The importance of sandeel (*Ammodytes marinus*) for minke whales (*Balaenoptera acutorostrata*) and white-beaked dolphins (*Lagenorhynchus albirostris*) in Faxaflói Bay, Iceland

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Abstract

Faxaflói Bay, located at the southwest coast of Iceland, has been noted as important feeding grounds for both minke whales (*Balaenoptera acutorostrata*) and white-beaked dolphins (*Lagenorhynchus albirostris*). These two cetacean species are both known to prey on lesser sandeels (*Ammodytes marinus*), a high-energy prey, which are found in high density in Faxaflói Bay.

The aim of the study was to investigate the predator-prey relationship between sandeels and both minke whales and white-beaked dolphins, and whether changes in population parameters of the sandeel stock influence the abundance of these cetacean species in Faxaflói Bay.

Whale abundance was estimated from observational data collected in regular whale watching tours in July 2008-2013. Sandeel data from the same period comes from a monitoring programme where fish was caught by a dredge or a trawl. Age structure of the sandeel stock was determined by ageing individuals with otolith analysis.

Minke whale abundance showed a significant correlation to the proportion of older sandeels (one year old and older). When the proportion of older sandeel in the stock was high more minke whales were seen. A similar analysis found no relationship between the abundance of white-beaked dolphins and the proportion of older sandeels. The results from this study suggest that the abundance of older sandeels is of greater importance for minke whales than for white-beaked dolphins. How these two predator species respond to fluctuations in prey populations might be linked to differences in their foraging behaviour and their dependency of prey density.

Útdráttur

Faxaflói er staðsettur á suðvestur strönd Ísland og hefur verið talinn vera mikilvægt fæðu svæði fyrir bæði hrefnu (*Balaenoptera acutorostrata*) og hnýðing (*Lagenorhynchus albirostris*). Þessar tvær tegundir nýta sandsíli, há-orku fæðutegund, sem finnst í miklum þéttleika í Faxaflóa.

Markmið rannsóknarinnar var að rannsaka afræningja-bráðar sambandið á milli sandsíla og bæði hrefnu og hnýðinga, og hvort breytingar í sandsíla stofninum hefði áhrif á fjölda hrefnu og hnýðinga í Faxaflóa.

Fjöldi hvala var metinn út frá gögnum sem var safnað í hvalaskoðunarferðum í Júlí 2008-2013. Sandsíla gögn frá sama tímabili komu frá rannsóknarleiðöngrum þar sem fiskur var veiddur með trolli eða plóg. Aldurssamsetning sandsíla stofnsins var ákvörðuð með því að aldursgreina einstaklinga út frá kvarna greiningu.

Fjöldi hrefna sýndi marktækt samband við hlutfall eldri sandsíla (eins árs eða eldri) í stofninum. Þegar hlutfall eldri sandsíla í stofninum var hátt var fjöldi hrefnu á svæðinu meiri. Svipuð greining fann ekkert samband á milli hlutfalls eldri sandsíla og fjölda hnýðinga á svæðinu. Niðurstöður rannsóknarinnar benda til þess að þéttleiki eldri sandsíla sé mun mikilvægari fyrir hrefnu heldur en fyrir hnýðinga. Hvernig þessir afræningjar bregðast við sveiflum í bráðarstofni gæti verið tengt mismunandi fæðuöflunar aðferðum og hversu háðar tegundirnar eru þéttleika bráðar.

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Acknowledgements

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1 Introduction

1.1 Predator-prey relationship in a patchy environment

The relationship between two populations that involves the predation of one population on the other for the purpose of obtaining food has been widely studied, mainly because of the influences that these interactions have on the behaviour, physiologies, morphologies, and life-history traits strategies of both the predator and the prey species that are involved (Taylor, 1984, as cited in Trites, 2009).

Changes in environmental factors can have significant effects on survival and recruitment of organisms, but how they respond to these changes varies between species. Environmental changes might have indirect effects on the distribution and abundance of cetaceans due to the influences that they have on the distribution and abundance of their prey species (Piatt et al., 1989). Cetacean species may respond differently to variations in prey abundance due to different density preferences and diet flexibilities. When species are flexible in their choice of food, decrease in main prey species usually result in diet shift towards other prey species with higher abundance, while species that are not as flexible in prey choice and highly depend on a single prey item, might be forced to move to a different feeding area (Friedlaender et al., 2006; Piatt et al., 1989).

Cetaceans as predators require a constant rate of food to maintain themselves between breeding season (Smith and Slatkin, 1973). When the prey abundance falls below a certain level, the predator fitness will decrease. The responses of predators to a lack of prey will reflect the fitness consequences of either staying in the same patch or searching for a better one (Sjödin et al., 2013). The optimal use of patches is likely to reflect abundance of prey within a patch since the amount of energy spent on hunting must be less than the energy gained from consuming the prey. If prey abundance in an optimal patch decreases, predators will have to spend more time hunting for efficient foraging. When the hunting time has significantly higher energy costs than the energy gained from the food unit, the predator must face a choice between staying in the patch or search for a new one (MacArthur and Pianka, 1966).

1.2 Faxaflói Bay – Feeding grounds of minke whales and white-beaked dolphins

In the ocean around Iceland, the lesser sandeel (*Ammodytes marinus)* are an important forage fish species, found in the diets of many commercial fish species, seabirds and marine mammals. In recent years the population has suffered from recruitment failure, and with that a decline in the stock. How these changes in the sandeel population affect the marine ecosystem is not fully known, but breeding failure of many seabird species has been linked to the recruitment failure of sandeels (Bogason and Lilliendahl, 2009).

In Faxaflói Bay, located at the southwest coast of Iceland, sandeels are found in high density and are believed to have high importance for various predator species (Gunnarsson et al., 2008). This bay is a very productive area that provides suitable spawning and nursing areas for many fish species (Stefánsson and Guðmundsson, 1978) and has been noted to be important as feeding grounds for both minke whales and white-beaked dolphins (Bertulli, 2010). Minke whale stomach sampling in Icelandic coastal waters showed sandeels being the single most important prey species in the southern and western areas. When sandeel abundance decreased, significant changes were seen in the diet of minke whales along with reduction in minke whale abundance, indicating that there might be a relationship between the densities of the two species (Bogason and Lilliendahl, 2009; Víkingsson and Elvarsson 2011). Little is known about the prey preferences of white-beaked dolphins but their diet is known to consist mainly of fish (Sigurjónsson and Víkingsson, 1997). Visual observations suggest that the white-beaked dolphins prey on sandeels, among other things, in Faxaflói Bay during the summer months (Rasmussen et al., 2013).

Although marine mammals are generally thought to be opportunistic predators, which select their prey according to availability, their diets are typically dominated by five or fewer species. How these animals choose their main prey species is not fully known, but presumably their choice is affected by the nutritional value of prey, the foraging energy needed to capture the prey species and prey digestibility (Mackinson et al., 2003; Trites, 2009). Cetacean species may respond differently to variations in prey abundance due to different density preferences and diet flexibilities, but even when predator diet contain variety of species, their condition and abundance can be strongly influenced by one prey type, if it has high calorific value (Engelhard et al., 2013; Wanless et al., 2005).

1.3 Aims

The aim of this study is to investigate the predator-prey relationship between sandeels and both minke whales and white-beaked dolphins. Sandeels are a high-energy prey (Hislop et al., 1991 as cited in Engelhard et al., 2013) that is thought to be the most “universally important” forage fish species as prey to predators (Engelhard et al., 2013). Because of the sandeels high calorific value, the recruitment failure and changes in the age structure of the population might affect the abundance of these cetacean species in Faxaflói Bay. Here the sandeel population is defined as a feeding patch and the two cetacean species as opportunistic predators. Theory predicts that changes in population parameters of the sandeel stock are likely to be reflected in cetacean abundance.

2 Materials and Methods

2.1 The study area: Faxaflói Bay

Faxaflói Bay (N64°24 W23°00) is located at the southwestern coast of Iceland, between two large peninsulas. The bay is less than 50 km long and 90 km wide. The inner part of the bay is rather shallow, particularly the northeastern part where depths less than 20 m extend 5-10 miles offshore. The area inside the 50 m isobath is almost 60% of the total area inside the bay, while depths between 50 and 100 m occupy a little over 30%. Near the mouth there is a small region, around 9-10% of the total area, with depths greater than 100 m. Faxaflói Bay is a highly productive area that provides suitable spawning and nursing areas as well as hunting grounds for various species (Stefánsson and Guðmundsson, 1978). In the south part of the bay, a bank called Syðra-Hraun is located. The middle of the bank consists of a lava field that is known to be relatively shallow and with high diversity of organisms (Gunnarsson et al., 2008).

The area can be divided in to three categories after substrate composition. The middle of the lava field is characterized by hard bottom, surrounded by gravel. Around the field of gravel, there is a sandy substrate. At the outermost edge, there is a rough substrate, sometimes with patches of sand within (Thors, 1975).

In some areas of Syðra-Hraun, especially those with sandy substrates, sandeels are found in high abundance and are known to spawn there (Gunnarsson et al., 2008), also Syðra-Hraun is thought to be important feeding grounds for both minke whales and white-beaked dolphins (Bertulli, 2010).

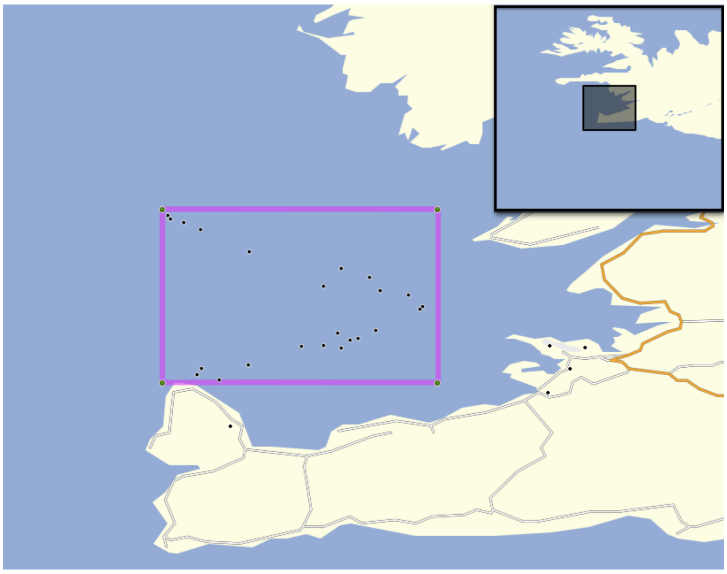

Fig. 2.1.1 A map of the study area. The pink frame shows the study area. Syðra-Hraun is located in the eastern side of the frame.

2.2 Study species

2.2.1 Lesser sandeel (*Ammodytes marinus*)

Ammodytes marinus (hereafter sandeels) are lipid-rich, schooling fish species that can reach 20 to 25 cm in length. The sandeels have a proportionally short lifecycle as they reach sexual maturity at a size of 11-12 cm and start spawning after the first year. Usually the bulk of the population consists of fishes that are three years old or younger (Bogason 2001; Jónsson and Pálsson, 2006).

Fig. 2.2.1.1 Lesser sandeel (Ammodytes marinus). Drawing © Jón Baldur Hlíðberg

Sandeels lack a swim bladder and thus have to remain in movement when they are in the water column in order to avoid sinking to the bottom. As a potential energy conservation strategy, sandeels tend to burrow themselves in the sand and seldom emerge, unless for the purpose of feeding (Hassel et al., 2002). The active season of the sandeels is during spring/summer. where they emerge to the water column in large schools to forage and build up their energy reserves. Over the winter the sandeels go into hibernation and are mostly buried in the sand, accept during October to December when spawning takes place (Bogason 2001; Jónsson and Pálsson, 2006)

Sandeels usually occur in coastal and shallow open-ocean waters on sandy substrates and are most abundant around the south, southwest and west coast of Iceland. They seem to occupy the same areas each year, using the same location for both feeding and spawning (Bogason, 2001; Jónsson and Pálsson, 2006; Winslade, 1971, as cited in Hassel et al., 2002).

Monitoring researches in Iceland have shown a significant decline in the sandeel population for the past years. Four different research areas all showed a recruitment failure in the years 2005 and 2006. Although the research showed that the year-class of 2007 had better recruitment than the two previous years, the sandeel population is still thought to be declining. Because of their short lifetime the missing year classes might have significant influences on both size and age structure of the population (Bogason and Lilliendahl, 2009).

2.2.2 Minke whale (*Balaenoptera acutorostrata*)

The minke whale (*Balaenoptera acutorostrata* Lacépède, 1804) is the most abundant baleen whale species in Icelandic coastal waters (Víkingsson and Elvarsson, 2011). Their occurrences are seasonal as they undertake long-distance migrations between high-latitude feeding grounds in the summer and low-latitude breeding grounds in winter (Horwood, 1990, as cited in Skaug et al., 2004).

Fig. 2.2.2.1 Minke whale (Balaenoptera acutorostrata). Drawing © Jón Baldur Hlíðberg

The diet of minke whales exists with regional differences, but in general, krill and capelin are an important part of the diet (Víkingsson and Elvarsson, 2011). Over the summer time the energy consumption for minke whales in Icelandic waters is estimated to be about 426,400-428,700 kcal per day for each individual (Sigurjónsson and Víkingsson, 1997). Collection of stomach samples in Icelandic coastal waters led to the conclusion that krill, sandeel, pelagic fish and gadoids were the most important prey groups, sandeels being the single most important prey type. The diet composition varies between geographical locations with sandeels being dominant in the southern and western areas while the diet seems to be more diverse in the northern and eastern areas (Víkingsson and Elvarsson, 2011). Arial surveys have shown drastic reduction in minke whale numbers around Iceland. Minke whale abundance was estimated to be 24.532 animals in 1987 and 43.633 in 2001. In 2007 minke whale abundance drastically reduced with estimates of 10.680 animals (Borchers et al., 2009). Most recently the Marine Research Institute in Iceland estimated the abundance in 2009 to be 9.588 animals (Pike et al., 2011).

2.2.3 White-beaked dolphin (*Lagenorhynchus albirostris*)

The white-beaked dolphins (*Lagenorhynchus albirostris*) are year-round residents in Icelandic waters and are most commonly found off southwest, northeast and southeast Iceland (Magnúsdóttir, 2007; Pike et al., 2009; Rasmussen et al., 2013). They are believed to be the most common dolphin species in Icelandic waters with abundance estimated to be about 31,653 animals from the sighting survey in 2001 (Pike et al., 2009).

Fig. 2.2.3.1 White-beaked dolphin (Lagenorhynchus albirostris). Drawing © Jón Baldur Hlíðberg

Although little is known about the reproduction behaviour of the white-beaked dolphin in Iceland, the calving is known to take place over the summer time, approximately from May to August after 11 months of gestation (Víkingsson and Ólafsdóttir, 2004).

Knowledge about the diets of white-beaked dolphins is very limited, but Sigurjónsson and Víkingsson (1997) estimated that dolphins in Icelandic coastal waters fed predominantly on fish (95% of stomach content) and cephalopods (5% of stomach content), with energy consumption per day of about 14,000-20,000 kcal for each individual. White-beaked dolphins are thought to be generalist in food selection, preying on variety of fish species of different sizes. From diet research in Icelandic waters, gadoids seem to be dominant in their diet along with a few pelagic fish species (Víkingsson and Ólafsdóttir, 2004). In Faxaflói Bay, white-beaked dolphins are believed to prey on sandeels (Rasmussen, 1999) and according to fishermen in Iceland, they are often sighted in great numbers at the southwest of Iceland during the spawning season of the capelin (Magnúsdóttir, 2007).

2.3 Cetacean data collection

In this paper, observational data of minke whales and white-beaked dolphins in Faxaflói Bay, Iceland, collected in July, over six field seasons from 2008-2013, is used.

Data collection is described in Bertulli (2010). The collecting was weather permitting and only carried out in wind speeds of less than 10 m/s (20 knots), or less, and sea state of zero to four (but mostly below three) on the Beaufort scale. The surveys were conducted using two whale watching vessels provided by the whale watching company "Elding", which is located in Reykjavík. In July 2008-2009 the company performed three trips per day but in July 2009-2013, six trips were conducted each day. Each tour lasted about three hours. An average of one to two surveys were conducted per day with suitable conditions, and the majority of the research took place with one boat, *Hafsúlan*. Additional boat, *Elding,* was used when *Hafsúlan* was not available. The reason why only one boat was chosen is related to the opportunity to standardize the methodology of data collection.

2.3.1 Effort

Every encounter of a cetacean was allocated a new sighting number, despite the possibility that the animal/animals had been encountered before. Information about time of the observation, GPS-coordinates of position, number of individuals, behaviour and the potential presence of calves was noted in the data for each encounter (Bertulli, 2010).
By viewing the GPS-coordinates from the data, using Garmin base camp, it was possible to only include data from the tours that overlapped the chosen study area around for the analysis.

Sightings were expressed as the number of sightings per unit effort (SPUE) in July, each year. The following formula was used: SPUE = n/T, where *n* is the total number of sightings and *T* is the number of tours conducted in the research area or total effort.

2.4 Sandeel data collection

The sampling of the sandeel data is described in Bogason et al. (2013). The data used in this paper comes from research area number two, Faxaflói Bay, which has 23 dredge stations (Fig. 2.4.1). The sandeels are length measured and counted while out at sea, but further analysis was then conducted on land so time could be utilized as well as possible.

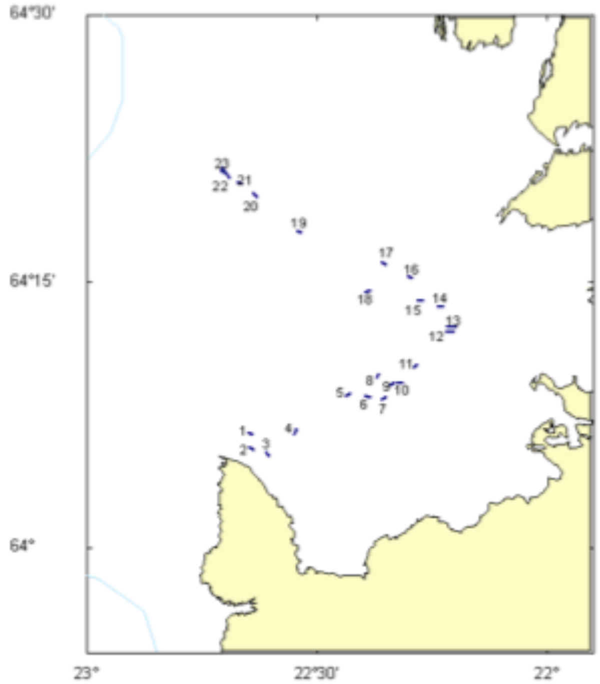

Fig. 2.4.1 - Dredge stations in Faxaflói Bay. Each station has a fixed number inside the area (Bogason et al.2013).

2.4.1 Fishing gear

Two types of trawling nets were used for data collection. From 2006-2010, fishing gear nr.23, a pelagic trawl was used. The trawl had a perimeter that had been delimited to 230 meters, 7 mm meshes and 16-17 meters opening (7%). In the year of 2011, fishing gear nr.24, a smaller pelagic trawl, with about 6-8 meters opening and a perimeter of 84 meters and 7 mm meshes, was taken in use.

Two types of dredges were used for data accumulation, fishing gear nr.172 and nr.173. In the years 2006-2007, a dredge with teeth that turn forward and down, was used. Because of the small mesh size, the net sometimes got full of sand after a short time. This was traced back to arrangement of the teeth. In the sandeel expedition in 2007, a design draft was made for the building of a new sandeel dredge that would do the same job as the old one, but without gathering sand into the net. This new dredge was brought into use in the expedition in 2008. Comparison of the two dredges has shown that there is no significant difference in the fishing efficiency. The dredges were 65 cm wide, 30 cm in height and were 3 meters long. They had a perimeter of 2 meters and the mesh size was 7 mm (Bogason et al., 2013).

2.4.3 Effort

Two types of fishing gear were used for the data sampling. The trawls were only used when the fish finder located schools of fish that were likely to be sandeels. The length and position of the haul depended on the conditions each time. Fishing gear nr.172, the new dredge, was the only dredge used in the sampling of the data used in this paper. The dredge was towed for 300 m^2 at the speed of 2 nautical miles/hour.

The total fishing effort was very similar between the sampling years, ranging from 26-29 hauls. The trawls were only used once a year from 2008-2010, five times from 2011-2012 and four times in 2013. The usage of dredge ranged from 22-28 hauls (Table 2.4.3).

Table 2.4.3 Total fishing effort and frequency of fishing gear usage, trawl and dredge, in the sandeel data collection in 2008-2013.

	Year					
Fishing gear	2008	2009	2010	2011	2012	2013
Trawl	1	1	1	5	5	4
Dredge	28	25	27	24	22	25
Total	29	26	28	29	27	29

If a station had 150 or more sandeels then only 100 were measured and the rest counted. 50 sandeels were then taken from the counted ones from each station and put in a bag with a marking tag on it, placed in a box and then frozen. Further analysis was then conducted on land. A station with 150 or less sandeels has the same analysis as the one above but all of the sandeels from the station were frozen after measurements had been conducted.

Further analyses on land involved examination of otoliths under a microscope, length measurements and weighting of the samples (Bogason et al. 2013). The examination of otoliths is used for age determination, the number of growth rings (zones) on the otoliths represent the age in years (Eliasen, 2008).

2.5 Statistical analysis

Correlation between each of the two main species and the proportion of older sandeels was established through statistical analysis using the R software (R 2.15.1). The average sightings per unit effort, for both minke whales and white-beaked dolphins, were plotted against the proportion of older sandeels, age groups 1-6, for all study years. A Spearman's rank correlation test was used to assess if there was a significant statistical relationship between the variables.

3 Results

3.1 Data analysis

220 tours were conducted in the research area, during July in 2008 to 2013. Minke whales were sighted 1194 times while white-beaked dolphins were sighted 524 times. Values for the mean number of animals, in the tours where the species were sighted, varied between years. For minke whales, the mean number of individuals ranged between 2.29-9.74 (SD range= 1.81-5.80) and for the white-beaked dolphins the mean ranged between 5.19-8.78 (SD range= 2.30-6.40) (Table 3.1.1).

Table 3.1.1 Number of tours conducted in the research area and number of sightings, as well as the mean number of individuals per tour sighted and the standard deviation (SD), for minke whales and white-beaked dolphins in July from 2008-2013.

		Minke whale			**White-beaked dolphin**		
Year	Tours	Sightings	Mean	SD	Sightings	Mean	SD
2008	41	380	9.74	5.80	132	5.5	3.13
2009	42	305	7.26	3.48	83	5.19	2.30
2010	29	108	4.15	1.88	79	8.78	4.98
2011	41	238	5.76	3.22	34	6.17	4.54
2012	28	55	2.29	1.85	51	5.67	3.64
2013	39	108	3.27	1.81	145	7.63	6.40
Total	220	1194			524		

Sightings per unit effort (SPUE) for both minke whales and white-beaked dolphins varied between sampling years. SPUE for the minke whales showed a decline from 2008-2010, increased slightly in 2011 but decreased again the year after. The SPUE for white-beaked dolphins fluctuated between years, increasing from 2009-2010 and from 2011-2013, but decreased from 2008-2009 and 2010-2011 (Table 3.1.2).

Table 3.1.2 Sightings per unit effort (SPUE) for minke whales and white-beaked dolphins, in July from 2008-2013. SPUE=sightings/tours

	SPUE	
Year	**Minke whale**	**White-beaked dolphin**
2008	9.27	3.22
2009	7.26	1.98
2010	3.72	2.72
2011	5.76	0.9
2012	1.96	1.82
2013	2.77	3.72

The age distribution in the sandeel population varied considerably in the years 2008-2013. The 0-group of sandeels was most frequent in the samples from 2010, 2012 and 2013, but in 2008, 2009 and 2011, older sandeels, age groups 1-6, were in higher proportion.

Table 3.1.3 Frequency of year-classes for sandeels sampled in the years 2008-2013.

%			**Year**			
Age	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**
0	4.17	22.8	48	16.4	87.1	70.07
1	66.3	1.67	12.3	11.8	0	0.48
2	18.5	62.5	9.93	17.3	0.49	3.72
3	8.66	12	26.9	18.6	0.62	12.02
4	1.85	1.06	2.17	35.2	3.21	3.49
5	0.46	0	0.72	0.24	8.28	2.76
6	0	0	0	0.48	0.25	7.45
n=	647	659	554	415	809	832

3.2 The Spearman's rank correlation test

Sightings per unit effort for the minke whales was plotted against the proportion of older sandeels, age groups 1-6, to assess whether the proportion of older sandeels had any significant influences on the SPUE for minke whales.

The Spearman's rank correlation test found the rho to be 0.9428571 and the p-value=0.01667, which indicates the variables compared are monotonically related and that there is a significant relationship between the SPUE of minke whales and proportion of older sandeels. As the proportion of older sandeels increased the SPUE for the minke whales increased as well (Fig.3.2.1).

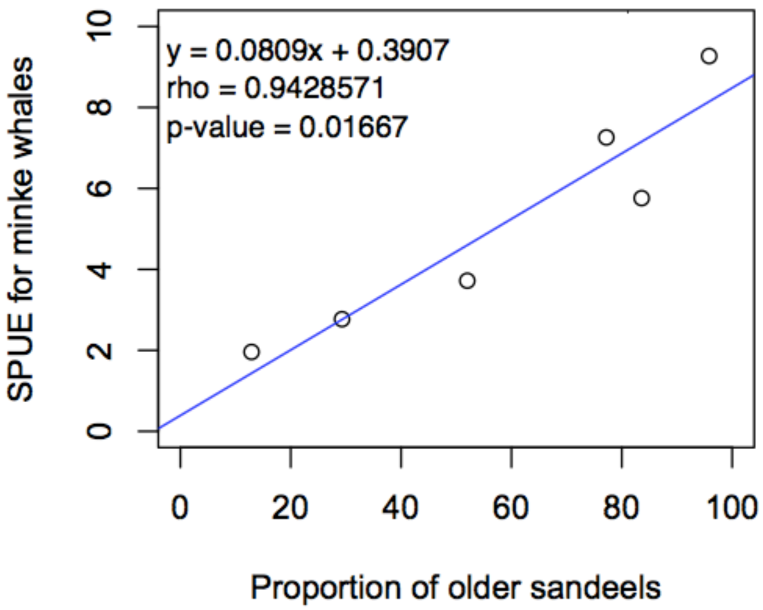

Fig. 3.2.1 Plot of sightings per unit effort for minke whales and proportion of older sandeels (age groups 1-6), in July 2008-2013. The blue line represents best line of fit. The y-axis represents the SPUE for minke whales with a scale from 0 – 10 and the x-axis represents the proportion (%) of older sandeels, in July 2008-2013. The dots represent SPUE and proportion of older sandeels in each research year (2008-2013).

SPUE for the white-beaked dolphins was plotted against the proportion of older sandeels, age groups 1-6, to assess whether the proportion of older sandeels had any significant influences on sightings per unit effort for the white-beaked dolphins.

The Spearman's rank correlation test found the rho= -0.02857143 and the p-value=1. These results show that there is not a significant relationship between the two variables (Fig. 3.2.2).

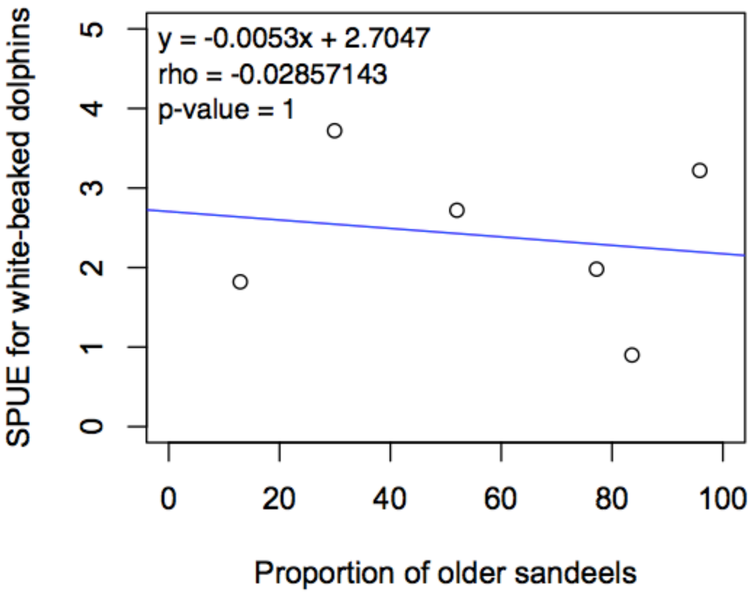

Fig. 3.2.2 Plot of sightings per unit effort for white-beaked dolphin and proportion of older sandeels (age groups 1-6), in July 2008-2013. The blue line represents best line of fit. The y-axis represents the SPUE for white-beaked dolphins with a scale from 0 to 5 and the x-axis represents the proportion of older sandeels. The dots represent SPUE and proportion of older sandeels in each research year (2008-2013).

4 Discussion

Abundance of minke whales showed a significant correlation to the variable proportion of older fish in the sandeel stock. SPUE being higher when older sandeels were dominant in the population. Minke whales have been reported as highly opportunistic predators, but the results indicate that they show some preference for older sandeels as prey. The preferences of older sandeels could very well be because of their higher energy value as compared to the 0-group fish. Immature sandeels tend to use their energy for rapid growth but after maturity has been reached, less energy is required for weight gain and maintenance, and instead more energy is stored as lipid reserves (Calow, 1981, as cited in Anthony et al., 2000). The sandeels are known to reach maturity after the first year, at the size of 11-12 cm (Jónsson and Pálsson, 2006), which indicates that sandeels in age groups 1-6 have higher lipid content than immature sandeels in the 0-group. The present results and hypothesis are also supported by a recent study of minke whale diets. Víkingsson et al. (2014) found that the age of sandeels eaten by minke whales, in Faxaflói Bay, ranged between 0 to 6 years old with the mean fish size of 12.8 cm, which roughly corresponds to one-year-old fish (Jónsson and Pálsson, 2006).

The white-beaked dolphins did not show any significant relationship to the proportion of older sandeels, and SPUE for the dolphins was relatively high despite low proportion of older sandeels. White-beaked dolphins are thought to be among the most generalist species of toothed whales, consuming a wide range of prey size, including both relatively small and large prey (Macleod et al. 2006). Although it has been shown that the diet of white-beaked dolphins consists mainly of fish (95%), very little is known about their prey preferences. Macleod et al. (2006) suggested that toothed whales might not simply base their choice on the availability of the prey, but seemed to consume larger, less abundant prey species in preference to smaller prey in higher abundance, which might explain the lack of relationship found between the white-beaked dolphins and proportion of older sandeels.

Although both minke whales and white-beaked dolphins are known to prey on sandeels, the results indicate that the importance of sandeels as a prey item is greater for minke whales than for white-beaked dolphins. A possible explanation is the differences between morphological traits used for foraging. The two predator species belong to distinct suborders, Mysticeti and Odontoceti. White-beaked dolphins belong to the suborder Odontoceti, or toothed whales, which are characterized by having teeth that they use to pierce and hold their prey, while minke whales belong to Mysticeti, or baleen whales, and have baleen plates, instead of teeth, that serve as a filter-feeding system (Cope, 1890; Norris and Mohl, 1983). These different foraging traits and methods influence the prey selection of the species and might explain why the results show that sandeels are more important for minke whales than for white-beaked dolphins. The mechanism of filter feeding makes the minke whales able to feed on numerous prey items at once. By choosing small, energy rich prey that is found in high density, instead of feeding on large prey items in low density, they might increase their energy gain. However, toothed whales typically capture and swallow a single prey item and are capable of using their teeth to tear large prey items apart. Benoit-Bird (2004) suggested that the energy that dolphins use to catch a single prey item is relatively the same for both large and small prey items. He found that spinner dolphins foraging rates for maintenance, increased dramatically if smaller prey was consistently consumed. If this applies for white-beaked dolphins as well, they might prefer larger prey items to increase their gain of energy.

The minke whales are migratory animals and are found in Faxaflói Bay, among other locations, during their feeding season. They depend on high availability of prey in order to build up their energy reserves, which they use to support the costs of reproduction, before migrating back to the breeding grounds. White-beaked dolphins are however resident and spend both the feeding and the breeding season in Icelandic coastal waters. Dolphins, like most toothed whales, are income breeders which use current energetic income to support reproduction, making building of reserves unnecessary as they continue to feed through out the reproductive cycle (Costa, 1993; Christiansen et al., 2013).

Canning et al. (2008) suggested that white-beaked dolphins may not be actively following prey in summer, but instead they are seeking protection while calving in areas where prey is also available. Although little is known about the reproduction behaviour of the white-beaked dolphin, the calving is known to be over the summer time, approximately from May to August. Females might move inshore during that period and the males might follow them in order to mate after the calves are born. This might explain the lack of relationship between white-beaked dolphin and older sandeels as the data used in the analyses were collected in July. Unfortunately the data does not provide information about the age of the dolphins or frequency of sexually mature individuals so this hypothesis might only partly apply to the dolphins seen in Icelandic coastal waters

5 Conclusion

The abundance of older sandeels is of greater importance for minke whales than for white-beaked dolphins. How these two predator species respond to fluctuations in prey populations might be linked to their foraging behaviour and their dependency of prey density. Minke whales require prey in high density for efficient foraging, if prey density falls below a certain level more energy will be spent per item caught, resulting in decreased energy gain. White-beaked dolphins might not be as dependent on prey density because they are not capable of feeding on large numbers of prey at the same time. Same amount of energy will be spent per item caught regardless of the density of the prey. Minke whales as capital breeders are depending on the amount of energy acquired during their feeding season to support the costs of reproduction on their breeding grounds. White-beaked dolphins as income breeders, however, feed all year-around and are not restricted to maximize their energy gain in a short time.

These findings could be important for insight into how predator species abundance, distribution and behavioural patterns might reflect not only the availability of prey but also variations in prey population parameters.

Further studies on prey preferences and habitat use of white-beaked dolphins are needed to better understand their population structure and distribution in Icelandic coastal waters.

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