Electrolyte Levels and Net Fluid and Electrolyte Movements in the Gastrointestinal Tract of Weanling Swine

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ABSTRACT

Electrolyte concentrations, osmolality and pH were determined in conventionally raised weanling swine fed a liquid diet. Incorporation of a dilution marker into the diet in combination with frequent feeding enabled estimations as to the sites of relative fluid and electrolyte absorption and secretion along the gastrointestinal tract. Unlike many other species the weanling pig depends largely on its large intestine for absorption of fluid and electrolytes with small changes in net fluid movement occurring along the jejunal and ileal segments. Additional observations included the absorption of water by the porcine stomach which increased dilution marker concentration by approximately twofold and the high osmolality values recorded in the small and large intestine. The implications of these observations are discussed with regard to pathogenesis of colibacillary diarrhea in the weanling pig.

RÉSUMÉ

Cette expérience visait à déterminer les concentrations d'électrolytes, l'osmolalité et le pH, chez des porcelets récemment sevrés et élevés de façon conventionnelle, auxquels on servait une diète liquide. L'incorporation à la diète d'un marqueur de dilutions, de concert avec plusieurs repas quotidiens, permit d'obtenir certaines données concernant les sites approximatifs d'absorption et de sécrétion de liquide et d'électrolytes, le long du tube gastro-intestinal. Contrairement à ce qui se passe chez plusieurs autres espèces, c'est surtout à la hauteur du côlon que le porcelet récemment sevré absorbe le liquide et les électrolytes, tandis que des changements minimes, relatifs au flot net du liquide, se produisent dans le jéjunum et l'iléon. D'autres observations portaient sur l'absorption de l'eau par la muqueuse stomacale du porc, en utilisant une dilution environ deux fois plus grande du marqueur, et sur les valeurs élevées de l'osmolalité, enregistrées dans l'intestin grêle et le côlon. Les auteurs commentent les implications de ces observations en rapport avec la pathogénèse de la diarrhée à colibacilles, chez le porcelet récemment sevré.

INTRODUCTION

Quantitative information on the sites and relative extent of net absorption and secretion of gastrointestinal fluid as a background for an understanding of diarrheal disease in weanling swine is quite limited. Alexander (1) has reported on electrolyte concentrations of ingesta from selected sites along the gastrointestinal tract of slaughtered adult swine. Presnell (29) has studied electrolyte flux in the small intestine of swine using a perfusion technique which employed multilumen catheters introduced through Maydl fistulas. Although Presnell found demonstrable relative pore size differences between ileal and duodenal or jejunal segments, net ion and water flux measurements did not differ significantly in these regions. Balance studies can only provide indirect information as to the digestion and absorption of feedstuffs (9). Investigation into the processes of absorption and secretion of fluid and electrolytes should include examination of the entire digestive tract during the digestion and absorption of food.

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During this study D. L. Hamilton was a fellow of the Medical Research Council of Canada. This work was supported by the Alberta Agricultural Research Trust and the Alberta Hog Producers' Marketing Board.

Submitted June 30, 1976.

The extent of absorption and secretion that occurs at various levels of the digestive system may be determined by means of water soluble markers incorporated into the test meal. This permits estimation of net transmural movements of water and other constituents by comparison of digesta concentrations with the unabsorbed dilution marker. Interpretation is facilitated if a steady state situation with respect to the marker can be established. Studies in sheep (17) with polyethylene glycol 4000 (PEG) as a dilution marker have been successfully used to follow the sites of electrolyte and water absorption and secretion throughout the entire abomasum and intestinal tract. An approximation of steady state movement of marker and ingesta is approached in this type of study due to the regular emptying of the rumen into the abomasum. Due to the intermittent feeding and gastric emptying of monogastric animals, marker concentrations following a single test meal containing a dilution marker have not approached a steady state (11, 23, 24). To circumvent or minimize this problem we have employed very frequent feeding of a commercial feed suspended in water and containing PEG as a nonabsorbable dilution marker.

The objective of this study was to determine electrolyte concentrations and sites of relative fluid and electrolyte absorption and secretion along the gastrointestinal tract of the weanling pig.

MATERIALS AND METHODS

EXPERIMENTAL DESIGN

One litter of eight, four week old, creep-fed piglets consisting of four castrated males and four intact females were weaned to a liquid diet. The diet was prepared by mixing an unmedicated commercial 18% with water at a 3:1 volume/volume ratio of water to feed. PEG[2] was added to the water at a concentration of 0.5 mg/ml. The liquid feed was provided two times daily for the duration of the experiment on days other than those used for sampling. Immediately prior to sampling the following feeding regime was instituted. The animals were fed a predetermined quantity of feed every hour for four hours and then every half hour for two more hours. The amount fed per pig per unit time was constant and based upon previous eating habits to ensure immediate and complete intake of each portion. Preliminary work with pigs fistulated at the level of the ligament of Treitz indicated that this feeding regime resulted in satisfactorily constant marker concentrations at the time of sampling (14).

Following completion of the feeding regime, general anesthesia was induced with an intravenous injection of sodium pentobarbital (30 mg/kg). A venous blood sample was removed and serum collected for electrolyte analysis. The abdomen was entered by a midline incision and the pylorus, proximal jejunum at the ligament of Treitz and the ileocecal junction were quickly ligated to reduce movement of ingesta during further manipulation of the gastrointestinal tract. Next the animals were sacrificed with an overdose of anesthetic and the entire gastrointestinal tract removed. Ingesta was sampled from the pyloric area of the stomach, duodenum, four equally spaced regions of the jejunum, ileum, cecum, three equally spaced areas of the spiral colon and descending colon. Direct pH determinations were immediately made on all samples of ingesta following removal from the gastrointestinal tract. To separate the fluid from the solids all samples were centrifuged at 20,000 x g at 0°C for 30 minutes and the supernatant analyzed for osmolality, electrolyte and PEG concentrations. All animals were studied between the age of five and eight weeks.

In addition, osmolality and electrolyte concentrations of sodium, potassium and chloride were determined in fecal fluid collected from feces of weanling swine fed the same diet but in the dry form with water *ad lib* to compare with those values observed in the above study. Collection was made at the time of defecation and immediately processed using the same methodology.

ANALYTICAL

Sodium and potassium concentrations were determined by flame photometry with

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[1] Co-op 18% Pig Starter, Federated Co-operatives Ltd., Saskatoon, Sask. Crude analysis: crude protein 18%, crude fat 2.5%, crude fiber 6.0%, NaCl 0.5%, Ca 1.0%, and P 0.8%.

[2] Carbowax 4000, Union Carbide Chemicals Co., New York.

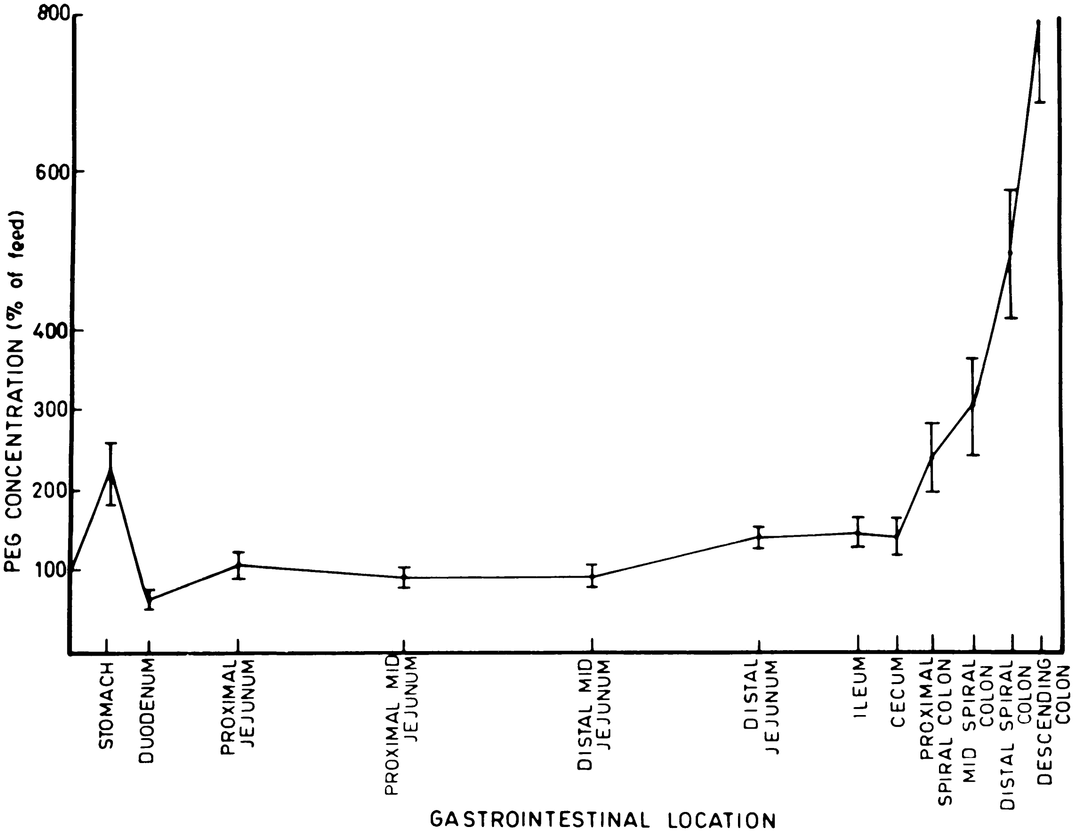

Fig. 1. Mean concentrations ± SE of PEG at the various gastrointestinal locations expressed as a percentage of the concentration in the liquid feed. The scale of the ordinate axis is approximately proportionate to the length of the various gastrointestinal locations.

lithium as internal standard. Chloride concentration was determined by coulometric-amperometic titration. PEG concentration was measured spectrophotometrically essentially according to the method of Boulter and McMichael (4). The pH was determined with a combination thin glass electrode and the osmolality by freezing point depression.

In order to indicate absorption or secretory transmural movement between adjacent segments of the gut, the mean electrolyte data was expressed to indicate amounts relative to the stomach. The relative concentration per unit of PEG was calculated from the formula:

$$\text{Relative concentration} = \frac{[\text{PEG}]_s \times [\text{E}]_o}{[\text{PEG}]_o \times [\text{E}]_s}$$

PEG and E represent polyethylene glycol and electrolyte respectively and the subscripts s and o refer to the stomach and to a specified region of the intestinal tract distal to the stomach.

A randomized block analysis of variance in combination with Duncan's multiple range test for significance (Table I) was used for comparison of electrolyte and PEG concentrations between the various regions of the digestive tract (19).

RESULTS

POLYETHYLENE GLYCOL CONCENTRATIONS AND NET WATER MOVEMENT

Figure 1 shows the mean concentrations of reference substance collected at the specified levels of the gastrointestinal tract expressed as percent of concentration in the fluid feed. PEG concentration doubled in the stomach followed by a two to threefold dilution in the duodenum. Throughout the small intestine the level of PEG did

TABLE I. Data and Duncan's Multiple Range of Study[a]

Position in G-I Tract[b]	1	2	3	4	5	5	6	8	9	10	11	12	Blood	Feed	Feces
PEG............	227 (32)[c]	64 (7)	106 (13)	95 (9)	96 (10)	135 (10)	150 (17)	146 (23)	243 (46)	308 (61)	503 (80)	796 (120)	—	100	—
Na (mEq/1)......	24 (1)	99 (3)	83 (4)	81 (2)	86 (2)	78 (7)	95 (5)	87 (6)	72 (6)	63 (5)	44 (5)	40 (5)	147 (1)	42 (3)	23[d] (5)
K (mEq/1).......	25 (1)	38 (2)	26 (4)	17 (3)	13 (2)	12 (1)	14 (1)	10 (1)	15 (2)	20 (2)	31 (3)	43 (2)	5.0 (0.3)	35 (3)	98[d] (7)
Cl (mEq/1).......	112 (5)	93 (3)	88 (8)	81 (8)	60 (8)	40 (3)	35 (3)	26 (1)	29 (1)	24 (1)	22 (1)	24 (1)	100 (1)	35 (3)	13[d] (2)
Osmolality (mOsm)........	283 (4)	494 (32)	575 (28)	609 (31)	585 (26)	441 (13)	396 (6)	370 (5)	398 (9)	398 (5)	395 (7)	391 (9)	312 (5)	274 (24)	399 (10)
pH..............	3.62 (0.11)	6.00 (0.06)	6.14 (0.09)	6.53 (0.22)	6.55 (0.10)	6.71 (0.12)	6.68 (0.12)	6.27 (0.12)	6.11 (0.09)	6.27 (0.17)	6.87 (0.15)	7.22 (0.16)	7.36 (0.02)	5.34 (0.04)	—

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[a] The 12 mean values for each variable measured throughout the gastrointestinal tract were arranged according to their ascending magnitude. The shortest significant range for each group of measurements was determined and the differences between means tested at the 0.01% level. Once statistical significance was determined between mean values they were rearranged according to their natural order with those adjacent mean values that were not statistically different underscored

[b] Positions in G-I tract 1-12 are stomach, duodenum, proximal jejunum, proximal midjejunum, distal midjejunum, distal jejunum, ilean, cecum, proximal spiral colon, midspiral colon, distal spiral colon and descending colon respectively

[c] Standard error of mean in brackets beneath mean values of eight animals fed liquid diet, except data on feces which is the mean value and standard error of mean of 12 animals fed dry commercial feed with water *ad lib*

[d] Statistically different from values of the descending colon (column 12) $P < 0.01$

not differ significantly. In the large intestine PEG concentration increased rapidly to almost eight times the concentration in the small intestine.

The relative net volume changes of fluid in relation to those found in the stomach are shown in Fig. 2. A three and one-half-fold increase in net fluid volume occurred within the duodenum. Following an initial net decrease in the proximal jejunum, the net absorptive change in fluid volume occurring along the entire length of the jejunum, ileum and cecum was about 30% of that entering the proximal jejunum. The most significant absorption occurred in the spiral colon and descending colon of the large intestine, amounting to 57% of the fluid entering the proximal jejunum.

SODIUM

Stomach fluid only contained 24 mEq/l of sodium (Fig. 3) which increased abruptly to 99 mEq/l in the duodenum. Sodium concentration was relatively uniform along the small intestine with no significant decrease occurring before the midspiral colon. In the descending colon the mean sodium concentration had decreased to only 40 mEq/l.

The relative net sodium movement estimated from changes in PEG and sodium concentrations (Fig. 2) demonstrated that the increase in sodium concentrations occurring between the stomach and the duodenum (Fig. 3) also reflected an absolute increase which was greater than the increase in water. Net sodium absorption was greatest in the proximal jejunum where it closely parallelled water movement. In the distal small intestine and large intestine most of the remaining sodium was absorbed at a rate that closely paralleled water movement.

POTASSIUM

The mean potassium concentration in the stomach was 25 mEq/l (Fig. 3). This increased significantly to 38 mEq/l in the duodenum. Mean potassium concentrations fell gradually along the jejunum and ileum to only 10 mEq/l in the cecum. Thereafter the potassium concentration increased steadily to 43 mEq/l in the descending colon.

Net potassium change as shown in Fig. 2 exceeded fluid movement between the stomach and duodenum. Between the proximal jejunum and cecum net potassium absorption occurred at a rate that slightly exceeded net fluid absorption. Throughout the large intestine negligible changes occurred in the relative amounts of potassium.

CHLORIDE

Chloride concentrations (Fig. 3) were highest in the stomach with a mean of 112 mEq/l. Thereafter mean chloride levels fell steadily to a minimum of 24 mEq/l in the descending colon. Net changes in the relative amounts of chloride (Fig. 2) indicated that net secretion of chloride in the duodenum was less than water. Along the rest of the intestinal tract net chloride absorption consistently exceeded net water absorption.

OSMOLALITY AND pH

The mean osmolalities of the gastrointestinal contents are shown in Fig. 4. The osmolality of gastric fluid was consistently less than that of serum (283 vs 312 mOsm). Thereafter osmolality rose rapidly to 494 mOsm in the duodenum with a peak of 609 mOsm in the midjejunum. Thereafter the osmolality fell to 370 mOsm in the cecum and remained slightly less than 400 mOsm throughout the large intestine. While large variations in osmolality were observed in the duodenum and proximal jejunum, readings in the stomach, ileum, cecum and large intestine were confined within narrow limits.

The gastric contents had a mean pH of 3.6 (Fig. 4). The pH of the intestinal contents was relatively constant with greatest fluctuations occurring in the midjejunum. A gradual increase in pH from a mean of 6.0 in the duodenum to 6.7 in the ileum was recorded. An abrupt drop in pH from 6.7 in the ileum to 6.1 was observed in the cecum and proximal portion of the spiral colon, followed by a steady increase to 7.2 in the descending colon.

FECAL ELECTROLYTE CONCENTRATIONS AND OSMOLALITY

The mean electrolyte concentrations and

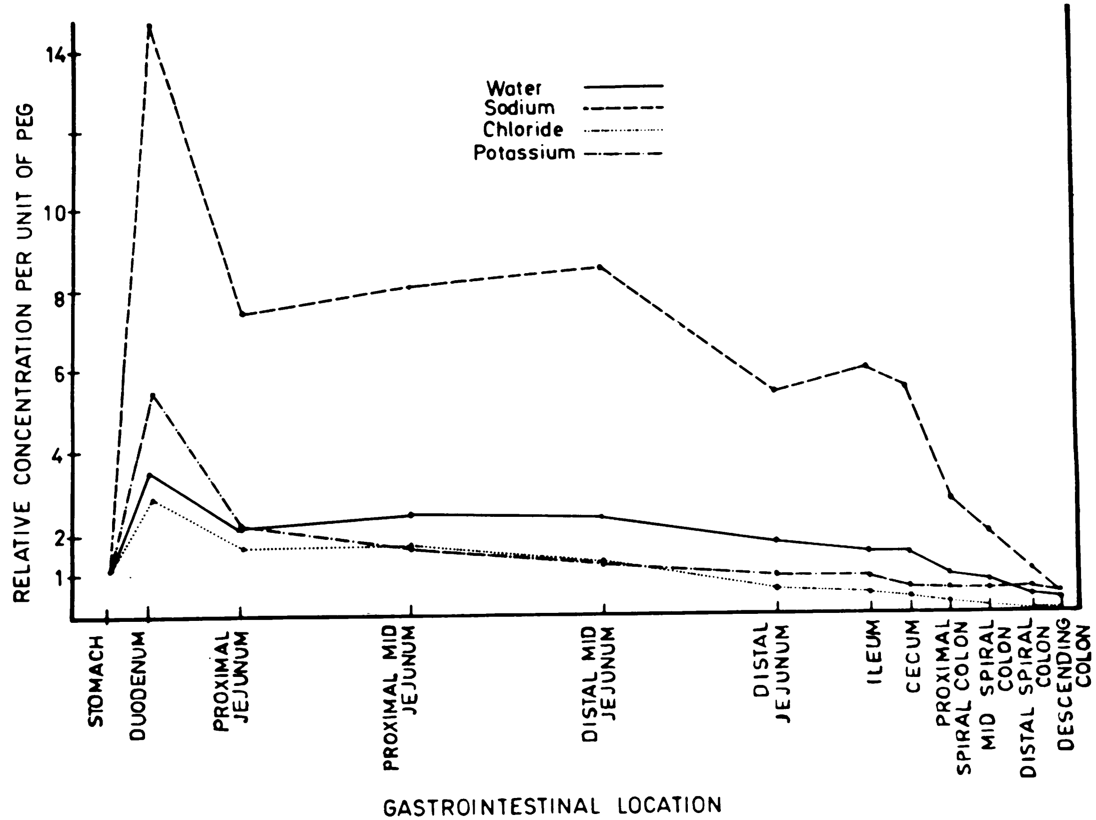

Fig. 2. Relative net changes in water, sodium, chloride and potassium that occurred along the intestinal tract of weanling swine using the gastric levels as a reference point. Mean data for each parameter for all eight pigs were used in this calculation of relative concentration.

osmolality of feces from conventionally raised weanling swine fed the same diet except in the form of dry crumbles with water *ad lib* are shown in Table I. The mean sodium and chloride values were significantly lower ($P < 0.01$) and the potassium values significantly greater ($P < 0.01$) than samples from the descending colon of the pigs fed the liquid diet (Student's unpaired t-test). Osmolality values, however, were not significantly different.

DISCUSSION

Currently, both dry and liquid feeding of swine are practiced commercially although liquid feeding may be superior in some respects. Varying the ratio of water to dry feed above those used in this study has resulted in no significant effects on digestibility, nitrogen retention, growth rate, feed conversion efficiency and carcass quality (18).

Feeding small amounts of the liquid diet at short time intervals permitted the entire gastrointestinal tract to approach a constant flow of ingesta. While this was not a normal feeding procedure it did lend itself to the study of ionic concentrations and net changes in volume and electrolytes during digestion along the entire intestinal tract.

An unexpected observation was the increase in marker concentration that occurred in the stomach ingesta (Fig. 1). This indicated a net absorption of fluid by the porcine stomach. Studies involving net fluid absorption by the stomach of monogastrics are limited (30) and certainly absorption of this magnitude has not been reported previously. The stomach of the dog is quite permeable to water (6) and the unidirectional absorption of water by the dog stomach has been reported (7) but measurements of net fluid absorption are not documented. The increase in marker

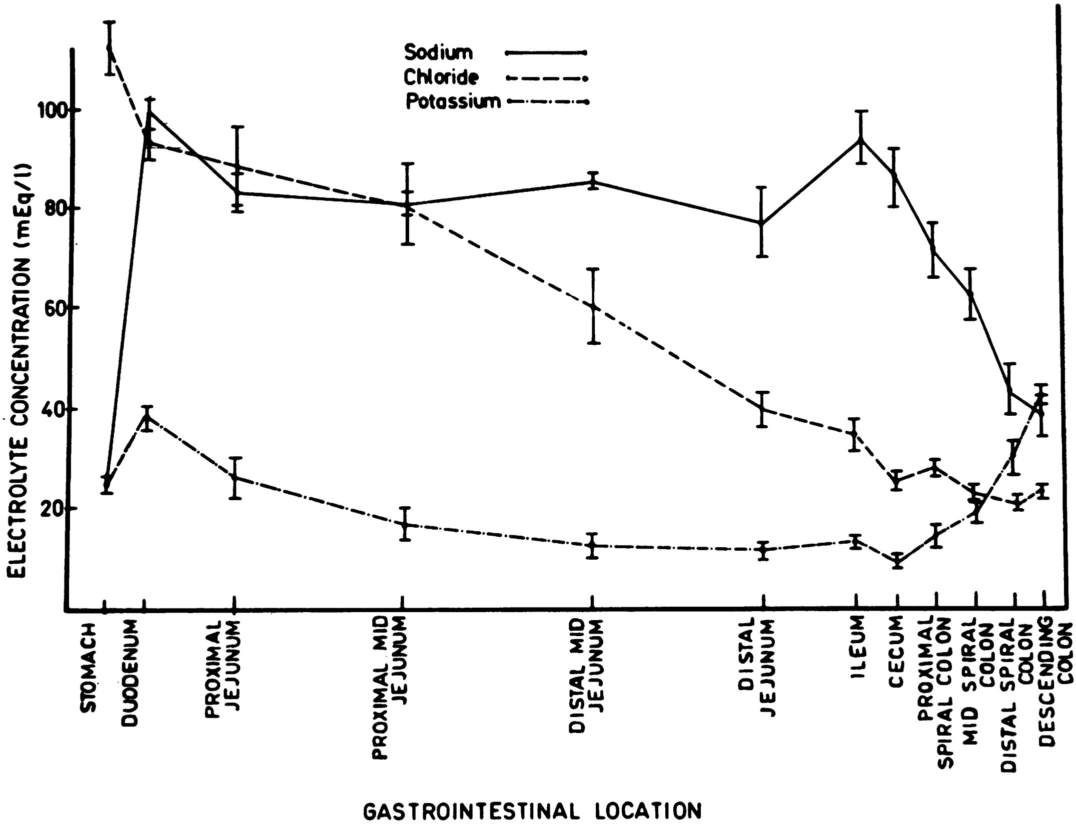

Fig. 3. Concentrations of sodium, chloride and potassium in luminal fluid plotted against the specified gastrointestinal locations and expressed in milliequivalents per liter ± SE.

concentration was not due to latent water imbibition by the feed subsequent to ingestion since preparations of the feed-water mixture which were stirred *in vitro* for up to six hours did not demonstrate a change in marker concentration (unpublished observations). It is also unlikely that a differential passage of fluid and marker out of the stomach exists for polyethylene glycol as it is highly water soluble. Therefore it is likely that actual net absorption of water by the stomach occurred perhaps as a result of volatile fatty acid absorption by the diverticulum ventriculi area of the porcine stomach which is not present in the simple stomachs of dog or man.

Only a small amount of net water absorption occurred from jejunum to cecum. Similar studies in adult cows, young calves and man, utilizing a test meal and dilution marker, have indicated that most of the fluid and electrolytes presented from the duodenum and stomach was absorbed before reaching the distal region of the small intestine (11, 17, 24). This variation may be due to species differences, dietary discrepancies in crude fibre or feeding regime. However this is not unique to the pig as Powell and co-workers (28) have reported that the small intestine of the guinea pig spontaneously secretes into the lumen of the gut at a rate which exceeds absorption. Perfusion and isolated loop studies of the small intestine of clinically normal weanling swine in our lab have indicated that it is not unusual for the pig small intestine to be in a state of net secretion (14, 29).

The osmolality values recorded in the small intestine exceed previously published data in swine and other mammals (11, 15). Frequent feeding of a liquid diet may have permitted large amounts of ingesta to enter the small intestine and thereby exceed the absorptive capacity of the intestinal mucosae. The resultant digestion and consequent liberation of osmotically active products may have caused the high osmolality values. Alternatively, the osmolality may have increased following removal of the ingesta from the gut but this was unlikely as all samples were quickly cooled at 0°C immediately following removal. The establishment and maintenance of this large osmotic gradient may be the result of an intestinal fluid circuit or countercurrent exchange as originally proposed by Florey (10) and more recently by Lundgren (21). Bellamy *et al* has described the vascular anatomy of the porcine small intestine (3) and like the rabbit, dog, rat and man it met the requirements for the formation of a fluid circuit.

However, osmolality as measured by freezing point depression refers to a theoretic osmotic pressure that would be achieved with a perfectly semipermeable membrane. The effective osmotic pressure depends on the concentration of ions and nonelectrolytes in solution and on the permeability of the solutes. Since the solutes of gastrointestinal fluids and plasma are permeable to intestinal mucosa to a variable extent, the theoretic and effective osmotic pressure may differ considerably and it is possible for a fluid which has a theoretic osmolality that is more than plasma to have an effective osmotic pressure that is less than plasma. Thus an osmolality different from plasma may not necessarily indicate that a driving force for fluid movement is present.

The osmolality of the pig's stomach fluid was hypotonic to plasma. This is believed to be the result of secretion and mixture of two fluids, one isotonic HCl and the other similar to an ultrafiltrate of plasma. The reaction of H^+ with HCO_3^- and the consequent loss of CO_2 results in a hypotonic fluid (20).

The mean osmolality of fluid in the large intestine was consistently greater than plasma and did not vary appreciably from ileum to distal colon. These values agree with those determined in fecal fluid obtained from weanling swine fed the same dry diet with water *ad lib* (Table I). Therefore they probably represent the normal osmolality of fecal fluid in these animals.

Gastrointestinal electrolyte levels were

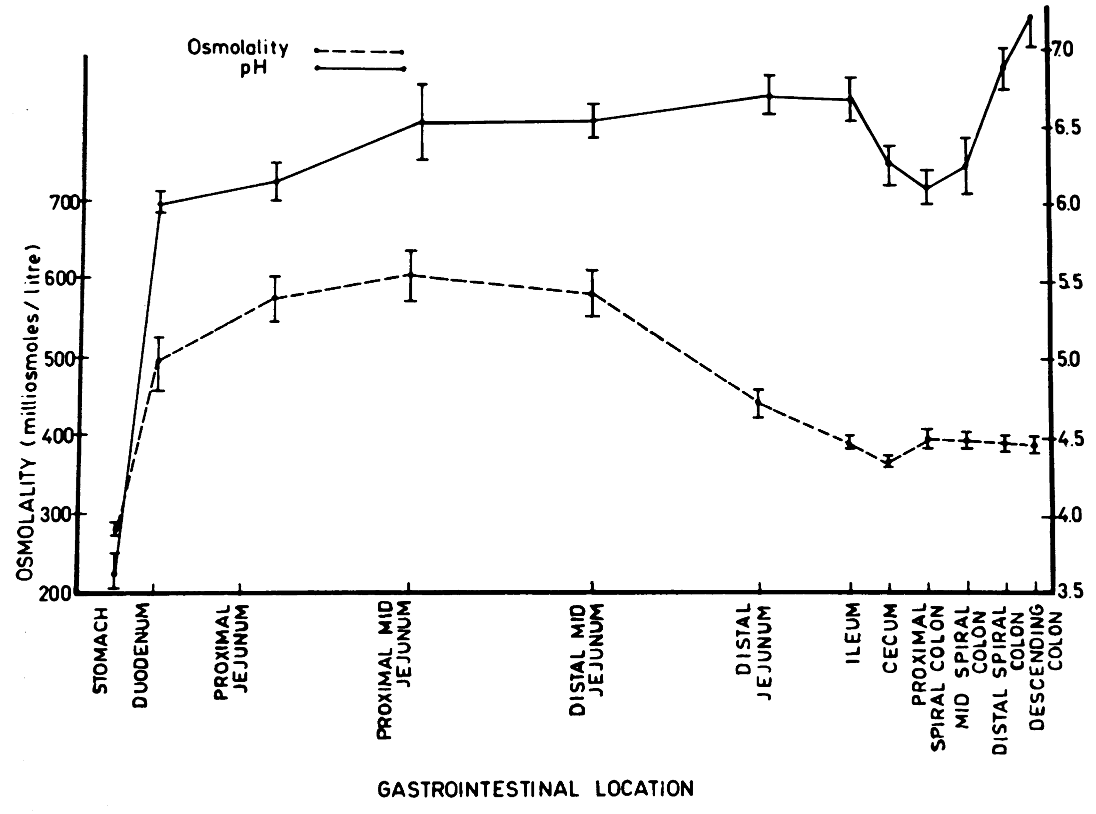

Fig. 4. Osmolality in milliosmoles and pH of gastrointestinal contents along the gastrointestinal tract of weanling swine (Mean values ± SE).

quite similar to previous reports in other mammals (2) and the pig (1). Sodium levels were lower than reported in fasting animals (16, 22). Mylrea (24) has reported that sodium concentrations in the small intestine of the calf decrease in response to feeding. The low sodium levels observed in this study may be the result of frequent feeding. A large increase in concentration and absolute amount of sodium occurred during passage of ingesta through the duodenum (Figs. 2 and 3). This was probably the result of biliary, pancreatic and duodenal secretions. A large proportion of sodium and water was absorbed in the proximal jejunum, presumably occurring with the absorption of readily digestible and actively absorbed nonelectrolytes. With the exception of the duodenum, net sodium and water changes closely paralleled each other in agreement with the transport of water along the osmotic gradients established by the absorption of sodium. In the duodenum the net increase in sodium exceeded the increase in water (Fig. 2). A cation exchange of Na^+ for some other ion such as K^+ or H^+ could explain the excessive net gain of sodium.

The potassium concentrations observed in the duodenum and proximal jejunum are higher than reported for fasting animals (8, 16). However they are similar to those observed by Alexander in the nonfasted adult pig (1). An increase of potassium following feeding has been reported in man (11) and the calf (24) and it probably results from its release during the degradation of feedstuffs. Thereafter potassium levels can be accounted for by passive absorption. While the concentration of potassium increased in the large intestine (Fig. 3) no significant relative change in the amount of potassium was observed (Fig. 2). Potassium is believed to be transported passively in both the small (26, 27, 32) and large (13, 26) intestine of mammals and this increase in potassium concentration is probably the result of a large negative transmembrane potential that is known to occur along the lumen of the colonic mucosa (13).

Chloride concentrations in the pig's gastrointestinal tract closely followed the levels reported in other animals (16). Chloride levels in the proximal jejunum and duodenum were less than reported for fasting mammals but again this is probably an effect of feeding as reported in calves (24). The authors have observed chloride levels of 125-135 mEq/l in the fasting duodenal fluid of normal weanling pigs (personal observation). Net absorption of chloride exceeded water absorption along the entire intestinal tract. A chloride-bicarbonate exchange has been proposed and described by other workers to explain this phenomena (27, 33).

The pH values (Fig. 4) in the small intestine were similar to those recorded in other animals. The drop in pH recorded in the cecum and proximal spiral colon may be peculiar to the pig (1) and other postgastric fermenters such as the rabbit, guinea pig and horse (1, 31). Volatile fatty acid levels are increased in these areas during feeding, with concentrations between 100 to 300 mmoles/liter recorded in the pig (5, 12). These acids constitute the major anions in the large intestine and may explain the lower pH in these areas of the intestinal tract (5). The differences in sodium and potassium concentrations between fecal samples collected from dry fed versus rectal samples in the liquid fed weanling swine may be due to differences in water intake affecting such factors as routes of excretion and aldosterone secretion.

The susceptibility of the weanling swine to colibacillary diarrhea is well established (25). This work indicates that the small intestine of weanling swine is in a delicate and precarious situation with regard to net fluid balance. The addition of more fluid would increase the already significant burden on the colon. Wilkinson and McCance found that removing the large intestine from newborn pigs resulted in the passing of voluminous watery feces (34). The pathogenesis of enteric colibacillosis in weanling pigs is believed to require the colonization, rapid proliferation and production of enterotoxins in the proximal small intestine by enteropathogenic *E. coli* (25). This study indicates that the presence of an enterotoxin which enhances net secretion of more fluid would add an excessive quantity of fluid to the distal small and large intestine. If the absorptive capacity of the colon is exceeded diarrhea will occur.

In conclusion, the weanling swine while having the same ionic constituents as described for other mammalian species appears to be able to maintain high osmotic gradients within its small and large intestine during digestion of feed and to depend extensively on its large intestine for absorption of fluid and electrolytes.

Since the weanling swine is a natural model for studying colibacillary diarrhea and its small intestine is in a delicate fluid balance it is an animal model of choice for studies involving intestinal secretion and the effects of various enterotoxins on the intestinal absorption and secretion of fluid and electrolytes.

ACKNOWLEDGMENTS

The invaluable technical assistance of Mrs. M. Johnson and the advice and encouragement of Dr. N. O. Nielsen is greatly appreciated. We also thank Miss B. Paproski for preparing the manuscript.

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