EGG INCUBATION AND YOLK UTILIZATION IN THE ISOPOD

*LIGIA OCEANICA*

by T. J. Pandian*, Biologische Anstalt Belgoland, Meeresstation, Helgoland, Germany; and Zoology Department, Bangalore University, Bangalore, India

The egg number, which averages to 53 (± 9.5 eggs) per female *Ligia oceanica* of Helgoland, shows no definite correlation to body size of the mother animals. In between the incubated eggs, the occurrence of nematodes *Gammarinema ligiae*, *Rhabditis* sp. and *Diplogaster* sp. is observed. The course of embryonic development of *L. oceanica* exhibits progressive increases in content of ash (4.4 to 31.6 per cent) and non protein nitrogen (from 1.5 to 2.7 per cent) and steady decreases in content of protein (from 41.8 to 36.8 per cent), fat (from 48.8 to 27.4 per cent), carbohydrate (from 3.5 to 1.5 per cent) and energy (from 5956 to 4175 cal/g dry weight). Water content of fresh egg is 76.1 per cent and after an initial decrease to 77.2 per cent in the eggs prior to hatching, it decreases to 72.1 per cent in the freshly hatched juveniles. A single egg contains 301 (± 34.4) μg dry substance equivalent to 1.79 calories. Cumulative yolk utilization efficiency during the total development is 72.1 per cent for energy, 90.5 for protein, 57.8 per cent for fat and 43.8 per cent for carbohydrate. Of the total energy expended on embryonic metabolic processes, oxidation of protein contributes only 10.1 per cent, while the rest is supplied by non-proteinous substances (fat 86.9 per cent and carbohydrate 3.0 per cent).

INTRODUCTION

Ecophysiological studies on the rate and efficiency of transformation of matter and energy in the developing eggs of aquatic crustaceans have received considerable attention in recent times [e.g. Branchiopoda: Urbani 1959, Hentig 1970; Ostrocodae: Theisen 1966; Copepoda : McLaren 1966; Taube and Nauwerck 1967; Cirripedia : Patel and Crisp 1960; Barnes 1965; Amphipoda: Kinne 1960; 1961; Decapoda : (Caridae) Pandian 1967, (Macrura) Pandian 1970 a, b, (Anomura) Pandian and Schumann 1967]. Considering the various important systematic groups, little work has been done with regard to yolk utilization in two groups, namely, Mysidacea and Isopoda. From the point of ecophysiology, this aspect of yolk utilization in developing eggs of terrestrial and semiterrestrial crustaceans remains a virgin field; comparative studies on changes in chemical composition and calorific content of developing eggs of aquatic and terrestrial crustaceans may indeed greatly stimulate and enhance our appreciation of the different ecological niches occupied, the adaptive changes in number and sizes of crustacean eggs and the varying morphological stages at which their larvae hatch. This paper reports on egg incubation and yolk utilization in the developing eggs of a semiterrestrial isopod *Ligia oceanica*.

*Present address :* Madurai University P. G. Centre, Sri Palaniandavar Arts College, Palni (Tamil Nadu).

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Material and Methods

*Ligia oceanica* Linnaeus (Oniscoidea) breeds almost throughout the year; during the period from May to August almost all the matured females carry developing eggs in their brood pouches for about 35 days*. For the present study, the specimens of *L. Oceanica* were collected from the holes and crevices situated in the supratidal zone of the harbour walls in the vicinity of the Ökolabor of the Biologische Anstalt, Helgoland (Southern North Sea). Collections were made once in August 1967 and again in June 1968. In the laboratory, these animals were kept at 20° ± 2°C in glass cylinders (Capacity 2 l) with a thin layer of fine wet (with sea-water: 31%, salinity) sand at the bottom and old pieces of wet bricks and stones above. The animals were let to feed on green algae.

For chemical and calorific analyses, the following arbitrary developmental stages were chosen:

**Stage I**: Undeveloped eggs and early cleavage stages; the earliest stages obtainable; the eggs are slightly oval, golden yellow, they are extremely delicate and are easily injured while handling.

**Stage II**: Oval eggs which are not so delicate; they exhibit definite, recognisable signs of embryonation at the animal pole, whose golden yellow surface is thickly studded with dull green spots.

**Stage III**: Dull green eggs with almost fully developed embryos ready to hatch; large eye spots, beating heart, segmented body and well developed appendages are seen in the embryos.

**Stage IV**: Just freshly hatched juveniles; even after hatching, the juveniles are known to continue their stay in the mother’s brood pouch for a shorter or longer period (Saudray and Lemercier 1960); in the present study, the mothers carrying egg stage III were kept separately and were observed from time to time and once the juveniles hatched out, they were forced to emerge out of the brood pouch.

Of each of the above-mentioned stages, eggs or juveniles were removed from the brood pouch of the chosen mother animals, and washed free from the adhering seawater by exposing them twice to distilled water, 15 sec each time (Flüchtler and Pandian 1968). After blotting, the test material was weighed in a Sartorius balance (Type 2604, sensitivity 10 µg). Water content was determined by weighing the test material before and after drying at 80°C for five hours.

Ash content was estimated by incinerating the test material (of about 15 mg dry substance) in a muffle furnace kept at 560°C for a period of five hours and weighing the residue, as recommended by Paine (1964).

Protein and non-protein nitrogen contents were determined following the standard procedure of micro-Kjeldhal method described by Roth (1958). Protein was precipitated by grinding the sample (of about 15 mg dry substance) with 0.5 ml of cold trichloroacetic acid in a glass mortar; the content was subsequently centrifuged. The supernatant contained non-protein nitrogen and the precipitate protein

*For further details on the bionomics of *L. oceanica* refer to Nicholls (1931).*
nitrogen. Protein content was estimated as albumin equivalent by estimating the protein nitrogen and multiplying the values by 6.25.

Fat content was estimated as the difference between dry weight (of about 40 mg dry substance) and fat-free dry weight of the test substance determined after six–eight hours extraction with chloroform : methanol mixture (2:1) in a semi–micro soxhlet apparatus.

Calorific content was determined with a Parr 1412 semi micro-bomb calorimeter. As the sample available was less than 20 mg in most cases, a known amount of benzoic acid was added as trigger substance.

RESULTS

Egg incubation

Almost all the females ranging from 1.5 to 2.4 cm body length were found to incubate developing eggs during the period from May to August. The number of eggs incubated at any one time varied from 39 to 63 and averaged to 53±9.5 eggs per female. When the number of eggs incubated is plotted as a function of body size (length) of the mother animals, which were randomly chosen from a large collection made in August 1967, no definite correlation could be established between these parameters (Fig. 1). For instance, the smallest female of 1.5 cm body length incubated as many as 60 eggs, while the medium sized one (2.0 cm body length) carried 39 eggs and the largest females of 2.3 and 2.4 cm body length 42 and 63 eggs, respectively.

In between the incubated eggs of *L. oceanica*, the occurrence of nematodes

![Figure 1](image-url)  
**Fig. 1.** Number of eggs incubated as a function of body size (length) of the females of *Ligia oceanica*. 
Gammarinema ligiae, Rhabditis sp. and Diplogaster sp.* was noted. Of the 120 berried females observed, as many as 113 (95 per cent) females were found to have been "infected", and one to five nematodes were present in any one of these "infected" females. These three species of nematodes have recently been described by Gerlach (1967) and he is of the opinion that these nematodes are free living (not parasitic). However, in the present study 1–15 eggs were found not to have successfully completed the embryonic development in any one of these "infected" females. While the parasitic or free-living nature of these nematodes remains to be investigated, the space between the incubating eggs of many crustaceans seems to offer one of the best ecological niches for the nematodes. Thus, Kinne and Gerlach (1953) reported the occurrence of a new species of commensal nematode Gammarinema gammari from a number of amphipods belonging to the genus Gammarus. Barnes (Scotland) and Balakrishna Nair (India) (personal communications) inform me that they have found the occurrence of a few species of nematodes in between the incubated eggs of barnacles.

Changes in chemical composition

During the course of embryonic development, the relative proportion of various constituents of an egg undergo considerable changes; changes in general biochemicals composition of developing eggs of L. oceanica were estimated and the values obtained are presented in Table I. Water content increased from 76.1 per cent in the fresh eggs (stage I) to 77.2 per cent in stage III (i.e. developing eggs that are just one or two days prior to hatching); thereafter, it decreased to 72.1 per cent in the freshly hatched juveniles.

Ash content, which was 4.4 per cent in the fresh eggs, increased to 31.6 per cent in the freshly hatched juveniles (Table I). The increase in ash was considerably more during the later stages (from 6.2 per cent in stage II to 20.5 per cent in stage III and to 31.6 per cent in stage IV) than during the earlier stages (from 4.4 per cent in stage I to 6.2 per cent in stage II). In general, the values obtained for the ash contents of the later stages (III and IV) displayed considerable range of deviation from their respective means. Ashes of all four stages were bluish white, indicating the presence of copper-containing pigments.

As mentioned above, after hatching the juveniles were forced to emerge out from the mother's brood pouch; but left undisturbed, the juveniles are known to continue their stay in brood pouch for considerable period and also increase their body weight owing to the accumulation of salts, probably of material origin. As high as 50 to 60 per cent ash content values have been reported for the freshly hatched juveniles of L. oceanica by Saudray and Lemercier (1960). While the freshly hatched planktonic larvae of other crustaceans have only about 10 to 15 per cent ash content, it is not known why the juveniles of supralittoral L. oceanica contain 30 to 60 per cent ash in their body.

Protein content showed a progressive decrease from 41.8 per cent in stage I to 36.8 per cent in stage IV (Table I). During the corresponding stages, non-protein

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*Identification of these nematodes was made by Prof. S. A. Gerlach, Institute für Meeresforschung, Bremerhaven, Germany.
nitrogen increased from 1.5 to 2.7 per cent. As much as 35 per cent of the net increase in non-protein nitrogen has been shown to be due to the synthesis of chitin during the embryonic development of some crustaceans (Pandian 1970 a).

**Table I**

*Changes in chemical composition of developing eggs and freshly hatched juveniles of Ligia oceanica*  
(Percentage values represent means of three to six estimates and are based on dry weight; only water content values are given as percentage of live weight)

<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>Water (%)</th>
<th>Ash (%)</th>
<th>Protein (%)</th>
<th>Non-protein nitrogen (%)</th>
<th>Fat (%)</th>
<th>Carbohydrate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I (egg)</td>
<td>76.1</td>
<td>4.4</td>
<td>41.8</td>
<td>1.5</td>
<td>48.8</td>
<td>3.5</td>
</tr>
<tr>
<td>Stage II</td>
<td>76.8</td>
<td>6.2</td>
<td>40.8</td>
<td>1.8</td>
<td>49.0</td>
<td>2.2</td>
</tr>
<tr>
<td>Stage III</td>
<td>77.2</td>
<td>20.5</td>
<td>37.8</td>
<td>2.1</td>
<td>37.8</td>
<td>1.8</td>
</tr>
<tr>
<td>Stage IV (Juvenile)</td>
<td>72.1</td>
<td>31.6</td>
<td>36.8</td>
<td>2.7</td>
<td>27.4</td>
<td>1.5</td>
</tr>
</tbody>
</table>

**Table II**

*Changes in calorific content of developing eggs and freshly hatched juveniles of Ligia oceanica*  
(Calorific values represent means of four to six estimates)

<table>
<thead>
<tr>
<th>Developmental stage</th>
<th>Energy content (cal/g dry weight)</th>
<th>Coefficient of variation (%)</th>
<th>Energy content (cal/g dry organic substance)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Stage I (egg)</td>
<td>5956±135</td>
<td>2.3</td>
<td>6229</td>
</tr>
<tr>
<td>Stage II</td>
<td>6062±51</td>
<td>0.8</td>
<td>6463</td>
</tr>
<tr>
<td>Stage III</td>
<td>5061±420</td>
<td>8.3</td>
<td>6366</td>
</tr>
<tr>
<td>Stage IV (Juvenile)</td>
<td>4175±366</td>
<td>8.8</td>
<td>6102</td>
</tr>
</tbody>
</table>

Fat content was relatively high (48.8 per cent) in the fresh eggs (stage I; Table I); an initial increase to 49.0 per cent in stage II was followed by a steady depletion of fat content throughout the subsequent course of development; thus, it was 37.8 per cent in stage III and only 27.4 per cent in stage IV.

Carbohydrate was not directly estimated; since ash, protein, non-protein nitrogen and fat contents are known, carbohydrate was calculated. It decreased from 3.5 per cent in stage I to 1.5 per cent in stage IV.

Table II shows the changes in calorific content of the eggs during the developmental stages; energy content was 5956 cal/g dry weight in the fresh eggs (stage I); an initial increase to 6062 cal/g dry weight in stage II was followed by a remarkable decrease during the ensuing developmental stages, especially from 5061 cal/g dry weight in stage III to 4175 cal/g dry weight in stage IV. The trend in the changes of calorific content is parallel to that of fat.
Considering the calorific contents of the corresponding stages of the other crustaceans (only about 5800 and 5300 cal/g dry organic substance for the eggs prior to hatching and freshly hatched larvae, respectively [Pandian 1967, 1970 a, b]), the calorific values (6366 and 6102 cal/g dry organic substance for the stages III and IV) obtained for the stages III and IV of L. oceanica are very high. This seems to be the reason for the high energy utilization efficiency value (72.1 per cent) obtained for the total development of L. oceanica. The main source of error seems due to the high ash content (20.5 and 31.6 per cent) of these two stages; the presence of large quantities of calcium carbonate alters the calorific content during the estimation process [Paine 1966].

Yolk utilization

To have deeper insight into the embryonic growth and metabolism, the data on changes in chemical composition and calorific content should be related to the weight of a single egg. Table III gives the mean dry weight of a single freshly laid egg and the changes in its mean dry weight during the ensuing developmental stages. The mean dry weight of an egg decreased from 301 \( \mu \)g in stage I to 290 \( \mu \)g in stage II, and subsequently, it increased to 308 \( \mu \)g in stage III and to 310 \( \mu \)g in a freshly hatched juvenile of L. oceanica. In other words, the dry weight of a freshly hatched juvenile is more than that of a single egg; this observation was confusing; however, the mean dry weight values obtained for a single egg and juvenile in August 1967 were confirmed by the data collected from the specimens of June 1968. As it can be seen from Table IV, due to a greater ash content (98 \( \mu \)g/juvenile), a freshly hatched juvenile is heavier than the freshly laid egg (only 13 \( \mu \)g ash/egg). Organic substance and calorific content of freshly hatched juvenile are lower than those of the freshly laid egg. Percentage values of ash content available in the literature [Saudray and Lemercier 1960] for the eggs and juveniles of L. oceanica also suggest and support the present observation.

In general, the values obtained for the dry weight of any one of the four stages deviated considerably from their respective means, although the size range of the mother animals from which these eggs or juveniles were collected, was restricted to 1.9 to 2.4 cm body length. Such deviations in egg size seem not uncommon among crustaceans; it has, for example, been demonstrated for Cirripedes by Barnes and Barnes (1965) and for decapods by Pandian (1967; 1970 a, b).

From the values presented in Tables I–III, average changes in the chemical composition and calorific content of a single egg from stage I to stage IV have been calculated; the values obtained are presented in Table IV. The course of embryonic development exhibits progressive increases in content of ash (from 13 to 98 \( \mu \)g) and non-protein nitrogen (from 4.5 to 8.4 \( \mu \)g), and steady decreases in content of protein (from 126 to 114 \( \mu \)g), carbohydrate (from 10.5 to 4.6 \( \mu \)g) and fat (from 147 to 85 \( \mu \)g). The remarkable decrease in fat content of the egg is reflected in the heavy depletion of the energy content of the egg, which decreases from 1.79 to 1.29 cal.

Cumulative yolk utilization efficiency of the total development has been calculated using Gray's (1928a) ratio “body formed/body formed + yolk used for metabolism”. The efficiency values are 73.6 per cent for organic substance, 72.1 per cent
for energy, 90.5 per cent for protein, 43.8 per cent for carbohydrate and 57.8 per cent for fat. The difference, in the values shows that the efficiency, with which different substances of yolk are utilized, varies considerably.

During the course of embryonic development, a certain amount (a little more than 0.5 cal) of energy was expended on metabolism; the sources of energy have been the oxidation of 12 µg protein, 6.1 µg carbohydrate and 62 µg fat (Table IV). Thus, oxidation of protein contributed only 10.1 per cent, while rest was supplied by non-proteinous substances (fat 86.9 per cent and carbohydrate 3.0 per cent).

**DISCUSSION**

The results presented bring out several interesting aspects in regard to the eco-physiology of embryonic metabolism and growth of the semi/terrestrial isopod
Ligia oceanica. However, I shall restrict the discussion to some adaptive features exhibited by the embryos of this semiterrestrial isopod to conserve and produce water. Water content of the freshly laid eggs of L. oceanica is 76.1 per cent; it increases to 77.2 per cent in the eggs that are ready to hatch, and subsequently, decreases to 72.1 per cent in the freshly hatched juveniles. Water content of freshly laid eggs of the other (fully) aquatic crustaceans, for instance the lobster Homarus gammarus is about 50 per cent; it increases to about 59 per cent on being attached to the setum; subsequently, it increases progressively to 72.3 per cent in the eggs that are ready to hatch and to 83.1 per cent in the freshly hatched larvae (Pandian 1970 a). Two important differences may be noted: (i) while the water content of developing eggs of aquatic of H. gammarus exhibits a steady and continuous increase, that of semiterrestrial eggs of L. oceanica, after an initial increase, decreases; (ii) water content of freshly laid eggs of the semiterrestrial eggs of L. oceanica is quite higher than that of the aquatic eggs of H. gammarus. In an attempt to give a convincing explanation, I have summarized the available data on water contents of the eggs and larvae or juveniles of crustaceans (Table V). These crustaceans are classified into Section I: Sublittoral-Benthic; Section II: Intertidal–1, (sandy shore) and Intertidal–2 (rocky coast); and Section III: Supratidal-Semiterrestrial zone. The crustaceans belonging to Sections I and II carry the fertilized eggs; these attached (and hence demersal) eggs hatch into planktonic (free floating) larvae; the inflow of water into these eggs leading to the reduction in specific gravity, makes the larvae to float, and hence, these eggs imbibe water throughout the embryonic development. The semiterrestrial isopod L. oceanica (Section III), on the other hand, hatches into a fully developed juvenile, which is also semiterrestrial (unlike the aquatic larvae of the terrestrial crabs; cf. Costlow and Bookhout 1968) and evidently, there has been no need to imbibe water and to reduce the specific gravity.

Since the animals belonging to the Section II are intertidal, the developing eggs, which are attached (to the abdomen of hippa, or to the mantle cavity of the barnacles) to the females, are also subjected to the alternate exposure and submersion twice in a day. During the exposure, relatively a greater quantity of capillary water is retained and made available to the burrowing inhabitants like Emerita analoga in the sandy shore, while in the rocky coast, the availability of water is relatively very little. On the other hand, developing eggs carried by the crustaceans belonging to the Section III (e.g. L. oceanica) are submerged only during the spring tide periods recurring once a fortnight. Freshly laid eggs of fully submerged sublittoral benthic lobsters and crabs contain only 53 per cent water (Table V); the eggs of inhabitants from the intertidal sandy shore like the hippa contain 63 per cent water; the eggs of inhabitants of the rocky coast like the barnacle contain 75 per cent water; and the eggs of inhabitants of the supritudal zone like L. oceanica contain as much as 76 per cent. Thus, the lesser the availability, the greater is the amount of water with which the eggs are laid by the mother animals.

The high initial water content seems to have offered a certain degree of independence to the semiterrestrial eggs of L. oceanica from the environment for water.

*For a detailed discussion on the role of the high initial water content in the terrestrial eggs during the course of evolution, refer to Gray (1928 b).
TABLE V
Changes in water content of developing eggs of marine crustaceans

<table>
<thead>
<tr>
<th>Species and habitats</th>
<th>Water content (%)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>egg</td>
<td>larva</td>
</tr>
<tr>
<td>I Sublittoral : benthic</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Crab <em>Maja verrucosa</em></td>
<td>56.4</td>
<td>77.1</td>
</tr>
<tr>
<td>Hermit crab <em>Eupagurus</em></td>
<td>45.6</td>
<td>83.1</td>
</tr>
<tr>
<td>Lobster <em>Homarus gammarus</em></td>
<td>54.0</td>
<td>86.8</td>
</tr>
<tr>
<td>Lobster <em>Homarus americanus</em></td>
<td>56.2</td>
<td>86.8</td>
</tr>
<tr>
<td>Average</td>
<td>53.0</td>
<td>82.3</td>
</tr>
<tr>
<td>II Intertidal : 1 Sandy shore</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hippa Emerita anolaga</em></td>
<td>63.3</td>
<td>83.7</td>
</tr>
<tr>
<td>II Intertidal : 2 Rocky coast</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barnacle <em>Balanus balanoides</em></td>
<td>72.6</td>
<td>88.3</td>
</tr>
<tr>
<td>Barnacle <em>Balanus balanus</em></td>
<td>78.2</td>
<td>89.4</td>
</tr>
<tr>
<td>Average</td>
<td>75.4</td>
<td>88.8</td>
</tr>
<tr>
<td>III Supratidal : Semi terrestrial</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Isopod Ligia oceanica</em></td>
<td>76.1</td>
<td>72.1</td>
</tr>
</tbody>
</table>

TABLE VI
Estimation of protein metabolized during conversion of yolk substances equivalent to one calorie in the developing eggs of some animals

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>Amount of protein metabolized (µg)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chick (<em>Gallus</em>)</td>
<td>Terrestrial</td>
<td>18.4</td>
<td>Needham (1931, pp. 983 and 997)</td>
</tr>
<tr>
<td>Silkworm (<em>Bombyx</em>)</td>
<td>Terrestrial</td>
<td>22.0</td>
<td>Needham (1931 p. 997)</td>
</tr>
<tr>
<td>Salmon</td>
<td>Freshwater</td>
<td>122.0</td>
<td>Needham (1931, p. 997)</td>
</tr>
<tr>
<td>Hermit crab</td>
<td>Marine, 60 m depth</td>
<td>40.6</td>
<td>Pandian and Schumann (1967)</td>
</tr>
<tr>
<td>Limpet (<em>Crepidula</em>)</td>
<td>Marine, 20 m depth</td>
<td>33.3</td>
<td>Pandian (1969)</td>
</tr>
<tr>
<td>Shrimp (<em>Crangon</em>)</td>
<td>Marine, 10 m depth</td>
<td>31.3</td>
<td>Pandian (1967)</td>
</tr>
<tr>
<td>Lobster (<em>Homarus</em>)</td>
<td>Marine, 5 m depth</td>
<td>15.7</td>
<td>Pandian (1970 a)</td>
</tr>
<tr>
<td>Isopod (<em>Ligia</em>)</td>
<td>Marine, supratidal</td>
<td>9.3</td>
<td>Pandian (present paper)</td>
</tr>
</tbody>
</table>

during the course of embryonic development; for instance, a single lobster egg (3.69 mg wet weight) requires as much as 4.88 mg water for a successful completion of embryonic development, while a *Ligia* egg (1.26 mg wet weight) requires only
about 83 μg water. In other words, assuming an equal wet weight of 1 mg, a lobster egg requires 1.322 mg water, while a Ligia egg only 0.066 mg. Furthermore, even this limited quantity of water required for the successful completion of development of Ligia egg seems to be mainly met by the production of metabolic water. Metabolization of yolk substances (62 μg fat release 66.3 μg water, 12 μg protein 5.0 μg water and 6 μg carbohydrate 3.0 μg water)* in a Ligia egg might have released as much as 74.3 μg or 89.5 per cent of the total required water. A lobster egg is reported to release only 473 μg metabolic water equivalent to 9.7 per cent of the total required water (Pandian 1970 a).

The primary energy source for the embryonic metabolism of L. oceanica is fat oxidation. Of the total energy expended on metabolism, as much as 87 per cent is supplied by fat oxidation, while that of protein amounted to only 10 per cent. During the development of a number of marine crustaceans fat serves as the main energy source, e.g. Balanus balanus, B. balanoides (Barnes 1965; Pandian 1970 a), Crangon crangon, Homarus gammarus, H. americanus, (Pandian 1967, 1970 a, b) and Eupagurus bernhardus (Pandian and Schumann 1967). In the other marine demersal eggs of crustaceans (and in fact molluscs too) oxidation of fat yields as much as 68 per cent of the energy required for the metabolism, while that of protein is only 24 per cent. Thus, in all these marine demersal eggs, protein metabolism is considerably suppressed and fat metabolism is "geared up". Upon oxidation, fat releases large quantities of water (1 g fat 1.07 g water; 1 g carbohydrate 0.56 g water; 1 g protein 0.41 g water; Baldwin 1964); unlike protein, fat oxidation does not result in ammonia production, the removal of which costs considerable water. These two properties of fat, namely production and conservation of water, obviously represent advantages for eggs of marine organisms to which water is not as readily available as to freshwater inhabitants. Considering these two metabolic properties, namely suppression of protein metabolism and "gearing up" of fat metabolism, the marine demersal eggs are closer to the terrestrial cleidoic eggs than to the non-cleidoic eggs of freshwater animals. Such a generalization differs from the concept of Needham (1950) and the merits and demerits of his concept have been extensively discussed by the author elsewhere (Pandian 1967; 1969, 1970 a, c).

From the available data, the amount of protein metabolized during the conversion of yolk substances equivalent to one calorie from the egg into the larva or juvenile in some animals has been calculated and the data are presented in Table VI. Non-cleidoic eggs of freshwater animals, for instance, that of salmon, oxidize as much as 122 μg protein in order to convert yolk substances equivalent to one calorie, while those of cleidoic terrestrial eggs of birds and insects only about 20 μg, and those marine demersal eggs about 30 μg protein. In other words, suppression of protein metabolism is one-sixth in terrestrial cleidoic eggs, and one-fourth in the marine demersal eggs, as compared to the eggs of non-cleidoic freshwater animals. Moreover, suppression of protein metabolism among the marine eggs is more and more intensified as the animal's habitat is closer and closer to the coast. The hermit crab, the data pertaining to which are given in Table VI, was trawled at 60 m depth (off from Helgoland); the limpet was dredged from the shallow waters near

*See Baldwin 1964, Table 4, p. 52 for calculation procedure.
Bremerhaven (Germany) at about 15 to 20 m depth; the shrimp was netted at
about 10 m depth; the lobster was caught by divers in the coastal waters of Helgoland
at about 5 m depth, and Ligia was collected from the supratidal zone of Helgoland
harbour. To convert yolk substances equivalent to one calorie, the hermit crab
oxidizes as much as 40.6 µg protein, the limpet egg 33.3 µg protein, the shrimp egg
31.3 µg protein, the lobster egg 15.7 µg protein and Ligia egg 9.3 µg protein. The
fact that in Ligia the amount of protein oxidized during the processes of conversion
of yolk substance equivalent to one calorie is only less than a half of that oxidized
in the cleidoic terrestrial eggs of birds and insects is of great interest and suggests
that the developing eggs of Ligia are adapted to the semiterrestrial life primarily
through suppressing protein metabolism rather than converting the end product of
protein metabolism into urea or uric acid.

In this connection, it is interesting to note the results obtained by Dresel and
Moyle (1950), who showed that fully marine adult isopod like Orchestia sp. excrete
as much as 6.0 mg nitrogen per 10 g body weight per day, while those of semi-
terrestrial isopod Ligia oceanica and terrestrial isopod Armadillidium vulgare only
1.3 and 0.3 mg nitrogen/10 g/day, respectively. A general suppression of nitrogen
metabolism by the semiterrestrial and terrestrial isopods has been considered by
them as the chief adaptation for life on land, rather than a conversion from ammo-
notely to ureo—or uricotely.

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