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Post-weaning growth of the Harp Seal, *Phoca groenlandica*

by

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1. INTRODUCTION

Harp seals, *Phoca groenlandica*, in the northwest Atlantic give birth to their young on pack ice in the Gulf of St. Lawrence and on the Front off Newfoundland in late February and early March. At birth pups lack a substantial blubber layer but this rapidly develops. Within hours, the pup begins nursing on milk which contains approximately 23% lipid. Fat content in the milk increases steadily to more than 40% (Lavigne *et al.*, 1981) during the lactation period which lasts about 9 days (Stewart & Lavigne, 1980). Total body weight increases rapidly with the pup gaining approximately 2.5 kg. per day, 1.9 kg. of which is sub-cutaneous fat (Stewart & Lavigne, 1980). At weaning the pup, now about 35 kg, is left to fend for itself (Stewart & Lavigne, 1980). Moulting occurs soon after weaning and is usually completed within a few days (Stewart, pers. comm.). This moult reduces the passive insulation afforded by the lanugo (Frisch & Oritsland, 1968) and reduces the pup's ability to utilize solar radiation as an external heat source (Oritsland, 1970; Oritsland & Ronald, 1973).

The moulted pup, or beater, soon enters the water. To feed, the beater, which may have already fasted several days before entering the water, must develop its swimming and

diving abilities and learn to forage. This period of learning to cope with the aquatic environment is initially a period of negative energy balance and is probably one of the most critical periods in the life of a harp seal.

It has been previously assumed that harp seal pups rely on the blubber layer as an energy source during fasting. The lightness and high energy yield relative to carbohydrate or protein makes it the favoured storage form of potential energy in most mammals. Another significant use of fat in marine mammals is as a thermal insulator. In a medium such as water, which transports heat away from the body twenty times as fast as air (Hart & Fisher, 1964), effective insulation is especially necessary. In harp seals, it appears that the insulation is critical since post-weaning harp seal pups lose weight from the core as opposed to the sculp (Stewart & Lavigne, 1980). The objective of the present study was to investigate in greater depth the responses of beaters to fasting and their ability to recover and grow when feeding begins.

2. MATERIALS AND METHODS

Twenty male harp seal pups, all in the early ragged-jacket age category (Stewart & Lavigne 1980), were collected by helicopter from the pack ice in the Gulf of St. Lawrence on 17 March 1980. These animals were flown to Charlottetown, P.E.I. and then transported to Guelph, Ontario by truck. Three additional animals were sampled in the field on 17 March to provide a reference point for subsequent changes in morphometrics.

The animals arrived in Guelph on 20 March and were weighed and tagged for future identification. Blood samples were taken for routine examination of hematology and blood chemistry . The monitoring of blood levels of circulating enzymes and metabolites, as well as routine hematology is an indespensible part of maintaining animals in captivity (Hunter & Madin 1976, Englehardt 1979, Geraci et al. 1975).

In the original experimental design, nine animals were randomly selected to be fasted while the remaining eleven were to be offered food. Two salt water tanks, at 10 C, were used for each treatment, and the animals within each treatment were randomly assigned.

One corollary of Murphy's Law states that in a carefully designed behavioural experiment, the well-trained animal does as it damn well pleases. It follows, then, that several seals in the present study had their own ideas about experimental design. A number of animals assigned to the treatment receiving food refused to eat, and this necessitated changes in the experimental protocol as the experiment progressed.

Four treatments were eventually examined. One group was force-fasted for the duration of the study and three groups were offered, and accepted, food after differing durations of fasting. The 'fed' group consisted of five animals which were fasted for a period of 8 days prior to being offered food. Recovery group 1 consisted of three animals: two of which began feeding after being force-fasted for a period of 29 days and one of which self-fasted for 29 days before beginning to eat. Recovery group 2 consisted of three animals: one of which refused food for 36 days , another which refused food for 44 days, and a third which was force-fasted for 29 days and then refused food for a further 15 days.

Food consisted of whole Pacific herring, Clupea pallasi , which was initially cut into 2.5 cm pieces. Once animals were feeding regularly, vitamin and mineral supplements were included as part of the diet (Table 1). Since the animals were in salt water, no NaCl supplements were given. Animals were offered a known weight of food twice daily. If an animal did not eat all of the fish offered, the remnants were weighed and subtracted from the weekly total intake record (Table 2) and discarded.

Each week, all animals were weighed and blubber thickness measured at 4 points along the mid-dorsum using an ultra-sonic depth detector (Scanoprobe, Ithaco, Ithaca, New York).

Physical and chemical blood properties were monitored weekly throughout the study to provide an indication of the general 'health' of the animals. All blood samples were taken from the hind venous plexus of restrained animals using a Vacutainer assembly (Becton Dickinson and Co., Canada, Ltd., Clarkson, Ontario). Blood was placed in K-EDTA (potassium ethylene diamine tetra-acetic acid) and Li-heparin tubes for routine hematology and sodium and potassium determinations and into serum tubes for blood chemistry. Samples for determination of blood glucose were placed in serum tubes containing sodium fluoride. All tubes, except the K-EDTA tubes, were centrifuged within one hour of sampling and the serum or plasma removed to dry ice for future analysis. The K-EDTA tubes were stored at 5 C and the hematology analyses were performed within 3 days of sampling (Geraci & Englehardt 1974).

Packed cell volume (PCV) was obtained using the micro-hematocrit technique (Simmons 1976). Red and white blood cell counts were done electronically (Coulter Counter) using 'Isoton' to dilute the sample (Coulter Electronics Inc, Hialeah, Florida). 'Zaponin' (Coulter Electronics Inc.) was used to produce erythrocytolysis to facilitate white cell counts, and for hemoglobin determination. Hemoglobin was measured on a Hemoglobinometer (Coulter Electronics Inc.). Mean cell volume (MCV), mean cell hemoglobin (MCH), and mean corpuscular hemoglobin content (MCHC) were calculated from the RBC count, hematocrit and hemoglobin values (Simmons 1976). Sodium and potassium levels were measured on a flame spectrophotometer (Radiometer, Copenhagen) using heparinized plasma. Total protein and blood glucose were measured using colorimetric

techniques as outlined in technical bulletin no.'s 540 and 115 respectively (Sigma Chemical Co., St. Louis). Serum levels of calcium, phosphorus, blood urea nitrogen (BUN), uric acid, serum glutamic - pyruvic transaminase (SGPT), serum glutamic oxalo - acetic transaminase (SGOT), lactate dehydrogenase (LDH), creatinine phosphokinase (CPK), alkaline phosphatase (alk. phos.), and creatinine levels were measured on an auto-analyzer (KDA, American Monitor, Indianopolis; Ontario Veterinary College, University of Guelph).

At bi-weekly intervals, three animals, two fasted and one fed, were selected at random for carcass analysis. At this time all routine morphometrics were obtained (American Society of Mammalogists 1967). In addition blubber thickness was measured at 10 locations with the ultra-sonic depth detector (4 mid-dorsally, 4 mid-ventrally and 2 laterally). These animals were sculped in sealing tradition to obtain sculp weights (weight of skin with blubber attached) and core weights, which were comparable with results obtained in the field. Core weight was further divided into weight of viscera and weight of the remainder of the carcass.

Percentage moisture was determined for the carcass and viscera by comparing the weight of a ground and homogenized freeze-dried sample with its wet weight.

Coincident with the laboratory study, beaters were also sampled in the area of White Bay, Newfoundland on the long liner, Cindy Elizabeth, from 14 to 23 April 1980 (n = 109) and from 9 to 20 May 1980 (n = 70). Most of these animals were shot in the water, but some were shot on ice. Total body weight was measured immediately to the nearest kilogram, uncorrected for blood loss due to the bullet wound. During the first trip, standard morphometric measurements were taken from all specimens within 2 hours of death. On the second trip this was also generally the case, but on one occasion some animals were killed late one day

and could not be measured until the next day. In the field, only the standard supraxyphysial blubber thickness measurement was obtained. Two intact carcasses, obtained between 14 and 16 May 1980, were analyzed in the same manner as the experimental animals described above.

3. RESULTS

3.1 GROWTH

Three animals sampled during the collection of the experimental animals on 17 March weighed 33.80 1.53 (S.D.) kg. On arrival in Guelph, mean weight of the remaining 20 animals was 32.14 3.28 kg, declining to 28.64 3.03 kg after seven days in captivity. This weight change amounted to a decrease of 3.5 kg over seven days or 0.5 kg per day. If this rate is used to extrapolate mean weight at capture three days prior to arrival, the result is 33.64 kg, or similar to that obtained for the three animals sampled at that time. These body weights are within the confidence intervals for both greycoat and ragged-jacket age categories (Stewart & Lavigne 1980) and suggest that age at capture was about 12 days post-partum.

Growth of individuals in the four treatment groups is summarized in Fig. 1. Also shown are data from beaters sampled on the Front between 14 and 23 April and 9 and 20 May 1980. The field data are not significantly different ($P = 0.05$) from the non-feeding study animals at age 43 days (April 18) and recovery group 2 animals at age 71 days (May 14), using Fisher's (protected) LSD procedure (Kleinbaum & Kupper 1978).

An analysis of covariance of weight versus age with weight on arrival in Guelph as the covariate, was performed on the four treatment groups (Fig. 2) (Statistical Analysis System, version 79.3 general linear models procedure). Fisher's (protected) LSD procedure ($P = 0.05$) was used to

test for significant differences between treatments at each age. At age 22 days, there were no significant differences ($P = 0.05$) between any of the treatments. The 'fed' group was offered food starting at this time and by age 36 days there was a significant difference between the 'fed' group and the three other groups that were all fasting at that time ($P < 0.05$). A week after food was introduced to recovery group 1 (age 50 days), the group was significantly heavier than the two non-feeding groups, but remained significantly lighter than the 'fed' group ($P < 0.05$). Recovery group 2 was significantly heavier than fasted seals, seven days (age 64 days) after it started feeding ($P < 0.05$). Also by age 64 days, the animals of recovery group 1 were not significantly different from the 'fed' group. By age 78 days, there was no significant difference between the two recovery groups, although recovery group 2 was still significantly lighter than the 'fed' group ($P < 0.05$), and all three feeding groups were significantly heavier than the 'fasted' group ($P < 0.05$).

To compare the growth rates of the different feeding groups, an analysis of covariance was done on weight versus days after initial feeding, with weight at the commencement of feeding as the covariate. Again Fisher's (protected) LSD procedure ($P = 0.05$) was used to test for significant differences between treatments (Fig. 3). At 14, 21, and 35 days after the commencement of feeding, there were no significant differences between the three feeding groups ($P < 0.05$). There were, however, significant differences between the two recovery groups and the 'fed' group at 7 and 28 days post commencement of feeding ($P < 0.05$). The adjusted mean weight of the 'fed' group was always lower than the adjusted mean weights of the two recovery groups (Fig. 3).

Total weight of field beaters ranged from 16 to 34 kg in April and from 16 to 32 kg in May. The distribution of these

animals, with respect to total weight, did not change appreciably between samples (Fig. 4). Experimental fasting animals at age 36 days had total weights between 20 and 24 kg, while fed animals were between 25 and 29 kg. In contrast the 'fasted' group animals at age 71 days ranged from 15 to 19.4 kg, recovery group 2 animals were 20 to 24 kg, and animals in both the 'fed' group and recovery group 1 were >30 kg.

The 'fed' and 'fasted' groups and field animals were also compared with respect to core weight, sculp weight and total weight (Fig. 5). Mean core, sculp, and total weights of the animals sampled in the field were intermediate to fed and fasting animals at age 43 days (April 18). At age 71 days mean sculp weight was similar but mean core and total weights were higher in the field and 'fed' groups than in the 'fasted' group (Fig. 5). Due to the small numbers of experimental animals involved, no tests of significance were performed on these data. Distribution of sculp weights for April and May field beaters indicated a trend to a lighter sculp (Fig. 4). The distributions of core weights remained unchanged (Fig. 4).

Core weight of the fasting animals declined 58% between the greycoat stage (age 9 days) and age 43 days (Fig. 5); from this point on core weight (now approximately 8 kg) did not change appreciably and approximated core weight of newborn animals (Stewart & Lavigne 1980). Percentage water of the carcass and viscera did not change over the entire study period (Fig. 6). Sculp weight of the fasting animals declined to 80% of the greycoat stage sculp weight by age 29 days. The weight of the viscera as a percentage of total weight remained constant, but when carcass and sculp weights were expressed as a percentage of total weight there was a dramatic change in percentages between age 57 and 71 days (Fig. 7). Up to age 57 days the sculp comprised approximately 38% of total weight and the carcass 34%. After

age 57 days, the sculp comprised approximately 46% of the total.

In animals which were feeding, there was also an initial decline in sculp weight (Fig. 5) but after day 43 sculp weight remained quite constant. Core weight of the feeding animals increased over time (Fig. 5). Sculp weight as a percentage of total weight declined due to an increase in core size and weight (Fig. 7). In a recovery group 1 animal killed at age 71 days which had been feeding since age 44 days, the sculp comprised only 39.1% of the total weight (Fig. 7).

3.2 CHANGES IN BLUBBER THICKNESS

The Scanoprobe's accuracy and precision in measuring blubber thickness was checked whenever animals were killed by comparing with the standard field measurement technique (American Society of Mammalogists 1967). Accuracy was determined to be -1.1 2.2 mm (95% C.I.).

A covariate analysis of blubber thickness at each of the four points monitored, using initial thickness as the covariate, and subsequent comparison of adjusted means using Fisher's (protected) LSD procedure ($P = 0.05$), revealed very few significant differences between treatments (Fig. 8). The 'fasted' group exhibited the largest decline in blubber thickness at all four points, whereas the 'fed' group maintained blubber thickness. The two recovery groups, especially recovery group 2, continued to show declines in blubber thickness even after the onset of feeding.

Blubber thicknesses obtained from field beaters showed a decline in mean thickness from 31.0 5.0 mm (S.D.) in mid-April to 26.5 4.7 mm in mid-May. The distribution of blubber thicknesses indicated a definite trend to a thinner blubber layer over time (Fig. 4).

3.3 CHANGES IN BLOOD PARAMETERS

Red and white cell numbers, hemoglobin and PCV remained constant throughout the study, regardless of treatment (Table 3). There also were no significant differences between treatments with respect to MCV, MCH or MCHC (Table 3).

In monitoring the levels of creatinine, BUN, uric acid and total proteins, no significant differences were noted ($P < 0.05$) (Table 4). Levels of uric acid of the non-feeding animals often appeared higher than those of feeding animals but again these differences were not significant ($P < 0.05$).

The values of blood glucose also showed no significant differences between treatments at any point in the study ($P < 0.05$). The levels did show a decline over the initial three weeks of the study, from a mean of 173.1 mg/dl to a level fluctuating around 150 mg/dl (Fig. 9).

Levels of sodium and potassium showed no significant differences between the four treatments (Table 4). In contrast, however, the level of blood calcium in the 'fasted' group appeared to be related to the feeding regime, with levels in the non-feeding animals significantly ($P < 0.05$) lower than those of the feeding animals (Fig. 10). The same relationship was noted for blood phosphorus levels, although not statistically significant ($P < 0.05$), the levels of the 'fasted' group animals were approximately 50% of the feeding animals at age 85 days (Fig. 10).

Alkaline phosphatase (alk. phos.) levels in the feeding animals remained constant, whereas those of the non-feeding animals declined significantly ($P < 0.05$) (Fig. 11). When animals commenced feeding alk. phos. levels rose into the same range of levels as feeding animals.

SGOT showed significant differences between treatments

at age 43 days and between ages 57 and 85 days, with the 'fed' group always having the highest value ($P < 0.05$) (Fig. 12). SGPT also appeared to be related to feeding activity. SGPT levels were always lower in the non-feeding animals and increased upon commencement of feeding ($P < 0.05$) (Fig. 12). CPK showed some significant differences ($P < 0.05$) (Fig. 11), with the 'fed' group always having the highest values. Again, there was an increase in the level of CPK with the commencement of feeding.

3.4 ENERGY INTAKE VERSUS GROWTH

Energy intake was calculated by multiplying the weight (gm) of fish ingested over a one week period by 2.6 kcal/gm (Lavigne et al. 1976, Kelver pers. comm.). This energy intake was used to calculate assimilated energy by allowing a fecal energy loss of 10% (of intake) and a urinary energy loss of 3% (of intake) (Phillipson 1966, Lavigne et al. 1976). Energy requirements for maintenance were estimated using Kleiber's equation (Kleiber 1975, Gallivan this volume):

$$M = 70\ W^{0.75} \qquad (1)$$

where M is basal metabolic rate (kcal day^{-1}) and W is body weight in kg at the beginning of the week. Multiplication by 7 provided an estimate of BMR in kcal week^{-1} (Table 2). This was then doubled to account for the higher metabolic activity of a young animal (Brody 1945, Moen 1973, Kleiber 1975).

The difference between energy available (assimilated energy) (kcal) and the estimate of energy required (kcal) was plotted against weight change (kg) (Fig. 13) and used to obtain the prediction equation:

(energy avail.- energy req.)=4903.68(wt. change)+1334.45 (2)

$$R^2 = 81.53$$

The inverse, or x on y, equation was:

$$\text{weight change} = 0.00020(\text{energy avail.} - \text{energy req.}) - 0.27 \quad (3)$$

$$r^2 = 81.53$$

4. DISCUSSION

At birth, newborn harp seal pups are exposed to weather conditions that are often severe. Superficially they would appear to be poorly adapted for survival with very little insulating blubber present and a pelage that is a poor insulator when wet (Blix et al. 1975, Frisch & Oritsland 1968). In reality, pups are able to compensate for the lack of insulation during the first few days of life, through shivering thermogenesis and the utilization of brown fat deposits beneath the skin and in association with venous plexuses (Grav et al. 1974, Blix et al. 1975). Deposition of the blubber layer is rapid with the onset of nursing (Stewart & Lavigne 1980).

Weaning for the harp seal pup, unlike that for most mammals, is quite abrupt. The mother does not usually initiate the pup into the water nor does she teach it to swim or forage. Soon after weaning, moulting occurs and the pup is generally forced into the water by the break-up of the pack ice.

At this time the pup must contend with the thermal properties of water in order to thermoregulate. The thermal conductance of water is more than 20 times that of air (Hart & Fisher 1964), meaning in simple terms that heat potentially will be lost from the body at a much greater rate. The animal can compensate for this by having a well-developed insulative layer, or by increasing its heat production markedly. Harp seal pups enter the water with a blubber layer which is 4 to 5 cm thick and preliminary evidence suggested that priority was given to maintaining this blubber layer. Stewart & Lavigne (1980) reported that

beaters showed a 10% decline in sculp weight and a 35% decline in core weight between the greycoat stage (age 9 days) and age 30 days. The results of the present study showed similar weight declines over the same period. Since water content of the core does not change appreciably, a preferential useage of core material as an energy source is indicated. George et al. (1971) have shown that adult harp seal muscle has a low fat content and it has therefore been suggested that the prime source of energy in these fasting seals may be protein (Stewart & Lavigne 1980, Bailey et al. 1980). From age 30 days until age 43 days (days 15-28 of the fast), the animal continues to utilize core tissues until the core approaches its size at birth. During this period, the sculp weight to body weight ratio remains constant. Blubber and core during this time are actually used in a ratio which prevents the rapid depletion of either, thus allowing the maintenance of an effective insulative layer and at the same time prolonging the useage of the core musculature as an energy source. By age 57 days (day 42 of the fast) the sculp weight to body weight ratio changes, with the sculp comprising less of the total body weight. From age 57 days on, the sculp was used preferentially. Since fat alone cannot support life, at least some core proteins must still be utilized.

There were no significant differences in blubber thickness between any of the treatments until after age 49 days. After this age, the 'fasted' group exhibited a more rapid decline in blubber thickness than did any of the other three treatments, indicating a more extensive utilization of blubber reserves. The two recovery groups did not demonstrate increases in blubber thickness after feeding commenced, possibly indicating that the blubber present was sufficient to maintain thermoneutrality in water. Gallivan (1977) has, in fact, shown that temperatures between 1.8 and 28.2 C are within the thermoneutral zone of adult harp seals

in water. Irving & Hart (1957) found no metabolic increase at 0 C in harp seals weighing 35.0-41.7 kg. They did find that the lower critical temperature of 4 harbour seals (Phoca vitulina) was 10 C, and that in one extremely thin harbour seal the lower critical temperature was elevated to 20 C. Skin temperatures of fasted animals in this study reflected water temperature and rectal temperatures were in the normal range (35 to 37 C) (Worthy unpubl. observ., Gallivan & Ronald 1979) indicating the presence of effective insulation.

The general sequence of events in starving mammals usually involves: (1) a depletion of glycogen reserves in the liver (1-2 days into the fast) ; (2) utilization of core proteins as gluconeogenic precursers (first week of the fast); (3) decreasing useage of glucose as an energy source by tissues, except the central nervous system and red blood cells, and increasing ketosis indicating extensive fat mobilization concommittant with decreasing protein depletion (3-4 days and onward); and (4) when the triacylglycerol supply has been consumed, the final depletion of core proteins (Cahill 1978). Harp seal beaters during the post-weaning fast appear to follow this general sequence of events, but the duration of each stage differs. Stage (2), the utilization of core proteins, appears to last 6 weeks rather than 1 week. Also, stage (4), the final depletion of core proteins may be reached before all of the blubber is consumed, because of the requirement of the blubber for insulation.

Harp seal beaters, which are in an environment where heat retention is critical to survival, must maintain heat balance either by maintaining their insulative blubber layer or by increasing their metabolic rate. An increased metabolic rate causes increased depletion of energy stores and potentially increased heat loss. In reality these seals attempt to maintain their insulative layer, making the

energy stored in the blubber generally unavailable to the animal for energy, until the depletion of proteins becomes critical. It appears that, at least for the initial 40-50 days of the fast, beaters should not be looked upon as animals with very large fat stores but as animals that are actually quite lean, with a very effective insulative layer around them. It is quite feasible that protein will be irreparably depleted before all of the fat stores can be used, and, in fact, one animal which apparently died of starvation on day 54 of the fast, still had 1.7 cm of blubber remaining.

Other investigations indicate that protein may actually be extensively utilized during fasting in several species of animals not only to meet energy demands but also water requirements. Fasting bottlenosed dolphins, Tursiops truncatus, and Pacific white-sided dolphins, Lagenorhynchus obliquidens, lose muscle as fast as body fat and apparently meet their glucose requirements from protein (Ridgeway 1972). Fasting willow grouse, Lagopus lagopus, obtain 40% of their energetic requirements from protein breakdown (Grammeltvedt 1978). Animals that maintain blood glucose levels by utilizing protein as a precursor or alternatively using protein directly as an energy source, must rid their body of nitrogenous wastes. This can result in marked water losses. The seals in this study did not become dehydrated as shown by the maintenance of a normal PCV, as well as maintenance of water levels in the carcass and viscera. Since fasting seals have been shown not to drink sea-water (Depocas et al. 1971), these seals must be able to derive sufficient water metabolically and from free water in the tissues.

Blntz et al. (1979) found that thin Richardson's ground squirrels, Spermophilus richardsoni, when starved, catabolized skeletal muscle tissue preferentially. Starved, water-deprived Richardson's ground squirrels catabolized

even greater quantities of skeletal muscle and recycled nitrogen to conserve some of the water that would be required to clear nitrogenous wastes (Rintz and Mackin 1979).

Muscle tissue, being approximately 72% water in both feeding and fasting animals (Worthy unpubl. results), could then serve not only as an energy source but as a source of preformed water. The catabolism of blubber, which results in 1.07 g of water/g of fat catabolized (Prosser and Brown 1961), would also provide metabolic water. Thus it appears that these fasting seals maintain water balance and meet caloric requirements by metabolizing blubber and core in a ratio which prevents the rapid depletion of either.

Several animals which were offered food starting 8 days after their arrival in Guelph refused to eat. Three of these animals eventually started feeding on their own; one after 29 days of fasting, one after 36 days and the other after 44 days. Another animal was force-fasted for 29 days and then offered food. This animal refused food for another 15 days. These animals pose an interesting question - why would they fast in the presence of food and other animals which were feeding and what prompted them to start feeding?

Brodie & Pasche (in press) commented that a seal under fasting conditions would not consume its propulsive tissue to the point of eliminating its effectiveness as a predator. Qualitative observations of fasted animals in this study did not indicate a decline in swimming ability, either in speed or agility, even in the final days of the study. These animals did have difficulty in moving when on the haul-out, but swam as fast and as frequently as fed animals. The occurrence of a large number of beaters in the wild (up to 15.7% of the total number of animals sampled in May) which weighed less than 20 kg indicates that indeed these smaller animals also exist in nature. The ability of recovery group animals to increase in size rapidly upon commencement of

feeding, and the apparent lack of interest in food in some seals until this weight range was reached, shows that animals of this size are also quite capable of recovering.

The recuperative powers of young harp seals, once feeding does commence, are impressive. Within 4 weeks, recovery group 1 seals were not significantly different in total body weight from animals which had been feeding for 8 weeks. Animals of recovery group 2 also showed a rapid gain of weight and by age 78 days were not significantly different from recovery group 1 animals. Beaters sampled in the wild during April appeared to be in a condition similar to non-feeding animals of this study. Animals sampled in the field during May resembled the recovery group 2 animals. This possibly indicates that the field beaters had started feeding during the preceeding two weeks, at about the same time as self-fasting seals of this study (Fig. 2).

Rates of weight gain of the two recovery groups were virtually identical, and were always higher (though not always significantly) than the 'fed' group. There is some indication that there may be compensatory growth, ie increased efficiency in food utilization, but this requires further investigation.

Blood analyses indicated that perhaps fasting seals can maintain homeostasis until they are very near to dying from starvation. For most blood parameters, fasting seals in this study maintained their levels similar to other phocids, exemplifying this ability (Worthy & Lavigne in prep'n.). Declines were noted in levels of calcium and phosphorus in fasting seals over the duration of the fast, consistent with the effects of long term fasting (Worthy & Lavigne, in prep'n.). alk. phos. levels declined in the non-feeding animals, consistent with observed trends in sheep (Healey 1974) and chickens (McDaniel and Dempsey 1962), but increased upon commencement of feeding, as did SGPT, SGOT

and CPK levels (which remained low in non-feeding animals) (Worthy & Lavigne in prep'n.).

The difference between assimilated energy and energy required by the animal, if positive, is that which is available for growth. If this difference is negative, the animal loses weight as it draws on its energy stores. The equation that was developed relating this difference to weight change (equation 3) enables calculation of the minimum caloric intake which will maintain body weight (or the basal energy requirement). This equation could be used to predict food intake required, and perhaps to calculate food consumption for beaters (of known biomass) in the wild.

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Table 1: Vitamin supplements given to all feeding animals on a daily basis.

One vitamin B capsule (1)	
(thiamine hydrochloride)	100 mg
One Novo-B capsule (2)	
vitamin B	10 mcg
thiamine mononitrate	35 mcg
riboflavin	15 mcg
niacinamide	50 mcg
pyridoxine HCl	5 mg
calcium d'Pantothenate	20 mg
ascorbic acid	300 mg
One vitamin A capsule (2)	25000 IU
One halibut liver oil capsule (2)	
vitamin A	5000 IU
vitamin D	400 IU
One vitamin E capsule (1)	
(73.5 mg of d-alpha tocopheryl acetate)	100 IU
One Latan capsule (3)	
vitamin A	5000 IU
vitamin C	1000 IU
vitamin B_{12}	2 mcg
thiamine mononitrate	3 mcg
riboflavin	3 mg
niacinamide	20 mg
pyridoxine	3 mg
calcium carbonate	250 mg
folic acid	2 mg
iron (ferrous fumarate)	66 mg

(1) ICN Canada Ltd., Montreal, Canada.

(2) Novopharm Ltd., Toronto, Canada.

(3) Ayerst Laboratories, Montreal, Canada.

Table 2: The food intake, calculated caloric intake, observed weight change and the energy requirement (2 x Kleiber) on a weekly basis for all animals that eventually did feed. Blank cells occur after an animal was sacrificed. Dashed lines refer to a week with no intake of food.

(1) fed group animal
(2) recovery group 1 animal
(3) recovery group 2 animal

ACE		781 (3)	782 (2)	786 (2)	787 (3)	789 (3)	790 (1)	792 (1)	794 (2)	795 (1)	796 (1)	797 (1)
29	food intake (gm)	-	-	-	-	200	4615	5255	-	3870	3970	4155
	caloric intake (kcal)	-	-	-	-	520	11999	13653	-	10322	10322	10803
	weight change (kg)	-2.15	-1.65	-1.15	-1.35	-2.00	0	+0.40	-1.95	-0.60	-0.70	-0.25
	predicted caloric requirement (kcal)	12404	12484	12718	11976	10258	12294	13344	12342	10090	11636	12404
36	food intake (gm)	-	-	-	-	-	8760		-	7885	7885	8760
	caloric intake (kcal)	-	-	-	-	-	22776		-	20501	20501	22776
	weight change (kg)	-1.50	-2.50	-2.50	-1.40	-0.85	+2.10		-2.30	+1.10	+1.90	+0.50
	predicted caloric requirement (kcal)	12246	11688	11938	11526	9972	12952		11608	10460	12262	12420
43	food intake (gm)	-	-	-	-	-	10000		-	10000	10000	10000
	caloric intake (kcal)	-	-	-	-	-	26000		-	26000	26000	26000
	weight change (kg)	-3.75	-2.15	-2.50	-1.80	-2.55	+2.50		-2.00	+0.25	+2.20	+0.95
	predicted caloric requirement (kcal)	11038	10990	11446	10940	8494	13722		10956	10544	12952	12718
50	food intake (gm)	-	8965	8265	-	-			7250	9260	9260	14150
	caloric intake (kcal)	-	23309	21489	-	-			18850	24076	24076	36790
	weight change (kg)	-1.75	+2.40	+2.65	-1.35	-1.50			+2.60	+0.15	-0.25	+2.25
	predicted caloric requirement	10460	11768	12294	10494	8544			11800	10592	12874	13416
57	food intake (gm)	-	13250	14995	-	5600			11000	12000		13000
	caloric intake (kcal)	-	34450	38987	-	14560			28600	31200		33800
	weight change (kg)	-1.85	+3.75	+3.40	-0.50	+0.40			+2.15	+2.35		+2.40
	predicted caloric requirement (kcal)	9836	12952	13354	10666	8706			12484	11364		14148
64	food intake (gm)	1300	11100	11100	10100	13000			13000	13000		13200
	caloric intake (kcal)	3380	28860	28860	26200	33800			33800	33800		34320
	weight change (kg)	-1.15	+0.20	+0.30	+1.40	+2.10			+2.50	+2.85		+1.55
	predicted caloric requirement	9442	13014	13446	11120	9440			13262	12278		14612
71	food intake (gm)	10750	12000	12000	12000	11000			11000	11000		10750
	caloric intake (kcal)	27950	31200	31200	31200	28600			28600	28600		27950
	weight change (kg)	+2.10	+2.10	+2.90	+2.45	+1.50			+1.10	+1.35		+0.90
	predicted caloric requirement (kcal)	10158	13662	14326	11912	9954			13600	12704		14880
78	food intake (gm)	12430	12357		12807	13000			13000	13000		12730
	caloric intake (kcal)	32318	32318		33298	33800			33800	33800		33098
	weight change (kg)	+4.00	+1.30		+3.10	+1.60			+1.85	+0.75		+0.15
	predicted caloric requirement (kcal)	11478	14056		12890	10494			14162	12936		14924
85	food intake (gm)	12000	12000		12000	12000			12000	12000		12000
	caloric intake (kcal)	31200	31200		31200	31200			31200	31200		31200
	weight change (kg)	+2.20	+1.90		+1.95	+1.65			+1.05	+2.30		-0.25
	predicted caloric requirement (kcal)	12184	14628		13494	11038			14478	13646		14850

Table 3: The mean (± S.D.) and range for the pooled data for packed cell volume (PCV), hemoglobin (HMG), red cell count (RBC), white cell count (WBC), mean cell volume (MCV), mean cell hemoglobin (MCH), and mean corpuscular hemoglobin content (MCHC). Reported normal values are shown.

	Units	n	$\bar{x}$ + S.D.	Observed Range	Reported Range	Source
RBC	(10^6 /mm)	158	5.2 + 0.56	4.0 - 6.9	3.8 - 6.9	1,2,3,4
WBC	(/mm)	158	10976 + 3974	3892 - 26104	3800 - 37565	1,2,3,4
HMG	(g/dl)	158	20.0 + 1.92	15.4 - 24.1	15.8 - 28.8	1,3,4
PCV	(%)	158	54.8 + 4.6	42.5 - 68.0	38.5 - 68.0	1,3,4
MCV	(μ^3)	158	106.0 + 11.3	77.5 - 141.3	88.0 - 139.0	1,4
MCH	($\gamma\gamma$)	158	38.7 + 4.8	28.5 - 54.8	30.0 - 56.0	1,4
MCHC	(%)	158	36.6 + 2.0	33.1 - 43.2	33.0 - 47.0	1,4

1. Geraci, 1971. ..... pups up to 6 months old
2. Englehardt, 1979. ..... 3 month old pups
3. Ronald et al. 1969 ... captive young animals
4. Ronald et al. in press . pups up to 2 months old

Table 4: The mean (± S.D.) and range for the pooled data for sodium, potassium, total proteins, creatinine, blood urea nitrogen (BUN), uric acid and lactate dehydrogenase (LDH). Reported normal values are shown.

	Units	n	$\bar{x}$ + S.D.	Observed Range	Reported Range	Ref.
Total Proteins	(mg/dl)	145	5.5 + 0.46	4.1 - 6.8	5.5 - 7.9	1,2,4*
BUN	(mg/dl)	139	38.8 + 11.7	15.9 - 71.5	20 - 69	1,3
Uric Acid	(mg/dl)	139	1.3 + 0.39	0.5 - 2.8	0.3 - 2.6	1,3
Creatinine	(mg/dl)	139	0.9 + 0.26	0.3 - 1.5	1.1 - 1.7	1,4
LDH	(IU/l)	139	159 + 47.4	57 - 294	134 - 187	1,4
Sodium	(mEq/l)	159	153.5 + 8.1	135 - 166	140 - 161	1,2
Potassium	(mEq/l)	159	3.8 + 0.42	2.7 - 4.8	3.3 - 6.1	1,2

1. Geraci, 1970. ..... captive adults
2. Englehardt, 1979. ..... 3 month old pups
   10 month old pups *
3. Geraci et al. 1979. ..... captive young adults
   (Phoca hispida).
4. Ronald et al. in press. ... up to 2 month old pups

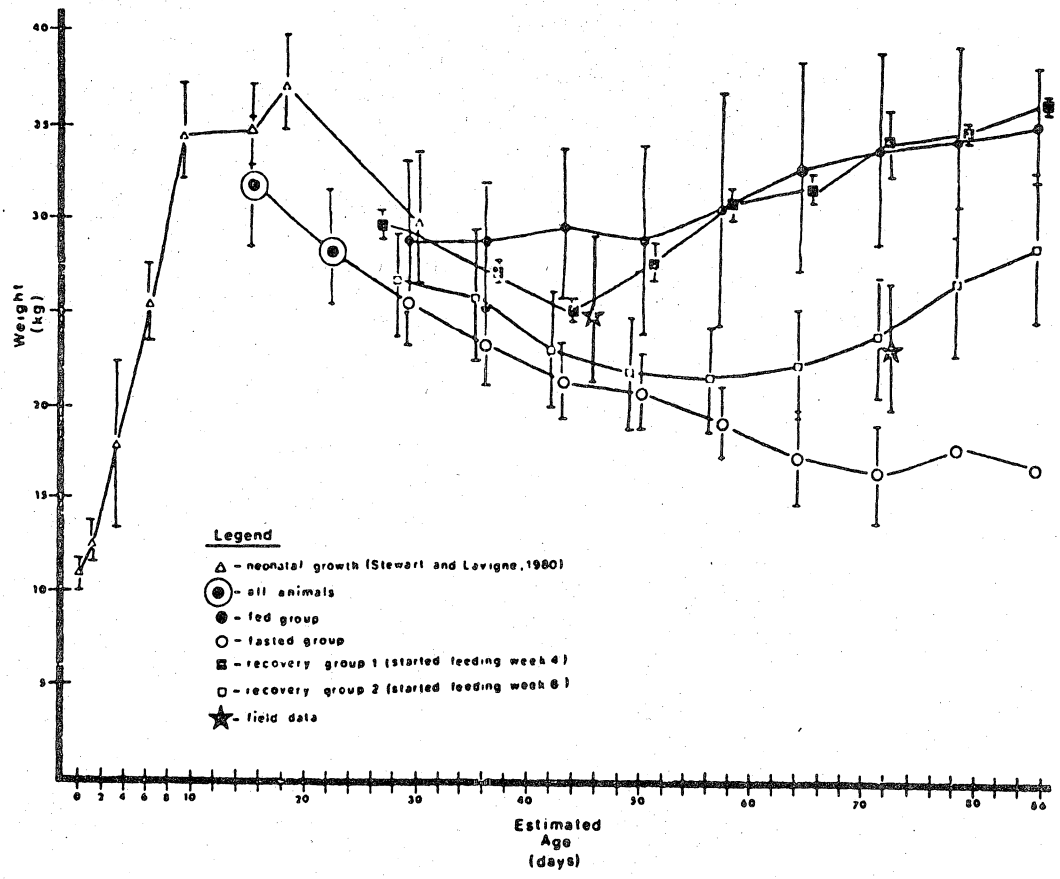

Fig. 1. Total weight (kg) versus estimated age (days) for neonates (± 95% C.I.) (Stewart & Lavigne 1980) and for all of the treatment groups in this study (± S.D.). Comparable data are presented for beaters collected in the field (± S.D.).

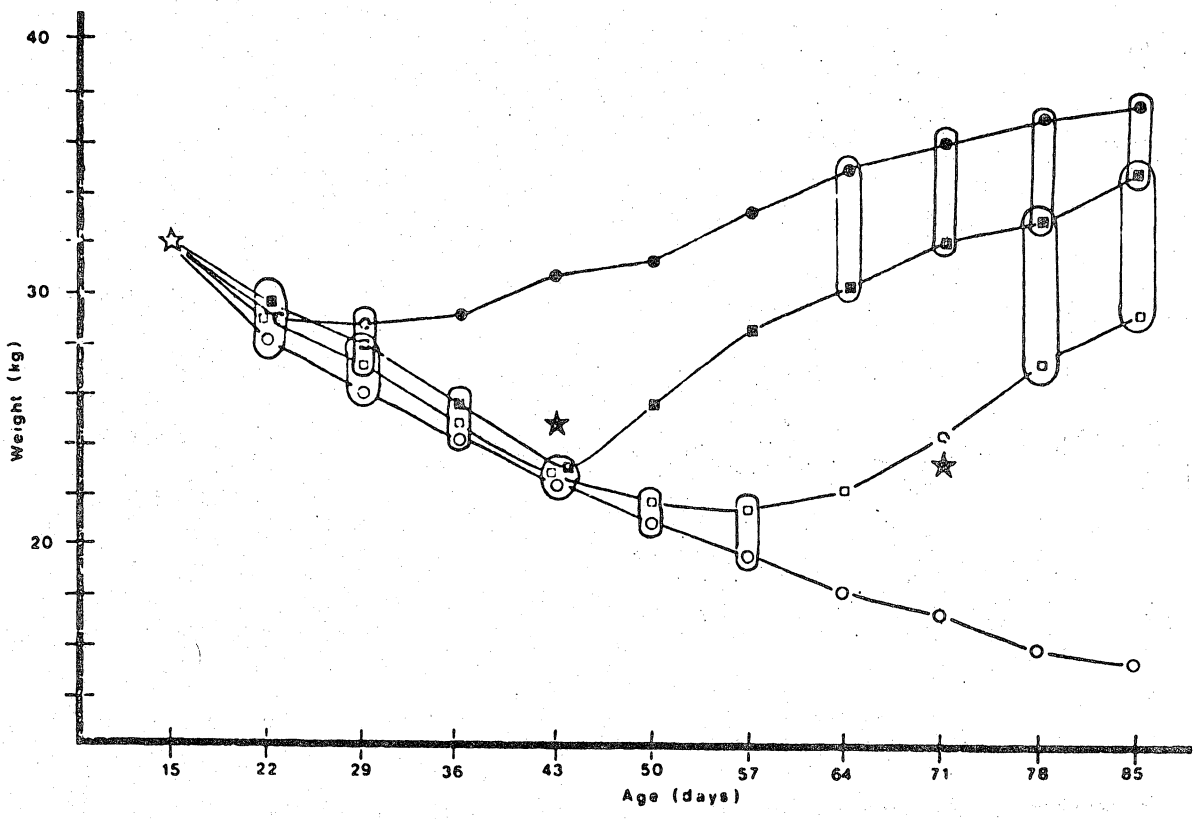

Fig. 2. A comparison of all treatments using adjusted means (obtained using analysis of covariance with starting weight as the covariate). Circled points are not significantly different using Fisher's (protected) LSD procedure ($\underline{P}$ = 0.05). Comparable field data are also shown, although no statistical test was done.

● 'fed' group
○ 'fasted' group
■ recovery group 1
□ recovery group 2
★ field data

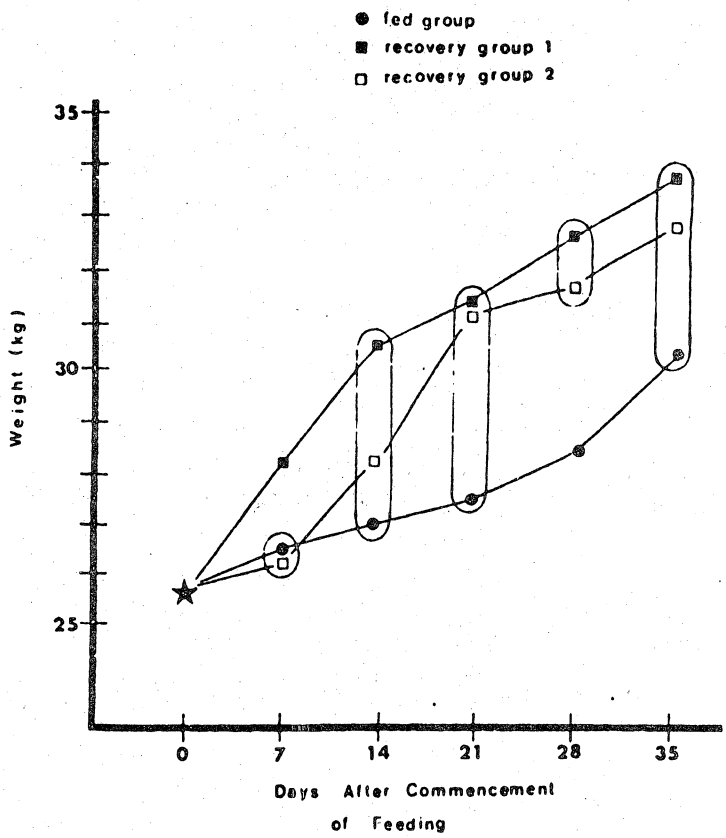

Fig. 3. A comparison of the rates of weight gain of the three feeding groups using adjusted means of body weight (obtained using analysis of covariance with body weight at the time of commencement of feeding as the covariate). Circled points are not significantly different using Fisher's (protected) LSD procedure ($\underline{P}$ = 0.05).

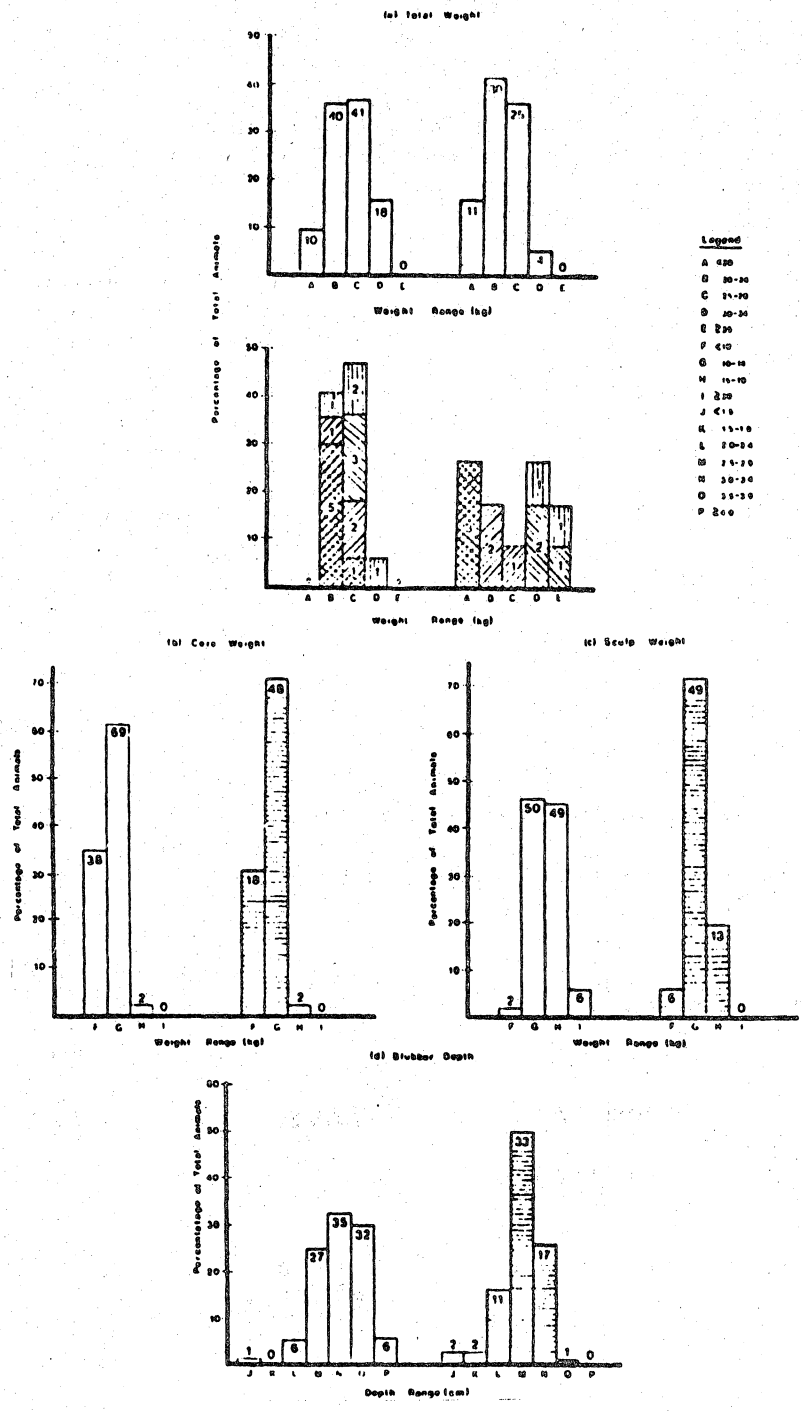

Fig. 4. A comparison of beaters sampled in the field in mid-April and mid-May, 1980 with respect to the distribution of (a) Total weight, (b) Core weight, (c) Sculp weight, and (d) Blubber depth. The distribution of total weights for experimental animals of this study are shown for the same dates. The numbers in the bars are the numbers of animals sampled or are the number of animals in a particular feeding regime.

April field beaters
May field beaters
'fed' group
recovery group 1
recovery group 2
'fasted' group

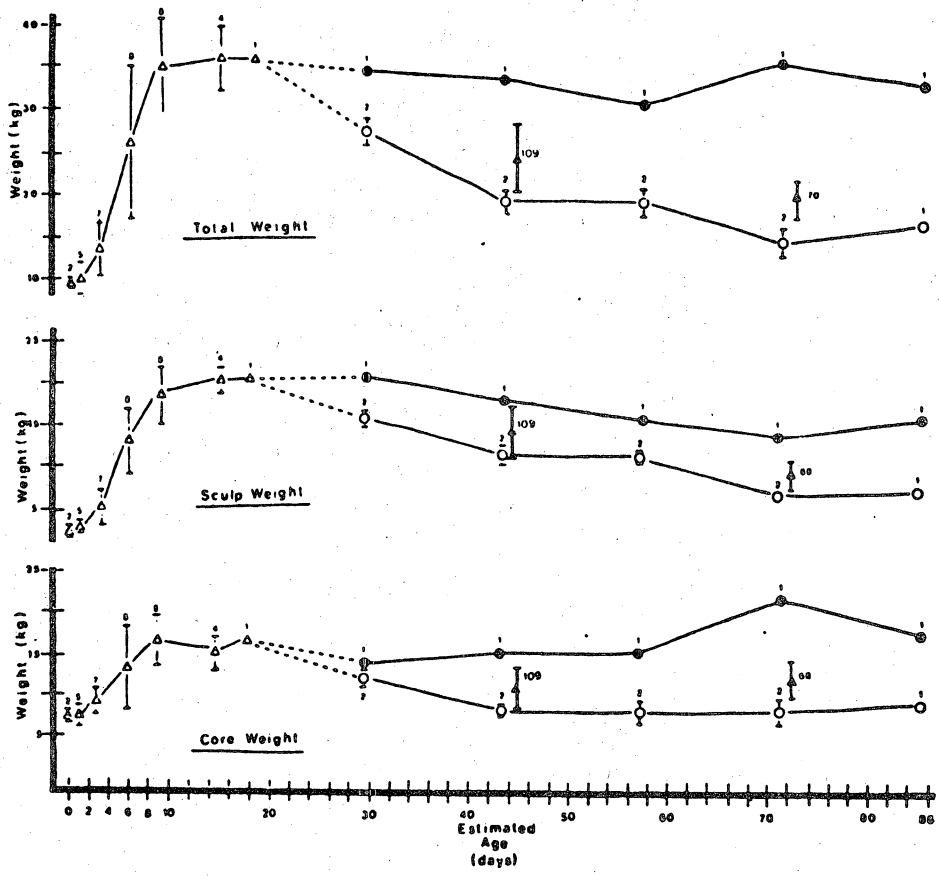

Fig. 5. Total weight, sculp weight, and core weight (± S.D.) expressed as a function of the estimated age of the animal, for animals collected in the field in March, April, and May, 1980 as well as animals sacrificed from fed and fasted groups. Numerals indicate sample size.

△ 1980 neonates
▲ 1980 field beaters
● 'fed' group
○ 'fasted' group

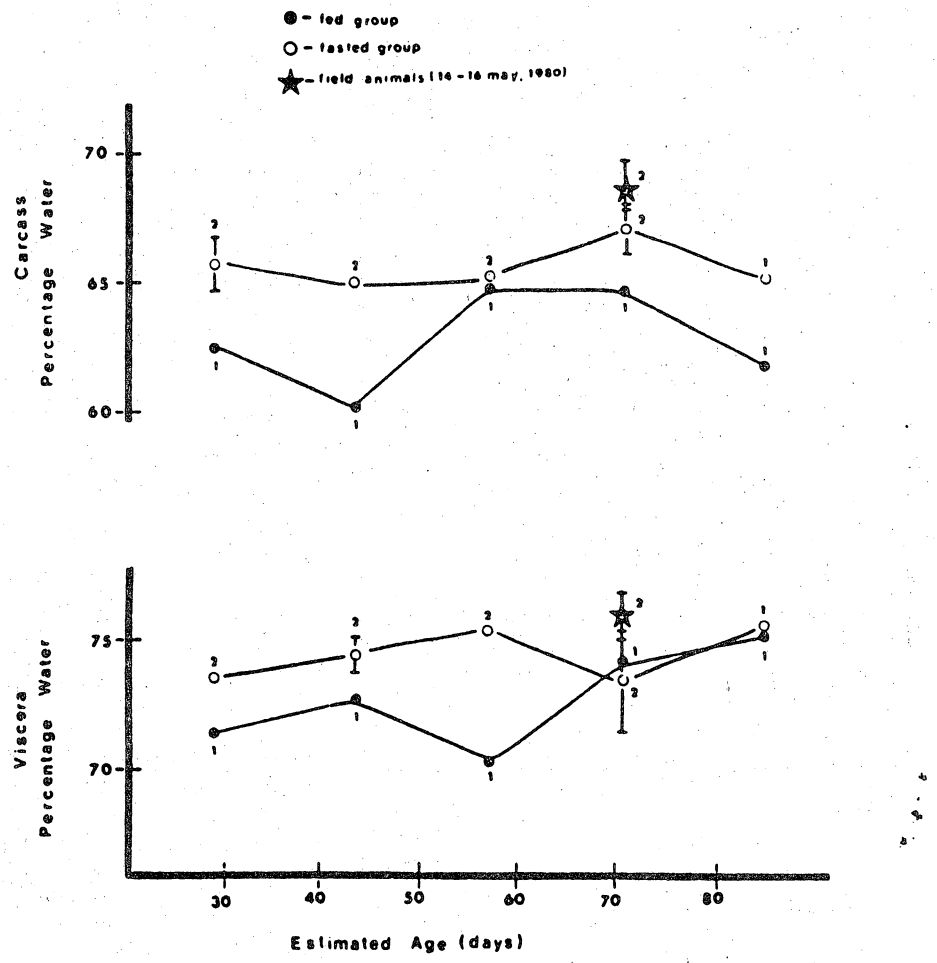

Fig. 6. Changes in the percentage water (± S.D.) of the carcass and viscera of animals sacrificed from fed and fasted groups of this study and for carcasses collected during 14-16 May, 1980.

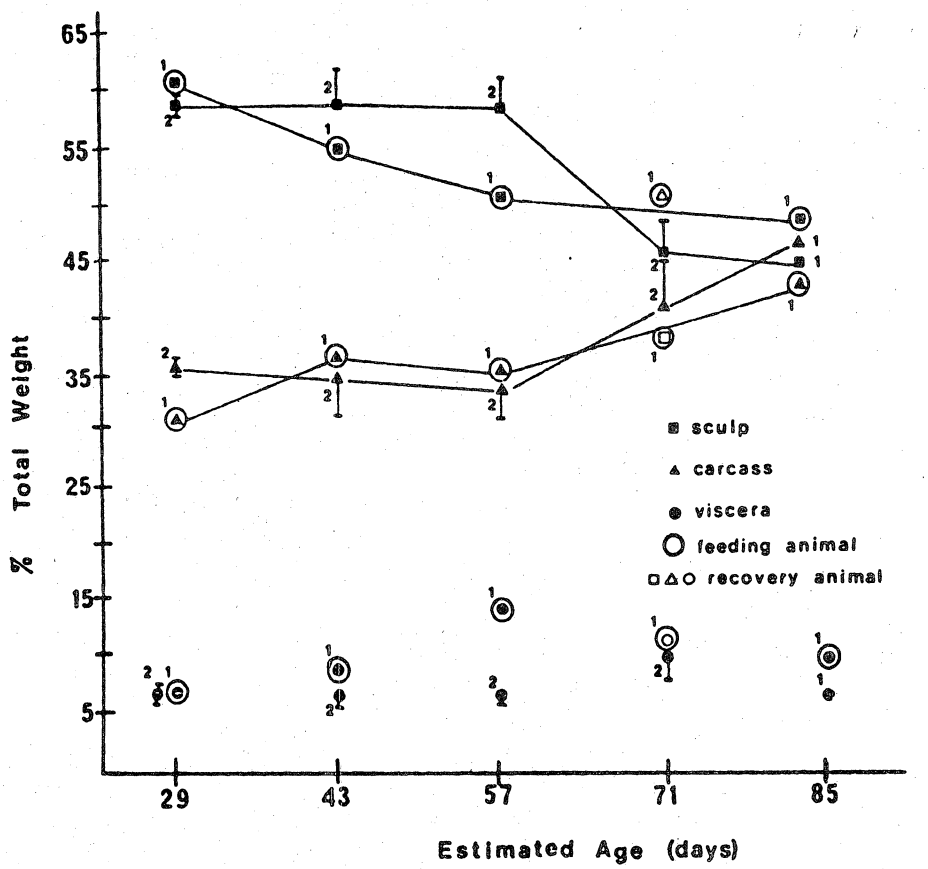

Fig. 7. Changes in the proportion of sculp weight and core weight with respect to total weight for sacrificed animals. Sample sizes are indicated.

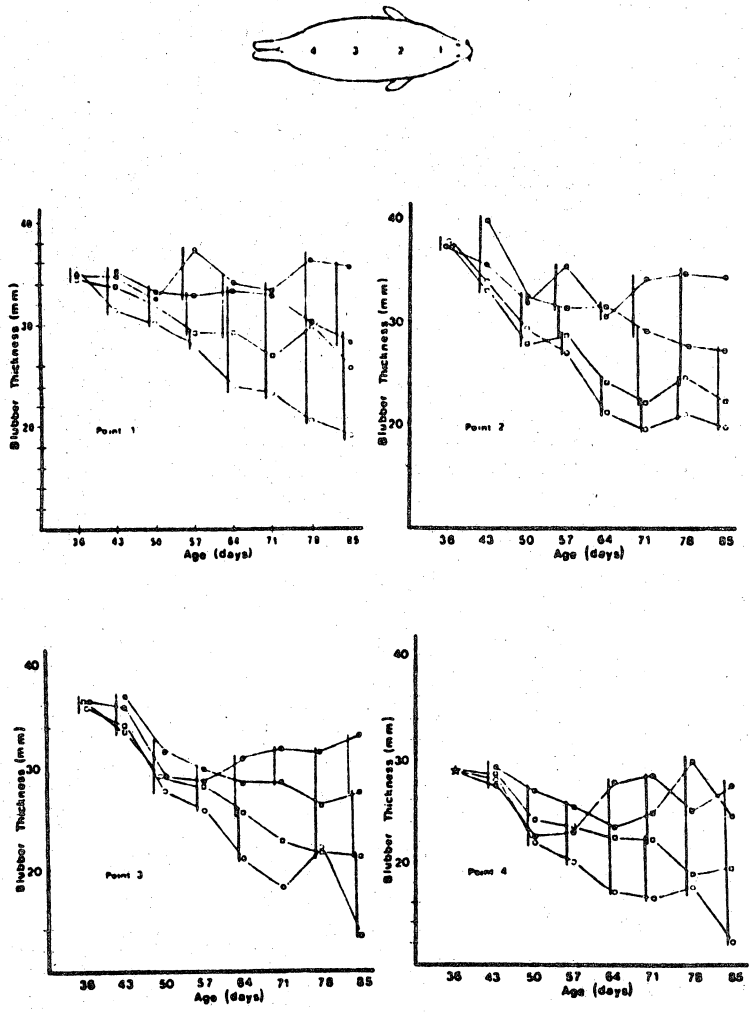

Fig. 8. Changes in blubber thickness over time, in the four treatment group measured at points 1 through 4, are shown on the diagram. Points joined by bars are not significantly different using Fisher's (protected) LSD procedure ($\underline{P}$ = 0.05).

● 'fed' group
■ recovery group 1
□ recovery group 2
○ 'fasted' group
★ point common to all 4 groups

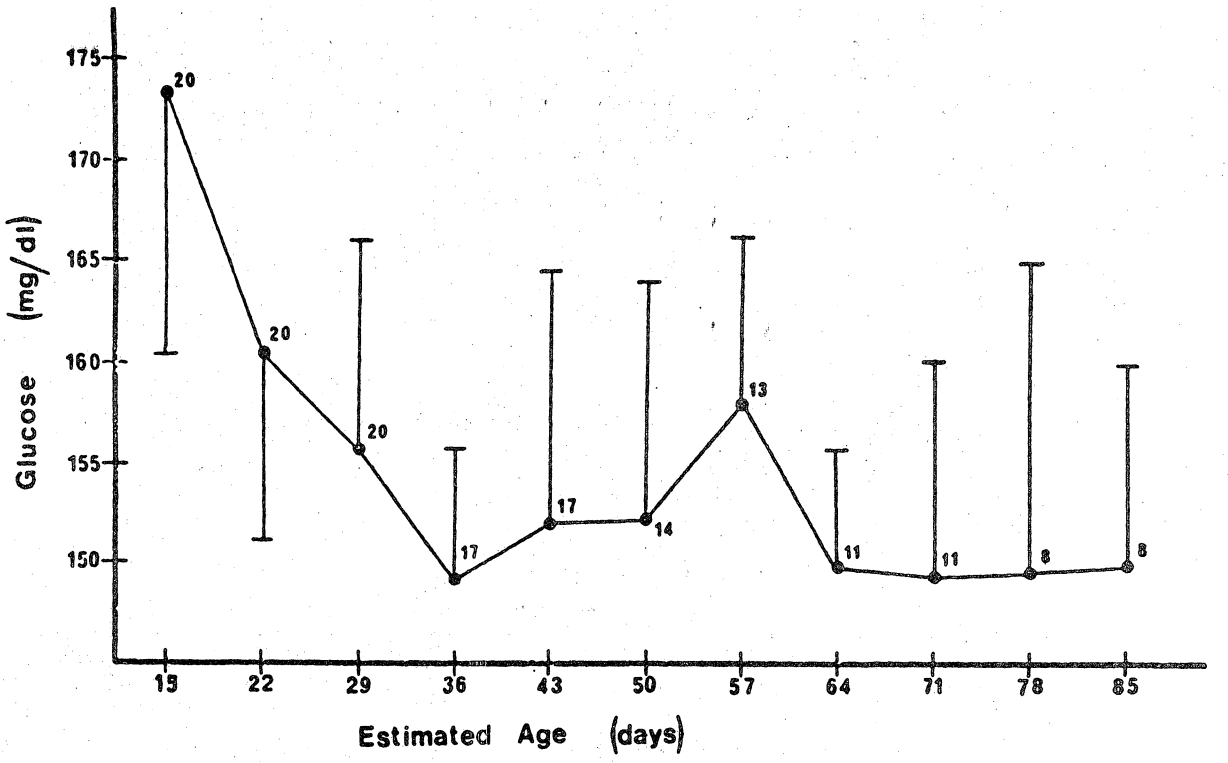

Fig. 9. The means (± S.D.) of the pooled data for blood glucose levels of all treatments for each sampling period . Sample sizes are indicated.

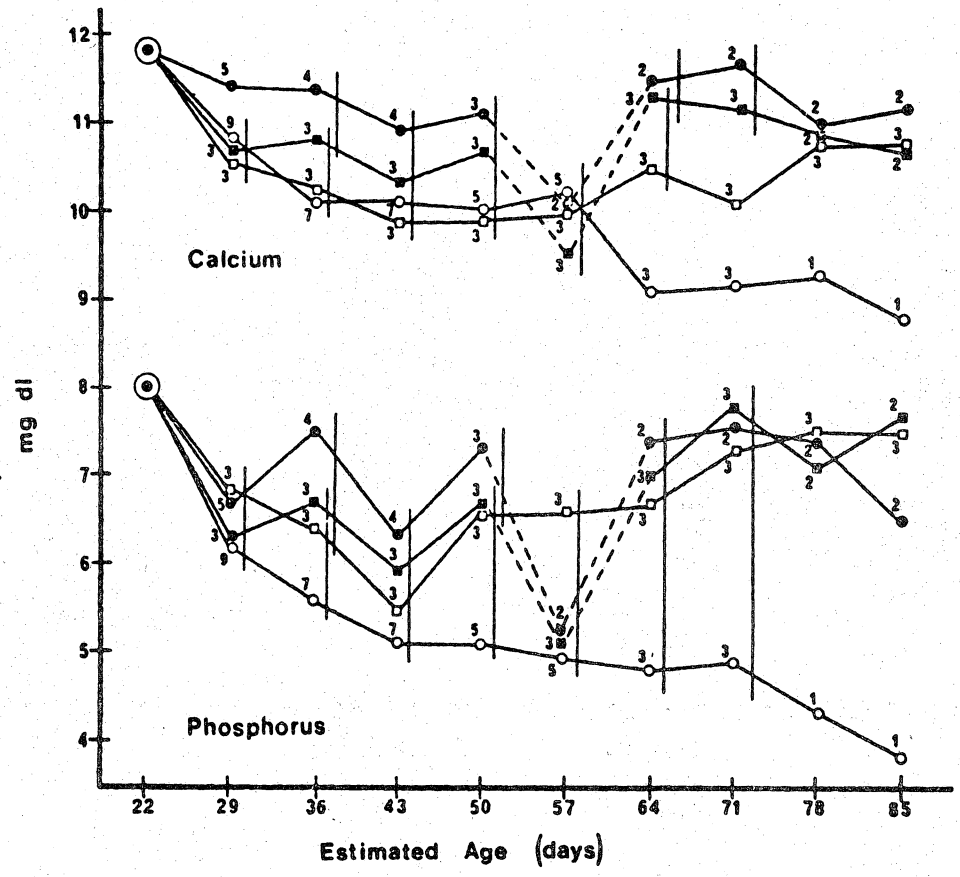

Fig. 10. The adjusted mean value for calcium and phosphorus (obtained from an Analysis of Covariance, using the initial value as the covariate) for each treatment. Points joined by bars are not significantly different using Fisher's (protected) LSD procedure ($P < 0.05$). The depression in the values of both calcium and phosphorus of the feeding animals at age 57 days occured after the animals were in fresh water for 4 days. Sample sizes are indicated.

● 'fed' group
■ recovery group 1
□ recovery group 2
○ 'fasted' group

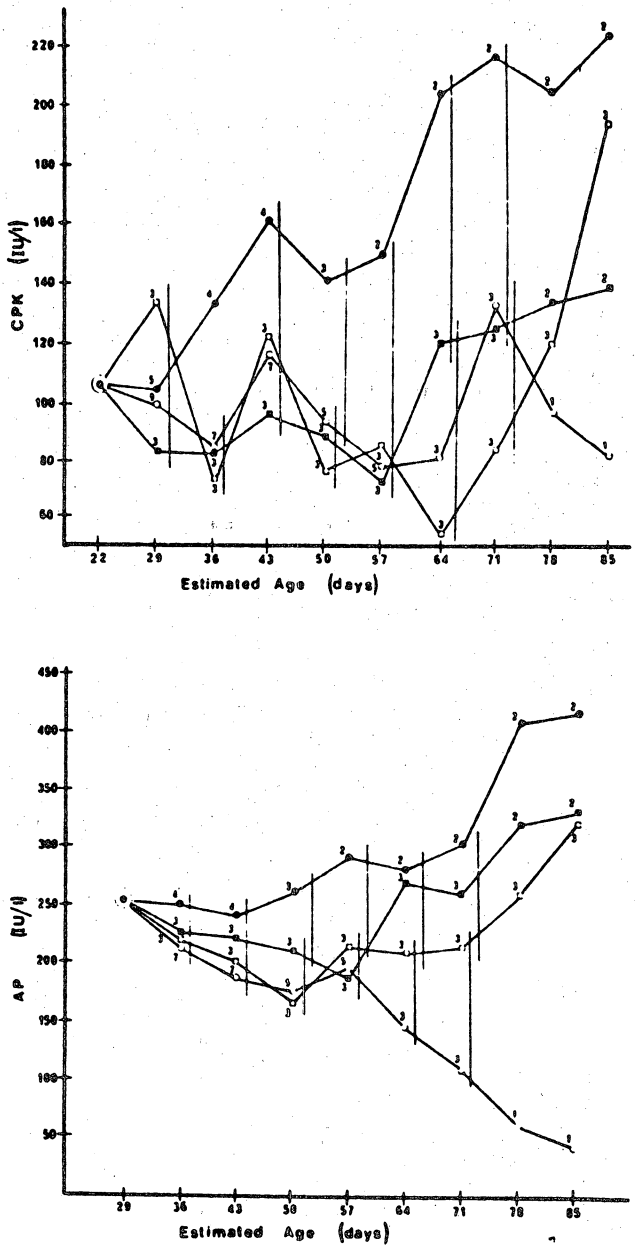

Fig. 11. The adjusted mean values for CPK and AP (obtained from an Analysis of Covariance, using the initial value as the covariate) for each treatment. Points joined by bars are not significantly different using Fisher's (protected) LSD procedure ($\underline{P} < 0.05$). Sample sizes are indicated.

● 'fed' group
■ recovery group 1
□ recovery group 2
○ 'fasted' group

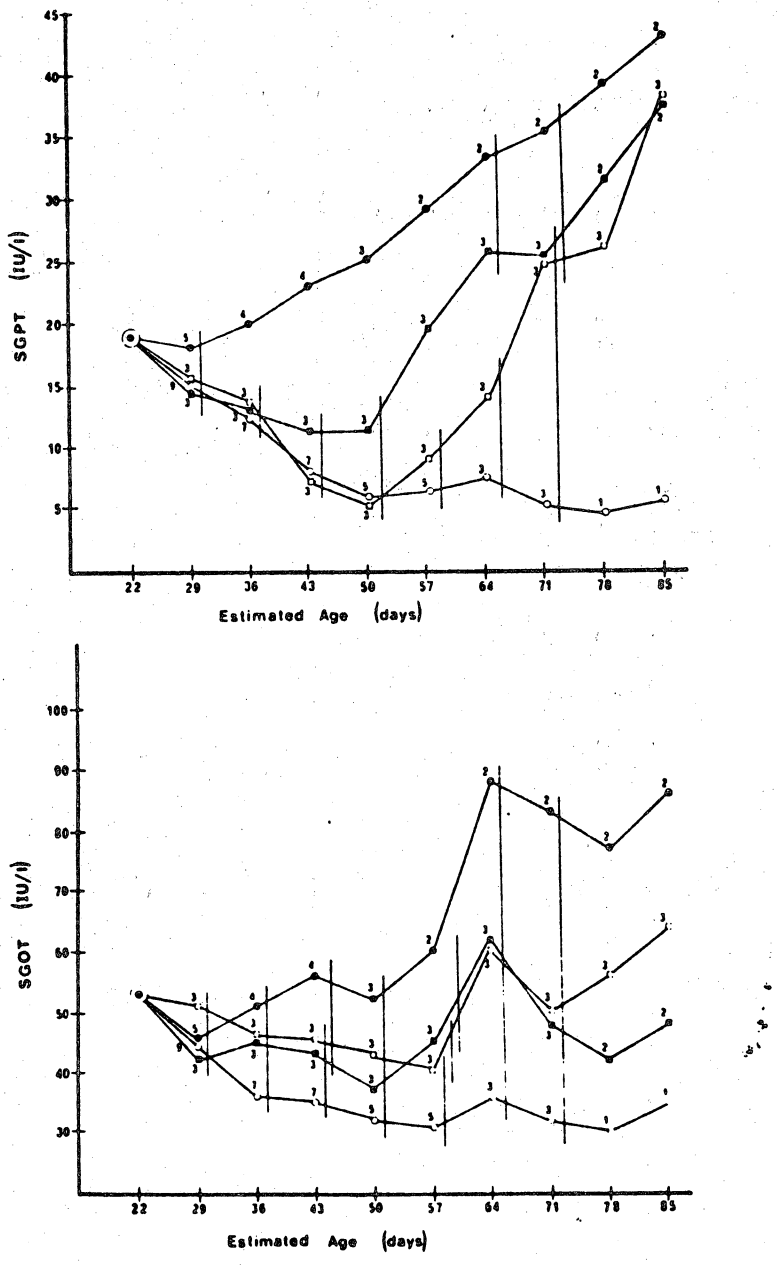

Fig. 12. The adjusted mean values for SGOT and SGPT (obtained from an Analysis of Covariance, using the initial value as the covariate) for each treatment. Points joined by bars are not significantly different using Fisher's (protected) LSD procedure ($P < 0.05$). Sample sizes are indicated.

● 'fed' group
■ recovery group 1
□ recovery group 2
○ 'fasted' group

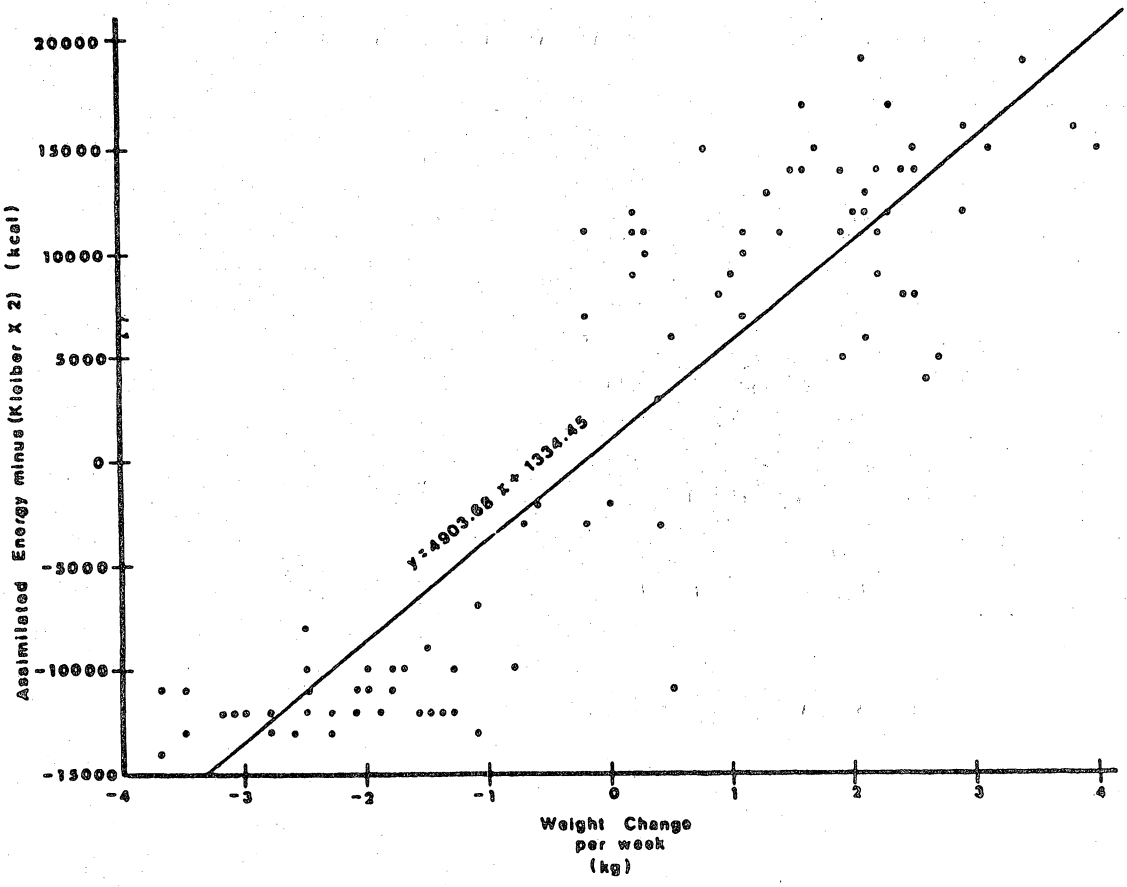

Fig. 13. An estimate of the energy available for growth (assimilated energy minus energy requirement) versus weekly weight change.