section PAL are compared to traditional pingers addressing two major concerns that have been raised around pingers: displacement and habituation. Further, and although this thesis did not quantify PAL's impact on reducing porpoise bycatch in the Belt Sea, it reviews previous findings on its bycatch reduction capacity in comparison to pingers to provide a more comprehensive picture.

Displacement and habitat exclusion

In this study, harbour porpoises were visually and acoustically recorded within hearing ranges of the PAL (Chapter 4 and 5) which is estimated to be between 90 - 320 m depending on the weather conditions (Chladek *et al.* 2020). Porpoises were even observed swimming over a modified bottom set net structure equipped with a PAL in several occasions during experimental trials in the Belt Sea in Denmark (Chapter 4). Porpoises were also frequently acoustically detected near nets with PAL during the regular commercial fishing activity in Germany and Denmark with only one recorded bycatch event during 8 800 hours of net deployment during the trials of this study (Chapter 5).

The observations made in this thesis support previous findings that measured only limited displacement of porpoises when PAL was active, with porpoises increasing their distance to the PAL by 32 m (from 131 to 163 m) (Culik *et al.* 2015). The absence of a strong displacement was considered a good sign as long as it would also be paired with effective bycatch reduction. Despite this, measurements by Culik *et al.* (2015) were made using a theodolite, thus only capturing positions of porpoises at the water surface. As seen in Chapter 3, more detailed information on the movement of porpoises under the water surface can be obtained through drone footage. As a matter of fact, Chladek (2022) suggested that habitat displacement remains an important aspect to be researched in order to confidently assess the expected effect of PAL. The findings in Chapter 4 respond to this question, as drone footage revealed that porpoises moved closer to the PAL than the 131 m previously measured by Culik *et al.* (2015). Porpoises were even observed swimming over a modified net with PAL. The fact that porpoises are not displaced by the signal emitted by PAL, is an important conservation advantage to pingers and responds to the concerns of potential habitat exclusion associated with traditional pingers (Carlström *et al.* 2009; Larsen *et al.* 2013; Kyhn *et al.* 2015).

In contrast, pingers have shown to affect the distribution of harbour porpoises in West Scotland (UK) by displacing them from the ensonified areas (Carlström *et al.* 2009) as well as in the Belt Sea (Denmark) (Kyhn *et al.* 2015) showing porpoise displacement ranges from 125 m (Laake *et al.* 1998), 200 m (Cox *et al.* 2001) and up to 380 m (Carlström *et al.* 2009). Considering that the position of set nets are not fixed, and that fishers often use different locations, the effect of pingers can affect the distribution of porpoises on a wide scale (Kyhn *et al.* 2015). The extent of the negative effect of habitat exclusion produced by pingers will depend on several factors such as the distribution of pingers, the effective range of the pingers and the availability for alternative habitats for porpoises (Larsen and

Eigaard 2014). In light of these concerns, it was suggested that alternative long-term solutions should be developed to avoid displacement, especially in critical areas (Carlström *et al.* 2009).

One limitation of the experimental set up in Chapter 4 was that the experimental design did not provide full visual coverage by drones on the entire area encompassed by the PAL (Chladek *et al.* 2020). The maximum flight height for drones flown under the A1/A3 open category is limited to 120 m above take off point (Regulation (EU) 2019/947) which in turn limited the recording frame of the drone to an area of approximately 80 m wide and 180 m long. At this altitude, it was challenging to identify porpoises in the footage, as the animals are rather small and their coloration is well adapted to the murky water of the Belt Sea, making it hard to find and follow them when analyzing the footage. Covering the full area encompassed by the PAL would have required at least four drones to be operated simultaneously which in turn would have required more resources to buy drones, getting a sufficient number of drone operators as well as other resources (e. g., charging capacity, data storage space, personnel for post-processing of footage). Due to these limitations, the information collected in Chapter 4 does not allow us to determine the number of porpoises that were deterred by the PAL sound at further distances, but reveals that at least some porpoises enter the area encompassed by the PAL and move in very close proximity of the net with the PAL.

To collect data for the analysis described in Chapter 3 and Chapter 4, a theodolite was used to track the surfacing positions of porpoises within the whole study area as well as around the net, with and without PAL in trials in Fyns Hoved (Denmark). This data provide some additional information on the distribution of porpoises around the net equipped with the PAL. It can be observed that porpoises entered the estimated hearing radius of PAL (approx. 200 m) (Chladek *et al.* 2020) (**Figure 6.2.**). The distribution of surfacing events within and around the 200 m area encompassed by the PAL are in agreement with the findings that suggest that PAL do not exclude porpoises from the areas encompassed by the PAL. The absence of a clear pattern of point distribution also suggests that a deterring effect is not produced elsewhere. This would nevertheless have to be further analyzed, looking at theodolite tracks for individual porpoise pods, to see whether porpoises turned around at some points suggesting aversion. **Figure 6.2.** only shows the aggregated data of surfacings for all sightings together and does not give information on individual or pod reactions towards the PAL or the net.

Habituation

Habituation is considered one of the most important concerns around pingers (Cox *et al.* 2001; Larsen *et al.* 2021) and was also suggested to be investigated for the PAL (Chladek *et al.* 2020). Habituation of harbour porpoises towards the PAL signal was studied for the first time (Chapter 5) after PAL have been implemented in German fisheries in Schleswig-Holstein in 2017 (OIC 2018). Echolocation baseline data of porpoises before the implementation of PAL was not recorded in Germany. Therefore, the study in Chapter 5 used the echolocation of porpoises in an area in Denmark where PAL has not been implemented previously as alternative baseline. Both areas are inhabited by porpoises from the Belt Sea, and while movement of porpoises between areas might occur, it is likely that a higher proportion of animals in Denmark are naïve to the PAL signal. Porpoises in Denmark did not show a strong reaction towards the PAL, with only minor decreases in average sound pressure and minimum ICI near PAL-equipped nets compared to their echolocation without PAL. As the response to PAL measured in the four click train parameters recorded by the F-PODs was similar in German porpoises to that of porpoises in Denmark, this study did not provide evidence of habituation to the PAL signal in German porpoises.

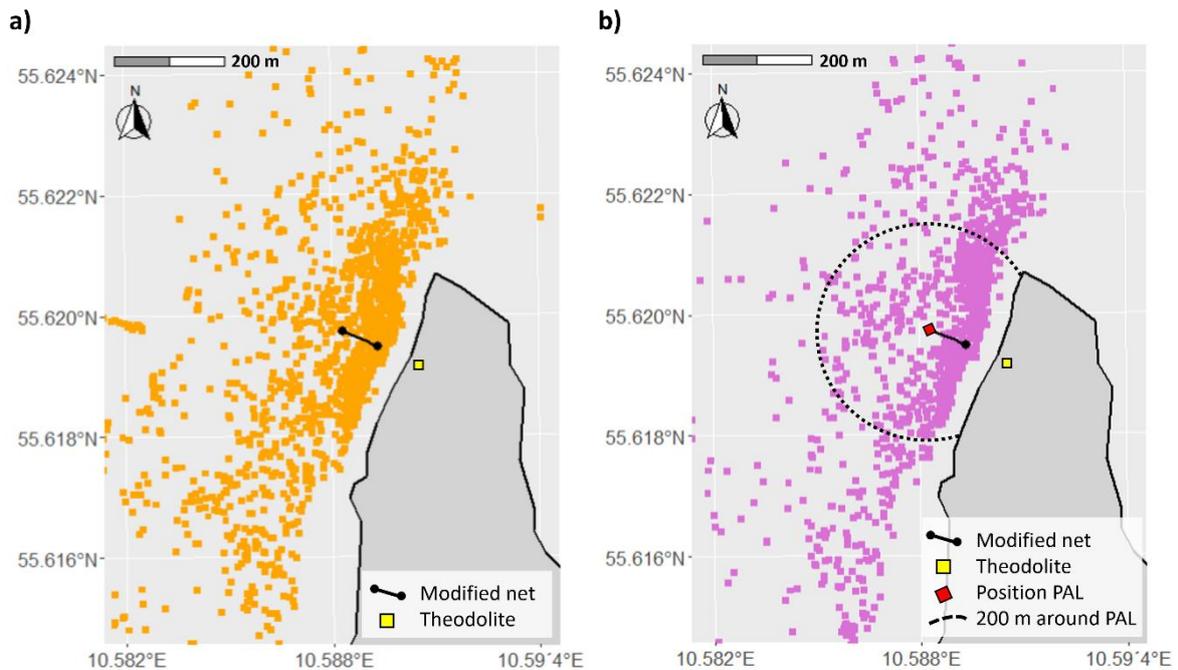


Figure 6.2. a) Harbour porpoise surfacing positions recorded with the theodolite when only the modified net was in the water. A total of 1762 surfacings were recorded over 19 sampling days during the 2022 field campaign. These 19 days were randomly selected from 31 net treatment days to provide a weighted comparison with the sampling size of PAL treatment days; b) harbour porpoise surfacing positions recorded with the theodolite when the modified net with PAL was in the water. 1276 surfacings were recorded during 19 sample days during the field campaign in 2022. Study area Fyns Hoved (Denmark).

The acoustic reaction of porpoises towards the PAL was also recorded during the net interaction trials described in Chapter 4. While no significant differences were found in the number of clicks per two minute period of individuals before and after crossing the net with the PAL, the number of clicks were slightly higher in the two minute period before swimming over the net compared to the two minute period after swimming over the net, which could indicate some increased exploration of the net before swimming over it. The duration of the click trains in milliseconds and the minimum ICI were both significantly shorter after the porpoises had crossed the net with the PAL compared to before the crossing giving some further evidence towards echolocation adaptation in porpoises in the presence of the PAL (Chapter 4). In fact, reduced minimum ICI were also detected near commercial fishing nets with PAL compared to their baseline echolocation without PAL in both countries (Germany and Denmark) (Chapter 5). This suggests that the PAL has an effect on this click train parameter and further exploration could be of interest. Variations in ICI could be attributed to porpoises exploring the area in anticipation of a new target at different distances (Koschinski *et al.* 2008). Results on habituation of harbour porpoises to normal pingers show both, absence of habituation (Palka *et al.* 2008; Carretta and Barlow 2011; Kyhn *et al.* 2015; Larsen *et al.* 2021; Königson *et al.* 2021) as well as some evidence for habituations (Cox *et al.* 2001; Carlström *et al.* 2009; Kyhn *et al.* 2015; Kindt-Larsen *et al.* 2019; Teilmann *et al.* 2006).

There are a few considerations to be made when assessing and interpreting habituation which can also play a role in future habituation experiments towards pingers and the PAL. For example, although individual repeatability is often assumed in habituation studies (Díaz *et al.* 2013), reactions have not been equal across group members of chacma baboons (*Papio ursinus*) when their habituation towards humans approaching them was studied (Allan *et al.* 2020). Differences in individual reactions towards

pinger-like sounds were also observed between two porpoises in captivity (Teilmann *et al.* 2006) which could suggest variability also in the wild.

Moreover, generally habituation studies are response-centric as they concentrate on measuring a single-response metric or a limited amount without considering other components of behaviour, which provides an incomplete picture of the overall behaviour (Ardiel *et al.* 2017). In the case of studies of habituation to pingers, differing results may be related to the various approaches of measuring habituation: among those are, long-term fisheries bycatch monitoring schemes (Palka *et al.* 2008; Carretta and Barlow 2011); assessing approach distances to pingers over time observed either visually (Cox *et al.* 2001) or based on passive acoustic monitoring (Kyhn *et al.* 2015; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021); behavioural and physiological responses to pingers (Teilmann *et al.* 2006), variations in echolocation activity (Carlström *et al.* 2009; Kyhn *et al.* 2015; Kindt-Larsen *et al.* 2019; Königson *et al.* 2021) or looking at particular acoustic parameters of porpoises as a response to pingers (Kindt-Larsen *et al.* 2019; Chapter 5). Besides different methods, it is also possible that some parameters are more suitable for detecting habituation than others or that they would have to be combined to get the full picture. As a matter of fact, while in the study presented in Chapter 5 no habituation was detected using the four selected click train parameters, it could be possible that the parameters are inadequate to detect or describe habituation. This was the first time that three of the click train parameters (median frequency of a click train, average sound pressure and minimum ICI) were used to test for potential habituation towards an acoustic signal in harbour porpoises. The four parameters used in the study were selected based on a bibliographic review and considering expert knowledge (Michael Dähne and Jakob Tougaard, pers. comm., 2024). When PAL was first tested, a 10 % increase in click rate of porpoises near PAL was observed (Culik *et al.* 2015). The same parameter was not used in Chapter 5 as the experimental set up did not allow accounting for differences in harbour porpoise density between Denmark and Germany or between net setting spots of the fishers within countries, which might have affected the click activity. The study prioritized recording porpoises near real fishing nets with PAL in both countries and in contrast take a higher variability of environmental factors into account that could not be controlled. Click train properties were thus considered more suitable to look for echolocation reactions as they are more independent on the abundance of porpoises.

Lastly, and although habituation is generally described as the prototypical example of non-associative learning (learning independent of the context), different examples from humans, non-human mammals, birds and invertebrates have shown that habituation can be context specific (Dissegna *et al.* 2021). A lot of variables are often suggested to play a role in bycatch events such as gear types, mesh size, hanging ratio, soak times as well as environmental factors such as noise and topography (Northridge *et al.* 2017). The context specific habituation effect could also be a potential explanation on why the same pinger type revealed different habituation results depending on the area in one study (Kindt-Larsen *et al.* 2019), or that the bycatch reduction capacity of the same pinger showed an order of magnitude difference in the same study between different net types (wreck fishery and flat bottom/stony ground fishery) (Larsen and Eigaard 2014). In Chapter 5, porpoises did not show a country specific reaction to PAL when analyzing the four selected click train parameters.

In general, studies on habituation towards bycatch mitigation strategies often emerge as a response to a lack of information on the performance of the mitigation strategy in terms of bycatch estimations in the real fishery where it is employed. As described in this section, it is nevertheless challenging to assess whether habituation is occurring. The fact that even the same instruments can provide different results adds to the scientific challenge. A final conclusion regarding habituation should therefore be interpreted with caution, and the findings of this study could not be extrapolated to a final answer to the question whether PAL is still effective after several years of use.

Bycatch mitigation efficiency

During the only experimental test conducted to date to estimate the bycatch reduction effect of PAL, it was shown that PAL significantly reduce harbour porpoise bycatch by up to nearly 80 % in the German and Danish Belt Sea gillnet fishery (Chladek *et al.* 2020). Application of pingers in bottom set net fisheries around the world have shown to significantly reduce the bycatch of harbour porpoises with estimated reduction rates between 67 and 100 % for different areas such as in the Norwegian commercial gillnet fisheries (Moan and Bjørge 2023), the Danish North Sea (Larsen and Eigaard 2014), the salmon gillnet fishery in Northern Washington (Gearin *et al.* 2000), and the commercial sink gillnet fishery in New Hampshire and southern Maine (Kraus *et al.* 1997). In two of the longest bycatch monitoring studies conducted in commercial fisheries, the effect of pingers was lower than those obtained in dedicated field experiments. For example, the swordfish and thresher shark driftnet fishery in California was monitored between 1990 and 2009 and the effect of the introduction of pingers in 1996 indicated bycatch reduction rates of cetaceans (dolphins and porpoises) of 50% (Carretta and Barlow 2011). At the same time, between 1999 and 2007 the US Northeast gillnet fishery was also monitored, showing a reduction of harbour porpoise bycatch of 50 – 70% due to pinger introduction (Palka *et al.* 2008). In both long-term studies, there was no evidence for temporal trends in the bycatch rates, suggesting that the lower bycatch rates were not related to habituation (Carretta and Barlow 2011; Palka *et al.* 2008).

Palka *et al.* (2008) estimated bycatch reduction rates in the US Northeast gillnet fishery during a controlled experiment and compared it to the bycatch reduction effect measured in real fisheries. The reduction during the controlled experiment was of 92 % compared to the lower 50 - 70 % achieved during long term operational fishery. This difference was attributed to the real fishery employing a larger variety of fishing nets with different mesh sizes which might have influenced pinger effectiveness (Palka *et al.* 2008). Targeted experiments thus might overestimate the efficiency of pingers (and the PAL) due to an oversimplification of real fisheries conditions which often show a larger variation in mesh sizes, areas of deployment as well as environmental conditions (Palka *et al.* 2008).

The potential of oversimplification influencing results in experimental set ups should be considered and calls for long-term monitoring approaches in the real fishery to reveal the real efficiency of instruments in reducing porpoise bycatch. In any case, the bycatch reduction estimation of PAL in the Belt Sea is comparable and within ranges of bycatch mitigation rates of traditional pingers during dedicated studies.

6.5. Methodological contributions to small cetacean research

During this thesis several methods were employed to study different aspects of harbour porpoise behaviour. A theodolite and drones were used for land-based observations while click-detectors (F-PODs) were used for underwater recording of the echolocation of porpoises. All of these methods are well suited for behavioural observations of porpoises and small cetaceans as they allow to record the undisturbed 'natural behaviour' when properly used (Piwetz *et al.* 2018; Aniceto *et al.* 2018).

In Chapter 3 the advantages and shortcomings of the theodolite and the drones were discussed and recommendations were made towards method selection for different research aims for land-based observations. These findings are based on the observation of the harbour porpoise which is particularly challenging due to its inconspicuous nature (Aniceto *et al.* 2018) but more importantly, are transferable to small cetaceans with near shore distribution. This is the first study that compares the performance of the two land-based observation methods in the context of small cetacean observations and provides evidence-based guidance for researchers to select a method when looking at: group-size estimations, behavioural observations and location data on a small and broader scale (Chapter 3). A

similar study comparing the efficiency of drones with boat-based surveys during the observation of bottlenose dolphins (*Tursiops truncatus*) was previously carried out with a similar aim (Fetterplace *et al.* 2023). Furthermore, since the theodolite has been a standard tool for recording marine mammal positions since the 1970s (Piwetz *et al.* 2018), the results in Chapter 3 confirm that its positional accuracy is comparable to GPS data from drones. This establishes a baseline for comparing research conducted using both methods.

Based on the findings in Chapter 3, drones were used to study the behaviour of porpoises near a bottom set net structure in Chapter 4. This was the first time porpoises were filmed in the wild near a modified bottom set net structure. The effort involved to obtain the data for this chapter was extensive counting with 687 effective observation hours during two summer campaigns in which 1 029 harbour porpoise pods (pod sizes between one and six porpoises) were observed within or in the vicinity of the study area. Despite the elevated number of porpoise sightings, only 140 interactions of porpoises with the modified net (or control treatment without the net) were recorded with drones, out of which 88 sightings were classified as suitable for the analysis. The low number was mainly related to the scarcity of events in which porpoises approached the experimental set up exactly where the 50 m net was set out, as well as due to missed interactions due to delay of drones being flown into position. To solve the latter problem of missing interactions, it was decided to permanently fly a drone recording the modified net during the observation hours. The scale of this effort is indicative of the challenges of conducting drone-based behavioural studies on wild porpoises near fishing nets and underscores the scarcity of research examining behavioural causes that lead to bycatch through visual observations (Northridge *et al.* 2017). It further underlines the uniqueness of the effort presented in Chapter 4. In any case, Chapter 4 presents a methodology that can be used to record reactions of rather large marine species in coastal areas towards different items (e.g. mitigation tools, structures in the water). Such studies can be important to further broaden our understanding of bycatch mechanisms of small cetaceans and their reaction to mitigation strategies (Larsen *et al.* 2021).

Additionally to the effort collecting data, a big challenge in Chapter 4 was processing the drone footage after data collection. The drone footage required multiple visualizations to detect net interactions, as identifying porpoises was challenging due to their small size and coloration blending with the murky water as drones recorded from 120 m altitude. Further, extracting GPS coordinates from the footage was also carried out manually using the CetTrack app. Future research using drone imagery could benefit from automated image recognition and artificial intelligence, as demonstrated in applications such as marine mammal monitoring with satellite images (Khan *et al.* 2023) and automated cetacean photo identification (Maglietta *et al.* 2022). Artificial intelligence was not explored to help processing the data in Chapter 4.

The advantages of artificial intelligence, specifically the subset of machine learning, were utilized in Chapter 5 of this thesis. A main challenge in this chapter was the differentiation of the narrow-band high-frequency PAL signals from narrow-band high-frequency signals of real porpoises in the data. To automate the filtering task, a binary classification model was developed to identify PAL signals and to filter the data. This procedure allowed working with a larger data set than it would have been possible if the PAL signal had to be extracted manually in the same amount of time. A machine learning algorithm was also used to complement the traditional statistical approach of data analysis in Chapter 5, which helped testing more complex interactions between acoustic parameters. While statistical approaches are able to include four acoustic parameters, the difficulty of analysis and interpretation increases with a growing number of included factors. This shows one advantage of machine learning in complex data situations and allowed exploring the acoustic data in Chapter 5 with a second approach complementing the conventional statistics. This is especially relevant, when working with passive acoustic monitoring data which often involves large data volumes that ideally require reliable

automated classification tools (Ivanchikova and Tregenza 2023). The study in Chapter 5 shows one approach that can be considered when processing large acoustic data volumes as those often obtained when using F-PODs. In fact, the application of artificial intelligence has been progressively growing and has already been applied in research on echolocation of odontocetes and other marine species. A semi-automatic deep learning approach was used to rapidly extract contours from audio recordings of wild free-ranging short-beaked common dolphins (*Delphinus delphis*) providing the first characterization of whistle features for a population in the Bay of Biscay (Lehnhoff *et al.* pre-print). An automatic identification algorithm was also presented to identify the critically endangered Yangtze finless porpoise (*Neophocaena asiaorientalis*) (Song *et al.* 2015). Artificial intelligence has also been applied to analyze vocal repertoires of other marine mammals such as the application of neural networks to detect and classify for manatee calls (Schneider *et al.* 2024) or bearded seal vocalizations (Escobar-Amado *et al.* 2022).

Collaboration with the field of machine learning and artificial intelligence are encouraged to be explored to study more complex relationships in data, and to help processing data that is otherwise time and labor intensive such as manually filtering acoustic signals from a data set (Chapter 5) or visually screening hours of drone footage (Chapter 4).

6.6. Management implications and future research directions

In this thesis two targeted experiments were conducted to increase our understanding on the behaviour of porpoises near nets and the PAL as well as the effect of PAL on harbour porpoises in the Belt Sea. The two main findings revealed that PAL seems not to displace porpoises from their habitat and indications for habituation in Germany could not be detected looking at four acoustic click train parameters. Considering that bycatch reduction rates measured with PAL are similar to those of traditional pingers, suggests that PAL should be considered as an alternative to pingers in the Belt Sea. In this section some considerations for the further use of PAL and research directions are discussed. It further addresses that the implementation of PAL should be accompanied by a long-term monitoring scheme including dedicated studies, to understand if the measured bycatch reduction efficiency persists over time, on a larger scale and in the different types (métiers) of fishing with nets.

PAL for other areas

A comprehensive bycatch mitigation study using the so-called Porpoise-PAL that is programmed with a specific harbour porpoise communication (F3) signal was only conducted one time in the Belt Sea (Chladek *et al.* 2020). The F3 signal was selected after a dedicated experiment in which three synthetic porpoise signals were tested analyzing the echolocation activity of porpoises as well as the displacement from the PAL (Culik *et al.* 2015). The F3 signal produced an increase in click activity in wild porpoises and had only a slight deterring effect with porpoises increasing their distance to the PAL by a 32 m (Culik *et al.* 2015). The increased click activity was suggested to potentially reduce bycatch of porpoises by increasing awareness due to enhanced echolocation (Culik *et al.* 2015). It has to be considered that the F3 signal was recorded from a female porpoise in captivity, stemming from the Belt Sea population. A preliminary trial using PAL with this signal was conducted in Iceland (Iceland Sea, Atlantic Ocean) where PAL did not significantly reduce the bycatch rate of porpoises (ICES 2018). Although the Icelandic study was only limited in time and extent, it can be inferred that prior to an implementation in the fisheries, the PAL should be tested in areas outside of the Belt Sea, and ideally should be programmed with a sound of the respective (sub-)population whose suitability has ideally been tested in advance through (field) trials. (Chladek 2022). It is nevertheless challenging to identify specific sounds of porpoises to be used to programme PAL as it ideally requires the observation of the behaviour of porpoises that accompanies the sound, similarly to the set up by Clausen *et al.* (2011). For species or (sub-)populations without trained or captive individuals, different sounds from wild

porpoises could be recorded through passive acoustic monitoring. These sounds would then have to be tested in the field or captivity, or linked to different observed behaviour or reactions to other individuals. With the broad repertoire of sounds that porpoises can produce (Clausen *et al.* 2011; Sorensen and Vermeiren 2018) testing different sounds under experimental conditions requires a large effort.

If PAL were to be proposed as a mitigation tool for the critically endangered Baltic Proper population in the Baltic Sea, its effectiveness would have to be studied first as it is a different population to the Belt Sea (Wiemann *et al.* 2010; Sveegaard *et al.* 2011; Galatius *et al.* 2012). However, a zero mortality threshold has been agreed upon for the Baltic Proper porpoise (HELCOM, 2023). Therefore, traditional pingers are not recommended as bycatch mitigation tool for the Baltic Proper population (Rogan *et al.* 2021) as they have proven to reduce bycatch but not to eliminate bycatch completely (Dawson *et al.* 2013). As bycatch reduction rates achieved with PAL are below 100% (Chladek *et al.* 2020) it is at this point not recommended to test nor implement the PAL as mitigation tool for the Baltic Proper population.

It could also be considered to use a more generic sound to programme the PAL that might be more comprehensive and be applied more generically. For example, the CETSAVER-DOLPHINFREE is a bio-inspired acoustic beacon prototype designed to inform common dolphins (*Delphinus delphis*) of the presence of a fishing net (Lehnhoff *et al.* 2022). Instead of emitting a dolphin's echolocation sound, it plays back the "returning echoes" that were recorded from a common dolphin's echolocation clicks reflecting off a fishing net and of a fishing net with an entangled dolphin (Lehnhoff *et al.* 2022). Similarly to PAL, this bio-inspired beacon was also developed as a response to the noise pollution produced by pingers and the diverse results obtained from bycatch mitigation studies (Lehnhoff *et al.* 2022). As a response to the CETSAVER-DOLPHINFREE, common dolphins increased their acoustic activity (echolocation clicks and whistles) when the bio-inspired beacon was on, and visual observations revealed attentive behaviour by the dolphins while keeping their distance from the beacon (Lehnhoff *et al.* 2022). It was thus suggested that the bio-inspired beacon signals the presence of fishing nets to common dolphins and has the potential to limit their bycatch, although this latter still has to be tested in the commercial fishery (Lehnhoff *et al.* 2022). This more generalized approach of emitting the echoes produced by a species onto a net seems less complicated than isolating aggressive or warning signals for different populations and species, allowing alerting devices to be species specific while reducing potential displacements and noise pollution. The CETSAVER-DOLPHINFREE is under further development and aims to include passive listening to only activate echo sounds when dolphins are present to reduce noise pollution (Lehnhoff *et al.* 2022).

Combination of PAL with other mitigation strategies

Considering distraction as a potential leading cause for porpoise bycatch, alarming or alerting devices could be a good solution to increase awareness. As the PAL does not completely eliminate the bycatch of porpoises, it was suggested to combine acoustic alerting devices with other measures such as net material enhancement to also increase the visibility of the nets (Larsen *et al.*, 2007; Chladek 2022; Chapter 4). Combining alerting devices with net material enhancements could increase detection while also compensate increased bycatch rates observed due to pinger failure (Carretta and Barlow 2011; Palka *et al.* 2008). Pingers can stop working for several reasons including expired batteries, physical damage from fishing operations or water intrusion (Carretta and Barlow 2011). Fishing strings with more than one non-functional pingers of all pingers in the net were detected to have higher bycatch rates than nets with a fully functioning set of pingers (Carretta and Barlow 2011), while Palka *et al.* (2008) even observed that bycatch rates in nets with some pingers that did not work were higher than rates in nets without any pingers at all. A potential explanation for higher bycatch rates in sets with malfunctioning pingers is that porpoises might interpret the gap in pingers sound to be a gap in the

net and try to swim through it (Palka *et al.* 2008). Magnitudes of pinger failure were in the dimensions of 3.7 % (Carretta and Barlow 2011) and 13 % (Palka *et al.* 2008) of fishing sets. During bycatch trials with PAL it was also observed that an increase in the suggested spacing of PAL led to lower bycatch reduction estimates of 64.9 % (spacing > 200 m) compared to the 79.7 % (spacing ≤ 200 m) (Chladek *et al.* 2020). Pinger spacing has also shown to influence the bycatch rates of harbour porpoises in the Danish North Sea (Kindt-Larsen *et al.* pre-print). Enhanced net material could compensate the effect of pinger failure by making the net more visible in potential gaps, as an increased perception was mentioned as the main driver behind reduced bycatch rates of harbour porpoises in trials with enhanced net materials (Trippel *et al.* 2003; Kratzer *et al.* 2021). The success of the combination of the methods would have to be tested, but findings in this thesis support this approach.

In any case, implementation of pingers is already associated with a cost and this cost will even increase if this mitigation strategy is to be combined with net enhancing materials. This makes both pingers, and even more so the combination of pingers with net enhancing material, a viable option only under a certain socio-economic condition, being less of a feasible option for many small scale fisheries in developing countries worldwide even with initial subsidies (Dawson and Lusseau 2013). For example, the cost of pingers was addressed as a challenge in the Peruvian small-scale driftnet fleet where porpoises are often bycaught (Mangel *et al.* 2013). Further investigations should thus also focus on more cost-effective strategies to reduce the bycatch of harbour porpoise and other small cetacean species in static net fisheries, as it is one of the most widely used fishing gears in coastal areas worldwide (Suuronen *et al.* 2012), while at the same time causing the highest bycatch rates of small cetaceans (Lewinson *et al.* 2004). If the bycatch issue around bottom set nets remains and continues to threaten populations, it should be considered to use alternative gears that substitute bottom set nets altogether.

PAL and Passive acoustic monitoring

Passive Acoustic Monitoring (PAM) is often used in the study of odontocetes as it allows for long-term monitoring and extensive bibliography is available. Despite this, PAM data often involves large data volumes that require reliable automated classification tools (Ivanchikova and Tregenza 2023). At present, signals of interest are generally detected through visual inspection of spectrograms (Song *et al.* 2015) which is time consuming. During Chapter 5 of this thesis click-detectors (F-POD) were used to record harbour porpoises near fishing nets with PAL. The main challenge when processing the data recorded on the F-POD was to filter out the narrow-band high-frequency signal programmed in the PAL, to separate it from the narrow-band high-frequency signals from real harbour porpoises. It is possible to filter out the PAL signals based on visually checking the spectrograms in the F-POD app, but this is an extremely time consuming task. An automated filter was therefore developed to support the filtering process, but the filter was not able to exclude all PAL signals from the data and showed less efficiency in recognizing weaker signals, coming from distant PALs (Chapter 5).

The distribution, habitat use and density of harbour porpoises in the Belt Sea have been previously estimated using PODs (SAMBAH 2016) and are currently being investigated using F-PODs (HaMoNa Project, Project Number. 3522520300). If nets with PAL are set near F-PODs used for monitoring, the narrow-band high-frequency signal could either drastically falsify the estimations or causing the need for resource consuming PAL signal filtering efforts. This problem is particularly caused and exacerbated by the fact that PAL emit signals randomly emitting an average of 5.5 signals/minute (Chladek *et al.* 2020), thus fulfilling the requirements for acoustic deterrent devices set in (Regulation (EU) 2019/1241). A solution for this could be to add a watermark to the PAL signal to allow for automated filtering. This will be especially relevant if the implementation area of PAL would increase in the Belt Sea. However, this presents a conflict between preventing bycatch and the need to monitor porpoises in the Belt Sea.

Management implications

Although assessing the continued effectiveness of PAL in reducing bycatch was not the aim of this thesis, the results do not provide a definitive answer to this question. The previously estimated bycatch reduction rates during a field experiment in the Belt Sea were based on three full-time commercial fishing vessels measuring bycatch rates over two years (Chladek *et al.* 2020). In any case, as suggested previously by Palka *et al.* (2008), there remains the risk that the bycatch reduction estimations might overestimate the efficiency of PAL considering the complexity of the fishery and its effect over a longer time period. The best way to confirm whether the effect of a bycatch mitigation tool is achieved in the long run, is through a proper bycatch monitoring scheme, being especially important during the first years of a large-scale implementation in the fishery. This monitoring scheme can provide real numbers of bycatch events that can be used to estimate real reduction effect in the long term and considering the variability of the real fishery, as long as any potential changes in the abundance of the population of interest are measured at the same time. Two good examples for this were the long term monitoring of the driftnet fishery in the Gulf of Maine (Palka *et al.* 2008) and the gillnet fishery in California-Oregon (Carretta and Barlow 2011). Such a long-term monitoring scheme is also recommended for the PAL in the Belt Sea.

This suggestion is not new, and it is general knowledge that successful management of anthropogenic activities relies on information on the species and the impact of a threat on it (Koschinski *et al.* 2024). Despite this, monitoring of bycatch events in the Baltic Sea is often insufficient or covers just short time periods at a low spatio-temporal resolution (Kindt-Larsen *et al.* 2023) and as for now, the information on bycatch rates of the harbour porpoise in the Baltic Sea continues to remain limited hindering our understanding of bycatch mortality (Glemarec *et al.* 2021). This highlights the broader issue that scientists often undertake expensive and time-consuming studies to assess the long-term effectiveness of mitigation tools, a necessity arising from the initial lack of efficient monitoring systems.

Three informations are necessary to obtain reliably bycatch estimates: bycatch records (Glemarec *et al.* 2021), representative fishing effort (Kindt-Larsen *et al.* 2023) and population abundance estimates (Glemarec *et al.* 2021). The three elements are described below providing where possible data on the *status quo* of the bycatch of harbour porpoise for Germany.

Bycatch records and Regulatory Framework

Under the EU Habitat Directive (Council Directive 92/43/EEC 1992) all Member States of the European Union are required to monitor the level of bycatch of harbour porpoises. This directive provides the legal basis for protecting species and their habitats within the EU, and establishes an obligation to the Member States to ensure that bycatch levels do not negatively affect the conservation status of harbour porpoises or other protected species. The EU Regulation 2019/1241 *on the conservation of fishery resources and the protection of marine ecosystems through technical measures* sets out the specific fisheries regulations that EU Member States must follow, which also includes measures on how the bycatch should be monitored. The basic rules on the collection, management and use of standardized data in line with the Common Fisheries Policy are defined within the Data Collection Framework (DCF) (Regulation (EU) 2017/1004).

The bycatch measures adopted for cetaceans within this regulation are nevertheless considered not sufficient to effectively mitigate bycatch in European waters (Dolman *et al.* 2021). While the regulation states the obligation to monitor bycatch of sensitive species, including cetaceans, it does not state requirements for dedicated observer schemes on the different types of vessels (Dolman *et al.* 2021). Further, the recommended monitoring scheme to be undertaken on an annual basis to monitor cetacean bycatch is established only for vessels of an overall length of 15 m or more (Regulation (EU)

2019/1241). This approach is considered insufficient as the majority of the European static net fishing vessels are smaller than 12 m (Rogan *et al.* 2021), which is also the case in the Baltic Sea in Germany (Federal Ministry of Food and Agriculture 2024).

Although there are no universal or legally defined required levels of observer coverage to monitor the bycatch of ETP species (Carpentieri *et al.* 2024), some recommendations to obtain reliable bycatch estimates of ETP species range from: 20 % for common species and up to 50 % for rare species (Babcock *et al.* 2003), 20 – 35 % coverage as recommended under the US Marine Mammal Protection Act (Barlow, 1989), while it is also suggested that a 10 % coverage can give initial rough bycatch estimates (Carpentieri *et al.* 2024). As many other countries, also Germany failed to achieve full compliance with the bycatch monitoring scheme between 2006-2014, which was back then regulated by Council Regulation (EC) No 812/2004 (Read *et al.* 2017). During this period the required level of coverage was not achieved, and static nets were underrepresented (Read *et al.* 2017). The new EU Regulation 2019/1241 does not state requirements for dedicated observer schemes on the different types of vessels (Dolman *et al.* 2021). In 2023 and in ICES areas subdivision 22 and 24, the total effort of German vessels using set nets was 12 387 days at sea, from which 136 days at sea were monitored by at sea observers (1.1 % on-board observer coverage) recording zero bycatch events of harbour porpoise (Christian von Dorrien, pers. comm., 2025). However, these zero bycatch events may express a bycatch that was not observed because it does not exist or because the monitoring effort is too low (ICES, 2024c). Thus, although Germany, as well as most other member countries, respond to the yearly data call of the Working Group on Bycatch of Protected Species (WGBYC) of the International Council for the Exploration of the Sea (ICES) by submitting data about fishing and monitoring effort, together with recorded bycatch events stemming from the DCF programme, the data seems insufficiently to representatively calculate harbour porpoise bycatch. Several countries in Europe have bycatch monitoring programs additionally to the DCF for marine mammals; Germany did not report additional programs (ICES 2024c).

Up to date, the only available bycatch estimate of harbour porpoises in the German Baltic Sea is 57 individuals per year, which were estimated for the years 1996-2004, based on stranding events, bycatch submitted by fishers and interviews with fishers (Rubsch and Kock 2004). Although newer estimates are not available, bycatch of porpoises takes place in the German static net fishery in the Baltic Sea, as has been documented through the statements of fishers in interviews (Barz 2023), based on cadavers submitted by fishers over the years (Siebert *et al.* 2006; Dähne *et al.* 2011) or bycaught animals in scientific studies (Chladek *et al.* 2020). Currently, only one regional law in Germany addresses the obligation to record bycatches of porpoises: fishers in Schleswig-Holstein are obliged to report bycaught harbour porpoises to the fisheries authority (Schleswig-Holstein 2018). However, these numbers are not available to the Thünen Institute of Baltic Sea Fisheries (Christian von Dorrien, pers. comm., 2025).

While logbooks represented the largest proportion of monitored bycatch data submitted by all countries to the WGBYC in 2023, most bycatch incidents in the data came from at-sea-observers or electronic monitoring records (**Figure 6.3.**) (ICES 2024c). Based on these results, the WGBYC does not consider self-reporting in logbooks as reliable method to quantify ETP species bycatch rates. This calls for the implementation of either more on-board-observer coverage or electronic monitoring (ICES 2024c; Dalskov *et al.* 2021). Video based electronic monitoring is considered a more cost-effective alternative to independent fisheries observers to collect data in small scale fisheries (Dalskov *et al.* 2021). Challenges associated with observer coverage in small scale fisheries are the small size of the boats, that make it difficult to place scientific observers on vessels in some occasions (Rubsch and Kock 2004), and the fact that - due to the low bycatch rates per vessel - it requires an elevated monitoring coverage of fishing operations to achieve reliable and accurate bycatch estimates (ICES 2024a) which

is (much too) costly. Electronic monitoring is also suggested to be more reliable as on-board observers often have other tasks and might miss some bycatch that get lost during hauling process (ICES 2024c). Denmark and Sweden have implemented electronic monitoring to collect harbour porpoise bycatch and static net fishing effort at a fine spatial and temporal scale in the Belt Sea (Kindt-Larsen *et al.* 2023). While electronic monitoring is generally applied on larger vessels as more space is available, systems adapted for small-scale vessels are available (different systems adapted to small scale fisheries can be found in Dalskov *et al.* (2021)). A particular example in the Belt Sea is the HafsAuga MobileEM system (Fetterplace *et al.* 2023). The system has been field-tested and is ideal for small-scale fisheries monitoring, due to easy transferability between vessels which allows for random and thus more representative sampling (Fetterplace *et al.* 2023). As of 2022, the HafsAuga MobileEM system has been implemented as the main monitoring tool in Sweden to collect data on bycatch of ETP species for the EU Data Collection Framework (Fetterplace *et al.* 2023). To facilitate the analysis of electronic monitoring footage, an automated detection and classification machine learning tool is already under development in Sweden (Svensson *et al.* 2023) and further research is conducted on applied machine learning or artificial intelligence tools to automate image classification for the detection and classify bycatch of ETP species in Europe such as OPTIFISH (www.optifish.eu), or part of the Marine Beacon project (www.marinebeacon.eu) to mention just two.

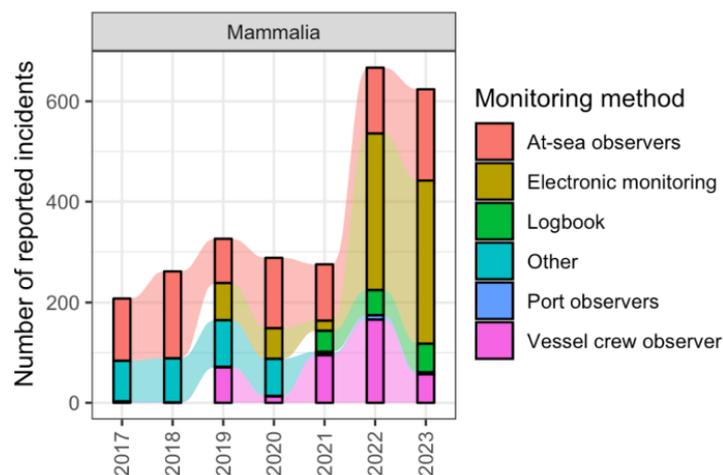


Figure 6.3. Total number of reported bycatch incidents of marine mammals by monitoring method (2017 – 2023) for all countries reporting to the 2024 WGBYC data call. The category ‘Other’ is defined as: other unspecified monitoring methods, e.g., interviews with fishers. Modified from ICES 2024c.

The trials conducted in Chapter 5 relied on self-reporting of fishers on whether a bycatch event had occurred or not. One harbour porpoise was bycaught in a net with the PAL at around 64 m from the PAL position. The trials were run over 8 months, with a total of 226 fishing trips being conducted were only one net was monitored within the study (118 nets in Germany with mean soak time of about 21 hours per net and 108 nets in Denmark with mean soak times of 41 hours). These numbers give an example of the relative low frequency of bycatch events of porpoises and in turn is an indicator of the potential monitoring effort required to collect a representative number of bycaught animals. Systems such as the HafsAuga, which are already developed and in use, are encouraged to be implemented in Germany to increase the monitoring. This monitoring could provide additional information on the effectiveness of PAL or alternative mitigation strategies while reducing the cost of on-board observers. Further, it would show Germany’s commitment to a representative monitoring effort allowing estimation of bycatch rate for the entire Belt Sea area.

Fishing effort

In recent years, Denmark and Sweden have provided bycatch estimations of harbour porpoises for the Belt Sea population based on fishing effort and recorded bycatch events (Kindt-Larsen *et al.* 2023; Glemarec *et al.* 2021). Data on German gillnetters effort was not included as bycatch estimates were not available and the fishing effort data was not standardized with the other events (Kindt-Larsen *et al.* 2023; Glemarec *et al.* 2021). The lack of accurate total fishing effort has been described as the main limiting factor to properly evaluate the magnitude of bycatch mortality since a long time (ICES 2014).

In Chapter 5, fishing effort was collected either using the Mofi - Mobile Fisheries Log (www.anchorlab.dk) - or via paper protocols, recording only the net that had the F-POD attached. The Mofi App was developed as a digital option to record fishing effort with high spatio-temporal resolution for all vessel sizes which can be used for electronic self-reporting (Meyer *et al.* 2022). Only two fishers in Germany expressed a willingness to adopt the mobile application during the study in Chapter 5, while the rest of the fishers in Germany and Denmark opted for paper protocols. Fishers who did not want to use the app said that they perceived it as complicated to use. One of the two fishers that used the app in Germany, kept on having minor problems with the operation of the app despite initial instructions, such as forgetting to end trips. Despite this, the two fishers in Germany that used the app reported that they did not find it hard to use. Similar problems were encountered when the Mofi app was first tested with fishers in the Baltic Sea (Meyer *et al.* 2022). Nevertheless, smaller issues can be addressed through more intense training as well as get better with increased use. The Mofi app has the potential to improve fishing effort data collection providing more detailed information on important fishing parameters such as soaking times, gear dimension and fishing positions, without which, bycatch risk can only be estimated at coarse spatial and temporal resolution (ICES 2024b). A mobile application such as the Mofi App would also be an interesting solution for smaller vessels (< 12 m) where information on fishing effort and gear characteristics remain limited (ICES 2024a).

More complete fishing effort data should be available within the following years as the EU has established the baselines for vessel monitoring systems for all vessels operating under EU flag or within EU waters. Vessels above 12 m length shall have installed on board a functioning tracking device transmitting automatically the vessel position data at regular intervals; while union fishing vessels of less than 12 m in length must also carry a device on board to allow the vessels to be automatically located and identified while at sea through recording and transmitting the vessel positional data at regular intervals, this device does not have to be installed on board (Regulation (EU) 2023/2842). The frequency of transmission of the data is not established yet and will be laid down by the Commission through the implementation of acts. Regulation (EU) 2023/2842 will be fully applicable as of 31 December 2029, after which all transitional exemptions for small-scale vessels under 9 m will cease.

Population abundance

As seen in Section 1.3. estimations of harbour porpoise abundance are assessed in regular intervals for the Baltic Sea area through the SCANS surveys since 1994 (Gilles *et al.* 2022). The abundance estimates allow for the calculation of different removal thresholds, even in the absence of bycatch data or fishing effort, which are often unavailable. One example is the Potential Biological Removal (PBR) control rule that was developed to compute limit reference points for anthropogenic removals from marine mammal stocks (Wade 1998). The PBR can be compared to the concept of maximum sustainable yield level often used for fish stock assessments (Wade *et al.* 2021). In the Baltic Sea, ASCOBANS set this conservation objective to keep the populations at or restore it to 80 % of its carrying capacity (ASCOBANS 1997). The carrying capacity is not known for the harbour porpoise in the Belt Sea, which has led different researchers to use approximations in the past years based on abundance estimations obtained in the SCANS surveys (Kindt-Larsen *et al.* 2023; Owen *et al.* 2024). As a result, the modified PBR (mPBR) (Genu *et al.* 2021) allows calculating a removal threshold for the harbour porpoise Belt

Sea population based on the ASCOBANS conservation objective. These abundances were used to calculate different values of mPBR or mortality limit for the harbour porpoise in the Belt Sea population with the latest estimates ranging from 24 animals (Owen *et al.* 2024) to 99 (Kindt-Larsen *et al.* 2023) individuals per year. Both of these values are exceeded by the current estimated bycatch rates in the Belt Sea, ~ 758 animals/year (NAMMCO and IMR 2019) ~ 900 animals/year (Kindt-Larsen *et al.* 2023).

Similarly, the HELCOM has established a precautionary threshold based on population abundance estimates. This threshold suggests that harbour porpoise bycatch in the Belt Sea should be kept below 1 % of the best available population size estimates (HELCOM 2018). Based on upper and lower limits of population sizes of the Belt Sea estimated in the last SCANS survey (9 555 – 21 769) (Gilles *et al.* 2022) this threshold would allow significantly fewer removals than the current bycatch levels, which again far exceed sustainable limits.

6.7. Call for action

This thesis has focused on advancing knowledge of underlying mechanisms that drive harbour porpoise bycatch in the static bottom set net fishery as well as broadened the understanding of the effect of a bycatch mitigation tool, the PAL, implemented voluntarily partly at the German Baltic coast. While interesting new findings are made, it remains a challenge to conclude whether the PAL is an efficient mitigation tool in the long term. As seen in bibliography (Palka *et al.* 2008), targeted experiments may overestimate the efficiency of mitigation tools due to an oversimplification of the fishing characteristics and environmental conditions. A long-term monitoring scheme accompanying any implementation of a bycatch mitigation measure would therefore be the preferred approach to fully understand the efficiency of the PAL or pingers as bycatch mitigation tools, also in the long-term.

Although regulations are in place, a clear framework for reducing porpoise mortality in fisheries to sustainable levels has yet to be fully defined in Europe (Rogan *et al.* 2021). This is partly due to the absence of quantitative conservation objectives, with vague bycatch targets in the EU Habitat Directive and Common Fishery Policy, and the complexity of shared management responsibilities (Rogan *et al.* 2021), which make implementation and compliance more challenging. An important step to be made in near future is the establishment of an appropriately designed monitoring program. It should allow for statistical meaningful analysis of the data, collecting information on the bycatch numbers as well as on the fishing effort for each fishing métier at appropriate spatial and temporal scales (Rogan *et al.* 2021; Kindt-Larsen *et al.* 2023; Owen *et al.* 2024). The good news is that a lot of important work to allow for good monitoring, and as a consequence reliable bycatch estimates, has been done in the past years:

- I. Range-wide **abundance estimates** are available for porpoises in the Belt Sea and estimates keep improving over the years (Gilles *et al.* 2022).
- II. **Biological reference points** are available such as the mPBR (Genu *et al.* 2021) for porpoises in the Belt Sea (Kindt-Larsen *et al.* 2023; Owen *et al.* 2024).
- III. **Electronic monitoring methods** have been developed, tested and **adapted for small scale fisheries** (Dalskov *et al.* 2021) and are in occasions already being used to collect **fishing effort** and **bycatch data** as shows the example of Denmark and especially Sweden where it is already being implemented as primary monitoring tool for the DCF (Fetterplace *et al.* 2023)
- IV. **Technical expertise** and scientific advice is provided by several international bodies, including the Scientific Committee of the International Whaling Commission, ASCOBANS, and the ICES WGBYC (Rogan *et al.* 2021).
- V. **New regulations** that intend a better **fishing effort coverage** (Regulation (EU) 2023/2842) are on their way.

- VI. **Advances in technology** including **AI tools** such as automated image recognition software are under development (Svensson *et al.* 2023) which can reduce the monitoring cost considerably while ensuring reliable data collection (ICES 2024c).

Making use of the available information and technologies would allow closing the gap between the current available information and the real magnitude of harbour porpoise bycatch in the Belt Sea and other areas in Europe. For this to happen, support by policy making bodies defining clear quantitative management objectives (Dolman *et al.* 2021; Rogan *et al.* 2021) as well as determination of Member States to follow up on requirements which is not always the case (Read *et al.* 2017) will be crucial.

In general this discussion highlights that, often auxiliary studies such as the ones conducted withing Chapter 4 and 5 of this thesis try to compensate the lack of a sufficient bycatch monitoring scheme that should follow the implementation of a bycatch mitigation strategy. We are still far away from understanding the real impact of German static bottom set net fisheries on the harbour porpoise population in the Western Baltic Sea and we do not fully understand the efficiency of PAL in reducing harbour porpoise bycatch in Germany. This further points to the difficulty for Germany to answer to the requirement of the Marine Strategy Framework Directive (Directive 2008/56/EC) whether populations are in good environmental status. The available bycatch estimations based on Danish and Swedish data largely exceed different calculated bycatch threshold by several orders of magnitude (Kindt-Larsen *et al.* 2023; Owen *et al.* 2024). This suggests that the harbour porpoise in the Belt Sea requires urgent attention.

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List of Abbreviations

ADD: Acoustic Deterrent Device	IUCN: International Union for Conservation of Nature
ASCOBANS: Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas	KW (test): Kruskal-Wallis test
AUC: Area Under the (Receiver Operating Characteristic (ROC)) Curve	medianKHz: median frequency of click train
avSPL: average Sound Pressure Level	MinICI_us: minimum inter click interval in a train (milliseconds)
CI: Confidence Interval	mPBR: modified Potential Biological Removal
CMS: Convention on the Conservation of Migratory Species of Wild Animals	nActualClx: number of clicks in a click train
C-POD: Cetacean-PORpoise Detector	NBHF: narrow-band high-frequency
DCF: Data Collection Framework	OIC: Ostsee Info-Center in Eckernförde
DE: Germany	PAL: Porpoise ALert
DK: Denmark	PAL-CE (project): PAL: Current Efficiency and mode of operation
D_{t-d}: Distance theodolite - drone	PAM: Passive Acoustic Monitoring
E²: epsilon squared	PBR: Potential Biological Removal
ETP species: Endangered, Threatened and Protected species	POD: PORpoise Detectors
EU: European Union	ROC: Receiver Operating Characteristic
F-POD: Full wave capture PORpoise Detector	SCANS (survey): Small Cetacean in European Atlantic Waters and the North Sea
GAMM: Generalized Additive Mixed Model	SD: Standard Deviation
GLM: generalized linear model	SH: Schleswig-Holstein
GPS: Global Positioning Networks	SHAP (values): SHapley Additive exPlanations
HP: Harbour porpoise	SWOT (analysis): Strengths, Weaknesses, Opportunities and Threats
HELCOM: Baltic Marine Environment Protection Commission – also referred to as the Helsinki Commission	T-POD: Timing PORpoise Detector
ICES: International Council for the Exploration of the Sea	TrDur_us: click train duration in microseconds
ICI: Inter Click Interval	UTC: Universal Time Coordinated
IQR: inter quartile range	UTM: Universal Transverse Mercator
	WGBYC: Working Group on Bycatch of Protected Species
	XGBoost: eXtreme Gradient Boosting

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Chapter 3. Performance of theodolites versus drones in land-based studies of marine mammals

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Chapter 4. Bycatch events of small odontocetes are not directly related to detectability of fishing nets

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Chapter 5: Harbour porpoise reaction to PAL (pinger alternative) in the Western Baltic Sea

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Confirmation of correctness of authors contribution:

Hamburg 13.03.2025



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