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SEASONAL AND DIEL PATTERNS OF HARBOUR PORPOISE (*PHOCOENA PHOCOENA*) ACTIVITY IN HARDANGERFJORD, NORWAY

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Seasonal and diel patterns of harbour porpoise (*Phocoena phocoena*) activity in Hardangerfjord, Norway

The harbour porpoise is a small cetacean species that mainly inhabits coastal areas. A passive acoustic monitoring study was carried out in Hardangerfjord, Norway, where porpoises are abundant, but little is known about their seasonal movements and diel activity patterns. The acoustic data showed significant differences in porpoise echolocation activity between different months. Harbour porpoise activity was highest in winter and lowest in summer, suggesting that porpoises may be migrating towards the open sea in summer. Analysis of diel patterns revealed that porpoises are significantly more active nocturnally than diurnally. To confirm the finding and to further explore the causes and extent of the observed patterns, additional data collection methods must be used in future studies.

B260 Hydrobiology, marine biology, aquatic ecology, limnology

Keywords: porpoise, acoustic monitoring, bioacoustics

Hariliku pringli (*Phocoena phocoena*) sesoonsed ja ööpäevased aktiivsusmustrid Hardangeri fjordis Norras

Harilik pringel on peamiselt rannikuvetes leiduv vaalaline. Norras Hardangeri fjordis, kus pringlite populatsioon on suur, kuid nende aktiivsusmustrite kohta on vähe informatsiooni, kasutati pringlite uurimiseks passiivset akustilist seiret. Kogutud akustilistest andmetest ilmnes oluline erinevus pringlite aktiivsuses aasta lõikes. Aktiivsus oli kõrgeim talvel ja madalaim suvel, viidates võimalikule hooajalisele rändele avamere ja fjordi vahel. Ööpäevaste mustrite analüüsis selgus, et pringlid on öösiti oluliselt aktiivsemad kui päeval. Järelduste kinnitamiseks ja vaadeldud mustrite põhjuste ja ulatuse edasiseks uurimiseks on vajalik täiendava andmekogumismeetodi kasutamine edaspidistes uuringutes.

B260 Hüdrobioloogia, merebioloogia, veeökoloogia, limnoloogia

Märksõnad: pringel, akustiline seire, bioakustika

CONTENTS

1. INTRODUCTION

The harbour porpoise (*Phocoena phocoena* (Linnaeus, 1758)) is a small odontocete found in coastal habitats in the Northern Hemisphere. Much of the species' range overlaps with human high-use areas and as a result, interactions between fisheries and harbour porpoises, including bycatch incidents, are very common (Bjørge & Tolley, 2009). Bycatch – the accidental entanglement of species or sizes that are not the target catch of the fishery – is largely considered to be the primary threat to cetaceans worldwide (Leaper & Calderan, 2018). Species that mainly inhabit coastal and shelf areas, such as the harbour porpoise, are particularly and heavily affected by bycatch (Reeves *et al.*, 2013).

The harbour porpoise is likely the most abundant small cetacean in the North Sea, with over 40% of the global population concentrated in this region (Hammond *et al.*, 2002; Carwardine, 2020). Norwegian coastal waters and fjords such as Hardangerfjord are optimal habitats for harbour porpoises and the porpoise population in the waters of Norway is estimated at over 180 000 individuals (Leonard & Øien, 2020; Hammond *et al.*, 2021). Annually, approximately 1500–2000 harbour porpoises are bycaught in Norwegian coastal gillnet fisheries, which is currently within bycatch limits – 1% of the best population estimate as recommended by ASCOBANS (2006) – but has been unsustainable for several of the recent years (Moan *et al.*, 2020).

To reduce porpoise mortality, various bycatch reduction methods are used around the world – acoustic deterrent devices (ADDs, also known as pingers), gillnet modifications, general fisheries management and time-area closures (Leaper & Calderan, 2018). ADDs are recommended for use in coastal fisheries, but in narrow and enclosed fjords they may drive porpoises away from their preferred habitat (Bjørge *et al.*, 2019; Dawson *et al.*, 2013). Time-area closures may be more effective for bycatch reduction in fjords, but implementing this method requires an adequate information base about porpoise behaviour and seasonality. While there are studies about porpoise migrations and diel activity in other regions (Zein *et al.*, 2019; Nachtsheim *et al.*, 2021), little is known about the porpoise population in Hardangerfjord and other Norwegian fjords. The existing information about seasonal movements in harbour porpoises shows a considerable degree of geographical variation (Scheidat *et al.*, 2012). Therefore, time-area closures should not be designed based on data collected in a different region. More information is available about the diel activity pattern of harbour porpoises, with the general conclusion that porpoises are more active at night (Wisniewska *et al.*, 2018), but it is unknown how much the behaviour and feeding strategies of porpoises in Hardangerfjord differ from porpoises in better-studied areas such as German and Danish waters.

To study the presence and activity of harbour porpoises, five passive acoustic monitoring (PAM) devices were deployed in Hardangerfjord from September 2020 to October 2021. The devices, called C-PODs, detect trains of echolocation sounds that porpoises and other cetaceans produce and the corresponding software can be used to filter out cetacean sounds from background noise.

The objectives of this thesis are to determine seasonal differences in the presence and activity of harbour porpoises and to describe diel patterns in porpoise activity. The research questions are:

1. Are harbour porpoises present in Hardangerfjord year-round and what seasonal movements or patterns in porpoise activity can be observed?
2. Are harbour porpoises more active during the day or at night, and what can this activity pattern reveal about porpoise feeding strategies and prey species?

1.1. THE HARBOUR PORPOISE

1.1.1. Biology

The harbour porpoise is a species of cetacean belonging to the taxon Odontoceti, the family Phocoenidae and the genus *Phocoena* (Braulik *et al.*, 2020). The harbour porpoise is among the smallest of all cetaceans with an average length and weight of about 160 cm and 60 kg for females and 145 cm and 50 kg for males (Bjørge & Tolley, 2009).

The harbour porpoise has a robust and stocky body shape and a blunt head with a short, almost indistinguishable beak (Figure 1). The dorsal fin is short and triangular, rarely sickle-shaped. The pectoral fins are small, dark and blunt-tipped, and the caudal fin has a concave trailing edge with a distinct median notch (Carwardine, 2020). Although colouration can vary greatly between populations and individuals, the dorsal side is always a darker colour (shades of grey or brown) that merges with lighter shades on the flanks with the ventral side being whitish or light grey (Bjørge & Tolley, 2009). The border between the dorsal and ventral colouration is diffused on the front half of the body, but clearer on the peduncle. Other distinguishing features include an upward-sloping mouthline and variable darker stripe from the mouth to the pectoral fin (Carwardine, 2020).

Figure 1. The harbour porpoise (Carwardine, 2020, illustration by Martin Camm).

The harbour porpoise primarily inhabits shallow (<200 metres) coastal areas and is frequently observed in bays, fjords, estuaries and harbours (hence the common name). The species is only found in temperate to sub-Arctic waters in the North Atlantic, the North Pacific and the Black Sea (Bjørge & Tolley, 2009). Several subspecies are recognised (Carwardine, 2020):

- *P. p. phocoena* – Atlantic harbour porpoise,
- *P. p. vomerina* – Eastern Pacific harbour porpoise,
- *P. p. relicta* – Black Sea harbour porpoise,
- *P. p. meridionalis* – Afro-Iberian harbour porpoise,
- Unnamed subspecies in the Western North Pacific.

Global population estimates of the species range from 700 000 to over 1 000 000 individuals (Bjørge & Tolley, 2009; Braulik *et al.*, 2020). In the North Sea alone, harbour porpoise abundance is estimated at over 340 000 individuals (Hammond *et al.*, 2002). Based on ship and aerial surveys, the total population of harbour porpoises in Norwegian waters is estimated to be about 180 000 animals (Leonard & Øien, 2020; Hammond *et al.*, 2021).

Harbour porpoises are not considered to be highly social animals, often being seen solitarily, in mother-calf pairs, or small groups of up to 8 individuals (Bjørge & Tolley, 2009). They avoid vessels and are difficult to approach and observe due to their inconspicuous surfacing behaviour consisting of low rolling movements without showing face or flukes, and rarely leaping out of the water (Carwardine, 2020).

Harbour porpoises become sexually mature at 3–4 years of age and females can give birth multiple years in a row (Carwardine, 2020). Mating takes place in summer and autumn and calves are born from May to August after a gestation of 10–11 months; weaning takes place at 8–12 months of age (Bjørge & Tolley, 2009).

Seasonal movement patterns of harbour porpoises have been noted in a few regions, exhibiting significant geographical variation. The methods used to study seasonal variation of harbour porpoise activity include acoustic monitoring, aerial surveys, land-based surveys, analysis of bycatch or stranding data, satellite telemetry, and combinations of these. In the German North Sea, porpoise abundance peaked in spring and summer (Gilles *et al.*, 2009). A similar pattern was observed in the German Baltic Sea (Verfuß *et al.*, 2007). However, Nachtsheim *et al.* (2021) found that even within the German North Sea, porpoise abundance trends vary between different Special Areas of Conservation (SACs). Slightly different movements, where porpoises were most abundant from February to April, were found in Belgian waters (Haelters *et al.*, 2011). In Dutch waters, harbour porpoise density was also highest in winter and spring (Scheidat *et al.*, 2012). Bycatch and stranding data have also showed differing results in different regions – in the Gulf of Maine, bycatch rates were highest in September (Murray *et al.*, 2000), and in the Black Sea, a clear peak in stranding occurred during the calving season in summer (Vishnyakova & Gol'din, 2014). As these results are extremely variable, it is necessary to conduct such studies in more areas, particularly when the purpose is to implement time-area closures for bycatch mitigation.

A few studies have also analysed changes in porpoise distribution and abundance over longer periods of time (Nachtsheim *et al.*, 2021). In the North Sea, the size of the harbour porpoise population remained relatively stable from 1994 to 2005, but a noticeable southward shift was observed in distribution (Hammond *et al.*, 2013). It is possible that population shifts are caused by changes in the distribution of primary prey species (Bjørge & Tolley, 2009).

1.1.2. Feeding

Harbour porpoises primarily feed on fish, but also consume cephalopods, crustaceans, and other invertebrates (Bjørge & Tolley, 2009; Andreasen *et al.*, 2017). The diet is highly variable and depends on the location, season, time of day, and age (Santos & Pierce, 2003). Harbour porpoises are considered opportunistic feeders, utilising diverse hunting strategies and feeding on benthic, pelagic and mesopelagic species (Aarefjord *et al.*, 1995; Bjørge, 2003; Andreasen *et al.*, 2017).

Atlantic herring (*Clupea harengus*) is the most important prey species in the diet of harbour porpoises in Scandinavian and Baltic waters (Aarefjord *et al.*, 1995; Andreasen *et al.*, 2017). Demersal fish species have been found to be more common in the diet of the porpoises in Danish and Swedish waters, whereas pelagic and mesopelagic prey are more prevalent in Norwegian waters (Aarefjord *et al.* 1995). Cod (*Gadus morhua*) and other Gadidae species are also significant prey species, especially in the diet of adult harbour porpoises, while juveniles may consume larger amounts of smaller fish such as gobies (Gobiidae) and crustaceans such as krill (Euphausiidae) (Aarefjord *et al.*, 1995; Andreasen *et al.*, 2017).

In addition to herring and gadids, other species frequently found in the stomachs of harbour porpoises in Norwegian waters include pearlsides (*Maurolicus muelleri*), argentine (*Argentina sphyraena*), greater argentine (*Argentina silus*), sprat (*Sprattus sprattus*), hake (*Merluccius merluccius*) as well as sandeels (Ammodytidae sp.) (Aarefjord *et al.*, 1995).

In a 1995 study of harbour porpoise diets, Aarefjord *et al.* recorded that out of all porpoises sampled in Norwegian waters, two thirds had been bycaught in salmon driftnets, but no traces of salmon (*Salmo* sp.) were identified in the stomach contents. Other studies in British and Baltic waters have also found no evidence of salmon in porpoise stomachs (Santos & Pierce, 2003). It is unclear whether salmon was simply not the preferred prey of the porpoises or only the soft parts of the fish were consumed, leaving no identifiable remains (Aarefjord *et al.*, 1995).

Harbour porpoises have a higher metabolic rate than most other odontocetes (Reed *et al.*, 2000). Due to their small body size and cold-water habitat, they must forage nearly continuously throughout the diel cycle (Wisniewska *et al.*, 2016). Distribution of prey items and the use of different hunting strategies appear to be the primary factor influencing diel patterns in harbour porpoise activity (Zein *et al.*, 2019). Studies using acoustic tags on harbour porpoises have determined that foraging activity is higher at night than during the day (Carlström, 2005; Wisniewska *et al.*, 2016; Wisniewska *et al.*, 2018). As a result of the need to continuously search for prey, harbour porpoises are particularly vulnerable to disturbances such as sonar and other noise from vessels as well as offshore wind farms (Wisniewska *et al.*, 2018; Booth, 2019; Nachtsheim *et al.*, 2021).

The differences in diet between Norwegian waters and Danish/Swedish waters suggest that porpoises in Norwegian fjords are more likely to forage pelagically as opposed to "bottom-grubbing", where the porpoise acoustically scans the seabed in a vertical position (Lockyer *et al.*, 2003). Establishing peak times of porpoise activity can aid in determining the primary prey species in a given area – for example, if harbour porpoises in Norwegian fjords are more active at night, it can be presumed that they are feeding on fish species that are found near the surface at night rather than during the day.

Even though harbour porpoises are generally considered to be rather unsocial, a highly specialised form of collaborative hunting has recently been observed in Danish waters (Ortiz *et al.*, 2021). The study found that harbour porpoises use role specialisation, where each individual displays only one or two specific behaviours during foraging, and the behaviours of each animal are different, whereas during solitary hunting all behaviours are displayed by a single individual (Ortiz *et al.*, 2021). In this case, the strategy of the group was to repeatedly force a school of fish to split and join (Ortiz *et al.*, 2021). Previous studies have also noted porpoises herding schools of fish towards the surface (Bjørge & Tolley, 2009).

1.1.3. Echolocation and communication

Unlike many other odontocetes, porpoises do not produce whistles and calls, instead using narrow band high frequency (NBHF) clicks to both hunt and communicate (Clausen *et al*., 2011; Sørensen *et al.*, 2018). The clicks produced by harbour porpoises have a modal frequency of ~132 kHz and mean inter-click intervals of ~60 ms (maximum ICI ~250 ms) (Villadsgaard *et al.*, 2007; Tregenza, 2013). In comparison to delphinids, porpoises use higher frequencies and produce quieter sounds (Villadsgaard *et al.*, 2007).

High frequency sounds such as porpoise clicks are well suited for echolocation because they are powerful and highly directional (Hansen *et al.*, 2008). However, they are not ideal for communication between individuals because higher frequency sounds attenuate faster than lower frequency sounds. This results in a small active space and therefore porpoises must remain closer to one another in order to communicate acoustically – it is estimated that porpoise sounds have a maximum range of about 1000 metres, significantly lower than other cetaceans communicating with various calls and whistles at lower frequencies (Clausen *et al.*, 2011). Because high frequency sounds are also highly directional, porpoises call repeatedly in different directions to communicate with others, as evidenced by frequent vocalisations and short pauses (Sørensen *et al.*, 2018).

Another issue is the limited ability to encode information within these NBHF clicks – if the sounds are also used for communication, other porpoises must be able to discern between echolocation clicks and communication clicks (Sørensen *et al.*, 2018). Clausen *et al.* (2011) concluded that porpoises communicate using click patterns that have the same source properties as echolocation clicks, but encode information within the repetition rates of these click patterns. Click trains with lower and higher repetition rates than foraging clicks ("feeding buzzes") are used for intraspecific communication, with higher click repetition rates being used in aggressive behaviour displays as an example (Clausen *et al.*, 2011; Sørensen *et al.*, 2018).

Andersen & Amundin (1976) report that in addition to the strong high frequency component, harbour porpoise clicks also contain a much weaker low frequency component at ~2 kHz and suggest that this component may be used for intraspecific communication. This hypothesis was tested by Hansen *et al.* (2008), but no evidence of communication through the low frequency component was recorded, concluding that it is merely a byproduct of the production of high frequency clicks.

It has been hypothesised that vocalisations consisting solely of NBHF clicks have evolved as a form of acoustic crypsis, a way of avoiding predators such as killer whales (Orcinus orca) (Andersen & Amundin, 1976; Morisaka & Connor, 2007). The hearing of killer whales is most sensitive in the range of 18–42 kHz (Szymanski *et al.*, 1999), well below the 120–140 kHz range of porpoise vocalisations. Killer whales may be able to weakly hear sounds at 120 kHz but sounds at 130 kHz and higher are entirely outside of the predator's hearing range (Andersen & Amundin, 1976; Szymanski *et al.*, 1999).

The small active space and high directionality of harbour porpoise clicks pose a challenge for the passive acoustic monitoring of the species, as the detection range for porpoises is much smaller than for species using lower frequency calls (Hansen *et al.*, 2008). Nevertheless, in areas where little background noise and few other cetacean species are present, PAM devices such as C-PODs are excellent tools for studying porpoise activity and NBHF clicks are easier to distinguish and identify than lower frequency sounds (Tregenza, 2013).

1.1.4. Threats and bycatch reduction

As the harbour porpoise most commonly inhabits coastal waters and often enters harbours, bays and fjords, they are heavily influenced by human activity and interactions between fisheries and porpoises are very common. While fisheries bycatch is considered to be the main threat to harbour porpoises, they are also significantly affected by environmental pollutants such as PCBs, prey depletion due to overfishing, shipping traffic, and noise from offshore wind farms (Bjørge & Tolley, 2009).

While the species as a whole is classified as Least Concern by the IUCN, some subspecies and populations such as the Black Sea and Baltic Sea harbour porpoises are endangered and more populations may require separate assessments (Braulik *et al.*, 2020). The species is protected under Appendix II of the Convention on the Conservation of Migratory Species of Wild Animals (CMS, 2020).

The harbour porpoise is the only species of cetacean that continuously inhabits the Baltic Sea, and the Baltic population is genetically distinct from the North Sea population (Palmé *et al.*, 2004). While this population is not recognised as a separate subspecies, it is considered Critically Endangered by the IUCN (Braulik *et al.*, 2020). The size of the Baltic Sea population is estimated at less than 500 individuals (SAMBAH, 2016). The Black Sea harbour porpoise is classified as Endangered due to bycatch, targeted exploitation, and prey depletion (Birkun, 2002; Braulik *et al.*, 2020).

In Norwegian coastal gillnet fisheries, bycaught harbour porpoises are primarily found in cod and monkfish (*Lophius piscatorius*) nets (Bjørge *et al.*, 2013). It is estimated that approximately 1500–2000 porpoises are bycaught each year in Norwegian coastal waters (Moan *et al.*, 2020). To stay within sustainable limits, fisheries-related mortality should not exceed 1% of the best population estimate (ASCOBANS, 2006). As the total number of harbour porpoises in Norwegian waters is estimated to be over 180 000 individuals, the current bycatch rates are only just within the recommended limits and during several of the last 13 years have likely been unsustainable (Moan *et al.*, 2020).

As previously mentioned, porpoises utilise different feeding strategies and forage for food both near the seabed and near the surface. This exposes them to different types of fishing gear, including bottom-set gillnets and driftnets hanging from the surface (Bjørge & Tolley, 2009). Gillnets are typically made of thin and light material that is difficult to detect by echolocation – it is estimated that porpoises are able to detect nets no more than 26 metres away (Villadsgaard *et al.*, 2007), and in unfavourable conditions the detection distance may be reduced to only a few metres, resulting in entanglement.

To mitigate bycatch, various methods have been implemented around the world. These include: acoustic deterrent devices or ADDs (also known as pingers), gillnet and fishing gear modifications, general fisheries management, PALs (Porpoise Alert or Porpoise Alarm) and time-area closures (Leaper & Calderan, 2018; Chladek *et al.*, 2020).

ADDs or pingers are small battery-operated devices that attach to gillnets and produce loud artificial acoustic signals typically around 145 dB meant to deter cetaceans from pinger-equipped nets (Leaper & Calderan, 2018). Pingers have been used in numerous areas of the world to reduce bycatch of a wide variety of odontocetes, and in some cases also to reduce depredation (Dawson *et al.*, 2013). These devices are often the preferred bycatch reduction method because their use does not require a change in fishing activity or gear type (Leaper & Calderan, 2018), and in the European Union certain vessels longer than 12 m are required to use pingers to reduce cetacean bycatch as regulated by the EU Council Regulation 812/2004.

However, there are also issues with pinger use. Multiple studies noted that although properly used pingers can reduce cetacean bycatch by up to 70%, nets with improperly placed or failed pingers had higher bycatch rates than nets without any deterrents at all (Palka *et al.*, 2008; Dawson *et al.*, 2013). Therefore, pinger placement and spacing is critical – in a study conducted in Danish fisheries, nets with pingers placed 455 m apart had a bycatch frequency of 0 per haul, whereas a spacing of 585 m resulted in 0.12 bycatch incidents per haul (frequency for nets with no pingers was 0.54) (Larsen *et al.*, 2013).

Habituation and displacement are further concerns associated with pingers. As reviewed by Dawson *et al.* (2013), habituation to pinger noise does not seem to be a significant effect in the case of harbour porpoises, but is a considerable problem with other species of porpoises as well as delphinids (Leaper & Calderan, 2018). Displacement from habitats is a leading concern when it comes to pinger use in narrow and semi-enclosed habitats such as fjords (Bjørge *et al.*, 2019) as great amounts of loud artificial noise could displace porpoises from entire bays and inlets (Dawson *et al.*, 2013).

Recently, alternatives to pingers have been developed. The devices, called PALs, emit synthetic harbour porpoise communication signals instead of artificial noise (Culik *et al.*, 2015; Chladek *et al.*, 2020). Trials conducted in gillnet fisheries in the Baltic Sea showed a bycatch reduction of up to 80%, although trials in the Danish North Sea did not achieve reduced bycatch rates compared to control nets and more studies are necessary to assess the efficiency of these devices. (Culik *et al.*, 2015; Chladek *et al.*, 2020)

Gillnet modifications, which make the nets acoustically visible to porpoises in order to enable detection at a greater distance, have also been used as a bycatch reduction method (Leaper & Calderan, 2018). Infusing the material of the net with substances such as iron oxide or barium sulphate does increase acoustic reflectivity and reduces bycatch rates, but also results in significantly lower catches of target species due to the stiffness of the net (Leaper & Calderan, 2018). Thus, they cannot be considered feasible methods of bycatch mitigation. New acoustically visible gillnets using small acrylic glass balls have been developed and tested, but further testing is required to prove the potential for bycatch reduction (Kratzer *et al.*, 2020; Kratzer *et al.*, 2021).

Time-area closures, where fisheries activity is limited or banned in a certain area for a certain amount of time, have been used in attempts to reduce bycatch of small cetaceans such as Hector’s dolphins (*Cephalorhynchus hectori*), franciscana (*Pontoporia blainvillei*), vaquita (*Phocoena sinus*) and harbour porpoises (Leaper & Calderan, 2018). The objective of such closures is to utilise natural differences in the presence and absence of targeted and bycatch species (Murray *et al.*, 2000. However, in numerous documented cases the closures were not implemented early enough, were not in place for long enough, or were not enforced strongly enough (Murray *et al.*, 2000; Slooten, 2013).

There are numerous conditions that must be met in order for time-area closures to be an effective bycatch reduction method (Murray *et al.*, 2000; Leaper & Calderan, 2018):

- There is an adequate information base on which to plan closures, including data about the seasonal movements, feeding habits and behaviour, and mobility of the species affected by bycatch.
- Bycatch occurs in a small part of the entire fishing area.
- Bycatch occurs in predictable spatio-temporal patterns.
- Limiting or stopping fishing activity in the protected area does not cause an increase in bycatch rates outside the protected area.
- The closures are successfully enforced.
- The closures are economically viable for the fisheries and fishermen cooperate with and support the regulations.

In the case of harbour porpoises, time-area closures have been used in the sink gillnet fishery of the Gulf of Maine in 1994, being in place for one month (Murray *et al.*, 2000). The closures failed to meet several of the conditions named above, including being in place over a long enough period of time and a large enough area, and the unpredictable variation in bycatch rates in both time and space. As a result, the overall bycatch rates were not reduced and fishing effort was purely displaced outside the protected area (Murray *et al.*, 2000). Time-area closures have the potential to be effective if implemented correctly and in suitable locations, such as in the Sea of Azov, where a clear seasonal pattern has been observed in harbour porpoise strandings and bycatch rates (Vishnyakova & Gol’din, 2014).

1.2. Passive acoustic monitoring

As cetaceans are heavily reliant on sound for both communication and foraging, acoustic monitoring provides insight into the activity and behaviour of these animals. Passive acoustic monitoring refers to methods that only record existing sounds in the environment, whereas active acoustic monitoring involves emitting loud signals and recording the returning echoes from animals. Harbour porpoises may be difficult to detect visually due to their small size, inconspicuous surfacing behaviour, and avoidance of boats (Carwardine, 2020). However, because they forage and echolocate nearly constantly (Wisniewska *et al.*, 2016; Sørensen *et al.*, 2018), PAM devices are commonly used to monitor and study this species (Kyhn *et al.*, 2012).

PAM devices include audio file loggers, which are capable of recording a wide variety of sounds in the environment and create audible files, or devices such as C-PODs and F-PODs, which are only able to record clicks, but can collect data for much longer periods of time because they do not retain audio files and instead create summary data files that display the parameters of the recorded sound (Chelonia Limited, 2018). The advantages of using PAM devices to study cetaceans include the ability to be left in the environment for long periods of time (several months for the PODs), no additional noise being introduced into the environment, and significantly lower cost and effort compared to visual surveys (Kyhn *et al.*, 2012).

Nonetheless, for some applications, PAM devices on their own may not provide enough information. For example, particularly with species that only produce clicks, such as porpoises, it is not possible to determine whether a number of acoustic detections is several different animals, or the same animal being detected more than once (Kyhn *et al.*, 2012). Animals may also pass by the PAM device undetected if they are not echolocating at the moment of passing. Depending on the application, it may be necessary to use another method in combination with PAM to produce reliable results (Kyhn *et al.*, 2012). As previously mentioned, harbour porpoise sounds are highly directional and have smaller detection ranges than delphinid sounds. Various studies have estimated the detection range for harbour porpoises using C-PODs at approximately 100-400 metres (Villadsgaard *et al.*, 2007; Hansen *et al.*, 2008; Kyhn *et al.*, 2012).

2. MATERIALS AND METHODS

2.1. Study area

The study area is located in the Hardangerfjord in Western Norway. Hardangerfjord is the second longest fjord in Norway with a length of 179 km. The maximum depth in the fjord is 852 metres. For this project, approximately half the length of the fjord was studied, from the innermost parts to the island of Varaldsøy in the central part of Hardangerfjord. Hardangerfjord was chosen for this study because based on visual surveys, harbour porpoises seem to be exceptionally abundant in this area compared to not only the North Sea, but also other fjords in Western Norway (Øien, 2018). The narrow and semi-enclosed fjords provide a favourable habitat for harbour porpoises, whereas other cetaceans are much less frequent in the area. Further visual surveys of porpoises were conducted in June 2020 and it is estimated that the summer population of harbour porpoises is close to 500 individuals with a population density of 0.62 porpoises/km2 (Leonard, 2022, unpublished data).

Each C-POD is equipped with an identifying number by the manufacturer, and each station was provided a name. The names and coordinates of used C-POD stations are shown in Table 1. Among the C-POD stations, the fjord is narrowest at Bagnstrond (approximately 1.5 km wide) and widest at Årsnes with a width of roughly 5.5 km.

Table 1. C-POD station names and coordinates.

C-POD ID	Station	Latitude (N)	Longitude (E)
1958	Bagnstrond	60°31'06.3546"	6°56'47.1532"
1254	Smedvik	60°29'20.2315"	6°51'46.3824"
1268	Ystanes	60°23'10.1375"	6°40'59.5865"
1375	Alsåker	60°23'30.3069"	6°30'01.4332"
1249	Torsnes	60°14'03.9935"	6°11'28.6430"

3111	Årsnes	60°02'54.1938"	6°01'02.2454"

2.2. Acoustic monitoring

The C-POD is a passive acoustic monitoring device developed by Chelonia Limited, UK. The device was originally designed to specifically detect harbour porpoise echolocation clicks, but newer versions can log clicks from 20 kHz to 160 kHz, which enables it to detect all toothed whales except for the sperm whale (*Physeter macrocephalus*) (Chelonia Limited, 2018). The device consists of an outer polypropylene casing that houses a hydrophone in one end of the tube with a removable lid at the other end. The outer casing is 67 cm long with a diameter of 9 cm and the device weighs 3.5 kg with batteries.

It is important to note that the C-POD does not retain any digitised sound files, but records the duration of every click (with a resolution of 10 ms) as well as the centre frequency, intensity, time of occurrence, bandwidth and frequency trend of clicks. Ambient temperature and angle from vertical are recorded every minute. Without storing audio files, the C-POD is capable of logging significantly larger amounts of data than traditional hydrophones and can be left in the water for several months. Another feature that enables the device to maximise storage capacity is a limit on logged clicks per minute. The limit is set at 4096 clicks per minute as default. According to Chelonia Limited, when cetaceans are detected in any given minute, it is highly likely that the detection occurs within the first 4096 clicks, so the total number of Detection Positive Minutes or DPM should not be affected by this feature. The limit prevents the SD-card from being filled up by sediment transport noise – as many as 120 000 clicks per minute could be logged due to this. When the limit is reached, the device stops logging data until the start of the next minute.

The C-POD contains a timer but not a clock, which means that the user must note the exact date and time of deployment and manually add it to the data later in the CPOD.exe software. The angle from vertical is relevant because the C-POD only records clicks when the hydrophone is higher than the other end of the device. This feature saves power and memory when the device is stored horizontally or upside down before deployment; however, being deployed at the wrong angle may prevent data logging. The CPOD.exe software shows angle data alongside acoustic data, so it is easy to view whether the device was deployed correctly and whether any major disturbances occurred.

Each C-POD is supplied with two 8GB SD-cards that have been formatted for the specific data logger and therefore are not interchangeable between C-PODs. The device requires 10 alkaline D-cell batteries to run and maximum deployment time is dependent on battery quality. While the batteries can last for a maximum of 212 days (Chelonia Limited), they should be changed more often to prevent loss of data.

In this project, the SD-cards and batteries were changed every 7-14 weeks, resulting in 5 data collection periods over a total of 374 days (396 days for C-POD 3111):

- Period 1: 27.09.2020–03.12.2020 (67 days);
- Period 2: 03.12.2020–04.03.2021 (91 days);
- Period 3: 04.03.2021–10.06.2021 (98 days);
- Period 4: 10.06.2021–26.08.2021 (77 days);
- Period 5: 26.08.2021–06.10.2021/28.10.2021 (41/63 days).

6 C-PODs were deployed in Hardangerfjord on September 27, 2020, in locations shown on Figure 2. In order to minimise interactions with and noise from boats, the devices were placed close to shore at a depth of approximately 5 metres, in water about 25 metres deep. Even though porpoises are known to feed on the bottom of the sea (Bjørge & Tolley, 2009), C-PODs should not be moored to the seabed because the noise from sediment transport and crustaceans can interfere with porpoise detections (Chelonia Limited, 2018). A small marker buoy was attached to the mooring line to simplify retrieval.

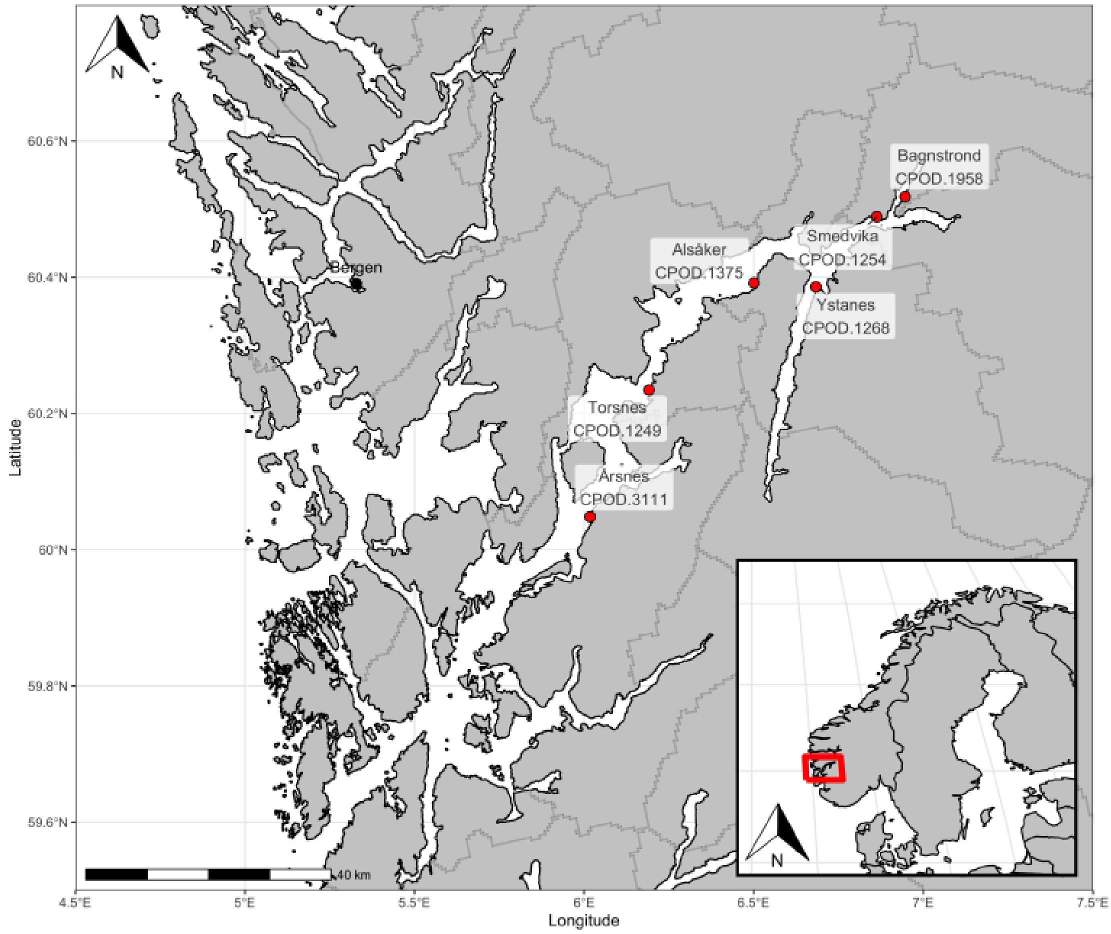


Figure 2. Map of C-POD stations in Hardangerfjord, Norway.

C-POD number 1375 disappeared during the first deployment period and has not been found, which is why there is no data from the Alsåker station. In the second data collection period, C-POD number 1249 was started incorrectly, resulting in no data being logged in the Torsnes station between 03.12.2020 and 04.03.2021. Devices number 1254 and 1268 could not be retrieved on 26.08.2021, but continued logging and were found in their correct locations at the end of the study period. Four out of five remaining C-PODs were successfully retrieved on 06.10.2021. C-POD number 3111 could not be retrieved on 6.10.2021 because the marker buoy had sunk underwater and was not visible from the surface, but the device was successfully retrieved on 28.10.2021 using a submarine drone. The retrieval of C-PODs is shown on Figure 3.

Figure 3. Retrieved C-PODs with anchors on 06.10.2021.

2.3. Validation and analysis of C-POD data

The CPOD.exe software (Version 2.044) was used to analyse the collected data. The raw data on the SD-cards is stored in .CHE files, which cannot be read or used directly. Therefore, the software firstly generates a .CP1 file, which contains all logged clicks as well as temperature and angle information. The .CP1 file can be processed using the KERNO classifier, which generates a .CP3 file containing only the clicks that have been identified as belonging to a train. The CPOD.exe interface is shown in Appendix I, Figure 10. The KERNO classifier algorithm divides identified trains into four categories:

- "NBHF" (in this study, the harbour porpoise is the only source of NBHF clicks)
- "dolphin" or "other cetacean" (other toothed whale species, who produce short broad band clicks),
- "sonar" (long narrow band clicks with regular cycles and patterns coming from vessels),
- and "unclassed" (the software has identified a train, but the source is unclear, includes noise from sediment transport, crustaceans and other sources).

The algorithm also assigns click trains a quality rating depending on the likelihood of the train coming from the identified source (in this case, harbour porpoises):

- "Hi Q" (high probability of click trains coming from porpoises),
- "Mod Q" (moderate probability of click trains coming from porpoises),
- "Low Q" (low probability of click trains coming from porpoises),
- "?" (trains likely coming from other sources).

Manufacturer recommendations to include only Hi Q and Mod Q trains in data analysis were followed. While all classes of detections were viewed during initial assessment of the data, only NBHF trains were included in further analyses.

To determine whether and how many false positive detections are present in the data, the cetacean detections must be manually validated. Because the total number of detections is far too high to validate each one manually, the recommended method for data validation is to inspect 10 trains, scroll through about 10% of the file, and repeat (Tregenza, 2013). Inspection of a click train includes looking at the parameters of the train itself (amplitude or SPL (sound pressure level), frequency, bandwidth, click rate, ICI (inter-click interval), duration) and other features such as the presence of background noise and clusters of similar trains. A harbour porpoise click train in CPOD.exe is shown in Appendix I, Figure 11.

Characteristics of NBHF click trains include (Tregenza, 2013):

- Frequency of 132kHz ± 7 kHz (Appendix I, Figure 12).
- Continually changing click rate and ICI (Appendix I, Figure 13).
- Smooth amplitude profile with a rise and fall.
- Groups of similar trains over several minutes.
- Low bandwidth.

2.4. Statistical analysis

Microsoft Excel and R (Version 1.4.1103) were used for all further statistical analyses. In MS Excel, a summary was created for every C-POD station, including values for total DPM, DPM/day, total clicks, clicks/day, clicks/h, clicks/min, number of Hi Q trains, percentage of Hi Q trains, and temperature. Figures and graphs were created to visually summarise differences in DPM/day and clicks/h values over all locations.

For analysis of seasonal migration, the dependent variable is "DPM/day" and the independent variable is "month". Because the data is not normally distributed, the non-parametric Kruskal-Wallis test was used to determine whether DPM/day values differ significantly throughout the year. The same test was conducted to test for differences between C-POD stations and Dunn's test was used as a post-hoc test to determine which months and locations differ significantly from each other.

For analysis of diel patterns, the dependent variable in "Clicks/h" (mean clicks, not total) and the independent variable is "time" (groups "night" and "day"). "Day" is defined here as the period between sunrise and sunset, and was calculated for each month and station based on the average day length of the month. "Night" is used to describe the period between sunset and sunrise, although there is no true night in the study area from mid-April to mid-August, only twilight. The Mann-Whitney U test was used to determine differences between nocturnal and diurnal porpoise activity. In addition to testing for an overall diel pattern across all locations, the data from each station and month was tested separately in order to find possible differences between stations.

2.5. Role of the author

The author of the thesis directly participated in data collection and the retrieval of the C-PODs, spending one month (03.10.2021–01.11.2021) in Norway. On October 6, 4 C-PODs were successfully retrieved from Hardangerfjord and transported to the University of Oslo. The last remaining device was retrieved on October 28. The author extracted and processed the most recent batches of C-POD data using the CPOD.exe software. Although the data from previous time periods had been processed earlier, it had not been validated or analysed further. Therefore, the author of the thesis was also responsible for the manual validation of the data as well as all consequent analyses, the majority of which were completed during the time spent in Norway.

3. RESULTS

3.1. Quality and validity of C-POD data

Total recording effort across all stations was 1801 days. Over the study period, 5 232 151 NBHF clicks (Hi Q and Mod Q only) were detected, and a total of 79 142 Detection Positive Minutes were recorded. The total number of DPMs, clicks, and the percentage of Hi Q clicks for each location is shown in Table 2, and the stations are listed from innermost parts of the fjord to the furthest parts of the study area. The 3-month long data gap in the Torsnes station should be considered when comparing this station to others.

Table 2. Total amounts of recorded DPM and clicks, and percentage of Hi Q clicks.

Station	**DPM**	**Total NBHF clicks**	**Hi Q of total**
Bagnstrond	27 227	2 590 098	31.6%
Smedvik	28 451	1 775 643	27.1%
Ystanes	7899	186 191	27.6%
Torsnes	4453	148 668	27.9%
Årsnes	11 112	531 551	28.5%
Total	79 142	5 232 151	28.5% (average)

During manual validation of the C-POD data, no probable false positive detections were found. False positives in acoustic data may occur in areas with high amounts of sediment transport noise or sonar activity and result in click trains being incorrectly classified as NBHF trains (Tregenza, 2013). While only approximately 250 of detected trains were inspected in detail following manufacturer recommendations for data validation, all data files were visually examined in their entirety. This visual examination revealed very little overall background noise. In all locations, a small number of time periods with high sonar activity were observed, but there was no clear pattern in the presence of sonar noise. The vast amounts of total porpoise detections and consistently high percentage of Hi Q clicks indicate an overall very high-quality data set.

A low number of probable false negative detections were found. When sonar noise occurs at the same time as porpoise clicks, the KERNO classifier is still capable of finding present click trains, but does not recognise them as porpoise/NBHF click trains. Due to this, as well as the increased difficulty of authenticating these trains, they were not included in the analyses.. Because only a few such co-occurrences were observed among thousands of reliable porpoise detections, they do not affect the overall quality of the data. An example of a porpoise and sonar noise co-occurrence is shown in Appendix 1, Figure 14.

3.2. Seasonal patterns

The echolocation activity recorded by the C-PODs shows that harbour porpoises can be found in Hardangerfjord year-round, but the level of activity varies through the seasons. In all C-POD stations, there was a significant difference in porpoise detections between the winter season and summer season (Kruskal-Wallis test, p-value = 2.987×10^{-5}) with most detections between November and February as shown on Figure 4. The difference between C-POD stations was not found to be significant (Kruskal-Wallis test, p-value = 0.0685).

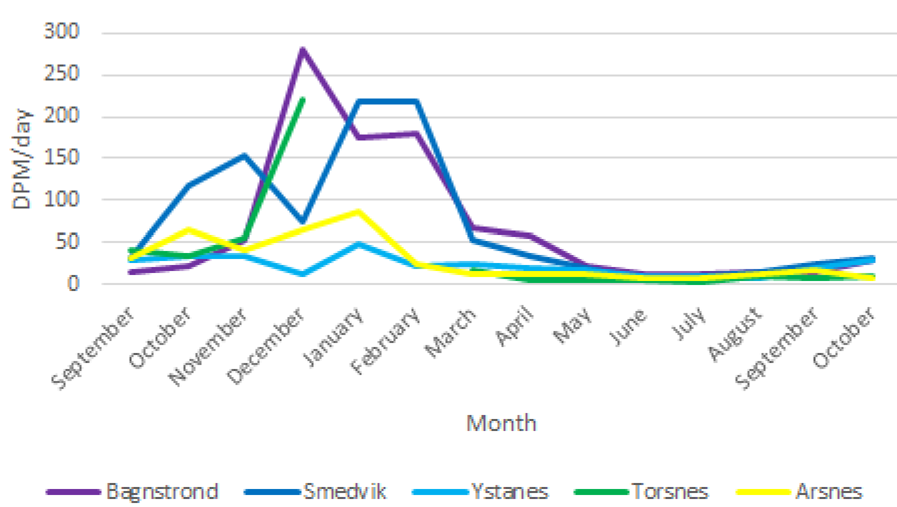


Figure 4. DPM/day values throughout the study period.

Dunn's test showed that DPM/day values differed significantly between November and June (p-value = 0.034), November and July (p-value = 0.043), December and June (p-value = 0.025), December and July (p-value = 0.032), January and June (p-value = 0.01), and January and July (p-value = 0.013).

By far the most detections (70% of total DPM and 83.4% of total recorded NBHF clicks) were recorded in two stations in the innermost part of the fjord: Bagnstrond and Smedvik (Figure 5). Although a difference between winter and summer months was observed in all locations, it is most noticeable in these two locations.

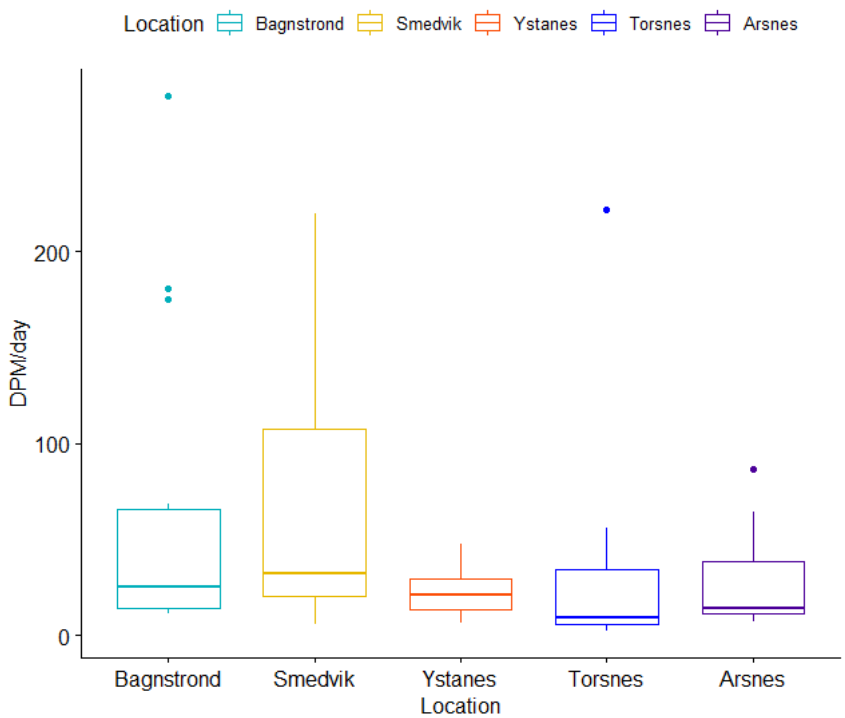


Figure 5. DPM/day for each C-POD station, in order from innermost to outermost areas.

3.3. Diel patterns

Only full 24-hour days were included in the diel pattern analysis due to limitations set by the CPOD.exe software, thus excluding the few days when the C-PODs were deployed, retrieved, or temporarily removed from the study environment. Additionally, the data from September 2020 was excluded from analysis as there are only 3 full days of data, which does not provide a reliable and accurate representation of the porpoise activity for the whole month.

Mean values for clicks per hour were used in this analysis. When testing for the differences between day and night across all locations, the result was significant (see Table 3) in all months, indicating an overall pattern of porpoises being more active at night than during the day. However, when testing each station separately, the pattern was not as clear. In all stations except for Årsnes, at least one of the spring/summer months (May, June, July) was not found to have a statistically significant difference between diel periods of porpoise activity. The results for the analyses for each location separately are shown in Appendix 2, Table 4.

Table 3. Mann-Whitney U test results for the diel activity pattern.

Month	W	p-value
October 2020	0	3.882×10^{-5}
November 2020	0	0.000101
December 2020	1	0.000465
January 2021	1	0.00013
February 2021	0	4.693×10^{-5}
March 2021	25	0.0077
April 2021	4	0.000269
May 2021	15.5	0.0113
June 2021	4	0.00595

July 2021	3	0.00176
August 2021	0	0.000101
September 2021	9	0.000395
October 2021	0	3.867×10^{-5}

As shown on Figure 6, porpoise echolocation activity is higher at night throughout the year, although the difference is greatest during the winter months. Clicks/h values in this analysis ranged from as little as 33 (June, 07:00) up to 37 216 (December, 23:00).

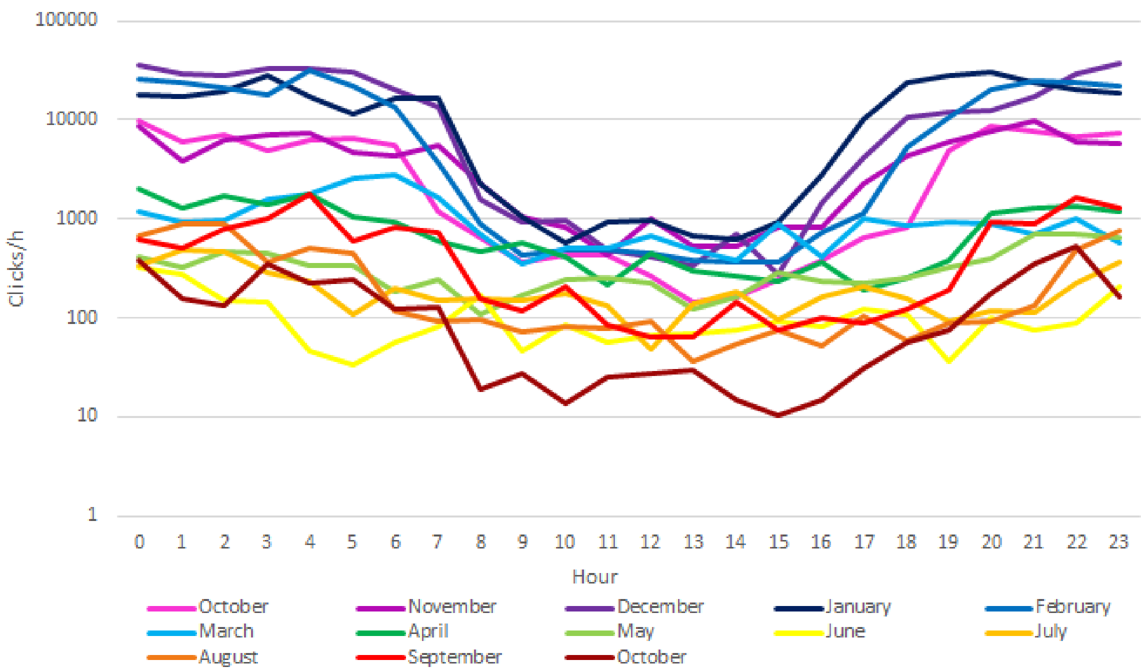
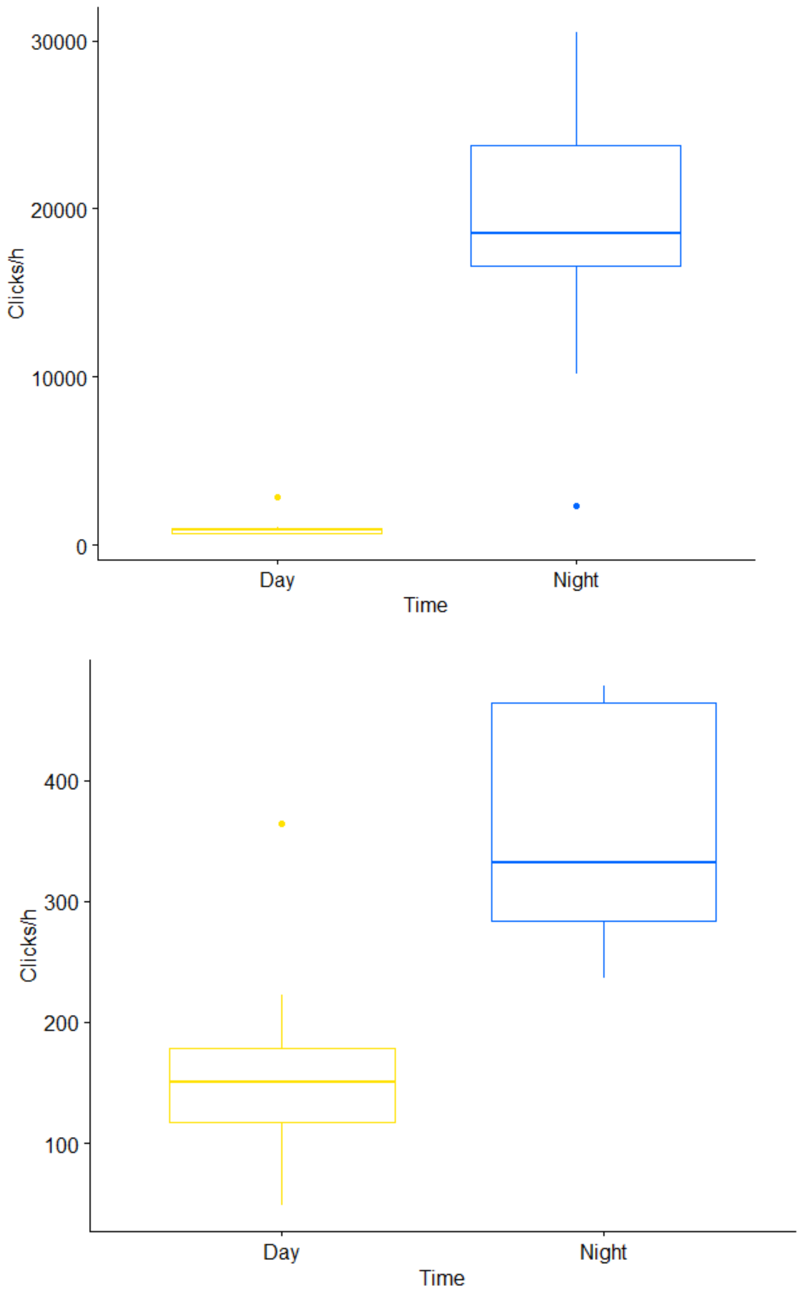


Figure 6. Clicks/h across all locations on a logarithmic scale. Colder colours denote the first half of the study period and warmer colours denote the second half of the study period.

The seasonal pattern is also clearly visible in the differences between clicks/h values through the year. While a notable difference is present between diurnal and nocturnal activity in both winter (represented by January on Figure 7a) and summer (represented by July on Figure 7b), the vast difference in activity between the seasons should be noted.



a.

b.

Figure 7. Differences between diurnal and nocturnal echolocation activity in January (a) and July (b).

3.4. Other detections

In the Smedvik and Ystanes stations no possible other cetacean click trains were detected. In the Torsnes station, click trains detected on 21.07.2021 were identified as “other cetacean” by the KERNO classifier in the CPOD.exe software. However, a detailed inspection of the click train parameters revealed that this detection is most likely sonar noise falsely identified as cetacean clicks. The pattern consisted of short loud pulses at 72–80 kHz with extremely consistent durations and intervals, leading to the conclusion that the noise is artificial in origin. This detection is shown in Appendix 1, Figure 15.

The Bagnstrond station, located in the innermost and narrowest part of the fjord within the study area, is the only C-POD station where other cetacean click trains were detected throughout the study period, although in small numbers (total DPM = 27). These detections were also inspected in detail and they appeared to match general characteristics of delphinid click trains as described by Tregenza (2013). The highest number of other cetacean detections (DPM = 11) in this station was observed during the summer season (June–August). In the Årsnes station (the outermost part of the fjord within the study area), other cetacean click trains were only detected on 16.10.2021 (DPM = 3). At this time, all other C-PODs had already been retrieved from the fjord.

Most of the detected click trains were in the frequency range of 40–100 kHz (therefore, high bandwidth) and exhibited continuously changing click rates and ICIs characteristic of cetacean vocalisations (as opposed to sonar noise) (Appendix I, Figure 16). In all stations where other cetaceans were detected, these detections occurred separately from harbour porpoise detections and there appeared to be no porpoise activity when other cetaceans were present.

4. DISCUSSION

4.1. Data quality and limitations

There are several characteristics that indicate that the data collected in this study is of great quality and that Hardangerfjord is an excellent location for conducting passive acoustic monitoring studies on porpoises.

These features, based on Tregenza (2013), include:

- Generally very quiet background with only a few periods of sonar and background noise present. The depth of the fjord allows for C-PODs to float far enough from the bottom that sediment transport noise does not affect the data.
- Vast amounts (almost 80 000 DPM over the study period) of genuine harbour porpoise detections.
- Apparent lack of false positive detections, and lack of factors that often cause false positive detections in C-POD data.
- Consistently high percentage of high quality click trains across the study area.
- Very few other cetacean detections that could complicate identification and analysis of porpoise detections.

The primary limitation of this study is the small number of C-POD stations. Data from only five stations does not provide a reliable representation of Hardangerfjord as a whole, and definitive conclusions about what might cause variation between different parts of the fjord cannot be made on this data alone. A second limitation is the lack of data collected with different methods. Particularly in the case of bycatch reduction and the implementation of time-area closures, the acoustic data from this study unfortunately does not establish an adequate information base about harbour porpoise seasonal movements and diel patterns, because the causes remain unclear. Ideally, acoustic detections should be validated with visual detections which would provide information that C-POD data cannot, such as the number of animals being detected. So far, visual porpoise surveys in Hardangerfjord have only been carried out during the summer season (Øien, 2018; Leonard, 2022).

4.2. Seasonal patterns

The first objective of this study was to determine possible seasonal differences in the presence and activity of harbour porpoises in Hardangerfjord. Based on the results it can be stated that harbour porpoises are undoubtedly present in the fjord throughout the year, but there are significant differences in seasonal activity. In Hardangerfjord, porpoise echolocation activity is highest during the coldest months – November to February.

Previous studies on seasonal movements of harbour porpoises have found variable results, but it should be noted that these studies have been conducted in numerous different locations using different methods. Several studies have found that porpoise activity in different parts of the North Sea peaks during the spring and summer, but there is considerable geographical variation in these patterns (Verfuß *et al.*, 2007; Gilles *et al.*, 2009; Haelters *et al.*, 2011). In both Belgian and Dutch waters, which are the southernmost areas of the North Sea reviewed here, porpoise abundance and density peaked in winter and spring (February–April) (Haelters *et al.*, 2011; Scheidat *et al.*, 2012). These are the results most similar to the patterns observed in this study, although in Hardangerfjord, the echolocation activity already decreases noticeably in March. The porpoise detections in the innermost area of the fjord continue to decrease drastically throughout the spring, possibly indicating that porpoises are migrating towards the open sea for the summer, and returning in autumn.

When reviewing related studies across the North Sea, a larger geographical pattern emerges – harbour porpoises seem to move northward for summer, with abundance and density peaking earlier in the south and later in the north. As mentioned, in Belgian waters, porpoise abundance is highest in late winter and early spring (Haelters *et al.*, 2011), in the German North Sea abundance peaks in spring/summer (Nachtsheim *et al.*, 2021), and in Danish waters, the peak occurs in summer (Sveegard *et al.*, 2011). Additionally, summertime inshore movements and wintertime offshore movements have been observed in several of these areas (Sveegard *et al.*, 2011; Haelters *et al.*, 2011). Data from Hardangerfjord does not seem to fit these patterns and the contradicting results raise questions about not only the porpoise population itself, but also about the reliability of the passive acoustic monitoring method for studying seasonal movements. Validation of acoustic data with other methods will be necessary in order to confirm whether this pattern is as strong in reality as it seems to be based on acoustic detections.

While the difference in echolocation activity between seasons is clearly significant, the difference between C-POD stations in Hardangerfjord was found to be just outside the limit of statistical significance (Kruskal-Wallis test, p-value = 0.0685). It is likely that the amount of stations is simply too small to produce a significant result and more C-POD stations should be used in future studies to reliably assess variation between different parts of Hardangerfjord. Nevertheless, it is visible that there is some level of variation between the stations in this study.

As shown on Figure 8, porpoise echolocation activity was remarkably higher in two stations – Bagnstrond and Smedvik, in the innermost part of the fjord. Based on DPM/day rates, shown as a line graph on Figure 8, the Torsnes station may have had great amounts of porpoise activity similar to the two aforementioned stations, but due to incorrect deployment the C-POD only recorded data in the first 3 days of December, resulting in a low number of total DPM but a high rate of DPM per day. In Årsnes and Ystanes, the echolocation activity does not change as dramatically throughout the year. The lowest detection rates were recorded in Ystanes, perhaps partly because the station is located on the inshore side of a commercial ferry route, which the porpoises may avoid due to noise and disturbances.

Although a difference in activity between winter and summer was observed in all stations, it is most visible in these two stations. These results may indicate that porpoises are gathering in the inner parts of the fjord during colder months. As winter is neither the breeding nor the calving season for harbour porpoises (Bjørge & Tolley, 2009), this possible gathering must have a different reason. Prey distribution and availability is believed to be the main factor influencing harbour porpoise movements (Santos & Pierce, 2003). It is possible that schools of one or more primary prey species are migrating inshore in winter, providing porpoises with a valuable food source during the coldest months. Conversely, the possible spring-summer migration towards the open sea may also be caused by changes in prey distribution. However, there is little to no information about seasonal migration of fish species in Hardangerfjord so this is purely speculation.

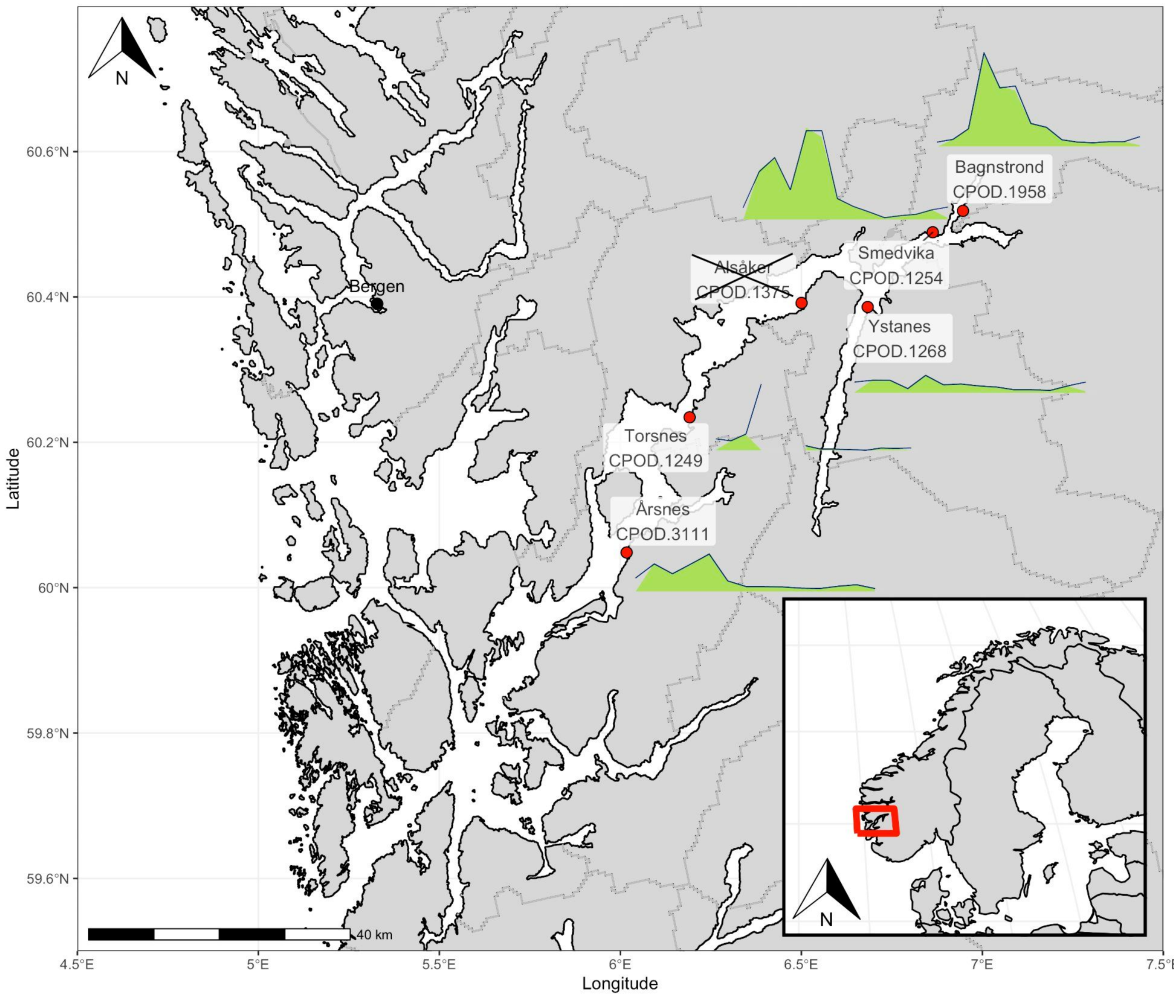


Figure 8. Differences in porpoise detections between C-POD stations across the whole study period. The total amount of DPM is shown as green areas on a scale of 0 to 9000 and DPM/day is shown as blue lines on a scale of 0 to 300.

An alternative explanation would be that the apparent differences between inner and outer parts of the study area are a result of the small acoustic detection range and width of the fjord at C-POD stations. All C-PODs were deployed very close to shore, but the width of the fjord was different at each station, being the narrowest at Bagnstrond (~1500 m) and widest at Årsnes (~5500 m). With a maximum detection range of 400 m in optimal conditions (Kyhn *et al.*, 2012), a C-POD at Bagnstrond would have a greater porpoise detection probability than one at Årsnes, meaning that in wider parts of the fjord many porpoises may remain undetected simply by being outside of the detection range. Again, the number of stations in this study is too small to prove or disprove this hypothesis.

4.3. Diel patterns

The second objective of this study was to determine whether porpoises are more active during the day or at night, and discuss possible feeding strategies and prey species based on the results. An analysis of diel patterns across the whole study area showed a significant difference in porpoise echolocation activity between day and night. Throughout the year, porpoises in Hardangerfjord are more active at night. This finding is in line with numerous previous studies which have also found that porpoise echolocation activity and foraging activity is higher at night (Carlström, 2005; Wisniewska *et al.*, 2016; Zein *et al.*, 2019).

When analysing each C-POD station separately, the patterns vary considerably (Figure 9). Again, the highest level of activity was recorded in Bagnstrond and Smedvik, as well as the highest degree of difference between day and night. The relatively incoherent pattern in Torsnes is likely the result of the period of data loss, but in all stations higher nocturnal activity can be observed. While this aspect is complicated to illustrate on a single graph, a difference in the intensity of the diel variation can be observed through the year. The diel pattern is the strongest in winter and the weakest in summer.

Numerous studies have found that porpoises forage throughout the diel cycle due to their high metabolic rate, but activity is higher at night (Reed *et al.*, 2000; Carlström, 2005; Wisniewska *et al.*, 2016). It is likely that the use of different feeding strategies also plays a role in the diel activity pattern. Although it is possible that porpoises may use their vision for hunting during the day and rely on echolocation at night, there is no evidence that darkness is the cause for increased echolocation activity at night (Verfuß *et al.*, 2009). Considering that maximum water depth in Hardangerfjord is 852 metres and the deepest recorded harbour porpoise dive reached a depth of just over 400 metres (Carwardine, 2020), it is highly unlikely that porpoises in Hardangerfjord use the bottom-grubbing behaviour as a primary feeding strategy.

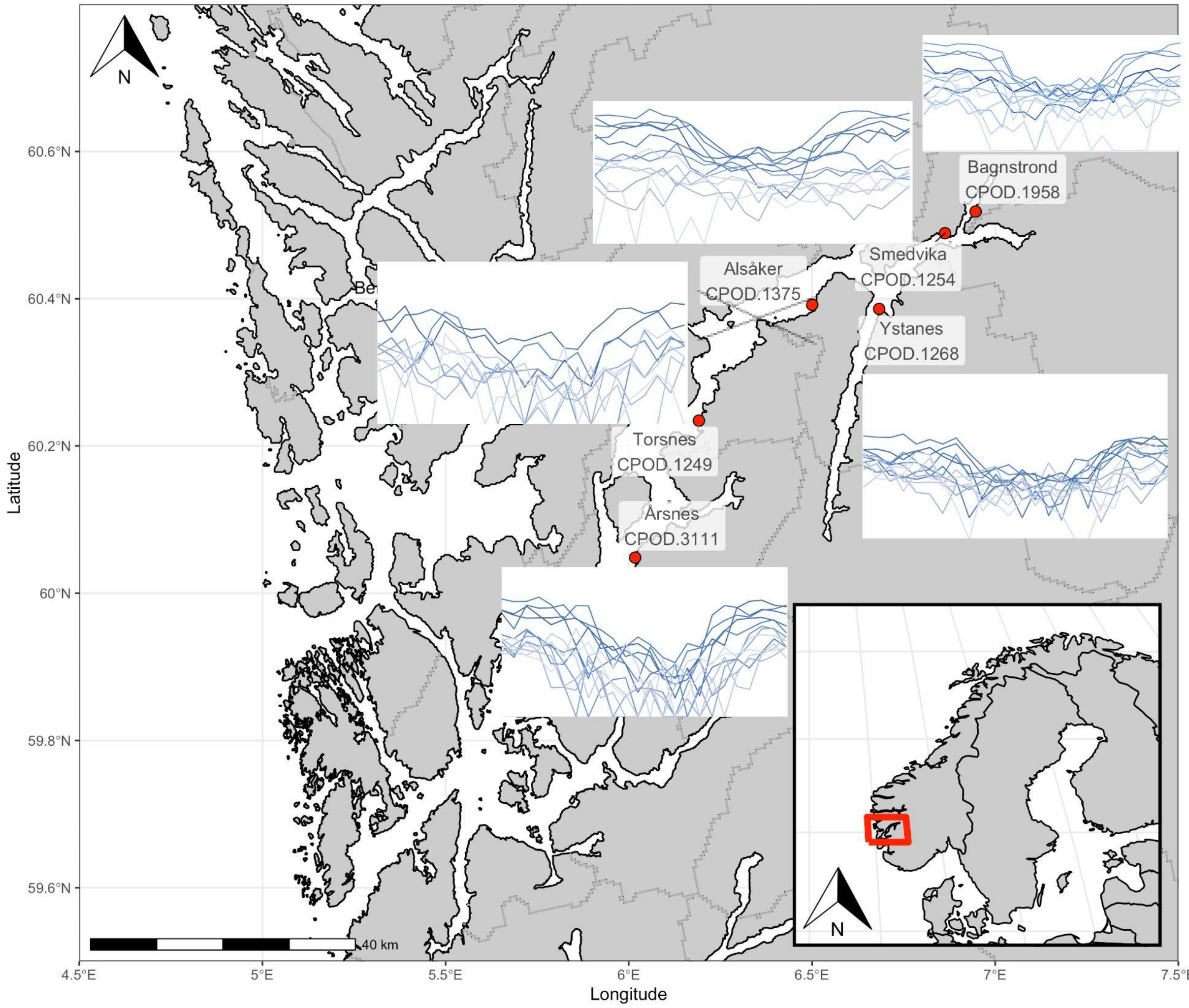


Figure 9. Diel activity patterns for each C-POD station, represented as the mean number of clicks per hour on a logarithmic scale of 1 to 1 000 000. Darker colours denote the first half of the study period and lighter colours denote the second half of the study period.

Previous studies examining the stomach contents of harbour porpoises have found that in Norwegian waters, pelagic and mesopelagic fish species are more prevalent than benthic species in porpoise diets (Aarefjord *et al.*, 1995). This supports the hypothesis that porpoises in Hardangerfjord also feed pelagically. Higher nocturnal echolocation activity indicates that porpoises are feeding on fish that are found at or near the surface at night. Diel vertical migration has been observed in several fish species that porpoises in Norway are known to feed on, such as pearlsides, argentines and various gadids (Bjørge, 2003). Pelagic feeding also contributes to the quality of the data discussed in chapter 4.1. – in areas where bottom-grubbing is a primary feeding strategy, such as the shallower and muddier waters in the Baltic and North Seas, harbour porpoises are more difficult to detect by PAM methods. Because porpoise sounds are highly directional (Hansen *et al.*, 2008), echolocation clicks used for bottom-grubbing do not reach acoustic monitoring devices. On the other hand, porpoises feeding pelagically will be scanning the environment in various directions and are more likely to be detected by devices like C-PODs.

In order to study how patterns in porpoise behaviour are influenced by prey species, more information is required about the fish in Hardangerfjord. Linking catch data from fisheries to porpoise activity may provide an insight into whether porpoises are following the distribution of certain species or opportunistically feeding on the species that are available to them.

Similarly to the seasonal patterns, the diel patterns in porpoise activity observed in Hardangerfjord cannot be confirmed without supporting data collected through another method. It is unknown how much of the variation in activity between day and night as well as the variation in the diel pattern between different seasons is caused by the use of different feeding strategies or seasonal changes in the porpoise population.

4.4. Other detections

In two stations (Bagnstrond and Årsnes), other cetacean click trains were detected. Besides the harbour porpoise, the only cetacean species known to enter Hardangerfjord is the killer whale. Therefore these other cetacean detections in the C-POD data are most likely killer whales. While the studies are still ongoing, more killer whale sightings in Hardangerfjord have been reported in recent years and two pods of killer whales that enter the fjord during the winter months have been identified (Eve Jourdain, pers. comm., May 2022).

There has also been at least one instance of killer whales hunting and killing a harbour porpoise in this fjord. The presence of killer whales may affect the behaviour and distribution of harbour porpoises in Hardangerfjord. Perhaps predator avoidance is part of the reason porpoise echolocation activity is higher in the innermost parts of the fjord in winter. Interestingly, nearly all the other cetacean detections in this study were also recorded in the innermost station, Bagnstrond.

In order to reach this area, the killer whales clearly had to pass all other C-PODs and yet remained undetected.

Broadband and lower frequency sounds such as killer whale vocalisations can be detected at significantly greater distances than NBHF clicks. According to Chelonia Limited, C-PODs may detect delphinid sounds from more than 1000 metres away. At all C-POD stations except for Årsnes, the width of the fjord does not exceed 2200 metres, so assuming that the conditions are good, the mean probability that passing killer whales are in the detection radius of a C-POD placed near the shore is at least 50%. It is also possible that killer whales were silent when passing the detectors despite being in the detection radius. As photo-identification is used to study killer whales in Hardangerfjord (Eve Jourdain, pers. comm., May 2022), it could be possible to match visual detections to acoustic detections and the locations of the C-PODs.

One factor that should be considered is that the C-PODs may have detected a greater number of killer whale click trains, but they were not identified by the classifier algorithm. As this study focuses on harbour porpoises and not other cetaceans, no explicit effort was made to filter out other cetacean detections from background noise. The algorithm used to filter out porpoise sounds – the KERNO classifier – is not ideal for identifying detections of killer whales and other non-NBHF species. Because the frequency and bandwidth of dolphin sounds greatly overlap with sediment noise, the KERNO classifier is conservative and often fails to classify delphinid click trains in order to minimise the amount of false positive detections (Chelonia Limited, 2014). A classifier specifically developed for the identification of non-NBHF species would be more suitable for this purpose.

4.5. Suggestions for future research

Even though significant variation was observed in both seasonal and diel patterns of harbour porpoise echolocation activity, it is clear that conclusions about the true causes of these patterns cannot be made without supplemental data collected through a different method such as visual surveys.

Based on the analysis and discussion of data collected in Hardangerfjord, the following recommendations for future studies are proposed:

- In passive acoustic monitoring studies, more C-POD stations should be used. Having a larger data set will provide more reliable data on how much porpoise activity varies in different parts of Hardangerfjord. Increasing both the number of C-POD stations in the current study area as well as the size of the study area itself would be beneficial.
- At least one entire year-round visual survey should be conducted alongside the PAM study to validate the acoustic data and determine the number of porpoises in the fjord. This will allow for the calculation of detection functions for acoustic monitoring, and continuous visual validation of acoustic data will not be necessary once reliable
- Different possibilities for the placement of C-PODs in the fjord should be explored. Perhaps it is possible to find a small area of the fjord with low ship traffic, to test whether placing C-PODs further from the shore will result in a different number of detections.

Beyond the scope of this thesis, the objective of the Hardangerfjord porpoise project is to provide information about porpoise behaviour and ecology in order to establish bycatch mitigation methods and reduce fisheries-related porpoise mortality. Unfortunately, the acoustic data collected in this project does not provide an extensive information base suitable for designing time-area closures in the fjords. The study area is too small to draw conclusions about Hardangerfjord as a whole, and protecting porpoises only within the study area may result in an increase in fishing effort and bycatch incidents outside the protected area. Therefore it is necessary to survey a larger area, possibly even the whole fjord, to be certain that any fishing bans or closures are an effective bycatch reduction method. Additionally, the collected acoustic data does not provide a reliable depiction of porpoise abundance and density in Hardangerfjord, highlighting the need for further studies.

SUMMARY

The harbour porpoise is a small cetacean that is heavily affected by bycatch due to its coastal habitat. Norwegian coastal waters and fjords have a large harbour porpoise population as well as high rates of porpoise bycatch, but little is known about the seasonal and diel patterns in porpoise activity in this area. Common bycatch reduction methods such as pingers may be effective in coastal waters, but inside the narrow fjords they may negatively affect porpoises by excluding them from preferred habitats. Implementing time-area closures requires an adequate information base about porpoises, which this study aimed to establish.

In order to study the seasonal and diel activity of porpoises, passive acoustic monitoring devices were deployed in Hardangerfjord, Norway for a period of one year. The devices record the narrow band, high frequency echolocation clicks produced by porpoises. However, it is not possible to discern the number of echolocating animals from acoustic data alone.

Results showed that porpoise echolocation activity is highest during the winter and lowest during the summer, with the most detections being recorded in two stations in the innermost part of the fjord. A clear diel pattern was also observed, with echolocation activity being significantly higher at night than during the day. The intensity of the diel pattern changed through the year, being most pronounced in winter and less distinct in summer. The diel pattern observed in Hardangerfjord corroborates previous findings on harbour porpoise activity in other regions, whereas the apparent seasonal movements do not seem to match migration patterns observed in the North Sea.

In order to establish time-area closures for bycatch reduction, further studies with more C-POD stations should be conducted in Hardangerfjord. Additionally, another data collection method such as visual surveys, must be used to confirm the results from this study. Because acoustic data may not accurately represent the size of the population, the extent and causes of the seasonal movements remain uncertain.

KOKKUVÕTE

Harilik pringel on hammasvaalaline, kes asustab peamiselt rannikualasid ning seetõttu satub tihti võrkudes kaaspüügi ohvriks. Norra rannikuvetes ja fjordides on erakordselt palju pringleid, kuid ka kaaspüügi sagedus on seal kõrge. Kõige tavalisem kaaspüügi vähendamise meetod on pingerite lisamine võrkudele, mis võib küll efektiivne olla avatud rannikuvetes, kuid kitsastes fjordides võivad pingerite tekitatud valjud helisignaalid pringlid elupaikadest välja tõrjuda. Eelistatum oleks kasutada ajalisi ja piirkondlikke piirangualasid, mille rajamiseks on vaja teavet pringlite aktiivsusmustrite kohta. Pringlite hooajalisi ja ööpäevaseid aktiivsusmustreid ei ole selles piirkonnas uuritud ning see ongi töö eesmärk.

Aktiivsusmustrite uurimiseks kasutati passiivse akustilise seire seadmeid, mis paigutati viite jaama Hardangeri fjordis üheks aastaks. Pringlid kasutavad kajalokatsiooniks kitsaribalisi kõrgsageduslikke helisid, mida eelmainitud seadmed tuvastavad. Siiski ei ole ainult akustiliste andmete põhjal määrata häälitsevate isendite arvu.

Tulemused näitavad olulisi sesoonseid muutusi - pringlite aktiivsus on kõrgeim talvel ja madalaim suvel. Kõige rohkem tuvastusi pärineb kahest jaamast, mis asuvad fjordi kõige sisemises osas. Hardangeri fjordis nähtav sesoonne muster ei ühti enamikes varasemates uuringutes vaadeldud mustriga, kuid mittevastavuse põhjused ei ole selged. Seevastu tuvastati selge ööpäevane muster, mis kinnitab varasemate uuringute tulemusi – pringlid on öösel oluliselt aktiivsemad kui päeva ajal. Ööpäevase mustri tugevus varieerus aasta lõikes, olles talvel kõige selgem ja suvel veidi ebamäärasem.

Kalapüügipiirangute kehtestamiseks selles uuringus kogutud akustilistest andmetest siiski ei piisa. Samas fjordis oleks vaja korraldada täiendavaid uuringuid rohkemate seirejaamadega ning akustilisi andmeid tuleks kinnitada mõnel muul meetodil kogutud andmetega, näiteks loendusandmetega. Kuna vaid akustiliste andmete põhjal ei saa usaldusväärselt määrata populatsiooni suurust, jäävad sesoonsete mustrite ulatus ja põhjused veel ebaselgeks.

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APPENDIX I. Analysis of data in the CPOD.exe software

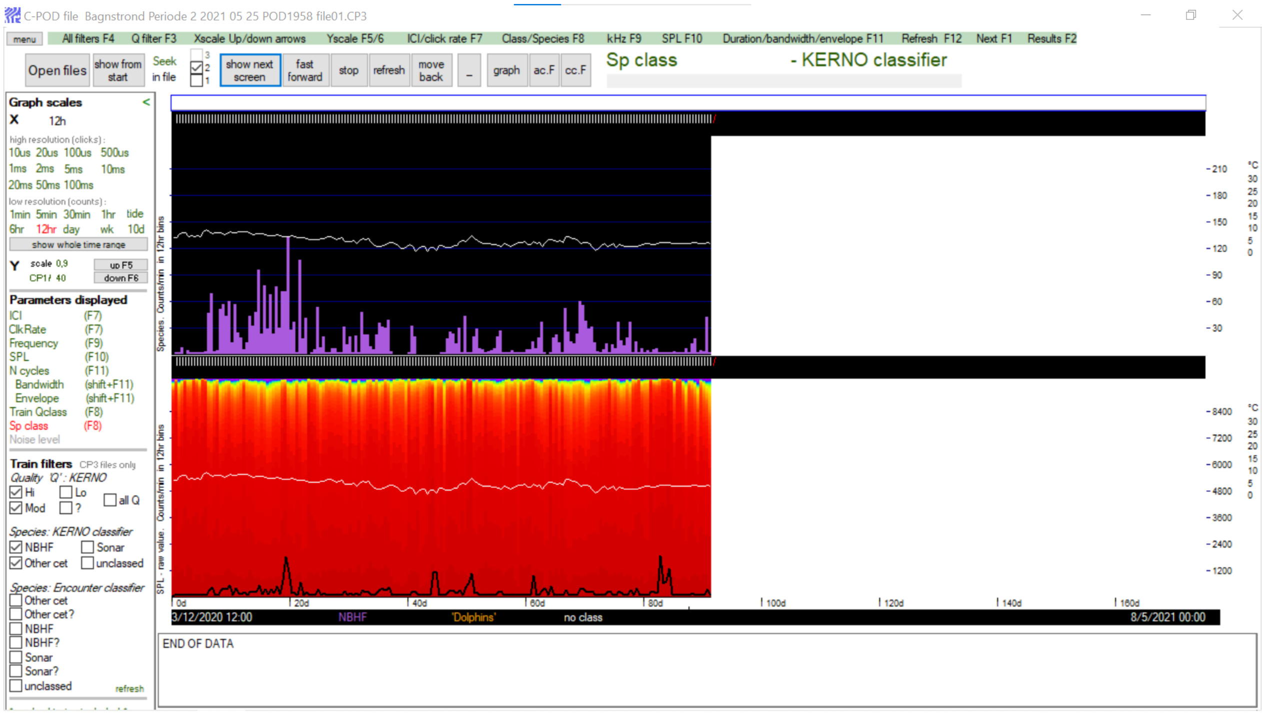

Figure 10. The interface of the CPOD.exe software, showing the .CP1 file at the bottom, the .CP3 file (porpoise detections) on top, and options for scales, parameters and various filters on the left side.

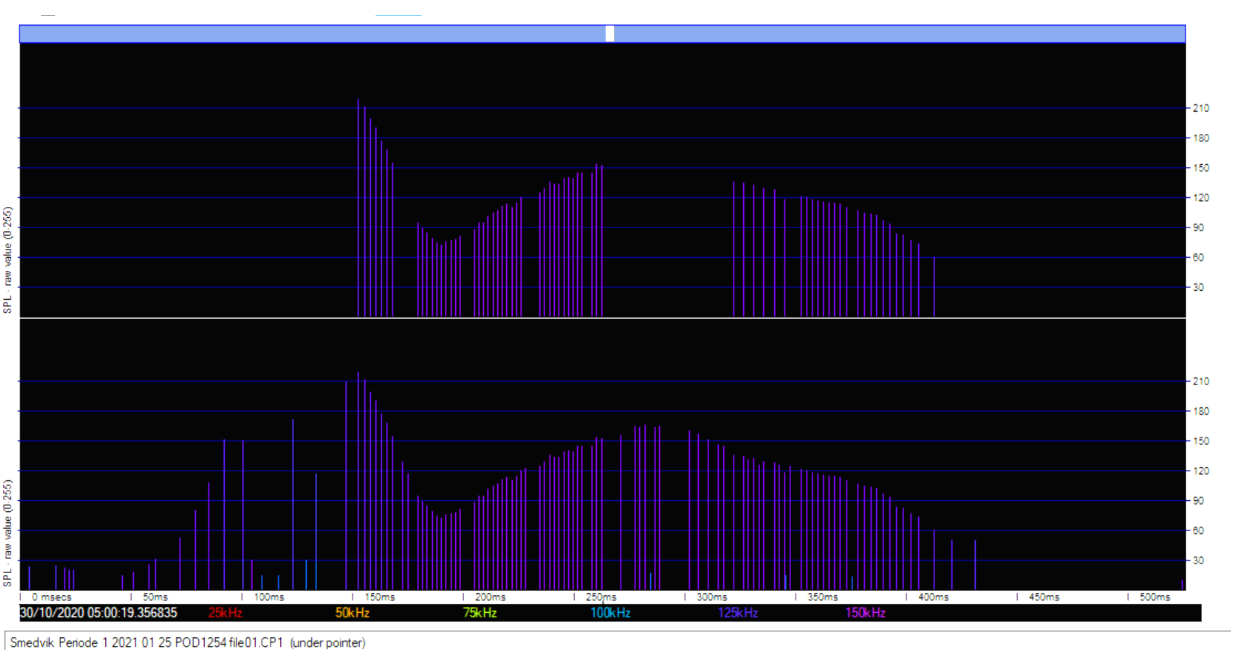

Figure 11. A harbour porpoise click train. The bottom file shows all recorded clicks, whereas the top file only shows clicks that were identified as part of a click train.

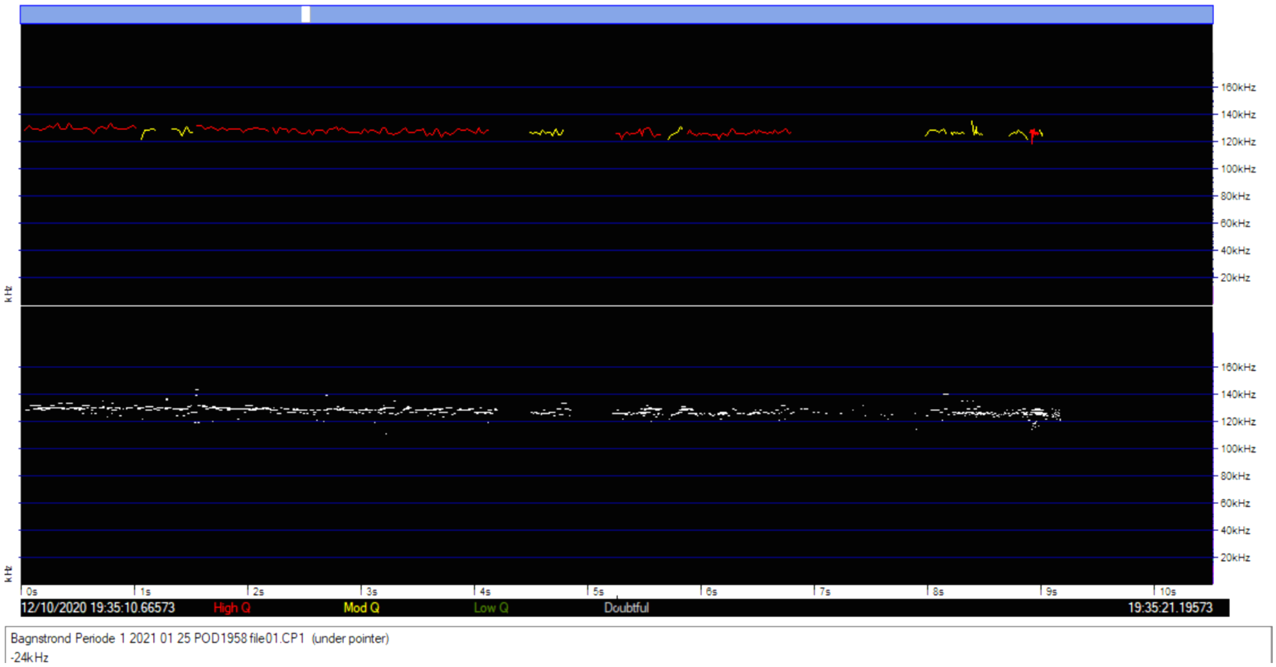

Figure 12. A harbour porpoise click train showing the narrow frequency range of 120–140 kHz.

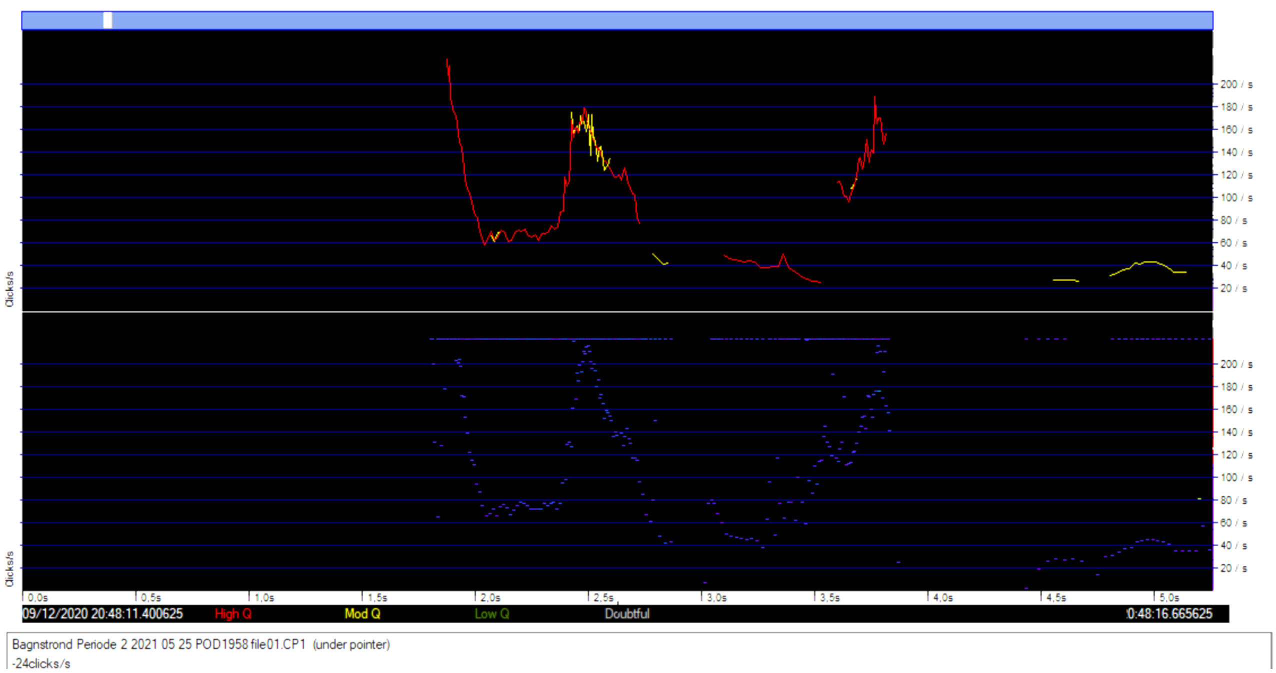

Figure 13. A harbour porpoise click train showing the continuously changing click rate with rises and falls.

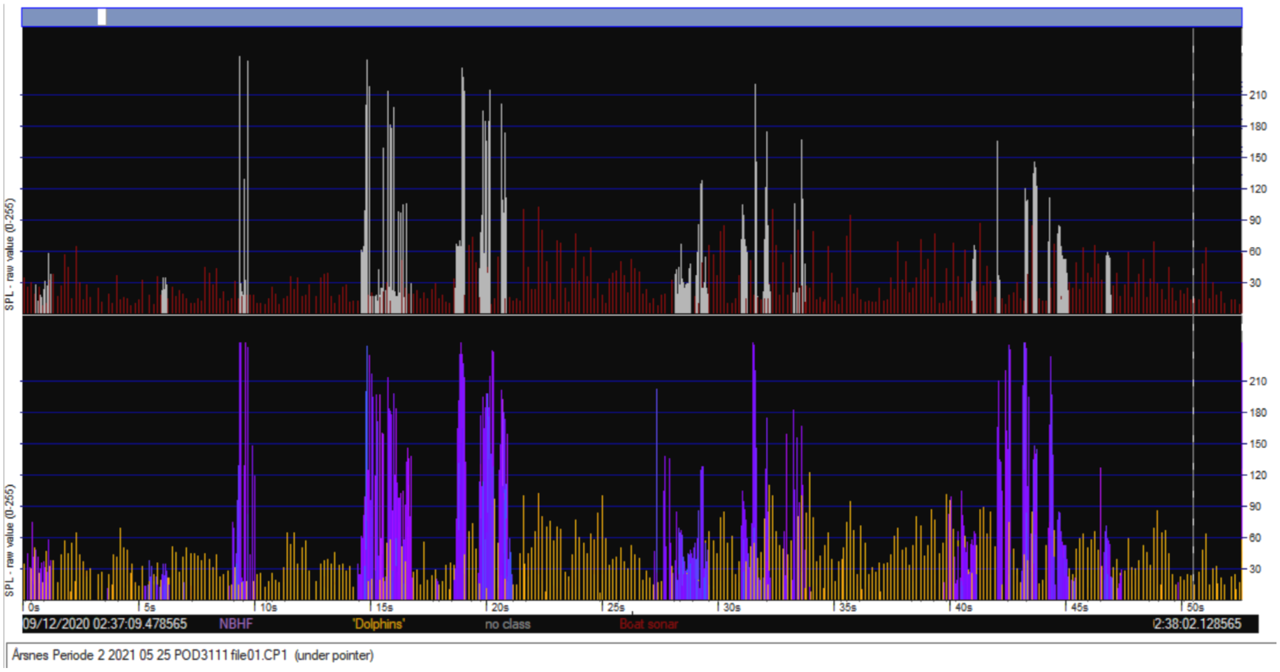

Figure 14. Probable harbour porpoise click trains (purple/grey) in the presence of sonar noise (orange/red). The algorithm has failed to classify the trains as NBHF.

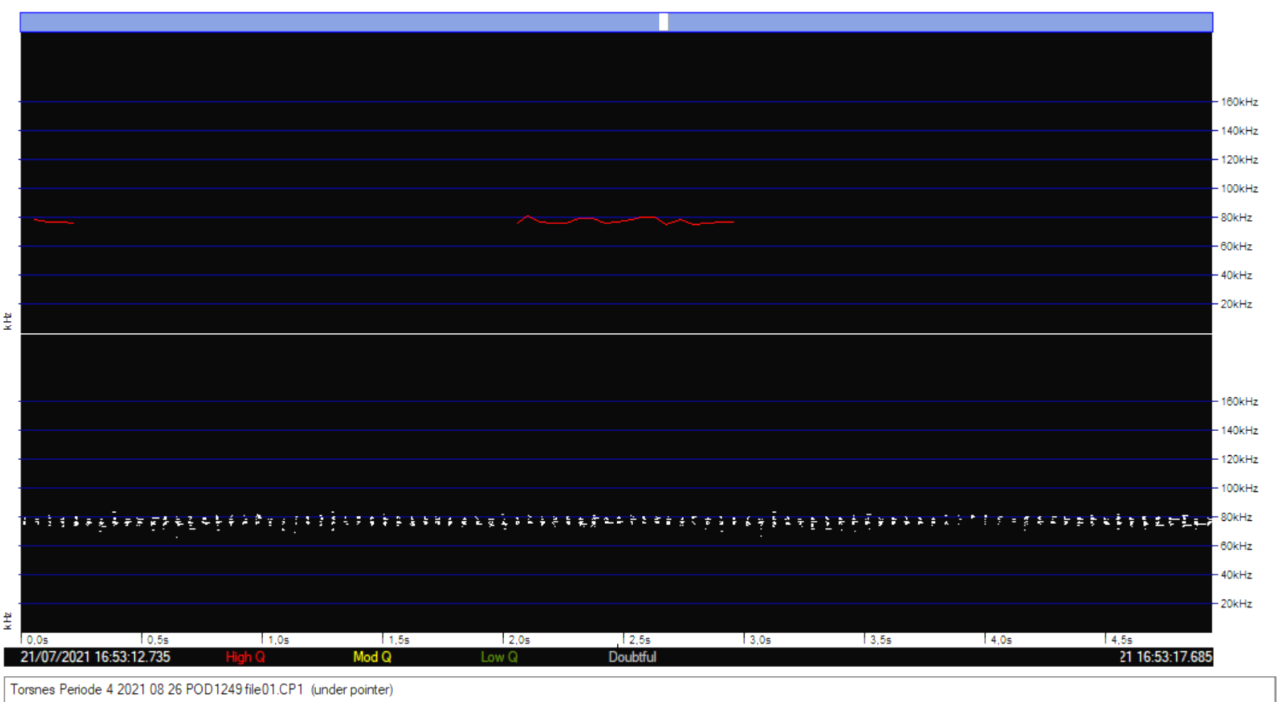

Figure 15. Probable sonar noise that has been classified as a cetacean detection by the software despite the unnaturally consistent click pattern and frequency.

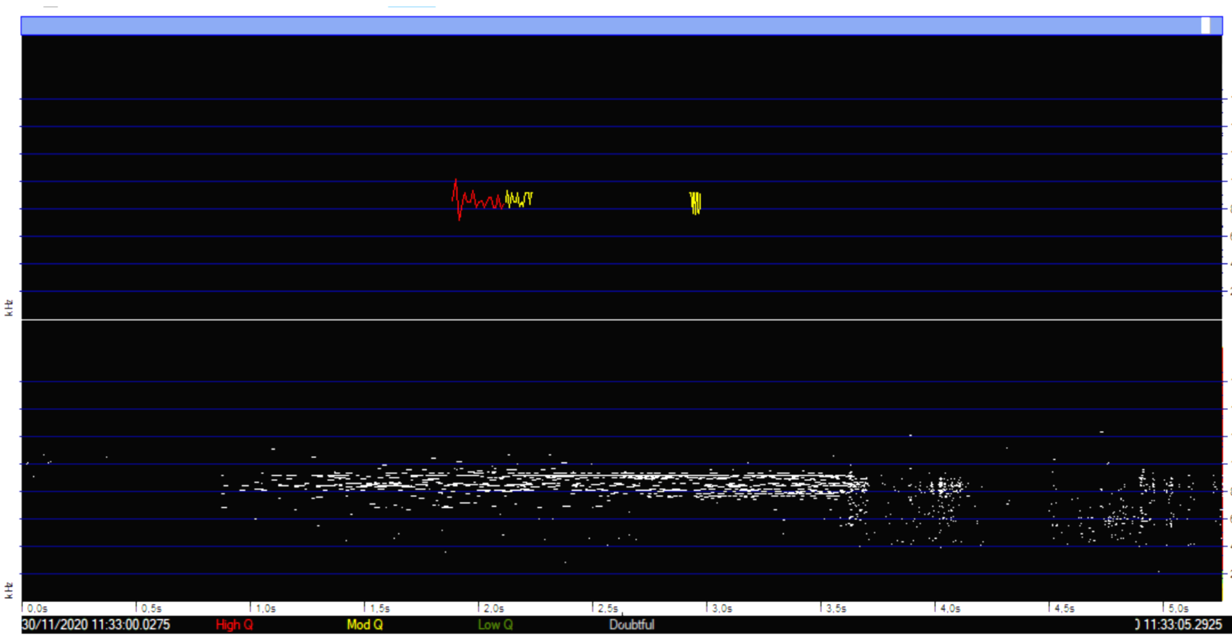

Figure 16. A probable killer whale click train identified by the software, showing a natural click pattern with a frequency range of 40–100 kHz.

APPENDIX II. Diel analysis results by each station

Table 4. Mann-Whitney U test results (p-values) for each C-POD station separately.

Month	Bagnstrond	Smedvik	Ystanes	Torsnes	Årsnes
October 2020	8.159×10^{-5}	3.897×10^{-5}	5.001×10^{-5}	0.0001037	3.882×10^{-5}
November 2020	0.002435	0.0001008	0.0002115	0.0001295	6.466×10^{-5}
December 2020	0.0009668	0.0003616	0.0136	-	0.0004775
January 2021	0.0002299	0.0001295	0.0001295	-	0.0001295
February 2021	4.711×10^{-5}	4.711×10^{-5}	6.048×10^{-5}	-	0.004513
March 2021	0.01496	0.643	0.2024	0.03206	0.003228
April 2021	0.0001295	0.3425	0.00105	0.006793	0.0005357
May 2021	0.336	0.003732	0.001935	0.06189	0.01174
June 2021	0.9075	0.642	0.003661	0.01307	0.004499
July 2021	0.03316	0.003535	0.2863	0.02175	0.00685
August 2021	0.001196	0.0002115	0.01557	0.009252	0.0002606
September 2021	0.001155	4.711×10^{-5}	0.0007603	0.002102	0.0009386
October 2021	0.0175	0.1914	0.0004485	0.03823	0.0002614

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