Porpoises and their prey

Diet and foraging behaviour of Belt Sea harbour porpoises

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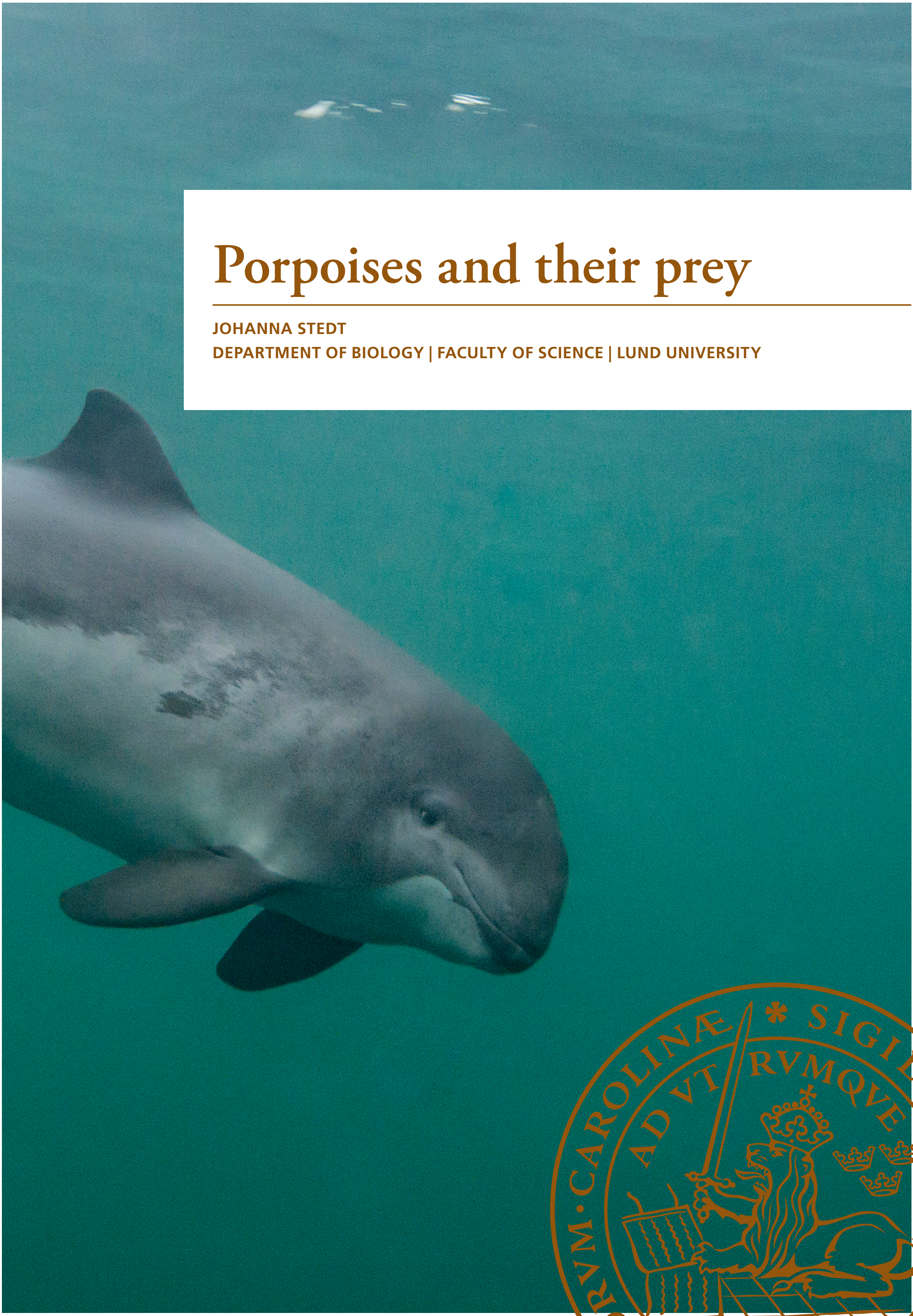

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Porpoises and their prey

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Johanna Stedt

DOCTORAL DISSERTATION

Doctoral dissertation for the degree of Doctor of Philosophy (PhD) at the Faculty of Science at Lund University to be publicly defended on 6th of December at 09.30 in the Blue Hall, Department of Biology, Ecology building, Sölvegatan 37, Lund.

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Title and subtitle: Porpoises and their prey – Diet and foraging behaviour of Belt Sea harbour porpoises

Abstract: The harbour porpoise (*Phocoena phocoena*) is a small toothed whale with a mainly coastal distribution in the northern hemisphere. As a marine top predator, the species can act as an indicator for early warning signs of ecosystem changes. At the same time, harbour porpoises are globally threatened by human activities and in need of conservation. Successful protection of harbour porpoises requires understanding how they interact with the local ecosystem, perhaps most importantly, how they interact with prey.

This thesis provide some answers to three seemingly simple questions: '*When and where do porpoises forage and eat?*', '*What do porpoises eat?*', and '*How do porpoises catch the fish that they eat?*'. By doing so, it aspires to provide information that can ultimately be used to identify conflict areas between human activities and harbour porpoises, in turn enabling effective conservation measures. The questions are explored by studies of wild harbour porpoises in Swedish and Danish coastal waters, mainly the Belt Sea population. A broad variety of techniques and methods are used for data collection and analyses, including e.g. passive acoustic monitoring, post-mortem examinations of deceased porpoises, and visual observations by drones.

Acoustic data on harbour porpoise activity show that porpoise presence and foraging are highly correlated in both space and time, suggesting that the main driving force for porpoise presence is prey occurrence. This reveals how tightly linked porpoises are to their foraging areas and that porpoise presence is in itself a good indicator of areas of energy intake, which in turn represents important habitats to protect.

Further, diet studies performed on deceased harbour porpoises in Swedish waters indicate that porpoises target a variety of fish from a diverse menu of both benthic and pelagic prey species. The estimated diet composition is similar to results from previous years in the same area, with preferred prey families being Gadidae, Gobiidae and Clupeidae. Our estimates do however provide some indications of changes in relative contribution of some prey species, possibly reflecting a response by harbour porpoises to changing prey abundance.

Finally, drone video recordings reveal porpoises to be flexible predators that forage on both single fish and schools of fish, as well as individually and in groups of varying sizes. In addition, porpoises display complex collaborative group hunting by role specialization. Some of these described behavioural adaptations and context-dependent strategies for prey capture might be based on information transfer and social learning, possibly indicating the presence of harbour porpoise culture.

Collectively, the results from this thesis provide new insights into the lives of harbour porpoises and provide valuable information to guide conservation actions for the species.

Key words: cetacea, *Phocoena phocoena*, spatiotemporal distribution, habitat use, macroscopic analysis, metabarcoding, UAS, drone, predator-prey interactions, fish, marine ecosystem, conservation

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Everyone you meet knows something you don't know but need to know.
Learn from them.

CARL JUNG

Table of Contents

Abstract

The harbour porpoise (*Phocoena phocoena*) is a small toothed whale with a mainly coastal distribution in the northern hemisphere. As a marine top predator, the species can act as an indicator for early warning signs of ecosystem changes. At the same time, harbour porpoises are globally threatened by human activities and in need of conservation. Successful protection of harbour porpoises requires understanding how they interact with the local ecosystem, perhaps most importantly, how they interact with prey.

This thesis provide some answers to three seemingly simple questions: '*When and where do porpoises forage and eat?*', '*What do porpoises eat?*', and '*How do porpoises catch the fish that they eat?*'. By doing so, it aspires to provide information that can ultimately be used to identify conflict areas between human activities and harbour porpoises, in turn enabling effective conservation measures. The questions are explored by studies of wild harbour porpoises in Swedish and Danish coastal waters, mainly the Belt Sea population. A broad variety of techniques and methods are used for data collection and analyses, including e.g. passive acoustic monitoring, post-mortem examinations of deceased porpoises, and visual observations by drones.

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Finally, drone video recordings reveal porpoises to be flexible predators that forage on both single fish and schools of fish, as well as individually and in groups of varying sizes. In addition, porpoises display complex collaborative group hunting by role specialization. Some of these described behavioural adaptations and context-dependent strategies for prey capture might be based on information transfer and social learning, possibly indicating the presence of harbour porpoise culture.

Collectively, the results from this thesis provide new insights into the lives of harbour porpoises and provide valuable information to guide conservation actions for the species.

Populärvetenskaplig sammanfattning

Förlust av biologisk mångfald är ett av de största hoten mot ekosystem och deras funktioner. Nästan 500 arter i den marina miljön i Sverige anses idag vara hotade eller sårbara. En av dessa är Sveriges enda val, tumlaren (*Phocoena phocoena*), som lever längs hela Sveriges kust och rör sig över stora områden i sin jakt på fisk att äta. Mänsklig påverkan, framför allt genom oavsiktliga bifångster vid garnfiske, miljögifter och försämrad födotillgång och -kvalitet, gör att tumlare är i behov av skydd i alla områden där de förekommer. Särskilt utsatt är arten i Östersjön. Här är populationen akut utrotningshotad med färre än 500 individer kvar.

Sverige har genom lagar och förordningar förbundit sig att införa åtgärder för att skydda tumlare och deras livsmiljö. Sådana åtgärder står dock ofta i konflikt med mänskliga intressen, såsom fiske, sjöfart och exploatering av grunda havsområden. I den marina förvaltningen är tumlare därför en nyckelart att förhålla sig till. Som toppredator högst upp i näringskedjan fungerar tumlare dessutom som en utmärkt indikator för hur havet mår, eftersom artens förekomst och hälsa speglar förändringar i det ekosystem som den lever i.

För att skydda tumlare och på samma gång minska risken för konflikt med andra intressen krävs kunskap om hur arten interagerar med det lokala ekosystemet. Eftersom tumlare har ett stort energibehov, och kräver nästan kontinuerlig tillgång till fisk att äta, är dess interaktioner med bytesarter särskilt viktig att studera för att bättre förstå tumlares utbredning, beteende och habitatbehov.

Denna avhandling gör en ansats att besvara tre till synes enkla frågor: '*När och var födosöker tumlare?*', '*Vad äter tumlare?*' och '*Hur jagar och fångar tumlare den fisk som de äter?*'. Studierna fokuserar på vilda tumlare tillhörande framförallt Bälthavspopulationen, vilken återfinns längs Sveriges sydvästkust och i inre danska vatten. Datainsamling sker med hjälp av såväl passiv akustisk övervakning, insamling av maginnehåll från upphittade döda tumlare, och visuella observationer från drönarvideo. Forskningen bedrivs med målsättningen att den ska ge förbättrade möjligheter att identifiera konfliktområden mellan tumlare och mänskliga aktiviteter, och på så vis möjliggöra effektivt skydd av tumlare och deras livsmiljö.

Det visar sig, genom akustisk övervakning av tumlares aktivitet inom ett nyckelområde för arten, att förekomsten av tumlare i både tid och rum är starkt knuten till födosöksbeteende. Detta tyder på att förekomst av bytesfisk är en av de starkast drivande krafterna bakom tumlares fördelningsbeteende, och att födotillgång kan förklara observerade stora skillnader i tumlaraktivitet mellan platser som ligger med bara några hundra meters avstånd från varandra. Våra studier demonstrerar även hur starkt knutna tumlare är till sina födosöksområden, vilket innebär att tumlarnärvaro i sig själv kan användas för att identifiera områden som är betydelsefulla för arten och därmed viktiga att skydda.

Våra studier av maginnehåll, från döda strandade och bifångade tumlare som påträffats i svenska vatten, bekräftar att tumlare äter från en varierad meny av fisk innehållande såväl bottenlevande som pelagiska arter. Tre familjer av bytesfisk dominerar dock dieten: torskfiskar (Gadidae), sillfiskar (Clupeidae) och smörbultar (Gobiidae). I stort skiljer sig inte den nuvarande dieten avsevärt från vad tumlare ätit för 15-40 år sedan i samma område. Det finns dock vissa tecken på att det skett en förändring i artsammansättningen, vilken skulle kunna spegla en potentiellt förändrad bytestillgång.

Visuella observationer av tumlare som födosöker i grunda danska vatten avslöjar för oss att arten är en flexibel jägare som jagar såväl individuell fisk som fisk i stim, och som ibland jagar ensam men även i grupper av varierande storlek. Tumlare verkar därutöver vara kapabla till sofistikerat samarbete. Detta visar sig genom att individer i en grupp vid gemensam jakt på stim av fisk fördelar arbetet mellan sig och genomför olika uppgifter. Några av de observerade födosöksstrategierna tyder på att information sprids mellan tumlarindivider genom social inlärning, vilket öppnar upp för potentiell förekomst av kultur hos tumlare.

Sammantaget bidrar forskningen i denna avhandling med flertalet viktiga nya insikter gällande tumlarens ekologi och beteende, vilka ger förbättrade möjligheter till effektiva bevarandeåtgärder för tumlare i alla hav där de förekommer.

List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals:

I. **Stedt, J.**, Wahlberg, M., Carlström, J., Nilsson, P. A., Amundin, M., Oskolkov, N. & Carlsson, P. (2023) Micro-scale spatial preference and temporal cyclicity linked to foraging in harbour porpoises. Marine Ecology Progress Series 708:143-161. https://doi.org/10.3354/meps14268

II. **Stedt, J.**, Brokmar, L., Neimanis, A., Englund, W. F., Carlsson, P. & Roos, A. Combining DNA metabarcoding with macroscopic analysis increase the number of detected prey taxa in the estimated diet for a marine top predator. *Submitted to Frontiers in Marine Science.*

III. **Stedt, J.**, Hamel, H., Ortiz, S. T., Højer, J. K. & Wahlberg, M. Harbour porpoises are flexible predators displaying context dependent foraging behaviours. *In revision in Ecology and Evolution.*

IV. Ortiz, S. T., **Stedt, J.**, Midtiby, H. S., Egemose, H. D. & Wahlberg, M. (2021). Group hunting in harbour porpoises (*Phocoena phocoena*). Canadian Journal of Zoology, 99(6), 511-520. https://doi.org/10.1139/cjz-2020-0289

Author's contribution to the papers

Paper I

JS conceptualised and designed the study with input from MW and PC. JS conducted field work. JS extracted, curated and analysed the data with support from PC, MW, JC, NO and PAN. JS wrote the manuscript. All authors contributed to revision of manuscript drafts and approved the final version.

Paper II

JS, LB, AN and AR conceptualised and designed the study with input from PC. AN, AR, JS and LB collected samples during post-mortem examinations. LB performed macroscopic analysis with support from AR. WFE performed DNA analysis. JS curated and analysed all collected data with support from LB and WFE. JS wrote the manuscript. All authors contributed with comments on manuscript drafts and approved the final version.

Paper III

JS conceptualised and designed the study with input from MW. STO, HH and JHK performed field work. JS extracted, curated and analysed the data. JS wrote the manuscript. All authors contributed with comments on manuscript drafts and approved the final version.

Paper IV

STO, JS and MW conceptualised and designed the study from an original idea by JS. STO performed field work. STO and JS extracted and analysed the data. HSM and HDE developed the software and supported data analysis. STO and JS wrote the manuscript. All authors contributed to revision of manuscript drafts and approved the final version.

Authors:

Johanna Stedt (JS), Per Carlsson (PC), Magnus Wahlberg (MW), Julia Carlström (JC), P. Anders Nilsson (PAN), Mats Amundin (MA), Nikolay Oskolkov (NO), Linnea Brokmar (LB), Anna Roos (AR), William F. Englund (WFE), Aleksija Neimanis (AN), Sara Torres Ortiz (STO), Héloïse Hamel (HH), Jakob Højer Kristensen (JHK), Henrik Skov Midtiby (HSM) and Henrik Dyrberg Egemose (HDE).

All authors in the list of papers have given their consent for the use of their work in the thesis.

Abbreviations

CFP	Common Fisheries Policy
CMS	Convention on the Conservation of Migratory Species
CR	Critically Endangered
DNA	Deoxyribo-Nucleic-Acid
DPM	Detection Positive Minute
EU	European Union
FPP	Foraging-to-Presence Percentage
HP	Harbour Porpoise
ICI	Inter-Click Interval
IUCN	International Union for Conservation of Nature
MSFD	Marine Strategy Framework Directive
PAM	Passive Acoustic Monitoring
SAC	Special Area of Conservation
sDNA	stomach DNA
SIA	Stable Isotope Analysis
UAS	Unmanned Aerial System
VU	Vulnerable

Aim of thesis

The aim of this thesis is to further our knowledge of how harbour porpoise (*Phocoena phocoena*) distribution and behaviour can be affected by their direct and indirect interactions with prey. Like most aquatic mammals, wild harbour porpoises are difficult to study and many aspects of their basic biology and ecology remain unknown. As top predators in the marine environment they hold an important role as an indicator species for early warning signs of ecosystem changes. At the same time, harbour porpoises are globally threatened by anthropogenic activities and in need of effective conservation measures. Successful protection of harbour porpoises requires understanding how the species interacts with the ecosystem it inhabits, perhaps most importantly, how the presence and behaviour of prey species govern porpoise distribution and foraging.

To advance the research field within the area described above, the papers in this thesis address the following research questions:

I. *When and where do porpoises forage and eat?*

In **Paper I**, I investigate how the presence of harbour porpoises in time and space relates to prey occurrence by exploring if regularly observed spatiotemporal patterns in their acoustic activity can be linked to foraging.

II. *What do porpoises eat?*

In **Paper II**, I compare two methods for dietary analysis to examine the current diet of harbour porpoises in Swedish waters using stranded and bycaught individuals.

III. *How do porpoises catch the fish that they eat?*

In **Paper III**, I use visual data collected by Unmanned Aerial Systems (UAS) to describe harbour porpoise foraging techniques for a range of prey types, group constellations, and water depths. In **Paper IV**, I explore one of the techniques further by detailed analysis of foraging events where several porpoises simultaneously predate on the same school of fish.

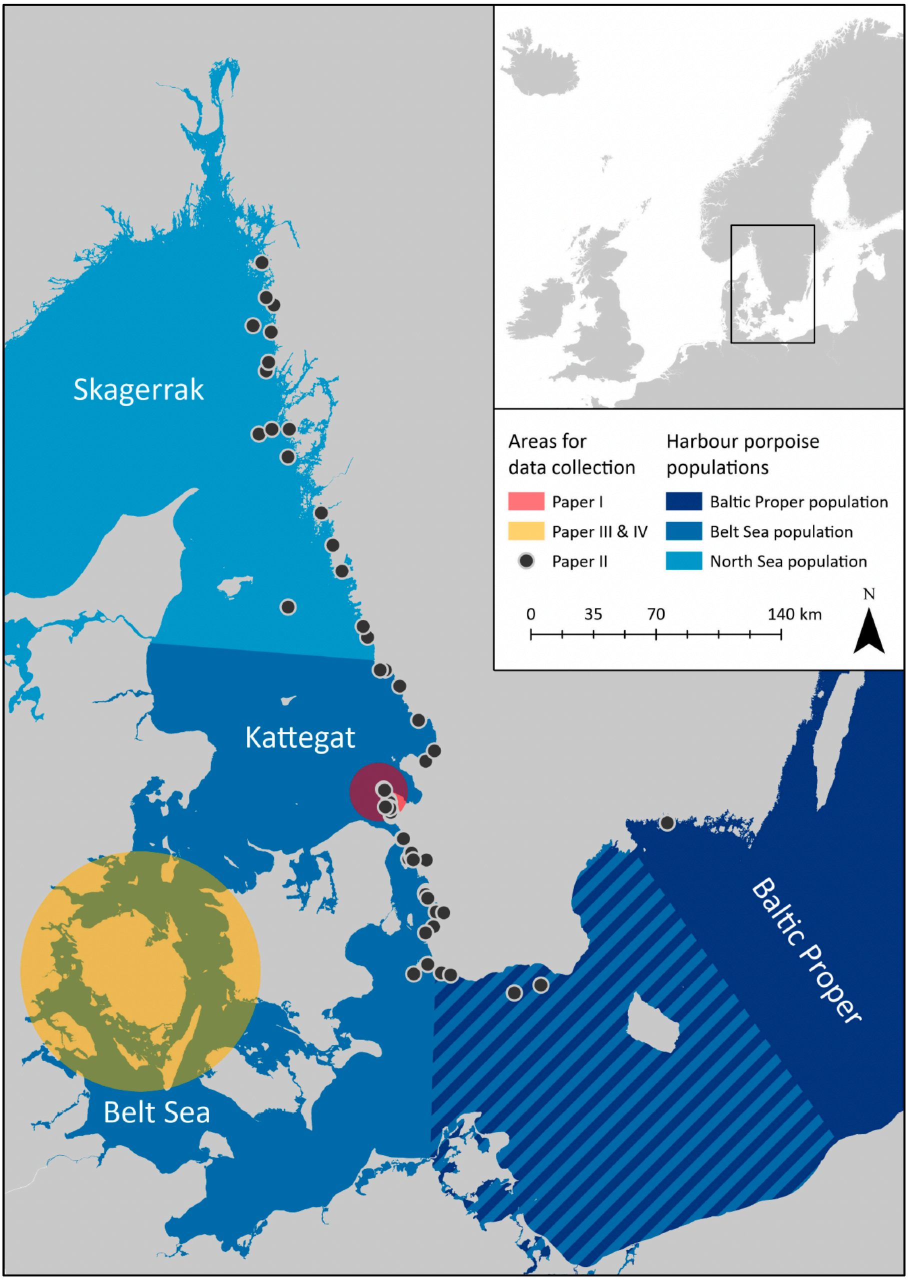

Figure 1. Summer management areas of harbour porpoise populations in the Baltic region overlayed with areas of data collection for **Paper I, III** and **IV**. Black round symbols represent encounter locations for deceased harbour porpoises used for data collection in **Paper II**. Dashed area between the Belt Sea population and the Baltic proper population represent overlap area between populations, in which individuals from both populations are found during May-October (Carlén et al., 2018; Sveegaard et al., 2015). No management areas have been defined for the remaining part of the year. Management area layers created and provided by I Carlén.

Setting the scene

Globally, biodiversity is declining at an alarming rate due to human activities, with negative impacts on ecosystems and their functionality (IPBES, 2019). At present almost five hundred marine species in Sweden are considered threatened (SLU Artdatabanken, 2020). One of these is the harbour porpoise (*Phocoena phocoena*), which is the only cetacean species resident in Swedish marine waters and a top predator with high ecological importance (Machovsky-Capuska & Raubenheimer, 2020). By moving across ocean basins and amplifying trophic information across spatiotemporal scales (Hazen et al., 2019), porpoises and other cetaceans can provide insights into marine ecological processes. These wide-ranging predators act as indicators of the state of the marine ecosystem, as their individual- and population-level status reflect local prey communities and available habitat quality, and signal changes in its structure and function which are otherwise difficult to directly observe (Hazen et al., 2019).

Worldwide, cetacean populations are under high pressure from human ocean-based activities (Plon et al., 2024; Sanganyado & Liu, 2022). Managing conflicts with human interests requires knowledge of which areas the animals use and when and why they are there. Central for successful protection of any animal species is to understand the factors shaping its distribution and behaviour (Lascelles et al., 2014; Lindenmayer, 2000). For harbour porpoises, knowledge of their diet and foraging behaviour is fundamental for effective implementation of conservation measures, as prey availability and quality have large impacts on their overall distribution and health (Spitz et al., 2018).

This thesis explores interactions between porpoises and their prey by investigation of spatiotemporal patterns in porpoise presence and foraging, dietary studies, and detailed descriptions of harbour porpoise foraging strategies. By doing so, it aspires to provide information which can ultimately be used to identify conflict areas between human activities and harbour porpoises, in turn enabling effective conservation measures. The studies are geographically located in Swedish and Danish coastal waters with focus on the Belt Sea population of harbour porpoises – one of three harbour porpoise populations in Sweden (Figure 1).

An introduction to the harbour porpoise

Biology

Small whale in cold water

The harbour porpoise (*Phocoena phocoena*) (Figure 2) is one of the smallest and most widely distributed toothed whales (Read, 1999), with a mainly coastal distribution in the temperate and subarctic waters of the northern hemisphere (Carwardine, 2020). It has a robust body shape, with a low, triangular dorsal fin and short rounded flippers. The head is rounded and with no distinct beak. The body colour is dark grey on the back and completely white on the belly, with pigmentation on the sides transitioning from dark to light through flecking and streaking in varying shades of grey (Carwardine, 2020). Adult harbour porpoises are approximately 1.5-1.7 m long and weigh 45-70 kg, with females being larger than similar-aged males (Cervin et al., 2020; Murphy et al., 2020).

Harbour porpoises swim at an average velocity of 0.6-2.3 km/h, but are capable of sustaining a speed of ~7km/h over longer periods of time (Kastelein et al., 2018). This allow them to travel over large distances, sometimes up to 60 km per day (Read & Westgate, 1997; Sveegaard, 2011). In the deep waters around West Greenland individual porpoises have demonstrated the capacity to perform dives down to 410 m (Nielsen et al., 2018) but in the Kattegat and Belt seas, where the water depth generally is less than 50 m, most dives are shallower than 25 m (Rojano-Donate et al., 2024; Teilmann et al., 2007). Maximum recorded dive depths typically reflect the local water depth (Nielsen et al., 2018; Otani et al., 1998; Teilmann et al., 2007; Westgate et al., 1995), suggesting that porpoises frequently explore the seabed. The dive frequency is high, with 30-40 dives per hour (Teilmann et al., 2007; Westgate et al., 1995) and a mean dive duration close to 1 min (Rojano-Donate et al., 2024). However, longer dives of 5-6 min (Teilmann, 2000; Westgate et al., 1995) or possibly over 10 min (Teilmann et al., 2007) have been reported.

Short and hectic life

The maximum life expectancy of a harbour porpoise is ~20 years, but the average lifespan is between 8 and 10 years (Carwardine, 2020) with <5% surviving to an age beyond 12 years (Lockyer, 2003). Sexual maturity is reached at the age of 3-4 years (Carwardine, 2020; Lockyer & Kinze, 2003; Murphy et al., 2020). The main reproductive season, with mating and calving, occurs between May and August (Camphuysen & Siemensma, 2015; Learmonth et al., 2014; Lockyer & Kinze, 2003) during which especially female harbour porpoises are believed to express site fidelity and return to their own area of birth for parturition and mating (Huggenberger et al., 2002; Tiedemann et al., 1996). The mating system is promiscuous, with sperm competition hypothesized to be the primary way males compete to fertilize the female egg (Keener et al., 2018). After a gestation period of 10-11 months the female gives birth to a single calf, which is then nursed for 8-12 months (Börjesson & Read, 2003; Camphuysen & Siemensma, 2015).

Figure 2. A wild harbour porpoise (*Phocoena phocoena*) on the west coast of Sweden.

Echolocate using clicks

Like other toothed whales, harbour porpoises navigate, forage, and communicate using biosonar (Figure 3) (Clausen et al., 2011; Sørensen et al., 2018; Verfuß et al., 2005; Villadsgaard et al., 2007). The echolocation clicks produced by harbour porpoises consist of narrowband, high frequency signals with the main energy between 120 and

140 kHz (Au et al., 1999; Koschinski et al., 2008). The sounds are produced by forcing pressurized air through the so-called phonic lips in the nasal passages (Madsen et al., 2023) and propagated through a fatty structure called the melon where the directionality of the narrow beam can be adjusted (Koblitz et al., 2012). Returning echoes from objects in the water are picked up by the lower jaw and transmitted to the inner ears (Cranford et al., 1996; Ketten, 2000) where they evoke nerve impulses that transmit to the auditory cortex (Wahlberg et al., 2015).

Harbour porpoise clicks have a duration of approximately 50-100 µs (Villadsgaard et al., 2007) and are emitted singularly or in series called click trains (Carlström, 2005). The interval between consecutive clicks is adjustable and while searching for prey or navigating the inter-click interval (ICI) normally varies between 30-100 ms. When the porpoise approaches prey the interval becomes progressively shorter and finally ends in a terminal 'buzz' (often referred to as a 'feeding buzz'), with ICIs less than 10 ms and sometimes down to about 2 ms, when the prey is only a few meters away (Koschinski et al., 2008; Miller & Wahlberg, 2013; Verfuß et al., 2009; Wisniewska et al., 2012). The variation in ICIs thus allows analysis of foraging behaviour in studies using harbour porpoise acoustic activity data (e.g. Todd et al., 2009; Zein et al., 2019).

Although diel variation in echolocation activity exists, harbour porpoises have been documented to echolocate almost continuously both day and night (Linnenschmidt et al., 2013). Infrequent silent periods do however occur and are thought to represent shorter periods of unihemispheric sleep (resting with one half of the brain while the other half remains alert) (Wright et al., 2017).

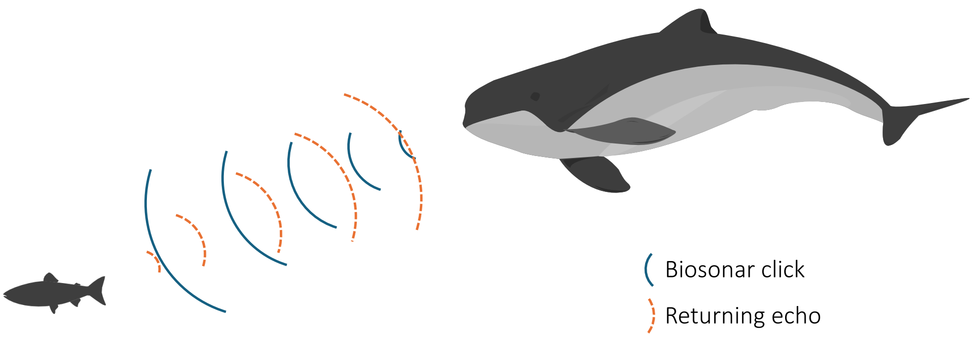

Figure 3. Schematic illustration of a porpoise echolocating at a fish.

A fish diet to cover high energy demands

Since harbour porpoises are small marine mammals that live in the cold waters of the northern hemisphere, they have a very high metabolic rate and an almost constant need to feed (Rojano-Doñate et al., 2018; Wisniewska et al., 2016). To meet their high energetic demand, porpoises need to catch and eat 2-6 kg of fish every day, which corresponds to 4-9.5% of their body weight depending on body size and reproductive state (Gallagher et al., 2018; Kastelein et al., 1997; Lockyer et al., 2003; Rojano-Doñate et al., 2018). This requires harbour porpoises to spend the majority of time foraging. Wild harbour porpoises carrying high-resolution tags in Danish waters have been observed to search and hunt for prey nearly continuously day and night, targeting several hundred small fish or shrimp every hour with an estimated capture success rate of >90% (Rojano-Donate et al., 2024; Wisniewska et al., 2016).

Studies utilizing stranded and bycaught porpoises have shown that porpoises in the Northeast Atlantic feed on small benthic and pelagic fish and that the diet is often dominated by a few species (Santos & Pierce, 2003). Sprat (*Sprattus sprattus*), herring (*Clupea harengus*) and cod (*Gadus morhua*) represented main prey for most porpoises in Swedish and inner Danish waters in 1980-2011, although dietary differences between geographical areas, seasons, age classes and sexes are known to exist (Aarefjord et al., 1995; Andreasen et al., 2017; Angerbjörn et al., 2007; Börjesson et al., 2003). Atlantic hagfish (*Myxine glutinosa*) have for example been found to contribute considerably to adult diet (Börjesson et al., 2003), while gobiids have been more important for juveniles (Andreasen et al., 2017). The more recently described ultra-high foraging rates of tagged porpoises (Wisniewska et al., 2016) do however suggest that porpoises might target smaller prey than before. Also, drastic regime shifts of fish populations in Swedish and Danish waters (Blocker et al., 2023; 2009; Casini et al., 2008; Svedang, 2003) during the last decades provide additional support for potential shifts in top predator diet.

Ecology and behaviour

Distribution and habitat use linked to prey availability

Based on the current knowledge, three morphologically and genetically distinct porpoise populations (Celemin et al., 2023; Galatius et al., 2012; Wiemann et al., 2009) exist in the Baltic region (Figure 1); the North Sea population which extends into the Skagerrak and northern Kattegat, the Belt Sea population which distributes from Kattegat through Öresund and inner Danish waters to the southwestern Baltic Sea, and the Baltic Proper population with a main distribution within the Baltic Proper.

Population-level distribution of porpoises has been found to be strongly linked to the distribution and abundance of main prey species (Lawrence et al., 2016; Sveegaard, 2011). On an individual level, porpoises exhibit large-scale movement patterns over hundreds to thousands of kilometres, thought to represent seasonal migration between foraging and reproductive areas (Johnston et al., 2005; Nielsen et al., 2018; Sveegaard et al., 2011; Verfuß et al., 2007). In addition, more fine-scale distribution patterns have been identified in numerous studies. These have found spatial variations over a few to tens of kilometres (Booth et al., 2013; Brandt et al., 2014; Williamson et al., 2022) thought to reflect a corresponding fine-scale spatial distribution of suitable prey, and temporal differences in activity linked to the diel (Benjamins et al., 2017; Schaffeld et al., 2016; Wisniewska et al., 2016) and lunar cycle (Brennecke et al., 2021).

However, harbour porpoises tagged with satellite positioning transmitters show large individual differences in their movements (Read & Westgate, 1997; Sveegaard et al., 2011; Teilmann et al., 2022). The only conclusion that can be drawn with confidence regarding the species' spatial distribution is that, although individual home-ranges of porpoises can be quite large, they seem to periodically remain and focus their activities in smaller restricted areas (Hamel et al., in press; Johnston et al., 2005; Nielsen et al., 2018; Teilmann et al., 2022).

Non-social with a fluid group structure

Harbour porpoises are typically considered to be non-social, with a loose, fluid group structure of one to ten individuals (Teilmann & Sveegaard, 2019) and a mean group size close to two (Berrow et al., 2014; Keener et al., 2018). Intraspecific social encounters have been reported (Sørensen et al., 2018) and might be more common than previously thought. The stability of such encounters and patterns over time are unknown and the only social bound known to be stable over several months is that between a mother and her calf (Camphuysen & Krop, 2011; Hamel et al., in press; Teilmann et al., 2007) (Figure 4). However, large aggregations of porpoises, sometimes as many as several hundred individuals, are occasionally observed during favourable feeding conditions at foraging hotspots (Teilmann & Sveegaard, 2019).

Figure 4. A harbour porpoise mother swimming with her calf in inner Danish waters.

The fact that porpoises exclusively communicate using ultrasonic clicks (Clausen et al., 2011; Sørensen et al., 2018; Wahlberg et al., 2015) has been hypothesised to be linked to their seemingly rather solitary lifestyle. While in contrast most dolphins, which are presumably more social, communicate using a more complex communication system comprised of click-based calls and tonal whistles (Janik & Sayigh, 2013).

Threats and conservation

Vulnerable to human impact

Harbour porpoises are threatened by anthropogenic impacts in all areas where the species occurs (Wisniewska et al., 2016). The main threat to harbour porpoises is bycatch in fisheries, especially in static nets (Brownell Jr et al., 2019). For the Belt Sea population the most recent total bycatch estimate is ~900 animals per year (Kindt-Larsen et al., 2023) which, given a population of approximately 14 400 individuals (Gilles et al., 2023), corresponds to a bycatch rate of ~6%. The mortality limit for the same population, indicating the number of animals per year that can be sustainably removed from the population, has however been estimated to 24 individuals (Owen et al., 2024b). This clearly demonstrates that the current bycatch rate is far too high to allow the Belt Sea population, and most other harbour porpoise populations in areas where bycatch commonly occur, to attain a good environmental status.

Bycatch apart, one of the predominant causes of mortality in harbour porpoises is starvation and related health effects (MacLeod et al., 2007; Neimane et al., 2020). Given their energetic need and dependence on continuous access to prey, harbour porpoises are highly sensitive to decreased prey quality and quantity (Gallagher et al., 2021; Koschinski et al., 2024). Studies of Baltic grey seals (*Halichoerus grypus*) are observing shifting diets and smaller prey items (Kauhala et al., 2017) and on the Swedish west coast harbour seal (*Phoca vitulina*) populations display decreasing reproductive output (Infantes et al., 2022), which are signs of food limitation. Investigations if porpoises are under similar pressure are lacking but highly needed, as they would provide important information for its conservation.

Like other cetaceans, harbour porpoises are negatively impacted by underwater noise from human marine activities, such as construction work (Dähne et al., 2013), shipping (Dyndo et al., 2015; Wisniewska et al., 2018), seismic surveys (Hermannsen et al., 2015; Sarnocińska et al., 2020), acoustic deterrence devices on fishing nets (Nowacek et al., 2007), and recreational boat traffic (Hermannsen et al., 2019). Other threats to their conservation include decreased fertility and immune responses due to pollutants (Beineke et al., 2005; 2007; Desforges et al., 2016; Murphy et al., 2015) and habitat loss and degradation (ASCOBANS, 2012; Nachtsheim et al., 2021).

In need of protection

As a result of the above-mentioned conflicts with humans, all three porpoise populations occurring in Swedish waters are threatened and in need of protection (Amundin et al., 2022; Carlén et al., 2021; Owen et al., 2024b). The population in the Baltic Proper is listed as critically endangered (CR) in the IUCN Red List (Carlström et al., 2023), with only about 500 individuals left (Amundin et al., 2022). None of the two populations of porpoises on the Swedish west coast meet their conservation objectives with regard to bycatch (Taylor et al., 2022). The Belt Sea population is in decline (Owen et al., 2024b) and listed as Vulnerable (VU) in the HELCOM Red List (HELCOM, 2013).

The harbour porpoise gained protection in Sweden already in 1973 and is still under a range of national and international laws. By inclusion in Annex II of the European Union (EU) Habitats Directive (Council Directive 92/43/EEG) harbour porpoises are under strict protection and Member States are obliged to designate Special Areas of Conservation (SACs) for the species. The Baltic Proper population of harbour porpoises was recently listed in Appendix I of the Convention on the Conservation of Migratory Species (CMS) (CMS, 2024), which contains migratory species that are endangered throughout all or a significant portion of their range. All three populations found in Swedish waters are included in Appendix II of the CMS, which also has a special agreement focused on cetaceans (ASCOBANS, the Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas) which include population-specific conservation and recovery plans (ASCOBANS, 2002,2009,2012). Other examples of European legislation relevant for porpoise conservation are the EU Common Fisheries Policy (CFP) (regulation 1380/2013) and the Marine Strategy Framework Directive (MSFD) (directive 2008/56/EC).

In Sweden, active protection of harbour porpoises and their habitat is also required through national action plans (HaV, 2021) and directly relevant with regard to environmental quality objectives (Naturvårdsverket, 2024). In coastal and shallow areas the porpoise is a key species for managers to handle, as the habitat is not only important for porpoises but also for human activities such as fishing and development of renewable energy production. However, to date the information available to aid assigned managing bodies in their work to protect the harbour porpoise and its habitat is deficient. Identified major gaps include knowledge of harbour porpoise key habitats and ecological needs (ASCOBANS, 2012; HaV, 2021), diet and distribution patterns (HELCOM, 2020; OSPAR, 2013), behaviour (HELCOM, 2020), and impacts from anthropogenic activities (HaV, 2021; HELCOM, 2020; OSPAR, 2013). Scientific research focusing on these areas is required to support an ecosystem-based management in which both porpoise conservation and other marine interests are taken into account.

When and where do porpoises forage and eat?

Spatiotemporal distribution patterns

Most resources are unevenly available in space and time

The necessary resources for any consumer are typically heterogeneously distributed in space and time, and affected by changes in environmental conditions (van Langevelde & Prins, 2008). A consumer's ability to adjust its spatiotemporal distribution and behaviour, on a varying range of scales, provides energetic benefits since it allows maximum utilization of available resources (Stevick et al., 2002). Most species are therefore not uniformly dispersed within their range of distribution, but instead migrate between important areas used for foraging, reproduction, or predator avoidance (see for example Bollens & Frost, 1989; Boyd, 2004; Cox, 1985; James et al., 2005).

As the search for food by animals is unavoidably uneven in space and time (van Langevelde & Prins, 2008) foragers often aggregate within certain restricted geographical regions, referred to as 'hotspots' (Davoren, 2013; Myers, 1988). The functional mechanisms causing animals to aggregate at foraging hotspots are likely to be based on individual foraging decisions made in response to environmental cues (Russell et al., 1992; Stephens & Krebs, 1986). Important environmental cues are found at both large and fine scales and include static and dynamic biological and physical variables. For marine animals environmental cues can be oceanographic features and hydrodynamics, such as reefs, headlands, wakes and regions with high relative current velocity (Jones et al., 2014; Swartzman, 1994; Thompson et al., 2012), seasonal availability of prey (Sveegaard et al., 2012; Womble & Sigler, 2006), or chemical gradients (Owen et al., 2021) making regions with beneficial foraging opportunities predictable to predators.

To understand the distribution pattern, density, and behaviour of a predator species thus requires knowledge on how it interacts with its environment, including prey, at a range of spatiotemporal scales (Embling et al., 2012; Fauchald & Erikstad, 2002). For species in need of protection, like the harbour porpoise, this is especially important as it allows development of efficient conservation actions, such as optimal zonation of human activities within designated protected areas.

Eavesdropping on cetacean vocalizations

Using passive acoustic monitoring to study distribution and behaviour

Harbour porpoises are notoriously difficult to study in the field due to their small size, anonymous appearance and fast movements (Amundin & Amundin, 1974; Elliser et al., 2022). However, the past decades' technical development has revolutionized the way scientific data is collected within marine mammal research. Traditional visual data collection by surface observations, which are extremely time consuming and limited to the time animals spend close to the surface, are now routinely combined with or replaced by new techniques.

During the past twenty years, passive acoustic data recorders and loggers that detect the species-specific sounds produced by cetaceans have been frequently used to study a range of species worldwide, for example to monitor their distribution and behaviour (Ivanchikova et al., 2024; Pearson et al., 2023; Schaffeld et al., 2016; Verfuß et al., 2007), estimate the abundance of critically endangered populations (Amundin et al., 2022; Jaramillo-Legorreta et al., 2019), and describe effects from weather events (Fandel et al., 2020) and human ocean-based activities (Dähne et al., 2013; Owen et al., 2024a; Sarnocińska et al., 2020). These autonomous battery-powered passive acoustic monitoring devices work in depths down to several hundred meters and are typically placed close to the seabed using an anchor, where they can be deployed for several weeks or months while continuously collecting data.

Paper I – Micro-scale distribution patterns linked to foraging

Exploring high-resolution presence and foraging in a key area for porpoises

In **Paper I** we took advantage of that harbour porpoises almost continuously emit echolocation clicks (Verfuß et al. 2005, Villadsgaard et al. 2007, Clausen et al. 2011, Amundin et al. 2022) and used passive acoustic monitoring (PAM) data to investigate spatiotemporal patterns in harbour porpoise presence and foraging. We did this on a spatial micro-scale within a known high-density area for harbour porpoises (**Paper I** area in Figure 1), with monitored sites separated only by a few hundreds of meters up to a few kilometres (Figure 1b in **Paper I**), as well as on a detailed temporal scale, ranging from diel phases to seasons, which provided us with very high-resolution spatiotemporal distribution data.

Using the feeding buzz as a proxy for foraging, we examined the connection between harbour porpoise presence and foraging to explore the hypothesis that prey occurrence is driving not only large-scale porpoise distribution (Sveegaard, 2011) but also micro-scale porpoise presence. We analysed the data by application of dynamic time warping and spectral methodology, which are widely used in time series data analysis, but represent a novel approach for passive acoustic monitoring studies.

Striking spatial differences and highest activity during midnight at full moon

Our study demonstrated that the acoustic activity of harbour porpoises, measured as both presence and foraging, can vary considerably and consistently over a fine spatial scale (hundreds of meters to a few kilometres) (Figure 5 and 6). In addition, we demonstrated presence of diel cyclicity in both activity measures with highest activity during midnight (Figure 5), and cyclic patterns corresponding to the lunar cycle with increased porpoise presence and foraging during full moon (Figure 5 in **Paper I**).

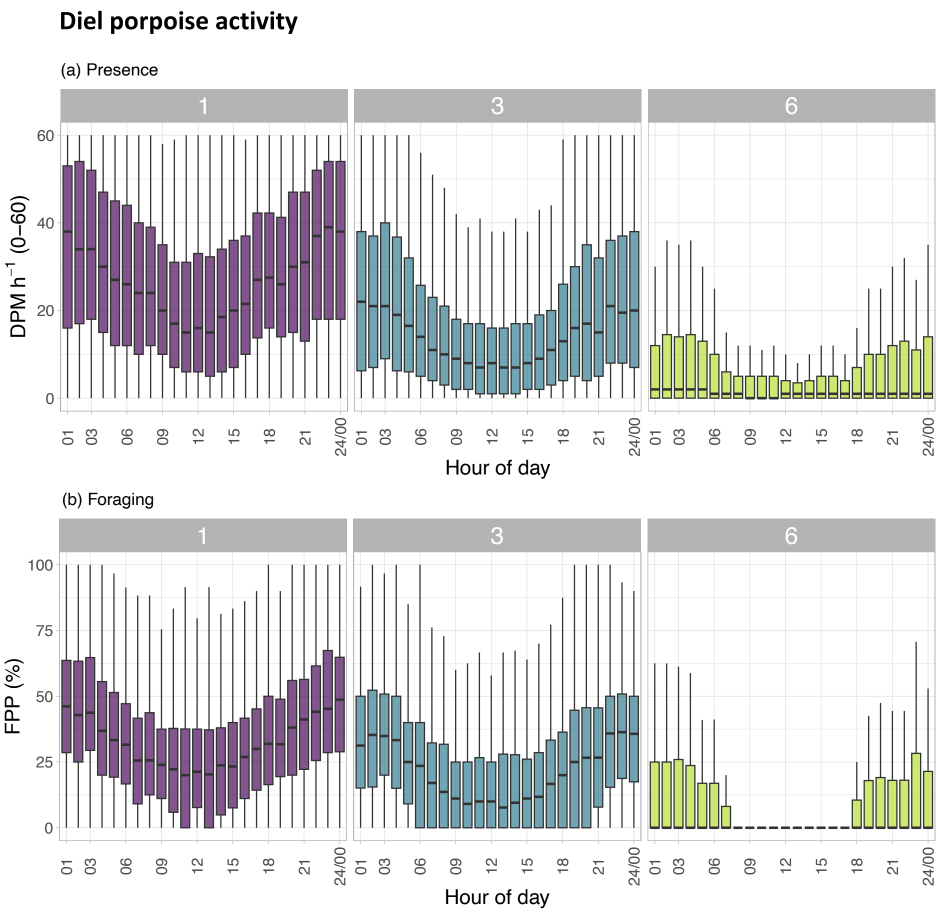

Figure 5. Harbour porpoise activity for each hour of the day: (a) presence (detection positive minutes, DPM h^{-1}, 0–60) and (b) foraging (foraging-to-presence percentage, FPP, %), for three of the survey sites (1, 3 and 6). Lower and upper box boundaries: 25th and 75th percentiles; lower and upper error lines: 10th and 90th percentiles. Black line inside each box: median value. Note that scales on the y-axes are different. Figure modified from **Paper I**.

The diel pattern has been observed previously and then proposed to be linked to increased foraging during nighttime, probably reflecting a higher numerical or behavioural availability of prey (Brandt et al., 2014; Schaffeld et al., 2016; Todd et al., 2009). To the best of our knowledge, **Paper I** was however the first study to report lunar cycle effects on harbour porpoise foraging behaviour in an area without any notable tidal forcing. This suggest that, apart from the indirect effects of the lunar cycle through tidal changes, harbour porpoises can be affected by the lunar cycle in other ways, such as through direct and indirect effects of varying light availability, possibly influencing predator-prey interactions and foraging efficiency.

Frequently used areas represent important foraging habitats

Perhaps most interestingly, at least from a conservation point of view, our results showed that the more frequently an area was used the higher degree of foraging occurred (Figure 6).

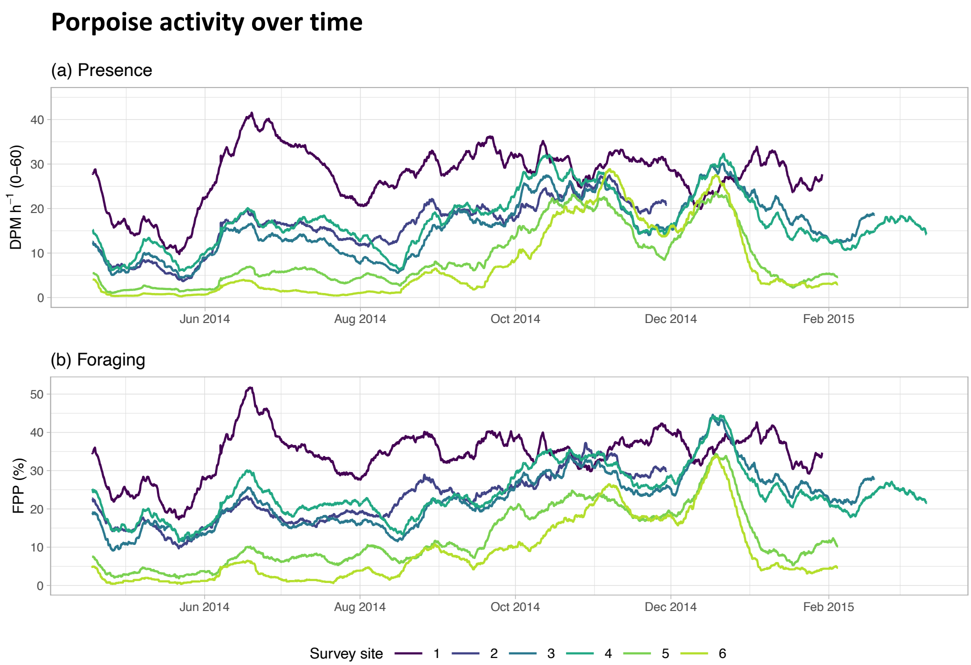

Figure 6. Porpoise activity over time: (a) presence (detection positive minutes, DPM h–1, 0–60) and (b) foraging (foraging-to-presence percentage, FPP, %), and all survey sites (1–6). Note that scales on the y-axes are different. Figure modified from **Paper I**.

As our foraging metric was calculated as a proportion of presence, the positive correlation between the two activity measures showed that harbour porpoises spent more time in areas with good foraging opportunities and used a higher proportion of the time foraging when being there. Conversely, in areas where porpoises were detected to a lesser extent of the time, they also spent a smaller proportion of the time present foraging. Put simply, porpoises present in high density areas were more likely to be engaged in foraging when compared to porpoises present in low density areas.

Our results thus strongly suggest that, similar to observed large-scale distribution patterns, the main driving force for porpoise presence, also on a micro-scale, is prey occurrence. This is important information for national managing bodies when designing protected areas and actions within. It also suggests that porpoise presence in itself is a good indicator of areas of energy intake, which in turn represent important habitats to protect. In addition, our study highlights the need to consider potential presence of micro-scale differences in species presence in the design of cetacean studies utilizing PAM, as the exact placement of a PAM device might heavily influence conclusions when single positions are used to infer general activity.

Exploring the connection between porpoises and fish

Environmental drivers of porpoise activity

In **Paper I** we argue that the observed differences in porpoise activity are likely to be linked to micro-scale variations in environmental variables, such as bottom substrate, current velocity, and light regime, causing prey availability to vary accordingly. However, neither prey availability nor potential environmental drivers of porpoise spatial distribution were included as collected data in **Paper I**.

To investigate direct links between habitat dynamics, prey occurrence and spatiotemporal distribution of harbour porpoises, simultaneous detailed monitoring of porpoises and important prey species over a range of environmental variables is required. Some studies have identified that areas and times of tidal flow or increased relative current velocity result in increased harbour porpoise activity (Ijsseldijk et al., 2015; Jones et al., 2014; Marubini et al., 2009). However, as harbour porpoises occupy a highly heterogenous and complex habitat in which they can easily travel over large distances, identification of factors that can be used to spatiotemporally predict harbour porpoise presence and foraging would provide important knowledge regarding their habitat needs and preferences. In addition, it would allow identification of important areas for the species and aid optimization of conservation actions.

Fine-scale temporal links: from zooplankton to fish and porpoises

Environmental drivers apart, a detailed understanding of the movements and distribution of harbour porpoises also requires an understanding of the underlying mechanisms that primarily drives their behaviour. As previously discussed, the fine-scale differences in porpoise activity discovered in **Paper I** are likely to be linked to variations in prey availability. This is based on the fact that neither the fish that the porpoise prey upon, nor the prey of the fish, e.g. zooplankton for Clupeids, are stationary available for predation. Instead they regularly move in space and time over both large and small scales, for example during the seasonal migration of fish or vertical migration of planktivorous fish and zooplankton (Brönmark et al., 2014; Romare & Hansson, 2003). For species that occupy different trophic levels in the same habitat this can result in an offset in behavioural reactions, so that the behaviour of one species stimulates a reaction in another species and so on (Bollens et al., 2011; Romare & Hansson, 2003). Consequently, the small-scale spatiotemporal distribution patterns observed in **Paper I** needs to be studied in connection with neighbouring trophic levels in the marine food web to explore interactions between predators and prey as driving forces behind porpoise movements and activity.

Parallel to this thesis work, we attempted to study the fine-scale temporal correlations between harbour porpoises, fish and zooplankton to investigate if the diel movement patterns of these three trophic levels are linked (Figure 7). We hypothesized that the temporal movements and behaviour of harbour porpoises might be governed, at least in part, by migration patterns of prey species of planktivorous fish, which in turn follow the diel vertical migration of zooplankton. Data for analysis of fine-scale temporal links between porpoises and lower trophic levels in the ecosystem, e.g. fish and zooplankton, were collected in the same area as in **Paper I** (**Paper I** area in Figure 1) during a high-intensity field sampling period in July to September 2019.

During this period, detailed (minute resolution) time series data on harbour porpoise presence and foraging activity was collected by passive acoustic data loggers (C-PODs, Chelonia Ltd.) at two positions approximately 1 km apart. In addition, data on fish relative abundance and zooplankton vertical distribution were sampled 16 times at both survey sites during the same time period; eight times during midday and eight times during midnight. At both sites, data on fish were collected along transects with echosounder (GPSMAP 1222xsc, Garmin) and by recording the echosounder output for later analysis. Zooplankton vertical migration data were collected by net sampling, using a closable net with 200 µm mesh size (WP-2 Zooplankton net, KC Denmark A/S) at three different depths (bottom, halocline and surface). Data on temperature, salinity, chlorophyll a concentration and oxygen concentration were collected at each sampling event and site using a CTD-probe (CTD 90, Sea and Sun Technology) in order to determine thermoclines, haloclines, and layers of phytoplankton biomass.

The complete dataset remains to be analysed in detail, but preliminary results reveal a significant increase in harbour porpoise activity and a close to significant ($p=0.051$) increase in fish abundance during nighttime compared to daytime, indicating a temporal correlation between harbour porpoises and fish. A corresponding link to zooplankton was however not detected as no diel vertical migration pattern of zooplankton was observed. This might in part be due to the characteristics of the study area, with shallow (30 m) depths and strong pycnoclines, but most likely also reflects the complexity of trophic interactions in heterogenous ecosystems.

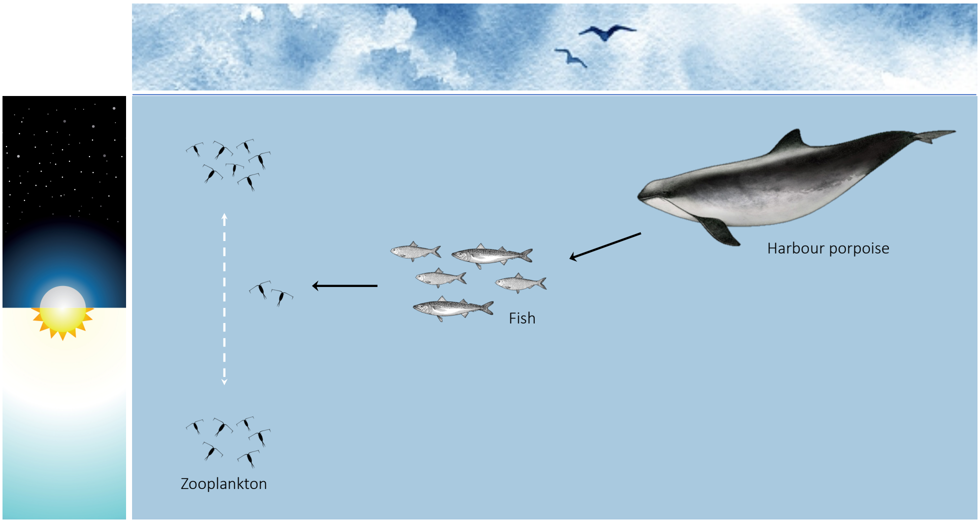

Figure 7. Schematic illustration showing the three trophic levels in the marine food web that were hypothesized to be linked. The harbour porpoise prey upon small fish, which in turn feed on zooplankton. Both zooplankton and fish move in time and space, in both small and large scale, to avoid predation and to feed. Zooplankton migrate vertically in the water column during day and night, while planktivorous fish migrate both vertically and between different habitats in larger scale. To understand the movements of harbour porpoises and their ecological role in the marine ecosystem thus requires knowledge not only regarding the behaviour of harbour porpoises but also an understanding of the predator prey interactions in neighboring trophic levels.

What do porpoises eat?

Diet tracing in ecology

A range of available methods

Knowledge of animal diets is fundamental in ecology, as species interactions and food web dynamics give powerful insight into the structure, function and resilience of entire ecosystems (Nielsen et al., 2017). Understanding what animals feed on also allows understanding of intra- and interspecific niche specialization (Kratina et al., 2012; Xia et al., 2020), and insight into nutritional physiology and energetics (Birnie-Gauvin et al., 2017; Rojano-Donate et al., 2024).

When trying to answer the question '*What does this animal feed on?*' ecologists are offered with a variety of dietary estimation methods. These include, for example, (*i*) traditional visual techniques, such as macroscopic analysis of stomach, intestinal or faecal content, (*ii*) analysis of organic macromolecules, such as fatty acids, stable isotope analysis (SIA) of bulk or specific compounds in animal tissue, and (*iii*) identification of prey remains through DNA metabarcoding. The different methods all come with inherent limitations and benefits and differ in their ability to correctly identify and quantify an animals diet (Nielsen et al., 2017; Traugott et al., 2013). For example, DNA metabarcoding is a time-efficient way to obtain large sample sizes with high taxonomic resolution (Nielsen et al., 2017), while traditional macroscopic analysis is time consuming and labour intensive. For piscivorous predators, macroscopic analysis can however provide information on size, body mass and age of detected prey species through detailed analysis of fish otoliths and inference of species-specific relationships (Nielsen et al., 2017, Hyslop, 2006).

Another important consideration when deciding which method to use for diet analysis is the type of material it requires, as the respective techniques use different material and thus measure the diet at various stages of consumption and degradation (Nielsen et al., 2017). Visual analysis of stomach, intestine or faeces content detects the ingested and digested diet items (Hyslop, 2006; Pierce & Boyle, 1991). A fraction of the ingested material is assimilated and incorporated in the consumer's tissue, where it can be detected by analysis of stable isotopes (Newsome et al., 2010) or fatty acids (Iverson, 2009), while ingested material which is not assimilated by the consumer is respired or excreted.

Dietary analysis provides estimates of the true diet

The aim of most diet studies is to provide a diet estimation which reflects the true diet of the consumer, which represent a fraction of the potential diet available in the ecosystem. The estimated diet is the diet identified by the specific method used for diet analysis, but might be erroneous due to a mismatch between estimated and true diet, for example by missed detection of true dietary items or detection of false dietary items (Figure 8) (Nielsen et al., 2017). The selected dietary analysis method should thus maximise the overlap between true and estimated diet. Further, as the diet is a mixture of consumed items, the method selected for analysis should be able to correctly separate and identify these (Figure 8b). Most methods also provide information on proportional contribution to estimated diet by individual diet items (Figure 8c). This allows calculation of metrics on relative contribution by specific taxa to individual- or population-level diet (Hyslop, 2006), e.g. numeric occurrence, weight, and energy content, reflecting dietary importance from different ecologically relevant perspectives.

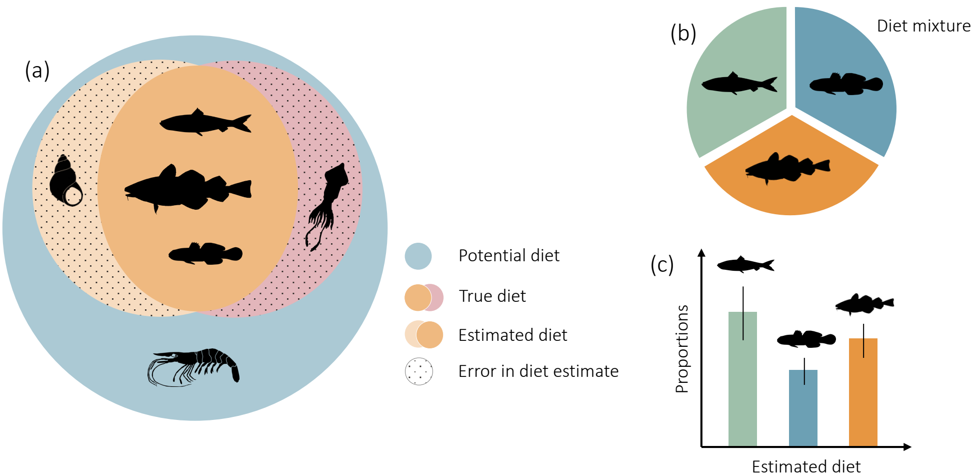

Figure 8. Conceptual sketch of diet tracing. (a) The true diet of an animal (bright orange and pink) represents a fraction of the potential diet available in the ecosystem (blue). Estimated diet is the diet identified by the specific method used for diet analysis (bright orange and pale orange) and might result in a mismatch (dotted black) between estimated and true diet. Mismatch can e.g. be caused by the method not detecting an ingested diet item (the squid) or by detection of possible diet items in the environment which were not ingested (the gastropod). (b) The diet is a mixture of consumed items and the method selected for analysis should be able to separate these. (c) The selected method should also be able to quantify proportional contribution to estimated diet by individual diet items. Figure inspired by illustration in Nielsen et al. (2017).

Dead useful

Using stranded and bycaught porpoises for research

Deceased stranded and bycaught harbour porpoises offer a unique opportunity to collect data to further our understanding of their basic biology and ecology (Börjesson & Read, 2003; Neimanis et al., 2022; Read, 1990), while also allowing monitoring of population health (Ijsseldijk et al., 2020). Stranded and bycaught harbour porpoises are collected along the Swedish coast and necropsied for national health monitoring and research. Since 2016, up to approximately 30 harbour porpoises are collected annually and examined postmortem by the Swedish Veterinary Agency and the Swedish National Museum of History through a national environmental monitoring program funded by the Swedish Marine and Water Management. During post-mortem examinations, tissue samples (e.g. liver, muscle and skin) from most of the collected porpoises are taken and preserved in the national environmental specimen bank where they are available for research. Necropsy results and the health status of analysed individuals are summarized in yearly monitoring reports.

Figure 9. Dead animals provide unique opportunities for research. (a) A recently deceased harbour porpoise found at the Swedish coast. (b) Post-mortem examinations of stranded or bycaught porpoises allow collection and investigation of stomach content for diet analysis. (c) Prey hard parts (e.g. otoliths, eye lenses and skeletal bones) are separated and extracted for macroscopic analysis by carefully rinsing the stomachs and passing the content through a series of sieves with small (0.5-2 mm) mesh sizes.

Past diet of harbour porpoises in Swedish waters

Diet studies on porpoises stranded or bycaught during 1980-2011 show that harbour porpoises in the waters around Sweden have previously targeted a variety of small benthic and pelagic fish, mainly gadid, gobiid and clupeid species (Aarefjord et al., 1995; Andreasen et al., 2017; Angerbjörn et al., 2007; Börjesson et al., 2003). More recent studies on live porpoises equipped with high-resolution biologgers however suggest that porpoises in inner Danish waters might predate on smaller prey than before (Wisniewska et al., 2016). As harbour porpoises are thought to exhibit prey switching behaviour, meaning that they change their preferred primary prey species depending on prey abundance (Ransijn et al., 2021), such a dietary switch could potentially have been induced by recent shifts in local prey fish species assemblages (Blocker et al., 2023; 2009; Casini et al., 2008; Svedang, 2003).

Reduced energy input by food limitation could have large impacts on harbour porpoises given their high energy need. Potential conservation implications include effects on individual-level fitness and health, as well as effects on population-level structure and density. To investigate if the vulnerable populations of porpoises in Swedish waters are under pressure from decreased prey quantity and quality updated dietary estimates are needed.

Paper II – Current diet of harbour porpoises in Swedish waters

Combining macroscopic analysis of hard parts with DNA metabarcoding

In **Paper II,** we performed dietary analysis on gastrointestinal content from harbour porpoises stranded and bycaught in Sweden during 2017-2022 (**Paper II** symbols in Figure 1, Figure 9), thereby providing updated diet estimates for porpoises in Swedish waters and allowing detection of potential dietary changes. We did this by parallel use of two methods for dietary estimation; macroscopic analysis of prey hard parts found in porpoise stomachs (macroscopic analysis) and DNA metabarcoding of gastrointestinal content (stomach DNA (sDNA) analysis), which allowed us to compare and evaluate the methods' respective and combined performance. By contrasting the two methods we investigated if a quick DNA sample from the gastrointestinal tract provide an alternative approach for diet estimation, possibly as a replacement or complement to the more traditional macroscopic analysis which is time consuming, labour intensive and dependent on performer experience.

Porpoises in Swedish waters still feed primarily on gadids, gobiids and clupeids

Three prey families (Gadidae, Gobiidae and Clupeidae) were clearly identified as main prey for harbour porpoises in Swedish waters, irrespective of the method or metric used to estimate diet contribution (Figure 10).

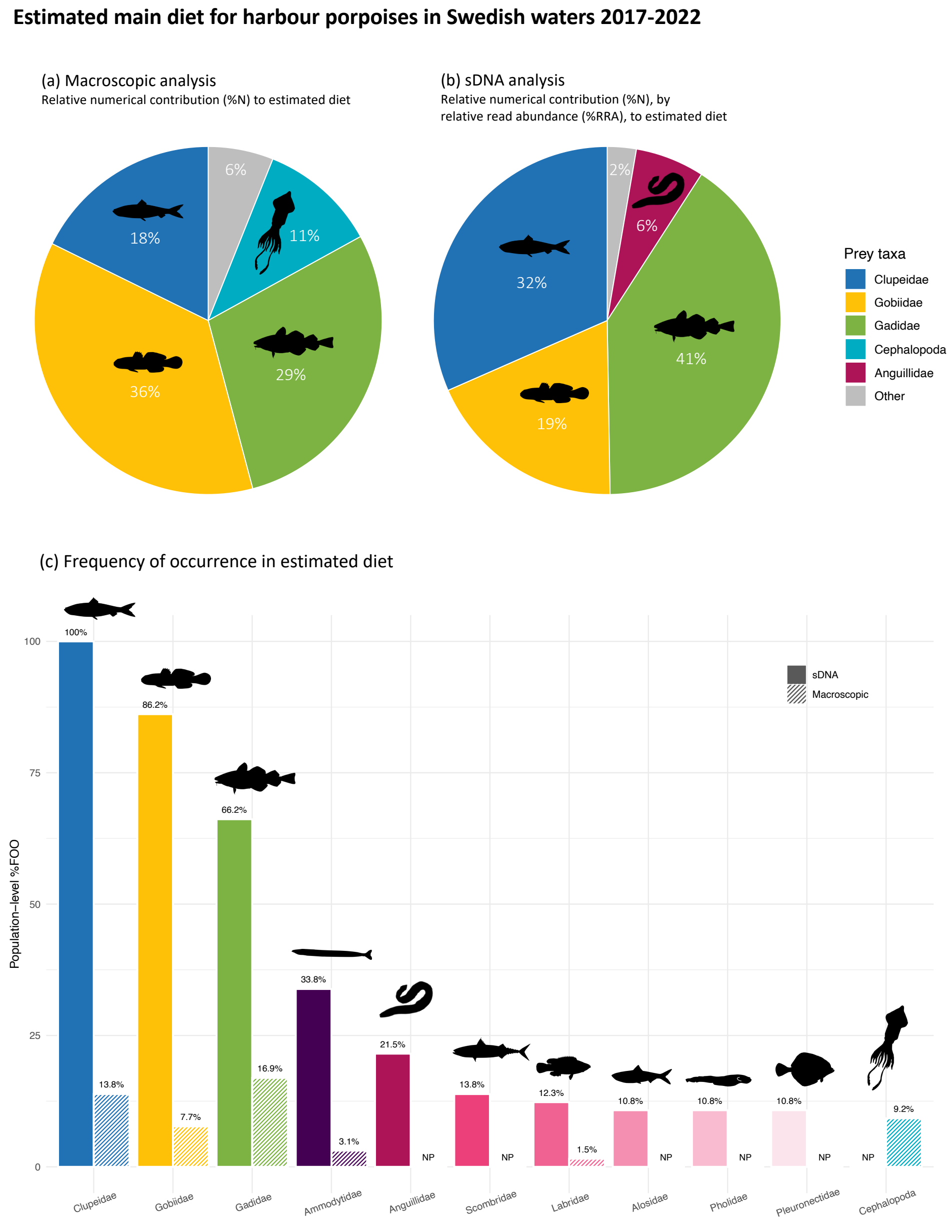

Figure 10. Estimated harbour porpoise population-level diet. Numerical contribution (%N) of detected prey species by (a) macroscopic analysis and (b) sDNA analysis, as well as (c) frequency of occurrence (%FOO) in side-by-side comparisons of results from sDNA and macroscopic analysis. For sDNA results the relative numerical contribution is relative read abundance expressed as a percent (%RRA) and comparable to %N (Deagle et al., 2019). In (a) and (b) taxa contributing with <5%N to estimated diet by the respective method are combined into the category ‘Other’. In (c) frequency of occurrence (%FOO) is shown for the 11 most common prey taxa (by any of the methods or metrics). NP = ‘Not present’. Figure from **Paper II**.

This is consistent with results from previous diet studies in the same area (Aarefjord et al., 1995; Andreasen et al., 2017; Angerbjörn et al., 2007; Börjesson et al., 2003), highlighting the importance of gadids, gobiids, and clupeids as main prey for harbour porpoises along the Swedish west coast. The diet however included a range of different prey, with in total 36 detected prey species belonging to 21 different taxa (20 fish families and class Cephalopoda). These had varying dietary importance, with 11 prey taxa contributing with >10% to estimated dietary contribution by any of the methods or metrics (Figure 10c). Again, these results are similar to previous estimates of the dietary composition of harbour porpoises in Swedish waters, and provided corroborating evidence that the harbour porpoise forage on a variety of prey species and switch their diet in response to prey abundance (Ransijn et al., 2021).

No clear evidence for a decrease in target prey size

In Danish waters, concerns have been raised for decreased prey target sizes and potential food limitation for harbour porpoises with studies suggesting that most prey targeted is only 3-10 cm in size (Wisniewska et al., 2016). Such a decrease in prey size was not supported by our dietary estimations in **Paper II**.

The mean estimated prey size in Swedish waters for years 2017-2022 was 13.3 cm (min-max range 2.5-40.6 cm) , which are in the range of estimated prey sizes for the same populations for years 1985-2011 (Aarefjord et al., 1995; Andreasen et al., 2017; Börjesson et al., 2003). Our results thus suggest that porpoises overall target larger prey in Swedish waters than they do in some Danish waters. However, since the tagged porpoises in Danish waters mainly were distributed in inner Danish waters during the short data collection period, they might reflect only local or regional prey choice and availability, but fail to mirror conditions on population-level scale. Similar local dietary trends might be present also in Swedish waters.

Differences between sexes, age classes, quarters of the year and sea districts

Both methods used in **Paper II** demonstrated that male and female porpoises had clear differences in their diet, with males predominantly targeting gadids and gobiids, while females predated on a larger number of different prey taxa (Figure 11a). A dietary difference between sexes has been found in one previous study in the area (Andreasen et al., 2017), but not all (Andreasen et al., 2017; Santos & Pierce, 2003). In addition, the sDNA analysis showed occurrence of eels (*Anguilla anguilla)* only in female diet and macroscopic analysis revealed that females fed on cephalopods to a much larger extent than males. Our findings, that females targeted a larger number of prey taxa than males, might indicate that females have a broader dietary niche than males, which could possibly be linked to their higher energetic need for reproductive investment (Santos & Pierce, 2003).

We also found evidence of dietary differences between porpoises belonging to different age classes (calves/juveniles/adults) (Figure 11b), quarters of the year (Q1-Q4), and sea districts (Skagerrak/Kattegat/Öresund/Southern Baltic) (Figure 1 in **Paper II**). For example, our dietary estimates indicate that cephalopods are only preyed upon by juvenile female porpoises in Öresund during the first quarter of the year.

In addition, gobiids seem to be lacking by proportional importance in adult diet (Figure 11b). This is surprising given that previous macroscopic diet studies of harbour porpoises in the same area have found gobiids in 31% of adult stomachs, representing 12% of the numerical contribution to estimated adult diet (Börjesson et al., 2003). Instead, our macroscopic diet estimates suggest an increased numerical contribution of gadids to adult harbour porpoise diet from approximately 20% during 1989-1996 to more than 60% in recent years (Figure 11b). In our macroscopic results, the high estimated numerical contribution (36%) of small gobiid prey species to population-level diet (Figure 10a) is affected by the inclusion of calves, which seemed to have a preference for gobiids (Figure 11b). Although this preference was shifted to juvenile individuals when using sDNA analysis for diet estimation, our results indicate that along the Swedish west coast gobiids are almost exclusively targeted by non-adult harbour porpoises. A switch in preferred prey for adult harbour porpoises in these Swedish waters during the past 30 years could reflect a functional response by porpoises to a simultaneous change in local prey abundance (Ransijn et al., 2021), but this needs to be investigated further.

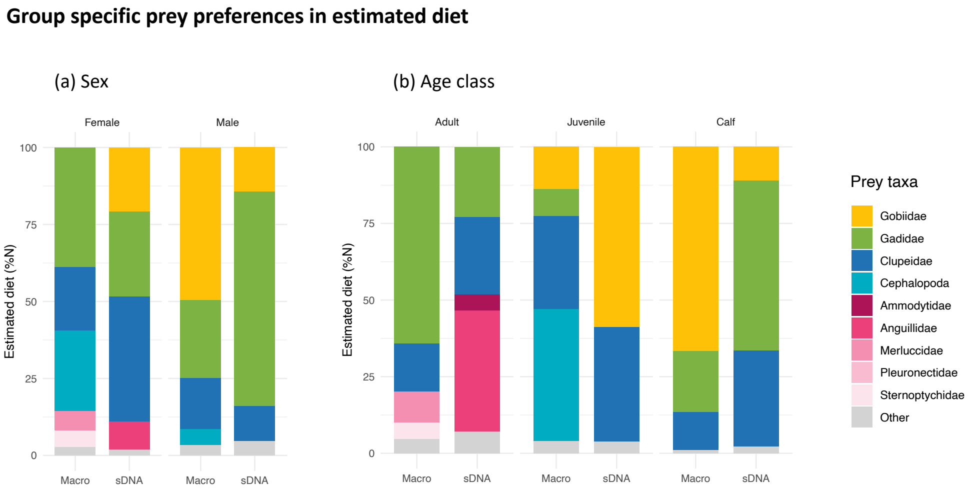

Figure 11. Side-by-side comparisons of estimated diet by relative numerical contribution (%N) by sDNA and macroscopic analysis for (a) sex and (b) age class reveal group specific prey preferences. Notice for example the higher number of taxa present in female diet in (a), the exclusive presence of Cephalopoda in juvenile diet in (b), and the exclusive presence of Anguillidae in adult females in (a) and (b). Figure modified from **Paper II**.

DNA metabarcoding increases taxonomic resolution

Our comparison in **Paper II** of estimated diet by macroscopic and sDNA analyses revealed that the two methods were overall in high agreement, especially when exploring diet contribution of prey at family level. sDNA analysis however clearly increased the number of detected prey taxa, in individual stomachs as well as in population-level estimates. At the same time, sDNA analysis increased sample size by allowing extraction of dietary data from, in terms of macroscopic hard parts, empty stomachs and intestines (Figure 12).

The detection probability of some occurring prey taxa however appears to be method dependent, cephalopods for example were almost only detectable in macroscopic data while eels frequently occurred in sDNA data but were not found by macroscopic analysis (Figure 10 and 11). However, our results showed that metabarcoding of gastrointestinal DNA (i.e. sDNA analysis) overall offered reliable semi-quantitative dietary estimates. The results from **Paper II** therefore suggest that sDNA analysis can be a useful supplement, or even replacement, for the traditional macroscopic analysis in studies of cetacean diets.

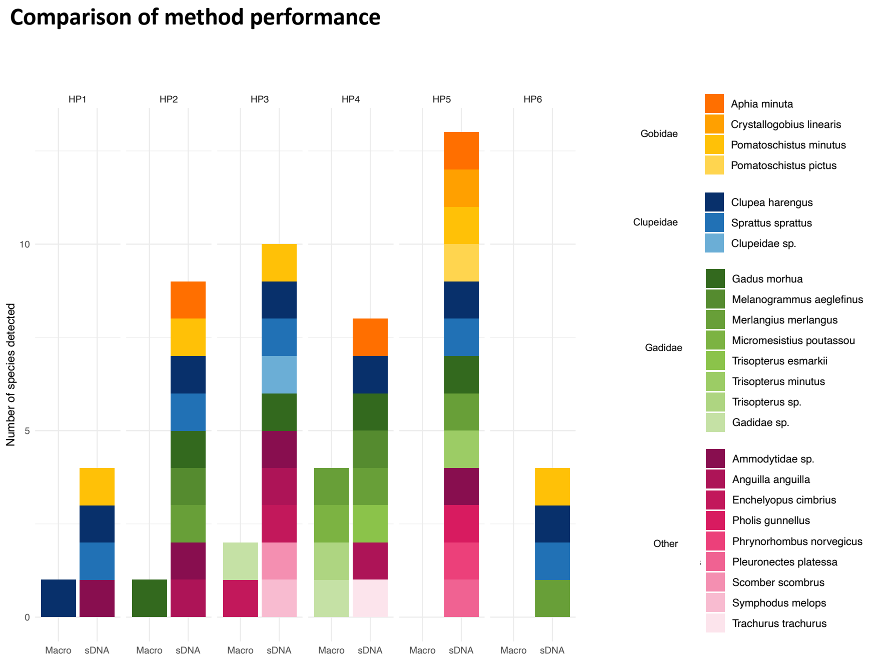

Figure 12. Number of species detected in individual-level diet estimates by macroscopic and sDNA analysis respectively for a subset of six porpoise individuals (HP1-HP6) analysed in **Paper II**. The agreement between results in terms of prey family detected for an individual porpoise by both methods is high, but DNA metabarcoding (sDNA) clearly increased number of detected prey families and species and also allowed retrieval of dietary data from seemingly macroscopically empty stomachs (HP5 and HP6). Note for example that HP5 was considered macroscopically 'empty', but renderred 13 prey species detected by use of sDNA analysis. Figure from **Paper II**.

Prey fish and porpoise health

Linking status and trophic position of porpoise prey to porpoise health

Following on **Paper II**, the impact of prey quality and quantity on harbour porpoise individual health and population status would be an interesting area to further explore. Such studies could increase the understanding of ecosystem dynamics, in terms of how the status of lower trophic levels impact top predators, and provide important conservation insight for the marine ecosystem as a whole.

Potential changes in the trophic level at which harbour porpoises feed can be studied by application of stable isotope analysis to historical tissue samples available through the national environmental specimen bank. The historical diet of porpoises in Swedish waters, during the past 40-50 years, could thus be analysed in combination with available biological and pathological parameters from the same individuals. This would allow relating prey consumption to porpoise health status over time, using e.g. data on blubber thickness, body mass index (BMI), and reproductive success as indicators of porpoise nutritional condition.

Combined with long-term monitoring data from fish population surveys, it would be possible to relate the results on porpoise diet and health to the composition and status of relevant fish populations. This would be highly informative from an overall conservation and management point of view.

How do porpoises catch the fish that they eat?

Strategies for foraging

Foraging tactics 'should' maximize net energy gain

As foraging typically requires investment of significant energy, the incentives for animals to develop foraging strategies that maximize their net energy gain are strong (Schoener, 1971). This results in large behavioural variation, both within and between species. Animals differ in the variety of food they consume, in time and effort they spend searching for food, in their choice of foraging tactics, as well as in the size and structure of the groups in which they feed (Ceia & Ramos, 2015; Cohen, 1993; McHuron et al., 2018; Overington et al., 2008).

Behavioural variation within a species is expected when natural selection favours individuals that are capable of expressing flexibility in their response to the environment, leading to so called conditional strategies (Alcock, 2009). A conditional foraging strategy, in order to maximize energetic gain, could for example be to switch between prey types or change search mode as a strategy become more or less profitable given the environmental conditions (Geary et al., 2019). Another strategy could be to change foraging habitat or patch. However, as the cost of switching from one foraging habitat or patch to another will usually be higher than the cost of changing prey type or search mode, foragers are expected to change their behaviour more often than their habitat (Stephens & Krebs, 1986).

Generalists, specialists and everything in between

The degree of foraging variability places animal species on a scale with generalists, which eat a wide variety of food, on one end of the spectrum and specialists, with narrow diets, on the other (Kassen, 2002; Overington et al., 2008). However, there can be considerable intraspecific variation, with many generalist species or populations containing specialized individuals whose niches represent small subsets of the overall species or population niche (Araujo et al., 2011).

Variation in foraging strategies and diet width are considered to be driven by environmental predictability, specifically resource distribution and availability. Foraging specializations are assumed to develop in stable environments with predictable and diverse resources, as it will reduce niche overlap and competition with conspecifics (Araujo et al., 2011; Rodriguez-Malagon et al., 2020). Unpredictable and unstable resources are on the other hand thought to favour development of generalists, since a broad diet and ability to use a variation of foraging strategies will be more beneficial (Futuyma & Moreno, 1988).

There is growing evidence that the degree of intraspecific variability in foraging behaviour can be used to study a species' ability to cope with changes in the environment, with increasing flexibility and behavioural plasticity providing greater resilience to changes in the habitat (Charrette et al., 2006; Overington et al., 2008; Shultz et al., 2005). Foraging behaviours can thus be valuable indicators for conservation, as they represent both the current and future prospects of a species. A shift in foraging strategies in response to changes in the animals' environment could for example be used as a first indicator of potential changes in population size (Stephens et al., 2007).

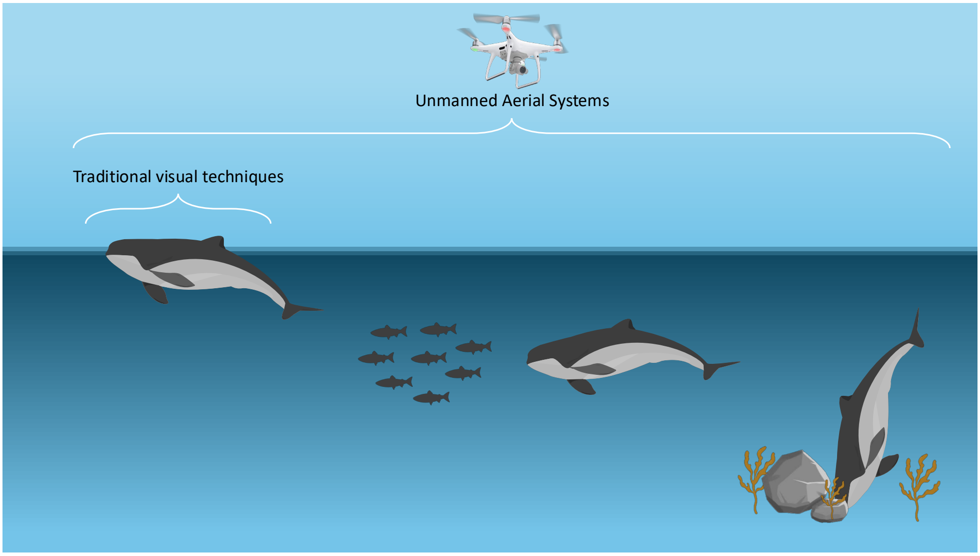

Figure 13. Compared to traditional visual techniques, Unmanned Aerial Systems (UAS) increase the potential time when visual observations of harbour porpoises and other marine mammals can be collected. Tradtional techniques typcially only observe the animals when they are at the surface, while detectability by UAS is possible also when animals leave the surface for e.g. foraging at depth. Visability of animals is dependent on depth, visibility and local conditons (for example turbidity, wave movement and sun glare), but harbour porpoises are typically detecable down to at least a few metres depth in Danish and Swedish waters. Figure inspired by illustration in Torres et al. (2018).

New perspectives from a bird's eye view

Using drones to study marine mammal behaviour

In recent years commercially available Unmanned Aerial Systems (UAS), commonly known as drones, have been increasingly used in studies of cetaceans and other marine animals (reviewed in Fiori et al., 2017; Schofield et al., 2019). Although the use of drones is limited to observations during daylight and in shallow waters or close to the surface in deeper waters, UAS have provided a completely new and important perspective from above with longer and more detailed behavioural observations than traditional land- or boat based methods (Fettermann et al., 2022; Torres et al., 2018) (Figure 13).

As the underwater noise effect from drones on marine mammals is small, even close to the surface, the technique provides undisturbed records of animals and behaviours (Christiansen et al., 2016) and have, for example, been used to describe behavioural development in southern right whale calves (Nielsen et al., 2019), sexual behaviour in a range of cetacean species (Ramos, 2023), and effects of whale-watching activities on endangered species (Sprogis et al., 2023).

Limited insight into how porpoises hunt and catch prey

Very little is known about the foraging behaviour of harbour porpoises, as the species is notoriously difficult to visually observe and study in the wild. Previous diet studies and our results in **Paper II** demonstrate that they predate on a range of different prey species, which occupy a diversity of habitats and express a variety of predator avoidance strategies (Linehan et al., 2001; Pitcher & Wyche, 1983; Turesson et al., 2009). This suggest that harbour porpoises should be capable of adjusting their behaviour in response to specific foraging contexts to maximize their net energy gain. However, for harbour porpoises no detailed visual observations or descriptions of foraging behaviours exist and it is unknown what tactics they use to catch the fish that they eat.

In addition, almost nothing is known about the group structure of harbour porpoises and whether the species forage alone or in groups. Foraging in a group typically includes several benefits, for example working together to locate prey (Pitcher et al., 1982), cooperative capture of large prey that a single individual would be unable to secure alone (Creel & Creel, 1995; Stander, 1991), and information transfer such as learning (Allen, 2019; Cantor & Whitehead, 2013; Greene, 1987). There are however also costs of grouping, including rapid depletion of food resources and reduced food availability (Alcock, 2009; Vijayan et al., 2012), lower reproductive rates (Borries et al., 2008), and increased intraspecific competition (Krause & Ruxton, 2002). As a result, there is remarkable variation in group size and stability within the animal kingdom both between and within species (Hintz & Lonzarich, 2018).

There are also large variations in the stability of groups formed. Some groups are very stable with strict hierarchies, such as family packs of wolves (Mech & Boitani, 2003), while others are more fluid temporary aggregations, such as the fission-fusion pods of bottlenose dolphins where individuals associate in groups dynamically and merge or split within the same aggregation several times per day (Connor et al., 2000).

Paper III and IV – Visual observations of foraging behaviour

Foraging in wild harbour porpoises observed from above

In **Paper III** and **IV** we used a large UAS video dataset (>130 hours) manually collected over nine years (2015-2023) in Danish shallow waters (**Paper III** and **IV** area in Figure 1) and provided novel insights into the foraging behaviour of wild harbour porpoises. From the complete dataset, sequences containing behaviours indicative of foraging were identified by manual examination and coded in detail to allow categorization, descriptions of observed behaviours, and more detailed analysis of potential collaboration by individual porpoises in a group.

Flexible predators with context-dependent strategies for prey capture

In **Paper III** we identified and described six different foraging strategies of harbour porpoises, as well as the context in which they occur. Most of the identified behaviours were previously unstudied and indicate use of context-dependent foraging strategies as they vary between different environmental contexts and targeted prey types. The observations align well with the broad diet of porpoises (**Paper II**), as successful predation on a diverse prey fish assemblage, with both benthic and pelagic prey that occupy a diversity of habitats and express a variety of predator avoidance strategies, can be expected to require an equally diverse behavioural repertoire in harbour porpoises.

A commonly observed foraging behaviour was '*bottom foraging*' where harbour porpoises performed vertical foraging in the sand or by rocks and algae at the seabed with head down and fluke up (Figure 14a). This behaviour was previously described for captive harbour porpoises (Wahlberg et al., 2023) and has been suggested to result in formation of large amounts of seafloor pits in the North Sea (Schneider von Deimling et al., 2023). It was however undocumented in the wild.

Occasionally multiple harbour porpoises and seabirds predated on the same fish school in a '*mixed-species feeding aggregation*' (Figure 14b), where all participating individuals are thought to benefit from the combined resource targeting effort. Harbour porpoises were also seen interacting alone with schools of fish in '*solo hunting on school*' (Figure 14c), where they swam in close proximity to the school and affected prey movements, sometimes forcing the school to split and achieving separation of individual prey which were actively chased and sometimes captured.

The visually spectacular '*turn & chase hunt*' was seen performed by single porpoises during active chase of predominantly large prey close to the surface and include multiple fast turns (180°), rapid accelerations and fast halts (Figure 14d and Figure 8 in **Paper III**). This behaviour was sometimes seen performed during several minutes when attempting to catch a specific prey, thereby providing a contrasting picture to the suggested ultra-high foraging rates of tagged porpoises in Danish waters (Wisniewska et al., 2016).

Figure 14. Harbor porpoises display a variety of foraging techniques and hunting behaviours, including (a) bottom foraging; vertically foraging in the sand or by rocks and algae at the sea bed with head down and fluke up, (b) mixed-species feeding aggregation; a special case of group hunting on schools of fish where multiple harbour porpoises and seabirds predate on the same prey resource, (c) solo hunting on school; interaction by a single harbour porpoise with a school of fish e.g. affecting school movements, and (d) turn & chase hunt; active chase of predominantly large prey close to the surface with multiple fast turns (180°), rapid accelerations and fast halts. Figure modified from **Paper III**.

Capable of complex collaborative group hunting

In **Paper IV** we investigated presence and conditions for social foraging and grouping as a foraging tactic in harbour porpoises. Given that the harbour porpoise is considered a non-social species, we hypothesized that individuals would mostly be seen foraging alone and that groups of foraging porpoises would show unstructured behaviours with no evidence of cooperation.

Our analysis showed, contrary to what was hypothesized, that harbour porpoises often foraged in groups targeting the same school of fish. In addition, detailed analysis of individual harbour porpoise movements in relation to targeted fish schools even suggested presence of collaborative hunting by role specialization (Figure 15) which is a very sophisticated kind of collaboration requiring complex social structures and communication.

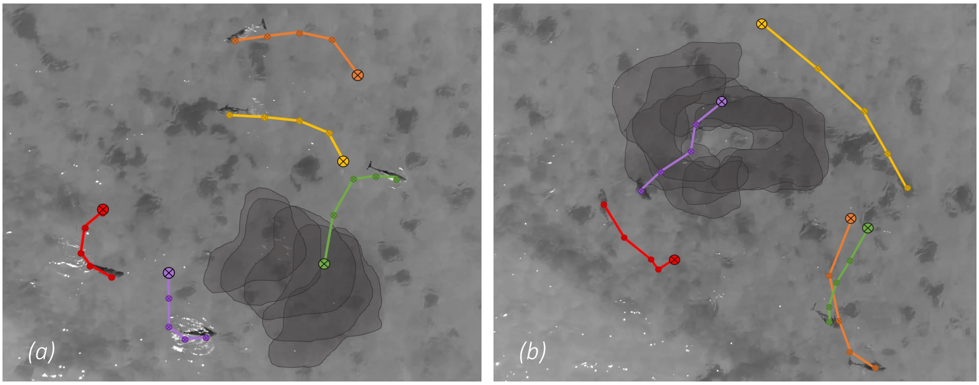

Figure 15. Two examples of 5-second tracks of five harbour porpoises performing collaborative group hunting on a school of fish in shallow Danish waters with sandy bottom and sea floor visible. Each porpoise is represented by an individual color, the X marks the start of the movement track and each following dot represents the position of that porpoise during the consecutive second. The fish school and school movement is shown by the grey area. In (a) the individual porpoises are moving the fish school forward by performance of coordinated herding and bordering movements. In (b) one individual (purple) is crossing the school in an assumed attempt to cause confusion and decrease school cohesion, while the other individuals (especially red and yellow) are restricting school movements by boardering.

Culture and social learning

More social than typically described

The behaviours described in **Paper III** and **IV** suggest that harbour porpoises are involved in social structures that are yet to be described scientifically. Further investigations of group foraging and sociality in harbour porpoises require studies on formation and stability of foraging groups over time, the division of roles within groups formed, and potential maintenance of specific group-hunting roles in the same individuals between foraging occasions. This is however not an easy task given that harbour porpoises display very few distinct characteristics that can be used to track individuals over time using e.g. photo-ID (Elliser et al., 2022), which is otherwise a commonly used technique for studies of the social lives and group structure in cetaceans (Ballance, 2018).

Social information transfer and culture in harbour porpoises

Regardless of the social group structure of harbour porpoises, information is likely to be transmitted socially between individuals, especially between a mother and her calf (Rendell & Whitehead, 2001). In **Paper III** we made observations of porpoise calves seemingly practicing foraging behaviours used by adults in their proximity, and of mother-calf interactions during accompanied foraging (Figure 16). This supports presence of social learning, which for example could be further investigated by exploration of whether harbour porpoise mothers take longer time to capture prey, adapt their body movements while hunting in presence of their calves (which has been observed in Atlantic spotted dolphins (*Stenella frontalis*) (Bender et al., 2009)), or predate on other species as indicated by diet studies (Paper II, Börjesson et al., 2003).

As social learning is a prerequisite for cultural transmission of behaviour (van Schaik, 2010), observations of imitation and teaching in harbour porpoise mother-calf pairs could indicate that hunting techniques are passed on to offspring through vertical cultural transmission (Rendell & Whitehead, 2001). Within Cetacea, such mother-offspring similarities in hunting behaviour are observed in orcas (*Orcinus orca*) (Baird, 2000) and bottlenose dolphins (*Tursiops sp.*) (Sargeant & Mann, 2009; Sargeant et al., 2005) where feeding specializations are learned by the offspring while swimming together with the mother.

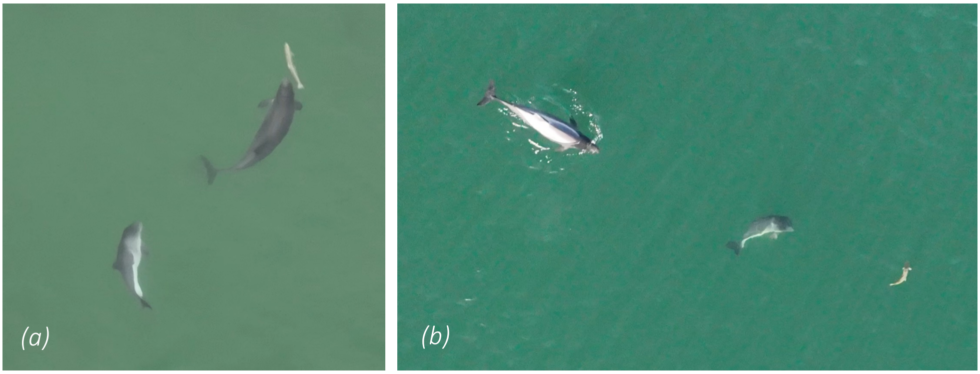

Figure 16. Potential social observational learning by a harbour porpoise calf in presence of its mother, with (a) the calf closely following the hunt of a bbig fish while fixating its head direction on the prey, and (b) the mother increasing her distance to the prey and the calf mimicking hunting behaviours previously performed by the mother. Figure from **Paper III**.

Over the last 70 years, research on culture in the animal kingdom has revealed it to be widespread in nature (Whiten, 2021). Examples from a range of socially complex cetacean species include the evolution of orca ecotypes, foraging traditions and song culture in humpback whales (*Megaptera novaeangliae*), and vocal clans in sperm whales (*Physeter macrocephalus*) (reviewed in Garland & Rendell, 2023). To date, no studies exist on culture in harbour porpoises. However, potential presence of harbour porpoise culture could, for example, be explored by comparative studies of existing foraging tactics in different geographic areas and populations.

Conclusions and outlook

While there is still much unknown, the studies included in this thesis provide important new insights into the basic ecology of harbour porpoises and their interactions with prey. In conclusion, our findings regarding fine-scale spatiotemporal activity, diet, and foraging behaviour of Belt Sea harbour porpoises convey three key messages which are reviewed below.

High density areas are important for foraging

The high correlation between presence and foraging found in **Paper I** indicate that harbour porpoise presence is a good indicator of areas of energy intake and reveals how tightly linked the species is to its foraging areas. The tight link signals that high-density porpoise areas cannot easily be replaced by other areas, stressing the importance of low levels of disturbance and other pressures within these regions.

The large differences in porpoise presence and foraging activity on a micro-scale, detected in **Paper I,** were previously undescribed and offer insights for development of conservation measures. Investigating if porpoises exhibit similar local activity patterns in other regions could provide crucial information for optimal zonation of human activities within protected areas and may both improve the efficiency of implemented measures and ease up challenges with conflicting interests.

In addition, we found temporal cyclicity in porpoise presence and foraging corresponding to the lunar cycle. Even if some previous studies have found the lunar phase to impact harbour porpoise distribution (de Boer et al., 2014) and bycatch risk (Brennecke et al., 2021), **Paper I** was the first to describe this cyclic frequency in an area without notable tidal forcing. The strong diel pattern in **Paper I** indicates that there might also be a fine-scale temporal variation in bycatch risk, a factor that has achieved little attention so far (Northridge et al., 2017) and could be worth investigating further.

However, the next step crucial for understanding porpoise habitat use is to study the underlying mechanisms that drives the observed fine-scale patterns in porpoise activity. This requires detailed studies on how porpoises interact with prey over a range of spatiotemporal scales, and identification of environmental factors that can be used to predict porpoise presence and foraging. This would in turn enable identification of important areas to protect in both space and time.

Feed from a diverse menu of fish

The dietary estimates for harbour porpoises in Swedish waters during 2017-2022 delivered in **Paper II** provide an important contribution to both research and marine management, as the previous most recent estimates for the region were 13 years old (Andreasen et al., 2017).

We showed that harbour porpoises along the Swedish west coast target a broad variety of fish from a diverse menu of both benthic and pelagic prey species, which is consistent with previous studies in the area (Aarefjord et al., 1995; Andreasen et al., 2017; Börjesson et al., 2003). On population-level, the preferred targeted prey families are Gadidae, Gobiidae and Clupeidae. Together they represented more than 80% of the relative numerical contribution to estimated diet, irrespective of the method used for analysis. Identification of these three families as main prey for harbour porpoises in the Baltic region is well in line with previous knowledge of the species' diet.

Our results in **Paper II** do however provide indications of changes in relative contribution of some prey species, with an increased consumption of gadids by adults whereas gobiids almost lack by proportional importance to their diet. This might reflect a functional response by a predator to changing prey abundance (Ransijn et al., 2021), which could be investigated by combination of historical data on porpoise diet and long-term data on the composition and nutritional status of relevant fish populations.

In addition to updated diet estimates, **Paper II** delivers a comparison of two methods for dietary studies using stomachs from deceased animals: macroscopic analysis of prey hard parts (macroscopic analysis) and DNA metabarcoding (sDNA analysis). Our comparison shows that the two methods are overall in high agreement, but that sDNA analysis increases the number of detected prey taxa. sDNA analysis also increases the sample size by allowing extraction of dietary data from seemingly empty stomachs. The detection probability of some occurring prey taxa however appears to be method dependent, which requires attention upon method choice.

However, as **Paper II** show that sDNA analysis overall offers reliable semi-quantitative dietary estimates this method can be a useful supplement, or even replacement, for the traditional macroscopic method when utilizing deceased animals to study individual- and population-level diet composition.

Flexible predators capable of complex group hunting

In **Paper III**, we provided the first detailed visual descriptions of harbour porpoise foraging behaviour using UAS data and in **Paper IV** we made one of the first attempts to study group hunting in harbour porpoises. Both studies provide important contributions to the general understanding of the species' foraging behaviour.

Paper III suggest that harbour porpoises are flexible predators that use conditional foraging strategies and adapt their behaviour in response to environmental circumstances. This is in accordance with the expectations for a species utilizing a range of different habitats and predating on a diversity of prey. However, the foraging behaviours described in **Paper III** are unlikely to reflect the full repertoire of porpoise foraging techniques, as the UAS data analysed is limited to observations during daytime and in shallow water. Our observations do however provide an important contrasting picture to the suggested ultra-high foraging rates of porpoises in the Kattegat and Belt Seas (Rojano-Donate et al., 2024; Wisniewska et al., 2016). To fully understand harbour porpoise foraging behaviour and strategies requires combining results from complementing studies utilizing different techniques.

The detailed analysis in **Paper IV** revealed that harbour porpoises are capable of complex group hunting by role specialization, which was surprising given their lack of apparent stable group structure and presumed non-social lives. The findings in **Paper IV** provide an important contribution to the general understanding of harbour porpoise behavioural ecology, and highlights the importance of considering presence of social foraging also in other seemingly non-social species.

Descriptions of foraging strategies in top predators are crucial not only for understanding species specific behaviours, but are also needed to study a species resilience to habitat alterations (Charrette et al., 2006; Overington et al., 2008; Shultz et al., 2005) and allow for early detection of ecosystem change. As such, the descriptions in **Paper III** and **IV** provide valuable information to guide conservation actions for porpoises which in turn will have positive conservation effects on marine biodiversity at large.

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