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Enzyme potentialities of the abomasum and pancreas of the calf. I. — Effect of age in the preruminant

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Summary. The effect of age on the enzyme potentialities of abomasum (chymosin and pepsin) and pancreas (chymotrypsin, trypsin, lipase, colipase and amylase) was studied in the preruminant calf. Three foetuses were collected after slaughter of their dams (260 d of gestation) and 32 calves were maintained as preruminant and slaughtered between birth and 147 d of age. The abomasal mucosas and pancreata were collected and analysed.

The abomasal and pancreatic glands of the foetus contained large amounts of enzymes, except pepsin and amylase. On a liveweight basis, the amount of chymosin was maximal at 1.5 d post partum and decreased thereafter ; the amount of pepsin increased until 21 d and then did not change. The development of pancreatic enzyme activities was usually the reverse of that of chymosin ; amylase activity was particularly low at birth.

After birth, the development of secretory potentialities could be divided into three phases : during the colostral period, the trend of pancreatic activities was the reverse of that observed for abomasal activities ; from 1.5 to 21 d, most of the enzyme potentialities (except those of chymosin and amylase) appeared to be stimulated by intake level ; after 21 d (1.5 d for chymosin and amylase), the development of secretory potentialities appeared to depend more on age than on intake.

Introduction.

Recent work on the preruminant lamb (Guilloteau *et al.*, 1983) has shown that, on a liveweight basis, the quantity of pepsin found in the abomasal mucosa does not change with age, whilst that of chymosin decreases after 2 d ; the development of pancreatic trypsin, chymotrypsin, amylase and colipase activities was the reverse of that of chymosin. To our knowledge, this phenomenon has not been reported before. Other authors have shown certain effects of age on some

enzyme secretions or contents of abomasum (Henschel, Hill and Porter, 1961 ; Alais, 1963 ; Garnot *et al.*, 1977) or of pancreas (Siddons, 1968 ; Track *et al.*, 1972 ; Track, Creutzfeldt and Bockermann, 1975 ; Ternouth, Roy and Shotton, 1976) in the preruminant. Only Huber *et al.*, (1961) studied at the same time the development of the enzyme activities of the abomasum, the pancreas and the small intestine in the young calf ; but these authors did not assay chymosin and pepsin separately and they used only two calves per stage. In many other works, it is difficult to distinguish the effect of age from that of weaning (Walker *et al.*, 1959a, b ; Morrill *et al.*, 1970) since the animals received milk and solid food at a young age. From most of these studies it is not easy to ascertain the development of enzyme potentialities with regard to liveweight and food intake. The aim of the present work was to determine whether the phenomenon observed in lamb occurred in calf.

Material and methods.

Thirty-five calves (30 Friesian and Friesian × Holstein and 5 Charolais) were used. Three foetuses were collected after slaughter of their dams (260 d of gestation). Ten calves were sacrificed at birth before feeding and two others at 1.5 d after 2 or 3 meals of colostrum. The other 22 animals were given colostrum for 2 d and then a milk substitute diet containing 21.9 % fat and 24.6 % protein on a dry matter (DM) basis. In this diet, protein was provided almost exclusively by skim milk powder ; the calves were bucket-fed twice daily and were slaughtered at different ages (table 1), 16 to 17 h after the last meal.

Abomasal mucosas and pancreata were collected and analysed according to the methods described by Guilloteau *et al.* (1983). The amounts of pepsin and chymosin were expressed in mg ; chymotrypsin activity was expressed in μmoles of benzoyl arginine ethyl ester (BAEE) hydrolysed per min and lipase and lipase + colipase activities in μmoles of fatty acids released per min ; amylase activity was expressed as the number of reducing terminals released after 20-min hydrolysis of a soluble starch. The results were compared by t-test analysis.

Results.

At birth, the only significant difference between breeds was the amount of pepsin per kg liveweight, which was higher in Friesians than in Charolais (1.05 mg instead of 0.70 ; $P < 0.05$) ; therefore, only overall results are given. The DM, nitrogen and fat intakes in relation to liveweight increased between 1.5 and 21 d of age (fig. 1), after which these amounts did not change or decreased slowly.

Organ development. — The abomasal mucosa grew rapidly during about the last 3 foetal weeks, whilst the weight of the pancreas did not change during that period (table 1). On a liveweight basis, the weight of the abomasal mucosa increased from birth (20 g/kg) to 21 d (27 g/kg) and then decreased until 147 d

TABLE 1

Experimental design and animal and organ weights (Mean ± SD).

Diet	Origin	—	—	Colostrum		Milk replacer		
	Method of distribution	—	—	*Ad libitum* from the dam		2 meals/d open pail		
Age at slaughter (days)		Foetus 260 d	0	1.5	21	71 (1)	133 (1)	147 (2)
Number of calves		3	10 (3)	2	5 (3)	2	2	12
Live weight (kg)		34.4 ± 2.2[a]	44.5 ± 3.4***	37.8 ± 3.9[c]*	62.5 ± 5.6[a]***	101.5 ± 2.1[a]***	181.0 ± 2.8[a]***	219.5 ± 13.5[a]***
Live weight gain (g/d) (4)		—	—	—	820 ± 63	948 ± 36*	1 007 ± 16	1 347 ± 33***
Abomasum (fresh weight)								
Musculosa (g)		84.0 ± 14.3	92.4 ± 22.3	—	205.3 ± 47.1[a]	—	—	439.9 ± 51.2[a]
Mucosa (g)		50.9 ± 15.9	87.0 ± 16.7***	98.4 ± 25.0	166.3 ± 24.2[a]*	201.9 ± 30.3[a]	265.0 ± 12.7[a]	230.8 ± 59.6[a]
Pancreas								
Fresh weight (g)		22.3 ± 2.2	22.7 ± 4.5	23.1 ± 2.3	49.4 ± 12.9[a]*	—	—	168.5 ± 22.8[a]
Total protein (g)		2.77 ± 0.06	3.43 ± 0.68	3.37 ± 0.88	6.32 ± 0.99[a]*	—	—	27.39 ± 4.12[a]

(1) Pancreas not collected.
(2) Only 11 pancreata collected.
(3) Four and one Charolais calves at birth and 21 d, respectively.
(4) From birth to slaughter.
Means with a superscript (a, b or c) are significantly different from those at birth ($P \leq 0.001$, 0.01 or 0.05).
Means with three or one asterisks are significantly different from those of the preceding column ($P \leq 0.001$ or 0.05).

(10 g/kg) ; the weight of the pancreas increased until 21 d (8 g/kg) and did not change thereafter.

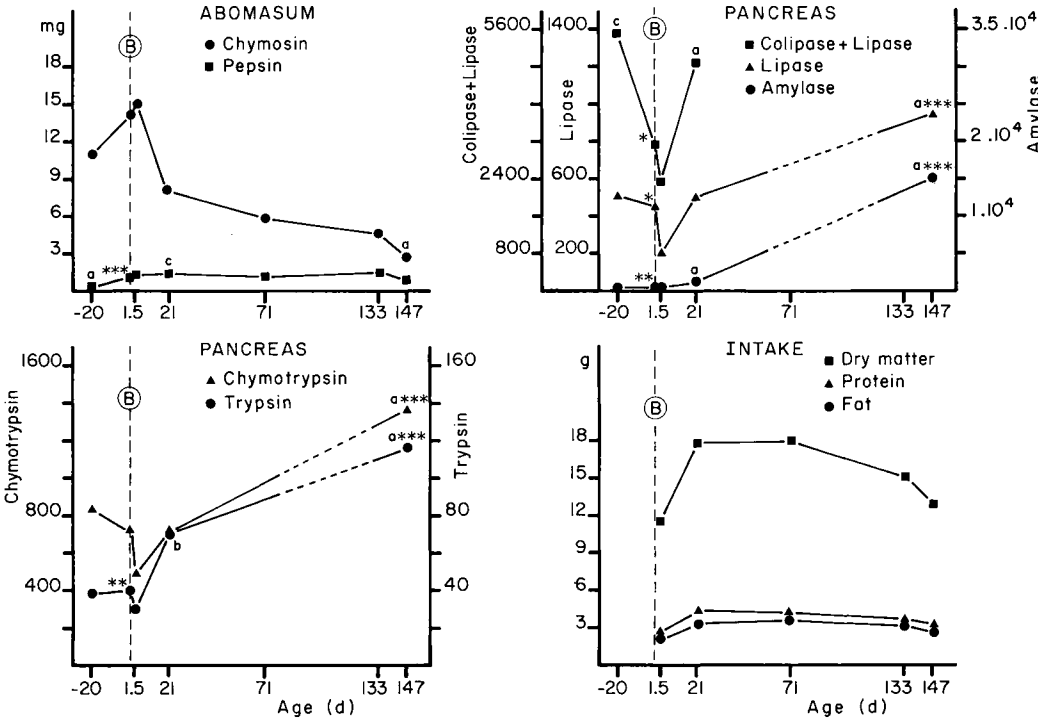

FIG. 1. — *Changes with age in the amounts of abomasal enzymes and in the activities of pancreatic enzymes* (per kg liveweight) *and in dry matter, protein and fat intakes* (g/kg liveweight). B : birth. Values with a superscript (a, b or c) are significantly different from those at birth ($P \leq 0.001$, 0.01 or 0.05). Values with three, two or one asterisks are significantly different from those at 21 d ($P \leq 0.001$, 0.01 or 0.05).

Gastric enzymes. — The amount of chymosin per g of mucosa was high in the foetus (table 2) ; it did not change during the last part of intra-uterine life but decreased after birth. The amount of pepsin was 4.4-fold higher at birth than in the foetus ; it did not change during the first 71 postnatal days, but increased rapidly thereafter. The chymosin/pepsin ratio was very high in the foetus because there was little pepsin ; it remained high at birth and during the first 2 postnatal days but decreased significantly thereafter.

The total amount of chymosin did not change significantly but that of pepsin always increased with age (fig. 2). On a liveweight basis, the amount of chymosin tended to increase during the last part of foetal life (fig. 1) ; after 1.5 d of age, it decreased rapidly, being 5.8-fold lower at 148 d than at 1.5 d. The amount of pepsin was 7.9-fold higher at birth than it was 3 weeks earlier ; it increased slightly during the first 3 postnatal weeks and did not change thereafter.

Pancreatic enzymes. — Among the pancreatic enzymes assayed, only colipase had a decreasing specific activity during the end of foetal life (table 2) ; after birth, all the enzyme activities were minimal at 1.5 d and increased thereafter. The chymotrypsin/trypsin ratio was high in the foetus and in the very young calf, but from 21 d it was significantly lower than at birth. The colipase/lipase ratio was higher than 1.

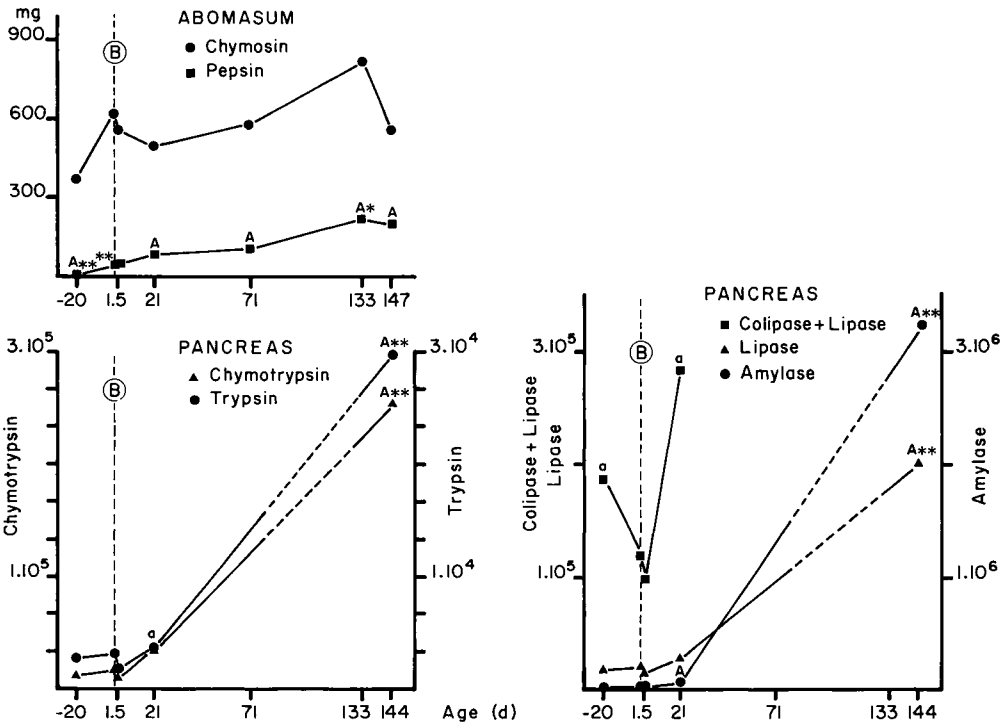

FIG. 2. — *Changes with age in the total amounts of abomasal enzymes and total activities of pancreatic enzymes.* B : birth.
Values with a superscript (a or A) are significantly different from those at birth ($P \leq 0.05$ or 0.001). Values with two or one asterisks are significantly different from those at 21 d ($P \leq 0.001$ or 0.02).

The total activities of trypsin, chymotrypsin, lipase and amylase were not modified between the foetal stage and 1.5 postnatal days, but they increased rapidly with age from 1.5 d (fig. 2). The total activity of lipase + colipase decreased during the end of foetal life and became very high at 21 d.

On a liveweight basis, only lipase + colipase activity changed towards the end of foetal life, the value observed at birth being 1.7-fold lower than it was 3 weeks earlier (fig. 1). After birth, the activities of all the enzymes tended to decrease until 1.5 d but increased rapidly thereafter.

TABLE 2

Development with age of amounts of chymosin (Ch) *and pepsine* (P) *per g of abomasal mucosa and of the specific activities of chymotrypsin* (Ct), *trypsin* (T), *lipase* (Lip), *colipase* (Colip) *and amylase* (Amyl). Mean ± SD.

Age at slaughter (days)		Foetus 260 d	0	1.5	21	71 (1)	133 (1)	147 (2)
Quantity of (mg)	Ch	7.28 ± 0.57	7.33 ± 4.14	5.82 ± 1.18	3.05 ± 1.28^{c}	2.71 ± 2.45	3.07 ± 1.20	2.30 ± 1.11^{a}
	P	0.11 ± 0.05^{b}	0.48 ± 0.17**	0.45 ± 0.16	0.50 ± 0.11	0.51 ± 0.28	0.85 ± 0.31^{c}	0.85 ± 0.38^{b}
Specific activity of	Ct	10.48 ± 1.12	9.04 ± 2.19	5.36 ± 2.04^{c}*	5.63 ± 0.61^{b}	NA	NA	10.73 ± 1.81
	T	0.48 ± 0.02	0.51 ± 0.17	0.34 ± 0.04	0.56 ± 0.07**	NA	NA	0.93 ± 0.16^{a}
	Lip	6.00 ± 0.86	5.59 ± 1.08	2.01 ± 0.27^{a}***	4.49 ± 0.30^{c}***	NA	NA	7.36 ± 1.02^{a}
	Colip	67.47 ± 17.19^{b}	31.28 ± 9.88** (3)	24.00 (4)	45.16 ± 8.32^{c}	NA	NA	NA
	Amyl	4.27 ± 1.83	3.09 ± 0.86	2.80 ± 0.56	10.63 ± 2.78^{a}*	NA	NA	119.43 ± 27.66^{a}
Enzyme ratios	Ch : P	85.3 ± 53.7^{b}	16.1 ± 7.0**	14.2 ± 7.5	5.9 ± 1.4^{c}	4.7 ± 2.2^{c}	4.2 ± 3.0^{c}	2.8 ± 1.4^{a}
	Ct : T	21.6 ± 2.0	18.3 ± 4.2	15.2 ± 2.5	10.1 ± 1.2^{b}*	—	—	11.7 ± 2.4^{a}
	Colip : Lip	11.4 ± 3.4	5.2 ± 1.0** (3)	10.9 (4)	10.1 ± 1.7	—	—	—

(1) Pancreas not collected.
(2), (3) and (4) : only eleven (2), six (3) or one (4) pancreata analysed.
NA : Not assayed.
Means with a superscript (a, b or c) are significantly different from those at birth ($P \leq 0.001$, 0.01 or 0.05).
Means with three, two or one asterisks are significantly different from those of the preceding column ($P \leq 0.001$, 0.01 or 0.05).

Discussion.

Methodological aspects. — To estimate changes in the concentrations of the enzymes or their activities, the amounts were first expressed in relation to abomasal weight or to pancreatic protein. Values for the whole of the organs were then determined and finally related with the liveweight of the calves. The latter expression appeared the most suitable for comparing secretory potentialities at the different stages under study ; moreover, these potentialities could be studied in parallel with amounts of food intake expressed on the same basis.

It is not easy to obtain a series of organs from slaughtered calves of precisely known age. Therefore, only two calves were used at 1.5, 71 and 133 d. However, the changes observed between birth and 1.5 d were similar to those previously reported in lamb (Guilloteau *et al.,* 1983), and the values at 71 and 133 d were in keeping with the preceding and following ones. These difficulties have also been reported by other authors (Huber *et al.,* 1961 ; Siddons, 1968) who used only one, or sometimes two, calves at each stage studied.

It would have been interesting to measure the enzyme activities in the digestive contents too since Peyraud (1983) showed that amylase, maltase and lactase activities in the intestinal contents were 25-50 % of the total activities of the digestive tract of preruminant lamb. However, our calves were slaughtered at least 16 h after the last meal, and it has been shown that abomasal and pancreatic enzyme secretions in preruminant calf are low at that time (Ternouth, Roy and Shotton, 1976 ; Davicco, 1978 ; Guilloteau and Toullec, 1983). From the data of Gorrill and Thomas (1967), one can estimate that, as far as trypsin and chymotrypsin are concerned, the total activities found in the small intestine contents of calves slaughtered 60-90 min after feeding represent only about 11 % of the activities measured in the pancreas.

Enzyme potentialities and age. — On a liveweight basis, the changes observed with age in the secretory potentialities of preruminant calf were very close to those previously described in preruminant lamb (Guilloteau *et al.,* 1983). At birth, trypsin, lipase and lipase + colipase activities were similar in the two species ; however, the amount of pepsin and the activities of chymotrypsin and amylase were 3, 2 and 12-fold higher, respectively, in lamb. Chymosin was the only enzyme studied which showed a higher content (2-fold) in the calf. Amylase activity and pepsin amounts remained higher in the lamb, at least until 21 d of age (15 and 4-fold, respectively). The amount of chymosin and the activities of trypsin and chymotrypsin were at similar levels in both species at 2 and 21 d, whilst the activities of lipase and lipase + colipase were 2-fold lower in lamb at 21 d.

In the foetal pig, Foltmann *et al.* (1981) did not detect any gastric enzyme 40 d before birth ; a large amount of chymosin was found 20 d later but there was no pepsin. Likewise, in the foetal lamb, Alais (1963) observed an important clotting activity (assayed on cow milk at pH 6.7) during the 24 d preceding birth. Track *et al.* (1972) and Track, Creutzfeldt and Bokermann (1975) reported chymotrypsin and trypsin activities but none for amylase in the pancreas of

bovine and human foetuses. Therefore, chymosin, trypsin, chymotrypsin, lipase and colipase seem to be present in large amounts towards the end of foetal life, whilst pepsin and pancreatic amylase stay at very low levels until the perinatal period.

The decrease in mucosal chymosin concentration observed after 1.5 d of age agrees with the results reported on clotting activity or chymosin content of calf abomasum (Kirton, Paterson and Clarke, 1971 ; Hagyard and Davey, 1972 ; Andren, Björck and Claesson, 1980 ; Valles, 1980). Patterns of protease secretion similar to our results on abomasal mucosa have been observed in gastric pouches of preruminant calves (Williams, Roy and Gillies, 1976 ; Guilloteau and Toullec, unpublished results). However, Pelletier *et al.* (1983) observed a decrease between 1 and 14 days in the pepsin concentration/mg protein in calf mucosa.

Protease, trypsin, chymotrypsin, lipase and amylase activities found in the pancreas (Walker, 1959a, b ; Huber *et al.,* 1961 ; Siddons, 1968 ; Pelletier and Dunnigan, 1983), the duodenal content (Brown and Perry, 1981) and the pancreatic juice (Morrill *et al.,* 1970 ; Ternouth, Roy and Shotton, 1976 ; Davicco *et al.,* 1979) also increase with age in the preruminant. Contrary to other authors, Huber *et al.* (1961) and Brown and Perry (1981) did not observe any increase after 8 and 14 d in calf and lamb, respectively. To our knowledge, the development of colipase activity has not yet been described in the preruminant calf. From the foetal stage until 21 d after birth, the colipase/lipase ratio was higher than 1, showing that pancreatic lipase was saturated and thus that lipolytic activity was theoretically entirely expressed when the pancreatic juice arrived in the intestinal lumen.

Enzyme potentialities and feeding. — At birth, before a meal, all the proteolytic and lipolytic enzymes studied exhibited high secretory potentialities probably due to the accumulation of zymogenic stores during the last part of foetal life. Just after birth, during the colostrum feeding period, abomasal potentialities increased or remained high, whereas pancreatic potentialities tended to decrease. This probably favoured casein coagulation in the abomasum and low extracellular protein digestion in the small intestine of the newborn ; therefore, most of the macromolecules could be absorbed intact, a necessary process in the preruminant calf which must absorb immunoglobulins for protection.

At pH 6.3-6.4, 1 mg of chymosin coagulates 1.0-1.5 liters of milk in 100 sec at 30 °C (Raymond *et al.,* 1973 ; Martin *et al.,* 1981). The clotting activity of pepsin is 2.0 to 2.6-fold lower than that of chymosin. Thus the total clotting activity/casein intake ratio decreased as age increased. However, at 147 d, the gastric mucosa still contained 50-fold more chymosin and 9-fold more pepsin than was required to coagulate the daily milk intake at pH 6.3-6.4. Abomasal content pH is about 5 just after feeding (Guilloteau *et al.,* 1975), facilitating coagulation. The abomasal lumen always seems to contain enough chymosin and pepsin to coagulate the amount of casein supplied by a meal.

On a liveweight basis, pepsin, chymotrypsin, trypsin, lipase and colipase activities increased between birth and 21 d, probably corresponding to an adaptation to intake level since the amounts of dry matter, nitrogen and fat

intakes augmented during the same time. After 21 d, these activities (except that of pepsin) continued to increase but the intake level did not change or decreased. Thus, after 21 d, enzyme potentialities depended more on age than on the amount of food intake. After birth, amylase activity increased like that of the other pancreatic enzymes, whereas the starch level in the milk replacer was always low (less than 3 % in DM). Therefore, in our experimental conditions, the development of amylase activity, like that of chymosin, appeared to depend more on age.

The amounts of food intake were about 4 and 2-fold lower in the calf than in the lamb at 2 and 21 d, respectively (Guilloteau *et al.,* 1983). Therefore, except for pepsin and amylase, the preruminant calf appeared to have higher enzyme potentialities in relation to food intake than did the preruminant lamb. However, the amounts actually secreted are not accurately known in either species.

In conclusion, the abomasal and pancreatic glands of the bovine foetus already contain large amounts of enzymes, except pepsin and amylase. After birth, the development of secretory potentialities is similar to that observed in lamb (Guilloteau *et al.,* 1983) and can be divided into three phases : during the colostrum feeding period, the trend of pancreatic potentialities is the reverse of that observed for abomasal potentialities ; from 1.5 to 21 d, most of the enzyme potentialities (except those of chymosin and amylase) appear to be stimulated by intake level ; after 21 d (1.5 d for chymosin and amylase), the development of enzyme potentialities probably depends more on age than on intake.

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Résumé. *Potentialités enzymatiques de la caillette et du pancréas du veau. I. — Effet de l'âge chez le préruminant.*

Trois fœtus sont collectés dès l'abattage de leur mère (260 j de gestation) et trente-deux veaux sont maintenus au stade préruminant et abattus entre la naissance et l'âge de 147 j. La muqueuse de la caillette et le pancréas sont collectés et analysés.

La chymosine, la trypsine, la chymotrypsine, la lipase et la colipase sont déjà présentes en quantités importantes chez le fœtus, contrairement à la pepsine et à l'amylase. Après la naissance, la quantité de chymosine rapportée au poids vif de l'animal est maximum à 1,5 j et décroît ensuite ; celle de pepsine augmente jusqu'à 21 j puis ne change plus. L'évolution des activités enzymatiques du pancréas est généralement l'inverse de celle de la chymosine ; l'activité amylasique est particulièrement faible à la naissance.

Après la naissance, l'évolution des potentialités de sécrétion peut être scindée en 3 phases. Pendant la période d'ingestion du colostrum, les potentialités pancréatiques évoluent en sens inverse de celles de la caillette. De 1,5 à 21 j, la plupart des potentialités enzymatiques (sauf celles de la chymosine et de l'amylase) semblent être stimulées par le niveau des quantités ingérées. Après 21 j (ou 1,5 j pour la chymosine et l'amylase), l'évolution des potentialités enzymatiques doit être davantage influencée par l'âge de l'animal que par son niveau d'ingestion.

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