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Notes

Fitisýrur í spiki av grindahvali, *Globicephala melas*, í Føroyum. Fitisýrur sum føðsluevni og markørur. Samfelagsligur týdningur av grind

Fatty acids in blubber of long-finned pilot whales, *Globicephala melas*, in the Faroe Islands. Fatty acids as nutrients and pod marker. Societal importance of pilot whales as a local marine food resource

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Faculty of Science and Technology University of the Faroe Islands

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Fatty acids in blubber of long-finned pilot whales, *Globicepala melas*, in the Faroe Islands. Fatty acids as nutrients and pod marker. Societal importance of pilot whales as a local marine food resource

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Abstract

The history of subsistence whaling is long and unique in the Faroe Islands, mainly because relevant information about the catch and distribution of meat and blubber has been recorded for centuries. The long-finned pilot whale, *Globicephala melas*, has been and still is an important food resource as well as an integrated and essential part of the Faroese society and culture. Although the blubber is sub-clinically polluted, it is still utilized for human consumption. Recently conducted investigations show that life expectancy for Faroese women (85.6 years) and men (82.4 years) is among the highest globally, and age-standardized incidence and prevalence of dementia is amid the lowest worldwide. Lipid extraction followed by gas chromatographic analysis showed that pilot whale blubber sampled in the summer season contains the following fatty acids: 16:0, 16:1ω7 and 18:1ω9 in relatively high proportions. Additionally, also smaller amounts of the long chained monounsaturated fatty acids, 20:1ω9, 20:1ω11, 22:1ω11, which are beneficial and healthy for humans. Multivariate analysis revealed the potential use of the fatty acid profile as a natural marker for discrimination among pods of long-finned pilot whales in Faroese waters.

Key words. Pilot whale, *Globicephala melas*, blubber, lipids, fatty a~~s~~cids (FA), long chain monounsaturated FAs, contaminants, sustenance, pod-switching, sustainability, local marine resources, gas chromatography, multivariate analysis.

Fitisýrur í spiki av grindahvali, *Globicephala melas*, í Føroyum. Fitisýrur sum føðsluevni og markørur. Samfelagsligur týdningur av grind

Úrtak

Hvalaveiða í Føroyum og tíðarlanga skrásetingin av henni er serlig í heimshøpi. Staðfestast kann, at grindahvalurin, *Globichepala melas*, er ein týðandi partur av føroyskari mentan, lógum, fyriskipanum og sum heild samfelag landsins. Tvøst og spik hevur verið og er framvegis ein vældámdur partur av kosti føroyinga. Sjálvt um spik er sub-kliniskt solkað av evnafrøðiligum dálkingarevnum, so verður tað framvegis skynsamt nýtt sum mannaføði. Lutfalsliga nýggjar kanningar vísa, at mettur livialdur hjá føroyskum kvinnum (85,6 ár) og monnum (82,4) er millum teir hægstu í heimi, og at aldursjavngjørdur títtleiki og útbreiðsla av minnissvinni er millum lægstu her á jørð. Gaskromatografisk kanning av sýnum um summarið vísti, at spik av grindahvali inniheldur lutfalsliga stórar nøgdir av fitisýrunum: 16:0, 16:1ω7 and 18:1ω9, eins og smærri nøgdir av gagnligum og heilsufremjandi langketaðum monoómettaðu fitisýrunum: 20:1ω9, 20:1ω11, 22:1ω11. Margbrigdlagreining avdúkaði, at fitisýruprofilur í spiki kann nýtast sum náttúrligur markørur til at skilja millum grindabólkar.

Introduction

Whaling - an old profession

The evidence of whaling for food in costal and nearshore waters in the arctic regions dates 5,500 years back in time (Freeman et al. 1998:59). This practice of local residents for provision of nutrients is not surprising, when the options for food supply and survival are kept in mind. The opportunities for subsisting on agricultural sustenance have been limited in these regions due to harsh climate, geography and a steep and rocky topology. Sustainable utilization of local marine resources in the arctic and boreal areas has therefore been and still is crucial and vital for the local populations. This is a modus vivendi, which is favourable for the environment and in total agreement with Sustainable Development Goal number 14 (https://sdgs.un.org/goals) of the United Nations.

Whales – a celestial gift

In the Faroe Islands, the infield is only 7,8 % (Fosaa et al. 2006) of the total land area, equivalent to of 1399 km^2. Large scale agriculture has therefore been and still is quite challenging. The staple local food has therefore been proteins and fat (Svangberg 2021), mainly, from different species of marine and terrestrial mammals, but also from various sorts of birds and fish. The Faroe Islands have been blessed with frequenting pods of long-finned pilot whales (*Globicephala melas*) for ages (Joensen 2009). These pods have been regarded as celestial gifts from the Almighty. The whales seem to have approached the near-shore waters of the Faroe Islands while foraging the country´s coastal waters, and as a consequence have been an easy catch in a relatively brief drive fishery. Occasionally, pods of pilot whales as well as single and small groups of bottlenose whales (*Hyperoodon ampullatus*) have beached themselves (Debes 1673), and still do so in some specific whale bays. Having noticed the stranded animals, the locals have relieved the animals immediately from gravity induced suffering by quickly severing the large arteries, rete mirabile and spinal cord (Bloch 2007, Bjørnsson et al. 2014). Subsequently, the carcasses were shared within the community for food, fishing tackles and domestic utensils. The last two mentioned cetacean derived commodities are not exploited any longer but were crucial in former times.

Social significance

Due to the improved livelihood from the regular arrivals of pods of pilot whales, these have been and still are essential for local communities in the Faroe Islands (Joensen 2009), both culturally (Brú 1940, Kawashima 2021), socially and economically (Kerins 2010). This sociological significance is reflected in acts, rules and regulations in the Faroese society (Bjørk 1963a, Joensen 2009), and especially so in the grind law (Grindalógin), the public law which regulates the hunt and sharing of pilot whales (Grind law 2020). The Faroese Grind law is old and dates back to 1832.

Biology of long-finned pilot whales

Even if quite a few aspects and facets of long-finned pilot whale´s biology and value as a food resource still remain in obscurity, then several clarifying and illuminating findings have been made and conclusions reached from studies carried out the last decades. Faroese and foreign scientist have conducted several national and international research projects on long-finned pilot whales in the North Atlantic. By and large, the research fields comprehend general biology, genetics, abundance, and contaminants of the long-finned pilot whale. Several topics have been covered and published, and encompass a range of biological studies, like ecology (Bloch et al. 1993a, Desportes et al. 1994a), morphometric analysis (Bloch and Lasstein 1993b), age and growth parameters (Bloch et al. 1993c), external characters (Bloch et al. 1993d), distribution (Buckland et al. 1993), abundance and sustainability (Pike et al. 2019; Bogadóttir 2020), age, growth and social structure (Bloch 1994), variation in foetal and postnatal sex ratios (Desportes et al. 1994b), modelling the school structure (Bloch and Lasstein 1995), diving behaviour (Heide-Jørgensen et al. 2002), tagging for movement registration (Bloch et al. 2003), interspecific introgression in pilot whales (Miralles et al. 2013), and furthermore interspecific hybridisation between tropical short-finned pilot whale and north east Atlantic long-finned pilot whales induced by global warming (Miralles et al. 2016).

Contaminants

The industrialized part of the world has been dumping and releasing a range of chemicals, poisons, and contaminants the last century and have thereby polluted the atmosphere, the lithosphere, and the hydrosphere more or less globally. This inconsiderate, hazarded, and dangerous conduct is an increasing peril and if continued unconstrained will threaten slowly but surely all life on earth, included the marine biota, which constitute the main food resource of the Faroese people. In order to circumvent ill health effects from pollutants, scientist in the Faroe Islands together with intercontinental researchers have been monitoring and registering negative impacts on human and cetacean health. The multitude of national and international projects completed have shed light on several health related issues, like the high concentrations of PBDEs and PCBs in human milk in the Faroe Islands (Fängström et al. 2005), accumulation of anthropogenic contaminants such as poly- and perfluoroalkyl substances (PFOS and FOSA) and its influence on human population (Dassuncao et al. 2018), adverse effect of polychlorinated biphenyls (PCBs) and perfluorinated alkylate substances (PFAS) on semen quality of humans (Petersen Skaalum et al. 2018), epigenetic changes in humans due to prenatal exposure of a mixture of contaminants (Leung et al. 2018), toxokinetic studies of mercury isotopes and selenium in several whale tissues (Li et al. 2020) and analysis of mercury and mercury associated neurochemical biomarkers in the brains of long finned pilot whales (Desforges et al. 2021).

Conundrum

Despite numerous reports and papers describing the ill effects of contaminants found in pilot whales, people in the Faroe Islands live longer and suffer less from age-related mental illnesses than inhabitants in most other countries worldwide. Life expectancy (2021) for men and women in the Faroe Islands was 85.6 years and 82.4 years, respectively. In average 83.5 years. The corresponding figure for the Nordic Countries was 82.4 years. (https://hagstova.fo/fo/folk/livsaevi/livialdur). Moreover, research shows that age-standardized incidence and prevalence of dementia in the Faroe Islands are lower than in most other countries globally (Petersen Skaalum M. et al. 2019).

Healthy LCMUFA

In the sub-clinically polluted meat and blubber of long-finned pilot whales in the North Atlantic there are also many healthy nutrients. Several animal and human, interventional and observational studies have shown a variety of beneficial effects from consumption of marine products rich in long chain monounsaturated FAs, LCMUFA (20:1 and 22:1). Thus, supplemental intake of seal oil, cod liver oil and notably whale oil, which was richest in LCMUFA, had favourable effects on concentrations of several types of biomolecules linked to cardiovascular and thrombotic diseases (Osterud et al. 1995, Vognild et al.

1998). Moreover, analysis have revealed downregulated expression of lipogenic genes, *Srebp-1*, upregulation of FA oxidative genes, *Cpt-1*, and energy-spending linked genes, *Pgc-1alpha*, as a response to LCMUFA intake (Yang et al. 2011a). Likewise, ingestion of LCMUFA-rich food down-regulated genes involved in cholesterol metabolism, *Hmgcr*, (Yang et al. 2011b), increased expression of the insulin signalling genes *Irs* and *Inrs* and decreased expression of inflammation mediating gene *Tnf-alpa* (Yang et al. 2015). Furthermore, dietary LCMUFA upregulates expression of lipid oxidation involved genes such as citrate synthase, *Cs*, and carnitine palmitoyltransferase 1A, *Cpt1a* (Yang et al. 2013). In blood vessels, inflammation and lipid accumulation are suppressed and cholesterol effluence increased by ingestion of C20:1 and C22:1 FAs, i.e. gondoic acid (20:1ω9), gadoleic acid (20:1ω11), erucic acid (22:1ω9) and cetoleic acid (22:1ω11). Altogether LCMUFA-rich diet improved lipid metabolism, insulin sensitivity, atherosclerosis and generally increased cardiovascular health (Yang et al. 2016). Finally, LCMUFA seems to be able to improve endothelial functions and have beneficial effects on the gut microbiota in humans (Tsutsumi et al. 2021).

Purpose

Although long-finned pilot whales in Faroese waters have been investigated thoroughly in many different ways, analysis of health promoting nutrients such as FAs in the subcutaneous fat has, to the best of knowledge, never been carried out in the Faroe Islands before. The purpose of this study is to present the importance of pilot whales in a broad context comprising relevant aspects of history, religion, society, biology, pollutants, and health, moreover, to quantify the fatty acids in blubber of long-finned pilot whales beached in the Faroe Islands in the summer season, and lastly, explore whether fatty acid profiles could be used as an ecological pod marker.

Materials and Methods

Sample collection

In connection with occasional non-commercial drive fishery of long-finned pilot whales (*Globicephala melas*) 14 blubber samples were collected, 7 from Miðvágur (Date: 06 June 2015. $N_{sampled}$ = 7, L = (445 ± 79) cm, L_{max} = 569 cm, L_{min} = 350 cm; N_{total} = 154) and 7 from Sandagerði (Date: 23 July 2015. $N_{sampled}$ = 7, L = (432 ± 62) cm, L_{max} = 540 cm, L_{min} = 370 cm; N_{total} = 142) in the Faroe Islands (Figure 1). The sampling took place after the whales had laid their bones– i.e. were dead - and prior to the ancient and socially well-organized sharing and distribution of meat, blubber, ribs, and scapulae, free of charge. The expression, having "laid their bones" is a common euphemism in Faroese used for whales only. It is not so common but does exists in English. After demise the carcasses were opened by cutting free passage into the abdominal cavity in order to facilitate cooling of meat and entrails (Figure 2). The openings, large enough for excision of the kidneys, were made by three incisions roughly in the middle of the abdomen along and perpendicular to the anteroposterior axis just behind the dorsal fin. Samples of blubber and muscle were excised at the ventral and caudal side of these abdominal rectangular incisions, i.e. near the genitals.

Samples of blubber were deposited in polyethylene bags and stored at – 20 ^{o}C until subsampling and delivery for analysis at Eurofins Steins Laboratory Ltd. in DK-6600 Vejen, Denmark.

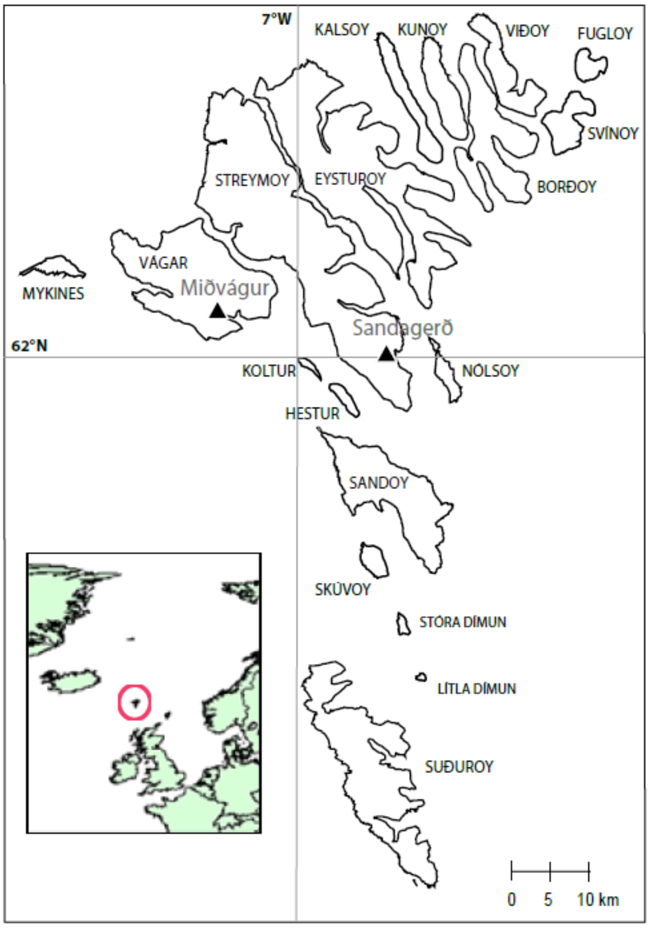

Figure 1. **Map of the Faroe Islands in the North Atlantic.** Faroe Islands and two authorized whale bays: Miðvágur and Sandagerði, marked by black triangles (▲), where whale pods laid their bones on 06 June 2015 and 23 July 2015, respectively. By courtesy of associated professor Eyðfinnur Magnussen, Faculty of Science and Technology, University of the Faroe Islands, Thorshavn, Faroe Islands.

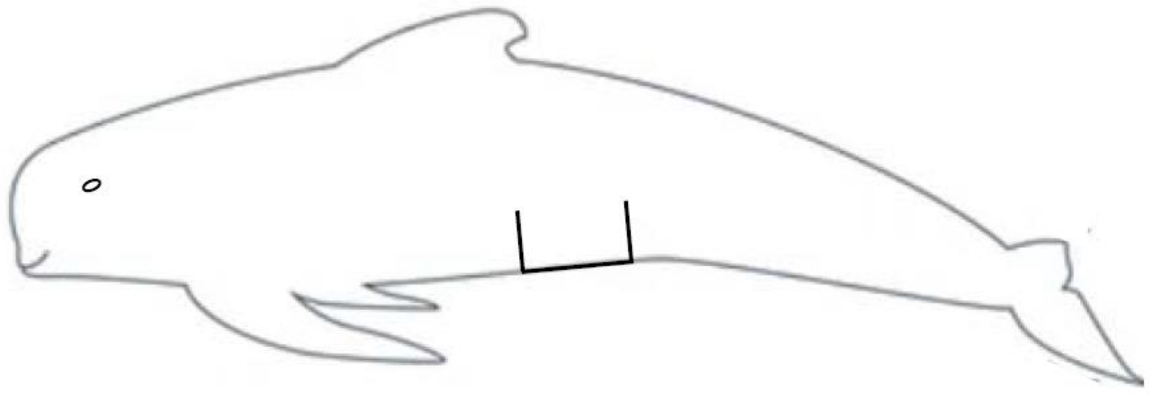

Figure 2. **Pilot whale, *Globicephala melas*, with cooling openings indicated by three black lines.** Pilot whale (*Globicephala melas*) contour. Free passage was made into the abdominal cavity of the carcass in order to facilitate cooling of meat and entrails. The hatch-like opening, large enough for excision of the kidneys, were made by three incisions roughly in the middle of the abdomen along and perpendicular to the anteroposterior axis just behind the dorsal fin. Samples of blubber and muscle for analysis were excised at the ventral and caudal side of these abdominal rectangular incisions, i.e., near the genitals.

Laboratory analysis

The methods used for analysis of FAs in the blubber were: 1) DHF19, NMKL 131: 1989 and Gravimetric Analysis. Fat: Schmid-Bondzynski-Ratzlaff > 99.8g/100g. 2) DHF24 GC-FID. FA factor: 0.956. 3) DHF26 AOCS 1f-96. GC-FID.

Univariate analysis

The raw data consisting of the relative mass of 27 different FAs in blubber (g of FA/100 g of blubber) from each of the 14 whales were processed univariately. Average values and standard deviations were calculated for the FAs quantified in the Miðvágur-pod and Sandagerði- pod, separately. Moreover, numerical values for the following stub entries were calculated for the two mentioned whale-pods: the sum of saturated fatty acids FAs, the sum of monounsaturated fatty acids FAs, the sum of polyunsaturated fatty acids FAs, the sum of ω3 fatty acids FAs, the sum of ω6 fatty acids FAs and the ratio between the sum of ω3 fatty acid FA and the sum of ω6 fatty acids FAs. Finally, the differences between the content of fatty acids FAs in the Miðvágur-pod and the Sandagerði -pod were tested by Student´s t-test. Significance level was 1% ($p<0.01$).

Multivariate statistics

After GC-FID analysis of the fatty acid FA methyl esters, the chromatographic data were normalized, log-transformed and since investigated by PCA (principal component analysis) available in the SIRIUS program package (Kvalheim and Karstang 1987). The total number of FAs analysed was 27. The resulting PC-biplot displays the major feature of data. Two clearly separated groups appeared on the plan spanned by the two principal components, PC1 and PC2, which explained the highest and next highest variance, respectively. The original variables, the FAs, were also displayed in a biplot. Hereby, the correlation among samples and FA became evident. A sample lying close to a FA in the biplot contains larger amounts of that particular FA than a sample lying far from that fatty acid FA. Close positioning of FAs in a biplot means that they are positively correlated. FAs on opposite sides of the origin are negatively correlated. After PCA, the data were subjected to agglomerative hierarchical cluster analysis and fuzzy cluster analysis (Dunn 1973; Bezdek 1981). The outcomes of these investigations confirmed the result in the PC-biplot. It is, however, not possible to decide from the PC-biplot whether the FA-based difference between the samples from the Miðvágur-pod and the Sandagerði-pod is statistically significant or not. In order to carry out a proper classification a second step of multivariate analysis was conducted. This additional investigation comprised SIMCA-analysis (soft independent modelling by class analogy) (Wold and Sjøstrøm 1977), of the normalized and standardized data. SIMCA is available in the SIRIUS package.

Results

Univariate analysis

The average quantitative amounts and standard deviations of FAs in pilot whale blubber from pods beached in Miðvágur and Sandagerði were calculated and summarized in Table 1. The major components are the monoenic FAs: oleic acid, 18:1ω9 (24-28 g FA/100 g blubber), palmitoleic acid, 16:1ω7 (11 g FA/100 g blubber), and the saturated FA: palmitic acid 16:0 (9-10 g FA/100 g blubber). The long chain monoenic FAs (LCMUFA) 20:1 (20:1ω9 and 20:1ω11) and 22:1 (22:1ω9 and 22:1ω11) totalled 8-9 g FA/100g blubber and

4-7 g FA/100g blubber, respectively. Altogether, the sum of the LCMUFA was 11-16 g FA/100 g blubber. The amounts of the long chain polyunsaturated FAs (LCPUFA), 20:5ω3 and 22:6ω3 were lower and constituted approximately 1 g FA/100g blubber and 3-4 g FA/100 g blubber, in that order. The ratios of total ω3- to total ω6-unsaturated FAs (Table 1) indicate general differences in the FA contents of the two pilot whale pods. Evaluated univariately, it becomes clear that quantities of equivalent FAs in each pod differ in several cases. When subjected to Student´s t-test, significant concentration differences were found for the following FAs: 14:0, 18:0, 18:1ω7, 18:3ω3, 20:2ω6, 20:4ω6, 22:1ω11 and 22:6ω3 (Table 1).

Table 1. Quantitative amounts (g FA/100g blubber) ± SD of fatty acids in blubber from two pods of long finned pilot whales, *Globicephala melas*. The fatty acids are assigned by the shorthand notation, A:BωC. A gives the number of carbon atoms in the molecule. All double bonds are separated by one methylene group, therefore, only the position of the first one is given. N is the number of whales sampled. The cases in which the absolute amounts of fatty acids were significantly (P < 0.01) different between the pods are marked with an s.

Fatty acids	Two pods of long-finned pilot whales beached in		T-test between the pods
	Miðvágur N=7	Sandagerði N=7	P < 0.01
12:0	0.21 ± 0.05	0.27 ± 0.06	
14:0	4.6 ± 0.7	7.0 ± 0.7	s
14:1ω5	0.9 ± 0.2	1.1 ± 0.2	
15:0	0.49 ± 0.06	0.50 ± 0.03	
16:0	10 ± 2	9.1 ± 0.8	
16:1ω7	11 ± 1	11 ± 2	
17:0	0.32 ± 0.07	0.25 ± 0.03	
17:1ω7	0.8 ± 0.1	0.56 ± 0.06	
18:0	1.9 ± 0.3	1.5 ± 0.2	s
18:1ω7	2.8 ± 0.2	2.2 ± 0.2	s
18:1ω9	28 ± 3	24 ± 2	
18:2ω6	1.2 ± 0.2	1.5 ± 0.1	
18:3ω3	0.5 ± 0.2	0.9 ± 0.1	s
18:3ω6	0.21 ± 0.03	0.19 ± 0.02	
18:4ω3	0.4 ± 0.3	0.7 ± 0.2	
20:1ω9	4.8 ± 0.9	5.4 ± 0.7	
20:1ω11	2.8 ± 0.8	3.9 ± 0.3	
20:2ω6	0.22 ± 0.03	0.17 ± 0.03	s
20:3ω3	0.14 ± 0.02	0.10 ± 0.06	
20:4ω3	0.5 ± 0.2	0.6 ± 0.1	
20:4ω6	0.42 ± 0.06	0.26 ± 0.03	s
20:5ω3	1.4 ± 0.4	1.3 ± 0.3	
22:1ω9	0.5 ± 0.1	0.49 ± 0.07	
22:1ω11	3 ± 1	6.3 ± 0.7	s
22:5ω3	1.2 ± 0.2	0.8 ± 0.2	
22:6ω3	4.1 ± 0.7	2.5 ± 0.7	s
24:1ω9	0.25 ± 0.04	0.27 ± 0.04	
ΣSFA	17 ± 3	19 ± 2	
ΣMUFA	55 ± 8	56 ± 6	
ΣPUFA	10 ± 3	9 ± 2	
Σω3	8 ± 2	7 ± 2	
Σω6	2.0 ± 0.4	2.1 ± 0.2	
Σω3/Σω6	4 ± 1	3.2 ± 0.9	

ΣSFA = total saturated fatty acids ; ΣMUFA = total mono unsaturated fatty acids; ΣPUFA = total polyunsaturated fatty acids, Σω3 = total w3-unsaturated fatty acids, Σω6 = total w6-unsaturated fatty acids; Σω3/Σω6 = the ratio of total ω3- to total ω6-unsaturated fatty acids; FA = fatty acids

Multivariate analysis

It is impossible to get an overview of the resemblance between the two pods by inspecting FAs in Table 1 univariately. In order to make comparison based on all measured FAs in the blubber samples simultaneously, a multivariate analysis, principal component analysis, PCA, of the normalized and logarithm-transformed data matrix was undertaken. The program package: SIRIUS was used for this purpose (Kvalheim and Karstang 1987). With two specimen exceptions, the resulting PC-plot showed a clear distinction along the the first principal component (PC1) between the Miðvágur-pod and the Sandagerði-pod (Figure 1). The exceptions were one male- and one female pilot whale. These had FA profiles similar to the Sandagerði-pod, but laid their bones, i.e. died, in Miðvágur together with the Miðvágur-pod (Figure 3). This overlap in the PC-plot could be the result of a pod-switch, shortly before demise. For clarity, only the FAs with the highest discriminatory power are given in the PC-biplot (Figure 3). The biplot shows that blubber of the pilot whales in Sandagerði-pod together with the two just mentioned exceptions is richer in the following FAs: 22:1ω11, 20:1ω11, 20:1ω9 and 16:1ω7 and 14:0 than the corresponding tissue from the Miðvágur-pod. Similarly, the biplot demonstrates a higher content of 22:6ω3 and 18:1ω9 in the Miðvágur -pod than in the Sandagerði -pod.

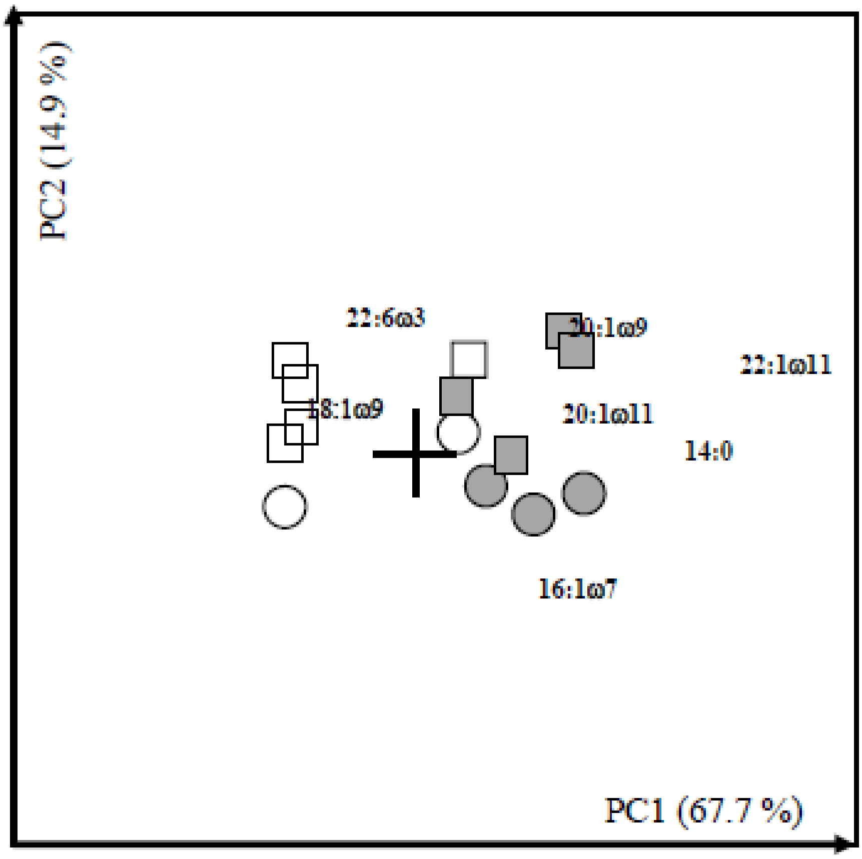

Figure 3. **Biplot of pilot whale, *Globicephala melas*, samples and fatty acids.** Pilot Whales, *Globicephala melas*. Biplot of PC1 versus PC2 of *Globicephala melas* samples based on the composition of the 27 variables measured in blubber. Each symbol represents an individual pilot whale. The male and female pilot whales from the Miðvágur-grind and the Sandagerði-grind are represented with white filled-in squares (□) and circles (○), and grey filled-in squares (■) and circles (●), respectively. Seven of the most important discriminating fatty acids are shown. The percentage of the total variance along each principal component (PC) is given.

Euclidian dendrogram

Agglomerative hierarchical cluster analysis of the blubber samples, resulting in an Euclidian dendrogram (Figure 4), supports the revealed change in affiliation of the two pilot whales (Figure 3). These two pilot whales – a male and a female laid their bones (i.e. died) in Miðvágur as a part of the Miðvágur-pod, but separated themselves lipid-wise from the Miðvágur-pod by having a FA profile similar to the the Sandagerði-pod. As a result, they clustered together with the Sandagerði-pod (Figure 4).

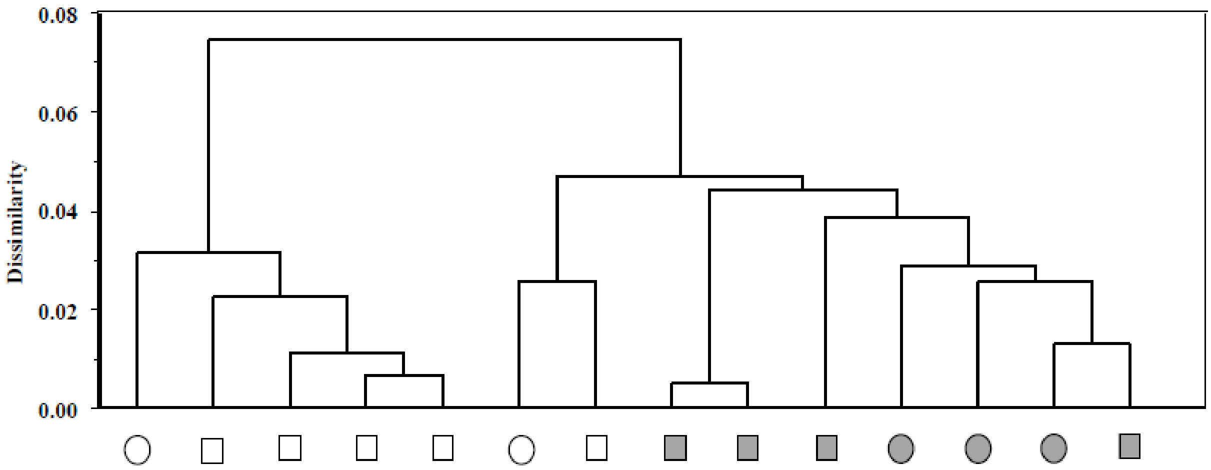

Figure 4. **Euclidian dendrogram of blubber samples from pilot whales, *Globicephala melas.*** *Globicephala melas*. Euclidian dendrogram, resulting from an agglomerative hierarchical cluster analysis of the blubber samples, shows a change in association, in which one male and one female pilot whale from the Sandagerði-pod have joined the Miðvágur-pod before laying their bones (i.e. death) in Miðvágur. The male and female pilot whales from the Miðvágur-grind and the Sandagerði-grind are represented with white filled-in squares (□) and circles (○), and grey filled-in squares (■) and circles (●), respectively.

Fuzzy cluster analysis

Based on the first principal component (PC1), the score values and and cluster exponent equalling 2, fuzzy cluster analysis (in PRS Sirius statistical package) was made of the data. In fuzzy cluster analysis the membership coefficients for each data point are generated based on clusters centroids and distance from each cluster centroid. These membership coefficients can range from 1 to 0. The resulting column chart clearly shows two distinct clusters, which are identical with the Euclidian dendrogram groups (Figure 5).

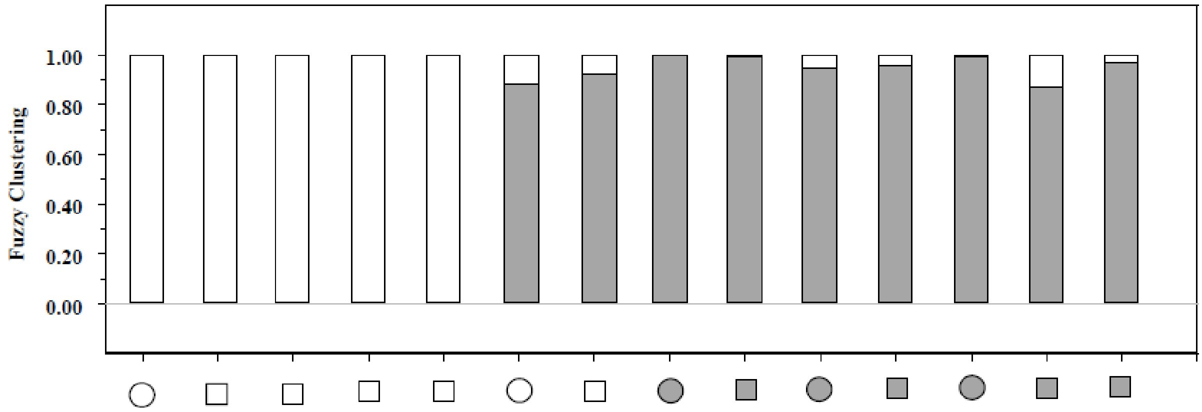

Figure 5. **Column chart shows fuzzy clustering of blubber samples from pilot whales, *Globicephala melas.*** *Globicephala melas.* Column chart based on scores of PC1 and cluster exponent 2, shows fuzzy clustering of sample. The male and female pilot whales from the Miðvágur-grind and the Sandagerði-grind are represented with white filled-in squares (□) and circles (○), and grey filled-in squares (■) and circles (●), respectively. Given their high membership coefficients in the Sandagerði-cluster, one male and one female pilot whale seem to have changed affiliation from the Sandagerði-pod to the Miðvágur-pod before laying their bones (i.e. death) in Miðvágur.

SIMCA analysis

The resulting PC-plot (Figure 3) from PCA displays the samples on a plane spanned by the first two principal components, PC1 and PC2. These PCs explain the highest (67.7 %) and next highest variation (14.9 %) of the data in the multidimensional vector space. Since all of the 27 FAs were used in the calculation, the dimensionality of the original vector space was 27. The PC-plot (Figure 3) reveals a distinction, but it is not possible to decide from the PC-plot whether the difference between the Miðvágur-pod and the Sandagerð-pod is statistically significant or not. In order to carry out a proper and valid statistically classification of the blubber samples, space-filling models of the mentioned whale pods were made by way of SIMCA (Wold and Sjøstrøm, 1977). The created models were based on the three highest discriminating PCs . The critical sizes of the statistical models based on the RSD (residual standard deviation) of the samples were calculated at 99% level. Thereafter the distances expressed as RSD of all 14 samples to each of the two models were calculated. The result, given in a Cooman plot (Figure 6), shows a statistically significant difference between the samples from the two whale pods, which laid their bones (i.e. died) in Miðvágur and Sandagerði. It is clear that one male and one female beached in Miðvágur fall in the same class as the Sandagerði-pod.

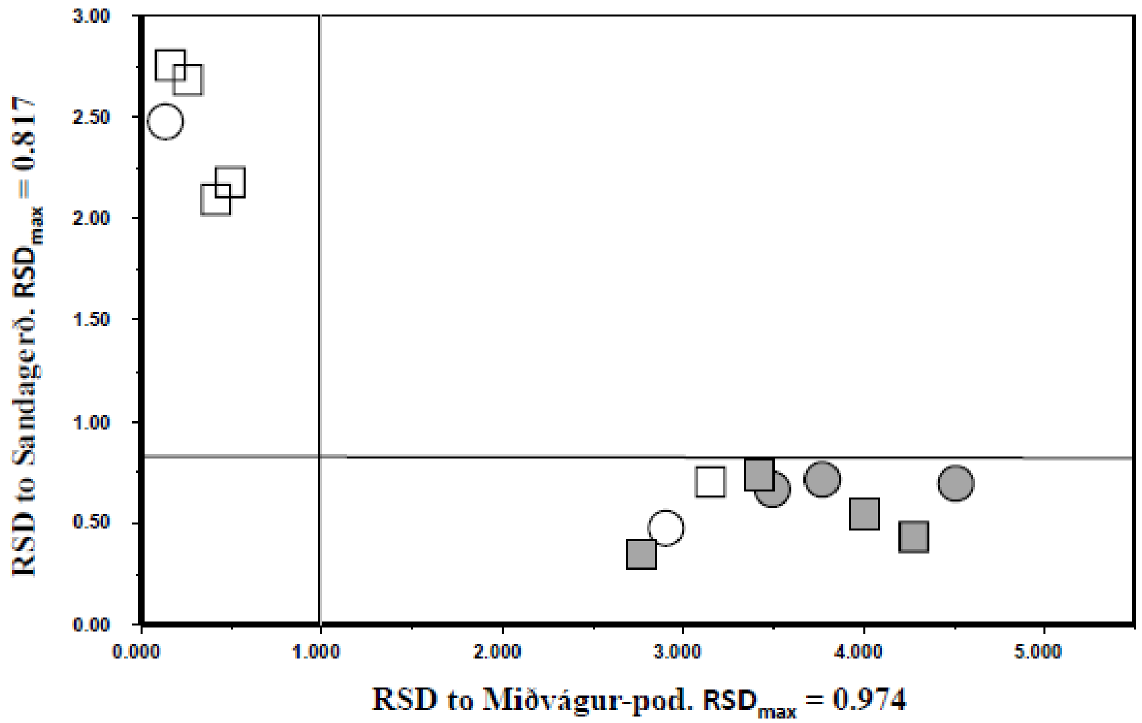

Figure 6. **Cooman plot of blubber samples from pilot whales, *Globicephala melas.*** Cooman plot of samples from 14 pilot whales (*Globicephala melas*), which laid their bones (i.e. died) in the following authorized whale bays: Miðvágur and Sandagerð, in the Faroe Islands. The male and female pilot whales from the Miðvágur-grind and the Sandagerði-grind are represented with white filled-in squares (□) and circles (○), and grey filled-in squares (■) and circles (●), respectively. The plot shows the orthogonal distances from the samples to the two different models simultaneously. The membership limits (RSD_{max}, p = 0.001) are indicated. Samples belonging to a model are within the membership limit that is to the left of the vertical line or below the horizontal line. Samples outside the boundaries belong to neither of the SIMCA-models. The plot shows total and significant separation between two groups of pilot whales. Two whales from the Miðvágur-pod grouped together with the Sandagerði-pod.

Discussion

Distinctive statistics

A unique Faroese long-finned pilot whale catch statistics cover relevant data from the present and back to 1584. (Bjørk 1963b, www.hagstova.fo). According to these statistics, the number of pilot whales beached in Faroese whaling bays the last 70 years, i. e. from 1951 to 2020, was 86.476 animals. The measured value of these whales, by the old Norse value in skinn, was 519.458 skinn (www.hagstova.fo). The annual catches these years was 1.235 whales corresponding to 7.421 skinn (7.421 skinn x 75 kg/skinn = 557 tons) in average. The mean value of each whale these years was 6.0 skinn. The conventional value-unit: one skinn, corresponds to 50 kg of meat and 25 kg of blubber (Poulsen et al. 1998), i.e., 75 kg. A corrective proposal (Bloch and Zachariassen 1989) suggests a bit different distinction between the ratio of meat and blubber. Their result was as follows: one skinn is 38 kg meat and 34 kg blubber, totalling 72 kg.

Importance of free whale meat and blubber

The question, whether the inhabitants of the Faroe Islands need the food from pilot whales frequenting the country´s bayes annually, have often been raised the last decades, mainly from foreign critics. The short answer is affirmative. A brief monetary evaluation of the average amount of meat and blubber received annually from the ocean gives a numerical reason to the confirmatory reply to the question set forth. If the price/kg of meat and blubber is set to 100 DKK/kg, – the price of cheap beef - the annual value will be: 7.421 skinn x 75 kg/skinn x 100 DKK/kg = 56 million DKK = 7.5 million EUR (Rate of exchange: October 2021). Furthermore, the value of the annual average import of meat and meat product from January 1988 to March 2020 (www.hagstova.fo) was 93.5 million DKK = 12.5 million EUR (Rate of exchange: October 2021). Consequently, the value of sustenance from pilot whales is approximately 60% of all yearly imported meat and meat products.

For many inhabitants, meat and blubber free of charge is highly appreciated and valued, and even if this kind of marine food is not directly necessary to stave off starvation it reduces the spending on nutriments. This kind of household cost cutting is important, because the Faroe Islands is an expensive country with a taxation rate among the highest in the world. As a result, a relatively large group of the Faroese population – in average 10.1 % (anno 2018) – has an equivalent income so low that it is characterized as a Risk of Poverty (60%) Remuneration, according to EU standards. The mentioned percentage varied from 8.9% and up to 18.1% in different residential areas of the country (www.hagstova.fo). Due to the low wages, pilot whaling is of importance generally, and especially so for segments of the rural population, whose existence is based on barter economy in addition to a low monetary income. The large proportion, which whale meat and blubber free of charge constitutes of the total meat consumption in the Faroe Islands, indicates the nutritional and financial importance.

The Almighty and Death

Up to these days, culture and religion have been tightly interwoven with pilot whale drive fishery. The divine guidance, care and support from the Providence have been and still is of spiritual importance in cetaceous based food provision. As a sign of gratitude and request for assistance from the Almighty to get success and blessing during the beaching process and the death-dealing, the front door of the local church and the shutters in the tower had to be open and the church bell chiming (Poulsen et al. 1998:198; personal observation). This has been practiced from time immemorial and up to these days. The main reason for the mentioned ecclesiastical ritual is the fact that pilot whale hunting does not always end successfully, and furthermore, it is by no means without risk. Skilful pilot whale hunters have been injured and even lost their lives during the pursuit (Joensen 2009) and the slaying process. These days, the death-dealing is quickly and professionally executed with spinal lances and sharp whale knifes (Bjørnsson et al. 2014), and cannot be compared with the long lasting, exhausting, and excruciating suffering and death in nature committed by killer whales (Samarra et al. 2018; Bloch and Lockyer 1988) and the less dramatic long-lasting destruction by parasites (Deliamure 1955; Ridgway and Dailey 1972; Ridgway 1979).

Fatty acid profile marker - pod-switch

Literature analyses have revealed that chemotaxonomy generally and the fatty acid FA profile method (FAPROM) specifically have potential to discriminate among several terrestrial and marine taxa in the animalia and plant kingdom (Joensen 2002). The method has been tried out at species level (Joensen and Grahl-Nielsen 2000), stock level (Joensen and Grahl-Nielsen 2004) and individual level (Joensen and Grahl-Nielsen 2014). Investigations of specimens of redfish (*Sebastes mentella*) showed that FAPROM compared well with enzyme-electrophoresis, microsatellites and morphometrics (ICES CM 2005, Joensen and Grahl-Nielsen 2004). Depending on fatty acid profiles either generated from selected tissues rich in triacylglycerols or phospholipids, it is possible to discover phenotypic and genotypic populations, respectively (Joensen 2002).

Regarding marine mammals, research in potential effects of biotic and abiotic factors on long-term stability of the fatty acid profiles in different types of tissues is to the best of knowledge not carried out yet thoroughly. In hypothetical cases with many samples from several ecological pods foraging in the same or adjacent waters for extended periods of time, some overlap may probably occur in PC-plots.

FAPROM has been tried out on blubber of baleen whales successfully. Thus, it was possible to discriminate between two internationally recognised management stocks of minke whales in the Norwegian Sea and the North Sea by using blubber FA profiles as population markers (Olsen and Grahl-Nielsen 2003). Likewise, FA profiles in blubber of long-finned pilot whales have been utilized successfully as a marker for discrimination among populations in three large regions in the North Atlantic: the seas off the north-western Iberian Peninsula, the United Kingdom and the United States (Monteiro et al. 2015).

But to the best of knowledge, FA profiles have not been utilized earlier for pod-discrimination in one and same area as was done with the FA data from the Miðvágur-pod and Sandagerði-pod (Figure 3). The result of the unsupervised multivariate analysis revealed that one male and one female pilot whale dispatched in the village Miðvágur bore close FA resemblance to the school slain in Sandagerði (Figure 4 and 5). These two pilot whales belonged therefore most probably to the Sandagerði-pod and may have left their own school and joined the Miðvágur-pod shortly before laying their bones (i.e. died) in Sandagerði (Figure 6). Even if the results show clearcut distinction, it must be kept in mind that the low number of specimens in the present multivariate analysis is a statistical weakness. Further and future corroborating studies of the utilized and additional samples could include analysis of microsatellites and/or single nucleotide polymorphisms, SNPs.

Pedigree structure - Fission-Fusion-Societies

A lot of research has been carried out on the social life of long-finned pilot whales. Genealogical analysis of pilot whale pods which laid their bones (i.e. died) in the Faroe Islands showed that several generations of maternally related males and females constituted the school, and that breeding within the school did not occur (Amos et al. 1993a, 1993b; Fullard 2000). Research has also shown that the cetacean bulls do not stay put in the native school through their entire life but visit or merge with other passing pods for breeding purposes or they join large transient fusion-societies of pilot whales sometimes observed out at sea (Amos et al. 1991). The social structure of long-finned pilot whales can generally be described as complex dynamic clusters of labile large groups composed of more stable small groups. In these fission-fusion societies long-term stable subgroups may unite in large labile short-term supergroups followed by breakup (Augusto et al. 2017). The average size of whale pods frequenting Faroese shores is approximately 135 animals, according to (1709-2016) official statistics (www.hagstova.fo). Accurate observations and analysis of social units of free-swimming long-finned pilot whales in Canada showed a more nuanced picture and revealed short-term associations of 3 to 135 animals over hours and days and long-term association of 11 to 12 animals over years (Ottensmeyer and Whitehead 2003).

Aggregations and fragmentations - driving forces

The driving forces behind large aggregations and subsequent fragmentations are many and could be feeding opportunities and/or mating urgency (de Stephanie et al. 2008) as well as competition and aggression between various matrilineal social groups. Moreover, intermale competitive fighting and pecking order harassment such as mobbing of smaller and younger whales by larger whales (Bloch 1994) could also be some of the many social factors driving individuals from pod to pod. Actually, cetacean aggression has been observed in nature, where eyewitnesses have registered a fully grown mature male long-finned pilot whale been chased and driven off by three adult females (Robson 1984).

Prominent fatty acids

The FAs, which occurred in highest proportions in the Miðvágur-pod and the Sandagerði-pod were palmitic acid 16:0 (10 and 9 g FA/100 g blubber), palmitoleic acid 16:1ω7 (11 g FA/100 g blubber) and oleic acid 18:1ω9 (28 and 24 g FA/100 g blubber), respectively (Table 1). These FAs are endogenous and can be synthesized by marine mammals generally (Guerrero and Rogers 2017). By utilization of principal component analysis (PCA), Dr. Andrea Walters (2005) showed that the mentioned three FAs had the highest discriminative power to distinguish significantly between juveniles and adult pilot whales (Walters 2005). The same result was not possible to reach by subjecting the present data material to PCA or bivariate analysis (calculations not shown). Maybe the age and maturity difference between the whales analysed in the Miðvágur-pod and the Sandagerði-pod was too small to detect the discriminatory power of the three FAs mentioned. Based on length, the whales were probably all mature (Bloch et al. 1993c), since the shortest and the longest whales were 350 cm and 569 cm long, respectively.

It is not always possible to compare the obtained results properly with FA data found in literature. This is due to various biotic and abiotic factors, differing sampling seasons and different sampling sites on the whale carcasses, varying number and kind of FAs included and presented, and lastly dissimilar units. A plain comparative evaluation shows though that the sum of long chain monounsaturated FAs, ΣLCMUFA: (55 ± 8) (g FA/100 g blubber) and (56 ± 6) (g FA/100 g blubber) from the Miðvágur-pod and the Sandagerði-pod in the Faroe Islands, respectively, (Table 1), are similar to the corresponding results, ΣLCMUFA: (53 ± 4) %, achieved from long-finned pilot whale blubber in Tasmania (Walters 2005), and the following ΣLCMUFA results: (50 ± 8) %, (59 ± 5) % and 57 ± 6) % from Nortwestern Iberian Peninsula, United Kingdom and United States of America, respectively (Monteiro et al. 2015). However, an equivalent comparison of the sums of polyunsaturated FAs, ΣLCPUFA, showed significant differences: (10 ± 3) (g FA/100 g blubber) and (9 ± 2) (g FA/100 g blubber) (Table 1) versus (6 ± 2) % (Walters 2005), and (24 ± 9) %, (18 ± 5) % and (21 ± 6) % (Monteiro et al. 2015).

Healthy nutrients

The increasing obesity prevalence more or less world-wide has contributed to a range of health-related problems and diseases including sleep disorders, hypertension, dyslipidaemia, type 2 diabetes and cardiovascular diseases (Powell-Wiley et al. 2021). Well known are the many studies of long chain polyunsaturated FAs (LCPUFA) – especially eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) (Nettleton 1995). Together with aspirin these have shown beneficial effects in preventing cardiovascular diseases (Wang et al. 2021). Until recently, however, little focus has been on the long-chain monounsaturated FAs (LCMUFA), i. e. 20:1, 22:1, and their preventive and restorative health effects.

The results of the conducted FA analysis of blubber of long-finned pilot whales in the summer season show noticeable occurrences of LCMUFA, with aliphatic tails longer than 18 C atoms. The absolute amount of 20:1 and 22:1 is approximately 8 and 6 (g/100g blubber), respectively (Table 1). The mentioned LCMUFA encompass 20:1ω9 (gondoic acid; (11Z)-icos-11-enoic acid), 20:1ω11 (gadoleic acid; (9Z)-icos-9-enoic acid), 22:1ω9 (erucic acid; (13Z)-docos-13-enoic acid) and 22: 1ω11 (cetoleic acid; (11Z)-docos-11-enoic acid).

Several prophylactic and curative results have been demonstrated in animals administered LCMUFA. The mentioned LCMUFAs, 20:1 and 22:1, were tested as food supplement on mice. The results showed a number of health improving effects, like increased insulin resistance and lowered blood lipids, mainly due changed expressions of relevant genes linked to the glucose-lipid metabolism as well as inflammation (Yang et al. 2011c), improved obesity associated metabolic dysfunction in comparison with a well-defined reference diet (Yang et al. 2013), attenuation of atherosclerosis (Yang et al. 2017a), and a cardio protective effect (Yang et al. 2017b).

Affirmative and conclusive health improvements have also been confirmed in humans. In an experiment conducted as a double-blind, randomized, crossover clinical trial for several weeks the result showed that supplementation with saury oil, rich in LCMUFA (20:1 and 22:1), reduced low-density lipoprotein (LDL) particle counts, plasma triacylglycerol (TG) levels, TG-rich lipoprotein (LP) particle counts and, moreover, increased high density lipoprotein cholesterol (HDL-C) effluence capability compared with reference control oil (Yang et al. 2020).

Conclusion

Analysis of FAs in blubber of long-finned pilot whale during the summer season showed that blubber contains mainly oleic acid (18:1ω9), palmitoleic acid (16:1ω7), palmitic acid (16:0) and noticeable amounts of nutritious, beneficial and healthy long chain monounsaturated FAs such as gondoic acid (20:1ω9), gadoleic acid (20:1ω11) and cetoleic acid (22: 1ω11). Furthermore, the multivariate study demonstrated that the FA profile can be utilized as a potential marker for discrimination among different whale pods in local areas.

Finally, a summary of the social, cultural, and economic importance of meat and bubber shows that non-commercial whaling and sustainable utilization of local food resources is deeply rooted in the Faroese national mind.

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