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Nutritional and Bioenergetic Considerations in the Development of the American Lobster *Homarus americanus*[1]

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To better understand the early life history stages of the American lobster *Homarus americanus*, nutritional and bioenergetic aspects of development have been investigated. These studies focused on physiological and biochemical processes during transitional periods between extrusion of the eggs, hatching, larval development, molting, metamorphosis, and attainment of the juvenile stage. Biochemical changes during embryogenesis reflect catabolism of various substrates for energy. Exposure to different thermal regimes resulted in considerable variation in the rates of utilization of energy substrates during embryogenesis. Embryos raised at elevated temperatures had yolk remaining at the time of hatching. The first three larval stages have similar energy requirements. Lipid is of prime importance and the turnover rate for lipid can be rapid. Weight-specific metabolism increases with successive larval stages. In stage IV lobsters, the dependency on lipid as a substrate is diminished and lipid reserves serve a storage function. Metabolic rates of premolt stage IV lobsters are decreased in comparison with earlier stages. These changes in physiology correlate with changes in the developing midgut gland, specifically with the appearance of droplets of lipid in the lipid-storing cells of the midgut gland of stage IV lobsters. By stage VI, lobsters have energy storage and metabolic patterns similar to those of adults, and the midgut gland has the adult morphology. The transitions from hatching to attainment of the juvenile form are reflected in differences in physiological and biochemical processes that influence food selection and diet.

Pour mieux comprendre les premiers stades du cycle vital du homard américain (*Homarus americanus*), les aspects alimentaire et bioénergétique du développement ont été examinés. Ces études ont été axées sur les processus physiologiques et biochimiques au cours des périodes de transition entre la sortie des oeufs, l'éclosion, le développement larvaire, la mue, la métamorphose et l'atteinte du stade juvénile. Les changements biochimiques au cours de l'embryogenèse reflètent le catabolisme de divers substrats au point de vue énergétique. L'exposition à différents régimes thermiques a amené une variation considérable des taux d'utilisation de substrats énergétiques pendant l'embryogenèse. Les embryons élevés à des températures élevées avaient encore du vitellus au moment de l'éclosion. Les trois premiers stades larvaires avaient des exigences énergétiques semblables. Les lipides sont d'une importance primordiale et le taux de roulement des lipides peut être rapide. Le métabolisme qui est fonction du poids augmente avec les stades larvaires successifs. Chez les homards du stade IV, la dépendance à l'égard des lipides en tant que substrat diminue et les réserves lipidiques ont une fonction d'entreposage. Les taux métaboliques des homards du stade IV avant la mue sont réduits par rapport aux stades antérieurs. Ces changements physiologiques présentent une corrélation avec les changements de la glande de l'intestin moyen en développement, particulièrement avec l'apparition de gouttelettes de lipides dans les lipocytes de la glande de l'intestin moyen des homards du stade IV. Au stade VI, les homards ont des régimes métaboliques et d'entreposage d'énergie semblables à ceux des adultes et la glande de l'intestin moyen a la morphologie de l'adulte. Les transitions entre l'éclosion et l'atteinte de la forme juvénile se reflètent par des différences dans les processus physiologiques et biochimiques qui influent sur le choix de la nourriture et sur le régime alimentaire.

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Development and metamorphosis of planktotrophic larvae, including those of decapod crustaceans, require efficient and coordinated utilization of available metabolic resources. Of many factors affecting resource utilization during the development period, nutrition is of prime importance. Nutrition involves endogenous and exogenous dietary sources, and the yolk reserve can be important during early postembryonic development. Consequently the nutritional aspects of embryogenesis are important for a complete understanding of development.

In the life cycle of the American lobster *Homarus americanus* Milne Edwards, there are several transitional periods where nutrition and bioenergetic processes may influence development. Embryogenic development of the lobster was described first by Bumpus (1891) and extends for 9–11 mo, depending on temperature (Templeman 1940; Perkins 1972; Branford 1978). During the embryogenic period, catabolism of yolk reserves serves as the sole source of nutrients for the developing embryo. At hatching and initiation of feeding, there

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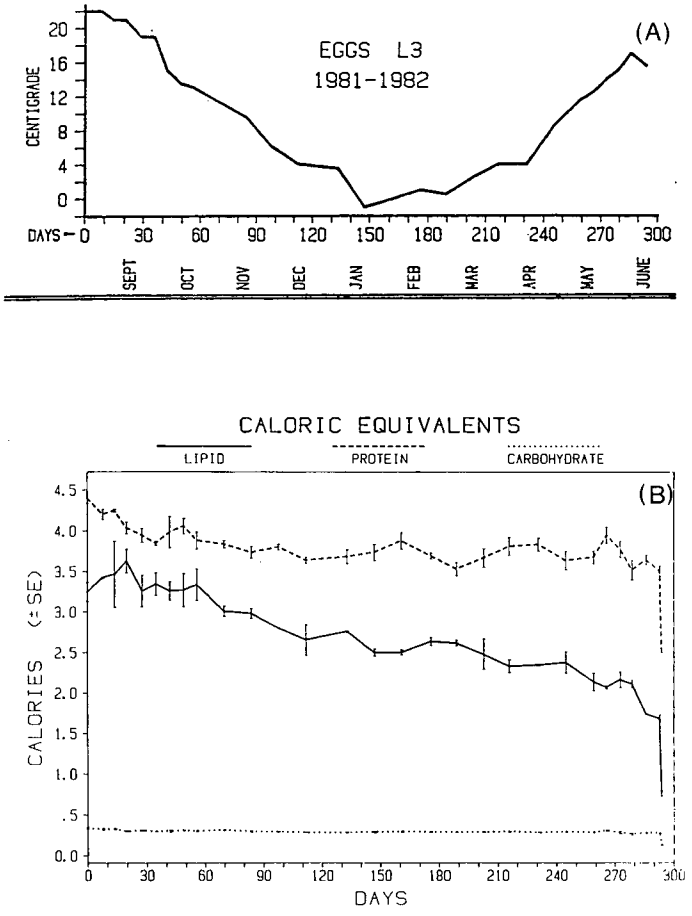

FIG. 1. (A) Temperature profile during embryogenesis study. (B) Caloric equivalents of protein, lipid, and carbohydrate during embryogenesis; values are presented as calories per individual ± SE; last point represents hatched larvae.

is a shift in dependence from endogenous to exogenous energy resources. Early development in the lobster includes four planktonic stages (Herrick 1896), although there is considerable debate whether or not these are all larval stages (Williamson 1982; Charmentier et al. 1984), as metamorphosis occurs at the molt between stages III and IV, but settlement does not take place until stage V. During development of the first three stages, there are gradual changes in morphology and concomitant changes in swimming behavior. After attainment of the fourth stage, claws are developed and more pronounced behavioral changes are evident. Stage IV lobsters are active swimmers but may remain among the plankton for several days before seeking a benthic habitat (Cobb 1976; Hughes and Matthiessen 1962). With the molt to stage V the shift to benthic habits is complete and feeding behavior is altered. With these changes, changes in metabolism, energy utilization, and biochemical composition may be expected and if so, may provide clues to changes in feeding requirements of young lobsters.

Capuzzo and Lancaster (1979) reported that weight-specific metabolism (oxygen consumption and ammonia excretion) of larvae of *H. americanus* increased with each stage (I–IV) and decreased with stage V. The rate of change in metabolism was greater than the rate of change in body size, indicating increased energy demand in the later larval stages. Reductions in O:N ratios among stages IV and V revealed an increased dependence on protein catabolism for energy. This paper presents an analysis of the physiological, biochemical, and morphological aspects of energy storage and metabolism in the early life history of *H. americanus*. Further elucidation of stage-specific changes in nutrition and bioenergetics is needed before the energetic costs of development are fully understood.

Materials and Methods

Culture Methods

Embryogenic period

To study the embryology of the lobster, gravid female lobsters were obtained prior to extrusion of their eggs. This was accomplished by examining the cement glands of the pleopods of female lobsters collected in local waters (Vineyard Sound, MA, and Buzzards Bay, MA). Cement gland morphology was examined according to the method described by Aiken and Waddy (1982). Lobsters that appeared ready to extrude eggs were placed individually in 95-L aquaria supplied with seawater (30–31‰ salinity) at ambient temperature (−0.5–22°C). The lobsters were fed frozen squid, clams, and fish twice a week. After extrusion, eggs were sampled from one female at weekly intervals at temperatures >6°C or biweekly intervals at temperatures <6°C until hatching occurred (295 d).

To examine the hatching period, eggs were sampled from lobsters that had extruded eggs before capture (offshore Buzzards Bay, MA). These lobsters were transferred to a 95-L aquarium supplied with flowing heated seawater (22–24°C) to accelerate embryogenesis. Hatching began after 120 d. Sampling of eggs began at the initiation of hatching and five samples were taken: (1) eggs 7–3 d from hatch, gold in color; (2) eggs 3 d to 12 h from hatch, gold; (3) eggs 1 d to hatching, blue; (4) prelarvae, or just prior to the molt to stage I; and (5) larvae within 6–36 h after hatching. The time until hatch for each sample was estimated and adjusted according to the time of the hatch.

Samples were assayed for biochemical composition according to the procedures described below. The morphology of the midgut gland in embryos and prelarvae were examined.

Larval development

Egg-bearing lobsters were obtained from offshore Buzzards Bay by fishermen and were transferred to individual 95-L aquaria, supplied with flowing seawater at ambient temperature and salinity (12–19°C; 30–31‰). Adult lobsters were fed frozen squid, clams, and fish twice weekly until hatching occurred. Hatching occurred over a 1- to 2-wk period, with the majority of larvae being released during 2–4 d. To provide animals as identical as possible, only larvae from one hatch, collected within 30 min of release, were used for each experiment. Each batch of larvae was placed in a separate fiberglass plankton-kriesel (Hughes et al. 1974), supplied with flowing, filtered (100 μm) seawater at ambient temperature (18–22°C); larvae were fed frozen *Artemia* (San Francisco Bay Brand) with a fatty acid supplement prepared from freeze-dried cod liver oil (Sasaki 1984) three to four times daily ad libitum). Larvae were sampled periodically and each larva was molt-staged according to the procedure of Sasaki (1984). Larvae were examined for changes in physiology, biochemical composition, and development of the midgut gland according to procedures described below.

Physiological Measurements

Respiration rate of individual lobsters was measured at 20–

TABLE 1. Weight and eye dimensions of embryos of *Homarus americanus* (n = 10).

Date 1981–82	Wet weight (mg) ±1 SD	Dry weight (mg) ±1 SD	Egg diameter (range in mm)	Eye length (range in mm)	Eye width (range in mm)
Aug. 24	2.10±0.11	1.03±0.05	1.4–1.6		
Sept. 1	2.08±0.05	1.01±0.04	1.4–1.5		
Sept. 7	2.17±0.06	1.07±0.03	1.4–1.6		
Sept. 13	2.15±0.09	1.01±0.04	1.5–1.6		
Sept. 21	2.20±0.08	1.03±0.05	1.5–1.6	0.09–0.11	
Sept. 28	2.31±0.08	1.02±0.02	1.5–1.6	0.15–0.16	
Oct. 5	2.39±0.08	1.03±0.05		0.22–0.24	0.13–0.15
Oct. 12	2.37±0.04	1.02±0.02	1.5–1.6	0.25–0.27	0.16–0.18
Oct. 19	2.48±0.08	1.04±0.04	1.5–1.7	0.26–0.33	0.19–0.21
Nov. 2	2.63±0.09	1.04±0.03	1.6–1.8	0.36–0.40	0.24–0.28
Nov. 16	2.63±0.09	0.99±0.05	1.7–1.8	0.43–0.50	0.30–0.33
Nov. 30	2.67±0.07	1.00±0.04	1.7–1.8	0.43–0.46	0.30–0.31
Dec. 14	2.71±0.06	1.01±0.03	1.7–1.8	0.43–0.46	0.30–0.32
Jan. 4	2.60±0.03	0.97±0.02	1.7–1.8	0.40–0.46	0.26–0.30
Jan. 18	2.62±0.12	0.97±0.06	1.7–1.8	0.41–0.48	0.26–0.30
Feb. 1	2.54±0.09	0.94±0.04	1.7–1.8	0.43–0.46	0.26–0.30
Feb. 16	2.61±0.06	0.98±0.03	1.7–1.8	0.42–0.46	0.30–0.35
Mar. 1	2.61±0.02	0.96±0.03	1.7–1.8	0.43–0.47	0.26–0.30
Mar. 15	2.58±0.10	0.96±0.04	1.7–1.8	0.44–0.47	0.30–0.33
Mar. 28	2.62±0.05	0.98±0.03	1.7–1.8	0.43–0.47	0.30–0.34
Apr. 12	2.61±0.08	0.95±0.03	1.7–1.8	0.43–0.47	0.30–0.34
Apr. 26	2.57±0.10	0.92±0.05	1.7–1.8	0.40–0.46	0.30–0.33
May 10	2.64±0.08	0.92±0.05	1.7–1.8	0.43–0.46	0.30–0.33
May 17	2.62±0.07	0.92±0.04	1.7–1.9	0.44–0.46	0.30–0.36
May 24	2.60±0.13	0.93±0.05	1.7–1.8	0.44–0.48	0.30–0.33
May 30	2.74±0.10	0.88±0.05	1.7–2.0	0.46–0.53	0.30–0.33
June 6	3.18±0.13	0.92±0.03	1.7–2.0	0.50–0.56	0.33–0.39
June 13	3.32±0.22	0.91±0.03	1.8–2.1	0.49–0.59	0.36–0.40

TABLE 2. Losses in lipid classes associated with hatching (n = 3).

Sample	Total lipid	Triacylglycerol (mean μg·individual^{-1} ± SD)	Phosphatidyl choline (mean μg·individual^{-1} ± SD)
Gold egg A	287	121.2±8.0	99.7±7.0
Gold egg B	254	88.0±6.4	94.6±6.7
Blue egg	221	67.9±8.4	82.7±9.2
Prelarva	215	64.4±1.3	88.2±4.0
St. I larva	207	59.7±2.1	81.7±3.0

22°C after acclimation to 20°C using a microrespirometer and a Gilson differential respirometer according to techniques described by Capuzzo and Lancaster (1979). Equilibrium between the gas and liquid phase of O_2 diffusion in the respirometer flasks was enhanced by gently shaking the flasks. At the end of each set of oxygen uptake measurements, the seawater in the respirometer flasks was analyzed for NH_4^+-N by the method of Solorzano (1969) in order that an in situ O:N ratio (atomic ratio of oxygen consumed to NH_4^+-N excreted) could be made; ammonia levels were compared with control blanks.

Biochemical Analyses

Eggs were detached from their surrounding cement matrix and measured with an ocular micrometer in a dissecting scope and the greatest egg diameter was recorded. If present, the embryonic eye width was measured (Perkins 1972). Eggs were then dipped into distilled water to remove external salt and blotted dry on a paper towel. Larvae were placed on a fiberglass mesh, dipped in distilled water, and blotted dry on a paper towel. Three samples of two eggs were pooled and taken for ash analysis, four samples of two eggs were pooled and taken for protein and carbohydrate analyses, and two samples of 10 eggs were pooled and taken for lipid analyses. For larval samples, three individuals were used for determination of ash values, four for protein and carbohydrate, and two groups of two to five individuals were pooled for lipid analyses. Each sample was measured for wet weight to the nearest 0.1 mg on a Mettler H15 balance. Samples for ash, protein, and carbohydrate analyses were frozen and lyophilized, weighed to the nearest 0.01 mg on a Mettler M5 microbalance, and stored at −20°C until analysed. Ash levels were determined after combustion at 475°C, carbohydrate levels were determined according to the procedure of Dubois et al. (1956), and protein levels were determined by the Lowry procedure (Hartree 1972) or using a Coomassie blue procedure (BioRad Laboratories 1979). For lipid analyses, egg and larval samples were weighed (wet weight) and extracted immediately for lipids (Folch et al. 1957; Sasaki and Capuzzo 1984). Total lipid was determined gravimetrically and lipid classes were determined using a Newman-Howells Iatroscan TH-10 according to the procedure described by Sasaki and Capuzzo (1984). A more detailed

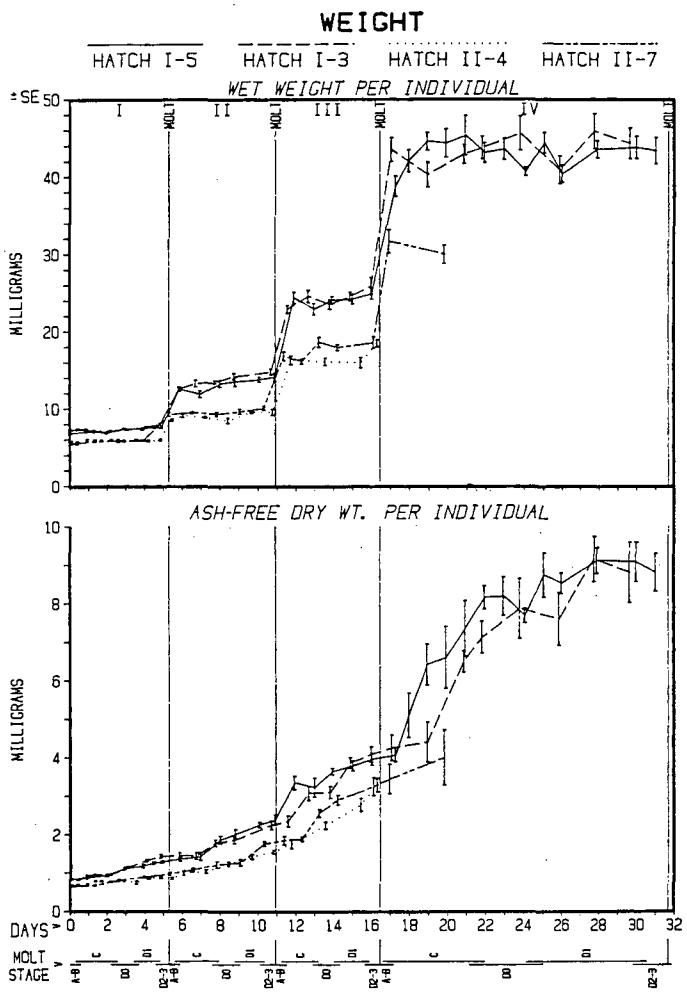

FIG. 2. Wet weight and ash-free dry weight of four hatches of lobsters; each value is the mean of seven measurements ± SE. The vertical lines labelled "MOLT" indicate the time of molting; the roman numerals (I–IV) at the top of the graph indicate each stage.

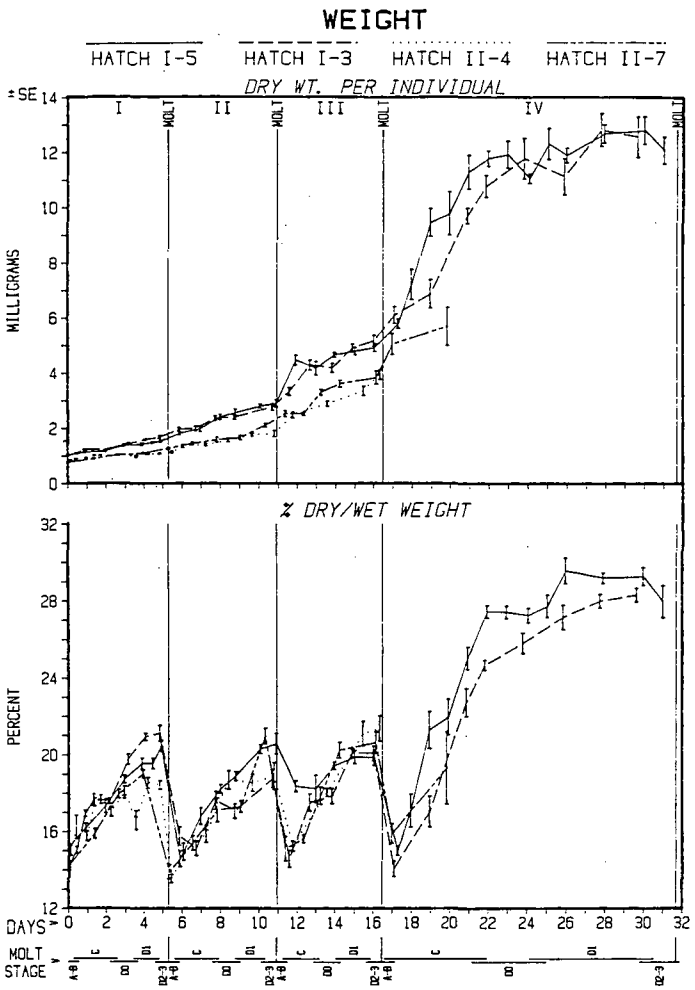

FIG. 3. Dry weight and percent dry to wet weight ratios of larval lobsters; each value is the mean of seven measurements ± SE.

description of analytical procedures is presented in Sasaki (1984).

Histological Methods

Embryos used to examine the morphology of the developing midgut gland were removed from the egg mass of a lobster. Larval and juvenile lobsters were sampled from laboratory cultures; animals were molt-staged and only intermolt animals were used. Whole animals were fixed in 3% phosphate-buffered glutaraldehyde, pH 7.2, for 1.5–2 h at 7°C. The tissues were washed in cold 0.1 *M* phosphate buffer and run through a dehydration series from 50 to 95% ethanol. Plastic embedding medium (methacrylate) was used according to the manufacturer's instructions (Polyscience, Inc.). The tissues were sectioned at 2 μm on a Sorvall JB-4 microtome and mounted on clean glass microscope slides. The sections were stained with Lee's methylene blue-basic fuchsin. To demonstrate the presence of yolk in the midgut gland, newly hatched stage I larvae were held separately for 12 h until attainment of molt stage C before being sampled; the larvae were fixed in glutaraldehyde as described above. After fixation, the midgut glands were dissected out and washed in buffer. They were postfixed for 2 h on ice in 1% osmium tetroxide buffered with 0.1 *M* phosphate buffer plus 0.75 g sucrose $\cdot L^{-1}$ and washed in cold buffer. The tissues were dehydrated and embedded as described above.

Statistical Methods

Differences in parameters among the various developmental stages were assessed by Student's *t*-test and analysis of variance (Sokal and Rohlf 1969; Zar 1974).

Results

The temperature profile of the incubation period for the embryological study is presented in Fig. 1A. Egg diameter, weight, and eye width and length measurements of the developing embryo are presented in Table 1. The wet weight of the egg increased for 10 wk and remained constant until approximately 3 wk prior to hatching when a second increase occurred. Wet weight increase, due to water absorption, was reflected in an increase in egg size. There was a decline in dry weight throughout embryogenesis. Loss of both wet weight and dry weight occurred at hatching and produced a large drop in the dry to wet weight ratio. The greatest change in biochemical composition was observed during the month after fertilization and in the month prior to hatching. Protein, lipid, and carbohydrate levels, expressed as their caloric equivalents, are

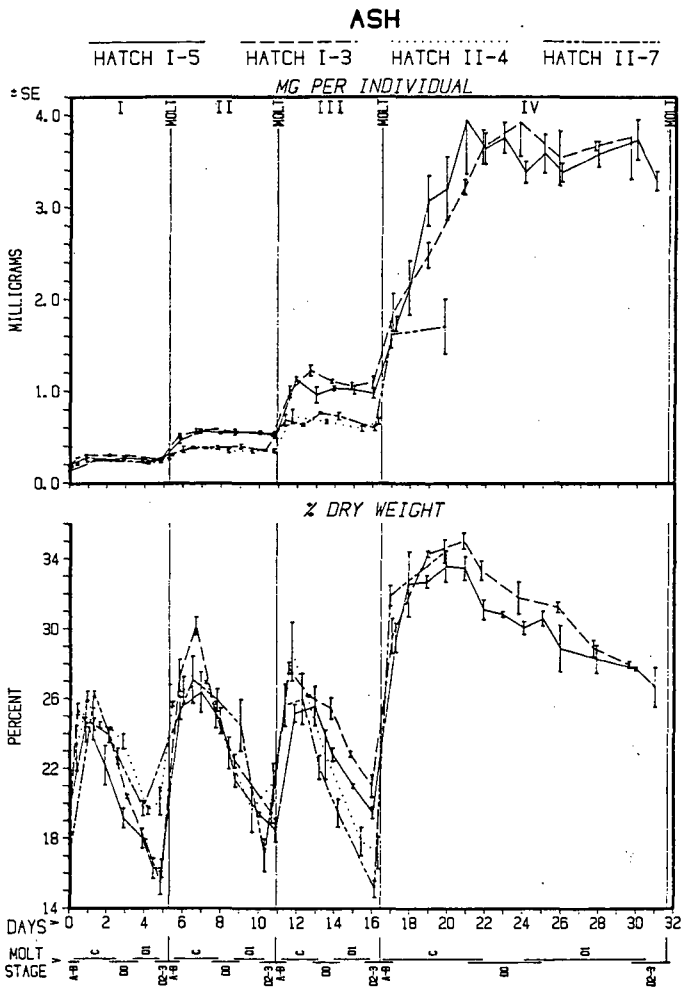

FIG. 4. Ash levels of larval lobsters; each value is the mean of three measurements ± SE.

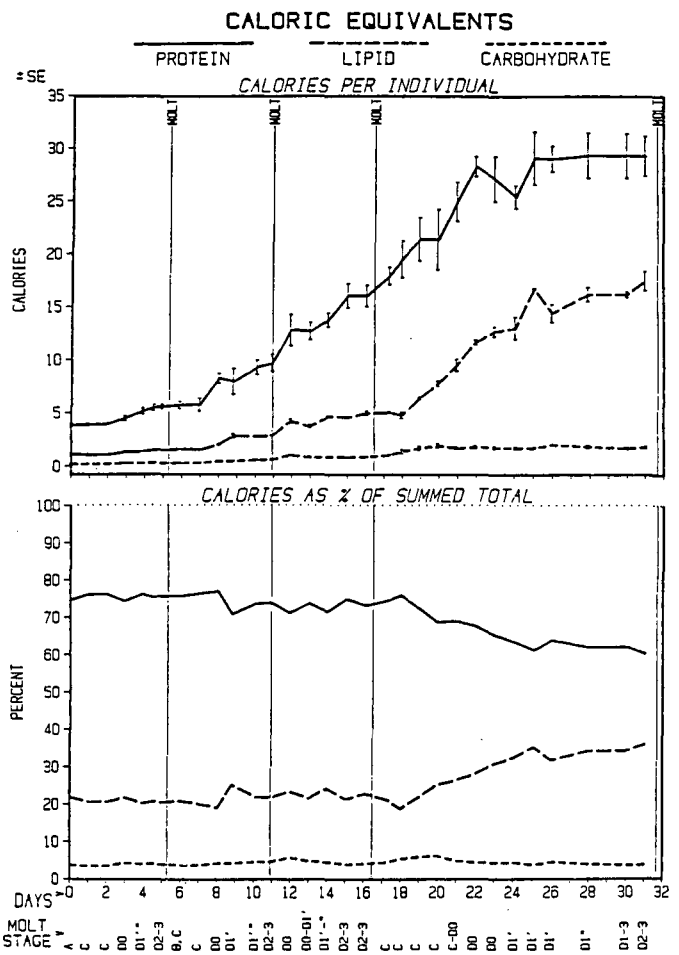

FIG. 5. Caloric equivalents for protein, lipid, and carbohydrate levels of larval lobsters; each value is the mean of four measurements for protein and carbohydrate and two measurements for lipid ± SE.

presented in Fig. 1B. Little or no change in carbohydrate level occurred, whereas protein levels decreased gradually during the initial phases of embryogenesis and then stabilized until hatching. Lipid levels decreased throughout the embryonic period and the loss was accentuated at hatch. The change during embryogenesis was greatest for lipids, followed by protein and carbohydrate. Using heat of combustion factors (Kleiber 1975) for protein (5.7 cal·mg^{-1}), carbohydrate (4.0 cal·mg^{-1}), and lipid (9.5 cal·mg^{-1}), it was determined that protein declined by 0.90 cal·egg^{-1} and lipid declined by 1.57 cal·egg^{-1} during embryogenesis (fertilization to the last egg sample). Losses of protein, carbohydrate, and lipid were used to estimate the caloric cost of embryogenesis; a value of 2.53 cal was estimated, indicating a yolk utilization efficiency of 68.4%. If the increased energetic costs of hatching are included in this estimate (including the caloric loss of the egg membrane = 0.33 cal; Pandian 1970), then yolk utilization efficiency was 46.7%. The decreases of triacylglycerol, phosphatidyl choline, and phosphatidyl ethanolamine throughout embryogenesis accounted for 74, 23, and 9%, respectively, of the total lipid loss.

Differences in biochemical composition of larvae at hatch were observed between samples from the embryogenesis study and the hatching period study, with larvae from the latter study having relatively larger energy reserves at hatch. It is speculated that this extra energy represents the energy not required for maintenance during periods of low temperatures. The main difference was in the amount of lipid remaining at hatch (0.12 mg·individual^{-1}; 1.14 cal·individual^{-1}). Eggs sampled during the embryogenesis study showed a decline of 0.05 mg of lipid during the period when the temperature was <6°C. The difference in these lipid values provides an approximation of the metabolic cost of maintenance under the temperature regimes experienced under ambient conditions and indicates a possible increased efficiency of development at higher temperatures. This excess lipid can serve as a supplemental energy store during the early posthatch period (Sasaki 1984). Changes in lipid composition (total, triacylglycerols, and phosphatidyl choline) at hatching are presented in Table 2.

The wet weight of larvae increased at each molt (Fig. 2). After this increase, the weight remained relatively stable until the next molt. The increase in wet weight at molt ranged from 70 to 80%. Dry weight (Fig. 3) and ash-free dry weight (Fig. 2) increased gradually and were not affected strongly by the molt. When the dry weight data are presented as a percentage of wet weight, a consistent relationship is seen for the first three larval stages. In stage IV lobsters, the dry weight increased to 28% of the wet weight.

Ash level increased after each molt and reached maxima during intermolt in each stage (Fig. 4); as a percentage of dry weight values, ash declined after intermolt in each stage. In stage IV lobsters, ash comprised a relatively greater proportion

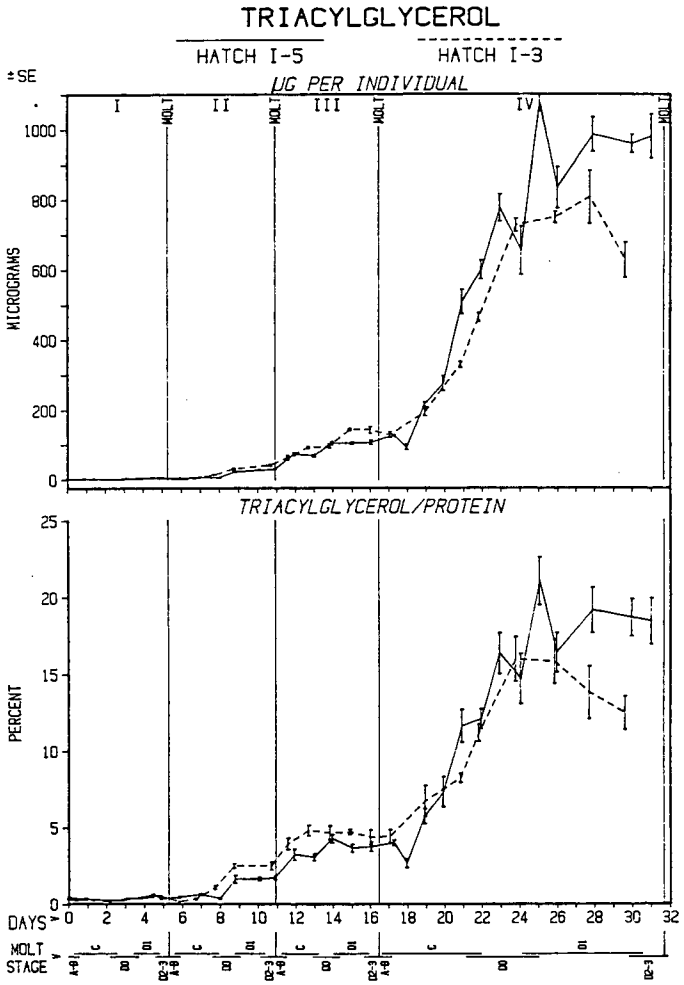

FIG. 6. Triacylglycerol levels and triacylglycerol to protein ratios of larval lobsters; each value is the mean of three measurements ± SE.

of total weight than in stages I–III.

Protein, lipid, and carbohydrate levels, reported as caloric equivalents, are presented in Fig. 5. Protein was the largest biochemical constituent in all stages; as a percentage of all biochemical components, however, protein decreased in stage IV lobsters as lipid levels increased. Carbohydrate remained at a low but stable level throughout larval development. Triacylglycerol levels did not increase until the middle of the second larval stage (Fig. 6). Accumulation of triacylglycerol then occurred at a steady rate until stage IV-C when it increased rapidly until stage IV-D_1, when it began to stabilize. As a percent of total lipid content, triacylglycerol increased from <3% at hatch to >50% in stage IV-D_1 lobsters and was the major lipid component. Triacylglycerol to protein ratios increased throughout development, indicating no constant relationship between the two parameters.

Respiration rates of larval lobsters (stages I–III) increased slightly during the molt cycle (molt stage B-D_1) following a slight decline during the postmolt recovery period (A–B). Increases in respiration rate were evident with the molt to subsequent stages with the exception of the molt to stage V (Fig. 7). Weight-specific respiration rates increased with each molt stage and were highest among stage IV larvae, and then decreased just prior to the molt to stage V (D_3). Ammonia excretion rates followed similar patterns as respiration rates in stages I and II, increased with stage III and stage IV, and

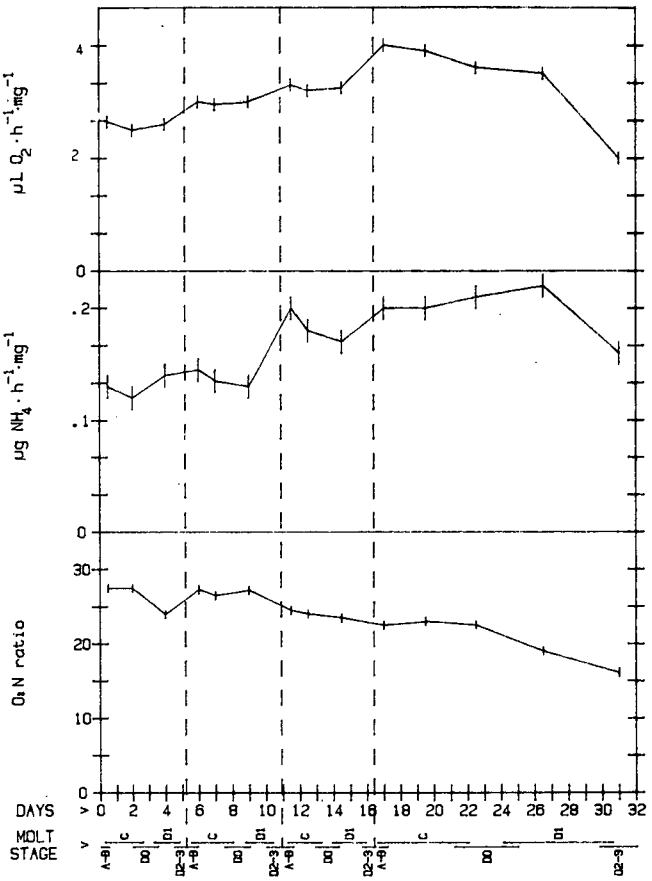

FIG. 7. Respiration rates, ammonia excretion rates, and O:N ratios of larval lobsters; each value is the mean of 24 measurements ± SE.

decreased just prior to the molt to stage V; in stages I, II, and III, ammonia excretion rates increased immediately after molting. O:N ratios were similar for stages I and II, decreased slightly for stage III, and showed a steady decline among stage IV lobsters, with the lowest value recorded just prior to the molt to stage V. The level of significance for differences in metabolic rates among each larval stage was $P < 0.01$.

The R-cells of the midgut gland, which function in adult crustaceans to store lipids, serve a similar purpose during early development of the American lobster. Late embryos, prelarvae, and unfed stage I larvae have lipid droplets, derived from the yolk, stored in R-cells (Fig. 8). Larval stages (stages I, II, and III) show no sign of lipid storage in the midgut gland (Fig. 9). Stage IV lobsters begin to store lipids, as evidenced by the appearance of a few lipid droplets in the R-cells. By stage VI, there are extensive lipid stores in the digestive gland. The morphology of the lipid-storing cells in juvenile lobsters is indistinguishable from that of adult lobsters, although the tubule formation in the midgut gland is less extensive. A more detailed description of the morphology of the midgut gland is reported by Biesiot (1986).

Discussion

The most active periods during embryogenesis, in terms of rates of utilization of biochemical constitutents, were the month after fertilization and the month prior to hatching. Utilization of lipid and protein reserves during embryogenesis had different patterns; loss of protein and lipid did not occur at the

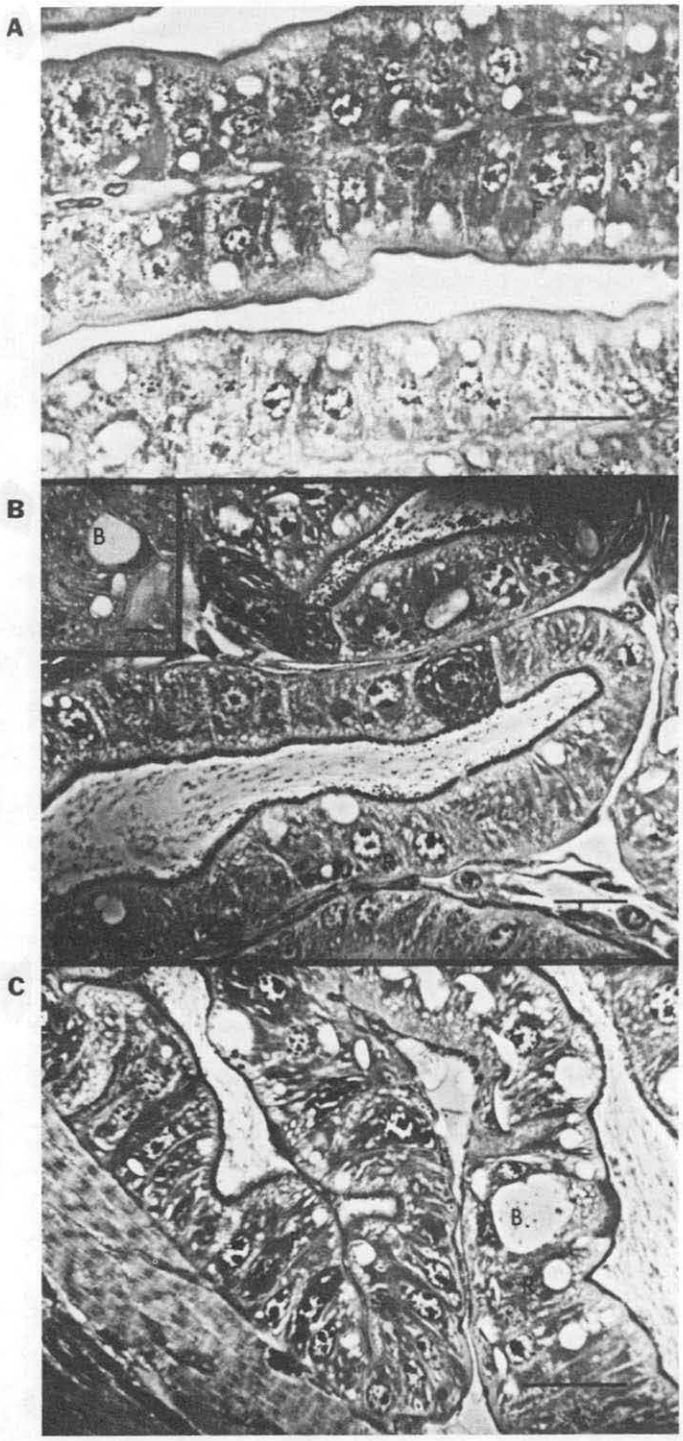

FIG. 8. Cell types comprising the midgut gland in embryonic stages: (A) gold egg, 3 d prior to hatch, scale bar = 5 μm; (B) blue egg, early in hatching process, scale bar = 5 μm; inset, B-cell, scale bar = 2 μm; (C) prelarva, late in hatching process. R = R-cell, F = F-cell, B = B-cell, a = apical complex of B-cell.

same rate throughout embryogenesis. Lipid provided the major portion of metabolic energy during embryogenesis, consistent with observations on other crustaceans (Barnes 1965; Pandian 1967, 1970; Pandian and Schumann 1967). If lipid reserves were sufficient to provide all the energy necessary for embryogenesis, then the loss of protein (~20%) during this period may be due to inefficient conversion from yolk protein to tissue and not due to respiratory needs. A latent period during mid-embryogenesis was observed when no change in protein level was evident. In contrast, lipid showed a steady decline throughout embryogenesis. Most of the lipid catabolized was triacylglycerol, but phosphatidyl choline was also used to some extent and may provide a secondary energy source when triacylglycerol is depleted. Increased conversion efficiency of embryos incubated at elevated temperatures suggests that subtle variations in the energetics of embryogenesis may be apparent among different populations where thermal regimes are different (Cooper and Uzmann 1980). Yolk in posthatch larvae may delay feeding and prolong periods of starvation resistance (Sasaki 1984; Anger et al. 1985) and would be of considerable adaptive advantage to newly hatched larvae.

The biochemical composition of lobster larvae reveals several clues as to the comparative aspects of bioenergetics during larval development and metamorphosis. Upon ecdysis, larvae absorbed water, increased in size, and began formation of the new exoskeleton. Decreases in carbohydrate and protein were likely related to chitin formation and, with decreases in lipid, energy utilization. Higher O:N ratios and a lack of evidence of lipid storage in the early larval stages suggest a reliance on catabolism of mixed energy substrates. Stage IV and V animals showed an increased dependence on protein catabolism. Carbohydrate, protein, and lipid increased from intermolt to early premolt stages, either through synthesis of new tissue and/or accumulation of energy reserves. Although respiration rates, ammonia excretion rates, and O:N ratios were fairly consistent within the molt cycle of an individual larval stage, significant increases in ammonia excretion rates, evident in the early postmolt periods, may reflect protein-fueled gluconeogenesis to produce chitin for the exoskeleton. The increased ash content of stage IV lobsters is indicative of the development of a more heavily calcified exoskeleton in postmetamorphic animals.

Accumulation of energy reserves may be related to life style, whereby active, rapidly growing animals with quick molt recoveries (stages I, II, and III) store less reserves than larger, slower growing animals (juveniles and adults) with more prolonged molt recovery periods. Thus, the transitions observed between stage I and stage IV lobsters may reflect comparative energetic strategies for different habitats. Postmetamorphic animals accumulated greater proportions of lipid, as evidenced by both biochemical studies and histological studies of the midgut gland. The reasons for this accumulation are unknown. On a caloric basis, the increased triacylglycerol content of late stage IV lobsters accounts for 3–5 d of metabolic reserves, based on measurements of routine oxygen consumption. As new feeding behavior must be adopted in benthic habitats, newly settled lobsters may rely temporarily on stored reserves. Premetamorphic larvae show little evidence of lipid storage and appear to utilize lipid rapidly. The lipid storage patterns seen in stage IV lobsters were consistent with the findings of increased protein catabolism (lower O:N ratios) and a reduction in metabolic activity of late premolt animals.

The physiological and biochemical observations made in this study have several implications for assessing the early life history of lobster populations. The large changes seen in energy storage and utilization patterns between pre- and postmetamorphic animals suggest that lipid stores may have an advantage for newly settled lobsters in that sufficient reserves may be available for searching for a suitable substrate, burrow construction, and adapting to a new habitat before feeding is a

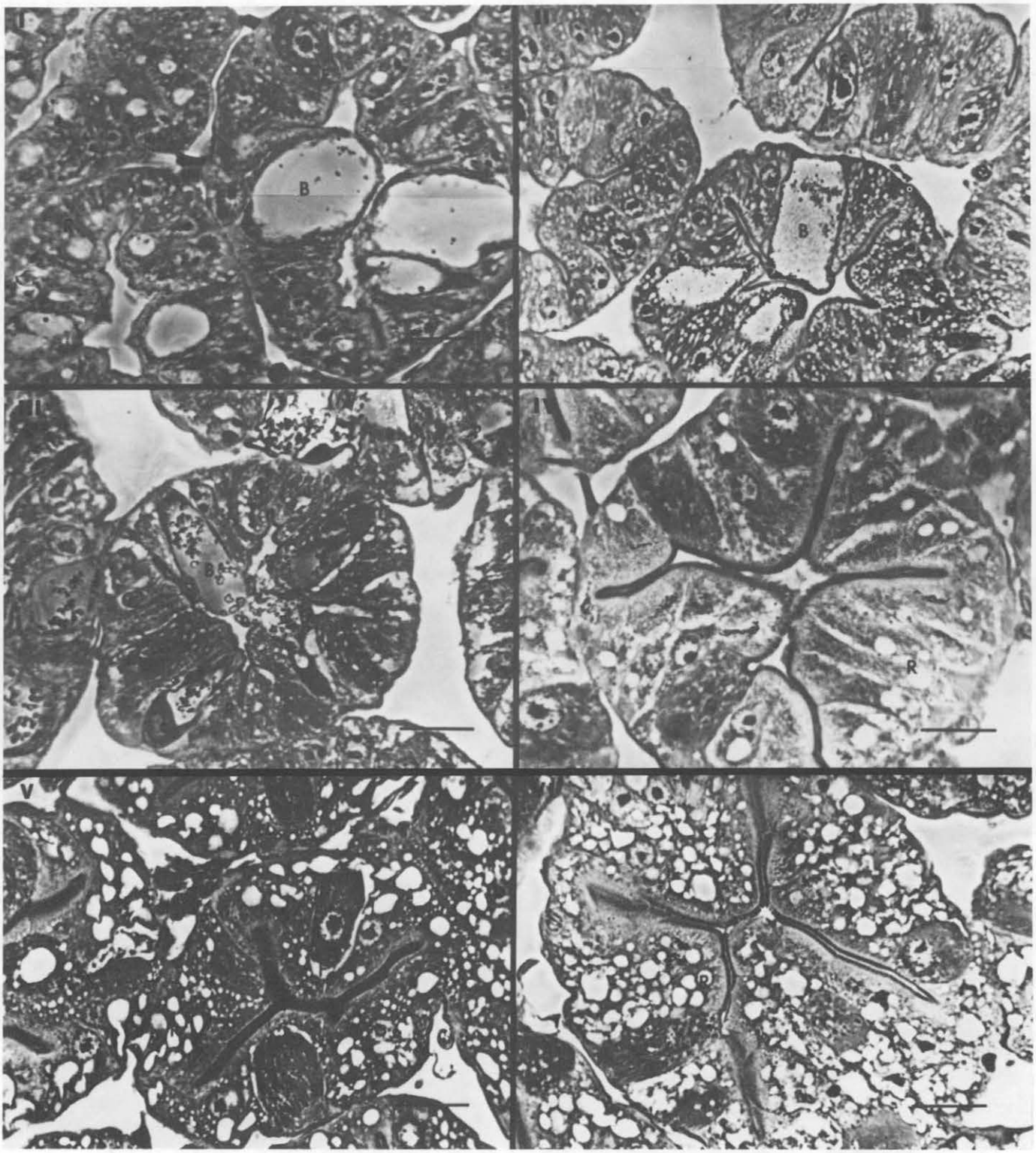

FIG. 9. Cell types comprising the midgut gland intermolt stages I–VI.

necessity. These studies also suggest that the transitional period between planktonic and benthic existence correlates with the capacity for increased energy stores and that larvae at molt stage IV-D_0–D_1 are at a considerable energetic advantage in selecting a benthic habitat. Settlement of larval lobsters may therefore be delayed until after this energetic transition.

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