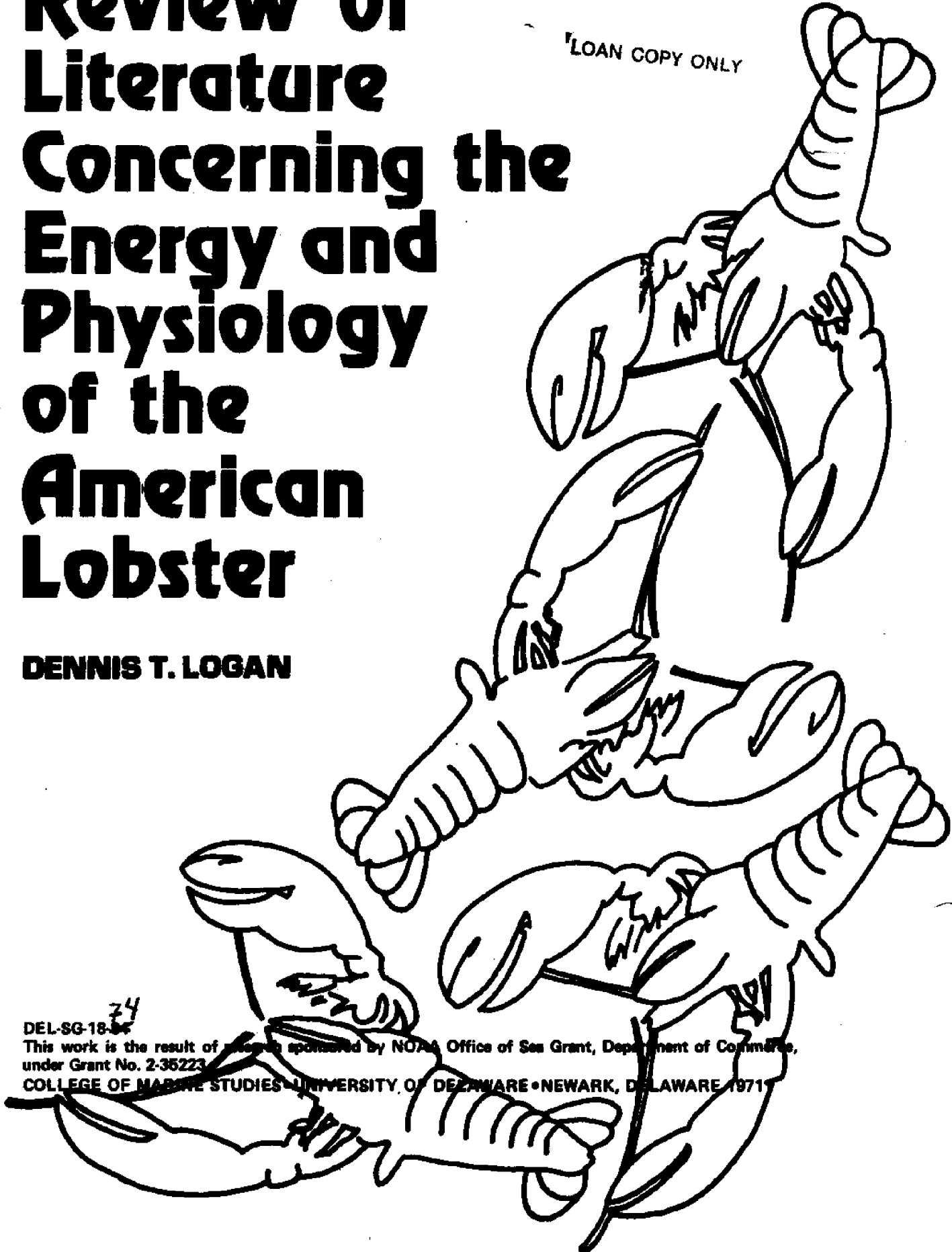


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# Review of Literature Concerning the Energy and Physiology of the American Lobster

**DENNIS T. LOGAN**

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COLLEGE OF MARINE STUDIES UNIVERSITY OF DELAWARE • NEWARK, DELAWARE 1971

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**REVIEW OF LITERATURE  
CONCERNING THE ENERGY AND PHYSIOLOGY  
OF THE AMERICAN LOBSTER**

by

Dennis T. Logan

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## INTRODUCTION

The American lobster, Homarus americanus, is now an important commercial organism and shows promise of being an important commercial organism in future mariculture. Before lobster mariculture can become an economically profitable venture, better understanding of the lobster's physiology, nutrition, behavior, parasites, diseases, and tolerances must be gained. This report summarizes most of physiological data concerning lobsters that is available in published literature.

Literature was collected and reviewed in preparation for a study at the University of Delaware of the energy budget throughout the life cycle of the American lobster. Such a study is basic to understanding much of the physiology and nutrition of Homarus. This report synthesizes relevant information into a hypothetical energy budget and analyzes weaknesses of this synthesis. An introduction to energetics is provided for those less familiar with this area.

## ENERGY BUDGETS AND PHYSIOLOGY

Energy budgets. An example of the conventional scheme for the utilization of energy by domestic animals is given in Fig. 1 (after Harris, 1966). All values are expressed as energy (calories) or energy flow (calories per unit time). The gross energy of food consumed is termed "food-intake gross energy" and abbreviated as "GE<sub>i</sub>." This may leave the organism as "fecal energy" (FE), which is the gross energy of the undigested fraction of the food, or become digested and absorbed into the organism as "apparent digestible energy" (DE). A fraction of the digestible energy may be lost as "gaseous products of digestion" (GPD), which will be assumed to be negligible in non-ruminants, and a fraction will be lost as "urinary energy" (UE), measured as the gross energy of the urine. The remaining digestible energy is available to do work and is termed "metabolizable energy" (ME).

In the process of metabolic work, energy is lost as a "heat increment" (HI). The remaining metabolizable energy is termed "net energy" (NE<sub>m + p</sub>) and is used for "maintenance" (NE<sub>m</sub>) and "production" of biomass (NE<sub>p</sub>). Maintenance is the fraction of net energy expended to insure and maintain the organism in internal chemical and physical equilibrium. Production is the fraction of net energy incorporated into new tissue growth.

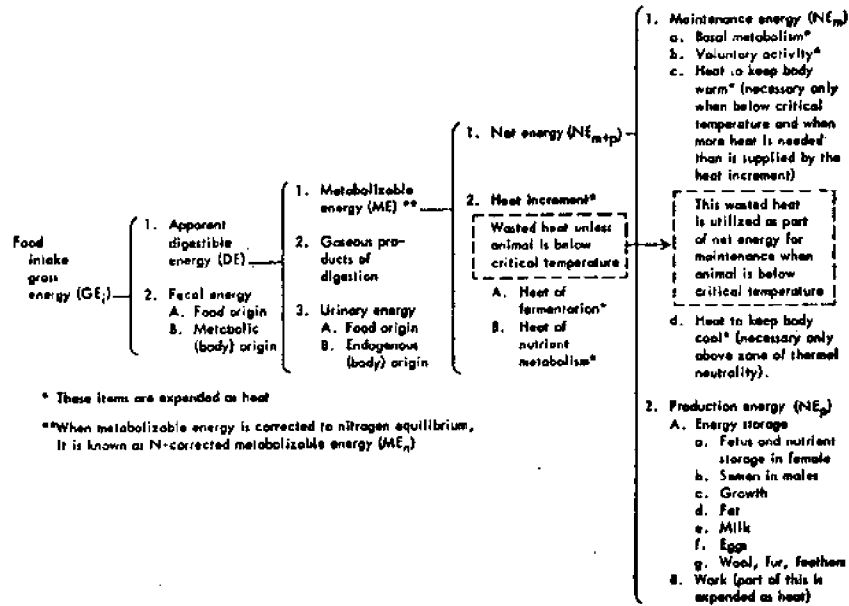


Figure 1. Utilization of energy (conventional scheme).  
(After Harris, 1966).

In the conventional scheme fecal energy and urinary energy of body origin (sloughed off cells, enzymes, and secretions) are considered as losses in digestion and metabolism respectively. These are actually losses from maintenance energy and a true theoretical scheme for the utilization of energy can be formulated with these changes (Harris, 1966). Unfortunately, differentiation of the origins of the energy contained in feces or urine is very difficult and the true scheme has seldom been utilized.

An example of a simplified energy budget for an organism is taken from Petruszewicz and Macfadyen (1970). Matter consumed (C) is either digested (D) or egested as feces (F); digested energy may be assimilated (A) or removed by excretion (U). Assimilated food energy may be used for production (P), which is subdivided into growth ( $P_g$ ), reproduction ( $P_r$ ), secretions and exuviae (E). Energy lost from nutrient metabolism, maintenance, and voluntary activity will appear as heat and can be measured as respiration (R). The Petruszewicz and Macfadyen scheme (Fig. 2) is generally used in ecological and non-mammalian studies and terms are operationally defined. The basic scheme will be used in this study.

Crustacean energetics. Although many investigators have researched problems of energy relationships, very few complete energy budgets for crustaceans exist. One of the first and most complete is Richman's (1958) study on laboratory populations of Daphnia pulex. Richman has determined



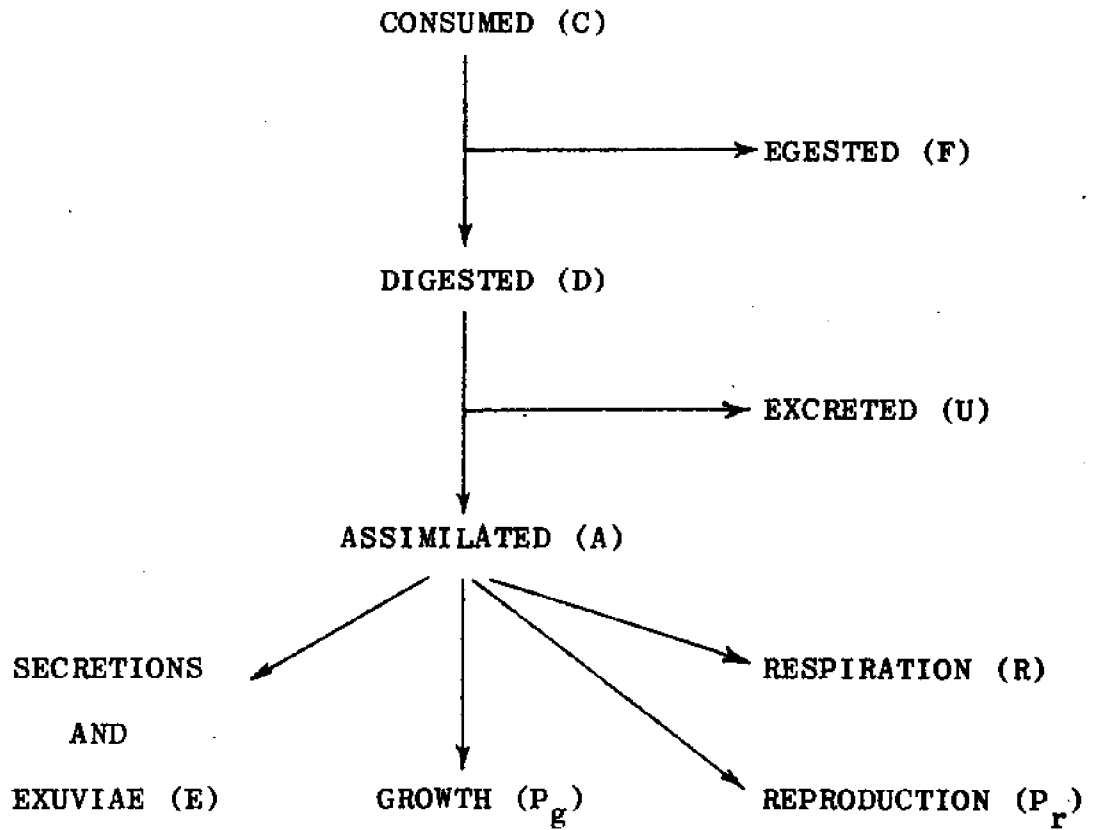


Figure 2. The utilization of energy. Illustration of scheme proposed by International Biological Program and described by Petruszewicz and Macfadyen (1970).

consumption, oxygen utilization, carbon-dioxide production, reproductive and growth productions. Rejecta (egesta plus excreta) is determined by subtraction. Energy budgets are composed for both adults and pre-adults.

Cummins et al. (1969) studied the energetics of a population of the predacious cladoceran Leptodora kindtii. In the 6-12 mm size class this species is carnivorous, but when below 6 mm it is believed to eat bacteria, algae, and detritus. A fairly complete energy budget for a population of Leptodora in the 6-12 mm size class is presented. Consumption, respiration, assimilation, production, egestion, reproduction (as over-wintering eggs), and yield are reported. Consumption is estimated from life tables of principle prey species. Assimilation is assumed to be 30 percent of the consumption; egestion is derived from the difference between consumption and assimilation. Respiration is estimated. Yield is estimated from fish gut analysis and fish populations (to determine predation) as well as from Leptodora life tables.

Clutter and Theilacker (1971) present an energy study of a population of mysid shrimp. Production (both as reproduction and growth), respiration, and exuvia production are measured. The rate of energy loss to catabolism is estimated as 5-6 percent of the energy content of the body per day.

A study by Hargrave (1971) on the amphipod, Hyallela azteca, is especially complete. Ingestion rates are cal-

culated from radiotracer experiments. Production rates from growth observed by another author are used. Egestion is measured, but the caloric content of digested sediment is assumed to be equivalent to that of undigested sediment, which is the food. This is possibly the largest source of error. Excretion of dissolved organics is measured by total carbon analysis. Excreted material is assumed to be 40 percent carbon; total excretion is estimated from this assumption. Mean calorific content of excreta is assumed to be 5000 cal/g; calorific content of total excreta is calculated from this assumption. Hargrave concludes that a surprising 36 percent of energy assimilated is released as soluble organic substances. This opens to question many previous studies which assume that excretion is an insignificant part of the total energy loss and can be ignored. A complementary study of Hyallolella azteca records the energy budget of a natural population in the field (Mathias, 1971).

Kibby (1971) studied energetics and population dynamics of a copepod, Diaptomus gracilis, in two reservoirs. Feeding rates are determined from radiotracer experiments. Assimilation is estimated from the sum of growth and respiration ( $A = P + R$ ) and by radiotracer experiments to determine egestion (excretion is considered negligible). Respiration is determined by micro-Winkler. Calorific content is determined by Gentry-Wiegert micro-bomb calorimeter. Carbon-dioxide production is calculated

## Tables I-III

Tables I-III summarize various ecological efficiencies (ratios) from a number of energetic papers. These tables are not comprehensive.

## Energy Flow Abbreviations:

C = Consumption  
D = Digestion  
A = Assimilation  
F = Egestion  
U = Excretion  
FU = Rejection  
R = Respiration  
P = Production  
P = Growth  
 $P_r^g$  = Reproduction

## Trophic Level Abbreviations:

C = Carnivore  
H = Herbivore  
O = Omnivore  
D = Detritus feeder  
F = Filter feeder

## Footnotes:

\*Calculated by this author

\*\*From Tsikhon-Lukanina, Soldatova, and Nikolayeva (1968)

Table I

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>g</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
Crustacea														
Actinia aquina	C			60										Ivleva 1964**
Artemia salina	H			54										Sushchenya 1962, 1968**
Asellopsis intermedia (copepod)	H					o 9.81 ♀ 18.42								Lasker et al. 1970
Asellus aquaticus	Allochthonic material			68										Levanidov 1949
Calanus finmarchicus (copepod)	O			55-60										Conover 1964, 1966
Calanus finmarchicus	H Skeletonema				38.4									Corner et al. 1967



Table I (con't.)

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>g</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
Hippolyte inervis (shrimp)	C				15 @ 24° C 41 @ 19° C									Regnault 1969
Hyalinella azteca (amphipod)	D	18.1*	69.5*	13.1*	18.2*		59*	36.5*	82*	87.5*		31	42	Hargrave 1971
Hyriopsis schlegelli	D													Satoru Higashi 1966**
Idothea baltica (isopod)	H													Tsikhon-Lukanina, Soldatova, and Nikolayeva, 1968
Idothea baltica larvae	H													Tsikhon-Lukanina and Lukashneva 1970

urine  
not  
tested

12-18

0

4.85\*

Table I (con't.)

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>E</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
<i>Limnea stagnalis</i>	H			75										Ivlev 1938**
<i>Macrocyclops albidus</i>	C			50										Kiekovskiy and Sushkina 1966**
<i>Metamysidopsis elongata</i>	C			90		19-36	56.9	5-6% of body dry wt/ day goes to urine			0			Clutter and Theilacker 1971
<i>Menippe mercenaria</i>	C			98										Sushchenya and Kiaro 1966
<i>Pontogammarus mecuticus</i> (amphipod)	H			65 ± 4.1		5	87							Soldatova 1970 Tsikhon- Lukanina, Soldatova, and N-ko- layeva, 1968



Table I (con't.)

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>g</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
Rithropanopeus harrisi (brachyuran)	C			95 ± 1.1										Tsikhon-Lukanina, Soldatova, and Niko-layeva, 1968
Sphaeroma pulchellum larvae (isopod)	H			90	5.9*	94.5*	10				6.25*			Tsikhon-Lukanina and Lukasneva 1970

Table II

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>g</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
Mollusks														
<i>Littorina planaxis</i>					20.0									North, 1954
<i>Mytilus californianus</i>	F				0-1 yr = 15.26 1-2 yr = 10.15 2-3 yr = 7.49									Fox and Coe, 1943
<i>Mytilus edulis</i>	F				0-1 yr = 84-29 1-2 yr = 29-11									Jorgensen, 1952
<i>Nucula sulcata</i>	D				9.22									Trevallion, 1965 (in Trevallion, 1971)
<i>Scrobicularias plana</i>	F				60.5	21.0*	78.7*	39.2				26-27*		Hughes, 1970; 1972
<i>Tellina tenuis</i>	D				13-29									Trevallion, 1971

Table III

Species	Trophic Level	D/C	A/D	A/C	P/A	P <sub>g</sub> /A	R/A	U/D	F/C	FU/C	P <sub>r</sub> /A	P/R	U/A	Author
Insects														
Hedriodiscus truquii larvae	H			56.8- 60.0		21.9- 39.1	60.0- 77.1	No urine tested	40.1- 42.2*			32.8- 58.0*		Stockner, 1971
Pardosa luqubris	C			100	26.5*	24*	71	No urine tested	0		2.5*	36.1		Edgar, 1971
Pogonomyrus badius	H											2		Golley and Gentry, 1964
Pyrrhocoma hymphula larvae	C			86-95	47.6- 52.0*	47.6- 52.0*	41.6- 47.6	No urine tested	10- 11.5*		0	98		Lawton, 1970; 1971

from pH change. Changes in calorific content and energy efficiencies are noted throughout the life cycle.

Partial energy studies have been done for many crustaceans. These studies fall into two categories: complete energy budgets for partial life cycles and partial energy budgets in which only certain pathways are considered.

The latter type usually deal with the ratio of assimilated to consumed food or with the ratio of production to assimilation. The former type is typified by energy budgets for the young of two species of marine isopods (Tsikhon-Lukanina and Lukasheva, 1970). Tables I-III summarize the results of both complete and incomplete energy studies on some species.

Respiration. Oxygen consumption can be related to metabolism by the formula  $4.7 \text{ kcal/l O}_2$  (STP) consumed, which is based on the evolution of heat from the complete oxidation of fat, carbohydrate, or protein (Kleiber, 1961). Evolution of heat will be the same for oxidation of these substances no matter what the oxidation process (second law of thermodynamics). Total loss of food energy to heat is termed metabolism and represents the energy expended for maintenance (homeostasis), locomotion, and heat loss at each metabolic step.

Oxygen uptake of the European lobster, H. vulgaris, was first studied intensely by Thomas (1954) who reviews earlier observations. He has measured ventilation rate, respiration rate in air, and oxygen uptake in water.

Uptake in seawater is proportional to oxygen concentration (1.0-6.0 ml/l) over a temperature range of 6°-18° C. No apparent difference in oxygen consumption between sexes is observed and oxygen uptake per gram body weight decreased with size of individuals at 15° C. Uptake increases with increasing temperature (6-18° C) in seawater of constant oxygen tension.

Thomas' data has been replotted in Fig. 3 as respiration per animal. Curve I is Thomas' oxygen consumption relationship at 15° C; points 1 and 2 are his data from 21° and 19°, respectively. At 15° oxygen uptake is proportional to weight to the 0.75 power ( $R = aW^{0.75}$ ).

McLeese (1964) finds lower oxygen consumption rates in H. americanus than those reported by Thomas (1954) for H. vulgaris. McLeese attributes this to heightened activity of animals resulting from Thomas' methods. Oxygen consumption by individuals increases as oxygen concentration increased at 10° and 15° C and increased as individual activity increased with crowding. Oxygen uptake almost doubles after feeding and does not return to normal after 72 hours. Weight specific oxygen consumption decreases with increasing size (0.9-12,300 g at 15° C). McLeese (1956) also reports acclimation and lethal limits of combinations of salinity, temperature, and oxygen consumption.

McLeese's data are also plotted on Fig. 3. His respiration curve at 15° (curve II) is lower and slightly rotated in comparison to Thomas' curve. This may be due to both a difference in species and a difference in activity levels. McLeese has measured oxygen consumption at various temperatures; that data is plotted on Fig. 3 as points A, B, C, and D. McLeese finds a greater change in metabolism with temperature than Thomas. It is interesting to note that McLeese's 15° data in this experiment (curve C) falls on Thomas' 15° weight specific oxygen consumption curve (curve I), and not on his own (curve II).

Two data points from Bosworth et al. (1936) are also plotted on Fig. 3. Bosworth's points a and b, Thomas' points 1 and 2, and McLeese' points A and B are the total data available for lobster respiration above 20° C. These data are not sufficient to assume a respiration curve at 22°-24° C, because they are too scattered to use as a possible point through which to draw the curve; and because it is not known whether the weight specific oxygen curve will simply be translated with increasing temperature or if rotation will also occur.

Growth and development. Herrick (1896) discusses developmental rates for early lobster embryos at 20°-22° C. Templeman (1940) has determined times required to reach formation of eye pigment at various temperatures. Perkins (1972) reports rates of development from formation of eye pigment

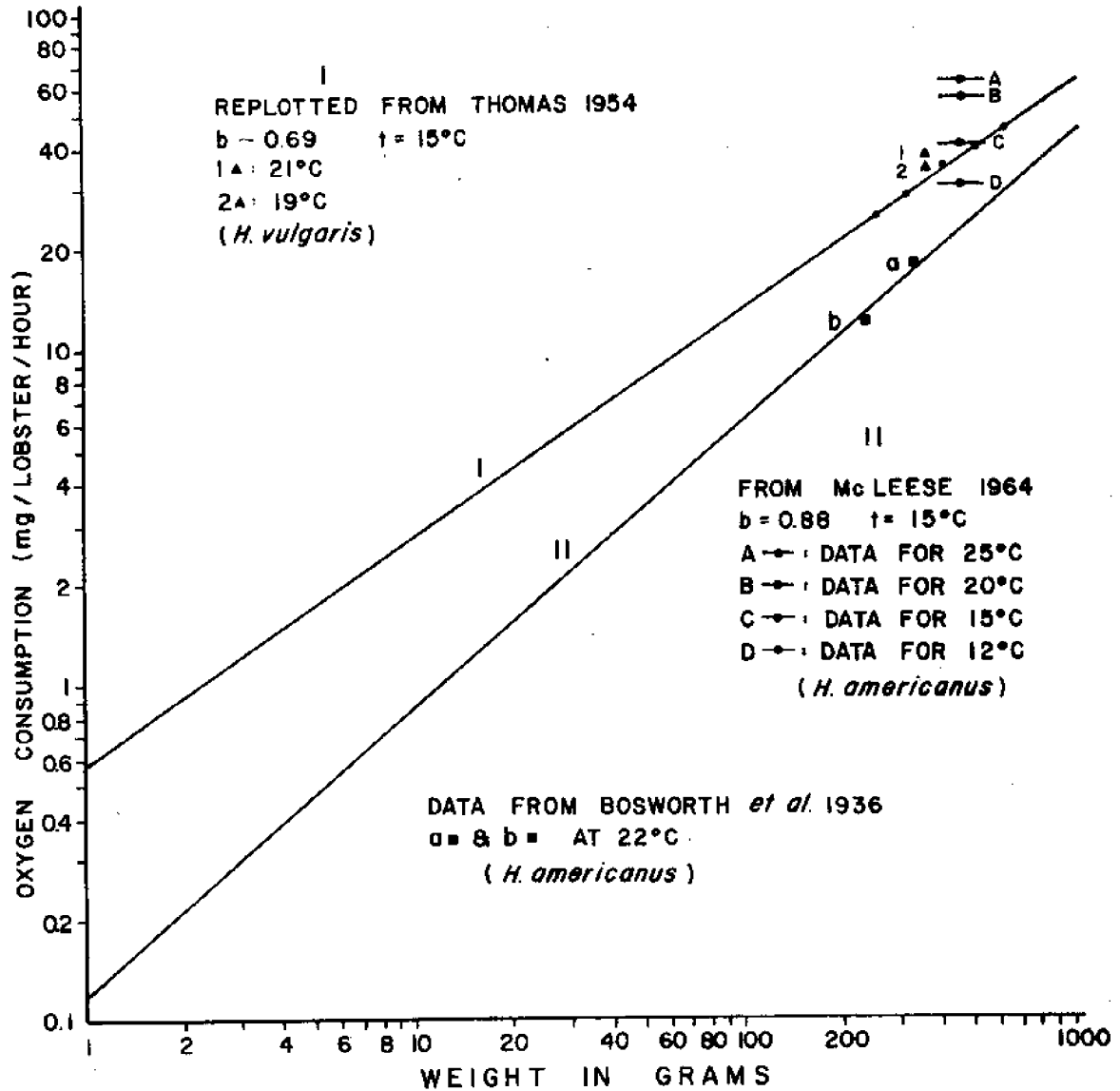


Figure 3. Respiration for Homarus. Data from three investigators are summarized on the same coordinates. Weight specific respiration at  $15^{\circ}$  from Thomas (1954) is curve I and from McLeese (1964), curve II. Data for elevated temperatures are from Bosworth *et al.*, 1936 (points a and b); Thomas (points 1 and 2); and McLeese (points A, B, C, and D).

to hatching at various temperatures ( $6.9^{\circ}$ - $24.6^{\circ}$  C) and formulates a relationship between development and temperature. According to his findings, the rate of lobster larval development may be manipulated to ensure periodic hatchings throughout the year. Pandian (1970) records dry weight, ash, water, and calorific content of lobster eggs and newly hatched larvae. Energy of metabolism is estimated from loss of energy content of the egg through time.

Hadley (1906) reports the first studies for lobster growth in captivity, concluding that lobsters take 12 years to grow to sexual maturity (about one pound or 454 g). MacKay (1929) has observed growth of larval and postlarval lobsters in a submerged box and reports a slower rate of growth. Both Herrick (1911), in his monograph, and Hadley (1906) state that greater growth occurs in nature than in artificial conditions used for determining these rates. Templeman's studies on larval and post-larval lobsters (reviewed by Wilder, 1953) collected in plankton tows indicate that this was true. Wilder's (1953) studies confirm Templeman's conclusions. Wilder reports growth in length per molt for wild lobster larvae in plankton tows and growth per molt of wild tagged lobsters. Empirical equations relating intermolt period to stage from Templeman's data and carapace length after molting to carapace length before molting from his own and Templeman's data are given. Male lobsters grow slightly more than females.



Hughes and Matthiessen (1962) report a slightly higher rate of growth for hatchery reared lobsters than that reported by Wilder (1953). Hughes, Sullivan, and Shleser (1972) report verification of Wilder's (1953) equations of growth increments in hatchery-reared animals in both ambient and 22° C water. Greatly increased growth rates at 22°-24° C (Hughes et al., 1972) make it possible to grow mature (one pound) lobsters in about two years instead of 8-12 for wild lobsters.

Ennis (1972) using tagged American lobsters find growth increments which also agree with Wilder's (1953) empirical growth increment equations. Within the 50-90 mm carapace length class males grow more than females, attributed to sexual development differences. In reviewing tagging experiments, Ennis notes variability in patterns of growth and molt increments for both H. vulgaris and H. americanus in the wild state.

McLeese (1972) observed the effects of temperature, feeding rate, diet, sex, and shelter on the rate of growth of American lobsters in captivity. He reports no difference in length or weight increments with sex, although these increments are inversely associated with population density. Mortalities are also inversely related to population density. Dunham (1972) reports that after a period of acclimation lobsters held in "group-housing" are less aggressive than those housed individually. There are no differences in levels of activity.

Production of exuviae. Rate of production of exuviae is temperature dependent (Ennis, 1972; Hughes and Matthiessen, 1962; Hughes et al., 1972; Templeman, 1936; and Wilder, 1953). Rate of molt production at 22°-24° C can be calculated from Hughes' et al. (1972) tables. Size increments of molts can be found from Wilder's (1953) empirical formulae.

Cobb (1968) reports delay of molt with no effect on mortality from fourth to fifth stage larvae when held over unfavorable substrates. Stewart and Squires (1968) also report inhibition of ecdysis in American lobsters subjected to adverse conditions.

Elevated production. An estimation of lobster growth at 22°-24° can be made from present data. Lobster growth is generally recorded as linear growth; what is needed here is biomass accumulation. Fig. 4 relates linear growth, measured as carapace length, to weight using data from wild lobsters (Krouse, 1973) and laboratory grown stock (Hughes et al., 1972) at 22°-24° C. The relationship is virtually the same.

Hughes et al. (1972) report growth increments (carapace length) per molt of lobsters at elevated temperatures. Their data has been replotted on Fig. 5. They reported that the data followed Wilder's (1953) growth equations; I found that it did not and graphed only the points from Hughes' data in Fig. 5. Increase in carapace length per molt (Fig. 5) is a constantly

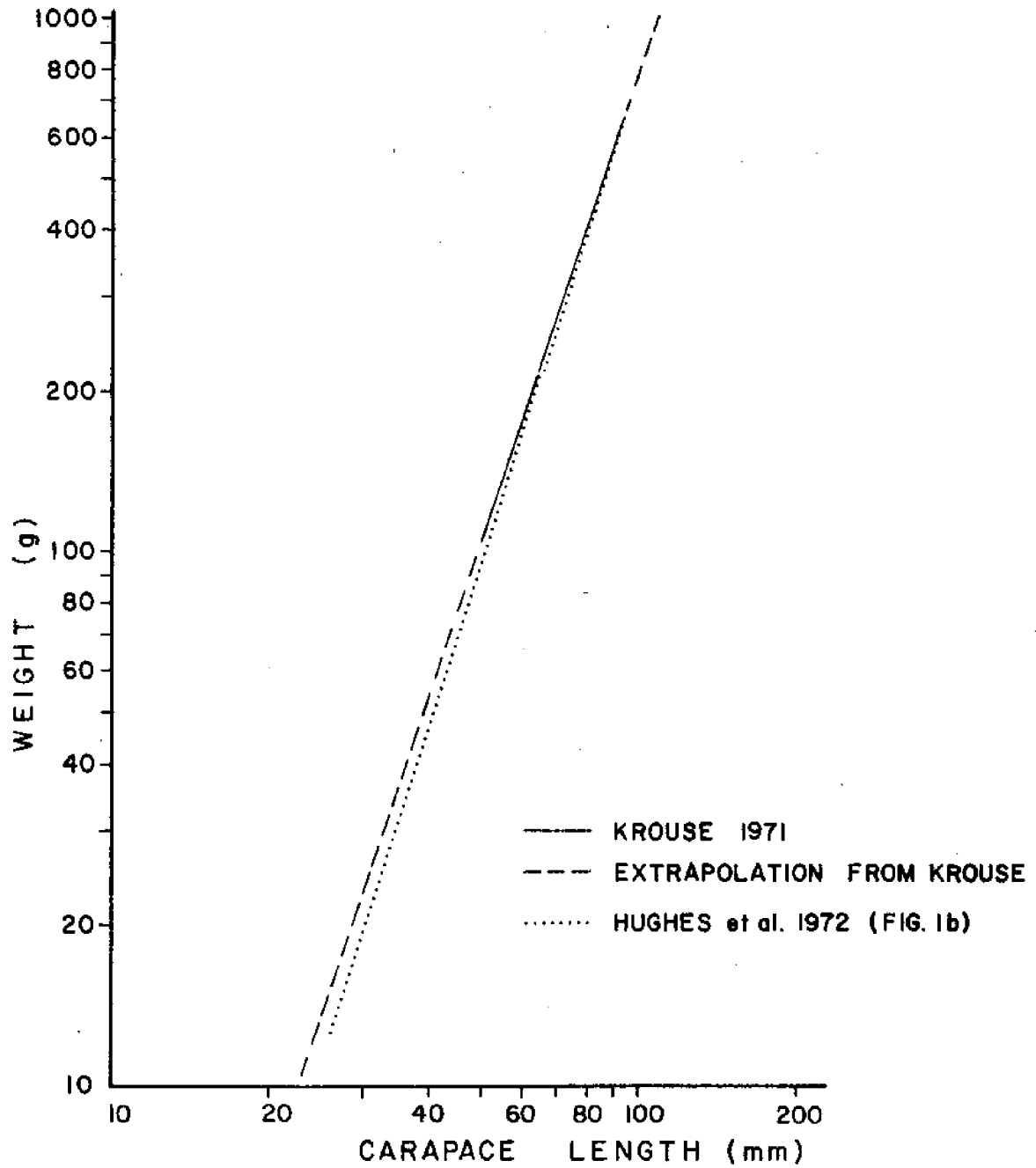


Figure 4. Relation of lobster weight to carapace length. Data from Krouse (1973) on wild lobsters and from Hughes et al. (1972) on laboratory stock. Data replotted onto double logarithm paper.

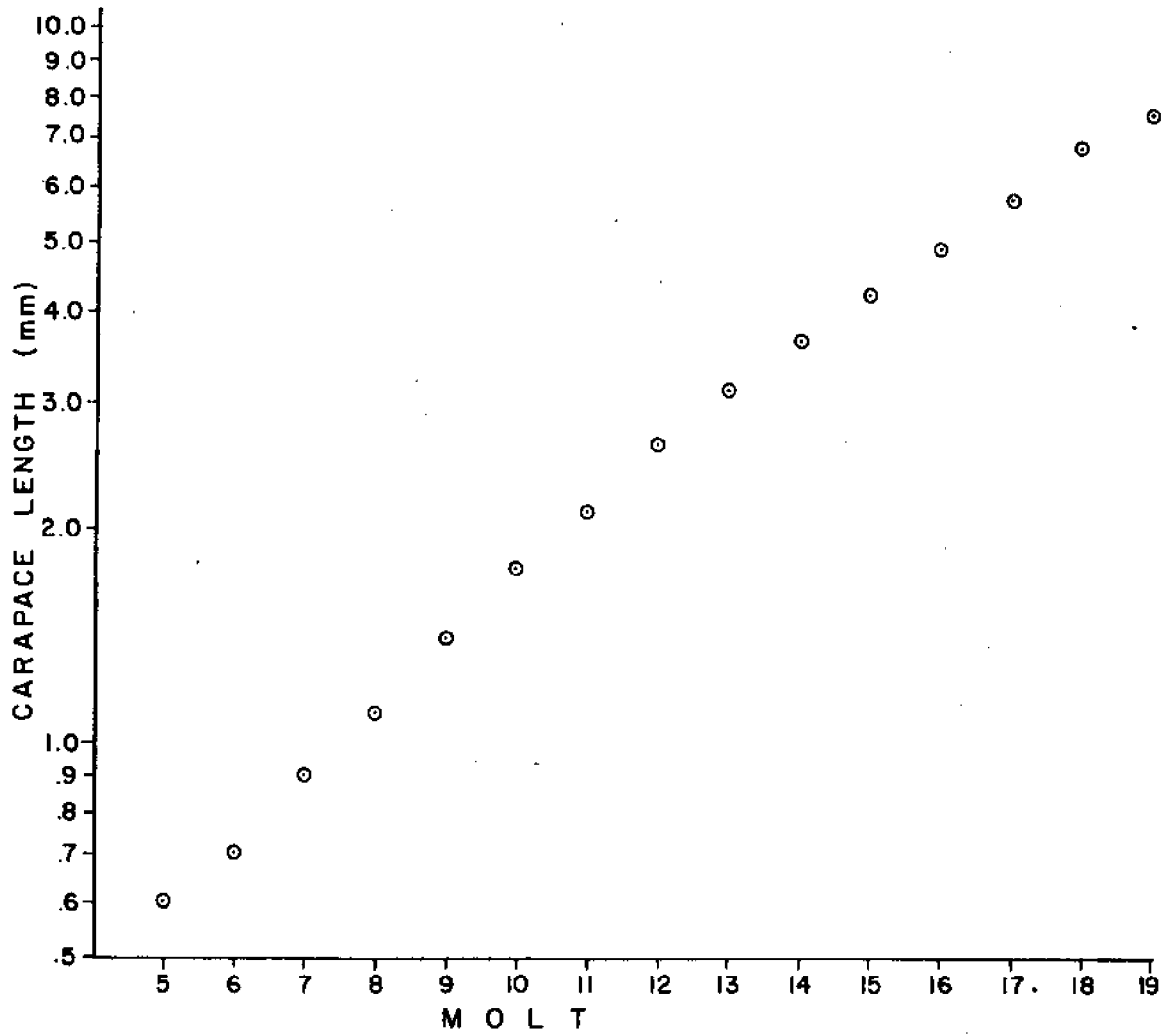


Figure 5. Relationship of carapace length to molt number. Points replotted on arithlog paper from data by Hughes et al. (1972) for lobsters at elevated temperature.

decreasing proportion of the previous carapace length (the rate of change of the slope is negative).

Lobster growth at elevated temperature can be replotted from Hughes et al. (1972). When replotted on arithlog paper (Fig. 6), one can observe that the rate of growth is in the self-inhibiting phase. This can be seen from the decreasing slope of the growth-time curve. Molts 14-19 are plotted on the growth curve and are determined from Figs. 4 and 5. Growth rate is extrapolated by a method explained later.

From data taken from Figs. 4, 5, and 6 (using only data taken directly from Hughes et al., 1972), the rate of exuvia production can be found and plotted (Fig. 7). The intermolt period increases by a constant fraction for each molt from 14 to 19. Extrapolation of this line allows one to find the time to any molt, assuming the constant fractional increase in time per molt is true in the extrapolated area. Molt 4 precedes lobster stage 1.

The relationship between weight and molt (Fig. 8) can be found from Figs. 4 and 5. Weight increases by a constant fraction at each molt. Weight at any molt down to molt 5 can be found by using Hughes' data (Fig. 5) and an extrapolation of Hughes' data (Fig. 4) or by Krouse's data (Fig. 4).

Lobster biomass accumulation (Fig. 6) can then be extrapolated to the early stages by using Figs. 7 and 8.

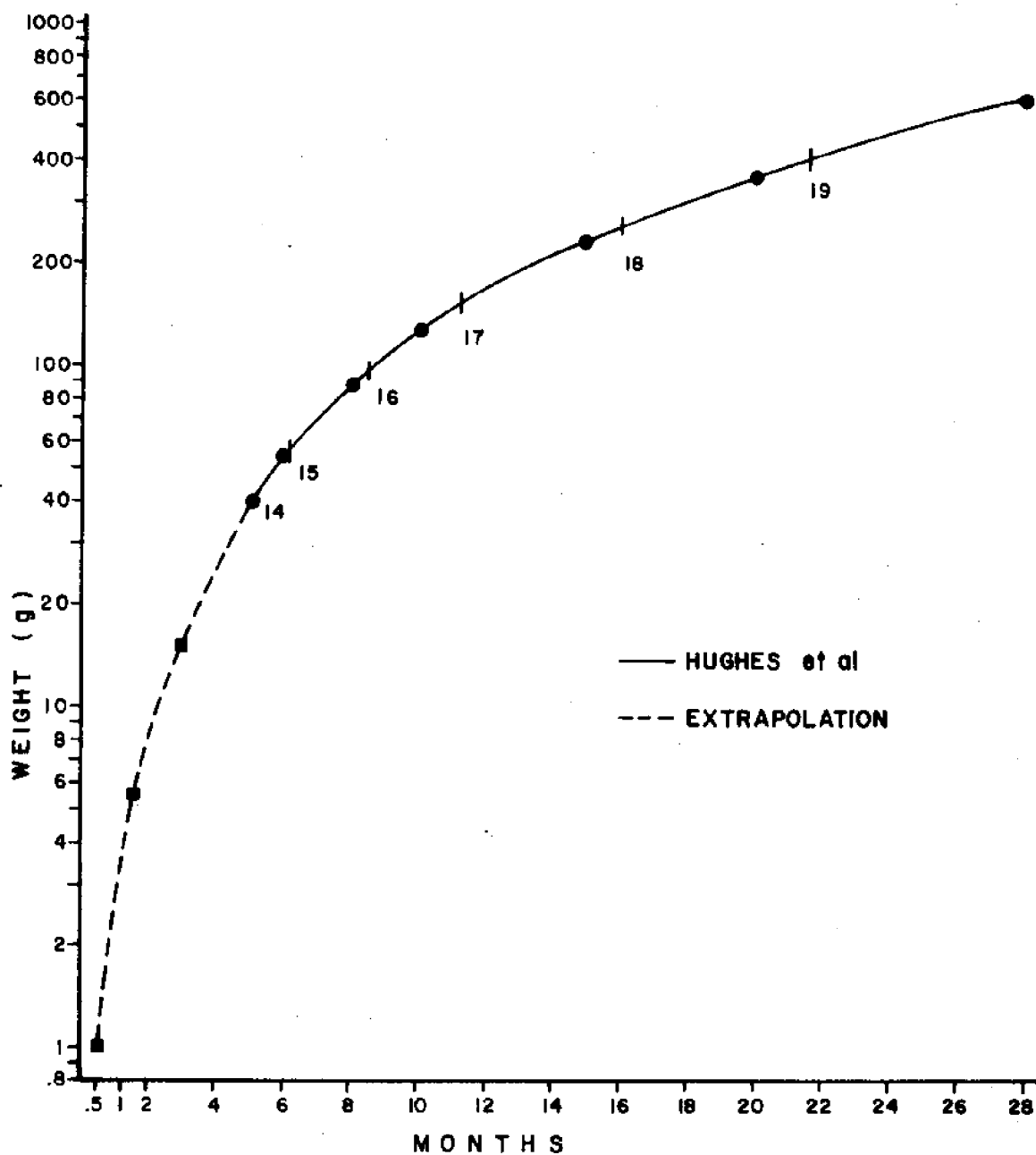


Figure 6. Lobster growth rate at elevated temperature (22° - 24° C). Replotted on arithlog paper from Hughes et al. (1972). Extrapolation explained in text. Points of molt numbers 14 through 19 indicated.

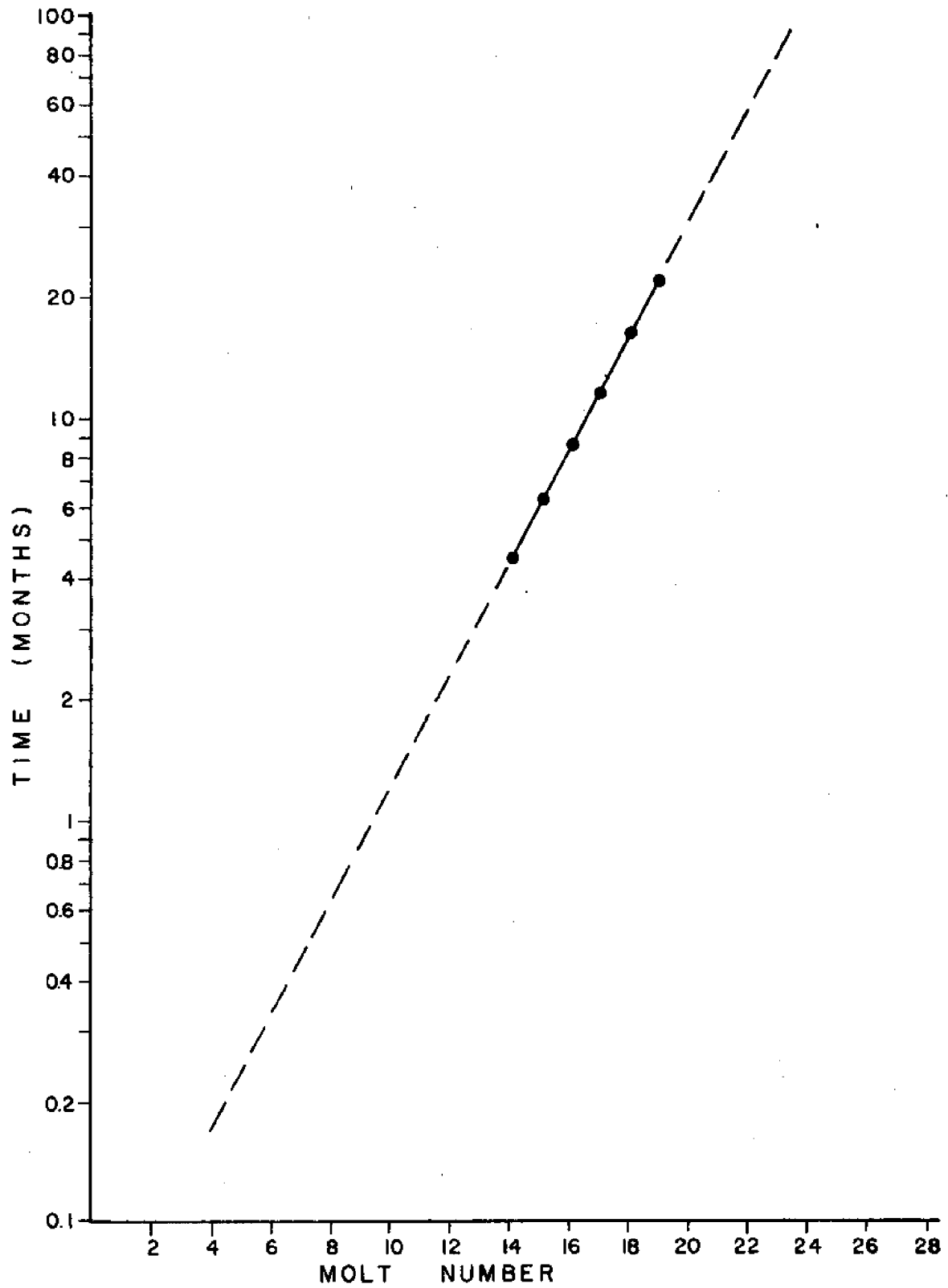


Figure 7. Rate of exuvia production at elevated temperature. Calculated from Figs. 4, 5, and 6.

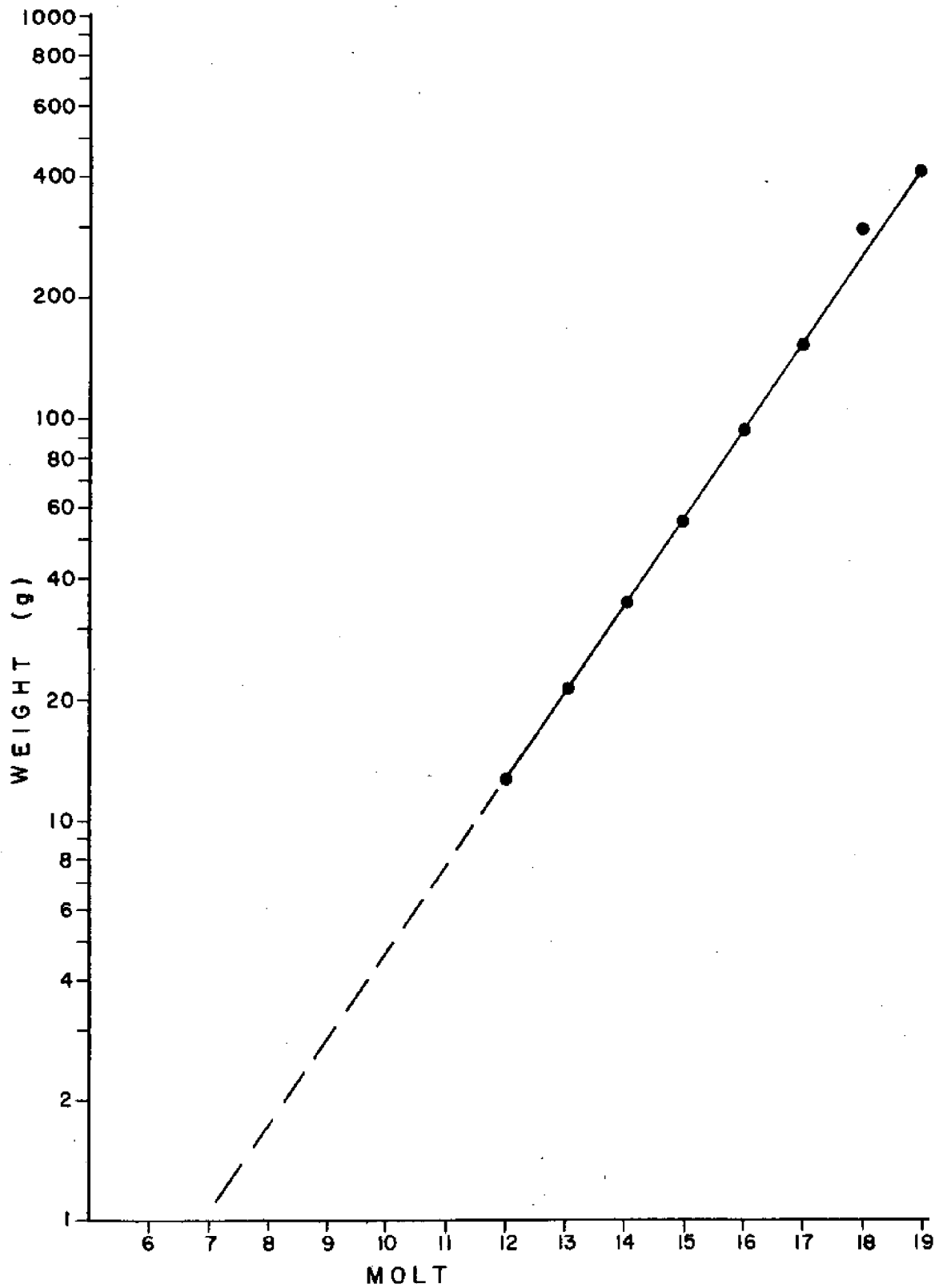


Figure 8. Relationship between weight and molt number. Calculated from Figs. 4 and 5.



This has been done on Fig. 6. The extrapolated area of the curve needs experimental verification.

Reproduction. Energy lost to reproduction is considered as the energy lost to the products of reproduction (eggs, sperm) and not the energy involved in the formation of those products. Energy involved in the formation and maintenance of eggs and sperm is considered part of adult maintenance.

Fecundity of females according to weight can be plotted from Herrick's data (1896) on 4645 lobsters (Fig. 9). His data (his table 15) compare fecundity to total length in inches. I have converted total length to millimeters and substituted into Wilder's (1953) equation relating Total Length (mm) to Carapace Length (mm):  $CL = 0.344TL - 0.13$ . Carapace lengths have been converted to weight from Fig. 4. Only Herrick's data from whole inch increments of total length are used. Weight is plotted against fecundity (Fig. 9). Egg production can be related to weight by the equation:  $Eggs = 0.964W - 2500$ .

Herrick's "law of Production" (1896) formulated from the same data can be written in the form:  $Eggs = 5000 \times 2^{(TL-8)}$ , where TL is the total length in inches. He admits (p. 53) that this "Law" only predicts the fecundity of smaller females.

Fecundity of many animals follows the relation given by Brody (1945) that fecundity (in energy or mass) is proportional to the metabolic body size or weight to

the 0.7 power. Energy lost to reproduction is therefore proportional to metabolism. Fig. 9 shows lobster reproduction to be linearly proportional to weight, at variance to most known instances.

The controlling factor in lobster reproduction may not be weight, but may be the area of the abdomen on which the eggs may be attached. The eggs are attached to a strictly defined area on the ventral abdomen. Assuming that the abdominal width and swimmeret length (onto which the eggs are glued) increase proportionally to length increases in the mature female, egg carrying capacity will increase as the cube of the length. Since weight also approximately increases as the cube of the length, it is possible that the controlling factor for fecundity is length cubed and not weight.

Reproductive energy loss in kcals can be found in the right axis of Fig. 9. This is assuming Pandian's (1970) value of 6.4 cal/egg at time of extrusion. The amount of energy expended on producing a particular brood may then be read from Fig. 9.

To compute cumulative loss to reproduction, one must take into account the observation that lobsters probably only spawn in alternate years. This is based on field data and anatomical data (Herrick, 1896), and will be assumed to be true at elevated temperature until proven otherwise. Cumulative loss to reproduction can be cal-

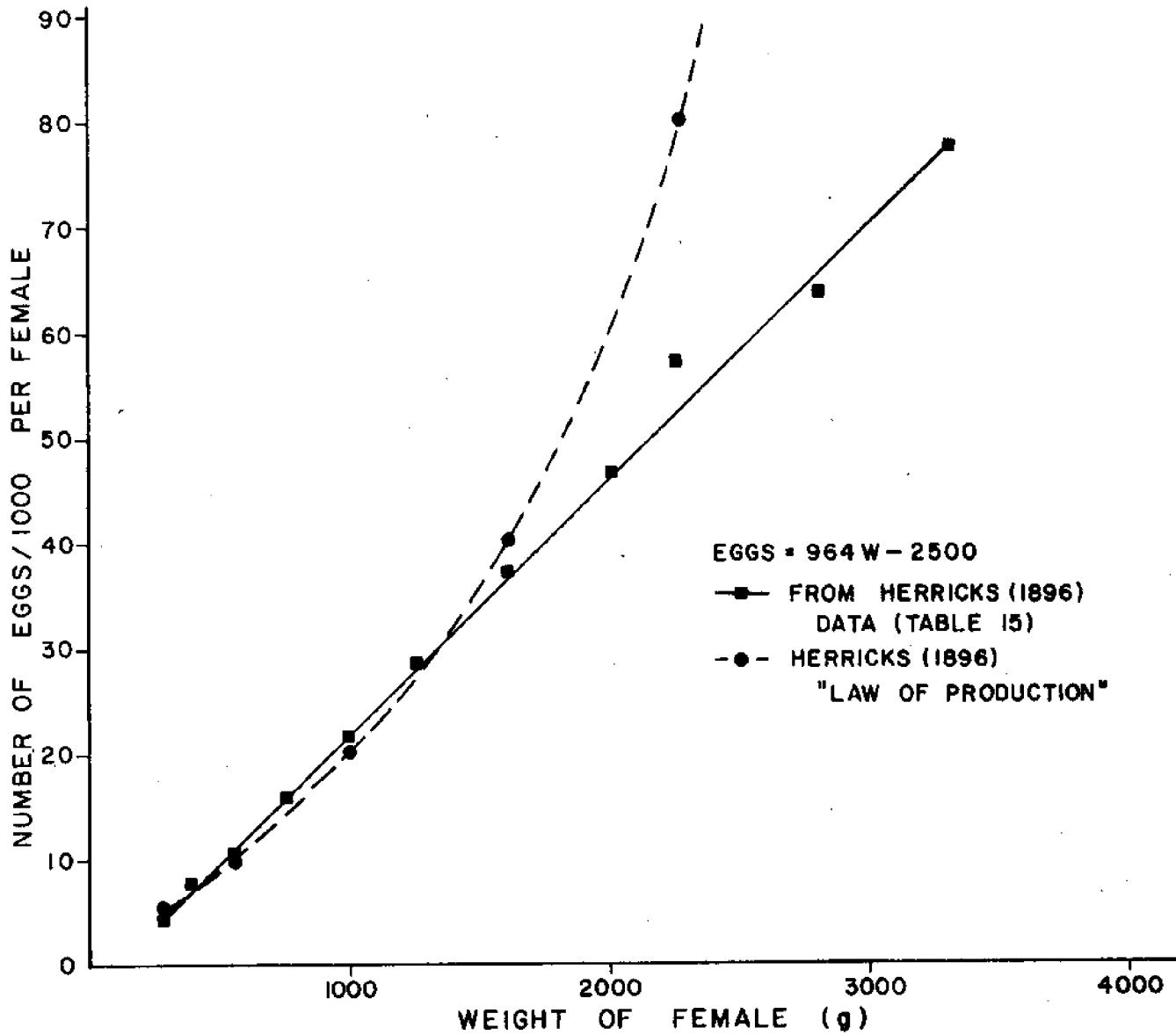


Figure 9. Fecundity as a function of body weight. Data taken from Herrick (1896). Herrick's "Law of Production" for lobsters also shown.

culated from Fig. 9, but will not be presented as a separate figure.

Reproductive energy loss for males (sperm) will be assumed negligible.

Egg energetics. Rate of energy loss of lobster eggs at approximately 22° can be calculated. Data on calorific content of eggs at four different stages was collected by Pandian (1970). Time from extrusion (Pandian's stage I) to eclosion (Pandian's stage IV) can be found from Perkins (1972). Stage III occurs about 4 days before hatching at 14° (Pandian, 1970) and I have assumed it would occur between 1 and 3.5 days before hatching at 22°. Stage II will occur between 1 and 2 weeks after extrusion at 21° (Herrick, 1896; Templeman, 1940).

Rate of energy loss by lobster eggs can then be plotted (Fig. 10). All energy loss will be assumed to be from respiration since mainly fat, not protein, is metabolized, and since loss to the sloughed egg membrane is insignificant (0.18cal/egg) (Pandian, 1970).

Rejecta. Rejecta can be subdivided into ejecta, or feces, and excreta, usually urine. In many energetic studies ejecta and excreta are measured together, or more commonly, rejecta is approximated by subtracting total measured energy outflows from total measured energy inflows (Petrusewicz and Macfadyen, 1970). Physiologically, ejecta and excreta are different. Ejecta is a combination of undigested food material and metabolic pro-

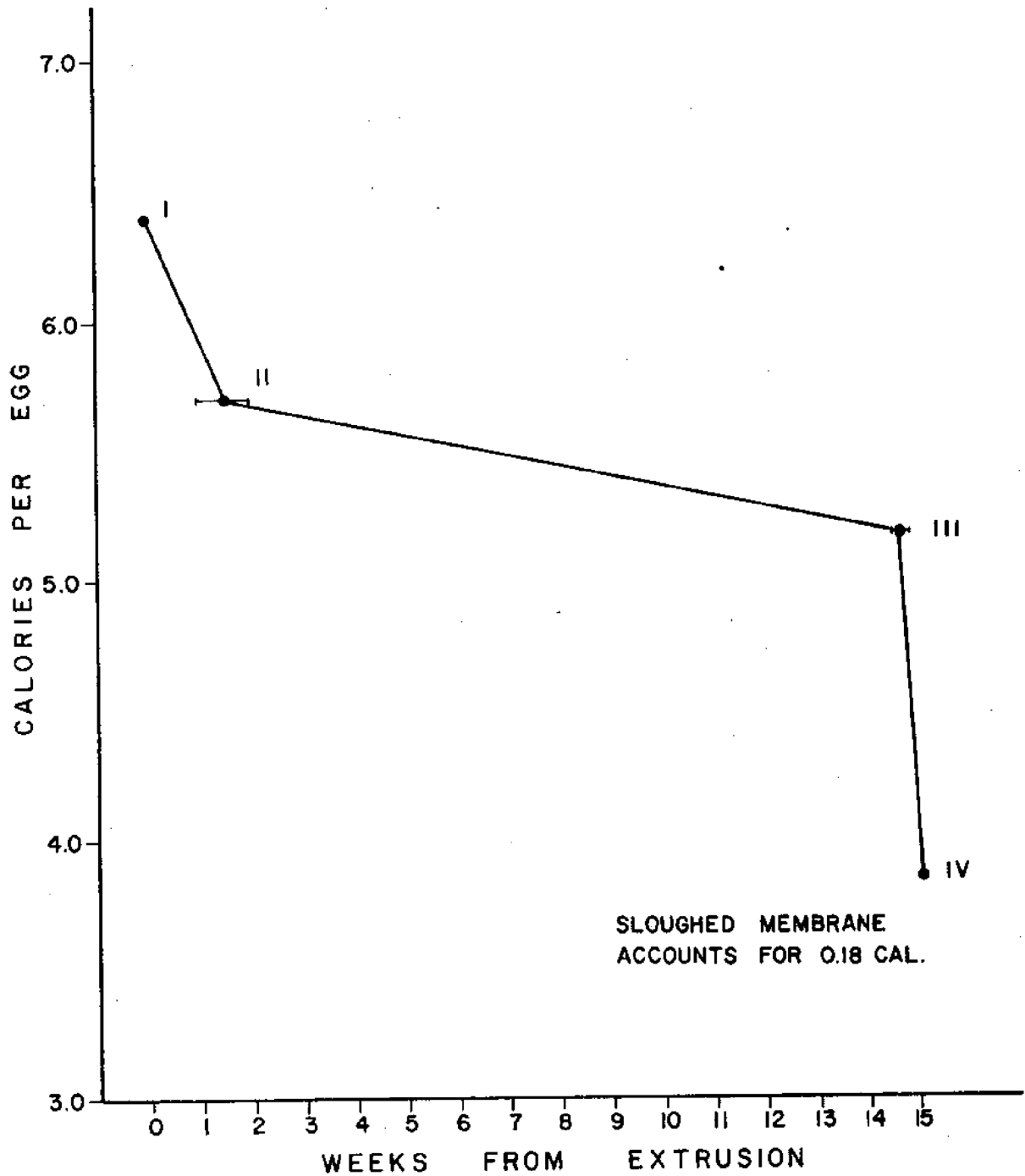


Figure 10. Energy content of *H. americanus* eggs during development. Energy content at four stages from Pandian (1970). Correlation of Pandian's stages to time from extrusion at 22° from Herrick (1896), Templeman (1940), and Perkins (1972). See page 35.

ducts (sloughed epithelial cells, digestive enzymes, mucus, secretions, etc.); excreta is a combination of unusable products of metabolism (such as nitrogenous wastes from protein catabolism) and complete metabolic products (again, sloughed epithelium). In each case the complete metabolic products are considered a negligible fraction.

In the lobster, ammonia and exogenous urea are not lost through the kidney-like nephridia, but through the gills (Burger, 1957). However, the nephridia are capable of secreting some organic substances.

Digestibility of food substances has been determined for crustaceans by the use of inorganic tracers. Ash has been used in copepods (Conover, 1966) and Penaeid shrimp (Condrey, Gosselink, and Bennett, 1972) and chromic oxide in Palaemonid and Pandalid shrimp (Forster and Gabbott, 1971). Chromic oxide has been used successfully in digestibility experiments with terrestrial organisms also (Crampton and Lloyd, 1951; Kane, Jacobsen, and Moore, 1950; Maynard and Loosli, 1969; and Schurch, Lloyd, and Crampton, 1950).

A lobster energy budget. From the existing data and some assumptions a possible energy budget for post-larval lobsters can be constructed. This budget can be compared to another energy budget independently constructed from field data. The comparison may be helpful in evaluating some basic assumptions used in making these models, and in evaluating the models themselves. The comparison

will also be helpful in illuminating areas where work should be done.

Miller et al. (1971) presented an energy budget for a population of wild lobsters in eastern Canada. The energy budget is reproduced as Fig. 11a. Biomass is estimated from commercial stock estimates, estimates of the relationship between total stock and commercial stock, and calorific constants. Respiration rates were taken from McLeese (1964) assuming a  $Q_{10}$  of 2.05. Production is estimated from population respiration. Assimilation efficiency is assumed to be 80% for carnivores (lobsters) and was calculated by dividing the sum of respiration and production (obtained from respiration) by 0.8. Egestion is then the difference between consumption and the sum of respiration and production; it is 20% of consumption. Excretion, reproduction, and production of exuviae are considered negligible.

A possible energy budget can be constructed for lobsters cultured at 22°-24° C. A male animal of 450 g will be considered; this is a commercial size and approximately the size at sexual maturity. It may well be representative of wild stock since smaller sizes are probably more numerous, and larger lobsters probably much less so because of commercial exploitation which starts at about the 450 g size. Energy of reproduction would be negligible; energy of exuvia production would be very small compared to production and assumed to be negligible. Biomass is

estimated using an energy density of 3500 cal/g dry weight and assuming the lobster is 80% water. These are values found for the crayfish Pacifastacus leniusculus (Cummins and Wuycheck, 1971). Biomass is 315 kcal:  $450 \text{ g wet wt.} \times .20 \frac{\text{g dry wt}}{\text{g wet wt}} \times 3.5 \text{ kcal/g dry wt} = 315 \text{ kcal}$ . Respiration will be taken from McLeese's data as 60 mg/lobster/hr, a value between his 25° and 20° points (points A and B on Fig. 3). Energy of metabolism can then be calculated using an oxy-calorific coefficient of 3.5 cal/mg O<sub>2</sub> (Kleiber, 1961);  $60 \text{ mg O}_2/\text{hr} \times 3.5 \text{ cal/mg O}_2 \times 24 \text{ hr/day} = 5040 \text{ cal/day}$ . Production of biomass at 22°-24° can be found from Fig. 6 to be approximately 0.8 g/day or  $0.8 \text{ g wet wt/day} \times .2 \text{ g dry wt/g wet wt} \times 3.50 \text{ kcal/g dry wt} = 0.56 \text{ kcal/day}$ . As in Miller et al. (1971) assimilation efficiency will be considered to be 80% and ingestion can be estimated by dividing the sum of growth and respiration by 0.8. Consumption is 7.00 kcal/day. Rejecta is then 20% of ingestion or 1.4 kcal/day. The energy budget (Fig. 11b) is complete.

Energy flows for the wild population (Miller et al., 1971) and the laboratory animal appear in Table IV. For comparison, energy flows are calculated as a ratio of biomass in Table IV. Miller et al.'s data have been multiplied by 365 days/yr; all tabulated values are then in units of % biomass/day.

Experimental animals at 22°-24° grow at a rate 3 to 5 times faster than that of wild lobsters (Hughes et al.,



Figure 11.

Two models of lobster energy budgets. a. From Miller et al. (1971) for a population of wild lobsters. Biomass in kcal/m<sup>2</sup>, all other units are kcal/m<sup>2</sup>/yr. b. A laboratory animal reared at 22-24° C; a male lobster weighing 450 g. Biomass in cal, all other units are cal/day.

C = consumption

P = production

P<sub>g</sub> = growth

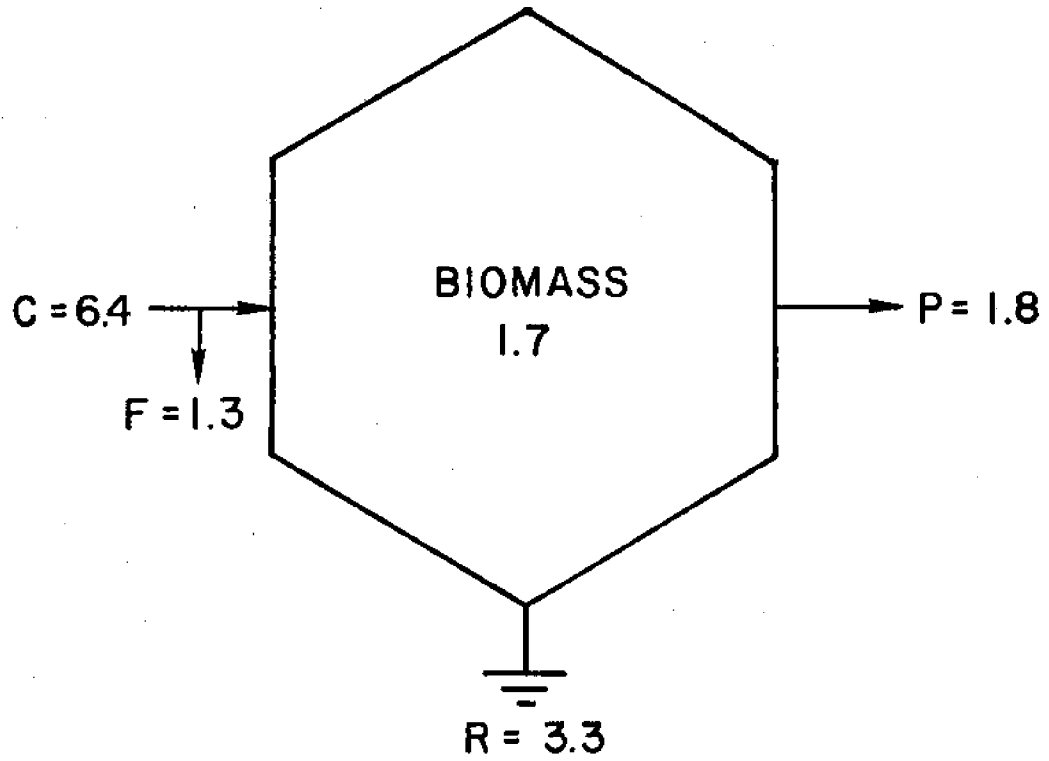
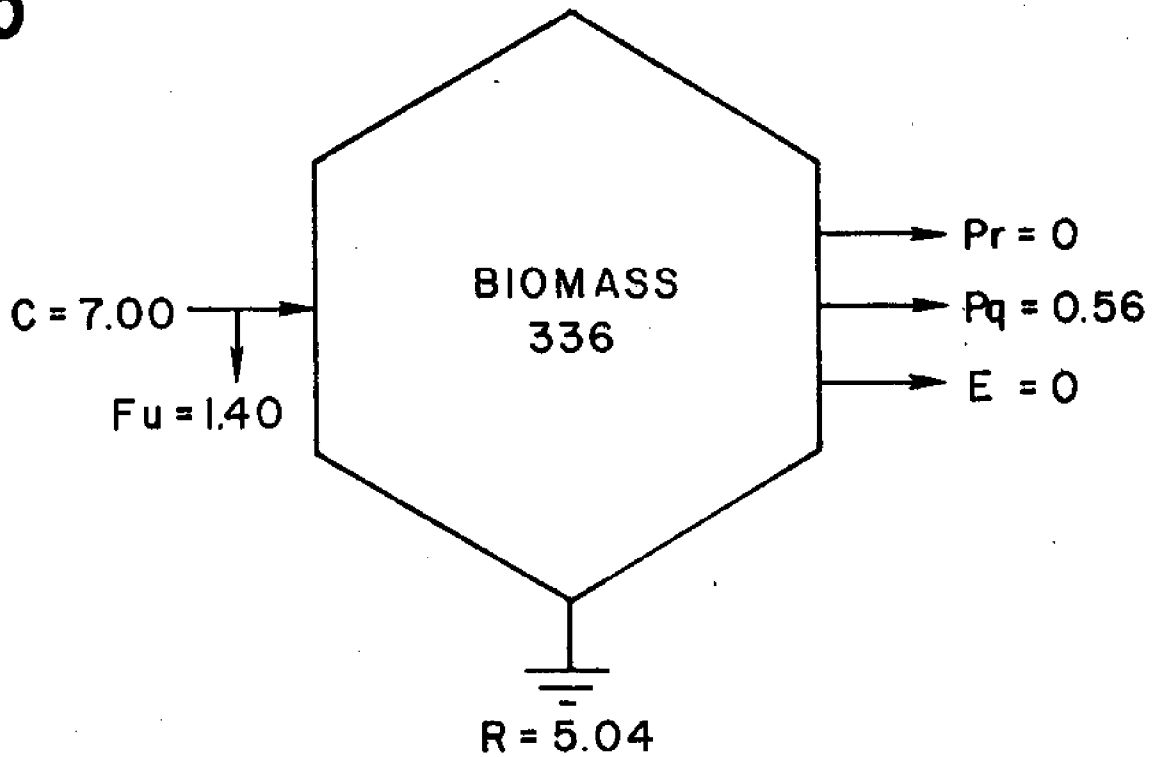
P<sub>r</sub> = reproduction

E = exuvia production

R = respiration

F = egesta

FU = rejecta

**a****b**

1972). However, the relative growth of a 450 g experimental lobster is calculated to be 2/3 that of the wild population. The hypothetical experimental lobster is a recently mature male with no reproductive loss, thus maximizing his calculated growth. Respiration of the experimental animal is over three times that of the wild population, a value which may be high but is within reasonable limits. Both consumption and rejection by the hypothetical experimental animal are twice that of the wild population. Thus, although some energy flows are within reasonable limits for the two models, one (growth) is not. For mariculture interests growth is a very important parameter.

Both models are hypothetical and neither has been substantiated. Part of the similarity of the two is due to the use of the same method of estimating consumption and rejection from respiration and production. This forces an artificial balance on both models by setting identical proportions for consumption, rejection, and assimilation. Of the independently determined flows, respiration is an acceptable range and production is not.

Both models could be greatly improved by testing. The assumption of 80% assimilation efficiency used in both models has not been tested. Excretion has been ignored in both models and may conceivably vary from negligible to 30-40% of ingested calories. The relative energy flow to production is not in agreement for the

Table IV.

Comparison of lobster energy budget models. One model is for a 450 g male reared at 22-24° C, using available literature data; the other is from Miller et al. (1971) for a population of wild lobsters.

Ratio	22-24° Animal	Wild Population
R/B	1.60	0.53
C/B	2.22	1.03
P <sub>g</sub> /B	0.18	0.29
FU/B	0.44	0.21

All values are % Biomass/day.

two models and this question may only be resolved by measurement.

Estimates of energetic pathways could be greatly improved by tightening constraints on respiration estimates, growth estimates over the earliest molts, ingestion and egestion estimates. Even a sketchy model of larval energetics cannot be constructed due to lack of data. With solid data at one temperature, data relating consumption, production, and rejection to metabolic body size, field models could be corrected to give more accurate predictions. The problem of imprecision in the lobster field model is discussed by Miller et al. (1971). The object of this research is to improve precision of the hypothetical experimental-lobster energy-budget model by testing and to extend that model to the entire life cycle.

## CONCLUSION

Present data indicate that the optimum temperature for the culture of lobsters is 22-24° C. Incomplete physiological and energy data are available at this temperature regime. Rate of growth and exuvia production are known. Good respiration data at 15° C are available, although extrapolation of these data to 22-24° cannot be done accurately. Production of excreta and egesta may be approximated from metabolic data; however, the accuracy of these approximations depends upon the accuracy of both metabolic (respiration) data and estimations of assimilation and digestion efficiencies.

Recognizing these possible errors, a hypothetical energy budget may be constructed. This may be used to give rough estimates of physiological processes which may be useful in the design of culture facilities. Research is now being carried on at the University of Delaware to improve the accuracy of an energy budget for lobsters at elevated temperatures suitable for lobster mariculture.

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