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Traditio et Innovatio

Activity pattern of the harbour porpoise *Phocoena phocoena* in the coastal waters of Fyn (Denmark)

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Master thesis

MNF Marine Biology

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I. Abstract

The harbour porpoise *Phocoena phocoena* is the only cetacean species, which occurs regularly in the Baltic Sea. Its abundance has decreased dramatically within the last several decades, so that it was classified as "Critically Endangered" in the Baltic Sea in 1996. In order to recover the harbour porpoise population, it is protected in the EU waters by several national and international agreements. These agreements demand the immediate creation of marine protected areas for the harbour porpoise, which is only possible with the knowledge about its abundance, distribution and activity pattern.

In this study, the activity pattern of the harbour porpoise in the coastal waters of Fyns Hoved, Denmark was investigated acoustically with C-PODs as well as visually with a theodolite. C-PODs are passive acoustic monitoring devices, which can automatically detect harbour porpoises by recording the echolocation clicks they produce. 10 C-PODs were deployed throughout 24 hours over a period of five weeks in Fyns Hoved. The visual observation was conducted during the day on an around 19 m high cliff in the study area.

The results have shown a diel as well as a geographical activity pattern of the detected harbour porpoises. More harbour porpoises were detected during night and evening than during morning and day. The detections of harbour porpoises were significantly higher at the deeper C-POD stations than at the remaining, shallow stations during the evening. The comparison of the acoustic with the visual harbour porpoise sightings have demonstrated that the ability to sight harbour porpoises visually is limited to a maximum distance to the observer of between 266 m and 325 m.

These findings have extended the current knowledge about the diel activity pattern of the harbour porpoise. It can be hypothesized that the harbour porpoise may be feeding pelagic prey in deeper waters at night, while it may be hunting mainly benthic prey in shallow waters during the day. Its hunting method during the day could be mainly visually or with the special feeding behavior. During this "bottom-grubbing", the harbour porpoise scans the sea bottom by swimming in a vertical position with the mouth close to the bottom. The visual hunting as well as the "bottom-grubbing" would both have the consequence that the harbour porpoise could not be detected by the C-PODs. These findings should be taken into consideration when planning further monitoring studies of the harbour porpoise. However, more research on this topic needs to be undertaken before a general conclusion can be made. It is recommended to compensate this potential limitation of the C-PODs during the day with visual monitoring methods to secure precise data collection.

II. Zusammenfassung

Der Schweinswal *Phocoena phocoena* ist die einzige Walart, die in der Ostsee regelmäßig vorkommt. Seine Abundanz hat innerhalb der letzten Jahrzehnte dramatisch abgenommen, so dass er seit 1996 in der Ostsee als „stark gefährdet" eingestuft wird. Damit die Schweinswalpopulation sich wieder erholen kann, werden die in den EU-Gewässern lebenden Schweinswalen durch verschiedene nationale und internationale Abkommen geschützt. In diesen Abkommen wird die sofortige Einrichtung von Meeresschutzgebieten für den Schweinswal gefordert, was jedoch nur möglich ist, wenn seine Abundanz, sein Vorkommen und seine Aktivitätsmuster bekannt sind.

In dieser Studie wurde das Aktivitätsmuster von Schweinswalen sowohl akustisch mit C-PODs als auch visuell mithilfe eines Theodolits in den Küstengewässern von Fyns Hoved in Dänemark untersucht. C-PODs sind passive akustische Monitoring Geräte, die Schweinswale erkennen, indem sie deren Echoortungsklicks aufnehmen. 10 C-PODs wurden über einen Zeitraum von fünf Wochen 24 Stunden lang in den Küstengewässern von Fyns Hoved ausgebracht. Die visuelle Beobachtung fand tagsüber auf einer ca. 19 m hohen Klippe im Untersuchungsgebiet statt.

Die Ergebnisse zeigen sowohl ein Tag/Nacht- als auch ein geographisches Aktivitätsmuster. Es wurden mehr Schweinswale am Abend und in der Nacht als am Morgen und am Tag registriert. Am Abend wurden häufiger Schweinswale an den tieferen C-POD Stationen entdeckt als an den flacheren Stationen. Der Vergleich zwischen der akustischen und der visuellen Schweinswalsichtungen hat gezeigt, dass die Beobachtung von Schweinswalen, auf eine maximale Entfernung von 266 m bis 325 m zum Beobachter beschränkt ist. Die Erkenntnisse haben den aktuellen Wissensstand über das Aktivitätsmuster von Schweinswalen erweitert. Es ist anzunehmen, dass der Schweinswal nachts vor allem pelagische Beute im tieferen Wasser frisst, während er am Tag hauptsächlich benthische Beute im flachen Wasser jagt. Sein Jagen am Tag könnte mehrheitlich visuell basiert sein oder ist mit einem speziellen Fressverhalten zu erklären, dem „bottom-grubbing". Dabei „tastet" der Schweinswal den Meeresboden mithilfe seines Sonars ab, in dem er vertikal mit der Schnauze nah über den Meeresboden schwimmt. Sowohl das visuelle Jagen als auch „bottom-grubbing" haben zur Folge, dass der Schweinswal nicht von C-PODs erkannt werden kann. Diese Erkenntnisse sollten bei der Planung zukünftiger Monitoringstudien mit Schweinswalen berücksichtigt werden. Dennoch muss mehr Forschung zu diesem Thema durchgeführt werden, bevor allgemeine Schlussfolgerungen gemacht werden können. Es wird empfohlen, dass die möglichen Einschränkungen von C-PODs während des Tages

mit visuellen Monitoringmethoden ausgeglichen werden, um eine genaue Datensammlung zu gewährleisten.

III. List of Figures

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V. List of Abbreviations

ASCOBANS	Agreement on the Conservation of Small Cetaceans of the Baltic and North Sea
Bft	Beaufort
BP	Baltic Proper
CI	Confidence Interval
CMS	Convention on the Conservation of Migratory Species of Wild Animals
C-POD	Cetacean Porpoise Detector
CTD	Conductivity, Temperature and Depth
CV	Coefficient of Variation
dB	Decibel
DMI	Danish Meteorological Institute
DPM	Detection Positive Minute
DST	Data Storage Tag
eds.	Editors
e.g.	exempli gratia (for example)
ft	feet
GB	Gigabyte
GPS	Global Positioning System
HELCOM	The Baltic Marine Environment Protection Commission or Helsinki Comission
Hi	High
ICI	Inter-Click-Interval
IDW	Inner Danish Waters
IUCN	International Union for Conservation of Nature
kn	knots
Lo	Low
mbar	Millibar
Min ICI	Minimum Inter-Click-Interval
Mod	Moderate
m	Meter
min	Minute
ms	Milliseconds

mS	Micro Siemens
NBHF	Narrow Bandwidth, High Frequency
n.d.	No date
NS	North Sea
kHz	Kilohertz
OSPAR Convention	Convention for the Protection of the Marine Environment of the North-East Atlantic
Other Cet	Other Cetacean
POD	Porpoise Detector
POPs	Persistent Organic Pollutants
RTK	Real Time Kinematic
s	Second
SAC	Special Areas of Conservation
SAMBAH	Statistic Acoustic Monitoring of BAltic Harbour porpoise
SCAN-I, SCAN-II	Small Cetaceans in the European Atlantic and North Sea
SD	Secure Data
STELLA	STELlnetzfischerei-LösungsAnsätze
T-POD	Timing Porpoise Detector
UTC	Universal Time Coordinated
µPa	Micropascal
µs	Microsecond

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1. Introduction

1.1. The harbour porpoise *Phocoena phocoena*

1.1.1. Biology

The harbour porpoise *Phocoena phocoena* is a small odontocete, which inhabits temperate to cold waters throughout the northern hemisphere (Bräger 2011, Scheidat *et al.* 2008). This species belongs taxonomically to the odontocetes (Odontoceti, suborder), Phocoenidae (family) and Phocoena (genus) (Kremer & Maywald 1991, Schulze 1996). Within the odontocetes, the harbour porpoise is the smallest species with a mean size of 150 cm length and 50 kg in males and 165 cm and 65 kg in females (Jefferson *et al.* 1994, Schulze 1996).

The body shape of the harbour porpoise is shown in Fig. 1: It has a short stocky body with a rotund shape (Bruhn 1997, Culik 2011, Kremer & Maywald 1991). Its dorsal side is dark grey while the belly is light grey to white which goes in a light grey over its side (Bruhn 1997, Culik 2011, Jefferson *et al.* 1994). Besides this color pattern, there is a dark stripe from the mouth to the flippers (Bruhn 1997, Culik 2011, Kremer & Maywald 1991).

Both sexes of the harbour porpoise reach sexual maturity at an age of three to four years (Lockyer & Kinze 2003, Lockyer 2007, Read 1995). After a gestation period of around 11 months, their offspring are born in the summer months (Börjesson & Read 2003, Lockyer & Kinze 2003, Lockyer 2007). Hasselmeier *et al.* 2004 has noted a geographical variation in the exact birth period of harbour porpoises in the North Sea and the Baltic Sea: between June and July in the North Sea and between July and August in the Baltic Sea. The lactation period lasts for about eight months, but the calves start already to hunt fish after five months (Kremer & Maywald 1991). Most female porpoises become pregnant each year after they are sexually mature, so that they are lactating and pregnant at the same time (Read 1995). Because of their intense reproduction cycle, they rely on enough energy-rich prey (around 3.5 to 4 % of their body weight/ day) (Kremer & Maywald 1991, Lockyer 2007). Therefore, the harbour porpoise is an opportunistic feeder and switches from one to another prey species depending on what is available, such as herring (*Clupea harengus*), cod (*Gardus morhua*), goby (*Pomatoschistus sp.*), sprat (*Sprattus sprattus*), sole (*Solea solea*) and squid (*Loglio sp.*) (Börjesson & Read 2003, Culik 2011, Schulze 1996). The harbour porpoise lives on average eight to ten years (Culik 2011). However, the age of the oldest stranded animal so far recorded was 24 years old (Lockyer 1995).

Harbour porpoises normally swim alone or in small groups of two or three animals (Bjørge & Tolley 2009, Bruhn 1997, Culik 2011), whereby these groups often consist of a mother with her calf (Bjørge & Tolley 2009). When they come for breathing to the water surface, they just show their dorsal side for a few seconds (Bjørge & Tolley 2009). Accordingly, they are difficult to observe, so that studies from cliffs above calm fjords or coastal waters yield the best observations (Culik *et al.* 2001). This species spends most of the time at depth shallower than 10 m and the majorities of dives have on average a duration of 1 min (Otani 1998, Teilmann *et al.* 2007). Dive depths of up to 220 m and a duration of 5 min have also been found (Westgate e*t al.* 1995).

Fig. 1: The harbour porpoise *Phocoena phocoena* (Culik 2011)

1.1.2. Abundance and distribution

According to the known geographical distribution of this species, it can be assumed that three reproductively isolated subpopulations exist: *Phocoena phocoena vomerina* in the North Pacific, *Phocoena phocoena phocoena* in the North Atlantic and *Phocoena phocoena relicta* in the Black Sea (Bjørge & Tolley 2009, Gaskin 1984). Within these subpopulations, they can be divided into several genetically distinct population units (Bjørge & Tolley 2009). The population units in the North Sea and in the Baltic Sea belongs to the subpopulation *P.p. phocoena* (Koschinski 2001), which include on the current state of knowledge a total number of 30 population units (Bjørge & Tolley 2009). With the help of genetic analysis (Andersen *et al.* 1997, Andersen *et al.* 2001, Wang & Berggren 1997, Wiemann *et al.* 2010), skull measurements (Galatius *et al.* 2012), tooth ultrastructure (Lockyer 1999) and contaminant investigations (Berggrena *et al.* 1999), three distinct population units of harbour porpoises can be differentiated in the North Sea and in the Baltic Sea (Fig. 2): (1) the North Sea population unit (North Sea, Skagerrak, northern part of the Kattegat), (2) the Inner Danish Waters population/ Belt Sea population unit (Southern Kattegat, Belt Seas and the Sound and western Baltic) and (3) the Baltic Proper population unit around the island of Rügen and northwards to Finland (Gillespie *et al.* 2005, Sveegaard 2011a, Wiemann *et al.* 2011).

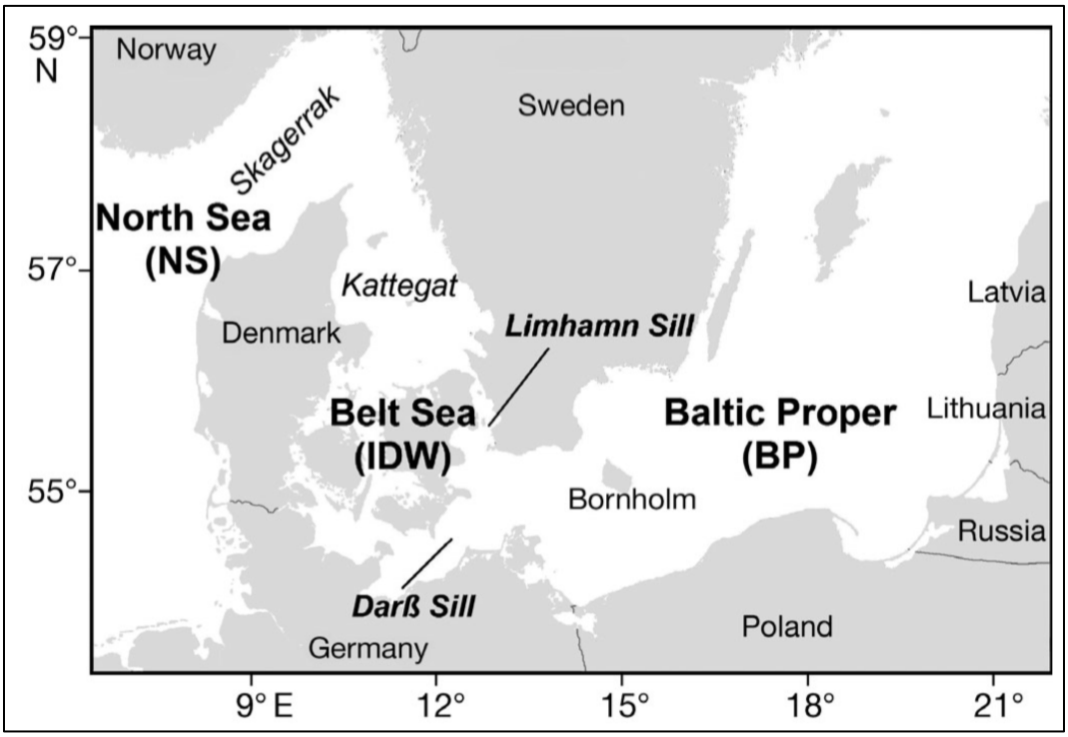


Fig. 2: Overview of the three population units: North Sea (NS), Belt Sea (IDW: Inner Danish Waters) and Baltic Proper (BP) population unit (Gallus *et al.* 2012).

To estimate the abundance of harbour porpoise in European Waters, two large, international aerial survey projects have been conducted: SCAN-I (**S**mall **C**etaceans in the European **A**tlantic and **N**orth Sea) in 1994 (Hammond *et al.* 2002) and SCAN-II in 2005 (SCANSII 2008). The total estimated abundance for harbour porpoises in the North Sea and adjacent waters was 341,366 porpoises (coefficient of variation (CV)= 0.14; 95% confidence interval (CI) = 260,000-449,000) in 1994 (Hammond *et al.* 2002) and 385,617 animals (95% CI: 261,266-569,153) in 2005 (SCANSII 2008). The abundance in the Kattegat, Skagerrak, Belt Sea and western Baltic Sea was calculated to be 31,715 (CV=0.25) porpoises in 1994 and 15,557 (CV=0.30) porpoises in 2005 (Hammond *et al.* 2008). Additionally, the acoustic survey project SAMBAH (**S**tatistic **A**coustic Monitoring of **BA**ltic **H**arbour porpoise) was carried out with the aim to estimate the abundance and distribution of the harbour porpoise in the Baltic Sea (SAMBAH 2016). With the deployment of over 300 acoustic data loggers (C-PODs) from 2011 to 2013 in the Baltic Sea, the harbour porpoise abundance of the Baltic Proper population unit was estimated at 497 porpoises (95% CI 80 - 1091) (SAMBAH 2016). Thus, the Baltic Proper population unit contains the lowest number of harbour porpoises in comparison to the North Sea- and the Belt Sea population unit.

Several studies have shown a geographical variation within the Baltic Proper population unit (Koschinski 2001, Gallus *et al.* 2011). This means a significant decrease in the abundance of harbour porpoises from west to east with the lowest abundance in the Pomeranian Bay (Benke *et al.* 2014, Heide-Jørgensen *et al.* 1993, Scheidat *et al.* 2008, Siebert *et al.* 2006). In addition to the geographical variation, a seasonal variation within the Baltic Proper population unit can be found as well: the harbour porpoise seems to stay in the Baltic Proper during spring and summer, while this species migrates in the Pomeranian Bay during cold winters (Benke *et al.* 2014, Gallus *et al.* 2012, Verfuß *et al.* 2007). This observation (higher distribution in summer compared to winter) and the fact that the breeding as well as the 11 months later entering birth occur in the summer months led to the conclusion that the Baltic Proper represents an important breeding and mating habitat for the harbour porpoise (Benke *et al.* 2014, Verfuß *et al.* 2007). This assumption was confirmed by the peak of calves in late summer (Siebert *et al.* 2006). While the exact cause of their movement is still unknown, the distribution of the harbour porpoise during the seasons is probably linked to the distribution of its prey (Sveegaard 2011b, Sveegaard *et al.* 2011).

Beside the seasonal variation of the Baltic Proper population unit, a seasonal migration pattern of the population unit in the North Sea (Gilles 2009) and in the Inner Danish Waters could also be identified (Schulze 1996): The harbour porpoise, which belongs to the North Sea population unit, seems to move during spring and autumn in the Skagerrak and it remains the rest of the year in the North Sea (Gilles 2009). The animals of the Inner Danish Waters population unit seem to migrate during spring and summer in the Pomeranian Bay, while they seem to stay the autumn and winter in the Inner Danish Waters (Gilles 2009).

1.1.3. Echolocation

Echolocation can be defined as "the process in which an animal obtains an assessment of its environment by emitting sounds and listening to the echoes as the sound waves reflect off different objects in the environment" (Au 2009). This capability of echolocation is called biosonar (Wahlberg *et al.* 2015) and probably all toothed whale species (Odontoceti) are able to echolocate (Huggenberger *et al.* 2009). Because sound spreads in water on average 4.5 times faster than in air (depending on salinity, temperature and pressure of the water bodies) and because sound travels farther than light in water, hearing is the most important sensory system for a whale (Wahlberg *et al.* 2015, Watzok & Ketten 1999). Thus, echolocation provides information about the environment of the whale so that it can be used for orientation and navigation, communication as well as for foraging (Gallus *et al.* 2011, Miller & Wahlberg 2013, Verfuß *et al.* 2009, Villadsgaard *et al.* 2007).

The anatomical structures, which are involved in the generation and reception of echolocation signals, are highly conserved within the toothed whales and they were evolved about 36-34 million of years in the evolution of the toothed whales (Steeman *et al.* 2009). The relevant structures for the harbour porpoise are illustrated in Fig. 3 (Wahlberg *et al.* 2015). The harbour porpoise produces high frequency acoustic pulses, called clicks, due to the flow of air through a pair of phonic lips (Gallus e*t al.* 2011, Goodson & Sturtivant 1996). The phonic lips, which are like a vocal fold organ, are located in the nasal air passage below the blowhole (Miller 2010). The press of air through the phonic lips causes them to open and close shut for each click (Cranford & Amundin 2004, Cranford *et al.* 2011). The melon, which is a fatty organ in front of the skull, bundles and emits the sound in the water (Goodson *et al.* 2004, Koblitz *et al.* 2012). When they reach an object in the surrounding, like prey, stones or rocks, the echo is sent back to the porpoise, which receives the sounds with the help of its lower jaw (Brill *et al*. 1988). There are located specialized fat channels, which send the sounds through the middle ear into the inner ear (Brill *et al*. 1988, Miller 2010). Subsequently, the echo is transformed into neural impulses, which are transferred to the brain and the new information can be processed (Ketten 2000).

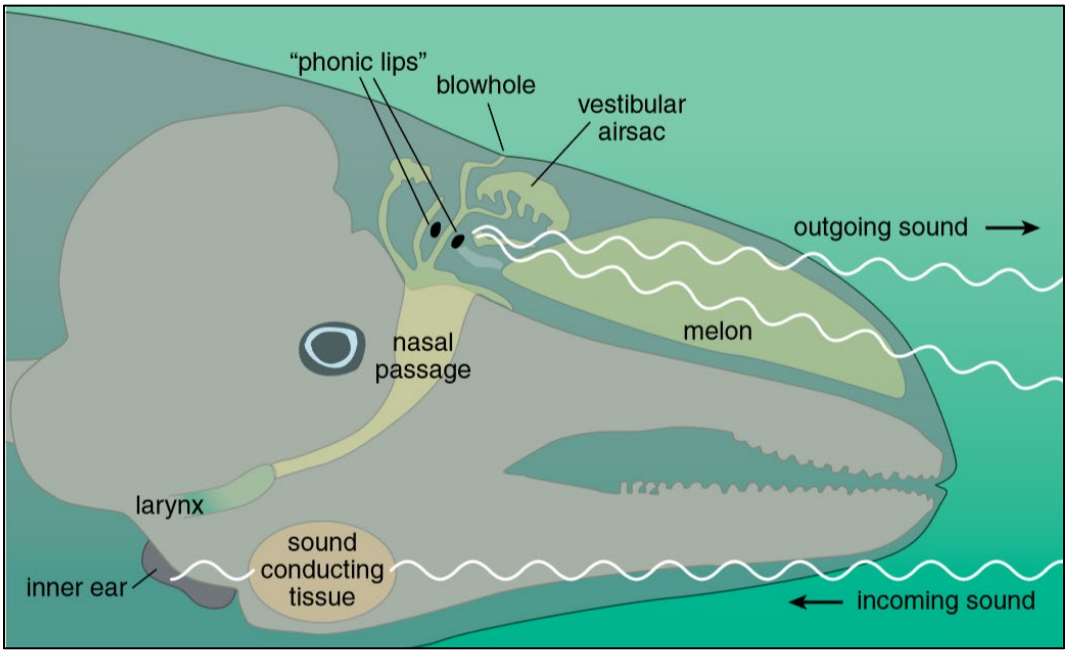


Fig. 3: Anatomical structures of harbour porpoise, which are involved in the echolocation sound production (Wahlberg *et al.* 2015).

The produced echolocation signals can be differentiated within the toothed whale species in regard to the duration, waveform and frequency of the generated clicks (Frankel 2009). The harbour porpoise emits a series of clicks, called trains, which are **n**arrow in **b**andwidth and **h**igh in **f**requency (NBHF, Au 1997). The latter one means that most of the clicks are centered in a frequency between 130 and 140 kHz, whereas its hearing capabilities range from about 100 to 150 kHz (Kastelein *et al*. 2002, Wahlberg *et al.* 2015). In comparison, humans can hear between 0.02 and 20 kHz (Gallus *et al*. 2011). A typical harbour porpoise click has on average a duration of 100 µs (Fig. 4 a), Miller 2010). The frequency spectrum can be seen in Fig. 4 b. The bandwidth is the frequency width within which a significant fraction of the total energy of the signal lies (Lew 1996). For example, a broadband signal has a significant amount of its energy distributed over a wide range of frequencies and a narrowband signal accordingly over a small range of frequencies (Lew 1996). The bandwidth refers to a threshold value of 3-decibels (dB), so that the 3-dB bandwidth can be defined as the angle between the directions at which the sound pressure level is reduced by 3-dB (Koblitz *et al.* 2012). The harbour porpoise' clicks have on average a 3-dB bandwidth of 16° (Koblitz *et al.* 2012). The sound pressure level, also known as the source level, is an indication for the loudness of a sound in dB (Frankel 2009). It is characterized as a ratio of measured sound pressure level to a reference sound pressure level at a distance of 1 m (Frankel 2009). This sound pressure level has on average a value of 157 dB re 1 µPa at 1 m for the emitted clicks of the harbour porpoise (Au *et al.* 1999, Teilmann *et al.* 2002).

A further feature of the harbour porpoise echolocation system is that the clicks are emitted in a narrow, forward oriented beam between 11-13° (Koblitz *et al.* 2012). This highly directional beam has the advantage that it reduces the clutter and reverberation from the surface and the bottom of the sea (Koblitz *et al.* 2012).

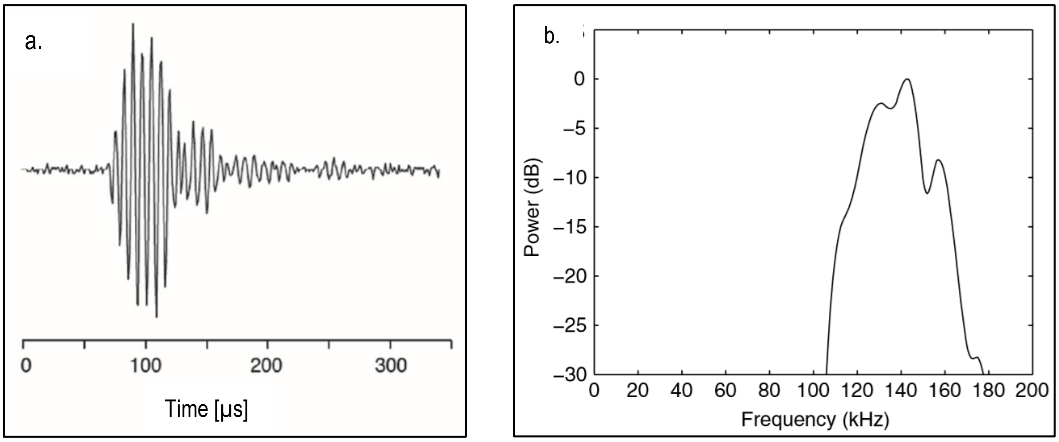


Fig. 4: **a.** Typical click from a series emitted by a harbor porpoise (modified after Miller 2010), **b.** Frequency spectrum of a harbour porpoise click (modified after Villadsgaard *et al.* 2007)

Another important parameter for analyzing echolocation activity is the Inter-Click-Interval (ICI), which is defined as the time interval between two transmitted clicks (Philpott *et al.* 2007). This ensures that the echo is not disturbed by subsequent clicks (Koschinski *et al.* 2008). The preferred mean ICI of the harbour porpoise is around 60 ms, but intervals up to 200 ms and down to a few milliseconds were also observed (Villadsgaard *et al.* 2007, Teilmann *et al.* 2002). Several studies have found that the ICI changes depending on what the animal is doing (Koschinski *et al.* 2008, Miller 2010, Miller & Wahlberg 2013, Verfuß *et al.* 2009). Thus, it was concluded that a variation in ICIs can be used to identify different acoustic behaviors of the porpoise (Koschinski *et al.* 2008). For example, the echolocation behavior of foraging porpoises can be divided into two different phases due to changes in ICI (Verfuß *et al.* 2009, see Fig. 5). In the first phase, called search phase, the porpoise is waiting for echoes of potential prey within its sonar range (Verfuß *et al.* 2009). It is assumed that this phase offers the porpoise the possibility to adjust its ICI to a specific search range (Verfuß *et al.* 2009). The following second phase, defined as approach phase, can be differentiated into an initial and a terminal part (Melcón *et al.* 2007). The initial part starts when the porpoise detects a suitable prey and it is characterized by an almost constant ICI of around 50 ms (Verfuß *et al.* 2009, Miller & Wahlberg 2013). When the porpoise is around 1-2 body length (around 2-4 m) from the prey away, the terminal part is initiated by a sudden and rapid decrease in ICI to a value of 1.4 ms to 1.6 ms (DeRuiter *et al.* 2009). This short ICI results in a click rate of around 320 clicks/s up to 640 clicks/s (DeRuiter *et al.* 2009). The terminal part can also be called “buzz” (Surlykke *et al.* 1993) and the mean buzz duration was calculated to be 1.37 s (DeRuiter *et al.* 2009). However, the duration of the buzz depends on how rapidly the prey is captured (Miller 2010). The porpoise echolocates even after catching (Miller 2010), which can be seen in an increase of the ICI after the end of the buzz (see Fig. 5).

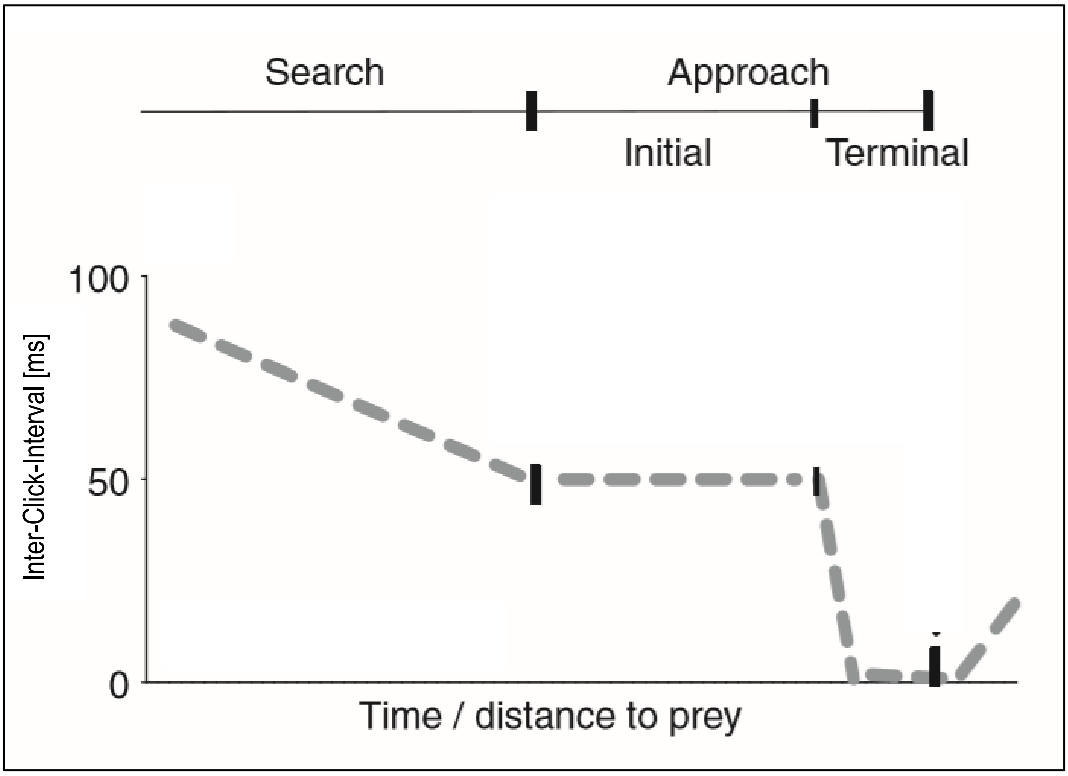


Fig. 5: Echolocation phases of harbour porpoise during foraging due to changes in Inter-Click-Interval (ICI), modified after Verfuß *et al.* 2009.

1.1.4. Current status of the harbour porpoise population

As mentioned above, the harbour porpoise is found abundantly in coastal waters all around the northern hemisphere (Miller & Wahlberg 2013). At the beginning of the century, it has been detected widespread in German waters (Tougaard *et al.* 1996, Verfuß & Schnitzler 2002), but the population in the Baltic Sea has decreased dramatically within the last several decades (Benke *et al.* 2014, SAMBAH 2016). Since 1996, the harbour porpoise in the Baltic Sea has been regarded as "Critically Endangered" by the International Union for Conservation of Nature (IUCN) and the Baltic Marine Environment Protection Commission or Helsinki Commission (HELCOM) (Hammond *et al.* 2008, HELCOM 2013). The causes for this decline seem to be a combination of several, largely anthropogenic factors (Koschinski 2001): hunting, hard winters, pollution and bycatch. Until the end of the 19^{th} century, a commercial hunt on harbour porpoise led to a decrease in their abundance (Lockyer & Kinze 2003). This hunt was resumed during the two world wars, but at a smaller scale (Lockyer & Kinze 2003). The rapid decrease in the population size led to the ban of whaling at the end of the 1960s (Bruhn 1997). During the first half of the 20^{th} century, there were several hard winters, which had consequently led to an ice entrapment and to a drowning of many hundred harbour porpoises under the ice (Lockyer & Kinze 2003). Furthermore, chemical as well as noise pollution may have contributed to the decline of harbour porpoises in the Baltic Sea (Benke *et al.* 2014, Koschinski 2001). To the latter one belongs anthropogenic underwater noise, e.g. shipping (Tougaard *et al.* 1996, Verfuß & Schnitzler 2002), seismic surveys with airguns, offshore wind power generators and military activities (ASCOBANS 2016, Koschinski 2001). It is known that sound is more pervasive in water than in air and that it can thus disturb echolocating animals by masking communication or foraging signals (ASCOBANS 2016). Ship traffic can also be responsible for the injuries of harbour porpoises by collisions or contact with the propeller of the ship (Tougaard *et al.* 1996). Chemical contamination of the sea by anthropogenic input has increased strongly during the last century (Koschinski 2001). These chemical pollutants are e.g. persistent organic pollutants (POPs) (Jepson *et al.* 1999), heavy metals (Siebert *et al.* 1999) and pesticides (Granby & Kinze 1991). Due to that fact that the harbour porpoise feed at higher trophic levels, these chemicals can accumulate in their tissues and can then impair the health status of the animal (Bruhn 1997, Pierce *et al.* 2008). As reported in many studies, these chemicals can cause in general an increased disease risk and immunological and reproductive failures (e.g. Beineke *et al.* 2005, Culik 2011, Pierce *et al.* 2008, Reijnders 1986). Based on the current state of knowledge, the exact effect of pollutants on the health status of the harbour porpoise remains mostly unclear (Siebert *et al.*

1999). The reason is that there are a lot of different contaminants in the sea, which might contribute to the toxicity and which even interact with each other (Koschinski 2001). In addition, many pollutants are permanently being developed and released into the environment without their toxicity having yet been fully identified (Koschinski 2001).

However, the probably main threat to harbour porpoise is the incidental catch in fishing gear (Teilmann & Lowry 1996), especially in gillnets (Tougaard *et al.* 1996, Berggren e*t al.* 2002). In order to efficiently protect this species in the Baltic Sea, knowledge gaps concerning the harbour porpoise need to be closed, e.g. missing information about their distribution, activity, seasonal movements, bycatch etc. (Koschinski 2001). Due to its alarming decline, this species is protected by different national and international agreements: It is listed in Annex II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) with all other migratory species, which have an unfavorable conservation status and which require international agreements for their conservation and management (Convention on Migratory Species 2018). The CMS established in 1994 the Agreement on the Conservation of Small Cetaceans of the Baltic and North Seas (ASCOBANS), which has focused on the conservation status of the Baltic harbour porpoise (ASCOBANS 2018). Due to the critically endangered status of the harbour porpoise in the Baltic Sea, the ASCOBANS member states passed in 2002 a recovery plan, called the Jastarnia plan (ASCOBANS 2016). Its goal is to restore the Baltic harbour porpoise population to at least 80 % of its carrying capacity (ASCOBANS 2015). This means that the total anthropogenic removal levels (which includes bycatch as well as other human related mortalities) must be under 1.7 % of the estimated harbour porpoise population size to achieve the goal of a favorable conservation status for this species (ASCOBAN 2016). In other words, the bycatch of harbour porpoise in the Baltic Sea must be reduced to not more than two porpoises per year to stop the decline and possible extinction of this species (Bräger 2011).

1.2. Monitoring marine mammals

1.2.1. Brief overview about monitoring studies of marine mammals

As early as in the 18th and 19th century, people were interested in whales and dolphins, in their abundance and distribution (Samuels & Tyack 2000). However, this interest consisted particularly with the intention to hunt whales for food, oil and leather products (Samuels & Tyack 2000). Besides the whaling industry, new insights into the behavior of whales came from carcass studies (Samuels & Tyack 2000). These studies enable information about the biology of the species, like the age, sex, body length and reproductive status (Samuels & Tyack 2000), but an individual whale could be investigated only once (Andersen 1984). The interest in whales and dolphins for purely commercial purposes changed in the early 20th century, when the first zoos and aquariums started to keep them (Wood 1986). From then on, a lot of studies about the behavior of marine mammals in a captivity setting were conducted (e.g. Essapian 1963, Gubbins *et al.* 1999, Yamamoto *et al.* 2014).

This captive behavioral research declined since the 1970s (Samuels & Tyack 2000). While there is no definitive reason for this decrease (Samuels & Tyack 2000), it could be traced back to a risen ethological concern leading to the demand for new approaches to study marine mammals in wild (Payne 1983).

Due to the general need for the conservation of marine mammals, knowledge about the distribution, abundance and behavior of these species is necessary (Read & Westgate 1997). Therefore, different methods have been developed for monitoring marine mammals, which range from highly invasive and long-lasting to noninvasive and temporary methods (Whitehead *et al.* 2000). These methods can be assigned to three main categories:

1. monitoring via tags,
2. visual monitoring and
3. acoustic monitoring (Sveegaard 2011a).

Every method has advantages as well as disadvantages and the choice for the most suitable method depends in particular on the exact research question, on the species of interest and on the available budget (Evans & Hammond 2004).

1.2.2. Monitoring via tags

The first category comprises several **tagging techniques**, which have been developed over the last decades (Irvine *et al.* 1982). These tags can be attached nowadays to a variety of marine mammals (McIntrye 2014). For the harbour porpoise it is common to attach the tag with bolts through the dorsal fin (Sveegaard 2011a). With the help of the tags, information about the individual porpoise is possible (Sveegaard 2011a). This includes not only the behavior (swimming speed, diving depth) and the physiological state of the porpoise (like heart rate and body temperature), but also environmental data, for example the water temperature and the salinity (Heylen & Nachtsheim 2018, Samuels & Tyack 2000). Another advantage of using tags is the implementation of long-term studies on marine mammals, like Read & Westgate (1997) did. They attached the tags for up to a year and a half to the porpoises and could in this way gain information about its movement pattern and its distribution (Read & Westgate 1997). Moreover, high-density areas of the harbour porpoise in the North- and Baltic Sea have been identified, which contribute to establish Marine Protected Areas for this species (Sveegaard 2011 b). Besides all these advantages, there are still some disadvantages of using tags in studying marine mammals. Firstly, it can be difficult to capture the species, which you want to tag (Heylen & Nachtsheim 2018). Secondly, the attachment of the tag might cause pain and several stress responses (Whitehead *et al.* 2000). These stress reactions can range from tissue reactions and infections around the tags (e.g. Irvine *et al.* 1982, Norman *et al.* 2018) to behavior changes such as mating, aberrant swimming, feeding or escaping from predators (Irvine *et al.* 1981, Rosen *et al.* 2018, Walker *et al.* 2011). All these possible disabilities might result in an impaired energy balance of the tagged animal (Rosen *et al.* 2018).

However, studies on harbour porpoise showed that the attached devices have only a short-term effect on the porpoise's behavior (e.g. a change in diving behavior, Geertsen *et al.* 2004) as well as on the physiological status of the porpoise (like the heart rate and respiration rate, Eskesen *et al.* 2009). These changes lasted a few hours until a few days after tagging (Geertsen *et al.* 2004). Two long-term studies on harbour porpoises indicated that the implementation of tagging caused only a temporary and a low-grade inflammatory reaction at the dorsal fin tissue (Heide-Jørgensen *et al.* 2017, Sonne *et al.* 2012). These findings lead to the interpretation that the tagging didn't have a strong influence on the overall energetic condition of these animals (Heide-Jørgensen *et al.* 2017, Sonne *et al.* 2012). All in all, despite of the previously mentioned advantages that tags can provide, the ethical point of view must be taken into account by planning a tagging study with marine mammals.

1.2.3. Visual monitoring

The second category, the visual observation, can be implemented from so called "platforms of observation", including air, sea or land (Piwetz *et al.* 2018, Sveegaard 2011a). Visual observation is especially suitable for marine mammals' abundance and distribution estimation, but also for the analysis of the movement patterns, the behavior and the life-history of a species (Sveegaard 2011 a). A standard method for estimating the abundance of a species is the **line transect method** (Sveegaard 2011 a). Here, a survey region is studied by placing a number of lines in the region (Thomas *et al.* 2010). The observer records all animals along the lines (Sveegaard 2011 a) and extrapolates this density to the entire survey area (Evans & Hammond 2004). In the 1970s, the **Photo-identification** (Photo-ID) was developed by the Würsigs, who identified bottlenose dolphins with the shape of their dorsal fin, scars and notches on it (Würsig 1978, Würsig & Würsig 1977, 1979). This method assumes that certain natural markings are long-lasting and thus, they can be used to identify individuals of a species (Würsig & Jefferson 1990). These natural markings are for example dorsal fin shapes of spinner dolphins (Norris *et al.* 1994), dorsal fin marks of minke whales (Dorsey *et al.* 1990) and scars and nicks on the harbour porpoise's trailing edge of the dorsal fin (Gaskin & Watson 1985). It is a common tool for long-term studies of cetaceans, like movement patterns, population size and dynamics and life history parameters (Würsig & Jefferson 1990).

Additional to the Photo-ID, Roger Payne *et al.* developed in the early 1970s a shore-based method of tracking marine mammals by **theodolite** (Piwetz *et al.* 2018, Samuels & Tyack 2000). This surveyor instrument can be used to monitor movement patterns, habitat use and behavior of near-shore cetaceans in their natural environment and in a non-invasive manner (Harzen 2002, Samuels & Tyack 2000). The observation should be conducted from land on a high platform, from which a wide overview of the study area is possible. The principle of this tool is to mark the points at which animals come to the surface to breathe (Mayo & Goodson 1993). The theodolite measures horizontal angles in relation to a selected reference point and vertical angles relative to the gravity (Würsig *et al.* 1998). These angular measurements can be converted afterwards in x/y coordinates on a map (Würsig *et al.* 1998). Therefore, a theodolite enables precise geographical positions of the tracked cetaceans (Samuels & Tyack 2000). A description of how to use a theodolite is presented in this thesis in chapter 2.4.

The first monitoring research on cetacean with the help of a theodolite was implemented by Würsig, who investigated the behavioral ecology of the common bottlenose dolphin (*Tursiops truncatus*) and the dusky dolphin (*Lagenorhynchus obscurus*) in Argentina (Würsig

1978, Würsig & Würsig 1979, 1980). This initial survey was followed by theodolite studies on various cetacean species, like gray whales (Gailey *et al.* 2016), humpback whales (Best *et al.* 1995) and Hector's dolphins (Bejder *et al.* 1999). Also, the harbour porpoise has already been observed with a theodolite (Culik *et al.* 2001, Koschinski *et al.* 2003, Kyhn *et al.* 2012, Müller 2013).

Nowadays, the theodolite is world-wide a useful tool to study marine mammal behavior. Accordingly, 46 species of marine mammals from 14 families have so far been tracked by the theodolite (Piwetz *et al.* 2018). Besides the studies on cetacean' behavior and movement patterns with a theodolite, potential human-related impacts on marine mammals can be investigated as well (Gailey & Ortega-Ortiz 2002). For example, due to the possibility to track both cetaceans and boats with a theodolite, interactions between them can be studied (Acevedo 1991, Marley *et al.* 2017 b). Therefore, the theodolite has become a preferred method for conservation and management research (Gailey & Ortega-Ortiz 2002, Piwetz *et al.* 2018).

Such as other monitoring methods, the visual observation of marine mammals has advantages and disadvantages. The most important advantage is the non-invasive manner of studying marine mammals. Hence, they can be observed in their natural environment without any disruption of them (Piwetz *et al.* 2018). In contrast to tagging techniques, where the received data include only a few individuals, the theodolite provides information on several individuals or groups at the same time (Piwetz *et al.* 2018). Another advantage is the lower equipment cost by using a theodolite than by other monitoring devices, like tags (Piwetz *et al.* 2018).

One of the main disadvantages is the weather-dependency during visual observation (Teilmann 2003). This means that the sea state has a significant effect on the sighting rate of marine mammals; namely a decreasing visibility with increasing sea state (Palka 1996, Teilmann 2003). As a consequence, a valid observation is just possible under very calm weather conditions with a sea state less than three (Sveegaard 2011 a, see Tab. 5 for a classification of the sea state). Moreover, visual monitoring is limited on daylight hours, which reduces the observation time (Sveegaard 2011a). Furthermore, visual surveys are influenced by observer skills and his experience (Sveegaard 2011a). A potential limitation by using a theodolite could be that the observation is just possible for near-shore animals and not for species, which can be found in open waters (Würsig *et al.* 1998). Another disadvantage is the need of a high observation point (like a cliff), which can be, depending on the study area, hard to find (Würsig *et al.* 1998). Visual observation has compared to other monitoring methods, some challenges. Especially small cetaceans, like the harbour porpoise, can be difficult to follow, because they disappear during dives and they swim quickly over large distances (Mann 1999). When they come to the surface, they only show a small part of their dorsal fin for a few seconds (Evans & Hammond 2004). Therefore, visual observation is often combined with acoustic measurements to improve the data collection.

1.2.4. Acoustic monitoring

Acoustic measurement tools (third category) are for instance **hydrophones**, which record the echolocation clicks of a marine mammal (Sveegaard 2011 b).

In 1991, Nick Tregenza from Chelonia designed a passive acoustic monitoring device to monitor the occurrence of harbour porpoise in UK waters (Chelonia Limited 2018). This so-called **POD** (Porpoise Detector) can recognize automatically porpoises via a hydrophone by recording the echolocation clicks they produce. This self-contained data recorder uses an algorithm, which separated porpoise clicks from other sounds (Mikkelsen *et al.* 2016). More information about how to use a Porpoise Detector and how to analyze the collected data can be found in chapter 2.3.

The development of PODs enabled information on porpoise' habitat use, distribution (e.g. Bailey *et al.* 2010, Gallus *et al.* 2012, Simon *et al.* 2010, Verfuß *et al.* 2007) as well as on its behavior (Koschinski *et al.* 2008, Nuuttila *et al.* 2013). Its echolocation activity was assumed to be a proxy for its abundance and thus, for its density in the study area (Carstensen *et al.* 2006, Teilmann *et al.* 2002). Furthermore, the response and the echolocation behavior of harbour porpoises to anthropogenic activity, like the operation of offshore-windfarms (Brandt *et al.* 2011, Carstensen *et al.* 2006, Scheidat e*t al.* 2011) and the use of deterrent devices by fisheries (Brandt *et al.* 2013) have been investigated.

The original POD was modified in 2000 to a T-POD (Teilmann *et al.* 2002). Since 2008 its successor C-POD (Cetacean Porpoise Detector) has been produced to distinguish odontocete species by logging their echolocation clicks simultaneously (Dähne e*t al.* 2013). Due to this improvement, the C-POD is now applied in studies on a wide range of cetacean taxa (Rayment *et al.* 2009) in diverse acoustic environments from the Arctic to the Amazon (Chelonia Limited 2018). Thus, it is possible to identify for example bottlenose dolphins (Bailey *et al.* 2010, Philpott e*t al.* 2007, Simon *et al.* 2010), Hector's dolphins (Rayment *et al.* 2009) and Maui's dolphins (Rayment *et al.* 2011) with a C-POD. This wide applicability makes the

C-POD to the most commonly used passive acoustic device for odontocetes in Europe (Garrod *et al.* 2018).

There is a certain convenience by handling acoustic measurements instead of other monitoring devices (Rayment *et al.* 2009): They can be used automated throughout 24 hours, because they generally do not require daylight and they are less affected by the weather (Todd *et al.* 2009). Therefore, the data can still be collected when weather conditions are unsuitable for land- or boat-based observations (Philpott *et al.* 2007). Additionally, acoustic devices are independent of individual observer skill and experience and accordingly, the data collection is less susceptible to variability in skills between observers (Chappell *et al.* 1996). Consequently, passive acoustic monitoring is a common tool for studies on odontocetes, especially when land- or boat-based observations are not possible (Philpott *et al.* 2007).

In spite of the numerous benefits of acoustic monitoring, there are still some disadvantages. Firstly, acoustic monitoring devices are based on the assumption that toothed whales and dolphins emit sound regularly (Sveegaard 2011a). As a consequence, if the investigated species is silent during particular activities or at certain seasons, it will not be detected by acoustic devices (Evans & Hammond 2004). However, the harbour porpoise, which will be investigated in this study, is a highly vocal animal, which vocalize almost constantly (Akamatsu *et al.* 2007). It has been shown that this species produces click trains on average every 12.3 s (Akamatsu *et al.* 2007), so that the echolocation activity can be expected to be an indicator for the harbour porpoise presence (Scheidat *et al.* 2011). Secondly, another disadvantage could be that the whale must echolocate straight towards the C-POD, otherwise it can not be detected by the acoustic data logger (Kyhn *et al.* 2012). Thirdly, in some cases it could be difficult to figure out which vocalization comes from which species (Rayment *et al.* 2009). The harbour porpoise belongs to the minority of species that emits narrowband, high-frequency clicks within 100-150 kHz (Au *et al.* 1999, Chappell *et al.* 1996). Also, this species is the only known regularly detected and reproducing cetacean species in the Baltic Sea and accordingly, there should be no confusion with other echolocated marine mammals (Scheidat *et al.* 2008). Finally, in some areas it could be necessary to differentiate the echolocation sounds from other sounds in the marine environment, like noises coming from boats (Evans & Hammond 2004).

In conclusion, the pros and cons of each monitoring method should be weighed to choose an appropriate method for his own research. By taking into consideration of all the previously mentioned points, the best option for this study on the harbour porpoise's activity in Denmark is a combination of visual monitoring (theodolite) with acoustic monitoring (C-POD).

1.3. Current state of research about the activity pattern of the harbour porpoise

While several studies about the harbour porpoise exist, for instance, about its biology, abundance and distribution, the investigation of the activity has received less attention. To the author's current state of knowledge, just a few scientific papers are published about the diel echolocation activity of the harbour porpoise (Carlström 2005, Schaffeld *et al.* 2016, Todd *et al.* 2009). Carlström (2005) determined in her study a variation in the echolocation activity of wild harbour porpoises in Scottish waters within the day, namely a higher echolocation activity at night than during the day. Similar diel patterns have also been documented for wild harbour porpoises in the Baltic Sea (Schaffeld *et al. 2016*) and in the North Sea (Todd *et al.* 2009). Two possible hypotheses to explain the nocturnal increase in echolocation activity were discussed by the authors. Firstly, harbour porpoises increase their echolocation rate during darkness to compensate the lack of visual information (Carlström 2005). This explanation has been confirmed by Akamatsu *et al.* (1992), whereas two studies could not support this hypothesis (Kastelein e*t al.* 1995, Verfuß *et al.* 2009). Secondly, the diel echolocation activity could be associated with the diel activity and vertical movements of their prey (Todd *et al.* 2009). In this context, Linnenschmidt *et al.* (2013) have described a positive correlation between the diel echolocation – and the diving activity of harbour porpoises. This means a higher echolocation and diving activity at night than during the day (Linnenschmidt *et al.* 2013). An interpretation of this pattern is that harbour porpoise are feeding at night active fish, like herring (*Cluepea harengus)* and sprat (*Sprattus sprattus*) (Brandt *et al.* 2014, Linnenschmidt *et al.* 2013). For example, herring (*Cluepea harengus)* and sprat (*Sprattus sprattus*) are known to move up into the water column during night and the shoals, which were formed during day, are dispersing at night (Cardinale e*t al.* 2003). Hence, they are probably easier for porpoises to catch at night than during the day (Brandt *et al.* 2014). A higher nocturnal echolocation activity could indicate a higher foraging activity of harbour porpoise due to more food availability at night (Brandt *et al.* 2014, Todd *et al.* 2009).

1.4. Motivation and hypotheses

The motivation to conduct this study can be explained as follows:

As mentioned in chapter 1.1.4., the harbour porpoise in the Baltic Sea has decreased strongly within the last several decades (Benke *et al.* 2014, SAMBAH 2016). Especially, the incidental bycatch of harbour porpoise seems to be a major threat, which contributes to the alarming decline of this species (Teilmann & Lowry 1996). Gillnets are all year long very common in the Baltic Sea because they are relatively inexpensive, easy to handle and they can be deployed from small vessels at very low costs (He 2006, Read 2008). Additionally, gillnets are generally highly size selective in regard to fish species and fish size, making them to a worldwide using fishing net (Food and Agriculture Organization of the United States 2019, He 2006). However, this fishing net has two serious concerns: firstly, the loss of gillnets or any pieces of netting, called ghost-fishing (Breen 1989) and secondly, a high unwanted bycatch rate of marine mammals (Jefferson & Curry 1994, Lien 1995). This conflict between the gillnet fishery and the conservation of harbour porpoise should be resolved.

In order to efficiently reduce the bycatch and consequently protect the harbour porpoise in the Baltic Sea, knowledge gaps concerning the harbour porpoise need to be closed, e.g. missing information about their abundance, distribution and activity (Koschinski 2001). With knowledge about the general activity of the harbour porpoise, it is possible to make a statement about the optimal time during day and night for monitoring this species. Furthermore, a management plan can be made for the commercial fishery to minimize the bycatch of harbour porpoises. In this plan it could be determined in which sea areas and at which time of the day fishing is permitted and where and when it is forbidden due to high harbour porpoise activities. Additionally, a comparison between the two different monitoring tools, which will be presented in this study, could be helpful to choose an appropriate monitoring method for further studies on marine mammals.

This study is part of the project STELLA (**STEL**lnetzfischerei-**L**ösungs**A**nsätze) which aims to develop a holistic approach to mitigating the conflict between marine mammal protection and fisheries. This includes alternative management approaches, fishing gears and techniques to reduce the bycatch of harbour porpoises in the Baltic Sea.

The aim of this study is to examine the diel activity of harbour porpoise in the coastal waters of Fyn (Denmark). For this, the echolocation activity, recorded with C-PODs, and the visual sightings of harbour porpoise, recorded with a theodolite, are assumed to be an indicator for its presence/absence and hence, for its activity. Additionally, environmental parameters, which could affect the visual sightings of harbour porpoises, will be investigated. For this study, the wind speed and the wind direction were chosen as environmental parameters. The investigation of harbour porpoises' activity includes the following tasks and hypotheses derived therefrom:

1. Task: Identify potential differences in activity patterns during the diel cycle with the use of C-PODs and a theodolite

   Hypothesis: The harbour porpoise activity pattern varies during the diel cycle.

2. Task: Identify potential impacts (wind speed and wind direction) on harbour porpoise detection with a theodolite

   Hypothesis: The wind speed and the wind direction have an impact on the detection rate of harbour porpoises with a theodolite.

3. Task: Compare the number of harbour porpoises' sightings with C-PODs to that with a theodolite.

   Hypothesis: The number of harbour porpoises' sightings with C-PODs differ from that with a theodolite.

2. Materials and Methods

2.1. Study area

The study took place from 30th July to 2nd September 2018 at Fyns Hoved, which is located on the northern coast of Fyn in Denmark (see Fig. 6). This island is situated in the Western Baltic Sea between the two straits Little Belt and Great Belt, which both connect the Baltic Sea with the Kattegat (She *et al.* 2006). The Little Belt is a strait between the two islands Fyn and Jutland. Its most narrow part has a width of 400 m (She *et al.* 2006). The Great Belt, which connects the island Fyn with the island Zealand, is wider than the Little Belt; namely around 8 km at its most narrow part (She *et al.* 2006).

This area was chosen for two major reasons: Firstly, it has found to be a high-density area of the harbour porpoise (Teilmann *et al.* 2008) and secondly, Fyn has an around 19 m high cliff from which the visual monitoring was conducted (see Chapter 2.4. for the implementation of the visual monitoring). A high observation point is crucial to having a good overview of the study area. Especially because the harbour porpoise is very small and appears just for a few seconds, when it comes to the surface for breathing (Bjørge & Tolley 2009).

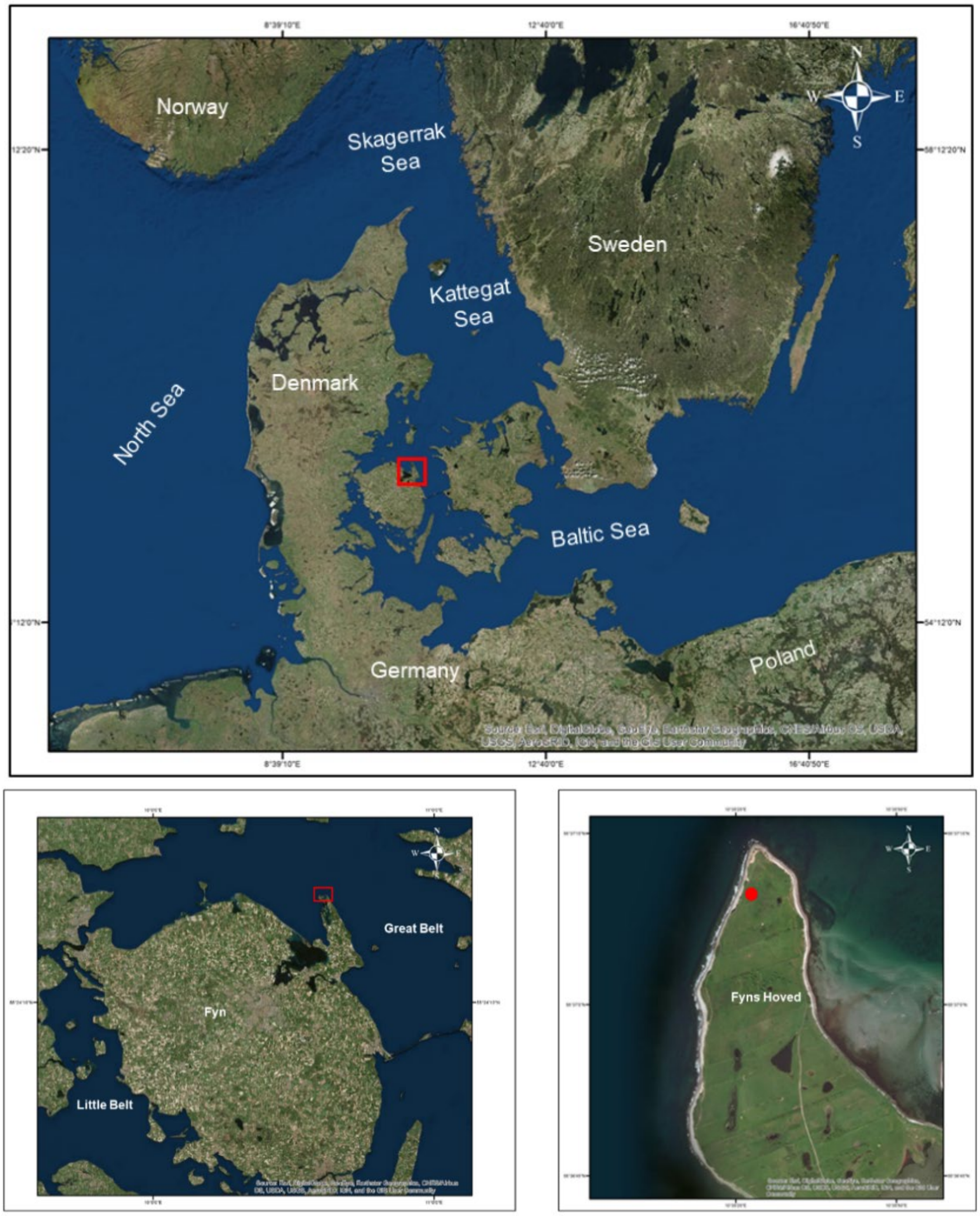


Fig. 6: Overview (top) and detailed map (bottom) of the study area in Fyns Hoved (Denmark). The red point on the map shows the observation place during the study period from 30th July to 2nd September 2018.

2.2. Environmental parameters

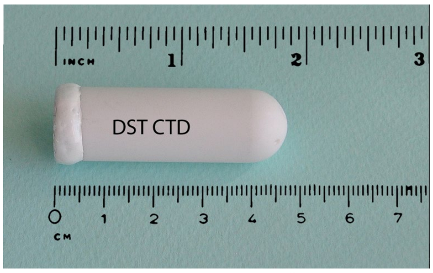
During the study period, several environmental parameters were collected with two different data loggers. These data loggers were attached to a hydrophone array.

The first used data logger was a DST-CTD (Data Storage Tag- Conductivity, Temperature, Depth) produced by the company StarOddi (StarOddi 2017, see Fig. 7 a.). The data logger has recorded the following parameters from 3rd August to 3rd September 2018 in intervals of 10 min: water temperature in °C, salinity in PSU, conductivity in mS/cm and sound velocity in m/s. Afterwards, the collected data were downloaded from the SeaStar software.

The second used data logger was a HOBO Water Level Data Logger U20L-02 (100 ft, Onset Computer Corporation 2019, Fig. 7 b.). It measured the water temperature in °C and the pressure in mbar from 28th July to 3rd September 2018 in intervals of 15 min. In addition to the data logger in the water, there was also a reference data logger onshore. After the measurement, the recorded data was read with the help of the HOBOware Pro software.

Furthermore, a FreeTec touchscreen weather station (REF-11171-919) was set up next to the observation place while the visual monitoring was conducted (FreeTec 2019, Fig. 7 c.). Every time a harbour porpoise was detected, the following parameters were noted in a protocol: air temperature in °C, wind speed in Bft and wind direction. A more detailed description of the performance of the visual monitoring can be found in chapter 2.4.

a.



b.

c.

Fig. 7: **a**. The data logger DST-CTD, **b.** the HOBO Water Level U20L-02 (100 ft) data logger and **c.** the FreeTec touchscreen weather station (REF-11171-919) were used during the study period.

As an addition to the measured parameters mentioned above, the Danish Meteorological Institute (DMI) made several parameters available for this study. The DMI measures meteorological, climatological and oceanographic parameters in the Commonwealth of the Realm of Denmark, the Faroe Islands, Greenland and their surrounding waters and airspace (Danish Meteorological Institute 2019). For this study, the following parameters were provided: Air temperature in °C, humidity in %, air pressure in mbar, wind speed in m/s and wind direction in degrees. These variables were measured from 29th July to 2nd September 2018 in intervals of one hour at the station “Odense Lufthavn” (station number: 06120, latitude:

55.4749, longitude: 10.3305, Vilic *et al.* 2013). The station has a height of 15 m (Vilic *et al.* 2013).

2.3. Acoustic monitoring

2.3.1. Study setup and procedure

The small self-contained data device C-POD was used (Chelonia Limited n.d.) for the acoustic monitoring of the harbour porpoise in Fyns Hoved (Denmark). The C-POD is a fully passive automated acoustic data logger originally developed to detect echolocation clicks of the harbour porpoise (Dähne e*t al.* 2013). Nowadays, the C-POD can detect all toothed whale species, except for the sperm whale, due to its ability to record clicks within the frequency range from 20 kHz to 160 kHz (Chelonia Limited n.d.). Therefore, the C-POD is a standard tool in the field of passive acoustic monitoring (Kyhn *et al.* 2008).

The C-POD, produced and developed by Nick Tregenza from Chelonia, UK, weighs around 3.5 kg (Chelonia Limited n.d.). It consists of an approximately 67 cm long polypropylene casing with a diameter of around 9 cm, a removable lid at one end and a hydrophone at the other end (Kyhn *et al.* 2008, Verfuß *et al.* 2013). The hydrophone is connected to two band-pass filters, called target filter A and reference filter B (Verfuß *et al.* 2013). The target filter must be set to the peak frequency of the species to be examined, while the reference filter B must be set to a frequency where there is little or no energy in the sonar signals of the investigated species (Philpott *et al.* 2007, Thomsen *et al.* 2005). As the clicks of the harbour porpoise have its peak frequency around 130 kHz and the energy of the clicks is not lower than 100 kHz (Kyhn *et al.* 2008), the target filter was centered at 130 kHz and the reference filter was centered at 90 kHz. The clicks of the harbour porpoise can be identified by comparing the signal energy between these two filters, (Koschinski *et al.* 2008, Scheidat *et al.* 2011). Each signal which has more energy in the target filter relative to the reference filter is likely to be a harbour porpoise (Scheidat *et al.* 2011). This filter settings secure that noise clicks as well as clicks from other odontocetes are excluded (Koschinski *et al.* 2008). The two filters are coupled with a microprocessor and a data logger, which continuously records the time and duration of each echolocation click in a 10 ms resolution, that fulfills the acoustic filter settings mentioned above (Kyhn *et al.* 2008).

Another acoustic setting criterium which must be determined by the user is the limit on number of clicks logged per minute (Thomsen & Piper 2004). A defined limit could be helpful in noisy areas to prevent exceeding the storage capacity too fast (Thomsen & Piper 2004). A limit of 4096 clicks per minute is recommended by the manufacturer and hence, this limit was set for this study. In this study, the C-POD continuously logged but it is also possible to run the C-POD intermittently to increase its total running time (Chelonia Limited 2011). The data can be stored on a single 4 GB SD (Secure Data) card. The C-POD is powered by 10 D-Cells, so that the logging time contains approximately five months (Dähne *et al.* 2013). A produced C-POD by Nick Tregenza can be seen in Fig. 8.

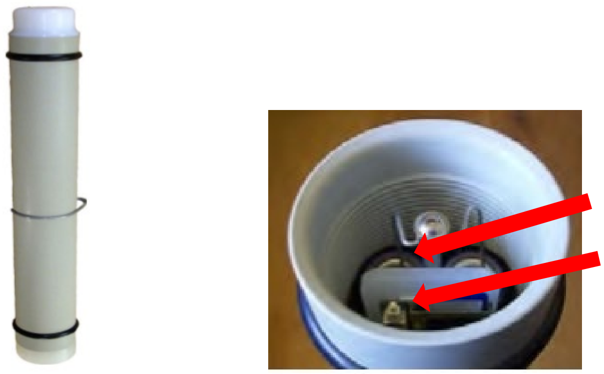


Fig. 8: A produced C-POD by Nick Tregenza, Chelonia (UK); left closed, right opened C-POD (Chelonia Limited 2011).

The C-PODs used in this study were kindly provided by Dr. Michael Dähne of the German Oceanographic Museum in Stralsund, Germany. It is recommended that C-PODs are calibrated prior to the deployment and after that, once every year (Dähne *et al.* 2013). A calibration is necessary to standardize each C-POD and allow the comparison between different C-PODs (Dähne *et al.* 2013). The C-PODs used in this study were calibrated in a test tank at the German Oceanographic Museum in Stralsund (Germany) prior to the begin of the study. A detailed description of the procedure of a C-POD calibration can be found in the paper by Dähne *et al.* (2013). After calibration and the setting of the acoustic parameters, 10 C-PODs were deployed in the coastal water of Fyns Hoved in Denmark (see Fig. 9 and Fig. 10).

For the deployment of the C-PODs, a 1.5 m long mooring line is attached around the middle of the C-POD. This line is connected to a rope, which has an anchor at its end. A yellow cross buoy at the sea surface shows the position of the C-POD (see Fig. 9). It is recommended to deploy the C-POD at least 3 m up from the bottom and at least 5 m down from the surface to prevent unwanted noise coming from the sea bed and the sea surface filling the memory card (Chelonia Limited 2011). When the C-POD is deployed in the sea, it floats vertically, which causes the hydrophone housing to move upwards and the C-POD starts logging automatically (Chelonia Limited 2011). This provides the possibility to transport the

C-POD before deployment without logging, which in turn saves power and memory (Chelonia Limited 2011).

The C-PODs deployed during this study are illustrated in Fig. 10. C-POD station 1 was deployed on the most northern point of the study area, while C-POD station 10 was located on the most southern point of the study area. The C-POD stations 2 to 9 were deployed in between them. The numeration of the C-PODs during their deployment is summarized in Annex, in Tab. 13. The GPS-position of each C-POD is shown in Annex in Tab. 14. The water depth varied between the different C-POD stations: The water depth at C-POD station 1 was around 11.3 m, while the water depth at C-POD station 10 amounted to around 14 m. The water depth at the remaining stations was around 6 m.

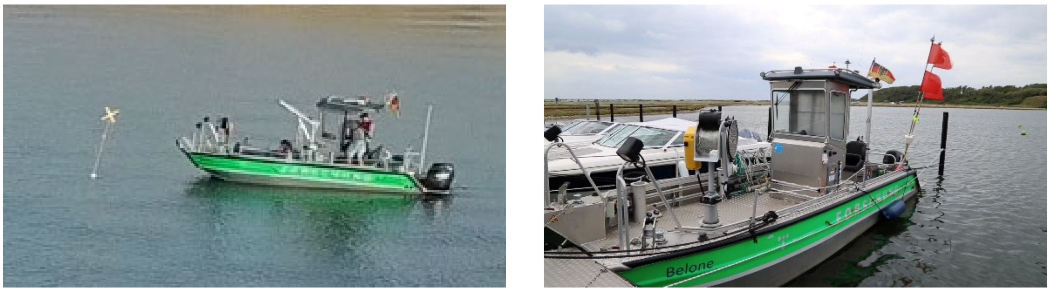


Fig. 9: Research vessel “Belone“ at one C-POD station (yellow buoy) (left) and at the harbor in Fyns Hoved, Denmark (right). Both photos were made by the Thünen-Institute for Baltic Sea Fisheries (Germany).

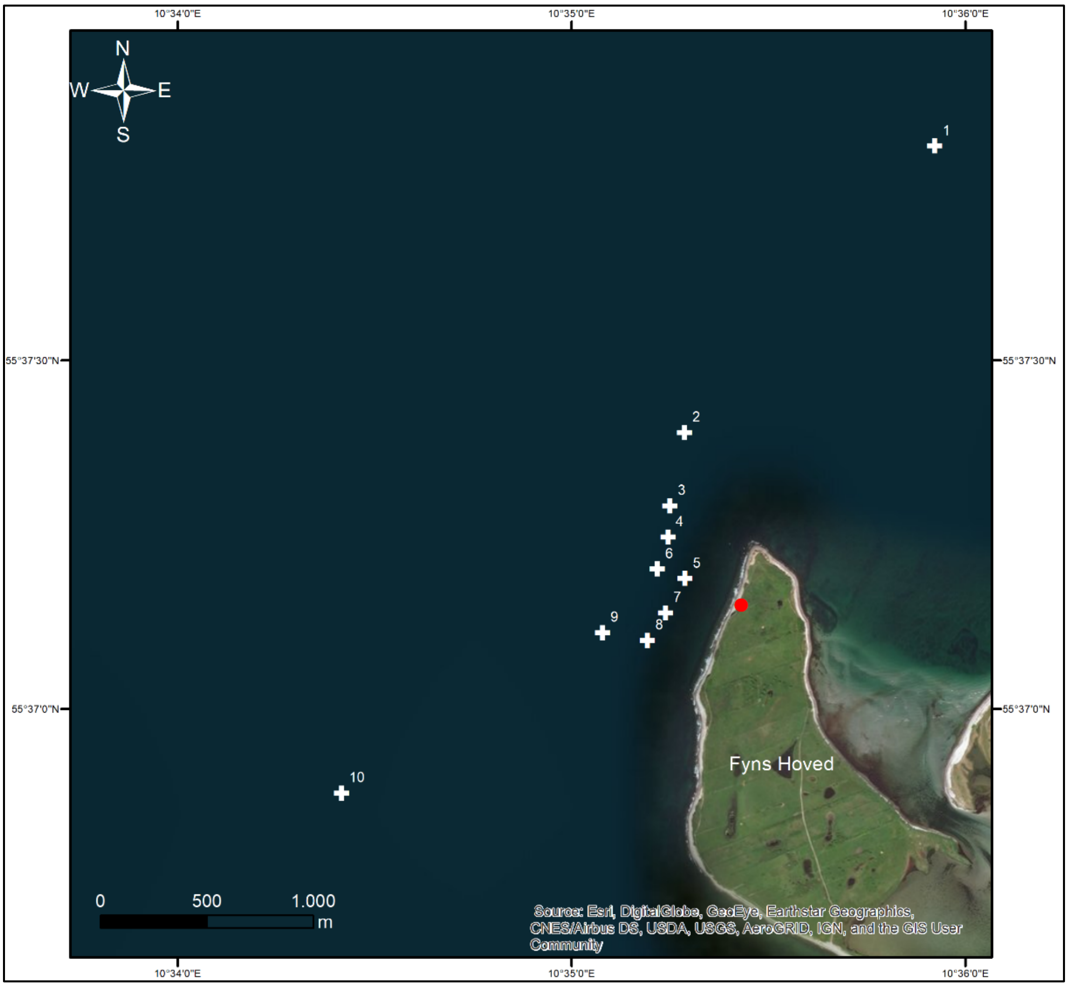


Fig. 10: Geographical position of the 10 deployed C-PODs during the study period from 30th July to 2nd September 2018 in Fyns Hoved (Denmark). The red point on the land shows the observation place during the study period.

Every few days, depending on the weather conditions, the C-POD devices were checked and the recorded data was saved. For this procedure, the C-PODs were removed from the sea and thus, there is no recording during this time period. As each C-POD was checked individually, the total hours of deployment differ between the C-POD stations (see Tab. 1). The date and time period of the deployment for each C-POD station can be found in Annex in Tab. 15. Additionally, at two C-POD stations (station 3 and 9), there is a greater amount of data missing - probably due to defects at the devices. The C-POD stations 5 and 6 were only deployed when another experiment was conducted by the Thünen-Institute for Baltic Sea Fisheries. The C-POD station 5 has recorded less than station 6 probably due to inaccuracies at the C-POD devices. The other experiment was running at the same time in the study area. The objective was to investigate the behavioral reactions of the harbour porpoise to a conventional gillnet and a modified gillnet in order to develop alternative fishing gears and techniques. To reduce the bycatch of harbour porpoises in the Baltic Sea, it was suggested to modify conventional gillnets (Jefferson & Curry 1996, Koschinski *et al.* 2006, Mooney *et al.* 2007). It was hypothesized that by increasing the acoustic reflectivity of a net, the porpoises could detect it easier and hence, the bycatch could be minimized (Jefferson & Curry 1996, Koschinski *et al.* 2006, Mooney *et al.* 2007). Thus, small acrylic glass spheres were attached to the gillnet as they have a large echo compared to their size. Each day, it was randomly chosen whether a conventional gillnet, a modified gillnet or no net (control) would be set. Possible reactions of harbor porpoises to these nets were observed on a cliff in Fyns Hoved.

Tab. 1: Total hours of deployment for each C-POD station during the study period from 30th July to 2nd September 2018 in Fyns Hoved (Denmark).

C-POD station	Total hours of deployment
1	804.84
2	821.47
3	578.50
4	821.60
5	33.08
6	65.86
7	820.55
8	821.25
9	380.65
10	821.60

2.3.2. Analysis of C-POD data

To analyze the recorded C-POD data, the software CPOD.exe (Version 2.044) was used. After having read the SD-card from a deployed C-POD (Fig. 11 a.), the software creates a CP1 file, which contains all the logged clicks (Tregenza 2014). When the CP1 file is processed via the “Kerno classifier button” on the “Trains” page (Fig. 11 b.), a CP3 file is generated (Tregenza 2014, Fig. 11 c.). This file contains only the clicks that have been identified by the KERNO classifier (Tregenza 2014). This classifier is the standard click train detection algorithm in the software which was used for this study. The algorithm classifies the logged trains in four categories depending on how likely they come from porpoises (Philpott *et al.* 2007, Rayment *et al.* 2009, Thomsen *et al.* 2005):

1. ”Hi” (“Cet High”): Trains with a high probability of coming from porpoises
2. “Mod“ (“Cet Moderate”): Trains with a moderate probability of coming from porpoises
3. **“Lo” (“Cet Low”):** Trains with a low probability of coming from porpoises
4. “?”: Doubtful trains, coming from other sources such as boats or rain

Additionally, it is possible to filter different species within the software (Tregenza 2014):

- **“NBHF” (Narrowband High Frequency):** Species who produce NBHF clicks. These include all porpoises of the family Phocoenidae, all dolphins in the genus Cephalorhynchus, some dolphins in the genus Lagenorhynchus and the dwarf and pygmy sperm whales in the genus Kogia, and Pontoporia.
- **“Other Cet” (“Other Cetacean”):** Species who produce broad band low frequency clicks. These include all non-NBHF toothed whales (Odontocetes), except for the sperm whale
- **“Sonar”:** Sonar sounds
- **“Unclassed”:** Trains from unrelated sources, like sediment noise

In this study, the species filter “NHBF” and the quality classes “Hi” and “Mod” were selected as following the recommendations of the manufacturer. After having run the algorithm, various parameters can be exported via the “Export” button in the software to conduct further analyses (Fig. 11 d.).

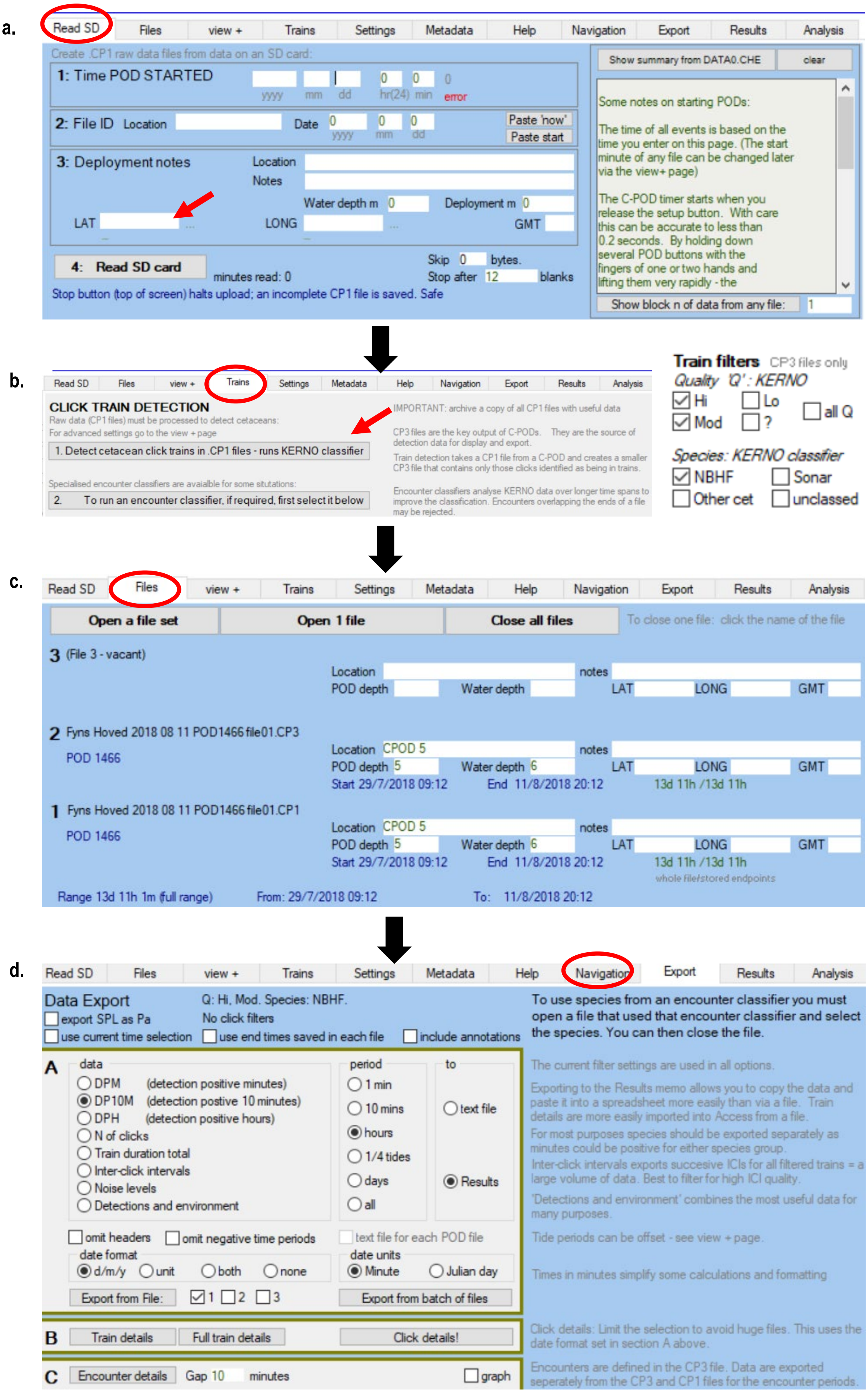


Fig. 11: Steps for analyzing recorded clicks with the software CPOD.exe (Version 2.044). **a.** Creating of a CP1 file after reading of the SD-card. **b.** Run of the Kerno classifier algorithm. **c.** Generating of a CP3 file. **d.** Export of the parameters to be studied.

To analyze the echolocation activity of the harbour porpoise in this study, the following parameter were exported from the C-POD software for each station: Modal frequency in kHz, Detection Positive Minutes (DPM) and Min Inter-Click-Interval per train in ms (Min ICI). These parameters are defined in Tab. 2. During the data analysis, it was recognized that the Kerno classifier algorithm has detected not only porpoises, but also dolphins. These potential echolocation signals of dolphins were seperated from these of the porpoises and they were analyzed in an additional chapter of this thesis.

Tab. 2: Definition of the analyzed echolocation parameters (modified after Carlström 2005 & Tregenza 2014).

Echolocation parameter	**Definition**
Modal frequency [kHz]	Modal frequency of a train in kHz
Detection Positive Minute [DPM]	1 minute period with at least one harbour porpoise train detection
Min Inter-Click-Interval per train (Min ICI) [ms]	Shortest period between two consecutive clicks within a train in ms

The DPM give for each minute on each day a value of “0” or “1”. A value of “0” inidcates that no harbour porpoise train was found by the C-POD detector within one minute. A value of “1” means that at least one harbour porpoise train was recorded within one minute. Thus, the DPM are a common indicator for the presence and absence of a porpoise. In order to compare the DPM between the different examination days and C-POD stations, the harbour porpoise detections per hour of C-POD recording was calculated for each day and station using Equation 1 (modified after Scheidat *et al.* 2011):

$$\text{Detections per hour of C} - \text{POD recording} = \frac{\sum \text{DPM per day at station}_\text{i}}{\sum \text{C} - \text{POD recording hours per day at station}_\text{i}} \qquad \text{Equation 1}$$

Another part of the study objective is to identify a possible diel pattern of the harbour porpoise presence and absence. For this investigation, the 24 hours of a day were divided into two phases: Day was defined as the period between sunrise and sunset and night was named as the period between sunset and sunrise. The time periods of day and night for each examination day can be seen in the Annex in Tab. 16. Subsequently, the detections per hour of C-POD recording were determined for each day, phase and station.

After detecting differences in the harbour porpoise activity during day and night, it would be interesting to gain a deeper insight into the period of its presence. This is possible with a more fine-scaled fragmentation of the day.

Therefore, the 24 hours of a day were divided into the four diel phases: morning, day, evening and night. This categorization is in accordance with other studies, in which the harbour porpoise activity was compared among the diel cycle (e.g. Carlström 2005, Todd e*t al.* 2009). The termination of the diel phases is based on the vertical angle of the sun, which is presented in Tab. 3 (Carlström 2005). Civil twilight begins in the morning and ends in the evening, when the center of the sun is geometrically six degrees below the horizon (Astronomical Applications Department 2017).

Tab. 3: Definition of the diel phases, which were used for this study (modified after Carlström 2005). As an example, the data of 30th July 2018 in Fyns Hoved are shown.

Diel phase	**Definition**	**Example**
Morning	Twice the time duration between beginning of civil twilight and sunrise	Begin civil twilight: 04:31 Sunrise: 05:19 Duration begin civil twilight – sunrise: 48 min Twice the duration: 96 min Morning: 04:31 + 96 min = 06:07
Day	Duration of the time between end of the phase morning and sunset	End of phase morning: 06:07 Sunset: 21:27 Day: 06:07 – 21:27
Evening	Twice the time duration between sunset and end of civil twilight	Sunset: 21:27 End civil twilight: 22:15 Duration end civil twilight – sunset: 48 min Twice the duration: 96 min Evening: 21:27 + 96 min = 23:03
Night	Duration of the time between the end of the phase evening and the beginning of civil twilight of the next day	End of phase evening: 23:03 Begin civil twilight: 04:33 Night: 23:03 – 04:33

The duration of the diel phases for each investigation day can be read in the Annex in Tab. 17. The detections per hour of C-POD recording were calculated for each day, phase and station.

After determining the period of the harbour porpoise presence, it is crucial to find out what it does during its presence. The Inter-Click-Interval is a common parameter to investigate the behavior of a porpoise (Kyhn *et al.* 2018). Following previous studies, a minimum ICI of below 10 ms was set as a proxy for potential feeding activity (Carlström 2005, Todd *et al.* 2009, Nuuttila *et al.* 2013, Verfuß *et al.* 2009). The threshold of 10 ms was chosen because it is supposed to be associated with foraging of porpoises (Nuuttila *et al.* 2013). The percentage of these feeding buzzes trains to non-feeding buzzes was calculated for each day, station and phase with the following equation (modified after Carlström 2005 & Kyhn *et al.* 2018):

$$\textbf{Feeding buzz trains}\,[\%] = \frac{\textbf{Number<10 ms}}{\textbf{Number>10 ms+Number<10 ms}} \times \mathbf{100}\% \qquad \text{Equation 2}$$

where Number < 10 ms is the number of ICIs less than 10 ms and Number > 10 ms is the number of ICIs more than 10 ms.

2.3.3. Statistical analysis

The conduction of the statistical tests, the analyses and the figures were made with R, Version 3.5.1 (R Foundation 2018). The indicated time throughout this thesis is the Universal Time Coordinated (UTC).

To examine whether there is a difference in the DPM between the different C-POD stations, the Kruskal-Wallis-Test was conducted. The Kruskal-Wallis-Test is a non-parametric test, which can be used to determine if there are statistically significant differences between a dependent, non-normally distributed variable and more than two groups of an independent variable (McKight & Najab 2010). In this study, the dependent variable is DPM, while the independent variable is “C-POD stations”. The one-way ANOVA is the parametric alternative to the Kruskal-Wallis-Test, which is only suitable for normally-distributed data (McKight & Najab 2010). Because the data in this study are not normally distributed, the Kruskal-Wallis-Test was chosen. The testing of normal distribution was conducted by the Kolmogorov-Smirnov-Test. It is important to mention that the Kruskal-Wallis-Test provides information on whether there is a significant difference between groups (McKight & Najab 2010). However, it cannot pinpoint which specific groups of the independent variable differ significantly from each other (McKight & Najab 2010). This question can be analyzed with a post-hoc test

(Dinno 2015). It was found that the Dunn Test is an appropriate post-hoc test following the Kruskal-Wallis-Test (Dinno 2015). It is based on a pairwise multiple comparison between groups in case the Kruskal-Wallis-Test has detected significant differences (Dinno 2015). In this study, the Dunn Test was conducted to check between which C-POD stations a significant difference was pronounced. By applying this post-hoc test, the risk of incorrectly rejecting the null hypothesis increased ("false positive finding", Armstrong 2014). This α risk rises, when multiple pairwise tests are performed simultaneously on a single data set (Armstrong 2014). To reduce this type I error, a Bonferroni correction was used in this study.
Furthermore, the detections per hour of C-POD recording were determined for each day, phase and station. The Mann-Whitney-U test was used to assess differences in the detections between day and night for each station. This test is similar to the Kruskal-Wallis-Test, but it is limited on the comparison of only two independent groups (Mann & Whitney 1947, Nachar 2008). In this study, the two independent variables are day and night. To investigate whether the harbour porpoise detections differ between the different stations during day or night, the Kruskal-Wallis test with the Dunn test was conducted.
Moreover, the detections per hour of C-POD recording were calculated for each day, diel phase (morning, day, evening and night) and station. Potential differences in the detections during the diel phases at each C-POD station and between the different C-POD stations were analyzed with the Kruskal-Wallis-test and the Dunn test as a post-hoc test.
Finally, the Kruskal-Wallis-test with the Dunn test was used to examine potential differences in the amount of feeding buzz trains during the diel phases at one C-POD station and between the different C-POD stations.

2.4. Visual monitoring

2.4.1. The theodolite

The theodolite is a surveyor's instrument, which is used for angular measurements in the field of geodesy (Vieira & Barros 2015). It is applied in many different areas like for example in automobile manufacturing, shipbuilding, the oil industry and railways constructions (Vieira & Barros 2015). Nowadays, it is a common tool to observe marine mammals in their natural habitats without disrupting them (Piwetz *et al.* 2018, see Chapter 1.2.3. for an overview about studies conducted with the theodolite). The theodolite measures horizontal- and vertical angles, which are used to calculate the surfacing position of an observed marine mammal species (Piwetz *et al.* 2018). The horizontal angle is defined as the difference between two determined directions (Resnik & Bill 2018). It is measured on a plane perpendicular to the vertical axis (Nathanson *et al.* 2017). The angle between the zenith and the target direction is called vertical angle (Resnik & Bill 2018). The zenith is perpendicular to the horizon, so that it is on the vertical axis directly above the instrument (Nathanson *et al.* 2017, Fig. 12). The typical unit of the measured angles is gon, whereby 1 gon = 0.9° (Kahmen 2006). Thus, 90° corresponds to 100 gon and 360° corresponds to 400 gon (Kahmen 2006).

During this study, the theodolite Leica Flexline TS06 plus was used for the visual monitoring of the harbour porpoise. The theodolite consists of three main parts: a tripod, a substructure and a superstructure (Fig. 12, Witte & Schmidt 2004). A secure standing of the theodolite is ensured by the tripod (Witte & Schmidt 2004). It must be screwed tightly with the substructure, which consists of a tribrach with three foot screws (Witte & Schmidt 2004). The rotatable superstructure is composed of a telescope carrier, a telescope with an ocular lens and a fine focusing drive (Witte & Schmidt 2004). The theodolite also includes a level (Resnik & Bill 2018). The level is used to precisely adjust the instrument and thus secure exact measurements (Witte & Schmidt 2004).

The used theodolite in this study is shown in Fig. 12. It has a memory capacity of 10 MB, which results in around 60.000 measurements (Leica Geosystems AG 2008). The batteries of the theodolite can run for approximately 30 h (Leica Geosystems AG 2008).

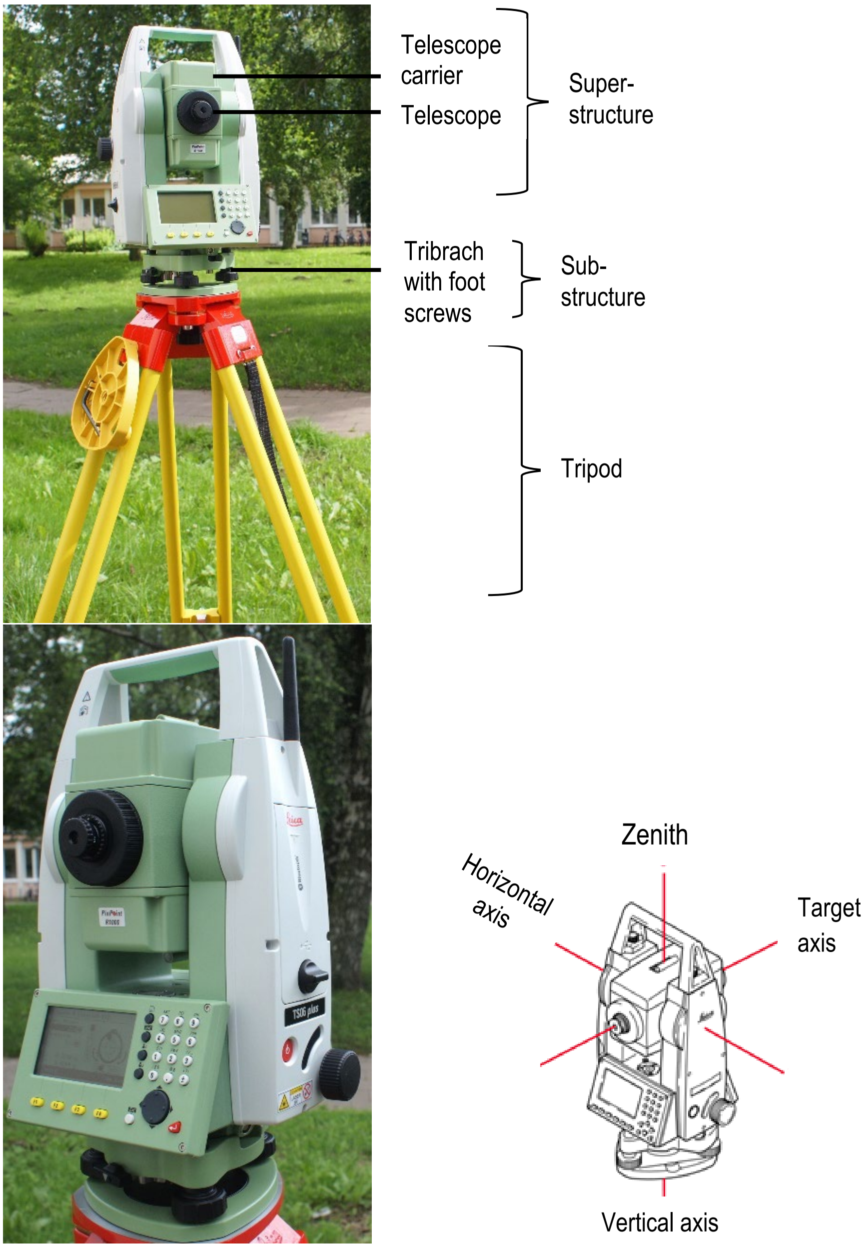


Fig. 12: The theodolite (Leica Flexline TS06 plus) was used for the visual monitoring of the harbour porpoise from 30th July to 2nd September 2018 in Fyns Hoved (Denmark). The two photos were made by Matthias Naumann (Faculty for Agricultural and Environmental Sciences, University of Rostock, Germany) and modified for this thesis by the author. The figure shows the different axes of a theodolite (modified after Zeiske 2000).

To obtain measurements as exactly as possible, the theodolite must be set up correctly. Firstly, the instrument must be centered above the observation point (Kahmen 2006). This means that the red laser point of the theodolite beams vertically into the center of the theodolite on the ground (Witte & Schmidt 2004). This is possible by rotating the foot screws of the tribrach (Witte & Schmidt 2004). Secondly, the vertical axis of the instrument must be adjusted perpendicularly (Witte & Schmidt 2004). This is the case, when the level bubble of the theodolite is in the middle of its level (Resnik & Bill 2018). The level bubble can be moved by changing the length of the tripod's legs (Kahmen 2006). It is important that nobody leans against the tripod or the instrument during the measurement (Nathanson *et al.* 2017). Otherwise, the setting up of the theodolite must be checked again (Nathanson *et al.* 2017).

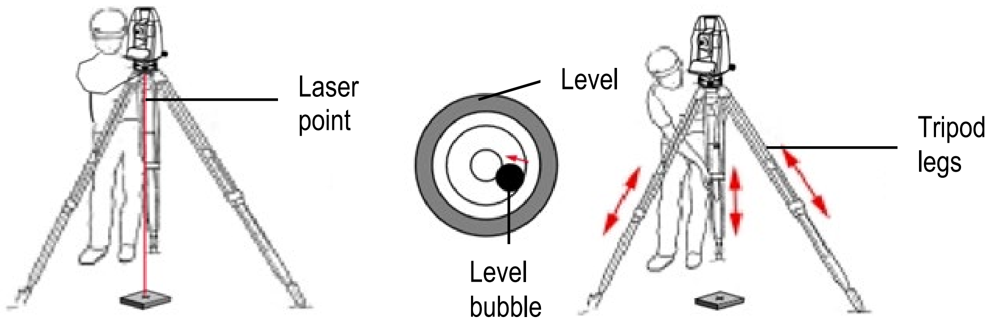


Fig. 13: Setting up the theodolite for angular measurements. The laser point is needed to center the theodolite. The level is used to adjust the instrument perpendicularly (modified after Zeiske 2000).

For this study, the measurement method "Freie Stationierung" was used. This means that the observation position can be chosen freely, depending on the local conditions (Resnik & Bill 2018, Zeiske 2000). The coordinates of this position can be calculated internally in the instrument by angle measurements to known fixed points (Zeiske 2000). Subsequently, the coordinates can be saved, so that the following measurements refer to the given coordinate system (Resnik & Bill 2018). Two fixed points, also called reference points, with known coordinates, are required for this method (Resnik & Bill 2018, Zeiske 2000). In this study, two boulders on the beach were the reference points: one was in the north (ref. point "A") and the other one was in the south (ref. point "B") of the observation area (see Fig. 14). Both were marked with color, so that they were used as reference points during each observation day. The GPS-position of these two reference points was measured with a Real Time Kinematic GPS device (RTK-GPS). This setting process was done on each observation day prior to the start of the measurements.

Fig. 14: Overview of the reference points "A" and "B" and the observation place during the study period from 30th August to 2nd September 2018 in Fyns Hoved (Denmark).

2.4.2. Study setup and procedure

Before the actual observation began, a "theodolite-training" was conducted for the observers on 30th July 2018 to standardize the data collection. This training was needed because it takes some experience to learn tracking marine mammals. This is especially the case for animals which only surface for seconds, like the harbour porpoise (Piwetz *et al.* 2018). The data collected during this day was not included in the analysis of the study.

The visual observation took place from 31st July to 25th August 2018 on a 19 m high cliff in Fyns Hoved in Denmark (see Fig. 15). It was found that the sightings of cetaceans decrease with increasing Beaufort Sea state (Clarke 1982). Teilmann (2003) concluded that a Beaufort Sea state of 3 is the maximum until which an exact detection of harbour porpoise is realizable without introducing errors. Consequently, to ensure accurate data collection, the observations were only implemented with a maximum Beaufort Sea state of 3. Therefore, an observation on a daily basis was not always possible. The dates and time periods of observation can be seen in Tab. 4. A classification of the sea states, developed by Beaufort, is shown in Tab. 5.

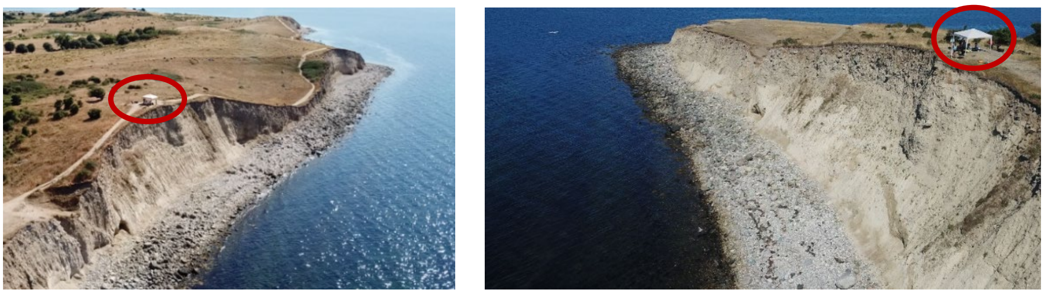


Fig. 15: Cliff in Fyns Hoved (Denmark), from which the visual monitoring of the harbour porpoise took place. The red circle shows the observation position during the study period from 30th July to 2nd September 2018. The photos were made by the Thünen Institute for Baltic Sea Fisheries in Rostock, Germany.

Tab. 4: Date and time period of the visual harbour porpoise observation during the study period from 30th July to 2nd September 2018 in Fyns Hoved (Denmark).

Date	Observation	Hours of observation
31.07.2018	08:30 - 16:40	8h 15min
01.08.2018	08:30 - 17:40	9h 10min
02.08.2018	08:30 - 17:30	9h
03.08.2018	09:00 - 17:00	8h
06.08.2018	13:30 - 17:15	3h 45min
07.08.2018	09:00 - 17:00	8h
08.08.2018	10:00 - 17:00	7h
09.08.2018	09:00 - 16:00	7h
13.08.2018	09:55 - 17:00	7h 5min
15.08.2018	09:00 - 17:00	8h
17.08.2018	09:40 - 17:40	8h
22.08.2018	08:30 - 16:30	8h
23.08.2018	08:30 - 16:15	7h 45min
24.08.2018	08:15 - 11:15	3h
25.08.2018	13:00 - 15:30	2h 30min
Total: 15 days		**Total: 104h 30min**

Tab. 5: Definition of the Beaufort's sea state from 0 – 3. The sea state scale ranges up to sea state 12. Here, only the description of the sea states is shown, at which the visual observation during this study period took place. Modified after Teilmann 2003 and after the National Centers for Environmental Prediction (Storm Prediction Center 2019)

Sea state	Wind speed [m/s]	Wind description	Appearance of wind effects
0	0 – 0.5	calm	Sea like a mirror
1	0.5 – 1.8	Light air	Patchy areas with ripples
2	1.8 – 3.4	Light Breeze	Small wavelets, no whitecaps
3	3.4 – 5.4	Gentle Breeze	Large wavelets, few whitecaps

If the weather conditions allowed, every observation day had the following procedure:

After setting up the theodolite, its height was measured with a tape measure. The method "Freie Stationierung" was chosen, the reference points were tracked with the theodolite and the theodolite position was calculated. All these values are needed to afterwards calculate the position of the tracked harbour porpoises (see chapter 2.4.3. for the calculation). Three persons with almost similar experience were grouped as observers during the whole study period. Some days, a fourth person helped as an additional observer.

The observation area was divided into two parts based on the position of the C-PODs deployed in this study. The first part ranged from C-POD station 10 in the south to C-POD station 5 and the second part ranged from C-POD station 5 to C-POD station 1 in the north (see Fig. 10 for the positions of the C-PODs). There were three different tasks implemented by the observers on each observation day. One person scanned the first part of the study area for harbour porpoises, whereas the second person looked for this species in the second part of the study area. For scanning, they used their eyes and binoculars. The third person waited until a porpoise was sighted. Then, this person had the task of taking notes. The break was necessary because the observation of marine mammals is a demanding task, which requires a high level of concentration.

After half an hour of observation, the three observers switched their tasks. This rotation in tasks was conducted to reduce observer-related differences in harbour porpoise sightings.

As soon as a harbour porpoise or a group of them was detected by the observers, their position was taken with the theodolite. Each time they were sighted again, they were repeatedly tracked with the theodolite. Thus, it was possible to follow their movement. The porpoises were tracked until they left the study area or until they were out of sight. One definition of a "group" was introduced by the researcher Shane (1990): "Dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity". This definition was applied for harbour porpoises in this study. A track was defined as a series of theodolite positions which were of the same porpoise group (Marley e*t al.* 2017 a).

Beside the tracking with the theodolite, the following data was reported in a protocol: date, time, number of sighted animals and their swimming direction, wind speed and -direction, temperature, Beaufort Sea state, number of points tracked with the theodolite and if possible, particular remarks. These remarks include e.g. mother with her calf or the number of boats within the observation area. A template of the protocol can be seen in the Annex in Tab. 18. At the end of each observation day, the collected data was transferred to a computer.

2.4.3. Analysis of theodolite data

With the help of the measured horizontal and vertical angles, it is possible to calculate the x- and y coordinates of the tracked porpoises. In geodesy, it is common that the axes of a coordinate system are interchanged in comparison to mathematics (Huber 2007). This means that the abscissa shows the y-axis as East-values (y_East), whereby the ordinate shows the x-axis as North-values (x_North, Huber 2007). The measured angles were converted in the unit radiant [rad] with the equation (Gruber & Joeckel 2007):

$$\mathbf{1\ rad} = \frac{\mathbf{200}}{\boldsymbol{\pi}}\ \mathbf{gon} \qquad \text{Equation 3}$$

To obtain the coordinates of the tracked harbour porpoises, the following calculation steps are required:

First, the total height of the theodolite at a given time (i) ($\mathrm{h_{sum}}\ (\mathrm{i})$) must be calculated. For this, the tripod height of the theodolite, the cliff height and the sea level changes are required. The measured cliff height at the first observation day was 19.73 m. This height value was used for the whole study. The sea level changes can be calculated from the data, recorded by the HOBO Water level data logger. One logger in the water measured the total pressure (air pressure + water pressure) in mbar and the other logger on the land measured the air pressure in mbar. The subtraction of the total pressure from the air pressure gives the water pressure in mbar (König & Lipp 2007):

$$\mathbf{water\ pressure\ [mbar] = total\ pressure -\ air\ pressure} \qquad \text{Equation 4}$$

The pressures in mbar were converted in the unit bar. Due to the fact that a water column of 1 m has a pressure of around 0.098 bar (König & Lipp 2007), the water depth at a given time (i) can be calculated for each given water pressure:

$$\mathbf{1\ m \sim 0.098\ bar}$$

$$\mathbf{10.20\ m \sim 1\ bar}$$

$$\mathbf{water\ depth\ (i)\ [m] = water\ pressure\ [i] * 10.20\ m} \qquad \text{Equation 5}$$

The calculated water depth at the deployment day of the HOBO Water level data logger was used as reference value of the water depth (water depth ref.). Subsequently, the change in the sea level at a given time (i) ($\mathrm{c_s}\ (\mathrm{i})$) can be calculated with the following equation:

$$\mathbf{c_s\ (i)\ [m] = water\ depth\ (i) - water\ depth\ ref.} \qquad \text{Equation 6}$$

The total height of the theodolite at a given time (i) ($\mathrm{h_{sum}}\ (\mathrm{i})[m]$) can be determined with the following equation:

$$\mathbf{h_{sum}}\ (\mathbf{i})[\mathbf{m}] = \mathbf{h_t}\ (\mathbf{i}) + \mathbf{h_c} + \mathbf{c_s}\ (\mathbf{i})$$ Equation 7

h_t (i) = tripod height of the theodolite at the day (i) [m]

h_c = cliff height [m]

c_s (i) = change of the sea level at the time (i) [m]

Next, the horizontal distance (d) is needed to obtain the coordinates of the porpoises. It can be calculated with the following trigonometric equations (Ebrecht e*t al.* 2003):

$$\boldsymbol{\alpha}' = \boldsymbol{\alpha} - \mathbf{1.5708\ rad}\ \ (1.5708 \text{ rad corresponds to } 90°)$$ Equation 8

Because α'' is an alternate angle of α', α'' has the same angle as α' (Erbrecht e*t al.* 2003).

$$\tan \boldsymbol{\alpha}'' = \frac{\mathbf{h_{sum}}\ (\mathbf{i})}{\mathbf{d}}$$ Equation 9

$$\mathbf{d} = \frac{\mathbf{h_{sum}}\ (\mathbf{i})}{\tan \boldsymbol{\alpha}''}$$ Equation 10

d = horizontal distance [m]

α = measured vertical angle with the theodolite [rad]

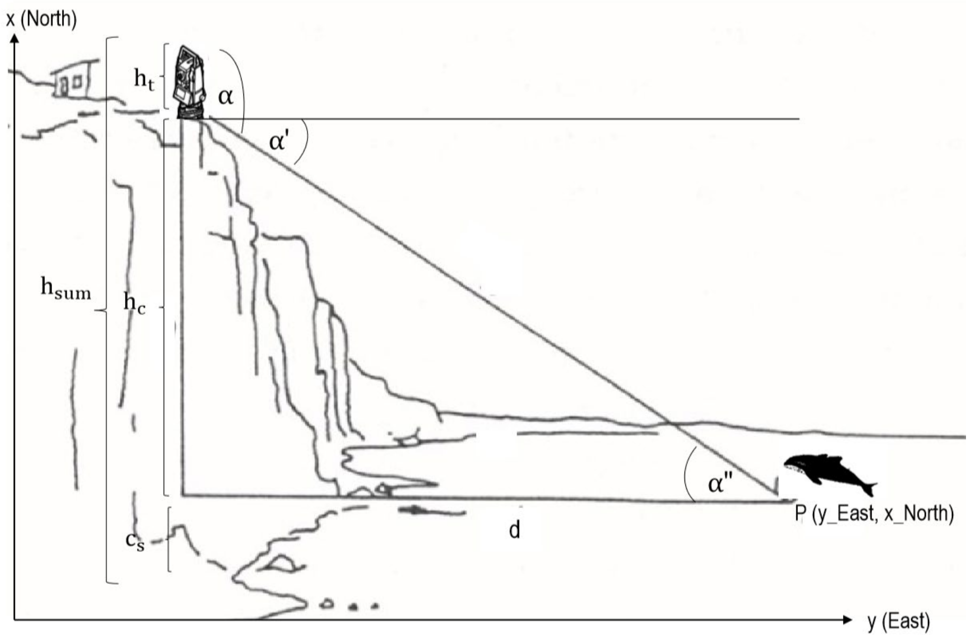


Fig. 16: Variables, which are required to determine the coordinates of a sighted porpoise. $\mathbf{h_{sum}}$ = total height of the theodolite, $\mathbf{h_t}$ = tripod height of the theodolite, $\mathbf{h_c}$ = cliff height, $\mathbf{c_s}$ = change of the sea level, d = horizontal distance, α = measured vertical angle with the theodolite, P = position of a sighted porpoise. Modified after Harzen 2002.

Finally, the coordinates of a sighted porpoise (P (y_East, x_North) can be determined with the equation (Gruber & Joeckel 2007):

$$\mathbf{P\ (y\_East) = T\ (y\_East) + \Delta y}$$ Equation 11

with: $\Delta \mathbf{y} = \mathbf{d} * \mathbf{sin}\,\boldsymbol{\beta}$ Equation 12

and: $\mathbf{P}\ (\mathbf{x\_North}) = \mathbf{T}\ (\mathbf{x\_North}) + \Delta \mathbf{x}$ Equation 13

with: $\Delta \mathbf{x} = \mathbf{d} * \mathbf{cos}\,\boldsymbol{\beta}$ Equation 14

$\mathrm{T\ (y\_East)} =$ East coordinate of the theodolite position

$\mathrm{T\ (x\_North)} =$ North coordinate of the theodolite position

$\beta =$ measured horizontal angle with the theodolite [rad]

$\mathrm{d} =$ horizontal distance [m]

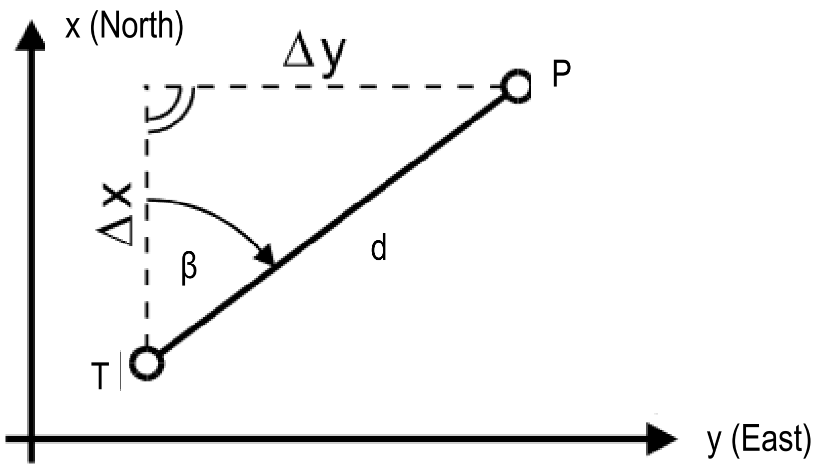


Fig. 17: Determination of the coordinates of a sighted harbour porpoise. **P** = sighted porpoise, **T** = theodolite position, **d** = horizontal distance, **β** = horizontal angle. Modified after Gruber & Joeckel 2007.

The tracked harbour porpoises were drawn on maps, which were created with ArcGIS, Version 10.3 (2013). All the maps were based on the UTM zone 33N (Universal Transversal Mercator) coordinate system. In order to compare the harbour porpoise sightings on the different days, the sightings per hour of observation were calculated for each observation day.

One aim of this study was a comparison of the harbour porpoise detections with C-PODs and that with a theodolite. It was found that the probability of detecting a porpoise decreases with the distance to the C-POD (Kyhn *et al.* 2012). Nuuttila *et al.* (2018) calculated that the mean maximum detection range for porpoises was 248 m (95% CI: 181 – 316 m). This means that only these visual sightings can be used for a comparison, which were in a certain range of the respective C-POD station. For this study, a distance of 100 m from the position of a visual sighting to the respective C-POD station was chosen. Thus, the distance of each visual porpoise sighting (P(x, y)) to each C-POD station (C(x, y)) was calculated with the following equation (Erbrecht *et al.* 2003):

$$\mathbf{Distance} = \sqrt{(\mathbf{P(x)} - \mathbf{C(x)})^{\mathbf{2}} + (\mathbf{P(y)} - \mathbf{C(y)})}^{2}$$ Equation 15

For the comparison, it is important to mention that the C-POD can only record Detection Positive Minutes and not absolute numbers of harbour porpoise detections. To make the two monitoring methods comparable, not the absolute number of visual sightings were used, but also Detection Positive Minutes. A value of “0” indicates that no harbour porpoise was sighted visually within one minute, while a value of “1” means that at least one harbour porpoise was sighted by the observers within one minute.

3. Results

3.1. Environmental parameters

The following chapter provides a presentation of the environmental parameters, which were measured from 29th July to 3rd September 2018.

Fig. 18 illustrates the environmental parameter, which was recorded at the measuring station "Odense Lufthavn" by the Danish Meteorological Institute (DMI). As Fig. 18 indicates, all parameters fluctuated from 29th July to 3rd September 2018. The first measured parameter was the air temperature (Fig. 18 a.). It ranged from 8.50 °C on 2nd September to 31.60 °C on 7th August. The mean air temperature amounted to 18.11 °C ± 4.42 °C.

Next, the humidity was recorded (Fig. 18 b.). The mean humidity amounted to 76.12 % ± 16.66 %. The lowest measured humidity amounted to 29.20 % on 7th August, while the highest measured humidity was 97.80 % on 24th August.

Furthermore, the air pressure was measured (Fig. 18 c.). Its mean was 1017 mbar with a standard deviation of 3.14 mbar. There was a sudden drop in the measured pressure to 1006 mbar on 25th August. The highest pressure was 1024 mbar on 29th August.

The wind speed in m/s was recorded as well (Fig. 18 d.). The wind blew with a speed between 0.200 m/s on 29th August and 11.60 m/s on 10th August. The mean wind speed was 3.58 m/s ± 1.76 m/s.

Finally, the wind direction was determined (Fig. 18 e.). A wind direction of 90 degrees means that the wind blew from the east, while a wind direction of 180 degrees indicates south wind. West wind has a direction of 270 degrees and north wind has a direction of 360 degrees. During this study period, the mean wind direction was 209 degrees. Thus, the wind mostly blew from southwest.

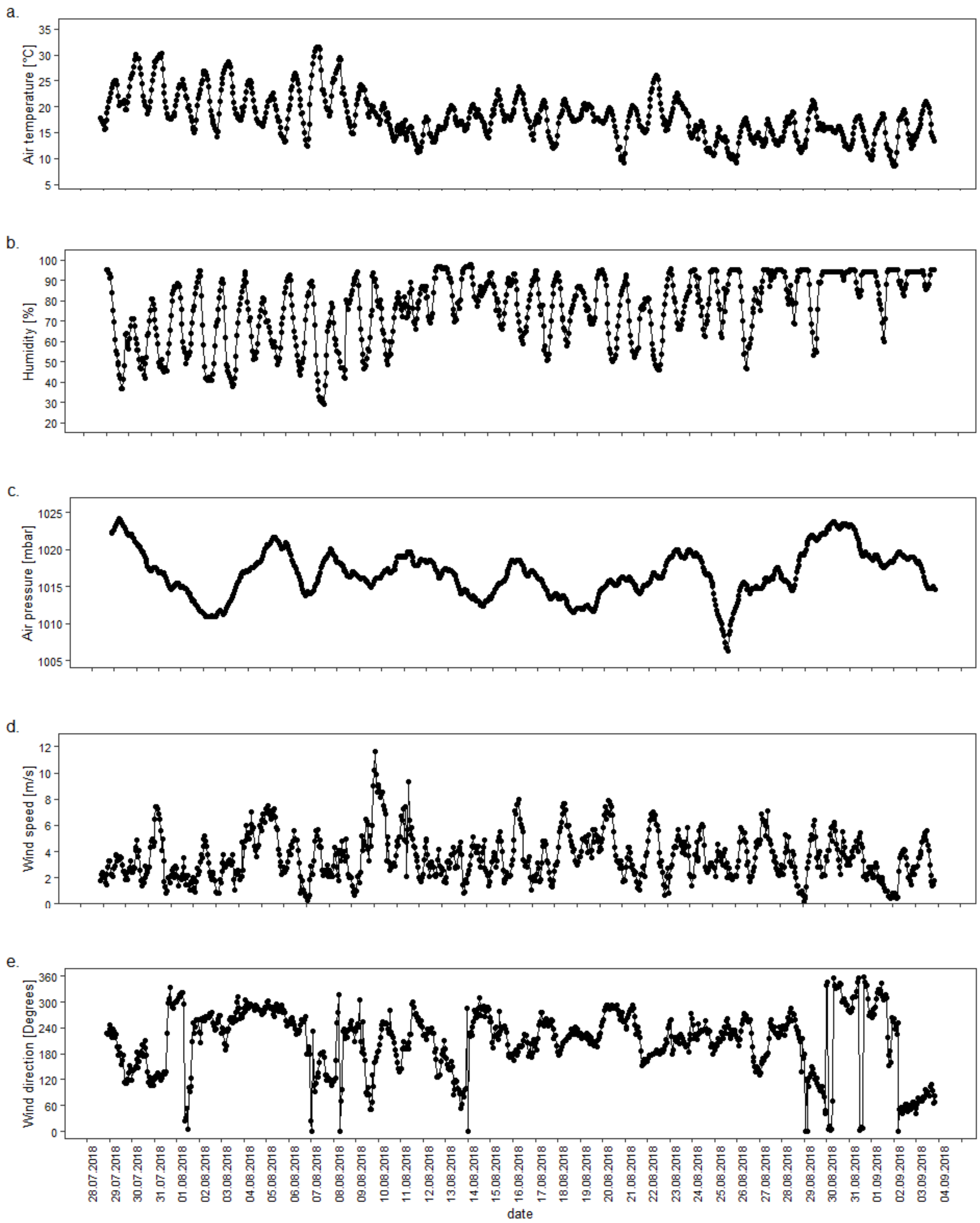


Fig. 18: Environmental parameter of the air at the measuring station "Odense Lufthavn" of the Danish Meteorological Institute (DMI) during the time period from 29th July 2018 to 3rd September 2018. **a.** Air temperature in °C, **b.** Humidity in %, **c.** Air pressure in mbar, **d.** Wind speed in m/s, **e.** Wind direction in degrees.

Additionally, a DST-CTD data logger and a HOBO Water Level Data Logger have measured the following parameter during the study period in Fyns Hoved, Denmark (see Fig. 19):

The first measured parameter was the water temperature in °C (Fig. 19 a.). The water has a mean temperature of 19.41 °C ± 1.66 °C. It is visible that the temperature increased slightly at the beginning of the study period. It reached its maximum on 4th August with a value of 22.52 °C. From then on, it decreased slightly until 30th August, when it reached its minimum of 14.5 °C. After this day, the temperature increased again and it remained more or less constant for the last four days of the study period.

Next, the salinity of the coastal water was recorded (Fig. 19 b.). As Fig. 19 b. shows, the salinity fluctuated during the beginning of the measurements. The lowest salinity was measured on 6th August with a value of 14.17 PSU. From 13th August on, the salinity remained more or less constant. There was a sudden increase in the salinity on 30th August with a maximum of 26.03 PSU. The mean salinity was 20.21 ± 2.15 PSU. In the Kattegat, the salinity has typical values between 18 and 26 PSU (Leppäranta & Myrberg 2009).

The third measured parameter was the water pressure in mbar (Fig. 19 c.). It ranged from 1563 mbar on 27th August to 1683 mbar on 20th August. The mean water pressure was 1637 mbar ± 18.36 mbar.

Moreover, the conductivity in mS/cm of the water was measured (Fig. 19 d). The lowest measured conductivity was 21.80 mS/cm on 6th August, while the highest measured conductivity was 32.67 mS/cm on 30th August. The mean conductivity amounted to 28.58 mS/cm ± 2.09 mS/cm.

Finally, the sound velocity of the water was measured (Fig. 19 e.). It can be seen that the sound velocity reached values up to 1511 m/s on 3rd August, whereby the mean was 1502 ± 3.0 m/s. The lowest sound velocity was recorded on 30th August with a value of 1494 m/s.

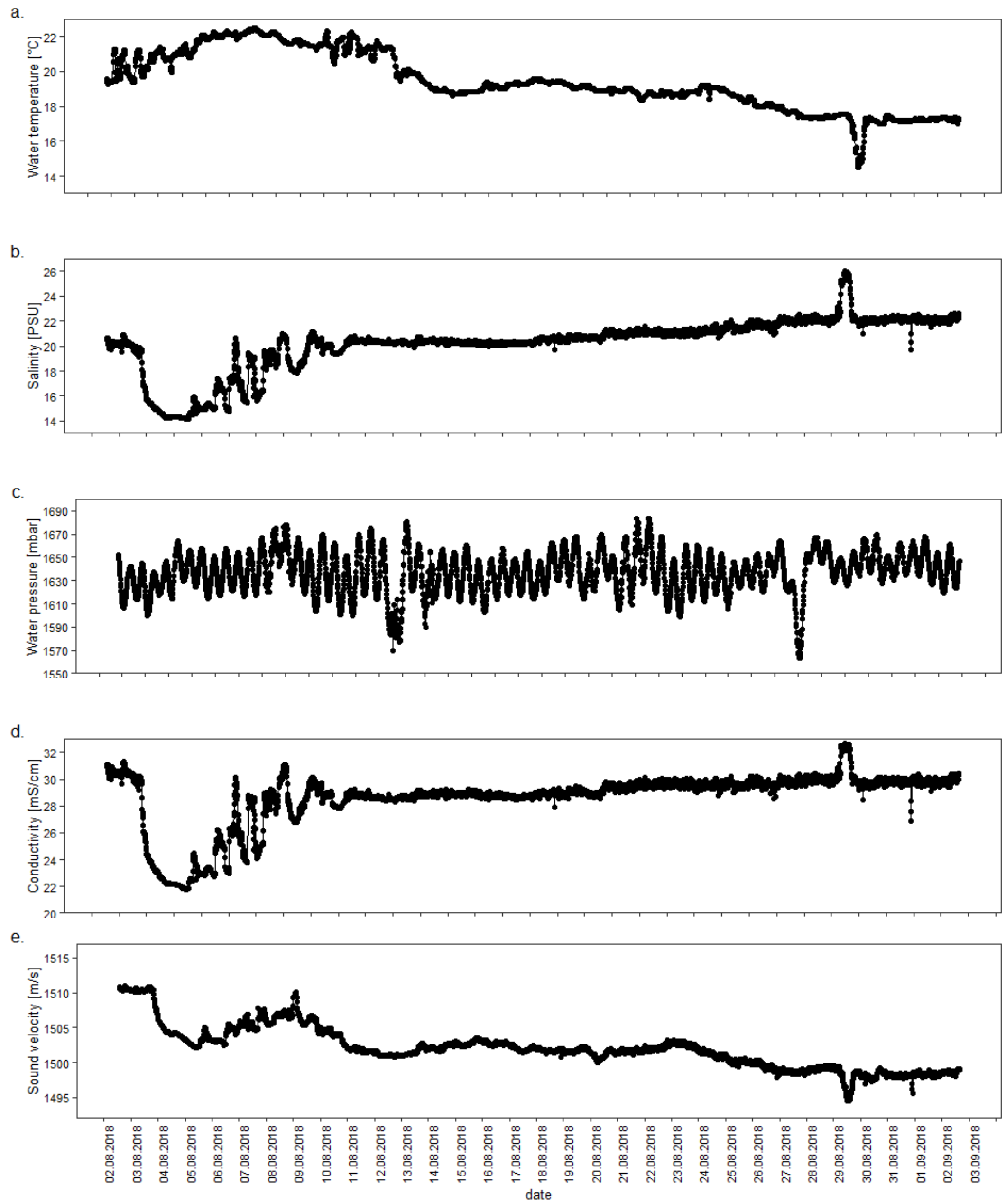


Fig. 19: Environmental parameter of the coastal water in Fyns Hoved (Denmark) during the time period from 29th July 2018 to 3rd September 2018. **a.** Water temperature in °C, **b.** Salinity in PSU, **c.** Water pressure in mbar, **d.** Conductivity in mS/cm, **e.** Sound velocity in m/s.

3.2. Acoustic detections of harbour porpoises

In the following, the harbour porpoise clicks recorded by the C-PODs will be analyzed. The first part of this chapter presents a potential seasonal pattern in the harbour porpoise detections, while the second part outlines a possible diel pattern of the harbour porpoise activity. In the following, the term “detections” will be used throughout this thesis. It does not represent the absolute numbers of detections. It relates to Detection Positive Minutes (DPM), unless it is mentioned explicitly otherwise.

The frequency spectrum of the identified harbour porpoise clicks is shown in Fig. 20. It is clearly visible that the frequency of the clicks per train ranged from 122 kHz to 143 kHz. The mean click frequency is 129.8 kHz with a standard deviation of 4.64 kHz.

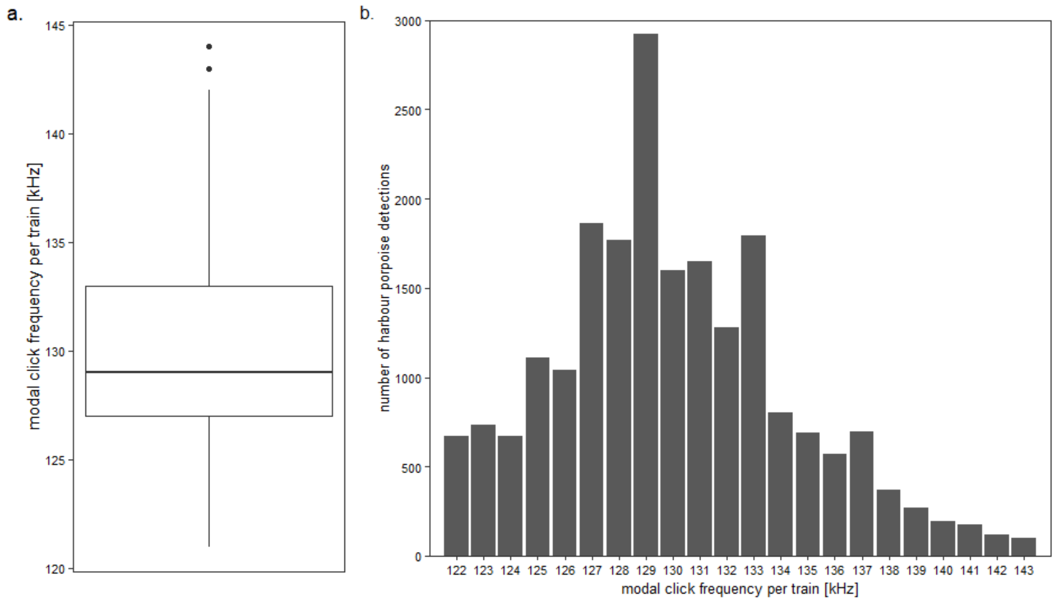


Fig. 20: Modal click frequency per train of the detected harbour porpoises during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark.

As a first overview, detections of harbour porpoises at each C-POD station are illustrated in Fig. 21. To investigate whether the harbour porpoise detections differ between the respective C-POD stations during the study period, the Kruskal-Wallis test was conducted. The results can be seen in Fig. 21. However, it is important to mention that the C-PODs at stations 5 and 6 were only deployed during day, while the other C-PODs were deployed during day and night. Thus, an exact comparison between stations 5 and 6 and the remaining stations was not possible for this illustration. Therefore, no statistical test was conducted between stations 5 and 6 and the other C-POD stations. The C-POD stations 5 and 6 were only illustrated for the sake of completeness in Fig. 21. The detections of the harbour porpoise varied significantly between the different C-POD stations (Kruskal-Wallis test, p-value = 2.939 ×

10^{-5}). The harbour porpoise was detected between zero and 8.46 times per hour at C-POD station 1. The Dunn test showed significant differences between C-POD station 1 and the stations 3 (p-value= 0.0117), 4 (p-value= 0.0036), 7 (p-value= 0.0019), 8 (p-value= 0.0072) and 9 (p-value= 0.0006). Significant differences between two stations are marked with the same symbol on top of the box plots. It is clearly visible that the median of detections was highest at C-POD station 1. At this station, the median amounted to 1.82 detections per hour of C-POD recording. In comparison, the median at the other stations ranged from 0.26 detections per hour at station 6 to 1.44 detections per hour at station 5. Additionally, the mean varied between the different stations: The mean at station 1 was 3.07 ± 2.66 harbour porpoise detections per hour of recording, while the mean at the other stations was between 0.36 ± 0.75 detections per hour at station 6 and 1.77 ± 1.53 detections per hour at station 2.

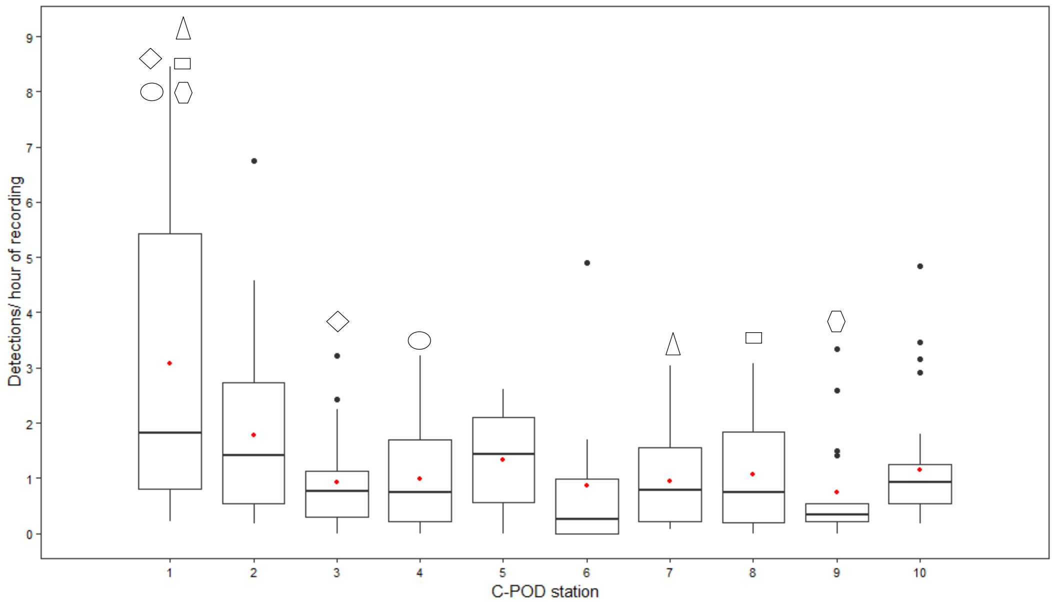


Fig. 21: Detections of harbour porpoise clicks per hour with at least one detection per minute from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark for C-POD stations 1 to 10 (see Fig. 10 for the position of each individual C-POD). The horizontal line inside the boxes is the median, while the red points show the mean. Box plots with the same symbol on top indicate a significant difference between each other. Significant differences were detected with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

3.2.1. Seasonal differences in harbour porpoise detections

The detections of harbour porpoises for each day of the study at C-POD station 1 and C-POD station 8 are illustrated in Fig. 22 and Fig. 23. These two stations were chosen because they differ significantly from each other. There was no proven significance between station 8 and the other remaining stations, so that station 8 can be used representatively for the other stations. The detections for each day of the study at the other stations can be seen in the Annex from Fig. 50 to Fig. 57. As Fig. 22 shows, more harbour porpoises were detected during the mid of August than during the beginning and end of August. Most harbour porpoises were detected on 15th August; namely 8.46 times per hour. The least porpoises were detected on 22nd August with 0.21 detections per hour. The sudden change in the number of detections between the days is recognizable. For example, on 21st August 7.04 harbour porpoises were detected per hour, while one day later, only 0.21 porpoises were recorded per hour.

In contrast to this station, at C-POD station 8 fewer porpoises were identified (Fig. 23). The highest number of detections was on 24th August with 3.08 detections per hour. No harbour porpoise was recorded on 5th August. More harbour porpoises were detected during the mid and during the end of August than during the beginning of the study period. This means that only between zero and 0.71 detections per hour were recorded until 13th August. After this day, the detections ranged between 0.46 and 3.08 per hour.

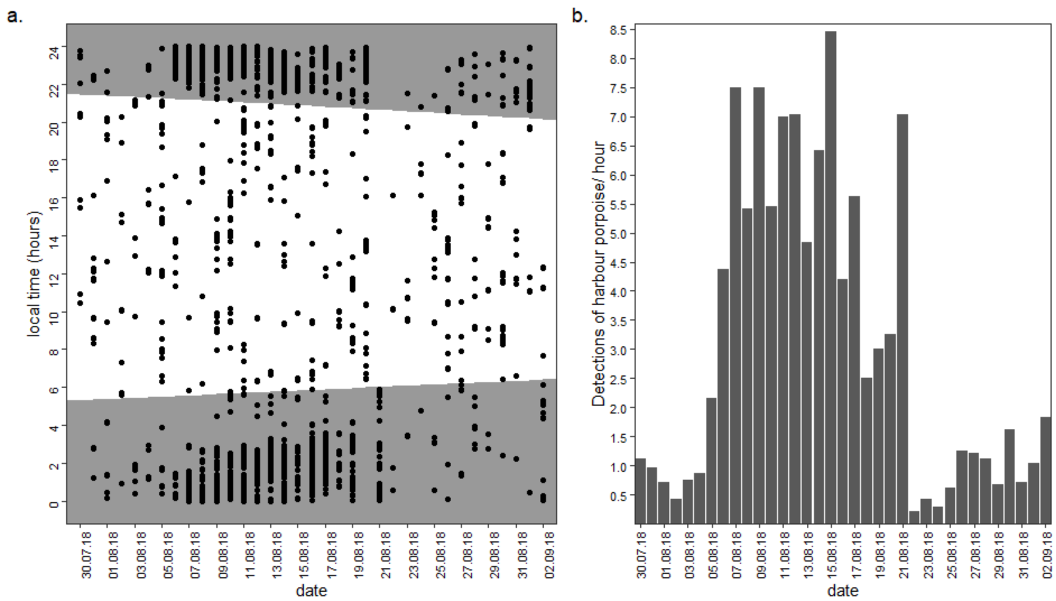


Fig. 22: C-POD 1: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

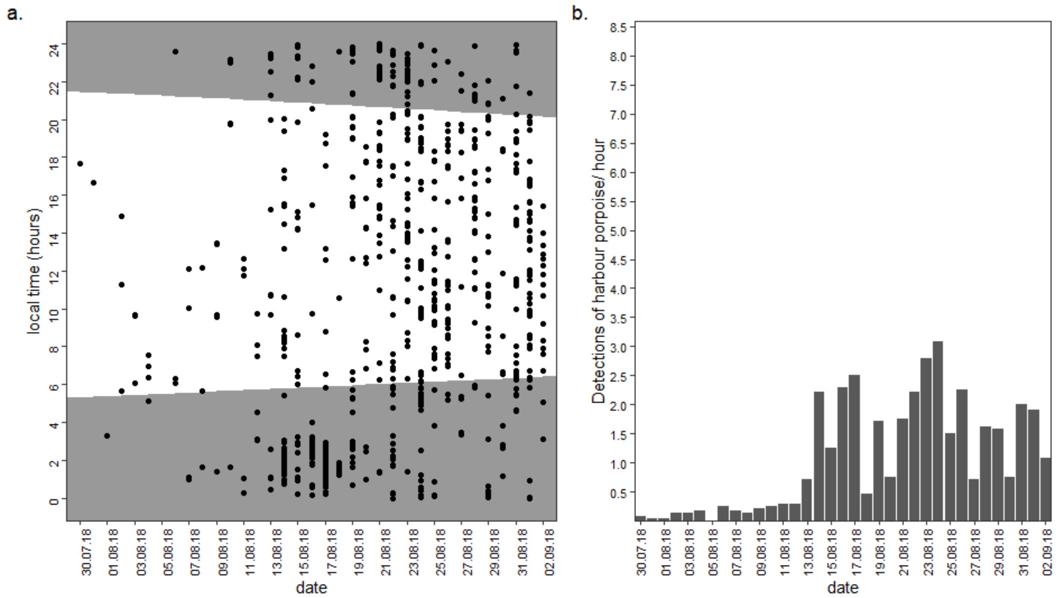


Fig. 23: C-POD 8: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

3.2.2. Diel differences in harbour porpoise detections

In this chapter, a possible diel pattern of the harbour porpoise activity will be presented. As a first step, it was investigated whether the number of detections differs between day and night. This was tested for each C-POD separately. The results are shown in Fig. 24 and in Fig. 25. Significant differences between day and night could be observed at C-POD station 1 (Fig. 24 a., Mann-Whitney-U test, p-value= 0.0005). Most harbour porpoises were detected at night with a maximum of 20.91 detections per hour on 13th August. During the day, the maximum amounted to only 2.16 detections per hour on 5th August. The mean detections per hour at night was 6.34 ± 7.10, while the mean during the day was 0.90 ± 0.59 detections per hour.

Furthermore, detections of the harbour porpoise differed significantly between day and night at C-POD station 2 (Fig. 24 b., Mann-Whitney-U test, p-value= 0.0010). It is evident that at this station, more harbour porpoises were detected at night than during the day. The mean harbour porpoise detections at night was 3.40 with a standard deviation of 4.33. In contrast, the mean detections during the day was 0.78 ± 0.62. The maximum of detected harbour porpoises at night was 13.41 detections per hour on 13th August. During day, the maximum of detected harbour porpoises was 2.27 detections per hour on 23rd August.

Moreover, the Mann-Whitney-U test revealed significant differences in the detections between day and night at C-POD station 10 with more detections at night than during the day (Fig. 25 d., p-value= 1.718×10^{-7}). As Fig. 25 d. shows, 7.96 was the maximum of detected harbour porpoises per hour at night. In comparison, the maximum of detections during the day was 4.31. The mean of detections at night amounted to 2.14 ± 1.94 detections per hour. During the day, the mean of harbour porpoise detections was 0.60 ± 0.98 detections per hour.

No significant differences in the detections between day and night could be found at the other C-POD stations. The C-POD stations 5 and 6 were not illustrated because they were only deployed during the day.

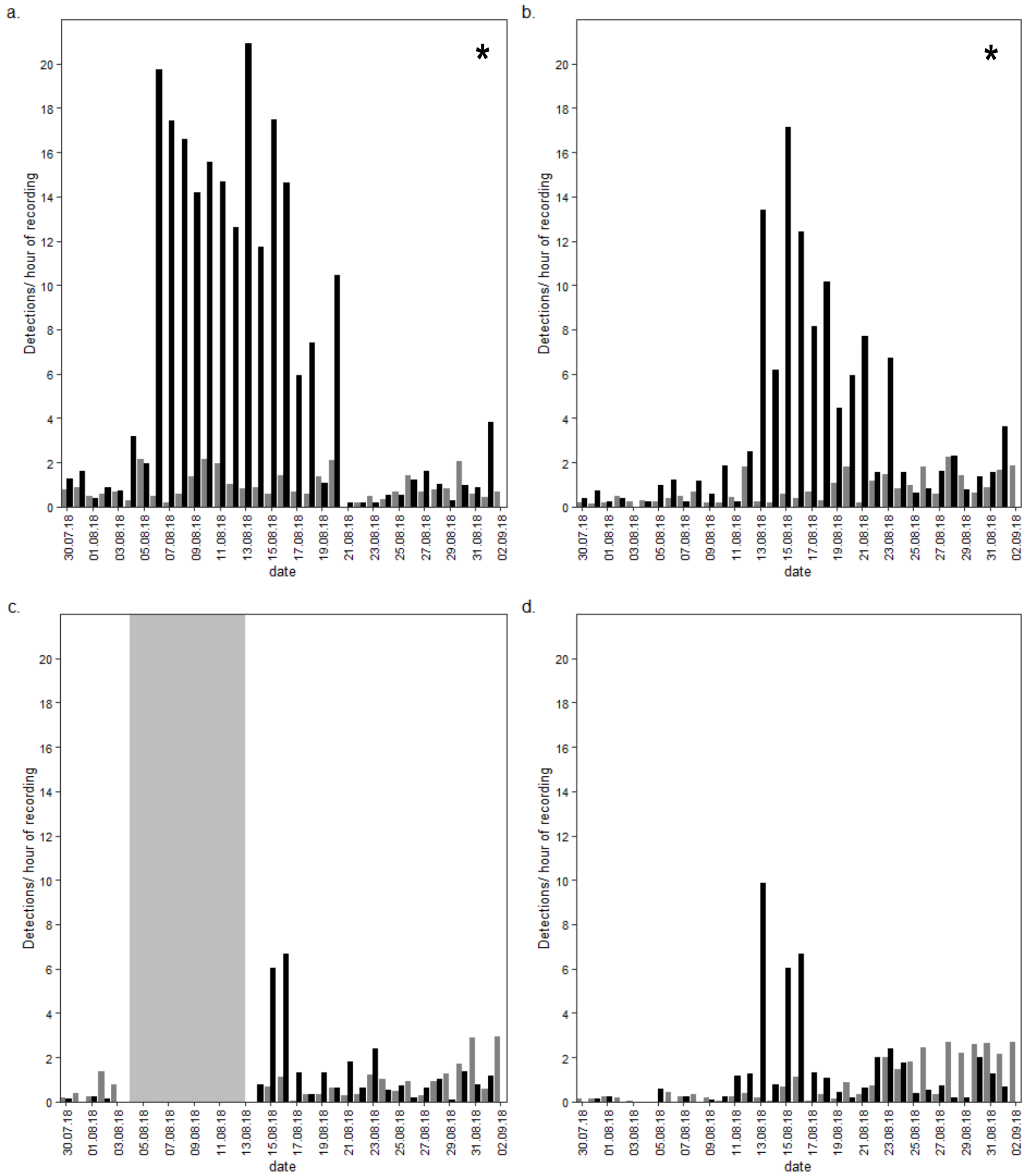


Fig. 24: Harbour porpoise detections per hour with at least one detection per minute at night (black bars) and during the day (grey bars) at C-POD stations **a.** 1, **b.** 2, **c.** 3 and **d.** 4 (see Fig. 10 for each individual C-POD position) in Fyns Hoved (Denmark). The grey area in Fig. 24 c. indicates a data gap. Significant differences between day and night at each C-POD station were tested with the Mann-Whitney-U test. The symbols in Fig. 24 a. and b. indicate significant differences between day and night.

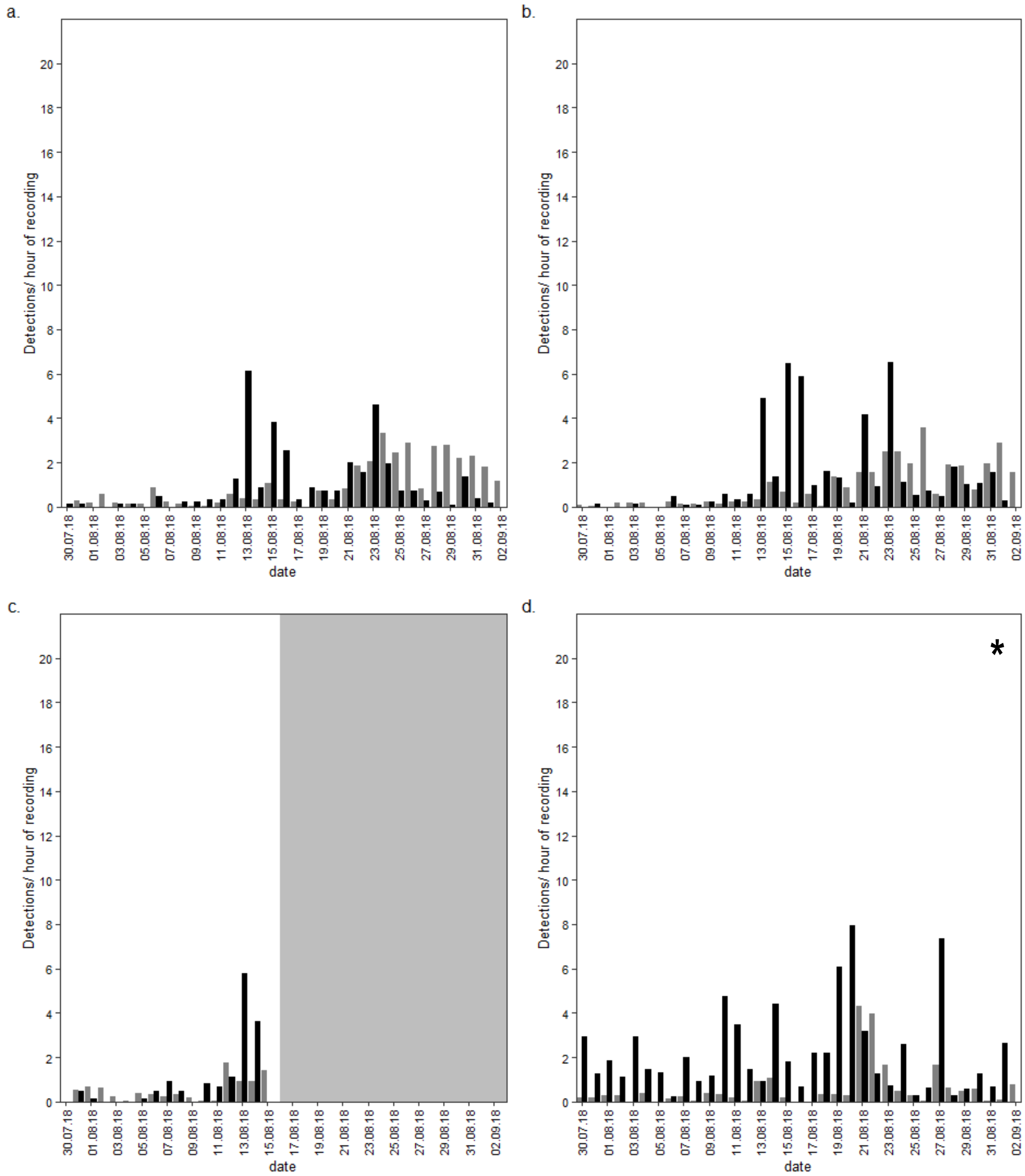


Fig. 25: Harbour porpoise detections per hour with at least one harbour porpoise detection per minute at night (black bars) and during the day (grey bars) at C-POD stations **a.** 7, **b.** 8, **c.** 9 and **d.** 10 (see Fig. 10 for each individual C-POD position) in Fyns Hoved (Denmark). The grey area in Fig. 25 c. indicates a data gap. Significant differences between day and night at each C-POD station were tested with the Mann-Whitney-U test. The symbol in Fig. 25 d. indicates significant differences between day and night at C-POD station 10.

As a second step, it was investigated whether the detections of the harbour porpoise differ significantly between the respective C-POD stations. This was tested for day and night separately. The results for the day can be seen in Fig. 26 and in Tab. 6. The detections per hour differed significantly between the individual C-POD stations during the day (Kruskal-Wallis test, p-value= 0.0002). For the day, the Dunn test identified significant differences between C-POD stations 1 and 6 (p-value= 0.0066), 1 and 10 (p-value= 0.0006), 2 and 6 (p-value= 0.0114), 3 and 6 (p-value= 0.0058) and between stations 7 and 6 (p-value= 0.0155).

At station 6, only a few porpoises were detected during the day (mean= 0.18 ± 0.38 detected porpoises per hour). In comparison, the mean value at the C-POD stations, which differ significantly from station 6, ranged between 0.78 ± 0.62 detected porpoises per hour at station 2 and 0.98 ± 1.01 detected porpoises per hour at station 7.

At night, the detections per hour significantly differed between the different C-POD stations as well (Fig. 26, Kruskal-Wallis test, p-value= 6.296×10^{-8}). The green fields in Tab. 7 indicates where there is a significant difference which was proven by the Dunn test. As can be seen in Fig. 26, at night the most porpoises were detected at station 1 (mean value= 6.34 ± 7.10 detections per hour of recording). Also, there were more detections of porpoises at station 2 than at the other stations (mean value= 3.40 ± 4.33 detections per hour of recording). The mean at the other stations varied between 0.92 ± 1.57 detections per hour of recording at station 9 and 2.20 ± 1.93 detections per hour at station 1.

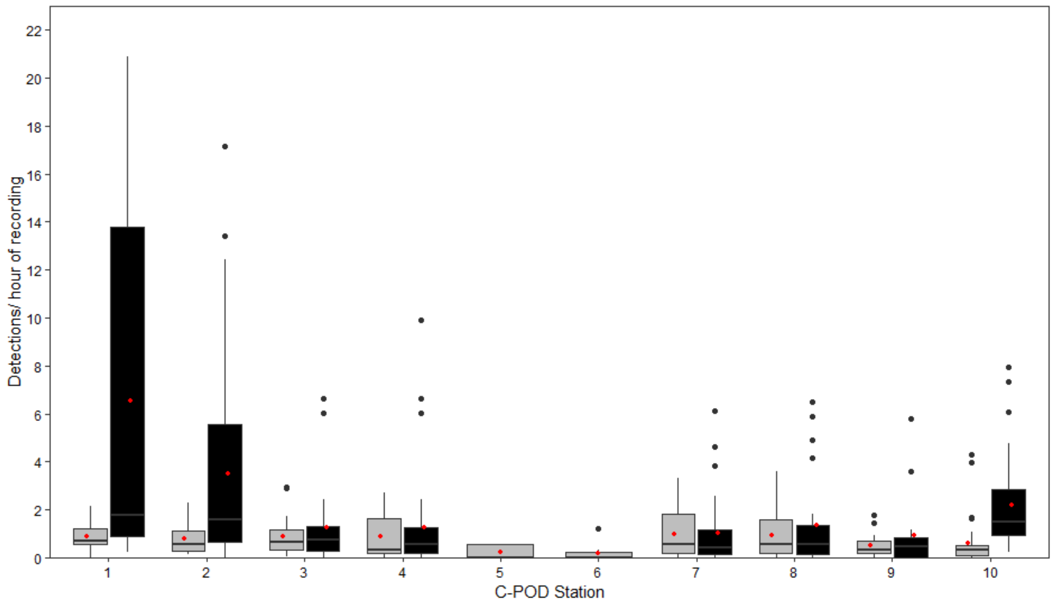


Fig. 26: Harbour porpoise detections per hour with at least one harbour porpoise detection per minute at night (black box plots) and during the day (grey box plots) for each C-POD station (see Fig. 10 for the position of each individual C-POD) from 30th July 2018 to 2nd September 2018 in Fyns Hoved (Denmark). The C-POD stations 5 and 6 have only box plots during the day because they were just deployed during the day. The horizontal line inside the boxes is the median, while the red points show the mean. Significant differences were revealed with the Kruskal-Wallis test and with Dunn test as a post-hoc test.

Tab. 6: Results of the pairwise comparison between the ten C-POD stations during the **day,** using the Dunn test. The green table fields indicate a significant difference between the respective C-POD stations during the day. The red table fields show where there was no significant difference between the respective C-POD stations during the day. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

	1	2	3	4	5	6	7	8	9	10
1										
2										
3										
4										
5										
6										
7										
8										
9										
10										

Tab. 7: Results of the pairwise comparison between the ten C-POD stations at **night,** using the Dunn test. The green table fields indicate a significant difference between the respective C-POD stations at night. The red table fields show where there was no significant difference between the respective C-POD stations at night. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

	1	2	3	4	7	8	9	10
1								
2								
3								
4								
7								
8								
9								
10								

With the division of the day into two phases, it was possible to identify differences in the detections of the harbour porpoise during day and night. The results showed significant differences between these two phases at some C-POD stations. The day was defined as the time between sunrise and sunset and the night as the time between sunset and sunrise. However, with a categorization of two phases, it was not possible to determine when exactly there were differences. For example: When significant differences were found during the day, it would be interesting to know whether more detections can be seen in the morning hours or in the afternoon. This is the same case for the night: With identifying differences in the detections at night, it is crucial to proof whether more detections can be reported in the evening hours or at night. Thus, with a more fine-scaled categorization of the day, these questions could be investigated. As a consequence, the day was classified into the four diel phases morning, day, evening and night.

Firstly, it was tested whether harbour porpoise detections differed between the single diel phases at each C-POD station. The results are shown in Fig. 27. The Kruskal-Wallis test demonstrated significant differences between the individual diel phases at all stations, except for stations 3 and 9. No tests were done for stations 5 and 6 because data at these stations was only collected during the day. With the help of the Dunn test, it was possible to identify between which diel phases there was a significant difference. Harbour porpoise detections, which differ significantly between two diel phases, have the same symbol on top of their box plot. It is visible that the detections did not differ significantly between all of the diel phases at each station. For example, at station 7, only the phases morning and evening differed significantly from each other. The most significant differences could be found at station 1 and 10. At both stations, four significant differences could be identified: between morning and evening, morning and night, day and evening and day and night. At C-POD stations 2, 4 and 8, most harbour porpoises were recorded at night. At C-POD station 7, most harbour porpoises were detected in the morning (mean= 1.42 ± 1.51 detections per hour). At C-POD station 10, most detections of harbour porpoises happened in the evening (mean= 3.37 ± 4.25 detections per hour).

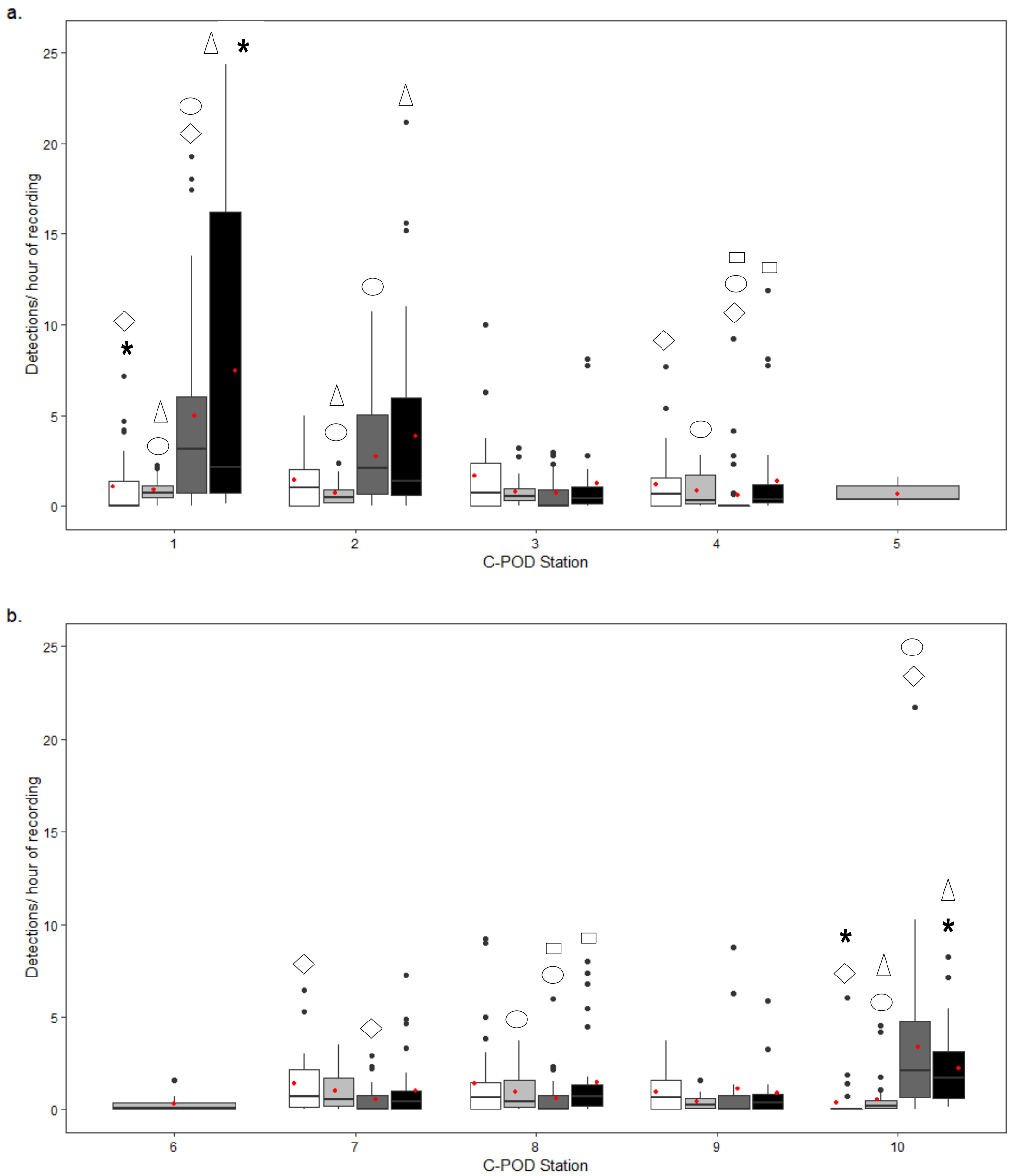


Fig. 27: Harbour porpoise detections per hour with at least one harbour porpoise detection per minute from 30^{th} July 2018 to 2^{nd} September 2018 in Fyns Hoved, Denmark for **a.** C-POD station 1 to 5 and for **b.** C-POD station 6 to 10 (see Fig. 10 for the position of each C-POD). The bar color indicates the day phase: white (morning), gray (day), dark gray (evening) and black (night) (see Tab. 3 for the definition of each diel phase). The horizontal line inside the boxes is the median, while the red points show the mean. Box plots with the same symbol on top indicate a significant difference between each other. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test. C-POD stations 5 and 6 have only data during the day, because they were deployed only during this time period.

Secondly, it was tested whether the detections of the harbour porpoise differ significantly between the individual C-POD stations at the different diel phases. The results are depicted in Fig. 28. In the morning, significant differences between the C-POD stations could be found (Fig. 28 a., Kruskal-Wallis test, p-value = 0.0008). The Dunn test showed that the detections differed significantly between stations 2 and 10 (p-value= 0.003), 3 and 10 (p-value= 0.0076) and 7 and 10 (p-value= 0.0006). At station 10, only very few harbour porpoises were detected in the morning. The mean amounted to 0.36 ± 1.11 detections per hour. In comparison, the means at station 2 is 1.44 ± 1.50 detections, at station 3 1.70 ± 2.39 detections and at station 7 1.42 ± 1.51 detections.

Furthermore, there were significant differences between the respective C-POD stations during the day (Fig. 28 b., Kruskal-Wallis test, p-value= 0.0010). The detections differed significantly between stations 1 and 6 (Dunn test, p-value= 0.0062) and between 1 and 10 during the day (Dunn test, p-value= 0.0019). At station 6, the least porpoises were detected with a mean of 0.30 ± 0.51 detections per hour. The mean at station 1 amounted to 0.89 ± 0.59 detections, while the mean at station 10 was 0.54 ± 1.02 detections.

In the evening, there were also significant differences between the individual C-POD stations (Fig. 28 c., Kruskal-Wallis test, p-value= 8.895×10^{-14}). It is visible that more harbour porpoises were detected at C-POD stations 1, 2 and 10 than at the remaining stations. The highest mean was calculated at station 1 with 4.96 ± 5.56 harbour porpoise detections per hour. At station 2 the mean was 2.75 ± 2.64 detections per hour, while the mean at station 10 was 3.37 ± 4.25 detections per hour. At the remaining stations, the mean ranged between 0.53 ± 0.77 detections per hour at station 7 and 1.15 ± 2.57 detections per hour at station 9.

Moreover, the Kruskal-Wallis test revealed significant differences between the C-POD stations at night (Fig. 28 d., p-value= 5.58×10^{-7}). During this diel phase, detections of the harbour porpoise differed significantly between C-POD station 1 and all other stations, except for stations 2 and 10. Furthermore, detections differed significantly between stations 7 and 10 (Dunn-test, p-value= 0.0110). Most harbour porpoises were recorded at station 1 with a mean of 7.45 ± 8.39 detections per hour. In contrast, the mean of detections at the other stations ranged from 0.91 ± 1.56 detections per hour at station 9 to 2.21 ± 2.06 detections per hour at station 10.

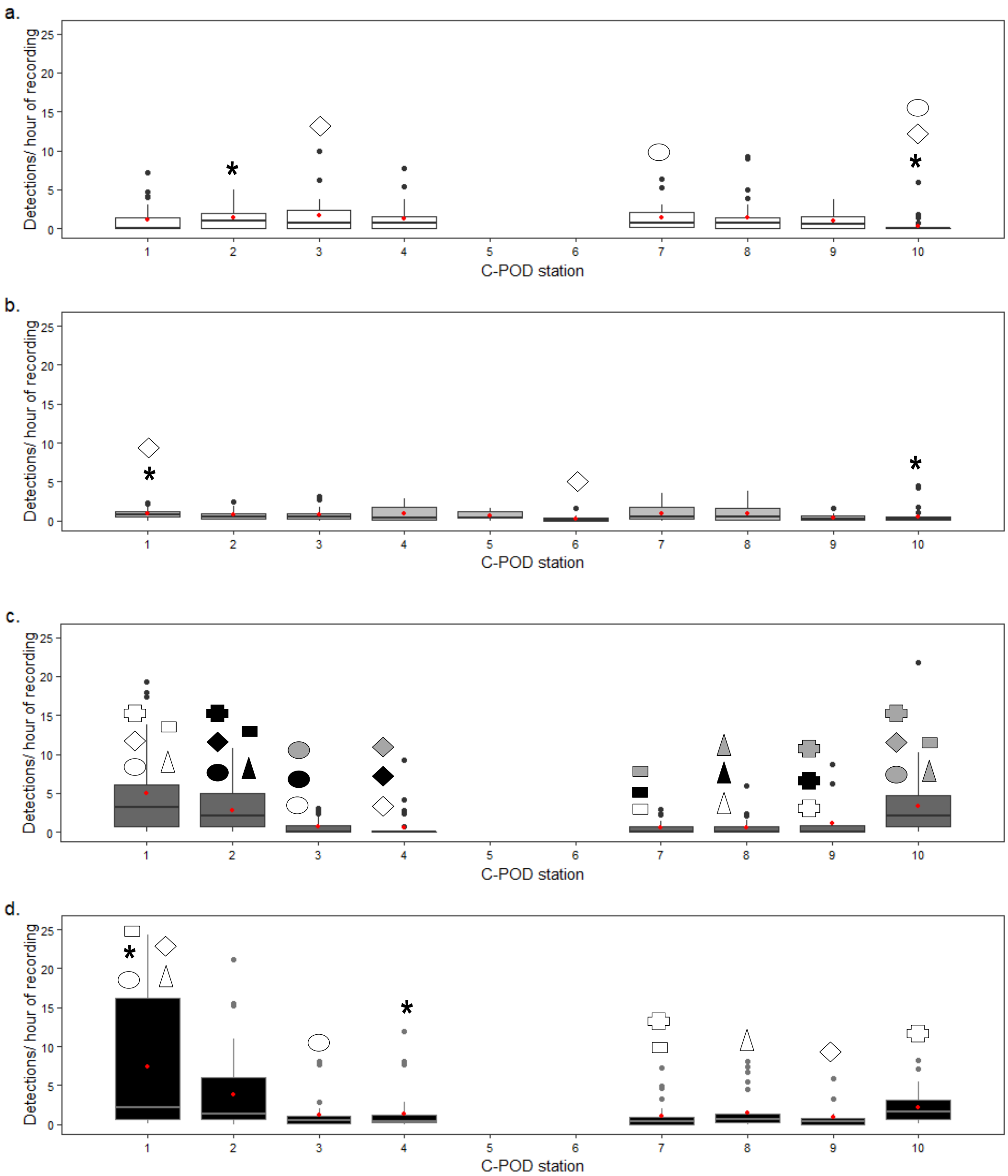


Fig. 28: Harbour porpoise detections per hour from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark for each C-POD station (see Fig. 10 for the position of each C-POD) during **a.** morning, **b.** day, **c.** evening and **d.** night (see Tab. 3 for the definition of each time period). The horizontal line inside the boxes is the median, while the red points show the mean. Box plots with the same symbol and color on top indicate a significant difference between each other. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

The main finding of this chapter can be summarized as follows: Significant differences could be found between the different diel phases at each C-POD station, except for station 3 and 9. Furthermore, significant differences were found between the C-POD stations during the four diel phases (morning, day, evening and night). Of particular note is the high number of detections at station 1 at night.

3.2.3. Behavior analysis of the detected harbour porpoises

After detecting differences in the activity of the harbour porpoise during the individual diel phases, it would be interesting to know what it does during each diel phase. A Minimum ICI below 10 ms (feeding buzz trains) was used as a potential indicator for feeding activity of the harbour porpoise. The findings are presented in this chapter.

At first, it was investigated whether the precentage of feeding buzz trains differs between the different diel phases at each C-POD station. At C-POD station 7, the percentage of feeding buzz trains differed significantly between each diel phase (Fig. 29 b., Kruskal-Wallis test, p-value= 0.03). The Dunn test showed significant differences between morning and night at station 7 with a higher porportion of feeding buzz trains in the morning than at night (p-value= 0.0238). The median of feeding buzz trains in the morning was 83.66 %, while it was 19.80 % at station 7 at night. The mean of feeding buzz trains amounted to 60.17 % with a standard deviation of 39.42 % in the morning. At night, the mean of feeding buzz trains was 32.31 % ± 31.06 %.

Furthermore, significant differences were detected during the different diel phases at C-POD station 8 (Fig. 29 b, Kruskal-Wallis test, p-value= 0.0225). It is visible that more feeding buzz trains were identified in the morning than in the evening (Dunn test, p-value= 0.0092). The mean of feeding buzz trains in the morning was 67.42 % ± 31.89 %, whereas it was 29.25 % ± 43.24 % in the evening.

No significant difference could be found between the different diel phases at the other C-POD stations. The C-PODs at stations 5 and 6 were only deployed during the day, so that data is only available for this time period.

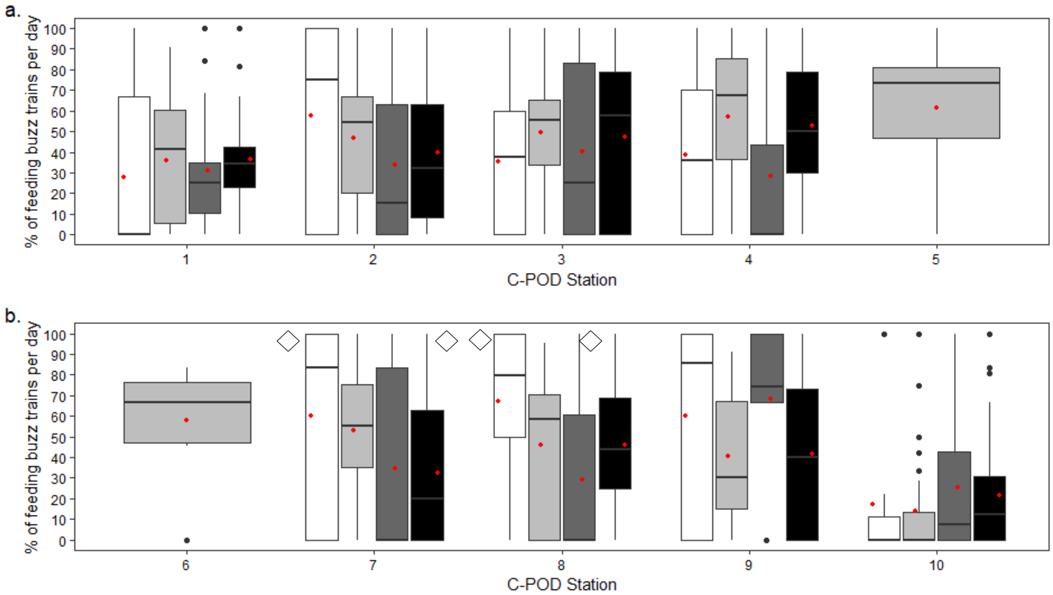


Fig. 29: Percentage of harbour porpoise feeding buzz trains (Minimum ICI < 10 ms) from 30^{th} July 2018 to 2^{nd} September 2018 in Fyns Hoved, Denmark for **a.** C-POD station 1 to 5 and for **b.** C-POD station 6 to 10 (see Fig. 10 for the position of each C-POD). The bar color indicates the diel phase: white (morning), gray (day), dark gray (evening) and black (night) (see Tab. 3 for the definition of each diel phase). The horizontal line inside the boxes is the median, while the red points show the mean. Box plots with the same symbol on top indicate a significant difference between each other. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

As a next step, the feeding buzz trains were statistically compared between the different C-POD stations within each diel phase. The results are presented in Fig. 30. In the morning (Fig. 30 a.) and in the evening (Fig. 30 c.), there were no significant differences in the feeding buzz trains between the individual C-POD stations. In contrast to these findings, the feeding buzz trains differed significantly between the respective C-POD stations during the day (Fig. 30 b., Kruskal-Wallis test, $p = 1.747 \times 10^{-5}$). A pairwise comparison using the Dunn test showed significant differences between C-POD Station 10 and 2 (p-value= 0.0019), 10 and 3 (p-value= 0.055), 10 and 4 (p-value= 0.0001),10 and 5 (p-value= 0.0013), 10 and 6 (p-value= 0.0189), 10 and 7 (p-value= 0.0001) and 10 and 8 (p-value= 0.0055). As the box plot at station 10 demonstrates, the percentage of feeding buzz trains was low during the day. The median was 0 % and the mean amounted to 13.74 % with a standard deviation of 25.20 %. By comparison, the median of feeding buzz trains at the other stations ranged from 30.43 % at station 9 to 77.85 % at station 5. The mean of feeding buzz trains between the other stations ranged from 36.16 % at C-POD station 1 to 64.87 % at C-POD station 5. During night, significant differences in the feeding buzz trains could be found between C-POD station 4 and C-POD station 10 (Fig. 30 d., Dunn test, p-value= 0.0022). As Fig. 30 d indicates, the median of feeding buzz trains was 12.5 % at C-POD station 10 and 50 % at C-POD station 4. The mean amounted to 21.34 % (standard deviation = 26.66 %) at station 10, whereas the mean at station 4 was 52.92 % with a standard deviation of 29.75 %.

It is important to mention that the C-POD stations 5 and 6 were only deployed during the day. Thus, data was just available for this time period at both stations.

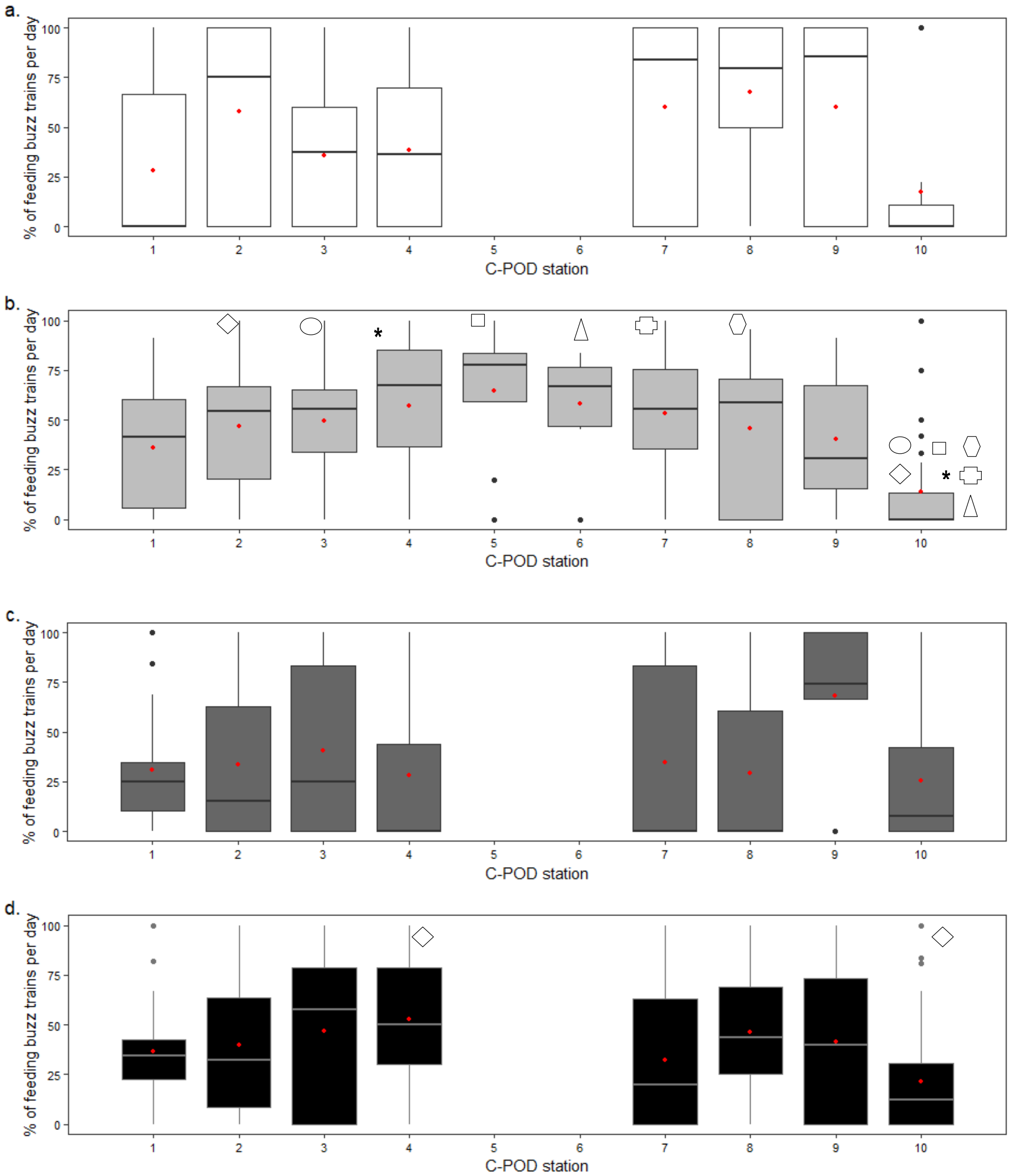


Fig. 30: Percentage of harbour porpoise feeding buzz trains (Minimum ICI < 10 ms) from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark for each C-POD station (see Fig. 10 for the position of each C-POD) during the diel phases **a.** morning, **b.** day, **c.** evening and **d.** night (see Tab. 3 for the definition of each diel phase). The white gaps at the C-POD stations 5 and 6 indicate a data gap. The horizontal line inside the boxes is the median, while the red points show the mean. Box plots with the same symbol on top indicate a significant difference between each other. Significant differences were tested with the Kruskal-Wallis test and the Dunn test as a post-hoc test.

As an example, the feeding buzz trains from two stations were plotted for each day of the study during the diel phases day (Fig. 31) and night (Fig. 32). The stations 4 and 10 were chosen because they differ significantly from each other. The black bars show the feeding buzz trains per day, whereas the grey bars show the non-feeding buzz trains per day. It is clearly visible that more feeding buzz trains were detected at C-POD station 4 than at C-POD station 10. This is recogniziable during the day as well as at night. However, it is important to consider that the the sample size per diel phase differed strongly between the different days. By way of illustration, the numbers inside the bars in Fig. 31 and in Fig. 32 represent the number of non-feeding buzz trains (red numbers) or the number of feeding-buzz trains (yellow numbers) per day. It is clearly visible that the amount of feeding buzz trains and non-feeding buzz trains varied between the individual days. For instance, on some days, only one train with a Minimum ICI below 10 ms was detected during the day at C-POD station 4, while on other days, over 80 trains with a Minimum ICI below 10 ms were detected during this diel phase (Fig. 31 a.). This is the same case for trains with a Minimum ICI above 10 ms at this station. On two days, even only two trains were recorded in total during the diel phase day at station 4. Similar results can be seen at station 4 at night and at station 10 during the day and at night.

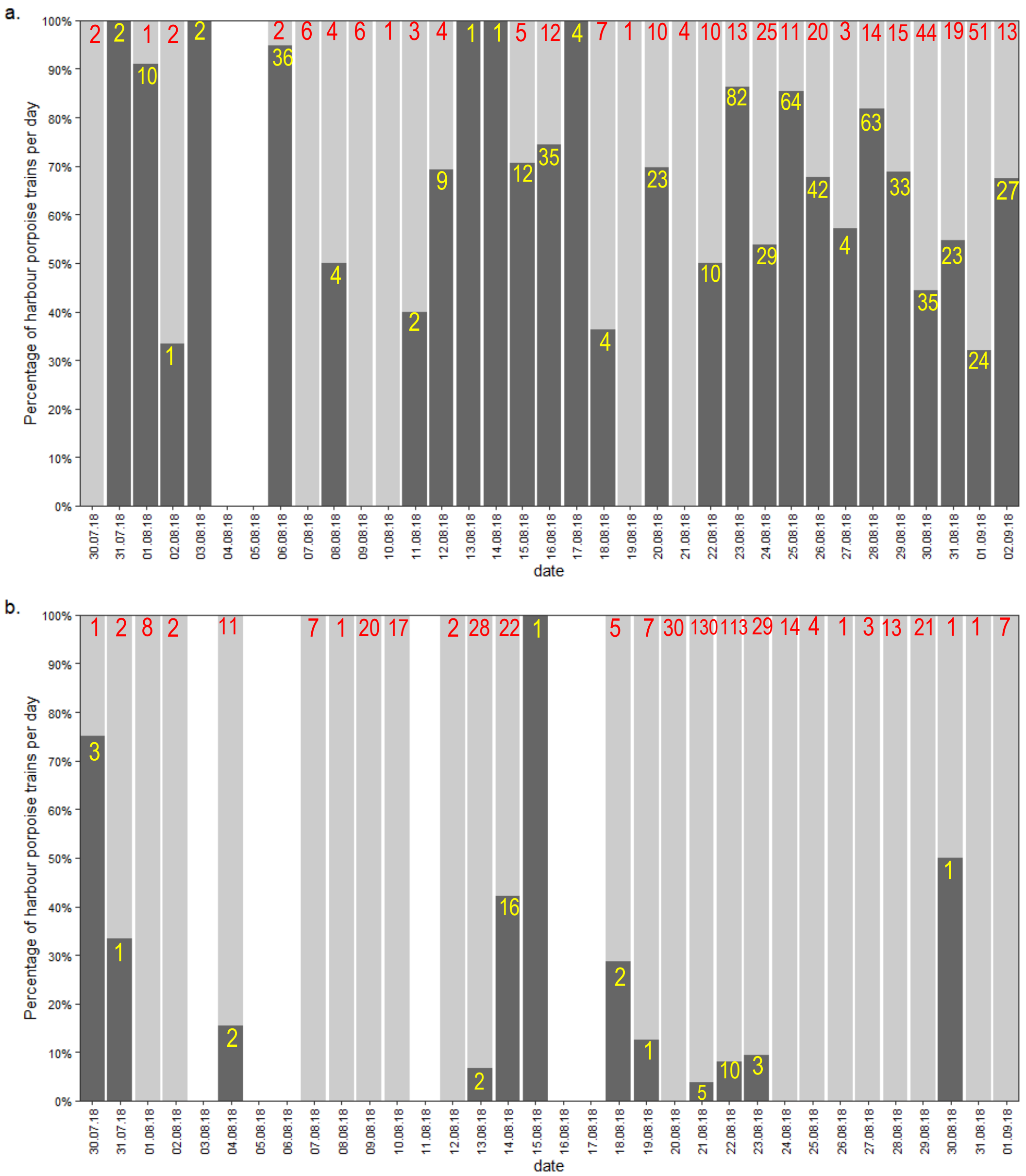


Fig. 31: Percentage of harbour porpoise trains during the diel phase **day** from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark at C-POD station 4 (**a.**) and at C-POD station 10 (**b.**) (see Fig. 10 for the position of the C-PODs and see Tab. 3 for the definition of each time period). Feeding buzz trains (Minimum < 10 ms) were shown as black bars (percentage per day) and as yellow numbers (amount per day). Non- feeding buzz trains (Minimum > 10 ms) were shown as grey bars (percentage per day) and as red numbers (amount per day). The white gaps indicate that no clicks were recorded on these days.

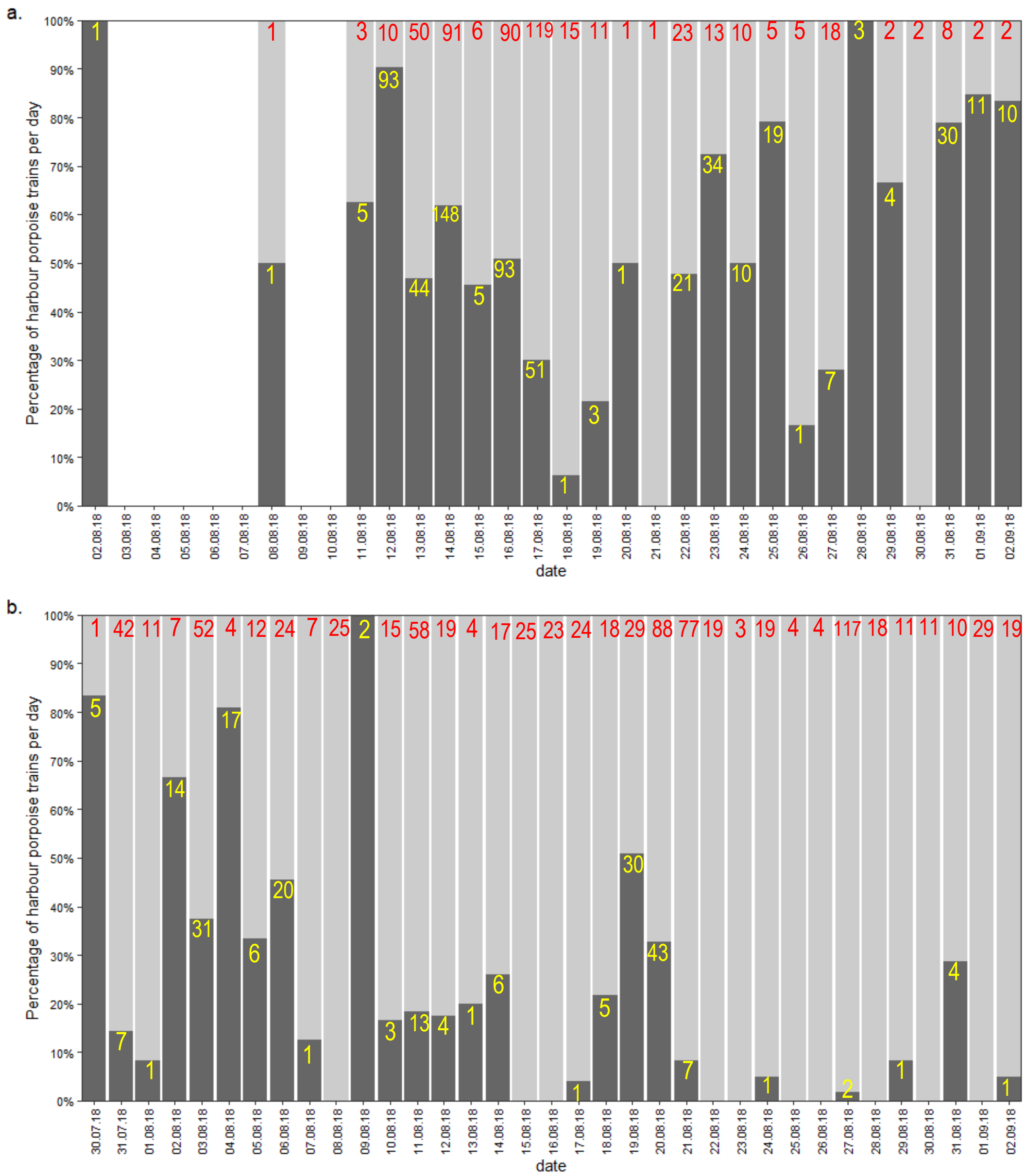


Fig. 32: Percentage of harbour porpoise trains during the diel phase **night** from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark at C-POD station 4 (**a.**) and at C-POD station 10 (**b.**) (see Fig. 10 for the position of the C-PODs and see Tab. 3 for the definition of each time period). Feeding buzz trains (Minimum < 10 ms) were shown as black bars (percentage per day) and as yellow numbers (amount per day). Non- feeding buzz trains (Minimum > 10 ms) were shown as grey bars (percentage per day) and as red numbers (amount per day). The white gaps indicate that no clicks were recorded on these days.

3.3. Visual detections of harbour porpoises

3.3.1. Seasonal and diel detections of harbour porpoises

In the following, the data of the visual harbour porpoise's monitoring is presented. Tab. 8 summarizes the observation period of this study. It is apparent from this table that the observation took place from 31th July 2018 to 25th August 2018. An every-day observation was not possible due to unfavorable weather conditions at some days. Thus, the visual monitoring was conducted on 15 days in total. As Tab. 8 shows, the observation time varied between the different days. It ranged from 2 hours and 30 min on 25th August to 9 hours and 10 min on 1st August. In total, the researchers spent 104 hours and 30 min in the field for the visual monitoring of the harbour porpoise.

Tab. 8: Time period of the visual harbour porpoise's monitoring with the theodolite in Fyns Hoved, Denmark.

Date	Observation	Hours of observation
31.07.2018	08:30 - 16:40	8h 15min
01.08.2018	08:30 - 17:40	9h 10min
02.08.2018	08:30 - 17:30	9h
03.08.2018	09:00 - 17:00	8h
06.08.2018	13:30 - 17:15	3h 45min
07.08.2018	09:00 - 17:00	8h
08.08.2018	10:00 - 17:00	7h
09.08.2018	09:00 - 16:00	7h
13.08.2018	09:55 - 17:00	7h 5min
15.08.2018	09:00 - 17:00	8h
17.08.2018	09:40 - 17:40	8h
22.08.2018	08:30 - 16:30	8h
23.08.2018	08:30 - 16:15	7h 45min
24.08.2018	08:15 - 11:15	3h
25.08.2018	13:00 - 15:30	2h 30min
Total: 15 days		**Total: 104h 30min**

In total, 209 harbour porpoise groups were tracked with the theodolite during the whole observation period. The group size varied between only one harbour porpoise and five harbour porpoises. Most of the sighted groups consisted of only one harbour porpoise (94 from a total of 209 groups) or of only two harbour porpoises (78 from a total of 209 groups), while a group of five porpoises was sighted only once. Fig. 33 summarized the size of each detected harbour porpoise group during this study.

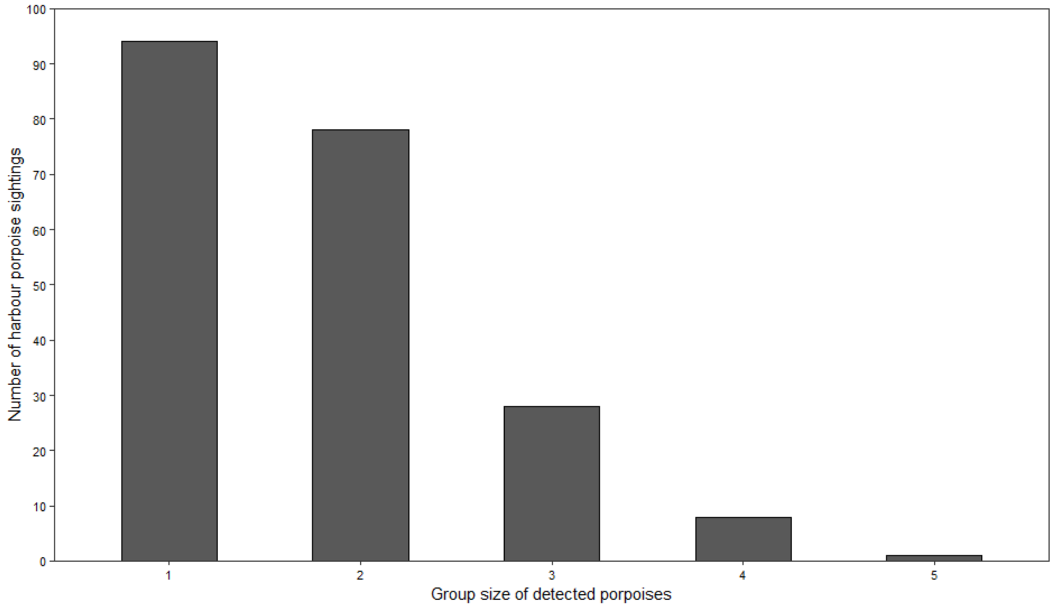


Fig. 33: Group size of the detected harbour porpoises during the visual observation from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

The sighted harbour porpoises during the observation are displayed in the following maps (Fig. 34 - Fig. 37). They show the first surfacing position of a sighted harbour porpoise group, which was tracked with the theodolite. This illustration was chosen for clarity reasons: The observers sighted a single group on some days around one hour, which resulted in up to 170 tracked positions with the theodolite for just one group. By adding the tracking, you can see that a total of 3588 points was tracked with the theodolite. Thus, the total number of tracked surfacing points for each group is not shown. As can be seen in the maps, most harbour porpoise groups were sighted on 25th August with a total number of 26 groups during this day. The least porpoise groups were detected on 6th August with only four groups.

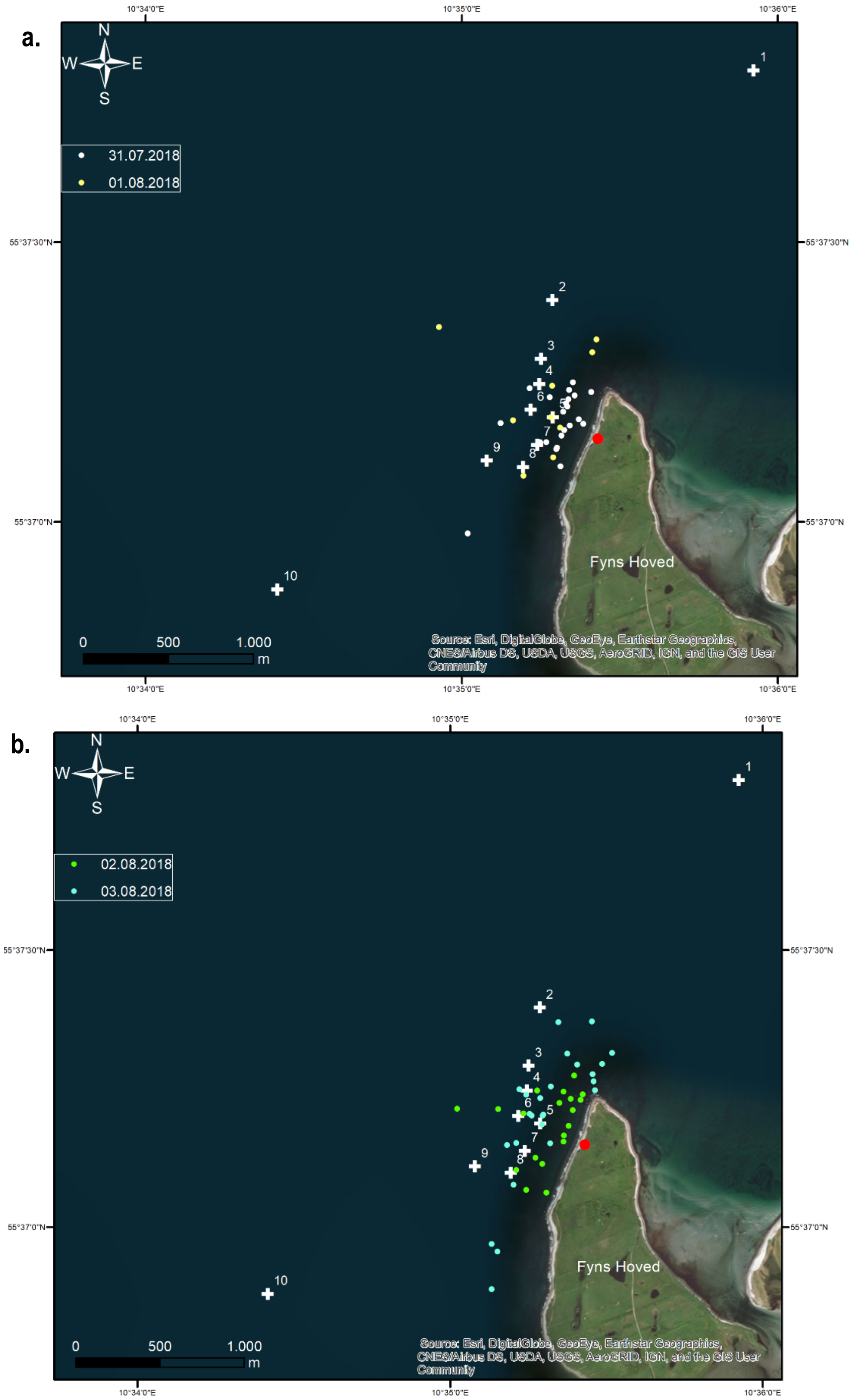


Fig. 34: Overview of the sighted harbour porpoise groups in Fyns Hoved on **a.** 31st July 2018 and 1st August 2018 and on **b.** 2nd August 2018 and 3rd August .2018. Each point presents the first surfacing point, which was tracked with a theodolite. The white crosses show the position of each deployed C-POD and the red point on the land shows the observation place during the study period.

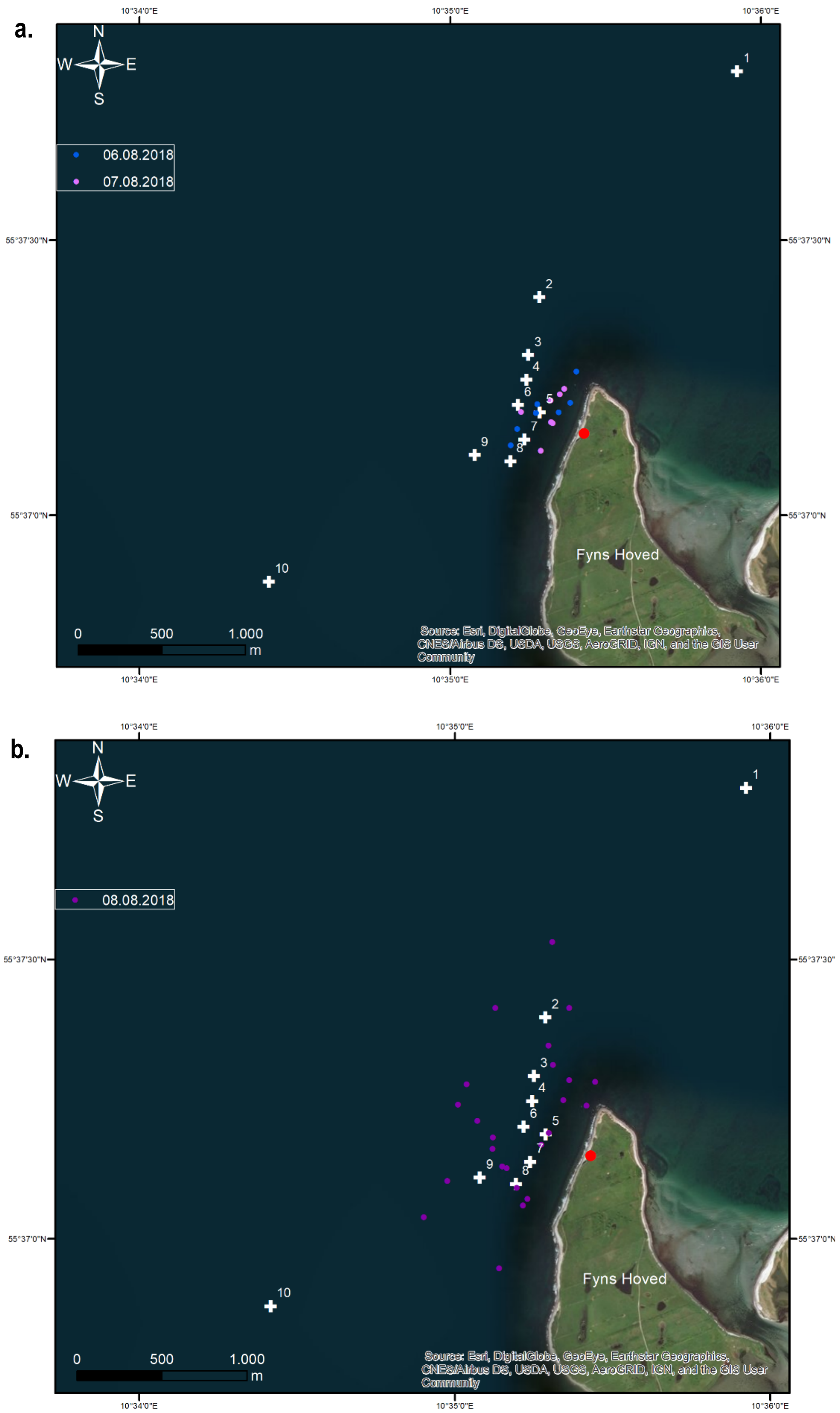


Fig. 35: Overview of the sighted harbour porpoise groups in Fyns Hoved on **a.** 6th August 2018 and 7th August 2018 and on **b.** 8th August 2018. Each point presents the first surfacing point, which was tracked with a theodolite. The white crosses show the position of each deployed C-POD and the red point on the land shows the observation place during the study period.

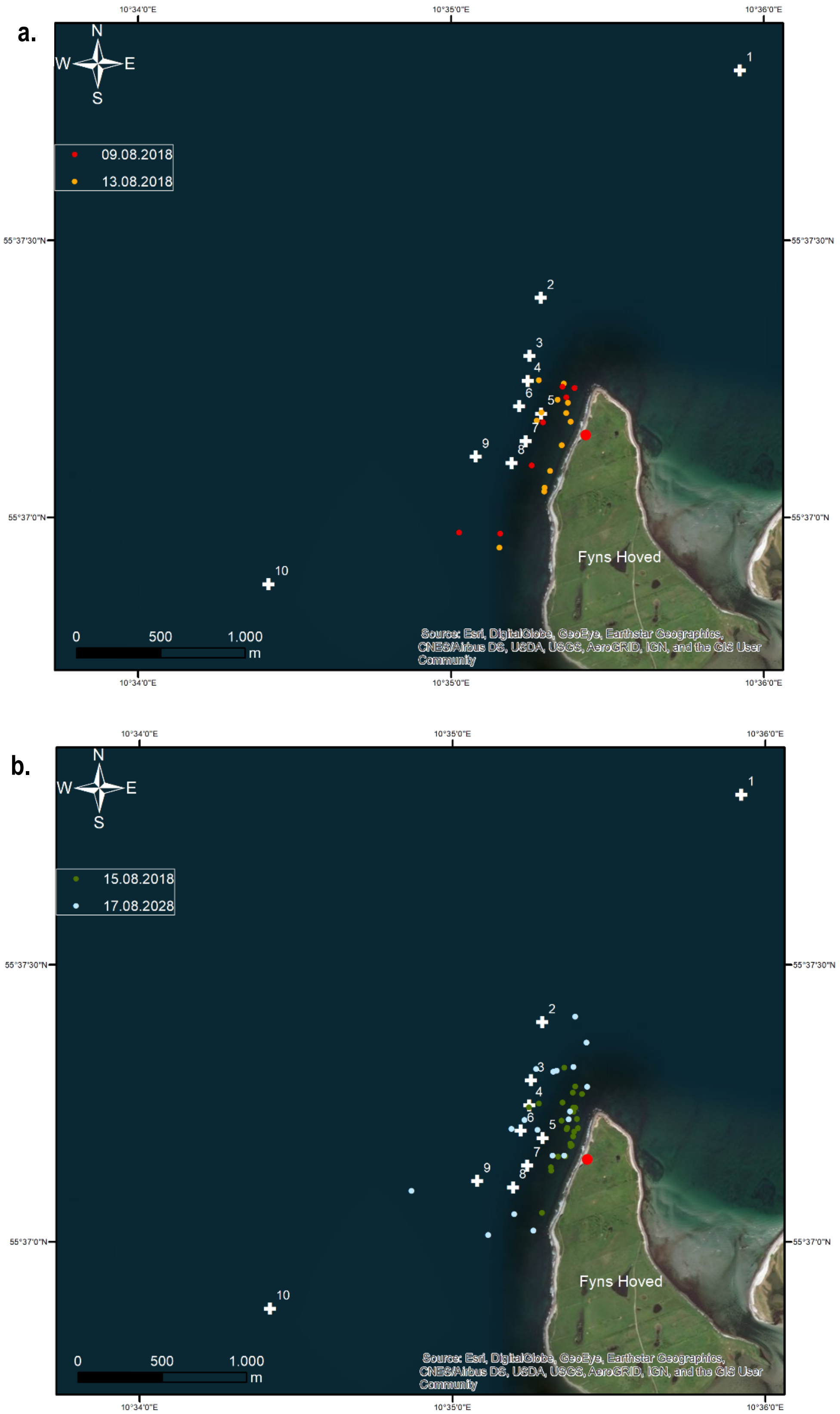


Fig. 36: Overview of the sighted harbour porpoise groups in Fyns Hoved on **a.** 9th August 2018 and 13th August 2018 and on **b.** 15th August 2018 and 17th August 2018. Each point presents the first surfacing point, which was tracked with a theodolite. The white crosses show the position of each deployed C-POD and the red point on the land shows the observation place during the study period.

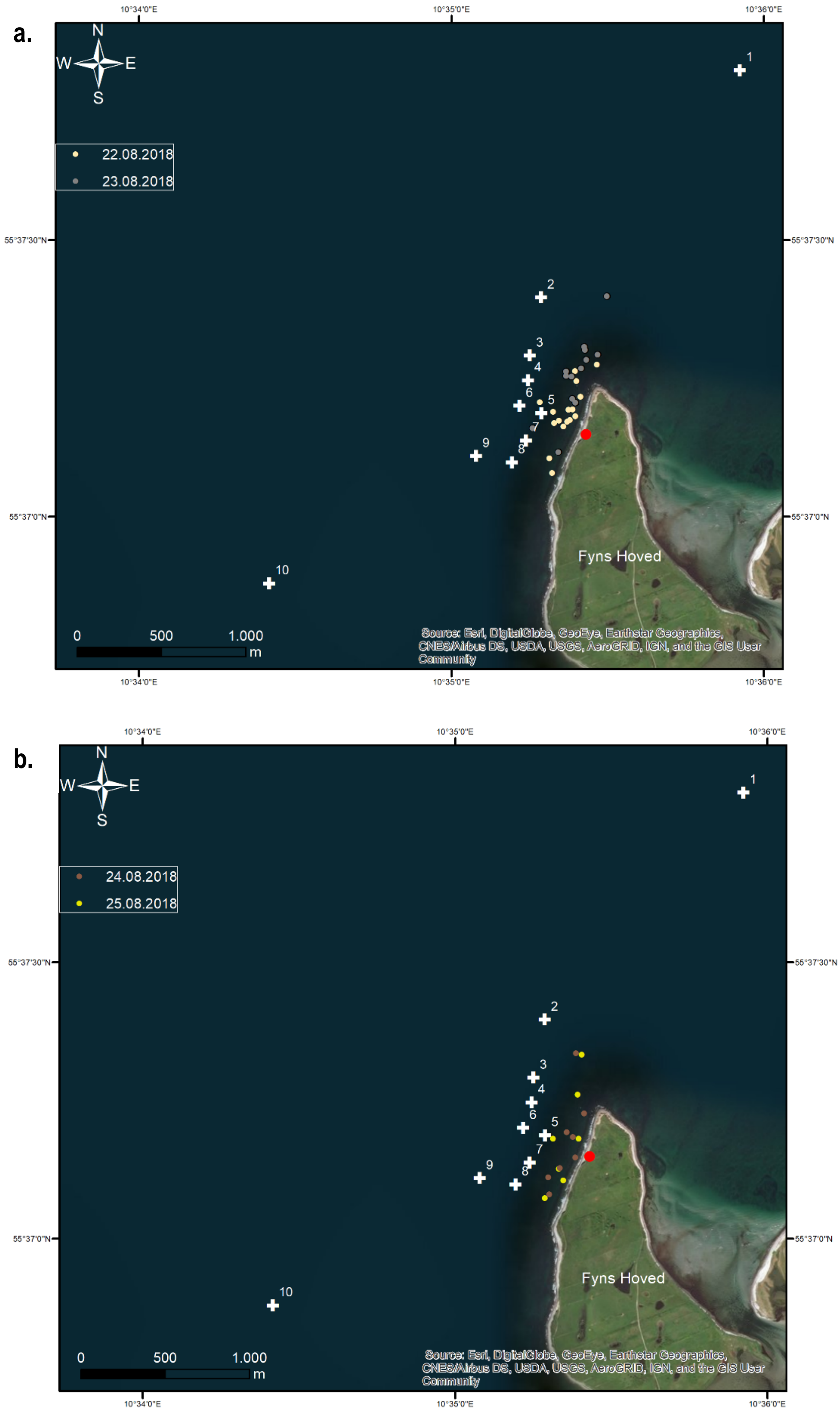


Fig. 37: Overview of the sighted harbour porpoise groups in Fyns Hoved on **a.** 22nd August 2018 and 23rd August 2018 and on **b.** 24th August 2018 and 25th August 2018. Each point presents the first surfacing point, which was tracked with a theodolite. The white crosses show the position of each deployed C-POD and the red point on the land shows the observation place during the study period.

Because the total hours of observation varied between the different days, the number of harbour porpoise groups per observation hour was calculated for each observation day. That way, a comparison in sightings between the different observation days is possible. Fig. 38 presents the harbour porpoise sightings per day and per observation hour from 31st July to 25th August 2018. It is visible that the detections of harbour porpoise groups varied during the study period. However, no clear seasonal sighting pattern was recognizable. They ranged from 0.98 sightings per hour on 1st August to 3.57 sightings per hour on 8th August. The mean sighting rate per hour amounted to 2.04 groups with a standard deviation of 0.83 sighted harbour porpoises per hour.

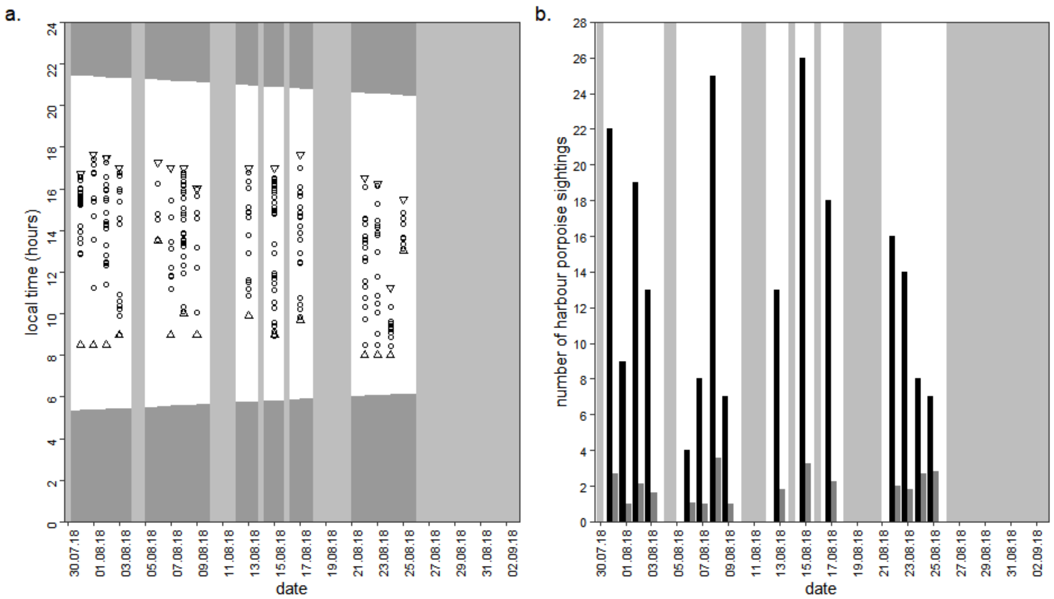


Fig. 38: Diel and seasonal sightings of harbour porpoise with the theodolite in Fyns Hoved (see Fig. 6 for the observation place). **a.**: Sightings of harbour porpoise (open points). The triangles show the start and end time of observation. The grey areas indicate no observation time. **b.**: Number of harbour porpoise sightings per day (black bars) and per hour (grey bars). The grey areas indicate no observation time.

To identify a potential diel pattern in the sighting rate of the harbour porpoise, Fig. 38 a. depicts the exact time when a group was tracked. In this figure, each point represents a sighted harbour porpoise group. It is clearly discernible that the porpoises were detected throughout the whole observation day. The time period of observation varied between the days, which is illustrated as triangles in Fig. 38 a. This figure gives a first overview of the harbour porpoise sightings during the day. In order to detect differences in the sighting rate during the day, the number of sightings from all observation days was counted for each hour from 08:00 to 17:00 (dark grey bars in Fig. 39). It is apparent that most of the porpoises were tracked in the afternoon between 14:00 and 15:00. The least harbour porpoises were detected between 17:00 and 18:00. However, it is important to mention that probably most of the porpoises were detected during the afternoon because the observation was conducted on each day during this time period. During other time periods, such as from 08:00 to 09:00 and from 17:00 to 18:00, a daily observation was not always possible. Hence, a comparison of the detections between the time periods is not exactly possible. To standardize these sightings, the total number of sightings from all days for each time period was divided by the total hours of observation from all days during the given time period. This is illustrated as light grey bars in Fig. 39.

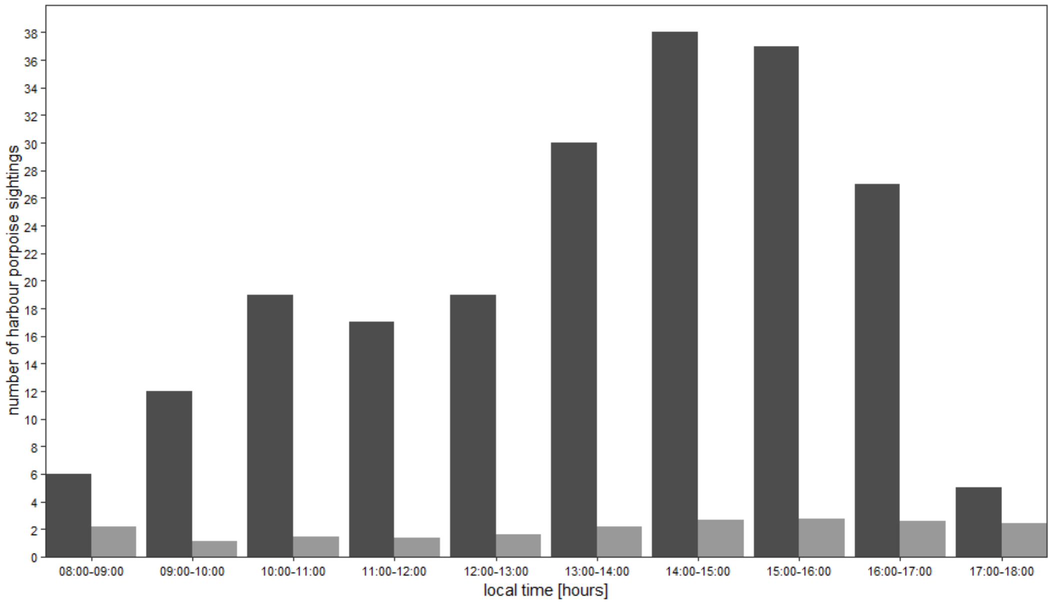


Fig. 39: Sighted harbour porpoises with the theodolite during the whole study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark (see Fig. 6 for the observation place). The dark grey bars show the absolute number of sighted porpoises and the light grey bars show the total number of sighted porpoises per sum of observation hours from all days for each time period.

As the light grey bars in Fig. 39 indicate, the harbour porpoise detections varied during the day. In general, it can be seen that less harbour porpoises were sighted from 09:00 to 13:00 than from 13:00 to 18:00. Most of the porpoises were tracked between 15:00 and 16:00, whereas the least porpoises were sighted between 09:00 and 10:00.

This chapter has provided information about the seasonal and the diel sighting rate of the harbour porpoise with a theodolite. The next chapter moves on to identifying possible impacts on the visual sighting rate of harbour porpoises.

3.3.2. Possible impacts on the visual detections of harbour porpoises

Firstly, it was investigated whether the wind speed has an effect on the visual detection of the harbour porpoise. For this, the number of tracked porpoises was counted for each given wind speed, which was measured by the weather station. The results are given in Fig. 40. It is visible that the porpoises could be tracked with a wind speed of up to 7.4 m/s. No animals were sighted below a wind speed of 1.4 m/s. Most of the porpoises were detected with a wind speed of 3.3 m/s. However, it is important to consider the predominant wind speed during the visual observation. Fig. 40 c. presents the measured wind speed at the station “Odense Lufthavn” during the time of the visual observation. The wind speed from the station in Odense was used for this illustration because it provided the wind speed for the whole observation time. The wind speed measured by the weather station, was only noted by the observers if a porpoise was sighted. It can be seen that the wind blew between 1.4 m/s and 7.4 m/s during the visual monitoring. The most frequent wind speeds during the observation were 3.3 m/s, 3.8 m/s and 4.3 m/s. When comparing Fig. 40 b. with Fig. 40 c., it can be seen that no harbour porpoise was sighted below a wind speed of 1.4 m/s because there was no wind speed below 1.4 m/s during the observation time. This is the same case for the wind speed of 7.4 m/s: The highest measured wind speed during the visual observation was 7.4 m/s and this was also the highest wind speed up to which porpoises were sighted.

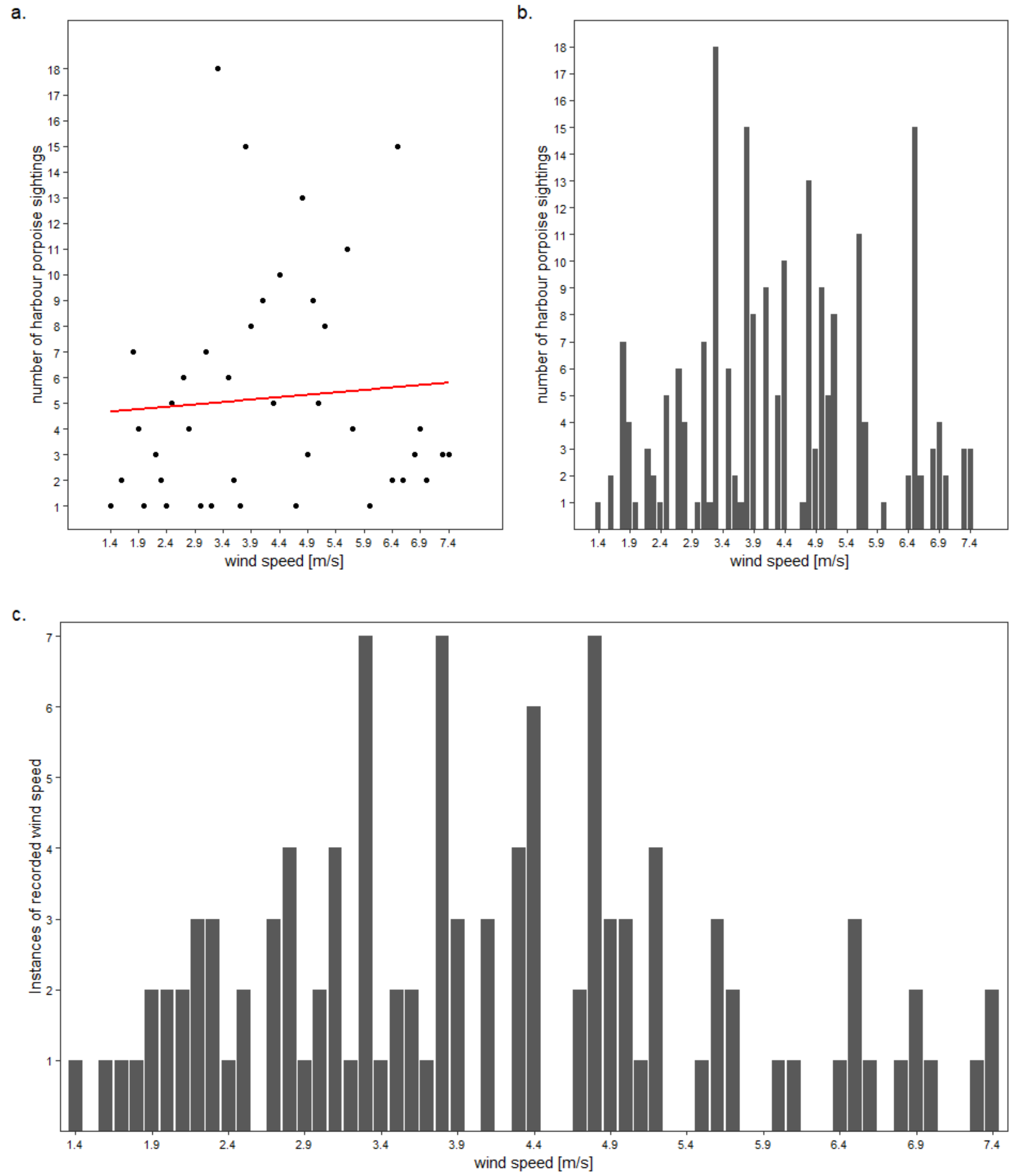


Fig. 40: **a.** and **b.**: Possible impact of the wind speed, recorded with the weather station, on the sighting rate of harbour porpoises with the theodolite in Fyns Hoved, Denmark during the study period from 30th July to 2nd September 2018 (see Fig. 6 for the observation place). **c.**: Recorded wind speed at the measuring station "Odense Lufthavn" from the Danish Meteorological Institute during the time of visual observation.

Secondly, the swimming direction of the tracked harbour porpoises was examined. The swimming direction was that direction of a group last noted before they were lost from sight or before they left the study area. Fig. 41 a. strongly shows, that most of the harbour porpoises swam either north or south. Only a few of them were sighted to leave the study area toward the coast or west. As an example, the swimming direction of the tracked harbour porpoises on 17th August 2018 is illustrated in Fig. 42. The arrows in the map indicate the swimming direction of the porpoises. It is clearly visible that all porpoises swam either north or south. No group was detected to swim east or west during this day. It is important to mention that the first and last surfacing point of an observed group can be seen in the map. The swimming behavior between these two surfacing points was not shown due to the large amount of tracking points. The swimming direction of the porpoises at the other observation days are illustrated in the Annex from Fig. 58 to Fig. 64.

Next, it would be interesting to know whether the wind direction had an impact on the swimming direction of the sighted harbour porpoises. The results are illustrated in Fig. 41 b. The size of the points represents the number of sighted porpoises. It is notable that the wind direction did not seem to have an impact on the swimming direction of the sighted harbour porpoises. This means that the harbour porpoises probably swam north and south, regardless of the wind direction.

As a next step, it was investigated whether the wind direction had an effect on the amount of tracked harbour porpoises. As Fig. 41 c. demonstrates, the porpoises could be sighted, when the wind came from all directions. Only a few porpoises were tracked when the wind blew from west and from north west. To understand this finding, the predominant wind direction during the visual observation must be taken into account. Fig. 41 d. illustrates the measured wind direction during the visual observation at the station in Odense. The wind direction from this station and not from the weather station was chosen for the same reason as indicated above for the wind speed. It can be seen in Fig. 41 d. that the wind blew only a few times from west and from north west. This could be the reason why only a few porpoises were sighted during these wind directions. However, also the wind directions north and north east were recorded only a few times during the observation. More harbour porpoises were sighted during these wind directions than when the wind blew from west and from north west. The most frequent wind direction during the visual observation was from south west, whereas the most porpoises were sighted when the wind came from east.

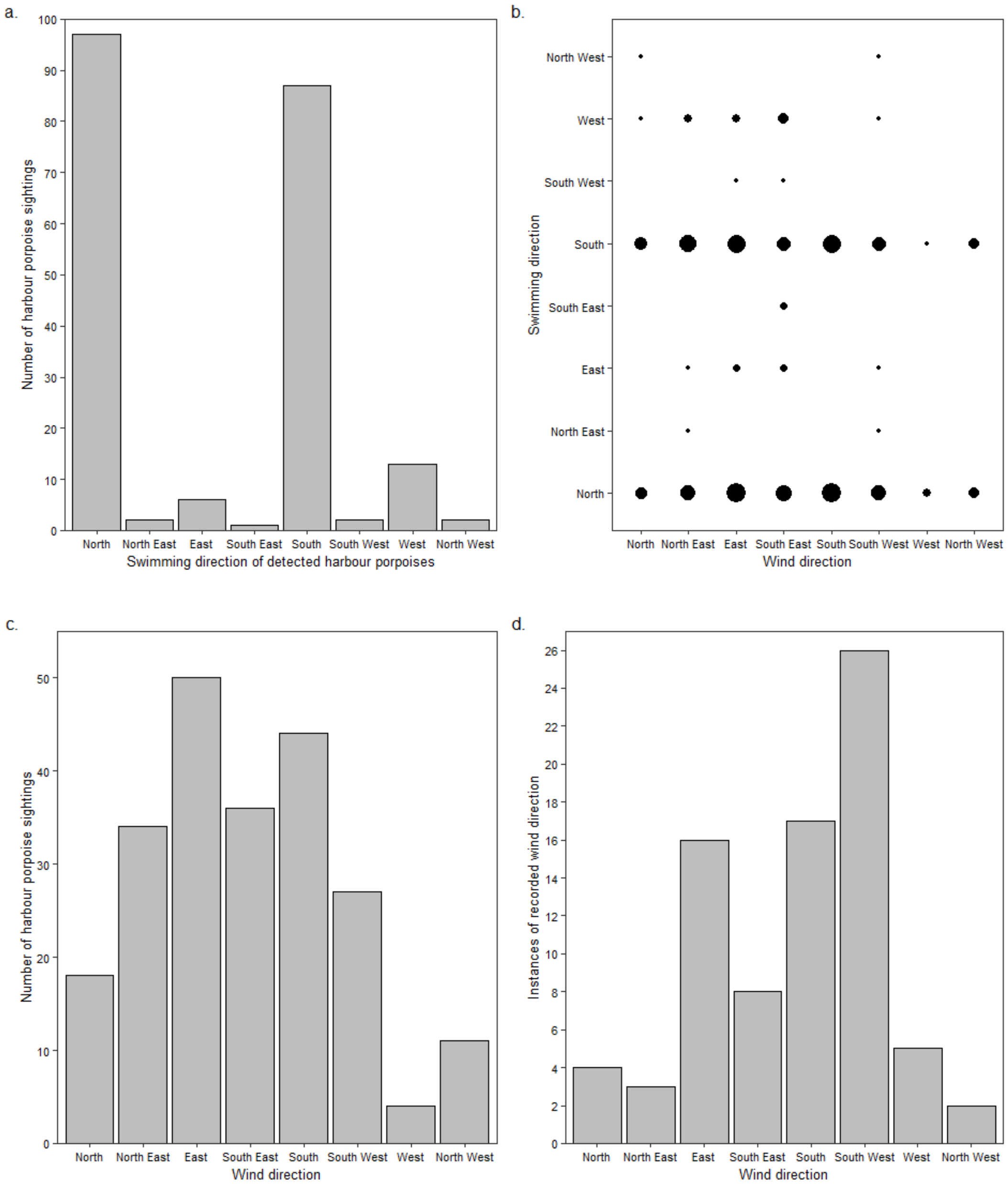


Fig. 41: **a.** Swimming direction of the tracked harbour porpoises with the theodolite in Fyns Hoved, Denmark during the study period from 30th July to 2nd September 2018 (see Fig. 6 for the observation place). **b.** Possible impact of the wind direction, measured with the weather station, on the swimming direction of the tracked harbour porpoises. **c.** Recorded wind direction at the measuring station “Odense Lufthavn” from the Danish Meteorological Institute during the time of visual observation. **d.** Possible impact of the wind direction, measured with the weather station, on the sighting rate of harbour porpoises.

Fig. 42: Swimming direction of the tracked harbour porpoises with the theodolite on 17th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

Thirdly, the distance up to which the harbour porpoises could be tracked, was studied. In addition, possible impacts on the distance were investigated. The results are presented in Fig. 43. It is clearly visible that 89 of a total of 209 sighted porpoises (corresponds to 42.58 %) were only between 100 and 200 m away from the observation place (Fig. 43 a.). Furthermore, 27.27 % of the sighted porpoises were tracked at a distance between 200 and 300 m. The finding that most of the harbour porpoises were tracked very close to the coast, can also be seen in the maps (from Fig. 34 to Fig. 37). Only one harbour porpoise group was detected around 1500 m away from the observation position. Next, it was studied whether the ability of the observers to see porpoises far away, is influenced by the wind speed. Fig. 43 b. indicates that the distance from the observer to a detected porpoise has decreased with increasing wind speed. Thus, it seems that the wind speed has slightly affected the distance up to which a visual detection of the harbour porpoise is possible. Finally, it was considered, whether the time of the day has an impact on the distance to a sighted porpoise. This was investigated for two reasons: Firstly, the observers could get tired with increasing time of monitoring, so that they could miss porpoises which are far away. Secondly, the sun is moving during the day and the sunrays could reflect on the water, so that less porpoises could be sighted. However, Fig. 43 c. shows that the distance from the observers to the tracked porpoises increased slightly the later it got.

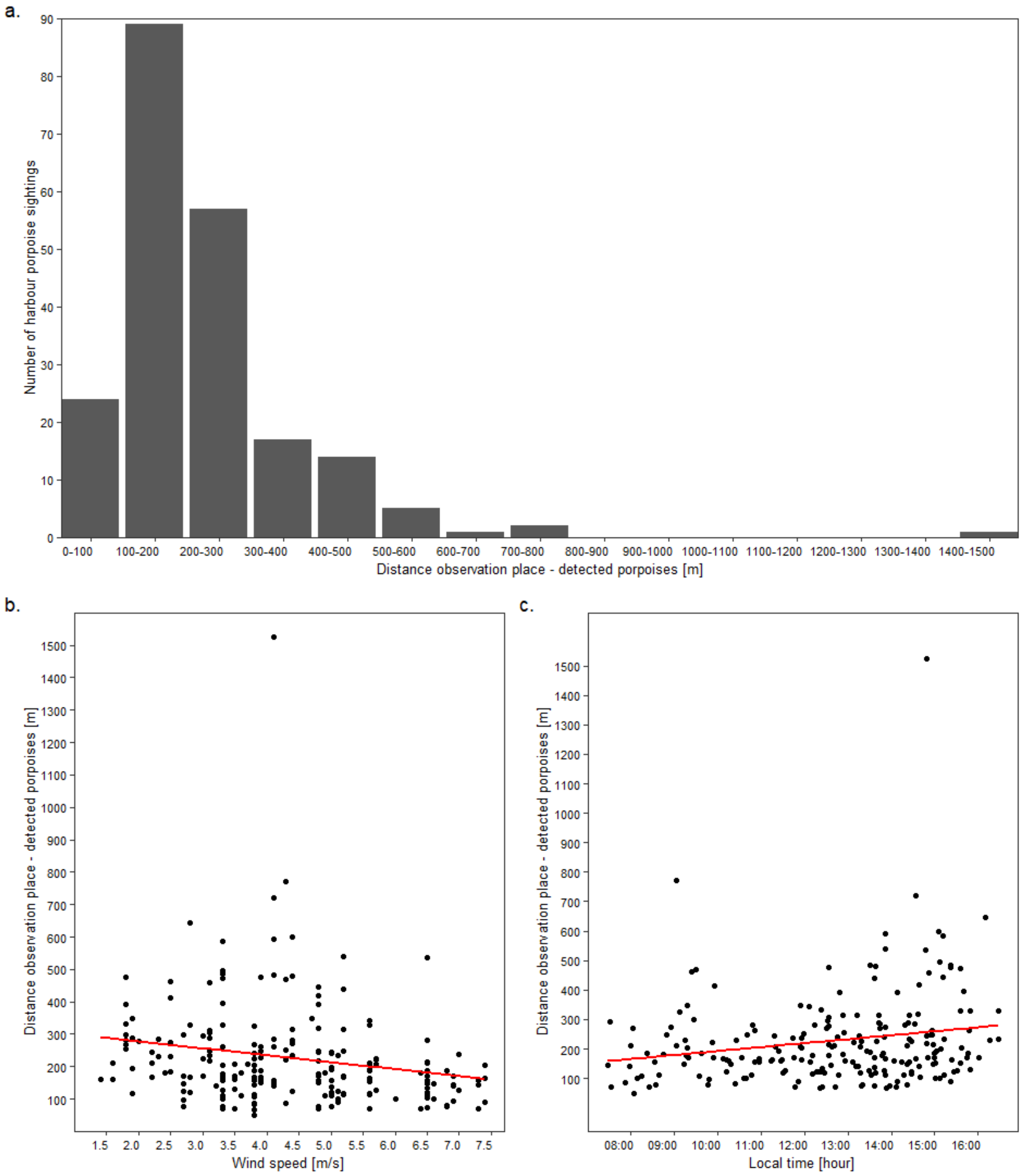


Fig. 43: **a.** Distance from the harbour porpoises detected with the theodolite to the observation place in Fyns Hoved (see Fig. 6 for the observation place). **b.** Possible impact of the wind direction, measured with the weather station, on the distance from the detected harbour porpoises to the observation place in Fyns Hoved (see Fig. 6 for the observation place). **c.** Possible impact of the time of day on the distance from the detected harbour porpoises to the observation place in Fyns Hoved (see Fig. 6 for the observation place).

3.4. Comparison of acoustic detections with visual detections

After analyzing the acoustic and the visual sightings of the harbour porpoise, this chapter provides a comparison between these two sighting methods. C-PODs only detect harbour porpoise clicks within a limited radius. Thus, only those visual sightings were used, that were within a 100 m radius of the corresponding C-POD. If this criterion was fulfilled, each visual sighting of a harbor porpoise was included in the comparison.

The comparison between the acoustic and the visual sightings of the harbour porpoise is presented in Tab. 9. The table shows the number of Detection Positive Minutes with the theodolite as well as with each C-POD. No harbour porpoise was sighted visually 100 m or closer to C-POD station 1 and 10. Therefore, a comparison between these stations and the sightings with the theodolite was not possible. As Tab. 9 indicates, more harbour porpoises were detected with the theodolite than with the C-POD at stations 4 to 8. At the remaining stations, more porpoises were recorded with the C-POD than with the theodolite. There is a strong mismatch between the number of harbour porpoise sightings with the theodolite and the sightings at some C-POD stations. The highest discrepancy between the sightings with the theodolite and with the C-POD was at station 7. Harbour porpoises were sighted 246 times with the theodolite and only 74 times with the C-POD. The smallest discrepancy between the visual and the acoustic sightings was at C-POD station 3. 29 detections were recorded with the theodolite, while 37 detections were noted by the C-POD.

Tab. 9: Comparison between the visual detections and the acoustic detections of the harbour porpoise at each C-POD station during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m apart from each C-POD station. The C-POD stations 1 and 10 were not included in the comparison because no visual sighting was 100 m or closer to these two stations.

C-POD station	Detection Positive Minutes with the theodo-lite	Detection Positive Minutes with the C-POD
2	13	64
3	29	37
4	98	65
5	208	38
6	90	32
7	246	74
8	96	62
9	8	27

A more detailed comparison between the visual sightings with the acoustic detections at two different C-POD stations is presented in the following paragraphs. As an example, a C-POD with a higher number of detections than these with the theodolite (C-POD station 2), and one C-POD, which has less detections than the number of visually detections (C-POD station 7) were chosen. Figures for the remaining stations can be seen in the Annex in the figures from Fig. 65 to Fig. 70 and in the tables from Tab. 21 to Tab. 28.

Firstly, the visual sightings and the acoustic detections at C-POD station 2 are compared in Tab. 10 and in Fig. 44. The open dots in Fig. 44 represent the visual sightings, while the black dots indicate the acoustic sightings of the harbour porpoise. It can be seen that more harbour porpoises were detected with the C-POD than with the theodolite, except for the 17th August. However, there is only a difference of one detection between these two monitoring methods on this day. The highest mismatch was on 23rd August with 15 detections with the C-POD and no detections with the theodolite. On 8th August, the same amount of detections was recorded with the theodolite and with the C-POD.

Tab. 10: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 2 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 2. Only these dates are shown, on which a visual observation took place.

Date	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 2
31.07.2018	0	2
01.08.2018	1	2
02.08.2018	0	5
03.08.2018	1	2
06.08.2018	0	0
07.08.2018	0	7
08.08.2018	5	5
09.08.2018	0	1
13.08.2018	0	3
15.08.2018	0	5
17.08.2018	6	5
22.08.2018	0	7
23.08.2018	0	15
24.08.2018	0	3
25.08.2018	0	2

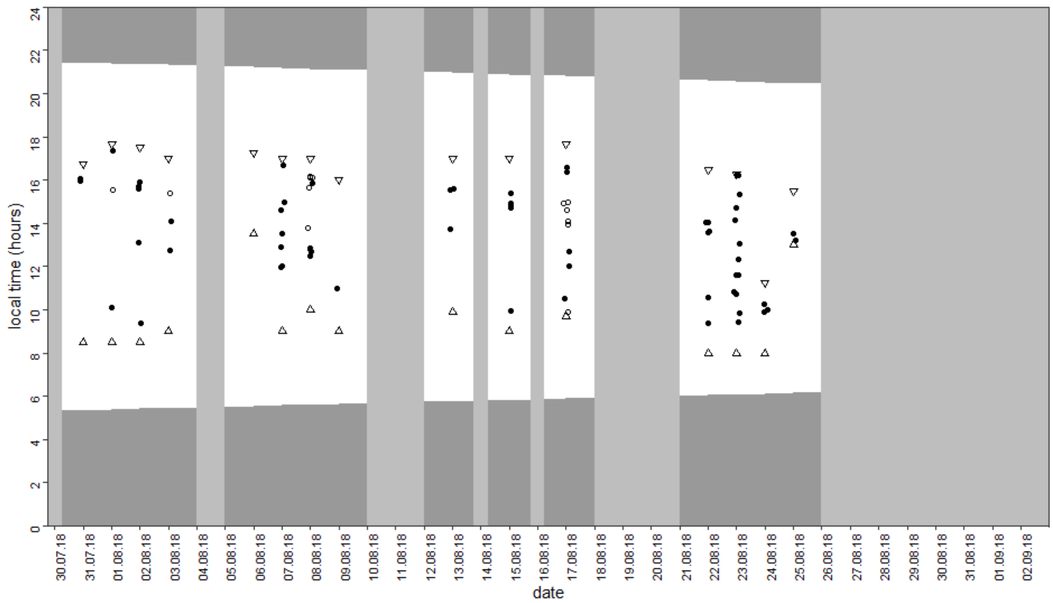


Fig. 44: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 2 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and see Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of the observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 2.

Secondly, a comparison of the visual sightings with the acoustic detections at C-POD station 7 is illustrated in Fig. 45. As in the figure above, the open dots in Fig. 45 represent the visual sightings and the black dots show the acoustic sightings of the harbour porpoise. Tab. 11 summarizes the number of visual detections and these of acoustical detections. It is clearly visible that more harbour porpoises were detected with the theodolite than at station 7. In general, harbour porpoises were sighted 246 times with the theodolite and only 74 times with the C-POD at station 7. When looking at each observation day, it is recognizable that the C-POD has recorded more detections than the observer on only four days. The largest discrepancy between the visual and the acoustic sightings can be noted on 23rd August, namely a difference of 32 detections. Small differences of only one detection can be reported on 6th and on 25th August.

Tab. 11: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 7 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. The number of Detection Positive Minutes with at least one harbour porpoise detection within one minute is shown. The visual detections are not more than 100 m away from C-POD station 7. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. Only these dates are shown, on which a visual observation took place.

Date	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 7
31.07.2018	14	4
01.08.2018	5	3
02.08.2018	19	7
03.08.2018	15	1
06.08.2018	3	4
07.08.2018	18	2
08.08.2018	18	1
09.08.2018	11	1
13.08.2018	17	6
15.08.2018	9	5
17.08.2018	19	1
22.08.2018	13	14
23.08.2018	49	17
24.08.2018	34	5
25.08.2018	2	3

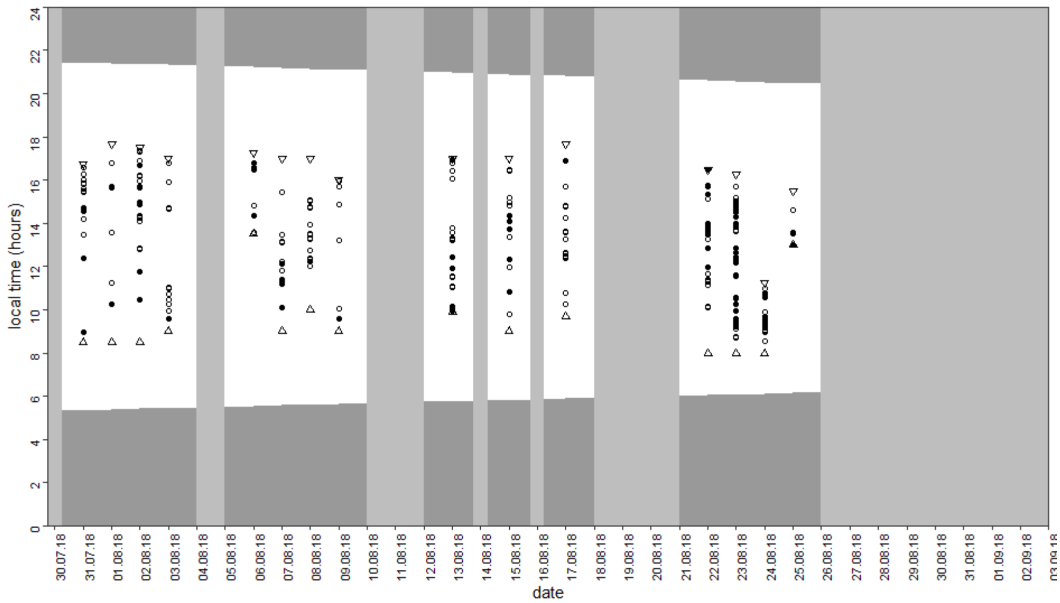


Fig. 45: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 7 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of the observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 7.

3.5. Other detected cetacean

In addition to the detected harbour porpoise clicks, the KERNO classifier algorithm has detected potential clicks, which could be produced by dolphins. These echolocation signals are presented in the following paragraph.

The frequency spectrum is shown in Fig. 46. It can be seen that the frequency of dolphin clicks ranged from 33 kHz to 133 kHz. The mean click frequency amounted to 83.99 kHz with a standard deviation of 13.90 kHz.

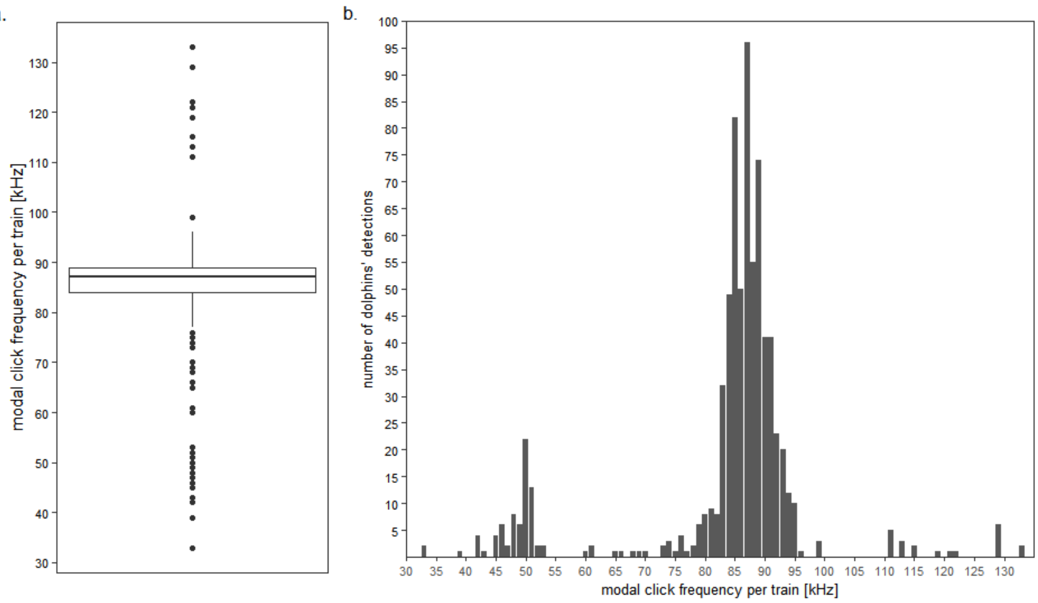


Fig. 46: Modal click frequency per train of the detected dolphins during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD).

The diel and seasonal detection of potential dolphin clicks is illustrated in Fig. 47. This figure summarizes the detected clicks from all C-POD stations. Figures of the recorded clicks for each C-POD station are presented in the Annex from Fig. 71 to Fig. 75. In total, 122 dolphin clicks were identified by the algorithm. In regard to a seasonal occurrence of detections, it can be seen that more dolphins were detected at the beginning of August. On 1st August, most dolphins were identified. In regard to a diel occurrence of detections, it seems that dolphins were recorded during the whole day. Only four clicks were recorded at night.

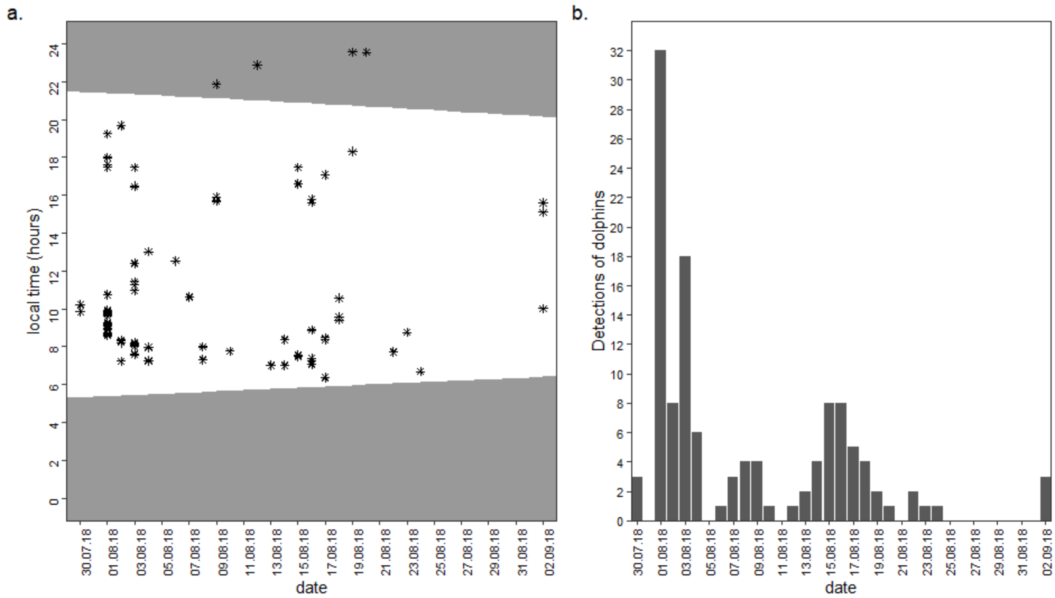


Fig. 47: **a.** Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute for all C-POD stations (see Fig. 10 for the position of each C-POD). Grey areas indicate night and white areas indicate day. **b.** Sum of dolphins’ detections per day for all C-POD stations.

4. Discussion

4.1. Acoustic detections of harbour porpoises

4.1.1. Diel differences in harbour porpoise detections

The first task of this study was to identify potential differences in activity patterns during the diel cycle with the use of C-PODs and a theodolite. The hypothesis was that the activity pattern of the harbour porpoise varied during the diel cycle.

This chapter will provide an interpretation of a potential harbour porpoise's activity pattern detected with acoustic monitoring (C-PODs), while chapter 4.2. will discuss its possible activity pattern during visual monitoring (theodolite).

C-PODs were used to investigate the echolocation activity of the harbour porpoise. As already mentioned in chapter 1.2.4., C-PODs are nowadays used in various research studies of the harbour porpoise, like for example the investigation of its habitat use and its distribution (e.g. Bailey *et al.* 2010, Gallus *et al.* 2012, Simon *et al.* 2010, Verfuß *et al.* 2007) or its reaction to anthropogenic noise pollution (Brandt *et al.* 2011, Carstensen *et al.* 2006, Scheidat e*t al.* 2011). On the current state of knowledge, this is the first study, which has examined harbour porpoise occurrence with C-PODs on a very small distance. The maximum distance between the separate stations was around 2.3 km. Although studies have been conducted to investigate the distribution range of harbour porpoises, it has been related to different sea areas (e.g. Bailey *et al.* 2010, Gallus e*t al.* 2012, Schaffeld e*t al.* 2016). This study has shown that the activity of harbour porpoises varied even between a very small distance of the C-POD devices.

A first result was that the mean click frequency was 129.8 kHz with a standard deviation of 4.64 kHz. These results are in accordance with the identified frequency in other studies (e.g. Kastelein *et al*. 2002, Wahlberg *et al.* 2015). They have identified a frequency range between 100 kHz and 150 kHz with a mean frequency between 130 kHz and 140 kHz (Kastelein *et al*. 2002, Wahlberg *et al.* 2015).

As a second result, the study showed that the harbour porpoises displayed a daily activity pattern: At stations 1, 2, 4 and 8, most harbour porpoises were detected at night. At C-POD station 7, most porpoises were recorded in the morning and at C-POD station 10, most were detected in the evening.

The third important result was that the detections of the harbour porpoise differed between the stations during the diel phases: More harbour porpoises were detected at C-POD stations 1, 2 and 10 than at the remaining stations during the evening. Moreover, the most porpoises were recorded at the station 1 at night.

These findings lead to the following question: Which are the main driving factors for the temporal activity pattern (second result) and for the spatial activity pattern (third result) of the harbour porpoise? Activity patterns already have been determined in several cetacean species (Klinowska 1986). The bottlenose dolphin, for example, (*Tursiops truncatus*) is more active during the day than at night (McCormick *et al.* 1969), while melon-headed whales (*Peponocephala electra*) and pilot whales (*Globicephala macrorhynchus*) are more active at night than during the day (Baumann-Pickering *et al.* 2015, Kritzler 1952). The activity pattern of the harbour porpoise has also been investigated in a few studies (Carlström 2005, Schaffeld *et al.* 2016, Todd *et al.* 2009, Williamson *et al.* 2017). In accordance with the present results, the previous studies have shown a significant variation in the echolocation activity of the harbour porpoise within the diel cycle. This study can be compared well to the studies by Carlström (2005) and Todd *et al.* (2009) as they both used the same classification of diel phases (morning, day, evening and night). Both found a significant higher echolocation encounter rate of harbour porpoises at night than during the day (Carlström 2005, Todd e*t al.* 2009). Echolocation encounters are an indicator for the presence or absence of a porpoise (Carlström 2005). They are defined as series of trains that are separated by periods of silence with a minimum duration of 10 min (Carlström 2005, Carstensen *et al.* 2006, Kyhn *et al.* 2012). These results confirm the results of this study that more porpoises per hour were detected during night (mean= 2.60 ± 4.60 detections per hour) and evening (mean= 1.94 ± 3.38 detections per hour) than during morning (mean= 1.20 ± 1.18 detections per hour) and day (mean= 0.77 ± 0.86 detections per hour). According to the current state of knowledge, there are several possible explanations for this activity pattern, which will be discussed in the following paragraphs.

One possible explanation for these results might be that harbour porpoises increase their echolocation rate during darkness to compensate the loss of visual information (Carlström 2005, Todd *et al.* 2009). On the one hand, this hypothesis can be supported by a study by Akamatsu *et al.* 1992, who demonstrated that a captive harbour porpoise increased its echolocation activity during darkness. On the other hand, DeRuiter *et al.* (2009) did not find any differences in the echolocation rate of porpoises during their prey capture experiments with and without eyecups. This discrepancy should be investigated in further studies.

Another possible explanation for the higher echolocation activity at night than during the day could be that the porpoises were eating more at night due to an increased availability of food during this period (Todd e*t al.* 2009). The underlying reason for this explanation could be the diurnal behavior of their prey species (Todd e*t al.* 2009). The harbour porpoise is an opportunistic feeder, which has a wide range of prey species (Recchia & Read 1989, Wright 2013). It mainly consumes sandeels (Ammodytidae), Atlantic herring (*Clupea harengus*), Atlantic cod (*Gadus morhua*) and gobies (Gobiidae) (Sveegaard *et al*. 2012), but the exact diet composition of the harbour porpoise seems to vary between its distribution areas (Börjesson *et al.* 2003, Jansen *et al.* 2013 and Santos & Pierce 2003). In the Kattegat, for example, it mainly forages Atlantic herring and gobies (Börjesson *et al.* 2003). To identify a potential diel activity pattern of the harbour porpoise, it is necessary to understand the diel activity pattern of its prey species. Thus, the diel movements of one of its prey species, the Atlantic herring, are presented in the following paragraph.

Herring exhibits a diel, vertical migration behavior, which means a downward vertical migration at dawn and an upward migration at dusk (Blaxter & Parrish 1965, Bollens e*t al.* 1992, Huse & Korneliussen 2000). Several studies have shown an aggregation in schools during the day and a dispersed distribution of herring at night (Blaxter & Batty 1987, Cardinale *et al*. 2003, Fréon *et al.* 1996). Diel vertical migrations are usually triggered by light intensity, but the extent of these patterns seems to be influenced by other factors as well, such as temperature, the oxygen content of the water and prey availability (Stepputtis 2006). The main biological functions of vertical migration are probably foraging, predator evasion and thermoregulation (Bollens & Frost 1989, Bollens *et al.* 1992, Espeland *et al.* 2010). It has been suggested that vertical migration enables the herring to catch prey near the surface in light intensities where they are less visible for predators (Blaxter & Parrish 1965, Espeland *et al.* 2010). Nonetheless, feeding makes the herring vulnerable to predators due to the breaking of the school formation during foraging (Blaxter & Parrish 1965).

Thus, it was suspected that it may be energetically more advantageous for harbour porpoises to hunt herring at night than during the day due to the vertical movements of herring (Read 2001). Moreover, it was speculated that the diel echolocation activity of the harbour porpoise is related to an alternation in feeding techniques and prey choice in deep and in shallow waters (Brandt *et al.* 2014, Schaffeld *et al.* 2016). It was hypothesized that harbour porpoises may be feeding pelagic prey, like herring, in deeper waters at night (Brandt *et al.* 2014, Schaffeld *et al.* 2016). During the day, they may be feeding mainly benthic prey in shallow waters, such as gobies and sandeels (Brandt *et al.* 2014, Schaffeld *et al.* 2016). It has been reported that harbour porpoises used a special bottom feeding technique to hunt hidden fish in the sediments of shallow waters (Lockyer 2000). This feeding technique has been called "bottom-grubbing" (Lockyer 2000, Lockyer *et al.* 2003). To use this technique, the harbour porpoise scans the sea bottom by swimming in a vertical position with the tail showing upwards and its mouth close to the bottom (see Fig. 48, Brandt *et al.* 2014, Lockyer 2000, Schaffeld e*t al. 2*016). This feeding behavior has been observed in captive and in wild harbour porpoises (Brandt *et al.* 2014, Lockyer 2000, Lockyer *et al.* 2003) as well as in other cetacean species, like the bottlenose dolphin (González & López 2000). Brandt *et al.* (2014) have argued that porpoises probably conserve energy when they use the bottom-grubbing in shallow waters rather than in deeper waters. Bottom-grubbing in deeper waters would not be efficient because it requires repeated deep and long dives and thus more energy (Brandt *et al.* 2014). Therefore, a variation in feeding techniques and in prey choices during day and night could be one reason for the different detections of harbour porpoises during the diel phases as well as between the different C-POD stations.

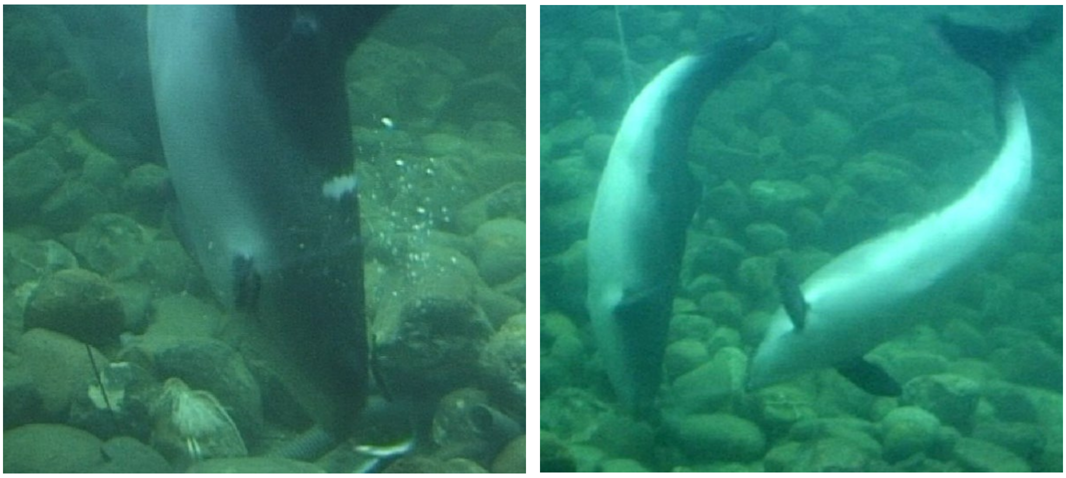


Fig. 48: Harbour porpoises during "bottom-grubbing", which were observed during a study by Lockyer (2000) at the Fjord and Baelt Center in Denmark. The photos were kindly provided by Geneviève Desportes.

This feeding behavior could have direct implications on the recording possibilities of a C-POD device. Bottom-grubbing was presumed to be missed by C-PODs due to the narrow echolocation beam of the harbour porpoise (Schaffeld *et al.* 2016). Its echolocation beam is directed towards the seafloor, while the C-POD is hanging with its hydrophone upwards (Schaffeld *et al.* 2016). Koschinski *et al.* (2008) have suggested that clicks may only reach the C-POD during the bottom-grubbing, when the harbour porpoise suddenly changes its orientation while hunting escaping fish. Therefore, it is possible that the C-PODs can record less clicks during the hunting of benthic prey in shallow waters than the hunting of pelagic prey in deeper waters (Schaffeld *et al.* 2016). Additionally, the harbour porpoise has the possibility to detect fish visually in shallow waters (Brandt *et al* 2014). A swim bladder amounts to 90 % - 95 % of the reflected acoustic energy in fish (Foote 1980, Didrikas & Hansson 2008, McCartney & Stubbs 1971). Because gobies and sandeels lack swim bladders, they have a low acoustic reflectivity (Freeman *et al.* 2004). The consequence is that they may be harder to detect by echolocation clicks than pelagic fish with a swim bladder (Brandt *et al.* 2014). Hence, it would be easier for porpoises to hunt gobies and sandeels visually during the day (Brandt *et al.* 2014, Schaffeld e*t al.* 2016).

These presumptions are in accordance with the research of Williamson *et al.* (2017). They have found that the detections of harbour porpoises varied with the water depth (Williamson *et al.* 2017). More harbour porpoises were detected in more shallow sandy areas during the day, while more harbour porpoises were sighted in deeper muddy areas at night (Williamson *et al.* 2017). The results of this study only partly support this hypothesis. Most harbour porpoises were detected at night at C-POD station 1, where the water was 11.3 m deep. The water at C-POD stations 2 to 9 was only around 5 m to 6 m deep and less porpoises were detected at these stations at night. This finding confirms the hypothesis that more porpoises were detected at night in deeper water than in shallow waters. However, less harbour porpoises were recorded at station 10 at night, where the water was around 14 m deep. This pattern of porpoises moving into deeper waters during darkness can already be observed in the evening. Significantly more harbour porpoises were detected at C-POD stations 1 and 10 during this time than at the more shallow stations. The reason why more porpoises were recorded at station 10 in the evening, but not at night, could be that the porpoises swam out of the study area into even deeper waters at night. During the day, no significant differences in harbour porpoise detections between shallow and deeper water could be identified, except for the stations 1 and 6. More harbour porpoises were detected at station 1 than at station 6 during the day. These contradictions should be analyzed in further studies.

Nonetheless, the possible indicated explanations need to be considered with caution for several reasons. Firstly, diel vertical migration patterns have so far only been proven in waters, which were much deeper than the water in this study. For example, Blaxter & Parrish (1965) have demonstrated vertical migration of herring in the north-western North Sea with a water depth of up to 100 m. Stepputtis (2006) has studied diel migrations of herring in the Bornholm Basin (central Baltic Sea) in a water depth of between 81 m and 87 m. In this study, the water depth ranged was around 14 m. However, Schaffeld *et al.* 2016 have

demonstrated that the diel activity pattern of harbour porpoises could be linked to the diel vertical movement of their prey even in more shallow waters of up to 28 m.
Secondly, it has been shown that the diet composition of the harbour porpoise is dependent on several factors (Santos & Pierce 2003, Santos *et al. 2*004, Vergeer 2006). Age-dependent variation in its diet has been classified e.g. by Andreasen *et al.* 2017, Santos & Pierce 2003. It was shown that juvenile porpoises mainly consume gobies (Gobiidae), while adult porpoises rather feed on herring and cod in the western Baltic Sea (Andreasen *et al.* 2017). Age-dependent differences in the diet composition of harbour porpoises have also been described in other areas, such as in Scottish Waters (Santos *et al.* 2004), in Dutch Waters (Schelling *et al.* 2014) and in Icelandic coastal Waters (Víkingsson *et al.* 2003). Furthermore, Santos & Pierce 2003 have discussed sex-related variability in the harbour porpoise diet. They suggested that a segregation of harbour porpoises in groups of different sex and age could show differences in diets of males and females (Santos & Pierce 2003). Adult males can form separate groups because they are more mobile than groups of juveniles or females with calves (Santos & Pierce 2003). Females accompanied by calves could be found more often in shallow waters and thus they could forage other prey species than males (Santos & Pierce 2003). Finally, there is a seasonal variation in the diet of harbour porpoises (Andreasen *et al. 2*017, Víkingsson *et al.* 2003). In general, juveniles have a more uniform diet composition throughout the year, whereas the diet of adults is more variable throughout the seasons (Andreasen e*t al. 2*017, Víkingsson *et al.* 2003). However, it is important to mention that most of these diet studies were conducted with stranded or caught animals.
It is not exactly known, which fish species were fed by the recorded porpoises during this study. Moreover, information about sex and age of the sighted harbour porpoises was not available in this study. Further investigations, which include more detailed information about the harbour porpoise as well as about its prey species should be undertaken to better understand the daily activity pattern of the harbour porpoise in this particular location.

Additionally, the harbour porpoise used its biosonar not only for foraging, but also for navigating and for perceiving obstacles in its surrounding (Gallus *et al.* 2011, Miller & Wahlberg 2013, Verfuß *et al.* 2009). Due to the high bycatch rate of harbour porpoises, it was hypothesized why they become entangled in fishing nets. Lockyer (2000) has suggested that the harbour porpoise pay not considerable attention to any obstacles, like nets, in its environment during the "bottom-grubbing" because its visual and acoustic attention is completely focused on the sea floor. This behavior might be compared to humans, who collide with a glass surface, in the attempt of joining a subject of interest on the other side (glass door syndrome, Lockyer 2000). Thus, the “bottom-grubbing” could be a possible explanation of the high bycatch rate of the harbour porpoise. However, further studies are required to examine this hypothesis.

To sum it up, the hypothesis that the activity pattern of the harbour porpoise varied during the diel cycle, can be confirmed so far as the harbour porpoises displayed a daily activity pattern at all C-POD stations, except for the stations 3 and 9. The detections of harbour porpoises differed between the stations especially during evening and night. Bottom-grubbing or the visual hunting of the harbour porpoise might be two possible explanations for fewer acoustically detected porpoises during the day than at night. Both explanations could have an immediate impact on passive acoustic monitoring devices as they are based on continuous echolocation of the investigated species. These findings should be considered in further studies, when the activity and distribution of an echolocated animal will be investigated.

To investigate whether the feeding behavior of the harbour porpoise could be a reason for a higher echolocation activity at night than during the day, the possible feeding buzz trains of the harbour porpoise were analyzed. The results will be discussed in the next chapter.

4.1.2. Behavior analysis of the detected harbour porpoises

The Minimum ICI below 10 ms was used as a potential indicator for feeding activity of the harbour porpoise. At first, the feeding buzz trains were compared between the different diel phases at each station. No clear feeding pattern between the diel phases was recognizable. A possible explanation for this might be that harbour porpoises need to feed nearly continuously throughout the day and the night to secure their metabolic demands (Wisniewska *et al.* 2016). Small marine mammals have higher energy intakes than similarly sized terrestrial mammals due to the high energy need for thermoregulation in water (Williams & Maresh 2016). This presumption can be supported by Wisniewska *et al.* (2016). With acoustic tags deployed on wild harbour porpoises, they showed that the porpoises foraged almost continuously with a capture of up to 550 small fish (3 – 10 cm) per hour (Wisniewska e*t al.* 2016). This finding was explained with the fact that the small size of porpoises limits their capacity to store energy (Koopman e*t al.* 2002, Wisniewska e*t al.* 2016). Therefore, they need to feed at high rates during the whole day (Wisniewska *et al.* 2016). On the other hand, these findings cannot be confirmed by Carlström (2005) and Todd *et al.* 2009. Both reported differences in the feeding ratio of the harbour porpoise within the day with a higher feeding ratio at night than during the day (Carlström 2005, Todd *et al.* 2009). It seems difficult to explain this discrepancy, but it could be a result of the different geographical position and time periods of their studies compared to this study. Todd *et al.* (2009) have investigated the harbour porpoise in the Dogger Bank region of the North Sea for one year from 2005 to 2006. The study by Carlström (2005) was conducted at the Isle of Mull in West Scotland from April to June 2001, while the present study was carried out from 30th July to 2nd September 2018 in Fyns Hoved in Denmark. However, these are only presumptions, which leave many questions for further research on this topic.

Next, the feeding buzzes between the different C-POD stations at each diel phase were compared. The main result was that significant more feeding buzzes were identified in shallow water (C-POD stations 2 to 8) than in deeper water (C-POD station 10) during the day. This finding is in line with the hypothesis mentioned in the chapter before that harbour porpoises probably hunt benthic fish in shallow water during the day. However, no significant differences could be found between C-POD station 1 and 9 and the remaining stations. Furthermore, the feeding buzzes did not differ significantly between the stations at night, except for station 4 and 10. More feeding buzz trains were classified at C-POD station 4 than at station 10 at night. This finding is in contrast to the suggestion that harbour porpoises move into deeper water at night to hunt pelagic fish. Possible explanations for this contradiction will be discussed in the following paragraphs.

One possible explanation could be the low variation in the water depth between the different C-POD stations. C-POD stations 2 to 9 were deployed close to the coast at a water depth of around 5 to 6 m. Only two C-PODs were located farther offshore at a depth of 11.3 m (C-POD station 1) and 14 m (C-POD station 10). If more C-PODs had been placed at different water depths, the possible pattern of harbour porpoise detections between shallow and deeper water could have been more significant. For example, in the study by Schaffeld *et al.* (2016), the C-PODs were deployed in water depths, which ranged from 8 to 28 m.

Another explanation could be that the number of feeding buzzes of a porpoise may depend on the features of its prey. For instance, if the quality of the prey is low in a certain area, the porpoise needs to catch more prey to meet its energy demand. This would lead to an increase of the foraging rate and hence to a raise of the feeding buzz ratio. If an area has a low density of the porpoise's prey, the porpoises must search longer. This means that they are clicking longer in the search phase for each caught fish. As a result, the feeding buzz ratio would decline. Kyhn e*t al.* 2018 have summarized possible factors, which could influence the feeding buzz ratio (see Fig. 49). However, it remains unclear whether one of these factors had an impact on the identified feeding buzz ratio during this study.

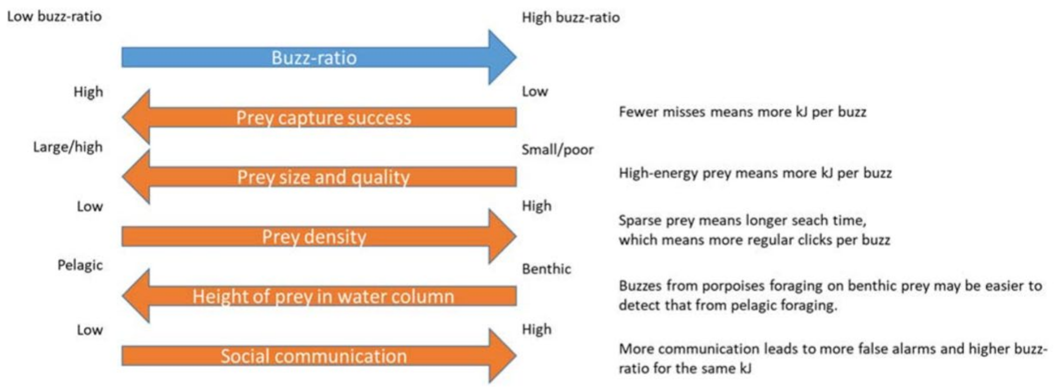


Fig. 49: Possible factors, which could influence the feeding buzz ratio of a harbour porpoise (Kyhn e*t al.* 2018).

Furthermore, there are still some discrepancies regarding the threshold up to which a click train can be classified as a feeding buzz train. In accordance with previous studies (Carlström 2005, Nuuttila *et al.* 2013, Todd *et al.* 2009, Verfuß *et al.* 2009), the author of this study has defined Minimum ICIs of less than 10 ms as a feeding buzz train. In contrast, Kyhn *et al.* (2018) have termed Minimum ICIs of below 15 ms as a feeding buzz train. They do not explain why they chose this specific threshold. Schaffeld *et al.* (2016) have argued that a Minimum ICI of below 10 ms can only be used as a first indicator for foraging activity as they determined that click trains show a high variation in ICI before they suddenly drop to below 10 ms (Schaffeld e*t al.* 2016). Additionally, it was found that harbour porpoises emit communication clicks, which could have a high similarity to feeding buzz trains (Clausen *et al.* 2011, Sørensen *et al.* 2018, Koschinski *et al.* 2008). Clausen *et al.* (2011) have investigated the acoustic and swimming behavior of harbour porpoises during different tasks in a pool at the Fjord and Baelt Center in Denmark. They demonstrated that harbour porpoises use specific click patterns that can be linked to specific behaviour categories (Clausen *et al.* 2011). These clicks during social communication were noted to consist of very short ICIs of below 7.7 ms, which were also reported for foraging activity (Clausen *et al.* 2011, Koschinski *et al.* 2008). After identifying potential communication clicks in captured porpoises, Sørensen *et al.* (2018) studied them with deployed tags on wild porpoises. They could show that wild harbour porpoises frequently produce communication clicks, which are separated by short silent periods (Sørensen *et al.* 2018). Communication clicks were detected 54 – 59 % of the time during

the recording of two tagged mothers and a calf, while 10 – 36 % of the time were found as communication clicks in a single tagged porpoise (Sørensen *et al.* 2018).
Thus, it was concluded that it could lead to inaccuracies if you only use a "buzz" as a criterion for feeding activity as it is not sure whether a click was emitted for echolocation or for communication (Schaffeld e*t al.* 2016). As a consequence, it was recommended to develop an algorithm for further studies, that can identify behavior categories automatically (Schaffeld e*t al.* 2016). In this study, Minimum ICIs of less than 10 ms were classified as feeding trains. Therefore, some of the identified feeding buzzes could have been communication calls. This could be especially true when a mother and a calf were sighted together. However, it is important to mention that the C-POD can sometimes record only fragments of a click train, depending on the position of the harbour porpoise (Koschinski *et al.* 2008). These fragments could be classified as different behavior categories although they are part of the same click train (Koschinski *et al.* 2008). Another problem could be that click trains of different individuals may overlap, which makes a categorization of an individual's click train difficult (Koschinski *et al.* 2008). By taking all these points together, it is clearly visible that further studies are required to clarify differences between foraging and communication click trains. This in turn would be helpful to identify a possible activity pattern of harbour porpoises.

As a next step, the absolute numbers of feeding buzzes of this study will be compared to other studies, which have also investigated the feeding buzz trains of harbour porpoises. In this study, the percentage of feeding buzz trains varied significantly between the stations during the day. The mean of feeding buzz trains ranged from 13.74 % at station 10 to 64.87 % at station 5 during the day. Also, significant differences in feeding buzz trains were found at night between stations 4 and 10. The mean amounted to 21.34 % at station 10, whereas the mean at station 4 was 52.92 %. When comparing these values to the calculated feeding buzzes of Carlström's study (2005), major differences can be seen. In her study, the feeding buzzes ranged from 1.7 % during the day to 4.8 % at night. This raised the question, why there is such a large discrepancy in the amount of feeding buzzes between this study and the study by Carlström (2005). Both studies used a Minimum ICI < 10 ms as an indicator for feeding activity. However, it is not known which customer settings were in the C-POD software in Carlströms study (Carlström 2005). In this study, the filters "Cet High" and "Cet Mod" were selected. Moreover, Carlström used the predecessor of the C-POD: the so called T-POD (Carlström 2005). Another aspect is that the sample size of trains per diel phase differed strongly between the days. On some days, only a total of one or two trains was detected during one diel phase. For instance, if only one train with a Minimum ICI < 10 ms and no train with a Minimum ICI > 10 ms was detected on one day, the feeding buzz ratio immediately amounted to 100 % (see chapter 3.2.3.). This could explain the high percentage of feeding buzz trains at some stations in this study. Furthermore, the Minimum ICI of below 10 ms can only be seen as an indicator for feeding activity. To proof whether a train is in fact a feeding train, it is necessary to look manually at each train. Due to the large amount of data, it was not possible to check each train individually during this study.

When comparing the calculated feeding buzz trains of this study with those of Kyhn *et al.* 2018, similar results can be identified. They found feeding buzz trains between 27.7 % in the southwest Baltic Sea and 61.6 % in the Baltic Proper at night. During the day, the feeding buzz trains ranged between 20.8 % in the Baltic Proper and 22.7 % in the southwest Baltic Sea. However, it is important to mention that they used a Minimum ICI of below 15 ms and not 10 ms as a threshold for feeding activity (Kyhn *et al.* 2018).

This chapter showed that further research projects are required to explain the discrepancies in the feeding activity of the harbour porpoise between different studies. Furthermore, it would be helpful for further research projects to use a unified method for analyzing feeding buzzes of harbour porpoises. For this, it must be determined which threshold of Minimum ICI is the most optimal one to use. Also, it must be investigated how to distinguish potential feeding trains from communication calls. It is recommended to create an algorithm, that can identify feeding activity automatically in order to facilitate the analyses in further studies.

4.2. Visual detections of harbour porpoises

This chapter will start by discussing potential differences in the visual harbour porpoise detections during the day. It was hypothesized that the harbour porpoise shows a diel activity pattern. As a next step, potential impact factors (wind speed and wind direction) on the visual harbour porpoise monitoring will be analyzed. The hypothesis was that wind speed and wind direction have an impact on the detection rate of harbour porpoises.

The harbour porpoise was observed visually with a theodolite during this study. In total, 209 harbour porpoise groups were tracked, which resulted in 3,588 tracking points. This affirms the use of a theodolite to observe harbour porpoises visually. The application of a theodolite to observe marine mammals visually was already reported in several studies such as by

Culik *et al.* 2001, Koschinski *et al.* 2003 and Kyhn *et al.* 2012. Furthermore, the harbour porpoises were sighted in groups of one to five animals during this study. Such a small group size has already been reported by Bruhn (1997) and Kremer & Maywald (1991). Bjørge & Tolley (2009) have found that small harbour porpoise groups often consist of a mother-calf pair. Moreover, the detections of harbour porpoises per hour differed over the day during this study. Fewer harbour porpoises per hour were sighted from 09:00 to 13:00 than from 13:00 to 18:00. One could have expected that the number of harbour porpoise's detections differs over the day e.g. due to sun glare or due to the reflection of the sun's rays on the water. The finding that more harbour porpoises per hour were sighted during midday (from 12:00 to 13:00) than in the morning hours would indicate that the position of the sun does not really seem to influence the ability to detect harbour porpoises. This would confirm that it is possible to observe harbour porpoises visually in their natural environment.

However, it is important to mention that the visual monitoring method has some limitations, which should be considered when planning a research project. Visual surveys can only be conducted if the weather is calm, the sea state is low and a good visibility of the study area is possible (Hammond *et al.* 2013). Due to unfavorable weather conditions during this study, the visual observation was only conducted on 15 days. This makes up to 43 % of the whole study days. In other words, during 57 % of the study period, it was not possible to observe the porpoises visually. This is a large proportion when considering that each day during a study project increases the costs of the study. When the weather was suitable and an observation was carried out, harbour porpoises could be detected during wind speeds of between 1.4 m/s and 7.4 m/s. Wind speeds of less than 1.4 m/s and more than 7.4 m/s were not measured during the observation. It could be assumed that wind speed may influence the ability to sight porpoises due to higher wave formations during high wind speeds. This could result in less harbour porpoise detections during periods of higher wind speed. During this study, no clear dependency between the number of harbour porpoise detections and the wind speed was recognizable (see Fig. 40). Therefore, it could be concluded that wind speeds of up to 7.4 m/s do not seem to have a strong impact on the ability to sight harbour porpoises in this study area. Teilmann (2003) has recommended not to observe with a Beaufort Sea state of more than 3 to minimize the probability of missing harbour porpoises. Berrow *et al.* (2008) have even suggested to conduct harbour porpoise surveys only at a sea state of 0 or 1 to ensure that all animals are detected. During this study, the observers have tracked porpoises with a wind speed of up to 7.4 m/s, which corresponds to a Beaufort Sea state of 4. Thus, some of the harbour porpoise sightings might have been false-positive detections. This means that e.g. higher water waves were wrongly identified as porpoises. Additionally, the reverse situation could have occurred as well: Some harbour porpoises could have been overlooked during high wind speeds. Especially because harbour porpoises are small and show only small parts of their body, when they come to the surface for breathing (Evans & Hammond 2004). However, the water in the study area was relatively shallow and the seabed was often visible so that the porpoises could be tracked pretty precisely.

Besides of the wind speed, the wind direction could influence the sighting rate of harbour porpoises as well. Depending on the direction of the wind, the shape of the waves could vary. This in turn could affect the ability to detect porpoises. The results in Fig. 41 have demonstrated that harbour porpoises could be sighted no matter of the wind direction. However, most porpoises were sighted when the wind blew from east, while the most frequent wind direction during the visual observation was from south west. This shows that the wind direction seems to have an impact on the detection rate of harbour porpoises. A possible explanation for this is the orientation of the cliff towards the west. When the wind blew from east, the observation area was more protected and thus shallower waves were to be expected. The magnitude of this possible impact and the exact number of porpoises that were missed or wrongly identified during some wind conditions, remains unclear in this study.

Another limitation could be the distance up to which a porpoise can be seen. It is clearly visible that most of the harbour porpoises were tracked very close to the cliff. 89 of 209 harbour porpoise groups were sighted between 100 m and 200 m away from the observation place. The maximum distance to a detected harbour porpoise group was around 1500 m. It remains unclear whether the porpoises truly swam very close to the coast or whether the observers were not able to spot porpoises further offshore.

An additional challenge during the visual observation was to make the decision whether a sighted porpoise group was already a new group or had already been sighted before. Therefore, it is possible that of the 209 observed groups some groups were wrongly tracked twice. This problem could be solved by taking photos of the observed porpoises and analyzing them afterwards. Furthermore, several harbour porpoise groups were sometimes detected within the study area. Because only one theodolite was available, it was only possible to track one group at once. The other, untracked group was only noted on the observation protocol. It would be helpful to use more than one theodolite in further studies. With several visual observation places along the coast, a larger area can be studied.

Overall, the hypothesis that the harbour porpoise shows a diel activity pattern can be verified in so far as more harbour porpoises were detected visually during the afternoon than in the morning and at noon. The hypothesis that the wind speed and wind direction influence the detection rate of harbour porpoises, can only be partly confirmed. Wind speeds between 1.4 m/s and 7.4 m/s do not seem to strongly influence the sighting rate of harbour porpoises, while the wind direction seems to have an impact on the ability to detect porpoises in this study. By taking into account all the points mentioned above, it is useful to combine visual and acoustic surveys to compensate possible limitations of both methods. How practicable a combination of these two methods during this study was, will be discussed in the next chapter.

4.3. Comparison of acoustic detections with visual detections

The third task of this study was a comparison of the acoustic harbour porpoise detections and the visual sightings. The hypothesis was formulated as follows: The number of harbour porpoises' sightings with C-PODs differs from that with a theodolite. To analyze whether both methods have obtained similar results, only these visual sightings were selected, which were not more than 100 m away from each C-POD. When comparing these two methods, it is clearly visible that more harbour porpoises were detected with the theodolite than with the C-PODs at stations 4 to 8. More harbour porpoises were detected at C-POD stations 2, 3 and 9 than visually. C-POD stations 1 and 10 were not included in the comparison because no visual sighting was closer than 100 m to one of these two stations.

These findings lead to the question why there is such a large discrepancy between these two observation methods. Possible explanations will be discussed in the following paragraphs.

Only C-POD stations 2, 3 and 9 have recorded more porpoises than it was possible with the theodolite. As Fig. 10 indicates, the C-POD stations were deployed in different distances to the coast of the study area. C-PODs 2, 3 and 9 were nearest to the C-PODs 1 and 10, which were deployed further offshore. They have a distance of around 484 m (C-POD 2), 325 m (C-POD 3) and 376 m (C-POD 9) to the observation place. The C-PODs 2, 3 and 9 were probably too far away so that an exact visual observation was not possible. This means that the ability to sight porpoises visually is probably limited to a certain distance to the observer. The C-PODs 4 to 8 were between around 165 m and 266 m away from the observation place. Thus, this seems to be the range up to which a precise observation during this study was possible. This finding should be considered when planning further visual monitoring projects. It remains unclear in this study whether a precise observation of harbour porpoises at distances between 266 m and 325 m was possible. The distance from each C-POD to the observation place is summarized in the Annex in Tab. 29.

One explanation for a higher detection rate with the theodolite than with the C-PODs could be a possible failure or inaccuracy of some C-POD devices. Every few days, the devices were removed to secure the data and they were replaced by another one. It is possible that some devices were more precise than others and thus they have detected more porpoises than the rest (Kyhn *et al.* 2008). The reason for this instrument variation could be for example a different standardization of the C-POD devices or different costumer settings of the detection filters in the C-POD software (Kyhn *et al.* 2008). It is recommended to standardize each C-POD before it is deployed (Dähne *et al.* 2013). Through a calibration in a test tank, the results of the C-PODs can be compared to each other (Dähne *et al.* 2013). All C-PODs used in this study were calibrated prior to the deployment. Moreover, the same costumer settings were selected for all C-PODs (see chapter 2.3.). For the analysis, the filters “Cet High” and “Cet Low” were chosen, which were recommended by the manufacturer. However, the detector in the C-POD software is a black box, so that it is not yet known how exactly it works (Tregenza *et al.* 2016). Thomsen e*t al.* 2005 wondered whether trains of the category “Cet Low” (low probability of coming from porpoises) and “?” (doubtful trains) should be included in the analysis or whether they should be left out. They found that a relatively high proportion of trains, which were classified as “Cet Low” and “?” came from harbour porpoises (Thomsen e*t al.* 2005). The consequence would be that trains of these categories should be investigated more carefully to reduce the risk of losing porpoise detections (Thomsen e*t al.* 2005). This would exceed the time frame for this study. Therefore, it is possible that some harbour porpoise trains were wrongly excluded from the data analysis in this study.

If some C-POD devices could detect more porpoises than other devices, it could be expected that during these days the difference between the visual and the acoustical detections would be lower. To proof this hypothesis, the days on which different devices were used, were compared to each other. As an example, the results for C-POD station 7 are shown in Tab. 12. The results for the remaining stations can be read in the Annex from Tab. 21 to Tab. 28. The gray fields in Tab. 12 show on which dates the devices were changed. In total, the C-POD device was changed three times at C-POD station 7. It is evident that most days more harbour porpoises were detected with the theodolite than with the C-POD, probably regardless of the deployed C-POD device. When comparing the days on which the first C-POD device was used (from 31st July to 13th August) to the days on which the next C-POD device was deployed (from 13th August to 17th August), no clear difference in the detections of harbour porpoises is recognizable. During both periods, the acoustic detections were much lower than the visual, except for 6th August. On this day, the difference between these two monitoring methods amounted to only one detection. Additionally, the other C-POD devices used at this station do not seem to influence the ability to detect porpoises. Similar results can be seen at the other C-POD stations (see Annex, from Tab. 21 to Tab. 28). Therefore, it seems rather unlikely that individual C-POD devices have recorded more porpoises than other devices. Hence, different C-POD devices seem not to be the reason for the mismatch between the visual and the acoustic harbour porpoise detections during this study.

Another explanation could be the possible impact of another experiment, which was conducted as part of the project STELLA during the same time in the study area. In this experiment, the behavior reactions of the harbour porpoise to a conventional gillnet, a modified gillnet or to no net (control) were observed on the cliff in Fyns Hoved. The background of this experiment was the high bycatch rate of harbour porpoises in gillnets throughout their distribution range. In order to reduce their entanglement in gillnets, you need to identify the reasons for this entanglement. One hypothesis was that harbour porpoises cannot see the net in time and become entangled (Cox & Read 2004). Secondly, solutions to reduce it need to be determined. It was suggested to improve the acoustic reflectivity of nets, so that they can be detected easier by the porpoise's biosonar (Jefferson & Curry 1996, Koschinski *et al.* 2006, Mooney *et al.* 2007). It has been found out that small acryl glass spheres have a large echo, which could be detected easier by harbour porpoises. Therefore, these glass spheres were attached to the modified gillnet before it was deployed. One could expect that the porpoises echolocate more frequently if a modified net (a possible more visible obstacle) was in the water than if only a conventional gillnet or even no net would be deployed. This in turn would mean that the difference between the visual and the acoustic sightings would be lower if a modified net would be in the water. This hypothesis will be analyzed in the following paragraph.

The type of net deployed on each observation day is listed in Tab. 12. The modified gillnet was deployed on four days, while the conventional gillnet was set on three days. The remaining days were control days. When comparing the days on which a modified gillnet was deployed, no clear pattern can be identified. For instance, on 6th August, a modified gillnet was deployed and the difference between the visual and the acoustical sightings amounted to only one detection. A modified gillnet was also deployed on 23rd August. On this day, the mismatch between the visual and the acoustic sightings was much higher, namely a difference of 32 detections. When comparing the days where a modified gillnet was deployed to the days with a conventional gillnet or without a net in the water, no clear differences can be recognized, either. This means that differences in porpoise detections between the visual and the acoustic method were high, probably regardless of a deployed net in the water. Similar results were noted at the other C-POD stations (see Annex, from Tab. 21 to Tab. 28). These findings demonstrate that the discrepancy between the visual and acoustic sightings can not be explained by the deployment of different gillnet types in the water. However, it is important to consider this interpretation with caution for two main reasons. Firstly, the nets were not deployed in the positions as desired by the researchers of this experiment. The nets stood only around ½ m to 1 m upright in the water column, whereas they should stand 3 - 4 m vertically in the water column. Secondly, as it was already noted in this thesis, most of the sighted porpoises swam very close to the coast (see Fig. 24 - Fig. 28). The nets on the other hand were deployed further offshore between C-POD stations 5 and 6. Thus, it is possible that the nets were not truly an obstacle for the porpoises. Further investigations on this topic will be conducted by Isabella Kratzer at the Thünen Institute for Baltic Sea Fisheries in Rostock (Germany).

Tab. 12: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 7 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 7. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. Only these dates are shown, on which a visual observation took place.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 7
31.07.2018	No net	14	4
01.08.2018	No net	5	3
02.08.2018	Modified gillnet	19	7
03.08.2018	No net	15	1
06.08.2018	Modified gillnet	3	4
07.08.2018	No net	18	2
08.08.2018	No net	18	1
09.08.2018	Gillnet	11	1
13.08.2018	No net	17	6
15.08.2018	Modified gillnet	9	5
17.08.2018	Gillnet	19	1
22.08.2018	No net	13	14
23.08.2018	Modified gillnet	49	17
24.08.2018	No net	34	5
25.08.2018	Gillnet	2	3

For the comparison, only these visual sightings were chosen, which were no more than 100 m away from each C-POD. It could be possible that C-PODs can detect only porpoises in a radius of less than 100 m. However, the manufacturer has indicated that C-PODs can detect porpoises in distances up to 400 m. Nuuttila *et al.* (2018) calculated that the mean maximum detection range for porpoises with C-PODs was 248 m (95% CI: 181 – 316 m). Therefore, it is rather unlikely that a too large distance could be the reason for the mismatch between the visual and the acoustic harbour porpoise detections in this study.

A more likely reason for the discrepancy between the visual and the acoustical sightings could be the echolocation behavior of the harbour porpoise. As mentioned in chapter 4.1.1., the harbour porpoise could be hunting visually during the day, which would result in less recorded echolocation clicks on the C-POD device. Furthermore, the harbour porpoise may use a special hunting strategy during the day, termed as “bottom grubbing” (Lockyer *et al.* 2003). During this sort of hunting, the harbour porpoise swims close to the bottom with the head downwards in search for prey (Brandt *et al.* 2014, Lockyer *et al.* 2003, Schaffeld e*t al.* 2016). It was argued that the echolocation clicks will only reach the C-PODs in an erratic way during this behavior, which is unlikely to be identified as an entire click train by the C-POD algorithm (Kyhn *et al.* 2012). The C-POD can only recognize clicks, when they have a sound source level above the detection threshold of the C-POD (Kyhn *et al.* 2012). This would be the case when the porpoise looks straight towards the C-POD. Dähne *et al.* (2013) have calculated that the detection threshold of a C-POD is 114.56 ± 1.2 dB re 1µPa at 130 kHz. Kyhn *et al.* (2012) have studied the harbour porpoise at the same location in 2003 and 2007 as in this study. They have observed that the harbour porpoise has used the “bottom grubbing” for a longer period during their study (Kyhn *et al.* 2012). Thus, the “bottom grubbing” of the harbour porpoise could be one reason why less porpoises were detected with the C-POD than visually during this study. However, further studies are recommended to investigate the extent of this behavior by the harbour porpoise. This information is needed when planning passive acoustic monitoring studies, which are based on continuous echolocation of the porpoise.

However, it is important to compare the observation methods with caution. During the visual observation, groups of harbour porpoises were counted and not individual porpoises. Each time they came up to the surface, they were tracked with the theodolite. The C-PODs have recorded the echolocation clicks of harbour porpoises and with these devices it is not possible to allocate single clicks to individuals. Furthermore, it should be kept in mind that not the absolute numbers of detections were compared to each other. The Detection Positive Minutes can give a value of “0” (no detections within one minute) or a value of “1”, which means that at least one harbour porpoise was detected within one minute. So far, it is not possible to identify how many porpoises have echolocated within a detected minute. Additionally, it is not possible to determine data whether consecutives click trains came from the same or from different animals based on the C-POD (Kyhn *et al.* 2012).

As a summary, the hypothesis that the number of harbour porpoises’ sightings with C-PODs differs from that with a theodolite, can be confirmed to the extent that more harbour porpoises were detected with the theodolite than with the C-PODs at the stations 4 to 8. More harbour porpoises were recorded at C-POD stations 2, 3 and 9 than visually.

4.4. Other detected cetacean

During this study, potential dolphin clicks were identified by the KERNO classifier algorithm. The frequency of dolphin clicks ranged from 33 kHz to 133 kHz. These results are consistent with the findings of Wahlberg *et al.* (2011), who have determined a frequency of dolphin clicks between 33 kHz and 109 kHz. A frequency up to 150 kHz has been noted by Au *et al.* 1974.

The results have shown that more dolphins were detected at the beginning of August than during the mid and the end of August. It is conspicuous that in general less harbour porpoises were recorded at the beginning of August than during the remaining study period. This finding leads to the question whether there is any connection between the occurrence of harbour porpoises and dolphins.

Several examinations of stranded harbour porpoises in the UK waters and in the Pacific Ocean have indicated attacks by bottlenose dolphins (Cotter *et al.* 2012, Patterson *et al.* 1998, Ross & Wilson 1996, Simon *et al.* 2010). These signs included multiple, ante-mortem injuries, like bruising around the head and thorax, multiple rib fractures, lung and soft tissue lacerations and contusions (Cotter *et al.* 2012, Patterson *et al.* 1998). All these injuries were bilateral, which led to the conclusion that the porpoises died due to an attack by another animal and not e.g. due to a boat collision (Cotter *et al.* 2012). The reasons for these attacks are still not completely clear (Patterson *et al.* 1998, Simon *et al.* 2010). One possible explanation could be a competition of food resources as bottlenose dolphins and harbour porpoises have an overlap in their prey species (Santos *et al*. 2001, Santos & Pierce 2003, Spitz *et al.* 2006). Another possible reason for these attacks could be that bottlenose dolphins practice infanticide since the found dead harbour porpoises had a size comparable to that of a bottlenose dolphin calf (Cotter *et al.* 2012, Patterson *et al.* 1998, Simon *et al.* 2010). This hypothesis could be supported by Patterson *et al.* 1998 who found attacked harbour porpoises as well as dead bottlenose dolphin calves during the same period with similar injuries at the coast of Scotland. Therefore, it is possible that harbour porpoises possibly avoid areas where dolphins appear (Simon *et al.* 2010). With the use of T-PODs, Simon e*t al.* 2010 found out, that dolphins were mainly abundant in the summer months in the Cardigan Bay in Wales, while porpoises were more abundant during the winter in this area. Because dolphin and porpoise click train were not recorded simultaneously on any T-POD device, they concluded that at least one species avoids echolocating in presence of the other species (Simon e*t al.* 2010). Thus, it could be hypothesized that the harbour porpoise in this study also avoids the time periods when bottlenose dolphins are around. As a consequence, less porpoises were detected in the time period where more dolphins were recorded. However, these explanations are only hypotheses, which should be investigated in further studies.

Furthermore, it is important to mention that the KERNO classifier algorithm has some limitations in regard to the identification of different species (Tregenza 2014). One limitation is that it classifies porpoises as dolphins when the environment is very noisy or when they are very close to the C-POD (Tregenza 2014). Thus, it remains unclear for this study, whether these clicks can be truly identified as dolphins, as there is also no visual confirmation of dolphin sightings.

5. Conclusion

The objective of this study was to investigate the activity pattern of the harbour porpoise in the coastal waters of Fyns Hoved in Denmark. Three main research tasks were investigated in this project.

The **first task** includes the identification of a potential diel activity pattern of the harbour porpoise with the use of C-PODs and a theodolite. The main results can be summarized as follows:

- The harbour porpoises detected by the C-PODs displayed a diel as well as a geographical pattern. More harbour porpoises were detected during night and evening than during morning and day. The detections of harbour porpoises were significantly higher at the deeper C-POD stations 1, 2 and 10 than at the remaining, shallower stations during the evening. The most porpoises were recorded at the C-POD station 1 at night.
- It was hypothesized that the echolocation activity of the harbour porpoise is related to an alternation in feeding techniques and in prey choice in deep and in shallow waters. The suggestion was that harbour porpoises may be feeding pelagic prey in deeper waters at night, while they may be hunting mainly benthic prey in shallow waters during the day. It was expected that the harbour porpoise is mainly hunting visually or with a special feeding behavior ("bottom-grubbing") during the day. The "bottom-grubbing" would have the consequence that the harbour porpoise could not be detected by the C-POD, because of its narrow echolocation beams.
- These findings have extended the current knowledge about the diel activity pattern of the harbour porpoise. Bottom-grubbing as well as visual hunting both have a direct impact on passive acoustic monitoring devices as they are based on continuous echolocation of the studied species. If harbour porpoises do not echolocate continuously, this could be a possible reason for the high bycatch rate of the harbour porpoise. Thus, there is an immediate need to conduct further studies on this issue. On the current state of knowledge, this is the first study, which has investigated the activity of harbour porpoises on a very small distance. It has shown that the occurrence of harbour porpoises varied on even a very small space. C-POD studies, which are so far known, have compared the distribution of harbour porpoises between different sea areas (e.g. Bailey *et al.* 2010, Gallus *et al.* 2012, Schaffeld *et al.* 2016).

- The visual monitoring has demonstrated that it is possible to observe harbour porpoises with a theodolite under the conditions of a maximum Beaufort Sea state of 3 to 4. More harbour porpoises were detected visually in the afternoon than during morning and noon.

As a **second task**, potential impacts on harbour porpoise detection with a theodolite were identified. The following findings were made:

- Wind speeds between 1.4 m/s and 7.4 m/s do not seem to strongly influence the sighting rate of harbour porpoises, while the wind direction seems to have an impact on the ability to detect porpoises in this study. Most porpoises could be sighted when the wind blew from east. The distance up to which harbour porpoises could be tracked, has decreased with increasing wind speed.
- These findings have led to the conclusion that the theodolite is an useful tool to observe harbour porpoises. However, effective and precise visual observation is limited to certain weather conditions, which should be taken into account during visual monitoring studies.

The **third task** involves a comparison of the number of harbour porpoises' sightings with C-PODs to that with a theodolite. The comparison has provided the following outcome:

- More harbour porpoises were detected with the theodolite than with the C-PODs at stations 4 to 8. At C-POD stations 2, 3 and 9, more harbour porpoises were detected acoustically than visually.
- This finding indicates that the ability to sight porpoises visually is probably limited to a certain distance to the observer. The comparison has demonstrated that around 266 m is the maximum distance up to which a precise observation during this study was possible. Distances of about 325 m to the observer could not anymore secure a precise observation of harbour porpoises in this study. This finding should be considered in further visual monitoring studies. It remains unclear in this study whether an exact monitoring at distances between 266 m and 325 m was possible.

6. Recommendations for future studies

The harbour porpoise is the only cetacean species, which occurs regularly in the Baltic Sea (Scheidat *et al.* 2008). Its abundance has decreased within the last several decades, so that it is listed as a threatened and/or declining species in the Northeast Atlantic by the OSPAR Commission (OSPAR 2008). In the Baltic Sea, the harbour porpoise is recognized as critically endangered (Hammond *et al.* 2008). In order to recover the harbour porpoise population, it is protected in the EU waters by being listed in several agreements (Annex II and IV of the EU Habitats Directive, Annex II of the Bern Convention, Annex II of the Convention on the Conservation of Migratory Species and in Annex V of OSPAR Commission) (Gallus *et al.* 2012, Gilles 2009, Verfuß *et al.* 2007). These listings demand the immediate identification of special areas of conservation for this species, which is only possible when its abundance, distribution and migration patterns are known (Berggren *et al.* 2002, Gallus *et al.* 2012). The OSPAR Commission has recommended that acoustic surveys, such as passive acoustic monitoring devices, should be used to effectively monitor harbour porpoises (Kyhn *et al.* 2018). However, just like any other method, acoustic monitoring has some limitations (Kyhn e*t al.* 2018): They are based on the assumption that the species echolocates continuously (Kyhn e*t al.* 2018). The probability of detecting harbour porpoises could be influenced by the narrow beam width of their echolocation clicks (Koblitz *et al. 2*012), certain feeding behavior (like the "bottom-grubbing", Lockyer *et al.* 2003) and background noise, such as wind speed, sediment noise and ship traffic (Tregenza *et al. 2*016). Thus, it was suggested to use a combination of visual and acoustic methods to create appropriate management plans for the protection of the harbour porpoise (Williamson e*t al.* 2017). In this study, the harbour porpoise was observed visually as well as acoustically in the coastal waters of Fyns Hoved. The results have demonstrated that the harbour porpoise was recorded less during the day by the C-POD than at night. This shows the need for the use of an additional monitoring method during the day, such as the visual monitoring. Secondly, the study has provided possible explanations for the diel activity pattern of the harbour porpoise. These explanations should be proven in further studies. Further research projects should include a wider range of water depths. It was hypothesized that the harbour porpoise moves into deeper water at night. This hypothesis could be proved by deploying more C-POD devices onshore as well as offshore. Furthermore, it would be interesting to simultaneously collect several parameters, which could possibly influence the abundance of harbour porpoises, like the occurrence of their prey species and human activities in the study area, as well as presence or absence of other cetacean species. According to the current state of knowledge, there are still different opinions on the most suitable threshold up to which a click train can be classified as a feeding buzz train. Therefore, it is recommended to conduct further studies in order to assess a uniform definition of a feeding buzz. Since this study has analyzed the activity pattern of the harbour porpoise during the summer, it would be important to identify a potential seasonal activity pattern of this species. Knowledge about the harbour porpoise abundance throughout the different seasons is necessary to effectively create a marine protected area for this species.

VII. References

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VIII. Eidesstattliche Erklärung

Hiermit bestätige ich, dass ich die vorliegende Arbeit selbständig verfasst und keine anderen als die angegebenen Hilfsmittel benutzt habe. Die Stellen der Arbeit, die dem Wortlaut oder dem Sinn nach anderen Werken entnommen sind, wurden unter Angabe der Quelle kenntlich gemacht.

Ort, Datum Unterschrift

IX. Annex

Tab. 13: Transformation of the number of the C-POD stations for data analysis.

Number of the C-POD stations during the study period	Transformation of the number of the C-POD stations for data analysis
1	4
2	3
3	2
4	7
5	8
6	9
7	5
8	6
9	10
10	1

Tab. 14: Geographical position of each deployed C-POD during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

C-POD	Latitude	Longitude
1	N55.63013°	E10.59872°
2	N55.62328°	E10.58812°
3	N55.62153°	E10.58751°
4	N55.62078°	E10.58742°
5	N55.61976°	E10.58812°
6	N55.61992°	E10.58694°
7	N55.61897°	E10.58732°
8	N55.61831°	E10.58656°
9	N55.6185°	E10.58466°
10	N55.61466°	E10.57361°

Tab. 15: Time periods of the deployed C-PODs during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark. The C-POD stations 2, 5, 6 and 9 have data gaps due to a probably defect of the devices.

C-POD station	C-POD ID	Start of deployment	End of deployment
1	1828	30.07., 09:38	08.08., 14:12
1	1825	08.08., 14:12	14.08., 07:02
1	810	14.08., 07:02	21.08., 14:24
1	813	21.08., 21:21	25.08., 09:14
1	1469	25.08., 09:14	02.09., 15:23
2	813	30.07., 10:02	13.08., 07:06
2	1469	13.08., 07:06	17.08., 09:06
2	1828	17.08., 09:06	23.08., 07:02
2	1825	23.08., 07:02	02.09., 15:30
3	810	30.07., 10:00	03.08., 06:43
3	1826	13.08., 09:45	19.08., 09:29
3	1469	19.08., 09:29	24.08., 06:22
3	1830	24.08., 06:22	02.09., 15:32
4	1474	30.07., 09:00	13.08., 08:35
4	813	13.08., 09:35	19.08., 09:34
4	1466	19.08., 09:34	24.08., 06:20
4	1828	24.08., 06:20	02.09., 15:36
5	1465	17.08., 08:55	17.08., 16:06
5	1465	22.08., 08:06	22.08., 17:20
5	1465	23.08., 06:59	23.08., 15:05
6	816	01.08., 09:21	01.08., 15:20
6	816	02.08., 09:00	02.08., 15:01
6	816	08.08., 07:46	08.08., 16:25
6	1465	15.08., 07:18	15.08., 17:02
6	816	17.08., 08:55	17.08., 16:15
6	816	22.08., 07:58	22.08., 17:25
6	816	23.08., 06:54	23.08., 15:15

C-POD station	C-POD ID	Start of deploy-ment	End of deploy-ment
7	1826	30.07., 10:10	13.08., 06:55
7	1466	13.08., 06:55	17.08., 09:20
7	1830	17.08., 09:20	23.08., 07:02
7	1473	23.08., 07:38	02.09., 15:43
8	1466	30.07., 10:30	09.08., 07:22
8	1828	09.08., 07:22	15.08., 07:17
8	1825	15.08., 07:17	22.08., 08:14
8	810	22.08., 08:18	02.09., 15:49
9	1469	30.07., 10:32	09.08., 07:18
9	1830	09.08., 07:19	15.08., 07:12
10	1830	30.07., 10:45	08.08., 16:30
10	1473	08.08., 16:30	14.08., 07:17
10	1474	14.08., 07:17	21.08., 14:37
10	1826	21.08., 14:37	25.08., 09:30
10	1866	25.08., 09:30	02.09., 15:08

Tab. 16: Duration of the defined time periods “Day” and “Night” for each day from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

Date	Day	Night
30.07.2018	05:19 – 21:27	21:27 – 05:19
31.07.2018	05:21 – 21:25	21:25 – 05:21
01.08.2018	05:23 – 21:23	21:23 – 05:23
02.08.2018	05:25 – 21:21	21:21 – 05:25
03.08.2018	05:26 – 21:19	21:19 – 05:26
04.08.2018	05:28 – 21:17	21:17 – 05:28
05.08.2018	05:30 – 21:15	21:15 – 05:30
06.08.2018	05:32 – 21:13	21:13 – 05:32
07.08.2018	05:34 – 21:11	21:11 – 05:34
08.08.2018	05:36 – 21:08	21:08 – 05:36
09.08.2018	05:38 – 21:06	21:06 – 05:38

Date	Day	Night
10.08.2018	05:40 – 21:04	21:04 – 05:40
11.08.2018	05:41 – 21:02	21:02 – 05:41
12.08.2018	05:43 – 21:00	21:00 – 05:43
13.08.2018	05:45 – 20:57	20:57 – 05:45
14.08.2018	05:47 – 20:55	20:55 – 05:47
15.08.2018	05:49 – 20:53	20:53 – 05:49
16.08.2018	05:51 – 20:50	20:50 – 05:51
17.08.2018	05:53 – 20:48	20:48 – 05:53
18.08.2018	05:55 – 20:46	20:46 – 05:55
19.08.2018	05:57 – 20:43	20:43 – 05:57
20.08.2018	05:59 – 20:41	20:41 – 05:59
21.08.2018	06:01 – 20:39	20:39 – 06:01
22.08.2018	06:03 – 20:36	20:36 – 06:03
23.08.2018	06:05 – 20:34	20:34 – 06:05
24.08.2018	06:06 – 20:31	20:31 – 06:06
25.08.2018	06:08 – 20:29	20:29 – 06:08
26.08.2018	06:10 – 20:26	20:26 – 06:10
27.08.2018	06:12 – 20:24	20:24 – 06:12
28.08.2018	06:14 – 20:21	20:21 – 06:14
29.08.2018	06:16 – 20:19	20:19 – 06:16
30.08.2018	06:18 – 20:16	20:16 – 06:18
31.08.2018	06:20 – 20:14	20:14 – 06:20
01.09.2018	06:22 – 20:11	20:11 – 06:22
02.09.2018	06:24 – 20:09	20:09 – 06:24

Tab. 17: Duration of the defined time periods “Morning”, “Day”, “Evening” and “Night” for each day from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

Date	Morning	Day	Evening	Night
30.07.2018	04:31 – 06:07	06:07 – 21:27	21:27 – 23:03	23:03 – 04:33
31.07.2018	04:33 – 06:09	06:09 – 21:25	21:25 – 23:01	23:01 – 04:35
01.08.2018	04:35 – 06:11	06:11 – 21:23	21:23 – 22:57	22:57 – 04:37
02.08.2018	04:37 – 06:13	06:13 – 21:21	21:21 – 22:55	22:55 – 04:39
03.08.2018	04:39 – 06:13	06:13 – 21:19	21:19 – 22:53	22:53 – 04:42
04.08.2018	04:42 – 06:14	06:14 – 21:17	21:17 – 22:49	22:49 – 04:44
05.08.2018	04:44 – 06:16	06:16 – 21:15	21:15 – 22:47	22:47 – 04:46
06.08.2018	04:46 – 06:18	06:18 – 21:13	21:13 – 22:43	22:43 – 04:48
07.08.2018	04:48 – 06:20	06:20 – 21:11	21:11 – 22:41	22:41 – 04:51
08.08.2018	04:51 – 06:21	06:21 – 21:08	21:08 – 22:38	22:38 – 04:53
09.08.2018	04:53 – 06:23	06:23 – 21:06	21:06 – 22:36	22:36 – 04:55
10.08.2018	04:55 – 06:25	06:25 – 21:04	21:04 – 22:32	22:32 – 04:57
11.08.2018	04:57 – 06:25	06:25 – 21:02	21:02 – 22:30	22:30 – 04:59
12.08.2018	04:59 – 06:27	06:27 – 20:59	20:59 – 22:26	22:26 – 05:02
13.08.2018	05:02 – 06:28	06:28 – 20:57	20:57 – 22:23	22:23 – 05:04
14.08.2018	05:04 – 06:30	06:30 – 20:55	20:55 – 22:21	22:21 – 05:06
15.08.2018	05:06 – 06:32	06:32 – 20:53	20:53 – 22:17	22:17 – 05:08
16.08.2018	05:08 – 06:34	06:34 – 20:50	20:50 – 22:16	22:16 – 05:11
17.08.2018	05:11 – 06:35	06:35 – 20:48	20:48 – 22:12	22:12 – 05:13
18.08.2018	05:13 – 06:37	06:37 – 20:46	20:46 – 22:10	22:10 – 05:15
19.08.2018	05:15 – 06:39	06:39 – 20:43	20:43 – 22:07	22:07 – 05:17
20.08.2018	05:17 – 06:41	06:41 – 20:41	20:41 – 22:03	22:03 – 05:19
21.08.2018	05:19 – 06:43	06:43 – 20:38	20:38 – 22:01	22:01 – 05:21
22.08.2018	05:21 – 06:45	06:45 – 20:36	20:36 – 21:58	21:58 – 05:24
23.08.2018	05:24 – 06:46	06:46 – 20:33	20:33 – 21:54	21:54 – 05:26
24.08.2018	05:26 – 06:46	06:46 – 20:31	20:31 – 21:53	21:53 – 05:28
25.08.2018	05:28 – 06:48	06:48 – 20:29	20:29 – 21:49	21:49 – 05:30
26.08.2018	05:30 – 06:50	06:50 – 20:26	20:26 – 21:46	21:46 – 05:32
27.08.2018	05:32 – 06:52	06:52 – 20:24	20:24 – 21:44	21:44 – 05:34

Date	Morning	Day	Evening	Night
28.08.2018	05:34 – 06:54	06:54 – 20:21	20:21 – 21:21	21:21 – 05:36
29.08.2018	05:36 – 06:56	06:56 – 20:19	20:19 – 21:37	21:37 – 05:39
30.08.2018	05:39 – 06:57	06:57 – 20:16	20:16 – 21:34	21:34 – 05:41
31.08.2018	05:41 – 06:59	06:59 – 20:13	20:13 – 21:32	21:32 – 05:43
01.09.2018	05:43 – 07:01	07:01 – 20:11	20:11 – 21:29	21:29 – 05:45
02.09.2018	05:45 – 07:03	07:03 – 20:08	20:08 – 21:25	21:25 – 05:47

Tab. 18: Protocol for the visual monitoring of the harbour porpoise during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

Date	Time	Number of sighted porpoises	Swimming direction	Start number theodolite	End number theodolite	Temperature [°C]	Wind direction	Wind speed [m/s]	Beaufort Sea state	Remarks

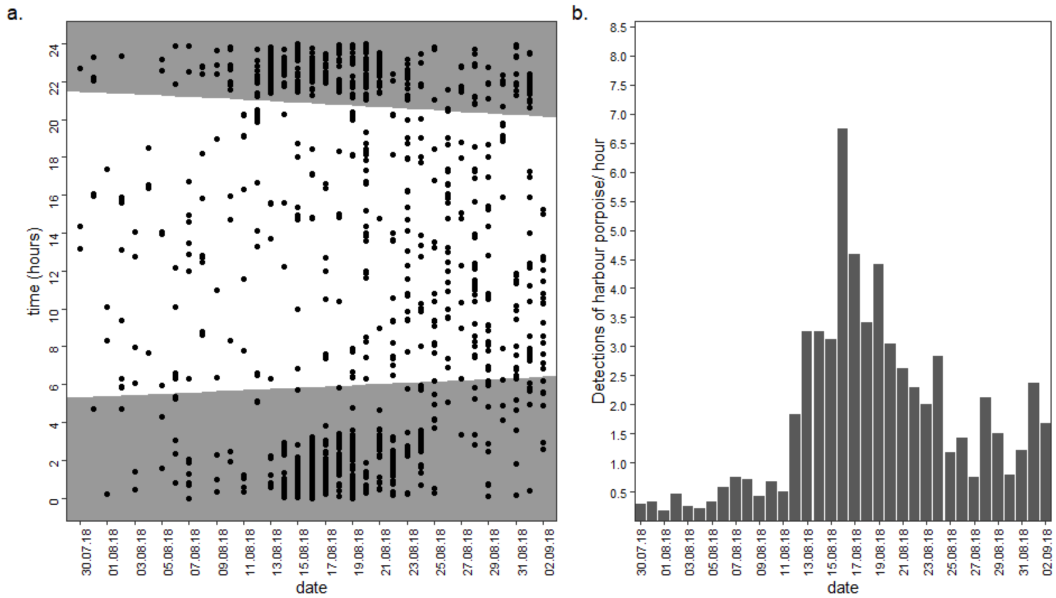


Fig. 50: C-POD 2: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

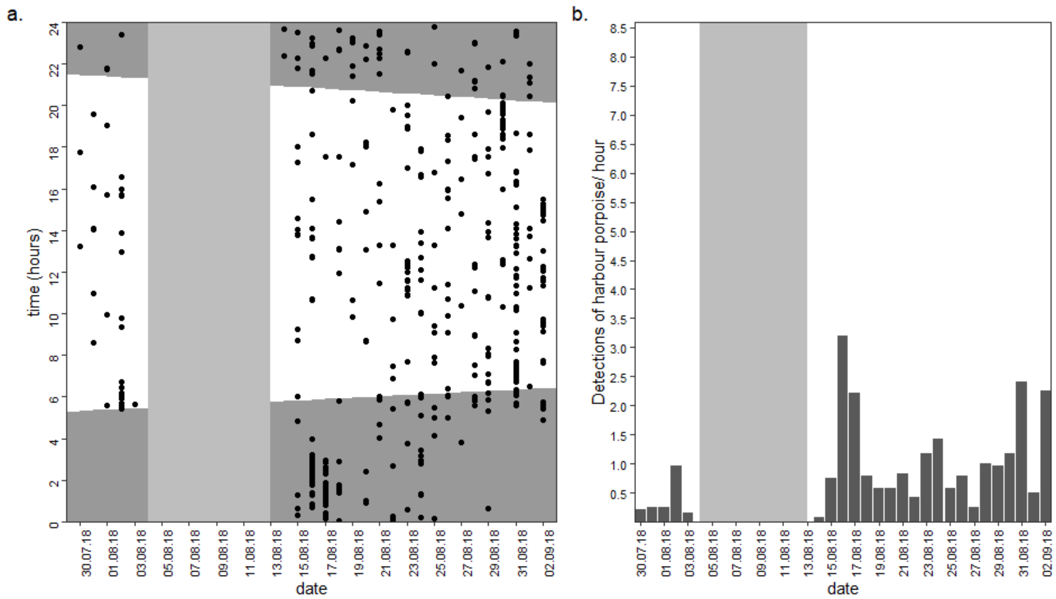


Fig. 51: C-POD 3: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bar indicates data gap. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute. The vertical grey bar indicates data gap.

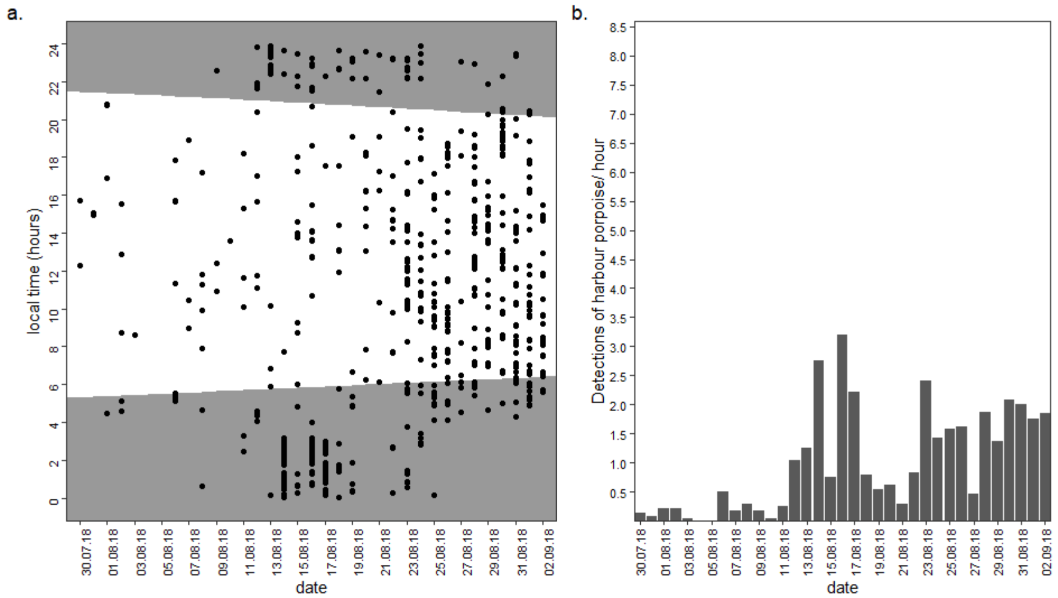


Fig. 52: C-POD 4: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

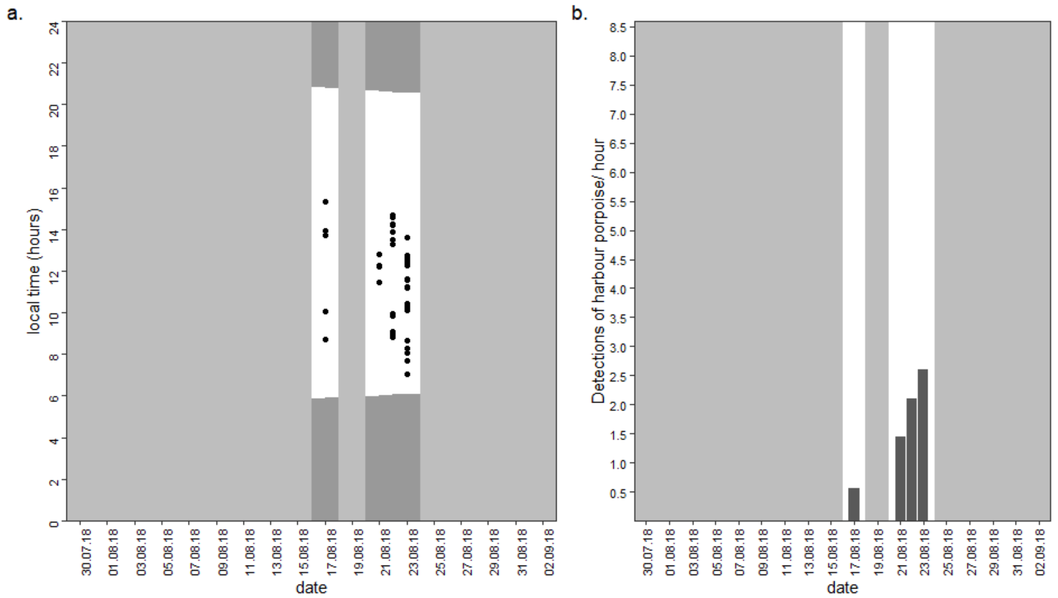


Fig. 53: C-POD 5: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical grey bars indicate data gap. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute. The vertical grey bars indicate data gap.

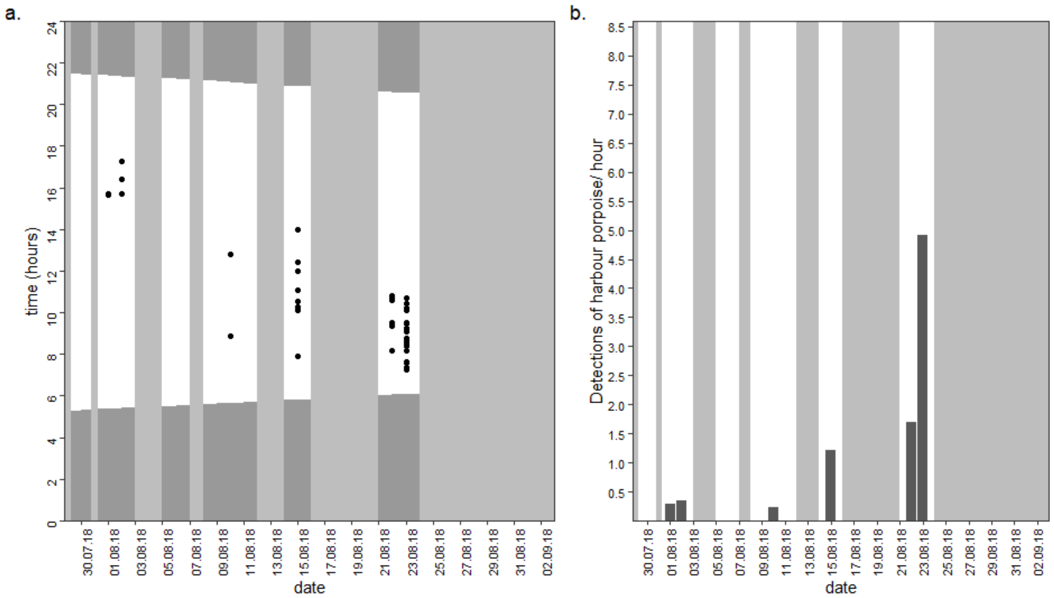


Fig. 54: C-POD 6: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate data gap. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute. The vertical grey bars indicate data gap.

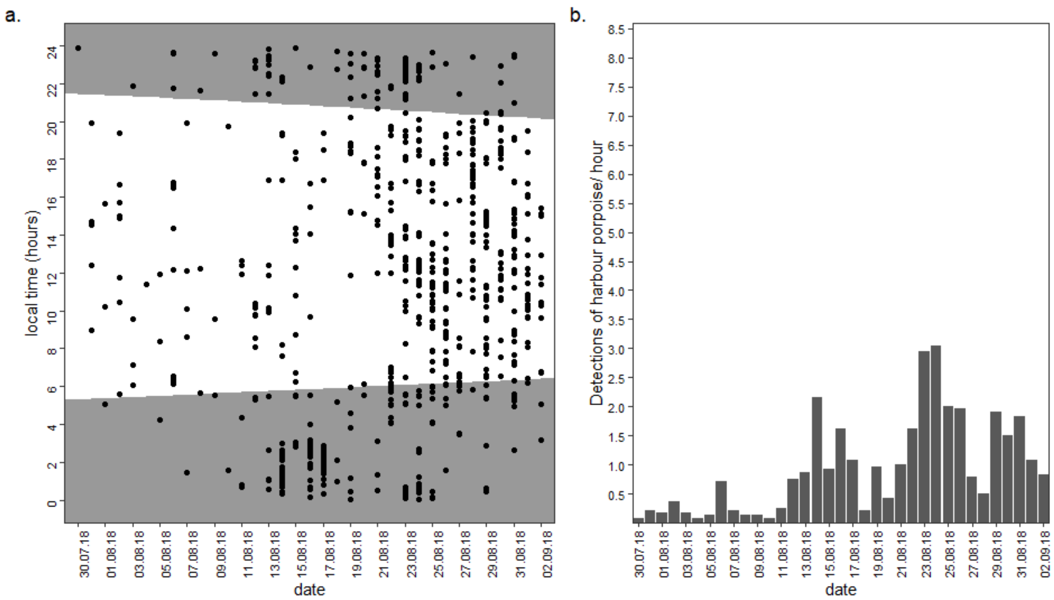


Fig. 55: C-POD 7: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

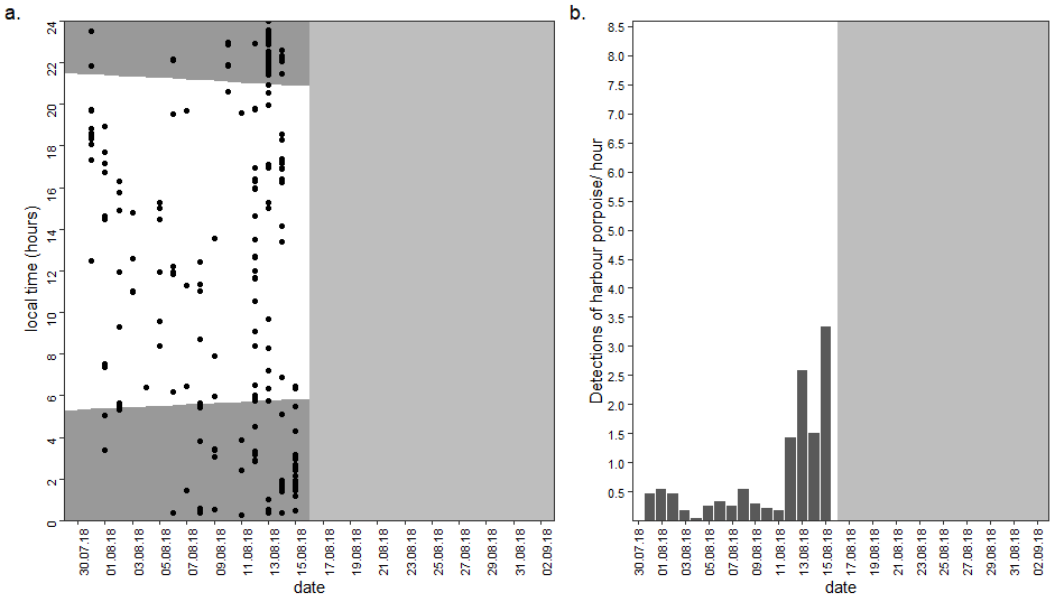


Fig. 56: C-POD 9: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bar indicates data gap. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute. The vertical, grey bar indicates data gap.

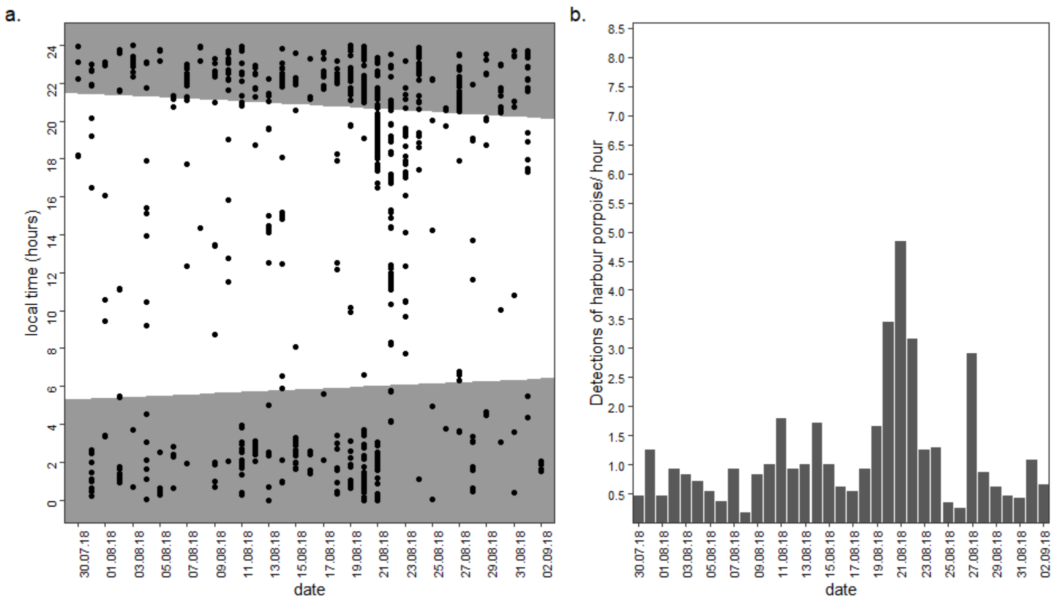


Fig. 57: C-POD 10: **a.** Diel and seasonal occurrence of harbour porpoise with at least one harbour porpoise detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** Detections of harbour porpoises per hour with at least one harbour porpoise detection per minute.

Tab. 19: Number of visual sighted harbour porpoises per day and per hour during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

Date	Observation	Hours of observation	Number of harbour porpoise sightings/ day	Number of harbour porpoise sightings/ hour
31.07.2018	08:30 - 16:40	8h 15min	22	2.67
01.08.2018	08:30 - 17:40	9h 10min	9	0.98
02.08.2018	08:30 - 17:30	9h	19	2.11
03.08.2018	09:00 - 17:00	8h	13	1.63
06.08.2018	13:30 - 17:15	3h 45min	4	1.07
07.08.2018	09:00 - 17:00	8h	8	1.00
08.08.2018	10:00 - 17:00	7h	25	3.57
09.08.2018	09:00 - 16:00	7h	7	1.00
13.08.2018	09:55 - 17:00	7h 5min	13	1.84
15.08.2018	09:00 - 17:00	8h	26	3.25
17.08.2018	09:40 - 17:40	8h	18	2.25
22.08.2018	08:30 - 16:30	8h	16	2.00
23.08.2018	08:30 - 16:15	7h 45min	14	1.81
24.08.2018	08:15 - 11:15	3h	8	2.67
25.08.2018	13:00 - 15:30	2h 30min	7	2.80
Total: 15 days		**104h 30min**	**209 sightings**	

Tab. 20: Number of visual sighted harbour porpoises from 08:00 to 18:00 during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

Time period	Absolute number of harbour porpoise sightings	Number of harbour porpoise sightings/ sum of observation hours from all days
08:00 – 09:00	6	2.18
09:00 – 10:00	12	1.52
10:00 – 11:00	19	1.46
11:00 – 12:00	17	1.39
12:00 – 13:00	19	1.58
13:00 – 14:00	30	2.22
14:00 – 15:00	38	2.71
15:00 – 16:00	37	2.74
16:00 – 17:00	27	2.57
17:00 – 18:00	5	2.39

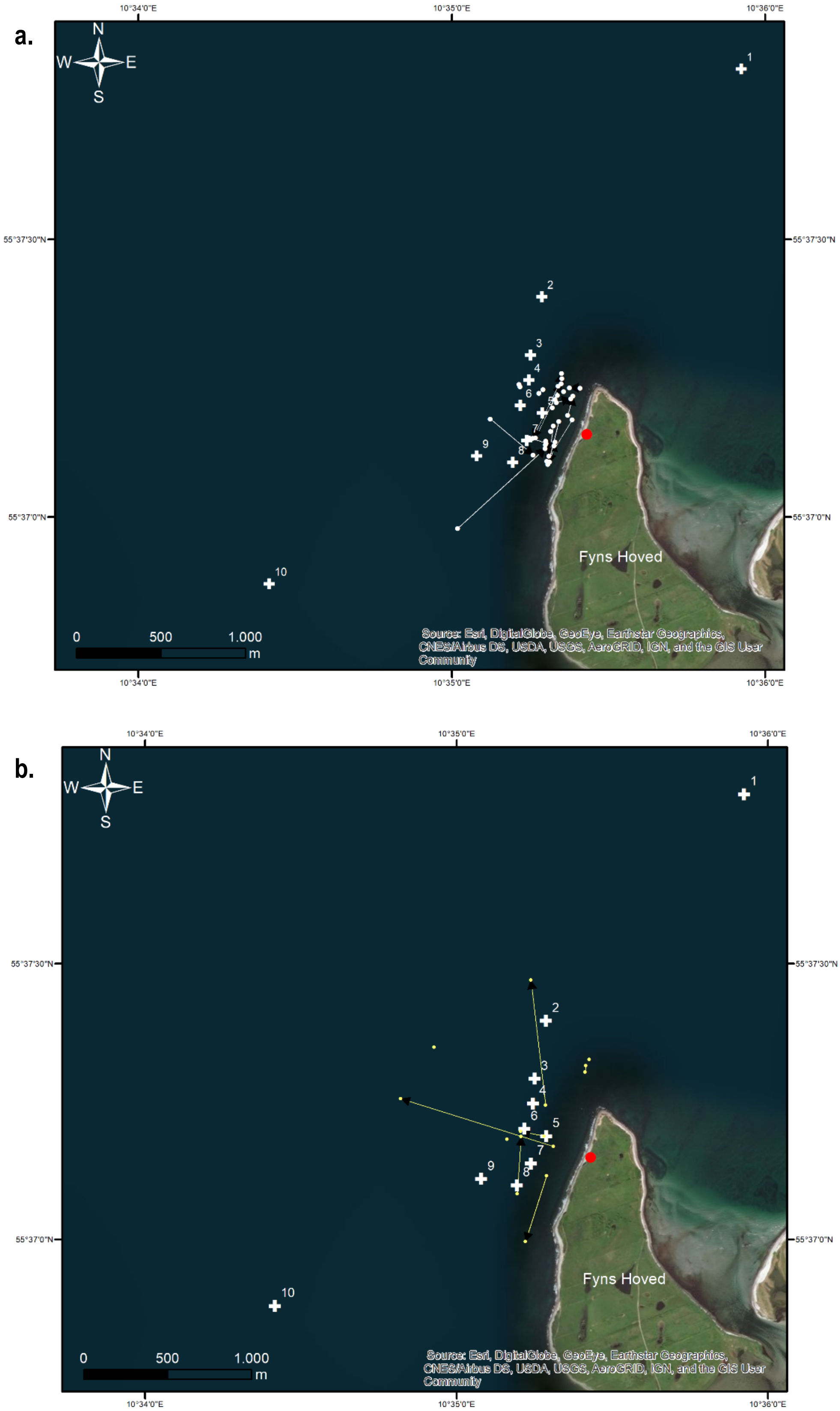


Fig. 58: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 31st August 2018 and **b.** on 1st August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

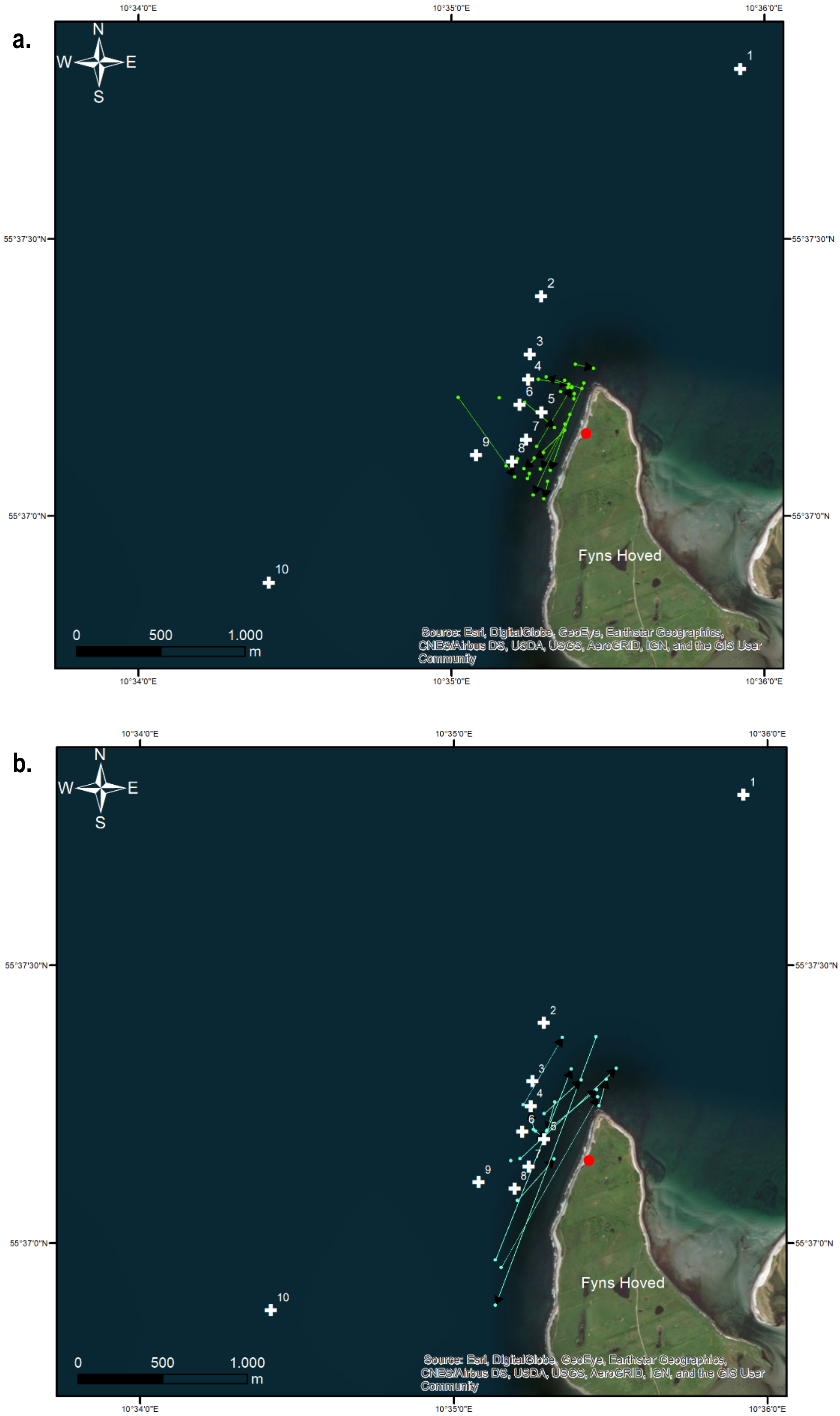


Fig. 59: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 2nd August 2018 and **b.** on 3rd August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

Fig. 60: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 6th August 2018 and **b.** on 7th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

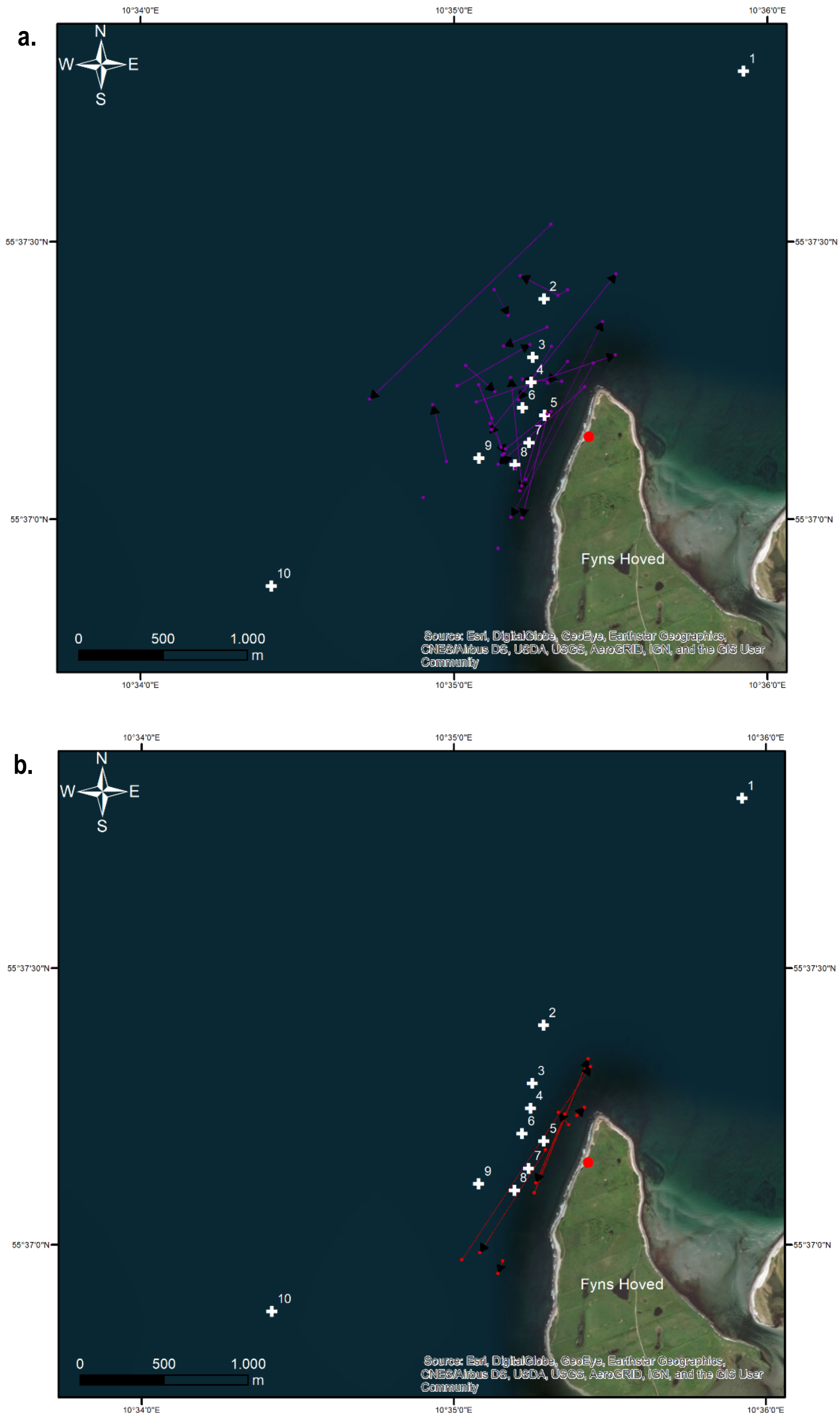


Fig. 61: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 8th August 2018 and **b.** on 9th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

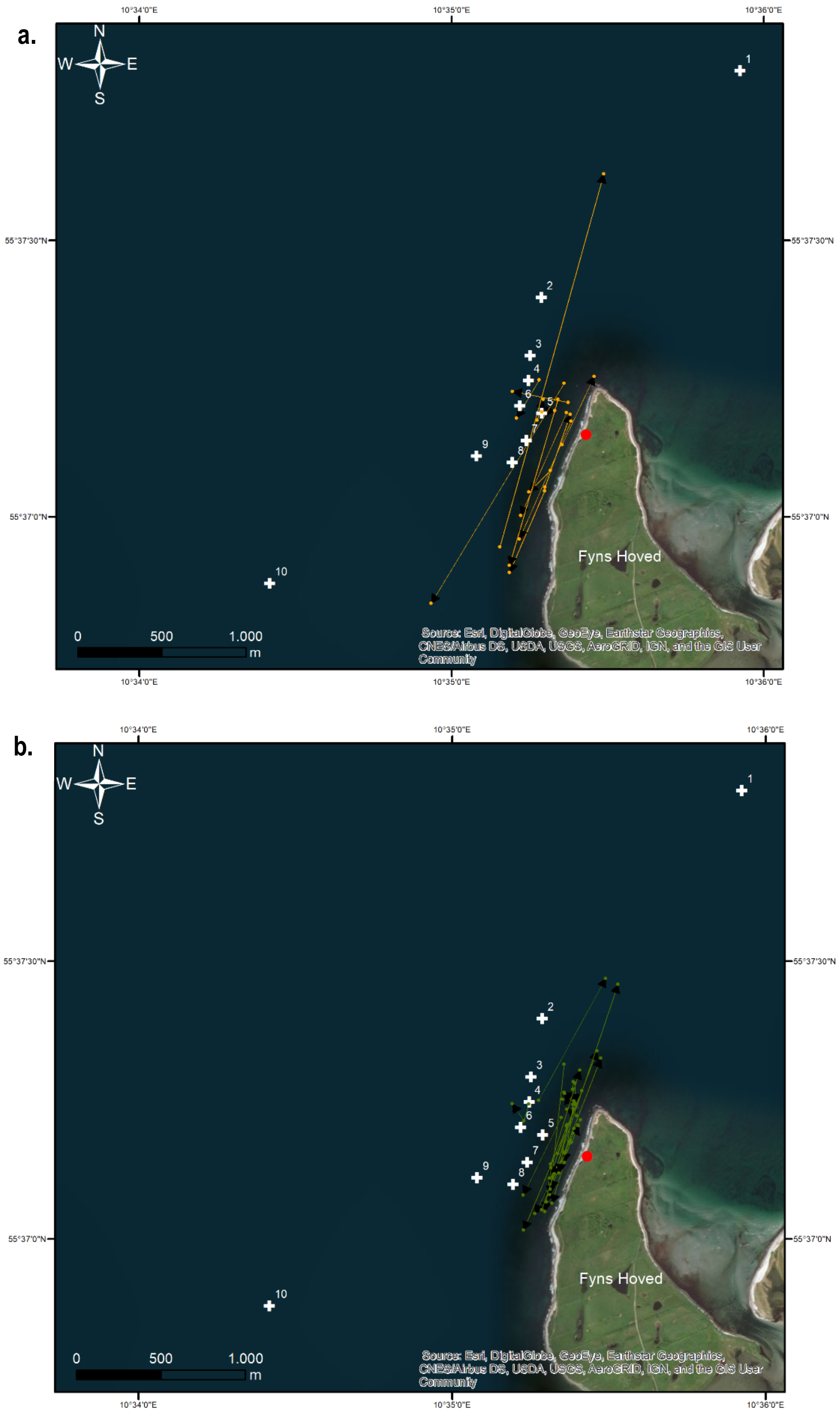


Fig. 62: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 13th August 2018 and **b.** on 15th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

a.

b.

Fig. 63: Swimming direction of the tracked harbour porpoises with the theodolite on **a.** 23rd August 2018 and **b.** on 24th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

Fig. 64: Swimming direction of the tracked harbour porpoises with the theodolite on 25th August 2018 in Fyns Hoved (Denmark). The points show the first surfacing point of an observed harbour porpoise group. The arrows show the swimming direction of the observed group and the points at the tip of the arrow show the last surfacing point of the observed group. The white crosses represent the position of each deployed C-POD and the red point on the land indicates the observation place during the study period.

Tab. 21: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 2 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 2. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. Only these dates are shown, on which a visual observation took place.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 2
31.07.2018	No net	0	2
01.08.2018	No net	1	2
02.08.2018	Modified gillnet	0	5
03.08.2018	No net	1	2
06.08.2018	Modified gillnet	0	0
07.08.2018	No net	0	7
08.08.2018	No net	5	5
09.08.2018	Gillnet	0	1
13.08.2018	No net	0	3
15.08.2018	Modified gillnet	0	5
17.08.2018	Gillnet	6	5
22.08.2018	No net	0	7
23.08.2018	Modified gillnet	0	15
24.08.2018	No net	0	3
25.08.2018	Gillnet	0	2

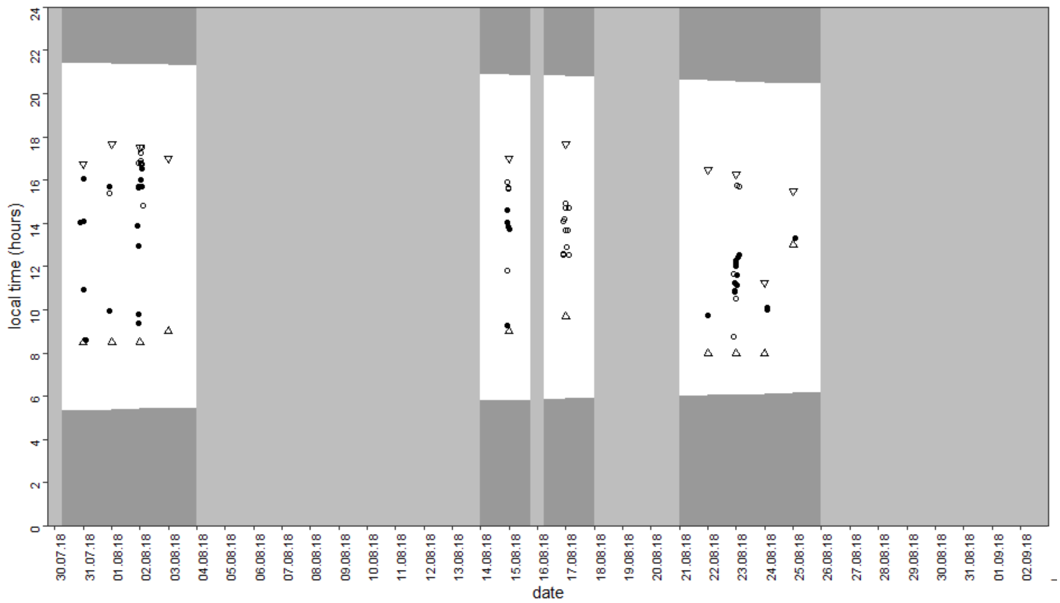


Fig. 65: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 3 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 3.

Tab. 22: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 3 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 3. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. From 3rd August to 13th August was no recording by the C-POD due to a probably defect at the C-POD device.

Date	**Type of experiment**	**Detection Positive Minutes with the theodolite**	**Detection Positive Minutes at C-POD station 3**
31.07.2018	No net	0	5
01.08.2018	No net	1	2
02.08.2018	Modified gillnet	8	10
03.08.2018	No net	/	/
04.08.-13.08.2018	/	/	/
15.08.2018	Modified gillnet	4	5
17.08.2018	Gillnet	11	0
22.08.2018	No net	0	1
23.08.2018	Modified gillnet	5	11
24.08.2018	No net	0	2
25.08.2018	Gillnet	0	1

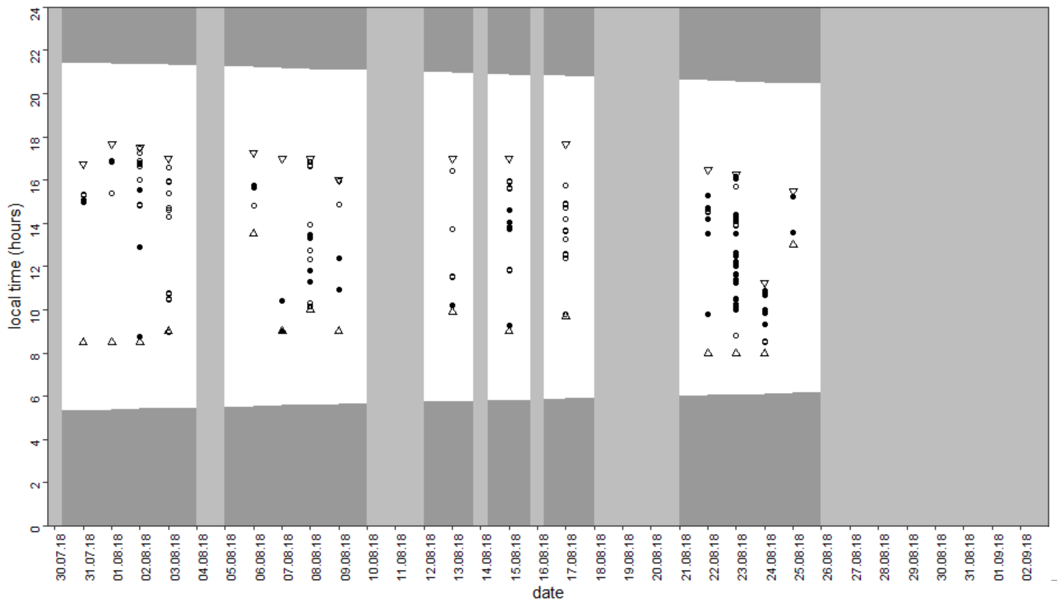


Fig. 66: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 4 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and see Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 4.

Tab. 23: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 4 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 4. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. Only these dates are shown, on which a visual observation took place. On 19th August 2018, no visual observation was possible due to unfavorable weather conditions.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 4
31.07.2018	No net	3	2
01.08.2018	No net	2	1
02.08.2018	Modified gillnet	11	3
03.08.2018	No net	14	0
06.08.2018	Modified gillnet	1	5
07.08.2018	No net	0	2
08.08.2018	No net	17	2
09.08.2018	Gillnet	2	3
13.08.2018	No net	5	1
15.08.2018	Modified gillnet	7	5
17.08.2018	Gillnet	19	0
19.08.2018	No net	/	/
22.08.2018	No net	3	6
23.08.2018	Modified gillnet	12	26
24.08.2018	No net	2	7
25.08.2018	Gillnet	0	2

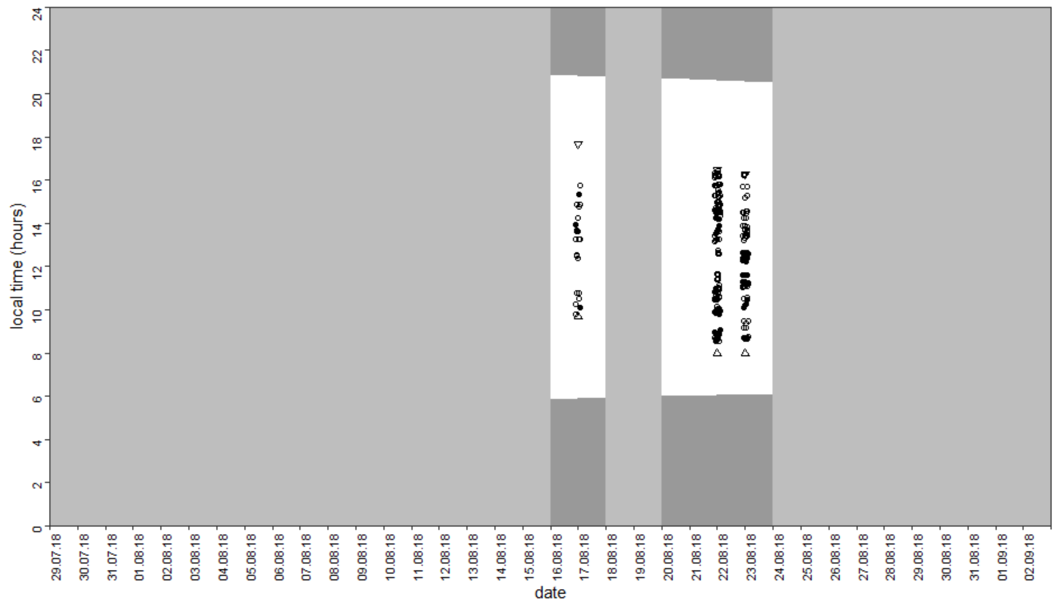


Fig. 67: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 5 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 5.

Tab. 24: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 5 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 5. Only three days are shown due to a probably defect at the C-POD device during the remaining days.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 5
17.08.2018	Gillnet	20	4
22.08.2018	No net	117	16
23.08.2018	Modified gillnet	71	18

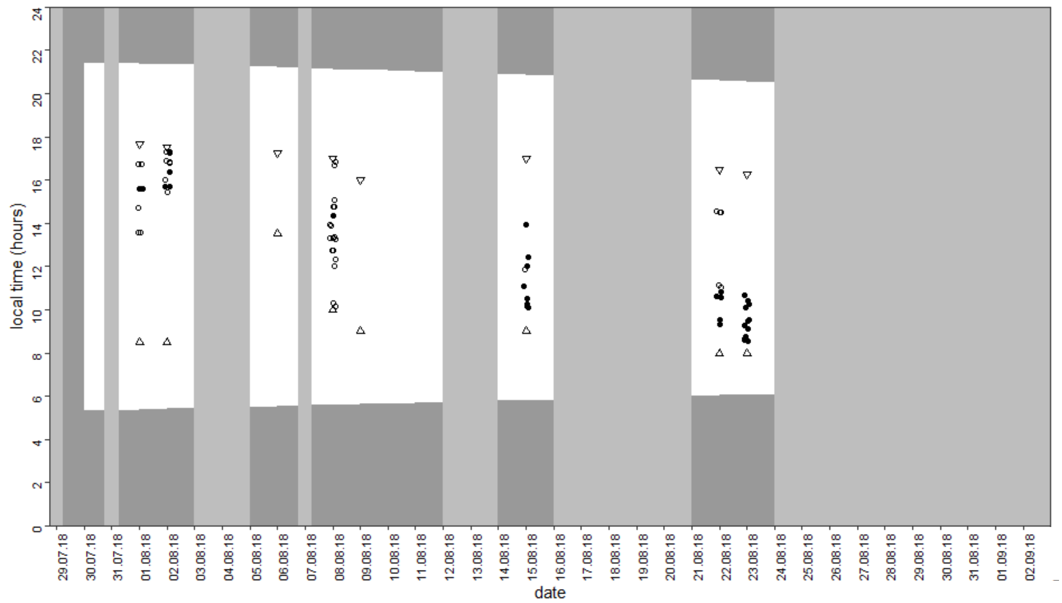


Fig. 68: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 6 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 6.

Tab. 25: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 6 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 6.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 6
01.08.2018	No net	5	2
02.08.2018	Modified gillnet	9	4
06.08.2018	Modified gillnet	0	0
08.08.2018	No net	18	1
09.08.2018	Gillnet	0	0
15.08.2018	Modified gillnet	6	8
17.08.2018	Gillnet	19	0
22.08.2018	No net	15	5
23.08.2018	Modified gillnet	18	12

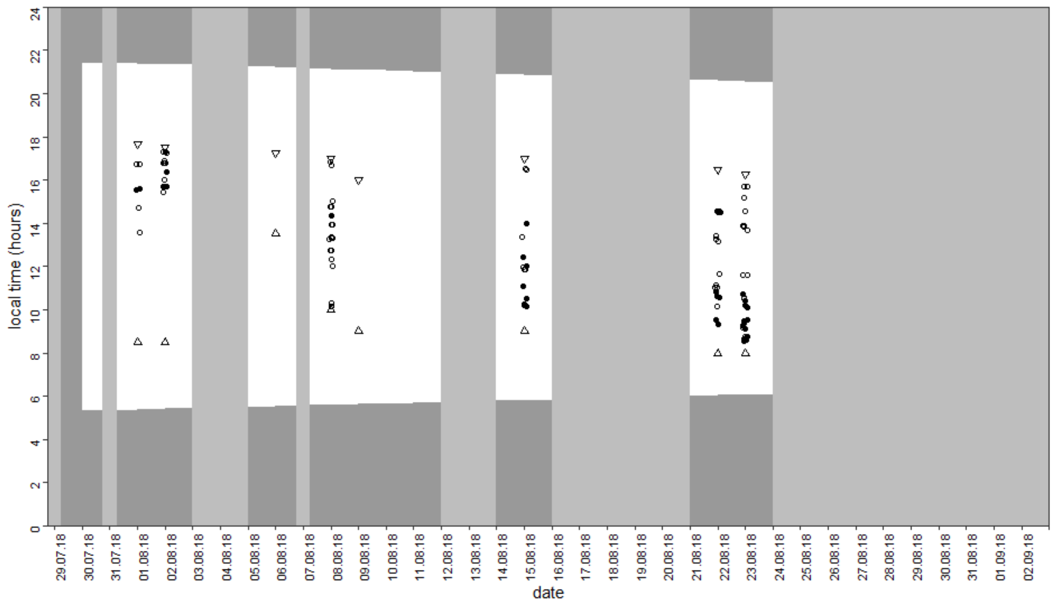


Fig. 69: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 8 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 8.

Tab. 26: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 8 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 8. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. Only these dates are shown, on which a visual observation took place.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 8
31.07.2018	No net	2	1
01.08.2018	No net	3	0
02.08.2018	Modified gillnet	13	2
03.08.2018	No net	10	2
06.08.2018	Modified gillnet	1	0
07.08.2018	No net	3	2
08.08.2018	No net	16	1
09.08.2018	Gillnet	7	4
13.08.2018	No net	12	3
15.08.2018	Modified gillnet	1	4
17.08.2018	Gillnet	17	3
22.08.2018	No net	1	7
23.08.2018	Modified gillnet	7	22
24.08.2018	No net	2	9
25.08.2018	Gillnet	1	2

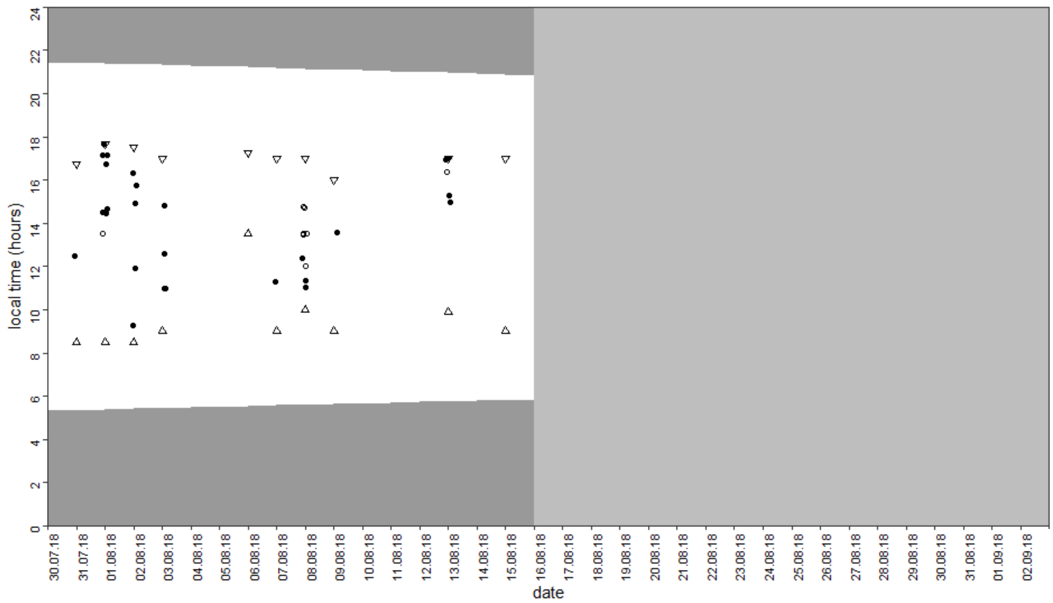


Fig. 70: Comparison between the visual harbour porpoise detections with the theodolite (open dots) and the acoustic detections at C-POD station 9 (black dots) in Fyns Hoved, Denmark (see Fig. 6 for the observation place and Fig. 10 for the position of each C-POD). It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The triangles show the start and end time of observation. Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate no observation time. The visual harbour porpoise sightings are not more than 100 m apart from C-POD station 9.

Tab. 27: Comparison between the visual detections and the acoustic detections of the harbour porpoise at the C-POD station 9 during the study period from 30th July 2018 to 2nd September 2018 in Fyns Hoved, Denmark. It shows the Detection Positive Minutes with at least one harbor porpoise detection within one minute. The visual detections are not more than 100 m away from C-POD station 9. The highlighted gray fields show the dates, on which the C-POD device was checked and replaced by another one. From 15th August to the end of the study project was no recording by the C-POD due to a probably defect at the C-POD device.

Date	Type of experiment	Detection Positive Minutes with the theodolite	Detection Positive Minutes at C-POD station 9
31.07.2018	No net	0	1
01.08.2018	No net	1	8
02.08.2018	Modified gillnet	0	5
03.08.2018	No net	0	4
06.08.2018	Modified gillnet	0	0
07.08.2018	Gillnet	0	1
08.08.2018	No net	7	3
09.08.2018	Gillnet	0	1
13.08.2018	No net	1	4
15.08.2018	Modified gillnet	0	0

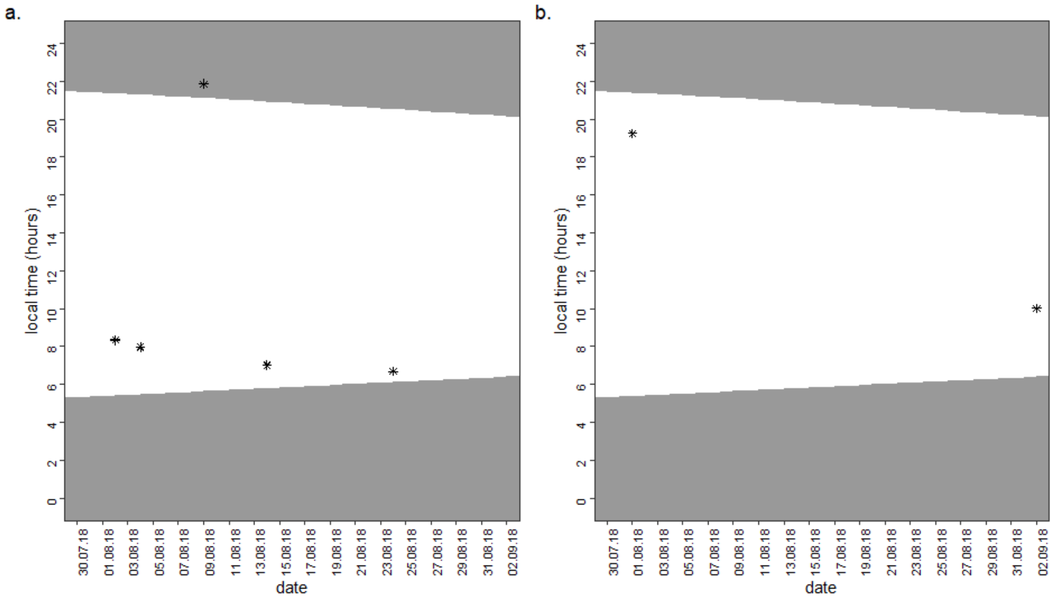


Fig. 71: **a.** C-POD 1: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** C-POD 2: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day.

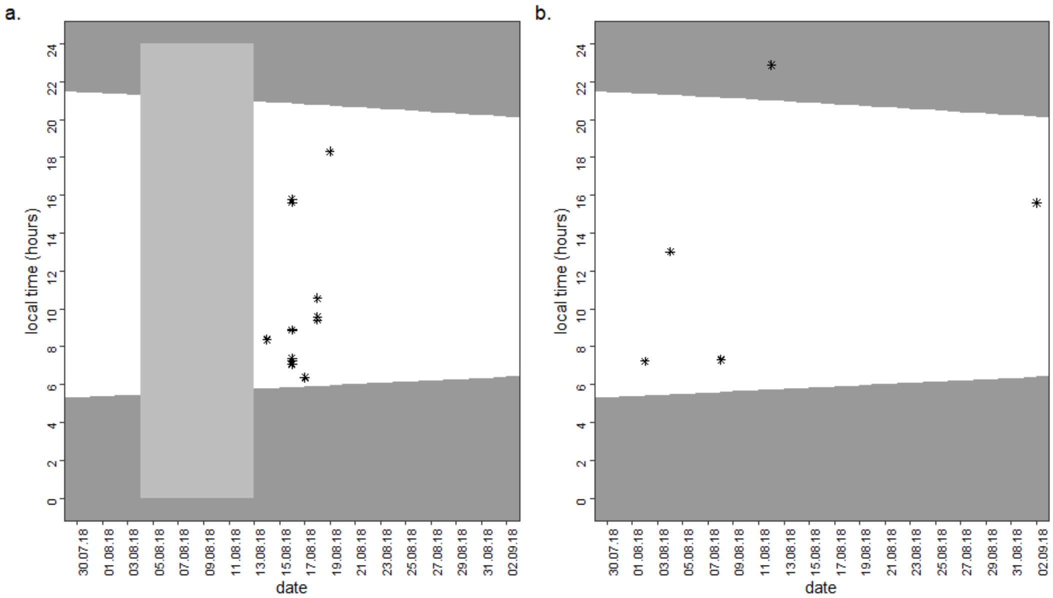


Fig. 72: **a.** C-POD 3: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bar indicates data gap. **b.** C-POD 4: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day.

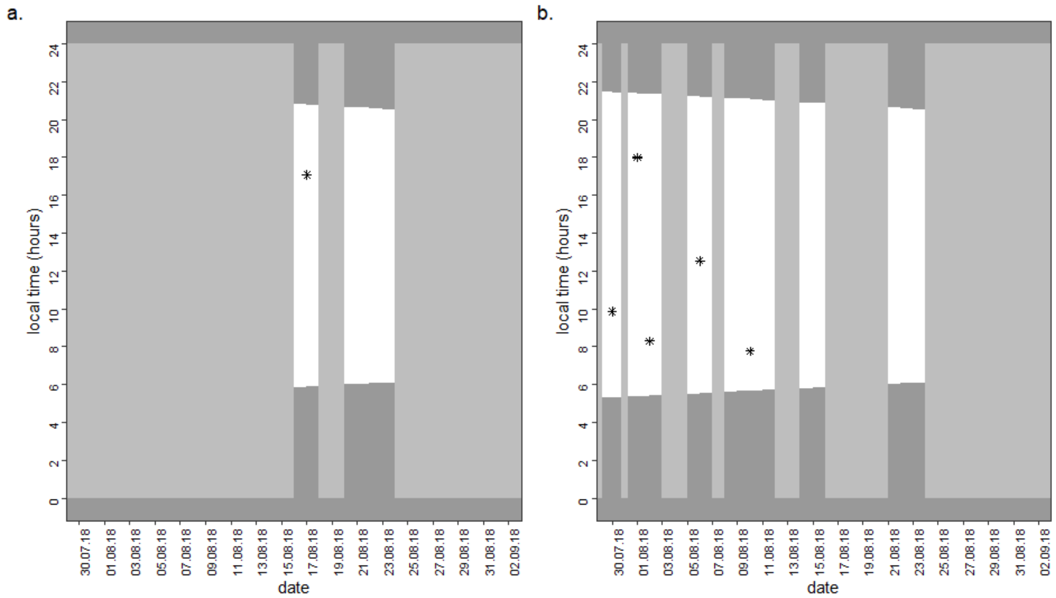


Fig. 73: **a.** C-POD 5: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate data gap. **b.** C-POD 6: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bars indicate data gap.

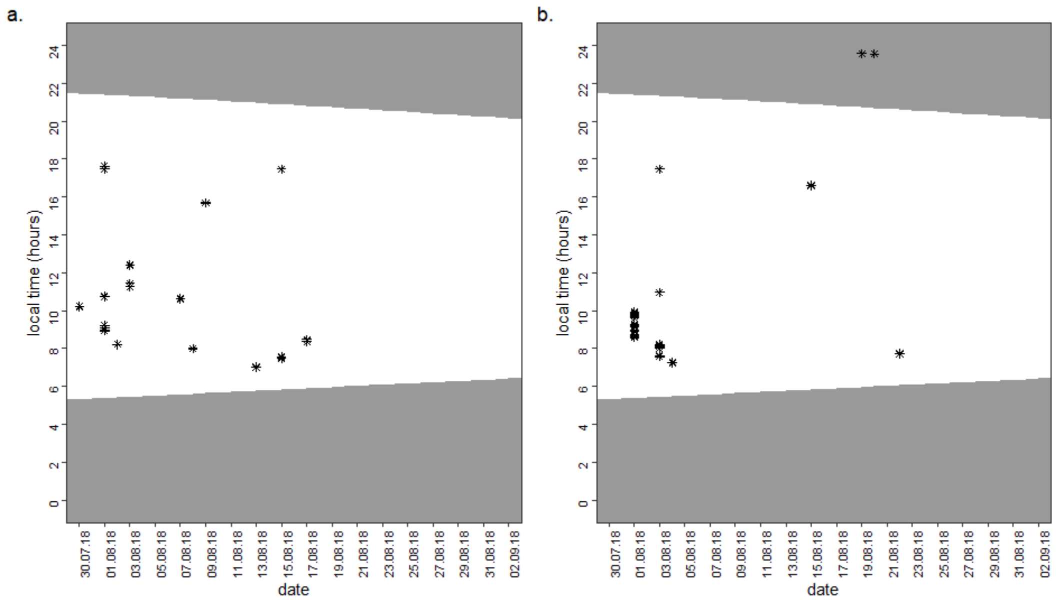


Fig. 74: **a.** C-POD 7: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. **b.** C-POD 8: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day.

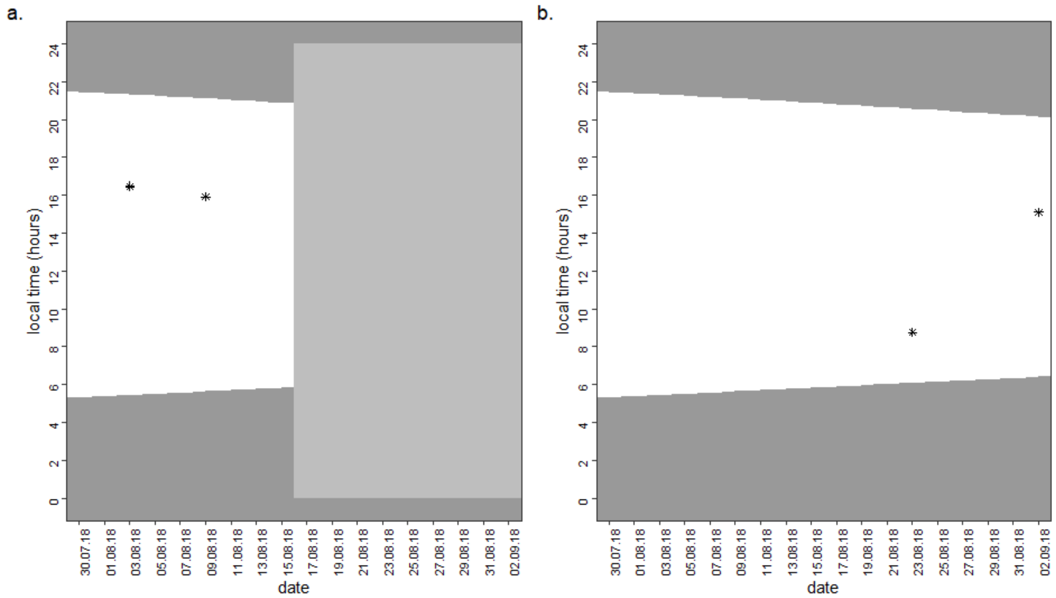
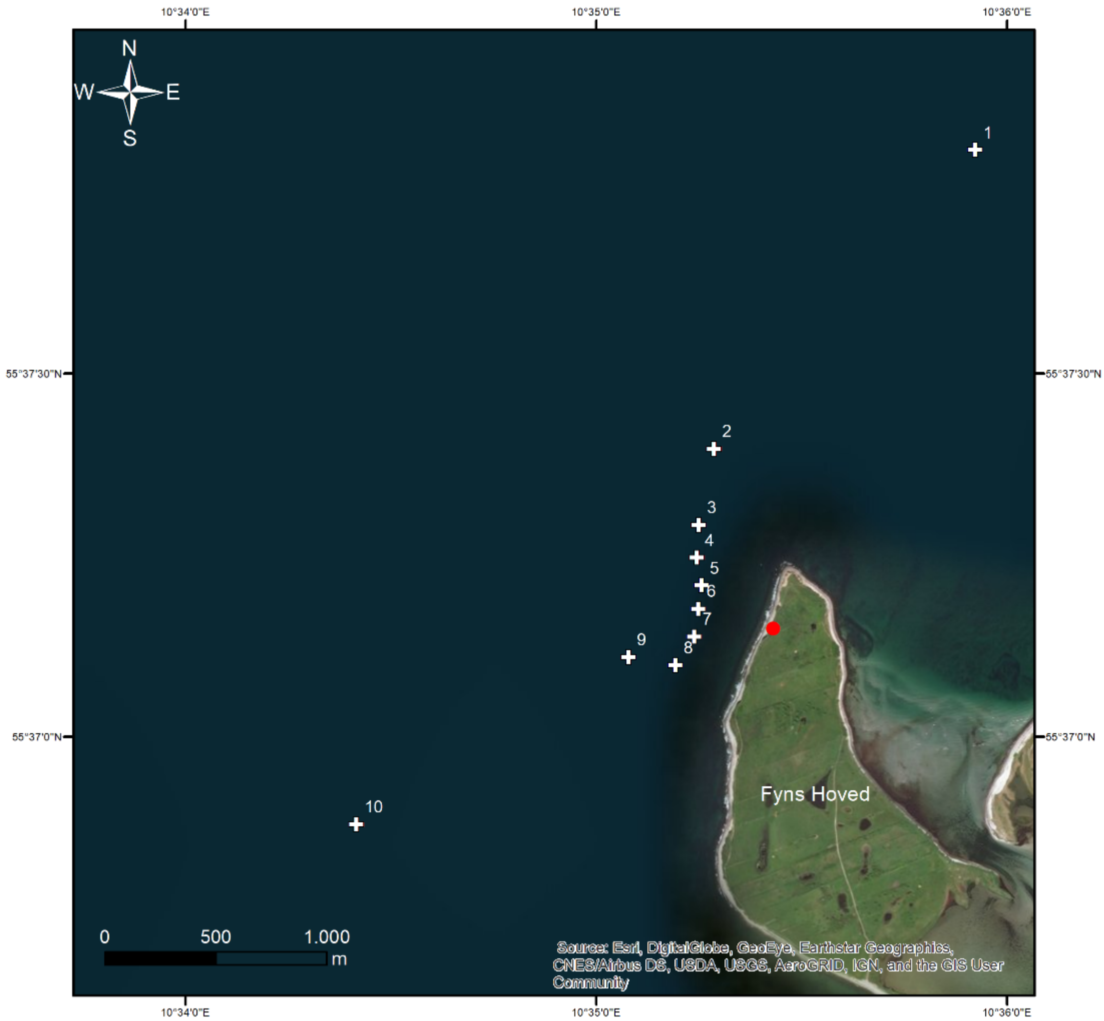


Fig. 75: **a.** C-POD 9: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day. The vertical, grey bar indicates data gap. **b.** C-POD 10: Diel and seasonal occurrence of dolphins with at least one dolphin detection per minute in Fyns Hoved, Denmark (see Fig. 10 for the position of each deployed C-POD). Grey areas indicate night and white areas indicate day.

Tab. 28: Distance from each C-POD station to the observation place during the study period from 30th July to 2nd September 2018 in Fyns Hoved, Denmark.

C-POD station	Distance to the observation place [m]
1	1327.47
2	483.65
3	325.35
4	266.10
5	165.51
6	242.93
7	202.40
8	266.45
9	376.18
10	1177.46


10°34'0"E
10°35'0"E
10°36'0"E
N
W
E
S
1
2
3
4
5
6
7
8
9
10
55°37'30"N
55°37'0"N
Fyns Hoved
0
500
1.000
m
Source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community