A statement in the literature that lobsters retain their original weight even after several months of fasting led to the present investigation. The constancy of body weight may be regarded as an index of physiological equilibrium, and its fluctuations indicate the internal condition of the organism. By the fall in body weight the normal course of a fast may be followed from day to day, just as normal growth may be studied by the periodic gains of the organism.

As far as we know, all organisms, temporarily deprived of nourishment, diminish progressively in mass, and this is registered by changes in weight. The observation of the constancy of the weight of fasting lobsters seemed, therefore, worthy of investigation. The two sides of the problem, i.e., the changes in weight and composition of the fasting lobsters, have been studied simultaneously.

Preparatory to weighing, the lobsters were wrapped in towels and the remaining traces of moisture were wiped off thoroughly from every portion of the body. Each animal was then placed in an aluminum can in which it was carefully weighed to 0.01 gm. The can was then weighed without the lobster, as the animals frequently excreted a small quantity of fluid during the weighing, and the weight of the lobster was calculated. The lobsters were kept in flat glass dishes partially filled with filtered
Changes in Fasting Lobsters

sea water, which was continuously aerated. The water was changed every second day, and the weighing was made every 2 weeks. The experiment lasted for nearly 2 months.

The data relating to the changes in total body weight are recorded in Table I, in which the percentage of the biweekly change and the per cent of the loss suffered in the 56 days of inanition are given. It will be observed that the losses ranged from 0.10 to 1.89 per cent during the 2 week periods. On two occasions a slight increase of 0.3 per cent was observed. It will be seen from the table that all the lobsters lost weight, though this loss was extremely small. Thus in the 56 days of fasting they lost, on an average, 4.83 gm. or 2.89 per cent of their initial weight. In view of the facts recorded here it is hardly justifiable to speak of a constancy of weight of lobsters subjected to inanition. The question naturally arises as to whether the singularly low rate of loss of body weight indicates that the metabolic activity of these animals is very low, or that the actual loss sustained by the lobster is masked by secondary occurrences. The study of the composition of normal and starved lobsters gives a definite answer to this question.

The following methods have been employed in the investigation of the chemical composition. Both the control and experimental animals were rinsed with clean water, thoroughly dried, weighed, and after being cut in small pieces they were desiccated at about 100°C. When no further diminution in weight was found, the dry material, shell and all, was ground to a fine powder which was again dried in the oven until the weight remained constant. The dry residues from the different lobsters were combined, thoroughly mixed, and used for the various analyses. The determinations made on these composite samples were as follows: total ash, non-volatile inorganic portion, total nitrogen, glycogen, and the ether-, alcohol-, and water-soluble matter. In the latter two portions the nitrogen was likewise determined.

In determining the total amount of ash a weighed portion of the dry material was at first charred over a low flame. This preliminary heating was never carried further than the incipient dull redness. The charred material was repeatedly extracted with boiling water until the test for chlorides was negative. The extracted material was then completely incinerated while the extract was evaporated. The combined weight of the two is the total ash content. The non-volatile inorganic constituents were determined separately by incinerating the dry matter directly in a muffle.

The glycogen was isolated according to Pflüger, and after hydrolysis it was measured by Allihn's gravimetric method.
<table>
<thead>
<tr>
<th>Date</th>
<th>No.</th>
<th>1 Weight</th>
<th>2 Bi-weekly loss</th>
<th>3 Weight</th>
<th>4 Bi-weekly loss</th>
<th>5 Weight</th>
<th>6 Bi-weekly loss</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>gm.</td>
<td>percent</td>
<td>gm.</td>
<td>percent</td>
<td>gm.</td>
<td>percent</td>
<td></td>
</tr>
<tr>
<td>July 12</td>
<td></td>
<td>175.50</td>
<td></td>
<td>168.33</td>
<td></td>
<td>143.87</td>
<td></td>
<td>167.51</td>
</tr>
<tr>
<td>&quot; 26</td>
<td></td>
<td>176.11</td>
<td>+0.35</td>
<td>167.20</td>
<td>-0.62</td>
<td>143.03</td>
<td>-0.60</td>
<td>163.56</td>
</tr>
<tr>
<td>Aug. 9</td>
<td></td>
<td>173.62</td>
<td>-1.42</td>
<td>165.67</td>
<td>-0.97</td>
<td>142.89</td>
<td>-0.10</td>
<td>161.18</td>
</tr>
<tr>
<td>&quot; 23</td>
<td></td>
<td>173.19</td>
<td>-0.25</td>
<td>165.35</td>
<td>-0.20</td>
<td>141.35</td>
<td>-1.08</td>
<td>161.72</td>
</tr>
<tr>
<td>Sept. 6</td>
<td></td>
<td>171.31</td>
<td>-1.08</td>
<td>163.17</td>
<td>-1.32</td>
<td>138.68</td>
<td>-1.89</td>
<td>160.77</td>
</tr>
<tr>
<td>Total loss</td>
<td></td>
<td>4.19</td>
<td>-2.39</td>
<td>5.16</td>
<td>-3.07</td>
<td>5.19</td>
<td>-3.61</td>
<td>6.38</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>4.83</td>
</tr>
</tbody>
</table>
Changes in Fasting Lobsters

The extraction with ether, then with alcohol and water, was made on the same sample of dry material, of which about 20 gm. were used for each determination. We used ether redistilled over sodium, and the alcohol was prepared from absolute alcohol by boiling it for 2 days with lime and distilling it over lime. This alcohol was kept over anhydrous copper sulphate.

The extraction with alcohol, which followed the ether extraction, was made in the same Soxhlet apparatus. By wrapping the apparatus with a layer of cotton it was possible to raise the temperature of the extraction cup so that a continuous flow of hot alcohol was maintained for 48 hours.

The material thus treated with ether and alcohol was boiled several times with distilled water until the filtered extract was perfectly colorless. The combined watery extracts were condensed and made up to 200 cc. Aliquot portions of this served for the nitrogen determination, as well as for the organic residue. This was determined by evaporation to dryness and analyzing the residue for its total yield of ash by the above method. The amount of organic extractives was obtained by subtracting the weight of the ash from the total dry weight.

Table II consists of two parts: in one the percentage composition of the dry matter of both normal and fasting lobsters is given; in the other these data are recomputed for the fresh material. Normal lobsters have on an average 67.33 per cent of water, the individual variations ranging from 65.9 to 69.5 per cent. About two-thirds (64.3 per cent) of the dry matter is organic. Of the inorganic matter about three-fourths is non-volatile constituents, while the volatile material consists chiefly of chlorides. The ether, alcohol, and water extractives represent 2.92, 5.61, and 10.53 per cent of the dry matter, respectively. The alcohol-soluble moiety contains 7.9 per cent of nitrogen, while in the water extractives there is 10.89 per cent of nitrogen. In determining the protein content I have departed from the customary way of giving as protein the product of the total nitrogen by the factor 6.25, but the nitrogen extracted by the various solvents which is not of protein origin has been deduced from the total amount of nitrogen found in the dry material. From the results of our experiments we may safely say that Moore is probably wrong in stating that “there is very little nitrogen other than protein nitrogen.” In my experiments the alcohol- and water-extracted nitrogen forms 22 and 24 per cent, respectively, of the total nitrogen of fasting and normal lobsters.

With the correction as stated above, the protein content of normal lobsters is computed as 31.54 per cent. But even this figure
<table>
<thead>
<tr>
<th></th>
<th>Dry matter</th>
<th>Water</th>
<th>Organic matter</th>
<th>Total inorganic matter</th>
<th>Non-volatile inorganic matter</th>
<th>Total glycogen</th>
<th>Ether extract</th>
<th>Alcohol-extracted nitrogen</th>
<th>Per cent of nitrogen in alcohol-extracted nitrogen</th>
<th>Water extractives</th>
<th>Water-extracted nitrogen</th>
<th>Per cent of nitrogen in water extractives</th>
<th>Total nitrogen</th>
<th>Protein (non-extracted nitrogen X 6.25)</th>
<th>Undetermined</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Control (average of five)</strong></td>
<td>32.572</td>
<td>67.328</td>
<td>21.010</td>
<td>11.662</td>
<td>8.953</td>
<td>0.161</td>
<td>0.954</td>
<td>1.831</td>
<td>0.145</td>
<td>2.582</td>
<td>3.285</td>
<td>0.374</td>
<td>3.558</td>
<td>2.168</td>
<td>10.315</td>
</tr>
<tr>
<td><strong>Fasting 50 days (average of five)</strong></td>
<td>21.374</td>
<td>78.626</td>
<td>10.766</td>
<td>10.608</td>
<td>8.933</td>
<td>0</td>
<td>0.051</td>
<td>0.361</td>
<td>0.019</td>
<td>1.100</td>
<td>1.248</td>
<td>0.171</td>
<td>2.924</td>
<td>0.957</td>
<td>4.793</td>
</tr>
</tbody>
</table>

**Percentage Composition of the Dry Matter of Normal and Fasting Lobsters.**

|                              | 64.305     | 35.695| 27.409         | 0.404                   | 2.919                       | 5.605          | 0.443        | 7.904                    | 10.528                                      | 1.146         | 10.891                   | 6.636                                      | 31.544        | 13.215                    |               |
| **Control (average of five)** | 50.370     | 49.630| 41.817         | 0                      | 0.238                       | 1.691          | 0.087        | 5.145                    | 5.767                                       | 0.876         | 15.190                   | 4.475                                      | 22.425        | 20.249                    |               |
is probably too high, since some of the nitrogen considered as 
belonging to the protein is really a component part of the chitin 
of which the shell is largely made up. Chitin contains about 
6 per cent of nitrogen (protein contains 16 per cent). Unfortu-
nately the weight of the shells was not determined, and it is there-
fore impossible to compute even approximately the chitin nitro-
gen fraction. But it is clear that the amount of protein is less 
than that given in the table and that the undetermined portion, 
recorded in the last column, should be correspondingly higher 
than 13.2 per cent.

The composition of fasting lobsters, as compared with that of 
the normal lobsters, shows an unusually large increase in the 
proportion of water, which was increased to 78.63 per cent, with 
individual variations ranging from 77.6 to 79.7 per cent. An 
increased content of water has been generally observed in fasting 
organisms, but the change from 67.3 to 78.6 per cent, i.e., by more 
than 11 per cent, must be regarded as entirely unparalleled in 
any other animal. The dry matter is made up of practically 
equal parts of organic and inorganic substance. About four-
fifths of the latter is non-volatile, a proportion greater than that 
found in normal lobsters, which is due to the predominant loss 
of chlorides and possibly also carbonates. The ether-, alcohol-, 
and water-soluble materials show likewise a marked reduction 
to 0.24, 1.69, and 5.77 per cent, respectively. The diminution is 
particularly noticeable in the case of the ether-soluble substances, 
the quantity of which decreased to less than one-twelfth the nor-
mal content. In comparison with that, the alcohol and water ex-
tractives have diminished much less, the former from 5.6 to 1.7 per 
cent, and the latter from 10.5 to 5.8 per cent. The nitrogen con-
tent of these extractives has not diminished in the same ratio. In 
the alcohol extractives it has changed from 7.9 to 5.1 per cent, 
while in the water extractives it increased from 10.9 to 15.2 per 
cent, or nearly one and a half times. It follows, therefore, that in 
the fasting lobsters the non-nitrogenous fraction of the extracted 
material decreased more rapidly than the nitrogenous.

It will be observed, furthermore, that the glycogen has been 
exhausted so that in the samples analyzed, at any rate, nothing 
could be recovered. It is possible, of course, that a slight trace 
may still have been present in the entire lobster.
The undetermined moiety of the dry matter of fasting lobsters is 20.25 per cent, and this is considerably higher than in the normal animal. It has already been pointed out that the undetermined fraction is doubtless chitin, and this would suggest further that the percentage of chitin is greater in fasting lobsters, which may be due either to the fact that the amount does not diminish as rapidly as that of the proteins, or that it does not diminish at all. In this connection the per cent of undetermined material found in the fresh substance gains particular significance. It will be seen that this was 4.46 per cent in the normal and 4.31 per cent in the fasting animals. We shall return to this subject later on.

The analyses here recorded differ considerably in their results from those given by Moore and Herdman. This may be partly accounted for by the consideration that these authors determined only the total nitrogen and, multiplying by the usual factor 6.25, expressed it in terms of protein. But apart from this they found in their lobsters a much higher proportion of fat, glycogen, and ash. Even in the series which fasted 235 days they still found 2.14 per cent of fat, whereas my lobsters contained barely over 0.2 per cent at the end of 56 days. The per cent of undetermined material is, therefore, much lower than in my experiments. But here again, since Moore and Herdman consider all the nitrogen of the dry matter of lobsters to be protein nitrogen and do not make any allowance for the chitin, it is obvious that the actual amount of undetermined matter must be greater than is shown in their tables.

With the data given in Table II we may now compute the average composition of the lobsters before and after the fast, in terms of the absolute quantities of the various components. This has been done in Table III. The interesting fact brought out by this comparison of the initial and final composition is that the water in the organism is not merely increased relatively, as has been ordinarily found in the case of starving animals, but that it increased absolutely. Thus it is computed that at the start there were 112.67 gm. of water per animal. The amount actually

---

TABLE III.

Average Composition, in Grams, of Lobsters before and after Fasting.

<table>
<thead>
<tr>
<th></th>
<th>Live weight</th>
<th>Dry matter</th>
<th>Water</th>
<th>Organic matter</th>
<th>Total inorganic matter</th>
<th>Non-collapsible inorganic matter</th>
<th>Total glycogen</th>
<th>Ether extract</th>
<th>Alcohol extractive</th>
<th>Alcohol-soluble nitrogen</th>
<th>Water extractive</th>
<th>Water-extractable nitrogen</th>
<th>Total nitrogen</th>
<th>Protein (calculated) X 5.5</th>
<th>Utdetermined</th>
<th>Per cent of organic matter determined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial (computed)</td>
<td>167.34</td>
<td>54.67</td>
<td>112.67</td>
<td>35.16</td>
<td>19.51</td>
<td>14.99</td>
<td>0.27</td>
<td>1.60</td>
<td>3.06</td>
<td>0.24</td>
<td>5.51</td>
<td>0.63</td>
<td>3.63</td>
<td>17.26</td>
<td>7.46</td>
<td>78.78</td>
</tr>
<tr>
<td>Final (determined)</td>
<td>162.58</td>
<td>34.75</td>
<td>127.83</td>
<td>17.50</td>
<td>17.25</td>
<td>14.53</td>
<td>0</td>
<td>0.08</td>
<td>0.59</td>
<td>0.03</td>
<td>2.03</td>
<td>0.28</td>
<td>1.56</td>
<td>7.79</td>
<td>7.11</td>
<td>59.95</td>
</tr>
<tr>
<td>Absolute loss in gm</td>
<td>4.76</td>
<td>9.92</td>
<td>+15.16</td>
<td>17.66</td>
<td>2.27</td>
<td>0.45</td>
<td>0.27</td>
<td>1.51</td>
<td>2.48</td>
<td>0.21</td>
<td>3.48</td>
<td>0.35</td>
<td>2.07</td>
<td>9.47</td>
<td>0.35</td>
<td></td>
</tr>
<tr>
<td>Loss in per cent...</td>
<td>2.73</td>
<td>57.3</td>
<td>+13.46</td>
<td>50.22</td>
<td>11.62</td>
<td>3.03</td>
<td>100.0</td>
<td>94.80</td>
<td>80.84</td>
<td>87.20</td>
<td>63.17</td>
<td>55.59</td>
<td>57.11</td>
<td>54.75</td>
<td>4.69</td>
<td></td>
</tr>
</tbody>
</table>
found at the end of 56 days of starvation was 127.83 gm., or 15.16 gm. more.

We may also point out the comparative constancy of the non-volatile portion of the ash. It was diminished by 0.45 gm., or 3.03 per cent, and it is doubtful if such a small diminution has any significance in view of the fact that the initial quantity is computed and not directly determined. It is probably more nearly true to assume that the non-volatile inorganic constituents remain practically unchanged through fasting.

It should further be observed that the various extractives suffer most heavily. Thus 94.8 per cent of the ether-soluble material is used up, while of the alcohol and water extractives 80.8 and 63.2 per cent, respectively, disappear. It is significant that the amount of material which remained undetermined in our analyses is nearly the same in the lobsters before and after the fast. The loss of 0.35 gm., or 4.69 per cent, does not seem large enough to merit much consideration, and, though it would not justify the assumption that this particular component does not undergo any change, it is clear that the change must be of slight importance.

If the different organic constituents are added together it is found that their weight makes up 78.78 per cent of the total dry matter in the normal condition, and only 59.95 per cent in the starved. At first thought this failure to recover more of the organic substance in spite of the more or less extensive analytical treatment would suggest that the analyses were faulty. I have assumed this attitude towards the results of the analyses, but the same data were obtained by repeating practically the whole work. The question has been cleared up, however, by the fact that chitin, which is apparently unaffected by inanition, forms a larger proportion of the fasting than of the normal lobster. It is of interest to observe that a substance comparatively rich in nitrogen and calorific value should remain untouched, while under the great stress produced by the inanition all other tissues of the organism contribute heavily to its maintenance. It raises the problem of the availability of glucosamines as a source of energy. This point will be studied in the future.

We shall now attempt to answer the question we have undertaken to solve at the beginning of this paper. A review of the
data in the last line of Table III shows that as far as the different organic substances of the lobsters are concerned the rate of their loss of weight was as great as in any other known instance on record. The changes we find here are in close agreement, for instance, with those which I observed several years ago in starving salamanders. The actual loss in body weight suffered by the lobsters is masked by the imbibition of water. We can easily compute what the probable loss was at the end of 56 days of fasting. The loss found from the change of the total body weight was only 2.73 per cent. But let us suppose that no imbibition of water had taken place. Furthermore, with the knowledge gained from other studies of fasting organisms we may assume that at this particular phase of starvation the quantity of water in the body would have diminished about 33.3 per cent. Starting with a quantity of 112.7 gm. of water, this would have decreased to 75.1 gm. at the end of 56 days of fasting. The weight of the lobsters would therefore have been 109.8 gm., and the loss 34.4 instead of 2.73 per cent. The hard shell protecting the entire body of the lobster and forming a solid supporting structure prevents the cells of the soft tissues from shrinking as they ordinarily do under the influence of inanition when the metaplasmic inclusions are being gradually used up. This may explain the extraordinary extent of the imbibition of water by the tissues as their reserves are being exhausted. The relative increase in the water content of the body which invariably occurs in inanition is unquestionably reduced the concentration of the body juices. But the great absorption of water by the tissues of starving lobsters is the result of primarily mechanical factors, the tissues imbibing an excess of water in the manner of a sponge.

My thanks are due to Mr. E. W. Fuller for the assistance which he rendered in the course of these experiments.
