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SYMPOSIUM ON 'QUANTITATIVE ASPECTS OF PIG NUTRITION'

The development of digestive function in the pig

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The newborn piglet has a digestive system which is well adapted to a diet of its own dam's milk, indeed if a sow has a plentiful supply of milk it is very difficult to interest her piglets in any alternative food, certainly for the 1st 1–2 weeks of life. Little supplementary food is actually eaten to start with. The piglets sniff the food, nuzzle it and taste it. Food that has been in the pen for some hours does not attract piglets and regular replacement of stale food with fresh is necessary if it is hoped to encourage piglets to learn to eat dry food. Some litters show much more interest than others, but by 21 d of age most will be eating appreciable amounts of supplementary food if one has persevered with the presentation of fresh food each day for the previous 10–14 d.

For trouble-free rearing of piglets it is desirable to provide supplementary diets which are suited to the digestive capacity of the piglet. To formulate such diets efficiently we need to know as much as possible about the efficiency of the piglet's digestive system and of any changes in digestive capacity which occur as it gets older. Studies of the reactions of artificially-reared piglets to various combinations of feeds have been valuable in showing up unsuitable ingredients, since such feeds will depress growth or cause scouring and, perhaps, even kill the piglet. Another approach is to study the digestive organs of pigs of various ages and compare histological development, or levels of enzymes and other digestive secretions produced. One can either slaughter the animal for study of the digestive tract, or the digestive system can be cannulated for continuous study of the process of digestion. Another useful way of studying the efficiency of a particular digestive process is to measure the rate of appearance of digestive products in the blood.

Conventional digestibility trials have also been valuable in showing up deficiencies in the digestive capacity of the piglet and in demonstrating some of the changes which take place as pigs mature in the over-all efficiency with which particular components are digested. For example, studies of the digestibility of fat by baby pigs have shown that artificially-reared pigs develop an increasing ability to digest fat as they become older (Cunningham & Brisson, 1955).

The naturally-reared piglet appears to have little difficulty in digesting its mother's milk, which is very rich in fat (420 g fat/kg dry matter) (Braude, 1964). This being so, why do we encounter problems in rearing pigs artificially on high-fat diets? There are various reasons. The suckled piglet gets its food in regular, small meals every hour of the day and night (Barber, Braude & Mitchell, 1955). Also, the fat in sow's milk is very finely divided (Whittlestone, 1952) compared with that in cow's milk (Whittlestone, 1954) so the suckled piglet is presented with fat in a form which facilitates digestion and absorption. The milk fat is well-digested as a rule. Frobish, Hays, Speer & Ewan (1967) found that the digestibility of sow's milk fat by 2-d-old pigs was 0·95. However, fairly regularly, we do see a condition in sow-reared pigs which we call white scours, often at about 2–3 weeks of age. Mouwen, Schotman, Wensing & Kijkuit (1972) have shown this to be a steatorrhoea due, apparently, to a disturbance of fat absorption. It merits further study since, although it does not appear to have a very serious effect on the piglet, its regular occurrence requires explanation.

Development of digestive function

As the pig gets older its digestive capacity, in all respects except one, gradually increases. The exception is the level of lactase (β-galactosidase; *EC* 3.2.1.23) in the intestinal mucosa, which decreases with advancing age. Previous work on lactase was reviewed by Manners & Stevens (1972). In that paper we presented results on the distribution of the enzyme along the mucosa of the small intestine of the pig at various ages from birth to maturity and we found that the sites of production of the enzyme contract as pigs grow older, the more distal parts of the intestine losing their activity first. More recently Dr D. E. Kidder and I have investigated the distribution of this enzyme along the small intestine more fully (Kidder & Manners, 1976).

Most other aspects of digestive capacity show considerable development as pigs grow older. Earlier reviews of digestive development are those by Lucas & Lodge (1961), Braude (1964), Manners (1970), Aumaitre (1971) and Kidder & Manners (1973). Within the limits of the present paper it will only be possible to summarize the changes which occur and only a selection of papers will be quoted to illustrate the changes.

The stomach, which was studied very comprehensively by Kvasnitskii (1951), shows increases in the volume and the acidity of secretion with age. Increasing amounts of pepsin (*EC* 3.4.23.1) are produced as pigs get older (Lewis, Hartman, Liu, Baker & Catron, 1957) and the full activation of pepsin by hydrochloric acid has to await the production of sufficient acid to overcome the buffering power of the stomach contents (see Manners, 1970). Sow's milk coagulates quickly and a soft curd is produced despite the low level of rennin (*EC* 3.4.23.4) present in the piglet's stomach wall (Hoynes & Fox, 1975).

In the small intestine, sucrase (glucosidosucrase; *EC* 3.2.1.20) and trehalase (*EC* 3.2.1.28) are not found in newborn pigs (Dahlqvist, 1961). The levels of both of these enzymes in the mucosa increase throughout much of the life of the pig (Kidder & Manners, 1976). Maltase (α-glucosidase; *EC* 3.2.1.20) levels are low at birth, increase from birth to 56 d and then decline somewhat (Tacu & Bianu, 1974*a*). The volume of bile found by Walker (1959) in the gall-bladder of sow-reared pigs increased slowly with increasing body-weight until pigs reached about 6 or 7 kg: above this body-weight the volume increased more rapidly. The volume of secretion from the pancreas increases with age from 500 ml/d at 5–6 weeks to over 8 l/d at 7–8 months (Kvasnitskii, 1951). Also, Kvasnitskii (1951) found a sharper response to feeding in the older pigs. Levels in pancreatic tissue of the four enzymes lipase (*EC* 3.1.1.3), α-amylase (*EC* 3.2.1.1), chymotrypsin (*EC* 3.4.21.1) and trypsin (*EC* 3.4.21.4) increase very considerably over the 1st 2 months of life (Aumaitre, 1971).

Fermentation in the gut of the pig

The proportions of the major end-products of fermentation differ in the very young pig from those in older pigs. Friend, Cunningham & Nicholson (1963) measured the changes in concentration of organic acids in the alimentary tract of pigs from 1 to 9 weeks of age. At the end of the 1st week of life the concentration of organic acids in the stomach and small intestine of the piglets was slightly less than that in the caecum and colon. As the pigs got older the levels in the stomach and small intestine tended to decrease while the levels in the caecum and colon increased. By 9 weeks of age levels of organic acids in the caecum and colon were about five times those in the stomach and small intestine.

Lactic acid formed a large proportion of the organic acid found in the stomach and small intestine throughout the 1st 9 weeks of life, although after supplementary feeding had begun the level of lactic acid in the stomach contents was less than when the piglets' diet consisted solely of milk. In the caecum and colon, lactic acid formed only a small fraction of the organic acids in the gut contents. The questions that arise when we consider the relevance of fermentation to the well-being and to the energy supply of the pig are those put by Cranwell (1968). Do pigs utilize the products of fermentation efficiently? If so, which do they utilize most efficiently? Does the ability of the pig to utilize fermentation products change with age? The quantities of fermentation products in the gut at any one time, as Cranwell (1968) pointed out, represent the difference between the amount produced and the amount absorbed. That metabolized by the gut wall and by bacteria must also be taken into account. It has proved difficult to quantify the importance of fermentation to the pig and it will be some time before we can even say whether we should encourage or discourage different types of fermentation. In slaughter experiments, the levels of organic acids found in the gut depend on the length of time elapsing between feeding and slaughter, as was shown by Argenzio & Southworth (1974), and, of course, the composition of the diets used will influence the results obtained.

Further studies of the fermentations which occur in the gut of both naturally and artificially-reared piglets would probably help us to understand better why our attempts to rear piglets away from the sow are often unsuccessful. For basic studies it would seem to me to be desirable not to include antibiotics in the diets.

pH in the gut of the pig

pH in the stomach. There is a great difference between the pH in the stomach of a piglet and that in the stomach of an adult pig. In the very young pig pH in the stomach remains close to that of the diet, even in the outer layers of the food mass, whereas in the adult, pH falls rapidly to the region of pH 2 in the outer layers. In the mature pig the high acidity of the contents of the stomach will prevent rapid bacterial multiplication but, in the piglet, pH in the stomach is such that bacteria can multiply fairly freely. There is very little that we can do to accelerate the gradual fall in stomach pH which occurs as piglets grow older. Both sows' milk and milk-substitute diets for piglets have very considerable acid-buffering power and this means that the HCl which is secreted is neutralized by the stomach contents, leaving no free acidity in the stomach. In our own studies we did not find low pH values in the contents of the stomach of pigs of less than 7 weeks of age (Manners, 1970). Kvasnitskii (1951), in very detailed studies of gastric acid production, found that acidity of gastric juice only approached that found in adult pigs when pigs reached 8–10 weeks of age. Certainly, there is a very long period during which the contents of the stomach of the young pig are insufficiently acid to inhibit bacterial multiplication, to say nothing of the effect of HCl on the activation of pepsinogen. I would say that the main practical result of the lack of gastric acidity is the susceptibility of the young piglet to outbreaks of gastrointestinal disease, especially under artificial rearing systems where piglets take in large amounts of food and thus swamp the acid-secreting power of their stomachs.

Schulman (1973) found that gastric pH in pigs weaned at 4, 5 and 6 weeks of age was higher, on average, than that in suckled piglets given the same feed, and gastric pH changes were less pronounced in the weaned piglets. He concluded that these differences would improve the growth conditions for coliform organisms in the stomach of weaned pigs.

Cereal-based diets, fed later in the life of the pig or used for piglets weaned at later ages, have lower acid-buffering power than milk-substitute diets (Manners, 1970) and this may be another practical reason why later weaning is attended by fewer digestive disturbances than early weaning onto milk-substitute diets.

Recently, Cranwell & Titchen (1974) have shown that HCl is secreted by the stomach of the suckled pig from a very early age, in contrast to the earlier report by Cranwell, Noakes & Hill (1968) that HCl secretion by the stomach of very young piglets was found only when the animals were kept in a clean environment. Cranwell & Titchen (1974) suggested that previous failures to detect acid-secretory capacity in piglets may have reflected a loss of capacity to secrete, rather than a failure to develop this capacity.

pH in the intestine. There is not a great deal of information on pH in the intestine of pigs, but that which does exist indicates that, in the small intestine of

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artificially-reared pigs, pH may be lower than that in sow-reared pigs and may restrict the activity of certain digestive enzymes (see Manners, 1970). It is possible that the few results so far available (Hartman, Hays, Baker, Neagle & Catron, 1961; Manners, 1970) are not typical of artificial diets in general. Further measurements on a wide variety of artificial diets would be valuable to show whether there is a general tendency for gut pH to be different in pigs given artificial diets from that in suckled pigs. The low pH levels found in the small intestine of artificially-reared pigs are closer to the pH optimums of carbohydrases than to the higher values required for optimum activity of proteases and lipase (see Manners, 1970). This could help to explain why carbohydrates generally form more useful energy sources than fats in artificial diets for very early weaning of pigs.

Possible deleterious effects of early weaning on the digestive capacity of the piglet

In my review of 1970 (Manners, 1970) I drew attention to the fact that Hartman *et al.* (1961) had found that piglets weaned at 7 d of age had shown a depression in pancreatic lipase and proteinase activity in the postweaning period compared with sow-reared piglets. This study by Hartman *et al.* (1961) is one of the few in which enzyme levels in both sow-reared and artificially-reared piglets have been compared. Very recently Tacu & Bianu (1974*a*, *b*) have found a similar situation with regard to certain carbohydrases. They found pancreatic amylase activity to be depressed in the 1st week after 7 d weaning and intestinal maltase activity was also depressed by 7 d weaning; 2 weeks after weaning the intestinal maltase levels returned to normal. Pancreatic maltase levels of 7 d-weaned pigs were not depressed at 14 d but in three groups of pigs slaughtered at 21 d of age the total levels of maltase activity in the pancreas were 9·5, 16·7 and 21·5 units for pigs weaned at 7, 14 and 21 d respectively.

These results indicate that one must be prepared for some derangement of digestive processes in the period following weaning and one must not assume that the normal processes of digestive development, as found in experiments where sow-reared pigs are studied, will proceed unhindered in early-weaned pigs. It emphasizes the need for further simultaneous studies in sow-reared and artificially-reared litter-mates.

Variation between pigs in digestive capacity

Another very important factor in relation to the likelihood of success in imposing particular feeding regimens on young pigs is the individual variation in digestive capacity that exists. Pigs develop at different rates and if, in a group, there are animals with poorly developed digestive capacities, these animals could be the ones which fall behind in growth and, perhaps, begin to scour. Just to give one example, my colleague J. A. Stevens and I found great differences in the levels of the enzyme sucrase in the mucosa of individual pigs in the 1st, 2nd, 3rd and 4th weeks of life. The level of the enzyme was tending to build up over this period, but some pigs at each of the four successive slaughter ages showed low levels. These are the individuals which would be likely to suffer if presented with a diet in which sucrose forms too large a proportion.

We have to aim to provide a feed which will be digestible by the least efficient animal in a group, based upon a knowledge of the normal variability in digestive capacity which exists. Also, it would be useful to know if there are breed variations in digestive capacity.

At present we are not in a position to say how likely it is that a pig of a certain age will have the capacity to digest this or that food. Some of the information which would enable us to make such predictions does exist but, in many instances, there just are not enough data. If we could make such predictions accurately we could design diets on which piglets could be reared artificially with a very high expectation of success.

We need to be clear about the size of sample of animals that need to be studied before reasonably accurate predictions can be made about likely digestive capacity at a certain age or body-weight in a particular breed. We should also consider the possibility that selective breeding for economy of food conversion may be changing the digestive physiology of the pig in some way. Are more efficient pigs ones in which the digestive system matures faster, or in which particular facets of the digestive process either mature faster or reach higher levels of digestive capacity? We should try to find out what happens when we select for improved economy of food conversion. Little work has been done on this topic and yet the material for study is available, virtually free of charge, all over the world in performance-testing stations.

Conclusion

The regular supply of highly digestible milk in small feeds suits the piglets' immature digestive system. In artificial rearing systems it has proved technically very difficult to duplicate the provision of an individual supply of hygienic and warm milk at regular intervals. Milks often become contaminated with micro-organisms in heated reservoirs. Dispensing apparatus tends to be very expensive and, even so, may be erratic in performance. In other words, it has proved almost impossible to provide a mechanical substitute for the sow which is as reliable and at the same time is economically competitive. This is not surprising when one considers how long it has taken for the sow to evolve. Also, there is a complex behavioural relationship between the sow and her offspring which ensures that each piglet gets a reasonable share of whatever milk is available. Overfeeding, one of the bugbears of artificial rearing systems, is almost impossible in natural piglet rearing because of the mechanics of the suckling process.

It has often been shown that it is possible to rear piglets fed artificially twice per d (compared with the twenty-four-times-daily feeding of the naturally-reared piglet). One can even use cold milk successfully, rather than milk at body temperature. However, large feeds, and particularly large cold feeds, are bound to be stressful. Piglets will eat dry food, especially if it is in the form of small pellets, and one advantage of this method of provision of food is that overeating is unlikely when solid food is given. However, again, there is a stress because before learning of necessity to eat solid food a piglet has to undergo a period of starvation and the latter is unlikely to be physiologically desirable.

In view of the steady maturation of the digestive system which occurs in the 1st 2 months of a piglet's life, it is clear that the earlier we try to wean pigs, the more trouble we must take to provide a highly digestible diet and to keep the piglets in hygienic surroundings. Because so many facets of digestive function are maturing at the same time, it is difficult to say which developments in particular are most important in relation to the increasing ease of weaning which one notices as pigs get older. The popularity of 5–6 week weaning probably results from a combination of factors, the most important being that at this age the piglet has had time to develop a substantial appetite for solid food, the acidity of its stomach contents is increasing and the hydrolytic power of its digestive enzymes is continuing to increase. It is possible that the development of stomach acidity is the most important single change which is necessary for trouble-free weaning of pigs.

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