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Feeding Ecology of Harbour Seals (*Phoca vitulina*) in Southern Norway

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Sammendrag

For å kunne forstå dynamikken og funksjonene som foregår i et økosystem er det viktig å ha kunnskap om samspillet mellom rovdyr og bytte. Steinkobba (*Phoca vitulina*) er et fiskespisende, marint pattedyr som finnes nært eller på toppen av marine næringsnett. Siden de hovedsaklig spiser fisk har steinkobba potensiale til å komme i konflikt med fiskere og fiskerier. I de senere år har steinkobbepopulasjonen i Skagerrak og Kattegat økt og det hevdes nå at selen nærmest tømmer sjøen for torsk. I denne masteroppgaven ble dietten hos steinkobbe estimert ved fire forskjellige lokaliteter langs sørlandskysten (Kragerø, Risør, Tvedestrand og Fevik) ved hjelp av innsamling av avføringsprøver og identifisering av otolitter. Dette er første gang seldiett blir estimert i dette området. Resultatene viste at totalt sett var seldietten variert og inkluderte 20 forskjellige arter og artsgrupper. De viktigste artsgruppene var torskefisk og flatfisk. Det ble funnet regionale forskjeller hovedsaklig mellom Fevik og de andre lokalitetene: Fevik viste en lavere artsrikhet. Det var mulig å dele resultatene fra Tvedestrand i to årstider (vinter/vår og sommer/høst). Både artsrikhet og diettoppbygning forandret seg med årstid her. Estimater for fiskestørrelser og -vekt viste at generelt sett foretrekker selen småfisk mindre enn minstemålene. Dette antyder at steinkobber ikke konkurrerer i stor grad med lokale fiskerier.

Abstract

In order to understand ecosystem dynamics and functions it is vital to have knowledge about relationships between predator and prey. Harbour seals (*Phoca vitulina*) are piscivorous marine mammals found at or near the top of marine food webs. Being mainly piscivores, harbour seals have the potential to come into conflict with fishermen and fisheries. Recently, as the Skagerrak and Kattegat population of harbour seals has increased, claims that seals are depleting the cod population have surfaced. Using scat sampling and otolith identification, harbour seal diet was estimated in four separate locations along the coast of southern Norway (Kragerø, Risør, Tvedestrand and Fevik). This is the first time harbour seal diet has been estimated in this area. The results showed that seal diet was overall varied and included 20 different species and species groups. The most important prey groups were gadids and flatfish. There were regional differences mainly between Fevik and the other locations: Fevik showing a lower species richness. It was possible to divide results from Tvedestrand into two seasons (winter/spring and summer/autumn). Both species richness and diet composition changed between seasons at this location. Fish length and weight estimates showed that seals generally prefer small fish below the smallest allowed catch size. This suggests that harbour seals do not compete on a large scale with local fisheries.

Preface

First, I would like to thank my excellent supervisors, Carla Freitas and Lars Korslund. You have guided me so well through field expeditions, laboratory work and thesis writing and for that I am grateful. I could have not have done this without you. I would also like to thank Lotta Lindblom (IMR) for invaluable help with the otolith handling and identification. Jan Atle Knutsen (IMR) deserves many thanks for providing the funds and logistics to conduct this study. The data set would have been very much smaller had it not been for Kjell Tormod Nilssen (IMR) collecting a large number of the samples last summer. Thank you very much for your contribution. I would also like to thank everyone else at IMR Flødevigen who helped me in ways big and small and made me feel so welcome during my weeks of fieldwork.

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Introduction

An important part of understanding ecosystem dynamics and functions lies in the relationships between predators and prey (e.g. Ford et al., 2016; Graham, Harris, Matejusová, & Middlemas, 2011; Pierce & Boyle, 1991; Riemer, Wright, & Brown, 2011; Staniland, 2002). These relationships can be better understood by mapping the diet composition of predators (Ford et al., 2016). Knowledge like this is important and necessary for sustainable management of ecosystems (Ford et al., 2016).

Because diets are not always readily discernible for many species in the wild, one can use several available methods to obtain information on the subject. These include otolith analysis from faeces (e.g. Andersen, Lydersen, Grahl-Nielsen, & Kovacs, 2004; Lance, Chang, Jeffries, Pearson, & Acevedo-Gutiérrez, 2012; Luxa & Acevedo-Gutiérrez, 2013), fatty acid analysis from faeces, (e.g. Andersen et al., 2004; Bromaghin et al., 2012), stable isotope analysis (e.g. Burns, Trumble, Castellini, & Testa, 1998), stomach content analysis (e.g. Pitcher, 1980), genetic analysis of faeces (e.g. Deagle et al., 2005; Ford et al., 2016; Janecka et al., 2008; Kohn, Knauer, Stoffella, Schröder, & Pääbo, 1995; Onorato, White, Zager, & Waits, 2006), etc. The latter method is especially useful for identifying prey remains from e.g. bones when otoliths are not available, especially fragile (i.e. salmonids) under-represented (Kvitrud, Riemer, Brown, Bellinger, & Banks, 2005; Matejusová et al., 2008; Parsons, Piertney, Middlemas, Hammond, & Armstrong, 2005) or to distinguish between closely related species (Matejusová et al., 2008).

Harbour seals (*Phoca vitulina*), also called common seals, are generalist predators, mainly piscivores, and are thus found near or at the top of marine food webs (e.g. Bromaghin et al., 2012; Ydesen et al., 2014). They inhabit coastal areas around the northern Pacific and Atlantic oceans (Havforskningsinstituttet, 2009). Harbour seals return to specific haul-out sites to socialize and rest with conspecifics between foraging trips, a behaviour generally called central place foraging (Geiger et al., 2013; Luxa & Acevedo-Gutiérrez, 2013). Several studies by P. M. Thompson and others on the harbour seal populations in Scotland's Moray Firth and the Orkney Islands have shed light on the details of their behaviour. In general, seals spend most of their time hauled out in daytime during low tide, while the majority of foraging trips take place at night (Thompson, Fedak, McConnell, & Nicholas, 1989; Thompson & Miller, 1990). Usually, several different such sites located within 75 km of each other (Thompson et al., 1996) are used by seals at different times with individual preferences (Thompson, 1989). Except for females with pups who seemingly prefer secluded haul-out sites for pupping, choice of site seems to be related to proximity to feeding grounds (Thompson et al., 1996). Preferring to stay relatively close to shore, seal foraging trips can vary both in distance and duration: one tagging study showed trips 25-46 km long lasting from less than twelve hours up to six days (Thompson & Miller, 1990), while a later study in the same area measured foraging trips up to 60 km (Thompson et al., 1996). There are also fairly large individual variations in this behavioural aspect as a tagging study in Oregon, USA saw one seal not leaving the bay wherein it was tagged, while another was found 225 km away from the tagging site (Brown & Mate, 1983). In late summer seals of both sexes generally spend more of their time on land due to pupping and moulting (Thompson, 1989; Thompson et al., 1996). After weaning their pups, females begin taking longer trips away from their haul-out sites, presumably in order to rebuild their fat reserves after the pupping season (Thompson et al., 1989). The researchers here also observed behaviour during the winter months and suggested that harbour seals spend much of their time during this season in offshore waters, while returning regularly to haul-out sites in the study area. As a contrast to what has been observed regarding haul-out patterns during the summer months (Thompson & Miller, 1990), in winter seals seem to spend most of their time hauled out during the night (Thompson, Pierce, Hislop, Miller, & Diack, 1991). The authors suggest this is due to tidal cycled and/or foraging, but this could not be confirmed.

Several earlier studies of harbour seal diet composition show that they are generalists and opportunists (e.g. Bromaghin et al., 2012; Geiger et al., 2013; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013; Pierce et al., 1991; Tollit & Thompson, 1996). In general they vary their diets according to season and geographical location, seeming to prefer the regionally and seasonally most abundant species, both benthic and pelagic (e.g. Bromaghin et al., 2012; Geiger et al., 2013; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013). There has also been observed a change in foraging grounds between seasons (Thompson et al., 1996), apparently due to winter prey changing its geographical distribution during overwintering (Pierce et al., 1991; Thompson et al., 1996; Thompson et al., 1991). In some areas seals seem to favour a small number of different prey species, while supplementing their diet with other species from time to time (Lance et al., 2012). Seasonal changes in diet can also be due to the addition of returning migrating fish species (Geiger et al., 2013; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013). As different populations of seals forage in different habitats, their diet composition also varies geographically (Andersen, Teilmann, Harders, Hansen, & Hjøllund, 2007; Härkönen, 1987).

Having such a varied diet, it is not surprising that harbour seals also prey on commercially important fish species (e.g. Bromaghin et al., 2012; Frost & Lowry, 1986; Graham et al., 2011; Spitz, Dupuis, Becquet, Dubief, & Trites, 2015), potentially creating conflicts of interest between seals and humans. These interactions can be divided into two categories: operational interactions that involve seals e.g. wrecking fishing gear or becoming entangled in it, and biological interactions that amongst other things involve seals and humans competing for the same species (Wickens et al., 1992).

As the population of harbour seals in Skagerrak and Kattegat has increased in later years (Bjørge, 2014; Reijnders et al., 2010), local fishermen now claim that harbour seals are depleting the cod (*Gadus morhua*) stocks and must be dealt with (Monrad, 2017; Mosberg, 2006). This development has been observed before with the rising seal population in the Bay of Somme, France (Spitz et al., 2015). However, as the diet of harbour seals along the coast of southern Norway (Telemark and Agder) has not yet been studied in detail, these statements lack scientific proof. Furthermore, it goes against the recommendations made by the government that isolated seal populations with fewer than 100 individuals (e.g. the population along the southern coast of Norway) and/or with special ecological adaptations should not be hunted (Fiskeri- og kystdepartementet, 2010).

Because of this, and in part to address the claims of local fishermen, it was decided to collect fish otoliths from seal scat samples in order to get a better overview of the different fish species included in the diet harbour seals in southern Norway. As with all methodology there are drawbacks and disadvantages to scat sampling. However, it is a fairly unobtrusive and cost-effective sampling technique (e.g. Andersen et al., 2004; Crimmins, Roberts, & Hamilton, 2009; Trites & Joy, 2005) making it suitable for the present study.

Objective

The objective of this thesis was to investigate the feeding ecology of harbour seals in southern Norway. Using scat samples collected at haul-out sites, the thesis aimed to identify prey items consumed by seals in this region, quantify the frequency of occurrence of the prey and estimate their body size and weight. This information is of high importance for evaluating the conflict between seals and fisheries, the ecological role of seals in the marine food web as well as filling gaps in knowledge.

Materials and methods

A total of 121 harbour seal scat samples were collected between June 2015 and August 2016. Samples were collected from Knallaren (58°54’24”N, 09°39’08”E), Ødegårdskilen (58° 51' 42’’N, 9° 31' 10’’E) and Gjesskjæra (58° 51' 51’’N, 9° 34' 20’’E) in Kragerø, Telemark county; Sørfjord (58°43’66”N, 09°07’86”E) near Risør, Aust-Agder county; Askerøy (58°37’02”N, 09°04’27”E) near Tvedestrand, Aust-Agder county; and Ryvingen (58°22’02”N, 08°44’24”E) outside of Fevik (Grimstad), Aust-Agder county (fig. 1 and 2). The sampling sites consisted of small islands and rocks available to the seals mostly during low tide. Some of the sampling sites were located in sheltered areas (Ødegårdskilen, Gjesskjæra, Risør and Askerøy), while other were more exposed to wave action (Knallaren and Ryvingen).

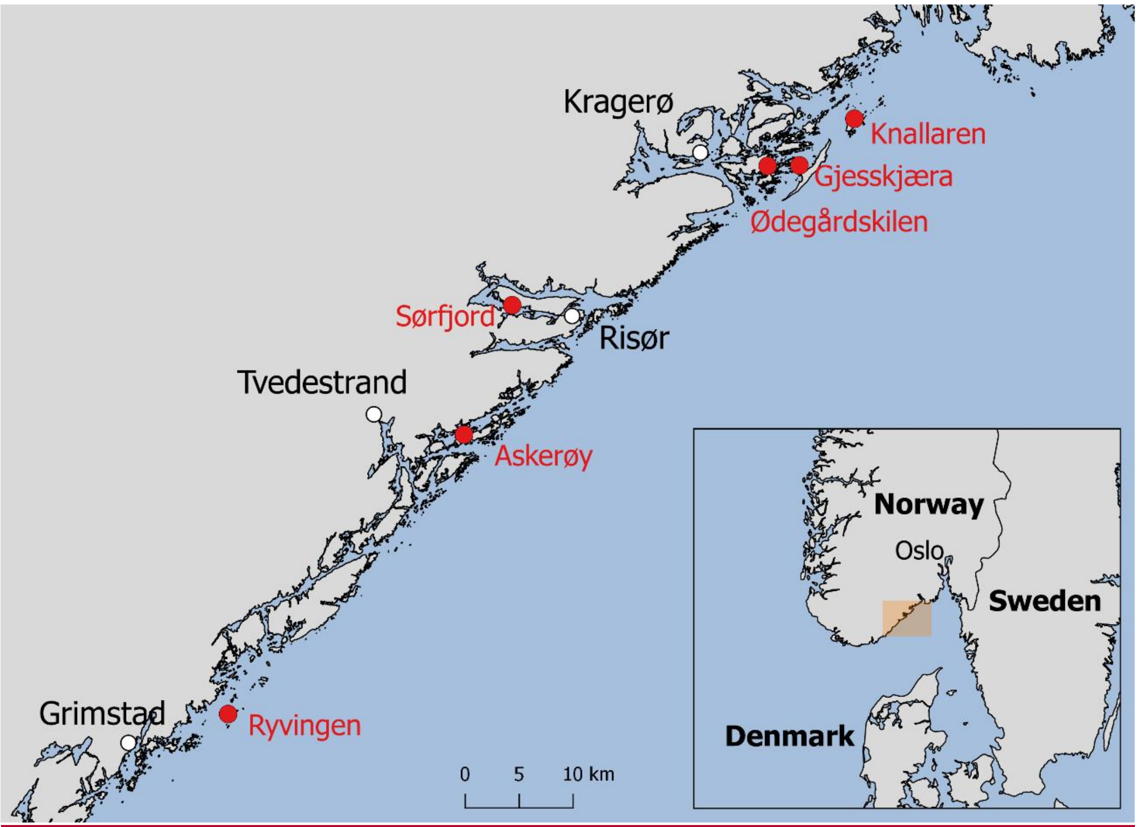

Figure 1: Map showing harbour seal scat sampling locations in red. Figure courtesy of Carla Freitas.

Samples from Askerøy and Ryvingen were collected during dedicated boat trips during low tide on days with no precipitation. Samples from Kragerø and Risør were collected during a seal counting expedition undertaken by the Institute of Marine

Research (IMR) during August 2016. Samples were collected in plastic bags and stored at -18 °C until further processing.

Thawed samples were rinsed with water through nested mesh sieves: 2, 1 and 0.5 mm from top to bottom. Residue from each of the three sieves was put in a water basin and otoliths were collected and stored in 80 % ethanol alcohol in glass vials. Later, otoliths were dried, measured (length and width) with a ruler and sorted by length and side (left/right). Otoliths were then identified to the lowest possible taxon using an otolith identification guide (Härkönen, 1986). This involved pooling data for species that could not be reliably distinguished: haddock/pollack/saithe [haddock (*Melanogrammus aeglefinus*), pollack (*Pollachius pollachius*) and saithe, (*Pollachius virens*)], genus Trisopterus [Norway pout (*Trisopterus esmarkii*), poorcod (*Trisopterus minutus*) and bib (*Trisopterus luscus*)] and long rough dab/witch [long rough dab (*Hippoglossoides platessoides*) and witch (*Glyptocephalus cynoglossus*)]. Data from families with few species and individuals (Labridae, Gobiidae and Bothidae) were also pooled together at family level. The groupings "Gadidae" and "Pleuronectidae" refers to Gadidae and Pleuronectidae species too degraded or otherwise not possible to reliably identify to species. The group "Pleuronectidae" could potentially contain species identified in other groups. However, this is not the case for "Gadidae" as after deciding to pool together haddock, pollack and saithe the data was re-examined. Any potential haddock, pollack or saithe otoliths previously put in "Gadidae" was moved to "haddock/pollack/saithe".

Figure 2: Resting harbour seals photographed during sampling trips. Photos taken by Carla Freitas (left) and Michael Poltermann (right).

Minimum number of individuals (MNI) (Orr et al., 2003) was counted from the side with the greatest number of otoliths from each species/group. More specifically, if e.g. there are eight left herring otoliths and five right herring otoliths in a sample the MNI would be eight. Otoliths occur in pairs in live fish and are mirror images of each other (Härkönen, 1986), but are not necessarily both found in scat samples. As the eight left otoliths would have to have come from different individuals, one can state that a minimum of eight herring were consumed. However, one cannot state with certainty there were 13 herring eaten as the five right otoliths could belong in a pair with five of the left ones. The same conservative method was applied when determining the number of unknown gadids and pleuronectids per sample.

Data is presented as frequency of occurrence (FO) and relative numerical FO (Berg, Haug, & Nilssen, 2002). FO is defined as:

$$\frac{Number\ of\ samples\ a\ species\ occurs\ in}{Total\ number\ of\ samples} * 100$$

while relative numerical FO is defined as:

$$\frac{Total\ number\ of\ otolith\ from\ a\ certain\ species}{Total\ number\ of\ otoliths\ identified} * 100$$

Frequencies of occurrence are given for the overall samples, as well as by location and season. Samples from Kragerø and Risør were collected in August 2016 and classified as “Kragerø summer” and “Risør summer”. “Fevik spring” contains data collected in March 2016, “Tvedestrand winter/spring” contains data from February to May 2016, and “Tvedestrand summer/autumn” contains data collected in June 2015, September 2015 and August 2016. Because data collection was fairly spread throughout the year it made sense to pool results according to seasons. This meant that for Tvedestrand it was possible to divide results into two seasons. Because data was not collected in January, July, and from October to December it was decided to divide into two seasons instead of four.

Fish length and weight was calculated from otolith length (width in some species) using regression functions from Härkönen’s otolith identification guide (Härkönen, 1986). No corrections for otolith degradation were made.

Results

All locations and seasons

A total of 757 otoliths from the six sampling locations were identified to the lowest taxonomic level. Of the 121 samples collected, 27 (22 %) contained no otoliths. Table 1 shows the number of otoliths and samples from each main location as well as the total number of otoliths and samples. The largest numbers of otoliths comes from Tvedestrand and Kragerø, which is also where the largest number of samples were gathered.

Table 1: Summary table with number of samples and number of otoliths per site. The location "Kragerø" consists of Knallaren, Ødegårdskilen and Gjesskjæra.

Location	Otoliths	Samples
Kragerø	257	45
Risør	149	18
Tvedestrand	282	53
Fevik	69	5
Total	**757**	**121**

A total of 11 separate fish species and nine pooled groups of either unknown or similar species were found in the samples collected (fig. 3). The most common species and groups found were genus Trisopterus, i.e. Norway pout/poorcod/bib (relative numerical FO = 27.34 %,), long rough dab/witch (13.74 %) and whiting (*Merlangius merlangus*) (12.68 %). Together, gadids and flatfish (families Pleuronectidae and Bothidae) comprised approximately 90 % of the diet (60.77 and 28.67 % respectively). Relative numerical FO for all species and species groups in descending order is shown in table 2.

Prey items more frequently found in the samples were genus Trisopterus (FO = 33.88 %) followed by haddock/pollack/saithe (29.75 %) and whiting (25.62 %) (fig. 3).

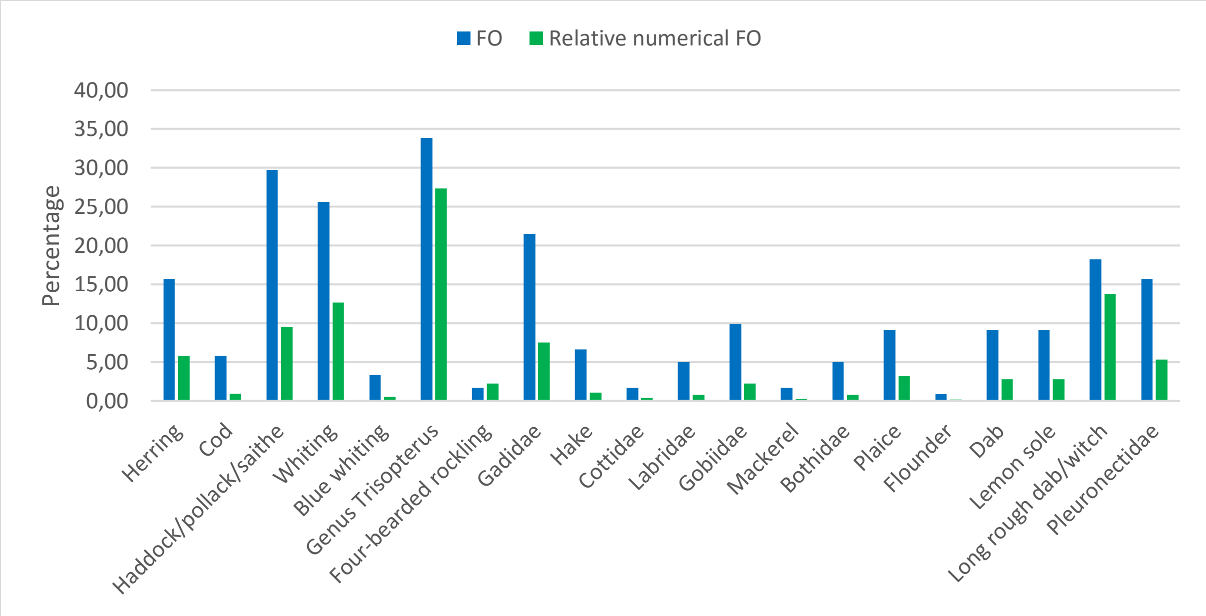

Figure 3: Percentage FO and relative numerical FO for all species and pooled groups for all locations and seasons.

*Table 2: Relative numerical FO in descending order for all species and pooled groups. Species pooled to family level include goldsinny (*Ctenolabrus rupestris*), cuckoo wrasse (*Labrus mixtus*), ballan wrasse (*Labrus bergylta*) and unidentified species from the Labridae family; black goby (*Gobius niger*), painted goby (*Pomatoschistus pictus*), common goby (*Pomatoschistus microps*), Fries's goby (*Lesuerigobius friesii*) and unidentified species from the Gobiidae family; and Norwegian topknot (*Phrynorhombus norvegicus*) and unidentified species from the Bothidae family.*

Species and species groups	Relative numerical FO
Genus Trisopterus	27.34
Long rough dab (*Hippoglossoides platessoides*)/ witch (*Glyptocephalus cynoglossus*)	13.74
Whiting (*Merlangius merlangus*)	12.68
Haddock (*Melanogrammus aeglefinus*)/ pollack (*Pollachius pollachius*)/saithe (*Pollachius virens*)	9.51
Gadidae	7.53
Herring (*Clupea harengus*)	5.81
Pleuronectidae	5.28
Plaice (*Pleuronectes platessa*)	3.17
Dab (*Limanda limanda*)	2.77
Lemon sole (*Microstomus kitt*)	2.77
Four-bearded rockling (*Enchelyopus cimbrius*)	2.25
Gobiidae	2.25
Hake (*Merluccius merluccius*)	1.06

Cod (*Gadus morhua*)	0.92
Labridae	0.79
Bothidae	0.79
Blue whiting (*Micromesistius poutassou*)	0.53
Cottidae	0.40
Mackerel (*Scomber scombrus*)	0.26
Flounder (*Platichthys flesus*)	0.13

Kragerø (summer)

Samples collected from the three locations in Kragerø contained otoliths from all species groups found, except for blue whiting, cottids, mackerel, and lemon sole (fig. 4). Overall, gadids formed the most represented prey group, comprising almost 60 % of the harbour seal diet in this area (57.59 %), followed by 38.91 % flatfish (Pleuronectidae and Bothidae). The rest of the species and species groups made up 3.5 % of the diet. The most common species or species groups was genus Trisopterus (19.84 %), followed by haddock/pollack/saithe (12.84 %), long rough dab/witch (12.84 %) and whiting (10.89 %). Flounder was only present in the diet here.

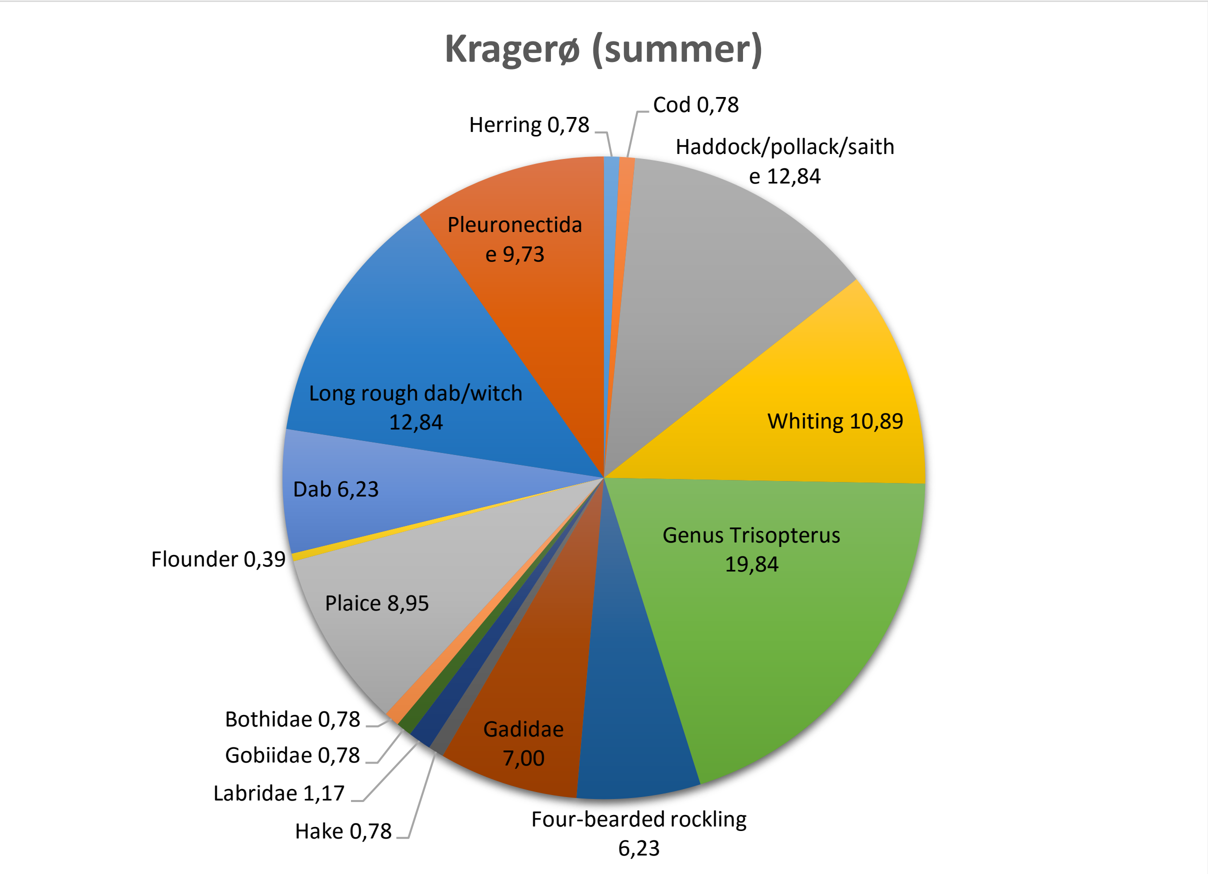

Figure 4: Relative numerical FO for all species and species groups present in Kragerø.

Risør (summer)

As in Kragerø, the diet composition in Risør during the summer was varied and contained a number of different species. Long rough dab/witch was the most common species group (30.20 %), followed by whiting (18.79 %), genus Trisopterus (16.78) and then haddock/pollack/saithe (12.08 %) (fig. 5). The general distribution of species groups was similar to Kragerø with Gadidae making up 52.35 % of the diet, followed by 42.28 % flatfish and 5.37 others. Four-bearded rockling, species from the Labridae family, plaice and flounder were not found here.

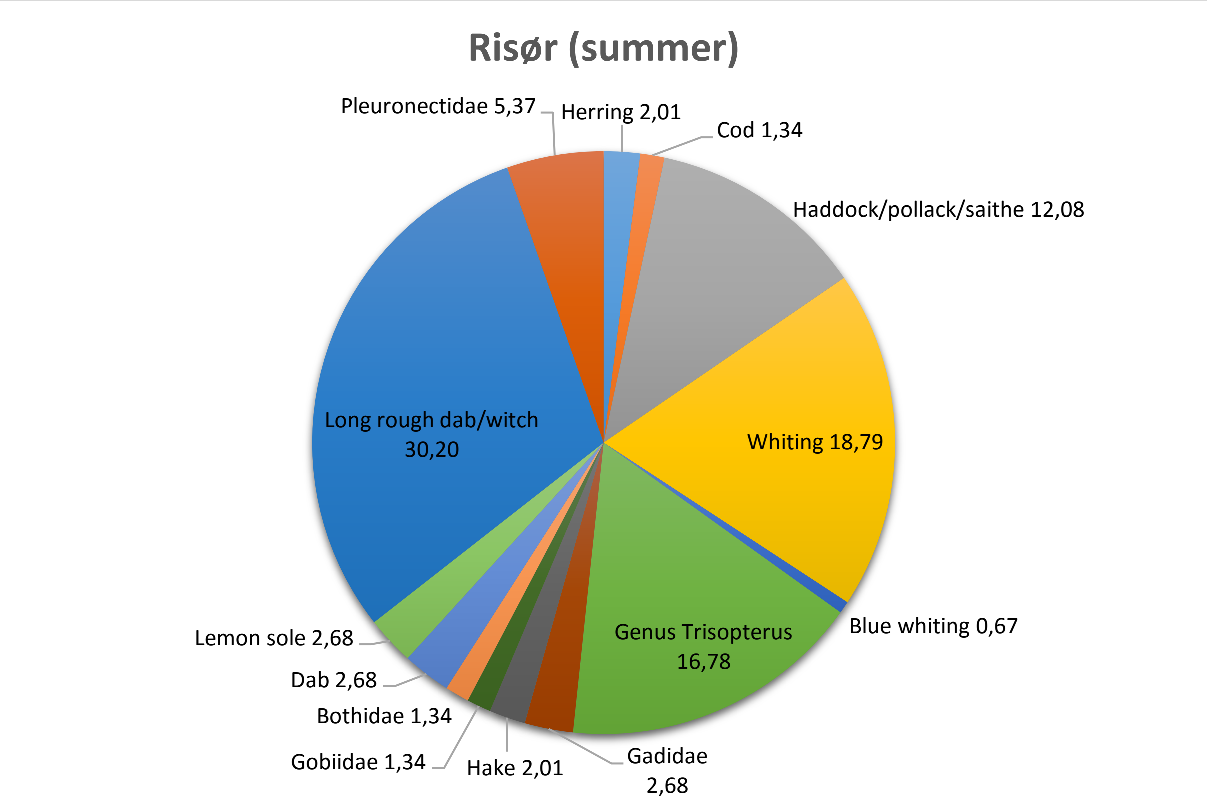

Figure 5: Relative numerical FO for all species and species groups present in Risør.

The percentages of genus Trisopterus found in both places are fairly similar, while long rough dab/witch constitute a much greater part of the diet in Risør than in Kragerø. This is also true for whiting, although to a somewhat lesser degree.

Fevik (spring)

Samples from Fevik were collected during spring and gives some insight into harbour seal diet during this season. Only seven species/species groups were found at this location: herring, cod, haddock/pollack/saithe, whiting, genus Trisopterus, unknown gadids and labrids. Gadids make up 97.10 % of the diet while others (herring and family Labridae) provide the rest. Genus Trisopterus is by far the most common (82,61 %) species group. Haddock/pollack/saithe and unidentified species of family Gadidae come second and make up 5.80 % each (fig. 6). Considering the number of samples from Fevik was fairly low (five samples) any conclusions drawn should be done so with caution.

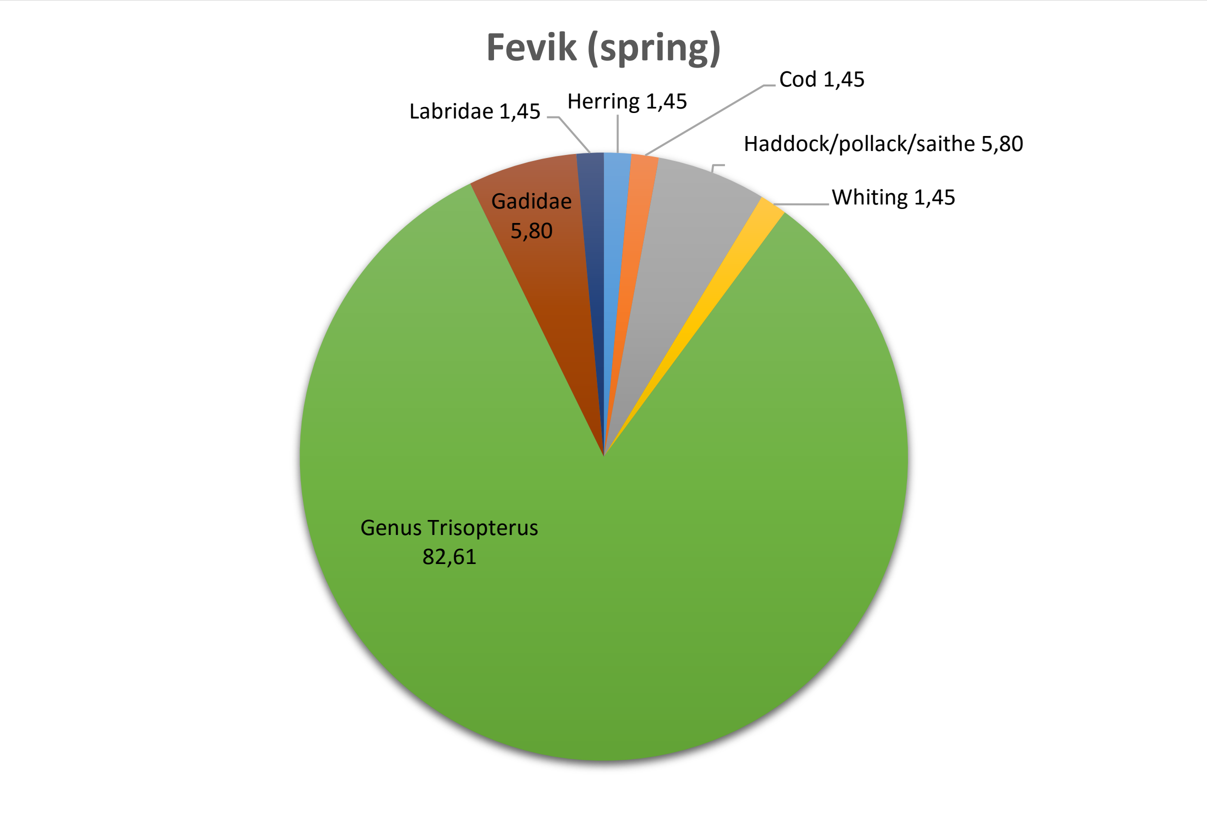

Figure 6: Relative numerical FO for all species and species groups present at Fevik.

Tvedestrand

In Tvedestrand, all twenty species or species groups are represented, except for flounder. Mackerel (summer/autumn) and cottids were only present here. As seen in the previous locations gadids were the most common prey group found here, comprising 59.22 % of the species found. The rest of the diet was almost equally made up of flatfish and others, contributing to 19.15 and 21.63 % of the diet, respectively. As seen in Kragerø and Fevik, genus Trisopterus was the most common prey (26.24 %), followed by whiting (13.83 %) and herring (13.48 %) (fig. 7).

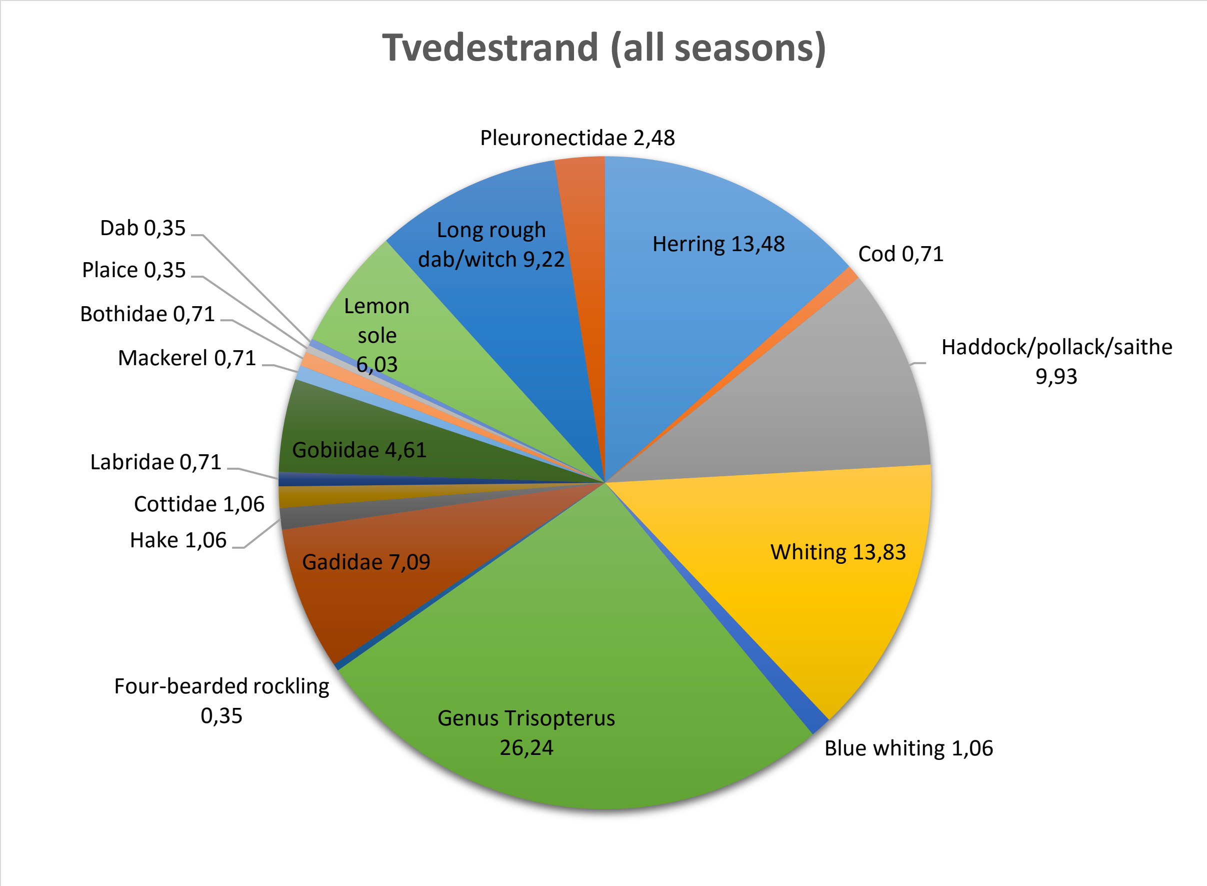

Figure 7: Relative numerical FO for all species and species groups present at Tvedestrand during all seasons.

Tvedestrand by season

As data from Tvedestrand was collected during different times of the year, it was possible to study the seal diet during different seasons. The species richness was higher during summer/autumn (19 species/species groups found) compared to winter/spring when only ten species/species groups were present. Gadids made up the main portion of the seal diet both in summer/autumn and in winter/spring, 61.11 and 50.00 % respectively. The contribution of flatfish however, decreased from 21.79 % in summer/autumn to only 6.25 % during winter/spring. This means other species and groups made up 43.75 % of the diet during winter/spring and 17.09 % during summer/autumn. Cod, whiting, four-bearded, hake, mackerel, family Bothidae, plaice, dab and lemon sole were only present in the diet during summer and autumn.

The most common species/species groups during summer/autumn were genus Trisopterus (26.07 %), whiting (16.67 %), haddock/pollack/saithe (11.54 %) and long rough dab/witch (10.26 %) (fig. 8). This changed somewhat in winter/spring. During this season the contribution of genus Trisopterus to the total diet increased by 1.1 % to 27.08 % (fig. 9). However, the main change in diet was an increase in the amount of herring consumed, from 8.97 to 35.42 % (fig. 9). Unknown gadids were also more prominent in the winter and spring diet than during summer/autumn, 18.75 vs. 4.70 %. As mentioned, whiting constituted a fair proportion of the seal diet during summer/autumn, but was absent in winter/spring. In addition, haddock/pollack/saithe and long rough dab/witch were also a larger part of the diet in summer/autumn than they were during winter/spring.

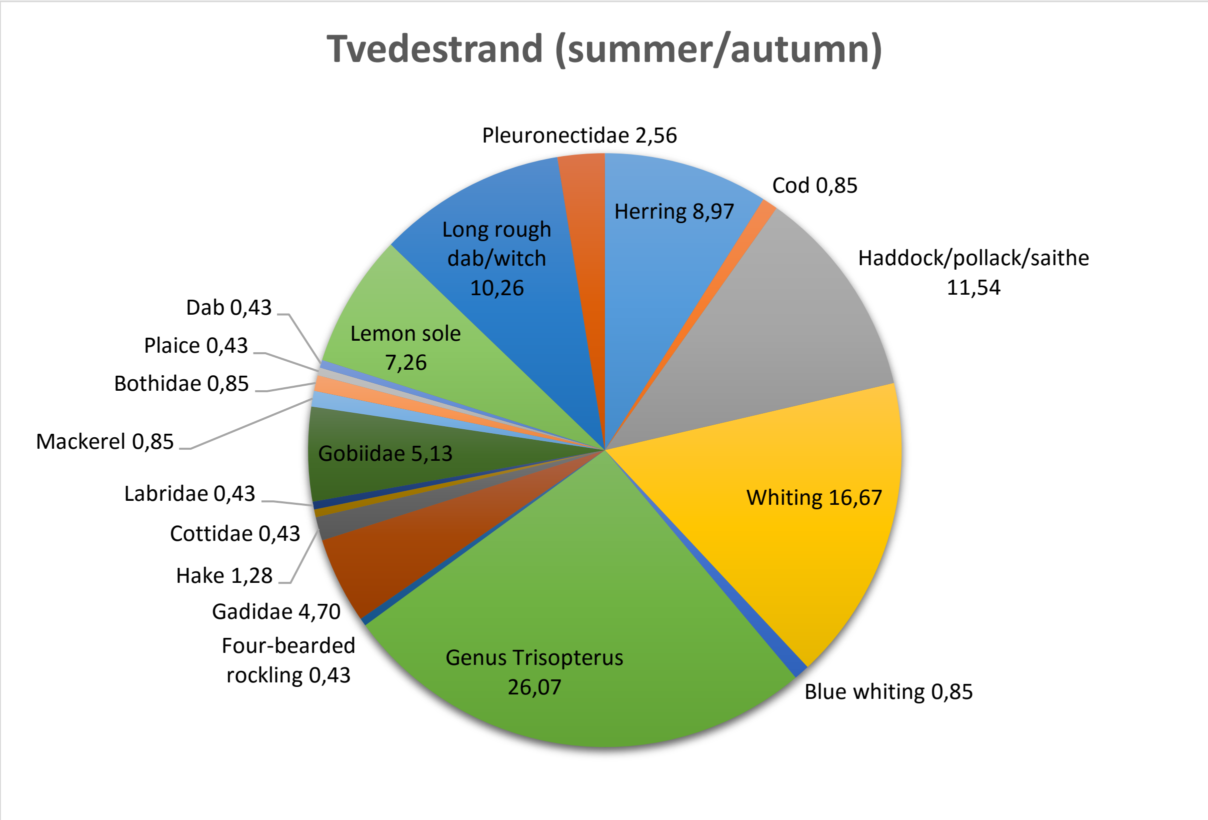

Figure 8: Relative numerical FO for all species and species groups present at Tvedestrand during summer and autumn.

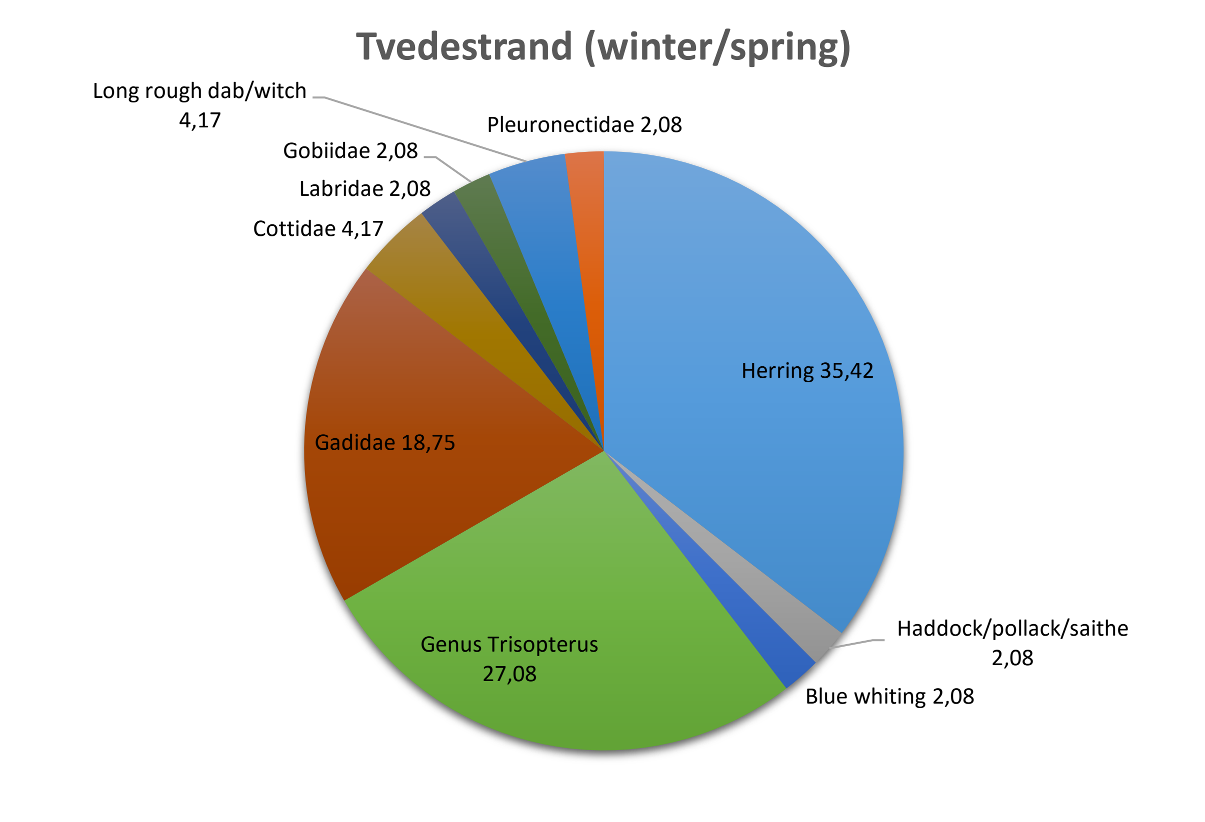

Figure 9: Relative numerical FO for all species and species groups present at Tvedestrand during winter and spring.

Fish length and weight

Fish lengths and weights were calculated for non-pooled species. The results show that overall fish length ranged from 77.67 mm (dab) to 393.26 mm (four-bearded rockling) (table 3). Average lengths varied from 148.25 mm (blue whiting) to 315.36 (flounder) (table 3). Put together, gadids had a slightly higher length range than pleuronectids, 80.65-393.26 and vs. 77.67-347.48 mm respectively. In descending order four-bearded rockling, herring and dab had the largest size ranges: 267.3, 258.15 and 239.73 mm, respectively.

Average fish lengths were lower than smallest allowed catch size (SACS) for cod, whiting, hake, mackerel, plaice and dab, and higher than SACS for herring, flounder and lemon sole. SACS was within total length range for herring, whiting, plaice, dab and lemon sole, while being above maximum fish length for cod, hake and mackerel. Regarding flounder, minimum fish length was higher than SACS.

Table 3: Minimum, maximum and average fish lengths in millimetres for species measured. Data on smallest allowed catch size is listed where found (Forskrift om utøvelse av fisket i sjøen, 2005).

Species	Min. fish length (mm)	Max. fish length (mm)	Average fish length (mm)	Number of individuals	Smallest allowed catch size(mm)
Herring	115.34	373.49	252.79	44	180
Cod	233.20	329.94	288.02	6	400
Whiting	80.65	252.04	158.74	96	320
Blue whiting	111.42	256.17	148.25	4	-
Four-bearded rockling	125.96	393.26	244.71	17	-
Hake	102.07	252.54	162.38	8	300
Mackerel	198.57	242.36	220.46	2	300
Plaice	181.95	329.60	244.86	24	270
Flounder	315.36	315.36	315.36	1	200
Dab	77.67	317.40	220.51	21	230
Lemon sole	205.54	347.08	268.71	21	250

Overall fish weights (table 4) varied from 2.73 gr (four-bearded rockling) to 572.25 gr (herring). Average weights ranged from 26.80 (four-bearded rockling) to 312.79 grams (flounder) (table 4). Gadids varied in weight from 2.73 to 284.83 grams. Pleuronectids had a somewhat wider weight range: from 4.37 to 489.29 grams. Herring, lemon sole, dab and plaice had the widest weight ranges: 564.20, 415.05, 327.78 and 326.38 grams, respectively.

Table 4: Minimum, maximum and average fish weights in grams for species measured.

Species	Min. fish weight (gr)	Max. fish weight (gr)	Average fish weight (gr)	Number of individuals
Herring	8.05	572.25	144.07	44
Cod	116.97	284.83	204.19	6
Whiting	3.02	122.42	32.84	96
Blue whiting	7.18	96.65	29.67	4
Four-bearded rockling	2.73	89.75	26.80	17
Hake	4.23	98.13	31.14	8
Mackerel	44.29	92.49	68.39	2
Plaice	51.47	377.85	149.05	24
Flounder	312.79	312.79	312.79	1

Dab	4.37	332.15	117.06	21
Lemon sole	74.24	489.29	208.05	21

Discussion

Overall results

The main finding in this study was that harbour seals have a varied diet consisting of fish species from several different families. Nine were identified here: Clupeidae, Gadidae, Merluccidae, Cottidae, Labridae, Gobiidae, Scombridae, Bothidae and Pleuronectidae. This is consistent with the findings of a large number of studies on the subject from all over the world where harbour seals are found (e.g. Andersen et al., 2004; Bromaghin et al., 2012; Herreman, Blundell, & Ben-David, 2009; Luxa & Acevedo-Gutiérrez, 2013; Pierce et al., 1991; Rae, 1973). As an example, a diet study performed in Skagerrak and Kattegat identified several of the same species found in this study, the most abundant species being cod, lemon sole, herring, sandeels, poorcod, long rough dab, whiting and Norway pout (Härkönen, 1987). In this study, gadids were the most common family of prey in all locations and seasons. Interestingly, cod was not one of the most abundant prey species found here. Genus Trisopterus was the most common group in all areas except for Risør, where whiting is slightly more common.

Following relative numerical FO, gadids and flatfish dominated the diet and the most common species were Norway pout/poorcod/bib (genus Trisopterus), long rough dab/witch and whiting. The distribution is different according to FO. The most common species group remains genus Trisopterus. However, the three following species/ species groups in descending order are haddock/pollack/saithe, whiting and unknown species from the Gadidae family. This means that these species and groups were present in a large number of samples, but not necessarily that they were preyed upon in large numbers. In fact, FO was higher than relative numerical FO in all but one group, four-bearded rockling, suggesting that harbour seals in this area do not specialize on a few select fish species. Rather, as has been reported in previously mentioned studies (Bromaghin et al., 2012; Geiger et al., 2013; Lance et al., 2012; Luxa & Acevedo-Gutiérrez, 2013; Pierce et al., 1991; Tollit & Thompson, 1996), they appear to be opportunists and generalists.

Härkönen's study in Skagerrak and Kattegat found mackerel to constitute only a very small part of the harbour seal diet, even though it is a commercially important species (Härkönen, 1987). This is similar to the results of the present study where only two individuals were identified. Härkönen suggests that the species is either avoided by seals or that they are simply not able to catch them; possibly the energetic cost is higher than the gain.

An analysis of harbour and grey seal diet based on stomach contents gathered over time showed that gadoids and clupeoids made up the majority of the diet of common seals, with whiting and herring being the most common species (Rae, 1973). Other important families include pleuronectids and salmonids. The author compares the results from this study with one of his own earlier studies and comments on the differences found in diet composition. In this study the higher proportion of clupeids found is attributed to the larger number of seal specimens obtained from inshore areas where young clupeoids tend to gather (Rae, 1973). This supports the theory that seals feed on the most numerous species in a given area at a given time. Their diet seems to change with seasonal movements and distribution of prey fish, along with annual fluctuations in year-class strength (Rae, 1973). The author believes this could explain why cod was to come extent replaced by saithe between the two time periods studied (Rae, 1973).

Sandeels were not identified as a part of the harbour seal diet in this study, as they have been in others (e.g. Härkönen, 1987; Sharples, Arrizabalaga, & Hammond, 2009).

No salmonids were identified as a part of harbour seal diet in this study. This is similar to results from older studies, both in the US and Scotland, where researchers using molecular genetic techniques found salmonid remains in only 5-10 % of samples (Kvitrud et al., 2005; Matejusová et al., 2008; Orr et al., 2004). One reason for the low amounts of salmonids found in harbour seal diet could be, as has been suggested, that salmonid abundance is still low compared to that of marine prey and therefore not an important part of the seals diet (Middlemas, Barton, Armstrong, & Thompson, 2006)

In addition to this, a study comparing stomach contents and faeces as indicators of harbour seal diet in Alaska found fragmented parts of salmonids in the stomachs, suggesting as other authors have that salmonids are often not eaten whole (Pitcher, 1980). If this is the case for seals in the present study area, otolith analysis alone would not have been able to identify salmonids in the diet. Had molecular genetic techniques been used in the present study, several more prey species might have been identified and the diet distribution would have looked different.

Kragerø, Risør and Tvedestrand (summer/autumn)

Harbour seal diet in Kragerø, Risør and Tvedestrand (summer/autumn) was varied and included most species and species groups identified in this study. Gadids were the most abundant species, followed by flatfish and the others. Genus Trisopterus, whiting and haddock/pollack/saithe were the three most common Gadidae prey species. Long rough dab/witch and unknown Pleuronectidae species were the most abundant flatfish in Kragerø and Risør, while long rough dab/witch and lemon sole were the most common in Tvedestrand. These results are largely consistent with the overall diet composition when viewing all sample dates and locations as a whole. The abundance of long rough dab/witch found suggests that one or both of these are the most common flatfish species in the areas, as harbour seals tend to prey on the most abundant species present in an area (Härkönen, 1987).

The wide variety of different species detected in seal diet in these areas could speak to the general species richness found here. This has been observed before in the Central Salish Sea (Luxa & Acevedo-Gutiérrez, 2013). Here, researchers found that seals foraging in species-rich estuaries consumed a higher number of species than seals foraging in other, rockier habitats.

Although the percentages of genus Trisopterus found in Kragerø and Risør are fairly similar, suggesting they are equally important parts of the diet in the two areas, long rough dab/witch constitute a much greater part of the diet in Risør than in Kragerø. This is also true for whiting, although to a somewhat lesser degree.

Fevik

Consistent with overall results and results from Kragerø and Risør, gadids made up the majority of the seal diet at Fevik, genus Trisopterus being the most common group. Herring and Labridae made up the remainder of the diet. The low number of species present in the diet here could be the results of the low sample size. On the other side, harbour seals have been known to specialize on a few or a single prey species while occasionally supplementing their diet with others. This has been observed in the Danish Limfjord. In one part of the fjord seals seemed to consume fewer, but larger fish in spring compared to summer and autumn, presumably to maintain energy uptake when higher quality prey was not available (Andersen et al., 2007). Contrastingly, seals in a different part of the fjord, closer to the ocean, had a summer diet made up mostly of flounder (Andersen et al., 2007). The authors suggest that harbour seals behave like specialist feeders and take advantage of a single prey species when it is abundant and easy to come by, while switching to generalist behaviour when prey abundance is lower or closer to equal between the different species (Andersen et al., 2007). If one or more species of genus Trisopterus were present in large numbers around Ryvingen during this time of year it seems likely seals would take advantage of this.

Flatfish comprised a fairly large part of the diet in Kragerø and Risør, 38.91 and 42.28 % respectively, while not being present at Fevik. This absence of flatfish in the diet could be due to the small sample size or could speak to the topography of the sea floor in this area. In his study, Härkönen (1987) found that at Anholt in the Kattegat, a sandy shore habitat, pleuronectids were the most common species consumed, namely dab, plaice and flounder. Rae (1973) attributed the low number of pleuronectids found in his study to the low sampling efforts in areas with sandy bays and estuaries.

As seen for the study area as a whole, as well as for Kragerø, Risør, Fevik and Tvedestrand (summer/autumn), gadids are an important part of the harbour seal diet. There are numerous studies supporting this (e.g. Rae, 1973; Steingass, 2017). Rae (1973) proposes that the reason gadids are such an important part of seal diet is not only because of their abundance, but because of their wide size range between species, making them suitable for both young and adult seals.

Tvedestrand (winter/spring)

Harbour seal diet composition changed during winter/spring and herring became the most consumed prey item. Gadids were still an important part of the diet, while the amount of flatfish consumed decreased to 6.25 %. Pleuronectids also appear to be more common in the summer diet of harbour seals in Scotland (Pierce et al., 1991).

Going by species and species groups herring was the most abundant, followed by genus Trisopterus and unknown Gadidae species. Diet changes with season have been observed in several other locations, among them the Salish Sea outside of Washington, USA (Luxa & Acevedo-Gutiérrez, 2013) and St. Andrews Bay in Scotland (Sharples et al., 2009). In the latter area harbour seals consumed mostly sandeels, especially in winter and spring, while supplementing their diet with gadids (chiefly whiting and cod), flatfish (flounder, common dab, plaice) and pelagic fish like herring at other times of the year (Sharples et al., 2009). Results from the same study, but a different location, Firth of Tay, showed that seals here prefer to prey mostly on salmonids in spring and summer, salmonids and sandeels in autumn, while switching completely to sandeels in winter (Sharples et al., 2009).

The abundance of herring found during winter and spring is consistent with other findings. A study performed in the Danish Limfjord showed that local harbour seals in one area of the fjord preyed largely on herring during the spring, while their diet during summer and autumn was more varied (Andersen et al., 2007). During that time seals fed on several different species, the diet dominated by plaice and eelpout in the summer and gobies and flounders in autumn. Harbour seals in the Moray Firth, North-East Scotland have been found to feed mostly on herring and sprat during the winter months (Pierce et al., 1991; Thompson et al., 1991).

As the results showed there was a change in both diet composition and richness with seasons observed in Tvedestrand. Such changes have also been found in several other harbour seal populations across the globe as the following examples will show. A study of harbour seal diet in Alaska found that their diet comprised mostly of pollock, eulachon, herring, flatfish, rockfish, salmon, sculpin and sand lance (Herreman et al., 2009). This study also found seasonal changes in diet based on prey availability, along with differences in diet between sexes and different age classes. In one of the study areas, sculpin and capelin comprised much of the spring and early summer diet, while the seals supplemented with eulachon, pollock and greenling in winter (Herreman et al., 2009). In the other study area the seals' diet included more species during spring and fall than it did in summer. They also consumed prey with a lower fat content, presumably being forced to do so due to increased interspecific competition (Herreman et al., 2009). The authors also observed differences in diets between sexes. This was more evident in adults and could be due to females hunting closer to shore and preying on intertidal and subtidal species during pupping and weaning (Herreman et al., 2009). Males can travel longer distances in search for food during this time and were found to prey more on pelagic species (Herreman et al., 2009).

In the San Juan Islands in Washington, USA, the diet of harbour seals there consisted mainly (but not only) of Pacific herring (*Clupea pallasii*) year-round; Pacific sand lance (*Ammodytes hexapterus*), northern anchovy (*Engraulis mordax*) and juvenile walleye Pollock (*Theragra chalcogramma*) in winter and spring; and adult salmon of different species during summer and fall (Lance et al., 2012).

A study on different aspects of harbour seal behaviour in two bays in Oregon discovered seasonal patterns in abundance in Netarts Bay with a peak during autumn (Brown & Mate, 1983). The authors found that this pattern coincided with the autumn return of chum salmon to the Whiskey Creek hatchery in Netarts Bay (Brown & Mate, 1983). The seasonal changes were different for Tillamook Bay, situated roughly 10 km north of Netarts Bay. Here there was a high abundance of harbour seals in the summer, during pupping (Brown & Mate, 1983). It is suggested in the article that this is because of Tillamook Bay's greater size and larger number of isolated, small channels with minimal disturbance, which makes it ideal for pupping (Brown & Mate, 1983). Otoliths collected from scat samples during late summer and autumn showed Pacific sand lance, English sole and five species of pleuronectids to be species most commonly consumed (presented as MNI and FO) (Brown & Mate, 1983).

Fish length and weight

Where possible, fish lengths and weights were estimated. Total fish lengths ranged from 77.67 mm (a dab) to 393.26 mm (a four-bearded rockling) with averages ranging from 148.25 mm (a blue whiting) to 315.36 mm (a flounder). Comparing the results to SACS (smallest allowed catch size) one can see that for most species the SACS is somewhere within the calculated length range. However, even the largest individuals consumed of cod, hake and mackerel are smaller than the smallest allowable catch length. For these three species it would seem that harbour seals are not in direct competition with fisheries and fishermen. Minimum, maximum and average lengths for flounder were based on only one individual, so even though all length measures were higher than SACS, results should be interpreted with caution.

Other studies have also shown a preference for smaller fish in harbour seals (e.g. Ramasco & Nilssen, 2015). With the exception of adult salmon, all the fish species consumed by seals in the San Juan Islands in Washington, USA were small (< 10 cm), rich in energy with a tendency for schooling (Lance et al., 2012). In France, seals in the Bay of Somme were found to prey almost exclusively on a small number of species of flatfish and dragonets in summer: mainly yellow, thickback and sand soles, along with plaice and dragonets (Spitz et al., 2015). 97 % of the diet in this study was composed of fish shorter than 20 cm.

Size estimation of seal prey in Limfjord, Denmark showed that, with the exception of herring, fish taken by seals are smaller than the ones taken by fisheries, suggesting minimal competition between seals and fisheries (Andersen et al., 2007). As for herring, seals do consume large fish also taken by the fishery, but the amount is six times less than what is taken by fisheries (Andersen et al., 2007). However, the authors did not apply correction factors for erosion of otoliths, biasing their size distribution of fish eaten by seals towards smaller fish. Even though this is also the case for the present study, the results here give an indication of the size range of fish species consumed by harbour seals.

Looking at fishery harbours in Aust-Agder, Telemark and the surrounding counties, there are several with which harbour seals could potentially come into conflict (Henriksen, 2014). In South Norway (Aust- and Vest-Agder) fishing vessels < 11 m landed approximately 650 tons of cod, 500 tons of pelagic fish (including herring, sprat and mackerel) and around 200 tons of "other codfish", which includes haddock and saithe (Henriksen, 2014). The numbers for vessels 11-14.99 m are ca. 1200 tons for pelagic species, ca. 600 tons cod and 200 tons other codfish.

In East Norway (Telemark, Vestfold, Buskerud, Akershus, Oslo and Østfold) fishing vessels <11 m caught ca. 400 tons pelagic fish, ca. 350 tons cod and approximately 100 tons of other codfish (Henriksen, 2014). Vessels 11-14.99 m landed ca. 1700 tons pelagic species. The amounts of cod and other codfish are all less than 100 tons each.

Vessels 15-20.99 m in South and East Norway caught approximately 200 tons other codfish, 200 tons cod and ca. 50 tons pelagic species (Henriksen, 2014).

When comparing these commercial catch numbers to fish weights calculated from results in this study, it seems likely that harbour seals are not serious competitors to fishery harbours. However, as weight was not calculated for pooled groups in this study, it follows that the total mass of fish consumed by seals in this time period is larger than presented. More data is needed in order to more accurately assess the degree to which seals compete with local fisheries and also with small-time fishermen.

Henriksen’s report states that in South Norway (Aust- and Vest-Agder) cod was the second most important species for the fishery vessels < 11 m in 2012, accounting for 24.6 % of the income (approximately 9 million NOK). Pelagic species, which includes herring and mackerel (mackerel being most important), accounted for 9.1 %, and other codfish, including haddock and saithe, accounted for just under 2 million NOK. All these were less important than “other species”, a group where wrasses dominate, that accounts for 47.8 % of the income. Other species is defined as “All other species. The most important are halibut, Greenland halibut, monkfish and different wrasses” (Henriksen, 2014). For vessels 11-14.99 m crustaceans was the most important species group and twice as important as cod. They accounted for 44 and 21.4 % of the income, respectively. The income from pelagic species constituted 21 %, around the same as from cod. Other codfish contributed approximately 1.5 million NOK to the income, making it the least important group.

The region East Norway consists of the counties Telemark, Vestfold, Buskerud, Akershus, Oslo and Østfold (Henriksen, 2014). Here, crustaceans is the most important species group, accounting for 56.4 % (approximately 32 million NOK) of the income for vessels < 11 m in 2012. Cod, pelagic species and other codfish are the least important groups, contributing 8.8, 5.6 and 2.9 % of the income, respectively. As in South Norway, mackerel is the most important of the pelagic species here (Henriksen, 2014). Crustaceans were the most important income for vessels 11-14.99 m, too, here accounting for 71.5 % of the income, followed by pelagic species (20.1 %). Here, herring and sprat was more important than mackerel. Cod and other codfish constitute only very low percentages of the income. For vessels 15-20.99 m in both regions, crustaceans contributed most to income in 2012, 68.4 %. Cod contributed 13.8 %, while the numbers for other codfish and pelagic species were even lower.

Looking at these numbers in comparison to harbour seal diet, it would seem like seals do not feed primarily on the most important species for these fishery harbours.

Methods used

Estimation of diet composition by gathering faecal samples and extracting otoliths from them is not necessarily as straightforward as it may seem. There are several different factors and parameters to take into account and gaining an accurate diet estimate can prove difficult. For example, not all prey classes are so easily detected using this method, and it reflects the diet during only a small window of time, specifically the time between two bowel movements (Bromaghin et al., 2012). However, seals foraging far from land might defecate before returning to shore and that sample would not be collected and analysed (Staniland, 2002). In addition to this, seals may only consume the soft parts of prey once it is captured, e.g. not the heads of fish, which is where the otoliths are found, leaving no discernible traces in faeces (Orr et al., 2004).

Digestion rate could also play a role in diet estimation. Presumably, prey with a high digestion rate that passes rapidly through the digestion tract will be underrepresented in scat samples collected at haul-out sites, and fish without sagittal otoliths, e.g. dogfish, lampreys and skates, will not be represented at all (Pierce & Boyle, 1991). The authors of this paper also suggested that small otoliths, crustacean remains etc. may be digested indirectly, through the fish preyed upon, and remains from small invertebrates like molluscs and crustaceans may be incorporated from the substratum.

Additionally, fish species with larger otoliths have a higher recovery rate than those with smaller otoliths (Grellier & Hammond, 2005). The authors suggest that a possible reason for this is that smaller otoliths are completely digested. Therefore, species with larger otoliths may well be overrepresented in diet estimates. In this study, sandeel otolith recovery rates were higher when this species was present at the same time as herring, leading the authors to suspect that meal composition could affect otolith digestion rate (Grellier & Hammond, 2005).

An experiment performed on Antarctic fur seals showed that only about 26 % of otoliths from fish fed to seals were recovered from faeces (Staniland, 2002). Missing otoliths were presumed eroded, fragmented or having remained in the stomach. If this were also the case for harbour seals, it would suggest that faecal sampling does not provide a complete assessment of the diet of these animals.

The above-mentioned study also mentions erosion of otoliths and the importance of taking this into account when estimating fish length from digested otoliths. However, in Staniland's experiment, specific equations accounting for erosion were used to estimate length and mass distribution of fish fed to seals. The resulting distribution differed from the actual distribution, and fish masses were underestimated. In conclusion, using equations to account for variables such as erosion, will not necessarily generate a completely accurate result. Where accurate fish length and/or mass cannot be calculated, size/weight classes might be of use instead (Staniland, 2002).

In order to map the diet of e.g. pinnipeds as accurate as possible it would be preferential to combine i.e. scat sampling with other methods. A study on northern fur seals in Alaska combined scat sampling with spew sampling, both methods showing different results (Gudmundson, Zeppelin, & Ream, 2006). Molecular genetic methods using different types of DNA and PCR techniques could also prove highly useful as they could identify prey items not detected by other means.

However, even by applying such techniques, diet estimates still might not be complete. Pierce et al., 1991 suggested that scat samples collected from haul-out sites would mostly reflect the diet of individuals foraging close to said haul-out sites. A previous study on harbour seal movement and foraging activity showed that seals taking shorter foraging trips hauled out more often (Thompson & Miller, 1990). Because of this it is possible that prey taken close to haul-out sites may be overrepresented in samples. Otolith erosion degree depends on time exposed to acids on stomach, while passage rates through the digestive system varies with activity level, food intake rate and meal composition (Pierce et al., 1991).

Despite these issues, scat sampling is still a valid sampling method suitable for giving an overview of the diet composition of the study animal. When applying estimations for digestion rates for food items and otoliths, as well as for length and duration of foraging bouts, the overview would be more accurate.

Conclusion

In summary, this study shows that harbour seals in southern Norway have a varied diet consisting mainly of gadids and flatfish. There are both regional and seasonal differences in diet composition and overall prey size (length and weight) is small. These results suggest that any competition for resources between seals and fisheries would happen at a small scale.

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