

THE EFFECT OF THE ADDITION OF VARIOUS FATS TO THE DIET OF WEANED PIGLETS ON SELECTED METABOLIC INDICATORS AND THE STRUCTURE OF THEIR DIGESTIVE TRACT

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Abstract

The study aim was to evaluate the effect of different dietary fats on gastrointestinal structure, and blood profile in weaned piglets. The study involved 42-day-old male piglets of synthetic line 990, weaned at 28 days of age, divided into 3 groups (n=6): control group fed a standard feed for weaned piglets, as well as LO and PO+L groups fed the same feed but supplemented with 10% of linseed oil or fractionated palm oil with lecithin, respectively. 21-day dietary supplementation of piglets with these fats did not show a significant effect on the final body weight of animals and ADFI and ADG throughout the experimental period compared to the control group ($P>0.05$). Statistically significant differences were demonstrated for FCR, which was significantly lower in both groups receiving the addition of oils compared to the control group ($P\leq 0.05$). In the case of the blood lipid profile, a statistically significant increase in TG concentration was found in the OP+F group compared to the control group ($P\leq 0.05$). The concentration of total cholesterol and HDL and LDL fractions did not differ between groups ($P>0.05$). It was observed that leptin concentration was significantly lower in both groups of piglets supplemented with oils compared to the control group, but significance was demonstrated only for the OP+F group ($P\leq 0.01$). On the contrary, ghrelin concentration was higher in both the OL and OP+F groups compared to the controls, but only in the OL group this difference was statistically significant ($P\leq 0.05$). Similar levels of T3 and T4 were also recorded in all three groups of piglets, while the concentration of rT3 was significantly higher in both experimental groups compared to the control ($P\leq 0.05$). The supplementation

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with fats resulted in a highly significant reduction in all tested morphometric parameters of the small intestine compared to the control group ($P \leq 0.01$).

Key words: gastrointestinal tract development, dietary fat, metabolism, piglets, weaning

Introduction

Gastrointestinal tract (GIT) plays the key role in regulating growth and development of juvenile mammals, as it is responsible not only for nutrient metabolism, but also the main source of organism immunity (Blikslager et al., 2007; Guilloteau et al., 2010). One of critical stages of the GIT development in piglets is the post-weaning period. Stress related to being separated from mother, diet change as well as new environment results in profound changes, both in physiology, as well as microbiology and immunology of the GIT (Hampson and Kidder, 1986; Brooks et al., 2001; Pluske et al., 2018, Lauridsen, 2020). The post-weaning changes within intestines include reduced length of intestinal villi and change of their shape, crypt hyperplasia and reduction of the small intestine mass and its mucosa (Hampson and Kidder, 1986, Lallès et al., 2004; Skrzypek et al., 2005). Reduced absorption capacity of an intestine significantly impairs digestion and nutrient absorption, which unavoidably leads to reduced growth performance of the animals. This, combined with the current intensive piglet rearing system, means that high-energy diets (with increased fat content) may become a necessity (Adeola et al., 2013).

In pig nutrition, fats constitute a highly digestible energy source, the content of which is 2–3 times higher as energy in an equivalent amount of carbohydrates (Cromwell, 2006). Importantly, it was determined that increased fat uptake in a diet correlates positively with the level of fatty acid absorption in the intestine (Wang et al., 2013; Lauridsen, 2020), and 1% increase of fat in the feed should result in improved conversion ratio by about 2% (Campbell, 2005). Furthermore, fat supplementation to animal diets slows down the passage and enhances digestibility of feed ingredients, contributes to reduced dustiness, improved palatability of feed and improved stability of fat soluble vitamins: A, D, E and K (Pettigrew et al., 1991; Cromwell, 2006; Adeola et al., 2013). It should be also highlighted that fats, and particularly fatty acids are highly bioactive compounds, regulating many cellular functions (Jazurek et al., 2008; Baker et al., 2011). Essential fatty acids (EFA) can be transformed into highly active hormone-like eicosanoids (Joncova et al., 2015), and, what is more, free fatty acids are compounds capable of regulating different nuclear receptors (Miyachi et al., 2010).

However, the efficiency of fat utilization depends on numerous factors, including their source, length of carbon chain, degree of saturation and branching of the chain, as well as the period of their supplementation or emulsification level (Price et al., 2013). Linseed oil is characterized by high polyunsaturated fatty acids (PUFA) *n-3* content, including α -linolenic acid (ALA), which have significant impact on the gastrointestinal, immune, reproductive and nervous systems (Tripathi et al., 2013; Lauridsen, 2020). On the other hand, palm oil, which contains mainly long-chain saturated fatty acids (SFA), may be efficiently used as energy source (Moussavi et al., 2008). The period of the most efficient fat utilization is the 3–5 week post-weaning, which may be linked to the adaptation of the GIT to the new feed type, or different (increased) lipase activity (Lindemann et al., 1986; Adeola et al., 2013).

With regards to the above, the aim of the study was to assess the effect of supplementation of different dietary fats: linseed oil and palm oil enriched with phospholipids on the structural development of the GIT, blood profile and growth performance in weaned piglets.

Material and methods

All experimental procedures were approved by the second Local Ethical Review Committee for Animal Experiments in Cracow, Poland (approval no 80/2020) and were performed according to the approved guidelines.

Animals and study design

A total of 18 male piglets of Polish synthetic line 990 from 4 litters were used in the study. Piglets were weaned at 28 days of age. The piglets were kept in individual pens and maintained under standard housing conditions. During a two-week adaptation period, all piglets were fed with a standard starter feed mixture. Feed and water were offered *ad libitum*. On the first day of the study, the 42-day-old piglets were randomly divided into 3 groups (n = 6) that received either a standard feed mixture alone (group C, control), starter feed mixture supplemented with linseed oil (Eurolen, Poland – group LO) or starter feed mixture supplemented with fractionated palm oil with lecithin (Bergafat HTL-306, Berg and Schmidt, Germany – group PO+L). Both oils were administered at a dose of 100 g/kg of feed. Feed rations were prepared according to Nutritional Requirements of Swine (2020) and computed using WinPasze Pro (2018) software. The composition and nutritional value of feed mixtures were analyzed using the AOAC method (2000) (Tables 1 and 2). The amino acid composition was determined with the chromatographic method using the AAA400 Amino Acid Analyzer from INGOS, after hydrolysis according to the content of Asp, Thr, Ser, Glu, Pro, Gly, Ala, Val, Ile, Leu, Tyr, Phe, His, Lys, Arg, Cys, Met – Regulation of the European Commission (EC) No. 152/2009 of 27/01/2009. The analysis of phosphorus in the feed was performed using the spectrometric method in accordance with the PN-ISO 6491:2000 standard.

The determination of calcium and sodium in feed mixtures was carried out using the flame atomic absorption method according to the PN-EN ISO 6869:2002 standard. Determination of the content of calcium, copper, iron, magnesium, manganese, potassium, sodium and zinc in feed was performed according to atomic absorption spectrometry method. The fatty acid profile of the feed mixtures is presented in Table 3.

After 21 days of treatment, blood samples from jugular vein were collected and transferred immediately into lithium heparin tubes (Equimed, Poland) for biochemical analysis or into EDTA tubes for hematological analysis. Heparinized blood samples were centrifuged (3000 rpm, 10 min, 4°C) and plasma samples were stored at -80°C until further handling. Next, pigs were sacrificed by an overdose of pentobarbital sodium salt (Morbital[®], Biowet, Poland). The gastrointestinal tract was removed, and samples of stomach pylorus, pancreas, duodenum, jejunum (divided into 3 equal-length segments: proximal, middle, distal) and ileum were collected and immediately fixed in 10% neutral formalin solution. Body weight of the piglets was recorded at the beginning (day 1; 42-day-old piglets) and at the end of the study (day 21; 63-day-old piglets), individual feed intake was determined daily.

Fatty acid profile of the feed mixtures

The fatty acid profile of the feed mixtures was determined by gas chromatography according to the modified method of Folch et al. (1957), as previously described (Pieszka et al., 2015). The analysis was performed on QP2010 Plus (Shimadzu, Japan) equipped with flame ionization detector (FID) and Restec (105 m) column. Fatty acids were identified by external standards of fatty acids (Sigma-Aldrich) using Internal Standard heptadecanoic acid. Fatty acid content was expressed as percentage of total fatty acids.

Table 1. The composition of feed mixtures used in the study. Piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Component (%)/Group	C	LO	PO+L
Casein	-	12.0	12.0
Wheat	40.0	40.0	40.0
Barley	31.0	28.0	28.0
Wheat bran	2.58	2.14	2.14
Soybean meal	19.0	-	-
Milk replacer	2.00	-	-
Corn starch	-	5.00	5.00
Ground limestone	0.80	0.80	0.80
Calcium phosphate	1.10	1.10	1.10
NaCl	0.35	0.35	0.35
L-lysine	0.46	0.06	0.06
L-threonine	0.14	0.04	0.04
L-tryptophan	0.02	0.01	0.01
PP Prestarter	0.50	0.50	0.50
DL-methionine	0.05	-	-
Soybean oil	2.00	-	-
Linseed oil	-	10.0	-
Palm oil	-	-	10.0

Table 2. The nutritional value of feed mixtures used in the study. Piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Item/Group	C	LO	PO+L	Requirements ¹
Dry matter (g)	892	902	896	
Metabolic energy (MJ)	13.0	15.3	15.0	13.0
Crude fat (%)	3.44	10.5	10.2	-
Lysine (g)	12.8	11.9	11.9	12.0
Methionine + Cysteine (g)	6.90	6.88	6.78	6.40
Tryptophan (g)	2.54	2.51	2.51	2.50

Fats addition for piglets and structure of digestive tract

Threonine (g)	6.59	7.63	7.63	7.60
Crude protein (g)	180	183	183	180
Calcium (g)	7.68	7.41	7.41	7.50
Total phosphorus (g)	6.02	6.06	6.06	6.00
Sodium (g)	1.58	1.55	1.55	1.50
Crude fiber (g)	34.8	25.2	25.2	35.0

Nutritional requirements for swine (2020).

Table 3. Fatty acid profile of feed mixtures used in the study. Piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Fatty acid (%) / Group	C	LO	PO+L
C14	0.37	0.11	1.29
C16	13.4	4.82	67.3
C16-1	0.18	0.06	0.05
C18	1.69	3.61	4.62
C18-1	13.6	24.3	13.4
C18-2	59.0	19.4	11.7
C20	0.17	0.19	0.28
C18-3	7.86	45.7	1.01
c22	0.26	0.11	0.09
C20-4	0.02	0.00	0.00
C22-1	0.07	0.01	0.01
EPA	0.24	0.15	0.002
DHA	0.33	0.00	0.00
SFA	17.7	10.6	73.6
MUFA	13.8	18.1	13.4
PUFA	67.5	66.2	12.8
PUFA <i>n-6</i>	59.0	20.6	11.7
PUFA <i>n-3</i>	8.44	45.6	1.01
PUFA <i>n-6/n-3</i>	6.99	0.45	11.6

Blood biochemical parameters

In the obtained blood plasma, the concentration of glucose, triglycerides (TG), total cholesterol, high- and low-density lipoproteins (HDL/LDL), as well as alanine aminotransferase (ALT) and aspartate aminotransferase (AST) were determined using ACCENT-200 biochemical analyzer (Cormay, Poland) and dedicated colorimetric kits (Cormay, Poland), following the manufacturer's instruction. In addition, the concentration of ghrelin and leptin (Phoenix Pharmaceuticals, USA), as well as insulin and thyroid hormones: triiodothyronine (T3), thyroxine (T4) and reverse T4 (rT4) (Merck Millipore, USA) were determined by radioimmunoassay and a gamma counter LKB Wallac type 1275 (Minigamma Counter, Australia).

Gastrointestinal tract histology

For histometry studies, gastrointestinal tissues samples were routinely dehydrated in a graded series of alcohol, embedded in paraffin, cut into 4.5 μm sections using a rotary microtome (Microm 350, Germany), placed on silane-treated glass slides, and then stained with hematoxylin and eosin (Woliński et al., 2020). For pancreas the surface area of pancreatic alveoli and cells and the number of follicular cells per pancreatic vesicle were determined. For stomach mucosa thickness and muscle membrane thickness were determined. For intestinal histometry, intestinal villi length, crypt depth, mucosa thickness and thickness of the muscle membrane. For each analysis, a minimum of 15 intact slides from each individual was assessed. The analyses were performed using a light microscope (Axioskop 40, Zeiss, Germany) coupled with computer software for image analysis (Axio Vision 4.2 Release, Zeiss, Germany) and a digital camera.

Statistical analysis

All data are expressed as mean \pm standard deviation (SD). ANOVA followed by the Tukey post-hoc test or Kruskal-Wallis test followed by Dunn post-hoc test was used to indicate the statistical differences among the groups. All analyses were carried out using Prism 7 (Graph Pad Software Inc., San Diego, CA, USA). In all statistical analyses $P\leq 0.05$ was considered significant.

Results

Growth performance

The initial body weight (BW) of piglets was similar in all groups of piglets 12.9 \pm 1.60, 12.9 \pm 1.60 and 12.7 \pm 1.46 kg in C, LO, PO+L respectively, ($P>0.05$). After twenty one days of treatment, the BW of piglets increased in all groups, however did not differ significantly between the groups (Figure 1). Dietary supplementation with oils also did not affect significantly average daily gain (ADG) of piglets and average daily feed intake (ADFI), however, a numerical increase in both ADG and ADFI might be noted in groups fed with the addition of oils (Figure 1).

The statistical significance was, however, demonstrated for feed conversion ratio (FCR), which was significantly lower in both groups receiving the addition of oils compared to the control group ($P\leq 0.05$, Figure 1).

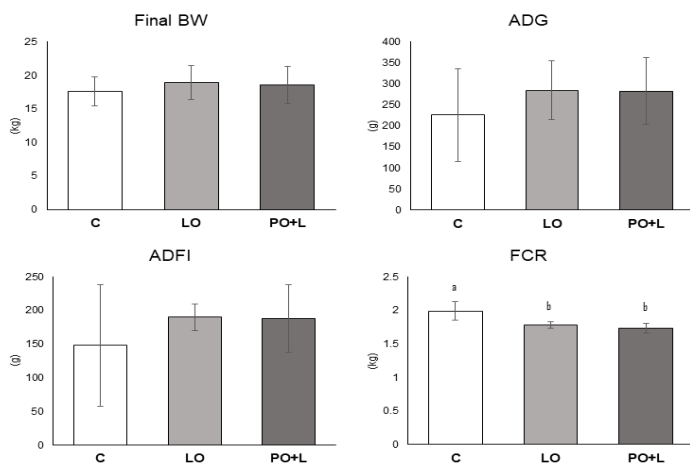


Figure 1. Effect of different dietary fats on body weight and feed intake in piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group). Values are given as means \pm SD. a,b Different letters indicate statistical significance at $P \leq 0.05$

Legend:

group C – control

group LO – linseed oil

group PO+L group – fractionated palm oil with lecithin

BW – body weight (kg)

ADG – average daily gain (g)

ADFI – average daily feed intake (g)

FCR – feed conversion factor, the amount of feed used per kilogram of animal body weight gain

Blood biochemical parameters

Pigs' blood parameters are presented in Table 4. In the case of the blood lipid profile statistically significant differences were found only for the concentration of TG, which was significantly higher in the PO+L group compared to the control group ($P \leq 0.05$). For total cholesterol and HDL, only a numerical increase was recorded in PO+L group compared to the control group, while the opposite trend was noted for LDL ($P > 0.05$, Table 4). There were also no statistically significant differences among the groups for plasma insulin and glucose levels ($P > 0.05$).

Leptin concentration was lower in both groups of piglets supplemented with oils compared to the control group, however, significance was shown only for the PO+L group ($P \leq 0.01$, Table 4). On the contrary, ghrelin concentration was higher in both LO and PO+L groups compared to the control group, but only in the LO group the difference was statistically significant ($P \leq 0.05$). The concentration of T3 and T4 hormones was similar in all three groups of piglets, while the concentration of rT3 was significantly higher in both experimental groups compared to the control ($P \leq 0.05$). In the case of liver marker enzymes, the concentration of ALT was significantly lower in the LO and PO+L groups compared to the control group ($P \leq 0.001$), while the concentration of AST was similar in all groups ($P > 0.05$, Table 4).

Table 4. Effect of different dietary fats on blood biochemical parameters in piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Parameter/Group	C ¹	LO ¹	PO+L ¹
Total cholesterol (mg/dL)	92.8±12.6	83.3±11.7	104±12.5
TG (mg/dL)	42.0±16.1 ^a	50.0±17.1 ^{ab}	113±44.1 ^b
HDL (mg/dL)	33.5±5.59	34.6 ±2.26	40.8±4.91
LDL (mg/dL)	49.8±6.22	46.9±6.01	41.0±5.29
Glucose (mg/dL)	112±14.6	113±21.9	110±11.8
Insulin (μU/mL)	15.0±1.53	13.9±2.19	13.3±0.92
Leptin (ng/mL)	5.53±0.62 ^a	4.90±0.37 ^a	3.26±0.63 ^b
Ghrelin (pg/mL)	61.0±8.50 ^a	75.6±12.6 ^b	73.3±4.58 ^{ab}
T4 (nmol/L)	39.7±7.96	38.3±6.61	30.3±5.45
T3 (nmol/L)	3.17±0.72	3.17±0.67	2.87±0.46
rT3 (nmol/L)	0.26±0.04 ^a	0.49±0.21 ^b	0.49±0.10 ^b
ALT (U/L)	67.8±9.36 ^a	33.0±6.56 ^b	31.3±5.69 ^b
AST (U/L)	77.7±13.6	69.3±15.3	76.0±6.08

¹ Values are given as means±SD.

^{a,b} Values within a row with different superscripts differ significantly at P<0.05.

Morphometric analysis of gastrointestinal tissues

The morphometric analysis of the pancreas and stomach is presented in Table 5. There was a statistically significant increase in the surface area of both the pancreatic alveoli and the pancreatic cells in LO and PO+L groups compared to the control group ($P \leq 0.05$). Additionally, in the PO+L group, the number of follicular cells was significantly lower than in the control group ($P \leq 0.05$). In the case of gastric analysis, the mucosa thickness was significantly lower in the PO+L group compared to the other two groups ($P \leq 0.01$), and also the mucosa thickness was significantly lower in the PO+L group compared to the LO group. ($P \leq 0.05$, Table 5).

Table 6 shows the results of the morphometric analysis of the small intestine of piglets. In the duodenum, there was a significant increase in the crypt depth and the mucosa thickness in the LO group, as well as a significant increase in the muscularis thickness in both groups receiving the addition of oils compared to the control group ($P \leq 0.01$). In the proximal jejunum (prox), the mucosa thickness increased significantly in both experimental groups, while the muscularis thickness was significantly smaller in the LO group compared to the other two groups ($P \leq 0.01$). In the middle jejunum, a significant increase in both the crypt depth and the mucosa and muscularis thickness was noted in the LO and PO+L groups compared to the control ($P \leq 0.01$, Table 6). On the contrary, in the distal part of the jejunum, a significant reduction in all parameters tested in both experimental groups was noted compared to the control group ($P \leq 0.01$). Additionally, in the ileum there was a significant increase in intestinal villi length in both groups of piglets supplemented with oils compared to the control group and a significant increase in muscularis thickness in PO+L groups compared to the

other two groups ($P \leq 0.01$, Table 6). Representative histological photographs of the small intestine of piglets are shown in Figure 2.

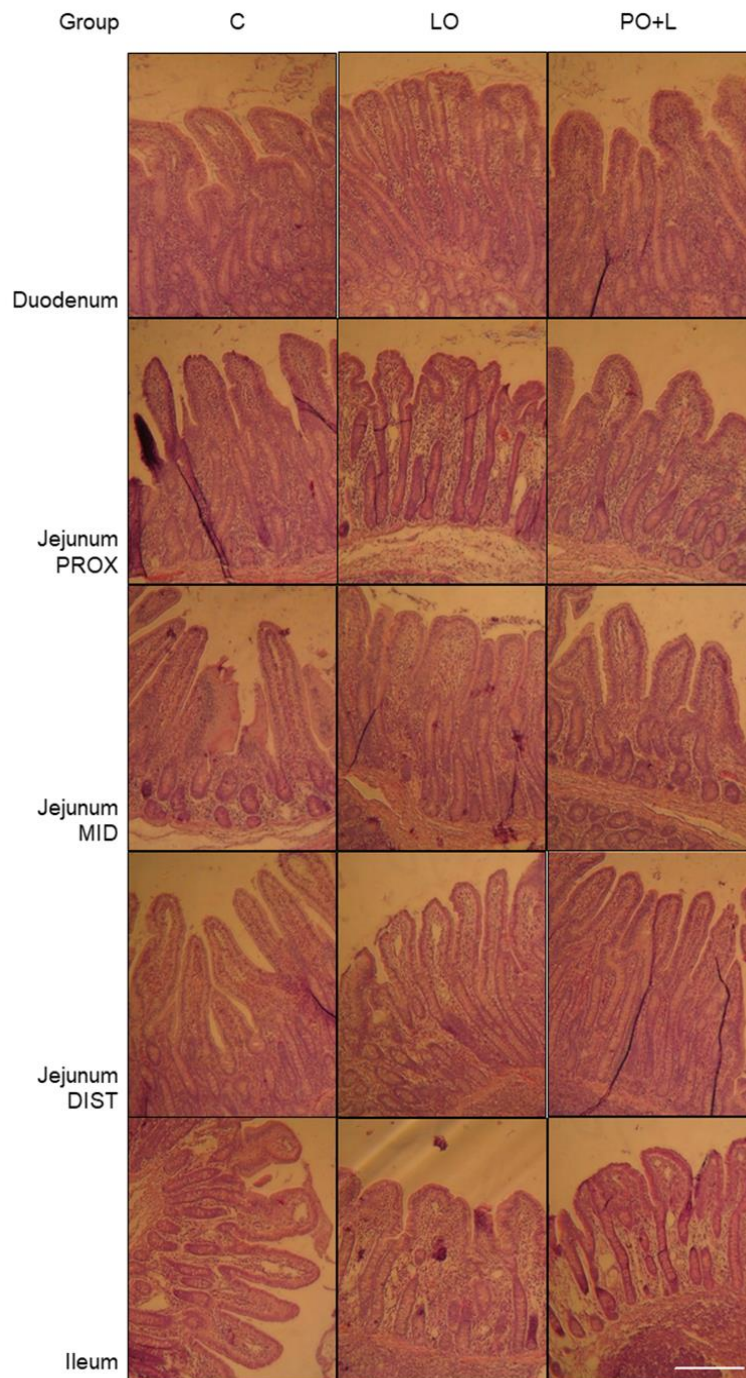


Figure 2. Representative histological photographs of hematoxylin and eosin stained sections from small intestine of piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group). Scale bar 100 μ m

Table 5. Effect of different dietary fats on histological parameters of pancreas and stomach in piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Parameter/Group	C ¹	LO ¹	PO+L ¹
Pancreas			
Surface area of pancreatic acini (mm ²)	692±202 ^a	855±226 ^b	830±271 ^b
Number of follicular cells per pancreatic acini	9.2±2.2 ^a	8.9±2.1 ^{ab}	8.0±2.6 ^b
Surface area of pancreatic cells (mm ²)	74±20 ^a	86±24 ^b	85±18 ^b
Stomach			
Mucosa thickness (µm)	596±79 ^a	609±105 ^a	536±91 ^b
Muscularis thickness (µm)	1774±448 ^{ab}	1855±408 ^a	1690±577 ^b

¹ Values are given as means±SD.

^{a,b} Values within a row with different superscripts differ significantly at P<0.05.

Table 6. Effect of different dietary fats on histological parameters of various small intestine segments in piglets fed either with a standard feed mixture alone (group C, control) or a starter feed mixture supplemented with 10% linseed oil (LO group) or 10% fractionated palm oil with lecithin (PO+L group)

Parameter/Group	C ¹	LO ¹	PO+L ¹
Duodenum			
Villi length (µm)	260±58	253±37	244±30
Crypt depth (µm)	227±70 ^a	257±50 ^a	240±46 ^{ab}
Mucosa thickness (µm)	553±125 ^a	572±57 ^b	548±65 ^a
Muscularis thickness (µm)	142±41 ^a	149±20 ^b	160±22 ^c
Proximal jejunum (prox)			
Villi length (µm)	226±58	231±33	224±38
Crypt depth (µm)	251±48	250±38	261±43
Mucosa thickness (µm)	450±74 ^a	493±69 ^b	509±63 ^c
Muscularis thickness (µm)	215±49 ^a	138±19 ^b	232±55 ^a
Middle jejunum (mid)			
Villi length (µm)	240±55	245±34	247±38
Crypt depth (µm)	193±34 ^a	234±24 ^b	212±35 ^c
Mucosa thickness (µm)	426±67 ^a	456±38 ^b	440±49 ^a
Muscularis thickness (µm)	102±24 ^a	114±25 ^b	117±22 ^b
Distal jejunum (dist)			
Villi length (µm)	324±96 ^a	234±33 ^b	234±30 ^b
Crypt depth (µm)	262±70 ^a	197±38 ^b	194±39 ^b
Mucosa thickness (µm)	602±146 ^a	370±149 ^b	422±60 ^b

Muscularis thickness (μm)	212 \pm 52 ^a	127 \pm 40 ^b	144 \pm 29 ^b
Ileum			
Villi length (μm)	215 \pm 40 ^a	230 \pm 38 ^b	224 \pm 31 ^b
Crypt depth (μm)	206 \pm 37	208 \pm 34	202 \pm 31
Mucosa thickness (μm)	416 \pm 60	435 \pm 56	429 \pm 54
Muscularis thickness (μm)	173 \pm 41 ^a	186 \pm 62 ^a	214 \pm 65 ^b

¹ Values are given as means \pm SD.

^{a,b,c} Values within a row with different superscripts differ significantly at $P < 0.05$.

Discussion

Reduced feed uptake is observed in the weaning period, which leads not only to reduced production capacity but also to a series of undesirable changes in the structure and function of the gastrointestinal tract (Pluske et al., 2018). In the presented experiment, 21-day-old piglet diet supplementation, 3 weeks post-weaning, with 10% addition of linseed oil or fractionated palm oil with phospholipids (lecithin) resulted in a statistically significant reduction of FCR as compared with control group (Figure 1). Reduced rate of intestinal food passage, increased digestibility of the remaining nutrients in the small intestine, reduced availability of net energy or a combination of these three events may be a possible cause for the enhancement of growth parameters in response to diet supplementation with fat (Pettigrew et al., 1991). Similar results were also obtained by Duran-Montgé et al. (2009), who observed reduction of FCR in slaughtering pigs fed with diet with 10% addition of lard, sunflower oil and linseed oil mix, although the same trend was not found in groups of animals receiving only one type of oil. Zhan et al. (2009) demonstrated that feeding pigs at final growth stages with a feed with 10% addition of linseed has a positive influence on growth parameters, which could be at least partially associated with the reduced inflammation. Vilarrasa et al. (2015) showed that the addition of palm oil results in significant differences in production parameters as compared with piglets fed with diet containing the same amount of soybean oil. Additionally, Duan et al. (2014) found that the highest increases of BW in pigs and lowest FCR is obtained when the feed is supplemented with PUFA *n-6/n-3* in 5:1 ratio, whereas with PUFA *n-6/n-3* ratio of 1:1 pigs were characterized by the highest muscle weight and lowest content of adipose tissue.

Furthermore, only in later rearing stages the supplementation of piglet diet with different types of oils leads to enhanced production parameters, in contrast to first two weeks after weaning (Cera et al., 1988; Howard et al., 1990; Schellingerhout et al., 2002a; Baudon et al., 2003; Jung et al., 2003; Adeola et al., 2013, Świątkiewicz et al., 2020). This phenomenon may result from the abnormal morphology of piglet intestine directly after weaning, which disables the proper absorption of nutrients, or with variable activity of pancreatic lipase (Adeola et al., 2013). Presence of an exogenous emulsifier in diet may have an additional positive effect on fat digestibility in weaned piglets (Jones et al., 1992; Xing et al., 2004; Kim et al., 2008), because weaning is accompanied by reduced secretion of bile and phospholipids, and thus reduced capacity to emulsify fat (Wang et al., 2013).

In the case of piglets' blood lipid profile, the addition of linseed oil did not result in significant changes in any of the measured parameters (Table 4), which is confirmed by the study of Schellingerhout et al. (2002a). On the other hand, many studies have provided evidence that PUFA *n-3*, including ALA, exhibit hypolipemic effect, leading to reduced total cholesterol and TG concentration in blood (Eidhin et al., 2003; Vijaimohan et al., 2006; Świątkiewicz et al., 2020). However, it should be mentioned that the majority of data

concerning the antiatherogenic properties of PUFA *n-3* originate from studies on individuals in which lipidogram exceeded physiological values, thus the biological effect of the supplementation used in the presented experiment could be limited. On the other hand, the concentration of TG in the group of piglets receiving addition of palm oil was significantly higher in comparison with control group C (Table 4). In rats, a 20% addition of palm oil also resulted in increased concentration of total cholesterol and TG as compared with individuals fed with the same amount of soybean oil (Sundram et al., 1990). Supplementation of diet with increased fat content with exogenous emulsifiers may, however, result in favorable changes in the lipid profile of the blood in weaned piglets (Jones et al., 1992).

Moreover, in the discussed experiment a significant reduction of leptin concentration was observed in the PO+L group as compared with control group. Leptin, a 'satiety hormone', regulates food intake and BW, however, its scope action is considerably broader (Friedman, 2011; Lu et al., 2015). Rats fed with diet containing about 30% fat (mainly LA and oleic acid) were also found to exhibit reduced leptin concentration in the plasma as compared with animals fed with standard, low-fat diet (Ainslie et al., 2000). On the other hand, administration of high-fat diet (60% energy from fats) containing palm oil resulted in increased leptin level in rats (Stachoń et al., 2006), which confirms the significance of the amount and type of dietary fats in regulation of metabolic response of the organism. However, the reduction of leptin concentration in the PO+L group could also be caused by the addition of lecithin, because diet supplementation with choline (whose level increases after ingestion of lecithin) in humans contributed to reduced concentration of leptin in blood (Elsawy et al., 2014).

Opposing results were obtained for ghrelin concentration, which is an antagonist of leptin, and which was significantly higher in the LO group ($P \leq 0.05$) as compared with control group. Ghrelin, the strongest orexigenic factor, causes increased food uptake, stimulates BW gain and secretion of the growth hormone, and also stimulates secretion of the gastric juice and gastric motor activities (Kojima et al., 1999). It was also demonstrated for pigs that regulation of ghrelin activity depends on the nutrition scheme and energy balance (Scrimgeour et al., 2008; Reynolds et al., 2010). The profile of fatty acids in the diet, including the length and level of saturation of the carbon chain, is significant for the regulation of ghrelin secretion, as shown by the research conducted on humans (Feltrin et al., 2006) and rats (Saidpour et al., 2012).

Changes in the concentration of leptin and ghrelin could also affect the increased feed uptake and BW gain observed in the present experiment for both experimental groups, because the reduced concentration of leptin was linked with reduced satiety, and as a consequence excessive energy consumption (Ainslie et al., 2000; Kocelak et al., 2009). What is more, intravenous administration of ghrelin to weaned piglets resulted in improved production parameters of the animals (Dong et al., 2009).

In the present study, the diet supplementation with oils did not have a significant effect on plasma concentration of insulin and glucose (Table 4). Although it has been demonstrated that the activity of the pancreas, including insulin secretion is strongly affected by the fats provided with food (López et al., 2010), the obtained results suggest that a 10% addition of fats does not impact the production and usage of glucose, and it does not result in the development of insulin resistance. Also, Duan et al. (2014) did not observe changes in the concentration of insulin in pigs fed with 3% linseed oil; similarly, Ostrowska et al. (2002) did not determine differences in plasma glucose concentration of pigs consuming 2.5% or 10% fat addition.

In the case of thyroid hormones, supplementation with selected oils resulted in a significant, almost two-fold increase of rT3 concentration as compared with control group, with concomitant absence of changes in the concentration of T3 and T4 (Table 4).

Maintenance of normal thyroid hormone levels in the blood is the key function of the hypothalamic–pituitary–adrenal axis and it is highly important for maintaining the normal rate and direction of metabolism. Despite the fact that rT3 is an inactive isomer of T3, due to the structural resemblance it can block T3 receptors and antagonize its action. In the study on slaughtering pigs, no differences in T3 and T4 concentration were found after diet supplementation with different types of fats, although the level of T3 was lower in the group receiving the addition of linseed oil in comparison with a group fed with tallow (Duran-Montgé et al., 2009). The study of Lachowicz et al. (2009) confirms that individual enzymes involved in thyroid hormone metabolism react differently to the quantitative and qualitative changes of fatty acids in the diet.

In the case of morphometric analysis of the pyloric part of the stomach, a significant reduction of the mucosa thickness was observed only in the PO+L as compared with control group and significant increase of the muscularis thickness of the LO group vs. PO+L group was observed (Table 5).

In the conducted study, no clear differences were observed in the length of the villi between individual segments of the small intestine, which is consistent with the results obtained by Pluske et al. (1996), although there is also data stating that in pigs the villi in the jejunum are longer compared to the duodenum or iliac intestine (Gancarčíková, 2012), or their length decreases with increasing distance to the stomach (Nabuurs et al., 1993; Pluske et al., 2003). The average length of villi of weaned pigs in the present experiment was smaller compared to the results obtained by other researchers (Peg et al., 2019), these discrepancies are probably due to individual variability, breed, age of pigs, intestinal section and the quantitative and qualitative composition of the diet (Redlich et al., 1997). Similar relationships also apply to the depth of the crypts: some authors found a negative correlation between the depth of the crypts and the distance from the stomach (Pluske et al., 2003), others noted the smallest crypt depth in the jejunum and the greatest in the duodenum (Gancarčíková, 2012), while others were unable to confirm any regularity (Pluske et al., 1996). In the present experiment, the crypts were deepest in the duodenum and shallowest in the iliac intestine, which may confirm that the rate of enterocyte proliferation and shedding is highest in the initial section of the small intestine. Via their impact on the receptors in the small intestine, fats provided with diet can cause inhibition of stomach emptying, prolonging its distention and regulating the rate at which nutrients reach the small intestine (Hunt and Knox, 1968; Warzecha et al., 2006). In addition, presence of fat in the GIT modulates the secretion of numerous gastrointestinal hormones known not only for affecting the rate of food transit, but also the trophic effect on the gastrointestinal mucosa, including cholecystokinin, prostaglandins, pancreatic polypeptide, gastrin, insulin, ghrelin, leptin and many others (Wong and Wright, 1999; Dembiński et al., 2004; Little et al., 2007). Considering that secretion of gastrointestinal hormones largely depends on the chemical structure of individual fats (Karhunen et al., 2008; Rasoamanana et al., 2012), perhaps the different effect of palm oil and linseed oil is linked to a different hormonal response.

Changes observed in pancreas morphometry, such as significant increase of the pancreatic cell surface area, or increase of pancreatic islet surface area in groups supplemented with oils may in turn indicate increased extrasecretory secretion of pancreas, and thus its adaptation to the type of food consumed (Table 5). Nutrients, via regulating the release of intestinal hormones and affecting the brain–gut axis have significant impact on the quality and amount of pancreatic fluid secreted (Jakob et al., 2000). It has been demonstrated that the intrainestinal infusion of oils rich in medium and long chain fatty acids leads to increased concentration of cholecystokinin in growing pigs, which in turn may stimulate changes in the extrasecretory action of pancreas, and this effect depends on the length of the carbon chain and the profile of fatty acids of the oils used (Jakob et al., 2000).

Weaning of piglets, particularly in the present intensive rearing system has a profound impact also on the morphology of the small intestine mucosa. Significant increase in the mucosa thickness in LO group vs. control group in the duodenum (Table 6), may suggest elevated intensity of cell proliferation within the mucosa or reduced apoptosis intensity. Proliferation of the intestinal mucosa, similarly to stomach, is also modulated by hormonal signals, peptides and growth factors secreted in the GIT (Wong and Wright, 1999; Little et al., 2007; Rao and Wang, 2010; Yang et al., 2013), and these peptides are strongly affected by dietary fatty acids (Sagher et al., 1991).

The observed increase of the mucosa thickness in both groups supplemented with oils in the proximal jejunum (prox) (Table 6) may be the result of elevated extrasecretory secretion of the pancreas. Research conducted on rodents provided evidence that this segment of the jejunum, reduced flow of pancreatic fluid and has led to villous atrophy (Balas et al., 1980). Furthermore, study on newly born piglets has shown that supplementation of diet with pancreatic enzymes stimulates the growth of the small intestine (Słupecka et al., 2012).

Similarly, in the middle jejunum (mid) no differences in the villi length were found (Table 6). However, it should be emphasized that the morphometric analysis was performed on tissues collected from piglets at the age of 63 days, 5 weeks after weaning, when the villi are fully developed and do not undergo such intense changes. Gu et al. (2002) demonstrated that beginning from day 36 of piglet age the villi in the duodenum, jejunum and ileum remain unchanged. Villi elongation typically occurs within 7–14 days post weaning, however, they remain shorter than prior to weaning (Cera et al., 1988). No differences in the length of the villi in response to the diet used could suggest that the absorption capacity of the intestine was also unchanged, but it should be noted that to determine this parameter, it is necessary to take into account the diameter of the villi and their shape due to their polymorphic appearance (Wiese et al., 2003).

In this growth phase, however, changes in the intestinal crypt depth are still observed, which are deepening even after the 7 week of life of piglets (Gu et al., 2002). A similar effect was also observed in this experiment, where in the middle section of the jejunum intestinal crypts were significantly deeper in both groups supplemented with oil compared to control group. This section of the small intestine is the main and most important place of hydrolysis and absorption of nutrients, where digestive and absorption processes are most intensive (Goodman, 2010). Therefore, the increase in cell proliferation in crypts and an increase in absorption surface in this section of the intestine is particularly important for optimizing the metabolism of nutrients and animal growth. The observed results may also stem from the aforementioned effect of gastrointestinal hormones. It should be added that lecithin can also support the structural reconstruction of the intestine (Mitchothai et al., 2010).

In turn, the morphometric analysis of the distal section of the jejunum was the only to show a drop in the length of the villi and the depth of crypts, and thus the mucosa thickness in groups of oils supplemented piglets compared to the control group (Table 6). However, it should be mentioned that in this part of the intestine processes of digestion and absorption of nutrients are no longer as intense, and the amount of bile salts and pancreatic enzymes secreted is significantly reduced, and all these factors may affect the local intestinal morphology variability (Lallès et al., 2004). Perhaps these results are linked to the microflora residing in the distal sections of the GIT and its activity in response to the differing diet composition and fiber content (Pluske et al., 1997). The increase in the villi length in groups supplied with oils in the last analyzed section, ileum, can also be related to differences in the quantitative and qualitative composition of intestinal microbiome (Martinez-Guryn et al., 2018) (Table 6). The recorded increased villi length could also be a specific mechanism compensating to reduce the absorption surface in the distal section of the jejunum (Piva et al., 2008).

Although there are few reports on the influence of exogenous lipids on intestinal mucosa in piglets, available data suggest that the effect of dietary fats is strongly dependent on the type and time of supplementation, as is the case for production parameters. Diet supplementation with oils in the direct post-weaning period resulted in an unfavorable effect on the intestinal epithelium (Cera et al., 1988), or it had no effect on the small intestine morphology (Schellingerhout et al., 2002b). Li et al. (1990) showed that the addition of soy oil or coconut oil into a diet of a piglet leads to the atrophy of the villi, however, the use of mixes of both oils, on the contrary, leads to an increase in their length. Price et al. (2013) reported a beneficial effect on the crypt depth in piglets supplemented with various types of fats that were administered in liquid form compared to dry diet. On the other hand, in the experiment of Jonecova et al. (2015), in which piglets were fed from 10 days before weaning to 21 days after weaning with the addition of linseed oil, a significant increase in the depth of the intestinal crypt was recorded on the day of weaning compared to the group receiving the same amount of sunflower oil.

Unfortunately there is absence of data on the influence of various types of fats on the morphometry of the GIT in piglets in a later post-weaning period, when the lipase activity increases and as shown in the present study, they may preferably affect the structure and physiology of the GIT. However, it should also be noted that most of the cited studies concern the impact of fats only on the middle part of jejunum, as the data differentiating their impact in individual intestinal fragments are also not available. It would be also interesting to conduct research enabling the determination whether the obtained effect would remain constant in further rearing stages, which could be significant also from the standpoint of breeding economy.

Conclusion

The data obtained in this experiment confirm the hypothesis that dietary supplementation of weaned piglets with linseed oil or fractionated palm oil with the addition of lecithin, starting from the 3rd week after weaning in an amount of 10% of the feed ration, may cause changes in metabolism that are beneficial from the point of view of productivity, leading to an increase in body weight, and a decrease in the FCR rate.

The body's metabolic response is highly dependent on the profile and structure of individual fatty acids in the diet, including the length and degree of saturation of the carbon chain, which may differently affect the blood lipid profile and the activity of hormones involved in the regulation of energy homeostasis, including leptin, ghrelin, insulin or thyroid hormones. Increasing the recommended fat content in the diet of weaned piglets does not cause inflammatory reactions in the body, as evidenced by the lack of increase in the values of cellular immunity parameters in the blood.

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WPLYW DODATKU RÓŻNYCH TŁUSZCZÓW DO DIETY ODSADZONYCH PROSIĄT NA WYBRANE WSKAŹNIKI METABOLICZNE ORAZ STRUKTURĘ ICH PRZEWODU POKARMOWEGO

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STRESZCZENIE

Celem niniejszej pracy była ocena wpływu różnych tłuszczów w diecie na strukturę przewodu pokarmowego i profil krwi u prosiąt odsadzonych od matki. Badaniami objęto 42-dniowe prosięta syntetyczne linii 990, odsadzone w 28. dniu życia, podzielone na 3 grupy (n=6): grupa kontrolna karmiona była standardową paszą dla prosiąt po odsadzeniu, natomiast grupy LO i PO+L karmione były tą samą paszą, ale uzupełnioną odpowiednio 10% olejem lnianym lub frakcjonowanym olejem palmowym z lecytyną. 21-dniowa suplementacja diety prosiąt tymi tłuszczami nie wykazała istotnego wpływu na końcową masę ciała zwierząt oraz ADFI i ADG w całym okresie doświadczenia w porównaniu z grupą kontrolną ($P>0,05$). Wykazano istotne statystycznie różnice dla FCR, który był istotnie niższy w obu grupach otrzymujących dodatek olejów w porównaniu z grupą kontrolną ($P\leq 0,05$). W przypadku profilu lipidowego krwi stwierdzono istotny statystycznie wzrost stężenia TG w grupie OP+F w porównaniu z grupą kontrolną ($P\leq 0,05$). Stężenie cholesterolu całkowitego oraz frakcji HDL i LDL nie różniło się pomiędzy grupami ($P>0,05$). Zaobserwowano, że stężenie leptyny było istotnie niższe w obu grupach prosiąt suplementowanych olejami w porównaniu z grupą kontrolną, przy czym istotność wykazano jedynie dla grupy OP+F ($P\leq 0,01$). Przeciwnie, stężenie greliny było wyższe zarówno w grupie OL, jak i OP+F w porównaniu z grupą kontrolną, ale tylko w grupie OL różnica ta była istotna statystycznie ($P\leq 0,05$). Podobne poziomy T3 i T4 odnotowano we wszystkich trzech grupach prosiąt, natomiast stężenie rT3 było istotnie wyższe w obu grupach doświadczalnych w porównaniu z grupą kontrolną ($P\leq 0,05$). Suplementacja tłuszczami spowodowała wysoce istotne obniżenie wszystkich badanych parametrów morfometrycznych jelita cienkiego w porównaniu z grupą kontrolną ($P\leq 0,01$).

Słowa kluczowe: rozwój przewodu pokarmowego, tłuszcz w diecie, metabolizm, prosięta, odsadzanie