Faculty of Biosciences, Fisheries and Economics
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The feeding ecology of harbour porpoises (*Phocoena phocoena*) in Norwegian coastal communities: a combined approach using stable isotope and stomach content analyses

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Camille Saint-André

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THE FEEDING ECOLOGY OF HARBOUR PORPOISES (*PHOCOENA PHOCOENA*) IN NORWEGIAN COASTAL COMMUNITIES:

A COMBINED APPROACH USING STABLE ISOTOPE AND STOMACH CONTENT ANALYSES

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Supervisors:

Ulf Lindstrøm: UiT –The Arctic University of Norway &

IMR – The Institute of Marine Research

Kirsteen MacKenzie: IMR – The Institute of Marine Research

ABSTRACT

The harbour porpoise is a key predator in Norwegian coastal communities, therefore studying its feeding ecology is important to understand its ecological role and may shed light on the dynamics of Norwegian coastal ecosystems. The diet of 134 harbour porpoises bycaught in Autumn 2016 (n = 61) and Spring 2017 (n = 73) in Norwegian coastal waters and fjords was investigated using both stable isotopes (δ15N and δ13C) and stomach contents. A total of 23 prey groups were identified in the stomachs, though most porpoises had consumed between 1 and 4 prey groups. Harbour porpoises mainly fed on gadoid fishes, and saithe (juvenile) was by far the most important prey species. Pelagic, lipid-rich prey species such as capelin and herring contributed much less to the diet. While lipid-rich prey species are thought to be essential for harbour porpoises, due to their high metabolic demands, this study highlights the importance of lean but more available prey in the diet. Harbour porpoises mainly fed on small prey species or on the juveniles of large-sized gadoids (e.g. saithe, cod). Both the stable isotope and stomach content analyses showed a significant ontogenetic shift, with differences in the isotopic and diet composition of calves compared to the more similar juveniles and adults. The stable isotopes may suggest a greater use of benthic or coastal resources, or a decreasing reliance on dietary lipids to synthesize muscle tissues with increasing body size. There was no significant difference in the isotopic and diet composition between male and female porpoises, suggesting both use similar habitats and prey resources. Although saithe was dominant in all sampling periods and areas, spatiotemporal variations in diet were observed and are likely related to seasonal and geographical changes in prey availability (i.e., prey spawning, seasonal migrations, species distribution). However, spatiotemporal variations in stable isotope composition cannot conclusively be linked to the diet, as knowledge on the isotopic baseline in time and space is lacking. The long-term differences in diet composition between the late 1980's and now suggest that prey availability has changed. This study confirms harbour porpoises are generalist predators that consume a wide variety of prey species and display a flexible foraging behaviour, feeding opportunistically on locally abundant and accessible prey.

Keywords: Norwegian coast, Diet composition, SIA, Otoliths, Foraging, Opportunist

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1. INTRODUCTION

The harbour porpoise (*Phocoena phocoena*, Linneaus 1758) is one of seven extant species belonging to the family Phocoenidae (Cetacea, Odontoceti). The family is divided into three genera: *Neophocaena* (finless porpoise *Neophocaena phocaeniodes* and narrow-ridged finless porpoise *Neophocaena asiaeorientalis*), *Phocoenoides* (Dall's porpoise *Phocoenoides dalli*), and *Phocoena*, in which we find the harbour porpoise, the Burmeister's porpoise (*Phocoena spinipinnis*), the vaquita (*Phocoena sinus*), and the spectacled porpoise (*Phocoena dioptrica*).

The harbour porpoise is among the smallest cetaceans, with adults usually measuring less than 1.8 m long. Harbour porpoises have a blunt short-beaked head, a stocky body, and a triangular dorsal fin. They are often described as "living life in the fast lane" due to their early maturation, relatively short gestation and lactation periods, frequent reproduction, and shorter lifespan than most marine mammal species (Read and Hohn 1995; Lockyer 2003). Most harbour porpoises do not live more than 12 years, though some individuals up to 24 years old have been observed in the wild (Lockyer 1995; Hohn and Brownell 1990 after Read and Hohn 1995; Lockyer 2003). Harbour porpoises generally live singly or in groups of less than 8 individuals, but occasionally form larger groups. These larger congregations are typically temporary and associated with high food concentrations (e.g. high prey concentration due to seasonal tides or upwelling) (Hoek 1992; Pierpoint 2008).

1.1. Distribution and habitat use

The harbour porpoise is widely distributed in the temperate to sub-polar waters of the Northern Hemisphere (Klinowska 1991; Bjørge and Donovan 1995). The species primarily inhabits coastal and continental shelf waters, usually shallower than 200 m (Bjørge 2003). Harbour porpoises can, however, be found in deeper oceanic waters and show important offshore movements (Bjørge and Øien 1995; Westgate et al. 1995; Read and Westgate 1997; Nielsen et al. 2018), which are mostly seasonal (Northridge et al. 1995; Read and Westgate 1997; Nielsen et al. 2018). Individuals are also common in rather deep Norwegian fjords (Hammond et al. 2017).

Five subspecies of *Phocoena phocoena* are currently recognised by the Committee on Taxonomy (Committee on Taxonomy 2018): *P. p. phocoena* in the North Atlantic; *P. p. vomerina* in the

eastern North Pacific; *P. p. relicta* in the Black Sea; and two yet unnamed subspecies, one in the western North Pacific and the other in the Iberian and Mauritanian waters. The porpoises from Iberia and Northwest Africa have only recently (September 2017) been recognised as a subspecies and are likely descendant from the extinct populations of the Mediterranean Sea (Fontaine et al. 2014).

1.2. Threats and conservation status

Due to its coastal distribution, the harbour porpoise is particularly vulnerable to incidental catches, or bycatch, by fisheries (IWC 1994; Stenson 2003; Moore et al. 2009). Harbour porpoises may get caught in different types of fishing gear (e.g. trawls, longlines, purse seines), however, the majority of porpoises are bycaught in bottom-set gillnets (IWC 1994; Jefferson and Curry 1994). Even though the harbour porpoise, as a species, is currently considered as being of "least concern" by the International Union for Conservation of Nature (IUCN), it is in danger in some parts of its distribution range. The populations in the Black Sea and in the Baltic Sea are listed as endangered and critically endangered, respectively (Birkun and Frantzis 2008; Hammond et al. 2008). While this is not the case in Norwegian waters, the current levels of bycatch are high and likely not sustainable.

No single, reliable abundance estimate exists for the harbour porpoise population along the entire Norwegian coast. In 2016, part of the Norwegian coastal waters was surveyed by an aircraft as part of the SCANS III survey. The area extended from 62°N to 68°N (Vestfjorden), including Trondheim Fjord, and the abundance was estimated at approximately 24 256 harbour porpoises (CV 0.28, CL low 14 035, CL high 40, 829) (Hammond et al. 2017). In order to be sustainable, ASCOBANS (Agreement on the Conservation of Small Cetaceans of the Baltic, North East Atlantic, Irish and North Seas) has recommended that bycatch not exceed 1.7% of the best available population estimate. Current bycatch of two gillnet fisheries (cod and monkfish) in Norwegian coastal waters is estimated to be about 2 200 to 3 200 individuals per year (Moan 2016) and represents about 80% of the total bycatch of harbour porpoise in Norwegian waters (NAMMCO and IMR 2019). At this rate, the population would have to exceed 129 400 to 188 250 individuals, which is considerably higher than the current available estimate suggests.

In addition to bycatch, anthropogenic threats to harbour porpoises include chemical pollution, noise pollution (e.g. through vessel traffic, seismic surveys, underwater explosions,

constructions of offshore wind farms), ship-strikes, and changes in prey availability (e.g. through overfishing, degradation of the sea floor by bottom trawling, climate change) (e.g. Goñi 1998; Learmonth et al. 2006; Weilgart 2007; Murphy et al. 2015). Such threats can act in synergy, with most of them having indirect, and potentially additive, effects. For example, long-term changes in prey availability can affect the fitness and survival of marine mammals through increased exposure to pollutants and susceptibility to disease, as well as lowered body condition and reproductive success(e.g. Aguilar et al. 1999; Geraci and Lounsbury 2002).

1.3. Feeding ecology

Harbour porpoises are considered generalist piscivorous predators (e.g. Santos and Pierce 2003; Víkingsson et al. 2003; Leopold 2015), with a diet mainly consisting of small pelagic schooling fishes (e.g. Atlantic herring *Clupea harengus*, capelin *Mallotus villosus*, mackerel *Scomber scombrus*, sprat *Sprattus sprattus*), and demersal or benthic fishes (e.g. Atlantic cod *Gadus morhua*, gobies Gobiidae, saithe *Pollachius virens*, whiting *Merlangius merlangius*). Occasionally, they also feed on crustaceans and cephalopods (e.g. Fontaine et al. 1994; Santos and Pierce 2003; Víkingsson et al. 2003).

Some previous feeding ecological studies indicate that harbour porpoise display an ontogenetic shift in diet. They found young porpoises mainly feed on small food items such as crustaceans (e.g. euphausiids) and small coastal, benthic fishes (mostly gobies) (Smith and Read 1992; Santos and Pierce 2003; Leopold 2015; Andreasen et al. 2017). As they grow, individuals feed on larger prey items and seem to diversify their diet, with a shift towards gadoids and pelagic fishes (mostly clupeids) reported by several authors (Smith and Read 1992; Santos and Pierce 2003; Schelling et al. 2014; Leopold 2015). This ontogenetic diet shift is likely a combination of experience and physiological constraints, as larger and more experienced porpoises are likely able to feed further offshore and to dive deeper than calves and juveniles (Santos and Pierce 2003). Indications of differences in diet composition and/or diversity between male and female adult harbour porpoises have been described as well (Santos and Pierce 2003; Víkingsson et al. 2003). These are thought to originate from differences in the distribution of male and female adult porpoises and the strong association of females with calves (Smith and Gaskin 1983; Santos and Pierce 2003; Pierpoint 2008). Additionally, pregnant and lactating females have been found to eat larger and/or different, more lipid-rich prey items than adult males, likely due to their coincidental higher energy requirements (Smith and Gaskin 1983; Yasui and Gaskin 1986;

Recchia and Read 1989; Schelling et al. 2014). However, no such differences have been found in other studies (Smith and Gaskin 1974; Fontaine et al. 1994), making the influence of age and sex on the harbour porpoise diet relatively unclear.

Due to their small size, limited body fat storage capacity, cold water habitat use, and high energy expenditure, harbour porpoises need to forage frequently and presumably on energy-rich prey items (Koopman 1998; Santos and Pierce 2003; Lockyer 2007; Spitz et al. 2012; Wisniewska et al. 2016). Kastelein et al. (1997a) and Lockyer et al. (2003) estimated that individuals need to consume about 4 to 9.5 % of their body weight in food per day. This makes the harbour porpoise particularly sensitive to changes in the energy density of available prey species or in the availability of energy-rich prey (Brodie 1995; Bjørge 2003; MacLeod et al. 2007). Additionally, important spatial and temporal variations in diet composition, including the species of prey and/or their relative importance, exist and are likely due to differences in prey distribution and availability (e.g. Aarefjord et al. 1995; Bjørge 2003; Santos and Pierce 2003; Víkingsson et al. 2003; Santos et al. 2004; Sveegaard 2011; Sveegaard et al. 2012). These are influenced by ecological (e.g. spawning, migration patterns) and physical factors (e.g. water temperature, bathymetry, slope gradient, substrate type), as well as aggregating oceanographic features (e.g. fronts, tidal flows, island wakes, upwelling; all spots of enhanced primary production) (Maravelias et al. 2000; Clark 2005; Johnston et al. 2005; Pierpoint 2008; Sveegaard et al. 2012).

Although harbour porpoises have a broad diet, it tends to be dominated by only a few species within a given area (e.g. Santos and Pierce 2003; Víkingsson et al. 2003; Santos et al. 2004). The last study on the diet composition of harbour porpoises in Norwegian waters showed the importance of capelin, herring, saithe, poor cod (*Trisopterus minutus*), and blue whiting (*Micromesistius poutassou*) in the diet using stomach contents (Aarefjord et al. 1995). Note that capelin was found to be important only off northern Norway.

1.4. The Norwegian fjords and coastal waters: ecosystems under change

The harbour porpoise is an important top predator in Norwegian fjords and coastal waters. Coastal ecosystems are complex and productive systems (Ray 1988; Duarte and Cebrián 1996; Agardy and Alder 2005). They provide necessary ecological functions such as spawning, nursing, and feeding grounds (Agardy and Alder 2005; Nyunja et al. 2009; Seitz et al. 2014), as well as goods and services for human society (Agardy and Alder 2005; Martínez et al. 2007;

Barbier et al. 2011). These ecosystems, however, are under pressure from human activities around the world through, for example, overfishing, land-based pollution, eutrophication, and modification of the coastline (e.g. Jackson et al. 2001; Lindeboom 2002; Halpern et al. 2008; Culbertson et al. 2009).

Important changes, altering the structure and functioning of the ecosystems, already happened in Norway. Such changes include the reduction in kelp forests (*Laminaria hyperborea*) due to intensive grazing by sea urchins (*Strongylocentrotus droebachiensis*) during the 1970-80s (Hagen 1983; Sivertsen 2006), and the large and rapid decline in cod populations in the 1980s (Mehl 1991; Broderstad and Eythórsson 2014). The causes are still poorly understood but are likely a combination of overfishing (both directly on cod and indirectly on sea urchins' predators and competitors), predator-prey interactions, life history traits (i.e. bet-hedging strategy of sea urchins), and climate change. Additionally, Norwegian coastal waters were influenced by the invasions of harp seals (*Phoca groenlandica*) and introduced red king crabs (*Paralithodes camtschaticus)* in the 1980s and early 1990s, respectively (Haug et al. 1991; Jørgensen and Nilssen 2011). This leads to conflicts between invasive species and fisheries (e.g. consumption of commercial fish or eggs of commercial fish, damages to fishing gear) and had significant impacts on the ecosystem (e.g. changes in benthic fauna including reduced benthic diversity and biomass) (Haug and Nilssen 1995; Falk-Petersen et al. 2011). Because of these major changes to the Norwegian coastal systems, the diet composition of harbour porpoises investigated around 30 years ago (Aarefjord et al. 1995) is likely not representative of their current feeding ecology, thus emphasising the need for a new dietary assessment.

1.5. Diet studies: stomach content and stable isotope analyses

To understand a predator's ecological role in its ecosystem, information on feeding preferences and foraging behaviour is essential. Because predation is a crucial ecological force (e.g. Tsou and Collie 2001; Estes et al. 2011), such knowledge might shed light on the ecosystem's dynamics and help predicting its response to potential changes. As direct observations of harbour porpoises feeding in the wild are difficult, especially because of their small size and elusive behaviour, diet studies have focused on stomach content analysis of dead animals, found either stranded or bycaught. Stomach content analysis can give detailed, qualitative information (i.e. prey species, size, and weight), but represent merely a snapshot of the diet, as only the last meal is often observed (Pierce and Boyle 1991). Alternative methods based on fatty-acid (e.g. in milk,

blood, blubber) and stable isotopes (e.g. in blood, skin, blubber, muscles, bones) can provide information on the assimilated diet over longer periods (i.e. days to years, depending on the tissue analysed and its turnover rate) and are increasingly used (e.g. Kelly 2000; Budge et al. 2006; Bowen and Iverson 2012; Mahfouz et al. 2017).

The analysis of stable isotopes (SIA) is a powerful tool to explore animals' feeding ecology, with sampling being relatively easy and less time-consuming than the investigation of stomach contents. Stable isotope analyses rely on the fact that the isotopic composition of a consumer tissues reflects the isotopic composition of what the animal eats (Kohn 1999). Ratios of nitrogen (^{15}N:^{14}N or $\delta^{15}N$) and carbon (^{13}C:^{12}C or $\delta^{13}C$) stable isotopes are the most commonly used in ecological studies (Michener and Lajtha 2007; Newsome et al. 2010); they can for example give insight on trophic relationships (Fry 1988; Hobson and Welch 1992), sources of primary production (France 1995; Rautio and Vincent 2007), habitat use (Clementz and Koch 2001; Fontaine et al. 2007), and migration patterns (Schell et al. 1989; Hobson 1999). In particular, nitrogen stable isotope ratios are used to determine trophic positions in the food web, as predators usually present an enrichment of 3–4 ‰ in ^{15}N compared to their prey (De Niro and Epstein 1981; Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002). The enrichment of carbon between trophic levels, on the other hand, is relatively low (i.e. generally 0–1 ‰), and $\delta^{13}C$ values are similar between a prey and its consumer (De Niro and Epstein 1978; France and Peters 1997; Post 2002). However, differences in carbon enrichment exist depending on the carbon source (e.g. terrestrial vs freshwater vs marine, offshore vs inshore), and carbon stable isotope ratios can help determine feeding location and habitat use. In the marine environment, benthic and coastal food webs tend to be more enriched in ^{13}C compared to pelagic or oceanic food webs (Fry and Sherr 1984; France 1995). Used in combination with traditional stomach content analyses, stable isotopes can help obtain a more comprehensive view on a consumer's feeding ecology.

1.6. Aims and predictions

The present study was part of a broader project exploring the ecological role of harbour porpoises in Norwegian coastal marine communities. The project will contribute to a better understanding of the importance of the harbour porpoise as a predator in the Norwegian coastal environment, its status in Norwegian coastal waters, and potential conflicts with human activities. This thesis attempts to give a detailed description of harbour porpoises' current diet composition in

Norwegian fjords and coastal waters, using both stomach content and stable isotope analyses. Differences in isotopic and diet composition between maturity classes, sexes, sampling periods, and sampling areas, are explored.

Differences in the feeding ecology of harbour porpoises in Norwegian coastal waters, studied by Aarefjord et al. (1995) almost three decades ago, are anticipated due to the large changes that occurred in Norwegian coastal systems. Additionally, according to previous studies (see above), I expect:

(i) an ontogenetic shift in diet, in both the composition and the diversity. In particular, younger porpoises are expected to eat smaller and relatively more coastal prey items than adults, and individuals are expected to show a more diversified diet as they mature

(ii) potential sexual differences in diet. Adult females are expected to stay closer to the coast with their calves while adult males migrate further offshore, feeding on different prey species

(iii) spatial and temporal differences in diet, linked to local habitat characteristics, as well as the distribution, life cycle, and migration patterns of potential prey species

2. MATERIALS AND METHODS

2.1. Study area and data collection

A total of 134 harbour porpoises bycaught in gillnets along the Norwegian coast in 2016 and 2017 were collected from recreational and commercial fishermen (Figure 1). The porpoises from 2016 (n = 73) were bycaught in the period September 12th–October 14th, between Rogaland (59.07°N, 5.83°E) in the south and Troms (70.14°N, 22.24°E) in the north. In 2017, however, the sampling was restricted to northern Norway for logistical reasons. A total of 61 porpoises bycaught from February 2nd to April 4th, between Senja (69.52°N, 17.50°E) and Varangerfjorden (71.05°N, 28.05°E), were collected then. The depth of the bycatches ranged from 20 to 160 m.

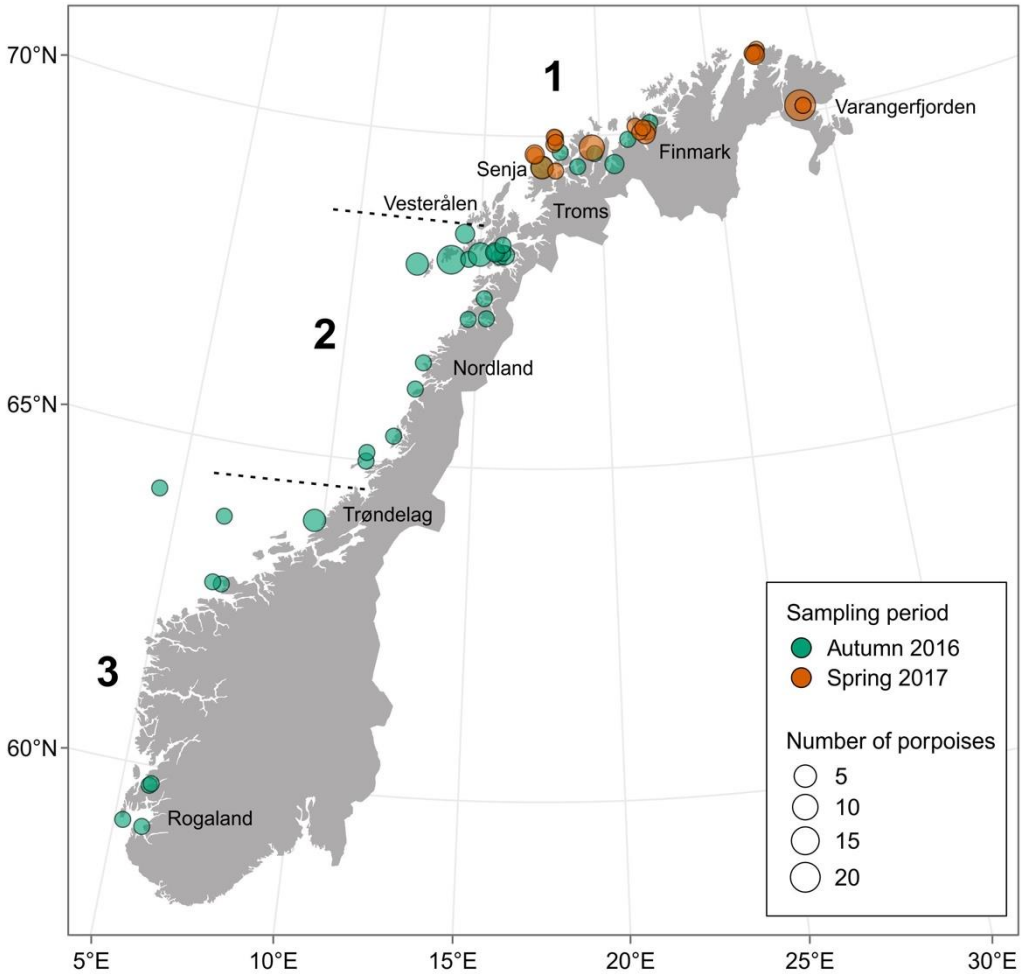

FIGURE 1: Sampling locations of harbour porpoises bycaught in September–October (Autumn) 2016 (green circles) and February–April (Spring) 2017 (orange circles). The size of the circles is proportional to the number of animals collected. Three areas are defined: (1) north of 68.55°N, Finmark and Troms counties; (2) between 64.40° and 68.55°N, Nordland and northern Trøndelag; and (3) south of 64.40°N, Western Norway (from southern Trøndelag to Rogaland).

The bycaught animals were frozen whole shortly after landing and transported to the Institute of Marine Research (IMR), Tromsø, Norway. The sex, body weight, and various morphometric measurements (length, maximum circumference, and blubber thickness) were registered prior to dissection. During dissection, the gastro-intestinal tract was removed and then was frozen (-20 °C) until further processing. Muscle tissues were collected for SIA and similarly frozen. Additionally, reproductive organs (i.e. ovaries and testes) and teeth from the lower jaw were collected and used for sexual maturity (Table 1) and age determinations by Cervin (2018). Age was converted into decimal years, assuming the porpoises were born on the first of July. Porpoises younger than one year old were classified as calves. Sexual maturity was unknown for three individuals and was instead assumed using the average age at maturity of other porpoises. The sampling distribution of harbour porpoises by area and sampling period is shown in Table 1.

TABLE 1: Sampling distribution of harbour porpoises bycaught along the Norwegian coast in 2016 and 2017, by area (see Figure 1), divided into four sex/maturity-status groups. In adults, M = males, and F = females. The sampling depth is presented as a range (mean ± sd).

Area	Sampling depth (m)	Year	Months	Calves	Juveniles	Adults	
						M	F
1 (n = 73)	20 – 160 (83 ± 33)	2016	Sept.–Oct.	3	7	0	2
		2017	Feb.–April	3	36	11	11
2 (n = 48)	20 – 130 (82 ± 29)	2016	Sept.–Oct.	8	27	4	9
3 (n = 13)	30 – 100 (84 ± 22)	2016	Sept.–Oct.	6	5	0	2
	Total			**20**	**75**	**15**	**24**

2.2. Laboratory work

2.2.1. Stable isotopes

Stable isotope of nitrogen and carbon were analysed in the muscle tissues. In muscle tissues, these stable isotopes reflect the diet integrated over weeks to a few months (Tieszen et al. 1983; Hobson 1999; Kurle and Worthy 2002). However, literature on the exact turnover rates in harbour porpoise tissues is lacking. Turnover rates might be higher in harbour porpoises than in other taxa due to their high metabolic rate (Kastelein et al. 1997a; Rojano-Donãte et al. 2018).

For the analyses, 1 to 2 cm^3 of muscle tissues were thawed, rinsed with deionised water, and freeze-dried at -80°C for approximately 72 hours. The samples were then ground in a fine

homogeneous powder using a pestle and mortar, which were cleaned thoroughly between samples using milli-Q water. Lipids were extracted for a part of the material (see below). Homogenised samples were weighed (± 0.001 mg) and loaded into tin cups. Samples were subsequently sent to Elemtex laboratories (Cornwall, UK), where analyses were performed using a Sercon 2020 isotope ratio mass spectrometer, coupled with a Thermo EA1110 elemental analyser. Stable isotope ratios are expressed in delta notation (δ) in parts per thousand (‰), following the equation:

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1\right) \times 100 \quad (1)$$

where X is ^{15}N or ^{13}C, and R is the ratio of heavy to light stable isotopes (i.e. ^{15}N:^{14}N, ^{13}C:^{12}C). The standards used for carbon and nitrogen were the Vienna Pee Dee Belemnite (VPDB) and atmospheric N_2 (AIR), respectively. Reference materials used were USGS 40, USGS 41, and BLS. The standard deviation was ± 0.19‰ and ± 0.16‰ for $\delta^{15}N$, and ± 0.15‰ and ± 0.05‰ for $\delta^{13}C$, for the 2016 and 2017 samples, respectively.

Lipid extraction and normalization model

Samples from 2016 and 2017 were treated in slightly different manners. From each 2016 sample, two aliquots were prepared: one aliquot was directly prepared for the SIA as described above, while in the second, lipids were extracted in cyclohexane following the method of Chouvelon et al. (2011), prior to the SIA. Lipid extraction is important in SIAs as lipids are depleted in ^{13}C compared to proteins (e.g. McConnaughey and McRoy 1979; Tieszen et al. 1983; Thompson et al. 2000); differences in fat content of tissues may mask prey preferences between individuals, hence confounding diet interpretation. Lipid extraction is therefore necessary for comparability of the samples. Extracting lipids can, however, alter $\delta^{15}N$ values, making it necessary to analyse both lipid- and non-lipid extracted samples. This increases the time and costs of analyses and lead to the development of lipid-normalization methods for $\delta^{13}C$ values. The following lipid-normalization model, modified from Kiljunen et al. (2006), was used to correct the $\delta^{13}C$ values from 2017.

$$L = \frac{93}{1 + (0.246 \times C{:}N - 0.775)^{-1}} \quad (2)$$

$$\delta^{13}C' = \delta^{13}C + D \times (I + \frac{3.9}{1+287/L}) \quad (3)$$

where L is the proportional lipid content of the sample and $\delta^{13}C'$ is the lipid-normalized $\delta^{13}C$ value. C and N are the proportions of elemental carbon and nitrogen in the sample, $\delta^{13}C$ is the measured carbon isotope value of the sample, D is the isotopic difference between protein and lipid (3.885 in this study), and I is a constant (-0.139 in this study). The parameters D and I were estimated to fit the observed data (i.e. the experimentally lipid-corrected $\delta^{13}C$ values from 2016 samples). To validate the modified model, lipid-normalized $\delta^{13}C$ values were estimated, observed vs predicted plots were produced (Figure 1A in Appendix A), and a modelling efficiency (EF; Mayer and Butler, 1993) was calculated as follows:

$$EF = 1 - \frac{\Sigma(y_i - \hat{y}_i)^2}{\Sigma(y_i - \hat{y}_i)^2} \quad (4)$$

where y_i is the observed value and $\hat{y}_i$ the predicted value. The modelling efficiency gives an indication of goodness of fit, with 1 corresponding to a perfect fit and values around 0 indicating a poor model performance. Negative *EF* values indicate that the average value of all measured values is a better predictor than the model used (Mayer and Butler 1993). Widely used models present in the literature (McConnaughey and McRoy 1979; Alexander et al. 1996) were inspected for comparison (Figure 1A & Table 1A in Appendix A). For consistency, the $\delta^{13}C$ correction from the modified model was applied to the 2016 samples as well.

2.2.2. Stomach contents

In the laboratory, the stomachs and intestines were thawed and cut open. Their contents were washed through a system of three interconnecting sieves of decreasing mesh sizes: 2.0, 1.0, and 0.5 mm. Invertebrates and hard remains of fish were preserved in 96% ethanol for later identification. Crustaceans were identified to the order level and a crude estimate of their numbers was determined based on carapaces, pairs of eyes, or other remains. When they were very numerous, a subsample was used. The biomass of ingested crustaceans was calculated using previously recorded mean weights of fresh specimens (U. Lindtstrøm, pers. comm.; see Table 4 notes). Cephalopod weight was back-calculated from the beak hood length using Clarke (1986) (Table 2A in Appendix A).

Sagittal otoliths were identified to the lowest taxonomic level possible using an otolith identification guide (Härkönen 1986) and a reference collection available at the IMR. Other hard remains of fish (e.g. vertebrae, jaw bones, secondary otoliths) were ignored in the presence of otoliths to avoid double counting (i.e. they were considered to be from the same fish as the otoliths), and were counted as "unidentified" individuals when they were found alone in samples. The 2016 material was analysed by the author while the 2017 material was analysed by a senior engineer (K. Windsland) and, consequently, slight differences exist in the method used. Digestion degrees were assigned to otoliths for the 2016 material for reference as follows: 0 for undigested, 1 for slightly digested, 2 for moderately digested, and 3 for very digested. Note that most of the contents were at least slightly digested, and a notable number of otoliths were broken, likely due to previous handling. Right and left otoliths were matched into pairs when both sides of the same species and of relatively similar size and digestion degree were present. The minimum number of individuals of each prey species was determined by adding the number of pairs to the number of remaining unpaired otoliths of the given species (i.e. matching left and right otoliths were counted as one fish together, while unpaired otoliths were counted as one fish each). When left- and right-side otoliths of the same species could not be distinguished, the total number of these otoliths was divided by two (i.e. one prey individual corresponded to two otoliths of undetermined side).

Otoliths were measured (± 0.01 mm) parallel to the sulcus (from the anterior tip of the rostrum to the posterior edge) using a Motic SWZ-168 stereomicroscope mounted with an ocular micrometer. For consistency, and because digestion degrees were not recorded for the 2017 material, the measurement of very digested otoliths was included. In cases where otoliths were very broken, the average length of otoliths from the same species was used. For the samples in which one prey species was represented by many otoliths (>100), a representative subsample of 30–70 measurable otoliths from that prey species was taken and the mean length was used as the length of the unmeasured otoliths. Otolith length to fish length and fish weight regressions from Härkönen (1986), and U. Lindstrøm and L. Lindblom (pers. comm.) were used to estimate the length and weight of the pre-ingested preys, respectively (Table 2A in Appendix A). For otoliths only identifiable with certainty to the family level (e.g. Gadidae), an educated guess (i.e. from identification or from the species distribution in the rest of the sample) was made to determine the most likely species and the corresponding regressions were used. In the case of ambiguity between several species, the average of the applicable regressions was used. No correction for erosion was made, as digestion degrees were not reported for all material; additionally,

determining digestion degrees and associated correction factors relies on subjective assessments. Eroded otoliths will therefore lead to underestimations of diverse extent, and all size and weight estimates must be considered minimum estimates. Note that length and weight of unidentifiable gadoid fishes will be particularly underestimated as the considerable digestion of their otoliths prevented the identification. Because most intestines were empty, or contained just one otolith, only stomach samples were considered in the analyses.

Stomach content analysis involves a certain degree of uncertainty and biases (e.g. Pierce and Boyle 1991; Pierce et al. 2007; Bowen and Iverson 2012). Often overlooked is the subjectivity of species identification and the consequent variations between readers, or over time by the same reader. Such intra- and inter-reader variability has never been quantified and is investigated in this thesis (Appendix B).

2.3. Data analysis

For the analyses of potential diet differences in time, samples collected in September–October 2016 were grouped together as "Autumn 2016", and samples collected in February–April 2017 as "Spring 2017". To explore spatial differences, the samples were divided into three geographical areas, following Aarefjord et al. (1995) for comparison: "northern Norway" (area 1), "mid-Norway" (area 2), and "southern Norway" (area 3) (Figure 1).

Data are presented as mean ± standard deviation unless stated otherwise. The level of statistical significance was set at $\alpha = 0.05$ for all analyses. All statistical analyses were performed with the software R, version 3.5.3 (R Core Team 2019), and plots were created with the packages *SIBER* (Jackson et al. 2011) and *ggplot2* (Wickham 2016).

2.3.1. Porpoise sample composition

The general composition of the porpoise samples was investigated in order to have a better overview of the dataset and the differences in the porpoises' biological characteristics (i.e. sex, age, length, weight) between sampling periods. Prior to statistical analyses, the data were tested for normality using Q-Q plots and a Shapiro-Wilk normality test. Homogeneity of variances (i.e. homoscedasticity) was evaluated with a Levene's test, which is robust to non-normality. Differences in age composition between the two sampling periods were tested using a Mann-Whitney U test. Differences in length and weight compositions between the two sampling

periods were investigated using a Welch's and a Student's t-tests, respectively. The Welch's t-test was used because the assumption of homoscedasticity was violated. Similarly, to test for differences in length and weight between male and female porpoises, a Mann-Whitney U test and a Welch's t-test were used, respectively.

2.3.2. Stable isotope analysis

Isotopic niche width

Stable isotope values are presented as biplots ($\delta^{13}C$ vs $\delta^{15}N$), which display the isotopic niche space (Newsome et al. 2007). The isotopic niches were investigated using metrics available in the Stable Isotope Bayesian Ellipses in R (SIBER) package (Jackson et al. 2011). Convex hulls (i.e. the smallest possible surface that encompasses all points) were constructed to estimate the total isotopic niche area (TA; expressed in $‰^2$) of the group of consumers. This metric can be interpreted as a measure of total diversity in the population or group studied; it is highly sensitive to the number of observations and must be interpreted with caution, in particular when comparing populations or groups of different sample sizes (Layman et al. 2007; Syväranta et al. 2013). To quantify isotopic niche widths, the standard ellipse area (SEA; expressed in $‰^2$) was used (Jackson et al. 2011). The SEA is equivalent to the univariate standard deviation and contains about 40% of the data, therefore representing the core isotopic niche of a population or group. An SEA corrected for sample size (SEA_C) was calculated as well. The SEA_C is considered robust for small sample sizes; sample size minima of 10 and 30 are recommended when the data follows a multivariate normal distribution and when it does not, respectively (Jackson et al. 2011; Syväranta et al. 2013). The SEA_C was used to visualize and calculate the degree of core isotopic niche overlap (CIO) between maturity classes, sexes, sampling periods, and sampling areas, following the equation (modified from Stasko et al. 2015):

$$CIO = \frac{\text{area of overlap between } SEA_{C1} \text{ and } SEA_{C2}}{(SEA_{C1} + SEA_{C2}) - \text{area of overlap between } SEA_{C1} \text{ and } SEA_{C2}} \times 100 \qquad (5)$$

A Bayesian estimation (Bayesian standard ellipse area; SEA_B), with corresponding 50, 75, and 95% credible intervals calculated using 10 000 iterations, was computed as well. The Bayesian framework uses probabilistic inference and allows quantification of uncertainty in isotopic niche widths by describing the range of possible values (posterior distribution), therefore overcoming differences in sample sizes (e.g. SEA_B exhibit more uncertainty with smaller sample size).

Standard ellipse areas were statistically compared by calculating the probability that the posterior distribution of one group's ellipse (SEA_{B1}) is larger (or smaller) than another's (SEA_{B2}). Multivariate normality was tested using Mardia's multivariate test from the *MVN* package (Korkmaz et al. 2014) and graphically with Q-Q plots. Three of the groups (area 1, area 2, and juveniles) did not meet the normality assumption but, since the sample size was large (n = 72, n = 47, and n = 74), SEA_C was robust to this violation.

Statistical analysis

Different statistical tests were used to investigate differences in isotopic values ($\delta^{15}N$ and $\delta^{13}C$) between maturity classes, sexes, time (sampling periods), and space (sampling areas). The parametric Student's t-test or the analysis of variance (ANOVA) were used when the assumptions of normality and homoscedasticity were met. Their non-parametric equivalent, Mann-Whitney U and Kruskal-Wallis tests, were used when they were not. Normality of the data (or the residuals in the case of the ANOVA) and homoscedasticity were assessed as in section 2.3.1. ANOVA and Kruskal-Wallis tests were used to compare more than two groups and were followed by a post-hoc Tukey's HSD (honest significant difference) or Dunn test, respectively. As multiple pairwise tests can lead to an increase in the type I error (i.e. rejection of a true null hypothesis), p-values were adjusted using the Bonferroni correction when necessary. The specific tests used for each variable and factor are presented in Table 2.

Notched boxplots were used to present differences in nitrogen and carbon stable isotope values separately between groups. Notches are a useful tool to visually compare groups; the notch displays the 95% confidence interval around the median and if two boxes' notches do not overlap there is "strong evidence" (95% confidence) that their medians differ. The relationship between porpoise length and stable isotope values was examined using linear regressions, with length as the explanatory variable and $\delta^{15}N$ and $\delta^{13}C$ as response variables.

TABLE 2: Summary of the statistical tests used to test for differences in $\delta^{15}N$ and $\delta^{13}C$ between maturity classes, sexes, and sampling periods and areas. The null hypothesis H_0 for normality is that the data, or residuals, follow a normal distribution. H_0 for homoscedasticity is that there is homogeneity of variance.

Variable – factor	No. of groups	Normality	Homoscedasticity	Tests
$\delta^{15}N$ – maturity status	3	H_0 not rejected	H_0 not rejected	ANOVA & Tukey's HSD
$\delta^{13}C$ – maturity status	3	H_0 not rejected	H_0 not rejected	ANOVA & Tukey's HSD
$\delta^{15}N$ – sex	2	H_0 not rejected	H_0 not rejected	Student's t-test
$\delta^{13}C$ – sex	2	H_0 not rejected	H_0 not rejected	Student's t-test
$\delta^{15}N$ – sampling period	2	H_0 not rejected	H_0 not rejected	Student's t-test
$\delta^{13}C$ – sampling period	2	H_0 rejected	H_0 rejected	Mann-Whitney U
$\delta^{15}N$ – sampling area	3	H_0 rejected	H_0 rejected	Kruskal-Wallis & Dunn test
$\delta^{13}C$ – sampling area	3	H_0 rejected	H_0 not rejected	Kruskal-Wallis & Dunn test

2.3.3. Stomach content analysis

Prey importance

Several indices are commonly used to measure the importance of prey species in diet studies, however, none of them give a complete overview of dietary composition (e.g. Hyslop 1980; Pierce and Boyle 1991; Cortés 1997; Liao et al. 2001). In this study, four feeding indices were used: (i) the frequency of occurrence, (ii) the relative frequency, (iii) the relative biomass, and (iv) a combined index:

(i) Frequency of occurrence: $$FO_i = \frac{S_i}{S_t} \times 100 \quad (6)$$

where S_i is the number of harbour porpoises (i.e. stomach samples) containing a prey group i, and S_t is the total number of non-empty samples.

(ii) Relative frequency: $$N_i = \frac{n_i}{n_t} \times 100 \quad (7)$$

where n_i is the number of individuals of a prey group *i*, and n_t the total number of individuals of all prey groups.

(iii) Relative biomass: $B_i = \frac{b_i}{b_t} \times 100$ (8)

where b_i is the total weight of a prey group *i*, and b_t is the total weight of individuals of all prey groups.

(iv) Combined index (Haug et al. 2007): $Q_i = \frac{B_i FO_i}{\sum_{i=1}^{m} B_i FO_i}$ (9)

where FO_i and B_i are the frequency of occurrence and relative biomass of a prey group *i*, respectively, and m is the number of prey groups. The combined index Q_i is a measure of "relative importance" that reduces the importance of large but rare prey items and increases the importance of smaller prey items that appear more frequently in the diet. This index contains information on both the contribution of prey groups to the nutrition of the predator (through weight consumed) and their frequency of occurrence in the stomachs, which gives a more balanced view of dietary importance.

Statistical analysis and visual representation

To investigate whether porpoises diversify their diet as they mature, differences in number of prey groups consumed between maturity classes were tested with a Pearson's Chi-square (χ^2) test. To obtain greater understanding of the biotic and abiotic factors that best explain variations in diet composition, a constrained ordination analysis was performed (e.g. Ter Braak and Verdonschot 1995; Legendre and Legendre 2012). A Detrended Correspondence Analysis (DCA) was used to examine the heterogeneity of the diet data and to determine the appropriate type of ordination model (Ter Braak and Prentice 1988). As there was a unimodal relationship (gradient length > 3) between the response matrix (dietary data) and the predictor matrix (explanatory variables), a Constrained Correspondence Analysis (CCA) was used (Legendre and Anderson 1999). A CCA is a direct gradient analysis that uses defined explanatory variables to explain the variation in the response variables. Prey biomasses (B_i) of relatively important or variable prey items (capelin, herring, mackerel, blue whiting, cod, saithe, silvery pout *Gadiculus argenteus thori*, *Trisopterus* spp., and whiting) were used as response variables, while the

porpoise maturity status, sex, and bycatch area (i.e. northern Norway, mid-Norway, or southern Norway) were used as explanatory variables. Sampling period was not included due to the unbalanced sampling. The response variables (the prey biomasses) were Hellinger-transformed prior to analysis to normalize the data, and lessen differences in variance and the effects of outliers. The explanatory variables were treated as nominal variables. The significance of the multivariate model, as well as that of each explanatory variable, was tested using a Monte Carlo permutation test (1000 permutations). The CCA was performed in R with the package *vegan* (Oksanen et al. 2019). As the CCA requires at least one non-zero value per row in the diet matrix, rows with a total biomass equal to zero were removed from the analysis, leaving a reduced dataset of n = 105. CCAs are commonly used in community ecology, e.g. to explore the environmental gradients explaining community composition, but have rarely been applied in diet studies, in particular for marine mammals (e.g. Labansen et al. 2007; Lundström et al. 2007, 2010; Lindstrøm et al. 2013).

To examine the effects of each factor (i.e. maturity status, sex, sampling period, and sampling area) on diet composition in more detail, univariate analyses were performed. For visual representation, the relatively most important or variable prey items were selected for each factor. For simplification, gadoid prey items with a combined index (Q_i) inferior to 2% were grouped with any unidentified gadoids into "Gadidae". Rare or relatively unimportant prey species were grouped into "other fishes", which included daubed shanny (*Leptoclinus maculatus*), haddock (*Melanogrammus aeglefinus*), hake (*Merluccius merluccius*), lanternfish (Myctophidae spp.), redfish (*Sebastes* spp.), sandeels (*Ammodytes* spp.), snailfish (Liparidae spp.), and snakeblenny (*Lumpenus lampretaeformis*). Invertebrates were negligible and therefore not included.

The length distributions of prey species that contributed more than 1% of the diet's relative importance (Q_i) (silvery pout, cod, capelin, herring, mackerel, blue whiting, and saithe) are displayed. *Trisopterus* species, not identifiable to the species level, were omitted, as the average of the Norway pout (*Trisopterus esmarkii*) and poor cod (*Trisopterus minutus*) equations was used to estimate the size of the consumed fish. Unidentified gadoids were also not included.

3. RESULTS

3.1. Porpoise sample composition

This study included a total of 134 harbour porpoises, bycaught in September–October 2016 (n = 73) and February–April 2017 (n = 61) along the Norwegian coast (Figure 1). The males dominated the bycatches in both 2016 (n_{males} = 42, $n_{females}$ = 31) and 2017 (n_{males} = 34, $n_{females}$ = 27) (Table 3). Calves and juveniles comprised 69% of the porpoises. The ages of all porpoises ranged from 0.2 to 12.7 years old, with an average of 3.7 ± 2.8 (mean ± standard deviation). There was a statistically significant difference in age between the two sampling periods (Mann-Whitney U test: U = 1147, p-value < 0.001), with the porpoises from Spring 2017 being older than the ones from Autumn 2016. Among the calves, i.e. porpoises less than one year old, the majority (n = 17) were bycaught in Autumn 2016, while the oldest porpoises were bycaught in Spring 2017. Harbour porpoise length ranged from 101 to 173 cm (138.6 ± 15.8 cm) and weight ranged from 17 to 74 kg (42.6 ± 12.1 kg). Overall, the individuals bycaught in 2017 were significantly bigger, both in terms of length and weight, than the ones sampled in 2016 (Welch's t-test (length): t = -3.03, df =129.4, p = 0.003; Student's t-test (weight), t = -3.52, df =132, p < 0.001), and females were significantly longer and heavier than males (Mann-Whitney U test (length): U = 1615.5, p = 0.008; Welch's t-test (weight): t = -2.97, df = 98.9, p = 0.004). Sampling and biological information are summarized by year and sex in Table 3.

TABLE 3: Sampling information (n = sample size) and characteristics of individual harbour porpoises bycaught along the Norwegian coast. Values are presented as ranges for sampling month, latitude, and longitude, and as mean ± standard deviation for age, length, and weight.

Year	Sex	n	Month	Latitude range (DD)	Longitude range (DD)	Age	Length (cm)	Weight (kg)
2016		73	9–10	59.07–70.16	4.28–22.28	2.6 ± 2	135.1 ± 17.4	39.4 ± 12.5
	M	42	-	-	-	2.4 ± 1.9	131.2 ± 15.5	36.2 ± 9.2
	F	31	-	-	-	2.8 ± 2	140.6 ± 17.9	43.8 ± 14.9
2017		61	2–4	69.47–71.05	17.18–29.03	5 ± 3	142.9 ± 12.6	46.4 ± 10.3
	M	34	-	-	-	5.7 ± 3.5	140.9 ± 10.3	44.5 ± 8.4
	F	27	-	-	-	4 ± 2	145. 5 ± 14.7	48.9 ± 12.1

3.2. Stable isotope analysis

A total of 133 muscle samples were used for the stable isotope analysis (note: one sample from 2016 was missing). One individual showed particularly high values of $\delta^{15}N$ and $\delta^{13}C$ ($\delta^{15}N$ = 15.9‰ and $\delta^{13}C$ = -18.65‰); it was considered to be an outlier and removed from further analyses. Among the remaining porpoises, individual $\delta^{15}N$ values ranged from 11.12 to 14.22‰ (12.64 ± 0.6‰) and $\delta^{13}C$ (lipid corrected) values ranged from -21.31 to -19.25‰ (-20.21 ± 0.39‰).

3.2.1. Ontogenetic variation in stable isotope values

The core isotopic niches, represented by the standard ellipse areas (SEA, ‰^{2}), of juvenile and adult harbour porpoises were similar (Figure 2). The standard ellipse area corrected for sample size (SEA_C) was 0.60‰^{2} for juveniles and 0.58‰^{2} for adults, and a nearly 50% overlap in the core isotopic niches was observed. Conversely, calves showed a larger SEA_C (1.02‰^{2}) but little overlap with the core isotopic niches of older porpoises (CIO = 13.6 and 16.0% with juveniles and adults, respectively). This separation between calves and juveniles/adults was driven by higher $\delta^{15}N$ and lower $\delta^{13}C$ values in calves. Based on Bayesian iterations, there was a nearly 100% probability that the Bayesian standard ellipse area (SEA_B) decreased from calves to juveniles or adults. For each maturity class, SEA_B and SEA_C showed the same trend (Figure 2B). Individual variation in isotopic values was greater in juveniles (TA = 3.64‰^{2}), followed by calves (TA = 2.72 ‰^{2}), and adults (TA = 2.48‰^{2}).

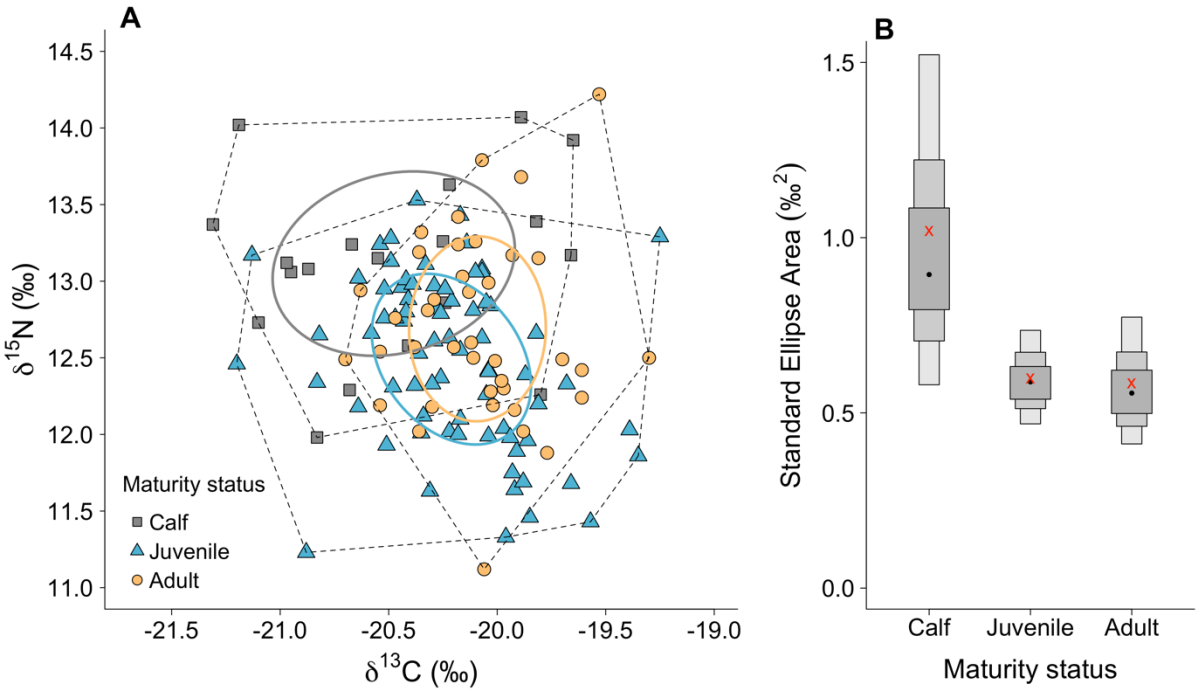

FIGURE 2: A) Bivariate stable isotope plot ($\delta^{13}C$ versus $\delta^{15}N$) with associated convex hulls (TA; dashed lines) and sample-size corrected standard ellipses (SEA_c; solid lines) of calf (grey squares), juvenile (blue triangles), and adult (orange circles) harbour porpoises bycaught along the Norwegian coast in September–October 2016 and February–April 2017. Standard ellipses include approximately 40% of the data and represent the core isotopic niches. B) Estimated posterior distribution of Bayesian standard ellipses (SEA_B), with grey-shaded density plots representing the 50%, 75% and 95% credible intervals. The black dots represent the mode, or most likely solution, of the SEA_B, and the red crosses represent the standard ellipse area corrected for sample size (SEA_C).

The $\delta^{15}N$ values ranged from 11.98 to 14.07‰ (13.11 ± 0.58‰) in calves, from 11.23 to 13.53‰ (12.49 ± 0.55‰) in juveniles, and from 11.12 to 14.22‰ (12.69 ± 0.59‰) in adults (Figure 3A). Similarly, the $\delta^{13}C$ values ranged from -21.31 to -19.65‰ (-20.48 ± 0.54‰) in calves, from -21.20 to -19.25‰ (-20.21 ± 0.36‰) in juveniles, and from -20.70 to -19.30‰ (-20.09 ± 0.31‰) in adults (Figure 3B). Adults showed the widest range in nitrogen and the narrowest range in carbon stable isotope values. Statistically significant differences between maturity classes were found for both $\delta^{15}N$ and $\delta^{13}C$ (ANOVA: $\delta^{15}N$, $F = 9.43$, $df = 2$, $p = 0.002$; $\delta^{13}C$, $F = 6.71$, $df = 2$, $p = 0.002$). In particular, calves' $\delta^{15}N$ were significantly higher than those of juveniles' and adults' (Tukey HSD post-hoc test: calves vs juveniles, $p = 0.022$, and calves vs adults, $p = 0.001$), while $\delta^{13}C$ values were significantly lower in calves (calves vs juveniles, $p = 0.019$, and calves vs adults, $p = 0.001$). There was no statistically significant difference between either the nitrogen or carbon stable isotope values of juveniles and adults (Tukey post-hoc test: $\delta^{15}N$, $p = 0.18$; $\delta^{13}C$, $p = 0.24$). Stable isotope values by maturity status had relatively similar

trends in each area (Figure C1 in Appendix C). Note that violin plots were used rather than boxplots due to the small sample size of some groups.

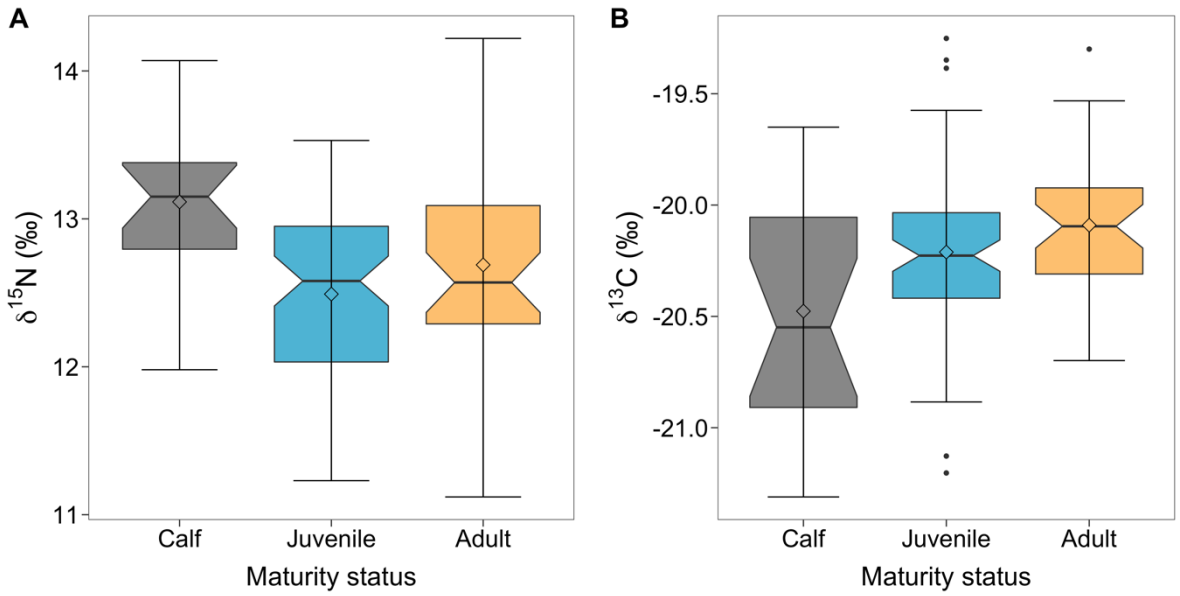

FIGURE 3: Notched boxplots of $\delta^{15}N$ (A) and $\delta^{13}C$ (B) values plotted against maturity status. The lower and upper hinges correspond to the first and third quartiles (i.e. 25th & 75th percentiles), and the whiskers extend to the largest value no further than 1.5 times the interquartile range (i.e. distance between the first and third quartiles). The median (full line), mean (diamond), and outliers (dots) are represented. The notches roughly represent the 95% confidence interval around the median and are used to compare groups: if the notches of two boxes overlap, it suggests that the medians are not significantly different.

There was no significant linear relationship between $\delta^{15}N$ values and length ($F = 3.12$, $df = 1$, $R^2 = 0.023$, $p = 0.08$) (Figure 4A). Conversely, porpoises displayed a weak but significant positive linear relationship between $\delta^{13}C$ and length ($F= 14.47$, $df = 1$, $R^2 = 0.10$, $p < 0.001$) (Figure 4B). Smaller individuals showed lower $\delta^{13}C$ values while larger individuals had higher $\delta^{13}C$ values in each area (Figure C2 in Appendix C).

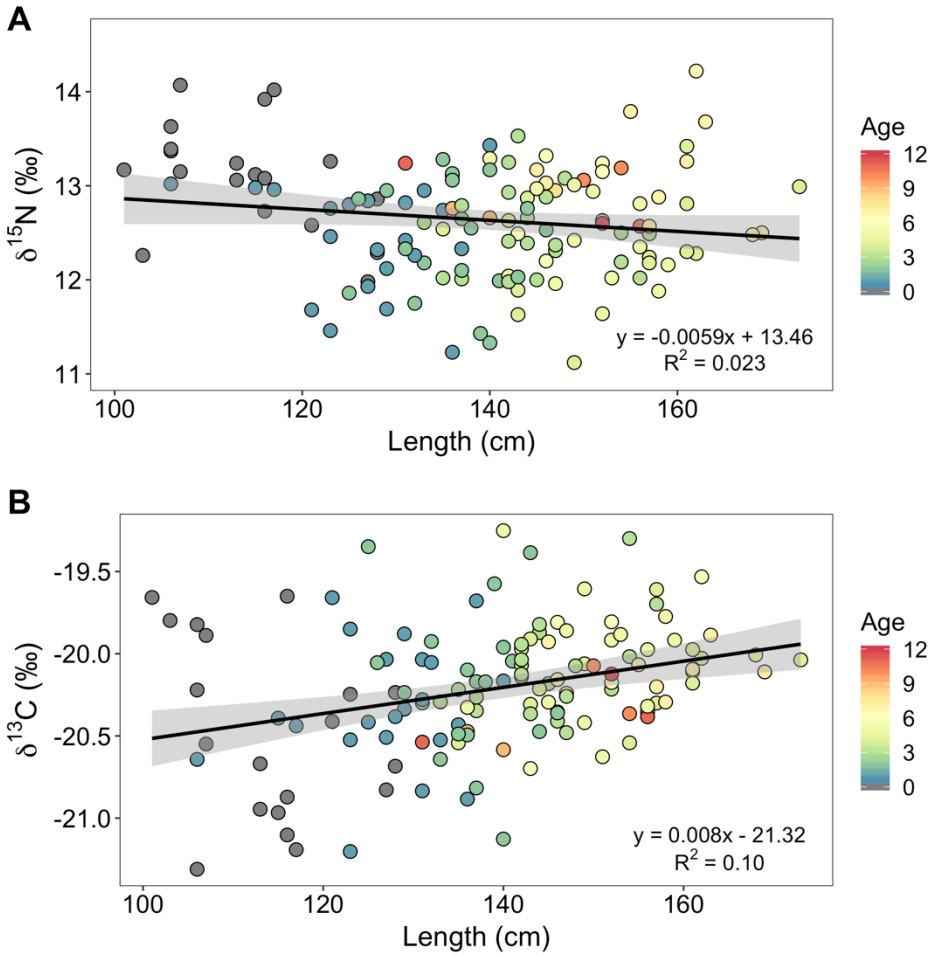

FIGURE 4: Scatter plots of harbour porpoise stable isotope data, $\delta^{15}N$ (A) and $\delta^{13}C$ (B), against length. Linear regressions with their respective equation and R^2 value are shown. The grey shaded areas represent the 95% confidence interval around the linear regression lines.

Carbon stable isotope values were corrected for the observed effect of length to further investigate sexual, temporal, and spatial variations. This correction was done using the following equation (MacKenzie 2010):

$$\widehat{Y}_i = \left[\frac{y_i}{\hat{y}_i}\right]\overline{y_0} \qquad (10)$$

where Y_i is the length-corrected $\delta^{13}C$ value, y_i is the initial $\delta^{13}C$ value of individual i, $\hat{y}_i$ is the expected $\delta^{13}C$ value of individual i given the regression equation shown in Figure 4 ($y = 0.008(x) - 21.32$), and $\overline{y_0}$ is the calculated $\delta^{13}C$ value for the mean length of all porpoises ($\overline{y_0} = 0.008(\overline{x}) - 21.32$).

3.2.3. Sexual variation in stable isotope values

The core isotopic niches of males and females were similar in size (SEA_{Cmale} = 0.66‰^{2}, $SEA_{Cfemale}$ = 0.74‰^{2}) and overlapped by 76.4% (Figure 5A). Additionally, both sexes showed important variation between individuals, with large and almost equal convex hull areas: TA = 4.06‰^{2} for males and TA = 3.90‰^{2} for females. The SEA_C was larger in females, while SEA_B was larger in males, but the uncertainty of the SEA_Bs overlapped (Figure 5B).

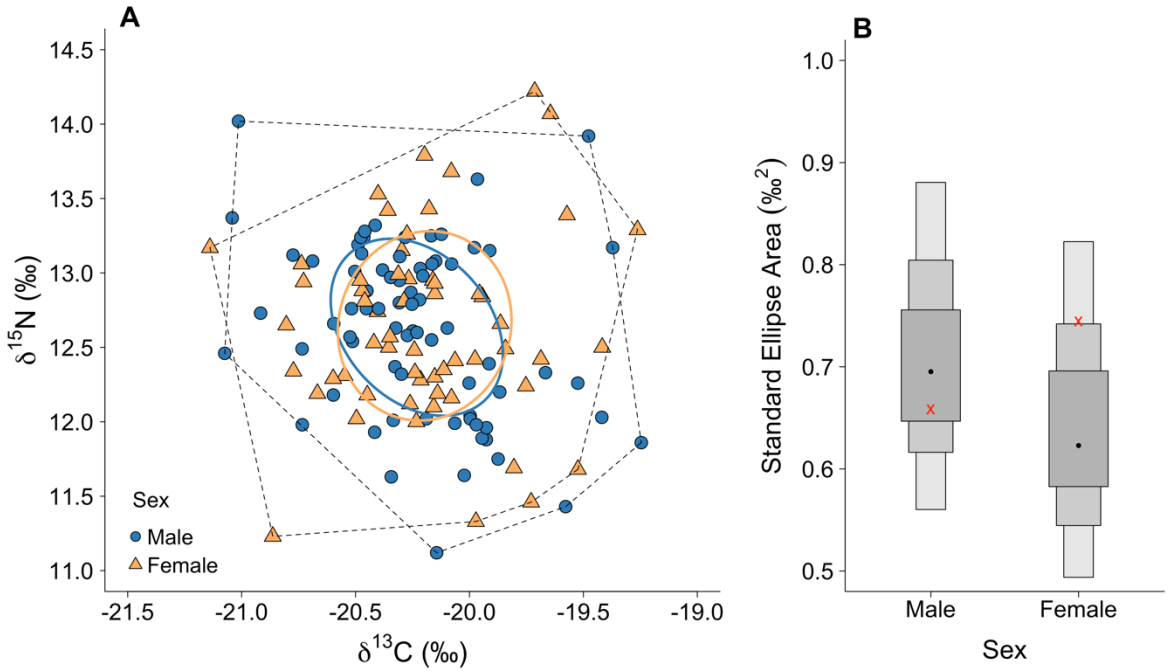

FIGURE 5: A) Bivariate stable isotope plot (length-corrected $\delta^{13}C$ versus $\delta^{15}N$) with associated convex hulls (dashed lines) and SEA_C (solid lines) of male (blue circles) and female (orange triangles) harbour porpoises, and B) estimated posterior distribution of Bayesian standard ellipses (SEA_B), as in Figure 2.

The $\delta^{15}N$ values ranged from 11.12 to 14.02‰ (12.64 ± 0.58‰) in males and from 11.23 to 14.22‰ (12.64 ± 0.62‰) in females. Similarly, $\delta^{13}C$ ranged from - 21.07 to -19.25‰ (-20.23 ± 0.37‰) for males and from -21.14 to -19.26‰ (-20.20 ± 0.37‰) for females (Figure 5A). There was no statistically significant difference between sexes for either $\delta^{15}N$ (Student's t-test: t = -0.09, df = 130, p = 0.93) or $\delta^{13}C$ (t = -0.53, df = 130, p = 0.60), supporting the isotopic niche width findings. Stable isotope values of males and females were similar in each area as well (Figure C3 in Appendix C).

3.2.4. Temporal variation in stable isotope values

The lack of a full factorial sampling design prevented the resolution of plausible temporal and spatial effects on diet and stable isotope composition. Instead, the temporal variation in $\delta^{15}N$ and $\delta^{13}C$ values was explored by comparing samples collected in the same sub-area (i.e. Troms county, between ~ 68.55 and 70.2 °N, and below 24 °E. See Figure 1) in Autumn (September–October) 2016 and Spring (February–April) 2017.

The individual variation in isotopic values was greater in porpoises bycaught in autumn than in spring, as reflected in the convex hull areas; TA = 1.18‰^{2} and TA = 0.76‰^{2} in autumn and spring samples, respectively (Figure 6A). Additionally, the core isotopic niche of harbour porpoises bycaught in Autumn 2016 was about 2.5 times larger than that of porpoises bycaught in Spring 2017, with a SEA_C of 0.57‰^{2} compared to 0.21‰^{2}. The Bayesian statistics indicated a nearly 100% probability that porpoises bycaught in autumn had a larger isotopic niche than the ones bycaught in spring (Figure 6B). The overlap between core isotopic niches of porpoises from the two sampling periods was only of 6%.

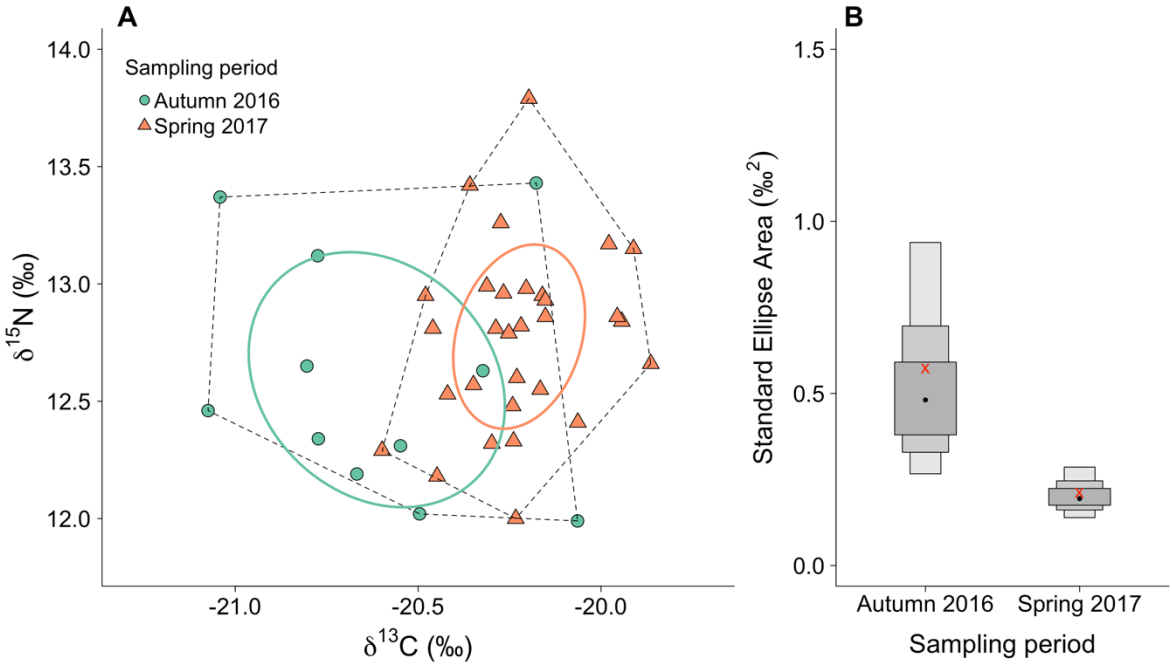

FIGURE 6: A) Bivariate stable isotope plot (length-corrected $\delta^{13}C$ versus $\delta^{15}N$) with associated convex hulls (dashed lines) and SEA_C (solid lines) of harbour porpoises bycaught in Autumn 2016 (green circles) and Spring 2017 (orange triangles), and B) estimated posterior distribution of Bayesian standard ellipses (SEA_B), as in Figure 2.

The $\delta^{15}N$ values ranged from 11.99 to 13.43‰ (12.59 ± 0.51‰) in Autumn 2016 and from 12 to 13.79‰ (12.78 ± 0.38‰) in Spring 2017, while $\delta^{13}C$ values ranged from -21.07 to -20.06‰ (-20.61 ± 0.33‰) in autumn and from -20.60 to -19.86‰ (-20.22 ± 0.18‰) in spring (Figure 7). The previously described difference in isotopic niche widths was mainly driven by differences in $\delta^{13}C$ ranges, with the porpoises from Autumn 2016 showing a larger variation in carbon stable isotope values (Levene test: $F = 7.01$, $df = 1$, $p = 0.011$). The harbour porpoises bycaught in Spring 2017 had significantly higher $\delta^{13}C$ values than those bycaught in Autumn 2016 (Mann-Whitney U test: $U = 53$, $p < 0.001$) while there was no statistically significant difference in $\delta^{15}N$ between autumn and spring (Student's t-test: $t = -1.24$, $df = 39$, $p = 0.22$).

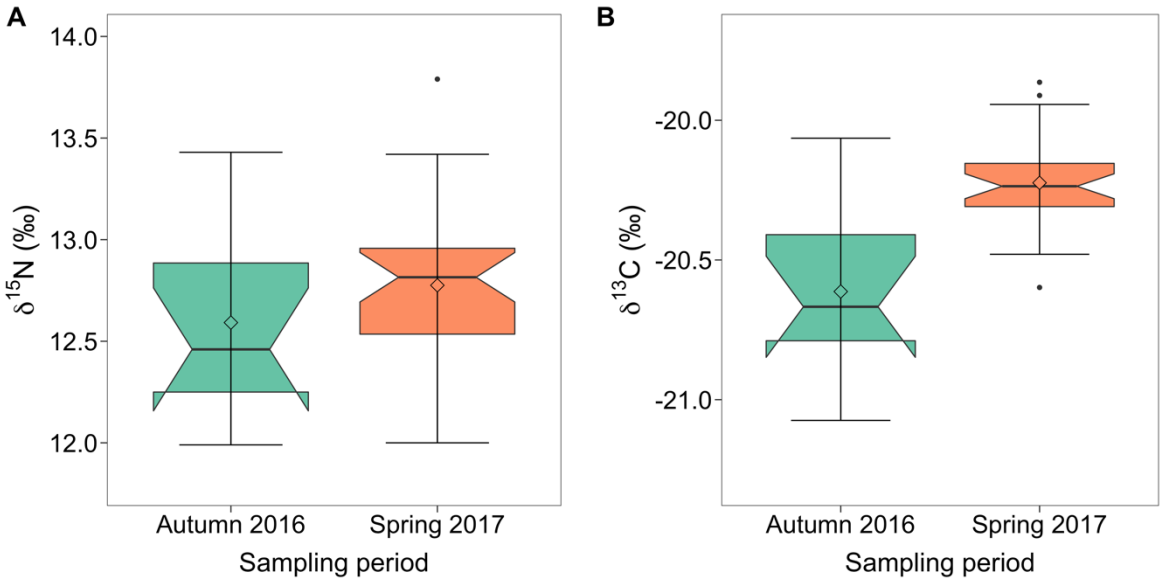

FIGURE 7: Notched boxplots of $\delta^{15}N$ (A) and length-corrected $\delta^{13}C$ (B) plotted against sampling period, as in Figure 2. Note that the odd behaviour of the lower notches means that the 95% confidence interval around the median is larger than the interquartile range.

3.2.5. Spatial variation in stable isotope values

Ellipse analysis showed distinct patterns between the different sites, in particular between northern and southern Norway (i.e. areas 1 and 3) (Figure 8). There was 4.3% overlap in corrected standard ellipse areas (SEA_C) between areas 2 (mid-Norway) and 3, and none between areas 1 and 3. Areas 1 and 2 overlapped at 17.4%. Area 2 displayed the highest variation in $\delta^{15}N$ and $\delta^{13}C$, with the largest convex hull area ($TA = 3.99‰^2$) compared to areas 1 and 3 ($TA = 2.03‰^2$ and $TA = 1.73‰^2$). Porpoises from area 3 showed the largest niche width, with a SEA_C of $0.85‰^2$. Area 2 presented a relatively large niche width as well, with $SEA_C = 0.71‰^2$. This was twice as large as the SEA_C for area 1 ($0.35‰^2$), where porpoises had the narrowest

niche width. Based on Bayesian iterations, there was a 100% probability that porpoises from area 2 and 3 showed a larger core isotopic niche than porpoises from area 1, while there was a 65% probability that porpoises from area 3 had a larger core isotopic niche than porpoises from area 2 (Figure 8B).

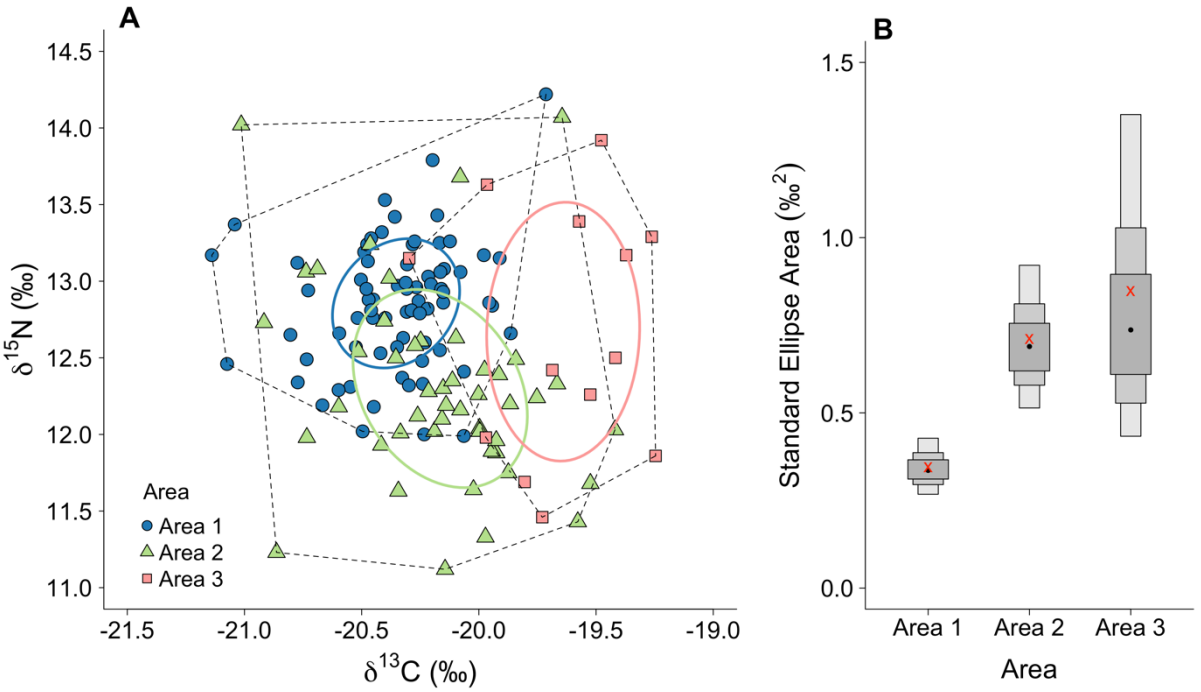

FIGURE 8: A) Bivariate stable isotope plot (length-corrected $\delta^{13}C$ versus $\delta^{15}N$) with associated convex hulls (dashed lines) and SEA_C (solid lines) of harbour porpoises bycaught in northern Norway (blue circles – area 1), in mid-Norway (green triangles – area 2), and in southern Norway (pink squares – area 3), and B) estimated posterior distribution of Bayesian standard ellipses (SEA_B), as in Figure 2.

Nitrogen stable isotope values ranged from 11.99 to 14.22‰ (12.86 ± 0.41‰), from 11.12 to 14.07‰ (12.30 ± 0.63‰) and from 11.46 to 13.92‰ (12.67 ± 0.80‰) for porpoises bycaught in areas 1, 2, and 3, respectively (Figure 9A). Similarly, carbon stable isotope values ranged from -21.14 to -19.71‰ (-20.35 ± 0.27‰) in northern Norway, from -21.01 to -19.42‰ (-20.16 ± 0.36‰) in mid-Norway, and from -20.30 to -19.25‰ (-19.64 ± 0.31‰) in southern Norway (Figure 9B). Both $\delta^{15}N$ and $\delta^{13}C$ values differed significantly between areas (Kruskal-Wallis test: $\delta^{15}N$, $\chi^2 = 28.51$, df = 2, $p < 0.001$; $\delta^{13}C$, $\chi^2 = 34.63$, df = 2, $p < 0.001$). In particular, porpoises from area 2 displayed significantly lower $\delta^{15}N$ values than porpoises from area 1 (post hoc Dunn test with Bonferroni correction: $\chi^2 = 28.51$, df = 2, $p < 0.001$). There were no significant differences in nitrogen stable isotope values between areas 1 and 3 (post hoc Dunn test with Bonferroni adjustment: $\chi^2 = 28.51$, df = 2, $p = 0.82$) and between areas 2 and 3 (post

hoc Dunn test with Bonferroni adjustment: $\chi^2 = 28.51$, df = 2, p = 0.098). The $\delta^{13}C$ values differed significantly between areas, and increased from northern to southern Norway (post-hoc Dunn test with Bonferroni adjustment: area 1 vs area 2, $\chi^2 = 34.63$, df = 2, p = 0.005; area 1 vs area 3, $\chi^2 = 34.63$, df = 2, p < 0.001; area 2 vs area 3, $\chi^2 = 34.63$, df = 2, p = 0.001).

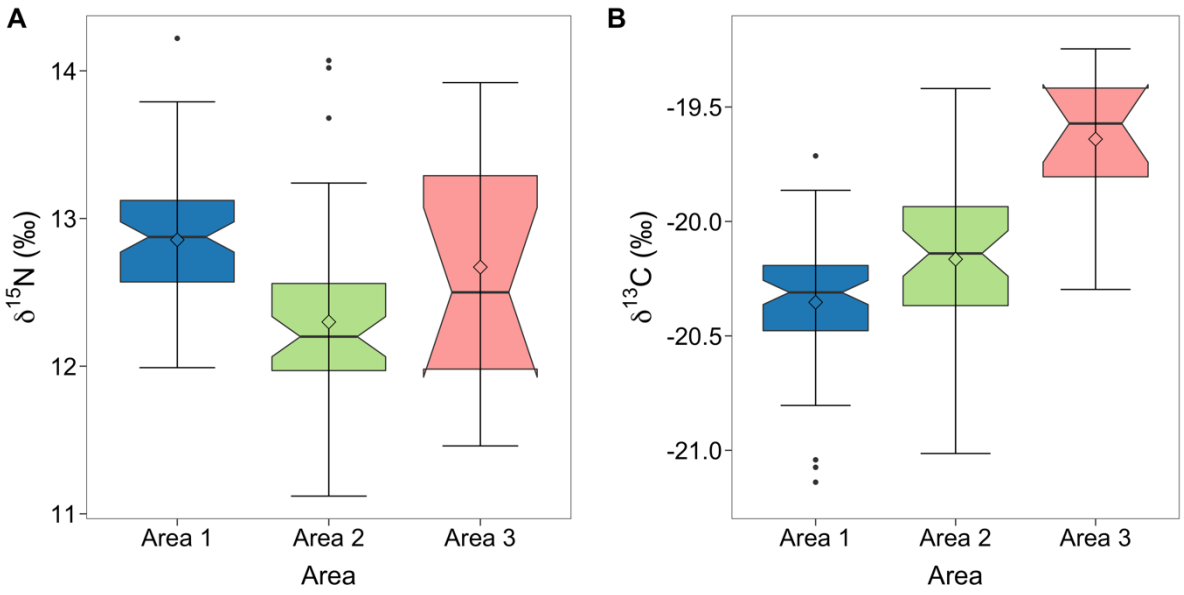

FIGURE 9: Notched boxplots of $\delta^{15}N$ (A) and length-corrected $\delta^{13}C$ (B) plotted against sampling area, as in Figure 2. Note that the odd behaviour of the lower notches means that the 95% confidence interval around the median is larger than the interquartile range.

3.3. Stomach content analysis

3.3.1. Overall diet composition

Of the 134 stomachs from harbour porpoises bycaught in Norwegian coastal waters, 12 (i.e. 9%) were empty. A total of 4157 prey individuals were found, of which only 0.1% were not identifiable. The total reconstructed biomass of the identified stomach contents was ca. 99.1 kg (Table 4).

The stomach contents comprised a wide range of fish species and some invertebrates, with a total of 23 different prey items found (Table 4). This included 19 fish groups, of which 12 were identified to the species level and 6 to the family or genus level; the last group consists of non-identifiable fish remains. Fish largely dominated the diet, both in terms of relative numerical abundance (N_i = 87.3%) and biomass (B_i = 99.1%). Fish remains occurred in 96.3% of the non-

empty stomachs and consisted principally of sagittal otoliths. Invertebrates prey were scarce and occurred in 18.7% of the stomachs with prey remains, accounting for 12.7% of the relative numerical abundance and 0.9% of the reconstructed biomass. One individual had eaten one squid and plastic material was found in the stomach of a juvenile porpoise.

The harbour porpoise diet was dominated by gadoid fish species (Table 4), which occurred in 83.7% of the non-empty stomachs and accounted for more than two-thirds of the diet regardless of the feeding index (N_i = 67.1%, B_i = 83.7%, Q_i = 92.6%). Unidentified gadoids were found in more than half the stomachs containing prey remains (FO_i = 57.7%); however, they constituted merely 3% of the diet's relative importance, according to the combined index (Q_i). Excluding the unidentified gadoids, saithe and *Trisopterus* spp. were the most common prey items with a frequency of occurrence of ca. 43.9 and 35.0%, respectively. Saithe was also the dominant prey species in terms of biomass (B_i = 57.5%), and when considering the relative importance, the dominance of saithe was even more pronounced (Q_i = 72.9%). *Trisopterus* spp. was the most numerous prey item (N_i = 22%), but the second most important prey group (Q_i = 8.5%), followed by blue whiting (Q_i = 5.2%). Lipid-rich prey species, i.e. capelin, herring, and mackerel, were not very common (FO_i = 21.1, 15.4, and 9.8%, respectively) and had relatively low importance in the general diet (Q_i = 3.9, 2.3, and 1.0%, respectively). Sandeels and daubed shanny were present in 11.8% and 8.1% of the stomachs, respectively, but were of virtually no importance in the diet (Q_i < 0.1%). Rare fish prey items included redfish, haddock, hake, snakeblenny, snailfish, and lanternfish. Krill appeared in about 16.3% of the stomachs but were negligible in terms of relative importance (Q_i < 0.1%). The other invertebrate groups were found in only one stomach each (FO_i = 0.8%) and their contribution to the diet was negligible as well, regardless of the feeding index considered (Table 4).

TABLE 4: Overall diet composition of 134 harbour porpoises bycaught along the Norwegian coast in 2016 and 2017. The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	Number of prey	FO_i (%)	N_i (%)	B_i (%)	Q_i (%)
Fishes					
Ammodytidae					
Ammodytes spp.[a]	104	11.79	2.50	0.27	0.09
Clupeidae					
Clupea harengus	92	15.45	2.21	5.06	2.26
Gadidae					
Gadiculus argenteus thori	323	26.83	7.77	1.80	1.40
Gadus morhua	210	21.95	5.05	1.83	1.16
Melanogrammus aeglefinus	3	0.81	0.07	0.83	0.02
Merlangius merlangus	224	21.14	5.39	0.82	0.50
Micromesistius poutassou	181	17.07	4.35	10.49	5.18
Pollachius virens	295	43.90	7.09	57.48	72.92
Trisopterus spp.[b]	916	34.96	22.03	8.39	8.47
Unidentified gadoids[c]	639	57.72	15.37	1.79	2.98
Stichaeidae					
Leptoclinus maculatus	38	8.13	0.91	0.19	0.04
Lumpenus lampretaeformis	2	1.63	0.05	<0.01	<0.01
Liparidae spp.	2	1.63	0.05	0.02	<0.01
Merlucciidae					
Merluccius merluccius	4	1.63	0.10	0.10	<0.01
Myctophidae spp.[d]	8	2.44	0.19	–	–
Osmeridae					
Mallotus villosus	452	21.14	10.87	6.39	3.90
Scorpaenidae					
Sebastes spp.	1	0.81	0.02	0.02	<0.01
Scombridae					
Scomber scombrus	129	9.76	3.10	3.67	1.03
Unidentified fish remains	5	4.07	0.12	–	–
Invertebrates					
Decapoda[e]	13	0.81	0.31	0.03	<0.01
Euphausiacea					
Euphausiidae spp.[f]	515	16.26	12.39	0.06	0.03
Cephalopoda	1	0.81	0.02	0.79	0.02
Unidentified invertebrates	1	0.81	0.02	–	–
Total Fishes	**3628**	**96.34**	**87.25**	**99.13**	**99.83**
Total Invertebrates	**530**	**18.70**	**12.75**	**0.87**	**0.17**
All prey	**4158**				

[a]The length-weight regression for *Ammodytes marinus* was used. [b]Either *Trisopterus minutus* or *Trisopterus esmarkii*, which were considered indistinguishable; the average of the respective equations was used. [c]Unidentified gadoids were too digested to make a precise identification to the species level; regressions of the most likely species were used. [d]No regression was available. [e]Assumed average weight of 0.2 g (U. Lindstrøm, pers. comm.). [f]Assumed average weight of 0.115 g (U. Lindstrøm, pers. comm.).

While up to 9 prey groups were found in an individual stomach, the majority of harbour porpoise (69%) stomachs contained between 1 and 4 different prey groups (Figure 10). There was no significant differences in number of prey groups ingested by different maturity classes when all were considered ($\chi^2 = 28.79$, df = 18, p = 0.051), nor when they were tested against each other with a post-hoc test (Chi square post-hoc test with Bonferroni adjustment: calf vs juvenile, p = 0.084; calf vs adult, p = 0.24; juvenile vs adult, p = 0.63). Although there were not statistically significant, differences could be observed in the distribution of number of prey groups consumed by the different maturity classes. Calves were highly skewed towards few prey groups, with 85% (i.e. 17 out of 20 individuals) consuming between 0 and 2 prey groups. In contrast, adults displayed a more homogenous distribution in the number of prey groups eaten, and 41% of the mature porpoises showed stomach contents composed of 0–2 different prey groups. Juveniles showed less of a skewed distribution in number of prey groups as well, although almost half (45%) of the individuals consumed prey items from 0–2 prey groups, with most of these juveniles eating from one single prey group, and very few individuals had eaten between 7 and 9 prey groups.

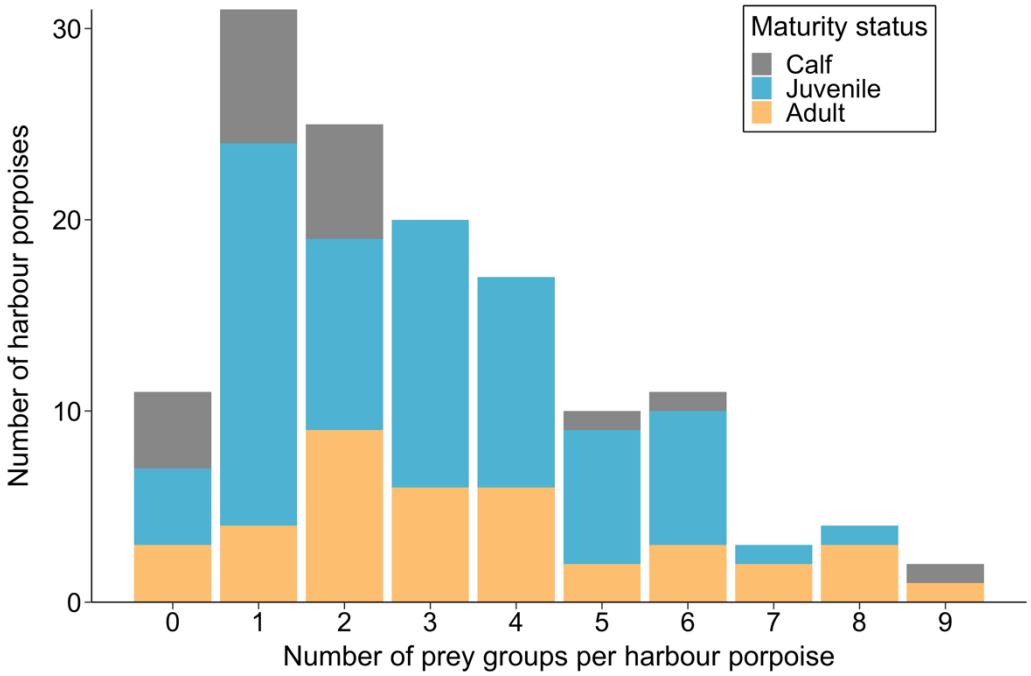

FIGURE 10: Number of different prey groups found in each stomach of the 134 harbour porpoises bycaught along the Norwegian coast in September–October 2016 and February–April 2017. Porpoises are divided into three maturity classes: calves (grey), juveniles (blue), and adults (orange).

The factors potentially explaining variations in diet composition were explored with a CCA. The CCA, with maturity status, sex, and sampling area as predictor variables, explained about 11.2% of the total variation in selected prey biomass (with Hellinger-transformed data) (Figure 11), 75% of which was explained by the first two axes. The first axis explained ca. 51% of the constrained variation (i.e. 5.7% of the total variation) and was related to geographical covariates. The second axis explained ca. 24% of the constrained variation (2.7% of the total) in the model and separated maturity classes. Differences in the diet composition of calves (StageC) explained most of the variation on the second axis. Area and maturity status were statistically significant (Monte-Carlo permutation test: area, F = 3.67, df = 2, p = 0.001; maturity status, F = 1.88, df = 2, p = 0.032), while sex did not explain a significant part of the variation (F = 1.35, df = 1, p = 0.20).

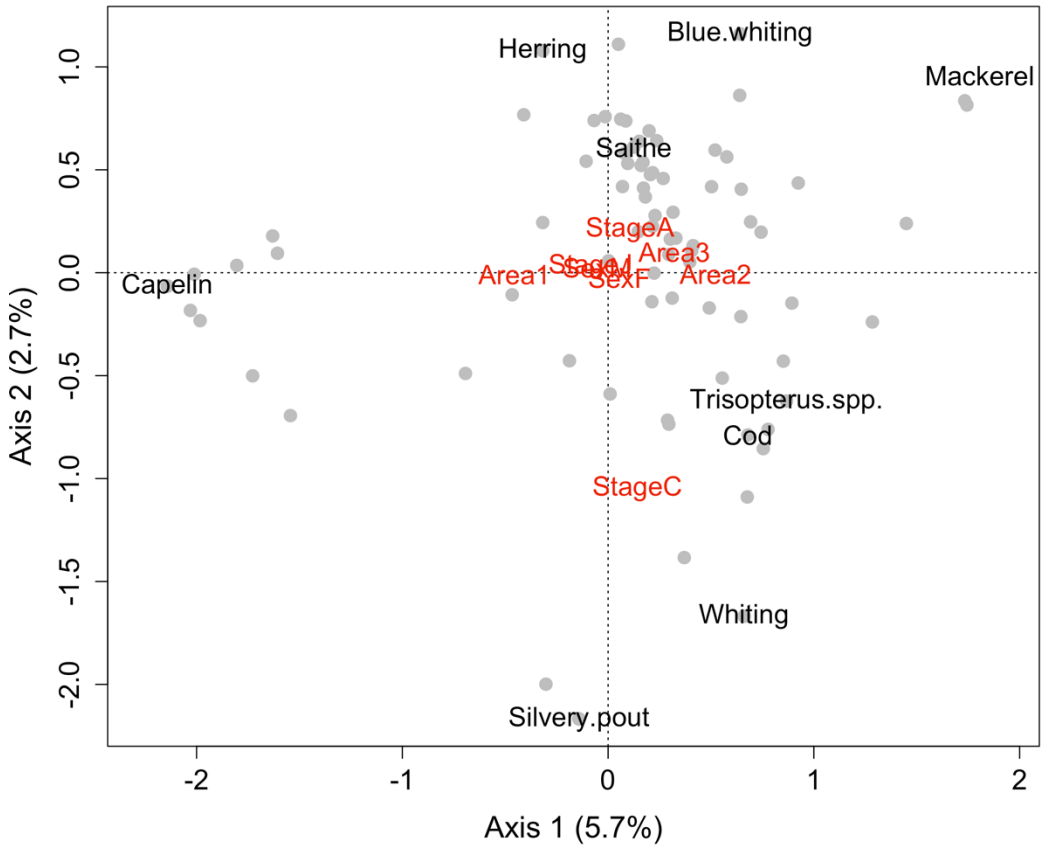

FIGURE 11: Canonical correspondence analysis (CCA) ordination biplot on reconstructed biomass (Hellinger-transformed) of selected prey species of harbour porpoises bycaught in Norwegian coastal waters (2016–2017). The porpoise individuals (grey dots), response variables (prey species – black) and explanatory variables (maturity status, sex, and area - red) are represented. The explanatory variables, being categorical, are displayed as a centroid. The explanatory variables explained 11.2% of the total variance in prey biomass. The first axis accounts for 5.7% and the second axis accounts for 2.7% of the total variation. Maturity status is abbreviated as StageC for calves, StageJ for juveniles, and StageA for adults. Male porpoises are defined as SexM and females are defined as SexF.

Porpoises bycaught in area 1 were strongly associated with capelin, while porpoises sampled in areas 2 and 3 were more associated with mackerel (Figure 11). The standard ellipse and convex hull for individuals bycaught in northern Norway (area 1) tend to the left of the ordination biplot, showing apparent dissimilarities in the diet of individuals from area 1 compared to the diet of individuals bycaught further south (area 2 and 3) (Figure 12A&B). Calves were distinctively associated with silvery pout and whiting, and to a lesser extent with cod and *Trisopterus* spp., while they were further away from (i.e. not positively associated with) saithe, herring, blue whiting, and mackerel centroids (Figure 11). The maturity classes "juvenile" and "adult" did not explain much of the variation in diet composition. Overall, calves seemed to have a distinct diet composition, in terms of biomass, from juveniles and adults, which appeared to have a similar diet composition with overlapping standard ellipses (Figure 12). Among all maturity classes, juvenile porpoises showed the greatest convex hull (Figure 12). The centroids "male" and "female" were very close to the origin of the ordination biplot and all prey items used in the CCA were consumed by individuals of both sexes, confirming the lack of significant explanation of the variance by sex (Figure 11, 12).

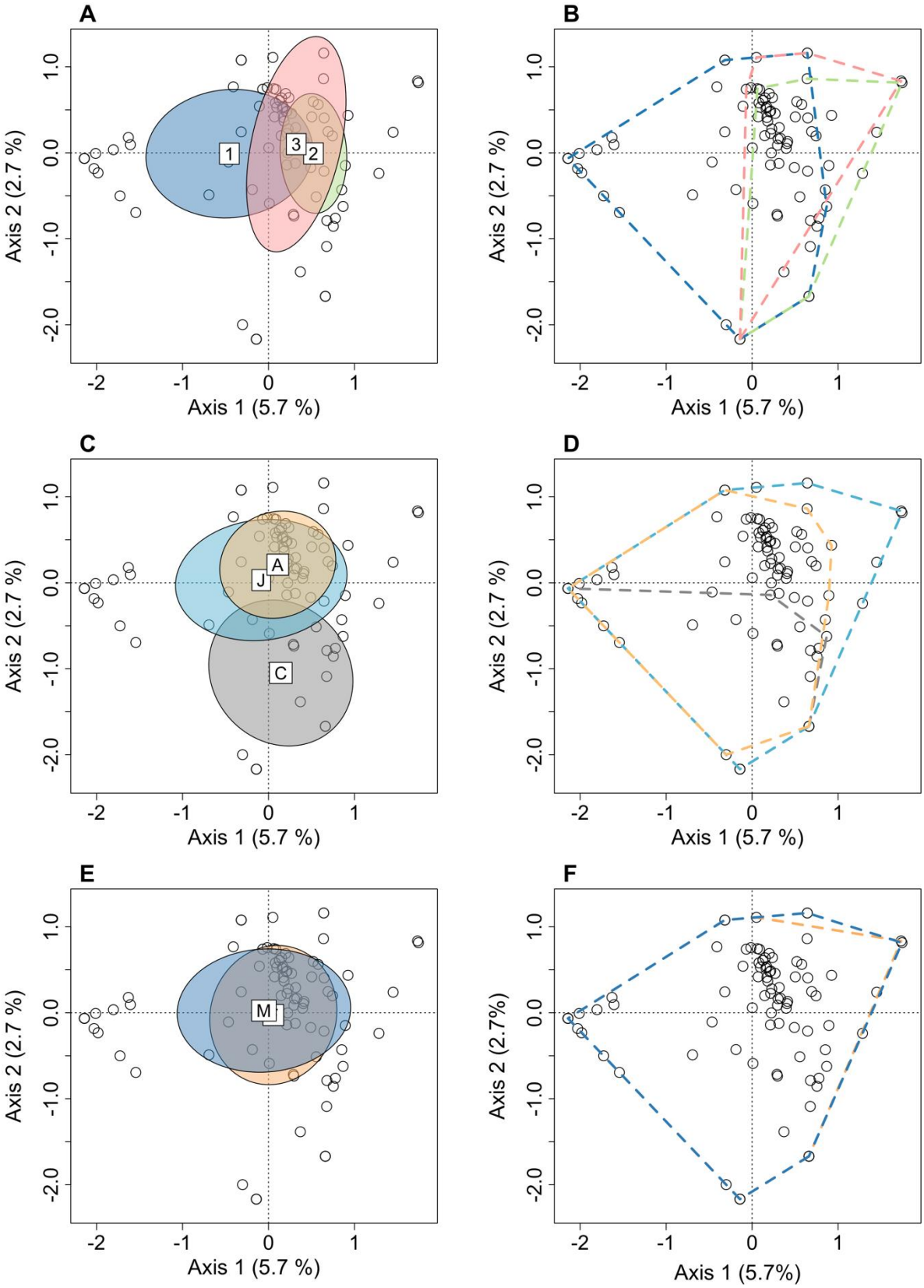

FIGURE 12: Canonical correspondence analysis (CCA) ordination biplots on reconstructed biomass (Hellinger-transformed) of selected prey species of harbour porpoises bycaught in Norwegian coastal waters (2016–2017). Standard ellipses (40%; left panels) and convex hulls (right panels) are represented for each explanatory variable: area (top panels A & B; area 1 in blue, area 2 in green, area 3 in pink), maturity status (middle panels C & D; calves (C) in grey, juveniles (J) in blue, adults (A) in orange), and sex (bottom panels E & F; males (M) in blue and females (F) in orange).

In the following sub-sections, univariate analyses were used to study the effect of each factor on harbour porpoise diet composition in more details. For these univariate analyses, the focus was on the relative importance, expressed by the combined index Q_i, of the most relevant prey items (i.e. most important prey items in the diet and prey items with interesting differences between groups). All other feeding indices are presented in Appendix C.

3.3.2. Ontogenetic variation in diet composition

Regardless of the maturity class, saithe was the dominant prey species in terms of relative importance (Q_i) (Figure 13, Table C1 in Appendix C). This importance increased with maturity, at ca. 32.3, 64.0, and 83.5% in calves, juveniles, and adults, respectively.

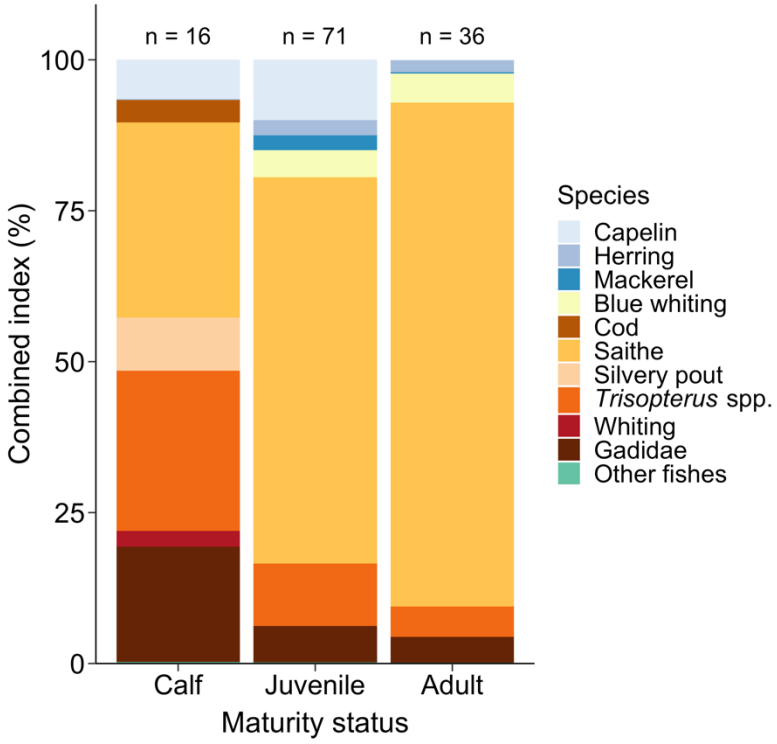

FIGURE 13: Diet composition, based on the combined index (Q_i), i.e. relative importance, of calf, juvenile, and adult harbour porpoises bycaught along the Norwegian coast in September–October 2016 and February–April 2017. Gadoids contributing less than 2% of the diet are incorporated to the group Gadidae, which also includes unidentified gadoids. The sample size n corresponds to the number of non-empty stomachs.

The calves' diet was clearly different from the one of older porpoises; silvery pout, cod, and whiting were relatively important (Q_i = 8.8, 3.7, and 2.6%, respectively), while they each accounted for less than 2% in the diet of juveniles and adults. *Trisopterus* spp. contributed ca.

26.5% in calves' diet and was decreasingly dominant in older porpoises (Q_i = 10.3% in juveniles, Q_i = 5.1% in adults). Additionally, unidentifiable gadoids were relatively more important in calves compared to juveniles and adults. Herring and blue whiting were only important in juveniles' and adults' diets and contributed between ca. 2.0 and 4.8%. Capelin was important only in immature porpoises (i.e. calves and juveniles) and comprised between ca. 6.5 and 10.0% of the diet composition. Mackerel constituted about 2.4% of the juveniles' diet, while it was negligible in the diet of calves and adults. The group "other fishes" was of virtually no importance regardless of the maturity status. Details on the diet composition of calves, juveniles, and adults, in each area, are presented in Figure C4 (Appendix C). Note that this is only for reference as sample sizes are too small to really explore potential prey preferences in time and space between maturity classes.

3.3.3. Sexual variation in diet composition

The diet composition of males and females did not differ much (Figure 14A, Table C2 in Appendix C). The main difference was the importance of capelin in male individuals only (Q_i = 9.7% in males vs 0.3% in females). Saithe amounted to 64.6% of the diet in males and was more dominant in female porpoises (79.9%). Herring comprised about twice as much of the diet in females (3%) as in males. Conversely, blue whiting and *Trisopterus* spp. had higher relative importance in the diet of male harbour porpoises, with Q_i = 5.7 and 10.3% compared to 3.8 and 6.3%, respectively. Males showed higher proportions of mackerel and other fishes as well, although the latter were of minor importance (Q_i < 0.5%).

The diet composition of males and females by area is displayed in Figure C5 (Appendix C). There were some differences from the overall (i.e. all areas together) diet. This is particularly the case in area 3, where saithe made up more than 95% of the males' diet, while the diet of females was dominated by *Trisopterus* spp. (Q_i = 40.0%), followed by saithe (Q_i = 34.5%), mackerel (Q_i = 16.3%), and herring (Q_i = 5.4%). Note, however, that sample sizes were especially small in this area. Additionally, some generally unimportant species increased in importance in specific areas; silvery pout was of some importance in the diet of females in area 3 (Q_i = 3.0%), and whiting constituted 2.5% for males in area 2.

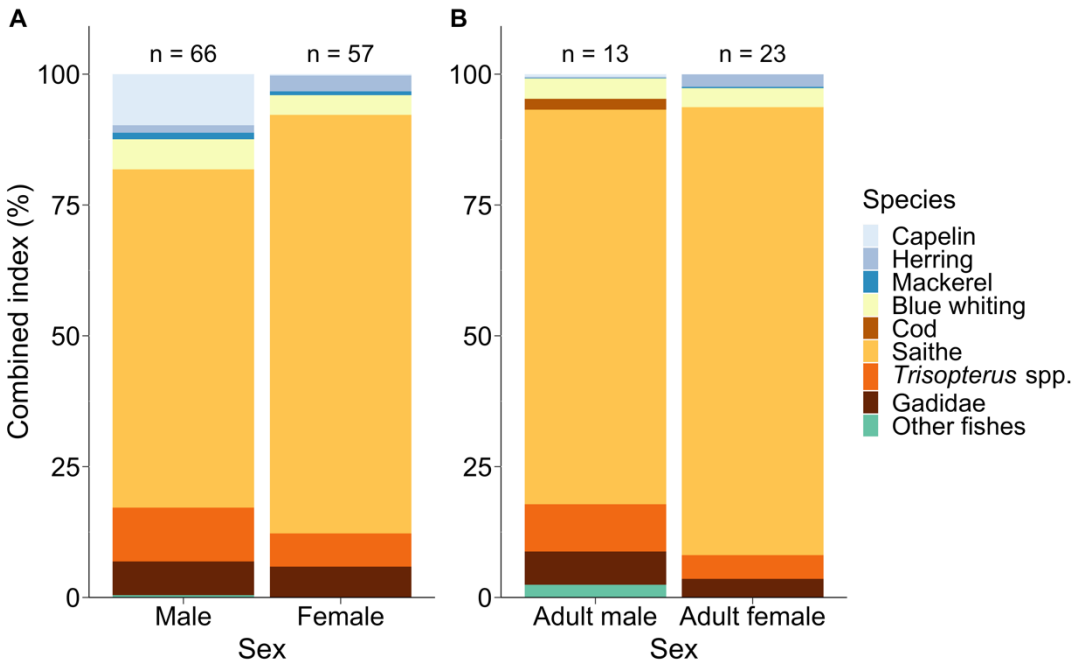

FIGURE 14: Diet composition, based on the combined index (Q_i), of all (A) and only adult (B) male and female harbour porpoises.

The diet of adult males and females only was also investigated in order to study potential differences between sexes after maturation. Adults of both sexes presented similar diet composition (Figure 14B, Table C3 in Appendix C). Saithe largely dominated the diet in both sexes, followed by *Trisopterus* spp. Saithe was relatively more important in adult females (Q_i = 85.6%) compared to adult males (Q_i = 75.4%), while *Trisopterus* spp. were more important for males (Q_i = 9.0%) than for females (Q_i = 4.5%). Cod and other fishes comprised a relatively higher proportion of the diet of adult males compared to adult females, with a combined index of ca. 2.0 – 2.4%. Regarding lipid-rich prey species, capelin and mackerel were of minor importance in both males and females, while herring constituted about 2.4% of the diet in adult females and was negligible in adult males (Q_i = 0.2%). Note that most unidentified gadoids (Q_i = 6.2%) consumed by adult males were most likely saithe.

3.3.4. Temporal variation in diet composition

The unbalanced temporal and spatial distribution of the sampling prevented the analysis of temporal variation of prey composition within areas, except for the sub-area of Troms county (area 1): the only zone in which sampling occurred in both September–October 2016 and February–April 2017 (Figure 1). Saithe dominated, in terms of relative importance, in both sampling periods although this prey species was relatively more important in autumn

(Q_i = 76.2%) than in spring (Q_i = 70.3%) (Figure 15, Table C4 in Appendix C). Herring, silvery pout, capelin, and *Trisopterus* spp., all of which constituted less than 2.5% of the diet in Autumn 2016, increased in relative importance in Spring 2017 and then contributed 7.5, 6.8, 5.4, and 4.6% of the diet, respectively. Note that capelin was only found in individuals sampled in Spring 2017. Conversely, blue whiting was found in the stomachs of porpoises bycaught in Spring 2017 but was relatively important (Q_i = 15.8%) in Autumn 2016 only. Several prey species were only present in Spring 2017, although their relative importance in the diet was negligible; this included sandeels, haddock, pricklebacks (i.e. *Leptoclinus maculatus* and *Lumpenus lampretaeformis*), and snailfish (Table C4 in Appendix C). Krill occurred relatively more frequently and were more numerous in Autumn 2016 than in Spring 2017 (FO_i = 27.3% in autumn vs 14.8% in spring; N_i = 28.3% in autumn vs 15.6% in spring). However, regardless of the season and year, they were of relatively no importance when the combined index Q_i was considered (Q_i < 0.1%). Other invertebrates were not present in the bycaught individuals from Troms county sub-area.

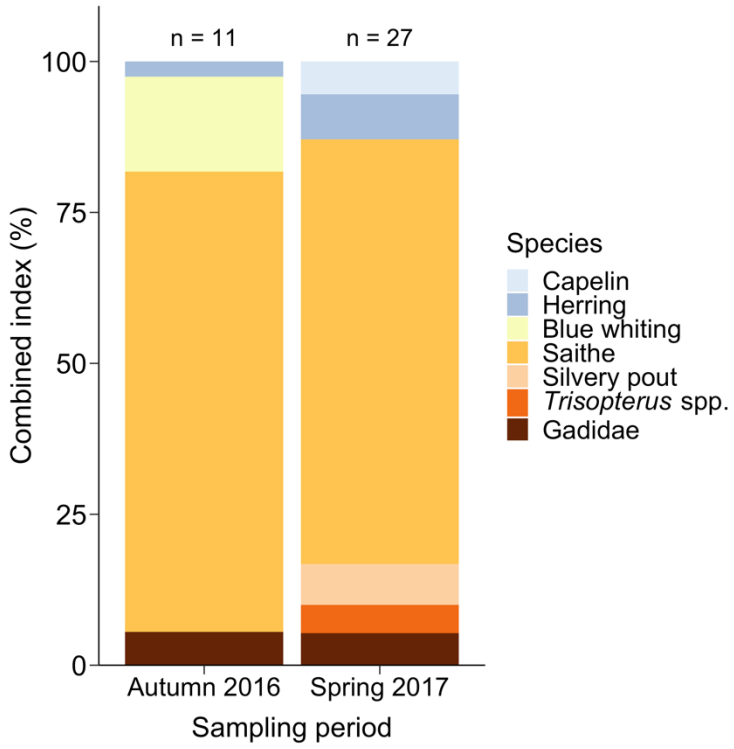

FIGURE 15: Diet composition, based on the combined index (Q_i), of harbour porpoises bycaught in Troms county waters in September–October 2016 (autumn) and February–April 2017 (spring).

3.3.5. Spatial variation in diet composition

Saithe was the dominant prey species in the diet of harbour porpoise in all areas along the Norwegian coast, although its relative importance was lesser in southern Norway (i.e. area 3); saithe comprised ca. 66.9, 69.3, and 54.3% of porpoises' diet in areas 1, 2, and 3, respectively (Figure 16). Differences in the relative importance of other selected prey items were observable between the three defined areas. The most obvious was the presence of capelin solely in northern Norway (i.e. area 1), where it accounted for 17.7% of the diet. Herring was present in all areas but was slightly more important in area 1 (Q_i = 4.0%), whereas mackerel was not present in this area (Table C5 in Appendix C) but contributed ca. 2.2% in area 2, and 8.5% in area 3. Blue whiting's contribution to the diet of southern harbour porpoises (i.e. area 3) was negligible (Q_i = 0.3%), and the species had greatest importance in area 2 (Q_i = 7.5%). The contribution of *Trisopterus* species increased along a geographical gradient, from northern to southern Norway (Q_i = <2, 14.6, and 31.4% in areas 1, 2, and 3, respectively). Other non-gadoid fishes were of minor importance in all areas ($Q_i \leq 0.6$).

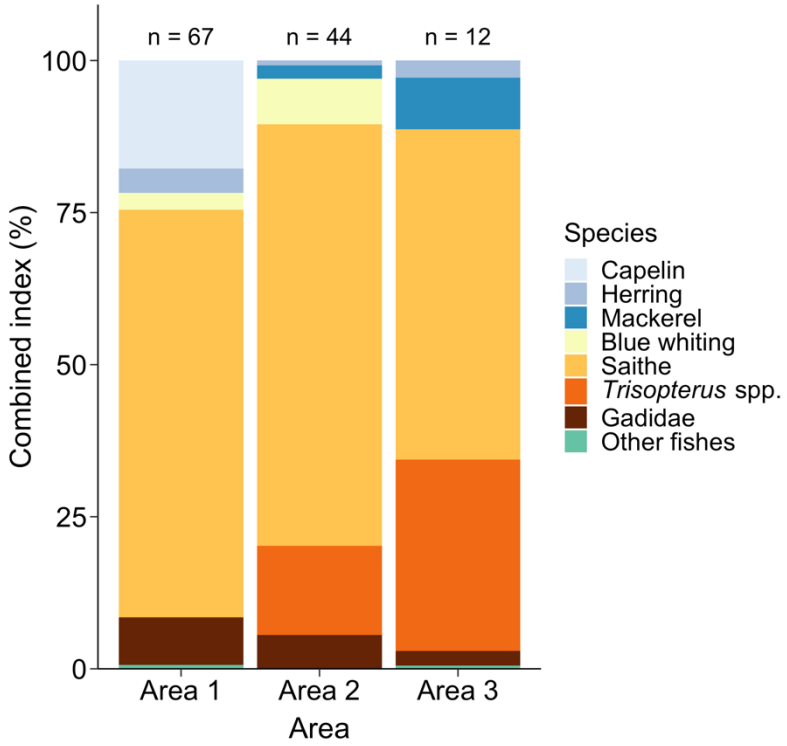

FIGURE 16: Diet composition, based on the combined index (Q_i), of harbour porpoises bycaught in three different areas along the Norwegian coast (1: northern Norway, i.e. Troms and Finmark; 2: middle Norway, i.e. Nordland; 3: southern Norway, i.e. Western Norway).

3.3.6. Prey size

Harbour porpoises consumed mainly small fishes, with the largest prey, a saithe, measuring about 49 cm (ca. 1 kg). The large majority of ingested fish had estimated lengths less than 40 cm. Length distributions are displayed for species that contributed to more than 1% of the diet, based on the combined index: silvery pout, cod, capelin, mackerel, herring, blue whiting, and saithe (Figure 17). Of these, silvery pout were the smallest individuals on average, with a mean length of ca. 6.7 cm and most individuals being smaller than 10 cm. Cod were generally small individuals as well, mainly ranging approximatively 8–11 cm, although larger specimens, up to 31 cm, were eaten occasionally. Capelin were also small, yet on average larger than cod, with a calculated mean length of ca. 13 cm. No capelin individuals larger than 18 cm were taken by the porpoises. Most mackerel were between 12–19 cm, although individuals up to 43 cm long were found. Herring and blue whiting ranged from 4 to 32 cm but were on average ca. 17 and 20 cm, respectively. Saithe were mainly larger individuals and showed the widest range in size, from about 6 to 49 cm. Most of the saithe identified in the stomachs ranged from ca. 16 to 33 cm, the mean value being ca. 25 cm.

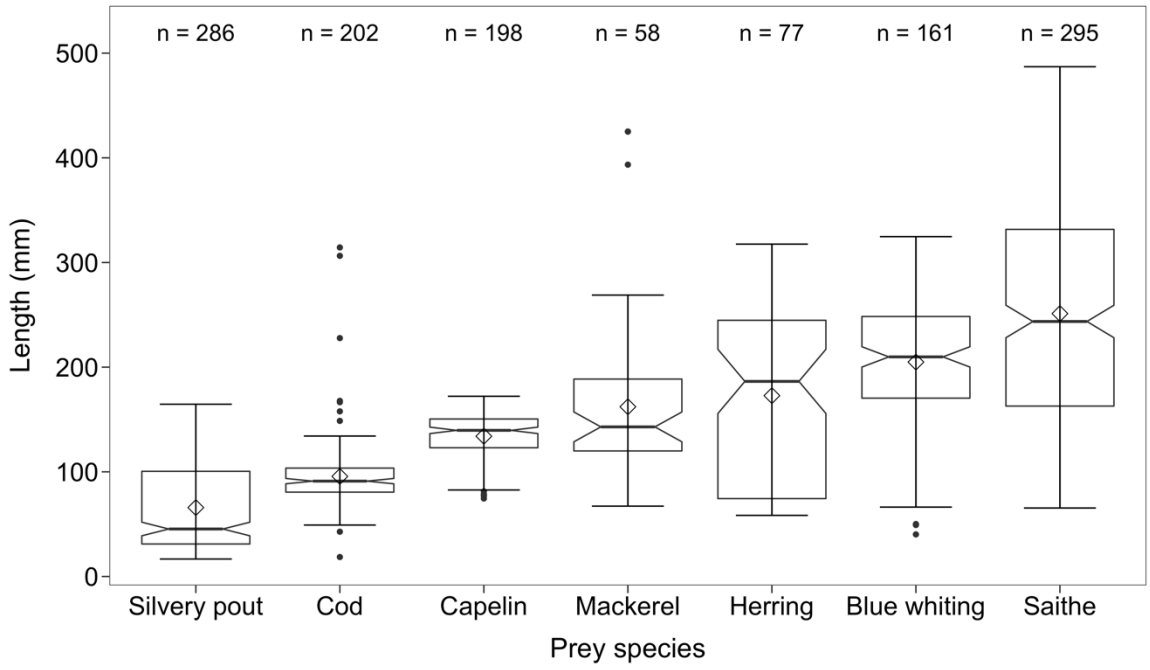

FIGURE 17: Length distribution of seven prey species (silver pout, cod, capelin, mackerel, herring, blue whiting, and saithe) identified in the stomachs of harbour porpoises bycaught along the Norwegian coast in September–October 2016 and February–April 2017. The boxplots show the median (black middle line), mean (diamond), interquartile range (IRQ; box), minimum and maximum values (no more than 1.5 x IRQ; lower and upper whiskers), and outliers (dots). The notches roughly represent the 95% confidence interval around the median and are used to compare groups. The fish lengths are estimated using otolith length–fish length regressions. The number of estimated fish individuals found in the stomachs is indicated (n).

4. DISCUSSION

This study confirms the diet of harbour porpoises in Norwegian coastal communities is mainly piscivorous. Harbour porpoises consumed a wide variety of fish species, though demersal gadoid fishes dominated. The analysis of stable isotopes and stomach contents revealed ontogenetic, temporal, and spatial differences, although saithe was dominant in all groups in the stomach contents. No differences were found in the isotopic and diet compositions of male and female porpoises. Changes in the diet composition of harbour porpoises in Norwegian coastal systems between 1988–1990 and 2016–2017 are described. Altogether, this study provides indications that harbour porpoises are opportunistic feeders, consuming the most available prey.

4.1. Overall diet composition

The proportion of empty stomachs was low, suggesting that most porpoises had foraged relatively recently. The number of recorded prey species in the stomachs and the variation in the isotopic composition suggest harbour porpoises in Norwegian coastal communities have a broad diet niche. This is in accordance with the generalist feeding behaviour commonly described in harbour porpoises (e.g. Aarefjord et al. 1995; Santos and Pierce 2003; Víkingsson et al. 2003). However, out of the 23 prey groups determined, only 9 (saithe, blue whiting, *Trisopterus* spp. capelin, herring, mackerel, cod, silvery pout, and unidentified gadoids) constituted more than 1% of the overall diet in terms of biomass (B_i) and relative importance (Q_i). Additionally, although up to 9 prey groups were found in individual stomachs, most harbour porpoises consumed between 1 and 4 different prey groups only. This suggests that either harbour porpoises display prey preferences at an individual level, or there is spatiotemporal heterogeneity in prey availability and they are feeding opportunistically on the most available prey.

The stomach contents were dominated by fish, and by prey species within the cod family (Gadidae) in particular. The piscivorous diet and the dominance of gadoid prey species observed herein are in line with previous studies (e.g. Santos and Pierce 2003; Leopold 2015). The importance of saithe in the diet of harbour porpoises in Norwegian coastal waters confirms findings from a study conducted ca. 30 years ago (Aarefjord et al. 1995). *Trisopterus* spp. (i.e. Norway pout, poor cod) and blue whiting also constituted an important part of the porpoise diet, which may be explained by their large distribution range along the whole coast of Norway (Olsen

et al. 2010; Froese and Pauly 2019).These prey species were also found to be important in the diet of harbour porpoises by Aarefjord et al. (1995).

Harbour porpoises have high energy demands and limited energy storage capacity and, as such, they need to feed frequently, preferably on lipid-rich prey (e.g. Brodie 1995; Spitz et al. 2012). Small schooling, lipid-rich prey species such as capelin, herring, and mackerel, have indeed been described to be an important part of harbour porpoises' diet (e.g. Recchia and Read 1989; Fontaine et al. 1994; Santos and Pierce 2003; Víkingsson et al. 2003; Mahfouz et al. 2017). While such species were present in the diet of the harbour porpoises studied here, they were of considerably lower importance than gadoids overall. According to Leopold (2015), harbour porpoises feed on a mixture of seasonally available lipid-rich prey and readily available but less energy-rich prey. The current study emphasises the importance of relatively lean prey items (i.e. gadoids) in the diet of harbour porpoises; if lean prey species are more available than energy-rich prey species, the net energy intake may be higher.

The harbour porpoises were found to generally feed on small fish: mean sizes of the most important prey species ranged from ca. 6.7 to 25 cm. The largest fish consumed was a 49 cm saithe, which is close to the prey size limit (48-51 cm) for porpoises described in other studies (Aarefjord et al. 1995; Víkingsson et al. 2003). Harbour porpoises are thought to use suction feeding to capture their prey (Kastelein et al. 1997b; Galatius and Kinze 2003) and do not usually seem to break fish in small pieces, but rather swallow them whole, therefore limiting the size of prey they can consume. Although the reconstructed lengths from otoliths are underestimates, a large part of the prey sizes of gadoid fishes likely corresponds to juvenile fish (Bergstad et al. 1987). Juvenile saithe, the most important prey item, settle in shallow coastal waters, where they stay in schools until they are 2-4 years old (Bergstad et al. 1987; Olsen et al. 2010). This shallow schooling behaviour likely make them easily accessible for porpoises.

Few invertebrate prey items (i.e. crustaceans and a squid) were found in the stomachs of harbour porpoises. Among crustaceans, krill was the most abundant, although it was present in only 20 stomachs (16.3% of non-empty stomachs) and never contributed much to the diet in terms of biomass or relative importance. Due to their limited importance, and because their remains were almost exclusively found with otoliths, crustaceans could also be secondary prey for most porpoises, initially consumed by the fish harbour porpoises preyed upon. However, one must keep in mind that the digestion rate of crustaceans is high, and they might therefore be

underrepresented in the diet. One harbour porpoise consumed one squid (ca. 700 g), showing that porpoises in Norwegian coastal waters may feed on cephalopods.

Plastic material was found in one individual. Interestingly, this was also the case in the study of Aarefjord et al. (1995). Plastic ingestion is widespread among marine wildlife (e.g. Derraik 2002; Kühn et al. 2015) and has been described for harbour porpoises in several papers (e.g. Baird and Hooker 2000; Unger et al. 2017).

4.2. Demographic variation: ontogenetic and sexual differences in diet

4.2.1. Ontogenetic variation

Calves had a distinct core isotopic niche from both juvenile and adult porpoises. Calves had higher $\delta^{15}N$ and lower $\delta^{13}C$ values, as well as a larger core isotopic niche, than juveniles and adults. The difference in nitrogen stable isotope ratios is likely the result of neonatal enrichment; if milk is synthesized from the catabolism of the mother's tissues, nursing calves should have higher $\delta^{15}N$ values (Hobson et al. 1997; Koch 2007; Newsome et al. 2010), which suggest they feed on a higher trophic level than their mother. This has been described in numerous marine mammal species (e.g. Newsome et al. 2006, 2009; Knoff et al. 2008; Jansen et al. 2012; Cherel et al. 2015; de Albernaz et al. 2017). Likewise, low $\delta^{13}C$ values might be the result of the high concentration of lipids, which are depleted in ^{13}C compared to proteins (De Niro and Epstein 1981; Cherel et al. 2015), in the milk the calves suckle. This would mean either calves use a portion of the lipids in the milk, rather than solely the protein portion of milk, to synthesize their tissues (Newsome et al. 2014; McMahon et al. 2015), or that mothers rely heavily on fat stores for the synthesis of proteins in the milk. Calves likely gradually wean, starting to feed on solid food while still being nursed; they would progressively learn to hunt on small and easily catchable prey such as crustaceans (e.g. euphausiids) and small coastal fish (Recchia and Read 1989; Lockyer 2003; Camphuysen and Krop 2011; Leopold 2015). The potential mixed diet of milk, crustaceans, and small fish in the first months of life might explain the larger isotopic niche in these young individuals.

Juveniles and adults, in contrast, had greatly overlapping and smaller isotopic niche widths, suggesting they specialize on prey species with similar isotopic compositions. These two maturity classes presented similar $\delta^{15}N$ and $\delta^{13}C$ values, and length did not significantly influence nitrogen isotopic ratios, suggesting that the trophic level harbour porpoises feed on is

independent of body size and maturity. However, there was a weak but significant increase in $\delta^{13}C$ with length, which might indicate porpoises eat more benthic or coastal as they grow. This could be explained by physiological capacities, as diving ability in marine mammals is believed to be linked to body mass and therefore closely related to size (Westgate et al. 1995; Halsey et al. 2006; Weise et al. 2010). Smaller porpoises might dive to lower depths or for less time, reducing their ability to search for and capture benthic or demersal preys. Additionally, larger porpoises are most likely to feed on larger fish (Santos et al. 1994; Víkingsson et al. 2003) such as saithe. Saithe juveniles in particular are closely associated to the littoral zone (Bergstad et al. 1987) and would therefore have high $\delta^{13}C$ values. Previous studies have found younger, smaller porpoises to feed more on coastal fishes (Santos and Pierce 2003), and this was therefore expected in this case as well. However, the results presented here might contradict this expectation. This may be due to the difference in study location, as the other studies were not conducted in Norwegian waters. Since different prey species will be more or less abundant and accessible to porpoises depending on their location, and predators choose prey with greater energy return per unit of time spent foraging, according to the optimal foraging theory, it is likely that ontogenetic shifts in harbour porpoise diet vary in space. It is also possible, and maybe more likely, that the porpoises show ontogenetic variation in how they utilize dietary macromolecules rather than in diet itself. Younger, smaller porpoises might rely more on dietary lipids, in addition to dietary proteins, in order to build their muscle tissues (Newsome et al. 2014; McMahon et al. 2015). This is possibly due to their relatively higher growth rates and increased metabolic demands for somatic growth (Andreasen et al. 2017), and would lead to lower $\delta^{13}C$ values sourced from ^{13}C depleted lipids. As they grow, their protein needs might be fully met by the dietary proteins.

An ontogenetic shift in diet was also observed with the stomach content analysis, with small fish prey species in calves and larger gadoids in juveniles and adults. Calves fed mostly on *Trisopterus* spp., silvery pout, capelin, cod, and, to a lesser extent, whiting. Small prey items, which are within the prey size small porpoises can swallow, are also likely easier to catch for young porpoises with less hunting experience. Saithe was considerably less important in calves than in juveniles and adults, likely because they are larger on average and harder to handle for young individuals, or/and because they are potentially difficult to catch due to their high swimming speed (Hess and Videler 1984). Crustaceans were of only minor importance in the stomachs of calves in this study; although euphausiids have been described to be potentially important for them in the literature (Smith and Read 1992; Santos and Pierce 2003), this was in

the western Atlantic. Differences in diet between calves and older porpoises have been described in the past (Santos and Pierce 2003; Schelling et al. 2014; Leopold 2015), yet not all studies found such differences. In Scandinavian waters specifically, Aarefjord et al. (1995) found no significant differences between the diets of calves (defined by the authors as <113 cm total length) and adult porpoises. It must be noted, however, that most calves in that study were sampled in Skagerrak waters rather than in Norwegian waters.

Similarly to the stable isotope results, the diet composition of juveniles and adults did not differ significantly, as supported by the CCA, and saithe was largely dominant in both. A few differences were apparent but are most likely the result of sampling distribution and spatial differences in prey availability. For instance, capelin was important in juveniles but not in adults; this could be a preference for lipid-rich prey species in growing juveniles, which need more energy to meet their higher metabolic demands (Andreasen et al. 2017), but the quantity of capelin ingested was only important for porpoises bycaught near Laksefjord in Finmark (Figure C6 in Appendix C). No adult porpoises (only one calf and five juveniles, all male) were bycaught near this fjord, so it is likely that the observed differences are rather due to spatial differences in where porpoises of different maturity classes were bycaught and the associated differences in prey availability.

There seemed to be a diversification in the number of different prey items consumed from calves to older porpoises, although this was not statistically significant. It is likely older porpoises can feed on a wider variety of prey, as they are larger and have more hunting experience. However, they seem to focus on the most available prey, as the overwhelming dominance of saithe in juveniles and adults suggest.

4.2.2. Sexual variation

Male and female harbour porpoises displayed no differences in isotopic composition; both core isotopic niches and convex hull areas overlapped greatly. Similar $\delta^{15}N$ and $\delta^{13}C$ values between the sexes suggest males and females feed on prey with similar trophic level and food source origin, in zones with similar isotopic compositions. This is line with the stomach content results, which showed no significant difference in diet composition between sexes. One small difference was the importance of capelin in males compared to females. However, the males that consumed large quantities of capelin are the same juvenile individuals mentioned above, from near

Laksefjord (Figure C6 in Appendix C). It is most likely that this, and other small differences, are therefore the result of prey availability near bycatch locations, rather than prey preferences between sexes.

Variations in diet between sexes have been described in previous studies (Smith and Gaskin 1983; Yasui and Gaskin 1986). These differences were attributed to sexual segregation in foraging areas and the use of different associated resources by adults (e.g. Smith and Gaskin 1983; Santos and Pierce 2003), or in differences in energy requirements due to gestation and lactation in adult females (e.g. Yasui and Gaskin 1986; Recchia and Read 1989; Schelling et al. 2014). The similarities in stable isotope and diet composition between sexes observed in this study were therefore not expected. They suggest that male and female porpoises use similar habitats and prey in Norwegian coastal waters on both the short- and longer-term. Additionally, although most of the adult females studied here were pregnant and/or lactating, their diet composition suggests they did not need to feed on lipid-rich prey. An absence of differences between sexes was also found by Aarefjord et al. (1995). It must be noted, however, that the number of adult females in *ibid* study was low (n=7).

4.3. Spatiotemporal variation: seasonal and geographical differences in diet

Harbour porpoises are considered generalist predators, feeding on a wide range of prey species and taking advantage of the most available prey species (e.g. Rogan and Berrow 1996; Santos and Pierce 2003; Víkingsson et al. 2003; Santos et al. 2004). Since prey availability varies in time and space, both temporal and spatial variation in the diet were expected.

4.3.1. Temporal variation

Temporal differences were observed in a small area in Troms county, where bycaught porpoises from both sampling periods were available. Due to the short (ca. 6 months) time difference between the two sampling periods, the temporal differences are likely the reflection of seasonal changes (autumn vs spring). Fish follow seasonal life cycles, with species-specific spawning times and migration patterns. Their seasonality is known to impact the diet of their predators (e.g. Dolgov 2002; Hovde et al. 2002; Santos and Pierce 2003), as they are more or less available depending on the time of the year.

The core isotopic niche and convex hull area were larger for porpoises bycaught in autumn, due to higher variability in $\delta^{13}C$ values in this season. This increased variability might indicate a larger spatial dispersion, and more diversified diet, of these porpoises in the summer and early autumn months, compared to the winter and early spring when they would have a more coastal and stationary distribution. The difference in $\delta^{13}C$ could also reflect a feeding on benthic or demersal fishes in winter and early spring, before the start of the spawning season of pelagic, lipid-rich prey species. The differences in $\delta^{13}C$ values might also be the result of the baseline isotope ratios varying seasonally and being transmitted to the upper trophic levels, rather than reflecting variations in the diet. Values of $\delta^{13}C$, and $\delta^{15}N$, at the base of the food web may indeed vary over time; variations can be linked to e.g. the size and time span of the phytoplankton bloom, phytoplankton species composition, upwelling, temperature, or external nutrient loadings (e.g. Kukert and Riebesell 1998; Michener and Lajtha 2007; Lara et al. 2010; Casey and Post 2011; Trueman et al. 2012). Norwegian fjords are particularly influenced by freshwater inputs from rivers, which have a seasonal discharge pattern (Wassmann et al. 1996; Skreslet 1997). In winter and early spring in Northern Norway, precipitation accumulates in snow and ice and the freshwater discharge is low (Wassmann et al. 1996; Skreslet 1997). It increases in late spring and summer when the snow melts, as well as during periods of heavy rain in autumn (Wassmann et al. 1996; Skreslet 1997). These freshwater runoffs release ^{13}C depleted organic matter (Vizzini et al. 2005; Michener and Kaufman 2007; Feder et al. 2011) and could explain the lower values in porpoises bycaught in autumn. On the other hand, spring samples might be enriched in ^{13}C due to the lack of primary production in winter and early spring. In the absence of new production, recycled consumption of production from the previous summer fuels the ecosystem, leading to a progressive enrichment in stable isotope ratios and higher isotopic composition values after the winter. No significant differences were found in the nitrogen stable isotope ratios between the two seasons. This suggests either there is no seasonal variation in the mean trophic level porpoises feed on, or the variation is masked by temporal variability in basal $\delta^{15}N$ values.

Slight seasonal variations were observed with the stomach content analysis. Capelin, herring, silvery pout, and *Trisopterus* spp. were relatively more important in the stomachs of porpoises bycaught in spring, while saithe and blue whiting were more important in the stomachs of porpoises bycaught in autumn. These variations support opportunistic feeding. For example, capelin and herring undertake major seasonal migrations to reach the coastal areas where they spawn in the late winter/early spring, likely making them more available to predators at this time. Capelin migrate from the northern Barents Sea to their spawning grounds along Troms and

Finmark in January–April, while herring spawn along the Norwegian west coast between February and April (Røttingen 1990; Gjøsæter 1998; Toresen and Østvedt 2008; Olsen et al. 2010). Their main spawning grounds are found off Møre, between 62 and 64°N, but some exist up to 70°N (Olsen et al. 2010; Slotte et al. 2018). Herring overwintering locally in the fjords, as well as juveniles in the nursery area, might have also been available (Olsen et al. 2010). Silvery pout was another pelagic fish that was relatively more important in the diet of porpoises bycaught in spring. Literature on this species is scarce, however, the species has increased in abundance along the Norwegian coast and is present in Troms waters (Skants 2019). Silvery pout spawns in spring as well, becoming more available for harbour porpoises then. It must be noted that even though blue whiting was relatively important in the autumn samples, the sample size was small and only one porpoise had consumed large quantities of this prey. Despite this, there was little seasonal variation in diet composition, and saithe was dominant regardless of the season, most likely due to the high availability of this prey species along the Norwegian coast throughout the year (Olsen et al. 2010; ICES 2018).

4.3.2. Spatial variation

Harbour porpoises bycaught in different areas showed dissimilarities in their isotopic niches. There was a clear separation in core isotopic niches between porpoises in the north (area 1) and south (area 3), with no overlap between the two areas. This was mainly driven by spatial differences in $\delta^{13}C$ values. Despite the low sample size in area 3, there was a 100% probability that the core isotopic niche of porpoises bycaught in southern Norway was greater than the niche of porpoises bycaught in the north, suggesting that porpoises in the south have a broader diet than those in the north. The core isotopic niche of porpoises bycaught in mid-Norway (area 2) overlapped with those of the two other areas to some degree, and seemed to be a transition zone between areas 1 and 3. They also showed the largest individual variation in isotopic values, although this is likely due to the higher sample size for this area. Differences in the harbour porpoises' stable isotope composition between regions along the Norwegian coast have been reported by Fontaine et al. (2008). The authors found higher $\delta^{13}C$ values in porpoises caught in southern Norway than in northern waters. The results from the stable isotope analysis presented in this study are consistent with those of Fontaine et al. (2008), with decreasing $\delta^{13}C$ values with latitude. Fontaine et al. (2008) suggested the variability in $\delta^{13}C$ values reflects a change in diet related to local bathymetry; in shallower waters in southern Norway, demersal and benthic prey species are more accessible, while in the deeper waters in the Barents Sea, the seafloor is harder

to reach and porpoises forage more in pelagic waters. However, bathymetry of the coastal waters, where the harbour porpoises were bycaught, does not vary much in space (EMODnet 2017). If the trend in $\delta^{13}C$ is related to a switch in diet from relatively more benthic prey in the south to pelagic prey in the north, it is unlikely this is due to bathymetric constraints, or it would mean porpoises undertake considerable onshore/offshore movements. It must be noted that even though most porpoises from northern Norway were bycaught in the spring, which was enriched in ^{13}C compared to the porpoises bycaught in autumn, they still had the lowest $\delta^{13}C$ values, suggesting the spatial effect might be stronger than the temporal one.

Differences in porpoise $\delta^{13}C$ values from southern to northern Norway could also be the reflection of the natural latitudinal cline in $\delta^{13}C$, which is closely related to temperature (Rau et al. 1982; Goericke and Fry 1994; Graham et al. 2010). At higher latitudes the sea temperature is lower, increasing the solubility of CO_2 (Lynch-Stieglitz et al. 1995). Phytoplankton, the base of the food web, are depleted in ^{13}C when $[CO_2]_{aq}$ is more available since the lighter isotope (^{12}C) is favoured by reaction kinetics, e.g. during photosynthesis (Laws et al. 1995; Hofmann et al. 2000). Additionally, temperature influences plankton growth rate; plankton cells tend to grow slower under cooler conditions, allowing higher isotopic fractionation (Laws et al. 1995; Popp et al. 1998; Hofmann et al. 2000). Temperature also influences phytoplankton species composition, for example, there is a higher abundance of diatoms, which are generally enriched in ^{13}C (Trueman et al. 2012), in colder waters (Leterme et al. 2005). This all contributes to decreasing $\delta^{13}C$ values with latitude. As of yet, no isotopic map (isoscape) exists for the coastal waters of Norway and, without knowledge on the local isotopic baseline, no conclusion can be drawn on the origins (i.e. changes in diet or at the base of the food web) of $\delta^{13}C$ variability.

Differences in $\delta^{15}N$ values between areas were also observed; porpoises bycaught in northern Norway had significantly higher $\delta^{15}N$ values than those bycaught in mid-Norway. The difference (ca. 0.5‰) was likely ecologically small, as one trophic level usually corresponds to ca. 3–4‰ enrichment in $\delta^{15}N$, although the specific value for harbour porpoises in this ecosystem is not known. Porpoises might have fed on relatively more juvenile or planktivorous fish, with lower trophic levels, in mid-Norway waters. This does not seem to be supported by the stomach contents; however, those only represent a snapshot of the diet. Differences may also arise from spatial variations in baseline values, which seems most likely in this situation. These can be the result of different factors, such as nitrogen source for primary production (terrestrial vs marine input, nitrate vs ammonium concentrations), temperature, phytoplankton uptake rate,

phytoplankton taxonomic composition, terrestrial inputs, depth, and salinity (e.g. Jennings and Warr 2003; Switzer et al. 2003; Michener and Kaufman 2007; Casey and Post 2011; Chouvelon et al. 2012).

Sampling area significantly explained part of the variation in the diet composition. Capelin in particular was relatively more important in the diet of porpoises bycaught in the north. This pelagic, lipid-rich prey species has also been found to be important in the diet of harbour porpoises off northern Norway in the past (Aarefjord et al. 1995). Demersal gadoid species were relatively, and similarly, more important in both mid- and southern Norway. *Trisopterus* spp. were relatively more important in mid-Norway, and even more in southern Norway, than in northern Norway. These differences are likely related to the distribution range of the fish prey species as, for example, capelin is especially important in northern Norway and in the Barents Sea (Olsen et al. 2010). *Trisopterus* spp. included two potential prey species, Norway pout and poor cod; the former is available along the entire coast while the latter is only distributed south of 66°N, with highest concentrations around the UK, in the North Sea, and off southern Norway (Froese and Pauly 2019). Therefore, the group *Trisopterus* spp. likely includes both species in the south, increasing the group's availability there. Geographic variations in diet, attributed to differences in prey availability, have been previously described in harbour porpoises from different waters in the northeast Atlantic (Aarefjord et al. 1995; Santos and Pierce 2003; Víkingsson et al. 2003; Santos et al. 2004). It must be noted, however, that in this study the porpoises were bycaught in different sampling seasons depending on the area. For example, most porpoises from northern Norway were bycaught in the spring, and their diet was therefore likely influenced by the increasing availability of spawning capelin. Also of note was the importance of mackerel in the diet of porpoises bycaught in the south, but this was due to only one individual that ingested this prey species in large quantities. Regardless of the area, saithe was the most important prey species, likely due to its availability along the entire Norwegian coast (Olsen et al. 2010).

In contrast to this study, saithe did not dominate the diet in all areas about 30 years ago; instead, capelin and poor cod dominated in areas 1 and 2, respectively (Figure C7 in Appendix C) (Aarefjord et al. 1995). Note that, for comparison, B_i rather than Q_i was used. Overall, in the Aarefjord et al. (1995) study, a greater number of prey species contributed to a large proportion (> 10%) of the total biomass than in this study. This seems to be in accordance with differences in prey resource between the two time periods (ICES 2018). The recruitment of saithe was low

in the 1980–1990's, leading to reduced stocks and low availability of this prey species for their predators. Porpoises taking advantage of the higher availability of saithe in 2016–2017 might have resulted in less heterogeneity in the stomach contents then. Some of the differences between the two studies might also come from differences in sampling months and associated changes in prey availability, as most of the porpoises were bycaught in May–June in Aarefjord et al. (1995). It must also be noted that the sample sizes varied greatly between areas and between studies. Because stomach contents only represent recent meals, interpretation of the diet may suffer from outliers, especially when sample sizes are small, and in particular when using biomass proportions: one or few individuals can largely impact the results if they consumed rare but very large prey items. Comparisons between diet studies would therefore largely benefit from consistent and large sample sizes for all areas and time periods investigated.

4.4. Sources of error and limitations

Several factors can affect the results and the interpretation of the diet. This include biases associated with the sampling procedure as well as ones common to diet studies, in particular when analysing stomach contents (Pierce and Boyle 1991). The results presented above should therefore be assessed with these biases in mind.

4.4.1. Sampling bias

Different sources of error exist in diet studies, the first being linked to sampling strategies and their inherent biases. Random sampling is rarely achieved in marine mammal studies. The samples for this study were collected opportunistically through cooperation with fishermen, leading to unbalanced data. The sampling period, September–October 2016 and February–April 2017, was restricted due to the seasonality of gillnet fisheries. Additionally, sampling distribution was different between seasons; porpoises south of the Lofoten islands were only bycaught in Autumn 2016, while in northern Norway, individuals were mainly bycaught in Spring 2017. Bycatches were also patchily distributed, with about half of the harbour porpoises bycaught in Vestfjorden and Varangfjorden. Due to the lack of a full factorial sampling design, it was not possible to resolve temporal and spatial effects on stable isotope and diet composition, although this was considered in the interpretation of the results. The small sample size, all too common in marine mammal studies, made the results vulnerable to outliers and the sub-division of samples reduce statistical power greatly. As such, differences described in maturity status and sex by area were limited and only qualitative. Börjesson et al. (2003) have suggested that a

minimum of 35-71 stomachs is needed so that all common prey species will be represented by at least one individual in the samples, at 95% confidence. This may be conservative but highlights the importance of a minimum sample size to describe diet composition and means it is possible that some prey species have not been described in the diet when divided in groups.

The harbour porpoises analysed were the result of bycatches, which also introduces biases. Firstly, bycaught porpoises can be biased towards smaller/younger individuals compared to studies that sample using direct catches (Hohn and Brownell 1994 after IWC 1994; Lockyer and Kinze 2003). The level of mortality from entanglements seems to be related to body size (IWC 1994), as smaller individuals are, in general, not strong enough to break the gear. Also, immature porpoises have less experience in avoiding fishing gear or may not recognise them as hazards. Nets are also a way to find aggregated prey, easily accessible to young porpoises still learning to hunt. The samples were also biased towards, with a sex ratio of 1.3:1.0 (males:females). This could be the result of behavioural differences between the sexes, with males being more mobile and dispersing more than females (Walton 1997; Lockyer and Kinze 2003). However, the lack of differences in both isotopic and diet composition suggest that harbour porpoises in Norwegian coastal communities are not sexually segregated. Alternatively, males may be more attracted to fisheries, or less responsive to hazards in their environment. Sampling from bycatch data might therefore not be representative of the whole population. Finally, bycaught samples are potentially biased towards fish species targeted by the fisheries, as bycatches in certain types of nets may select porpoises with a certain foraging behaviour and therefore diet composition (Recchia and Read 1989; Pierce and Boyle 1991; IWC 1994). The dominance of demersal prey species in the diet of harbour porpoises could therefore be accentuated by the type of fish targeted by the gillnets the porpoises were bycaught in. Despite these biases, bycatch is the most commonly used sampling method to investigate the diet composition of marine mammals; it prevents intentional killing and provides healthier individuals than strandings. The cause of death of stranded porpoises is often unknown, potentially giving biased information on their diet composition (i.e. diet of an unhealthy individual, bias towards empty stomachs) (Pierce and Boyle 1991; Toperoff 2002). On the other hand, bycaught porpoises, as used in this study, are likely healthier (Kuiken et al. 1994) and more representative of the general population.

4.4.2. Diet reconstruction

Identification of prey items by hard remains, specifically otoliths, is a widely used method in diet studies (Pierce and Boyle 1991). However, such analyses of faeces or gastrointestinal tract contents come with potential biases and sources of error that must be kept in mind in the interpretation of diet data. First and foremost, otoliths from related species (e.g. saithe, pollack, and haddock) can be hard to distinguish; misidentification of prey species occurs and is inherently linked to the reader's experience (Appendix B). Variation in prey identification between different readers was investigated (Appendix B), calling attention to the issue. In this study, the material from each year was identified by different readers for logistical reasons. However, one reader was experienced, and the other was guided by an experienced reader, differences were therefore assumed to be minimized.

Difficulties and differences in identification may be enhanced due to erosion; stomachs contain acid gastric, which is particularly corrosive and can heavily affect hard remains, potentially leading to failure of identification to the species level (Pierce and Boyle 1991). Also, a major problem is that otoliths erode at different rates depending on the prey species. The different digestion rates reflect the general robustness and shape of the otoliths; thinner, fragile otoliths (e.g. clupeids) are more likely to be completely digested and would then be under-represented in the diet, while larger, thicker otoliths (e.g. gadoids) would be over-represented (e.g. Jobling and Breiby 1986; Berg et al. 2002). This can lead to notable errors when estimating numbers and weights of fish consumed, and thus also when estimating the contribution of different prey groups to the diet. Other factors such as meal size and composition, metabolic rate, and individual activity are likely to impact otolith digestion in the digestive tracts (Helm 1984; Markussen 1993; Marcus et al. 1998; Trumble and Castellini 2005). Otoliths that do survive complete digestion may suffer large reductions in size (e.g. Pierce and Boyle 1991; Tollit et al. 1997), leading to underestimations in size and mass of digested fish prey.

Partial and complete digestion of otoliths can, to some degree, be corrected using species-specific digestion coefficients and numerical correction factors. Such factors have been developed for grey seals (Grellier and Hammond 2006) and for harbour seals (Harvey 1989; Tollit et al. 1997; Berg et al. 2002) in captivity, however, they do not exist for harbour porpoises. To use these correction coefficients on species other than the ones they have been determined for may generate biases. Additionally, digestion coefficients rely on digestion degrees

determined by the reader, which is subjective and may therefore add uncertainty. One way to overcome this subjectivity would be to standardize the determination of digestion degrees with an objective method to classify each degree (e.g. Tollit et al. 1997). To avoid these issues, one technique is to measure only uneroded otoliths and assume the eroded ones were of more or less the same size. However, digestion degrees were not available for the 2017 material in this study; all otoliths were therefore measured. Measuring all otoliths, and not applying corrections for partial and complete digestion, results in underestimations of the number and size of fish prey items. Lastly, otoliths can be lost or broken during preparatory laboratory work and previous handling.

Regression equations used to reconstruct the size and mass of consumed fish do not always exist for all prey species in the area studied. In this study, some equations were developed from prey species in the Norwegian and Barents Seas (pers. comm. from U. Lindstrøm and Lotta Lindblom) but most of them were based on fish from the North Sea (Härkönen 1986). Using local relationships to reconstruct the size and weight of ingested fish would greatly benefit the quality of diet data and there is a need for such equations to be developed for fishes in Norwegian coastal waters.

Despite these biases, stomach contents are extremely useful to obtain information on specific prey species eaten, as well as the mass and size of prey items. They provide both quantitative and qualitative data that could not be obtained otherwise. However, they represent merely a snapshot of an individual's diet, with only recent meals shown. Less traditional methods, such as stable isotope analysis, give a broader overview, with integrated diet information over a longer period, but are not absent of limitations. Stable isotopes can only give indications of the trophic level of the predator and the origin of prey sources. Additionally, many factors can influence stable isotope ratios, isotopic fractionation, and isotopic turnover rates (e.g. Jennings and Warr 2003; Michener and Kaufman 2007; Lara et al. 2010; Newsome et al. 2010; Casey and Post 2011), and complicate the interpretation of the diet (e.g. Schmidt et al. 2003; Casey and Post 2011; Chouvelon et al. 2012) All methods involve biases and limitations, but applying several methods gives a more reliable picture of animals prey use.

A CCA was performed to investigate the factors that drive variation in diet composition (biomass). Only ca. 11% of the total variation was explained by the factors used (sampling area, maturity status, and sex). Including additional explanatory variables seem essential to explain a

greater proportion of the total variation in diet composition. Although area seems to be a proxy for prey availability (i.e. spatial differences are likely the result of changes in prey availability rather than prey preferences), it is likely that adding prey abundance as a predictor variable would increase the power of the CCA. It should also be noted that CCA results are sensitive to the type of data transformation used. Area was always significant, while sex was never significant, whether the data was not transformed, log transformed, or Hellinger transformed. Maturity status was not significant when the data was not transformed, nor log transformed.

In the face of the biases described above, the results of this study still provide valuable information on the feeding ecology of harbour porpoises in Norwegian coastal systems. More generally, they highlight the importance of using complementary methods in diet studies.

4.5. Recommendations and future studies

Common problems in marine mammal studies include small and unbalanced samples, and a lack of longitudinal sampling allowing for exploration of changes in space and time. For future studies, I recommend working towards more balanced longitudinal sampling. This is hard in practice, particularly when depending on bycaught samples, but should drive tighter association with fishermen. More balanced sampling could be improved by using an adaptive stratified sampling design, where the number of bycaught samples collected is predefined, both in time and space. Additionally, including samples from other seasons would be interesting, although this is difficult owing to the seasonality of fisheries.

Traditional methods, such as the analysis of stomach contents, provide valuable data and will continue to be used to study the diet of marine mammals. Limitations should however be addressed and herein I present adjustments that could improve the reconstruction of the diet in the future. The development of digestion coefficients and numerical correction factors for harbour porpoises and their main prey species would help correct for digestion and avoid large underestimations of prey species number, length, and biomass. For this to not generate more biases, standardization of an objective method to defined digestion degrees (e.g. by using distinctive morphological features for each grade and prey species; Tollit et al. 1997) would be necessary. Identification of other hard remains than otoliths could be used to increase detection of prey species (e.g. Pierce and Boyle 1991; Cottrell and Trites 2002) Diet studies could also be improved through the use of DNA, be it to fully investigate the diet with DNA extraction

techniques or to distinguish unidentified prey species from the same family (e.g. unidentified gadoids) determined by the traditional hard-remains approach (e.g. Tollit et al. 2009; Nilssen et al. 2019). This study also highlights the influence of intra and inter-reader variability in otolith identification (Appendix B) and the importance of a standard protocol in stomach content analyses.

In most diet studies using stable isotopes, $\delta^{13}C$ values are corrected for lipids. To minimize cost and time, lipids are not always experimentally extracted but rather corrected using models. The comparison of lipid-normalization models and the large differences between models observed in this study (Appendix A) call attention to test for the model used and to potentially develop new models for the species studied in a specific area.

Stable isotope and stomach content analyses could be complemented by satellite tracking and/or cameras attached to the porpoises, in order to better understand habitat use and nearshore/offshore movements. This could provide information on where the different maturity classes and sexes forage (i.e. calves vs adults, males vs females), as well as on their diving behaviour. This would, for example, confirm if larger porpoises dive deeper to feed on benthic prey species and if males and females really do not segregate spatially. Additionally, using stable isotope composition to infer trophic level and food source depends on a reliable estimate of the isotopic baseline and a good understanding of spatiotemporal variations in this baseline. The development of isoscapes along the Norwegian coast is therefore essential to assess if changes in isotopic composition are the reflection of changes in diet or changes in the environment.

This study indicates that harbour porpoises in Norwegian coastal communities are opportunistic feeders, with ontogenetic and spatiotemporal variation in the diet. Prey preferences were, however, not investigated and would require comparing the diet to the prey availability in the environment. Resource and diet data cannot be collected concurrently when relying on bycaught animals but prey availability from resource surveys at the time of sampling could be used. Future feeding ecology studies could also include isotopic mixing models (SIAR), which utilize the stable isotope signatures from potential prey species to determine the relative contribution of each prey species to the diet. This would give an idea of the species composition in the long-term diet and would enable comparisons with the short-term diet information from stomach content analyses. Fatty acid analysis is another method that gives information on the diet over a longer time period and could also complement our understanding of the diet.

While this study does provide more information on the feeding ecology of harbour porpoises in Norwegian coastal communities, further studies are needed to better understand their ecological role. Harbour porpoises experience high bycatch mortality, which is most likely not sustainable (Moan 2016; Hammond et al. 2017). To improve management and conservation of harbour porpoises, knowledge on the population size and structure, and life history are required. Population size estimates, for example, do not yet exist for the entire harbour porpoise population in Norwegian coastal waters and fjords and should be developed in the future.

5. CONCLUSION

This study supports previous findings that suggest this small cetacean is a generalist predator, exploiting a wide range of prey species, primarily gadoid fish species. Juvenile saithe were by far the most important prey found in the stomachs. This is most likely due to their availability in shallow Norwegian coastal waters and fjords. Using both stable isotope and stomach content analyses gave a more comprehensive view of harbour porpoises feeding ecology, with information on both short and longer-term diet. Ontogenetic changes were observed, likely as a result of physical and physiological constraints. Ontogenetic variation in stable isotopes values might also indicate a gradual decrease in the use of dietary lipids to synthesize muscle tissues with length. No sexual differences in diet were found, which suggests a lack of spatial segregation between males and females and might indicate adult females do not require different prey species for their specific energy needs. Seasonal and geographical differences in the stomach contents likely indicate dietary variations related to prey availability. Differences in isotopic composition might, however, also result from temporal and spatial variations in isotopic baseline. To investigate if those differences are the result of changes in the diet or the isotopic baseline, isoscapes along the Norwegian coast, and how they change in time, must be determined. Changes in the diet composition of harbour porpoises bycaught along the Norwegian coast between 1988–1990 and 2016–2017 are most likely due to differences in the availability of prey, rather than a change in preferred food. The results of this study are important for the conservation of harbour porpoises and ecosystem-based management. Future studies with larger sample sizes and more balanced sampling, using telemetric data, and investigating resource availability are necessary to explore further the variations described herein and better understand the ecological role of harbour porpoises in Norwegian coastal communities.

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APPENDIX A

Supplementary information for Materials and Methods

TABLE A1: Model performance, expressed as modelling efficiency (EF), of the modified lipid-normalization model presented in this study and compared to models from the literature. Values close to 1 indicate a good fit while values around 0 indicate poor model performance. Models giving a negative EF values are not recommended (Mayer and Butler 1993).

	McConnaughey and McRoy (1979)	Alexander et al. (1996)	Kiljunen et al. (2006)	Present study (2019)
Modelling efficiency (EF)	0.63	-1.29	-9.28	0.87

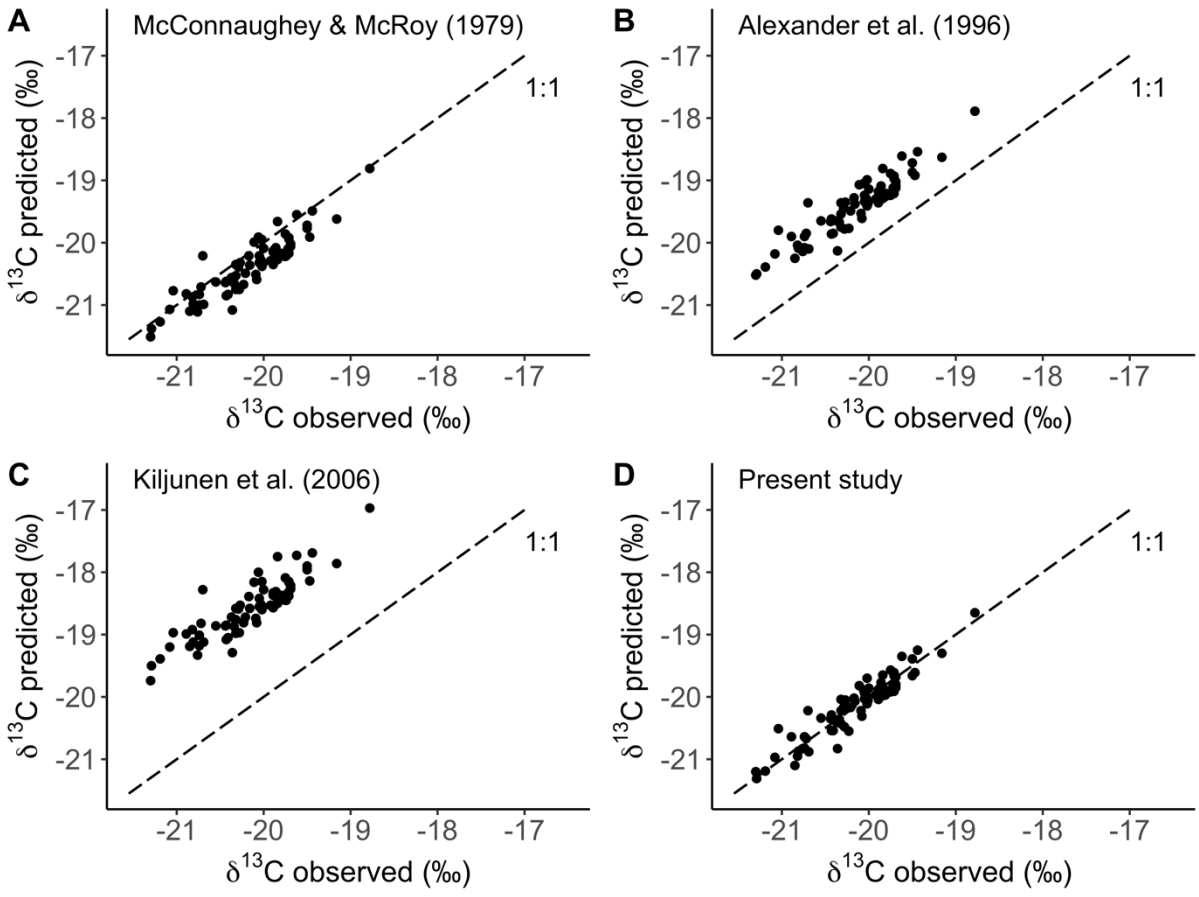

Figure A1: Observed (chemically determined) vs predicted (using the four different lipid-normalization models) lipid-extracted $\delta^{13}C$ values from harbour porpoises bycaught in Norwegian coastal waters in September–October 2016. The dotted line shows the 1:1 ratio for observed and predicted values.

TABLE A2: Regression equations used to infer the weight and length of the prey items consumed by harbour porpoises from otolith length (OL) and beak lower rostral length (LRL). All lengths are in mm. FW = fish length and FL = fish length. Equations marked with * are from Härkönen (1986), with ** from Clarke (1986) (the equation for *Gonatus* was used), and with *** from Windsland (2007). Others are from pers. comm. (U. Lindstrøm and L. Lindblom).

Prey item	Weight	Length
Ammodytes spp. (sandeel)	$FW = 0.61215\ OL^{2.71}$ *	FL = 8.776 + 51.906 OL *
Clupea harengus (herring)	$FW = 1.631\ OL^{2.9972}$	FL = 13.815 + 56.399 OL
Gadiculus argenteus thori (silvery pout)	$FW = 0.021289\ OL^{3.785}$ *	$FL = 19.449\ OL^{1.053}$ *
Gadus morhua (cod)	$FW = 0.0294\ OL^{3.5377}$	FL = -18.941 + 25.76 OL
Mallotus villosus (capelin)	$FW = 1.538\ OL^{2.778}$ **	FL = 44.333 OL + 41.951 **
Micromesistius poutassou (blue whiting)	$FW = 0.0067267\ OL^{3.892}$ *	FL = -40.94 + 25.394 OL *
Melanogrammus aeglefinus (haddock)	$FW = 0.002096\ OL^{4.58}$ *	$FL = 8.785\ OL^{1.38}$ *
Merlangius merlangus (whiting)	$FW = 0.012692\ OL^{3.535}$ *	FL = -11.936 + 19.7 OL *
Merluccius merluccius (hake)	$FW = 0.02628\ OL^{3.484}$ *	FL = -0.63 + 23.884 OL
Leptoclinus maculatus (daubed shanny)	FW = 3.7735 OL - 1.3259	NA
Lumpenus lampretaeformis (snakeblenny)	$FW = 0.374\ OL^{3.6684}$	NA
Pollachius virens (saithe)	$FW = 0.007288\ OL^{4.501}$ *	$FL = 8.97297\ OL^{1.53}$ *
Scomber scombrus (mackerel)	$FW = 1.094\ OL^{4.039}$ *	FL = -20.41 + 87.59 OL
Sebastes spp.	$FW = 0.071\ OL^{3.295}$ *	$FL = 16.165\ OL^{1.224}$ *
Trisopterus esmarkii (Norway pout)	$FW = 0.002805\ OL^{4.729}$ *	FL = -42.6 + 29.522 OL *
Trisopterus minutus (poorcod)	$FW = 0.003540\ OL^{4.57}$ *	FL = -49.9 + 29.091 OL *
Liparidae	$FW = 0.0921\ OL^{3.626}$	NA
Myctophidae	NA	NA
Squid	LnW = -0.655 + 3.33 lnLRL ***	NA

APPENDIX B

Intra- and inter-reader variability in otolith identification

Otoliths are widely used in diet studies to identify the fish prey of piscivore predators such as fish, marine mammals, and seabirds (Pierce and Boyle 1991). Even though the shape of otoliths, in particular sagittal otoliths, is species-specific, the distinctive characteristics are not always obvious (Härkönen 1986). Otolith morphology can be similar, especially for species of the same genera: e.g. saithe *Pollachius virens* and pollack *Pollachius pollachius*, or poor cod *Trisopterus minutus* and Norway pout *Trisopterus esmarkii*. This can be accentuated if otoliths are significantly worn out due to the digestive secretions in the stomach, which affect their original shape. Additionally, species identification retains an element of subjectivity. Variability in the identification of otoliths is therefore likely to exist between readers due to differences in experience and individual perception. Age-determination variability among readers has been the subject of several studies and workshops (e.g. ICES 1991; Kimura and Lyons 1991; Stransky et al. 2005) but no work has yet been done to assess variation in identification. Differences could also exist between different readings by the same reader over time, especially if the reader is gaining experience in otolith identification in the meantime.

B.1. Experimental set-up

The stomach contents from 2016 were used to investigate inter-reader variability, with readings from three readers, each with different experience with otolith identification (Table A1). Additionally, approximately half the stomach samples from the 2016 material were read by the author on two occasions (June and October 2018) in order to evaluate intra-reader variability in the case of a learning process (i.e. the reader becoming more knowledgeable and familiar with digested otoliths). The aim of the experiments was to qualify variability between readers of different experience and to examine the importance of consistency (in reader, or at least in experience) in stomach content analysis in diet studies. Note that crustaceans were not included in the inter- and intra-reader variability analyses.

TABLE B1: The different readers involved in the inter-reader variability experiment and their experience in otolith identification.

Year	Reader	Experience
2016	Reader 1	Inexperienced and unguided
2016	Reader 2	Expert who performed a quick reading
2016	Reader 3	Inexperienced but slightly guided by Reader 2

B.2. Results and discussion

Inter-reader variability

Differences in the frequency of occurrence (FO_i, i.e. the percentage of stomachs in which a prey item $_i$ was found) between readers was investigated (Figure B1). This feeding index was chosen because it gives information on species identification and because these data were complete and comparable between different readers.

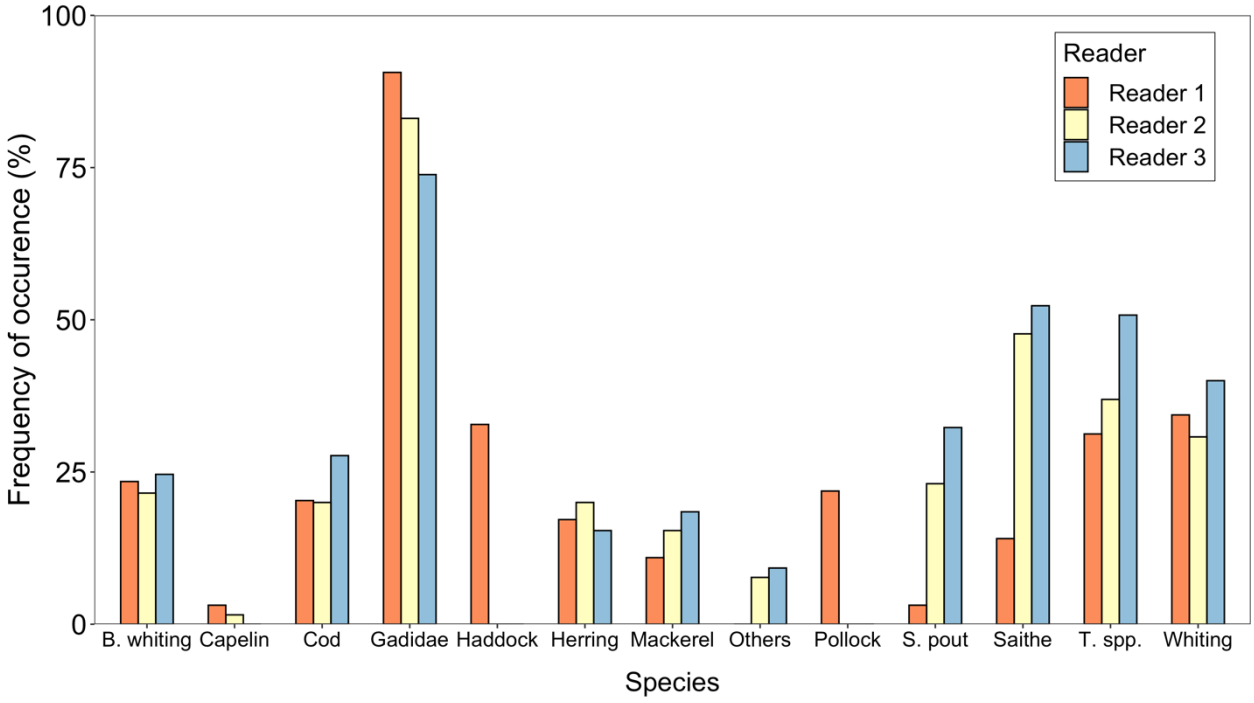

FIGURE B1: Frequency of occurrence of fish prey species identified from the stomach contents of harbour porpoises bycaught in 2016 according to three different readers (see Table B1). B. whiting stands for Blue whiting, S. pout for Silvery pout, and T. spp. for *Trisopterus* spp.

Reader 1 seemed to have more distinct results than readers 2 and 3, who had more similar results to each other. This is likely because reader 3 received more help and instructions from reader 2 than did reader 1.

Only reader 1 identified haddock and pollock (*Pollachius Pollachius*) in the samples, while not frequently identifying saithe. These three species have similar otolith structure and can be hard to distinguish from one another (Härkönen 1986), especially for someone with limited experience. Reader 1 also found silvery pout to be less frequently occurring in the stomachs than readers 2 and 3 did. Silvery pout has small otoliths with easily eroded distinguishing features (Härkönen 1986). It is likely that reader 1 could not identify this species, and often classified such otoliths as unidentified gadoids (i.e. Gadidae). Unidentified gadoids indeed occurred most frequently according to reader 1, compared to readers 2 and 3, suggesting the ability to identify otoliths to the species level increases with experience and/or guidance. Additionally, reader 2 had the lowest FO_i for unidentified gadoids, which could be explained by the fact that reader 3 only performed a quick reading, likely not spending as much time trying to identify very small and eroded otoliths as reader 2.

While lack of experience could lead to the under-identification of otoliths to the species level, it could also have contributed to an over-identification of some. For example, *Trisopterus* spp. were identified in more stomachs by reader 3 than by reader 2; a more experienced reader (i.e. reader 2) might be better able to realise when an otolith should be considered unidentifiable. However, this could also be explained by reader 3 performing a quicker reading. Capelin was not found by reader 3, this might be because capelin otoliths are fragile and easily broken and that this reader handled the material last. Additionally, it occurred so seldomly in the samples, as suggested by the other two readings, it is possible reader 3 did not realise this species was potentially present. This lack of experience and knowledge of which fish species to expect could also be the reason why reader 1 did not find other fishes (“others”, mostly Myctophidae) in the stomachs. Additionally, personal differences in perception and reasoning could impact the readings.

Intra-reader variability

Differences in both frequency of occurrence and numerical abundance (N_i) for the same reader before and after acquiring substantial knowledge and experience in otolith identification were investigated (Figure B2).

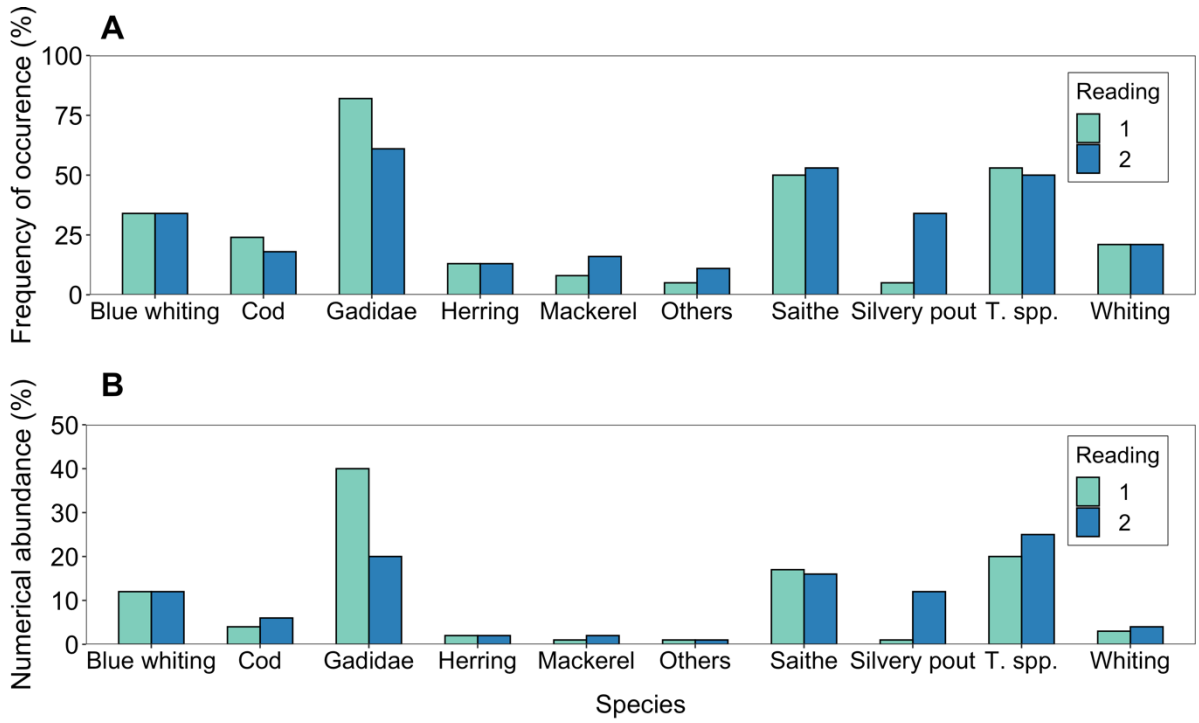

FIGURE B2: Frequency of occurrence and numerical abundance of fish prey species identified by the same reader on two occasions, before and after acquiring experience in otolith identification. T. spp. stands for *Trisopterus* spp.

The differences seem relatively small between the two readings. However, unidentified gadoids occurred at higher frequency and greater numbers in the first reading. In the second reading, some of these unidentified gadoids were likely identified as silvery pout, which increased in frequency and number. As mentioned above, silvery pout otoliths are small and erode easily in the stomach, affecting their distinguishing features. It is likely that, with no previous experience, the reader could not identify most of the silvery pout otoliths at the time of the first reading and classified them as unidentified gadoids. With experience, identification was easier and unidentified gadoids were found in fewer stomachs and in lower numbers. Both mackerel and "others" increased in frequency of occurrence and numerical abundance between the two readings and were likely easier to identify with experience as well. Cod were found in fewer stomachs in the second reading but were slightly more numerous than in the first reading. This is hard to explain and might be due to difficulties in discerning small and digested cod from

saithe otoliths in different stomachs and may depend on conditions the day different stomachs were analysed. Variability might arise day to day from differences in mental fitness and awareness as well as from past observations (i.e. if a species has been found a lot in previous samples, identification of future similar otoliths might be biased towards that species).

Conclusion

In conclusion, reader experience, level of guidance from an experienced reader, individual biases (e.g. awareness, effort taken, past observations) are likely to impact the identification of otoliths. In particular, a lack of experience may bias the frequency of occurrence estimates through incorrect identification of species. Additionally, an inexperienced reader is more likely to identify otoliths at the family level rather than species level. It seems that the inter-reader variability was more important than the intra-reader variability. Although the experimental design was not optimal, the results highlight the potential impact of inter-reader variability in particular and call attention to this issue in the interpretation of diet data. Future inter-reader variability studies should have a precise protocol and fully independent readers, who should not have information regarding results from the other readers nor share information regarding the identification of otoliths. It must be noted that it is impossible to know which reader is the most correct (at least without DNA analyses on each otolith), and that visual identification will always be impacted by subjectivity and human error.

APPENDIX C

Supplementary information for Results and Discussion

Section 1: Figures

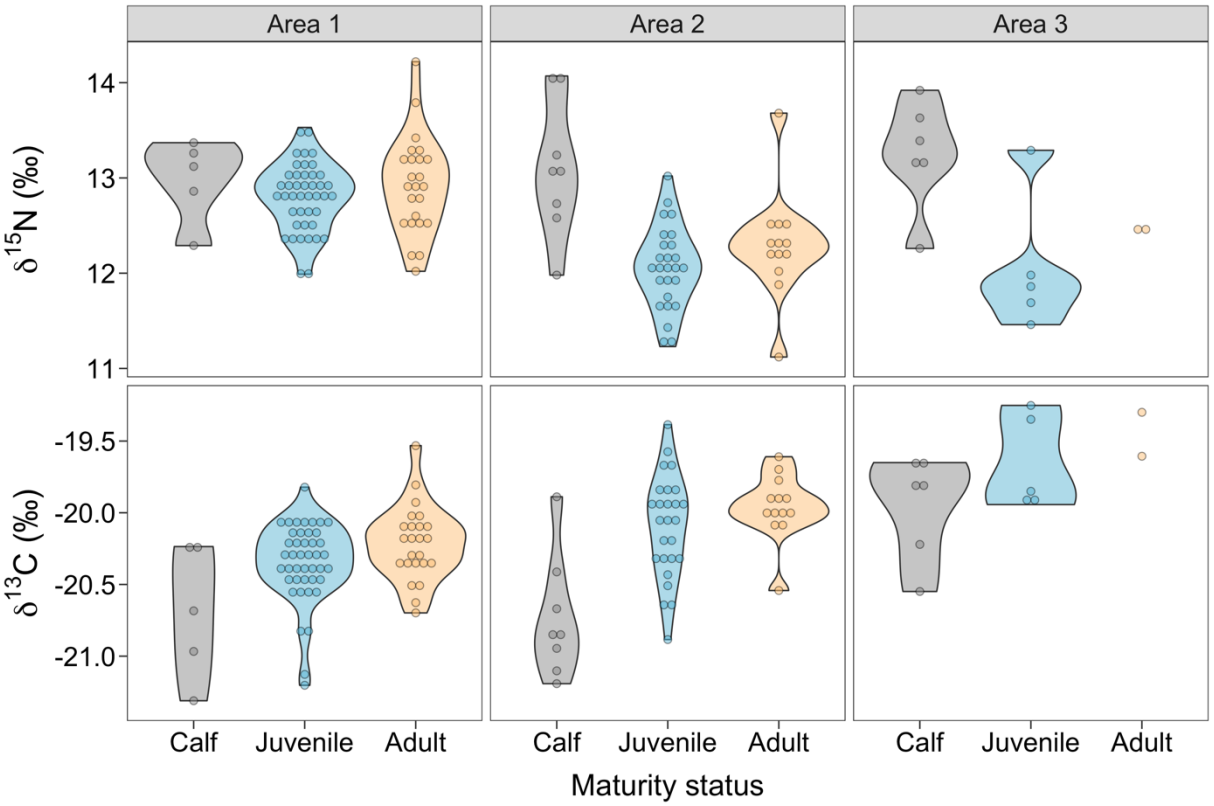

FIGURE C1: Violin plots of $\delta^{15}N$ and $\delta^{13}C$ against maturity status, by area.

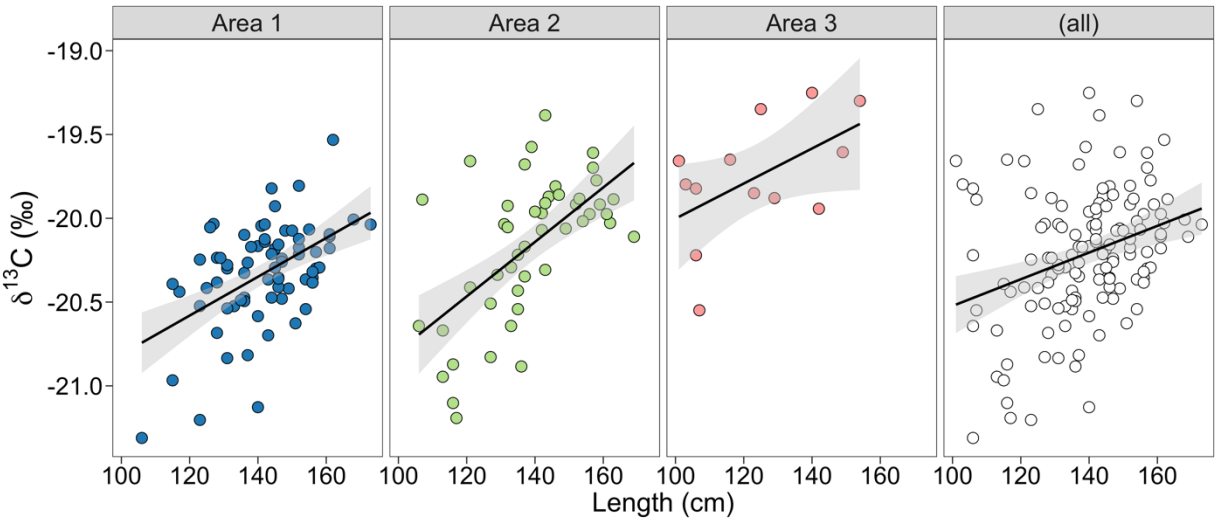

FIGURE C2: Scatter plots of harbour porpoise $\delta^{13}C$ values against length, by area. Solid lines and grey shaded areas represent the linear regression lines and their respective 95% confidence interval.

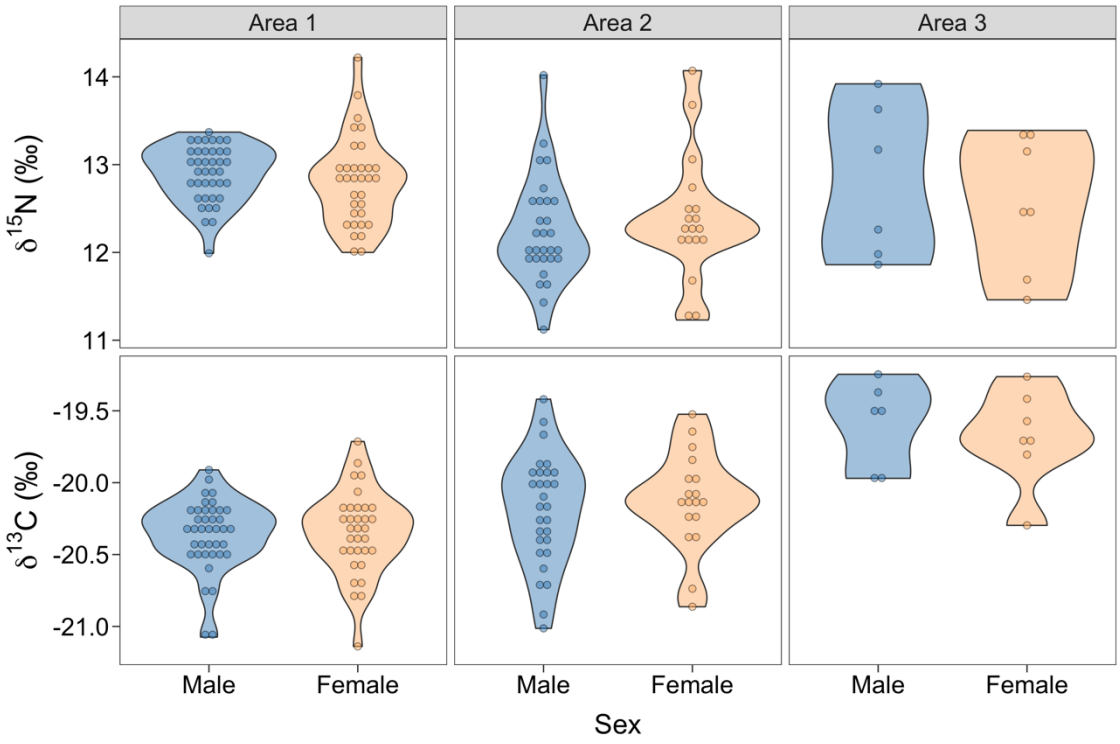

FIGURE C3: Violin plots of $\delta^{15}N$ and $\delta^{13}C$ against sex, by area.

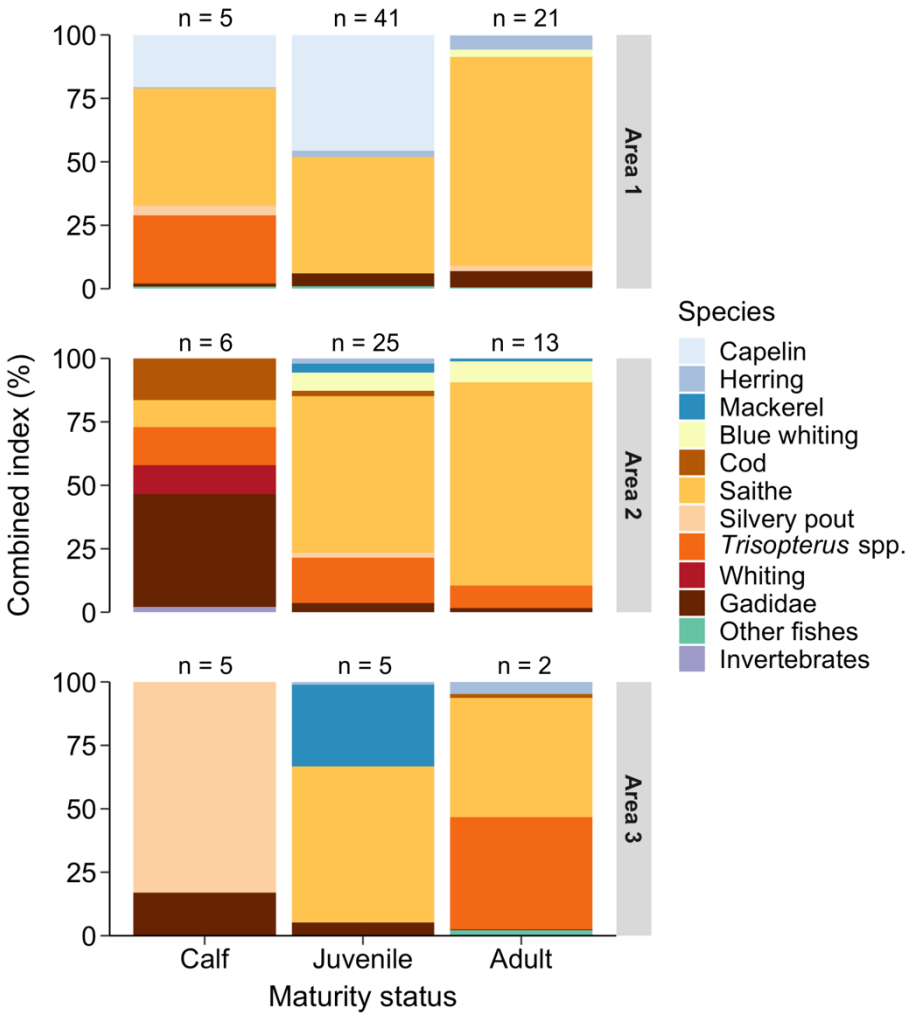

FIGURE C4: Diet composition, based on the combined index (Q_i), of calf, juvenile, and adult harbour porpoises, by area.

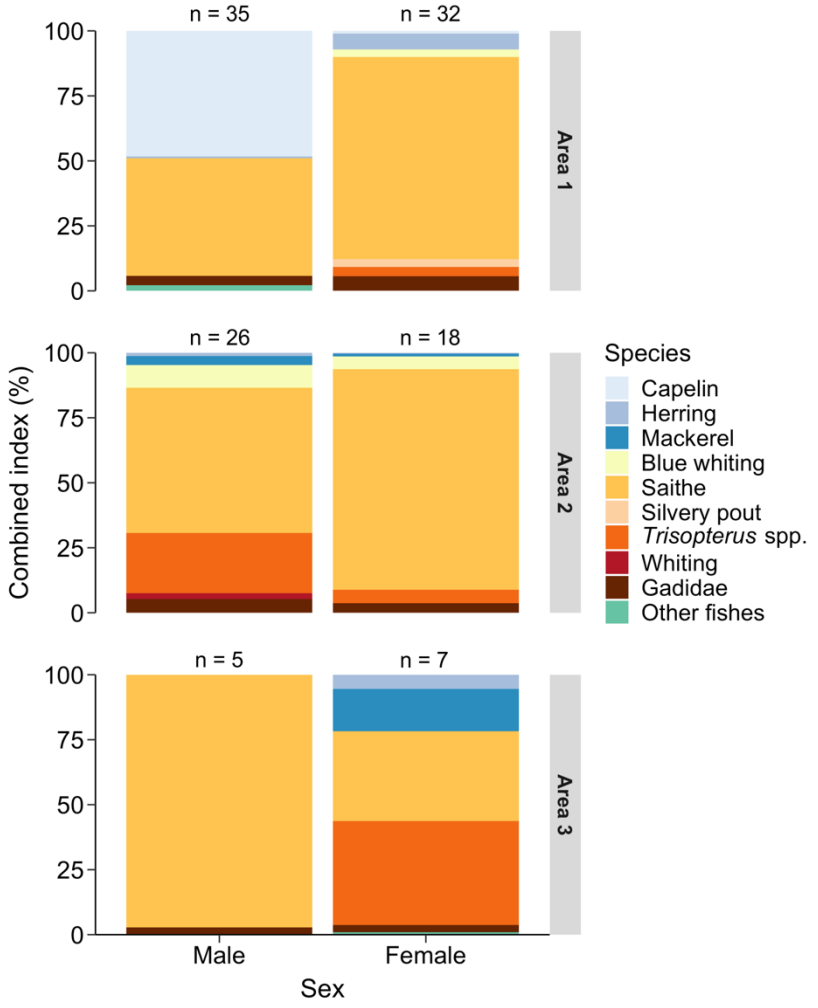

FIGURE C5: Diet composition, based on the combined index (Q_i), of male and female harbour porpoises, by area.

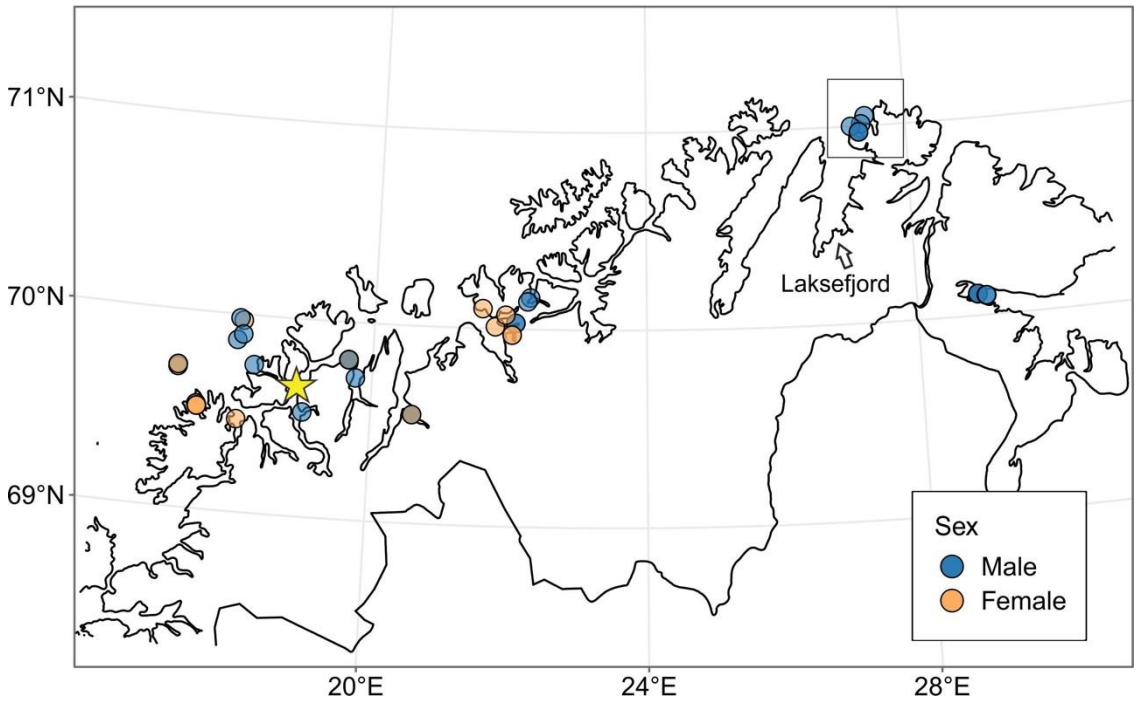

FIGURE C6: Map of northern Norway (Troms and Finmark) and sampling locations of male (blue circles) and female (orange circles) harbour porpoises. The square indicates porpoises bycaught near the mouth of Laksefjord, which are mostly juveniles (5 juveniles and one calf) and all male. Tromsø is indicated by a star for reference.

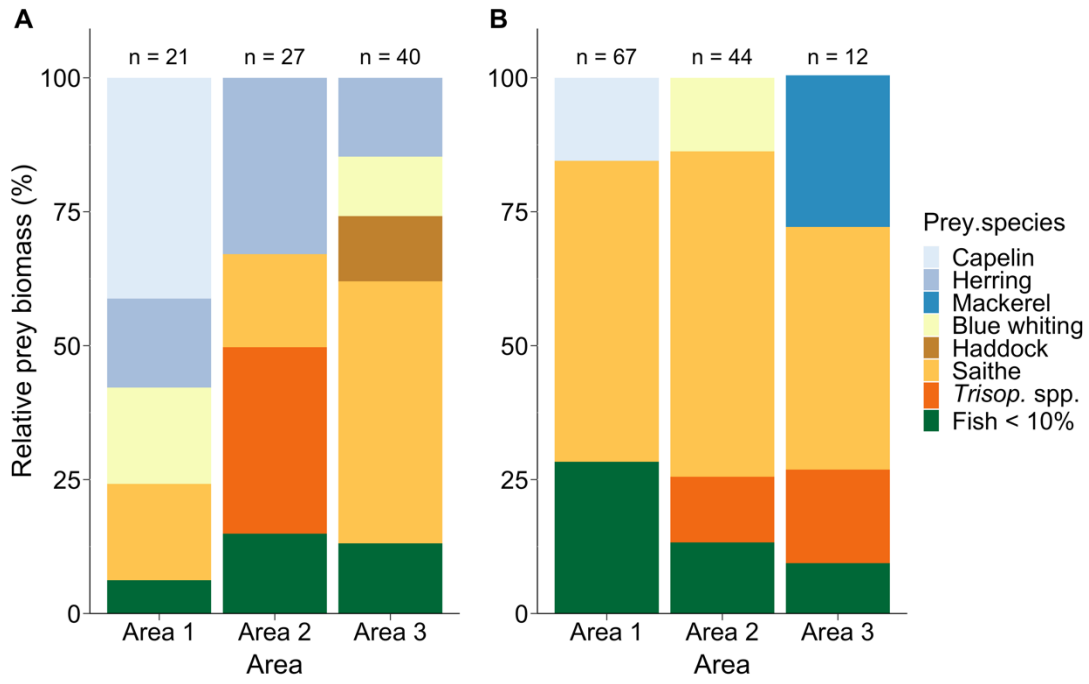

FIGURE C7: Diet composition, in terms of biomass (B_i), of harbour porpoises bycaught in three different areas along the Norwegian coast in 1988–1990 (A: Aarefjord et al. 1995) and 2016–2017 (B: this study). In Aarefjord et al. (1995), *Trisopterus* spp. (*Trisop*. spp.) defines prey identified as poor cod by the authors, whereas in this work no exact identification was considered possible and *Trisopterus* species can be poor cod or Norway pout.

Section 2: Tables

TABLE C1: Diet composition of harbour porpoises bycaught along the Norwegian coast (2016–2017), by maturity status (C = calf, J = juvenile, and A = adult). The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	No. prey			FO_i (%)			N_i (%)			B_i (%)			Q_i (%)		
	C	J	A	C	J	A	C	J	A	C	J	A	C	J	A
Fishes															
Ammodytidae															
Ammodytes spp.	5	79	20	12.5	13.4	8.3	1.5	3.6	1.2	0.4	0.4	0.1	0.2	0.2	0.2
Clupeidae															
Clupea harengus	1	70	21	6.3	12.7	25.0	0.3	3.2	1.3	0.5	6.1	4.2	0.1	2.5	0.2
Gadidae															
Gadiculus thori	44	148	131	43.8	22.5	27.8	12.9	6.7	8.1	4.1	1.8	1.7	8.8	1.3	0.1
Gadus morhua	27	116	67	18.8	16.9	33.3	7.9	5.3	4.1	4.0	1.6	1.9	3.7	0.9	2.1
Melanogrammus aeglefinus			3			2.8			0.2			1.8			<0.1
Merlangius merlangus	37	158	29	18.8	22.5	19.4	10.8	7.2	1.8	2.9	1.3	0.2	2.6	0.9	<0.1
Micromesistius poutassou		49	132		21.1	16.7		2.2	8.2		6.5	15.3		4.5	3.9
Pollachius virens	13	159	123	12.5	38.0	69.4	3.8	7.2	7.6	52.5	51.4	64.1	32.2	63.9	75.4
Trisopterus spp.	70	313	533	31.3	32.4	41.7	20.5	14.2	33.0	17.2	9.7	6.5	26.5	10.3	9.0
Unidentified gadoids	105	337	197	56.3	56.3	61.1	30.7	15.3	12.2	6.9	1.6	1.7	19.0	2.9	6.2
Stichaeidae															
Leptoclinus maculatus		10	28		5.6	16.7		0.5	1.7		0.1	0.3		<0.1	2.1
Lumpenus lampretaeformis	1		1	6.3		2.8	0.3		0.1	0.1		<0.1	<0.1		<0.1
Liparidae spp.			2			5.6			0.1			<0.1			<0.1
Merlucciidae															
Merluccius merluccius		1	3		1.4	2.8		<0.1	0.2		<0.1	0.2		<0.1	<0.1
Myctophidae spp.			8			8.3			0.5			–			–

Osmeridae															
Mallotus villosus	20	403	29	12.5	25.4	16.7	5.8	18.3	1.8	10.6	12.0	0.3	6.5	10.0	0.5
Scorpaenidae															
Sebastes spp.			1			2.8			0.1			<0.1			0.1
Scombridae															
Scomber scombrus		120	9		12.7	8.3		5.5	0.6		5.9	1.6		2.4	0.1
Unidentified fish remains		3	2		4.2	5.6		0.1	0.1		–	–		–	–
Invertebrates															
Decapoda	13			6.3			3.8			1.0			0.3		
Euphausiacea															
Euphausiidae spp.	6	231	278	12.5	19.7	11.1	1.8	10.5	17.2	<0.1	0.1	0.1	<0.1	<0.1	<0.1
Cephalopoda		1			1.4			<0.1			1.6			0.1	
Unidentified invertebrates	1			6.3			0.3			–			–		

TABLE C2: Diet composition of male (M) and female (F) harbour porpoises bycaught along the Norwegian coast (2016–2017). The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	No. prey		FO_i (%)		N_i (%)		B_i (%)		Q_i (%)	
	M	F	M	F	M	F	M	F	M	F
Fishes										
Ammodytidae										
Ammodytes spp.	100	4	15.9	7.0	5.0	0.2	0.6	<0.1	0.3	<0.1
Clupeidae										
Clupea harengus	58	34	12.1	19.3	2.9	1.6	3.5	6.4	1.5	3.0
Gadidae										
Gadiculus thori	153	170	22.7	31.6	7.7	7.9	1.6	2.0	1.3	1.5
Gadus morhua	98	112	19.7	24.6	4.9	5.2	1.4	2.2	0.9	1.3
Melanogrammus aeglefinus		3		1.8		0.1		1.5		0.1
Merlangius merlangus	180	44	24.2	17.5	9.0	2.0	1.5	0.3	1.2	0.1
Micromesistius poutassou	54	127	21.2	12.3	2.7	5.9	7.9	12.7	5.7	3.8
Pollachius virens	151	144	36.4	52.6	7.6	6.7	51.7	62.3	64.6	79.9
Trisopterus spp.	193	723	25.8	45.6	9.7	33.5	11.6	5.7	10.3	6.3
Unidentified gadoids	318	321	51.5	64.9	15.9	14.9	1.7	1.9	3.0	2.9
Stichaeidae										
Leptoclinus maculatus	31	7	10.6	5.3	1.6	0.3	0.3	0.1	0.1	<0.1
Lumpenus lampretaeformis	1	1	1.5	1.8	0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Liparidae spp.	1	1	1.5	1.8	0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Merlucciidae										
Merluccius merluccius	1	3	1.5	1.8	0.1	0.1	<0.1	0.2	<0.1	<0.1
Myctophidae spp.		8		5.3		0.4		–		–
Osmeridae										
Mallotus villosus	407	45	21.2	21.1	20.4	2.1	13.4	0.5	9.7	0.3
Scorpaenidae										
Sebastes spp.	1		1.5		0.1		<0.1		<0.1	
Scombridae										
Scomber scombrus	124	5	12.1	7.0	6.2	0.2	3.0	4.2	1.2	0.7
Unidentified fish remains	4	1	6.1	1.8	0.2	<0.1	–	–	–	–
Invertebrates										
Decapoda		13		1.8		0.6		<0.1		<0.1
Euphausiacea										
Euphausiidae spp.	121	394	15.2	17.5	6.1	18.2	<0.1	0.1	<0.1	<0.1
Cephalopoda	1		1.5		0.1		1.7		0.1	
Unidentified invertebrates	1		1.5		0.1		–		–	

TABLE C3: Diet composition of adult male (AM) and adult female (AF) harbour porpoises bycaught along the Norwegian coast (2016–2017). The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	No. prey		FO_i (%)		N_i (%)		B_i (%)		Q_i (%)	
	AM	AF	AM	AF	AM	AF	AM	AF	AM	AF
Fishes										
Ammodytidae										
Ammodytes spp.	19	1	15.4	4.3	8.3	0.1	0.7	<0.1	0.2	<0.1
Clupeidae										
Clupea harengus	3	18	15.4	30.4	1.3	1.3	0.7	4.6	0.2	2.4
Gadidae										
Gadiculus thori	22	109	30.8	26.1	9.6	7.9	0.1	1.9	0.1	0.8
Gadus morhua	19	48	38.5	30.4	8.3	3.5	2.4	1.9	2.1	1.0
Melanogrammus aeglefinus		3		4.3		0.2		2.0		0.1
Merlangius merlangus	4	25	7.7	26.1	1.7	1.8	0.3	0.2	<0.1	0.1
Micromesistius poutassou	9	123	23.1	13.0	3.9	8.9	7.4	16.3	3.9	3.6
Pollachius virens	28	95	53.8	78.3	12.2	6.8	61.7	64.4	75.4	85.6
Trisopterus spp.	43	490	23.1	52.2	18.7	35.3	17.3	5.1	9.0	4.5
Unidentified gadoids	28	169	53.8	65.2	12.2	12.2	5.1	1.3	6.2	1.5
Stichaeidae										
Leptoclinus maculatus	26	2	38.5	4.3	11.3	0.1	2.4	<0.1	2.1	<0.1
Lumpenus lampretaeformis	1		7.7		0.4		<0.1		<0.1	
Liparidae spp.	1	1	7.7	4.3	0.4	0.1	0.1	<0.1	<0.1	<0.1
Merlucciidae										
Merluccius merluccius		3		4.3		0.2		0.2		0.0
Myctophidae spp.		8		13.0		0.6	–	–	–	–
Osmeridae										
Mallotus villosus	18	11	23.1	13.0	7.8	0.8	1.0	0.2	0.5	<0.1
Scorpaenidae										
Sebastes spp.	1		7.7		0.4		0.3		0.1%	
Scombridae										
Scomber scombrus	7	2	7.7	8.7	3.0	0.1	0.6	1.7	0.1	0.3
Unidentified fish remains	1	1	7.7	4.3	0.4	0.1	–	–	–	–
Invertebrates										
Decapoda										
Euphausiacea										
Euphausiidae spp.		278		17.4		20.0		0.1		<0.1
Octopoda										
Unidentified invertebrates										

TABLE C4: Diet composition of harbour porpoises bycaught in Autumn 2016 (A) and Spring 2017 (S) along the Norwegian coast. The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	No. prey		FO_i (%)		N_i (%)		B_i (%)		Q_i (%)	
	A	S	A	S	A	S	A	S	A	S
Fishes										
Ammodytidae										
Ammodytes spp.		4		14.8		0.7		<0.1		<0.1
Clupeidae										
Clupea harengus	41	27	27.3	18.5	10.7	4.9	4.6	12.4	2.5	7.4
Gadidae										
Gadiculus thori	4	99	9.1	40.7	1.0	17.9	<0.1	5.2	<0.1	6.8
Gadus morhua	29	7	9.1	11.1	7.6	1.3	0.3	2.9	<0.1	1.1
Melanogrammus aeglefinus		3		3.7		0.5		4.3		0.5
Merlangius merlangus	85		54.5		22.1		1.6		1.8	
Micromesistius poutassou	1	2	27.3	7.4	0.3	0.4	29.2	0.1	15.8	<0.1
Pollachius virens	51	50	63.6	33.3	13.3	9.0	60.5	65.1	76.2	70.2
Trisopterus spp.	4	123	27.3	37.0	1.0	22.2	2.3	3.9	1.2	4.6
Unidentified gadoids	149	32	81.8	37.0	38.8	5.8	1.5	3.1	2.5	3.7
Stichaeidae										
Leptoclinus maculatus		5		11.1		0.9		0.2		0.1
Lumpenus lampretaeformis		1		3.7		0.2		<0.1		<0.1
Liparidae spp.		2		7.4		0.4		0.1		<0.1
Merlucciidae										
Merluccius merluccius										
Myctophidae spp.										
Osmeridae										
Mallotus villosus		73		63.0		13.2		2.7		5.4
Scorpaenidae										
Sebastes spp.										
Scombridae										
Scomber scombrus	1		<0.1		0.3		<0.1		<0.1	
Unidentified fish remains										
Invertebrates										
Decapoda	13		<0.1		3.4		<0.1		<0.1	
Euphausiacea										
Euphausiidae spp.	6	126	27.3	14.8	1.6	22.7	<0.1	0.1	<0.1	<0.1
Cephalopoda										
Unidentified invertebrates										

TABLE C5: Diet composition of harbour porpoises bycaught along the Norwegian coast (2016–2017), by area (area 1 = northern Norway, area 2 = mid-Norway, and area 3 = southern Norway). The feeding indices, frequency of occurrence (FO_i), relative numerical abundance (N_i), relative biomass (B_i), and the combined index (Q_i) are presented.

Prey items	No. prey			FO_i (%)			N_i (%)			B_i (%)			Q_i (%)		
	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Fishes															
Ammodytidae															
Ammodytes spp.	104			21.6			5.3			0.6			0.4		
Clupeidae															
Clupea harengus	76	14	2	17.9	11.4	16.7	3.9	0.8	0.6	7.4	3.2	4.7	4.0	0.8	2.8
Gadidae															
Gadiculus thori	143	163	17	22.4	29.5	41.7	7.2	9.0	4.7	2.4	1.5	0.2	1.6	1.0	0.2
Gadus morhua	24	181	5	14.9	36.4	8.3	1.2	9.9	1.4	1.6	2.1	1.1	0.7	1.6	0.3
Melanogrammus aeglefinus	3			1.5			0.2			2.0			0.1		
Merlangius merlangus	73	150	1	9.0	43.2	8.3	3.7	8.2	0.3	0.4	1.2	<0.1	0.1	1.1	<0.1
Micromesistius poutassou	82	97	2	11.9	25.0	16.7	4.2	5.3	0.6	7.8	13.7	0.5	2.8	7.5	0.3
Pollachius virens	153	134	8	40.3	52.3	33.3	7.8	7.4	2.2	55.1	60.7	45.3	66.9	69.3	54.3
Trisopterus spp.	344	269	303	19.4	54.5	50.0	17.4	14.8	83.5	2.4	12.3	17.5	1.4	14.6	31.4
Unidentified gadoids	253	371	15	49.3	70.5	58.3	12.8	20.4	4.1	2.6	1.2	0.8	3.9	1.9	1.6
Stichaeidae															
Leptoclinus maculatus	38			14.9			1.9			0.4			0.2		
Lumpenus lampretaeformis	2			3.0			0.1			<0.1			<0.1		
Liparidae spp.	2			3.0			0.1			<0.1			<0.1		
Merlucciidae															
Merluccius merluccius		1	3		2.3	8.3		0.1	0.8		–	1.7		–	0.5
Myctophidae spp.		4	4		4.5	8.3		0.2	1.1		–	–		–	–
Osmeridae															
Mallotus villosus	452			38.8			22.9			15.2			17.7		

Scorpaenidae																
Sebastes spp.	1			1.5			0.1			<0.1			<0.1			
Scombridae																
Scomber scombrus		127	2		25.0	8.3		7.0	0.6		4.0	28.3		2.2	8.5	
Unidentified fish remains	1	3	1	1.5	6.8	8.3	0.1	0.2	0.3	–	–	–	–	–	–	
Invertebrates																
Decapoda		13			2.3			0.7			0.1			<0.1		
Euphausiacea																
Euphausiidae spp.	222	293		14.9	22.7		11.2	16.1		0.1	0.1		<0.1	<0.1		
Cephalopoda	1			1.5			0.1			1.9			0.1			
Unidentified invertebrates		1			2.3			0.1			–			–		