

Enzyme potentialities of the abomasum and pancreas of the calf. II. — Effects of weaning and feeding a liquid supplement to ruminant animals

P. GUILLOTEAU, T. CORRING (*), R. TOULLEC, R. GUILHERMET

with the technical assistance of Marguerite BEAUFILS, S. BOUSSION, Mireille CONNAN, H. FLAGEUL, Anne-Marie GUEUGNEAU (*), Monique LESNE

*Laboratoire du Jeune Ruminant, I.N.R.A.,
65, rue de St-Brieuc, 35042 Rennes Cedex, France.*
(* *Laboratoire de Physiologie de la Nutrition, I.N.R.A.,
78350 Jouy-en-Josas, France.*

Summary. Thirty-nine male Friesian calves, divided into three groups (L, S and SL), were reared until they were 147 to 175 days old. Group L calves remained preruminant until slaughter. Group S calves were weaned between 5 and 9 weeks of age and then received a concentrate feed and dehydrated fescue *ad libitum*. Besides this diet, group SL calves received a liquid supplement containing whey powder and soyabean oil meal, supplying a total of 940 g of dry matter and 5,060 g of water per day. The slaughter age of the calves in each group was chosen so that carcass weight in the three groups was similar. At slaughter, the abomasum and pancreas of each animal were collected and the gastric (chymosin and pepsin) and pancreatic (chymotrypsin, trypsin, lipase and amylase) enzymes were assayed.

Weaning caused a decrease in the chymosin content and an increase in the pepsin content of the abomasum. The amount of chymosin per kg of carcass was on the average 2.8-fold lower and that of pepsin 1.9-fold higher in groups S and SL than in group L. The amount of pepsin tended to be higher in group S than in group SL, but only the difference observed (36 %) for the total amount was significant.

In group S, the pancreata showed more chymotrypsin, trypsin and amylase activities but less lipase activity than in group L; the observed differences in these activities per kg of carcass were 32, 49, 70 and 24 %, respectively. The activities of group SL were lower than those of group L for trypsin, chymotrypsin and lipase but higher for amylase (17, 12, 44 and 18 %, respectively). Group SL exhibited lower activities than group S (55, 67, 16 and 44 %, respectively, for trypsin, chymotrypsin, lipase and amylase).

Weaning appeared to induce large changes in abomasal and pancreatic enzyme potentialities which exhibited patterns similar to the variations in the amounts of substrate intake. In our experimental conditions, giving a liquid supplement to ruminant calves had a depressive effect on the activities of the enzymes (except chymosin), in the pancreas and the abomasum.

Introduction.

In preruminant calves ingested milk passes directly into the abomasum owing to the reflex of oesophageal groove closure. When the animal is ruminant, solid

food remains in the rumen where it is fermented by the microflora before passing into the abomasum. However, the reflex of oesophageal groove closure in weaned calves can be maintained and the rumen by-passed when a part of the diet is given in liquid form (Guilhermet, Patureau-Mirand and Toullec, 1976; Guilhermet, Coroller and Toullec, 1980). This technique permits better use of good quality protein and energy sources insofar as they can be efficiently digested by monogastric mechanisms. Transition from the preruminant to the ruminant stage and the distribution of a part of the diet in liquid form lead to physiological adaptations in animals which have been little studied from the point of view of digestive secretions (Andren, Bjorck and Claesson, 1980, 1981; review by Sissons, 1981). The aim of the present work was to measure the effect of the above two factors on the secretory potentialities of the abomasum and the exocrine pancreas in intensively-fed calves.

Material and methods.

Thirty-nine male Friesian calves, bought at about 8 days of age, were reared on straw in individual crates. Up to 4 weeks, they were muzzled and received a milk substitute diet (table 1) which was bucket-fed twice daily. The calves were then distributed into three groups (L, S and SL) of 13 animals each. Group L

TABLE 1
Diet composition

| <i>Constituents (%)</i> | | | | |
|------------------------------------|-----------------|------------------|-------------------|------------|
| Diet | Milk substitute | Concentrate feed | Supplement | |
| Skim milk powder | 65.0 | — | — | |
| Maize | — | 74.2 | — | |
| Soyabean meal | — | 12.0 | 25.0 (1) | |
| Dehydrated alfalfa | — | 6.0 | — | |
| Urea | — | 0.8 | — | |
| Tallow | 22.0 | — | — | |
| Beet molasses | — | 3.0 | — | |
| Pregelatinized starch | 2.0 | — | — | |
| Whey powder | 10.0 | — | 75.0 | |
| Mineral and vitamin mixture | 1.0 | 4.0 | — | |
| <i>Chemical composition (% DM)</i> | | | | |
| Diet | Milk substitute | Concentrate feed | Dehydrated fescue | Supplement |
| Protein (N. 6.25) | 24.6 | 17.6 | 16.9 | 22.9 |
| Lipid | 21.9 | 3.0 | 3.1 | 1.4 |
| Starch | 2.5 | 51.9 | — | — |
| Crude fiber | — | 10.2 | 24.4 | 1.9 |
| Minerals | 7.8 | 7.5 | 11.0 | 9.2 |

(1) Dehulled soyabeans, hexane-extracted, treated by damp heat and finely ground (Soyoptim from « Société Industrielle des Oléagineux », 59, rue de la Tour, 75016 Paris, France).

calves continued to receive exclusively the milk substitute diet and remained preruminant until slaughter. They were always muzzled and were fed twice daily, except on Sundays when no evening meal was given. The amounts distributed at each meal increased with age from 665 to 1,595 g of dry matter and the concentration increased likewise from 133 to 190 g of dry matter/kg of milk substitute.

The muzzle was removed from the other calves and they were gradually weaned between 4 and 9 weeks onto an exclusively solid diet (group S) or a semi-liquid diet (group SL) and thus became either strict or « semi » ruminant, respectively. These calves were given a concentrate feed, dehydrated fescue (table 1) and water *ad libitum* from 4 weeks of age. Group SL calves received a liquid supplement containing a mixture of whey powder and soyabean meal (table 1) diluted in water (156 g of dry matter/kg of liquid). During weaning, this supplement gradually replaced the milk substitute from 7 weeks of age. After weaning each calf was given a constant amount (6 kg/day) of the liquid supplement. It was bucket-fed twice daily up to 14 weeks and thereafter given once daily. Blood samples for plasma glucose determination were taken from the jugular vein 4 h after the morning meal during the last week before slaughter (Michel, 1973). All animals of a same group were slaughtered on the same day ; slaughter ages were chosen so as to obtain similar mean carcass weights in the three groups (table 2).

The abomasal mucosa and the pancreas were collected at slaughter and analysed according to methods described by Guilloteau *et al.* (1983). The amounts of pepsin and chymosin were expressed in mg ; chymotrypsin activity was expressed in μ moles of acetyltirosin ethyl ester (ATEE) hydrolysed per min, trypsin activity in μ moles of benzoyl arginine ethyl ester (BAEE) hydrolysed per min, lipase activity in μ moles of fatty acids released per min and amylase activity in the number of reducing terminals released after 20-min hydrolysis of soluble starch. The results were subjected to an analysis of variance and means were ranked according to the Newman-Keul's test (Snedecor and Cochran, 1971).

TABLE 2

Slaughter age, liveweight and weights of carcass, abomasum and pancreas (mean \pm SEM)

| Group (1) | L | SL | S |
|--|-------------------|-------------------|---------------------------------|
| Age (d) | 147 | 168 | 175 |
| Liveweight (kg) | 219.5 \pm 3.7** | 242.5 \pm 6.8 | 258.8 \pm 4.0a* |
| Carcass weight (kg) | 128.6 \pm 2.6 | 126.5 \pm 3.8 | 135.2 \pm 2.4 |
| Abomasum fresh weight (g/kg carcass) : | | | |
| • total | 5.17 \pm 0.16 | 5.96 \pm 0.37 | 5.69 \pm 0.16 |
| • mucosa | 1.79 \pm 0.12 | 2.09 \pm 0.20 | 2.40 \pm 0.10 ^b |
| Pancreas (g/kg carcass) | | | |
| • fresh weight | 1.33 \pm 0.05* | 1.62 \pm 0.11 | 1.71 \pm 0.04 |
| • total protein | 0.217 \pm 0.011 | 0.224 \pm 0.015 | 0.269 \pm 0.008 ^{b*} |

(1) Thirteen animals per group were slaughtered but 2 pancreata could not be used in group L.

** , * : Differed from group SL ($P \leq 0.01$ and 0.05) ; a, b : Group S differed from group L ($P \leq 0.01$ and 0.05).

Results.

Growth and intake. — The health and growth of the animals were very satisfactory ; from 4 weeks to slaughter the liveweight gains (means \pm SEM) were $1,346 \pm 33$, $1,344 \pm 41$ and $1,372 \pm 28$ g/day for groups L, SL and S, respectively. To obtain the same carcass weight, the ruminant animals were slaughtered 3 (group SL) or 4 (group S) weeks later than the preruminants (table 2) ; the carcasses of group S calves were slightly heavier than those of the other groups, but the differences were non-significant. These divergencies were mainly due to the fact that group S animals had a higher growth rate than expected during the last 2 weeks of the experiment. Contrary to expectation, the carcass yield of group SL calves was not higher than that of group S (about 52.2 % of liveweight in both cases) ; indeed Guilhermet *et al.* (unpublished data) observed a decrease in the weight of digestive contents when ruminant calves were given a liquid supplement supplying about 25 % of the dry matter intake. The amounts of dry matter, nitrogen and starch intakes per kg of carcass were significantly higher in groups S and SL than in group L (table 3), whereas the contrary was true for lipids.

In group SL calves, the level of plasma glucose measured 4 h after the morning meal was lower ($P < 0.01$) than in group L calves but it was higher ($P < 0.05$) than in group S calves (116 ± 6 , 148 ± 7 and 96 ± 3 mg per 100 ml, respectively). Thus a large part of the liquid supplement by-passed the rumen, in agreement with the results of Guilhermet, Patureau-Mirand and Toullec (1976) and Guilhermet, Coroller and Toullec (1980).

Since the carcasses of group S calves were slightly heavier than those of the other groups, the results are given not only as total activities and per g of mucosa or protein but are also expressed in relation to carcass weight. The relative weights of the abomasal mucosa and the pancreas were lowest in group L and highest in group S (table 2). Pancreatic protein content was lower ($P < 0.01$) in group SL than in the other groups (0.14 g/g of pancreas vs 0.16).

TABLE 3
Calf intakes during the week before slaughter
(g/d/kg of slaughter carcass) (mean \pm SEM)

| Intake | Group | | |
|------------|-----------------------|------------------|-------------------------|
| | L | SL | S |
| Dry matter | $22.45 \pm 0.44^{**}$ | 39.56 ± 1.28 | $45.75 \pm 1.44^{***}$ |
| Protein | $5.30 \pm 0.10^{**}$ | 6.60 ± 0.19 | $7.35 \pm 0.21^{a*}$ |
| Lipid | $4.72 \pm 0.08^{**}$ | 0.99 ± 0.03 | $1.30 \pm 0.04^{a***}$ |
| Starch | $0.53 \pm 0.01^{**}$ | 11.51 ± 0.42 | $15.83 \pm 0.46^{a***}$ |

** , * : Differed from group SL ($P \leq 0.01$ or 0.05) ; ^a : Group S differed from group L ($P \leq 0.01$).

Gastric and pancreatic enzymes. — The amounts of enzymes present per g of abomasal mucosa were similar in groups S and SL (table 4). However, the chymosin and pepsin contents of these organs were 3.6-fold higher and 1.6-fold lower, respectively, in group L than in groups S and SL (fig. 1). The chymosin : pepsin ratio was therefore very much higher (or an average 6.4-fold) in group L than in the other groups. The specific activities of chymotrypsin and amylase were 1.2 and 1.4-fold higher, respectively, whilst that of lipase was 1.5-fold lower in group S than in group L. There was no significant difference for trypsin between these two groups. Except for lipase, the specific activities of the enzymes of SL calves were generally lower than those of group S calves. They were also lower than those of group L for trypsin and lipase but higher for amylase.

TABLE 4

Amounts of gastric enzymes (mg/g of abomasal mucosa), specific activities of pancreatic enzymes and enzyme ratios (mean \pm SEM)

| Group | L | SL | S |
|---------------------------|--------------------|-------------------|----------------------------------|
| Amount (chymosin) | 2.30 \pm 0.31** | 0.66 \pm 0.10 | 0.71 \pm 0.14 ^a |
| (pepsin) | 0.85 \pm 0.11** | 1.29 \pm 0.11 | 1.41 \pm 0.08 ^a |
| (chymotrypsin) | 10.73 \pm 0.55 | 9.49 \pm 0.43 | 13.29 \pm 0.32 ^{a**} |
| Specific (trypsin) | 0.93 \pm 0.05** | 0.77 \pm 0.04 | 0.98 \pm 0.03** |
| activity (lipase) | 7.36 \pm 0.31** | 4.99 \pm 0.24 | 4.77 \pm 0.17 ^a |
| (amylase) | 119.43 \pm 8.34* | 138.20 \pm 5.46 | 161.78 \pm 4.91 ^{a**} |
| Ratio (chymosin : pepsin) | 2.82 \pm 0.40** | 0.48 \pm 0.07 | 0.48 \pm 0.09 ^a |
| (chymotrypsin : trypsin) | 11.70 \pm 0.72 | 12.68 \pm 0.82 | 13.64 \pm 0.40 |

** , * : Differed from group SL ($P \leq 0.01$ or 0.05) ; ^a : Group S differed from group L ($P \leq 0.01$).

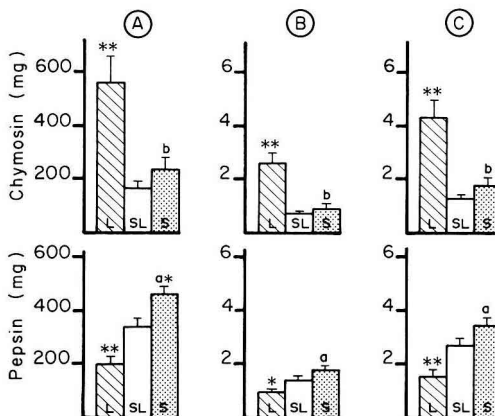


FIG. 1. — Amounts of gastric enzymes in whole abomasum (A) per kg of liveweight (B) and per kg of carcass (C) (means \pm SEM).

** , * : Group S differed from group L ($P \leq 0.01$ or 0.05) ; a, b : Groupe S differed from groupe L ($P \leq 0.01$ or 0.05).

Problems concerning the estimation of secretory potentialities from the amounts present in the organs have been discussed previously (Guilloteau *et al.*, 1984b). In the present experiment, observations of dietary effects on the potentialities of enzyme secretions were broadly the same whether results were expressed, for the whole abomasum or pancreas, per kg liveweight or per kg carcass (fig. 1, 2). In the abomasum, secretory potentialities were always lower for chymosin but they were always higher for pepsin in groups S and SL than in group L. Thus, chymosin content per kg of carcass in groups S and SL was on an average 2.8-fold lower, whilst pepsin content was 1.9-fold higher. These potentialities always tended to be greater in group S than in group SL, but only the difference between the total pepsin contents (37 %) was significant. In the pancreas, the potentialities of group S calves were higher than those of group L calves for chymotrypsin, trypsin and amylase, but lower for lipase, the observed differences in activities per kg of carcass were 49, 32, 70 and 24 %, respectively. Group SL had lower potentialities than group L for chymotrypsin, trypsin and lipase, but tended to have higher ones for amylase (12, 17, 44 and 18 %, respectively, per kg carcass). As far as chymotrypsin and trypsin are concerned, the differences were only significant for activities in relation to liveweight. Therefore, SL calves always exhibited clearly lower potentialities than S animals ; the observed differences in activities per kg of carcass were 67, 55, 44 and 16 % for chymotrypsin, trypsin, amylase and lipase, respectively.

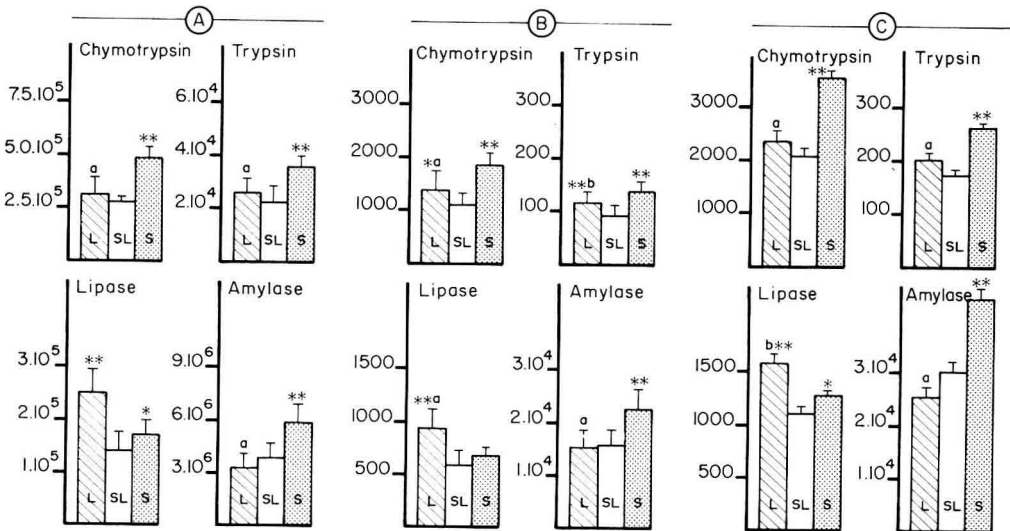


FIG. 2. — Pancreatic enzyme activities in whole gland (A) per kg of liveweight (B) and per kg of carcass (C).

** , * : Differed from group SL ($P \leq 0.01$ or 0.05) ; a, b : Group S differed from group L ($P \leq 0.01$ or 0.05).

Discussion.

With the chromatographic method we used (Garnot *et al.*, 1972), pepsin A was separated from chymosin and pepsin B, but the latter two enzymes remained mixed and were thus assayed together. Pepsin B constitutes about one-half of the chymosin-pepsin B mixture in adult cattle (Rothe, Harboe and Martiny, 1977 ; Valles, 1980) but only 12 % in calf commercial rennets (Rothe, Harboe and Martiny, 1977). Also pepsin B does not seem to represent more than 5 to 7 % of the sum of pepsin A + pepsin B and it is about 2.6-fold less active than chymosin on the α -casein we used as a substrate (Martin *et al.*, 1982). Therefore, the method of Garnot *et al.* (1972) would lead to an overestimate of chymosin of about 5 % in calves and 28 % in adult cattle. As far as our calves are concerned, it may be considered that the results on chymosin essentially correspond to this enzyme, whilst the values assigned to pepsin actually apply to pepsin A.

Group L calves were younger than those of the other groups at slaughter. From previous observations (Guilloteau *et al.*, 1983, 1984b), if the organs of group L calves had been analysed at the same age as those of groups S and SL, the potentialities of chymosin secretion would have been slightly lower and those of the other pancreatic enzymes slightly higher. Nevertheless, the changes would have been too slight (for example 10-13 %) for chymosin to cause modifications in the classifications we observed in relation to diet in this study.

Effect of weaning. — Weaning caused a considerable decrease in chymosin content per kg of carcass. This was solely due to a decline in the concentration of this enzyme in the abomasal mucosa because mucosal weight per kg of carcass increased. In contrast, pepsin predominated in weaned animals due to an increase in both enzyme concentration and organ weight. These results agree with those obtained on bovine (Andren, Bjorck and Claesson, 1980) and ovine (Guilloteau *et al.*, 1983) gastric mucosa or on the contents of calf abomasum (Garnot *et al.*, 1977). The same is true of gastric juice since the chymosin/pepsin ratio decreases during weaning (Hill, Noakes and Lowe, 1970 ; Guilloteau *et al.*, unpublished data). However, most of these studies do not allow a distinction between the respective effects of age and diet. In group S, chymosin concentration per g of mucosa was close to that reported by Andren, Bjorck and Claesson (1980, 1981) in 6-month old calves receiving a diet containing high amounts of concentrate feed, whilst the pepsin A concentration found by these authors was about 2.7-fold higher. This divergency could be at least partially due to methodological differences (mucosal area analysed, assay method, animal breed).

In group S calves, potentialities for pepsin secretion per kg of liveweight were similar to those observed by Valles and Furet (1981) in 17-month old Friesian bulls and 6-year old culled cows. Compared with pepsin, the potentialities for chymosin secretion were much higher in our calves (33 and 13-fold, respectively). Thus, the secretory potentialities for chymosin appeared to decrease continuously as the ruminants grew older, but those of pepsin changed little.

The secretory potentialities for chymotrypsin, trypsin and amylase were higher in weaned than in preruminant calves, contrary to those of lipase which

were lower. This resulted from the fact that the specific activities of the first three enzymes, as well as pancreas weight, were higher after weaning, although the increase in the size of the pancreas did not compensate for the drop in lipase specific activity. In 42-day old lambs, pancreatic trypsin, chymotrypsin and amylase activities per kg of empty liveweight also tended to be higher in weaned animals than in preruminants, but the same was true of lipase activity (Guilloteau *et al.*, 1983). Also, higher activities per kg liveweight of amylase, trypsin, chymotrypsin or protease were found in the pancreas, pancreatic juice or small intestine contents of weaned calves and lambs by Walker (1959a,b) and Gorrill, Schingoethe and Thomas (1968). In contrast, Schingoethe *et al.* (1970) did not observe an increase in the trypsin activity of small intestine contents, whilst Gooden (1973) reported that the daily secretion of pancreatic lipase was much higher in weaned calves. However, from these published results, except those of Guilloteau *et al.*, 1983, 1984b), it is not possible to separate the effect of age from that of weaning.

In our experiment, the effect of weaning on enzymatic activities may be the result of many phenomena : *e.g.* development of the forestomachs, more regular transit towards the abomasum and small intestine, the nature of the terminal products of digestion and modification of the mechanisms regulating digestive secretions. For example, plasma gastrin, CCK-PZ, pancreatic polypeptide (PP) and vasoactive intestinal peptide (VIP) levels are higher in ruminant than in preruminant calves before the morning meal (Guilloteau *et al.*, 1984a and c) ; however, the secretin level is lower.

Effect of giving a liquid supplement to ruminants. — In our experimental conditions, the use of a liquid supplement did not have a marked effect on enzyme potentialities in the abomasum compared to those observed with the exclusively solid diet. In contrast, Andren, Bjorck and Claesson (1981) noticed a slight increase in the chymosin content of the abomasal mucosa when skim milk was given twice daily for 7 weeks to ruminant calves having received an exclusively solid diet between 2 and 4 months of age. Also, the chymosin level of the abomasal contents increased slightly when milk was given to a calf having received an exclusively solid diet for 2 to 5 weeks (Garnot *et al.*, 1977). However, the augmentations observed by these authors were low, indicating that the changes in the potentialities for chymosin secretion induced by the intake of solid food could not be markedly reversed. Thus it appears that rumen development is a dominant factor in the regulation of abomasal enzyme potentialities. In our experiment the liquid supplement did not contain casein. That may have limited the enhancement of chymosin secretion potentialities since it has been reported that the replacement of milk protein by whey, fish, or soyabean protein in the diet of preruminant calves leads to a decrease in these potentialities (Garnot *et al.*, 1974, 1977).

Pancreatic enzyme potentialities were lower with the liquid supplement than with the exclusively solid diet. In the pig whose digestive physiology is very different, a depressive effect of a liquid diet on pancreatic and biliary secretions was also observed by Partridge *et al.* (1982) and Sambrook (1981, cited by Partridge *et al.*, 1982). In our animals, the massive arrival of the liquid supplement

in the abomasum and small intestine could limit the favourable effect of the relatively regular passage of products leaving the rumen. Another hypothesis would be that the calf is particularly sensitive to soyabean meal, even when appropriately cooked. This meal usually contains small residual amounts of antitryptic factors, a part of which (in bound form) is released by pepsin, acidification or alkalization (Delobez, Duterte and Rambaud, 1971). The soyabean meal incorporated into the liquid supplement was not treated to eliminate these bound antitryptic factors. When milk protein is replaced by soyabean meal containing these factors, trypsin activity in the pancreas and intestinal contents is decreased (Gorrill and Thomas, 1967).

Enzyme potentialities and diet. — In addition to young ruminants, chymosin or a similar enzyme has also been shown to be very active in young rabbits (Henschel, 1973), young rats (Kotts and Jenness, 1976; Nikolaevskaya and Chernikov, 1978), piglets, pups and kittens (Foltmann and Axelsen, 1980). This activity seems to disappear at weaning in these monogastric animals, indicating that it may be associated with milk feeding. The amount of chymosin found in young ruminants decreased at weaning. However, it was still important 100 days later in group S calves and thus, in agreement with the results of Andren, Bjorck and Claesson (1980), it declined very slowly with age. It should be noted that calves of nursing cows are not completely weaned before about 8 months of age, while those of group S were only 5.8 months old at slaughter.

The differences observed between group S and group L calves for the activities of proteolytic enzymes (except chymosin), amylase and lipase exhibited a pattern similar to the changes in the respective amounts of nitrogen, starch and lipid intakes (table 3). In ruminant animals, starch is largely degraded in the rumen. However according to the data of Thivend and Journet (1970), one can estimate that about 30 % of the starch intake of group S calves, i.e. 600-700 g/d during the last week, reached the duodenum in our experimental conditions. Thus, in the weaned calf the synthesis of these enzymes appeared to adapt to the intakes of the substrates. This hypothesis agrees with results on many species after weaning (see review by Corring, 1980) but has to be questioned. Clary *et al.* (1969) reported that cattle had more pancreatic amylase activity with a maize-rich diet than with grass. However, the substitution of starch for lactose had no effect on the amylolytic activity in the pancreas of the preruminant lamb (Peyraud, 1983). Also Hamza (1977) observed no increase in pancreatic amylase secretion when ruminant lambs were offered a supplement of maize starch suspension by bottle. Similarly, Corring, Lebas and Courtot (1972) showed in the rabbit that dietary changes during weaning were not the cause of the increased enzyme activities observed in the pancreas during this period.

Giving a liquid supplement to ruminant calves had a marked effect on enzyme : substrate intake ratios only in the cases of trypsin and chymotrypsin where they were 1.4 and 1.5-fold lower, respectively, in group SL than in group S. This supports the hypothesis of a possible depressive effect of the residual antitryptic factors of soyabean oil meal in the liquid supplement (Gorrill and Thomas, 1967).

As regards trypsin and chymotrypsin, the enzyme : nitrogen intake ratio was very little affected by forestomach development, but it increased by 57 % for pepsin. Chymosin particularly acts on coagulation and has a low proteolytic activity compared to pepsin (Chow and Bell, 1976 ; Jenkins, Mahadevan and Emmons, 1980 ; Martin *et al.*, 1982). Thus, it appears that enzyme potentialities per gram of protein arriving in the abomasum were at least as high in weaned as in preruminant calves. Nevertheless compared to milk protein, microbial protein and dietary protein undegraded in the rumen are probably less easily hydrolysed by pepsin and pancreatic proteolytic enzymes. Because of the very large differences in the intakes of starch and lipids between group S and group L calves, comparing the corresponding enzyme : substrate ratios would have no meaning.

In conclusion, weaning in calves causes large changes in abomasal and pancreatic secretory potentialities ; these modifications show a pattern similar with the changes observed in the intake of substrates. The secretory potentialities for lipase and chymosin decrease as the intake of lipid declines and casein disappears from the diet respectively. The secretory potentialities for pepsin and trypsin, chymotrypsin and amylase increase with higher intakes of protein and starch. Giving a liquid supplement to ruminant calves leads to a general decline in enzyme activities (except chymosin), whilst enzyme : substrate ratios are only modified for trypsin and chymotrypsin.

*Reçu en décembre 1983.
Accepté en janvier 1985.*

Acknowledgements. — Thanks are due to P. Martin for determining the correspondance between coagulation activities and amounts of abomasal enzymes, to A. Daifuku for translating the French text and to J. Quillet for collecting the documentation.

Résumé. *Potentialités enzymatiques de la caillette et du pancréas du veau. II. Effet du sevrage et de la distribution d'un supplément liquide à des animaux ruminants.*

Trente neuf veaux mâles de race frisonne, répartis en 3 lots (L, S et SL) sont élevés jusqu'à l'âge de 147 à 175 j. Les animaux du lot L restent préruminants jusqu'à leur abattage. Ceux du lot S sont sevrés entre les âges de 4 et 9 semaines et reçoivent ensuite *ad libitum* un aliment concentré et de la fétuque déshydratée. Les veaux du lot SL reçoivent en plus du régime des veaux du lot S, une buvée contenant de la poudre de lactosérum et du tourteau de soja apportant au total 940 g de matière sèche et 5 060 g d'eau par jour. L'âge d'abattage des veaux de chaque lot est choisi de manière à obtenir des poids de carcasse similaires dans les 3 groupes. A l'abattage, la caillette et le pancréas de chaque veau sont collectés puis les enzymes gastriques (chymosine et pepsine) et pancréatiques (chymotrypsine, trypsine, lipase et amylase) sont dosées.

Au niveau de la caillette, le sevrage entraîne une diminution de la quantité de chymosine et une augmentation de celle de pepsine ; ainsi, les quantités de chymosine présentes par kg de carcasse sont en moyenne 2,8 fois plus faibles et celles de pepsine 1,9 fois plus fortes chez les veaux des lots S et SL que chez ceux du lot L. La quantité de pepsine a tendance à être plus forte chez les veaux du lot S que chez ceux du lot SL, mais seule la différence observée pour la quantité totale (36 %) est significative.

Au niveau du pancréas, les activités des veaux du lot S sont supérieures à celles des veaux du lot L pour la trypsine, la chymotrypsine et l'amylase, mais elles leur sont inférieures pour la lipase : les différences observées dans les activités par kg de carcasse sont respectivement de 32, 49, 70 et 24 %. Les veaux du lot SL ont des activités plus faibles que ceux du lot L pour la trypsine, la chymotrypsine et la lipase mais plus élevées pour l'amylase (respectivement de 17, 12, 44 et 18 %) ; ils ont des activités toujours inférieures à celles des veaux du lot S (respectivement 55, 67, 16 et 44 % pour la trypsine, la chymotrypsine, la lipase et l'amylase).

Le sevrage entraîne de profondes modifications dans les potentialités de sécrétion des enzymes digestives étudiées qui vont dans le même sens que les changements observés dans les quantités de substrats ingérés. Dans nos conditions expérimentales, la distribution d'une buvée à des veaux ruminants a un effet dépressif sur les activités enzymatiques du pancréas et de la caillette (chymosine exceptée).

Références

- ANDREN A., BJÖRCK L., CLAESSION O., 1980. Quantification of chymosin (rennin) and pepsin in bovine abomasum by rocket immunoelectrophoresis. *Swedish J. agric. Res.*, **10**, 123-130.
- ANDREN A., BJÖRCK L., CLAESSION O., 1981. Effect of supplementary milk-feeding on content of chymosin in the abomasal mucosa of concentrate-fed calves. *Swedish J. agric. Res.*, **11**, 11-15.
- CHOW C., BELL J. M., 1976. Effects of various heat and pH treatments on digestibility of protein in pea protein concentrate (*Pisum sativum*). *Can. J. anim. Sci.*, **56**, 559-566.
- CLARY J. J., MITCHELL G. F., LITTLE C. O., BRADLEY N. W., 1969. Pancreatic amylase activity from ruminants fed different rations. *Can. J. Physiol. Pharmacol.*, **47**, 161-164.
- CORRING T., 1980. The adaptation of digestive enzymes to the diet : its physiological significance. *Reprod. Nutr. Dévelop.*, **20**, 1217-1235.
- CORRING T., LEBAS F., COURTOT D., 1972. Contrôle de l'évolution de l'équipement enzymatique du pancréas exocrine du lapin de la naissance à 6 semaines. *Ann. Biol. anim. Bioch. Biophys.*, **12**, 221-231.
- DELOBEZ R., DUTERTE R., RAMBAUD M., 1971. Dosage des facteurs antitrypsiques du soya. *Rev. Fr. Corps gras*, **18**, 381-389.
- FOLTMANN B., AXELSEN N. H., 1980. Gastric proteinases and their zymogenes. Phylogenetic and developmental aspects. *Fed. europ. Bioc. Soc. (FEBS Proc)*, **60**, 271-280.
- GARNOT P., THAPON J. L., MATHIEU C. M., MAUBOIS J. L., RIBADEAU-DUMAS B., 1972. Determination of rennin and bovine pepsins in commercial rennets and abomasal juices. *J. Dairy Sci.*, **55**, 1641-1650.
- GARNOT P., TOULLEC R., THAPON J. L., MARTIN P., MINH-THU-HOANG, MATHIEU C. M., RIBADEAU-DUMAS B., 1977. Influence of age, dietary protein and weaning on calf abomasal enzymatic secretion. *J. Dairy Res.*, **44**, 9-23.
- GARNOT P., VALLES E., THAPON J. L., TOULLEC R., TOMASSONE R., RIBADEAU-DUMAS B., 1974. Influence of dietary proteins on rennin and pepsin content of preruminant calf vell. *J. Dairy Res.*, **41**, 19-23.
- GOODEN J. M., 1973. The importance of lipolytic enzymes in milk-fed and ruminating calves. *Aust. J. biol. Sci.*, **26**, 1189-1199.
- GORRILL A. D. L., SCHINGOETHE D. J., THOMAS J. W., 1968. Proteolytic activity and in vitro enzyme stability in small intestinal contents from ruminants and non-ruminants at different ages. *J. Nutr.*, **96**, 342-348.
- GORRILL A. D. L., THOMAS J. W., 1967. Body weight changes, pancreas size and enzyme activity and proteolytic enzyme activity and protein digestion in intestinal contents from calves fed soybean and milk protein diets. *J. Nutr.*, **92**, 215-223.
- GUILHERMET R., COROLLER J. Y., TOULLEC R., 1980. Effet d'un apport post-ruminal d'énergie ou d'énergie et de protéines sur la prise alimentaire chez le veau ruminant. *Reprod. Nutr. Dévelop.*, **20**, 1645-1649.

- GUILHERMET R., PATUREAU-MIRAND P., TOULLEC R., 1976. Influence de la distribution sous forme solide ou liquide d'un supplément riche en protéines chez le veau ruminant. *Ann. Zootech.*, **25**, 281-286.
- GUILLOTEAU P., CHAYVIALLE J. A., TOULLEC R., GRONGNET J. F., DARDILLAT C., 1984a. Early life pattern of plasma secretin level in calves. *Can. J. Anim. Sci.*, **64** (Suppl.), 100-101.
- GUILLOTEAU P., CORRING T., GARNOT P., MARTIN P., TOULLEC R., DURAND G., 1983. Effects of age and weaning on enzyme activities of abomasum and pancreas of the lamb. *J. Dairy Sci.*, **66**, 2373-2385.
- GUILLOTEAU P., CORRING T., TOULLEC R., ROBELIN J., 1984b. Enzyme potentialities of the abomasum and pancreas of the calf. I. Effect of age in the preruminant. *Reprod. Nutr. Dévelop.*, **24**, 315-325.
- GUILLOTEAU P., DELANSORNE R., TOULLEC R., 1982. Répartition des concentrations enzymatiques dans la muqueuse abomasale du veau préruminant. Evolution avec l'âge. *Reprod. Nutr. Dévelop.*, **22**, 511-522.
- GUILLOTEAU P., TOULLEC R., CHAYVIALLE J. A., GRONGNET J. F., 1984c. Early life pattern of plasma gastro-enteropancreatic hormones in calves. *Fifth int. Symp. on gastrointestinal hormones*. Rochester, U.S.A., September 30 to October 3 (in press).
- HAMZA A. N., 1977. Pancreatic secretion in sheep. I. Adaptation of the pancreas to dietary starch. *Sudan J. Vet. Sci. Anim. Husb.*, **18**, 1-18.
- HENSCHER M. J., 1973. Comparison of the development of proteolytic activity in the abomasum of the preruminant calf with that in the stomach of the young rabbit and guinea-pig. *Brit. J. Nutr.*, **30**, 285-296.
- HILL K. J., NOAKES D. E., LOWE R. A., 1970. Gastric digestive physiology of the calf and piglet, 166-179. In Phillipson A. T. : *Physiology of digestion and metabolism in the ruminant*, 11rd int. Symp. on ruminant physiology, Oriel Press Limited, Newcastle Upon Tyne.
- JENKINS K. J., MAHADEVAN S., EMMONS D. B., 1980. Susceptibility of proteins used in calf milk replacers to hydrolysis by various proteolytic enzymes. *Can. J. Anim. Sci.*, **60**, 907-914.
- KOTTS C., JENNESS R., 1976. Rennin and pepsin in stomach of rats. *J. Dairy Sci.*, **59**, 1398-1400.
- MARTIN P., TRIEU-CUOT P., COLLIN J. C., RIBADEAU-DUMAS B., 1982. Purification and characterization of bovine gastricsin. *Eur. J. Biochem.*, **122**, 31-39.
- MATHIEU C.-M., 1961. Etude du développement du tractus digestif du veau. *Ann. Nutr. Alim.*, **15**, 263-266.
- MICHEL M., 1973. Recherches de tests biochimiques destinés à caractériser l'état nutritionnel et sanitaire d'un troupeau de veaux. *Ann. Rech. vétér.*, **4**, 113-124.
- NIKOLAEVSKAYA V. R., CHERNIKOV M. P., 1978. A study of the milk protein digestion in the stomach at a young age. *Vopr. Pitan.*, **4**, 33-36.
- PARTRIDGE J. G., LOW A. G., SAMBROOK I. E., CORRING T., 1982. The influence of diet on the exocrine pancreatic secretion of growing pigs. *Br. J. Nutr.*, **48**, 137-145.
- PEYRAUD J. L., 1983. *Rôle respectif des enzymes de l'hôte et de la flore intestinale dans la digestion de l'amidon et de ses dérivés (produits amylacés) chez le jeune agneau préruminant*. Th. Univ. Rennes I et E.N.S.A. Rennes. Numéro d'ordre 83/8, série B, 173 p.
- ROTHER G. A. L., AXELSEN N. H., JOHNK P., FOLTMANN B., 1976. Immunochemical, chromatographic and milk-clotting activity measurements for quantification of milk-clotting enzymes in bovine rennets. *J. Dairy Res.*, **43**, 85-95.
- ROTHER G. A. L., HARBOE M. K., MARTINY S. C., 1977. Quantification of milk-clotting enzymes in 40 commercial bovine rennets, comparing rocket immunoelectrophoresis with an activity ratio assay. *J. Dairy Res.*, **44**, 73-77.
- SCHINGOËTHE D. J., GORRILL A. D. L., THOMAS J. W., YANG M. G., 1970. Size and proteolytic enzyme activity of the pancreas of several species of vertebrate animals. *Can. J. Physiol. Pharmacol.*, **48**, 43-49.
- SISSONS J. W., 1981. Digestive enzymes of cattle. *J. Sci. Food Agric.*, **32**, 105-114.
- SNEDECOR G. W., COCHRAN W. R., 1971. *Statistical methods*. The Iowa State Univ. Press, Ames.
- THIVEND P., JOURNET M., 1970. Utilisation digestive de l'amidon du maïs chez le ruminant. *Ann. Biol. anim. Bioch. Biophys.*, **10**, 323-326.

- VALLES E., 1980. *Les protéases gastriques bovines utilisées en fromagerie*. Th. Doct. Ing., Paris, 246 p.
- VALLES E., FURET J. P., 1981. Etude des caillettes des bovins à l'état ruminant pour l'obtention d'extraits coagulants à base de pepsine bovine. II. Influence de la race, de l'âge et du sexe sur leur contenu enzymatique. *Le lait*, **61**, 590-618.
- WALKER D. M., 1959a. The development of the digestive system of the young animal. III. Carbohydrase enzyme development in the young lamb. *J. agric. Sci.*, **53**, 374-380.
- WALKER D. M., 1959b. The development of the digestive system of the young animal. IV. Proteolytic enzyme development in the young lamb. *J. agric. Sci.*, **53**, 381-386.
-